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ORIGINAL ARTICLE

Trophic interactions among the heterotrophic components of plankton in man-made peat pools

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ABSTRACT

Man-made peat pools are permanent freshwater habitats developed due to non-commercial man-made peat extraction. Yet, they have not been widely surveyed in terms of ecosystem functioning, mainly regarding the complexity of heterotrophic components of the plankton. In this study we analysed distribution and trophic interrelations among heterotrophic plankton in man-made peat pools located in different types of peatbogs. We found that peat pools showed extreme differences in environmental conditions that occurred to be important drivers of distribution of microplankton and metazooplankton. Abundance of bacteria and protozoa showed significant differences, whereas metazooplankton was less differentiated in density among peat pools. In all peat pools stress-tolerant species of protozoa and metazoa were dominant. In each peat pool five trophic functional groups were distinguished. The abundance of lower functional trophic groups (bacteria, heterotrophic nanoflagellates (HNF) and ciliates feeding on bacteria and HNF) was weakly influenced by environmental drivers and was highly stable in all peat pool types. Higher functional trophic groups (naupli, omnivorous and carnivorous ciliates, cladocerans, adult copepods and copepodites) were strongly influenced by environmental variables and exhibited lower stability. Our study contributes to comprehensive knowledge of the functioning of peat bogs, as our results have shown that peat pools are characterized by high stability of the lowest trophic levels, which can be crucial for energy transfer and carbon flux through food webs.

Key words: Microbial loop; classical food chain; metazoa; Crustacea; peatbog.

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INTRODUCTION

Food webs in aquatic ecosystems function *via* the channelling of energy and flux of materials among diverse assemblages of organisms organized into two chains: the microbial loop and the classical trophic chain. The microbial loop is composed of bacteria and heterotrophic protists (Azam *et al*., 1983), and the role of these communities consists in recovering carbon and nutrients and transferring them to higher trophic levels of the classical trophic chain. Distinct components of the microbial loop influence one another in predator-prey relations and are also influenced by metazooplankton, which are components of the classical grazing chain (Sanders and Wickham, 1993; Gasol *et al*., 1995; Bec *et al*., 2003). Likewise, distinct trophic levels of metazooplankton within the classical food chain affect one another and are directly influenced by planktivorous fish and indirectly by piscivorous fish. These complex predator-prey relations influence species composition and abundances of major components of food chains and in this way can alter their trophic relationships and stability. Countless possible relations between distinct levels of microbial and classical food chains have been described in marine and freshwater ecosystems (Beaver and Crisman, 1982; Güde, 1986; Gilbert *et al*., 1998; Wickham, 1995a, 1995b; Jürgens and Jeppesen, 2000). However, available information on diversity and correlations among components of food chains in other types of aquatic ecosystems, including humic wetlands, is particularly scarce. Humic wetlands have higher concentration of organic matter (OM) in comparison to other aquatic ecosystems, and large quantities of OM are in relatively recalcitrant dissolved form, mostly derived from moss decomposition (Rydin and Jeglum, 2013). As organic matter of low nutritive value is decomposed through a sequence of physical, chemical and biological processes, interactively coupled group of organisms must be recognised to properly evaluate the rate of organic matter regeneration in wetlands. Microbial loop may have significant role in transferring energy from allochtonous OM to metazoplankton, thus food web in these ecosystems may be largely sustained by bacterial production (Jones, 1992). Only a few studies around the world have surveyed plankton food webs in these systems, generally concluding that trophic interactions affecting food webs are dictated by a conjunction of specific morphology and abiotic features of wetlands (Sharma and Bhattarai, 2005; Druvietis *et al*., 2010; Quiroga *et al*., 2013). Peatbogs are wetlands with the capacity to accumulate dead organic matter (peat), in most cases from

slowly decomposing plants. For centuries, peat has been used as a heating fuel and for a wide variety of non-fuel purposes, including horticulture (Robertson, 1993; Cruickshank *et al*., 1995). As a result of non-commercial, small-scale extraction of peat, distinctive water bodies have developed. Owing to biological succession, they have semi-natural features enhancing the biodiversity of peatbogs (Beadle *et al*., 2015). Pools are critical habitats for biodiversity in natural peatlands. They serve as habitats for specific plant communities, foraging sites for amphibians, and breeding habitats for some species of arthropod (Larson and House, 1990; Poulin *et al.*, 1999; Mazerolle, 2005). Man-made peat pools have specific physical and chemical properties, including carbon budget, pH, conductivity, and nutrient concentrations. Pools situated within an ombrotrophic peat profile are characterized by low pH, low levels of primary production and nutrients and high levels of dissolved organic matter Pools that have any sort of minerotrophic input may differ from this pattern and have higher levels of pH and conductivity.

