Dynamics of Species and Size Structures of Phytoplankton at Different Levels of Bottom-Up and Top-Down Effects in Experimental Conditions

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Abstract—An experimental study of the impacts of trophic conditions and the activity of zooplankton and fish on the phytoplankton structure has shown that, at the beginning of the experiment, the species and size structures of algae were dependent on the N : P ratio. This parameter causes the differences in phytoplankton structures between mesotrophic and eutrophic conditions so that, in mesotrophic conditions, the dominant taxa are diatoms, dinoflagellates and chrysophytes while, in eutrophic mesocosms, cyanobacteria are most abundant. Later on, the differences in N : P ratio in the treatments are smoothed out and the dominance shifts to large filamentous green algae. Fish reduce zooplankton control over phytoplankton, thus promoting the development of edible diatoms; this is most clearly manifested in eutrophic conditions.

INTRODUCTION

The species and size structures of phytoplankton can be regulated bottom-up by nutrients and top-down by consumers, commonly by planktonic filter feeder crustaceans. To predict changes in the ecosystems, it is important to know which factors cause changes in the structure of primary producers and when. Furthermore, changes in environmental conditions may also alter the impact of the main drivers on the structure of algae communities. For example, a higher trophic level may reduce bottom-up control because nutrient concentrations increase but, on the other hand, top-down control may be enhanced.

The concentration of nutrients is believed to regulate the structure and abundance of phytoplankton. However, there are evidences that algae are influenced by the N : P ratio rather than by concentrations of nutrients (Levich and Bulgakov, 1995). In particular, the high abundance of cyanobacteria in Lake St. George (United States) was associated with a low ratio of nitrate nitrogen to total phosphorus (<5), while cyanobacteria were never abundant when this ratio exceeded 5 (McQueen and Lean. 1987).

Top-down control of phytoplankton communities is implemented via fish effects on the abundance of filter-feeder zooplankton (Feniova et al., 2007; Semenchenko et al., 2007). Fish predation was shown to increase zooplankton species richness (Feniova et al., 2007; Fott et al., 1980; Korinek et al., 1987; Declerck and De Meester, 2003; Semenchenko et al., 2007) and, in turn, affect the structure of phytoplankton. However, fish can have not only a top-down impact on phytoplankton but also exert bottom-up control. For example, algae passed through the gut of silver Prussian carp *Carassius auratus* L. can influence the dynamics of individual species, in particular, stimulate the growth of *Microcystis aeruginosa* (Kützing) Kützing or inhibit the growth of *Anabaena flos-aquae* Brébisson ex Bornet & Flauhault (Kolmakov and Gladyshev, 2003). Fish of the carp family can stimulate the development of cyanobacteria as a result of iron chelation (Brabrand et al., 1984).

Our goal was to establish how the species and size structures of phytoplankton respond to the changes in the trophic level and fish pressure. We carried out experiments to study the dynamics of the species and

size structures of phytoplankton at two trophic levels (mesotrophic and eutrophic conditions) in the presence and absence of fish. We hypothesized that the mechanisms of effects of these factors on the structures of phytoplankton communities may be different under mesotrophic and eutrophic conditions.

MATERIALS AND METHODS

We conducted experiments in 300 L mesocosms (0.94 × 0.64 × 0.50 m) in mesotrophic and eutrophic conditions. To create two trophic levels, mesocosms were filled with water containing phyto- and zooplankton from two lakes belonging to the Mazurian lake system (northeastern Poland), namely, mesotrophic Lake Majcz (area 163.5 ha, max. depth 16.4 m, mean depth 6.0 m) and eutrophic Lake Mikołajskie (area 498 ha, max. depth 26 m, mean depth 11 m) (Gliwicz et al., 1981). The experiments included four treatments: (1) mesotrophic conditions without fish (M), (2) mesotrophic conditions with fish (MF), (3) eutrophic conditions without fish (E), and (4) eutrophic conditions with fish (EF). In the fish treatments, one ruff *Gymnocephalus cernuus* L. (7.5–11 cm long) was added to each mesocosm. We placed the fish in 5-L plastic boxes that were suspended in the mesocosms. The boxes had large slots that allowed zooplankton to pass freely but kept the fish inside. The mesocosms were open but, in case of rain, we covered them with a multilayer polyethylene film to avoid contamination from rain water. All treatments of the experiment were triplicated. The experiment lasted 50 days.

The chlorophyll concentration was estimated using a PHYTOPAM fluorometer (Walz, Germany) on days 1, 10, 20, 30, 40, and 50. The fluorometer measures the total concentration of chlorophyll and the concentration of the main photosynthetic pigment in three groups of phytoplankton: greens, diatom algae, and cyanobacteria (*Phytoplankton Analyzer...*, 2003). The concentration of nutrients (P-PO$_4$, N-NH$_4$, N-NO$_2$, N-NO$_3$) in water was measured on days 1, 30 and 50 by the standard methods (*Standard Methods*, 2005). The concentration of total nitrogen was calculated as the sum of its compounds.

