NEMATODE FEEDING TYPES IN A TUFA-DEPOSITING ENVIRONMENT (PLITVICE LAKES, CROATIA)

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Free-living nematodes are an important group in all benthic habitats. They occur in high abundance and due to the feeding types they have strong influence on bacteria, algae, detritus and meiofauna in periphyton and sediments. The main aims of this study were to determine the vertical distribution of nematodes and their feeding types within the moss-covered tufa barrier over a one year period in Plitvice Lakes National Park. Altogether 23 taxa were identified with a maximum value of 198 ind. 10 cm^{-2} in spring. Stylet-bearing suction feeders were the dominant nematode feeding type in bryophytes and in the deeper layers of the tufa substrates. The domination of Adenophorea and the high value of the maturity index (MI) confirmed that this was clean, unpolluted water and showed the oligotrophic state of investigated habitat. The results demonstrated that nematodes, due to their high abundance and biomass, play an important role in karst water sediments.

Key words: freshwater nematodes, trophic structure, tufa-depositing systems, bryophytes

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Slobodnoživući, nenametnički oblići su važan segment u svim bentičkim staništima. Oni su prisutni u velikoj brojnosti te svojim prehrambenim navikama značajno utječu na bakterije, alge, detritus i meiofaunu u perifitonu i sedimentu. Glavni ciljevi ovog rada su bili utvrditi vertikalnu distribuciju oblića i njihove hranidbene skupine u mahovinom prekrivenim sedrenim barijerama Nacionalnog Parka Plitvička jezera tijekom jedne godine. Ukupno smo utvrdili 23 svojte oblića s maksimalnom brojnošću od 198 ind 10 cm^{-2} u proljetnom razdoblju. U mahovinama i u sedrenom sedimentu dominantna hranidbena skupina bili su oblići s bodežićem - „isisavači". Velika brojnost oblića iz skupine Adenophorea i visoke vrijednosti MI indeksa (*eng*. Maturity index) potvrdile su čisti, nezagađeni vodeni medij i oligotrofno stanje ekosustava. Navedeni rezultati ukazuju da oblići, brojnošću i biomasom, imaju važnu ulogu u sedimentima krških voda.

Ključne riječi: slatkovodni oblići, trofička struktura, sedrotvorni sustav, mahovine

INTRODUCTION

Free-living nematodes are ubiquitous organisms present in all types of freshwater sediments. They are one of the most abundant and diverse groups of the meiobenthos in aquatic ecosystems (Traunspurger, 2002). Nematode feeding types include a broad dietary spectrum: bacteria, algae, detritus, fungi, plants, protozoan and metazoan prey (Giere, 2009). Traunspurger *et al.* (1997) found that grazing by bacterial-feeding nematodes induced the activity and abundance of bacteria in freshwater sediments. Nematodes also serve as a food for higher trophic levels, such as the macrozoobenthos (Schwank, 1981; Toman & Dall, 1997; Beier *et al.*, 2004) or juvenile fishes (Spieth *et al.*, 2011). Nevertheless, knowledge about the diversity and ecology of lotic nematodes is still very

limited, especially in karstic (carbonate rock substrate) freshwater habitats. These habitats are characterized by calcite precipitation and tufa formation. Ford & Pedley (1996) defined tufa as the „product of calcium carbonate precipitation under a cool water (near ambient temperature) regime [that] typically contains the remains of micro- and macrophytes, invertebrates and bacteria". This process is highly sensitive to any environmental changes, especially to an increase of the trophic state of aquatic systems (Pentecost, 2005).

