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Research Article

Effects of zebra mussels (*Dreissena polymorpha*) on phytoplankton community structure under eutrophic conditions

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Abstract

We conducted two mesocosm experiments to determine how invasive zebra mussels affected phytoplankton community and size structure in the summers of 2014 and 2017. Water containing natural phytoplankton and zooplankton communities was collected from the eutrophic Lake Mikołajskie (Masurian Lake District, northeastern Poland) and used to start each experiment. We analyzed how the introduction of zebra mussels impacted chlorophyll and the biomass of individual algae taxa, with particular interest on cyanobacteria. The starting phytoplankton communities differed in the two study years, whereby cyanobacteria dominated in 2014 and dinoflagellates and diatoms dominated in 2017. The biomass of crustacean zooplankton (cladocerans and copepods) was not affected by zebra mussels; therefore, we attributed differences in phytoplankton between treatments to the presence of zebra mussels. Zebra mussels had contrasting effects on cyanobacteria in the 2014 and 2017 experiments. In 2014, zebra mussels decreased cyanobacteria, while in 2017 they had a positive effect on cyanobacteria chlorophyll. The contrasting effects of zebra mussels on cyanobacteria could be related to differences in starting nutrient concentrations and phytoplankton communities between the two experiments. Filamentous green macroalgae dominated at the end of the both experiments in the zebra mussel treatments while they were not very abundant in the controls. Therefore, zebra mussels can have indirect negative effects on higher trophic levels even when they decrease cyanobacteria because they shift the autotrophic structure in favor of attached green macroalgae, which are a poor resource for zooplankton.

Key words: phytoplankton taxonomic and size structures, nutrients, *Dreissena*-cyanobacteria interactions, zooplankton

Introduction

The invasive zebra mussel, *Dreissena polymorpha* (Pallas, 1771), is an effective grazer that can significantly reduce algal biomass and provide a buffer against the increasing effects of nutrient enrichment on phytoplankton abundance (Dzialowski and Jessie 2009; Dzialowski 2013). Zebra mussels consume cells within the range of 0.7–80 µm and exhibit

maximum consumption efficiency on cells between 5–35 µm in diameter (Sprung and Rose 1988; White and Sarnelle 2014). A large body of research has shown that zebra mussels can reduce phytoplankton biovolume and shape phytoplankton community composition (Vanni 2002; Conroy and Culver 2005; Conroy et al. 2005). However, their effects on cyanobacteria have been inconsistent (Raikow et al. 2004; Sarnelle et al. 2005). Several studies of phytoplankton species composition before and after zebra mussel invasion have highlighted complex zebra mussel–cyanobacteria interactions. For example, the biomass of *Microcystis aeruginosa* (Kützing) Kützing in the Bay of Quinte in Lake Ontario increased dramatically after zebra mussel invasion, whereas the biomass of *M. aeruginosa* in the Hudson River declined after zebra mussel invasion (Sarnelle et al. 2005). Raikow et al. (2004) suggested that the effects of zebra mussels on cyanobacteria, specifically *Microcystis* spp., were nutrient dependent. They found that zebra mussels increased abundance of *Microcystis* spp. in invaded lakes with relatively low total phosphorus (TP) concentrations (< 25 µg/L), but there was no relationship between zebra mussels and *Microcystis* spp. in invaded lakes with relatively high TP concentrations (> 25 µg/L).

Negative effects of zebra mussels on phytoplankton are caused by strong grazing pressure, while positive effects can be caused by alteration of nutrient concentrations through zebra mussel excretion (Vanderploeg et al. 2017). Nicholls et al. (2002) found that total phytoplankton biomass did not respond to the introduction of zebra mussels in the Bay of Quinte (northeastern Lake Ontario), while cyanobacteria abundances increased. They suggested that this increase was due to the development of grazing-resistant forms of cyanobacteria. Results of enclosure experiments by Sarnelle et al. (2005) were consistent with these studies and additionally demonstrated that the effects of zebra mussels on cyanobacteria can be context dependent. When phosphorus concentrations were very low (mean total phosphorus [TP] ~ 3 µg L^{-1}), the effect of zebra mussels on the biomass of *M. aeruginosa* was monotonically negative across the full range of mussel densities in the enclosures. When phosphorus concentrations increased (mean TP ~ 9 µg L^{-1}), there was a monotonically positive effect of zebra mussels on *M. aeruginosa* across the same mussel gradient.

Zebra mussels excrete nutrients into the water column, especially phosphorus, (Arnott and Vanni 1996; Wilson 2003; Wojtal-Frankiewicz and Frankiewicz 2011; Feniova et al. 2018) which can favor cyanobacteria growth (Smith 1986; Watson et al. 1997). However, the success of cyanobacteria may be more dependent on the nitrogen:phosphorus (N:P) ratio rather than on phosphorus availability (Levich and Bulgakov 1995). A strong negative relationship has been found between cyanobacteria dominance and N:P ratios (Palus 2015). Studies in Lake St. George (Ontario) demonstrated that cyanobacteria were abundant at N:P ratio < 5, while they were rare at higher N:P ratios (McQueen and Lean 1987). As such,

zebra mussels have the potential to either increase (through alterations of nutrient concentrations and ratios) or reduce (through strong grazing pressure) total algal abundance. Sarnelle et al. (2012) postulated, based on experiments in an oligotrophic lake, that the effect of zebra mussels on *Microcystis* growth rate was positive at low P and negative at high P because its growth stimulation exceeded grazing mortality at low P and vice versa at high P.

The goal of this experiment was to determine how phytoplankton taxa and size structure responded to the presence of zebra mussels under eutrophic conditions. While much data has shown how total phytoplankton abundance responds to zebra mussels, less is known about how zebra mussels affect individual taxa including cyanobacteria. We performed mesocosm experiments where we manipulated the presence/absence of zebra mussels in two different years using water with natural plankton communities from the eutrophic Lake Mikołajskie (Masurian Lake District, northeastern Poland). Since the experimental conditions in the mesocosms were eutrophic, we anticipated that mussels would reduce phytoplankton abundance including cyanobacteria based on previous research (zebra mussels–cyanobacteria/phytoplankton interactions) (Sarnelle et al. 2012; Dzialowski et al. 2018). We also hypothesized that zebra mussels would alter phytoplankton taxonomic structure including the relative abundance of cyanobacteria.

Materials and methods

We conducted 30-day mesocosm experiments in June–July of 2014 and again in 2017 using similar methodologies. Unfiltered lake water for the experiments was collected from 1 m below the surface within the pelagic zone of the eutrophic Lake Mikołajskie (Masurian Lake District, northeastern Poland, 21°35′E; 53°48′N; area 498 ha, max. depth 26 m, mean depth 11 m; Chróst et al. 2009) using a submersible water pump (Kärcher SP 1 DIRT), which does not harm zooplankton. The mesocosms (internal dimensions 940 × 640 × 500 mm; 300 L operative volume) were placed on the shore of Lake Mikołajskie at the Research Station of the Nencki Institute of Experimental Biology, Polish Academy of Sciences.