Currently, creating of artificial pools on peatland is a common tool used in restoration of degraded peatlands (Armstrong *et al*., 2009). However, the ecological status of these man-made pools is almost unknown. As environmental conditions can influence the structure and composition of planktonic communities in lake ecosystems and trophic relations between them (Persson, 1999; Adamczuk *et al*., 2015), we hypothesized that man-made peat-pools differ in heterotrophic assemblages according to their characteristic environmental constraints. An additional objective of the study was to estimate the stability of heterotrophic plankton as food web components in order to better understand the effect of environmental drivers on the functioning of food webs in man-made peat pools.

METHODS

Study area

We estimated biocenotic structures of man-made peat pools from peatbogs located in Polesie National Park (east-central Poland). The park is part of the West Polesie Biosphere Reserve protected under the Ramsar Convention as an important wetland site with valuable natural features. It covers 9764.31 ha, and peatbogs account for about 41% of its area (Radwan, 2002). The peatbogs in Polesie National Park are one of a very few groups of peatbogs in Europe formed during the Elsterian glaciation. Six man-made peat pools located on three types of peatbogs were selected for the study: two peat pools located on the carbonate fen Bagno Bubnów (hereafter CF), two peat pools located on the transitional peatland Jelino-Krugłe Bagno (TP), and two peat pools located on the high moor peatland Moszne (HM). CF (51°23′05.4″ N, 23°08′07.8″ E) is located in the eastern part of the park in a basin on chalk bedrock. It is a rare type of base-rich peatbog with small patches of purple moor grass meadows and poor-fen vegetation. TP (51°24′05.9″ N, 23°09′06.9″ E) lies in the western part of the major complex of the park and is probably fed by both precipitation and groundwater. HM (51°27′29.83″ N, 23°07′30.69″ E) is situated at the centre of the major complex of the park and is fed mainly by precipitation. The areas of the peat pits do not exceed 0.5 ha, and their depth reaches a maximum of 2 metres. They represent different vegetation types. The vegetation of TP is heavily dominated by *Sphagnum cuspidatus* and *Utricularia* sp., the vegetation of HM is dominated by *Chara fragilis*, and CF is colonized by *Utricularia* sp. and *Potamogeton* sp.

Field sampling

Environmental parameters

Environmntal variables were measured monthly from April to November 2013-2014. Temperature, dissolved oxygen (DO), electrical conductivity (EC) and pH were determined *in situ* with a YSI 556 MPS multiparametric probe. Other environmental variables were measured in the laboratory: total suspended solids (TSS), total organic carbon (TOC), biochemical oxygen demand (BOD) and chemical oxygen demand (COD) using a PASTEL UV spectrophotometer (Secomam, France); total phosphorus (P_{tot}) and dissolved ortho-phosphorus (P-PO_4) with a Schimadzu UV-1610 spectrophotometer (by the molybdate method after mineralization with a mixture of HNO_3 and H_2SO_4); and nitrate nitrogen N-NO_3 by the sodium salicylate method. Total solids (TS) were estimated according to NREL Laboratory Analytical Procedures (LAP) (Sluiter *et al.*, 2008). Chlorophyll *a* (chl-*a*) was determined spectrophotometrically after extraction with ethanol (Yentsch and Menzel, 1963).

Bacteria and protozoa

From each peat pool three replicate samples were collected once a month from April to November 2013-2014. The abundance of bacteria and HNF were determined with DAPI – 4′6-diamino-2-phenylindole (Porter and Feig, 1980). A 10-mL volume of water was preserved in formaldehyde to a final concentration of 2% and kept in darkness at 4°C. Preparations were made within 24 h after sampling. Sub-samples of 2 mL were condensed on polycarbonate filters (0.2 µm pore size) dyed with Irgalan black and enumerated by epifluorescence microscope. Ciliata communities were investigated using a 5 L planktonic sampler; three replicate samples of volume 0.5 L were fixed with Lugol's solution (0.2% final concentration). Densities of ciliates were determined with an in-

verted microscope by the settling chamber technique: 50 mL of sample was sedimented for at least 24 h and half of the bottom of the chamber was counted at 300 × magnification (Utermöhl, 1958).

Metazoa

From each peat pool, double samples of a 5 L volume were collected and pooled to reduce heterogeneity in metazooplankton distribution and sampling variability, so that the final volume of a sample measured 10 L. Each sample was taken in three replications. Samples were sieved through a 40 μm mesh net and initially fixed with Lugol's solution. Cladocera and Copepoda species were classified and counted using a Sedgewick-Rafter chamber.