Phytoplankton samples were collected on days 1, 10, 30, and 50 using a 0.5-L glass after thoroughly mixing the water column. We used the sedimentation method to concentrate phytoplankton samples (Kuz'min, 1975). Samples were fixed with an Utermöhl solution with formaldehyde. Algae were counted under a light microscope (Nikon Optiphot 2). Small algae were estimated in 3.2 mm^3 Fuchs-Rosenthal chamber, large forms were counted at low magnification in the grooves of the Bogorov chamber, and the largest algae (*Oedogonium* sp., *Mougeotia* sp.etc.) were processed in the entire chamber. The algae biomass was estimated based on geometric approximations assigning a geometric shape (Korneva, 2015). Cell

sizes were measured under a microscope using an ocular micrometer. The size structure of phytoplankton was represented by five classes: <10, 10–29, 30–49, 50–99, and >100 μm.

Zooplankton samples were collected with a 2.6 L Limnos sampler after thoroughly mixing the water on days 1, 10, 20, 30, 40, and 50. We measured the lengths of 100 individuals of each taxon for biomass estimates based on length : weight relationships from Balushkina and Vinberg (1979).

We analyzed the changes of nutrients, chlorophyll concentrations of different groups of algae, and biomasses of cladocerans and copepods. The significance of differences in these variables between the treatments was estimated using one-way analysis of variance ($p < 0.05$, one-way ANOVA). Correlation analysis of chlorophyll relations with cladoceran and copepod biomasses and with concentrations of nutrients was performed using Spearman's rank-order correlation coefficient. Statistical analysis of experimental data was conducted using integrated Biosystem office (Petrosyan, 2014) and R 3.3 software.

RESULTS

The concentrations of phosphate and total nitrogen did not differ significantly between the treatments (Table 1); however, the concentration of ammonium nitrogen was significantly higher under eutrophic conditions ($F = 37.2$, $p \ll 0.005$, Fig. 1). By the end of the experiment, the concentration of the total nitrogen in the treatments M and MF had decreased while in E and EF it did not change throughout the experiment ($p > 0.05$) (Fig. 2). There were no significant differences in the concentration of phosphorus between any treatments of the experiment ($p > 0.05$). In mesotrophic conditions, the N : P ratio was the highest at the beginning of the experiment and it significantly decreased by the end (Table 2). In EF treatment, N : P reached a peak on the 30th day, while, in the E treatment, this ratio did not significantly change in the course of experiment. The N : P ratio differed between mesotrophic and eutrophic conditions only at the beginning of the experiment ($F = 7.8$, $p = 0.01$).

Concentrations of total chlorophyll, chlorophylls of cyanobacteria, and diatoms in eutrophic conditions were significantly higher than in mesotrophic conditions (Table 1). Fish did not affect the concentration of total chlorophyll; however, the concentration of the main photosynthetic pigment of green algae in EF treatment was significantly higher than in M and MF treatments, but it did not differ relative to that in E treatment (Table 1).

In mesotrophic conditions, diatoms dominated (24–98% of total algae biomass) throughout the experiment regardless of the presence or absence of fish (Table 3). They were represented by *Fragilaria capucina* Desmazières, *F. crotonensis* Kitton, *F. vires-*

Table 1. Comparison (one-way ANOVA) of the main variables ($M \pm SD$) between the treatments of the experiment

Variable	M	E	MF	EF	F	P
PO$_4$-P, mg/L	0.02 ± 0.01	0.02 ± 0.00	0.02 ± 0.02	0.03 ± 0.03	1.1	0.357
Total N, mg/L	0.14 ± 0.23	0.09 ± 0.02	0.12 ± 0.20	0.12 ± 0.04	0.2	0.925
Total chlorophyll, μg/L	21.07 ± 5.78^A	51.17 ± 16.30^B	20.96 ± 5.59^A	50.01 ± 16.49^B	23.3	**≪0.005**
Chlorophyll of diatoms, μg/L	18.16 ± 4.94^A	27.07 ± 9.27^B	17.60 ± 4.32^A	29.18 ± 10.60^B	7.1	**≪0.005**
Chlorophyll of cyanobacteria, μg/L	1.70 ± 1.44^A	21.32 ± 13.37^B	2.00 ± 1.26^A	15.35 ± 12.32^B	13.9	**≪0.005**
Chlorophyll of greens, μg/L	1.31 ± 1.14^A	2.77 ± 2.85^{AB}	1.42 ± 1.03^A	5.47 ± 6.47^B	3.4	**0.025**
Copepoda, mg/L	0.16 ± 0.08^A	0.53 ± 0.23^B	0.25 ± 0.13^A	0.42 ± 0.24^B	10.5	**≪0.005**
Cladocera, mg/L	1.37 ± 1.33^A	0.48 ± 0.57^{BC}	1.09 ± 1.04^{AC}	0.29 ± 0.30^B	3.7	**0.019**

Statistically significant differences ($p < 0.05$) between the treatments are designated by different letters (A, B, and C) and highlighted in bold.

