Effect of water chemistry on zooplanktonic and microbial communities across freshwater ecotones in different macrophyte-dominated shallow lakes

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ABSTRACT

*Complex interactions between zooplankton and microbial food webs are vital to the ecosystem ecology of shallow lakes. However, little is known about how horizontal changes in environmental conditions may influence microbial and metazoan communities in shallow lakes. The specific goals of the study were i) to describe environmental variables responsible for the distribution of bacteria, flagellates, ciliates and crustaceans in an adjacent canal, ecotone and reservoir (littoral-pelagic zone) in two different types of lakes (*Ceratophyllum-*dominated and* Potamogeton-*dominated lakes); ii) to determine whether the contact zone waters differ in hydrochemical and biological terms from the waters of the canal and the open water zone; iii) and to evaluate the influence of particular macro-habitats (canal, canal/reservoir, littoral and pelagic zone) on the interactions between components of the planktonic food web. We studied four shallow, eutrophic lakes in Polesie Lubelskie (eastern Poland). The highest diversity and abundance of microorganisms and crustaceans were observed in the canal-reservoir contact zone, while the lowest values were noted in the pelagic zone. Hence, the contact zone in the investigated lakes could fulfil the function of an ecotone, distinguished by a significant increase in biodiversity, abundance, and species specificity of micro- and macroorganisms. Weak relations between food web components were found in the* Ceratophyllum-*dominated lakes, where environmental variables explained the bulk of the total variance in plankton abundance, whereas in the* Potamogeton-*dominated lakes, where environmental variables had a minor role in the total variance in plankton abundance, strong predator-prey relations were noted. Spatial structure of habitats proved to be another important factor for relationships between food web components, as our study indicated that habitat complexity can reduce negative correlations between food web components. Our study contributes to knowledge of the functioning of eutrophic lakes in the current era of increasing eutrophication caused by climate change and human activity.*

Key words: Eutrophication; macrophyte; microbial loop; crustaceans.

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INTRODUCTION

The presence of aquatic submerged vegetation is a very important factor in food webs of shallow lakes. Littoral habitats serve as important sinks for nutrients that enter the lake and are major regulators of nutrient dynamics in lake ecosystems through habitat coupling (Jeppesen *et al.,* 2000; Schindler and Scheuerell, 2002). The littoral zone in shallow lakes comprises a mosaic of vertical and horizontal microhabitats, provided by emergent and submerged macrophytes and open patches. Due to structural and spatial heterogeneity, it maintains a very diverse niche which may allow the coexistence of different life forms (Kairesalo *et al.,* 2000). One of the fascinating roles of macrophytes is their potential to provide refuge for large zooplankton species which, in turn, control the phytoplankton and may also affect the structure and function of the microbial community (Jürgens and Jeppesen, 1997; Kuczyńska-Kippen, 2005). However, little has been known about the microbial communities inhabiting lakes dominated by different types of macrophytes. Understanding the flow of matter and en-

ergy through an ecosystem, as described in food web theory, is of paramount importance (Pomeroy 1974; Segovia *et al.,* 2015). Food webs in aquatic ecosystems function via the flow of energy and matter among diverse assemblages of organisms, and are organised into two webs: the 'microbial loop' and the classical grazing chain. They are regulated both by top-predator grazing (top-down control) and nutrient resources (bottom-up control), and the strength of this control is dependent on trophic position and food web length (Pierce and Turner, 1992; Biyu, 2001; Xu *et al.,* 2005). Countless possible relations between distinct levels of microbial and classical food webs in freshwater ecosystems have been described (*e.g.* Hillbricht-Ilkowska and Węgleńska, 2003; Segovia *et al.,* 2015). While it is well established that metazoan grazing is an important process for the recycling of nutrients and the production of dissolved organic substrates for bacteria, it is also a controlling factor for heterotrophic protist community structure (Fermani *et al.,* 2013; Mieczan and Tarkowska-Kukuryk, 2013). The microbial loop plays an important role in carbon flow and nutrient cycling through microbial components of aquatic

communities. In addition to bacterial uptake of nonliving organic matter, many direct links exist between algae, bacteria, and other heterotrophic microbes (Azam *et al.*, 1983).

The influence of environmental factors is fairly well documented in the case of seasonal and spatial differences in the abundance and biomass of aquatic animals. However, studies on their relations to food web interactions in ecotonal zones (*e.g.* littoral zone) of shallow lakes are scarce. Boundaries between water bodies (lakes, ponds or reservoirs) and adjacent terrestrial patches play an important role in the coupling of terrestrial and aquatic ecosystems. Ecotones are transition zones between relatively homogenous areas or patches (di Castri *et al.*, 1988). They are zones in which environmental gradients are steeper and rates of change in ecological patterns and processes are increased relative to the surrounding zones. The canal–reservoir system may thus be perceived as a spatial system of two kinds of ecosystems or patches. Ecotonal zones of these patches are formed by the mixing of reservoir water with river/canal water (Hillbricht-Ilkowska and Węgleńska, 2003). The zone of river inflow to a reservoir functions as a barrier system and filter of incoming organic matter, nutrients and suspended minerals. Studies on the effect of ecotones on freshwater communities have focused on rotifers (Ejsmont-Karabin, 2003), bacteria and periphyton (Fleituch *et al.*, 2001). However, our knowledge of the distribution and regulating factors of micro- and macroorganisms in transitional zones in shallow lakes is still fragmentary. Because the canal/reservoir zone is recognised as an ecotone (the contact zone between two different ecosystems – water/water ecotone), it was postulated that it should exhibit significant differences in physical and chemical water parameters from adjacent habitats and be distinguished by high species richness and abundance of bacteria, flagellates, ciliates and crustaceans, including species typical of the zone. The specific goals of the study were to analyse the abundance of microbial and crustacean communities; to describe environmental variables responsible for the distribution of bacteria, flagellates, ciliates and crustaceans in an adjacent canal, ecotone and reservoir (littoral-pelagic zone); to determine whether the contact zone waters differ in hydrochemical and biological terms from the waters of the canal and the open water zone; and to evaluate the influence of particular macro-habitats (canal, canal/reservoir, littoral and pelagic zone) on the interactions between components of the planktonic food web.

METHODS

Study area

The study area comprised four shallow (depth 1.5-2.2 m), eutrophic and polymictic lakes (Dratów, Krzczeń, Domaszne and Białe Libiszowskie) in the Polesie Lubelskie region of eastern Poland (51° N, 23° E) (Fig. 1). Over 70-80% of the catchment area of the lakes is used for agriculture (mainly arable land and meadows). In 1961, these lakes were connected to the Wieprz-Krzna Canal (WKC) (Dawidek *et al.*, 2004). Due to feeding with canal waters, the rate of water exchange in the lakes increased and its quality and trophic condition improved. The hydrotechnological facilities are efficient, carefully maintained and fully functional. The water in the reservoirs is replaced several times in a hydrological year, irrespective of the natural feeding system (Dawidek *et al.*, 2004). The lakes represent two types of macrophyte community. Lakes Białe Libiszowskie and Dratów are classified as *Potamogeton*-dominated, with total coverage of the bottom ranging from 7% to 11%; *Potamogeton lucens* L. dominated in the species structure with five accompanying macrophyte species: *Ceratophyllum demersum* L., *Potamogeton crispus* L., *Myriophyllum spicatum* L. and *Stratiotes aloides* L. The other two lakes, Krzczeń and Domaszne, represent the *Ceratophyllum*-dominated type. The total area overgrown by submerged vegetation varied between 28% and 39%; *C. demersum* dominated in the species structure, with the accompanying species *M. spicatum*, *P. crispus* and *Potamogeton pectinatus* L.

