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DISENTANGLING FOOD WEBS INTERACTIONS IN THE LITTORAL OF TEMPERATE SHALLOW LAKES

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Elucidation of food web interactions provides a better understanding of ecosystem functioning, indicates anthropogenic impacts which often cause alterations in environmental conditions and deterioration in feeding networks in terrestrial and aquatic ecosystems. The importance of microfauna and macroinvertebrates in the littoral zones of shallow waters has been poorly studied regarding their trophic interactions. This study compares invertebrate assemblage and food web interactions among epiphyton, zooplankton and benthic macroinvertebrates across structural heterogeneity in the littoral zone of three temperate shallow water bodies. Submerged and structurally-complex stands of *Ceratophyllum demersum* inhabited a higher abundance of cladocerans and supported a higher diversity and biomass of epiphytic protozoans and invertebrates than floating-leaved *Nuphar lutea* stands. Analysis of the ecosystem functioning illustrated the increased biomass of macroinvertebrate predators and a preference of predation over planktonic crustaceans in more complex macrophyte stands. Food webs displayed higher complexity and size with habitat heterogeneity, while epiphyton and zooplankton shared an important fraction in food resources among the invertebrate trophic network. Results of food web modelling indicated zooplankton and epiphyton as more vulnerable to invertebrate predation in the complex submerged macrophytes than in the floating-leaved macrophyte stands. Integrated approaches to community, ecosystem and food webs in explanation of complex trophic interactions in the littoral zones confirmed an increase in diversity and food-web functional complexity with structural heterogeneity of microhabitats.

Key words: epiphyton, zooplankton, macroinvertebrates, tactile predators, macrophytes, relaxed niche food web model

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Razjašnjenje interakcija u hranidbenoj mreži omogućuje bolje razumijevanje funkcioniranja ekosustava te indikaciju antropogenih učinaka koji često uzrokuju promjene uvjeta okoliša i narušavanje hranidbene mreže kopnenih i vodenih ekosustava. Trofičke interakcije mikrofaune i makrozoobentosa slabo su proučavane u priobalnim (litoralnim) zonama plitkih vodenih tijela. Cilj ovog rada je usporediti interakcije beskralježnjaka i izvora hrane, uključujući epifiton, zooplankton i makrozoobentos u strukturno heterogenim litoralnim zonama triju plikih jezera umjerenog pojasa. U submerznim i strukturno složenim makrofitskim sastojinama vrste *Ceratophyllum demersum* rašljoticalci su razvili populacije velike brojnosti, a također je u njima zbilježena veća raznolikost i biomasa epifitskih protozoa i beskralježnjaka u usporedbi sa sastojinama plutajuće vrste *Nuphar lutea*. Analiza funkcioniranja ekosustava ukazivala je na to da je u heterogenim makrofitskim sastojinama povećana biomasa makrozoobentoskih predatora i izraženija je njihova predacija nad planktonskim rakovima. Hranidbene mreže bile su složenije u heterogenima staništima, a epifiton i zooplankton imali su važan udio u hranidbenim resursima unutar hranidbene mreže beskralježnjaka. Modeliranje hranidbenih mreža inidicira veću ranjivost zooplanktona i epifitona na predaciju beskralježnjaka u kompleksnijim, submerznim, makrofitskim sastojinama u odnosu na sastojine plutajućih makrofita. Integrirani pristup s aspekta ekologije biocenoza, ekosustava i hranidbenih mreža u objašnjenju složenih trofičkih interakcija u litoralnoj zoni potvrđuje povećanje raznolikosti i kompleksnosti hranidbenih mreža sa strukturalnom heterogenošću mikrostaništa.

Ključne riječi: epifiton, zooplankton, makrozoobentos, taktilni predatori, makrofiti, model hranidbenih mreža

INTRODUCTION

Littoral zones significantly determine environmental conditions and biotic interactions in shallow water bodies and may consist of a wide range of microhabitats, e.g. various macrophyte stands, harboring diverse faunal and floral entities (Meerhoff *et al*., 2003; Celewicz-Gołdyn & Kuczyńska-Kippen, 2017). Macrophytes are key organisms in modifying physico-chemical conditions (metabolic gasses, nutrients and light attenuation) and biotic interactions, *e.g.*, predation and zooplankton migration (Scheffer *et al*., 1993; Kuczyńska-Kippen & Wiśniewska, 2011; Meksuwan *et al*., 2014). They support various life styles, functional groups and food sources from organic matter, algae and epiphyton (Kuczyńska-Kippen & Nagengast, 2006) to littoral microfauna (Duggan *et al*., 2001; Malekzadeh-Viayeh & Špoljar, 2012), meiofauna (Ali *et al*., 2007) and macroinvertebrates (Habdija *et al*., 1995; Warfe & Barmuta, 2006; Kovačević *et al*., 2007; Cremona *et al*., 2008). The architectural complexity, age, size and density of macrophytes determine different environmental conditions and their efficiency in providing shelter for zooplankton and fish fry (Cattaneo *et al*., 1998; Bogut *et al*., 2007; Brothers *et al*., 2013) against fish, as visual, (Estlander *et al*., 2009) and macroinvertebrates as tactile (Gonzalez Sagrario *et al*., 2009), predators.

Study on aquatic food webs may reflect ecosystem equilibria or deterioration. Food-web ecology integrates community and ecosystem ecology, species interactions and ecosystem functioning (Thompson *et al*., 2012). Survey of food web connectance and linkage could predict their resilience and robustness due to species extinction or colonisation (Dunne *et al*., 2002; Thompson *et al*., 2012). The productivity of water bodies has been known to be an important constituent of feeding preference and positively influences the vertical extension of food-web structures (France, 2012). More recent studies have shown that low productivity supports omnivory and shortens the vertical food-web structure (Thompson *et al*., 2012). Spatial organisation of the food web within an ecosystem, *e.g.* the pelagial – littoral of lakes, can significantly influence trophic relationships and result in functionally different food webs (Compte *et al*., 2016).

Studies on food webs in standing or running freshwaters have been more engaged with trophic interactions related to fish and macroinvertebrates (Warren, 1989; Woodward & Hildrew, 2001; Dézerald *et al*., 2013; Schriever & Williams, 2013) than with microfauna (Martinez, 1991; Schmid-Araya *et al*., 2002a). Here we attempt to assess the impact of macroinvertebrate tactile predators and food resources (algae and epiphyton) in the littoral zones on the microfauna assemblages (*sensu lato* microscopic heterotrophic organisms: protozoans, rotifers, gastrotrichs, nematodes, ostracods, cladocerans and copepods), presented in zooplankton and epiphyton. Accordingly, the main objectives of this study were: (i) to identify epiphyton, zooplankton and macroinvertebrate assemblages and (ii) to analyse food web properties in the littoral zones of three temperate water bodies. We have focused on the differences in feeding interactions among the structurally different littoral zones as well as on the importance of microscopic epiphytic and planktonic organisms in macroinvertebrates feeding, organic matter cycling and trophic network.

MATERIALS AND METHODS

Study area

This study was conducted in North West Croatia in the vicinity of the city of Zagreb, in the littoral zones of three shallow water bodies of the Sutla backwater (S), Skrcev kut oxbow (Sk, Škrčev kut in Croatian) and Zajarki gravel pit (Z) differing in origin, morphology, anthropogenic impacts, transparency and macrophyte composition and coverage (Fig. 1, Tab. 1a). Sutla backwater is a natural water body, connected with the Sutla River and divided into two interconnected basins: a) the upper basin (UB) with a high coverage of submerged macrophytes, dominated by hornwort, *Ceratophyllum demersum*, and b) the lower basin (LB) without macrophyte stands, which is not considered in this study. Skrcev kut oxbow was moderately covered by yellow waterlily, *Nuphar lutea*; this water body was created during highway construction when a Krapina River meander was cut off 50 years ago. Zajarki gravel pit was built on alluvial deposits next to the inflow of the Krapina into the Sava River. Gravel excavation started in the year 1970 and lasted until 2010. The initial small basins created by digging were later joined to form the recent Zajarki gravel pit which is covered with sparse patches of *N. lutea.*

