



Effect of eutrophication and humification on nutrient cycles and transfer efficiency of matter in freshwater food webs

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Abstract We evaluated how eutrophication and humification impacted nutrient cycles and the efficiency of carbon transfer in the planktonic food webs of 12 lakes in north-eastern Poland that differed in trophic state. Our results indicated that the effectiveness of carbon transfer between phytoplankton and zooplankton varied from 0.0005% to 0.14%, which is much lower than the theoretical 10%. The highest efficiency of carbon transfer occurred in the mesotrophic lakes due to the higher hypolimnetic zooplankton production, while the lowest efficiency was observed in the dystrophic lakes and in one eutrophic

lake that was dominated by cyanobacteria. Inedible algae (e.g. *Gonyostomum semen*) and cyanobacteria appeared to be the main factors reducing the efficiency of the transfer of matter in pelagic food webs. The results of our study showed that plankton communities are a key component of the nutrient cycle in freshwater food webs. Phytoplankton were a very effective nitrogen sink, and in the mesotrophic lakes, up to 99% of the total nitrogen was sequestered in phytoplankton. As a result, there was a depletion of inorganic nitrogen in the upper water layer. Furthermore, zooplankton were an important phosphorus sink, thus significantly influencing the nutrient cycles.

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Introduction

Plankton communities are a key component in the ecosystems of freshwater lakes. Interactions between primary producers (phytoplankton or photoautotrophs) and primary consumers (zooplankton or heterotrophs) affect the overall functioning of freshwater ecosystems. Phytoplankton need a wide variety of chemical elements, but the two critical ones are nitrogen and phosphorous, as they often act as limiting factors (Vitousek & Howarth, 1991). In the organic matter, the ratio of carbon, nitrogen, and phosphorus

atoms is 106:16:1, respectively. Most algae cannot use atmospheric nitrogen directly but, instead, acquire chemically reactive forms of this element, such as nitrate (NO_3^-) or ammonium (NH_4^+). Similarly, algae use reactive forms of phosphorus (PO_4^{3-}). Therefore, phytoplankton are an important link in the transformation of nutrients from inorganic to organic forms, thus reducing the amount of reactive nutrient forms. As a result, inorganic phosphorus is usually less than 5% of the total phosphorus (TP) in lakes (Boyd, 2015). The uptake of oxidized and reduced forms of nutrients can be separated in time and space due to their association with different phytoplankton groups (Yu et al., 2018). Hence, changes in phytoplankton taxonomic structure and growth rates can affect their nutrient demand and uptake and, as such, can influence their carbon: nutrient stoichiometry (Sterner & Elser, 2002). Therefore, the nutrient cycles can depend on phytoplankton community structures.

Zooplankton act as vectors transferring energy and matter from primary producers to higher trophic levels and play a central role in the biogeochemical cycles. One of the pivotal paradigms of ecology is that only about 10% of organic carbon production of one trophic level is incorporated into new biomass of organisms of the next trophic level (Gladyshev et al., 2011). However, there are large discrepancies in the effectiveness of the transfer of matter between lakes with different trophic statuses. In oligotrophic systems, the energy transfer efficiency between phyto- and zooplankton commonly varies in the range of ca. 5–30% (Lacroix et al., 1999), and for higher trophic levels in pelagic food webs, it is around 10% (Schulz et al., 2004). However, hypereutrophic lakes usually have a very high primary production with relatively little zooplankton and fish production (Brett & Müller-Navarra, 1997) due to cyanobacterial blooms and the dominance of large inedible algae. Cyanobacteria are a poor food resource for zooplankton, which negatively influences large-bodied zooplankton through feeding interference, poor nutritional quality, and the production of toxins (Vanni & Lampert, 1992; Ferrão-Filho & Kozłowsky-Suzuki, 2011). Thus, there is a shift in zooplankton communities to the domination of small species (rotifers and small cladocerans), which feed on other resources, like bacteria or picoplankton. As a result of the removal of small size classes of phytoplankton, colonial cyanobacteria grow more intensively (Haney, 1987), further deteriorating the

water quality. However, it is not clear how differences in the phytoplankton and zooplankton structures affect the efficiency of carbon transfer in freshwater food webs. Nowadays, processes such as global warming and human activity intensify eutrophication in the freshwater lakes, resulting in a decrease in the efficiency of the transfer of matter and energy from phytoplankton to zooplankton. There are some evidences which suggest that efficient systems can support 25 times more biomass of zooplankton than inefficient eutrophic systems (Brett & Müller-Navarra, 1997), and this could significantly affect the nutrient cycles in the pelagic food web.

The main aim of our study is to assess the contribution of zooplankton and phytoplankton as sinks of phosphorus and nitrogen in lakes with different trophic conditions. We hypothesize that (i) the efficiency of carbon transfer from phytoplankton to zooplankton will decrease with the intensification of eutrophication and humification processes, (ii) efficiency of transfer of matter between phytoplankton and zooplankton will be associated with a reduction in inorganic nitrogen and phosphorus in the water, and (iii) under mesotrophic conditions most of the nitrogen and phosphorus will be accumulated in plankton communities. In addition, we aimed to find combinations of phytoplankton and zooplankton structures, which provide efficient transfer of matter and energy within lake food webs. We also predict that differences in plankton communities will be related to differences in the elemental composition of zooplankton.

Methods

Study sites

The study was conducted in 12 lakes in north-eastern Poland with different morphometric parameters (Table 1) and different trophic statuses (Table 2) during the peak of summer stagnation (July 16–24, 2018). The sampling stations were located close to the deepest point of each lake. The maximum depth of the lakes ranged from 4 to 73 metres, and the surface area ranged from 0.96 to 2118.3 hectares (Table 1). The Carlson trophic state indexes (Carlson, 1977) of harmonic lakes ranged from 46.4 to 59.2, and the visibility of the Secchi disc (SDV) ranged from 1.1 to

Table 1 Morphometric characteristics of the lakes

No.	Lakes	Latitude	Longitude	Area (ha)	Max depth (m)	Avg. depth (m)	V (thous. m ³)	Shor. dev.	Max length (m)
1	Białe Wigierskie	54° 01' 57"	23° 05' 41"	100.2	34	13.2	13,193.5	1.44	1875
2	Wigry	54° 00' 51"	23° 03' 45"	2118.3	73	15.8	336,726.7	4.43	17,500
3	Busznica	53° 56' 38"	23° 05' 00"	49.4	48	6.8	3350.6	1.05	950
4	Okrągłe	54° 01' 14"	23° 01' 22"	13.7	13	5.6	767.2	1.10	455
5	Długie Wigierskie	54° 01' 17"	23° 02' 03"	80.0	14.8	6.4	5227.6	2.16	2075
6	Leszczewek	54° 04' 18"	23° 03' 50"	21.0	6.5	3.6	755.3	1.51	1000
7	Garbaś	54° 07' 44"	22° 37' 42"	152.5	48	20.9	31,809.7	1.90	3450
8	Necko	53° 51' 43"	22° 57' 56"	400.0	25	10.1	40,561.4	1.84	5400
9	Wądołek	54° 07' 44"	23° 04' 02"	1.1	15	8.9	–	1.05	155
10	Suchar I	54° 05' 07"	23° 00' 54"	0.9	4	2.3	–	1.22	170
11	Suchar II	54° 05' 15"	23° 01' 04"	2.5	10	4.6	–	1.06	209
12	Suchar Wielki	54° 01' 40"	23° 03' 22"	8.9	9.6	3.9	–	1.68	760

shor. dev. shoreline development, avg. average, – it means no data available

6.6 metres (Table 2). The humic lakes were characterized by highly dystrophic conditions with hydrochemical dystrophy indexes (HDI) ranging from 66.5 to 69.4 (Table 2). The dystrophic lakes were mid-forest and small, usually oval (Table 1), without any inflows or outflows (Górniak, 2017). Mesotrophic lakes were generally large and deep (Table 1) and their catchment area was dominated by forests. Among them, Lake Wigry (no. 2) stands out because it is one of the deepest and largest lakes in Poland, characterized by a very diversified morphometry and developed shoreline (Table 1). The eutrophic lakes had large agricultural catchment, were more diverse, varying from small and shallow lakes, e.g. Lake Leszczewek and Lake Okrągłe, to large and deep lakes, e.g. Lake Necko and Garbaś (Table 1). Most of the lakes are located in the Wigry National Park, with the exception of Lake Busznica, Lake Garbaś, and Lake Necko (East Suwałki Lakeland).