Data processing

Differences in environmental conditions and density between the three peat pool types were analysed by one-way ANOVA. No significant differences between pools located on the same peatbog were revealed for any abiotic and biotic variable. Therefore, pools located on each peatbog were considered as grab samples and values of all variables were averaged per sampling date. All variables met the assumption of ANOVA without transformation. All data were previously analysed for distribution and homocedasticity of variables using normality and equal variance tests. In all the cases, the significance level used was 0.05. Tukey's post hoc comparisons (at $P<0.05$) were used to compare means when significant differences were found. Spearman's rank correlation coefficients were used to evaluate the correlation of all pairs of environmental variables to determine which variables were inter-correlated. Trophic groups were distinguished on the basis of feeding habits of taxa. Feeding habits were evaluated with the use of Foissner and Berger (1996), Dussart and Defaye (2001), Dumont and Negrea (2002). The coefficient of variation (CV) was used to quantify the temporal stability of each trophic group: CV (%) = 100σ/mean, where σ is the standard deviation. CV was computed on raw data of density of each trophic group.

In order to assess the influence of different environmental variables on the overall diversity as well as abundance of taxonomic and trophic groups, a Redundancy Analysis (RDA) was performed using raw data. This choice of linear ordination model was justified by the narrow range of the data (previously assessed by DCA with a gradient length <2 standard deviations). Automatic forward selection of environmental variables, performed by the Monte Carlo permutation test (999 permutations), was used to determine the most important variables (Lepš and Šmilauer, 2003). On the resultant plot, the arrows representing environmental variables indicate the direction of maximum change of that variable, and the length of each arrow is proportional to the rate of change. The ordination analyses were performed in CANOCO 4.5 for Windows.

RESULTS

Environmental parameters

Statistically significant differences between the peat pools were found for pH, TOC, chl-a, $P\text{-}PO_4$, COD, BOD ($P<0.01$), EC, and TS ($P<0.05$) (Tab. 1). The lowest pH values were recorded in HM, while values closer to 7 (neutral pH) were observed in CF. TOC, chl-*a*, $P\text{-}PO_4$, and COD had the lowest values in CF and the highest in HM, whereas BOD was lowest in TP and highest in HM. Conductivity and TS content were lowest in TP and highest in CF. Tukey post hoc comparisons detected the smallest differences between CF and TP, which differed in pH, EC, and TSS ($P<0.05$). CF and HM exhibited significant differences in pH, EC, TOC, chl-a, $P\text{-}PO_4$, COD, and BOD ($P<0.05$). TP and HM differed in TSS, TOC, chl-a, $P\text{-}PO_4$, COD, and BOD ($P<0.05$) (Tab. 1). Some environmental variables showed significant inter-correlations. pH showed positive correlations with TS, EC, $N\text{-}NH_4$ (Spearman's rank correlation, r range: 0.34 to 0.43, $P<0.05$), and negative correlations with TOC, COD and BOD (Spearman`s rank correlation, r range: -0.34 to -0.43, $P<0.05$). There were also inter-correlations between above variables, including TS and conductivity (Spearman's rank correlation, $r = -0.47$, $P=0.004$), and TS, TOC, COD, BOD (Spearman`s rank correlation, r range: 0.46 to 0.89, $P<0.001$). Other group of inter-correlating variables were DO, EC and biogenes, including $N\text{-}NO_3$, $P\text{-}PO_4$, and P_{tot} (Spearman's rank correlation, r range: 0.46 to 0.89, $P<0.001$). $N\text{-}NO_3$ correlated with TOC, COD, and BOD (Spearman's rank correlation, r range: 0.73 to 0.74, $P<0.01$). Another group of correlates were chlorophyll-a correlating negatively with pH (Spearman`s rank correlation, $r = -0.44$, $P=0.009$), and positively with $N\text{-}NO_3$, TSS, TOC, COD, and BOD (Spearman's rank correlation, r range: 0.52 to 0.89, $P<0.01$). Among this group of correlates, TSS showed significant correlation with COD ($r = 0.34$, $P=0.048$).

Heterotrophic plankton – composition, abundance and relation to environmental parameters