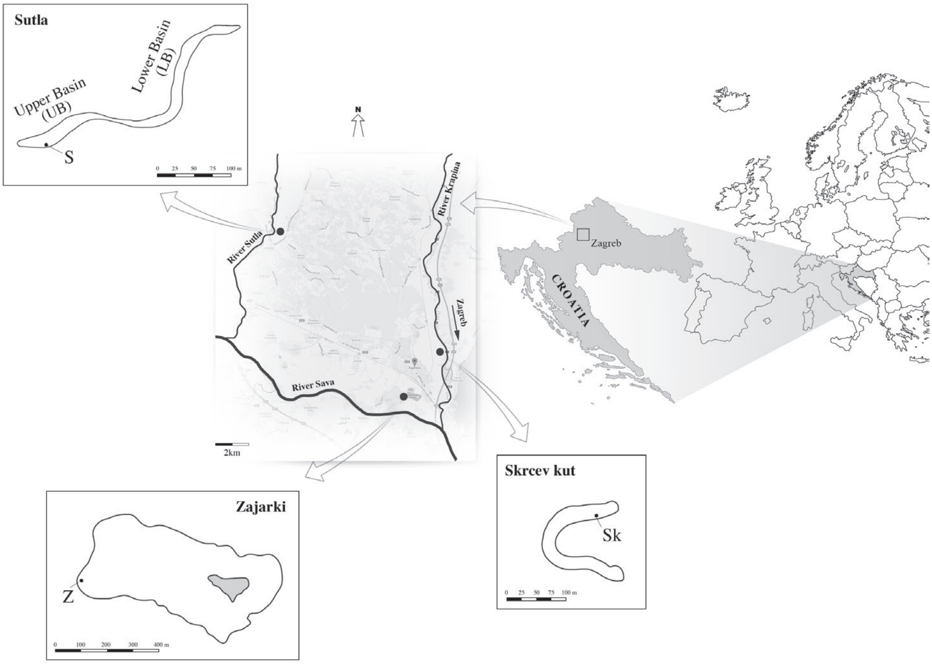

Fig. 1. Map of the investigated water bodies in North West Croatia with marked positions of sampling points in the littoral zones. S: Sutla backwater; Sk: Skrcev kut oxbow; Z: Zajarki gravel pit

Field and laboratory measurements and biocoenotic analyses

Environmental factor measurements and analyses were conducted with a procedure previously described by Špoljar *et al*. (2016). Macrophyte dry mass was measured after epiphyton was scraped off, dried in an oven at 104 °C for 24 h and weighed.

Planktonic, epiphytic and benthic samples were collected in the littoral zone of each waterbody during July, August and September of the year 2012 (3 waterbodies × 3 months × 3 replicates). Epiphyton was sampled from two macrophyte species differing in their stem architecture: first, the floating-leaved yellow waterlily, *N. lutea*, in the littoral zone of Skrcev kut oxbow and Zajarki gravel pit and second, the complex and submerged *C. demersum* in UB (Tab. 1a).

For epiphyton analysis, shoots of *Ceratophyllum* (each sample included a shoot of a single plant) were taken with a plexiglas core sampler (30 cm high, ∅ 8 cm, 26 µm mesh) according to Kornijów & Kairesalo (1994), and *Nuphar* leaves were collected by hand. After cutting 10 to 15 cm long shoots of the macrophytes, the epiphyton was scraped off using a small brush and washed into the plastic bottles, one set of macrophyte shoots was scraped for the identification of microfauna (transferred to the laboratory and the living material was identified ≤ 48 h after collection). Another set of epiphytic samples was collected for the measurement of algal biomass. All shoots were dried off and weighed and epiphytic abundance and biomass were estimated, ind g^{-1}dry mass of the macrophyte (DM) and µg g^{-1} DM, respectively.

Zooplankton samples were collected by filtering 20 L of the water through a plankton net (26 µm mesh) and were fixed with 4% formalin. Zooplankton comprising rotifers, cladocerans and copepods were analysed, while the epiphyton consisted of protozoans, rotifers, nematodes, gastrotrichs and oligochaetes. Zooplankton and epiphyton samples were identified and counted in three subsamples under an Opton-Axiovert 35 inverted microscope (125×to 400× magnification). For species identification, the following references were consulted: Voigt & Koste (1978), Ogden & Hedley (1980), Amoros (1984), Einsle (1993), Foissner & Berger (1996), and Rundle *et al*. (2002). Bdelloidea and Nematoda were counted but not identified.

Macroinvertebrates were sampled from the benthos (ind m^{-2}) and among the macrophytes (ind g^{-1} DM). Benthic macroinvertebrates were sampled using a 25×25 cm Surber sampler (300-µm mesh). A third set of macrophyte shoots was collected for analysis of the macroinvertebrates attached to the stems (pseudoepiphytic, in the further text epiphytic macroinvertebrates). Samples were washed and sieved through a 300-µm mesh net. Macroinvertebrate samples were preserved in 75% ethanol and analysed under an Olympus SZ61 stereomicroscope (10× to 40× magnification). Specimens were identified to the lowermost taxonomic level based on Hopkins (1961), Knoz (1965), Radoman (1983), Nilsson (1996), Nilsson (1997), Waringer & Graf (1997), Bauernfeind & Humpesch (2001), Glöer (2002), Sundermann & Lohse (2004) and Timm (2009).

Biomass of protozoan and metazoan invertebrates in the plankton and epiphyton, presented in dry weight, was calculated by using the biovolume data based on their geometric shapes, and converted to dry mass for protozoans (Gilbert *et al*., 1998), rotifers, cladocerans and copepods (Dumont *et al*., 1975; Malley *et al*., 1989). Macroinvertebrate biomass was determined on up to 30 randomly-selected individuals per taxon in each sample after being dried in the thermostat (104 °C).

We considered functional feeding guilds (FFG) in the plankton (rotifers, cladocerans and copepods) as microfilter-feeders, macrofilter-feeders and predators according to Špoljar *et al*. (2011) and macroinvertebrates were classified according to Moog (2002).

Food web model properties and analysis

To analyze the main properties of the food webs, we used equations and visualizations according to Yoon *et al*. (2004) and Williams (2010). Relationships among the invertebrate consumers (ID predator) and their food resources (ID prey, protozoan and metazoan invertebrates) were analysed through the three food webs consisting of epiphytic, planktonic and macroinvertebrate species. Main food resources were suspended phytoplankton (Ssalgae), epiphytic algae (Ealgae), suspended (SsPOM), sediment (SPOM) and epiphytic (EPOM) particulate organic matter, leaf litter (Ll), as well as protozoan and metazoan invertebrate species.

For the visualization of food webs, the relaxed niche model (RNM) introduced by Williams (2010) was selected, in which the species are placed on vertical axis Y using the convention that the basal species are at trophic level one, while their direct or indirect consumers are at higher trophic levels. Elements of network model, number of trophic species (*S*) and food resources are presented as nodes, and links (L) represent trophic interactions. Common properties of each food network model are analysed in this study: connectivity (L/S), number of link per species; connectance ($C, L/S^2$), the number of links; web complexity (SC) estimated as product $S \times C$ (Polis, 1991); the mean trophic level (TL) of all species computed using the short-weighted trophic level algorithm (Williams & Martinez, 2008) and predator:prey richness ratio (PPR), number of predatory taxa/number of prey taxa (Dézerald *et al*., 2013). In the presented food webs, species of some systematic groups were associated in one trophic node as follows: Testacea and Gymnoamoeba as Sarcodina on S and Sk, Ciliophora on S and Sk, and Gastropoda, Oligochaeta and Hydrachnidia on S, Sk and Z (see supporting information in Appendix S1). Copepod larvae, nauplii and copepodites were each classified as a separate node due to their different food resources through the development.

Tab. 1. Main characteristics of the investigated water bodies (a) and results of the Kruskal-Wallis test ($H_{(2,9)}$, $p < 0.05$) and *post hoc* multiple comparison test for the environmental variables (b)

a)

Localities	Sutla (S)	Skrcev kut (Sk)	Zajarki (Z)
Coordinates	45°54′51″N;	45°51′45″ N;	45°50′36″ N;
	15°42′11″E	15°49′29″ E	15°48′78″ E
Length $_{max}$ (m)	260	300	750
Width $_{max}$ (m)	20	12	310
Depth $_{max}$ (m)	3	2	6
Littoral zone depth (m)	1.43 ± 0.83	0.50 ± 0.10	0.53 ± 0.31
Area (m^2)	2500	2500	31000
Macrophyte coverage (%)	70 - 80	30 - 40	10
Type of macrophytes	Submerged	Floatant	Floatant
Species	*Ceratophylllum demersum*	*Nuphar lutea*	*Nuphar lutea*
TSI_{SD}	55 ± 1.20	69 ± 3.75	49 ± 0.46
TSI_{TP}	91 ± 1.27	91 ± 0.89	83 ± 0.89
TSI_{Chla}	53 ± 4.69	61 ± 1.28	35 ± 4.8
Anthropogenic impact	Leaching from the agricultural field	Leaching from the agricultural field, sport fishing	Arranged coast for sport fishing and recreation