The morphology of nematode mouthparts indicates their feeding habits and according to the shape of the buccal cavity they can be divided into four tropho-ecological groups (Traunspurger, 1997; Tab. 1): chewers, epistrate feeders, deposit feeders and suction feeders. This function-based approach offers several advantages: (i) in order to assign feeding category, it is not necessary to indentify specimens to species level and (ii) it focuses on the ecological role of nematodes in the benthos. Depending on freshwater substrate and available food sources, different parts of river beds and lakes basin are occupied by specific trophic nematode groups. For instance, in sand and mud sediments deposit feeders prevail (Beier & Traunspurger, 2001; 2003). These nematodes possess no teeth in the buccal cavity and feed mainly on bacteria and unicellular eukaryotes. Periphyton habitats harbor a rich and diverse nematode community, with domination of epistrate-feeding nematodes (Majdi *et al.*, 2011). This trophic group mostly feeds on diatoms, which are abundant in such habitats. Dražina *et al.* (2013) established the domination of suction-feeding nematodes in stream bryophytes. This trophic group also prefers the root regions of aquatic macrophytes (Prejs, 1977; 1987). A high percentage of suction feeding dorylaimid nematodes has been established in terrestrial mosses across Europe (Barbuto & Zullini, 2006). Suction feeders are an omnivorous group of nematodes, and piercing different kinds of food (algae, plants, fungi and animals) using their stylets (Traunspurger, 2002).

Nematode community structure is indicative and useful in biomonitoring studies (Bongers, 1990; Bongers & Ferris, 1999). They have several advantages compared with macrofauna in environmental bio-assessment: as mentioned above, they occur in high diversity and density, they are a trophically heterogeneous group and nematodes react rapidly to disturbances and organic enrichment (Beier & Traunspurger, 2001). Most used methods in bio-assessment interpreted by nematode community are the ratio of Secernentea and Adenophorea (two traditional nematode „classes"; Zullini, 1976) and the maturity index (Bongers, 1990).

Data on nematode trophic composition in karst water sediments are very scarce and this study will contribute to the biodiversity records and better understanding of trophic

Tab. 1. Classification of nematode feeding types (Traunspurger, 1997).

| Feeding type	Morphology of buccal cavity	Food
epistrate-feeders	small teeth present in buccal cavity	bacteria, uniceliliar eucariotes, diatoms and other algae
deposit-feeders	no teeth in buccal cavity	bacteria, unicellular eukaryote
suction-feeders	stylet present	omnivorous – algae, plants, fungi and animals
chewers	voluminous, sclerotized buccal cavity with one or more teeth	predators of protozoa, nematodes, rotifers and tardigrades
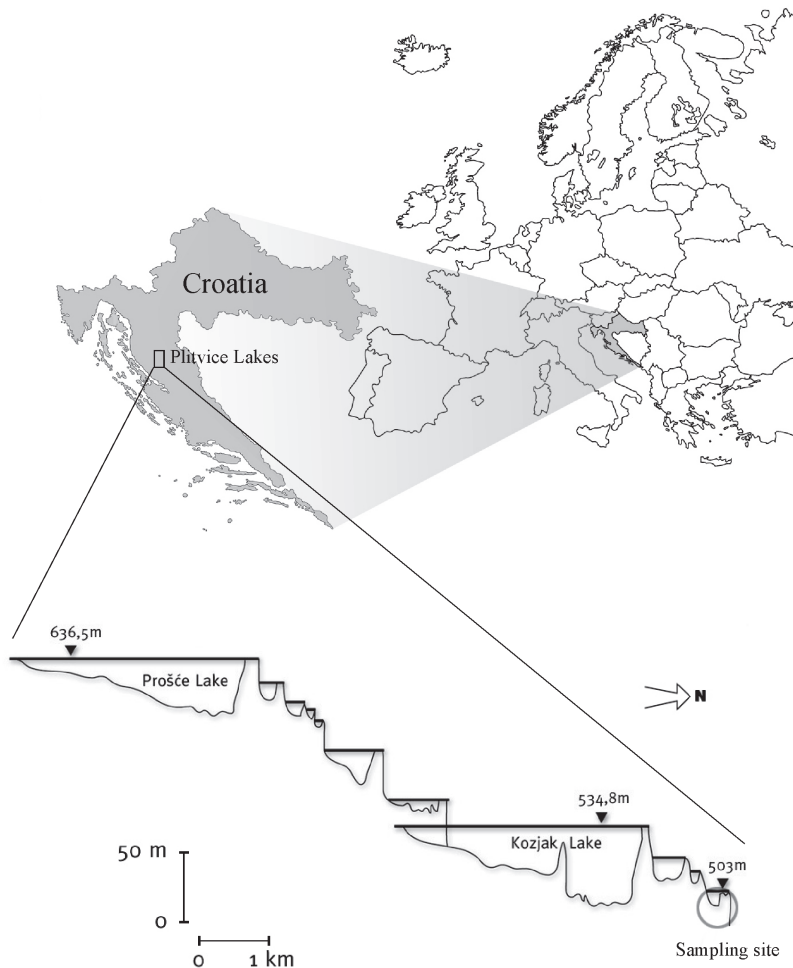
Fig. 1. Location of the sampling site in the Plitvice lakes National Park, Croatia.