cens Ralfs, and *Rhizosolenia longiseta* O. Zacharias. Chrysophytes (golden algae) and dinophytes were abundant (>20% of the total algae biomass) during the first 10 days. At the beginning, among the dinophyte algae, the most abundant were *Gymnodinium* and *Peridinium*, which reached 26−49% of the total algae biomass. Green algae (15−46%) appeared at the end of the experiment; they mainly consisted of attached algae *Rhizoclonium hieroglyphicum* (C. Agardh) Kützing, *Mougeotia* sp. and *Oedogonium* sp. Cyanobacteria in mesotrophic conditions were rare (1−7% of the total phytoplankton biomass).
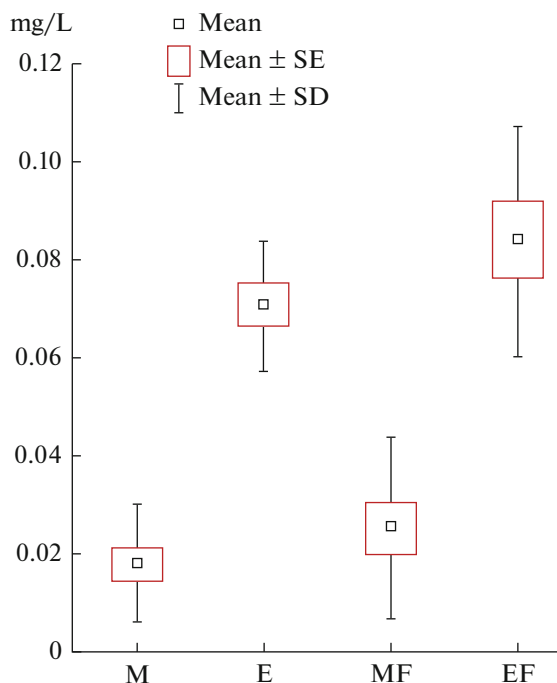
In eutrophic conditions, in both treatments, cyanobacteria dominated. During the first 10 days, their biomass varied from 64 to 77% of the total phytoplankton biomass (Table 3). Cyanobacteria were mainly represented by *Limnothrix planctonica* (Woloszynska) Meffert, *L. redekei* (Goor) Meffert, and *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek. On days 30 and 50, the largest proportion of the phytoplankton biomass was contributed by green algae, from 49 to 92%, due to the large cells of the genera *Mougeotia* and *Oedogonium*. The proportion of diatoms of the phytoplankton biomass in E treatment was insignificant (1−15%); however, in EF treatment, on days 30 and 50, their proportion increased to 10−45%. Golden and dinophyte algae accounted for <10% of total phytoplankton biomass.

At the beginning of the experiment in mesotrophic conditions, the largest proportion of algae was allocated to the size group of 30−50 μm (Table 4). Fish promoted the development of large algae (50−100 μm), which dominated on day 10, while small algae (10−30 μm) were more abundant in M treatment. On days 30 and 50, in both treatments in mesotrophic conditions, algae of 50−100 μm dominated.

Under eutrophic conditions, algae >100 μm dominated in both treatments during the first 10 days. In E treatment, algae with a size of >100 μm dominated until the end of the experiment, while algae of 50−100 μm were the most abundant.

In the eutrophic mesocosms, the average biomass of Copepoda was significantly higher, while that of Cladocera, on the contrary, was lower than in mesotrophic conditions (Table 1). This was true during the first 30 days. After that, in E and EF treatments, Copepoda biomass decreased and did not differ from that in M and MF. In M and MF, conversely, the biomass of Cladocera decreased and became similar to that in E and EF (Fig. 3).

The concentration of total chlorophyll was positively correlated with N : P in MF treatment. In E

Fig. 1. Concentration of ammonium ions in the four treatments of the experiment. M is mesotrophic conditions, E is eutrophic conditions, MF is mesotrophic conditions with fish, and EF is eutrophic conditions with fish.
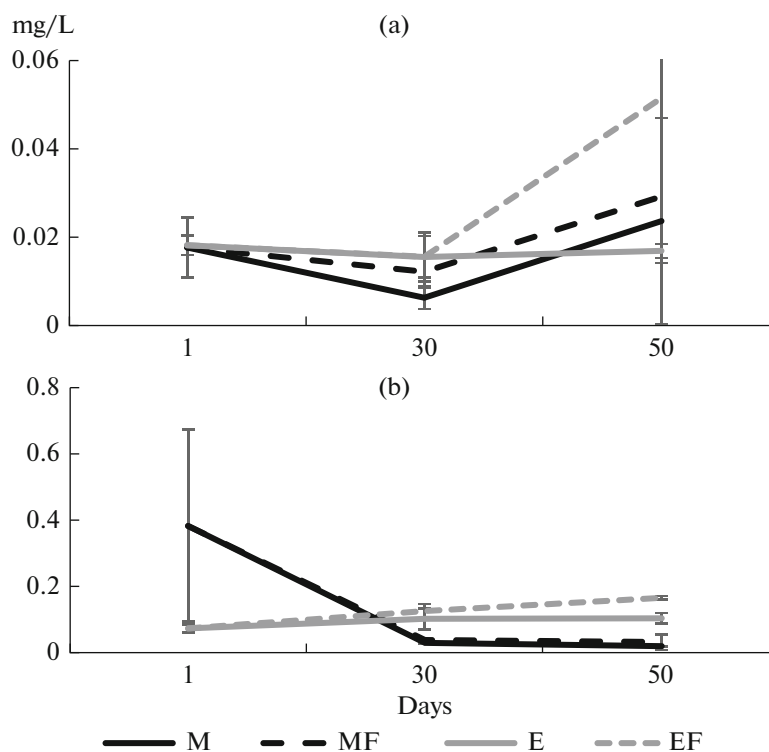
Fig. 2. Dynamics of concentrations of phosphorus (a) and nitrogen (b). M is mesotrophic conditions, E is eutrophic conditions, MF is mesotrophic conditions with fish, and EF is eutrophic conditions with fish.

