EFFECTS OF PHOSPHOROUS ENRICHMENT ON ZEBRA MUSSELS

By

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Abstract:
Cultural eutrophication has decreased overall water quality and increased the occurrence and intensity of cyanobacteria blooms. Eutrophication may interact with other stressors such as invasive species. Zebra mussels (*Dreissena polymorpha*) are an invasive species causing severe ecological and economic impacts. Zebra mussels are effective filter feeders on phytoplankton, causing top down control and redistributing nutrients from pelagic to benthic environments. It is less well known how zebra mussels affect aquatic food webs along a gradient of eutrophication. The objective of this research was to better understand the interactions between eutrophication and invasive zebra mussels. I conducted a series of mesocosm experiments to determine how phosphorus additions interacted with zebra mussels and influenced zebra mussel feeding rates. An outdoor mesocosm experiment tested if phosphorous enrichment and zebra mussels affected water quality and plankton. In an established phosphorous gradient, phosphorus had a significant effect on chlorophyll *a* but not zebra mussels. Cyanobacterial (measured as phycocyanin) biomass was affected by the interaction of phosphorus and zebra mussels. Cladoceran abundance increased with increasing phosphorus but decreased in mussel treatments. Copepod abundance also increased with phosphorus, but was not affected by zebra mussels. An indoor mesocosm experiment tested how zebra mussels were affected by phosphorus concentration in their algal resources. Zebra mussel filtering rates significantly decreased with increasing phosphorus enrichment. The feeding rate for low (no phosphorus) and medium (520 µg/L phosphorus) each differed from the very high treatment (5,200 µg/L) though this concentration is not likely to occur in natural settings. The findings of these two studies suggest that zebra mussel effects may not be as strong as suspected and that nutrients are a stronger driver than zebra mussel consumption in terms of algal biomass. Although mussel feeding was constrained at very high phosphorus, it only occurred at concentrations that are not biologically relevant.

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CHAPTER I

EFFECTS OF PHOSPHOROUS ENRICHMENT ON ZEBRA MUSSELS

Introduction

A major stressor affecting water quality in lakes and reservoirs is non-point source pollution (Schindler and Vallentyne 2008). Although legislation since 1979 has diminished point source pollution, such as industrial waste, in the United States, non-point sources of pollution have become more prevalent (Jeppesen et al. 2005, Schindler et al. 2012). Two significant sources of non-point source pollution are synthetic fertilizers and animal waste runoff from agricultural activities (Carpenter et al. 1998, Paerl and Fulton 2006). These substances contain large concentrations of nitrogen (N) and phosphorus (P) to stimulate higher agricultural yields, but surplus nutrients, particularly P, often enters adjacent water bodies leading to eutrophication, (Sardans et al. 2012, Arbuckle and Downing 2001). Nurnberg (1996) gives the following criteria for P levels for quantifying the trophic state of a water body: oligotrophic (0-12 µg/l (parts per billion/ppb) phosphorus), mesotrophic (12-24 µg/l), eutrophic (24-96 µg/l), and hyper eutrophic (96+ µg/l) In recent decades eutrophication has increased the overall productivity of many lakes, causing a shift from lower productivity (oligotrophic or mesotrophic) to higher productivity (eutrophic or hyper eutrophic) (Cooke et al. 2011).

One of the negative consequences of surplus nutrients entering lakes and reservoirs is an increase in the frequency and intensity of cyanobacteria (Wetzel 1990,

Anderson et al. 2002). Under high nutrient conditions, cyanobacteria undergo rapid population growth that is driven by P inputs in the system (Downing et al. 2001). The genus *Microcystis*, particularly *Microcystis augreonosia*, produces harmful toxins known as microcystin, as a defense against predation from phytoplankton grazers such as *Daphnia* (Lambert 1982). At high cyanobacteria densities, these toxins can concentrate and reach levels that lead to further habitat degradation and become severe health concerns for both wildlife and humans (Knoll et al. 2008, Pires et al. 2004, World Health Organization 2003).