Sampling and identification

Microbial communities (bacteria, heterotrophic flagellates and ciliates) and crustaceans (cladocerans and copepods) were examined in a horizontal transect including the following: 1, the Wieprz-Krzna Canal (WKC); 2, the canal/reservoir contact zone (WKC/R); 3, the littoral zone (L); and 4, the pelagic zone (P). The samples were taken in April, July and October 2012-2013. In each of the study seasons three samples were collected from each habitat, so that 72 (36 in 2012 and 36 in 2013) samples were collected in spring, summer and autumn in these lakes. Samples were collected with a 5-litre Bernatowicz sampler at all sites.

Abundances of bacteria were determined using DAPI - 4´6-diamino-2-phenylindole (Porter and Feig, 1980). Water samples of 10 mL were preserved in formaldehyde to a final concentration of 2% and kept in darkness at 4°C. Preparations were made within 24 h after sampling. Four slides were made from each sample, with 2-mL subsamples filtered on 0.2-µm-pore-size polycarbonate filters stained with irgalan black. Epifluorescence microscopy (Nikon, Eclipse) was used to determine total bacterial cell numbers (at 1250× magnification, epifluorescence illuminator HB2-RFL, a mercury lamp HB0-100W, neofluor objective lens 100/l.25). Bacteria were chosen from 5-10 randomly selected fields of each microscope slide and 250-300 cell per slide were counted.

Abundances of heterotrophic flagellates (HF) were determined with primuline solution (Caron, 1983). Water samples of 10 mL were collected into dark sterilised bottles. The samples were preserved in formalin to a final

concentration of 2% and kept in darkness at 4°C. Four preparations were made from each sample. Sub-samples were condensed on 0.8-µm-pore-size black Nucleopore filters and enumerated by epifluorescence microscopy (at 1250× magnification).

Abundances of ciliates and their community composition were determined using the Utermöhl method, at 600× magnification (Utermöhl, 1958). Ciliate samples (3 samples; 500 mL each) were sedimented for 24 h in a cylinder stoppered with Parafilm and then the upper volume of 400 mL was gently removed. To determine density and biomass, three samples were preserved with Lugol's solution. Additionally, live samples were observed for taxonomic identification. Because ciliates are highly perishable and their type of motility is a species-specific feature, species determination and measurements were carried out on live material immediately upon return to the laboratory and after silver impregnation (Augustin *et al.,* 1984). Morphological identification was mainly based on works by Foissner and Berger (1996), Foissner *et al.,* (1999). Crustaceans (Cladocera and Copepoda) were collected with a 5-L sampler. Double samples were collected and pooled to reduce heterogeneity in crustacean distribution and sampling variability. Samples were sieved through in a 40-µm mesh net and fixed with formalin-glycerine solution. In the laboratory, the classification and counts of crustaceans were made with a Sedgewick-Rafter cell (at 100× magnification); abundance was expressed as the number of individuals per L.

Physical and chemical parameters

Simultaneously to the biological examinations, a number of physical and chemical analyses were conducted. Visibility was estimated with a Secchi disc (SD). Temperature, conductivity, pH and dissolved oxygen (DO) were determined *in situ* with a multiparametric Probe (Hanna Instruments). Total suspended solids (TSS) were determined using a PASTEL UV spectrophotometer, and the remaining factors (total phosphorus), $P-PO_4^{3-}$, $N-NH_4$ and $N-NO_3$) were analysed in the laboratory (Golterman, 1969). Total phosphorus (P_{tot}) and ortophosphates were measured using a spectrophotometer UV-1610 Schimadzu (with molybdate method after mineralization with a mixture of HNO_3 and H_2SO_4), nitrate (with sodium salicylate method) and $N-NH_4$ by the Kjeldahl's method. Chlorophyll *a* concentration was determined by spectrophoto-
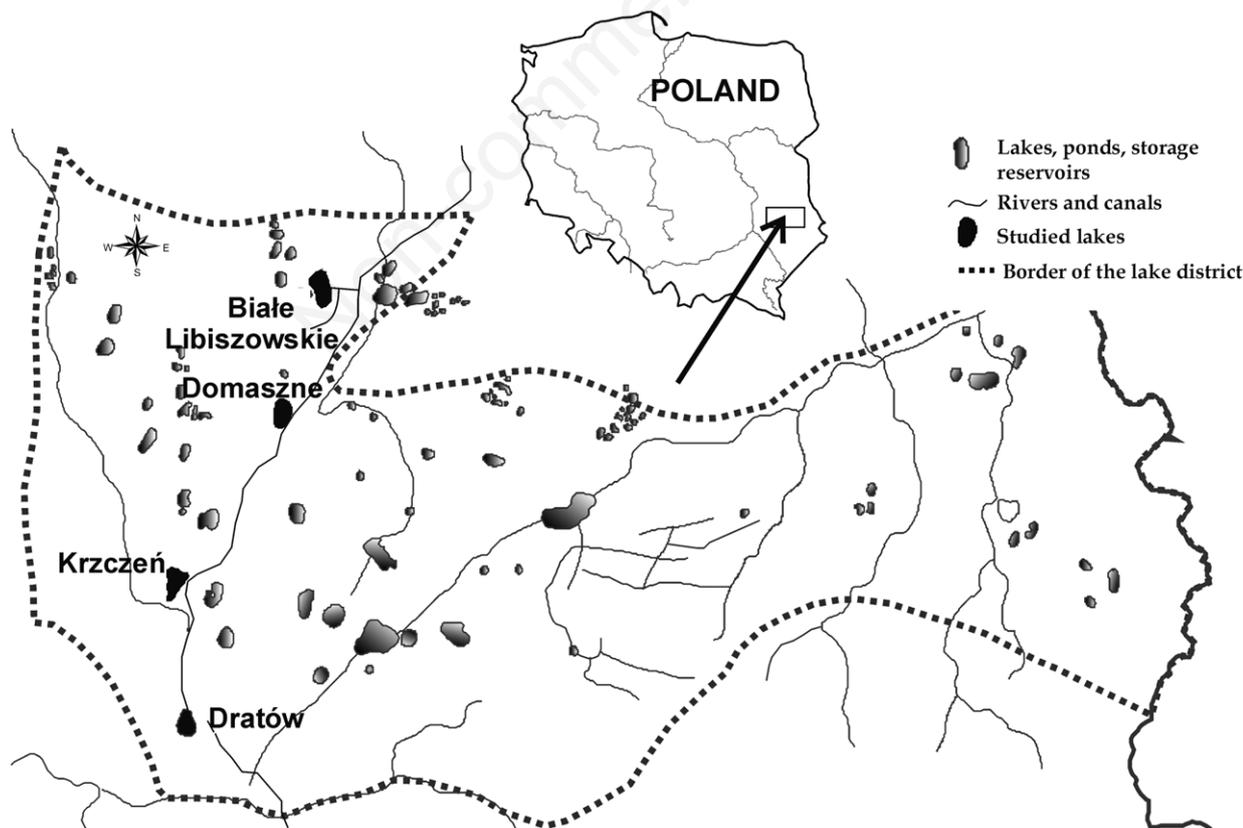

Fig. 1. Location of the studied lakes and sampling points.

metric analysis of acetone extracts of algae retained on Whatman GF/F filters (0.7 µm, 2.5 cm diameter) according to Golterman (1969).

Statistical analyses

Differences in the physical and chemical parameters and in abundance of microbial communities and crustaceans in the different sites were tested using ANOVA. When significant differences were observed, the post-hoc sequential Bonferroni test was performed (Quinn and Keough, 2002). The initial critical probability value was set at $P<0.05/n$, where n=number of samples collected in lake type (n=36). Ordination techniques were used to describe the relationships between groups of the planktonic food web and environmental variables. The length of the gradient indicated by Detrended Correspondence Analysis of the communities was <2 SD, which suggests that redundancy analysis (RDA) was an appropriate method (Ter Braak, 1988-1992). RDA analysis was performed in order to specify the effect of environmental variables on planktonic communities. Moreover, RDA was used to to recognize the importance of environmental conditions on the distribution of ciliate, cladoceran and copepod species along the horizontal gradient (WKC, WKC/R, L, P). The Monte Carlo permutation test (999 permutations) was applied to determine the significance (P<0.05) of variables. All analyses were performed using CANOCO 4.5 for Windows.