treatment, total chlorophyll was negatively related to total nitrogen and N : P ratio (Table 5). Total chlorophyll negatively correlated with the biomass of Cladocera in all the treatments (Table 5).

DISCUSSION

Higher concentrations of phytoplankton, especially cyanobacteria, in eutrophic conditions relative to mesotrophic mesocosms in our experiments are quite common (Lyashenko, 2003; Trifonova, 1998; Naselli-Flores and Barone, 2000; Babanazarova et al., 2011; Downing et al., 2001; Chen et al., 2003). Cyanobacteria *Limnothrix redekei*, *Planktothrix agardhii*, and

Table 2. N : P ratio on days 1, 30, and 50 in the four treatments of the experiment

Treatments	Days			F	p
	1	30	50		
M	20 ± 8^A	5 ± 2^B	1 ± 1^B	13.0	**0.01**
MF	20 ± 8^A	3 ± 1^B	3 ± 4^B	10.7	**0.01**
E	4 ± 1	8 ± 6	6 ± 1	0.8	0.51
EF	4 ± 1^A	8 ± 1^B	4 ± 3^A	4.4	**0.05**

Statistically significant differences ($p < 0.05$) between the treatments are designated by different letters (A and B) and highlighted in bold.

Pseudanabaena limnetica usually occur in highly productive systems (Babanazarova et al., 2011; Reynolds et al., 2002; Nixdorf et al., 2003; Wiśniewska et al., 2007). According to Reynolds Functional Groups classification (Reynolds et al., 2002), these species belong to the planktothrix-oscillatoria group.

Golden algae commonly reach high abundances in waters of low trophic level (Rosén, 1981; Negro et al., 2000). In our experiment in mesotrophic mesocosms, they constituted >20% of the total phytoplankton biomass, but they were rare in eutrophic conditions. The diatom alga *Rhizosolenia longiseta* and dinoflagellates were also abundant in mesotrophic mesocosms, which is in accordance with their preference to meso- (Reynolds et al., 2002) and oligo-mesotrophic lakes (Ilmavirta, 1975; Rosén, 1981). However, in our experiment, the algal groups in mesotrophic mesocosms shifted in the course of experiment to the large filamentous attached green algae *Mougeotia* sp. and *Oedogonium* sp.

Because in eutrophic conditions cyanobacteria were displaced by the large filamentous green attached algae in the second half of the experiments, we can conclude that attached filamentous algae more efficiently consumed nutrients than small plankton forms. Such a shift can occur in shallow lakes or inshore, where appropriate substrates are available and nutrients are not in shortage (Sakharova and Korneva, 2018). This group of algae is likely to gain competitive advantages due to their large surface area to use nutrients.

Table 3. Proportion of different taxa and dominant species in phytoplankton (% of the total biomass ± SD) in the four treatments of the experiment

