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Experimental effects of zebra mussels on crustacean communities under eutrophic conditions

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SUMMARY

Introduction

Zebra mussels are efficient filter feeders and the sizes of food particles that they consume overlaps with those of crustaceans. A large body of research has shown that zebra mussels can reduce algal biomass for crustaceans (Karatayev *et al*., 1997, 2002; Vanderploeg *et al*., 2002; Kelly *et al*., 2010). Experimental studies showed high selectivity of zebra mussel grazing (Baker *et al*., 1998, 2000). Zebra mussels can also promote cyanobacteria which are of poor nutritional quality, especially in systems with low trophy (Raikow *et al*., 2004). Therefore, introduction of zebra mussels has the potential to strongly influence algal nutritional quality in terms of elements (mainly studied as carbon [C], nitrogen [N], and phosphorus [P]) and/or polyunsaturated fatty acids (PUFA, mainly studied as eicosapentaenoic acid [EPA]). For example, experimental studies in mesocosms under mesotrophic conditions showed that zebra mussels increased the phosphorus content of the seston thus favoring the development of large *Daphnia* species (Feniova *et al.*, 2015). In support, a number of studies have shown that zebra mussels excrete nutrients, including phosphorus, into the water column (Wilson, 2003; Wojtal-Frankiewicz & Frankiewicz, 2011). In contrast, zebra mussels reduced the content of EPA in mesotrophic mesocosms (Feniova *et al*., 2015), ~~a~~nd they have been shown to selectively consumed EPA-rich seston (Makhutova et al., 2013). -Therefore, zebra mussels can potentially suppress crustaceans through food quantity as well as through food quality.

If zebra mussels alter the nutritional quality of algal resources, this could have important implications for crustaceans. For example, zooplankton can exhibit reductions in growth and reproduction when there is a mismatch between algal elemental quality and/or EPA and the body requirements of individual taxa (Urabe & Sterner, 1996; Hessen & Andersen, 2008). For example, copepods typically sequester more nitrogen in their tissue (Elser & Urabe, 1999) while cladocerans sequester more phosphorus relative to nitrogen (Sterner & Elser, 2002; Johnson & Luecke, 2012). Cladocerans such as *Daphnia* spp., which have low body N:P (Andersen & Hessen, 1991), tend to occur in lakes with low seston N:P (Hassett *et al* ., 1997). Conversely, copepods, with higher body N:P (Andersen & Hessen, 1991; Carrillo, Reche & Cruz-Pizarro, 1996; Villar-Argaiz *et al*., 2000) tend to appear in lakes with high seston N:P (Hassett *et al*., 1997).

There also appear to be differences in nutritional quality between large and small-bodied zooplankton (Andersen & Hessen, 1991). Large-bodied species are more likely to be successful when carbon is limiting because they are more effective filterers than small-bodied

species (Brooks & Dodson, 1965; Gliwicz, 2003; Sikora & Dawidowicz, 2014). However, large-bodied species may be more vulnerable to phosphorus limitation because phosphorus is used for somatic growth (Sterner & Schulz, 1998). Sikora, Dawidowicz & von Elert (2014) also showed that small-bodied *Daphnia* species were less vulnerable to temperature related decreases in algal quality than large-bodied species in terms of EPA. Results of their experiments with several species of *Daphnia* and their clones varying in body size showed that the saturation threshold for EPA-dependent growth increased with increasing species and/or clone body size (Sikora *et al*., 2016). Combined, these studies suggest that zebra mussel have the potential to modify crustaceans through bottom-up effects on the nutritional quality (e.g., C:N:P ratio and PUFAs) of algae.

We conducted a mesocosm experiment under eutrophic conditions where we manipulated the presence/absence of zebra mussels to determine how they influenced algal food quality and quantity and the community structure of crustaceans. Under eutrophic conditions, carbon is unlikely to be a limiting factor while phosphorus or EPA could be in shortage. Therefore, we hypothesized that zebra mussels would alter algal composition and nutritional quality for crustaceans with respect to dominance by cyanobacteria, C:N:P stoichiometry and/or EPA concentrations. We anticipated that small- and large-bodied cladoceran species would respond differently to changes in algal quality and quantity. Therefore, we also added large-bodied *Daphnia* to the mesocosms to test the hypothesis that zebra mussels positively influence their ability to establish by altering algal quality. Finally, we conducted a concurrent life table experiment where crustaceans were grown in water from the different mesocosms treatments to determine how zebra mussels affected algal structure and individual crustacean life history characteristics.