Physical and chemical parameters of the water and elemental analyses of seston and zooplankton

The field measurements included the Secchi disc visibility (SDV), electrical conductivity (EC), pH, and the concentration of dissolved oxygen (DO), which was measured using an HQ40D Multi Meter (Hach-Lange GmbH). Phytoplankton (green algae, cyanobacteria, diatoms, cryptophytes, and the total chlorophyll *a* concentration) and temperature were

both measured in situ with the submersible spectrofluorometer FluoroProbe (bbe-Moldaenke). Changes in the resulting chlorophyll emission provide fluorometric estimation of algal classes based on differences in class-dependent peripheral antenna pigments (Beutler et al., 2002). The FluoroProbe determines the four distinct phytoplankton classes: green algae (Chlorophyceae and Euglenophyceae), cyanobacteria (phycocyanin-rich Cyanobacteria), diatoms (Heterokontophyta, Haptophyceae, and Dinophyceae) and cryptophytes (Cryptophyta and the phycoerythrin-rich Cyanobacteria). The Chlorophyceae have a broad maximum of fluorescence at 470 nm, which is caused by chlorophyll *a* and *b*. The Cyanobacteria has a maximum at 610 nm due to the phycocyanin. Cyanobacteria also contain chlorophyll *a* whose intensity of fluorescence is observed at 470 nm, due to the masking effect from phycocyanin. Furthermore, the high peak at the 525 nm wavelength is originated from xanthophyll fucoxanthin for the Bacillariophyceae and peridinin for the Dinophyceae. Due to the presence of phycoerythrin, the Cryptophyceae have a significant fluorescence maximum at 570 nm (Kring et al., 2014; Karpowicz & Ejsmont-Karabin, 2018). Continuous measurements of phytoplankton by probe represent a great advantage over discrete sampling since some species of phytoplankton can be concentrated in a very thin layer (Gregor & Maršálek, 2004). In situ measurements of the chlorophyll *a* concentrations were used to calculate the gross primary

Table 2 Trophic characteristic of lakes (July 2018)

No.	Lakes	TSI*	HDI**	Trophic status	SDV (m)	PZ (m)	Thermocline depth (m)	chl <i>a</i> epi	chl <i>a</i> meta
1	Białe Wigierskie	46.4	19.2	Mesotrophic	5.7	14.5	6.5–11.0	2.3 ± 0.6	1.9 ± 0.1
2	Wigry	47.3	15.9	Mesotrophic	5.2	10.5	7.5–10.0	3.8 ± 1.1	3.1 ± 1.0
3	Busznica	47.3	26.1	Mesotrophic	6.6	8.5	4–10.0	4.5 ± 1.0	4.8 ± 0.8
4	Okrągłe	50.9	16.7	Eutrophic	3.1	7.5	3.5–8.0	4.6 ± 1.4	6.3 ± 2.0
5	Długie Wigierskie	54.1	22.3	Eutrophic	1.65	7.0	4.0–8.0	6.9 ± 1.8	22.8 ± 18.3
6	Leszczewek	56.2	19.4	Eutrophic	2.3	5.0	>3.0	12.2 ± 4.2	94.8 ± 48.8
7	Garbaś	57.9	16.1	Eutrophic	2.0	5.0	4.0–9.0	26.2 ± 5.5	34.5 ± 21.3
8	Necko	59.2	19.5	Eutrophic	1.1	5.0	4.5–10	15.5 ± 3.8	3.9 ± 1.8
9	Wądołek	67.7	68.6	Dystrophic	1.2	4.0	1.0–3.0	21.1 ± 3.5	61.9 ± 32.2
10	Suchar I	61.9	66.5	Dystrophic	1.1	2.0	1.2–4.0	27.1 ± 0.9	109.0 ± 45.6
11	Suchar II	53.9	69.4	Dystrophic	1.9	3.5	1.5–5.5	9.2 ± 2.0	49.3 ± 29.9
12	Suchar Wielki	55.8	68.2	Dystrophic	2.2	4.7	3.2–6.0	26.0 ± 3.1	61.0 ± 24.4

TSI trophic state index (Carlson 1977), HDI hydrochemical dystrophy index (Górniak 2017), SDV Secchi disc visibility, PZ photic zone, epi epilimnion, meta metalimnion

*TSI = [TSI(SDV) + TSI(chla) + TSI(TP)]/3; TSI(SDV) = 60 - 14.41 ln(SDV); TSI(chla) = 9.81 ln(chla) + 30.6; TSI(TP) = 14.42 ln(TP) + 4.15

**HDI = HDI₁ + HDI₂ + HDI₃/3; HDI₁ = 20 (9.5 - pH); HDI₂ = 100/log(EC); HDI₃ = 10 DOC/DIC

production (GPP) and enriched taxonomic identification of algae (described below). Field measurements of temperature, oxygen, conductivity, pH, and phytoplankton were made from the surface to a depth of 30 metres.

Chemical analyses of the water samples were conducted in the laboratory immediately after collection. The concentrations of ions (PO₄³⁻, NH₄⁺, NO₃⁻, NO₂⁻) were determined using a Dionex ICS 1100 ion chromatograph. The concentrations of total nitrogen (TN), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), and total carbon (TC) were analysed by high-temperature catalytic combustion in the Shimadzu TOC-L Series analysers. TP analyses were conducted according to the conventional photometric method (Murphy & Riley, 1962), modified by Neal et al. (2000).

We also collected samples of seston (< 100 µm) and zooplankton (> 100 µm) from every lake for elemental analysis. The seston represents all particles and live organisms (phytoplankton, small rotifers, and bacteria) that passed through a net with 100 µm mesh. However, in freshwater lakes, the main component of seston is usually phytoplankton (Feniova et al., 2019).

For the seston samples, we collected 0.5–1.0 l of water from different water layers (epilimnion, metalimnion, and hypolimnion) in each lake. Subsequently, we filtered them through pre-combusted glass-fibre GF/F filters (Whatman, USA). The zooplankton samples were collected by vertical hauls and filtered on mesh sieves (100 µm) and then placed on filter paper to remove the surface moisture. We kept filters for seston analyses at room temperature for 24 h, while zooplankton samples were dried at 75°C overnight and stored dry in a desiccator until further analyses. The TC concentrations in seston and zooplankton were measured using Shimadzu TOC-L Series analysers with Solid Sample Modules SSM-5000A. TN was determined with Koroleff's photometric method using TN Cell Tests by Spectroquant, Merc (KGaA). Contents of TP analyses in seston and zooplankton were estimated following the conventional photometric method (Murphy & Riley, 1962). In conclusion, we used similar methods to assess nutrient concentrations in water, seston, and zooplankton. We then determined the role of phytoplankton and zooplankton as nutrient sinks by comparing the concentrations of nitrogen and phosphorus in

phytoplankton and zooplankton to the total amount of nutrients in the water.

Plankton analyses

The 10 l samples for taxonomical analyses of zooplankton and phytoplankton were taken from the epilimnion, metalimnion, and hypolimnion in each lake with a 5 l Limnos sampler. The zooplankton samples were filtered through a 50 µm mesh sieve and fixed with 4% formaldehyde. Rotifers and crustacean species were identified and counted in the whole samples. Additionally, the lengths of 10 individuals of each species were measured. Mean animal lengths were used to estimate the wet weight of planktonic crustaceans by applying the equations after Błędzki & Rybak (2016). The biomass of rotifers was established following length–weight relationships in Ejsmont-Karabin (1998). Cladocerans were further divided into large (*Daphnia* spp. and *Diaphanosoma* spp.) and small species (*Ceriodaphnia* spp., *Bosmina* spp., *Chydorus sphaericus* (O.F. Müller, 1776), etc.) because body size is an important attribute of cladoceran functional biology and ecology (Hart & Bychek, 2011), and small- and large-bodied cladocerans respond differently to predation pressure and algal abundance (Feniova et al., 2018; Karpowicz et al., 2019b).

Water samples for phytoplankton analysis were fixed with Lugol's solution. Phytoplankton abundance was determined according to the Utermöhl method (Utermöhl, 1958). Cells, colony, and filaments with a length of 100 µm were counted. The biomass of the phytoplankton species was determined based on cell sizes and their approximations to simple geometric shapes (Hillebrand et al., 1999).

Primary and secondary production of plankton

The GPP was estimated by the chlorophyll fluorescence method with DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), as described by the Gaevsky et al. (2000). We measured, in situ, the vertical distribution of phytoplankton, and in the laboratory, we estimated the potential photochemical activity of photosystem II for different groups of algae with DCMU using the FluoroProbe with Workstation 25. The DCMU was added to the samples to inhibit the reoxidation of the reduced primary electron acceptor (Q) of photosystem

II, yielding maximum fluorescence (Ishimaru et al., 1985). The GPP ($\text{gO}_2 \text{ l}^{-1} \text{ h}^{-1}$) was calculated by the empirical equation (Gaevsky et al., 2000) for phytoplankton:

$$\text{GPP} = b F_v/F_m \text{Chl}aI,$$

where b is the empirical coefficient, 0.00042, F_v/F_m is the relative variable fluorescence (arb.units), $\text{Chl } a$ describes the chlorophyll a concentration of algae ($\mu\text{g l}^{-1}$), and I is the average intensity of photosynthetically active radiation (PAR, W m^{-2}). Relative variable fluorescence was calculated by the following formula:

$$F_v/F_m = (F_m/F_0)/F_m,$$

where F_0 is the steady-state level of fluorescence and F_m describes the maximum level after the addition of 10 µM DCMU. The relative variable fluorescence summarizes the general condition of alga cells and their instant photosynthetic capacity.

