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RESEARCH ARTICLE

Influence of environmental factors on vertical distribution of zooplankton communities in humic lakes

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Abstract – The influence of vertical environmental gradients on zooplankton communities was studied in five humic lakes with the high availability of food resources (phytoplankton and bacterioplankton) and low fish pressure. The factors that inhibit the development of large zooplankton in humic lakes are currently widely debated. We have found that relatively productive humic lakes do not offer many niches for zooplankton because of the sharp thermal gradient which results in a shallow layer of oxygenated waters. The results of this study indicated that different taxonomic groups of zooplankton are determined by a different set of environmental variables. This phenomenon explains very low species richness of zooplankton and a possibility of their coexistence in the narrow oxygenated layer. We concluded that due to sharp thermal gradient in humic lakes biomass of herbivores may be reduced which could promote development of phytoplankton.

Keywords: dystrophic lakes / Crustacea / Rotifera / phytoplankton / thermocline

1 Introduction

Dystrophic (humic) lakes are a very specific type of lakes due to small quantity of mineral substances dissolved in their waters. The waters are strongly acidic and contain a remarkable content of dissolved organic matter. The share of humus substances fed from the catchment basin also plays an important role in the dystrophication of these lakes. Humus substances dissolved in waters acidify them and have the ability to form complexes of phosphorus compounds, ammonia, and metal cations, including heavy metals (Górniak *et al.*, 1999a, b). Dystrophic lakes have a characteristic yellow-brown color of waters (Drzymulska and Zieliński, 2013). This results in several typical characteristics: unique light climate (rapid light attenuation and changes in wavelength proportions), rapid warming of the epilimnion and hence strong thermal stratification. The thermocline in humic lakes is usually steep and the epilimnion very shallow, *i.e.* the ratio of the epilimnion to the hypolimnion volume is small. Another typical feature of humic lakes is oxygen deficiency prevailing below the thermocline (Górniak, 2017). Besides strong thermal stratification, humic lakes often develop a distinct chemical stratification, as many of them are small and well protected from winds by the surrounding forests (Ojala and Salonen, 2001). Dystrophic lakes are characterized by strong influence of environmental factors (Cudowski *et al.*, 2013).

Described above characteristic patterns of dystrophic lakes create specific conditions for organisms occupying them. The lakes are traditionally viewed as unproductive with large numbers of bacteria (Klavins *et al.*, 2003), which are able to use humic substances as carbon source for their development (Jackson and Hecky, 1980). Food webs in humic lakes are often largely based on photoautotrophic bacterioplankton (Culver and Brunskill, 1969). There are lakes where photoautotrophic bacteria can account for 86% of the total biovolume of the entire water column (Guerrero *et al.*, 1985). Dense plates of autophototrophic bacteria are often met just below the oxic-anoxic layer, where there is enough light for photosynthesis (Murtaugh, 1985; Ojala and Salonen, 2001). An important component of primary production in humic lakes is also photoautotrophic picoplankton (cell size between 0.2 and 2.0 μm), which could take advantage of intensive nutrient recycling within the microbial loop in humic lakes (Jasser, 1997). Photoautotrophic pikoplankton may strongly influence food chain in a lake, where the high bacteria productivity reflects on a different food chain involving development of mixotrophic phytoplankton, possibly compensating for low light conditions (Nürnberg and Shaw, 1999). Many of the mixotrophs could form dense blooms in humic lakes. For example, *Gonyostomum semen* (Ehrenberg) Diesing is a large flagellate that can form dense blooms in dystrophic lakes of the Wigry National Park (Pęczuła *et al.*, 2017). Like many other

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Table 1. Characteristics of the studied dystrophic lakes in Wigry National Park. Abbreviations: SEC – transparency measured with the Secchi disk; EC – electrical conductivity.

No.	Lake name	GPS	area (ha)	max depth (m)	SEC (m)	pH	EC ($\mu S \cdot cm^{-1}$)	chlorophyll *a* range ($\mu g \cdot L^{-1}$)
I	Wądołek	54°06′39″N 23°02′38″E	1.09	15	1.1	6.15	18.6	32–141.7
II	Suchar Wielki	54°01′40″N 23°03′20″E	8.90	9.6	2.5	5.76	16.75	12.7–66.5
III	Suchar II	54°05′14″N 23°01′03″E	2.60	10	1.5	5.95	15.1	13.7–68.5
IV	Dembowski	54°06′39″N 23°02′38″E	3.30	8	2.5	6.04	12.14	48.3–166.6
V	Widne	54°00′44″N 23°07′25″E	2.10	5.7	1.4	6.72	38.1	15.3–75

flagellates, the species is able to swim, therefore it is often found unevenly distributed in the water column. However, the patterns of its distribution vary between lakes and the factors controlling this phenomenon are still under discussion (Pęczuła, 2013).