Methods

Mesocosm setup

We conducted our experiments in 12 mesocosms (0.94 ×0.64 ×0.50 m; 300 L, food safe, high density polyethylene (HDPE) containers) from 26 June to 18 August, 2014 (54 days total). The mesocosms were located on the shore of Lake Mikołajskie (Mazurian Lake District, northeastern Poland, 21°35′E, 53°48′N) at the Hydrobiological Station of the Nencki Institute of Experimental Biology, Polish Academy of Sciences. The mesocosms were filled with unfiltered water from the eutrophic Lake Mikołajskie (Chróst, 2009) that contained *in situ* phytoplankton, microzooplankton (rotifers, nanoflagellates, and ciliates) and mesozooplankton that were the source of mineral and organic forms of nutrients (Eccleston-

Parry & Leadbeater, 1995; Dolan, 1997; Ejsmont-Karabin *et al*., 2004). The cladoceran community that was added to the mesocosms from Lake Mikołajskie included *Chydorus sphaericus, Bosmina coregoni, Bosmina longirostris, Ceriodaphnia pulchella* and *Diaphanosoma brachyurum*. The copepod community included *Eudiaptomus gracilis, Eudiaptomus graciloides, Mesocyclops leuckarti, Thermocyclops oithonoides, Thermocyclops crassu*.

Experimental treatments

We established 4 treatments by manipulating the presence of alien large-bodied zooplankton and zebra mussels in a 2×2 factorial design. Each treatment was replicated in triplicate mesocosms. The treatment with unfiltered lake water only served as the control (C). The introduced alien zooplankton (Z) treatment was established by adding two large-bodied cladoceran species that were reared in laboratory cultures: *Daphnia magna* Straus (originated from Binnensee, Germany) and *Daphnia pulicaria* Forbes (originated from Lake Brome, Canada). *Daphnia magna* and *D. pulicaria* are not found in Lake Mikołajskie; therefore, they were alien to the zooplankton communities that were used to fill the mesocosms. We added both *D. magna* and *D. pulicaria* to mesocosms in the Z treatments at densities of 1.0 ind. L^{-1} for each species at the beginning of the experiment on Day 1. The zebra mussel (M) treatment was established by adding zebra mussels at a wet weight of 250 g/m^2, or approximately 200 individuals per mesocosm. Similar levels of zebra mussel biomass have been reported in two Polish lakes (lakes Licheńskie and Ślesińskie) where biomass ranged from 0.02-2.79 kg/m^2 (Sinicyna & Zdanowski, 2007). The zebra mussels were collected from nearby Lake Boczne and transported to the field station in coolers and added to the mesocosms within 24 hours of collection on Day 1 of the experiment. The size range of 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.

Water quality analysis

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 analyses of nutrient concentrations 4 times over the course of the experiment (on Days 1, 4, 24 and 54). Samples were collected with a Limnos sampler

(2.6 L) from the center of each mesocosm after they were gently mixed 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 Standard Methods (2005).

Biological analysis

Water samples were also collected (2.6 L Limnos sampler) from the center of each mesocosm after they were gently mixed for the analysis of chlorophyll concentrations and zooplankton identification and enumeration (on days 1, 4, 14, 24, 34, 44, and 54). Chlorophyll concentration was estimated using a PHYTOPAM fluorometer (Walz, Germany) which estimates total chlorophyll concentrations for three groups of algae individually (cyanobacteria, brown (mostly diatoms), and green algae). Zooplankton samples were preserved in a 4% formaldehyde solution and all crustaceans were identified to species. We also measured the lengths of up to 100 individuals of each taxon for biomass estimates based on length:weight relationships from Balushkina & Vinberg (1978).

Rotifers, nanoflagellates and ciliates were collected with a 1 L sampler from the center of each mesocosm. Rotifers were concentrated using a 30 μm mesh net and preserved in Lugol's solution and 4% formalin. We used length measurements (~10-25 inds./species) to estimate rotifer biomass using length:wet weight relationships (Ejsmont-Karabin, 1998). Nanoflagellates (NF) were fixed with formaldehyde (final concentration 2%), stained with DAPI (Porter & Feig, 1980), filtered through 0.8 μm pore size polycarbonate membrane filters and enumerated by epifluorescence microscopy (Nikon Optiphot 2). The NF biovolume was calculated from measurements of cells size and their approximations to simple geometric forms. Ciliate samples were fixed with Lugol's solution and then examined with a light microscope (Nikon Optiphot 2). Biovolume was calculated from measurements of cell dimensions and simple geometric shapes. Species identifications of ciliates were based mainly on Foissner *et al.* (1991–1995).