The trophic state index (TSI), calculated from chlorophyll *a* concentrations according to Carlson (1977), indicated that trophic status in each mesocosm was eutrophic (TSI > 50) prior to the start of the experiments.

The experimental design consisted of two treatments, each with three replicates. Mesocosms in the control treatment (C) were filled with unfiltered lake water containing natural phytoplankton and zooplankton. A zebra mussel treatment (ZM) was created by adding 200 mussels (250 g wet weight/m^2) to each experimental mesocosm. The control and zebra mussel treatments for the two experiments were designated as C-2014 and ZM- 2014 for 2014 and C-2017 and ZM- 2017 for 2017. Zebra mussels for

the experiments were collected from the nearby eutrophic Lake Boczne. Similar densities of zebra mussel biomass have been reported in two Polish lakes (Licheńskie and Ślesińskie) where biomass ranged between 0.02 and 2.79 kg/m^2 (Sinicyna and Zdanowski 2007). The size range of zebra mussels used in the experiment was 7–24 mm. Zebra mussel mortality was monitored on each sampling date and did not exceed 3% by the end of the experiment. Some of the 2014 treatments were the same as in Feniova et al. (2018), but we analyzed different response variables (phytoplankton communities) and compared them between the two years in the current research.

Planktonic crustaceans were collected in the mesocosms with a 2.6-L Limnos sampler and then concentrated using a 30 µm mesh plankton net and preserved with 4% formaldehyde. At the end of the experiment, a larger volume of water (60 L) was sampled from each mesocosm. Crustaceans were identified to species and enumerated under a microscope. At least 10 individuals of each species were measured to determine the body length. Length:weight relationships were used to determine the biomass of crustaceans using Balushkina and Vinberg (1979).

Chlorophyll *a* concentrations were estimated at a 10-day interval using a PHYTOPAM fluorometer (Walz, Germany) that estimates chlorophyll concentration for three groups of algae individually (cyanobacteria, diatoms and dinoflagellates (brown algae), and green algae). We removed filamentous large algae from the samples and measured chlorophyll concentrations in 5 ml cuvettes. Thus, chlorophyll concentrations were only measured for potential edible algae < 100 µm.

The concentration of chlorophyll is generally considered to be the basic characteristic of phytoplankton photosynthetic activity and is determined from the physiological state of algae cells and environmental conditions (Roy 1988; Brunet et al. 1996; Felip and Catalan 2000). Therefore, we used chlorophyll concentrations (measured with the PHYTOPAM) as indicators of phytoplankton quantity to compare between treatments.

In addition, we collected samples of phytoplankton species including macroalgae just below the surface of each mesocosm on Days 1, 10 and 30 with a 0.5 L glass beaker after thoroughly mixing the water. Samples were preserved with a Utremel solution and 4% formaldehyde. Phytoplankton samples were concentrated by settling (Kuzmin 1975). Algae were counted and identified under a light microscope (Nikon Optiphot 2). Algal cell sizes were measured under a microscope using an ocular micrometer. Algae biomass was calculated based on cell sizes and their approximations to simple geometric shapes (Vinberg and Lavrenteva 1982; Mikheeva 1989). We divided phytoplankton into three size groups < 30, 30–80 and > 80 µm. The smallest size group is preferred by crustaceans (Sommer and Sommer 2006) and zebra mussels (Sprung and Rose 1988), while the largest size group is less likely to be consumed by zebra mussels (White and Sarnelle 2014).

Temperature and dissolved oxygen concentrations were measured daily from the center of each mesocosm using a WTW multi-parameter probe 3410 with optical sensor FDO925. Water samples were collected for nutrient analysis 4 times over the course of the experiment on Days 1, 10, 20 and 30. Samples were collected with a Limnos sampler (2.6 L) from the center of each mesocosm after they were gently mixed and then filtered through 0.22 µm millipore filters for the analyses of phosphates ($P\text{-}PO_4$), nitrate and nitrite nitrogen ($N\text{-}NO_3$, $N\text{-}NO_2$), and ammonium concentrations ($N\text{-}NH_4$) according to the analytical procedures described in APHA (2005). The total concentration of inorganic nitrogen was determined as the sum of nitrate, nitrite, and ammonium.

We used two-way ANOVA with Year (2014 and 2017) and Treatment (C – control; ZM – zebra mussels) as factors with Generalized Linear Models (GLM) to determine if there were significant differences between the starting conditions on Day 0 in the 2014 and 2017 experiments. If there was a significant year effect (i.e., response variables differed on Day 0 in the 2014 and 2017 experiments), we then conducted analysis for the 2014 and 2017 experiments separately. We constructed mixed GLMs to determine the effects of Treatment, Day and interactions on the dependent response variables. Treatment and Day (repeated measure) were specified as fixed factors, while Mesocosm (treatment) was randomly nested within treatments. Dependent parameters that were used to determine the effects of zebra mussels over the course of the 2014 and 2017 experiments included the nutrients (dissolved phosphorus, dissolved nitrogen, and N:P ratio), algae (brown and green algae, cyanobacteria, total algae), and zooplankton (cladocerans and copepods) response variables. If significant Treatment effects were detected, we used Fisher's test ($P < 0.05$) to determine which variables differed. Then we used sequential Bonferroni Post hoc tests ($P < 0.05$) to establish significant differences in variables over time, and for comparison of each dependent variable between treatments on individual sample dates. Interaction effects of Treatment × Day on the dependent variables over time and the results of sequential Bonferroni Post hoc comparisons are given in the Supplementary material Tables S1–S18.

We used GLMs two-way ANOVA to compare the biomasses of five phytoplankton taxonomic groups (TG) on Days 1 and 30 between C and ZM treatments and between taxonomic groups in the 2014 and 2017 experiments. We distinguished the following taxonomic groups: (1) diatoms and dinoflagellates (brown algae), (2) filamentous green algae (*Zygnema* sp., *Oedogonium* sp., *Mougeotia* sp.), (3) other green algae (mainly small green algae of the order Chlorococcales and rarely occurring algae of the orders Chlamydomonadales, Volvocales, Ulotrichales, Desmidiales), (4) cyanobacteria and (5) others (Cryptophyta, Xanthophyta and Chrysophyta). Factors in these analyses were Treatment, TG and the interaction between Treatment × TG. We also used Repeated Measure (RM) ANOVA mixed GLMs to compare

the biomasses of the most abundant filamentous cyanobacteria *Planktothrix agardhii* (Gomont) and *Limnothrix redekeii* (Van Goor) in the 2014 experiment on Days 10 and 30.

We did not measure the biomass of the different phytoplankton size classes on every sampling date. Therefore, we used two way ANOVA GLMs (factors = Treatment, Size class and the interaction between Treatment × Size class) to compare differences in each size class (< 30 µm, 30–80 µm, and > 80 µm) between control and zebra mussel treatments and between size classes on Days 1 and 30 in 2014 and 2017.