Spearman rank correlation coefficients were calculated to determine the relationships between components of the pelagic food web with respect to the site studied, using Statistica 10.0 Software.

RESULTS

Abiotic variables

Physical and chemical water parameters varied between sites and lake types (Tab. 1). In *Potamogeton*-dominated lakes significant differences between the sites were found for conductivity (ANOVA, F=11.15, P<0.001), dissolved oxygen (ANOVA, F=16.15, P<0.001), N-NO$_3$ (ANOVA, F=14.34, P=0.0012), P-PO$_4$ (ANOVA, F=11.88, P=0.0013) and chlorophyll-*a* (ANOVA, F=15.73, P=0.0011). In *Ceratophyllum*-dominated lakes, four environmental parameters changed significantly along the horizontal gradient: conductivity (ANOVA, F=24.41, P<0.001), N-NH$_4$ (ANOVA, F=7.78, P=0.001), N-NO$_3$ (ANOVA, F=69.57, P<0.001) and P-PO$_4$ (ANOVA, F=83.25, P<0.001).

Bacteria, flagellates, ciliates and crustaceans

In *Potamogeton*-dominated lakes the highest mean bacterial numbers were noted in the littoral zone (L) ($18\pm2\times10^6$ cells mL^{-1}) and the highest mean flagellate

Tab. 1. Mean values (±SD) of physical and chemical water parameters at studied sites.

	Potamogeton-dominated lakes				*Ceratophyllum*-dominated lakes			
	WKC	WKC/R	L	P	WKC	WKC/R	L	P
Temperature (°C)	15.1 ±4.1	15.4 ±4.4	15.7 ±4.8	15.6 ±4.7	15.1 ±4.3	15.6 ±5.4	15.9 ±5.3	15.7 ±5.2
pH	7.7 ±0.3	7.8 ±0.5	8.1 ±0.4	8.4 ±0.3	8.1 ±0.4	7.8 ±0.5	8.3 ±0.4	8.2 ±0.4
Conductivity (µS cm^{-1})	385 ±132	260 ±112	258 ±102	251 ±103	415 ±115	295 ±105	239 ±103	234 ±113
Dissolved oxygen (mg L^{-1})	8.44 ±1.71	9.36 ±2.0	9.59 ±1.46	11.54 ±1.85	10.20 ±2.31	8.31 ±1.76	19.48 ±1.96	11.27 ±1.66
N-NH$_4$ (mg L^{-1})	0.242 ±0.072	0.143 ±0.047	0.139 ±0.040	0.127 ±0.058	0.116 ±0.277	0.117 ±0.054	0.115 ±0.063	0.097 ±0.061
N-NO$_3$ (mg L^{-1})	0.474 ±0.514	0.139 ±0.053	0.127 ±0.071	0.128 ±0.101	0.610 ±0.395	0.184 ±0.055	0.136 ±0.077	0.172 ±0.067
P-PO$_4$ (mg L^{-1})	0.093 ±0.031	0.029 ±0.034	0.040 ±0.043	0.033 ±0.025	0.114 ±0.055	0.055 ±0.028	0.029 ±0.017	0.038 ±0.027
P tot (mg L^{-1})	0.206 ±0.088	0.195 ±0.075	0.200 ±0.110	0.203 ±0.066	0.204 ±0.160	0.184 ±0.083	0.191 ±0.140	0.226 ±0.130
TOC (mg L^{-1})	6.2 ±1.6	6.0 ±0.7	6.1 ±0.9	6.4 ±1.1	5.9 ±0.9	5.5 ±1.2	5.0 ±0.7	4.9 ±1.3
Total suspension (mg L^{-1})	14.76 ±10.70	25.57 ±15.53	23.20 ±17.60	28.56 ±19.55	16.98 ±16.18	19.13 ±6.00	27.24 ±6.30	24.82 ±9.77
Chlorophyll-*a* (µg L^{-1})	31.08 ±27.26	63.58 ±26.01	57.99 ±34.20	65.84 ±41.08	41.41 ±21.27	87.56 ±19.01	131.73 ±7.88	91.36 ±11.46

WKC, Wieprz-Krzna Canal; WKC/R, contact zone; L, littoral; P, pelagic zone.

numbers in WKC/R ($2\pm1\times10^3$ cells mL^{-1}), while the lowest densities of both groups occurred in WKC ($6\pm2\times10^6$ cells mL^{-1} and $1\pm0.2\times10^3$ cells mL^{-1}, respectively) (Tab. 2). Species richness and density of ciliates and crustaceans showed horizontal variability. The highest taxa numbers for ciliates and copepods occurred in L and WKC/R (20 and 11 taxa, respectively), and for cladocerans in the pelagic zone (P) (25 taxa). The site showed the significant influence on the densities of bacteria (ANOVA, F=2.12, P=0.0011), flagellates (ANOVA, F=2.61, P<0.001) and ciliates (ANOVA, F=3.07, P<0.001). The dominance structure of ciliate communities showed no significant differences between sites. The highest abundances were attained by *Cinetochilum margaritaceum* (WKC, WKC/R, L), *Askenasia* sp. (WKC, L) and *Strombidium viride* (WKC/R, P). No horizontal differences were noted in the dominance structure of crustaceans. *Bosmina longirostris* and *Thermocyclops crassus* dominated in all of the sites. In *Ceratophyllum*-dominated lakes, densities of bacteria and flagellates showed a similar pattern to that observed in the *Potamogeton*-dominated lakes (Tab. 2). Density of ciliates and crustaceans exhibited horizontal variability (Tab. 2). The highest species richness of ciliate, cladoceran and copepod taxa occurred in the littoral zone (L) (24, 21 and 12 taxa, respectively). As in the *Potamogeton*-dominated lakes, densities of bacteria (ANOVA, F=2.87, P=0.0004), ciliates (ANOVA, F=4.56, P<0.001) and flagellates (ANOVA, F=1.06, P=0.0012) were shown to be significantly affected by the site. The dominance structure of ciliate communities did not differ significantly between the sites. The highest abundances in all sites were attained by *C. mar-*

garitaceum, with accompanying taxa dependent on the site: *Askenasia* sp. (WKC), *Coleps hirtus* (WKC/R, L, P) and *S. viride* (WKC/R, L, P). Horizontal differences were not noted in the dominance structure of cladocerans. *B. longirostris* dominated in all of the sites, accompanied by significant share of *Alonella nana* (WKC/R), *Chydorus sphaericus* (WKC/R, L, P) and *Daphnia cucullata* (L) and copepods - *Mesocyclops leuckartii* (in all sites).

Ordination analyses

In the *Potamogeton*-dominated lakes all the variables together explained 53.1% of the total variance. Variables that significantly (P<0.05, Monte Carlo permutation test) explained the variance in the abundance of planktonic communities were temperature ($\lambda=0.04$; F=2.59; P=0.048), visibility (Secchi depth) ($\lambda=0.06$; F=3.99; P=0.012), conductivity ($\lambda=0.10$; F=6.24; P=0.002) and N-NO$_3$ ($\lambda=0.19$; F=11.04; P=0.002). On the RDA triplot, axis 1 appears to separate individual components of the planktonic food web; bacteria, ciliates and cladocerans are separated from flagellates and copepods (Fig. 2A). Axis 2 separates samples collected in WKC from other sites (WKC/R, L and P). Samples collected in the littoral and pelagic zones may correspond with abundances of bacteria, ciliates and cladocerans, while the presence of flagellates corresponds with samples collected in WKC/R. However, RDAs performed separately for planktonic groups (ciliates, cladocerans and copepods) showed high variability in species-environment relations. The RDA for spatial distribution of ciliates showed that all the environmental variables together explained 73.7% of the total variance. The Monte Carlo permutation test showed the significance of temperature

Tab. 2. Mean densities (±SD) of the years 2012-2013 of components of planktonic food web in studied lakes.