Microbial plankton components showed significant differences in density between the peat pools (ANOVA, $F = 7.493\text{-}15.994$, $P<0.001$), reaching the lowest values in HM and the highest in CF. Mean abundance of bacteria ranged from 0.669±0.173 cells 10^6 mL^{-1} to 2.75±0.813 cells 10^6 mL^{-1}, and showed significant differences between CF and TP and between CF and HM (Tukey *post-hoc* comparisons, $P<0.01$ in both cases). HNF reached from 1±0.5 in HM to 2.87±1.03 cells 10^3 mL^{-1} in CF, and

differed significantly between all pairs of peat pools (Tukey post hoc comparisons, P<0.01 for CF-TP and CF-HM, P<0.05 for TP-HM). The highest species richness of ciliates was observed in CF (20 taxa) with dominant *Cinetochilum margaritaceum*, while TP had the lowest species richness, with 13 taxa observed, of which *Strombidium* sp. was dominant. In HM, 18 taxa were found and *Paramecium bursaria* was dominant. Mean density of ciliates varied from 19±1.19 to 34±12 ind mL^{-1}, and differed between CF and HM (Tukey *post-hoc* comparisons, P<0.01) and between CF and TP (Tukey *post-hoc* comparisons, P<0.05). Among metazooplankton, Cladocera showed greater differentiation in taxonomic composition between the peat pools, ranging from 13 species with dominant *Chydorus sphaericus* in HM and 15 species with dominant *Ceriodaphnia quadrangula* in TP to 22 species with dominant *Alona costata* in CF. Copepoda were represented by 6-7 species, with dominant *Mesocyclops leuckartii* in HM and TP and *Thermocyclops crassus* in CF. Crustacean plankton showed significant differentiation in density between the peat pools (ANOVA, F = 3.325-6.833, P<0.05). Both Cladocera and Copepoda displayed the lowest densities in HM and the highest in TP. Mean density of Cladocera ranged from 8±7 ind. dm^{-3} to 162±155 ind. dm^{-3}, while the mean density of Copepoda varied from 7±5 ind. dm^{-3} to 295±464 ind. dm^{-3}. Tukey *post-hoc* comparisons of Crustacea density between peat pools showed that HM was distinct from TP (P<0.01 for Copepoda and Cladocera) and CF (P<0.05 for both groups of Crustacea). RDA showed a clear influence of environmental variables on densities of heterotrophic plankton. All axes accounted for 40.3% of the total variance in the relationship between environment and density of planktonic communities and distinctly separated peat pools. Variables that significantly explained the variance in density of heterotrophic plankton were pH (Monte Carlo permutation test, λ=0.07; F=3.78; P=0.003), BOD (λ=0.09; F=4.36; P=0.003), DO (λ=0.08; F=4.59; P=0.004), Chl-a (λ=0.05; F=2.8; P=0.03), TS (λ=0.03; F=2.14; P=0.04), and COD (λ=0.02; F=1.4; P=0.04). The first axis explained 36.1% of the total variance in the relationship between environment al variables and density of planktonic communities and was mostly influenced by Copepoda and DO and correlated with HM. The second axis explained 4.1% of the total variance in the relationship between environmental variables and density of planktonic communities and was positively correlated with pH, bacteria, HNF, Cladocera, Ciliata and CF, and negatively with BOD, chl-a, TS and COD (Fig. 1).

Functional trophic groups within heterotrophic plankton and their stability

Analysis of the feeding habits of individual taxa within plankton communities made it possible to distinguish 5 functional trophic groups. The first two groups comprised bacteria (I) and HNF (II). Third group consisted of bacterivorous and HNF-feeding ciliates (IIIa) and naupli - larval stages of copepods (IIIb). The fourth group comprised omnivorous and predatory ciliates (IVa) preying on groups I-III and cladocerans (IVb) preying on groups I-IIIa. The fifth group consisted of omnivorous and

Tab. 1. Mean values (± standard deviation) of environmental parameters of water in the peat pools. Abbreviations of chemical parameters are detailed in the text.

	Mean values ± standard deviation			One-way ANOVA			Tukey HSD		
	CF	TP	HM	F	df	P	CF-TP	CF-HM	TP-HM
pH	7.04±0.51	4.73±1.01	4.65±1.17	15.994	33	0.00001	P<0.01	P<0.01	
Temperature (°C)	15.12±4.09	19.23±4.81	17.93±5.18	1.785	33	0.184			
Conductivity (µS·cm^{-1})	367±107.62	19.58±6.86	7.38±7.10	7.629	33	0.002	P<0.01	P<0.01	
Dissolved oxygen (mg·L^{-1})	7.08±1.31	7.73±2.16	7.32±2.78	0.001	33	0.999			
TS (mg·L^{-1})	70.5±7.12	11.45±9.64	159.91±92.53	3.658	32	0.037			P<0.05
TSS (mg·L^{-1})	68.27±17.19	137.79±33.39	298.69±125.94	7.230	31	0.0026	P<0.05		P<0.01
TOC (mg·L^{-1})	17.47±2.67	21.32±3.09	51.72±21.58	14.843	33	0.00003		P<0.01	P<0.01
chl-a (µg·L^{-1})	10.03±5.4	42.69±24.50	50.65±29.14	12.845	33	0.0001		P<0.01	P<0.01
Ptot (mg·L^{-1})	0.13±0.09	0.16±0.13	0.58±0.26	1.221	33	0.308			
N-NO_3 (mg·L^{-1})	0.17±0.12	0.62 ±0.58	0.72±0.47	2.844	33	0.73			
N-NH_4 (mg·L^{-1})	0.18±0.15	0.12±0.31	0.39±0.44	1.430	30	0.255			
P-PO_4 (mg·L^{-1})	0.07±0.04	0.050±0.036	0.09±0.11	8.231	33	0.001		P<0.01	P<0.01
COD (mg O_2·L^{-1})	39.89±8.58	46.11±10.10	110.76±48.83	12.058	33	0.0001		P<0.01	P<0.01
BOD (mg O_2·L^{-1})	23.64±5.94	27.97±4.64	68.78±28.73	14.776	33	0.00003		P<0.01	P<0.01