Taxon	Days						
	1	10		30		50	
	mesotrophic conditions						
	M	M	MF	M	MF	M	MF
Diatoms							
Fragilaria capucina	0	6 ± 10	9 ± 9	0	0	17 ± 17	24 ± 35
Fragilaria crotonensis	29 ± 34	12 ± 4	23 ± 21	59 ± 38	74 ± 47	16 ± 26	4 ± 8
Fragilaria virescens	0	0	0	0	0	10 ± 18	2 ± 3
Rhizosolenia longiseta	0	1 ± 1	4 ± 4	20 ± 22	9 ± 13	0	0
Other diatoms	16 ± 12	5 ± 1	17 ± 8	6 ± 3	15 ± 3	35 ± 5	23 ± 20
Diatoms totally	45 ± 43	24 ± 15	53 ± 34	93 ± 46	98 ± 38	83 ± 52	53 ± 48
Greens							
Oedogonium sp.	0	17 ± 29	20 ± 35	0	0	0	7 ± 11
Rhizoclonium hieroglyphicum	0	0	6 ± 6	0	0	13 ± 12	20 ± 21
Mougeotia sp.	0	0	0	0	0	0	18 ± 25
Other greens	6 ± 4	2 ± 1	3 ± 5	1 ± 1	2 ± 2	2 ± 1	1 ± 1
Greens totally	6 ± 4	19 ± 29	29 ± 35	1 ± 1	2 ± 2	15 ± 13	46 ± 46
Dinophytes							
Peridinium sp.	26 ± 1	25 ± 25	14 ± 12	5 ± 10	0	2 ± 3	0
Gymnodinium sp.	0	24 ± 42	0	0	0	0	0
Other dinophytes	0	0	0	0	0	0	0
Dinophytes totally	26 ± 1	49 ± 24	14 ± 13	5 ± 10	0	2 ± 3	0
Cryptophytes	1 ± 0	1 ± 1	2 ± 1	0	2 ± 1	2 ± 3	0
Cyanobacteria	7 ± 4	1 ± 1	2 ± 2	5 ± 10	0	0	0
Euglena algae	0	2 ± 4	0	0	0	0	1 ± 1
Golden algae	15 ± 11	4 ± 5	0	0	0	0	0
	Eutrophic conditions						
	E	E	EF	E	EF	E	EF
Diatoms	3 ± 2	3 ± 5	1 ± 2	15 ± 6	45 ± 16	5 ± 4	10 ± 9
Greens							
Muojeotia sp.	0	0	9 ± 16	32 ± 28	33 ± 11	79 ± 34	68 ± 9
Oedogonium sp.	0	0	0	0	7 ± 12	10 ± 17	3 ± 2
Other greens	23 ± 1	15 ± 9	8 ± 7	32 ± 4	9 ± 5	3 ± 0	12 ± 3
Greens totally	23 ± 1	15 ± 9	17 ± 8	64 ± 32	49 ± 26	92 ± 20	83 ± 24
Dinophytes	7 ± 3	5 ± 6	5 ± 5	3 ± 1	0	1 ± 1	3 ± 4
Cryptophytes	0	0	1 ± 2	0	0	1 ± 1	1 ± 1
Cyanobacteria							
Limnothrix (redeckii + planctonica)	51 ± 6	65 ± 1	63 ± 14	15 ± 11	2 ± 1	0	1 ± 0
Planktothrix agardhii	11 ± 5	9 ± 8	6 ± 4	3 ± 5	3 ± 2	1 ± 1	0
Other cyanobacteria	2 ± 1	1 ± 1	8 ± 2	0	1 ± 1	0	2 ± 1
Cyanobacteria totally	64 ± 2	75 ± 8	77 ± 17	18 ± 3	6 ± 3	1 ± 1	3 ± 1
Euglena algae	0	0	0	0	0	0	0
Golden algae	3 ± 2	2 ± 1	2 ± 2	0	0	0	0

Table 4. Proportion of size-classes of phytoplankton (% of the total biomass ± SD) in the four treatments of the experiment

Days	Size class, μm	M	MF	E	EF
1	>100	1	–	48–88	–
	50–99	17–25	–	2–5	–
	30–49	56–70	–	6–39	–
	10–29	3–7	–	6–11	–
	<10	6–15	–	0	–
10	>100	0–1	0	78–80	69–79
	50–99	30–39	38–91	0–2	1–5
	30–49	0–13	34–59	0–10	4–6
	10–29	53–65	2–6	8–18	14–21
	<10	0–2	0	1–0	0–9
30	>100	2–12	0	44–77	7–27
	50–99	66–89	85–94	1–3	43–80
	30–49	4–30	2–10	3–39	6–26
	10–29	1–4	2–5	13–45	4–14
	<10	0–1	0–1	0–3	0–1
50	>100	1–4	28–53	50–99	4–84
	50–99	55–94	41–92	0	11–87
	30–49	3–34	2–9	0–46	3–9
	10–29	1–26	1–6	1–7	3–9
	<10	0	0	0	0

In mesotrophic conditions, small species dominated, while large algae were more abundant in eutrophic mesocosms. This is consistent with the statement that the size of algae increases with the increasing trophic level (Watson and Kalff, 1981). Filamentous green algae were shown to be more competitive in eutrophic conditions due to their advantages in the consumption of nutrients (Cattaneo, 1987; Carrick and Lowe, 1989).

There were no significant differences in the nitrates, nitrites, and phosphates between the treatments, likely due to the active consumption of nutrients by phytoplankton. However, in eutrophic condi-

Table 5. Spearman's rank-order correlation coefficients of chlorophyll relations with biomasses of cladocerans and copepods and nutrient concentrations in the four treatments of the experiment

Treat-ments	Cope-poda	Clado-cera	PO$_4$-P	N total	N : P
M	−0.39	**−0.74***	0.57	0.42	0.47
E	0.38	**−0.63***	0.53	**−0.77***	**−0.78***
MF	−0.25	**−0.71***	0.27	0.54	**0.68***
EF	0.15	**−0.55***	0.15	−0.53	−0.58