Statistical analyses were conducted using the integrated software Biosystem office (Petrosyan 2014) and R 3.3 (R Core Team 2017). The RStudio Desktop version 1.1.463 was used as an IDE for R language (https://www.rstudio.com/).

Results

There was a significant year effect for several of the response variables including dissolved phosphorus, dissolved nitrogen, brown and green algae, cyanobacteria, and total algae indicating that there were differences on Day 0 between the 2014 and 2017 experiments (Table 1, Figure 1). Dissolved phosphorus, brown algae, cyanobacteria and total algae were lower at the start of the 2017 experiment than they were at the start of the 2014 experiment, while in contrast green algae was higher at the start of the 2017 experiment. Because of these significant differences between the starting conditions in the two years, we analyzed the 2014 and 2017 experiments separately.

Zebra mussels in the 2014 experiment had a significant positive effect on dissolved phosphorus and brown and green algae (Table 2, Figure 2), while they decreased N:P ratios and cyanobacteria. Total algae was significantly lower in the ZM treatment than in the control, but on Day 30 only (Table 2, Figure 2).

Zebra mussels in the 2017 experiment had an overall positive effect on dissolved phosphorus, dissolved nitrogen and cyanobacteria, but an overall negative effect on total chlorophyll and brown algae (Table 3, Figure 3). Comparison of these results from the 2014 and 2017 experiments highlight the contrasting effects that zebra mussel had on several response variables including cyanobacteria and brown algae between the two experiments. Zebra mussel also decreased N:P ratios in 2014, but did not affect N:P ratios in 2017 (Table 3).

Zebra mussels did not have a significant effect on cladoceran or copepod biomass in either the 2014 or 2017 experiment (Tables 2–3, Figures 2–3).

Cyanobacteria were dominant phytoplankton group (Figure 4A, Table 4, Table S19) at the start of the experiment in 2014. Among cyanobacteria, the filamentous species *Limnothrix redekeii* and *Planktothrix agardhii* were the most abundant. The biomass of both species decreased during the experiment

Table 1. Results of the two-way ANOVA comparing the starting conditions (Day 0) between the 2014 and 2017 experiments. Factors in the analyses are Year and Treatment. C – control, ZM – zebra mussel treatment; *P*-values were determined using GLM. Significant effects are bolded (P < 0.05).

Effect	F-ratio	P-value
Phosphorus (mg L^{-1})		
Year	23.94	**<< 0.00**
Treatment (C, ZM)	3.44	0.16
Year × Treatment	2.74	0.14
Nitrogen (mg L^{-1})		
Year	5.61	**0.04**
Treatment (C, ZM)	0.90	0.37
Year × Treatment	0.05	0.84
N:P ratio		
Year	4.42	0.069
Treatment (C, ZM)	0.52	0.49
Year × Treatment	0.58	0.47
Brown algae (µg L^{-1})		
Year	754.8	**<< 0.01**
Treatment (C, ZM)	0.19	0.68
Year × Treatment	0.13	0.72
Green algae (µg L^{-1})		
Year	16.26	**0.004**
Treatment (C, ZM)	0.85	0.39
Year × Treatment	0.85	0.38
Cyanobacteria (µg L^{-1})		
Year	2084.5	**<< 0.01**
Treatment (C, ZM)	0.69	0.43
Year × Treatment	0.01	0.94
Total algae (µg L^{-1})		
Year	1211.5	**<< 0.01**
Treatment (C, ZM)	0.06	0.81
Year × Treatment	0.00	0.99
Cladocerans (mg L^{-1})		
Year	0.54	0.48
Treatment (C, ZM)	0.00	0.95
Year × Treatment	1.26	0.29
Copepods (mg L^{-1})		
Year	0.06	0.82
Treatment (C, ZM)	2.24	0.17
Year × Treatment	2.85	0.13

(Figures 4–5) as indicated by significant Day and zebra mussel effects (Table 5). The decrease was greater in the zebra mussel treatment than it was in the control. The greatest difference in cyanobacteria between the control and zebra mussel treatments was observed on Day 10. On Day 30, the biomass of *P. agardhii* was low and did not differ between the treatments, while the biomass of *L. redekeii* was greater in the control although its biomass was also relatively low. In contrast, on Day 30, the biomass of total filamentous green algae and other green algae was significantly higher in the zebra mussel treatment than in the control (Figure 4B). The greatest difference was found in filamentous green algae between the control and zebra mussel treatments.

The most abundant phytoplankton groups at the start of the 2017 experiment were dinoflagellates and diatoms (Figure 4C, Table 4, Table S19),

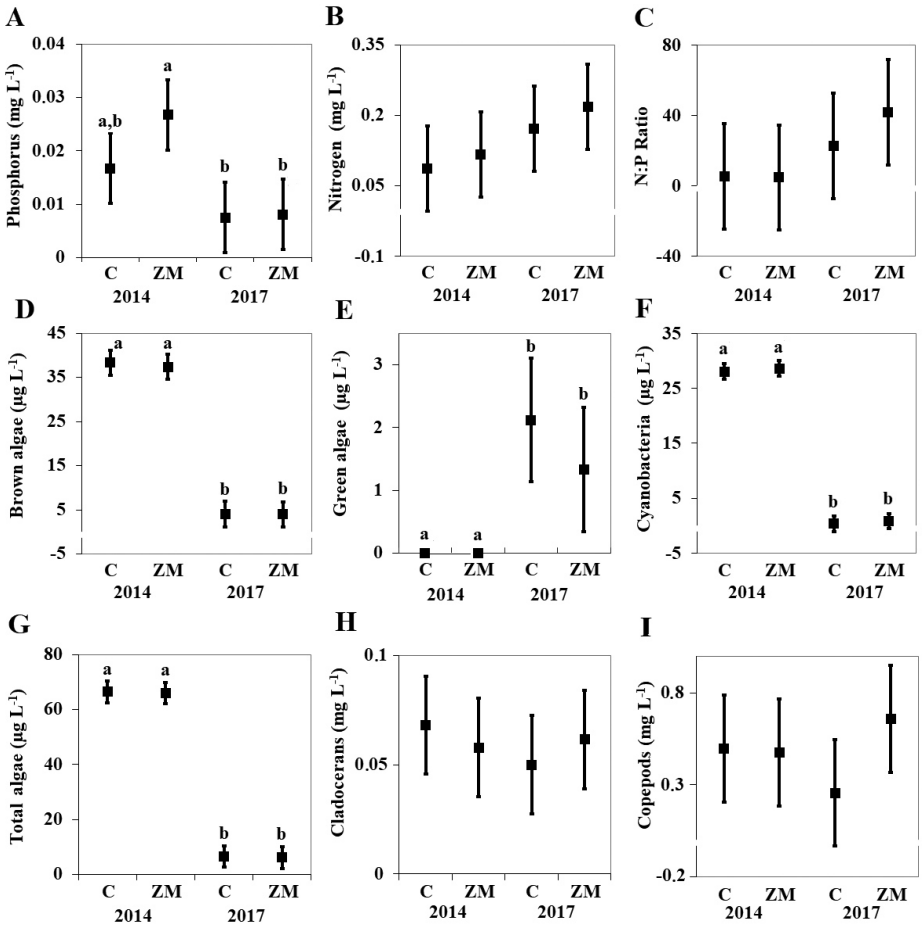

Figure 1. Comparison of mean response variables between treatments (C – control; ZM – zebra mussels) on Day 0 in the 2014 and 2017 experiments. Significant differences were determined using Bonferroni Post hoc test ($P < 0.05$). Error bars represent standard error of the mean. See Table 1 for statistical results from the two-way ANOVAs. Significant differences between 2014 and 2017 are depicted with the different letters.