CF, carbonate fen; TP, transitional peatland; HM, high moor peatland; df, degrees of freedom.

carnivorous copepods preying on groups IIIa-IV. Taxonomical characteristics and trophic relations between groups are presented in Tab. 2 and Fig. 2. Groups I-II showed significant inter-habitat differences in density (ANOVA, F=16.694–60.825, P<0.00001), and differenced between CF and TP and between CF and HM (Tukey *post-hoc* comparisons, P<0.05). Groups IIIa, IIIb and IVa showed weaker differences (ANOVA, F=3.535–8.489, P<0.03) and differed only between CF and HM (Tukey *post-hoc* comparisons, P<0.05), whereas groups IVb and V (ANOVA, F=2.902-4.540, P<05) differed significantly between TP and HM (Tukey *post-hoc* comparisons, P<0.05). In RDA analysis, all axes accounted for 41.1% of the total variance in the relationship between environment and density of trophic groups. However, influence of environmental variables on I-IIIa groups was weak. The Monte Carlo permutation test showed the significance of four variables: DO (λ=0.08, F=4.04, P=0.009), influencing mainly group V, temperature (λ=0.03, F=0.94, P=0.013), primarily affecting groups IIIb and IVb, and TS (λ=0.02, F=0.74, P=0.023) and TSS (λ=0.01, F=0.42, P=0.034), influencing group IVa (Fig. 3). Values of CV showed that stability of densities of distinct functional trophic groups decreased along with level in food chain, with groups I-IIIa showing greater stability (CV = 22%-65%) than the other functional groups (CV = 60%-204%). Trophic groups showed the highest stability in HM (33%-106%), whereas in CF the lowest stability of trophic groups was observed (36%-204%).

DISCUSSION

Although peatlands occupy extensive areas in the northern hemisphere, information on the ecology of peat pools is rare (Rydin and Jeglum, 2013). The present study represents one of the very few studies on interactions among heterotrophic plankton in man-made peat pools. Our studies showed that peat pools displayed very different chemical features that were in phase with chemical conditions of surrounding peatlands, similarly to natural freshwater ecosystems (Ferencz, 2016). They also differed in abundances of bacteria, protozoa and metazoa. Despite differences in bacteria densities, the abundances of these organisms were typical for humic water bodies within *Sphagnum* bogs, generally characterized by low abundance of these groups (Druvietis *et al*., 1998, 2010; Taipale *et al*., 2009). However, the bacterial abundances in the peat pools were much lower than those observed in other *Sphagnum*-dominated habitats, like hummocks and hollows (Langenheder *et al*., 2006: $1.39 \cdot 10^6$ cells mL^{-1}; Quiroga *et al*., 2013: $6.2\text{-}11.1 \cdot 10^6$ cells mL^{-1}) suggesting that although studied peat pools had anthropogenic origins, their biota were typical for natural water bodies in