Most zooplankton species typical of humic lakes can be found in all kinds of waters, but usually in lower abundance (Sarvala *et al.*, 1999). The large-bodied herbivorous cladocerans (*Daphnia obtusa* Kurz and *Daphnia longispina* Müller), are often dominating zooplankton species in Polish and Scandinavian small polyhumic lakes with few or no fish (Sarvala *et al.*, 1999; Karabin, 1999). *Daphnia* can outcompete other members of the zooplankton community by efficient filter feeding, and it also affects the abundance of its single-celled prey (*e.g.*, Gilbert, 1988; Arvola and Salonen, 2001). *Daphnia* can feed on a wide range of particles in dystrophic lakes from detritus, bacteria, heterotrophic flagellates to phytoplankton (Kankaala, 1988; Jürgens *et al.*, 1994). Even large algae like *Gonyostomum semen* could be consumed by large *Daphnia* and *Eudiaptomus gracilis* (Sars), which is common in humic lakes (Johansson *et al.*, 2013). However, previous feeding experiments with *G. semen* have shown contrasting results. Lebret *et al.* (2012) observed significant grazing on *G. semen* by *Daphnia magna* Straus, but neither *Daphnia pulex* Leydig nor *Eudiaptomus gracilis* had any significant impact on *G. semen* cell density. Williamson *et al.* (1996), on the other hand, observed a significant reduction in the number of *G. semen* cells in treatments with *Diaptomus oregonensis* Lilljeborg and estimated that 44% of their diet consisted of *G. semen*. They also recorded some feeding on *G. semen* by *Daphnia pulicaria* Forbes (estimated to 27% of diet). Large zooplankton could more effectively transfer energy and matter from phytoplankton to a higher trophic level, than smaller species (Gladyshev *et al.*, 2011; Feniova *et al.*, 2015). Sometimes zooplankton of humic lakes is dominated by small cladoceran species (genera of *Bosmina* and *Ceriodaphnia*), which was connected with the high abundance of fish like crucian carp (*Carassius carassius* L.) and european perch (*Perca fluviatilis* L.). These fish can tolerate organic acidity and they can thrive in dystrophic lakes despite the lack of cool and well oxygenated water (Rask, 1991; Sarvala *et al.*, 1999). The specific conditions in humic lakes could be preferred by a few species that can take advantage of different niches and achieve rapid growth. However, the factors influencing competition between large zooplankton (>1 mm), and small species in humic lakes are not clear.

The common statement that dystrophic lakes are unproductive (Klavins *et al.*, 2003) is not confirmed by the literature data from more than 600 freshwater lakes, in which primary and secondary productivity is as high or higher than in clear lakes due to high bacteria and phytoplankton productivity (Nürnberg and Shaw, 1999). Nevertheless, a common phenomenon in humic lakes is that the large amount of food for crustacean zooplankton and low fish pressure in these lakes usually do not result in rapid development of large zooplankton. The factors that inhibit development of large zooplankton in dystrophic lakes are still discussed. Some authors suggest that humic stress related to high dissolved organic carbon and humic substances could be the limiting factor for zooplankton, however, experimental results are not clear (Robidoux *et al.*, 2015). The main aim of our study is to determine a combination of factors that inhibit development of large-bodied zooplankton (>1 mm) in humic lakes with high concentration of food resources and low fish pressure. We especially focused on the vertical gradients of abiotic (thermal gradient, deficiencies of oxygen, chemical parameters with emphasis of carbon and nitrogen forms) and biotic (phytoplankton) factors influencing distribution of major groups of freshwater zooplankton (Rotifera, Cyclopoida, Calanoida, large and small Cladocera) in dystrophic lakes.

2 Study sites

The subjects of the investigation were five humic (dystrophic) lakes in the area of the Wigry National Park (WNP) in northeastern Poland. The lakes are mid-forest with a small area (Tab. 1), usually oval and without any outlets. The maximum depth of the lakes ranges from 5.7 to 15 m. (Tab. 1) and most of the lakes are thermally stratified. Oxygen deficiency below the thermocline was observed in all the studied lakes (Fig. 1). The lakes had also other features typical of humic waters: yellow-brown color, pH below 7, small quantity of mineral substances dissolved in water (Tab. 1). However, Lake Widne differs from the remaining lakes due to the highest value of pH, twice more of mineral substances dissolved in water (Tab. 1) and aquatic plants typical for eutrophic waters covering 30–40% of the lake surface. Macrophytes of Lake Widne were dominated by: *Potamogeton natans* L. *Myriophyllum verticillatum* L., *Nuphar lutea* (L.) Sibth. & Sm, which indicates humoeutrofication of the lake. Other studied lakes did not have typical aquatic vegetation, with the exception of a single assemblage of *Nuphar lutea* (L.) Sibth. & Sm in Lake Suchar Wielki and Suchar II (Górniak *et al.*, 1999a, b). All the studied lakes are surrounded by a coat of mosses and peat which extend in the lake to a considerable

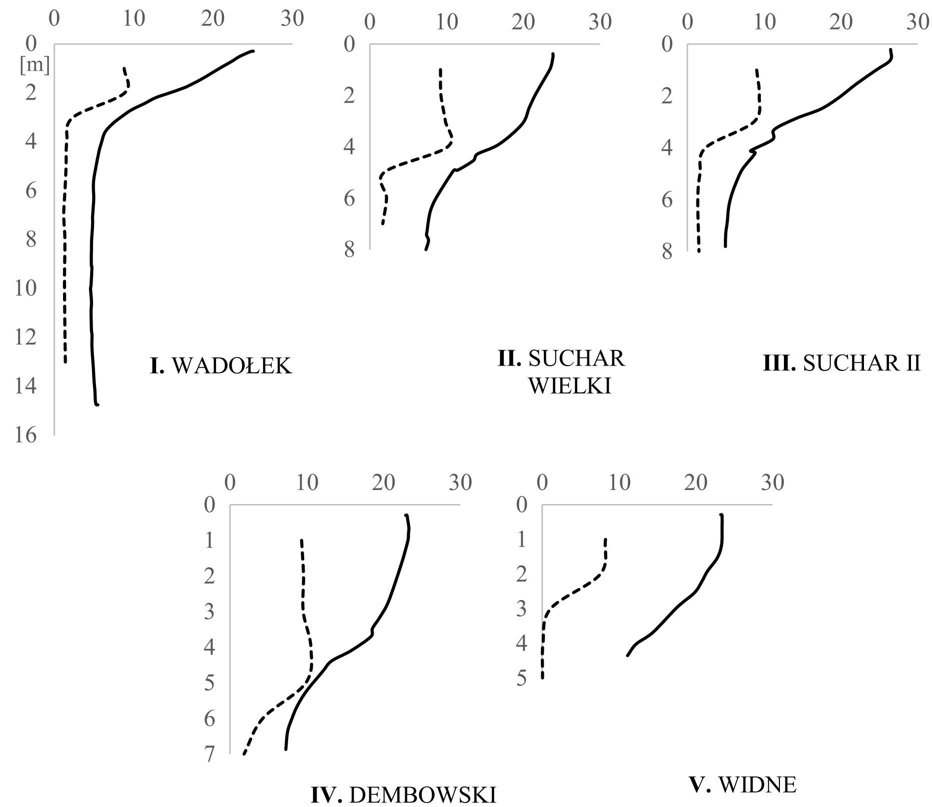

Fig. 1. Vertical gradients of temperature (°C) – solid line, and oxygen concentration ($mgO_2 L^{-1}$) – dotted line in five humic lakes.