GPP per hour was multiplied by daylight hours (using <https://www.timeanddate.com/>) for daily GPP calculations. In situ attenuation of PAR (W m^{-2}) was measured with a portable underwater irradiance metre with a Licor radiation sensor, LI-193SA Spectral Quantum sensor (USA). The conversion factor for GPP from mg O_2 to mg C was 0.32 (Alimov, 1989).

The production of zooplankton (secondary production) was calculated using regression models from Stockwell & Johansson (1997):

$$P = 10^{(-0.23 \log(M) - 0.73)} 1.12 MN,$$

where P is the daily production ($\mu\text{g DW l}^{-1} \text{ day}^{-1}$), M is the mean individual dry weight (μg), and N is the abundance (individuals l^{-1}).

Small rotifers from the seston subsamples were also included in zooplankton production estimations. Production of rotifer communities was established from the number of eggs counted in the samples. A curvilinear logarithmic generalized relationship between the rate of egg development and the temperature was used (Bottrell et al., 1976). Dry weight was converted into carbon units using a 1/2.3 quotient (Alimov, 1989).

The trophic transfer efficiency between the two trophic levels, phytoplankton (primary producers) and zooplankton (consumers), was calculated as the percentage ratio between the primary production and the

secondary (zooplankton) production in the whole water column (Gladyshev et al., 2011).

Statistical analyses

We used a one-way analysis of variance (ANOVA) with type III sums of squares (SS) to determine how the analysed parameters (zooplankton communities, the elemental composition of plankton, primary and secondary production, and the effectiveness of carbon transfer) differed between the trophic conditions. If significant treatment effects were detected, we used the Tukey HSD (Honestly Significantly Different) post hoc test ($P < 0.05$) to determine which means differed. To analyse the differences between the trophic levels, plankton production, and the effectiveness of carbon transfer, we used ANOVA with the least-squares means (LS). To test the importance of environmental parameters on zooplankton communities, we used the ANOVA with type III SS, and then, we used those parameters as factors in the multivariate analysis. Canonical correspondence analysis (CCA) was performed to find combinations of abiotic (nitrogen forms, TP, DO, and trophic status) and biotic (groups of phytoplankton based on Chl *a*) factors affecting the community structure of zooplankton.

Results

Hydrochemistry

The EC of the studied lakes in the eutrophic lakes group exceeded $400 \mu\text{S cm}^{-1}$, and in the mesotrophic lakes group, it was close to $250 \mu\text{S cm}^{-1}$. In the case of dystrophic lakes, it did not exceed $30 \mu\text{S cm}^{-1}$ (Table 3). The dystrophic lakes were distinguished by low pH values and high DOC concentrations (Table 3), while harmonic lakes had much more DIC (Table 3). The vertical profiles of DO in the eutrophic and dystrophic lakes were clinograde type, and in dystrophic lakes, oxygen depletion was just below the epilimnion (Table 3) at a depth of 2–3 metres. The mesotrophic lakes were characterized by the orthograde oxygen profile, with a well-oxygenated hypolimnion. The harmonic lakes had a higher concentration of nutrients in the lower water layers, especially those available for phytoplankton. The concentration of nitrates (NO_3^-) in the hypolimnion

was even 180 times higher than in the epilimnion of mesotrophic lakes (Table 3). The smallest differences between the investigated lake types were recorded for TN (Table 3).

Phytoplankton communities

The maximum concentration of chlorophyll *a* in the mesotrophic lakes was $5.89 \mu\text{g l}^{-1}$, while in the eutrophic and dystrophic lakes it was $144.72 \mu\text{g l}^{-1}$ and $143.75 \mu\text{g l}^{-1}$, respectively. The most eutrophic and dystrophic lakes had maximum concentrations of phytoplankton in the thermocline, while in the mesotrophic lakes, there were similar Chl *a* concentrations in the epilimnion and metalimnion (Table 2). The dominant group in the dystrophic lakes was green algae, which contributed to more than 60% of the total phytoplankton biomass (Fig. 1). The high share of green algae was also observed in most of the eutrophic lakes. Cyanobacteria dominated below the epilimnion in lake no. 5 and in the hypolimnion in lake no. 2. The dominant groups of phytoplankton in mesotrophic lakes were diatoms and cryptophytes (Fig. 1).

Microscopic analysis of the phytoplankton biomass (PB) of the three mesotrophic lakes indicated the dominance or co-dominance of Dinophyceae (48.9–96.5% of the PB in lake no. 2, 24.6% of the PB in the epilimnion of lake no.1) and Chlorophyceae (28.6% of the PB in lake no. 2, 62.8–65.2% of the PB in lake no. 3). Dinophyceae were represented mainly by *Ceratium hirundinella* (O.F.Müller) Dujardin, 1841; *Peridinium cinctum* Ehrenberg, 1838; and *Peridinium* spp., while Chlorophyceae was represented by *Phacotus lenticularis* (Ehrenberg) Diesing, 1866 (lake no. 2), *Dictyosphaerium* sp., and *Botryococcus braunii* Kützing, 1849 (lake no. 3, Table 4).

The main component of phytoplankton in the three eutrophic lakes (no. 4, 6, 8) were Chlorophyceae from the order Chlorococcales, which reached, respectively, 72–90%, 55.8–72.4%, and 33.7–55.2% of the PB. They were represented mainly by *P. lenticularis* (all lakes), *Coelastrum polychordum* (Korshikov) Hindák, 1977 (lake no. 8), and *Oocystis* spp., *Tetraedron minimum* (A.Braun) Hansgirg, 1888; *Tetrastrum komarekii* Hindák, 1977 (Table 4). In the case of lake no. 5, Chlorococcales (45.2%), represented mainly by *P. lenticularis* and *Dictyosphaerium* sp., co-dominated with Dinophyceae (38.3%, *C. hirundinella*) only in epilimnion. However, in the deeper layers,

Table 3 The mean vertical variation (\pm SD) of physical and chemical parameters and chlorophyll *a* in the lakes with different trophic statuses

	Mesotrophic			Eutrophic			Dystrophic		
	Epi (n = 3)	Meta (n = 3)	Hypo (n = 3)	Epi (n = 5)	Meta (n = 5)	Hypo (n = 3)	Epi (n = 4)	Meta (n = 4)	Hypo (n = 2)
Temp. (°C)	23.6 ± 1.7	14 ± 1.5	7.8 ± 2.3	24.1 ± 1.1	16.9 ± 1.6	8.6 ± 1.6	25.2 ± 0.9	13.5 ± 3.9	6.2 ± 2.3
pH	8.4 ± 0.3	8.0 ± 0.1	7.8 ± 0.1	8.5 ± 0.2	7.9 ± 0.3	7.5 ± 0.1	6.1 ± 0.2	5.3 ± 0.3	5.5 ± 0.4
EC (µS cm ⁻¹)	246 ± 118	270 ± 121	280 ± 133	407 ± 87	450 ± 73	438 ± 28	17 ± 2	24 ± 10	26 ± 10
DO (mg l ⁻¹)	9.8 ± 0.5	10.1 ± 4	7.6 ± 2.3	10.2 ± 1	5.8 ± 5.5	2.1 ± 2.1	8.5 ± 0.6	0.8 ± 0.9	0.2 ± 0.01
Chl <i>a</i> (µg l ⁻¹)	3.5 ± 1.2	3.3 ± 1.5	1.8 ± 1.0	12.5 ± 8.4	34.0 ± 8.4	5.2 ± 3.6	21.7 ± 8.4	77.1 ± 38.8	23.7 ± 10.8
DOC (mg l ⁻¹)	5.9 ± 1.2	5.6 ± 0.8	5.2 ± 0.8	7.8 ± 3.3	8.0 ± 3.6	5.6 ± 3.0	11.9 ± 5.1	17.0 ± 12.9	11.3 ± 4.1
DIC (mg l ⁻¹)	30.0 ± 9.1	30.2 ± 10.3	33.3 ± 11.7	43.5 ± 10.6	49.4 ± 9.2	52.7 ± 1.8	6.0 ± 1.2	9.1 ± 6.1	7.0 ± 1.5
TN (mg l ⁻¹)	0.98 ± 0.13	0.98 ± 0.06	1.35 ± 0.27	1.26 ± 0.27	1.52 ± 0.28	2.45 ± 0.31	1.30 ± 0.39	1.50 ± 0.74	1.65 ± 0.22
NH ₄ ⁺ (µg l ⁻¹)	1.2 ± 1.4	0.7 ± 0.2	5.1 ± 7.7	1.0 ± 0.8	6.2 ± 7.7	4.8 ± 6.6	0.7 ± 0.3	0.5 ± 0.5	0.4 ± 0.2
NO ₃ ⁻ (µg l ⁻¹)	1.0 ± 0.4	11.3 ± 15.7	187 ± 240	10.6 ± 18.5	170 ± 169	608 ± 526	6.0 ± 7.0	1.8 ± 0.8	3.3 ± 0.1
NO ₂ ⁻ (µg l ⁻¹)	1.9 ± 1.7	0.4 ± 0.2	0.8 ± 0.8	1.1 ± 0.8	1.3 ± 0.9	2.7 ± 1.8	0.4 ± 0.4	0.7 ± 0.7	0.7 ± 0.1
TP (µg l ⁻¹)	3.9 ± 0.6	3.9 ± 0.9	8.4 ± 7.0	4.7 ± 0.4	6.0 ± 1.7	11.3 ± 5.8	14.6 ± 20.0	5.2 ± 2.3	5.8 ± 1.9

cyanobacteria (*Aphanizomenon* sp.) created 57.9–79.4% of the PB. The reverse situation was observed in lake no. 6, where the highest share of Chlorococcales (*P. lenticularis*) was recorded in the hypolimnion, while in the epi- and metalimnion, *C. hirundinella* was clearly dominant (81.3–91.7% of the PB).