Bio-chemical analyses

We collected seston (all the particles and live organisms that passed through a 115 μm mesh sieve) and cladocerans on the first and final (Day 54) days of the experiment for elemental and fatty acid analyses. In particular, we were interested in determining how zebra mussels

affected seston quality. Therefore, we analyzed seston at the starting point just after taking it from Lake Mikołajskie and at the end of the experiments from the C, M, MZ treatments. We focused on these three treatments specifically because large alien species did not develop in the Z treatments; therefore, there was not an effect of the alien *Daphnia* on seston quality and the Z treatments was similar to control for all response variables that were measured in this study (see Results below). For seston analysis, we collected 7–15 L of water from each mesocosm and filtered it onto precombusted glass-fiber GF/F filters (Whatman, USA). The filters for fatty acid analysis were dried at ambient temperature for about 30 minutes, and then placed into vials containing 3 mL of chloroform-methanol (2:1, v/v) and stored at -20°C until further analysis. Filters for organic carbon and nitrogen were dried at 75°C overnight and stored dry in a desiccator until further analyses. The samples for particulate phosphorus were filtered onto membrane filters (Vladipor, Mytischi, Russia, pore size 0.75–0.85 μm) and kept wet at 4°C.

Live individuals of three dominant species *D. magna* (100–150 ind.), *D. pulicaria* (100–150 ind.) and *C. pulchella* (200–300 ind.) were collected from the zooplankton samples for elemental and fatty acid analyses. The cladocerans were kept in filtered water from their respective mesocosms for several hours before the analyses to allow them to empty their guts. Animals were then collected onto a mesh sieve and placed on filter paper to remove the surface moisture, and then they were subsampled for fatty acid analyses. The sample sizes ranged in 8–20 mg and 4–10 mg of wet weight for fatty acid and organic carbon analyses, respectively. The fatty acid subsamples were then transferred into a chloroform-methanol mixture and frozen.

The procedure for fatty acid analyses of the seston and cladocerans is described in detail elsewhere (Gladyshev *et al*., 2015). Briefly, lipids from the seston and cladocerans were extracted by chloroform-methanol (2:1, v/v). Prior to the extraction, a known volume of an internal standard solution (free 19:0 in chloroform, 0.5 mg mL^{-1}) was added to the samples. The total lipid extract was methylated in a mixture of methanol-sulfuric acid (20:1, v/v) at 85°C during 2 h. Fatty acid methyl esters (FAMEs) were analyzed and identified using a gas chromatograph-mass spectrometer (model 6890/5975C, 'Agilent Technologies', USA) equipped with a 30 m long, 0.25 mm internal diameter capillary column HP-FFAP (Gladyshev *et al*., 2014).

We have used a common shorthand notation for fatty acids of the form A:Bn-X, where A represents the number of carbon atoms in the molecule, B gives the number of double

carbon-carbon bonds and X gives the position of the double bond closest to the terminal methyl group. Organic carbon (C) and nitrogen (N) were measured using a Flash EA 1112 NC Soil/MAS 200 elemental analyzer (ThermoQuest, Milan, Italy), as described in Gladyshev *et al*. (2007). Calibration curves for the elemental analyzer were generated using aspartic acid and standard soil reference material. Contents of particulate total phosphorus (P) were estimated following the conventional photocolorimetric method (Murphy & Riley, 1962). The background P content of the filters was preliminarily measured and subtracted from the sample values.

Life-table-experiments

Life-table experiments were conducted to determine how demographic parameters of the alien species (*D. magna*, and *D. pulicaria*) and a dominant small-bodied cladoceran species from the initial zooplanton community (*C. pulchella*) changed under indirect effects of zebra mussels via modification of phytoplankton composition and abundance. We did not want to disturb the mesocoms in the experiment described above, therefore, we set up four additional mesocosms to obtain water for the life-table experiments. Two mesocosms were established without zebra mussels (i.e. the same as the control) and two were established with zebra mussels (i.e. the same as the MZ treatment) exactly as described above. Life table experiments were performed simultaneously with the mesocosm experiment.

Life-table experiments were conducted using a flow through system with 500 mL bottles. To start the experiment, 20 to 30 new born individuals (less than 24 hours) of each species were placed into bottles separately. Each species was grown in monoculture in triplicate bottles in both waters with and without zebra mussels for a total of 6 bottles for each species. The bottles were filled with water that was collected from the mesocosms and then filtered through the sieve with a mesh size 50 μm to remove crustaceans and other large material. The flow through system was designed so that the entire volume of each bottle was replenished twice a day (e.g. 1 L flow through per day) to ensure that resource abundance was similar to that in the mesocsoms. We collected the following parameters every 2 days from the start of the experiment until approximately the third clutch: the total number of individuals of each species, clutch sizes, the time of maturation. We limited our observations to the third clutch because previous studies on cladoceran life-histories have shown that later clutches contribute negligibly to population growth rate (*r*) (Pijanowska *et al.*, 2006; Porter, Feig & Vetter, 1983). We continued to collect data from the bottles over the course of two

generations of each species. The experiments with the first generation were conducted starting on Day 1 and the second generation after Day 24, which was the day when generations of each species reached the third clutch so these two generations did not overlap.