relations in karst benthic communities. The aims of this article are: (1) to analyze vertical distribution of nematodes in tufa; (2) to establish nematode feeding types in tufa and (3) to test nematodes as indicators of environmental changes in freshwater karst habitats. This paper will highlight the importance of nematodes in benthic community food webs and their role as indicator organisms in aquatic systems.

MATERIAL AND METHODS

We carried out this study in the Plitvice Lakes National Park (Croatia). According to FORD & PEDLEY (1996) the Plitvice Lakes system belongs to the „fluvial barrage model" and consists of 16 mutually connected lakes. This is an oligotrophic system with the following environmental conditions during the period of the investigation (February 2009 – January 2010): temperature ranged from 2.9 to 22.2 ºC, dissolved oxygen ranged

from 7.7 to 12.7 mg cm^{-1}, (oxymeter WTWOXI 96), pH was slightly alkaline (7.9–8.8; WTW 330i) and conductivity was high (348–563 μS cm^{-1}; Hach Sension 5). A detailed description of the Plitvice hydrosystem, the main limnological features and vascular vegetation are given in previous studies by Miliša *et al.* (2006), Špoljar *et al.* (2007), Sertić Perić *et al.* (2011) and Dražina *et al.* (2013).

In our investigation, we chose the last tufa barrier (44°54′11′′N; 15°36′36′′E), which divide the lakes Kaluđerovac and Novakovića Brod, just before formation of the Korana River (Fig. 1). We selected a constantly submerged microhabitat with a dense bryophyte cover and with an average flow velocity (FV) of 1.05 ± 0.24 ms^{-1} (P600, Dostmann electronic GmbH), measured 3 cm above bryophytes. We collected samples monthly in triplicates (February 2009 – January 2010) from the chosen microhabitat using a metal corer (Ø 4 cm). We cut every substrate core into three layers: bryophyte mats (2 cm, symbol B), loose tufa layer with encrusted bryophyte remains (4 cm, symbol R) and the layer of consistent tufa (4 cm, symbol T).

In the laboratory, we stored samples at 10 °C, counted and identified soft bodied meiofauna (defined as those animals which are retained on a 44 μm sieve) alive under the inverted microscope Opton-Axiovert 35 at 400× magnification, within 3 days of collection. After we finished determination of live material, we fixed samples with 4% formalin and stained with Rose Bengal. We randomly collected between 10 and 100 specimens of nematodes (depending on their density) from each replicate and mounted them on slides after Seinhorst (1959), and then measured and identified them to the lowest taxonomic level. We calculated the wet weight (WW) of nematodes after the formula of Andrássy (1956) and we classified nematodes into four feeding types following Traunspurger (1997).