Raphidophytes *Gonyostomum semen* (Ehrenberg) Diensig, 1866 reached the highest share in the three dystrophic lakes. The contribution of this species in the PB fluctuated between 67.7 and 92.7% (lake no. 9), 64.7–84.8% (lake no. 10), and 43.4–64.7 (lake no. 11). The predominance of Dinophyceae (45.6–80% of the PB), represented by *Gymnodinium* sp. and *Peridinium* sp., over Chlorophyceae (10.7–17.2% of the PB) was observed only in lake no. 12. The most numerous species were *Quadrigulla closteroides* (Bohlin) Printz, 1915 and Raphidophyceae (5.33–14.3%) (Table 4).

Zooplankton communities

In the mesotrophic lakes, the biomass of zooplankton ranged from 0.53 to 3.77 mg l⁻¹ (Fig. 2) and averaged 2.08 mg l⁻¹. The mesotrophic lakes are characterized by the greatest diversity of planktonic crustaceans, and the number of species ranged from 14 to 15. Rare and relict species were also detected: *Eurytemora lacustris* (Poppe, 1887) in lakes no. 1 and 2, *Hetercope appendiculata* Sars G.O., 1863 in lakes no. 1 and 3, *Cyclops lacustris* Sars G.O., 1862 in lake no. 1, *Bythotrephes brevis* Lilljeborg, 1901 in lake no.3, and *Daphnia longiremis* G.O. Sars, 1861 in lakes no.1 and 2. There was a large diversity of the *Daphnia* genus in lakes no.1 and 2, where four species were found. Besides the dominant *Daphnia cucullata* G.O. Sars, 1862 (Table 5), which contributed 65% of the total crustacean biomass in the mesotrophic lakes, we found *Daphnia cristata* G.O. Sars, 1862; *Daphnia longispina* (O.F. Müller, 1776) and *D. longiremis*. The genus *Bosmina* was also represented by 3 to 4 species in the mesotrophic and eutrophic lakes (Table 5). Large cladoceran species dominated in the zooplankton communities of lakes no. 2, 3, and 4 (Fig. 2), while the cyclopoid group comprised the highest share in lake no.1 (Fig. 2), with the

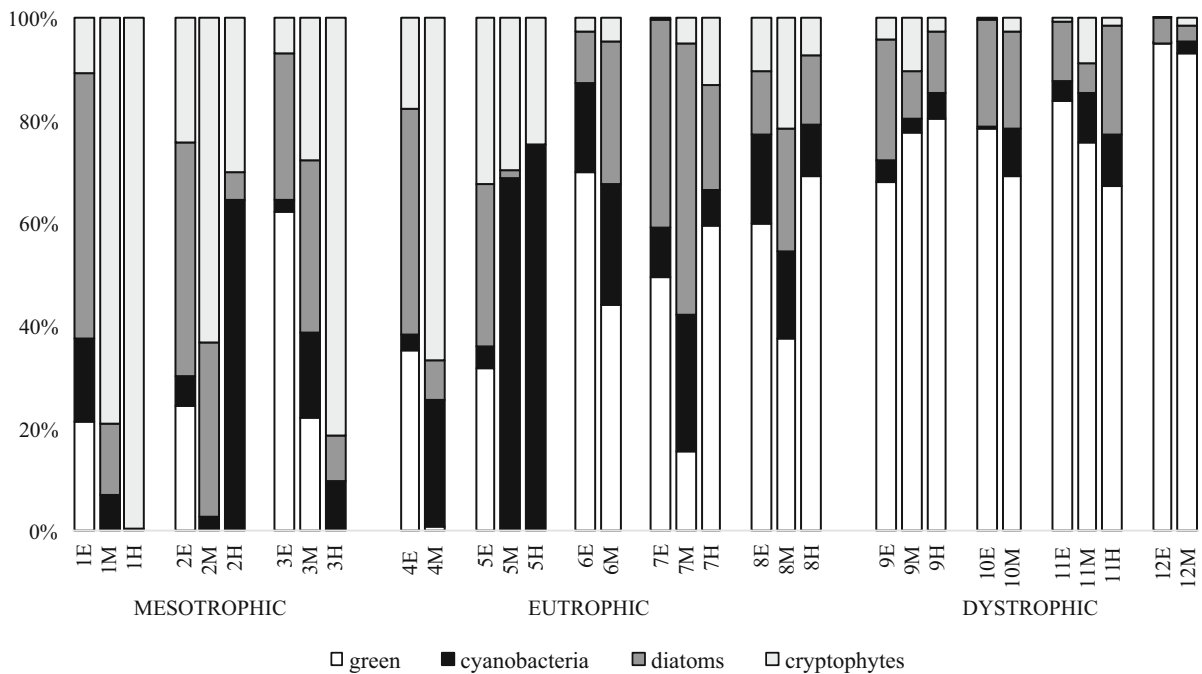


Fig. 1 The percentage share of main phytoplankton groups. Numbers 1–12 correspond to the lakes (Tables 1 and 2); *E* epilimnion, *M* metalimnion, *H* hypolimnion

domination of *Cyclops scutifer* Sars G.O., 1863 and relict *C. lacustris* (Table 5). Rotifer biomass in the mesotrophic lakes was relatively low, except for in the hypolimnion of lake no. 2, where the total rotifer biomass reached 0.35 mg l^{-1} in the epilimnion due to the mass development of the colonial species *Conochilus hippocrepis* (Schrank, 1803) (Table 5). In the other lakes, rotifer biomass in the epilimnion was very low, i.e. $0.01\text{--}0.05 \text{ mg l}^{-1}$. The other abundant rotifer species was *Keratella cochlearis* Gosse, 1851, which was especially dense in deep zones where its *macracantha* form was characterized by markedly higher body size.

In the eutrophic lakes, the biomass of zooplankton varied from 0.53 to 7.71 mg l^{-1} (Fig. 2), with an average of 3.39 mg l^{-1} . The species richness of the crustaceans in the eutrophic lakes ranged from 9 to 14, and the relic *Eurytemora lacustris* was found in one eutrophic lake (no. 7). In lakes no. 4 and 5, zooplankton was dominated by large Cladocera (mostly *D. cucullata* and *Diaphanosoma brachyurum* (Liévin, 1848)), while in the other eutrophic lakes, the shares of the main zooplankton groups were similar (Fig. 2). The highest contribution to the rotifer biomass in eutrophic lakes was made by the large predatory

rotifer, *Asplanchna priodonta* Gosse, 1850. This rotifer species was most abundant in the metalimnion of lakes no. 4, 6, and 7 and in the meta- and hypolimnion of lake no. 5. The other abundant rotifer species in all eutrophic lakes were *Gastropus stylifer* Imhof, 1891; *K. cochlearis*, *Pompholyx sulcata* Hudson, 1885, and 3 species of the genus *Polyarthra* (Table 5).

The biomass of zooplankton in the dystrophic lakes ranged from 0.015 to 3.25 mg l^{-1} (Fig. 2), averaging 0.67 mg l^{-1} . The number of crustacean species in the dystrophic lakes ranged from 3 to 6. The dominant crustacean species was *Ceriodaphnia quadrangula* (O.F. Müller, 1785), which contributed up to 93% to the total crustacean biomass in lake no. 12. The calanoid copepod *Eudiaptomus gracilis* (Sars G.O., 1863) was found in all the dystrophic lakes (Table 5) and made up to 75% of the total crustacean biomass in the lake no. 11 (Fig. 2). Rotifers in dystrophic lakes were represented by *Conochiloides dossuarius* (Hudson, 1885); *Polyarthra remata* Skorikov, 1896; *K. cochlearis*, and *A. priodonta* (Table 5); however, these species occurred in various combinations. *C. dossuarius* and *P. remata* dominated in lake no. 11 (ca. 84% of the total rotifer biomass) and lake no. 10 (ca.