Life table experiments were used to calculate population growth rate: $r = \ln\{\Sigma l(x)m(x)\}/T$, where $l(x)$ and $m(x)$ were the age of survival and fecundity, respectively, and T was the mean generation time.

Statistical analyses

Since water quality and biological parameters in the mesocosms were measured 3 times (nutrients) or 6 times (biomass of crustaceans and microzooplankton, chlorophyll concentrations) two-ways repeated-measures of variance ANOVA (RM-ANOVA) were used where treatment and time as the two factors. With respect to treatment, we analyzed three levels including C, M and MZ. We excluded the Z treatment from the analyses because *Daphnia* species failed to develop in this treatment and individuals that were added were only observed at the start of the experiment. Therefore, we believe that the Z treatment did not affect zooplankton dynamics in the mesocosms. In contrast, *Daphnia* did successfully establish in the MZ treatment; therefore, we considered the M and MZ treatments in the analyses.

If the data properties of symmetry according to Mauchley's criterion were violated in the RM-ANOVA, the degrees of freedom of the *F*-test for Time and Time*Treatment factors were adjusted using epsilon Greenhouse-Geisser corrections. If *P* in the Mauchley's test was less than 0.05, we did corrections of the degrees of freedom for the *F*-test. If significant treatment effects were detected with RM-ANOVA, we used Tukey's HSD post hoc test ($P < 0.05$) to determine which means differed. We also analyzed the effects of the two factor combination (Time*Treatment) to determine whether the Treatment factor was dependent on time. If the combined effects of two factors was insignificant, we assumed that there was no interaction effect between the two factors and that their effects were additive.

Since data on water quality and biological parameters did not meet the requirements of Leven criterion such as dispersion homogeneity of data and that the combined effects of two factors were not additive, we made log-transformation of the data to adjust them for statistical analysis. The figures of biological parameters dynamics were also made for log-transformed data to make them correspond to statistical results. RM-ANOVA analysis was conducted using Statgraphic XVII.II software.

Data on the juvenile development time violated the conditions of randomnicity of measurements and equality of variances, thus we could not use parametric one-way ANOVA of variance. Therefore, juvenile development time between *D. magna, D. pulicaria* and *C. pulchella* and between control and zebra mussel treatments for two generations were performed using nonparametric one-way ANOVA of variance on the basis of rank values according to the Kruskal-Wallis test (KW). If KW showed significance difference between means, we performed multiple Bonferroni post hoc procedure ($P<0.05$) to determine which means were significantly different. Statistical analysis of experimental data using one factor ANOVA was performed using the integrated software Biosystem office (Petrosyan, 2014).

We used one-way ANOVA to compare values of the food quality indicators (C:N:P and EPA) of seston and zooplankton. We used one-way ANOVA for these analyses because we only collected these data from select treatments (C, M and MZ) on the final sample date. In the absence of normal distribution (Kolmogorov-Smirnov one-sample test for normality D_{K-S}), Kruskal-Wallis test was used. The number of all variables (3 replicates × 4 treatments) was equal to 12, since we compare the whole data set rather than pairs of variables. Fatty acid composition of dominant cladoceran species was compared using principal component analysis (PCA). The calculations were carried out using STATISTICA software, version 9.0 (StatSoft, Inc.).

In order to analyze the linear relationships between total chlorophyll concentrations and the biomass of small cladocerans, *Daphnia* and copepods, we evaluated Pearson's correlation coefficients, and conducted two-tailed hypothesis test of these coefficients using Fisher's z –transformation.

For the life table experiment we used parametric one-way ANOVA to compare parameters including clutch sizes and population growth rate between *D. magna, D. pulicaria* and *C. pulchella* in the control and zebra mussel treatments for each species during the first and second generations. If *F* (Fisher's test) gave significant difference between the means, multiple Tukey's HSD post hoc tests ($P<0.05$) were used to determine which means were significantly different.

Results

Mesocosm experiments

Phosphorus ($P\text{-}PO_4$) and nitrogen concentrations (sum $N\text{-}NO_3$, $N\text{-}NO_2$ and $N\text{-}NH_4$) were significantly greater in the zebra mussel treatments (M and MZ) than they were in the control (Table 1, Fig. 1). The greatest differences between the control and zebra mussel treatments

were observed during the middle of the experiment for both nutrients. There were no significant differences between the M and MZ treatments for either nutrient.

Concentrations of green algae were significantly higher, while concentrations of cyanobacteria were significantly lower, in the zebra mussel treatments compared to the control (Table 1, Fig. 2). Concentrations of brown algae were significantly higher in zebra mussel treatments only after day 24 of the experiment. Total chlorophyll concentrations were not affected by zebra mussels and did not differ between the treatments (Table 1, Fig. 2 g, h).