For sediment quality assessment we used the ratio of Secernentea and Adenophorea (S/A ratio) and the maturity index (MI). Zullini (1976) found that in polluted and disturbed habitats the relative abundance of Secernentea is higher than in unpolluted and undisturbed habitats. MI was developed by Bongers (1990) and it can be defined as a measure of disturbance, with smaller values being indicative of a more disturbed environment and larger values characteristic of a less disturbed environment. In order to calculate MI, we classified nematodes into five cp-groups (colonizers versus persisters; Bongers, 1990). Nematodes that have a short life-cycle, high colonization ability and that rapidly increase their abundance under favorable conditions are considered colonizers (r-strategist in the loose sense) and they are classified into the cp1-group. In contrast, nematodes that have a low reproduction rate, a long life-cycle and low colonization ability are considered persisters (K-strategist *sensu lato*) are classified into the cp5-group. Nematodes with intermediate characteristics are classified from cp2- to cp4-groups. We used only free-living nematodes and all five cp values:

$$MI = \Sigma \, v_i * f_i / n$$

where v_i is the cp-value of taxon i, f_i is the frequency of taxon *i* in a sample and *n* is the total number of individuals in a sample.

We calculated the Shannon diversity index (H′), Pielou´s evenness (J′), the Bray Curtis index of similarity and cluster analysis using PRIMER (version 6; PRIMER-E, Plymouth, UK). We used multivariate analysis of similarities (ANOSIM) to identify differences/ similarities in functional feeding groups between sampling layers. Due to the low sample number, we carried out tests of differences between nematode abundance among sampling dates and microhabitats with the non-parametric Kruskal-Wallis test (STATISTICAsoftware, version 10.0; Statsoft, Tulsa, Oklahoma).

Tab. 2. Presence of nematode species through the vertical profile of bryophyte-tufa sediments at Plitvice Lakes (B, R, T). The cp-values (cp, Bongers, 1990) and feeding-types (f) are listed. The four classified feeding types are: chewers (c), epistrate-feeders (e), deposit-feeder (d) and suction-feeders (s).

ORDER	Layer				
Taxon	B	R	T	cp	f
ADENOPHOREA					
CHROMADORIDA					
Achromadora ruricola (de Man, 1880)	*	*	*	3	e
Ethmolaimus pratensis de Man, 1880	*	*	*	3	e
MONHYSTERIDA					
Eumonhystera dispar (Bastian, 1865)	*			2	d
Eumonhystera similis (Butschli, 1873)	*		*	2	d
Eumonhystera sp.	*			2	d
Eumonhystera vulgaris/filiformis	*	*	*	2	d
Geomonchystera villosa (Butschlii, 1873)	*	*	*	2	d
Theristus sp.		*		2	d
PLECTIDA					
Chronogaster typica (de Man, 1921)	*			3	d
Teratocephalus terrestris (Butschli 1873)			*	3	d
ARAEOLAIMIDA					
Cylindrolaimus communis de Man, 1880	*			3	d
MONONCHIDA					
Mononchus truncatus Bastian, 1865	*	*		4	c
DORYLAIMIDA					
Eudorylaimus carteri (Bastian, 1865)	*	*	*	4	s
Mesodorylaimus hofmaenneri (Menzel, 1914)	*	*	*	4	s
Paractinolaimus macrolaimus (de Man, 1880)		*		5	s
Dorylaimida Gen. sp. 1	*			4	s
Dorylaimida Gen. sp. 2	*	*	*	4	s
TRIPLONCHIDA					
Prismatolaimus intermedius (Butschli, 1873)	*	*		3	e
DESMODORIDA					
Prodesmodora sp.	*			3	e
SECERNENTEA					
TYLENCHIDA					
Tylenchorhynchus sp.	*		*	3	s
Tylenchus sp.	*		*	3	s
Tylenchida Gen. sp.		*		3	s
Nematoda unidentified/damaged	*	*	*		-

RESULTS

Altogether 23 nematode taxa were identified (Tab. 2). In diversity, representatives of orders Dorylaimida (5) and Monhysterida (4) dominated. Dorylaimida were the most abundant order led by the species *Mesodorylaimus hofmaenneri* (26% of all nematodes).