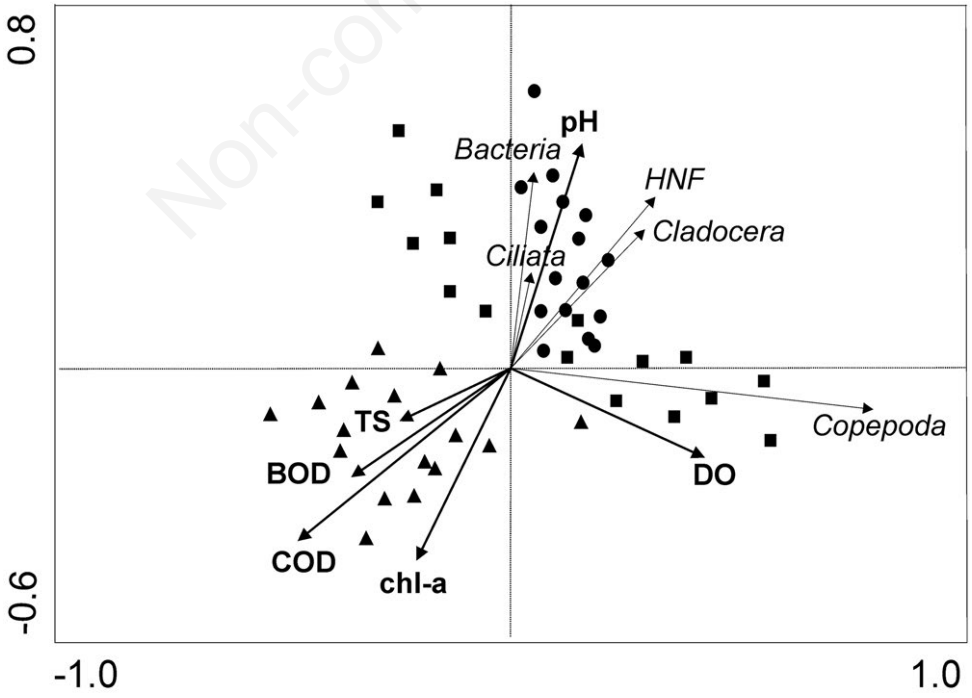

Fig. 1. RDA biplots showing relationships between environmental variables and abundances of heterotrophic plankton in peat-pools. Peat pools are designated as follows: ● carbonate fen (CF), ■ transitional peatland (TP), ▲ high moor peatland (HM).

peatlands. Densities of HNF shaped similarly to those reported in wetlands (Sinistro, 2009; Straskrábová *et al*., 2011). Their abundance was correlated with bacteria, a phenomenon often observed in aquatic ecosystems (Simon *et al*., 1998; Gurung *et al*., 2000). Mean abundances of ciliates were similar to those observed in various peatbog ecosystems (Mieczan, 2009, 2010; Quiroga *et al*., 2013). The peat pools were colonized by stress-tol-

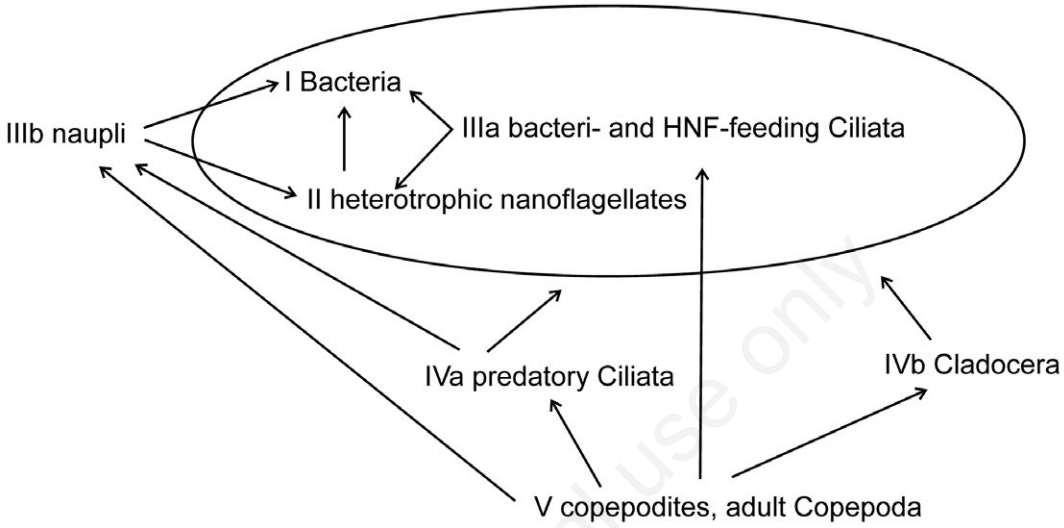

Fig. 2. Trophic relationships between functional trophic groups in peat pools. Meaning of trophic groups is detailed in Tab. 2.

Tab. 2. Functional trophic groups of plankton communities in the man-made peat pools.