Copepods, cladocerans, and small bodied species did not differ between the treatments and the control (Fig. 3 a, b, c, d, e, f). However, there were significant time effects for these variables (Table 1). There was a gradual increase in cladoceran biomass over the course of the experiment regardless of treatment. The biomass of *Daphnia* was significantly greater in the ZM treatment than it was in the Z treatment (Table 1, Fig. 3 g, h). *Daphnia* biomass increased in the ZM treatment, while it decreased in the Z treatment until day 24, after which no *Daphnia* were observed in this treatment. Furthermore, no *Daphnia* neonates were observed in the mesocosms from the Z treatment at any time during the experiment.

Microzooplankon biomass was the highest at the beginning of the experiments and gradually decreased in all the treatments (Fig. 3 i, j). There were no significance differences between microzooplankton in the zebra mussel treatments and the control, although the *P*-value was close to being significant (P=0.058) (Table 1).

Chlorophyll concentrations were not significantly correlated with the abundance of either copepods or *Daphnia* (Table 2). However, there was a significant negative correlation between total chlorophyll and the biomass of small species in the control and Z treatments (Table 2).

Nutritional quality of seston

Concentrations of eicosapentaenoic acids (EPA, 20:5n-3) were significantly higher at the start than at the end of the experiments in all of the treatments (Table 3). When comparing concentrations at the end of the experiments between the treatments, concentrations of EPA were significantly higher in the control than in both of the zebra mussel treatments (Table 3). Concentrations of particulate organic carbon (C) and particulate organic nitrogen (N) in the seston were significantly higher at the start of the experiment compared to the end of the experiment in all of the treatments (Table 3). In contrast, concentration of particulate organic phosphorus (P) showed the opposite pattern and were lower at the start than they were at the

end of the experiment. C:N values were significantly higher in MZ treatments indicating feasible limitation in nitrogen in this treatments (Table 3). C:P and N:P values decreased by more than an order of magnitude from the start to the end of the experiments in all the treatments indicating that food quality in terms of phosphorus content improved (Table 3). EPA:C values did not differ between the start and end of the experiments for any treatment (Table 3).

Fatty acid composition of dominant cladoceran species

Using PCA, the dominant cladoceran species were represented in two-dimensional space based on two factors corresponding to the largest eigenvalues from their fatty acid levels (Fig. 4). Factor 1 accounted for 55.0 % of the total variance and the highest contributions to Factor 1 were provided by 18:3n-3 and 16:2n-6 on the one hand, and by i17:0 and 15:0 on the other. The second factor accounted for 17.9% of the total variance and the highest contributions to Factor 2 were provided by 20:4n-6 and 20:5n-3 on the one hand, and by ai15:0 and 18:4n-3 on the other. According to the PCA, at the start of experiment, *D. magna* and *D. pulicaria* were close to each other in Factor 1, although differed moderately in Factor 2. At the end of the experiment in the mesocosms with zebra mussels *D. magna* shifted significantly upward Factor 2 while *D. pulicaria* moved left along Factor 1 (Fig. 4) and became close to *C. pulchella*, which were far from both *Daphnia* species at the start of experiment.

In general, the above results of the PCA suggest why *D. magna* and *D. pulicaria* did not displace one another and coexisted throughout the experiment (Fig. 5). Although when reared in the culture both *Daphnia* fed primarily on green algae, in the experiment *D. magna* added diatoms to their diet, and *D. pulicaria* dramatically switched to bacteria. Indeed, at the end of the experiment, the percentages of bacterial acids (i15:0, ai15:0, i15:1, 15:0, 17:0) significantly increased in *D. pulicaria* (Table 4). It does not concern cyanobacteria since they have different fatty acids (FA) composition. Thereby, FA composition of *D. pulicaria* at the end of the experiments was closer to that of *C. pulchella* because percentages of these bacterial acids, which differed significantly at the start of experiment, were similar at the end (Table 4). In contrast, the percentages of some of the bacterial FAs (ai15:0) significantly decreased in *D. magna* (Table 4). In both *Daphnia* species at the end of the experiments percentage of 16:2n-6, 16:3n-3,18:3n-3 significantly decreased (Table 4) indicating a decrease in the contribution of green algae in their diet. Besides in *D. pulicaria* at the end of experiment percentages of 18:2n-6 decreased indicating a stronger decrease in algal diet

compared to that of *D. magna* (Table 4). Percentages of 20:4n-6 increased significantly at the end of the experiments in both *Daphnia* species indicating an increase of proportion of allochthonous organic matter in their diet (Table 4). In *D. magna*, percentages of 20:5n-3 at the end of experiments increased significantly by about an order of magnitude indicating an abrupt increase in the proportion of diatoms in their diet (Table 4). In contrast, in *D. pulicaria* the percentage of 20:5n-3 increased by only 1.4 times (Table 4). In *D. magna* percentages of 18:0 and 18:1n-7 increased significantly (Table 4), providing a moderate left moving along Factor 1 (Fig. 4).