Invasive or non-native species are another stressor that has the potential to impact water quality and ecosystem health (Havel et al. 2005). Historically aquatic species were restricted to specific watersheds, isolated by geo-physical barriers, water body heterogeneity, and flow regimes which limited expansion (Rahel 2002). However, anthropogenic activity such as the intentional and unintentional movement of species, connected waterways, and modified aquatic habitats have reduced those barriers and led to species spreading into new environments on multiple spatial scales (Rahel 2002). A notable invasive species in North American aquatic ecosystems is the zebra mussel, *Dreissena polymorpha,* which invaded the Great Lakes in the late 1980's unintentionally via the ballast water of transatlantic cargo ships (MacIsacc et al. 1992, Johnson and Padilla 1996, Ricciardi and MacIsaac 2000). Since their introduction zebra mussels have spread across the Mississippi river drainage including 18 states and two Canadian provinces (Johnson and Padilla 1996), including rivers and reservoirs in Oklahoma (Drake and Bossenbroek 2004). Zebra mussel adults and larval veligers can be moved unintentionally by residing in boat live wells and other water filled containers, allowing

them to move to unconnected water bodies. These dispersal mechanisms have helped to greatly increase their distribution in the United States (Johnson and Padilla 1996, MacIsacc et al. 1992, Johnson and Carton 1996, Havel and Stelzleni-Schwent 2000).

Zebra mussels can attain high population densities in their nonnative range causing widespread economic and ecological impacts (Kelly et al. 2013, Johnson and Padilla 1996). Some of the ecological effects include increasing water clarity, modifying nutrient concentrations, and shifting native species distribution (Naddafi et al. 2009). In the United States, zebra mussels have contributed to increased water clarity of the Great Lakes, but also reduced phytoplankton community composition and abundance, leading to a top-down trophic cascade. Zebra mussels achieve this by removing P and other nutrients from pelagic food webs and distributing them to benthic habitats (Vanderploeg et al. 2010).

Key to the zebra mussel's success as an invader is that they are highly efficient filter feeders (Bastviken et al. 1998). A significant amount of research has quantified zebra mussel filtration rates, though rates vary across studies. Kryger and Rissgard (1998) and Kotta et al. (1998) found that individual mussels filtered up to 234ml of water per hour. Vanderploeg et al. found that mussels feeding in the presence of cyanobacteria, zebra mussel reduced algae at a rate of 18.5-51.0ml per square cm per hour (2009). MacIsaac et al. (1992) reported that some areas of Lake Eire, zebra mussels living at high densities could filter 132,000l of water per square meter per day.

With their high population densities and high filtration rate, zebra mussels can manipulate aquatic habitats by consuming particulates, particularly algae, which has major implications for all aquatic species because algae form the energetic base of

aquatic food webs (Johnson and Padilla 1996, Wojtal-Frankiewicz and Frankiewicz 2001, Vanderploeg et al. 2010). While zebra mussels can graze on cyanobacteria colonies, they are not a preferred food source (Vanderploeg et al. 2001). Rather, cyanobacteria can be extruded as pseudofeces in which the algae cells are filtered by the mussel, but wrapped in mucus and released back into the water column (Vanderploeg et al. 2001). This process does not kill the algae, allowing them to continue growing (Vanderploeg et al. 2001). Zebra mussels can also prey on microzooplankton (e.g. rotifers) and compete with macrozooplankton, (e.g. *Daphnia*) for algal resources (Wojtal-Frankiewicz and Frankiewicz 2001). Higgins et al. (2011) found that top down effects on phytoplankton from mussel filtration had a proportional effect on zooplankton species (Feniova et al. 2015). Zooplankton are important in aquatic ecosystem as they are an important linkage between primary producers and higher level consumers, distributing chemical energy throughout the food web (Bowen and Johannsson 2011).

A large body of research suggests that zebra mussels can interact with eutrophication to affect aquatic ecosystems. For example, zebra mussels can directly affect nutrient concentrations in invaded systems. Goedkoop et al. (2011) found that zebra mussels in Lake Ekoln were able to limit cyanobacteria growth by grazing on phytoplankton that had taken up excess P and N from effluent entering the lake. In contrast, Higgins et al. (2011) found that zebra mussels negatively affected relationships between P and chlorophyll *a* in lakes in the northern United States. Chlorophyll *a* concentrations decreased due to zebra mussel grazing while total phosphorus (TP) concentrations were not affected due to increased P excretion from mussels (Higgins et al. 2011). These effects of zebra mussels have important implications for lake and

reservoir health as the P released from zebra mussels has the potential to increase the intensity and frequency of harmful cyanobacteria blooms (Knoll et al. 2008).