TSI - trophic state index

b)

Environmental variables	Sutla (S)	Skrcev kut (Sk)	Zajarki (Z)	H	p	Multiple comparison
	Mean ± SD	Mean ± SD	Mean ± SD			
Transparency, SD (m)	1.40 ± 0.20	0.53 ± 0.21	2.07 ± 0.12	7.26	0.003	Z > Sk
Conductivity (μS cm^{-1})	343.33 ± 19.73	369.67 ± 29.40	537.33 ± 36.09	6.49	0.04	Z > S
COD_{Mn} (mg O_2 L^{-1})	17.59 ± 5.26	18.75 ± 1.59	6.82 ± 2.87	7.2	0.03	Sk > Z
Chlorophyll *a* plankton (μg L^{-1})	37.10 ± 21.70	27.43 ± 14.26	3.65 ± 2.81	5.8	0.054	
Chlorophyll *a* epiphyton (μg g DM^{-1})	63.14 ± 45.33	15.02 ± 6.50	8.09 ± 6.54	3.8	0.058	
	All localities (S, Sk, Z) p > 0.05					
Temperature (ºC)	24.00 ± 4.90					
Dissolved oxygen (mg L^{-1})	8.58 ± 2.33					
pH	8.15 ± 0.43					
Orthophosphates, PO_4^{3-}-P (mg L^{-1})	0.05 ± 0.02					
Nitrates, NO_3^- -N (mg L^{-1})	0.72 ± 0.82					
Nitrites, NO_2^- -N (mg L^{-1})	0.01 ± 0.01					
Ammonia, NH_3-N (mg L^{-1})	0.12 ± 0.05					
Total nitrogen (mg N L^{-1})	1.42 ± 0.71					
Total phosphorus (mg P L^{-1})	0.29 ± 0.12					
Suspended organic matter (mg AFDM L^{-1})	0.01 ± 0.001					

Eleven properties of the RNM are compared among the three food webs *B*, *I* and *T*: the proportions of basal (without prey), intermediate (with both predators and prey) and top (without predators) species; *GenSD*, *VulSD*, *LinkSD*, the normalized standard deviations of generality (the number of taxa a species eats), vulnerability (the number of taxa that feed on a species) and the number of consumers, resources, and consumers plus resources across the species. *Connectance*; *MeanSim*, the mean Jacardian similarity (Martinez, 1991); *PathLen*, the mean characteristic path length between species (Williams *et al*., 2002); *MeanShortChn*, the mean shortest chain to a basal species and *Cluster*, the mean clustering coefficient (Williams *et al*., 2002). For the analysis of prey vulnerability, the species were divided into four groups regarding their size categories and lifestyle: Ie, epiphytic protozoans; IIe, epiphytic metazoans; IIp, zooplankton and IIIb, macroinvertebrates (Tab. S1).

Comparing the empirical food-web structure with that produced by the niche model, we generated a set of a 1000 niche-model web (Dunne *et al*., 2008; Williams & Martinez, 2008). Based on the eleven properties of each network, we calculated niche model error, ME, to determine whether the value of a property in an empirical food web differs significantly from the model's distribution of values for that property; ME Mean is the average of ME means across 11 network properties, ME SD is the standard deviation of ME; $|\mathrm{ME}|$ is the proportion of MEs that fall outside ±1 (Dunne *et al*., 2008).

Data analysis

The mean values of triplicates across estimated variables were considered for the analyses (3 waterbodies × 3 months, $n = 9$). The trophic state index was determined according to Carlson (1977) based on water transparency (TSI_{SD}).

For biocoenotic and environmental analyses, all data were logarithmically transformed [$\log_{10}(x + 1)$] and their normality was checked using the Shapiro-Wilk test. The data of biomass were normally distributed and were compared by one-way ANOVA and *post hoc* Tukey's HSD test. As the rest of the data (abundance, diversity) did not follow a normal distribution even after transformation, the Kruskal-Wallis test (comparison between multiple independent samples for spatial distribution of environmental parameters and biotic components) accompanying *post hoc* multiple comparisons were implemented using Statistica 13.1 (Statsoft, Inc. 2015). Expectedly, as sampling was performed in a limited time period, no temporal oscillations of environmental and biocenotical parameters were established (Kruskal–Wallis test, $p > 0.05$), thus the analyses were focused on spatial/habitat peculiarities.

Multivariate analysis of similarities (ANOSIM) was used to identify differences/similarities in environmental conditions among the three water bodies employing the analytical package PRIMER v6 (Clarke & Gorley, 2006). ANOSIM generates a value of R ranging between −1 and +1; a value of zero indicates no difference among a set of samples (Clarke & Warwick, 2001). The relationships between: (1) the biomass and diversity of epiphyton (sarcodins, ciliates and rotifers), plankton (rotifers, cladocerans, nauplii and copepodites+adults) and epiphytic macroinvertebrate species, e.g., small snails and insect larvae against (2) the biomass of main benthic macroinvertebrates feeding guilds (grazers, active filtrators and predators) and environmental parameters (transparency and food resources), were explored by redundancy analysis (RDA) based on the logarithmically-transformed data. Prior to this, a detrended correspondence analysis (DCA) was performed and, as the data showed a linear response, the RDA was applied (ter Braak & Šmilauer, 2002). Statistical significance of the impacts of the macroinvertebrates and environmental parameters on the littoral plankton and epiphyton was tested by Monte Carlo permutation test (499 permutations).

RESULTS

Environmental parameters

Overall, values of the environmental parameters significantly differed among the water bodies (ANOSIM, $r = 0.60$, $p = 0.01$;). Transparency and conductivity were significantly higher in Z, while DOM values were notably higher in Sk. Trophic levels accounted as TSI_{SD} had maximum values in Sk and lowest in Z. The highest food resources for algivores were determined in plankton and epiphyton of the littoral zone in S (Tab. 1b).

Biodiversity

In total, 167 taxa (90 microfauna and 77 macroinvertebrates) of benthos, plankton and epiphyton were recorded during the study period among the macrophytes in the littoral zones of the three shallow water bodies (see Tab. S1). Only 25 taxa (16%) were common for all the three study sites; among these, 20 belonged to microfauna. Biodiversity assessment resulted in significant difference across the three water bodies (Kruskal-Wallis test $H_{(2, 9)} = 6.489$, $p = 0.04$). The highest diversity (127 taxa) was notified in the backwater S within the submerged macrophyte *Ceratophyllum,* and an almost twice as low diversity was registered in Sk and Z within floating-leaved *Nuphar*; 73 and 59 taxa, respectively. Plankton diversity did not differ significantly among the studied waterbodies (Kruskal-Wallis, $p > 0.05$). With regard to the epiphytic entities, the water bodies of higher trophic levels, S and Sk, reached higher diversity than Z. Macroinvertebrates reached the highest diversity within submerged macrophytes in S (Fig. 2).

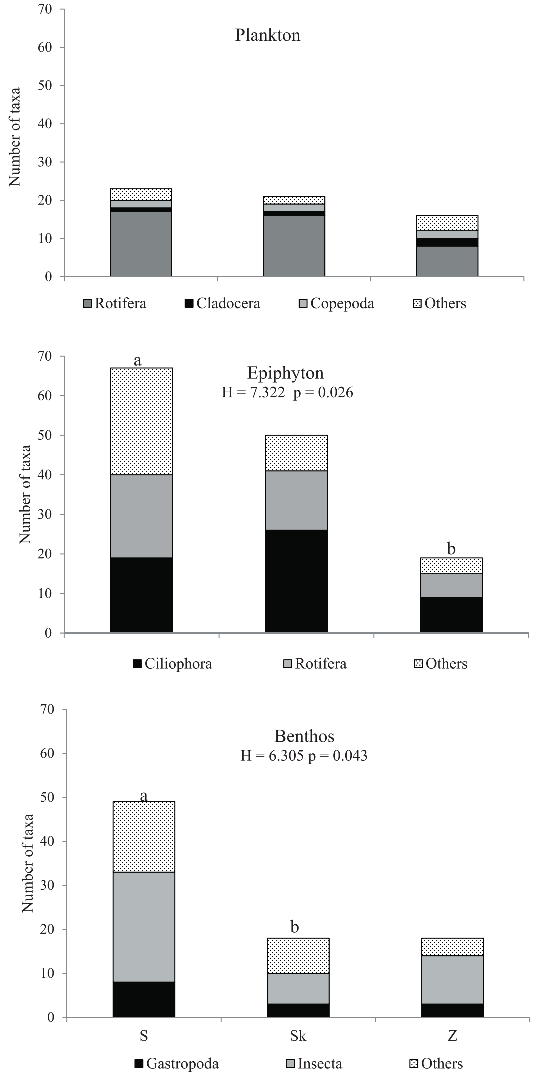

Fig. 2. Biodiversity variations of the dominant biocoenotic groups (plankton, epiphyton and benthos) across the three water bodies. Significant differences were realized by Kruskal-Wallis test ($H_{(2,9)}$, $p < 0.05$).