while diatoms and filamentous greens were dominant at the end of the experiment. The biomass of filamentous green algae at the end of the experiment was also higher in the zebra mussel treatment than in the control (Figure 4, Table 4). Cyanobacteria were rare in the 2017 experiment. Among them, there were coccoid forms including *M. aeruginosa, Aphanothece clathrata* West & G.S. West, *Gloeocapsa* sp. Filamentous cyanobacteria *Pseudanabaena* sp. and *Oscillatoria* sp. appeared at the end of the experiments but they were < 4% of total algae biomass. There were no differences in cyanobacteria biomass between treatments. Non-filamentous green algae were significantly less in zebra mussel treatments than in control (Figure 4D).

Initially, the biomass of filamentous algae that were greater than 80 µm were significantly greater than the other size classes in 2014, while in 2017 the smaller phytoplankton (dinoflagellates and diatoms) fraction was greater (Table 6, Figure 6). Therefore, the size class (< 30 µm) that is more preferable for cladocerans (Sommer and Sommer 2006) was more abundant in 2017. At the end of the 2014 experiments, the small fraction (< 30 µm)

Table 2. Results of repeated measures ANOVA for nutrients (dissolved phosphorus, dissolved nitrogen, and N:P ratio), algae (brown and green algae, cyanobacteria, total algae), zooplankton (cladocerans and copepods) from the 2014 experiment. Treatment (C – control, ZM – zebra mussel treatment) and Day are Factors in the analyses which were carried out using mixed GLMs. *F* is Fisher's test, DF is degrees of freedom, and P is *P*-value. Significant factor effects are bolded (P < 0.05). Results of post hoc comparisons between treatments (Tables S1–S9) were determined using sequential Bonferroni test (P < 0.05).

Effect	Dissolved P (mg L^{-1})			Dissolved N (mg L^{-1})		N:P ratio	
	DF1/DF2	F	P	F	P	F	P
Treatment	1/8	17.0	**0.04**	0.01	0.94	9.71	**0.01**
Day	2/8	1.91	0.21	1.44	0.29	1.69	0.24
Treatment × Day	2/8	3.02	0.11	2.61	0.13	0.82	0.48
GLM (DF1/DF2 = 9/8)	F = 3.70; **P = 0.04**			F = 1.07; P = 0.47		F = 3.29; **P = 0.05**	
	Brown algae (µg L^{-1})			Green algae (µg L^{-1})		Cyanobacteria (µg L^{-1})	
Treatment	1/8	12.67	**0.007**	56.4	**<< 0.01**	95.2	**<< 0.01**
Day	2/8	2.73	0.1244	2.61	0.13	12.2	**<< 0.01**
Treatment × Day	2/8	2.11	0.1839	3.58	0.08	9.83	**<< 0.01**
GLM (DF1/DF2 = 9/8)	F = 3.40; P = 0.049			F = 11.75; P << 0.01		F = 17.12; P << 0.01	
	Total chlorophyll (µg L^{-1})			Cladocerans (mg L^{-1})		Copepods (mg L^{-1})	
Treatment	1/8	5.1	**0.05**	0.58	0.47	0.23	0.64
Day	2/8	2.07	0.19	1.56	0.27	3.76	0.07
Treatment × Day	2/8	2.77	0.12	0.40	0.69	2.80	0.12
GLM (DF1/DF2 = 9/8)	F = 3.11; P = 0.05			F = 1.12; P = 0.44		F = 2.46; P = 0.11	

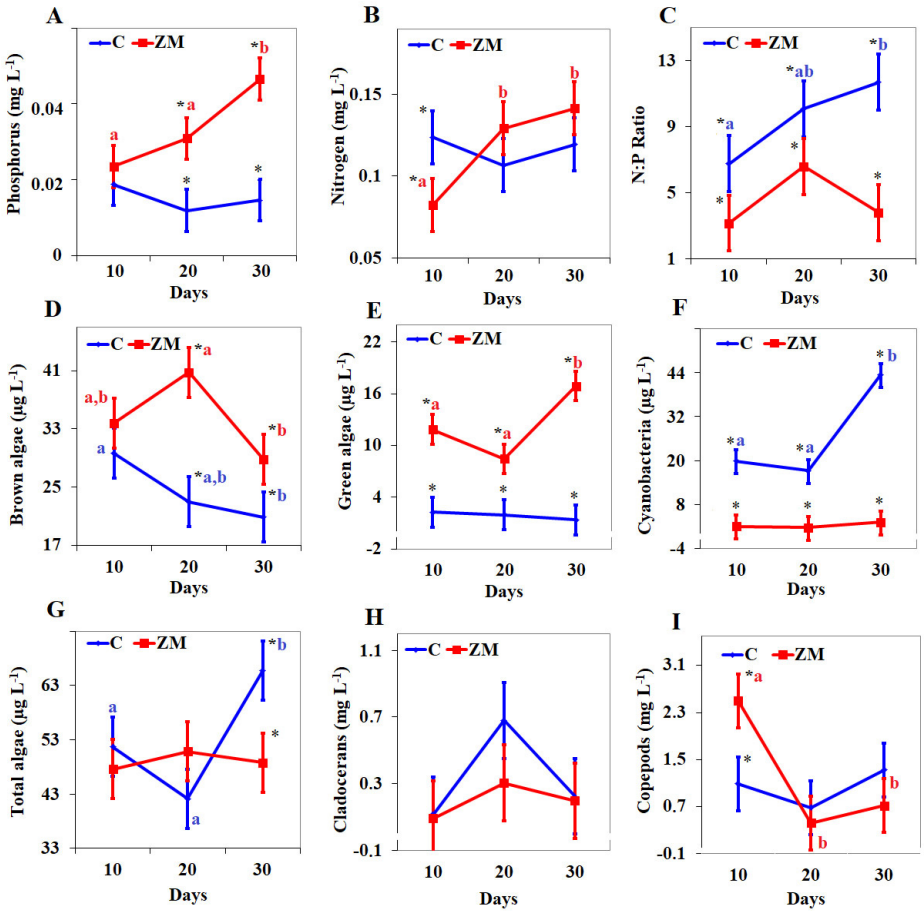

Figure 2. Comparison of mean response variables between experimental treatments (C – control; ZM – zebra mussels) over the course of 2014 experiment. Significant differences between treatments were determined using sequential Bonferroni test (P < 0.05). If a value of variable significantly differs between C and ZM treatments on the same date, it is designated by *. Significant differences between the dates are depicted by different letters. Results of post hoc comparisons of variables between dates and between treatments on each sampling date are given in Tables S1–S9.