	Potamogeton-dominated lakes							
	Białe Libiszowskie				**Dratów**			
	WKC	**WKC/R**	**L**	**P**	**WKC**	**WKC/R**	**L**	**P**
Bacteria (cells mL^{-1})	$4\pm2\times10^6$	$19\pm1.5\times10^6$	$20\pm3\times10^6$	$8\pm1\times10^6$	$8\pm2\times10^6$	$15\pm1\times10^6$	$16\pm3\times10^6$	$6\pm2\times10^6$
Flagellates (cells mL^{-1})	$1\pm0.3\times10^3$	$2.5\pm0.8\times10^3$	$1.8\pm0.8\times10^3$	$1.5\pm0.4\times10^3$	$1\pm0.3\times10^3$	$1.5\pm0.6\times10^3$	$1.4\pm1.2\times10^3$	$1.3\pm1\times10^3$
Ciliates (ind. L^{-1})	169±19	298±27	145±11	141±16	120±18	199±17	247±23	203±32
Cladocerans (ind. L^{-1})	233±13	161±26	3004±123	29608±324	803±27	337±22	10790±165	6364±152
Copepods (ind. L^{-1})	258±13	2421±39	1526±31	2728±31	464±22	3051±59	2057±42	3145±58
	Ceratophyllum-dominated lakes							
	Domaszne				**Krzczeń**			
	WKC	**WKC/R**	**L**	**P**	**WKC**	**WKC/R**	**L**	**P**
Bacteria (cells mL^{-1})	$11\pm1\times10^6$	$12\pm2\times10^6$	$14\pm1\times10^6$	$14\pm1\times10^6$	$9\pm1\times10^6$	$10\pm1.5\times10^6$	$12\pm3\times10^6$	$10\pm3\times10^6$
Flagellates (cells mL^{-1})	$3\pm1.1\times10^3$	$3.2\pm0.7\times10^3$	$1.3\pm0.6\times10^3$	$1.4\pm1.1\times10^3$	$1\pm0.8\times10^3$	$2.8\pm0.8\times10^3$	$0.9\pm1\times10^3$	$1\pm0.8\times10^3$
Ciliates (ind. L^{-1})	115±29	264±31	213±14	147±21	166±32	329±24	306±29	296±11
Cladocerans (ind. L^{-1})	236±13	581±19	2072±89	1314±27	59±12	416±32	976±52	2235±49
Copepods (ind. L^{-1})	216±19	2358±39	1698±42	3165±61	131±23	1374±49	1844±47	1174±54

WKC, Wieprz-Krzna Canal; WKC/R, contact zone; L, littoral; P, pelagic zone.

(λ=0.04, F=2.08, P=0.022), pH (λ=0.08, F=3.78, P=0.002) and P-PO$_4$ (λ=0.05, F=2.85, P=0.002) in explaining the variability of ciliates in all habitats. On the RDA triplot the species commonly observed in WKC/R, *Astylozoon* sp., *Codonella cratera* and *Urotricha* sp., and two species of WKC, *Askenasia* sp. and *C. margaritaceum*, correspond with the decreasing temperature gradient (Fig. 3A). The ciliates *Cyrtohymena muscorum*, *Paramecium bursaria* and *Spirostomum ambigum* correspond with the WKC habitat and the increasing gradient of P-PO$_4$. A large group of species inhabiting the littoral and pelagic zones, *Amphileptus cleparedei*, *A. pleurosigma*, *Chilodonella uncinata*, *Colpidium colpoda*, *Spathidium sensu lato* and *Stentor coeruleus*, correspond with the increasing pH gradient (Fig. 3A). The results of the RDA for cladocerans showed that all the environmental variables together explained 48.1% of the total variability. The Monte Carlo permutation test indicated the significance of two variables, visibility (λ=0.04, F=2.06, P=0.044) and total suspension (λ=0.09, F=4.71, P=0.036), in explaining the variability of cladocerans along the habitats studied. On the RDA triplot the abundances of *Alonella exigua*, *Leptodora kindtii*, *Pleuroxus laevis*, *Pleuroxus truncatus* and *Scapholeberis mucronata* correspond with the L and P habitats and the increasing gradient of total suspension (Fig. 4A). Secchi disc visibility was associated with the presence of three cladocerans, *Acroperus elongatus*, *Pseudochydorus globosus* and *Simo-*

cephalus vetulus, inhabiting the WKC and L habitats. For copepods, the environmental variables explained 70.3% of their total variance in analysed habitats. Three variables, visibility (λ=0.09, F=4.54, P=0.004), temperature (λ=0.11, F=6.38, P=0.002) and Ptot (λ=0.05, F=2.96, P=0.034), showed significant importance in the Monte Carlo permutation test. On the RDA triplot, two species inhabiting the P habitat, *Cyclops bicolor* and *Paracyclops poppei*, correspond with the decreasing gradient of Ptot (Fig. 5A). Temperature was found to significantly determine abundance of *Acanthocyclops trajani* and *A. robustus* in the L and P habitats. A large group of species (*Acanthocyclops einslei*, *Cyclops strenuus*, *Cyclops vicinus*, *Diacyclops bicuspidatus*, *Eudiaptomus graciloides* and *Mesocyclops leuckartii*) and copepodites of Calanoidae and Cyclopoidae correspond with the rising visibility gradient.

In *Ceratophyllum*-dominated lakes all the variables together explained 78.2% of the total variance. Variables that significantly (P<0.05, Monte Carlo permutation test) explained the variance in the abundance of planktonic communities were pH (λ=0.24; F=14.44; P=0.016), dissolved oxygen (λ=0.03; F=3.51; P=0.016), conductivity (λ=0.05; F=4.60; P=0.002), total suspension (λ=0.07; F=5.55; P=0.006), N-NH$_4$ (λ=0.06; F=4.94; P=0.010), N-NO$_3$ (λ=0.04; F=3.95; P=0.018) and P-PO4 (λ=0.13; F=9.54; P=0.002). On the RDA triplot, Axis 1 appears to separate components of the planktonic food web, with
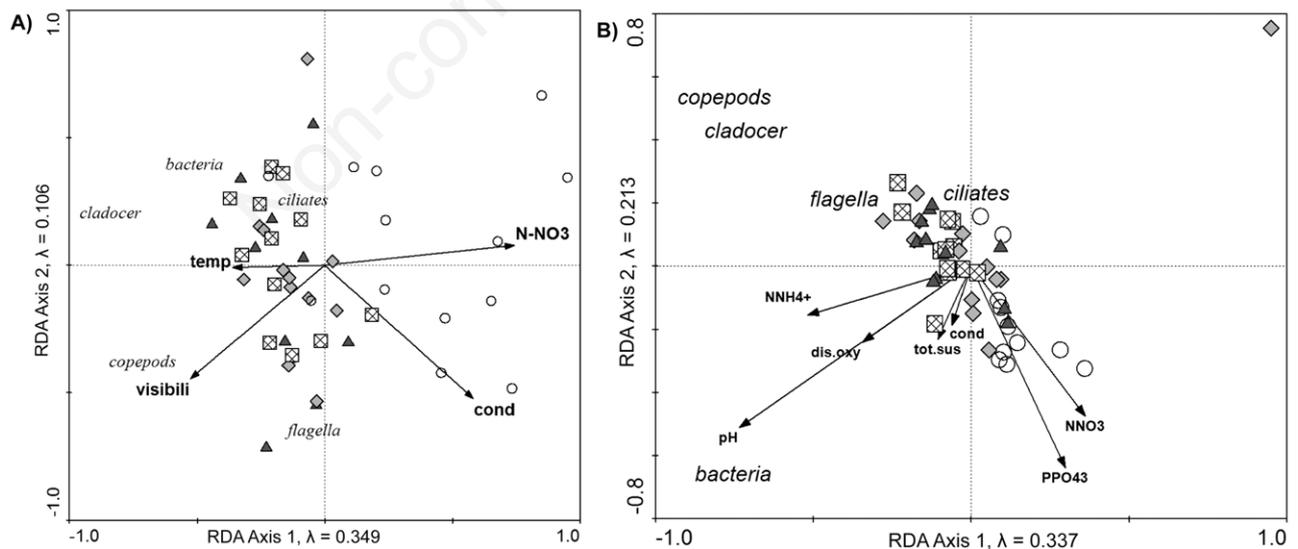