Functional group	Ecological characteristics	Trophic relations to other functional groups	Taxonomical characteristics
I	Bacteria		–
II	HNF	I	–
IIIa	Bacteri- and HNF-vorous ciliates	I, II	*Aspidisca costata*, *Chilodonella uncinata*, *Cinetochilum margaritaceum*, *Codonella cratera*, *Coleps spetai*, *Colpoda cucullus*, *Drepanomonas revoluta*, *Holosticha pullaster*, *Paramecium bursaria*, *Spirostomum ambigum*, *Strombidium viride*, *Strombilidium* sp.
IIIb	Naupli	I, II	–
IVa	Omnivorous and carnivorous ciliates	I, II, III	*Amphileptus cleparedei*, *Coleps hirtus*, *Euplotes* sp., *Lacrymaria olor*, *Paradileptus elephantinus*, *Prorodon sp.*, *Spathidium sensu lato*, *Stylonychia mytilus*- Komplex
IVb	Cladocerans	I, II, IIIa	*Acantholeberis curvirostris*, *Acroperus harpae*, *Alonella excisa*, *Alonella exigua*, *Alona costata*, *Alona guttata*, *Alona intermedia*, *Alona quadrangularis*, *Alona rectangula*, *Alona rectangula pulchra*, *Ceriodaphnia pulchella*, *Ceriodaphnia quadrangula*, *Ceriodaphnia reticulata*, *Chydorus latus*, *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Eurycercus lamellatus*, *Macrothrix hirsuticornis*, *Macrothrix rosea*, *Moina brachiata*, *Oxyurella tenuicaudis*, *Polyphemus pediculus*, *Pseudochydorus globosus*, *Scapholeberis mucronata*, *Scapholeberis microcephala*, *Simocephalus serrulatus*, *Simocephalus vetulus*
V	Adult copepods, copepodities	IIIa-IVb	*Cyclops strenuus*, *Eucyclops serrulatus*, *Macrocyclops albidus*, *Macrocyclops fuscus*, *Mesocyclops leuckartii*, *Cryptocyclops bicolor*

Microcyclops varicans, Thermocyclops crassus.

erant species. The dominant species of Ciliata, *i.e*., *C. margaritaceum*, *Strombidium s*p., and *P. bursaria*, were eurytopic species common in a wide variety of aquatic ecosystems (Mori *et al*., 1998; Mieczan, 2009). Among cladocerans, *C. sphaericus* and *C. quadrangula*, which have a high tolerance to wide range of pH values (Flössner, 2000) and the ability to utilize detrital food sources (Gliwicz, 1977; Vijverberg and Boersma, 1997), were dominant in the acidic HM and TP. In the alkaline CF, the acid-sensitive *A. costata* (Havens, 1991; Walseng *et al*., 2003, 2001) was dominant. All three species are widely encountered in different types of freshwater bodies (Duigan, 1992; Illyová and Némethová, 2005). Cladocerans present in peat pits were fairly eurytopic, as they also inhabit the macrophyte zone of hard-water lakes (Adamczuk, 2014). Similarly, Copepoda communities did not distinguish peat pools from other aquatic ecosystems, as *M. leuckartii*, dominant in the acidic peat pools, and *T. crassus*, dominant in the alkaline peat pools, are widely distributed in European freshwater bodies of many other types (Nilssen and Wærvågen, 2000). Both of these species are planktonic (Ueda and Reid, 2003), but they occasionally occur in small water bodies or in the littoral zone of lakes (Adamczuk, 2013).

The environmental variables taken together accounted for 40.3% of the total variance in abundance of food chain components, indicating that their distribution gradient corresponds to changes in the environment. Biochemical and chemical oxygen demand, indicating amount of organic compounds, as well as other environmental parameters potentially indicative of resource subsidy for microbial loop components, were highest in the acidic pool, and lowest in the alkaline pool. Nonetheless, microbial loop components displayed the reverse pattern of densities diminishing along with pH decreases. Thus, pH occurred to be the strongest explanatory variable of variation in the density of microbial loop components. Positive correlations between abundances of microbial loop components and pH have also been reported in lake ecosystems (Yannarell and Triplet, 2004; Lindström *et al*., 2005; Gaedke and Kamjunken, 2006). Resource subsidy is considered one of the most important factors influencing food web functioning (bottom-up *versus* top-down control). However, negative correlations between components of microbial loop and resource subsidies and positive correlations between their densities and pH may suggest that the microbial loop components were controlled by water pH rather than resource availability in the peat pools. Additionally, negative pH-BOD and pH-COD correlations suggested that low pH indirectly inhibited the decay of organic matter by its direct influence on the density of microbial loop components. This conclusion was also supported by negative correlations between pH and TOC, chl-a, and TS as well correlations of the second axis with