Life-table experiments

Clutch sizes of the three study species responded differently to the presence of zebra mussels (Table 5). In the first generation, clutch sizes of *D. magna* were significantly higher in water from the M mesocosms than from the control. In contrast, clutch sizes were lower for *C. pulchella* grown in the M treatment. In *D. pulicaria* clutch sizes were not significantly different between the treatments. During the second generation, clutch sizes of *C. pulchella* and *D. pulicaria* did not significantly differ between control and zebra mussel treatment while *D. magna* clutch sizes were significantly greater in zebra mussel treatment than in control (Table 5). In comparing clutch sizes between the first and second generations in control, clutch sizes of *D. magna* and *D. pulicaria* were significantly greater during the second generation, while in *C. pulchella* the difference in clutch size between generations were not significant. Clutch sizes of all three species did not differ between generations in the M mussel treatments.

The juvenile development time in the first generation was much longer in *D. magna* than in *D. pulicaria* which was also significantly longer than in *C. pulchella* both in control and zebra mussel treatments (Table 5). In the second generation, juvenile development time of *D. magna* did not differ from that of *D. pulicaria* in control. *Ceriodaphnia pulchella* developed equally fast in the first generation in zebra mussel treatment and control while in the second generation it developed a little bit longer in zebra mussel treatment.

Mortality was low and did not exceed 0.04 – 0.08 per capita a day which was in the limits of minimal physiological mortality for cladoceran species (Romanovski & Feniova, 1985) in either treatment for any study species.

The population growth rate in both *Daphnia* species was lower in the control than in the M treatment in the first generation (Table 5). *Ceriodaphnia pulchella* showed the opposite

trend as its population growth rate was greater in the control than in the M treatment in the first generation. In the second generation, population growth rates of both *Daphnia* species were greater in both the control and M treatment compared to the corresponding population growth rates in the first generation. In the control, *Ceriodaphnia pulchella* grew faster as compared to *Daphnia* species in the both generations but in zebra mussel treatment, it growth rate was slower or similar than that of *Daphnia* (Table 5).

Discussion

Zebra mussels may have affected crustacean abundances and promoted the introduction of *Daphnia* by either altering the quantity or the quality of algal resources in the mesocosms. Zebra mussels can out compete crustaceans if they reduce algal concentration below crustacean threshold levels (0.5 – 2.0 μg/L) (Semenchenko *et al*., 2007). Yet, no significant relationships were detected between chlorophyll and crustacean abundances in our experiment and concentrations of chlorophyll were always above the threshold levels for crustaceans. Therefore, we suggest that competition for food was not important for crustacean dynamics in the mesocosms. There is also a large body of research showing that zooplankton biomass is not always related to food concentrations, but instead related to the nutritional quality (McCauley, Murdoch & Nisbet, 1990; Müller-Navarra & Lampert, 1996). As such, we believe that food quality rather than food quantity helped to regulate crustacean dynamics in the mesocosms.

Zebra mussels significantly increased phosphorus and nitrogen in the mesocosms. Increases in nutrient concentrations via zebra mussel excretion have been reported in several studies (Wilson, 2003; Feniova *et al*., 2015). Zebra mussels were also recently found to selectively consumed EPA-rich seston (Makhutova et al., 2013). In response to changes in nutrient or EPA concentrations, phytoplankton nutritional value can alter. In fact, in zebra mussel treatments, abundance of green algae increased while that of cyanobacteria decreased, i.e. there was a shift in the phytoplankton structure although total chlorophyll concentration was not affected. Since cyanobacteria and green algae are of different nutritional value for crustaceans, we anticipated that food quality in terms of EPA or C:N:P ratios could cause the changes in zooplankton structure in zebra mussel treatments in relation to control.

EPA content (μg EPA mg C^{-1}) is an important indicator of the quality of natural phytoplankton for cladoceran species (Müller-Navarra, 1995; Müller-Navarra *et al*., 2000; Gladyshev *et al*., 2008; Wacker & von Elert, 2001; Hartwich *et al*., 2012) and potentially