Significant correlation coefficients are highlighted in bold* ($p < 0.05$).
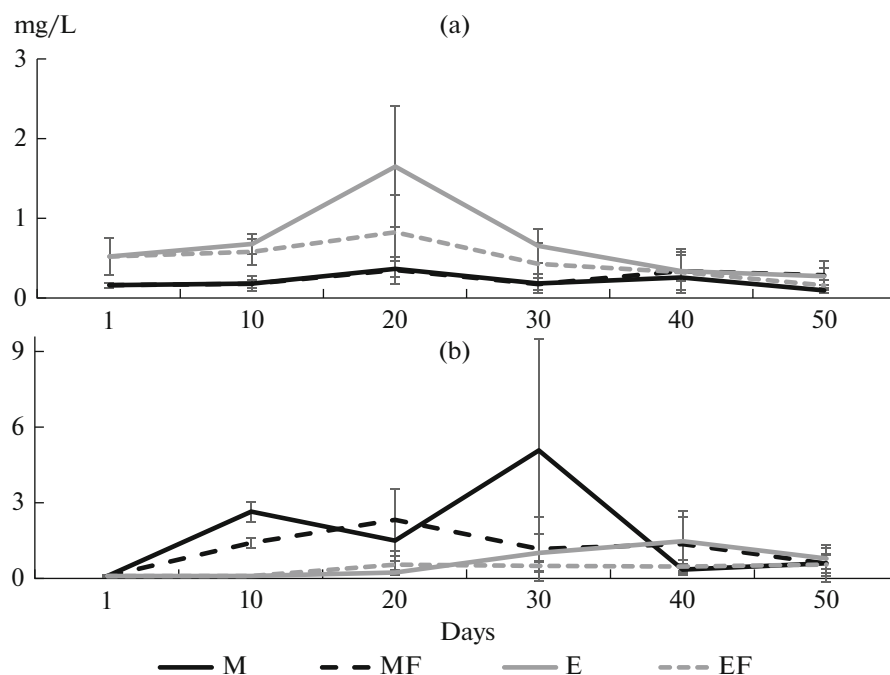
tions, concentrations of ammonium ions were higher relative to mesotrophic. High concentrations of ammonium nitrogen are common for waters experiencing a high organic load (Datsenko, 2007). However, for the development of algae, the N : P ratio may be more important than their individual concentrations (Levich and Bulgakov, 1995). We suggest that significant differences in the dominant taxa between the mesotrophic and eutrophic conditions at the beginning of the experiment could be associated with N : P ratios. Cyanobacteria usually dominate at low N : P ratios as a result of their competitive advantage over other species (Havens et. al., 2003). Indeed, at the beginning of the experiment, N : P was significantly lower than in mesotrophic conditions in eutrophic mesocosms. Although low N : P sustained in eutrophic conditions throughout the experiment, there was a shift from cyanobacteria to green filamentous algae *Mougeotia* and *Oedogonium*, which happened as a result of competition for nutrients (Schindler, 1975; Carrick and Lowe, 1989). In eutrophic lakes, these algae are able to form dense coverage (Simons, 1994; Gerrath, 2003; John, 2003). The decrease of N : P in mesotrophic conditions in the course of the experiment also led to the dominance of large filamentous green algae.

The chlorophyll concentration negatively correlated with N : P in the eutrophic mesocosms; conse-

Fig. 3. Dynamics of biomasses of Copepoda (a) and Cladocera (b). M is mesotrophic conditions, E is eutrophic conditions, MF is mesotrophic conditions with fish, and EF is eutrophic conditions with fish.

quently, algae community was controlled not only top-down by crustaceans but also bottom-up. For this reason, better adapted species to low N : P dominated. Attached filamentous green algae are not edible by zooplankton due to their large size, thus leading to a decline in zooplankton abundance if they are a dominant phytoplankton group (Burns, 1968; Lampert et al., 1986). Since chlorophyll concentration was negatively related to cladoceran biomass, by the end of our experiment, when filamentous algae became abundant, cladoceran biomass decreased in all the treatments. The dominance of copepods at the beginning of the experiment over cladocerans in eutrophic conditions was likely associated with lower concentrations of edible phytoplankton than those in mesotrophic mesocosms.

Fish can enrich water with nutrients (Feniova et al., 2016) but, in our experiment, nutrient concentrations did not respond to the presence of fish. The N : P ratio in MF and EF treatments also did not differ from that in M and E correspondingly. Fish also did not affect abundances of phyto- and zooplankton. We suggest that the active consumption of nutrients by phytoplankton smoothed out the differences between the treatments. Fish can reduce crustacean control on small species of phytoplankton (Gliwicz, 2002; Semenchenko et al., 2007; Feniova et al., 2015). Under eutrophic conditions, in the fish treatments of our experiment, on days 30 and 50, diatoms of 50−100 μm dominated while in fish-free mesocosms, filamentous green algae >100 μm in size were the most abundant.

Therefore, fish reducing zooplankton control on small algae promoted the development of edible diatoms.

To conclude, the main driver of the dynamics of phytoplankton communities is likely the N : P ratio, which determined the different species and size structures of algal communities in M and E treatments at the beginning of the experiment. When the differences in N : P between the treatments were smoothed out, phytoplankton structure became similar, being represented by large filamentous attached algae. Hence, we can conclude that, in shallow lakes or inshore, the impact of small plankton algae will be replaced by more competitive larger green algae.

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Statement of the welfare of animals. This article does not contain any studies involving animals or human participants performed by any of the authors.