depth, and are overgrown by roots of different plants and dwarf trees. Among the mosses (*Sphagnum* sp.) belts of *Carex limosa* L., *Rhynchospora alba* (L.) Vahl., and *Carex lasiocarpa* Ehrh. immediately adjoin the lakes' waters. Also *Scheuchzeria palustris* (L.) Dulac., *Menyanthes trifoliata* L., *Drosera rotundifolia* L., and *Drosera anglica* Huds. may be encountered there. On the borders the swamp forest *Vaccinio uliginoso* – *Pinetum* or spruce on peat *Sphagno* – *Piceetum* dominate (Górniak *et al.*, 1999a, b). The catchment basins of these lakes do not exceed 20 ha.

The studied lakes were characterized by very low fish density and a small number of fish species (Białokoz and Krzywosz, 1992). The stunted population of crucian carp (*Carassius carassius* L.) and european perch (*Perca fluviatilis* L.) were found in lakes Wądołek, Dembowski, and Suchar II. In Lake Widne and Suchar Wielki more fish species were found: *Carassius carassius* L., *Perca fluviatilis* L., *Tinca tinca* L., *Rutilus rutilus* L., and *Esox lucius* L. (Białokoz and Krzywosz, 1992).

3 Methods

The study was conducted in the peak of the summer stagnation (27–28 July 2016). The sampling stations were located close to the deepest point of each lake. Water samples for chemical analyses and zooplankton samples were taken every meter from the surface to the bottom with the 5 l Limnos sampler. Five-liter zooplankton samples were filtered through a 50 µm mesh size plankton net and fixed with 4% formalin. Rotifers and crustaceans were determined to species and counted in the whole samples. Additionally, 10 length measurements for each species were made. Species with a body length of >1 mm were classified as a large-bodied zooplankton (*e.g. Daphnia* sp., *Eudiaptomus* sp.). Mean values of the animal length were used to estimate the wet weight of planktonic crustaceans by applying the equations after Błędzki and Rybak (2016). Biomass of rotifers was established following Ejsmont-Karabin (1998).

The field measurements included the visibility of Secchi disc, conductivity (EC) and concentration of dissolved oxygen by the Hach Lange Sonde. Phytoplankton communities (green algae, blue green algae, diatoms, cryptophytes, total chlorophyll *a* concentration) and temperature were measured *in situ* by the submersible spectrofluorometer (FluoroProbe, bbe-Moldaenke). The measurements of temperature every few centimeters allow us to determine precisely the thermocline (metalimnion) zone. The FluoroProbe spectrofluorometer provides *in situ* measurements of total chlorophyll *a*, and algae classes determination using differences among fluorescence excitation spectra. Changes in the resulting chl *a* emission allow for fluorometric estimation of algal classes based on differences in species and class-dependent peripheral antenna pigments (Beutler *et al.*, 2002). The FluoroProbe identifies the four phytoplankton classes called: green algae (Chlorophyta and Euglenophyta), blue green algae (phycocyanin-rich cyanobacteria), diatoms (Heterokontophyta, Haptophyta, and Dinophyta) and cryptophytes (Cryptophyta and the phycoerythrin-rich cyanobacteria). The division of Chlorophyceae (green algae) shows a broad maximum of

Table 2. Average value of selected hydrochemical parameters and water transparency in the water column studied humic lakes. Abbreviations: E – epilimnion; M – metalimnion; H – hypolimnion; EC – electrical conductivity; TOC – total organic carbon; DOC – dissolved organic carbon; POC – particulate organic carbon; IC – inorganic carbon; TN – total nitrogen; DN – dissolved nitrogen.

		Transparency %	EC $\mu s \cdot cm^{-1}$	$Fe^{2+/3+}$ $mg \cdot L^{-1}$	SiO_4^{4-} $mg \cdot L^{-1}$	TOC $mg \cdot L^{-1}$	DOC $mg \cdot L^{-1}$	POC $mg \cdot L^{-1}$	IC $mg \cdot L^{-1}$	TN $mg \cdot L^{-1}$	DN $mg \cdot L^{-1}$
Wądołek	E*	82.11	18.6	0.21	0.07	14.69	13.79	0.9	3.29	2.2	1.6
	M	67.23	32.2	0.32	0.3	14.59	13.98	0.6	4.48	1.8	1.46
	H	80.26	40.7	0.53	0.46	15.22	14.38	0.83	4.57	3.26	2.64
Suchar Wielki	E	86.11	16.7	0.28	0.11	6.58	6.2	0.38	4.18	0.76	0.7
	M	85.16	19.4	0.1	0.13	6.55	6.02	0.53	4.74	0.9	0.72
	H	67.56	21.3	0.17	0.17	6.19	5.6	0.59	3.33	0.9	0.66
Suchar II	E	80.45	15	0.24	0.13	7.79	7.45	0.34	3.25	1.32	1.1
	M	77.02	17.8	0.17	0.15	8.03	7.37	0.66	3.17	1.26	0.92
	H	84.3	29.2	0.31	0.56	8.46	7.86	0.6	3.79	2.84	2.44
Dembowski	E	86.49	12	0.13	0.12	7.53	7.07	0.46	3.33	1.14	0.9
	M	86.05	12.8	0.26	0.07	6.33	5.98	0.35	3.42	1.2	0.92
	H	72.17	20.3	0.23	0.11	6.37	5.44	0.93	4.04	2.52	1.58
Widne	E	85.4	38.3	0.43	0.11	11.95	10.71	1.24	6.67	1.66	1.32
	M	76.99	49.4	0.13	0.13	11.06	10.33	0.73	6.59	1.74	1.32

fluorescence at the 470 nm LED, which is caused by chlorophyll −*a* and −*b*. The Cyanophyceae (blue-green algae) have their maximum at 610 nm due to the photosynthetic antenna pigment phycocyanin. Cyanophyceae also contain chlorophyll −*a* if there is low intensity at 470 nm. This is due to the masking effect of the phycocyanin. Furthermore, the high peak at the 525 nm region for the Bacillariophyceae originates from xanthophyll fucoxanthin and for the Dinophyceae from peridin. For the Cryptophyceae, a significant maximum can be found at 570 nm, which originates from phycoerythrin (Kring *et al.*, 2014).