Abundance and biomass

Rotifers constituted the greatest abundance of the littoral zooplankton in Z and Sk, ~46% and ≤ 96%, respectively (Fig. 3). There was almost ten fold higher abundance of rotifers in Sk (2170 ± 562 ind L^{-1}) than in Z (295 ± 70 ind L^{-1}). This was due, in part, to the populations of *Keratella tecta* (771 ± 606 ind L^{-1}) and *Trichocerca similis* (225 ± 93 ind L^{-1}). Planktonic rotifers represented 90% of the abundance in Sk, and considerably less, 44% and 32%, in S and Z, respectively (see Tab. S1). Littoral species took over larger part of abundance in the two latter water bodies: *i.e.* bdelloids in S and Z, 296 ± 131 ind L^{-1} and 29 ± 5 ind L^{-1}, respectively. Submerged macrophytes in S hosted the most abundant cladoceran population (Fig. 3).

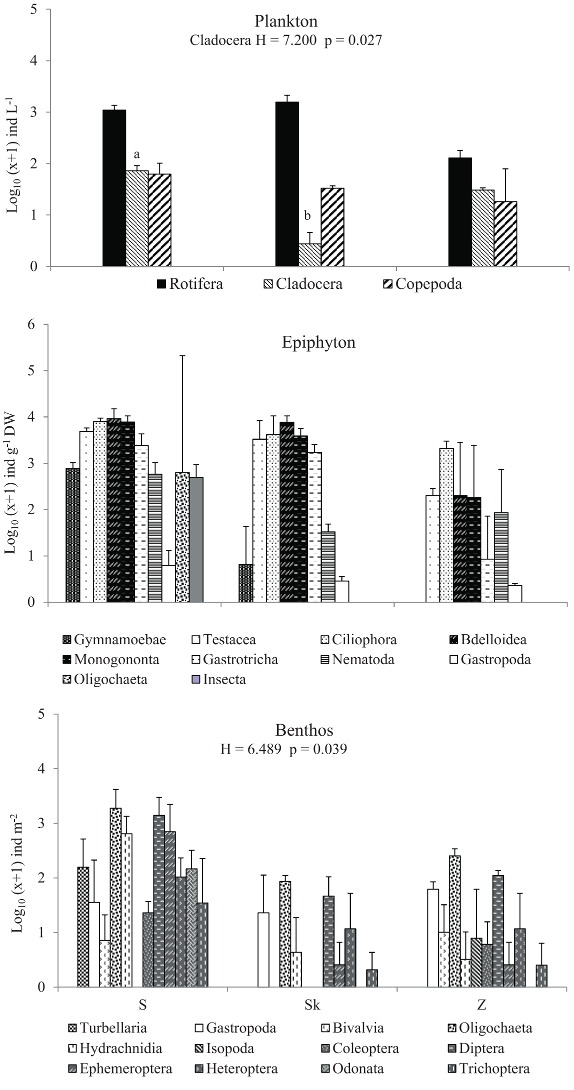

Fig. 3. Oscillations of abundances ($Log_{10(x+1)}$) in plankton, epiphyton and benthos across three water bodies. Significant differences were realized by Kruskal-Wallis test ($H_{(2,9)}$, $p< 0.05$).

Epiphyton, composed of protozoans, microscopic metazoans and macroinvertebrates (gastropods and insect larvae) developed the most diverse and abundant populations over submerged macrophyte stems in S. The bdelloids reached a density of 11124 ± 4044 ind g^{-1} DM, while among MZB in S most abundant were dipteran insect larvae and heteropterans (Fig. 3, Tab. S1). Benthic macroinvertebrates exhibited significantly higher abundances in sediments covered with the submerged *Ceratophyllum* in S, except gastropods, with increased abundance in Z (Fig. 3).

Planktonic biomass ranged from 10^{-5}g L^{-1} to 10^{-3} g L^{-1}. Copepods achieved three (S and Sk) to eleven (Z) fold higher biomass than the two other planktonic groups (Fig. 4). The microhabitats in S held significantly higher biomass of planktonic algivorous cladocerans (ANOVA $F = 11.84$, $p < 0.005$; Tukey's HSD) than Sk. Among the epiphytic metazoans, biomass of rotifers and nematodes was the most prominent. We noted that the complex macrophyte stands in S were favourable habitats for 21 predatory macroinvertebrate species, including turbellarians, phantom midges, notonectids, water mites, heteropterans and majority of dipteran larvae (Tab. S1). Decrease in biomass of the predators was significantly related to the reduction of habitat complexity (ANOVA $F = 9.85$, $p < 0.05$, S > Sk, Z; Tukey's HSD test). Among macroinvertebrates over macrophytes and in littoral sediment, grazers and detritivores also shared a considerable part (Fig. 4).

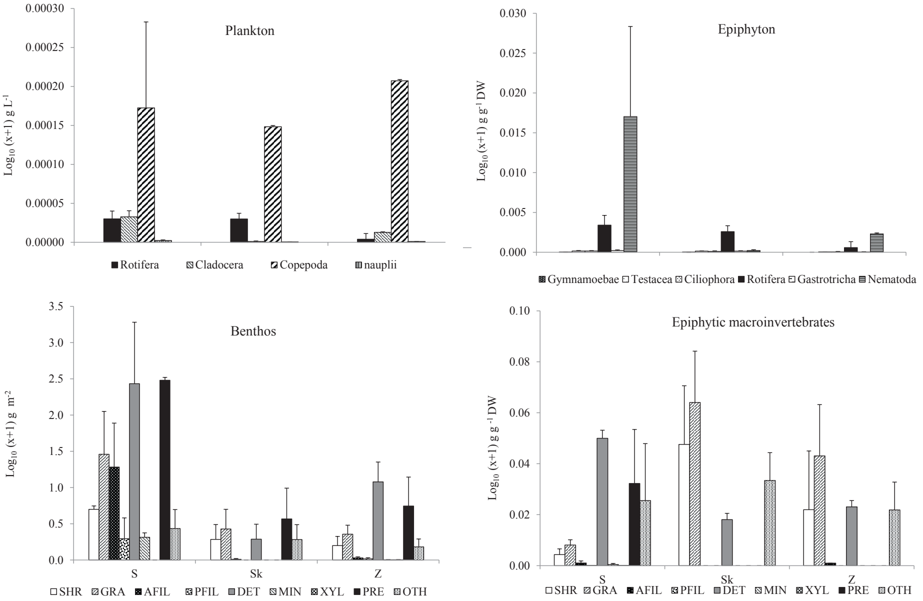

Fig. 4. Oscillations of the biomass ($\mathrm{Log_{10(x+1)}}$) for dominant groups in zooplankton, epiphyton and functional feeding guilds for epiphytic macroinvertebrates over macrophytes and in benthos across three water bodies. SHR: shredders; GRA – grazers, AFIL –active filterers, PFIL –passive filterers, DET – detritivores, MIN – miners, XYL – xylophage, PRE – predators, OTH – others.

Interactions of environmental variables and biotic components

The first two axes of the RDA plot explain 94% of variance, 76% and 15%, respectively. According to the Monte Carlo permutation test, macrophyte coverage ($F = 12$, $p = 0.002$) and biomass of the macroinvertebrate predators ($F = 5.4$, $p = 0.02$) explained 63% and 18% of variance, respectively, and significantly impacted the microfaunal biomass and diversity in the littoral zones (Fig. 5). Most of the evaluated factors strongly related to axis 1 ($r = –0.6$ to $–0.91$). Diversity and biomass of the epiphytic groups were positively affected by food resources and macrophyte structural complexity. Biomass of pelagic rotifers among the macrophyte stands was negatively affected by pelagial transparency, while water transparency increased the diversity of benthic invertebrates and the biomass of pelagic copepods and cladocerans. Increased suspended organic matter and epiphytic algae enhanced the biomass of benthic grazers and detritivores ($r = 0.65$ to 0.75).