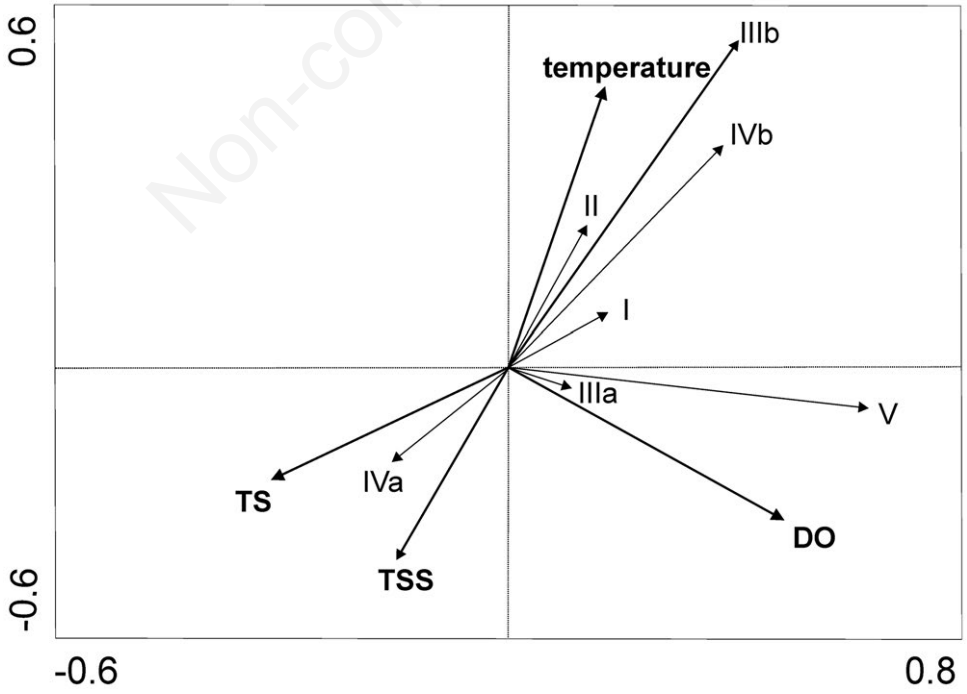

Fig. 3. RDA biplots showing relationships between environmental variables and biomasses of functional trophic groups in peat pools. Meaning of trophic groups is detailed in Tab. 2. Abbreviations of chemical parameters are detailed in the text.

these parameters in RDA. pH also influenced the distribution of cladoceran communities. The influence of pH on Cladocera has also been shown in studies in lake ecosystems, with the conclusion that low pH coincides with decreased abundances of these animals (Nilssen and Sandoy, 1990; Kurbatova, 2005; Nevalainen *et al*., 2011). Cladocera are components of the lowest trophic level in the classical food web and function as intermediaries between the microbial and classical food chains (Agasild *et al*., 2012). Thus, pH, through its direct effect on cladocerans, influenced higher trophic levels of the classical food chain. Copepoda density was correlated with DO concentrations. The crucial influence of DO concentration on successful development of Copepoda has been observed in both freshwater and brackish ecosystems (Tinson and Laybourn-Parry, 1985; Roman *et al*., 1993). Densities of heterotrophic plankton showed significant differences among peat pools, reaching the lowest densities in acidic peat pool and the highest densities in alkaline peat pools. Nonetheless, despite lowest density, heterotrophic plankton showed the highest stability in the acidic peat pools. I and II trophic groups (bacteria and HNF) were less influenced by environmental variables, and that was probably conducive to the stability of these groups. In the same way, group IIIa (bacterivorous and HNF-feeding ciliates) also showed resistance to environmental variables that coincided with their high stability. Higher trophic groups (naupli, omnivorous and carnivorous ciliates, cladocerans, copepodites and adult copepods) proved to be highly vulnerable to environmental variables, including DO, temperature, TS and TSS, and were less stable. In general, stability is thought to be mainly influenced by biodiversity (expressed as taxonomic richness) in plant and animal communities (Hector *et al*., 2010; Downing *et al*., 2014). However, Steiner (2005) found significant relationships between CV values and environmental variables in pond ecosystems. In the studied peat pools, we found similar relations but only for components of the classical food chain. Some papers have reported that in freshwater bodies stability of communities is linked to productivity, because it decreases with increasing system enrichment (Steiner, 2005) and eutrophication (Hautier *et al*., 2014). As the trophic status of peat pools and other humic water bodies differs from trophic statuses non-humic waters, the stability of food web components in these ecosystems is undoubtedly correlated with different environmental variables specific to this type of habitats.

CONCLUSIONS

Recently, man-made peat pools creating by drain blocking have been common restoration tool, however knowledge on the ecology of man-made pools is limited, especially in the domain of heterotrophic plankton. The present characterization of distribution and structure of heterotrophic plankton in correlation with environmental variables represents the first survey of the complete heterotrophic plankton food web from peat pools. In our studies, we found that the peat pools had different assemblages of food web components with respect to species composition, abundance, biomass, and distribution of dominant species. Despite these differences, food web components showed similar patterns of stability that showed inverse correlation with trophic level of organisms. Our studies deepen insight into the structure and functioning of artificial peat pools as surrogates for natural ecosystems with regard to trophic relations among heteroplanktonic organisms.

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