Table 4 The list of the dominant phytoplankton species (more than 5% of total biomass) in 12 lakes

	1	2	3	4	5	6	7	8	9	10	11	12
Cyanophyceae												
<i>Aphanizomenon</i> sp.					***							
<i>Dolichospermum lemmermannii</i> (Richter) P.Wacklin, L.Hoffmann & J.Komárek, 2009	**											
Euglenophyceae												
<i>Trachelomonas volvocina</i> Ehrenberg var. <i>volvocina</i>	*											
Dinophyceae												
<i>Ceratium furcoides</i> (Levander) Langhans, 1925							*					
<i>Ceratium hirundinella</i> (O.F.Müller) Dujardin, 1841		***	*	**	**		***					
<i>Gymnodinium fuscum</i> (Ehrenberg) Stein, 1978										**		
<i>Gymnodinium</i> sp.			*									***
<i>Peridiniopsis cunningtonii</i> Lemmerman, 1907				*		**						
<i>Peridinium cinctum</i> Ehrenberg, 1838		*		**								
<i>Peridinium gatunense</i> Nygaard, 1925				*								
<i>Peridinium inconspicuum</i> Lemmerman, 1899	**							*	**	*		*
<i>Peridinium</i> sp.												*
Cryptophyceae												
<i>Cryptomonas</i> spp.			*	*	**			*	*	*	**	
Chrysophyceae												
<i>Chromulina</i> sp.												*
Raphidophyceae												
<i>Gonyostomum semen</i> (Ehrenberg) Diensig, 1866								***	**	**	*	*
Bacillariophyceae												
<i>Fragilaria crotonensis</i> Kitton, 1869		*										
<i>Tabellaria fenestrata</i> (Lyngbye) Kützing, 1844							**					
Chlorophyceae												
<i>Botryococcus braunii</i> Kützing, 1849			**									
<i>Coelastrum polychordum</i> (Korshikov) Hindák, 1977								**				
<i>Crucigeniella fenestrata</i> (Schmidle) Schmidle, 1900											*	
<i>Dictyosphaerium</i> sp.			**	*						**		
<i>Oocystis</i> spp.	**	*	*		*							
<i>Phacotus lenticularis</i> (Ehrenberg) Diesing, 1866		*	**	*	**	**	**	**				
<i>Tetraedron minimum</i> (A.Braun) Hansgirg, 1888					*							
<i>Tetrastrum komarekii</i> Hindák, 1977					*							
Unicellular Chlorococcales						**				**		
<i>Quadrigulla closteroides</i> (Bohlin) Printz, 1915												**

*For species with biomass 5–10%

**For species constituting 10–50% of the biomass

***For species with biomass > 50% of total phytoplankton biomass

76%). Further both these species, together with *A. priodonta*, were observed in lake no. 9, accounting for up to ca. 88% of the total rotifer biomass. *A. priodonta*, *K. cochlearis*, and *P. remata* dominated in lake no. 12.

There were significant differences in the biomasses of Rotifera ($F = 5.59$; $P = 0.009$) and large Cladocera ($F = 4.65$; $P = 0.018$) between the eutrophic and dystrophic lakes. There were also differences in the

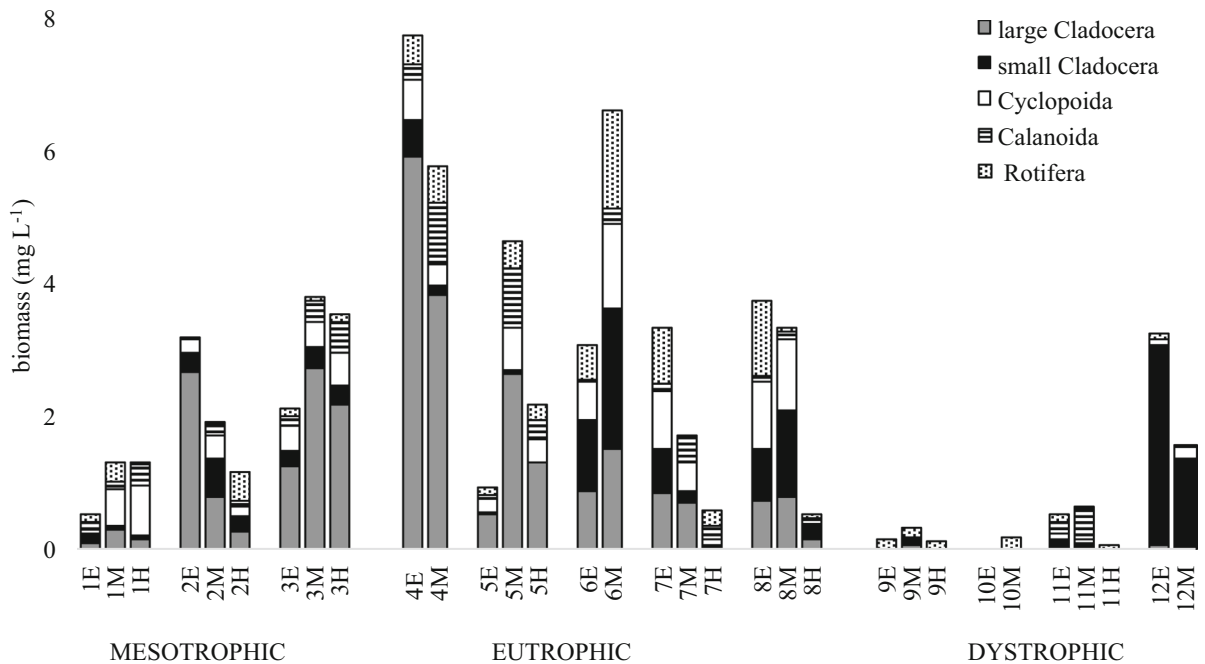


Fig. 2 Zooplankton biomass with a share of main zooplankton groups. Abbreviation as in Fig. 1

biomass of Cyclopoida between harmonic lakes (highest biomass) and dystrophic lakes (lowest biomass), while in the small bodied Cladocera and Calanoida, there were no significant differences in the biomasses between lakes with different trophic states. The CCA revealed that phytoplankton groups were the most important factor affecting the community structure of zooplankton. The Calanoida and large Cladocera could be positively linked with cryptophytes and diatoms while they were negatively linked with cyanobacteria and green algae (Fig. 3). On the contrary, small bodied Cladocera was related with a high abundance of cyanobacteria and green algae (Fig. 3). The CCA also clearly distinguished zooplankton communities in dystrophic lakes due to higher shares of small bodied Cladocera and Calanoida (Fig. 3).

Elemental composition of zooplankton

The dry weight of zooplankton was $7.8 \pm 1.4\%$ of the wet weight. The content of carbon, nitrogen, and phosphorus in zooplankton was $52.4 \pm 6.4\%$, $7 \pm 1.8\%$, and $1.1 \pm 0.3\%$, respectively. The carbon content in zooplankton showed the highest variability in the dystrophic lakes (Fig. 4A). The highest carbon content in zooplankton was found in lakes no. 10

(66.3%) and no. 11 (65.1%), where the zooplankton was mainly represented by Rotifera and Calanoida (Fig. 2). The lowest carbon content in zooplankton was found in lake no. 12 (47.1%), where small cladocerans dominated (Fig. 2). The carbon content of zooplankton in the eutrophic and mesotrophic lakes was similar (Fig. 4A) and accounted for $49.9 \pm 1.6\%$. There were no significant differences in nitrogen and phosphorus content in zooplankton between different trophic conditions (Fig. 4B, C). The analysis of variance revealed that differences in the community structure did not result in changes in the elemental composition of zooplankton. However, the type III SS test showed that Calanoida may be associated with a decrease in the amount of phosphorus in zooplankton ($F = 3.78$; $P = 0.091$), and large Cladocera were positively correlated with phosphorus content in zooplankton ($F = 3.36$; $P = 0.11$).