Fig. 2. Triplot of Redundancy Analysis showing components of planktonic food web, studied sites and environmental variables in A) *Potamogeton*-dominated lakes and B) *Ceratophyllum*-dominated lakes. Solid black arrows indicate significant variables based on Monte Carlo permutation test (*P*<0.05). Samples collected at studied sites are marked with geometric figures. White circles, Wieprz-Krzna Canal (WKC); grey diamonds, contact zone: canal/reservoir (WKC/R); crossed squares, littoral zone (L); grey triangles, pelagic zone (P); Chl-a, chlorophyll-*a;* cond, conductivity; dis.oxy, dissolved oxygen; N-NH4, ammonium nitrogen; N-NO3, nitrate nitrogen; Ptot, total phosphorous; P-PO4, dissolved orthophosphates; temp, water temperature; tot.sus, total suspension; visibili, Secchi disc depth; flagella, flagellates; cladocer, cladocera.

bacteria separated from flagellates, ciliates, cladocerans and copepods (Fig. 2B). Samples collected in WKC/R and the littoral zone correspond with abundances of flagellates and ciliates. However, RDAs performed separately for planktonic groups (ciliates, cladocerans and copepods) revealed substantial differences in relationships between species and environmental parameters. The RDA for spatial distribution of ciliates showed that all the environmental variables together explained 88.3% of the total variance. The Monte Carlo permutation test showed the significance of visibility (λ=0.05, F=2.62, P=0.010), total suspension (λ=0.07, F=3.53, P=0.006), dissolved oxygen (λ=0.03, F=1.74, P=0.040) and chlorophyll-a (λ=0.03, F=1.57, P=0.038) in explaining the variability of ciliates in all habitats. On the RDA triplot the species commonly observed in WKC, *Paradileptus elephantinus* and *S. ambigum*, correspond with the decreasing gradient of dissolved oxygen (Fig. 3B). The ciliates *A. cleparedei, Balanion planctonicum, Strombidium* spp., *S. viride* and *Urocentrum turbo* correspond with the WKC/R and P habitats and the rising gradient of visibility. A large group of species inhabiting the littoral and pelagic zones, *Aspidisca costata, Chlamydonella* sp., *C. colpoda, Colpoda*

cucullus, Colpoda steinii, C. uncinata, Euplotes sp., *Lacrymaria olor, P. bursaria, S. coeruleus* and *Vorticella companula*, correspond with the decreasing gradient of chlorophyll-*a* and total suspension (Fig. 3B). The results of the RDA for cladocerans showed that all the environmental variables together explained 46.4% of the total variability. The Monte Carlo permutation test indicated the significance of five variables, *i.e.* temperature (λ=0.04, F=1.89, P=0.048), total suspension (λ=0.03, F=1.83, P=0.044), N-NH$_4$ (λ=0.03, F=1.72, P=0.037), N-NO$_3$ (λ=0.06, F=2.80, P=0.036) and Ptot (λ=0.06, F=3.07, P=0.012), in explaining the variability of cladocerans along the habitats. On the RDA triplot the abundances of *Alona affinis* and *Pleuroxus uncinatus* correspond with the WKC habitat and the rising gradient of total phosphorous (Fig. 4B). Temperature corresponds with the presence of *Alona costata, Bosmina coregoni, Ceriodaphnia quadrangula, D. cucullata, Diaphanosoma brachyurum, Pleuroxus truncatus* and *Sida crystallina* inhabiting the L and P habitats. The presence of *Daphnia longispina* corresponds with the increasing gradient of total suspension and the L habitat. N-NH4 may influence the presence of *Alona guttata, Alona intermedia, Ceriodaphnia rec-*
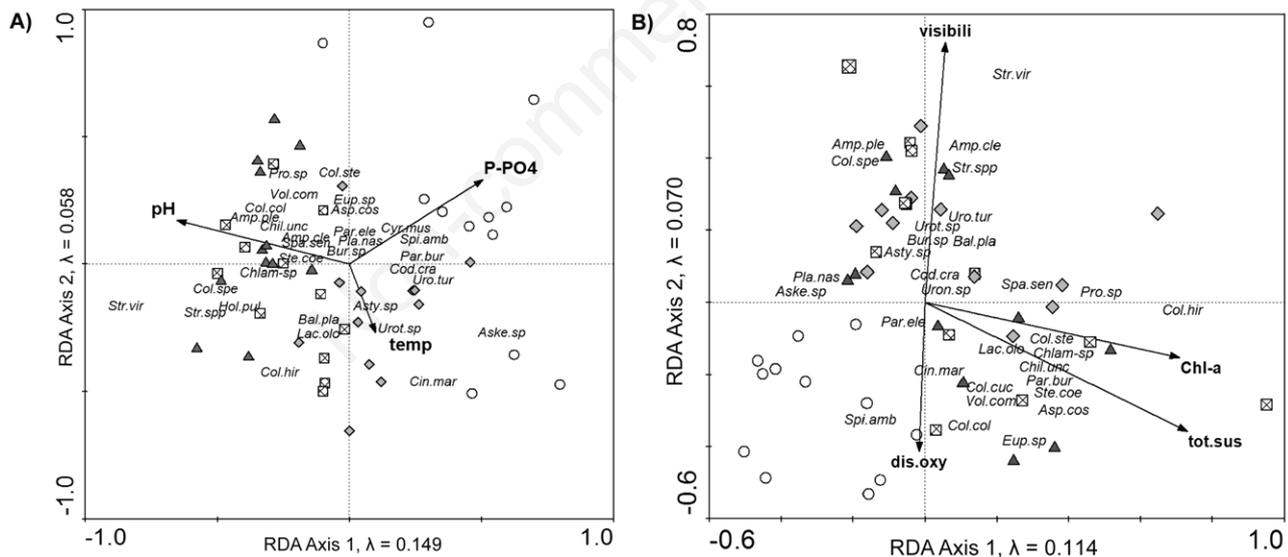

Fig. 3. Redundancy Analysis triplot showing ciliate species, studied sites and significant environmental variables based on Monte Carlo permutation test (P<0.05) in A) *Potamogeton*-dominated lakes and B) *Ceratophyllum*-dominated lakes. Explanations of studied sites and environmental variables are the same as on Fig. 2. *Amp.cle, Amphileptus cleparedei; Amp.ple, Amphileptus pleurosigma; Aske.sp, Askenasia sp.; Asp.cos, Aspidisca costata; Asty.sp, Astylozoon sp.; Bal.pla, Balanion planctonicum; Bur.sp, Bursellopsis sp.; Chil.unc, Chilodonella uncinata; Chlam-spr, Chlamydonella-spr; Cin.mar, Cinetochilum margaritaceum; Cod.cra, Codonella crater; Col.hir, Coleps hirtus; Col.spe, Coleps spetai; Col.col, Colpidium colpoda; Col.cuc, Colpoda cucullus; Col.ste, Colpoda steinii; Cyr.mus, Cyrtohymena muscorum; Dre.rev, Drepanomonas revolute; Eup.sp, Euplotes sp.; Hol.pul, Holosticha pullaster; Lac.olo, Lacrymaria olor; Oxy.sp, Oxytricha sp.; Par.ele, Paradileptus elephantinus; Par.bur, Paramecium bursaria; Pla.nas, Plagiopyla nasuta; Pro.sp, Prorodon sp.; Spa.sen, Spathidium sensu lato; Spi.amb, Spirostomum ambigum; Ste.coe, Stentor coeruleus; Str.vir, Strombidium viride; Str.spp, Strombilidium spp.; Sty.myt, Stylonychia mytilus-Komplex; Uro.tur, Urocentrum turbo; Uron.sp, Uronema sp.; Urot.sp, Urotricha sp.; Vol.cam, Vorticella campanula.*

tirostris and *Pleuroxus laevis*, and correspond with the WKC/R habitat.