Analyses of chemical parameters of water were conducted in a laboratory, immediately after collection of samples. The analyses of $Fe^{2+/3+}$ and SiO_4^{4-} ions were conducted according to the standard methods (APHA *et al.*, 2012). The concentrations of dissolved nitrogen (DN), total nitrogen (TN), total organic carbon (TOC), dissolved organic carbon (DOC) and inorganic carbon (IC) were analyzed by the high-temperature catalytic combustion in Shimadzu TOC-L Series analyzers. Particular nitrogen (PN) was calculated from the differences between TN and DN. Particulate organic carbon (POC) was calculated from the differences between TOC and DOC. Total carbon (TC) was calculated as the sum of TOC and IC (Cudowski *et al.*, 2015).

The differences between vertical distribution of plankton (phytoplankton, Rotifera, Crustacea) and hydrochemical parameters within lakes at different depths were tested with the non-parametric Kruskal–Wallis test with a 0.05 significance level. Principal component analysis (PCA) was performed to present complex spatial structure of hydrochemistry parameters in different depth of different lakes. The effect of environmental factors on the biomass of major group of freshwater zooplankton (Rotifera, Cyclopoida, Calanoida, large Cladocera, small Cladocera) in humic lakes was estimated using the Spearman rank correlation and by the Canonical Correspondence Analysis (CCA). The CCA is a very useful tool for ecologists to relate the abundance of species to many environmental variables (ter Braak, 1986). Cladocera were divided into small (<1 mm) and large-bodied (>1 mm) species, because the body size is an important attribute of cladoceran functional biology and ecology (Hart and Bychek, 2011). The small- and large-bodied cladocerans respond differently to changes in predation pressure (*e.g.* top-down effects) and algal resources (*e.g.* bottom-up effects) (Brooks and Dodson, 1965; Sommer *et al.*, 1986; McQueen *et al.*, 1989; Gliwicz *et al.*, 2000). Statistical analyses were performed with XLSTAT-Ecology (Addinsoft).

4 Results

4.1 Vertical hydrochemical gradients

The studied lakes were characterized by a high temperature of surface waters reaching 26.4 °C and sharp temperature gradients in the upper water layers (Fig. 1). It resulted in very shallow epilimnion zones and thermocline usually beginning at a depth of 1–2 m. However, the lakes showed some differences in their thermal profiles. A very sharp temperature gradient from the surface was observed in lakes Wądołek and Suchar II, and the temperature of water at a depth of four meters was 6.9 and 11.1 °C, respectively. The smoother thermal gradient was observed in the lakes: Suchar Wielki, Dembowski, and Widne (Fig. 1). The studied lakes were also characterized by specific oxygen conditions, with strong anoxic condition below the thermocline and well-oxygenated epilimnion zone (Fig. 1).

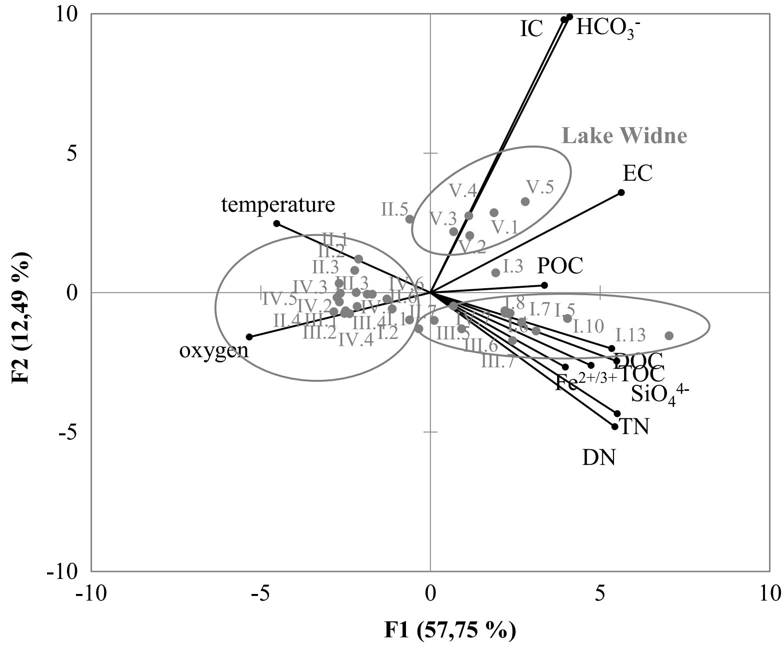

Fig. 2. Biplot of the hydrochemical parameters and sampling stations using principal component analysis (PCA). The code for stations: roman numerals represents different lakes (as in Tab. 1); the numbers after dot (1–13) are depth (m). Abbreviations: EC – electrical conductivity; TOC – total organic carbon; DOC – dissolved organic carbon; POC – particulate organic carbon; IC – inorganic carbon; TN – total nitrogen; DN – dissolved nitrogen.