The most abundant nematode community was observed in the surface, bryophyte layer and mean abundance was 103 ± 85 ind.10 cm^{-2}. With increasing depth, nematode abundance significantly decreased (Fig. 2), and reached mean values of 35 ± 22 ind. 10 cm^{-2} in R and 16 ± 18 ind. 10 cm^{-2} in deepest T layer (Fig. 2; Tab. 3). The mean ne-
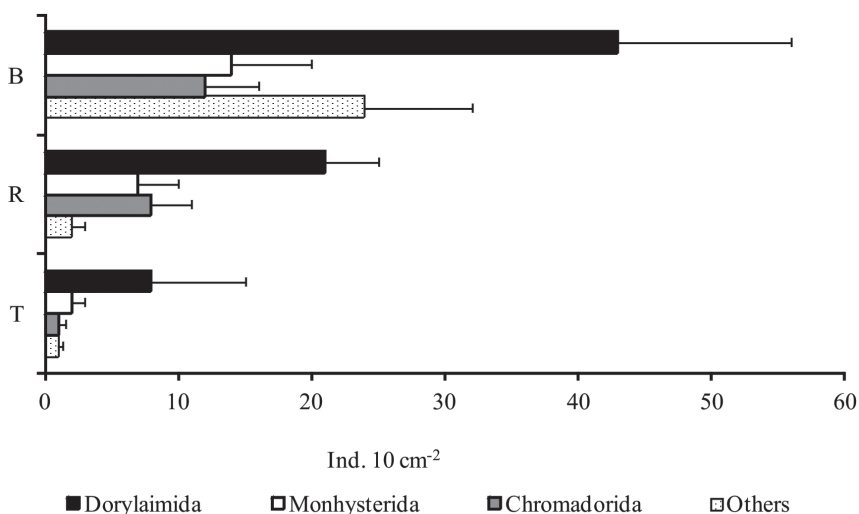
Fig. 2. Vertical distribution of main nematode orders (mean abundance ± standard error) in B, R and T layers.

Tab. 3. Number of species, mean abundance and biomass (wet weight –WW), mean diversity index, evenness, Maturity index and ratio of Secernentea/Adenophorea (S/A) in three layers of tufa sediments. Differences were analyzed by the Kruskal Wallis test (KW; N = 12; *** P < 0.001; n.s. = not significant).

	B	R	T	KW	Multiple Comparisons
Number of species	19	14	13	n.s.	
Mean abundance (Ind. 10 cm^{-2})	103±85	35±22	16±18	***	B ≠ R; B ≠ T
Mean biomass (μg WW)	112±125	37±29	13±28	***	B ≠ R; B ≠ T
Shannon diversity index (H′)	1.5	1.2	1.1	n.s.	
Pielou's evenness (J′)	0.9	0.8	0.9	n.s.	
Maturity index (MI)	3.11	2.35	2.05	n.s.	
S/A	11/89	2/98	5/95	n.s.	

matode biomass (WW) followed same pattern as abundance: with increasing depth nematode biomass decreased. These differences in abundance and biomass between bryophytes and tufa layers were statistically significant (Tab. 3).

Domination of dorylaimid nematodes was reflected in the composition of feeding types and at least 50% of the nematode populations in each layer were suction-feeders. Deposit-feeders, presented mainly by Monhisterida, accounted for 19% of all nematodes, epistrate-feeders 16% and chewers 8% (Fig. 3). ANOSIM analysis revealed similar structure of feeding types along the investigated vertical profile (R = 0,18; p = 0,002).