Table 3. Results of repeated measures ANOVA for nutrients (dissolved phosphorus, dissolved nitrogen, and N:P ratio), algae (brown and green algae, cyanobacteria, total algae), zooplankton (cladocerans and copepods) from the 2017 experiment. Treatment (C – control, ZM – zebra mussel treatment) and Day are Factors in the analyses which were carried out using mixed GLMs. *F* is Fisher's test, DF is degrees of freedom, and P is *P*-value. Significant factor effects are bolded (P < 0.05). Results of post hoc comparisons between treatments (Tables S10–S18) were determined using sequential Bonferroni test (P < 0.05).

Effect	Dissolved P (mg L^{-1})			Dissolved N (mg L^{-1})		N:P ratio	
	DF1/DF2	F	P	F	P	F	P
Treatment	1/8	5.31	**0.05**	14.7	**0.01**	1.64	0.27
Day	2/8	0.05	0.95	0.09	0.91	0.08	0.92
Treatment × Day	2/8	0.56	0.59	0.02	0.97	1.01	0.41
GLM (DF1/DF2 = 9/8)	F = 3.29; **P = 0.051**			F = 3.45; P = 0.047		F = 0.70; **P** = 0.7	
	Brown algae (µg L^{-1})			Green algae (µg L^{-1})		Cyanobacteria (µg L^{-1})	
Treatment	1/8	5.17	**0.05**	2.93	0.13	8.9	**0.02**
Day	2/8	0.79	0.49	2.07	0.19	0.61	0.57
Treatment × Day	2/8	0.63	0.55	0.89	0.45	0.30	0.75
GLM (DF1/DF2 = 9/8)	F = 3.44; P = 0.05			F = 3.05; P = 0.07		F = 3.41; P = 0.05	
	Total algae (µg L^{-1})			Cladocerans (mg L^{-1})		Copepods (mg L^{-1})	
Treatment	1/8	5.59	**0.05**	0.27	0.63	4.91	0.06
Day	2/8	1.49	0.28	1.42	0.3	2.12	0.18
Treatment × Day	2/8	0.94	0.43	0.16	0.86	0.15	0.86
GLM (DF1/DF2 = 9/8)	F = 3.32; **P** = 0.05			F = 2.63; P = 0.09		F = 1.67; **P** = 0.24	

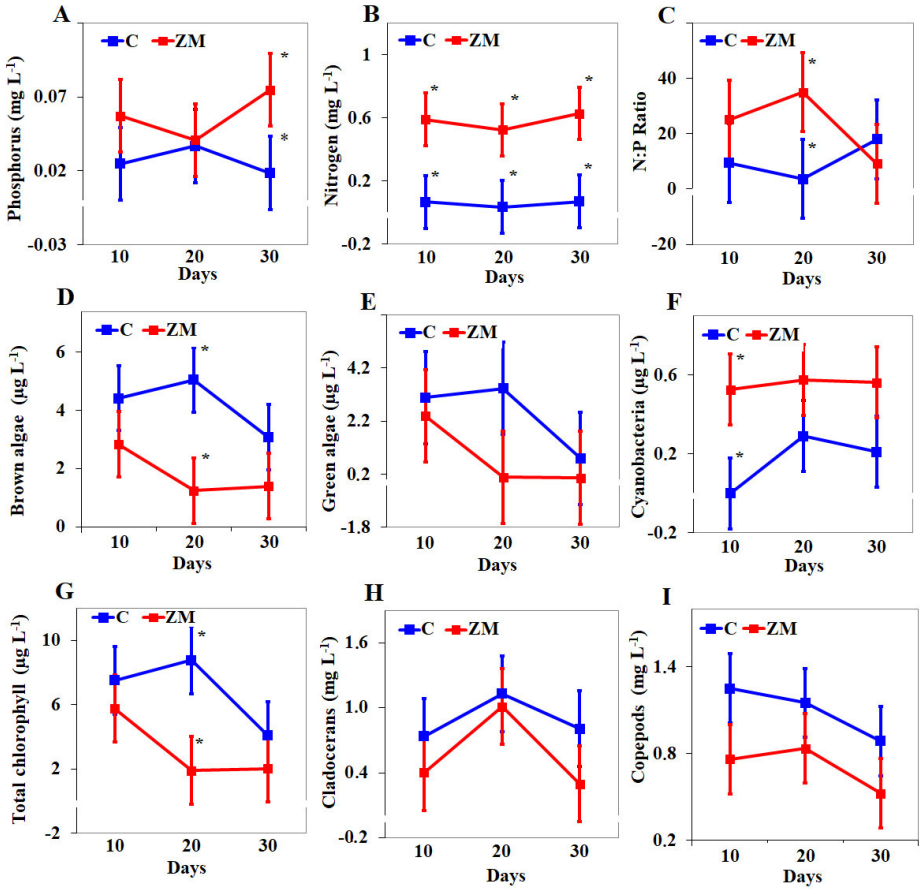

Figure 3. Comparison of mean response variables between experimental treatments (C – control; ZM – zebra mussels) over the course of 2017 experiment. Significant differences between treatments were determined using sequential Bonferroni test (P < 0.05). If a value of variable significantly differs between C and ZM treatments on the same date, it is designated by *. There were no differences between the dates. Results of post hoc comparisons of variables between dates and between treatments on each sampling date are given in Tables S10–S18.

Table 4. Results of GLMs two-way ANOVA for phytoplankton taxa on Days 1 and 30 in the 2014 and 2017 experiments. Treatment (C – control, ZM – zebra mussel treatment) and Day are Factors in this analysis. F is Fisher's test, DF is degrees of freedom. Significant effects are bolded (P < 0.05). Interactions plot between Treatment and Taxa are presented in Figure 4.

Effect	2014			2017	
	DF1/DF2	F	P	F	P
			Day 1		
Treatment	1/20	0.16	0.69	4.12	0.06
Taxa	4/20	7.96	**<< 0.001**	18.8	**<< 0.001**
Treatment × Taxa	4/20	1.93	0.15	1.42	0.26
GLM (DF1/DF2 = 9/20)	F = 4.41; P = 0.003			F = 9.6; **P << 0.001**	
			Day 30		
Treatment	1/20	17.0	**<< 0.001**	0.04	0.8
Taxa	4/20	14.8	**<< 0.001**	11.1	**0.001**
Treatment × Taxa	4/20	12.1	**<< 0.001**	4.04	**0.01**
GLM (DF1/DF2 = 9/20)	F = 13.9; **P << 0.001**			F = 6.74; **P << 0.001**	

and filamentous large green algae (> 80 μm) were significantly more abundant in zebra mussel mesocosms than in the control. In the 2017 experiment, the biomasses of all the size classes were similar and there were no differences between the control and zebra mussel treatments (Table 6, Figure 6).