could be the determinant of the zooplankton dynamics in the experiment. Noteworthy is that small and large-bodied cladoceran species can differently respond to EPA concentrations. In fact, Sikora *et al*. (2016) showed that EPA-saturation thresholds, which were defined as the minimal content of EPA per organic carbon above which the juvenile growth rate becomes saturated, increased significantly with increasing body size of the tested species. For the small-sized *D. longispina* complex, the content of EPA resulting in 75 % of the asymptotic growth rate varied between 0.74 – 1.80 (µg EPA mg C^{-1}), for the medium-sized *D. pulicaria* it varied between 2.21 – 3.49, and for large-sized *D. magna* it varied between 5.83 – 7.33 (Sikora *et al*., 2016). According to other published data for the medium-bodied *D. pulex* (similar in size as *D. pulicaria*) a lower EPA threshold for 90 % saturation was 1.3 µg EPA mg C⁻1 (Ravet, Persson & Brett, 2012), and for the large-bodied *D. magna* it was 2.0–4.9 µg EPA mg C^{-1} (Sperfeld & Wacker, 2011). Based on these thresholds, EPA contents (µg EPA mg C^{-1}) at the start and at the end of our experiments were not limiting for small-bodied species, but were close to the limiting threshold for large-bodied cladocerans. While EPA content (µg EPA mg C^{-1}) was not variable over the course of the experiments nor did it differ between the treatments, population growth rates of the study species differed distinctly. Therefore, we believe that these data suggest that EPA content per organic carbon did not cause the differences between the treatments with zebra mussels and those without zebra mussels. However, regarding sestonic EPA concentrations in the mesocosms (µg L^{-1}), it is worth noting that the threshold concentration for *Daphnia* was found to be 13 mg L^{-1} (Gladyshev *et al*., 2008). In the present study, the EPA concentrations were far below this threshold and therefore it may have constrained *Daphnia* growth rates. In support, *Daphnia* grown in the life table experiment never had clutch sizes greater than 3 eggs/clutch even when content of phosphorus in the seston was above threshold concentrations.

Copepods and cladocerans differentially recycle inorganic nutrients based on nutrient demands for their tissues. Copepods typically sequester more nitrogen in their tissue (Elser & Urabe, 1999) while cladocerans sequester more phosphorus relative to nitrogen (Sterner & Elser, 2002; Johnson & Luecke, 2012). Cladocerans such as *Daphnia* spp., which have low body N:P (Andersen & Hessen, 1991), tend to occur in lakes with low seston N:P (Hassett *et al* ., 1997). Conversely, copepods, with higher body N:P (Andersen & Hessen, 1991; Carrillo, Reche & Cruz-Pizarro, 1996; Villar-Argaiz *et al*., 2000) tend to appear in lakes with high seston N:P (Hassett *et al*., 1997). In our experiments, N:P ratio decreased over 10-fold from the start to the end of the experiments both in the zebra mussel treatments and control. Therefore, at the beginning of our experiments high molar N:P ratios (216) could have

467 favored copepod abundance, until the N:P ratio decreased afterwards cladocerans could
468 increase their abundance. In fact, in the experiments, there was a shift of domination from
469 copepods to cladocerans as seen in Fig. 5.
470 The N:P ratio in the tissues of cladocerans also depends on body size. Small-bodied
471 species have been shown to have a higher percentage of nitrogen and a lower percentage of
472 phosphorus content in their dry weight than larger daphnids (Bergström *et al*., 2015).
473 Therefore, the phosphorus demand is higher in large-bodied species due to their higher
474 somatic growth rate than in small-bodied species that grow more slowly (Sterner & Schulz,
475 1998). Because daphnids have a relatively higher P content in their body tissues than most
476 other freshwater zooplankton (Sterner & Hessen, 1994), stoichiometric theory predicts that
477 daphnids should be more sensitive to P limitation than other taxa (DeMott & Gulati, 1999).
478 For example, small-bodied cladocerans are predicted to be less sensitive than *Daphnia* to P
479 limitation because they have lower percentage of body P content but they are more sensitive
480 to N-limitation (Urabe &Watanabe, 1992; Schulz & Sterner, 1999). In mesocosm
481 experiments, Elser *et al*. (1988) showed that when manipulating zooplankton community
482 composition towards smaller sized herbivores, N-limitation in phytoplankton was induced.
483 According to N:P measurements in seston at the beginning and at the end of the experiment,
484 N:P ratio decreased over 10-fold in the course of the experiments. We can presume that N:P
485 ratio gradual decreased provoking a shift of dominance from microzooplankton to copepods
486 and afterwards from copepods to cladocerans. Since zebra mussels enhanced inorganic
487 phosphorus concentration in the water, N:P ratio in seston could decrease faster in zebra
488 mussel mesocosms, thus, favoring the development of large *Daphnia* species. Indeed, in the
489 life-table experiments, large *Daphnia* species had higher population growth rates than in
490 control, while the small-bodied species *C. pulchella* exhibited a higher growth rate in the
491 control.
492 The most likely critical molar C:P ratio in seston above which daphnid production will
493 be limited by seston P content is ~300 (Urabe, Clasen & Sterner, 1997; Sterner 1997, 1998;
494 Brett, Müller-Navarra & Park, 2000). At the start of our experiment the C:P ratio was much
495 higher than threshold C:P ratios. Therefore, large *Daphnia* species could not develop
496 successfully without zebra mussels. We assumed that zebra mussel could cause very abrupt
497 decrease of C:P thus allowing *Daphnia* abundance to grow. Similar effects were observed in
498 mesotrophic conditions (Feniova *et al*., 2015) where $P\text{-}PO_4$ enrichment by zebra mussels was
499 found to facilitate the successful development of large-bodied *Daphnia* only in mesocosms
500 with zebra mussels. C:P decreased over the course of the experiment and by the end it had