Community measures as number of species, Shannon diversity index, Pielou´s evenness, MI index and S/A ratio were not significantly different on a temporal scale and through the vertical profile of tufa barrier (Kruskal Wallis test, p > 0,05), suggesting a constant and stable community of nematodes in the studied habitat.

Adenophorea dominated in all layers and almost 90% nematodes belong to this class (Fig. 4). Highest value of MI index was recorded in B layer (Tab. 3) and with increasing depth MI values decrease. The cp3-nematodes were dominant (45%), followed by cp2-nematodes (27%), cp4-nematodes (23%) and cp5-nematodes (5%). Dominant dorylaimid nematodes have high cp values (cp4 and cp5) and this caused a relatively high value MI index, indicating unpolluted habitat. Fig. 5 shows the results of cluster analysis based on abundance of all nematode taxa. The most similar community structure is noted between the B and R layers.

DISCUSSION

In our research we found a rich and diverse community of nematodes in bryophyte and tufa substrates. Matoničkin (1987) recorded nematodes from the genus *Dorylaimus* in bryophytes along the longitudinal profile of Plitvice Lakes. Dražina *et al.* (2013) established 26 nematode taxa in bryophytes of Plitvice Lakes with the domination of doryla-
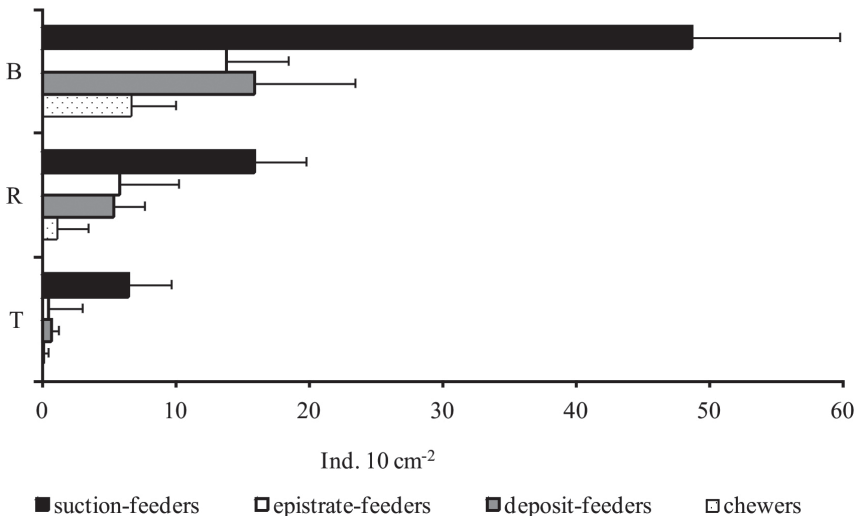