The surface waters of the studied lakes were characterized by small quantity of dissolved mineral substances. Electrical conductivity (EC) in epilimnion zones in most lakes was below 20 $\mu s \cdot cm^{-1}$. A higher value of EC in surface water was observed in Lake Widne (Tab. 2). Vertical gradients of EC in the lakes revealed a significant increase of dissolved mineral substances with increasing depth. The largest increase of EC in a thermocline was observed in the deepest Lake Wądołek with a sharp thermal gradient (Tab. 2). The sharp thermal gradient resulted also in the lowest water transparency in the metalimnion zone of Lake Wądołek and Suchar II, whereas in the lakes with a smoother thermal gradient, water transparency decreased with increasing depth (Tab. 2). There were significant differences in the vertical distribution of concentrations of organic carbon and nitrogen in lakes with different thermal conditions. The highest values of TOC and DOC were observed in the hypolimnion zones of the lakes with sharp thermal gradients, whereas the lakes with smoother thermal gradients had the highest values of TOC and DOC in the epilimnion zones (Tab. 2).

Spatial autocorrelation by the principal component analysis was performed to present structure of hydrochemistry parameters in different depth of different lakes. Hypolimnetic stations of Lake Wądołek and Suchar II were positively correlated with the first axis and were connected with the higher concentrations of organic carbon and nitrogen (Fig. 2), while Lake Dembowski and Suchar Wielki, as well as epilimnion station of Lake Wądołek and Suchar II, were negatively correlated with the first axis (Fig. 2). Furthermore, the results of the PCA analysis clearly divided all stations in the Lake Widne (Fig. 2).

Table 3. Average and maximum phytoplankton cell concentration ($cell \cdot mL^{-1}$) based on *in situ* fluorometric measurements.

	Wądołek	Suchar Wielki	Suchar II	Dembowski	Widne
average cell concentration ($cell \cdot mL^{-1}$)	29 953	15 519	20 248	33 049	20 867
maximum cell concentration ($cell \cdot mL^{-1}$)	76 726	37 540	55 451	92 598	79 003

4.2 Vertical distribution of phytoplankton

The maximum chlorophyll *a* concentration in the studied lakes ranged between 66.5 and 166.6 $\mu g \cdot L^{-1}$ (Tab. 1), and the maximum phytoplankton cell concentration – between 37 540 and 92 598 $cell \cdot mL^{-1}$ (Tab. 3). The highest phytoplankton biomass was found in Lake Dembowski and Lake Wądołek (Tab. 1). There were significant differences in vertical distribution of phytoplankton. The lowest phytoplankton concentrations were generally found in the epilimnion zone. A significant increase of phytoplankton was observed in the thermocline zone of the lakes. The lakes with a very sharp thermal gradient (Lake Wądołek and Lake Suchar II) had maxima of phytoplankton concentrations in the thermocline zone. The lakes with a smoother thermal gradient had maximum concentration of phytoplankton in the hypolimnion (Fig. 3).