reached ratios which were below the threshold ratios not only in zebra mussel treatments but also in control. We suggest that such decreases in C:P in the control were provided by regeneration of phosphorus by microzooplankton groups such as ciliates, nanoflagellates, rotifers which commonly excrete nutrients although not as intensively as zebra mussels (Vanni, 2002). We suggest that introduced large-bodied *Daphnia* species could not increase in population abundance in the treatment without zebra mussel at the start of the experiments because regeneration of phosphorus by microzooplankton occurred more slowly than it did in the zebra mussel treatments. It is possible that during the second half of the experiments, large-bodied species could have successfully developed in the control if they had been introduced later as indicated from life table experiments.

Based on the PCA analysis we found that two closely related species of *Daphnia (D. pulicaria* and *D. magna*) exhibited differences in resource use. These species were reared in culture and fed with *Scenedesmus quadricauda*: however, in the experiments *D. magna* mainly grazed on diatoms while *D. pulicaria* dramatically switched to bacteria. Such a divergence in their diet is likely to weaken potential competition between *Daphnia* species. Similar diet pattern was also observed in mesotrophic conditions (Feniova *et al*., 2015) where *D. pulicaria* also preferred bacteria while *D. magna* preferred diatoms. Cladocerans are known as nonselective filter feeders whose diet is constrained by food particle size (DeMott, 1986). Their diet spectrum varies from 1 to 20–30 μm (Sommer & Sommer, 2006). However, they could differently retain or assimilate particulate food items. In support, Taipale *et al.* (2016) found that cladoceran $\delta^{13}C$ values did not correlate with seston $\delta^{13}C$ values and instead correlated with the $\delta^{13}C$ values of the different phytoplankton taxa, indicating that *Daphnia* selectively assimilated phytoplankton. Selective feeding of *Daphnia* on natural microalgal assemblages was also demonstrated experimentally by Gladyshev *et al*. (2000).

Life table experiments supported that these two *Daphnia* species could coexist and according to the population growth rates they could have equal chances to develop in the experimental conditions. However, the relative abundance of these two species which was 1:2 (*D. pulicaria* : *D. magna*) in the mesocosms could be affected by copepod predation and/or other factors. These findings contradict the niche theory stating that the closely related species could experience more severe competition (Chesson, 2000; Shea & Chesson, 2002; Tilman, 2004). However, it gives one more reason for the ‘plankton paradox’ phenomenon for zooplankton (Ghilarov, 1981) where more than one potentially competitive species coexist in the plankton community.

In conclusion, the main driver of cladocerans in our experiment was likely food quality in terms of the phosphorus content in the food. The introduction of zebra mussels appeared to enhance phosphorus in the seston due to the excretion of inorganic phosphorus. In the treatments without zebra mussels phosphorus enrichment could be provided by regeneration processes of microzooplankton. C:P and N:P ratios were the most variable indicators of food quality and could operate as drivers of the shift in domination from microzooplankton to copepods, and then from copepods to cladocerans.

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Figure legends

Fig. 1 Dynamics of nutrient concentrations in control (A), in Z treatment with introduced large-bodied *Daphnia* species (B), in M treatment with introduced zebra mussels (D) and in MZ treatment with introduced large-bodied *Daphnia* species and zebra mussels (D).

Fig. 2 Dynamics of chlorophyll concentrations in control (A), in Z treatment with introduced large-bodied *Daphnia* species (B), in M treatment with introduced zebra mussels (D) and in MZ treatment with introduced large-bodied *Daphnia* species and zebra mussels (D).

Fig. 3 Dynamics of zooplankton biomass in control (A), in Z treatment with introduced large-bodied *Daphnia* species (B), in M treatment with introduced zebra mussels (D) and in MZ treatment with introduced large-bodied *Daphnia* species and zebra mussels (D).

Fig. 4 Principal component analysis of FA levels in zooplankton from mesocosms: Dms - *Daphnia magna*, start; Dps - *Daphnia pulicaria*, start; DmM – *D. magna* + mollusks, end; DpM – *D. pulicaria* + mollusks, end; cC –*Ceriodaphnia pulchella* control.