Phytoplankton and zooplankton as a sink of nitrogen and phosphorus

The average nitrogen content in phytoplankton varied from 53% (dystrophic lakes) to 65% (eutrophic and mesotrophic lakes) of TN (Fig. 5C). However, in one mesotrophic lake, the phytoplankton nitrogen content

Table 5 The list of the dominant zooplankton species (more than 5% of total biomass) in 12 lakes

	1	2	3	4	5	6	7	8	9	10	11	12
Cladocera												
<i>Bosmina berolinensis</i> Imhof, 1888		*	*	*	*	*		*				
<i>Bosmina (Eubosmina) coregoni</i> Baird, 1857	*		**	*			*	*	***	**		
<i>Bosmina (Eubosmina) crassicornis</i> Lilljeborg, 1887	*	**		*	*		**	**				
<i>Bosmina longispina</i> Leydig, 1860	*	*	*		*	*	*	*	*			
<i>Ceriodaphnia quadrangula</i> (O.F. Müller, 1785)			*	*		**		**			**	***
<i>Chydorus sphaericus</i> (O.F. Müller, 1776)				*		*		*				
<i>Daphnia cristata</i> G.O. Sars, 1862	*	*		*								
<i>Daphnia cucullata</i> G.O. Sars, 1862	**	**	***	***	***	**	**	**	**	**		*
<i>Daphnia longispina</i> (O.F. Müller, 1776)	*	*	*	*	*		*	*				*
<i>Diaphanosoma brachyurum</i> (Lévin, 1848)	*	*	**	**	*	*	*	*	*			
<i>Leptodora kindtii</i> (Focke, 1844)		*	*	*	*	*	*	*				
Cyclopoida												
<i>Mesocyclops leuckarti</i> (Claus, 1857)		*	*	*	*	*	*	**			*	*
<i>Thermocyclops oithonoides</i> (Sars G.O., 1863)	*	*	*	*	**	**	**	**	*		**	
<i>Cyclops scutifer</i> Sars G.O., 1863	**			*	*			*				
<i>Cyclops lacustris</i> Sars G.O., 1862	**											
Calanoida												
<i>Eudiaptomus gracilis</i> (Sars G.O., 1863)				*		*		*	*	*	**	*
<i>Eudiaptomus graciloides</i> (Lilljeborg, 1888)	*	*	*		*		**					
<i>Eurytemora lacustris</i> (Poppe, 1887)	*	*					*					
<i>Hetercope appendiculata</i> Sars G.O., 1863	*		*									
Rotifera												
<i>Ascomorpha ovalis</i> (Bergendahl, 1892)	*		*	*			*	*	*	*		
<i>Asplanchna priodonta</i> Gosse, 1850	**		*	*	*	*	*	**	**		**	*
<i>Conochiloides dossuarius</i> (Hudson, 1885)					*	*	**	*			*	*
<i>Conochilus hippocrepis</i> (Schrank, 1803)		**	*					*	*			
<i>Conochilus unicornis</i> Rousset, 1892	*	*	*			*	*	*	*			
<i>Gastropus stylifer</i> Imhof, 1891	*		*	*				*	*	**	*	*
<i>Keratella cochlearis</i> Gosse, 1851	*	*	*	*	*		*	*	*	**	*	*
<i>Keratella irregularis</i> (Lauterborn, 1898)	*		*	*			*	*		*		
<i>Keratella cochlearis tecta</i> (Gosse, 1851)		*	*				*	*	*	*	*	
<i>Polyarthra remata</i> Skorikov, 1896	*	*	*	*	*	**	*	*	*	*	**	*
<i>Polyarthra vulgaris</i> Carlin, 1943	*	*	*	*	*		*	*	*	*	*	*
<i>Pompholyx sulcata</i> Hudson, 1885	*	*	*	*			*	*	*	**	*	
<i>Trichocerca cylindrica</i> (Imhof, 1891)							*	*	*	*		*

*For species with biomass 5–10%

**For species constituting 10–50% of the biomass

***For species with biomass > 50% of total zooplankton biomass

comprised up to 99% of the TN. As a result of algae uptake, there was a depletion of inorganic nitrogen in the upper water layer. The concentrations of NO₃⁻

ions in the upper water layers of harmonic lakes were nearly 180-fold lower than in the hypolimnion (Table 3). The low concentrations of NO₃⁻ were

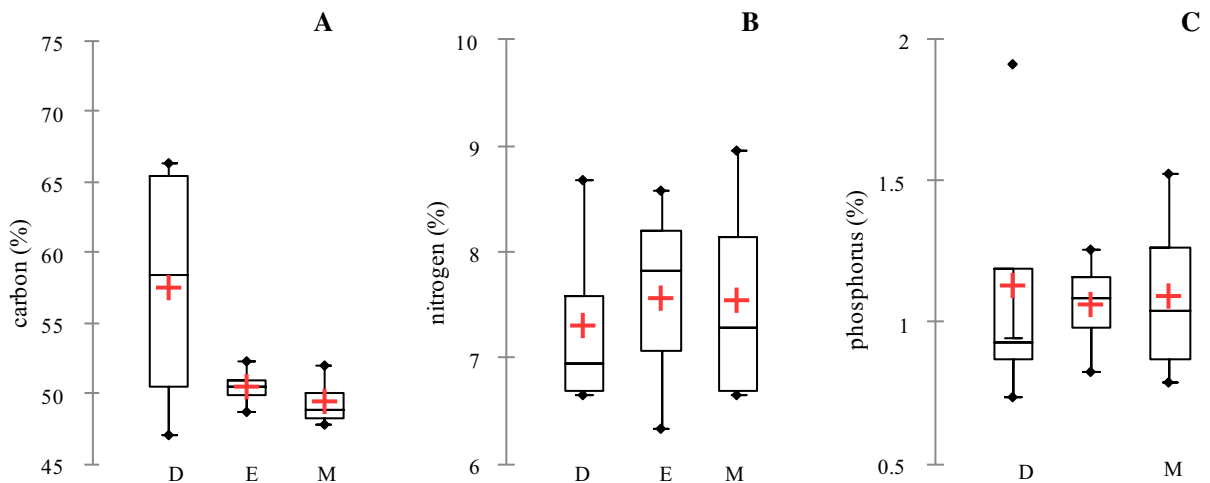


Fig. 4 Elemental composition of zooplankton (percentage share of C, N, P) in lakes with different trophic statuses. *D* dystrophic, *E* eutrophic, *M* mesotrophic

and mesotrophic lakes it was $0.08 \pm 0.8 \text{ gC l}^{-1} \text{ day}^{-1}$ and $0.01 \pm 0.01 \text{ gC l}^{-1} \text{ day}^{-1}$, respectively.

There were no significant differences in the secondary (zooplankton) production between the lakes of different trophic conditions (Fig. 6A), as well as in the vertical profile (Fig. 6B). The average (\pm SD) zooplankton production was $0.071 \pm 0.17 \text{ mgC l}^{-1} \text{ day}^{-1}$, with a maximum of $0.91 \text{ mgC l}^{-1} \text{ day}^{-1}$ in the metalimnion of eutrophic lake no. 4, and a minimum of $0.00036 \text{ mgC l}^{-1} \text{ day}^{-1}$ in the epilimnion of dystrophic lake no. 10. However, there were significant differences in the hypolimnetic zooplankton production between dystrophic lakes and harmonic lakes (eutrophic and mesotrophic). The hypolimnetic secondary production in the harmonic lakes was $0.05 \pm 0.05 \text{ mgC l}^{-1} \text{ day}^{-1}$, while in the dystrophic lakes it was $0.006 \pm 0.004 \text{ mgC l}^{-1} \text{ day}^{-1}$.

A comparison of primary and secondary productions in the whole water column revealed that the effectiveness of carbon transfer between phytoplankton and zooplankton ranged from 0.0005% to 0.14%. The highest efficiencies of carbon transfer were in lakes no. 4 (0.14%) and no. 3 (0.13%), where large Cladocera dominated in the whole water column (Fig. 2). The efficiencies of carbon transfer between phytoplankton and zooplankton in the mesotrophic and eutrophic lakes were 0.068% and 0.048%, respectively (Fig. 7). However, the low efficiency of carbon transfer between phytoplankton and zooplankton (0.006%) was noted in one eutrophic lake (no. 5)

with the highest share of cyanobacteria (Fig. 1). The lowest efficiency of carbon transfer was observed in the dystrophic lakes, where, on average, only 0.001% of organic carbon production by phytoplankton was incorporated into new biomass of zooplankton (Fig. 7).