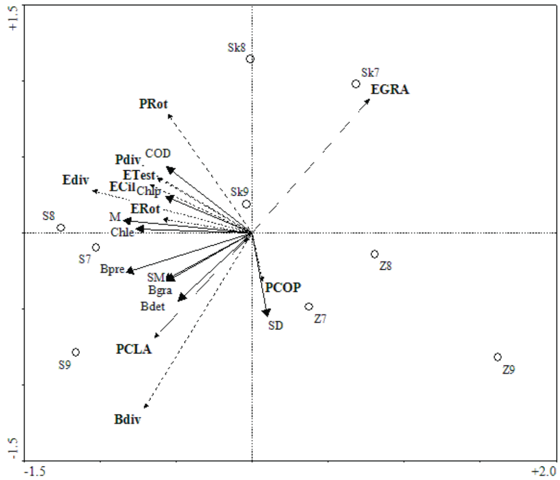

Fig. 5. The triplot of the redundancy analysis (RDA) indicating the interactions between the diversity of each biocenotic constituent, biomass of microfauna and epiphytic grazers (dash line) against environmental conditions and biomass of the benthic macroinvertebrates (solid line). Abbreviations: benthic (Bdiv), epiphytic (Ediv) and planktonic diversity (Pdiv); planktonic Rotifera (PROT), Cladocera (PCLA) and Copepoda (PCOP); epiphytic Testacea (ETes), Ciliophora (ECil), Rotifera (Erot) and grazers (EGRA); Transparency (SD), benthic grazers (Bgra), detritivores (Bdet) and predators (Bpred); phytoplankton biomass (Chlp), epiphytic algae biomass (Chle), dissolved organic matter (DOM), suspended organic matter (SM), macrophytes (M).

Food webs properties and interactions

Relaxed niche food-web models obtained between 41 and 83 trophic taxa (Fig. 6). Diversity, expressed as number of taxa, reduced in trophic species (*S*) up to 35%. The largest web size, linkage and complexity were evidenced in the Sutla backwater and decreased with reduction in habitat heterogeneity (Tab. 2). Connectance varied around 0.11 ± 0.02, and positively related to species generality ($r = 0.641$, $p < 0.001$) and vulnerability ($r = 0.512$, $p < 0.0001$). Thus, maximum C value was observed in Sk with the highest fraction of top predatory species among the estimated food webs. Otherwise, connectance negatively related to PPR ($r = -0.77$, $p > 0.05$). The ratio of *T*:*I*:*B* taxa mostly remained constant among the studied food webs, with a remarkable share of intermediate taxa (Tab. 3). Differences in properties between original and modelled food webs with significantly under- or overestimated values are shown in Tab. 3. The niche model tended to underestimate property values in S and Sk, while the property values were slightly overestimated in Z, mean MEs0.003 to 0.340 (Tab. 4).

Tab. 2. Basic properties of the food webs in the littoral zone of three water bodies. All abbreviations are explained in the section Materials and methods.

Food Web	Sutla	Skrcev kut	Zajarki	BS	LRL	SP
Diversity	127	73	59	85	181	35
S	83	43	41	79	92	25
L	732	239	162	378	994	198
L/*S*	8.82	5.56	3.95	4.45	10.8	7.9
C	0.106	0.129	0.096	0.052	0.118	0.315
SC	17.85	11.38	8.1	9	21.61	16.5
TL	2.47	2.28	2.21			
Tac/Totpred	0.72	0.31	0.50			
PPR	0.57	0.46	0.52			
$P_{Tac}PR$	0.42	0.17	0.29			

LRL, Little Rock Lake (Martinez, 1991); SP, Skipwith Pond (Warren, 1989); BS, Broadstone Stream (Schmid-Araya *et al.*, 2002b)

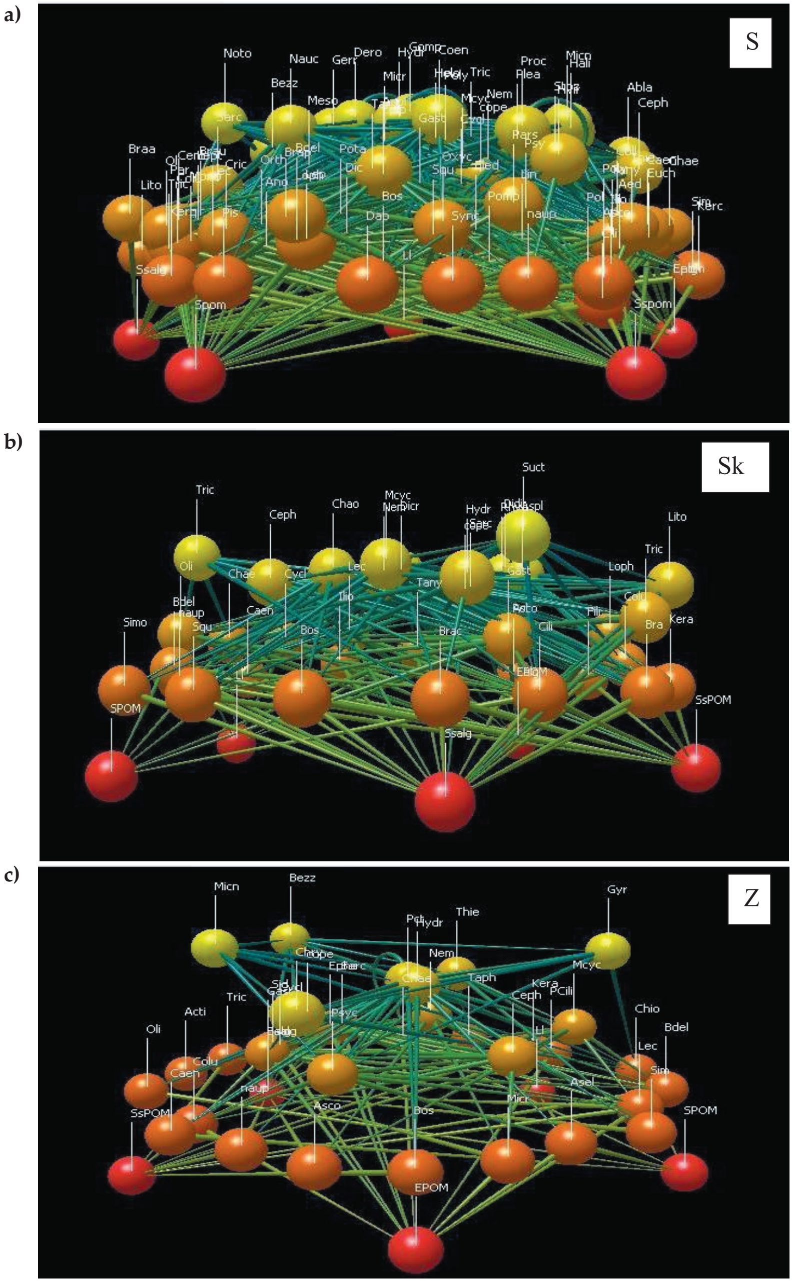

Fig. 6. Relaxed niche model of the food webs based on the original species in the littoral zone of Sutla backwater (S), Skrcev kut oxbow (Sk) and Zajarki gravel pit (Z). Spheres represent trophic species and elongated cones represent feeding links. Position of the taxa vertically corresponds to their trophic level (TL) with basal taxa (primary producers and detritus) shown at the bottom of the network in red, and uppermost taxa at the top in yellow. For species abbreviations consult Table S1. Main food resources were suspended phytoplankton (Ssalgae), epiphytic algae (Ealgae), suspended (SsPOM), sediment (SPOM) and epiphytic (EPOM) particulate organic matter and leaf litter (Ll).

The mean values of prey vulnerabilities for epiphytic metazoans (IIe, i.e. *Colurella, Lecane*, *Lepadella* and gastrotrichs) and planktonic (IIp) species were significantly high (ANOVA *F*= 3.9 – 7.0, $p < 0.05$) in comparison with the protozoans (Ie) and epiphytic macroinvertebrates (IIIb) (Fig. 7). Prey vulnerability for each life type and size category of IIe, IIp or IIIb was significantly higher among the complex submerged macrophyte stands in S (ANOVA *F*= 4.5 – 8.5, $p < 0.05$) than in the floating-leaved stands of Sk and Z.

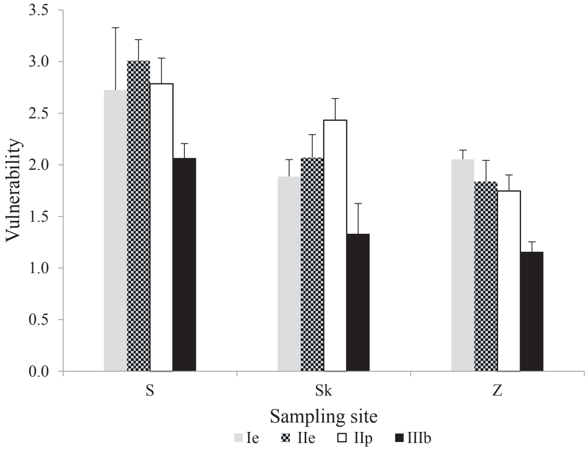

Fig. 7. Prey vulnerability are graded into size categories (I-III) and life style (epiphytic (e), planktonic (p) and benthic(b)) based on the observed food webs in Sutla backwater (S), Skrcev kut oxbow (Sk) and Zajarki gravel pit (Z).