Discussion

Zebra mussels did not affect the biomass of cladocerans and copepods in either the 2014 or 2017 experiments. Therefore, we attribute differences in phytoplankton between control and zebra mussels mesocosms to the presence of zebra mussels and not differences in zooplankton.

Phytoplankton individual taxa respond differently to environmental conditions, therefore, total chlorophyll may not always be the best indicator of environmental change. In contrast to zooplankton (Feniova et al. 2015, 2018), phytoplankton communities are more variable (Geider and La Roche 2002) and respond to a wider gradient of environmental factors (Sterner et al. 1997; Hessen et al. 2002). Responses of phytoplankton to different stressors can be measured not only in terms of the total phytoplankton abundance or total chlorophyll, but also in changes in phytoplankton taxonomic groups.

Zebra mussel–phytoplankton interactions can be complex. Although zebra mussels can decrease algal biomass (Dzialowski and Jessie 2009; Dzialowski 2013), some experimental and field studies did not show strong zebra mussel effects on total algal biomass (Nicholls et al. 2002; Sarnelle et al. 2005). However, this does not mean that zebra mussel did not affect algal assemblages. In the Bay of Quinte (Lake Ontario), the total phytoplankton biomass did not change after zebra mussel invasion, while the biomass of *M. aeruginosa* increased dramatically (Nicholls et al. 2002). In our experiments, phytoplankton changed in response to the introduction of zebra mussels mainly through changes in individual taxa. In particular, zebra mussels decreased cyanobacteria chlorophyll in the 2014 experiment, and increased cyanobacteria chlorophyll in the 2017 experiment relative to control mesocosms.

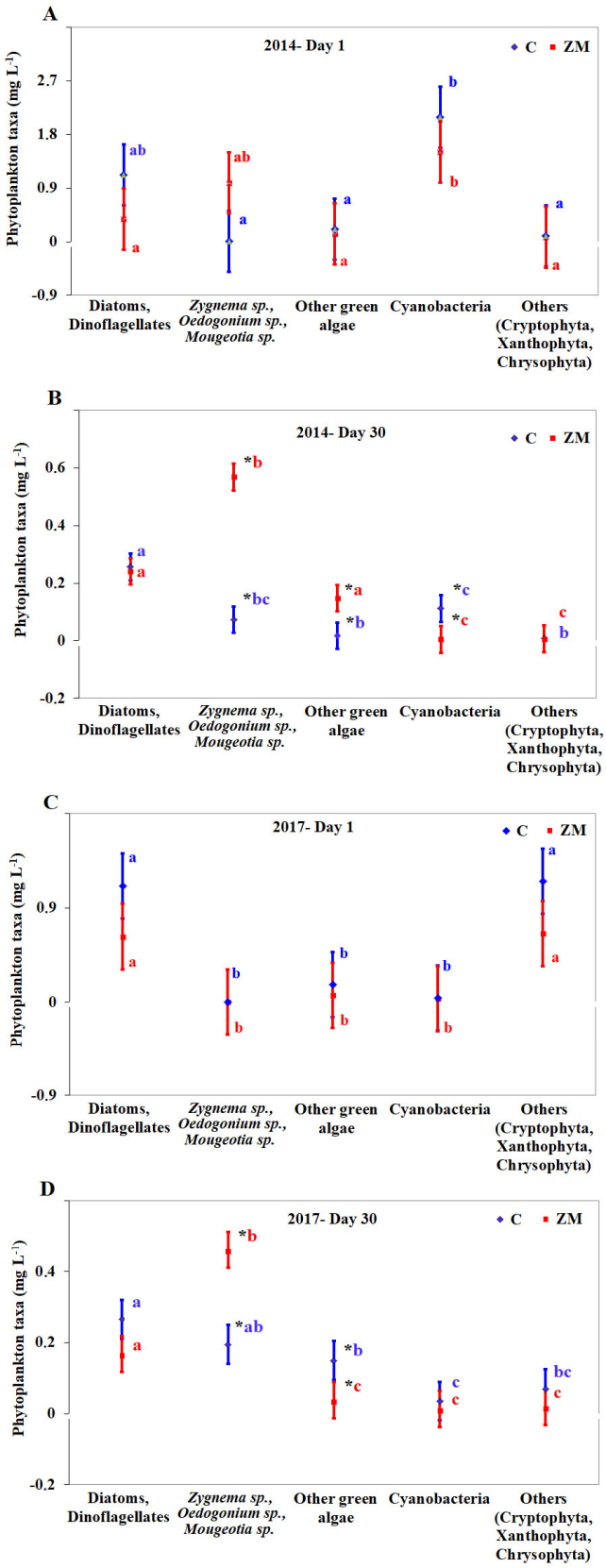

Figure 4. Comparison of mean biomasses of phytoplankton taxa on Days 1 and 30 between experimental treatments (C – control; ZM – zebra mussels), and between taxonomic groups in the 2014 and 2017 experiments. GLMs two-way ANOVA was used. Factors were Treatment, Taxa and interaction Treatment × Taxa. Data are presented as means with 95% Fisher's LSD intervals using Post hoc test. Significant differences between taxa are designated by different letters, but differences between treatments on each sampling date for the same taxa group are designated by symbol *.

Table 5. Results of repeated measures ANOVA for biomasses of *Limnothrix redekeii* and *Planktothrix agardhii* from the 2014 experiments. The analyses were carried out using mixed GLMs. Treatment (C – control, ZM – zebra mussel treatment) and Day are Factors in this analysis. F is Fisher's test, DF is degrees of freedom and P is *P*-value. Significant effects are bolded (P < 0.05). Results of post hoc comparisons between treatments using sequential Bonferroni test (P < 0.05) are presented in Figure 5.

Effect	*Limnothrix redekeii* (mg L^{-1})			*Planktothrix agardhii* (mg L^{-1})	
	DF1/DF2	F	P	F	P
Treatment	1/4	646.5	**<< 0.01**	540.4	**<< 0.01**
Day	1/4	640.0	**<< 0.01**	431.7	**<< 0.01**
Treatment × Day	1/4	613,6	**<< 0.01**	314.9	**<< 0.01**
GLM (DF1/DF2 = 7/4)	F = 271.84; **P << 0.001**			F = 190.9; **P << 0.001**	

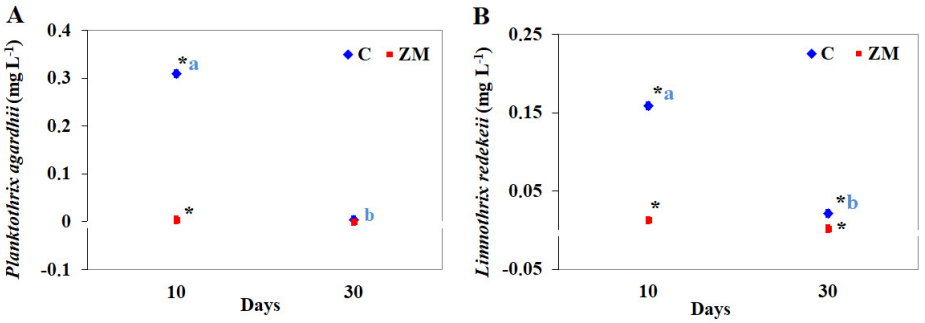

Figure 5. Comparison of mean biomasses of *Planktothrix agardhii* and *Limnothrix redekeii* between experimental treatments (C – control; ZM – zebra mussels) on Day 10 and 30 in the 2014 experiment. Mixed GLMs RM ANOVA was used. Factors were Treatment, Day and interaction Treatment × Day. Vertical bars indicate 95% of Bonferroni intervals. Different letters represent significant differences (sequential Bonferroni test, P < 0.05) between means of biomass over time. The differences between C and ZM are designated by *.