Discussion

The results of our study confirm that eutrophication and humification decrease the efficiency of the transfer of matter between phytoplankton and zooplankton. The lowest efficiency was observed in dystrophic lakes, where only 0.001% of organic carbon production of phytoplankton was incorporated into new biomass of zooplankton. These lakes were characterized by high biomass of phytoplankton, which was similar to that of the hypertrophic reservoir with cyanobacterial blooms (Grabowska & Wołowski 2014; Górniak & Karpowicz, 2014). The high biomass of phytoplankton was well documented for the dystrophic lakes of Wigry National Park (Karpowicz & Ejsmont-Karabin, 2018), with expansive development of flagellate *Gonyostomum semen* (Pęczuła et al., 2018). This flagellate was also dominant in all the studied dystrophic lakes, contributing to 92.7% of the PB. *G. semen* has been drawing much attention for many years due to frequent blooms observed in humic lakes in Northern Europe (Korneva, 2000), and

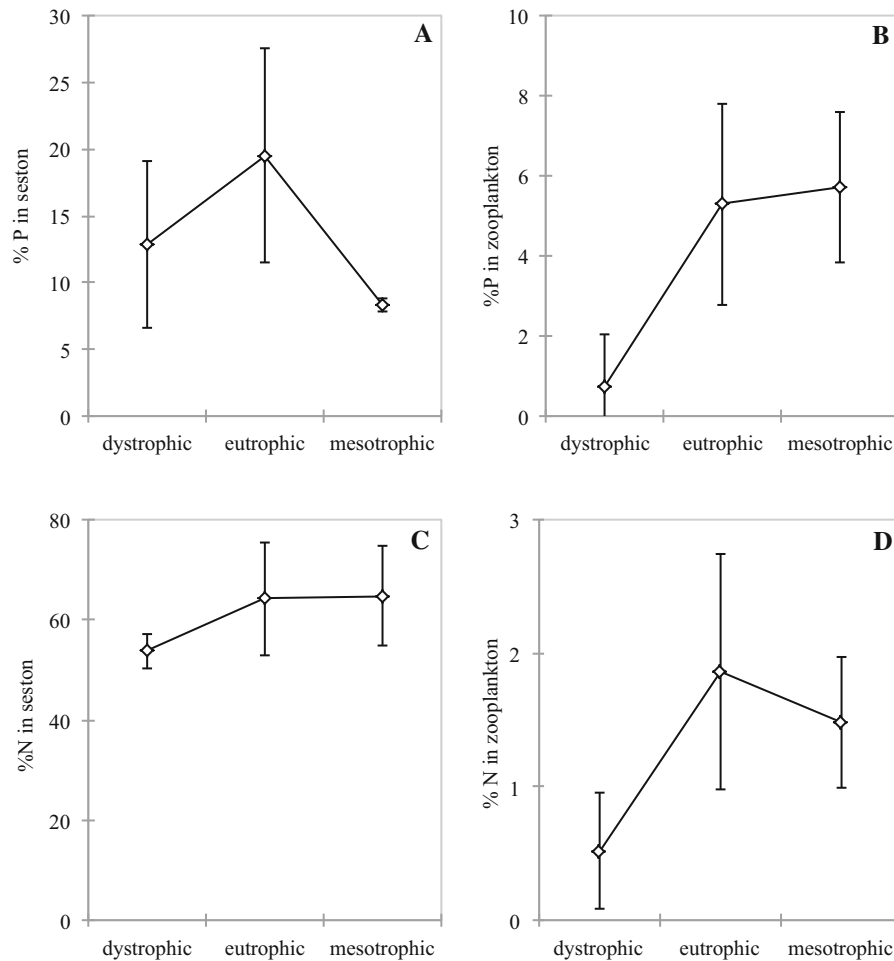


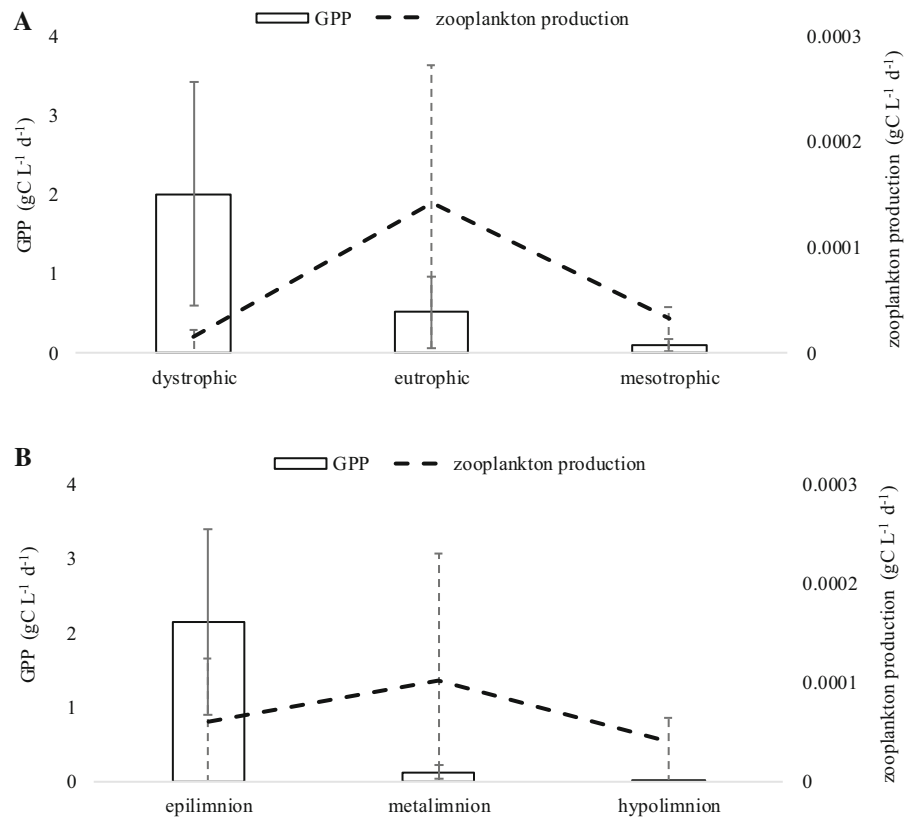
Fig. 5 The mean percentage (\pm SD) of phosphorus and nitrogen in zooplankton and seston compared to the total amount of phosphorus in the water

recently, also in Poland, Latvia, and Lithuania (Karosiene et al., 2014). Although this species is generally inedible for most zooplankton species due to its large body size (50–70 μm) and the presence of trichocysts, the research suggests that *G. semen* could be grazed by large zooplankton (*Asplanchna priodonta*, *Daphnia pulex*, *Holopedium gibberum*, and *Eudiaptomus gracilis*) (Williamson et al., 1996; Lebreton et al., 2012; Johansson et al., 2013; Pęczyła et al., 2018). These zooplankton species are also common components of humic lakes, which suggests that some part of the matter and energy accumulated in *Gonyostomum* can be transferred to higher trophic levels. However, during *Gonyostomum* blooms small zooplankton dominate over large zooplankton species, which strongly reduces the importance of

Gonyostomum as a food resource (Johansson et al., 2013). The high biomass of *G. semen* in the studied dystrophic lakes could be a reason of the very low efficiency of carbon transfer between phytoplankton and zooplankton.

Literature data from more than 600 lakes also confirmed that bacteria and phytoplankton production is higher in humic lakes than in harmonic lakes (Nürnberg & Shaw, 1999). The results of this study also indicate that in the dystrophic lakes, high biomass of phytoplankton contrasts with low biomass of zooplankton, which results in a very low efficiency of transfer of matter between phytoplankton and zooplankton. Noteworthy is that in humic lakes, the large amount of food resources for crustacean zooplankton and low fish pressure do not lead to the

Fig. 6 Differences in gross primary production (GPP) and secondary (zooplankton) production ($\text{mgC l}^{-1} \text{ day}^{-1}$) in different trophic conditions (A) and in vertical profiles (B) presented by least-squares means (LS) and standard deviation (solid vertical lines for GPP, and dashed vertical lines for zooplankton production)



massive development of large-bodied zooplankton. The factors that prevent the development of large-bodied crustaceans in humic lakes are still unclear. Some authors suggest that humic stress connected to the high concentrations of humic substances and DOC could constrain zooplankton development (Robidoux et al., 2015). Other researchers believe that food quality for zooplankton in humic lakes is low (Taipale et al., 2016). Our previous results suggest that the sharp changes in temperature and low oxygen concentration in humic lakes are the main factors which reduce the zooplankton biomass and can promote the development of phytoplankton (Karpowicz & Ejsmont-Karabin, 2018). This finding is also supported by our current data indicating that the high biomass of zooplankton was found in Lake Suchar Wielki (no. 12), which has a deep and oxygenated epilimnion. Nevertheless, the common statement that dystrophic lakes are unproductive (Berggren et al., 2009; Kostrzevska-Szlakowska & Jasser, 2011) should be revised. Some authors have more precisely specified that humic lakes are unproductive from a fishery point of view (Rask et al., 1995; Finstad et al., 2014). In

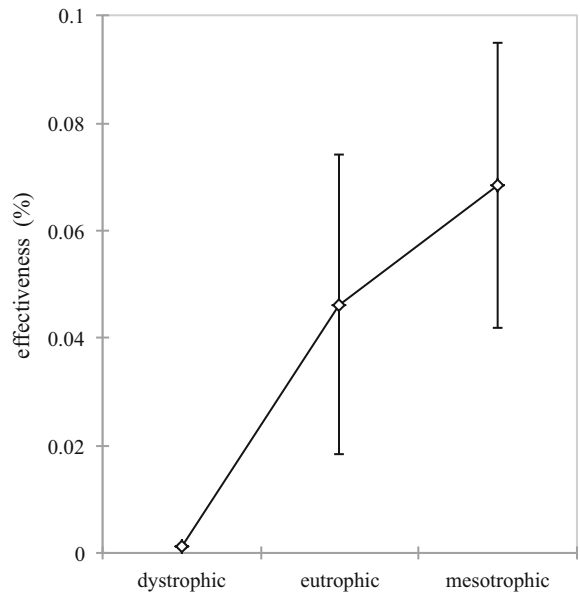


Fig. 7 Effectiveness (%) of carbon transfer between phytoplankton and zooplankton in lakes with different trophic statuses presented by least-squares means (LS) with standard deviation

regard to primary production, our data show that humic lakes are highly productive (Fig. 6), but the transfer of matter between phytoplankton and zooplankton is very ineffective (Fig. 7).