DISCUSSION

Studying complex trophic interactions in diverse water systems is challenging, but recenttly more attention has been drawn toward the discovery of such interactions (Martinez, 1991; Schmid-Araya *et al.*, 2002a; Dunne *et al.*, 2008; Compte *et al.*, 2016). In the current study, we attempted to define trophic interactions by taking into account the basic ecological components, *i.e.*, organism biodiversity, abundance and biomass, environmental variables and functional feeding guilds connected in the interpretation of food web complexity. The results of our study confirmed that in macrophyte stands of higher complexity zooplankton could find short-time refuge from visual predators, i.e. fish, However, among macrophytes, zooplankton simultaneousy encounters macroinvertebrate predators, occupying a significant trophic niche to higher trophic level in shallow water bodies.

Higher concentrations of DOM in the Sutla and Skrcev kut could be explained by the decomposition of considerable algal biomass in plankton and epiphyton, and also by the decay of macrophyte stems and probably due to resuspension as a result of the proximity of the sediment (Špoljar *et al.*, 2012 a,b; Brothers *et al.*, 2013). We assumed that the highest water transparency in Zajarki gravel pit and minimum Chl *a* and dissolved organic matter was an indication of low productivity. Domination of detritivores (i.e. *Keratella* and *Bosmina*) in the zooplankton appears to support ongoing organic matter decomposition, which complies with the results obtained by Špoljar *et al.* (2012a).

The structural heterogeneity of habitats in the Sutla backwater related to the complex macrophyte architecture, significantly enhanced the biodiversity (Kuczyńska-Kippen, 2003; Špoljar *et al.*, 2012a; Chaparo *et al.*, 2015; Dražina *et al.*, 2016), as different from the structural simplicity and biodiversity scarcity in Zajarki gravel pit (Špoljar *et al.*, 2011, Špoljar, 2013). Snails, water mites and insect larvae are the main consumers of epiphyton (Liboriussen *et al.*, 2005), maintain macrophyte light conditions i.e. stands, thus increase the diversity of benthic macroinvertebrates among the macrophyte stems. On the other hand, the substantial decline in macroinvertebrate diversity corresponded significantly to a reduction in the structural heterogeneity in the water bodies; this is similar to the results of studies on Lago di Candia, northern Italy (Cremona *et al.*, 2008) and peat ditches in the Netherlands (Whatley *et al.*, 2014). Rotifers and ciliates, which comprised a considerable proportion of the plankton and epiphyton diversity, did not differ significantly among the studied water bodies. Both of these organisms have high dispersal ability due to their small body size and dormant stages, showing broad distributions typical for microscopic organisms (Fontaneto *et al*., 2008; Wallace *et al*., 2008). Spatial distribution of plankton, epiphyton and macroinvertebrate abundances and biomasses accorded with their diversity pattern, the highest values of which occurred in the Sutla backwater with complex submerged *Ceratophyllum* stands. This phenomenon was also noticed in previous studies (Kuczyńska-Kippen, 2003; Meerhoff *et al*., 2003; Estlander *et al*., 2009; Špoljar *et al*., 2012a,b).

Results of the RDA suggested that planktonic cladocerans in littoral zone were strongly affected by macroinvertebrate predation, and rotifers were not directly affected by predation upon the macroinvertebrates. Romo *et al*. (2004) by conducting mesocosm experiments confirmed that macroinvertebrate predators attacked planktonic crustaceans, especially cladocerans and their nauplii. Our findings are also in accordance with the results of Gonzalez Sagrario *et al*. (2009) who employed both *in situ* and laboratory experiments to show that *Buenoa* sp. (backswimmer), adult *Palemonetes argentinus* (grass shrimp) and *Cyanallagma interruptum* (damselfly) controlled the abundance of cladocerans and copepods. However, copepods' escape strategies and their higher swimming velocities than cladocerans, have given them better adaptation against predators (Chaparro *et al*., 2015). Hampton & Gilbert (2001) suggested that macroinvertebrate predation could be pronounced, especially in the littoral zone or in fishless water bodies. They explained that the predatory insects, the notonectids *Notonecta lunata* and *Buenoa macrotibialis*, the smaller hemipteran *Neoplea striola* and the small (1.5 mm-long) aeschnid dragonfly are capable of direct suppression of rotifer populations, represented by *Hexarthramira, Plationus patulus* and small and large *Synchaeta pectinata*. This predator-prey interaction together with the habitat structure influences the prey density, and confirmed that the role of structurally-complex macrophytes as refuge for prey organisms is pronounced (Wafre & Barmuta, 2004).

According to Warren (1989), food webs are not static entities, either seasonally nor spatially. However, there is a strong persistence in the organization of trophic links where natural communities display non-random interaction patterns (Dunne *et al*., 2008; Dézerald *et al*., 2013). Many food-web studies performed in both terrestrial (*e.g.* grasslands and rainforest) and aquatic (freshwater and marine) environments suggest that network robustness increases with connectance (Dunne *et al*., 2002; Thompson *et al*., 2012). In comparison with surveys conducted by Martinez (1991) in Little Rock Lake (USA) and Schmid-Araya *et al*. (2002b) in different ecosystems across the UK, our biocoenotic analysis was conducted over small spatial distances, within short time periods, and among shallow water bodies with slight habitat differences. The empirical data-sets collected in this study could be used for further food web simulations and could contribute to comparative studies among diverse ecosystem networks (Bascompte, 2009). Food web topologies can be sensitive to sampling effort (Martinez *et al*., 1999) and taxonomical resolution (Martinez, 1992). As is shown by clustering the investigated food webs, taxonomical resolution impacts network size and complexity and determines the food web topology. High taxonomical resolution significantly decreased connectance, as evidenced particularly in the Sutla food web and in the former study of Broadstone Stream (Schmid-Araya *et al*., 2002a). The medium values of connectance (0.01 to 0.13) obtained in this study are in agreement with the typical range published for food webs, 0.05 to 0.3 (Thompson *et al*., 2012).

The mean niche errors indicate that the niche models are consistent with prior results for Skipwith Pond and Little Rock Lake (Dunne *et al*., 2008; Williams & Martinez, 2008). Fractions of top, intermediate and basal species corresponded with the well-resolved food webs in Broadstone Stream and the two latter water bodies (Warren, 1989; Martinez, 1991; Schmid-Araya *et al*., 2002a). The small proportion of basal species is a result of unthorough classification of food resources, *i.e.* POM and algae (Briand & Cohen, 1984). The increase in total invertebrate predators as well as in the tactile macroinvertebrate predators was observed in water bodies of higher transparencies, Sutla backwater and Zajarki gravel pit, probably as a consequence of reinforced fish predation in the pelagial (Špoljar *et al*., 2011, 2016). The enhanced proportion of predators reduces connectance, as was witnessed by the results of our study and those of PPR in tank-bromeliad ecosystems in French Guiana (Dézerald *et al*., 2013). Our results suggest the importance of epiphytic microfauna and zooplankton as the preferable prey among invertebrates. We observed that the vulnerability of microfauna increased with habitat complexity that favours inhabitation of numerous predatory invertebrates. Warfe & Barmuta (2004) revealed that macroinvertebrate abundance and diversity increase with macrophyte density and biomass. Also, macroinvertebrate abundance is positively correlated with epiphyton biomass (Cattaneo *et al*., 1998), indicating that this food source has a direct impact on the invertebrate community, while it is indirectly beneficial for fish colonisation, due to trophic cascade.

We observed the complementarity of the applied multilevel analyses, i.e. community, ecosystem and food web ecology, for the biocoenotic assemblage and their interactions in the shallow lakes. Community survey enriches the knowledge about the role of microhabitats in supporting the biodiversity, but leaves unanswered the question of energy flow within the system. The food-web approach provides general rules regarding the balance among its main constituents, applicable for each ecosystem. However, in the study of the functional feeding groups, the importance of individual species may be masked. Furthermore, while networks are associated with biodiversity and energy flow, high taxonomical resolution may decrease the network connectance. As a result, information about the interactions of some species is lost within the large-sized webs. To achieve a better understanding of the details of these interactions, studies on feeding interactions are the most accurate approaches under controlled experimental conditions. This study showed that habitat can alter food web properties even at a small spatial scale and with limited structural heterogeneity. It was intended to augment our knowledge of different biocoenotic features by resolving food webs' structure. Such investigations are essential for in-depth discovery of ecosystem disturbance and environmental changes.