For copepods, the environmental variables explained 83.3% of their total variance in the habitats studied. Four variables, visibility (λ=0.10, F=6.14, P=0.004), temperature (λ=0.08, F=5.61, P=0.002), conductivity (λ=0.04, F=3.28, P=0.034) and P-PO$_4$ (λ=0.20, F=11.81, P=0.002), showed significant importance in the Monte Carlo permutation test. On the RDA triplot, two species, *Eucyclops macruroides* and *M. leuckartii*, inhabiting the WKC/R, L and P habitats, correspond with the rising temperature gradient (Fig. 5B). A group of species (*Cryptocyclops bicolor*, *Eucyclops graciloides*, *Eucyclops macruroides* and *Thermocyclops crassus*) and copepodites of Calanoidae and Cyclopoidae correspond with the decreasing visibility gradient and with the littoral and pelagic zones. The presence of the species *Eucyclops serrulatus* corresponds with the rising conductivity gradient and with the WKC/R and L habitats.

Relationships between planktonic food web components

Generally, the number of significant correlations between the main groups of the planktonic food web differed between the sites and lake types (Tab. 3). In *Potamogeton*-dominated lakes, in WKC flagellates correlated positively with density of ciliates (r=0.52, P=0.028) and copepods (r=0.61, P=0.003). In WKC/R bacterial density correlated positively with the density of cladocerans (r=0.54, P=0.037), while flagellates showed a positive correlation with density of ciliates (r=0.58, P=0.035) and copepods (r=0.67, P=0.025). The number of significant correlations was highest in the littoral zone. The number of bacteria showed a significant positive correlation with ciliates (r=0.49, P=0.032), cladocerans (r=0.89, P=0.016) and copepods (r=0.81, P=0.041) and a negative relationship with the number of flagellates (r=-0.78, P=0.046). Flagellates showed a significant negative correlation with the number of cladocerans (r=-0.94, P<0.001) and copepods (r=-0.93, P<0.001). In the open water zone bacterial density exhibited a negative correlation with the density of copepods (r=-0.65, P=0.026), and densities of ciliates and cladocerans were negatively correlated (r=-0.85, P=0.029). In *Ceratophyllum*-dominated lakes, flagellates showed a significant positive correlation with the density of copepods (r=0.61, P=0.033, WKC) and ciliates (r=0.51, P=0.042, littoral zone) and negative relationships with bac-
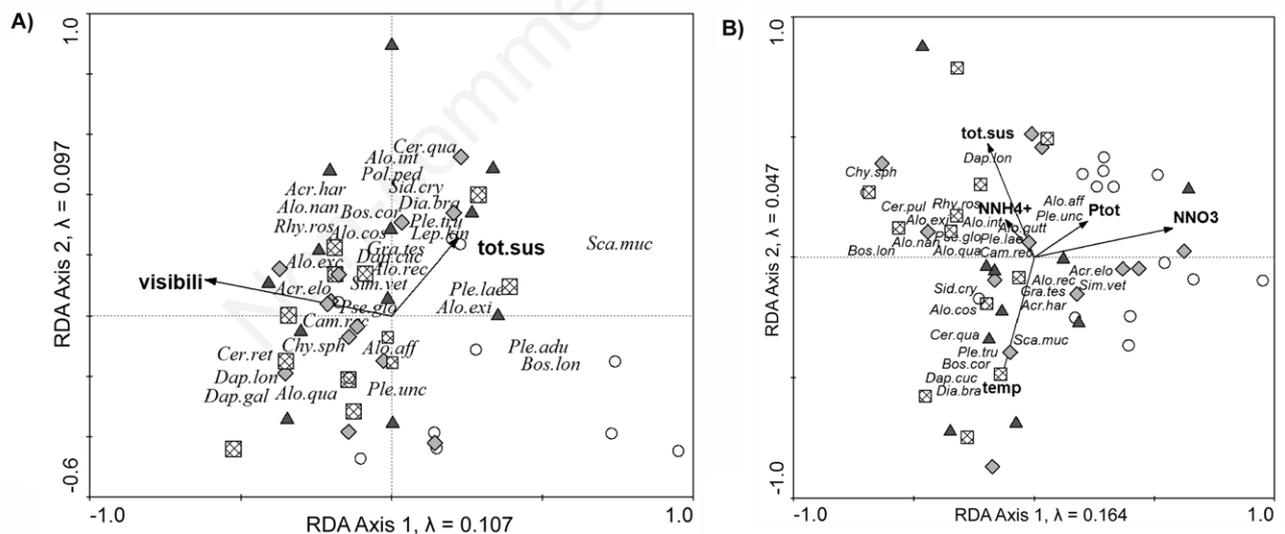

Fig. 4. Redundancy Analysis triplot showing cladocerans species, studied sites and significant environmental variables based on Monte Carlo permutation test (P<0.05) in A) *Potamogeton*-dominated lakes and B) *Ceratophyllum*-dominated lakes. Explanations of studied sites and environmental variables are the same as on Fig. 2. *Alo.aff*, Alona affinis; *Alo.cos*, Alona costata; *Acr.elo*, Acroperus elongates; *Anch.ema*, Anchistropus emarginatus; *Alo.exc*, Alonella excise; *Alo.exi*, Alonella exigua; *Alo.gutt*, Alona guttata; *Acr.har*, Acroperus harpae; *Alo.int*, Alona intermedia; *Alo.nan*, Alonella nana; *Alo.qua*, Alona quadrangularis; *Alo.rec*, Alona rectangular; *Bos.cor*, Bosmina coregoni; *Bos.lon*, Bosmina longirostris; *Cer.meg*, Ceriodaphnia megops; *Cer.pul*, Ceriodaphnia pulchella; *Cer.qua*, Ceriodaphnia quadrangular; *Cam.rec*, Camptocercus rectirostris; *Cer.ret*, Ceriodaphnia reticulate; *Chy.sph*, Chydorus sphaericus; *Dap.amb*, Daphnia ambigua; *Dia.bra*, Diaphanosoma brachyurum; *Dap.cuc*, Daphnia cucullata; *Dap.gal*, Daphnia galeata; *Dap.lon*, Daphnia longispina; *Gra.tes*, Graptoleberis testudinaria; *Lep.kin*, Leptodora kindtii; *Ley.ley*, Leydygia leydygii; *Ple.adu*, Pleuroxus aduncus; *Pse.glo*, Pseudochydorus globosus; *Ple.lae*, Pleuroxus laevis; *Pol.ped*, Polyphemus pediculus; *Ple.tri*, Pleuroxus trigonellus; *Ple.tru*, Pleuroxus truncates; *Ple.unc*, Pleuroxus uncinatus; *Rhy.ros*, Rhynhotalona rostrata; *Sid.cry*, Sida crystalline; *Sca.muc*, Scapholeberis mucronata; *Sim.vet*, Simocephalus vetulus.

teria (r=-0.66, P=0.020, WKC/R) and copepods (r=-0.94, P<0.001, littoral zone). Bacterial density correlated positively with ciliates (r=0.46, P=0.036, littoral zone) and cladocerans (r=0.81, P=0.049, littoral zone and r=0.65, P=0.022, pelagic zone).