Contrasting effects of zebra mussel on cyanobacteria have also been reported by Raikow et al. (2004) who suggested that the effects of zebra mussel were nutrient dependent. They found that zebra mussels stimulated the growth of cyanobacteria at low TP concentrations, while they had no effect on cyanobacteria at high TP concentrations. In support, Sarnelle et al. (2005) showed that in experimental enclosures filled with water containing phytoplankton taken from the oligotrophic lake (Gull Lake, Michigan), the effects of zebra mussels on cyanobacteria were negative in 2000, but positive in 2001 across the same experimental gradient of zebra mussel densities. Similarly, we conducted our experiments with water from the same eutrophic lake, yet, the response of cyanobacteria to mussels differed by year. We attribute differences between the 2014 and 2017 experiments to differences in zebra mussel activity between the two years.

Excretion by zebra mussels can vary based on nutrient conditions, algae composition, or seston stoichiometry (Vanderploeg et al. 2017). Zebra mussels excrete less phosphorus or nitrogen in habitats with lower phosphorus or nitrogen, likely as an adaptive response to nutrient deficiency (Vanderploeg et al. 2002, 2017). Therefore, nutrient conditions can help to alter zebra mussel-phytoplankton interactions. We suggest that zebra mussels enriched the water with nutrients differently in the 2014 and 2017 experiments. This assumption is supported by differing effects of zebra mussels on nutrient concentrations. In particular, phosphorus concentrations

Table 6. Results of two-way ANOVA for biomasses of algal different size classes from the 2014 and 2017 experiments on Days 1 and 30. The analyses were carried out using mixed GLMs. Treatment (C – control, ZM – zebra mussel treatment) and Day are Factors in this analysis and *F* is Fisher's test, DF is degrees of freedom, and P is *P*-value. Significant effects are bolded (P < 0.05). Results of post hoc comparisons between treatments using sequential Bonferroni test (P < 0.05) are presented in Figure 6.

Effect	Biomass of algal size classes (mg L^{-1})				
	2014 – Day 1			2014 – Day 30	
	DF1/DF2	F	P	F	P
Treatment	1/12	0.12	0.73	5.3	**0.04**
Size classes	2/12	12.27	**0.001**	1.2	0.34
Treatment × Size classes	2/12	0.04	0.96	0.47	0.64
GLM (DF1/DF2 = 5/12)	F = 4.9; **P = 0.01**			F = 1.7; P = 0.2	
	2017 – Day 1			2017 – Day 30	
Treatment	1/12	1.6	0.23	0.40	0.54
Size classes	2/12	22.0	**<< 0.001**	1.17	0.34
Treatment × Size classes	2/12	2.7	0.11	0.86	0.45
GLM (DF1/DF2 = 5/12)	F = 10.2; **P << 0.001**			F = 0.9; P = 0.5	

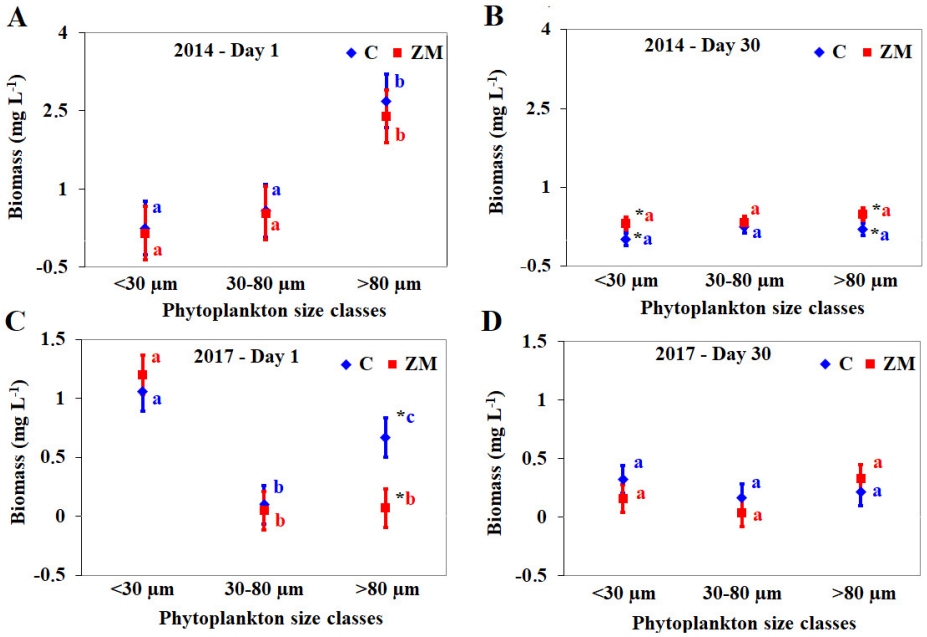

Figure 6. Comparison of mean biomasses of phytoplankton size classes on Days 1 and 30 in control (C) and zebra mussel (ZM) treatments in 2014 (A, B) and 2017 (C, D) experiments. The analyses were carried out using GLMs two-way ANOVA. Vertical bars are indicated with 95% Fisher's LSD intervals. Significant differences (Post hoc Fisher's LSD test, P < 0.05) between means of biomass on Days 1 and 30 were designated by different letters with different color, and significant differences between treatments on the same day are designated by *.

in the 2014 experiment were higher in the zebra mussel treatment than in the control, while nitrogen concentrations did not differ. In 2017, nitrogen concentrations in the zebra mussel treatment were higher than in the control, while phosphorus differed only on one date. Correspondingly, N:P ratios were lower in the zebra mussel treatment in 2014 relative to the control, while N:P ratios did not differ between the treatments in the 2017 experiment. Therefore, zebra mussels likely affected phytoplankton differently because the N:P ratio of their excretion differed in the two experiments. This is consistent with Vanderploeg et al. (2017) who stated that one of the advantages of zebra mussels over native mussels is their

ability to regulate nutrient excretion by altering their tissue stoichiometry. N:P ratios in the water can be even more essential for phytoplankton development than concentrations of each of these nutrients individually (Levich and Bulgakov 1995). Since zebra mussels had different effects on N:P ratios in the 2014 and 2017 experiments, phytoplankton taxonomic structure responded differently in the two years. Vanderploeg et al. (2017) suggested that zebra mussel effects on cyanobacteria were dependent on the balance between grazing and nutrient excretion. Sarnelle et al. (2012) explained that the contrasting effect of zebra mussels on cyanobacteria at low and high P loading occurred because cyanobacteria growth was stimulated by zebra mussel P excretion at low P, but grazing exceeded the effects of excretion at high P.