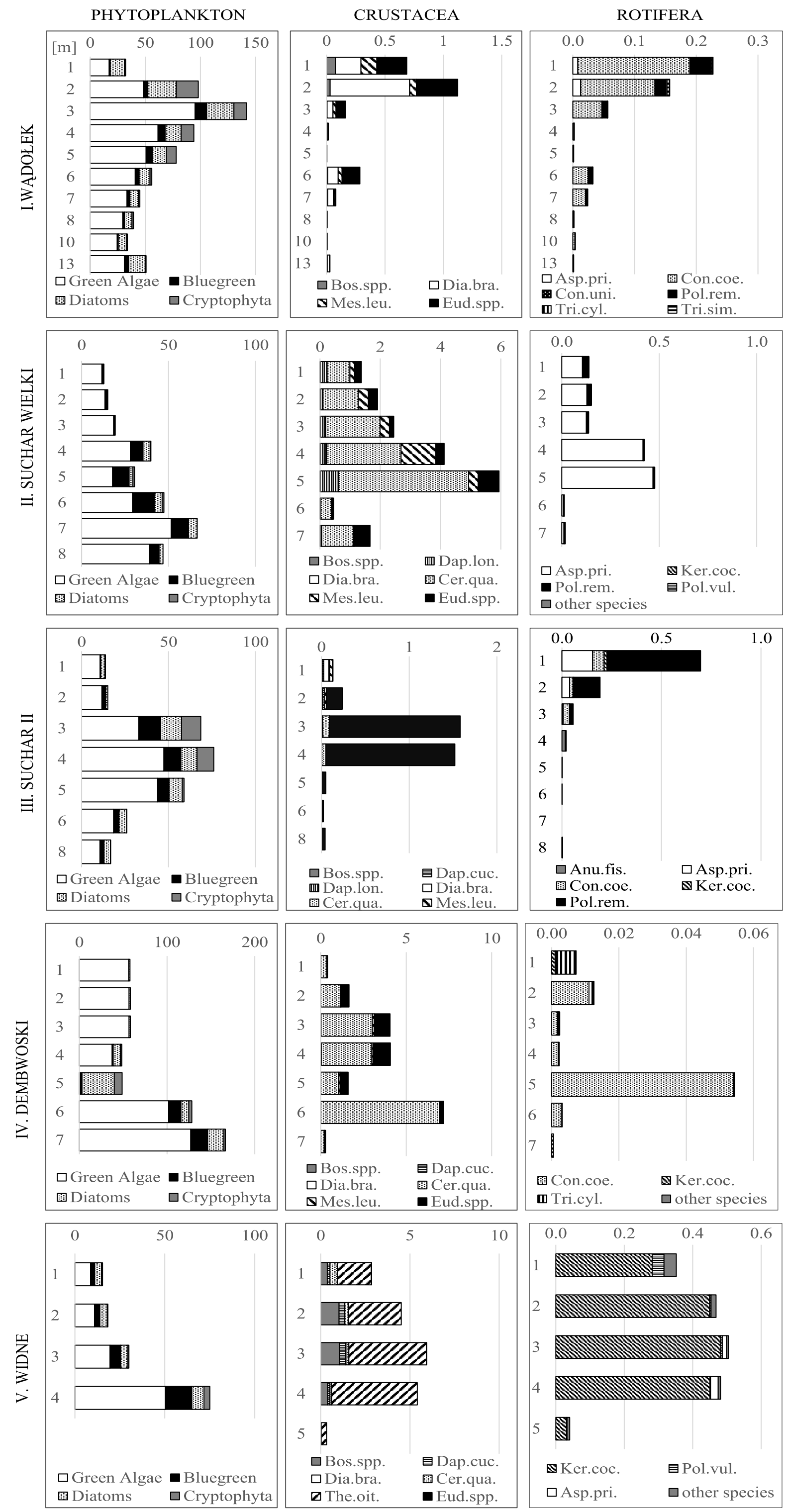

Fig. 3. Vertical distribution of phytoplankton communities (μg·L^{-1}), dominant crustacean species (WW mg·L^{-1}) and dominant Rotifera species (WW mg·L^{-1}). Abbreviations: Bos.spp. – *Bosmina* species; Dap.cuc. – *Daphnia cucullata*; Dap.lon. – *Daphnia longispina*; Dia.bra. – *Diaphanosoma brachyurum*; Cer.qua – *Ceriodaphnia quadrangula*; Mes.leu. – *Mesocyclops leuckarti*; The.oit. – *Thermocyclops oithonoides*; Eud.spp. – *Eudiaptomus* species; Asp.pri. – *Asplanchna priodonta*; Con.coe. – *Conochiloides coenobasis*; Con.uni. – *Conochilus unicornis*; Pol.rem. – *Polyarthra remata*; Pol.vul. – *Polyarthra vulgaris*; Tri.cyl. – *Trichocerca cylindrica*; Tri.sim. – *Trichocerca similis*; Ker.coc. – *Keratella cochlearis*; Anu.fis. – *Anuraeopsis fissa*.

Table 4. Correlation coefficients between the zooplankton communities and environmental variables in humic lakes. The values displayed in bold are significant at $p < 0.05$.

	EC	O_2	$Fe^{2+/3+}$	SiO_4^{4-}	TOC	DOC	POC	IC	TN	DN	chl *a*	temp.
Rotifera	−0.12	0.25	**−0.39**	**−0.47**	−0.14	−0.08	−0.03	0.11	**−0.40**	**−0.42**	**−0.41**	**0.64**
Cyclopoida	−0.15	**0.35**	**−0.35**	**−0.52**	−0.31	−0.28	−0.14	0.23	**−0.48**	**−0.49**	−0.32	**0.61**
Calanoida	**−0.70**	**0.60**	**−0.41**	**−0.46**	**−0.57**	**−0.57**	**−0.50**	**−0.57**	**−0.58**	**−0.57**	0.21	0.27
small Cladocera	**−0.50**	**0.54**	**−0.48**	**−0.68**	**−0.64**	**−0.62**	**−0.36**	−0.02	**−0.68**	**−0.68**	−0.10	**0.53**
large Cladocera	−0.08	0.15	−0.23	−0.23	**−0.40**	**−0.34**	−0.25	0.23	**−0.52**	**−0.52**	**−0.57**	**0.46**

The dominant group of phytoplankton were green algae, which contributed to 62–80% of phytoplankton biomass. The highest domination of green algae was observed in the epilimnion zones of Lake Dembowski and Lake Suchar Wielki (Fig. 3). Green algae reached maximum densities in the thermocline of the lakes with a sharp thermal gradient. In the lakes with a smoother thermal gradient, green algae had maximum densities in the hypolimnion. In the lower thermocline of Lake Dembowski a strange phenomenon was observed, *i.e.* dominant in water profile green algae completely disappeared between 4 and 5 m (Fig. 3). This niche was used by diatoms and cryptophyta. The repeated measurement gave the same result.

4.3 Vertical distribution of Crustacea

The lowest biomass of crustacean zooplankton was recorded in the lakes with a sharp thermal gradient. Maximum biomass of crustaceans in Lake Wądołek was 1.13 $mg \cdot L^{-1}$, and zooplankton was mostly distributed in the surface layer 0–2 m. In another lake with a sharp thermal gradient (Suchar II) zooplankton was mostly distributed between 3 and 4 m (Fig. 3). The significantly higher crustacean biomasses were recorded in the lakes with smoother thermal gradients. The biomass of zooplankton in the lakes generally increased with depth to upper hypolimnion, but near the bottom we observed its significant decrease (Fig. 3). In Lake Dembowski such decrease in crustacean biomass was observed at a depth of 5 m, thus concurrently to the phytoplankton distribution.

The crustacean communities of the studied lakes consisted of species common in all kinds of waters in the region. Dominant crustacean species were: *Bosmina longirostris* (Müller), *Ceriodaphnia quadrangula* (Müller), *Diaphanosoma brachyurum* (Liévin), *Daphnia cucullata* Sars, *D. longispina* (Müller), *Thermocyclops oithonoides* (Sars), *Mesocyclops leuckarti* (Claus), *Eudiaptomus gracilis* (Sars) and *E. graciloides* (Lilljeborg). The number of crustacean species ranged from 6 (Lake Wądołek and Lake Suchar II) to 9 (Lake Suchar Wielki). However, each lake had a specific combination of 1–3 species (Fig. 2). The crustacean zooplankton in the studied lakes was dominated mostly by small species. *Ceriodaphnia quadrangula* was the dominant species in Lake Suchar Wielki and Lake Dembowski. Vertical distribution of *C. quadrangula* in the lakes was similar to the distribution of phytoplankton (Fig. 3). *Diaphanosoma brachyurum* was the dominant species in the surface waters of the lakes with a sharp thermal gradient (Lake Wądołek and Lake Suchar II). *Bosmina longirostris* was an important component of zooplankton in Lake Widne and in the surface waters of Lake Wądołek. Larger species from the genus *Daphnia* were found in higher numbers in the thermocline zone of Lake Suchar Wielki and Lake Widne. Large calanoids *Eudiaptomus gracilis* strongly dominated in Lake Suchar II (Fig. 3). *E. gracilis* and *E. graciloides* were found in 4 lakes, and reached the highest abundance in the thermocline zones.