REFERENCES

Babanazarova, O.V., Kurmayer, R., Sidelev, S.I., Alexandrina, A.M., and Sakharova, E.G., Phytoplankton structure and microcystine concentration in the highly eutrophic Nero Lake, *Water Resour.*, 2011, vol. 38, no. 2, pp. 229–236.

Balushkina, E.V. and Vinberg, G.G., Dependence between length and weight of the body of planktonic crustacean and rotifers, in *Ekologo-fiziologicheskie osnovy izucheniya vodnykh ekosistem* (Ecological and Physiological Basis for the Analysis of Aquatic Ecosystems), Leningrad: Nauka, 1979, pp. 169–172.

Brabrand, A., Faafeng, B., Källqvist, T., and Nilssen, P.J., Can iron defecation from fish influence phytoplankton production and biomass in eutrophic lakes? *Limnol. Oceanogr.*, 1984, vol. 29, pp. 1330–1334.

Burns, C.W., The relationship between the body size of filter-feeding Cladocera and the maximum size of particle ingestion, *Limnol. Oceanogr.*, 1968, vol. 13, pp. 675–678.

Carrick, H.J. and Lowe, R.L., Benthic algal response to N and P enrichment along a pH gradient, *Hydrobiologia*, 1989, vol. 119–127, p. 179.

Cattaneo, A., Periphyton in lakes of different trophy, *Can. J. Fish. Aquat. Sci.*, 1987, vol. 44, pp. 296–303.

Chen, Y., Qin, B., Teubner, K., and Dokulil, M.T., Long-term dynamics of phytoplankton assemblages: *Microcystis*-domination in Lake Taihu, a large shallow lake in China, *J. Plankton Res.*, 2003, vol. 25, pp. 445–453.

Datsenko, Yu.S., *Evtrofirovanie vodokhranilishch. Gidrologo-gidrokhimicheskie aspekty* (Eutrophication of Reservoirs: Hydrological and Hydrochemical Aspects), Moscow: GEOS, 2007.

Declerck, S. and De Meester, L., Impact of fish predation on coexisting *Daphnia* taxa: a partial test of the temporal hybrid superiority hypothesis, *Hydrobiologia*, 2003, vol. 500, nos. 1–3, pp. 83–94.

Downing, J.A., Watson, S.B., and McCauley, E., Predicting Cyanobacteria dominance in lakes, *Can. J. Fish. Aquat. Sci.*, 2001, vol. 58, pp. 1905–1908. https://doi.org/10.1139/cjfas-58-10-1905

Feniova, I.Yu., Razlutskii, V.I., and Palash, A.L., The influence of raptorial behavior and competitiveness on the species structure of communities of Cladocera, *Biol. Vnutr. Vod*, 2007, no. 3, pp. 41–47.

Feniova, I., Dawidowicz, P., Gladyshev, M.I., Kostrzewska-Szlakowska, I., Rzepecki, M., Razlutskij, V., Sushchik, N.N., Majsak, N., and Dzialowski, A.R., Experimental effects of large-bodied *Daphnia*, fish and zebra mussels on Cladoceran community and size structure, *J. Plankton Res.*, 2015, vol. 37, pp. 611–625. https://doi.org/10.1093/plankt/fbv022

Feniova, I.Y., Petrosyan, V.G., Rzepecki, M., Kostrzewska-Szlakowska, I., Zilitinkevicz, N.S., Krylov, A.V., Majsak, N.N., Razlutskij, V.I., and Dzialowski, A.R., Experimental impacts of fish on small and large Cladocerans under eutrophic conditions, *Inland Water Biol.*, 2016, vol. 9, no. 4, pp. 375–381.

Fott, J., Desortova, B., and Hrbáček, J., A comparison of the growth of flagellates under heavy grazing stress with a continuous culture, *Proc. 7th Symp. "Continuous Cultivation of Microorganisms,"* Prague, 1980, pp. 395–401.

Gerrath, J.F., Conjugating green algae and desmids, in *Freshwater Algae of North America. Ecology and Classification*, Amsterdam: Elsevier, 2003, pp. 353–381.

Gliwicz, Z.M., On the different nature of top-down and bottom-up effects in pelagic food webs, *Freshwater Biol.*, 2002, vol. 47, pp. 2296–2312.

Gliwicz, Z.M., Ghilarov, A., and Pijanowska, J., *Food and predation as major factors limiting two natural populations of Daphnia cucullata Sars*, *Hydrobiologia*, 1981, pp. 80, vol. 205–218.

Havens, K.E., James, R.T., East, T.L., and Smith, V.H., N : P ratios, light limitation, and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution, *Environ. Pollut.*, 2003, vol. 122, no. 3, pp. 379–390.

Ilmavirta, V., Dynamics of phytoplanktonic production in the oligotrophic Lake Pääjärvi, southern Finland, *Ann. Bot. Fenn.*, 1975, vol. 12, pp. 45–54.

John, D.M., Filamentous and plantlike Green algae, in *Freshwater Algae of North America. Ecology and Classification*, Amsterdam: Elsevier, 2003, pp. 311–352.