Fig. 3. Vertical distribution of nematode functional feeding guilds (mean abundance ± standard error) in B, R and T layers.
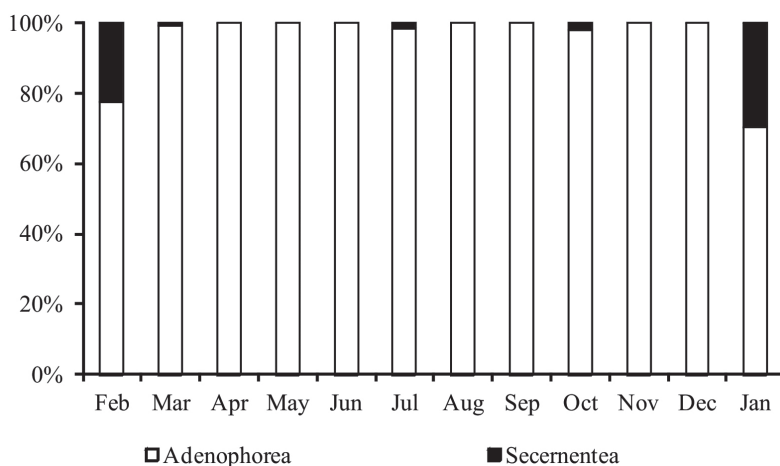
Fig. 4. Mean month ratio (%) of Secernentea and Adenophorea in the investigated period.
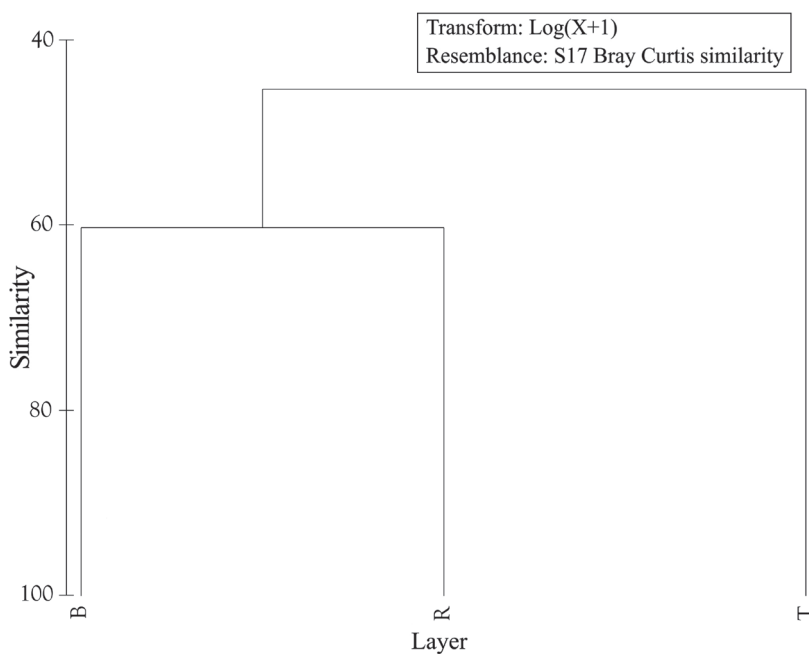

Fig. 5. Cluster analysis of B, R and T layers based on nematode abundance.

imid nematodes. This is comparable with the results of the present study, where we established altogether 23 different nematode taxa and where Dorylaimida dominated in diversity and abundance. Suren (1992), Linhart *et al.* (2002) and Dražina *et al.* (2013) established relatively high nematode abundance in aquatic bryophytes and their results are comparable with the data presented in this study. The high nematode abundance in the surface (B) layer can be explained by the nature of the bryophyte habitat. Aquatic

bryophytes in lotic systems are a specific substrate suitable for colonization by numerous invertebrates, primarily because they represent a refuge from high flow velocity (Suren, 1992; Dražina et al., 2013). Also, bryophytes have a large retention capacity and they accumulate organic matter, which can be the source of food for benthic organisms. Thus, nematodes have a refuge and numerous sources of food in bryophytes, where they create stable population. In other types of benthic habitats nematodes are also most numerous in surface layers of the substrate, while their abundance decreases with increasing depth (Giere, 2009). Although tufa is a porous sediment (Chafetz & Folk, 1984; Miliša et al., 2014), with increasing depth a large amount of carbonate silt fills the spaces between bryophyte debris which impedes the movement of organisms. This especially holds true for the deepest T layer considered in this study, which contained the largest amount of silt. This might have caused the decrease in the nematode abundance. This is comparable with the results of Radwell & Brown (2006), who found a lower number of nematodes and other meiofauna in substrates with a high silt percentage. The silt reduced habitat quality, even for minute metazoans.