Interestingly, at the end of the experiments in both years, filamentous green macroalgae contributed the greatest percentage to the total biomass in the zebra mussel treatments, while their relative abundance in the controls was much less. Zebra mussels facilitated the growth of attached green algae *Mougeotia* sp., *Zygnema* sp., and *Oedogonium* sp. in the mesocosms, which are inedible to zebra mussels and zooplankton. Attached green algae require nutrients for their development and can compete with cyanobacteria. Cyanobacteria decreased in the zebra mussel treatment in the 2014 experiment, while attached green algae increased relative to the control. In 2017 experiment, cyanobacteria were rare and grazing on them was likely weak so that they were stimulated by zebra mussel nutrient excretion while remaining at a low biomass as indicated by the chlorophyll data.

Higher trophic levels integrate benthic and pelagic food webs (Hecky and Hesslein 1995; Vander Zanden et al. 2011). The distribution of primary production between benthic and pelagic energy pathways has a strong effect on the structure of lake food webs and ecosystem functioning (Vadeboncoeur et al. 2003). The term "autotrophic structure" was referred to as the partitioning of total ecosystem primary production between phytoplankton and benthic primary producers (Higgins et al. 2014; Karpowicz et al. 2019). Our results suggested that zebra mussels shifted the autotrophic structure in favor of periphyton green algae regardless of the phytoplankton structure before zebra mussel introduction. This can be caused by either active zebra mussel consumption of pelagic algae including cyanobacteria or the competitive ability of large greens. Green algae from the genera *Mougeotia* and *Oedogonium* are more competitive than pelagic phytoplankton (Schindler 1975; Carrick and Lowe 1989) due to their ability to form dense thickets that have large absorbing surfaces (Simons 1994; Gerrath 2003; John 2003). Our results are in accordance with results from other mesocosm experiments. For example, zebra mussels promoted the growth of attached algae in experimental mesocosms filled with water collected from a eutrophic reservoir (Dzialowski 2013) and colonial green

algae *Hydrodictyon reticulatum* (L.) bloomed due to zebra mussels in an experimental study (Wojtal-Frankiewicz and Frankiewicz 2011).

Similar effects of zebra mussels on autotrophic structure were reported in invaded lakes. The invasion of the zebra mussel into Oneida Lake, NY, was associated with increases in macrophyte densities (Zhu et al. 2006). Shifts to attached algae after the introduction of zebra mussels have been documented in a number of natural lakes. For example, the introduction of zebra mussels in Lake Erie, USA, caused the development of filamentous green algae *Cladophora* sp. (Davies and Hecky 2005). In Saginaw Bay, Lake Huron, the algal structure shifted to benthic filamentous green algae (*Spirogyra* sp., *Stigeoclonium* sp., *Cladophora* sp., and *Mougeotia* sp.) soon after the introduction of zebra mussels (Pillsbury et al. 2002). In a field study on energy flow that compared food webs in two Minnesota lakes, USA, zebra mussels had community-wide impacts on energy flow, with invertebrate predators and many species of fish increasing their reliance on littoral energy sources (McEachran et al. 2019). Nutrient excretion by zebra mussels may be an important factor leading to increased *Cladophora* in zebra mussel invaded lakes (Vanderploeg et al. 2017). Sarnelle et al. (2012) suggested that it may be possible to ameliorate the negative effects of zebra mussel invasion on water quality (i.e., promotion of cyanobacteria) by adding P; however, we believe that this has the potential to cause growth of large filamentous green algae that also have negative impacts on water quality.

A study on the relative contribution of carbon from coastal filamentous green algae *Cladophora glomerata* (L.) Kutz. and *Ulva intestinalis* L. in the coastal food webs in the Neva Estuary (Baltic Sea) showed that filamentous green algae were a poor organic carbon source for consumers and they were not incorporated into the food web (Golubkov et al. 2018). In the case of zebra mussels which induced increase in attached algae, the biomass of higher trophic levels (zooplankton and fish) will likely decline similarly to the situation in the Neva Estuary. We believe that zebra mussel introductions can create similar effects by promoting the development of green macroalgae in lakes.

Overall, individual phytoplankton taxa responded differently to zebra mussels in the two years of the experiment, even though the mesocosms were filled with water from the same eutrophic lake. Some taxa including cyanobacteria can respond differently to the introduction of zebra mussels likely depending on nutrient concentrations. Zebra mussels can alter nutrient concentrations and ratios by differentially excreting nutrients, thus facilitating changes in taxonomic phytoplankton structure. In eutrophic conditions, zebra mussels can alter the autotrophic structure to favor of attached green macroalgae. Even if the introduction of zebra mussels results in decreased cyanobacteria abundance, they have the potential to deteriorate food resources for higher trophic levels by facilitating the growth of green macroalgae which are a poor resource for zooplankton.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Post hoc comparisons of dissolved phosphorus (P) in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S2. Post hoc comparisons of dissolved nitrogen (N) in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S3. Post hoc comparisons of N:P ratio in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S4. Post hoc comparisons of brown algae in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S5. Post hoc comparisons of green algae in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S6. Post hoc comparisons of cyanobacteria in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S7. Post hoc comparisons of total algae in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S8. Post hoc comparisons of cladocerans in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S9. Post hoc comparisons of copepods in each treatment over time (top) and between treatments on each sampling date (bottom) in 2014. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S10. Post hoc comparisons of dissolved phosphorus (P) in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S11. Post hoc comparisons of dissolved nitrogen (N) in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S12. Post hoc comparisons of N:P ratio in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S13. Post hoc comparisons of brown algae in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S14. Post hoc comparisons of green algae in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S15. Post hoc comparisons of cyanobacteria in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S16. Post hoc comparisons of total algae in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S17. Post hoc comparisons of cladocerans in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S18. Post hoc comparisons of copepods in each treatment over time (top) and between treatments on each sampling date (bottom) in 2017. Different letters represent significant differences (sequential Bonferroni, $P < 0.05$).
Table S19. Species composition and average biomass in phytoplankton: C-2014-1 and C-2014-30 are Day 1 and Day 30 respectively in the control in 2014; ZM-2014-30 is Day 30 in zebra mussel treatment in 2014; C-2017-1 and C-2017-30 are Day 1 and Day 30 respectively in the control in 2017; ZM-2017-30 is Day 30 in zebra mussel treatment in 2017.

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