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SAŽETAK

"Raspetljavanje" hranidbenih mreža u litoralu plitkih jezera umjerene zone

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Litoralna zona plitkih jezera često je pokrivena makrofitskim sastojinama koje predstavljaju staništa bogata izvorima hrane, velike brojnosti, biomase i raznolikosti beskralježnjaka i riba. Općenito, makrofitske sastojine smatrane su skloništima od predatora, a u biotičkim interakcijama najčešće je razmatran odnos predator-plijen na primjeru riba i zooplanktona. Razjašnjenje interakcija u hranidbenoj mreži omogućuje bolje razumijevanje funkcioniranja ekosustava te indikaciju antropogenih učinaka koji često uzrokuju promjene uvjeta okoliša i narušavanje hranidbene mreže kopnenih i vodenih ekosustava. Trofičke interakcije mikrofaune (epifitona, zooplanktona) i makrozoobentosa slabo su proučavane u priobalnim (litoralnim) zonama plitkih vodenih tijela. Cilj ovog rada je usporediti interakcije beskralježnjaka i izvora hrane, uključujući epifiton, zooplankton i makrozoobentos u litoralnim zonama različite heterogenosti staništa triju plitkih jezera umjerenog pojasa. Za dobivanje podataka o interakcijama abiotičkih i biotičkih čimbenika korištene su metode multivarijantne analize i primijenjen je program modeliranja hranidbene mreže. Najveća raznolikost (127 svojti) zabilježena je u litoralnoj zoni rukavca sa submerznim sastojinama zbog velike heterogenosti staništa vrste *Ceratophyllum demersum*, a gotovo dvostruko manje u plitkim mrtvicama čija je litoralna zona pokrivena sastojinama plutajućih makrofita vrste *Nuphar lutea*. Submerzne i strukturno složene makrofitske sastojine vrste *Ceratophyllum demersum* naseljavali su u većoj brojnosti rašljoticalci, a također je u njima zbilježena veća raznolikost i biomasa epifitskih Protozoa i beskralježnjaka u usporedbi sa sastojinama plutajuće vrste *Nuphar lutea*. Analiza funkcioniranja ekosustava ukazivala je na to da je u heterogenim makrofitskim sastojinama povećana biomasa makrozoobentoskih predatora i izraženija je njihova predacija nad planktonskim rakovima. Hranidbene mreže bile su složenije u heterogenim staništima, a epifiton i zooplankton imali su važan udio u hranidbenim resursima unutar hranidbene mreže beskralježnjaka. Modeliranje hranidbenih mreža inidicira veću ranjivost zooplanktona i epifitona na predaciju beskralježnjaka u kompleksnijim, submerznim, makrofitskim sastojinama u odnosu na sastojine plutajućih makrofita. Time su zooplankton i epifiton obilježeni kao važne karike u hranidbenim mrežama plitkih jezera. Velika heterogenost litoralne zone ujedno predstavlja ne samo kratkotrajni zaklon od predatora, već nasuprot, stalnu izloženost predaciji. Integrirani pristup s aspekta ekologije biocenoza, ekosustava i hranidbenih mreža u objašnjenju složenih trofičkih interakcija u litoralnim zonama potvrdili su povećanje raznolikosti i kompleksnosti funkcioniranja hranidbenih mreža sa strukturalnom heterogenošću mikrostaništa.

Appendix. Name, distribution, size categories and life style of the taxa, and the abbreviations connected with 3D food web models. a: adult; Ie - epiphytic protozoans, IIe - epiphytic metazoans, IIp - zooplankton, IIIb – benthic macroinvertebrates, S - Sutla backwater; Sk - Skrcev kut oxbow; Z - Zajarki gravel pit

Species	Study site			Abbreviation	Size + Life style
	S	Sk	Z		
GYMNAMOEBAE					
Amoeba proteus (Pallas, 1766) Leidy, 1878	*			Sarc	Ie
Thecamoeba striata (Penard, 1890)	*		*	Sarc	Ie
Thecamoeba verrucosa (Ehrenberg, 1838) Glaeser, 1912	*			Sarc	Ie
Vahlkampfia limax (Dujardin, 1841)	*			Sarc	Ie
Vampyrella lateritia (Fresenius, 1856) Leidy, 1879		*		Sarc	Ie
TESTACEA					
Arcella discoides Ehrenberg, 1843	*	*	*	Sarc	Ie

Species	Study site			Abbreviation	Size + Life style
	S	Sk	Z		
Centropyxis aculeata (Ehrenberg, 1838)	*	*	*	Sarc	Ie
Difflugia oviformis Cash & Hopkinson, 1909	*			Sarc	Ie
Pseudochlamys arcelloides Penard 1904		*		Sarc	Ie
HELIOZOA					
Actinophrys sol Ehrenberg, 1830			*	Sarc	Ie
CILIOPHORA					
Amphileptus sp.			*	Cili	Ie
Aspidisca costata (Dujardin, 1841) Stein, 1859		*	*	Cili	Ie
Aspidisca lynceus Müller, 1773		*		Cili	Ie
Carchesium polypinum Linnaeus, 1758		*		Cili	Ie
Chilodonella uncinata (Ehrenberg, 1838) Strand, 1928		*	*	Cili	Ie
Cinetochilum margaritaceum Perty, 1852	*	*	*	Cili	Ie
Coleps hirtus (Müller, 1786)	*	*		Cili	Ie
Cyclidium sp.	*	*	*	Cili	Ie
Didinium sp.		*		Didi, Cili	Ie
Epistylis sp.	*			Cili	Ie
Euplotes charon (Müller, 1786) Ehrenberg, 1830		*		Cili	Ie
Euplotes patella (Müller, 1773)	*	*		Cili	Ie
Glaucoma scintillans Ehrenberg, 1830		*		Cili	Ie
Halteria cirrifera Kahl, 1932		*		Cili	Ie
Halteria grandinella (Müller, 1773) Dujardin, 1840			*	Cili	Ie
Holosticha pulaster (Müller, 1773)	*	*		Cili	Ie
Litonotus lamella Schewiakoff, 1896	*	*	*	Lito, Cili	Ie
Microthorax pusillus Engelmann, 1862	*		*	Cili	Ie
Nassula ornata Ehrenberg, 1833	*	*		Cili	Ie
Opercularia articulata Goldfuss, 1820		*		Cili	Ie
Oxytrichidae	*	*	*	Cili	Ie
Paramecium bursaria (Ehrenberg, 1831) Focker, 1836	*	*		Cili	Ie
Podophrya sp.		*		Cili	Ie
Stentor sp.	*			Cili	Ie
Tetrahymena pyriformis Ehrenberg, 1830	*	*		Cili	Ie
Tokophrya lemnarum (Stein, 1859)		*		Cili	Ie
Uronema nigricans (O.F. Müller, 1786)	*		*	Cili	Ie
Urostyla grandis Ehrenberg, 1830	*	*		Cili	Ie
Vaginicola sp.	*	*		Cili	Ie
Vorticella campanula Ehrenberg, 1831	*	*		Cili	Ie
Vorticella microstoma Ehrenberg, 1830	*			Cili	Ie
Vorticella monilata Tatem, 1870		*		Cili	Ie
Vorticella similis Stokes, 1887	*	*		Cili	Ie
HYDROZOA					
Hydra viridissima Pallas, 1766	*			Hvir	IIe
TRICLADIDA					
Dugesia tigrina Girard, 1850	*	*		Tric	IIIb
ROTIFERA					
Ascomorpha ovalis (Bergendahl, 1892)	*	*	*	Asco	IIp
Asplanchna priodonta Gosse, 1850	*	*		Aspl	IIp
Bdelloidea	*	*	*	Bdel	IIe