Domination of dorylaimid nematodes directly influenced the trophic structure, making suction-feeders most abundant. Similar results were also established by Schwank (1985) and Zullini & Peretti (1986) who found dorylaimid suction-feeders in lotic bryophytes. Suction-feeders are omnivorous and this trophic group is known to inhabit exposed phytal habitats in freshwater and marine environments (Giere, 2009). Bryophytes and other phytal habitats are particularly suitable for suction-feeders. They puncture the cells of plants, fungi or small animals with their stylets and suck out their contents (Dražina et al., 2013). Chewers, as predators, are generally present in a small percentage in bryophyte and macrophyte habitats, while their importance is much higher in soft and sandy sediments of freshwater habitats (Bogut & Vidaković, 2002; Beier & Traunspurger, 2003). Bryophytes are the basis for epiphyton development, and deposit-feeders and epistrate-feeders are present in such habitats, feeding on bacteria or algae from epiphyton (Suren, 1992; Majdi et al., 2011). Community composition and trophic structure are uniform throughout the entire vertical profile and are primarily influenced by high nematode abundance in the surface sections.

Domination of Adenophorea on both the temporal and vertical scale and the high value of MI confirmed the unpolluted, oligotrophic state of the habitat investigated. Due to their frequency, nematodes are suitable organisms to be bioindicators. Ristau & Traunspurger (2011) found that nematode species richness and the composition of nematode feeding groups are affected by the nutrient condition in lakes. Future research should be focused on the relation between nematode communities and the trophic status of lotic systems. Nematode functional diversity influences the processing of detritus, nutrient recycling and their contribution to these processes should be considered for better understanding of food webs functioning in streams and rivers.

ACKNOWLEDGEMENTS

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SAŽETAK

Hranidbeni tipovi oblića u sedrenim staništima (Plitvička jezera, Hrvatska)

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Proces precipitacije kalcijevog karbonata i stvaranje recentne sedre (eng. *tufa* ili *travertine*) je temeljni fenomen odgovoran za nastanak jezerskih bazena te brojnih slapova i barijera Plitvičkih jezera. Navedeno područje Plitvičkih jezera je zbog iznimnih prirodnih ljepota 8. travnja 1949. godine proglašeno Nacionalnim parkom, a 29. listopada 1979. je ovaj Park upisan na UNESCO-vu Listu svjetske prirodne i kulturne baštine. Nakon više od stoljeća intenzivnih limnoloških istraživanja ovog područja, još uvijek postoje skupine organizama, poput slobodnoživućih oblića, koje do sada nisu sustavno istraživane na području Parka. Oblići su izrazito brojna i važna skupina organizama u svim bentičkim staništima. Svojim raznolikim prehrambenim navikama značajno utječu na bakterije, alge, detritus i meiofaunu u perifitonu i sedimentu. Glavni ciljevi ovog rada su bili utvrditi vertikalnu distribuciju oblića i njihove hranidbene skupine u mahovinom prekrivenim sedernim barijerama Nacionalnog Parka. Nadalje, po prvi put je ova skupina organizama korištena kao pokazatelj stanja okoliša. Koristili smo dvije metode: omjer dvaju (tradicionalnih) razreda oblića Secernentea i Adenophorea te MI indeks (*eng*. Maturity index).

Uzorci mahovine i sedre su uzimani jednom mjesečno (veljača 2009. – siječanj 2010.) na sedrenoj barijeri između jezera Kaluđerovac i Novakovića Brod. Ukupno smo utvrdili 23 svojte oblića. Brojem vrsta dominirale su skupine skupine Dorylamida (5) i Monhysterida (4). U površinskom, mahovinskom sloju je zabilježena najveća brojnost oblića (103 ± 85 ind. 10 cm^{-2}). S povećanjem dubine došlo je do statistički značajnog pada brojnosti, dok je sastav zajednice ujednačen. U mahovinama i u sedrenom sedimentu dominantna hranidbena skupina bili su oblići s bodežićem – „isisavači". Velika brojnost oblića iz skupine Adenophorea i visoke vrijednosti MI indeksa potvrdile su čisti, nezagađeni vodeni medij i oligotrofno stanje ekosustava. Navedeni rezultati ukazuju da oblići, brojnošću i biomasom, imaju važnu ulogu u sedimentima krških voda.