4.4 Vertical distribution of Rotifera

Vertical distribution of rotifer biomass was strongly differentiated among the lakes under study (Fig. 3). In general, it was similar to the distribution of crustacean biomass, except Lake Suchar II, in which algivorous *Polyarthra remata* Skorikov occupied the surface layer, whereas maximum of *Eudiaptomus* biomass was just below this layer. In all the studied lakes the maximum biomass of rotifers was strongly dominated by one species: *Conochiloides coenobasis* (Skorikov) at 1 m depth in Lake Wądołek and at 5 m depth in Lake Dembowski, predatory *Asplanchna priodonta* Gosse at 4–5 m depth in Lake Suchar Wielki, *Polyarthra remata* at 1 m depth in Lake Suchar II, and detritophagous *Keratella cochlearis* (Gosse) at 1–4 m depth in Lake Widne (Fig. 3).

4.5 Environmental factors influencing zooplankton communities

Zooplankton groups were negatively correlated with most of the hydrochemical parameters (Tab. 4). The strongest negative correlation was found between all of the zooplankton groups with nitrogen concentrations. DOC concentration was significantly negatively correlated with abundance of Cladocera and Copepoda (Tab. 4). Phytoplankton biomass expressed by chlorophyll *a* concentration was negatively correlated with Rotifera (−0.41; $p = 0.016$) and large Cladocera (−0.57; $p < 0.001$). The positive correlations were found between zooplankton groups with oxygen concentrations and temperature of water (Tab. 4). CCA was used to relate the zooplankton communities with the environmental variables. The two-dimensional Canonical Correspondence Analysis map obtains 92.34% of the inertia, with the most of inertia carried by the first axis (Fig. 4). The CCA results show that the abundance of small Cladocera and Calanoida could be associated with chlorophyll *a* and oxygen concentration (Fig. 4), while large Cladocera and Cyclopoida could be negatively influenced by the chlorophyll *a* and oxygen concentration. Rotifera seem to

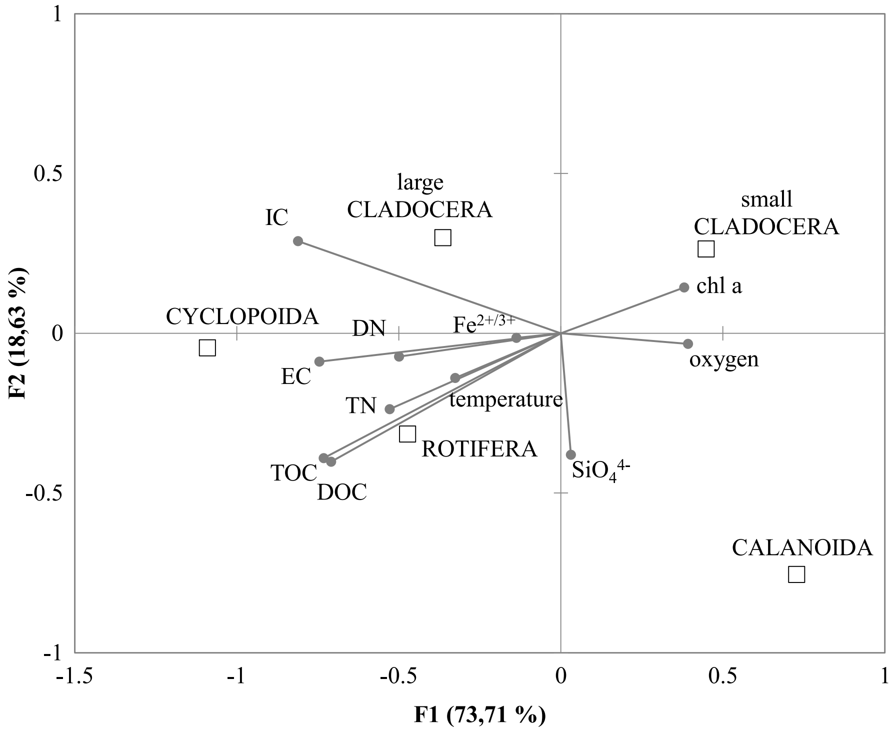

Fig. 4. The Canonical correspondence analysis map of major group of freshwater zooplankton and environmental variables in humic lakes.

be more sensitive to DOC, TN and temperature of water (Fig. 4). Generally, each of the taxonomic groups of zooplankton is determined by different set of environmental variables.

5 Discussion

The studied humic lakes were characterized by a high primary production and a low secondary production. Chlorophyll *a* concentrations in the lakes were much higher than in eutrophic lakes of the region (Jekatierynczuk-Rudczyk *et al.*, 2014; Karpowicz *et al.*, 2016). The concentrations of phytoplankton in the lakes were at a similar level as in a hypertrophic reservoir with strong cyanobacterial blooms (Górniak *et al.*, 2003; Górniak and Karpowicz, 2014; Grabowska and Mazur-Marzec, 2014). The high biomass of phytoplankton in humic lakes is a common phenomenon (Nürnberg and Shaw, 1999), and it was well documented for dystrophic lakes of the Wigry National Park (Górniak *et al.*, 1999a, b; Grabowska and Górniak, 2004). Phytoplankton in the humic lakes of WNP was composed of wide range of particles which could be available for herbivorous zooplankton. The dominant component of phytoplankton in these lakes were mainly small green algae like: *Chlorella* sp., *Dictyosphaerium* sp., *Chlamydomonas* sp., *Monoraphidium contortum* and *Crucigenia tetrapedia*. Other common components of phytoplankton were: *Peridinium inconspicuum* (Dinophyceae), *Dinobryon divergens* (Chrysophyceae) and *Gonyostomum semen* (Raphidophyceae) (Grabowska and Górniak, 2004). The last species is a large flagellate (length 36–92 μm, width 23–69 μm) that forms blooms in dystrophic lakes of Poland (Hutorowicz *et al.*, 2006; Pęczuła *et al.*, 2015). Many other studies have shown an increase in the geographical distribution and bloom incidence of *G. semen* in Northern Europe during recent decades. Increasing levels of DOC in freshwaters and rising temperatures are the potential drivers of the expansion, as the growth of *G. semen* is enhanced by humic substances (Johansson *et al.*, 2013). On the other hand, in humic lakes there is often observed an increased abundance of autotrophic picoplankton, which is the smallest fraction of phytoplankton (cell size of between 0.2 and 2.0 μm). Possibly, that picoplankton could take advantage of intensive nutrient recycling within the microbial loop in humic lakes (Jasser, 1997).