Species	Study site			Abbreviation	Size + Life style
	S	Sk	Z		
Brachionus angularis Gosse, 1851	*	*		Braa	IIp
Brachionus patulus O.F. Müller, 1786	*			Brap	IIp
Brachionus quadridentatus Hermann, 1783		*		Braq	IIp
Brachionus urceolaris O.F. Müller, 1773	*			Brau	IIp
Cephalodella forficula (Ehrenberg, 1838)	*	*		Ceph	IIe
Cephalodella gibba (Ehrenberg, 1832)	*	*	*	Ceph	IIe
Cephalodella spp.	*	*	*	Ceph	IIe
Collotheca mutabilis (Hudson, 1885)	*			Coll	IIe
Colurella obtusa (Gosse, 1886)	*	*		Colu	IIe
Colurella uncinata (O.F. Müller, 1773)	*	*	*	Colu	IIe
Dicranophorus sp.		*		Dicr	IIe
Epiphanes senta (O.F. Müller, 1773)	*			Epip	IIe
Euchlanis dilatata (Ehrenberg ,1832)	*			Euch	IIe
Filinia longiseta (Ehrenberg, 1834)		*		Fili	IIp
Keratella cochlearis (Gosse, 1851)	*	*	*	Kerc	IIp
Keratella quadrata (O.F. Müller 1786)	*			Kerq	IIp
Keratella tecta (Gosse, 1851)		*		Kera	IIp
Lecane closterocerca (Schmarda, 1859)	*	*	*	Lec	IIe
Lecane cornuta (Müller, 1786)	*			Lec	IIe
Lecane flexilis (Gosse, 1886)	*			Lec	IIe
Lecane luna (Müller, 1776)	*	*	*	Lec	IIe
Lecane lunaris (Ehrenberg, 1832)	*	*	*	Lec	IIe
Lepadella patella (O.F. Müller, 1786)	*			Lep	IIe
Lindia sp.	*			Lin	IIe
Lophocharis salpina Ehrenberg, 1832	*	*		Loph	IIe
Monommata sp.	*			Mono	IIe
Polyarthra spp.	*	*		Poly	IIe
Pompholyx sulcata Hudson, 1885	*			Pomp	IIp
Squatinella lamellaris. f. *mutica* (Ehrenberg, 1832)	*	*		Squ	IIe
Synchaeta pectinata (Ehrenberg, 1832)	*			Sync	IIp
Taphrocampa sp.			*	Taph	IIp
Trichocerca similis (Wierzejski, 1893)	*	*	*	Tric	IIp
GASTROTRICHA					
Chaetonotus sp.	*	*	*	Chae	IIe
NEMATODA					
Nematoda	*	*	*	Nem	IIe
GASTROPODA					
Bithynia tentaculata (Linnaeus, 1758)			*	Gast	IIIb
Ferrissia fragilis (Tryon, 1863)	*	*		Gast	IIIb
Galba truncatula (O.F. Müller, 1774)	*		*	Gast	IIIb
Gyraulus crista (Linnaeus, 1758)	*			Gast	IIIb
Gyraulus laevis (Alder, 1838)	*	*		Gast	IIIb
Hippeutis complanatus (Linnaeus, 1758)	*			Gast	IIIb
Lithoglyphus naticoides (C. Pfeiffer 1828)			*	Gast	IIIb
Lymnaea stagnalis (Linnaeus, 1758)		*		Gast	IIIb
Physella acuta (Draparnaud, 1805)	*	*	*	Gast	IIIb
Radix auricularia (Linnaeus, 1758)	*		*	Gast	IIIb

Species	Study site			Abbreviation	Size + Life style
	S	Sk	Z		
Radix labiata (Rossmässler, 1835)			*	Gast	IIIb
Valvata piscinalis (O.F. Müller, 1774)	*		*	Gast	IIIb
BIVALVIA					
Pisidium sp.	*	*	*	Pis	IIIb
OLIGOCHAETA					
Eiseniella tetraedra (Savigny 1826)	*		*	Oli	IIIb
Enchytraeidae	*	*	*	Oli	IIIb
Lumbricidae	*	*	*	Oli	IIIb
Lumbriculidae	*	*	*	Oli	IIIb
Naididae	*	*	*	Oli	IIIb
HIRUDINEA					
Helobdella stagnalis Linnaeus, 1758	*			Helo	IIIb
TARDIGRADA					
Macrobiotus sp.	*			Tard	IIe
HYDRACHNIDIA					
Arrenurus (Truncaturus) fontinalis K. Viets, 1920	*		*	Hydr	IIIb
Arrenurus globator (O.F. Müller, 1776)	*			Hydr	IIIb
Hydrodroma pilosa Besseling, 1940	*			Hydr	IIIb
Limnesia undulata (O.F. Müller, 1776)	*			Hydr	IIIb
Limnochares aquatica (Linnaeus, 1758)	*			Hydr	IIIb
Neumania angulata Sokolow, 1931	*			Hydr	IIIb
Piona conglobata (Koch, 1836)	*	*	*	Hydr	IIIb
Unionicola figuralis (Koch, 1836)	*			Hydr	IIIb
ARANEAE					
Argyroneta aquatica (Clerck, 1758)	*			Arg	IIIb
CLADOCERA					
Bosmina longirostris (O.F. Müller, 1776)	*	*	*	Bos	IIp
Daphnia obtusa Kurz, 1874	*		*	Dap	IIp
Iliocryptus agilis Kurz, 1878		*		Ilio	IIe
Iliocryptus sordidus (Liévin, 1848)	*			Ilio	IIe
Sida crystallina (O.F. Müller, 1776)			*	Sid	IIe
Simocephalus vetulus (O.F. Müller, 1776)	*	*	*	Sim	IIp
COPEPODA					
Macrocyclops albidus$_{l,a}$ (Jurine, 1820)	*	*	*	Mcyc	IIp
nauplii				naup	IIp
copepodites				cope	IIp
OSTRACODA					
Cyclocypris sp.	*			Cycl	IIp
ISOPODA					
Asellus aquaticus (Linnaeus, 1758)			*	Asel	IIIb
EPHEMEROPTERA					
Brachycercus harrisella Curtis 1834		*		Brac	IIIb
Caenis macrura Stephens 1835			*	Caen	IIIb
Caenis pusilla Navás, 1913	*			Caen	IIIb
Caenis rivolorum Eaton, 1884		*		Caen	IIIb
Centroptilum luteolum (Müller 1776)	*			Cent	IIIb
Ephemera danica Müller, 1764			*	Ephe	IIIb

Species	Study site			Abbreviation	Size + Life style
	S	Sk	Z		
Leptophlebia vespertina (Linnaeus 1758)	*			Lept	IIIb
Parameletus sp.	*			Par	IIIb
Potamanthus luteus (Linnaeus, 1767)	*			Pota	IIIb
ODONATA					
Coenagrion sp.	*			Coen	IIIb
Gomphus sp.	*			Gomp	IIIb
HETEROPTERA					
Gerris buenoi Kirkaldy, 1911	*			Gerr	IIIb
Mesovelia mulsanti White 1879	*			Meso	IIIb
Micronecta sp.	*		*	Micn	IIIb
Microvelia reticulata (Burmeister, 1835)	*			Micr	IIIb
Naucoris maculatus Fabricius, 1782	*			Nauc	IIIb
Notonecta glauca Linnaeus, 1758	*			Noto	IIIb
Plea minutissima Leach, 1817	*			Plea	IIIb
COLEOPTERA					
Bledius sp.$_a$	*		*	Bled	IIIb
Deronectes latus$_a$ (Stephens, 1829)	*			Dero	IIIb
Gyrinus sp.$_a$			*	Gyr	IIIb
Haliplus fulvus$_a$ (Fabricius 1801)	*			Hali	IIIb
Haliplus lineolatus$_a$ Mannerheim, 1844	*			Hali	IIIb
DIPTERA					
Ablabesmyia sp.	*			Abla	IIIb
Aedes sp.	*			Aed	IIIb
Anopheles maculipennis	*			Ano	IIIb
Bezzia sp.	*		*	Bezz	IIIb
Chaoborus sp.		*		Chao	IIIb
Chionea sp.			*	Chio	IIIb
Chrysops sp.			*	Chry	IIIb
Cricotopus sp.	*			Cric	IIIb
Dicrotendipes sp.	*			Dic	IIIb
Megaselia kovaci $_p$ Disney, 1991 pupae	*				IIIb
Oxycera pulchella Meigen, 1822	*			Oxyc	IIIb
Parakiefferiella sp.	*			Par	IIIb
Polypedilum sp.	*			Poly	IIIb
Procladius sp.	*			Proc	IIIb
Psychoda sp.			*	Psyc	IIIb
Stilobezzia sp.	*			Stbz	IIIb
Tanytarsus sp.	*	*		Tany	IIIb
Thienemannimyia sp.	*		*	Thie	IIIb
TRICHOPTERA					
Orthotrichia sp.	*			Orth	IIIb
Polycentropus sp.	*		*	Pct	IIIb
Psychomyia sp.	*			Psy	IIIb
Rhyacophila sp.		*		Rhya	IIIb
LEPIDOPTERA					
Parapoynx stratiotatum (Linnaeus, 1758)	*			Pars	IIIb