Kolmakov, V.I. and Gladyshev, M.I., Growth and potential photosynthesis of cyanobacteria are stimulated by viable gut passage in crucian carp, *Aquat. Ecol.*, 2003, vol. 37, pp. 237–242.

Korinek, V., Fott, J., Fuksa, J., Lellak, J., and Prazakova, M., Carp ponds in Central Europe, in *Managed Aquatic Ecosystems*, Amsterdam: Elsevier, 1987, pp. 29–62.

Korneva, L.G., *Fitoplankton vodokhranilishch basseina Volgi* (Phytoplankton of the Volga River Basin), Kostroma: Kostromsk. Pechat. Dvor, 2015.

Kuz'min, G.V., Phytoplankton, in *Metodika izucheniya biogeotsenoza vnutrennikh vodoemov* (The Method of Analysis of Biogeocenosis of Inland Reservoirs), Moscow: Nauka, 1975, pp. 73–87.

Lampert, W., Fleckner, W., Rai, H., and Taylor, B.E., Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase, *Limnol. Oceanogr.*, 1986, vol. 31, pp. 478–490.

Levich, A.P. and Bulgakov, I.G., Biogenic elements in environment and phytoplankton: ratio of nitrogen to phosphorus as independent regulating factor, *Usp. Sovrem. Biol.*, 1995, vol. 15, no. 1, p. 13.

Lyashenko, O.A., Comparative analysis of planktonic algological flora from the Nero and Pleshcheevo lakes, *Bot. Zh.*, 2003, vol. 88, no. 3, p. 30.

McQueen, D.J. and Lean, D.R.S., Influence of water temperature and nitrogen to phosphorus ratios on the dominance of blue-green algae in Lake St. George, Ontario, *Can. J. Fish. Aquat. Sci.*, 1987, vol. 44, no. 3, pp. 598–604.

Naselli-Flores, L. and Barone, R., Phytoplankton dynamics and structure: a comparative analysis in natural and man-made water bodies of different trophic state, *Hydrobiologia*, 2000, vol. 438, pp. 65–74.

Negro, A.I., De Hoyos, C., and Vega, J.C., Phytoplankton structure and dynamics in Lake Sanabria and Val-

paraíso reservoir (NW Spain), *Hydrobiologia*, 2000, vol. 424, pp. 25−37.

Nixdorf, B., Mischke, U., and Rücker, J., Phytoplankton assemblages and steady state in deep and shallow eutrophic lakes—an approach to differentiate the habitat properties of Oscillatoriales, *Hydrobiologia*, 2003. V 502, pp. 111−121.

Petrosyan, V.G., RF Inventor's Certificate no. 2014663194, 2014. http://www1.fips.ru/fips_servl/fips_servlet?DB= EVM&DocNumber=2014663194&TypeFile=html.

Phytoplankton Analyzer PHYTO-PAM and Phyto-Win Software V. 1.45: System Components and Principles of Operation, Effeltrich: Heinz Walz, 2003.

Reynolds, C.S., Huszar, V., Kruk, C. Naselli-Flotes, L., and Melo, S., Towards a functional classification of the freshwater phytoplankton, *J. Plankton Res.*, 2002, vol. 24, no. 5, pp. 417−428.

Rosen, G., Phytoplankton indicators and their relations to certain chemical and physical factors, *Limnologica*, 1981, vol. 13, pp. 2263−2290.

Sakharova, E.G. and Korneva, L.G., Phytoplankton in the littoral and pelagial zones of the Rybinsk Reservoir in years with different temperature and water-level regimes, *Inland Water Biol.*, 2018, vol. 11, no. 1, pp. 6−12.

Schindler, D.W., Whole-lake eutrophication experiments with phosphorus, nitrogen, and carbon, *Verh. Int. Ver. Limnol.*, 1975, vol. 19, pp. 3221−3231.

Semenchenko, V.P., Razlutskij, V.I., Feniova, I.Yu., and Aibulatov, D.N., Biotic relations affecting species structure in zooplankton communities, *Hydrobiologia*, 2007, vol. 579, pp. 219−231.

Simons, J., Field ecology of freshwater macroalgae in pools and ditches, with special attention to eutrophication, *Neth. J. Aquat. Ecol.*, 1994, vol. 28, no. 1, pp. 25−33.

Standard Methods for the Examination of Water and Wastewater, Washington: Am. Publ. Health Assoc., 2005.

Trifonova, I.S., Phytoplankton composition and biomass structure in relation to trophic gradient in some temperate and subarctic lakes of northwestern Russia and the Pre-Baltic, *Hydrobiologia*, 1998, vols. 369−370, pp. 99−108.

Watson, S. and Kalff, J., Relationships between nanoplankton and lake trophic status, *Can. J. Fish. Aquat. Sci.*, 1981, vol. 38, pp. 960−967.

Wiśniewska, M., Krupa, D., Pawlik-Skowrońska, B., and Kornijów, R., Development of toxic *Planktothrix agardhii* (Gom.) Anagn. et Kom. and potentially toxic algae in the hypertrophic Lake Syczynskie (Eastern Poland), *Oceanol. Hydrobiol. Stud.*, 2007, vol. 36, pp. 173−179.

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