Humic lakes have much higher bacteria productivity than eutrophic lakes, especially in anoxic hypolimnia (Klavins *et al.*, 2003; Zieliński *et al.*, 2011). Bacteria productivity in Swedish humic lakes was several times higher than primary production (Tranvik, 1989) and in general bacteria respiration in humic lakes exceeds primary production in oligotrophic waters (Del Giorgio *et al.*, 1997). An important group of bacterioplankton in humic lakes of north-eastern Poland are green sulphur bacteria – *Chlorobium limicola* (Czeczuga and Czerpak, 1968). The high biomass of bacterioplankton is well documented in humic lakes in the Wigry National Park (Czeczuga and Czerpak, 1968; Piotrowicz *et al.*, 2002). This could favor the development of mixotrophic phytoplankton and small zooplankton species.

Most literature data indicate a high secondary productivity in humic lakes (Nürnberg and Shaw, 1999). Several studies have found a higher zooplankton production than what could be supported by algal production alone (Hessen *et al.*, 1990). This was due to the ability of large zooplankton (*i.e. Daphnia*) to feed on a wide range of particles (detritus, bacteria, heterotrophic flagellates, phytoplankton) in dystrophic lakes

(DeMott, 1982). Experimental results have shown that even large algae like *Gonyostomum semen*, which are common in humic lakes, could be consumed by large *Daphnia* and *Eudiaptomus gracilis* (Williamson *et al.*, 1996; Johansson *et al.*, 2013). However, we have found low biomass of crustacean and rotifer zooplankton in humic lakes with high biomass of phytoplankton and bacterioplankton. Large amount of food for crustacean zooplankton and a small fish pressure (Górniak *et al.*, 1999a, b) do not result in significant development of large zooplankton in the studied lakes. The factors that inhibit development of crustacean zooplankton in the lakes with high bacterial and primary production are still debated (Robidoux *et al.*, 2015). We found that the sharp thermal and oxygen gradients in humic lakes significantly influence zooplankton abundance and their vertical distribution. All studied lakes were characterized by a lack of oxygen below the thermocline, which is common in humic lakes. The sharp thermal gradient from the surface results in a shallow oxygenated zone, reaching only 3–4 m. This, together with high ultraviolet radiation in surface waters, limits the vertical distribution of zooplankton to a very narrow water layer. Many laboratory and field studies show that zooplankton is negatively affected when exposed to high intensities of ultraviolet radiation (Rautio and Tartarotti, 2010). The investigated lakes with a sharp thermal gradient have the lowest biomass of zooplankton. Vertical distribution of crustacean and rotifer zooplankton in the lakes was strongly limited to the oxygenated zone. The avoidance of ultraviolet radiation was observed in *Eudiaptomus graciloides*, which was a dominant species in the lake with a sharp thermal gradient (Suchar II). The population of *E. graciloides* in the lake avoids surface waters and anoxic conditions, so its vertical distribution is limited to 3–4 m layer. The experimental results have shown that *E. graciloides* responded more readily to changes in UV radiation than daphnids (Rautio and Korhola, 2002). Low biomass of zooplankton in the lakes with sharp thermal gradients could also promote higher primary production. Additionally, the sharp thermal gradient results in the higher concentration of suspended particles in metalimnion zone (Gliwicz and Kowalczewski, 1981) which was expressed by the significantly lower water transparency, while the lakes with a smoother thermal gradient had higher secondary production, and the maximum concentrations of zooplankton were usually observed at the edge of hypolimnion.

Some authors suggest that humic stress related to the high content of dissolved organic carbon and humic substances could be a limiting factor for zooplankton (Robidoux *et al.*, 2015). We found that increasing DOC concentration could negatively influence zooplankton communities. Large amount of seston also could limit growth and reproduction of zooplankton (Muller-Navarra and Lampert, 1996; Nix and Jenkins, 2000). According to other authors *G. semen* during blooms form mucilaginous aggregates which may serve as mechanical traps for large daphnids and in this way may enhance organisms' mortality (Pęczuła *et al.*, 2017). Thus the food quality seems to be an important factor that limits the success of large zooplankton in brown water woodland ponds (Nix and Jenkins, 2000). The brownification of waters (DOC increase) changes phytoplankton composition and favors phytoplankton taxa which do not synthesize EPA + DHA or have a low PUFA:C ratio. Even a moderate increase of nutrients (eutrophication) and dissolved organic carbon (brownification) may decrease the transfer of DHA in aquatic food webs (Feniova *et al.*, 2015; Taipale *et al.*, 2016). However, *G. semen* which forms blooms in many humic lakes has a high content of nutritionally valuable fatty acids (Gutseit *et al.*, 2007). *G. semen* has also several physical adaptations that could limit grazing by zooplankton and limit the transfer of these fatty acids as well as other biochemicals, mineral nutrients and energy to higher trophic levels. The cell size of *G. semen* is above the preferred size range for many filter-feeding zooplankton, but large *Daphnia* and *Eudiaptomus* species could consume *G. semen* (Williamson *et al.*, 1996; Lebret *et al.*, 2012). The results of our studies indicated that food resources are not the limiting factor for zooplankton in humic lakes. We suggest that the sharp thermal and oxygen gradients in humic lakes significantly reduce the secondary production and promote the primary production.

Although relatively productive, humic lakes do not seem to offer very many niches. This conclusion is illustrated with the results of CCA analyses, which show that each of the taxonomic groups of zooplankton is determined by a different set of environmental variables. This phenomenon explains very low species richness of the zooplankton groups and a possibility of their coexistence in the narrow oxygenated layer.

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