The highest efficiency of the transfer of matter was in the mesotrophic lakes due to a higher hypolimnetic zooplankton production. The well-oxygenated hypolimnion zones promote a large species richness of crustacean zooplankton and create a favourable habitat for cold-water species with high environmental requirements (Karpowicz et al., 2019a). We found a high species richness and large size variability of zooplankton in the water column of the mesotrophic lakes. The well-oxygenated hypolimnion allowed the vertical niche segregation of *Daphnia* species, where 3–4 species were found in each lake. Different species of *Daphnia* could occupy different niches if they differ from each other by life-history strategies, habitat preferences, behaviour, morphology, body size, filtration rate, and vulnerability to predation (Brzeziński et al., 2012). The high species richness of the *Daphnia* genus in Lake Wigry has been well known for a long time (Kamiński, 1999; Karpowicz et al., 2019a). The migration of large species to deeper layers creates favourable conditions for small species in the upper layer (Karpowicz & Ejsmont-Karabin, 2017). This can promote the effective transfer of energy and matter to higher trophic levels because it critically depends on the size structure of the zooplankton (Rykaczewski & Checkley, 2008; Beaugrand et al., 2010). The large size variability of zooplankton in the water column also promotes niche partitioning of predators (Ye et al., 2013), which makes the transfer of energy throughout the whole lake food web more efficient. The lower water layers in the mesotrophic lakes were inhabited by large zooplankton, among which five relict and rare crustacean species occurred (*Eurytemora lacustris*, *Heterocope appendiculata*, *Cyclops lacustris*, *Bythotrephes brevimanus*, and *Daphnia longiremis*). These cold-adapted species spread over Europe, along with glaciers, during the last ice age and were able to survive only in deep lakes with well-oxygenated hypolimnion (Spikkeland et al., 2016; Karpowicz & Kalinowska, 2018). The high habitat requirements make them a very useful indicator of good ecological status in lakes and low trophic conditions (Ejsmont-Karabin & Karabin, 2013; Ochocka & Pasztaleniec, 2016). The results of our study revealed a high zooplankton production in

deeper layers of the mesotrophic lakes, which, together with large species richness, promotes the effective transfer of matter in the pelagic food web.

Recent research suggests that eutrophication and climate change are two processes that may promote the proliferation and expansion of harmful cyanobacterial blooms (O'Neil et al., 2012). Our results indicate that the eutrophication process also causes a decrease in the efficiency of carbon transfer between phytoplankton and zooplankton, but not so much as the humification process. We have found a similar efficiency of carbon transfer between phytoplankton and zooplankton in the mesotrophic and eutrophic lakes, which could be attributed to a small share of cyanobacteria in our lakes. The dominance of cyanobacteria was recorded only in Lake Długie Wigierskie (no. 5), which had a very low efficiency of carbon transfer between the phytoplankton and zooplankton. Cyanobacteria generally have many deleterious effects on zooplankton grazing, via production of toxins (Ferrão-Filho & Kozłowski-Suzuki, 2011; Holland & Kinnear, 2013; Mantzouki et al., 2018), low nutritional value (Vanni & Lampert, 1992; Sikora et al., 2016; Feniova et al., 2018), and filamentous colony structure which inhibit filtration processes (Gliwicz, 1990; Sikora & Dawidowicz, 2014). This indicates that cyanobacteria and/or inedible algae are the main factors reducing the efficiency of the transfer of matter in pelagic food webs.

One of the general paradigms of ecology is that only 10% of energy and matter pass to the next trophic level (Lindeman, 1942; Gladyshev et al., 2011). The primary producers convert inorganic carbon into organic carbon, which is incorporated into new biomass at higher trophic levels. Therefore, the production and effectiveness of matter transfer are frequently measured in carbon mass units (Pauly & Christensen, 1995; Schulz et al., 2004). The transfer efficiency in marine ecosystems ranged between 2 and 24% (Pauly & Christensen, 1995) and is similar to that in lakes where the transfer efficiency between phytoplankton and zooplankton ranges between 1 and 30% (Lacroix et al., 1999). However, the results of our study revealed much lower carbon transfer efficiency between phytoplankton and zooplankton in lakes with different trophic statuses, which varied between 0.0005% and 0.14%. Such very low efficiency in the algal-based pathway may be attributed to the dominance of large inedible algae in seston during the peak

of summer stagnation. However, more accurate methods to measure the efficiency of carbon transfer in planktonic food webs suggest that only 0.1% of the carbon produced by the phytoplankton is incorporated into zooplankton (Sherr & Sherr, 1987; Havens et al., 2000). Measurements of carbon transfer in algal and bacterial food webs revealed the same low efficiencies for both pathways (Ducklow et al., 1996; Koshikawa et al., 1996). This suggests that the effectiveness of carbon transfer through planktonic freshwater food webs is much lower than the theoretical 10%.

The results of our study showed that plankton communities are a key component of the nutrient cycle in freshwater food webs. Phytoplankton were a very effective sink of nitrogen and phosphorus. In mesotrophic lakes, up to 99% of TN was sequestered in phytoplankton, thus causing a depletion of inorganic nitrogen in the upper water layer. Phytoplankton have a high demand for nitrogen because they contain intracellular nitrogen in many forms, e.g. nitrate, ammonium, amino acids, protein, RNA, and pigments (Dortch, 1982). According to the Lagrangian model, algae acquires nutrients at the bottom of the habitat while it grows in shallower waters, and when their nutrient quota falls below a certain threshold, the cells start to sink (Grover, 2017). Field studies revealed that a deep chlorophyll layer is a common phenomenon in clear water lakes, as a result of a nutrient shortage in the epilimnion during summer stagnation (Camacho, 2006; Karpowicz & Ejsmont-Karabin, 2017). Our results indicated that a shortage of dissolved nitrogen in the epilimnion could be the main factor for formation of the deep chlorophyll layer in mesotrophic lakes. Also, mesocosm experiments confirmed that nitrogen was effectively accumulated by phytoplankton (Karpowicz et al., 2019b) and sequestration of nitrogen by phytoplankton was much higher than remineralization by zooplankton.

The results of our study also suggest that the zooplankton is an effective sink of phosphorus. However, zooplankton could act simultaneously as a phosphorus sink by incorporating P and as a source of phosphorus, by excretion of phosphate and organic phosphorus (e.g. Lampert et al., 1986; den Oude & Gulati, 1988; Lyche et al., 1996). This dualism in the functional role of zooplankton is very important for the nutrient cycle in lakes. The threshold elemental ratio model, which is a principal concept in ecological stoichiometry, assumes that the element in the least

supply is assimilated with maximum efficiency (Hessen et al., 2013). The excretion of phosphorus by *Daphnia* could drop to zero when there is low phosphorus content in algae (i.e. C:P ratio ranging from 320 to 430) (Olsen et al., 1986; Sterner et al., 1998). Therefore, low P content in algae, together with high demand for P by *Daphnia*, underlines the role of zooplankton as a sink of phosphorus. Finally, zooplankton also contributes to the translocation of nutrients within the water column (Karpowicz & Ejsmont-Karabin, 2017; Sługocki & Czerniawski, 2018), and its importance in nutrient cycles increases with lake size (Fee et al., 1994).

Conclusions

Our results indicated that the effectiveness of carbon transfer between phytoplankton and zooplankton varied from 0.0005% to 0.14%, which is much lower than the theoretical 10%. However, the highest efficiency of transfer of matter was in mesotrophic lakes due to the higher hypolimnetic zooplankton production. The well-oxygenated hypolimnion zones increases zooplankton species richness and creates a favourable habitat for cold-water species with high environmental requirements. The lowest efficiency was noted in dystrophic lakes, where only 0.001% of organic carbon production of phytoplankton was incorporated into new biomass of zooplankton. Our results indicated that cyanobacteria and/or inedible algae (*G. semen*) are the main factors reducing the efficiency of the transfer of matter in pelagic food webs.

The results of our study showed that plankton communities are the key component of the nutrient cycle in the freshwater food web. The phytoplankton was a very effective sink of nitrogen ($62.2 \pm 17.8\%$) and phosphorus ($13.2 \pm 12.4\%$). However, in mesotrophic lakes, up to 99% of TN was sequestered in phytoplankton, and as a result, there was a depletion of inorganic nitrogen in the upper water layer. The results of this study also suggest that zooplankton is an effective sink of phosphorus in eutrophic and mesotrophic lakes, where its average content in zooplankton reaches up to 5–6% of TP.

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Conflict of Interest: The authors declare that they have no conflict of interest.

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