DISCUSSION

Food web *vs* environmental parameters

The trophic status of lakes is usually estimated on the basis of several variables (Carlson, 1977). The lakes stud-

ied, while displaying insignificant differences in trophic status, varied significantly in other physical and chemical parameters that apparently influenced diversity in the food web components and the mutual relations among them. *Potamogeton*-dominated lakes displayed lower influence of environmental variables on plankton communities and showed higher densities of bacteria, Cladocera and Copepoda, whereas in the *Ceratophyllum*-dominated lakes higher influence of environmental variables on plankton communities were found and much lower densities of those communities were observed. In both lake types,
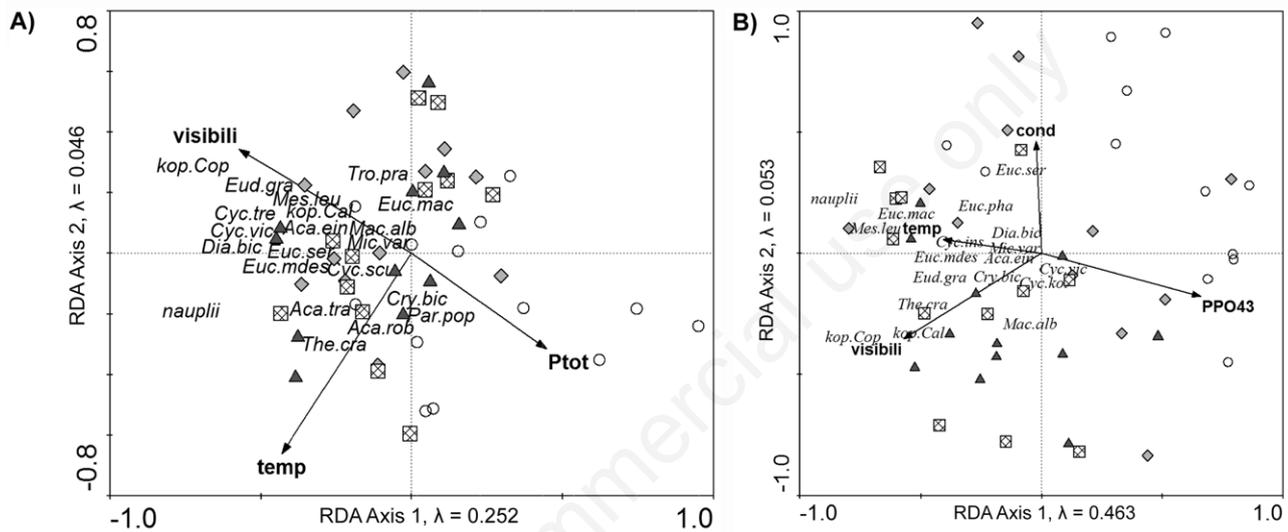

Fig. 5. Redundancy Analysis triplot showing copepods species, studied sites and significant environmental variables based on Monte Carlo permutation test (P<0.05) in A) *Potamogeton*-dominated lakes and B) *Ceratophyllum*-dominated lakes. Explanations of studied sites and environmental variables are the same as on Fig. 2. *Aca.ein*, *Acanthocyclops einslei*; *Aca.rob*, *Acanthocyclops robustus*; *Aca.tra*, *Acanthocyclops trajani*; *Cry.bic*, *Cryptocyclops bicolor*; *Cyc.ins*, *Cyclops insignis*; *Cyc.kol*, *Cyclops kolensi*; *Cyc.scu*, *Cyclops scutifer*; *Cyc.tre*, *Cyclops strenuus*; *Cyc.vic*, *Cyclops vicinus*; *Dia.bic*, *Diacyclops bicuspidatus*; *Dia.cra*, *Diacyclops crassicaudis*; *Eud.gra*, *Eudiaptomus graciloides*; *Euc.mdes*, *Eucyclops macruroides*; *Euc.mac*, *Eucyclops macrurus*; *Euc.ser*, *Eucyclops serrulatus*; *Mac.alb*, *Macrocyclops albidus*; *Mac.dis*, *Macrocyclops distinctus*; *Mes.leu*, *Mesocyclops leuckartii*; *Mic.var*, *Microcyclops varicans*; *Par.pop*, *Paracyclops poppei*; *The.cra*, *Thermocyclops crassus*; *Tro.pra*, *Tropocyclops prasinus*; kop.Cal, copepodites Calanoidae; kop.Cop, copepodites Cyclopoidae.

Tab. 3. Values of Spearman correlation coefficients between components of planktonic food web in investigated lakes.

	Potamogeton-dominated lakes				*Ceratophyllum*-dominated lakes			
	WKC	**WKC/R**	**L**	**P**	**WKC**	**WKC/R**	**L**	**P**
Bacteria:flagellates	-0.17	-0.17	-0.78*	-0.16	-0.49	-0.66*	-0.11	-0.48
Bacteria:ciliates	-0.39	-0.34	0.49*	0.37	-0.14	-0.14	0.46*	0.21
Bactera:cladocerans	-0.20	0.54*	0.89*	0.08	-0.23	0.03	0.81*	0.65*
Bacteria:copepods	-0.05	-0.05	0.81*	-0.65*	-0.27	0.08	0.21	0.26
Flagellates:ciliates	0.52*	0.58*	-0.05	-0.15	0.06	-0.21	0.51*	0.34
Flagellates:cladocerans	-0.02	-0.06	-0.94**	0.42	-0.04	0.14	-0.31	-0.14
Flagellates:copepods	0.61*	0.67*	-0.93**	0.24	0.61*	-0.03	-0.94**	0.25
Ciliates:cladocerans	-0.20	-0.02	-0.03	-0.85*	0.19	-0.07	0.52	0.22
Ciliates:copepods	0.28	0.28	0.27	-0.51	-0.17	-0.08	-0.29	0.23

*WKC, Wieprz-Krzna Canal; WKC/R, contact zone; L, littoral; P, pelagic zone. *P<0.05; **P<0.01.*

planktonic communities differed significantly in the horizontal gradient. Most ciliates dominant across the horizontal gradient were eurytopic species which have rapid ecological adaptability and a wide range of tolerance for environmental changes. Along the horizontal gradient bacterivorous ciliates prevailed. This suggests that ciliates in eutrophic ecosystems constitute a significant link in the flow of matter and energy between bacteria and higher invertebrates. The small proportion of algivorous and algae-diatom feeder ciliates in the habitats studied may have been caused by problems with food availability. Like ciliates, the cladocerans and copepods occurring in the horizontal gradient were eurytopic species found in lakes despite their trophic status. However, while macroplankton showed much higher abundances in the *Potamogeton*-dominated lakes, this group displayed higher species diversity in the *Ceratophyllum*-dominated lakes. In the former, despite differences in the horizontal distribution of Cladocera and Copepoda, both groups had a stable dominance structure in all sites, with *B. longirostris* as the dominant cladoceran and *T. crassus* as the dominant copepod. *B. longirostris* is a cosmopolitan species that prefers eutrophic conditions and displays wall-to-wall behaviour with even horizontal and vertical distribution (Adamczuk, 2012; Jensen *et al.,* 2013). Similarly, *T. crassus* is regarded as an environmentally-tolerant species with invasive ability (Duchovnay *et al.,* 1992; Gutiérrez-Aguirre and Su, 2000). In the *Ceratophyllum*-dominated lakes, low density of Crustacea coincided with quite high species diversity, which was seen in the dominance structure. Although both *B. longirostris* and *T. crassus* also obtained high densities, they were co-dominated by *D. cucullata*, *C. sphaericus*, *A. nana*, *M. leuckartii* and *M. albidus*. The significant correlations between microbial communities and copepods suggest that Copepoda may have a key role in transferring energy from the microbial to the classical food web, especially when we consider that their grazing effect occurs at each developmental stage, including larvae, immature and mature individuals (Adamczuk *et al.,* 2015).

The Monte Carlo permutation test showed that the food web components in the *Ceratophyllum*-dominated lakes were more strongly affected by water chemistry. Environmental variables were less important in the *Potamogeton*-dominated lakes for abundances of food web components. Interestingly, different trophic relations were observed in the two types of lakes. In the *Ceratophyllum*-dominated lakes, which were more strongly affected by environmental variables, the relationships between food web components were weaker. The influence of predator activity control on lower trophic levels generally decreases with increasing nutrient levels (McQueen *et al.,* 1986, 1989; Brett and Goldman, 1996), but some studies suggest that top-down control is in fact most pronounced

in nutrient-rich lakes (Leibold, 1989; Sarnelle, 1992; Jeppesen *et al.,* 1997). However, total suspension (TS) could have an important effect on trophic relations among food web components. This variable was found to be an important factor influencing the spatial distribution of all planktonic communities in the *Ceratophyllum*-dominated lakes. This variable was probably responsible for both the significant relationships between bacteria and higher trophic levels and the weak relationships between microorganisms and higher trophic levels. Detrital particles constituting mostly TS created a medium for bacterial development. Some studies have reported that more than half of the bacterioplankton in aquatic ecosystems may be attached to detrital particles (Simon 1987; Riemann *et al.,* 2000), and the abundance of those particles influences the density, biomass and production of the attached bacteria (Kepkay, 1994; Carrias *et al.,* 2002). Both ciliates and crustaceans can consume particles, including the attached bacteria (Shimeta 1993; Lemarchand *et al.* 2006; Suzuki *et al.,* 2014), and detrital particles with attached bacteria can often be more quantitatively important food for zooplankton (Gons *et al.,* 1992). It is generally accepted that cladocerans transfer energy by eating components of microbial food webs and being preyed on by higher components of the classical food chain, including predatory copepods. Many studies attribute a key role in energy transfer in food webs to *Daphnia* species. However, while *D. cucullata* had a substantial contribution in the dominance structure in the *Ceratophyllum*-dominated lakes, correlations between microbial food web components and cladocerans were weaker than in the *Potamogeton*-dominated lakes, where *B. longirostris*, currently regarded as a minor food web component, was the dominant species. Many reports suggest that *B. longirostris* can have much stronger influence on bacterial communities than Daphnia species (Porter *et al.* 1983; Vague, Pace 1992). Thus, it is possible that high abundances of bacteria as food source contributed to high densities of *B. longirostris* in *Potamogeton*-dominated lakes.

Interactions between food web components - horizontal changes

Comparative data concerning the distribution of bacteria, protozoa and crustaceans in the horizontal transect (WKC –WKC/C – L - P) have thus far been very scarce. Low density of planktonic communities was found in the WKC, probably due to current velocity, which confirms results obtained by Primc-Habdija *et al.* (1998). A visible increase in the density of microbial communities usually occurred in the canal-reservoir contact zone WKC/R. Most species found at all stations were eurytopic species, which have rapid ecological adaptability and a broad tolerance range for environmental changes. The ecotone zone is usually inhabited by a large number of species

(Harris 1988). At particular sites some physical or chemical water properties influenced the quality and quantity structure of planktonic ciliates. The increase in organic matter and nutrient concentrations was correlated with a higher number of taxa and abundance of microorganisms. The presence of emergent vegetation in the ecotone zone may also influence the abundance of zooplankton by slowing the current and the development of microhabitats. Several mechanisms may account for the contact zone and macrophyte beds being a more favourable habitat for zooplankton to develop (Bunn, Artington 2002). Macrophyte beds in eutrophic lakes provide zooplankton with a refuge against invertebrate and vertebrate predators (Jeppesen *et al.,* 1998; Mieczan, 2007). Cladocerans and copepods, although abundant along the whole horizontal gradient, attained the highest densities in the pelagic zone (P). Their density could be regulated by planktivorous fish, as the contact zone is a place of forage for obligatory planktivorous fish fry, which play an important role in eliminating zooplankton (Whiteside, 1988; Zalewski *et al.,* 1990).

As mentioned above, environmental variables had different effects on density and mutual relations of food web components in the two lake types, which suggest that the stronger effect of environmental variables weakens trophic relationships among food web components. Environmental variables also influenced trophic relationships within individual lakes. Analysis of the system bacteria-flagellates-ciliates-crustaceans reveals a clear differentiation and strength of mutual relations between the zones analysed. The highest number of significant correlations was determined in the canal-reservoir contact zone WKC/R and L, and the lowest number in WKC and P. In WKC/R and L, more mutual relations between food web components were determined than in the other zones analysed. Jeppesen *et al.* (1998) suggest that an increased abundance of microorganisms should be effectively reduced by zooplankton inhabiting the macrophyte zone. Our study, however, reveals high numbers of microbial communities in this zone despite a number of correlations between them and higher trophic levels. Foraging efficiency of invertebrate predators decline with increasing complexities of habitats (Adamczuk, 2013); thus the patchy structure of the ecotone zone apparently favoured the coexistence of prey-predator communities. It seems that in the fairly homogenous pelagic zone (P) crustaceans could diminish the abundance of microbial communities, which suggests that the spatial architecture of habitats is an important factor influencing mutual relationships between microbial communities and their predators. It seems also that morphology of macrophytes and range of their occurrence in a lake can have crucial influence on relations among food web components in a whole lake scale. In *Ceratophyllum*-dominated lakes that displayed wider area grown by macrophytes of more complex mor-

phology in comparison to *Potamogeton*-dominated lakes, weak relations among food web components were noted in all biotic zones. Thus, our results suggest that debilitating influence of complex habitats on relationships among food web components is not only restricted to those habitats but impacts a whole lake area.

CONCLUSIONS

The present study showed clear horizontal distribution patterns of bacteria, flagellates, ciliates and crustaceans in the horizontal gradient of shallow lakes. The analysis of trophic relationships in the system bacteria-ciliates-crustaceans reveals a clear differentiation and strength of mutual relations between the zones analyzed. The highest number of significant correlations was determined in the littoral zone. It can also be a place of very efficient matter and energy flow in freshwater ecosystem. Environmental variables influenced the density of planktonic communities but did not affect their spatial distribution, which probably resulted from the eurytopic habits of species commonly found in shallow, eutrophic lakes. Environmental variables apparently influenced the strengths of interactions between microbial communities and their predators. In the *Ceratophyllum*-dominated lakes, where environmental variables explained the bulk of the total variance in plankton abundance, weak relations among food web components were noted, whereas in the *Potamogeton*-dominated lakes, where environmental variables had a minor role in the total variance in plankton abundance, strong predator-prey relations were found. The spatial structure of habitats proved to be another significant factor for relationships among food web components, as our study revealed that habitat complexity can reduce negative correlations between food web components. Inter- and intra-lake differences in spatial structure are frequently ignored in field studies on functioning of eutrophic lakes. Yet our data suggest that trophic relations in eutrophic lakes are more heterogeneous that they have been considered by now, and variation in diversity and abundance of food components should be considered at small spatial scales. Without doing so, we cannot fully know biotic structure in eutrophic lakes that are often falsely perceived as quite homogenous ecosystems.

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