The effects of zebra mussels on plankton may also be context-dependent and vary based on the amount of P in a system. For example, lakes in Michigan with zebra mussels had higher *Microcystis* concentrations than lakes without mussels, but only at TP concentrations less than 25µg/l (Raikow et al. 2004). One hypothesis is that zebra mussel feeding rates are negatively affected by excess P. While under most environmental conditions P is limited and species growth and maintenance is restricted by the lack of this element, there is evidence that excess P and other nutrients can be detrimental to growth due to imbalances with other elements (e.g., C or N) (Plath and Boersma 2001, Acharya et al. 2006 Boersma and Elser 2006,). A growing body of research suggests that the growth of several algal grazers, including both *Daphnia* and zebra mussels, can be negatively impacted by excess P in their algal food resources (Morehouse et al. 2013, Plath and Boersma 2001). With respect to zebra mussels, Morehouse et al. (2013) found that zebra mussel growth was reduced when they were feed P-rich algae (low C:P ratio), which led to an increase in ammonia production from the breakdown of internal proteins due to lack of carbohydrates in their diets. As excess P is taken up by phytoplankton in eutrophic systems and then ingested by zebra mussels, surplus P in the zebra mussel diet allows them to meet their dietary P requirements for growth, leading to reductions in feeding rates. Similarly, Plath and Boersma (2001) observed that *Daphia* increased feeding rates in conditions of high C:P (low P) to increase their P intake. Alternatively, at lower C:P ratios (high P), *Daphnia* feeding rates were reduced as metabolic requirements were quickly attained. A similar reduction in feeding rate may occur in other filter

feeders such as zebra mussels and could explain the dynamics between zebra mussels and phytoplankton in high P environments.

The purpose of this study was to determine how the effects of zebra mussels varied along a gradient of P enrichment in two mesocosm experiments. I hypothesized that the overall effects of zebra mussels on aquatic ecosystems would be context-dependent and the strength of these effects would vary based on P concentrations in the mesocosms. At low P concentrations, mussel feeding rates will be higher, which will reduce phytoplankton and zooplankton. In contrast, as the concentration of P increases, zebra mussel feeding rates will decrease due to stoichiometric imbalances created by excess P, reducing impacts on phytoplankton and zooplankton.

Methods

I conducted two mesocosm experiments, one outdoors in 2014 and the other indoors in 2015. The first experiment (*Outdoor Mesocosm Experiment*) was designed to determine how zebra mussels impacted nutrients and plankton along a P gradient. The second experiment (*Indoor Mesocosm Experiment*) was designed to specifically determine how zebra mussel filtering rates varied along a P gradient.

Outdoor Mesocosm Experiment

I set up 32 individual mesocosms (Rubbermaid 568 liter cattletanks, 147.3cm x 99.1cm x 61.0cm) in the OSU pond facility at Lake Carl Blackwell (36° 8'0.37"N, 97°11'21.49"W). The mesocosms were placed in a single pond basin in a four by eight pattern in a random order. The mesocosms were filled with approximately 500L of water

from Lake Carl Blackwell that was pumped to the pond through an underground pipe. A sieve screen (5.0mm mesh) was placed on the inflow pipe to keep fish, larger invertebrates, and debris out of the mesocosms as they were being filled. Zooplankton were collected from Babcock Park (36° 6'15.25"N, 97° 5'27.09"W), Boomer Lake (36° 9'6.39"N, 97° 3'50.26"W), and Lake Carl Blackwell (36° 8'6.94"N, 97°13'0.72"W) using a 240.0µm net. The zooplankton from these sites were homogenized in a large carboy and then added to each mesocosm to allow zooplankton communities to develop. After the mesocosms were filled the holding pond was also filled around the mesocosms to provide thermal insulation and to help limit evaporation from the tanks. The mesocosms were left undisturbed for approximately two weeks before the P and zebra mussel treatments were established. After this two week establishment period the experiment was conducted for 49 days from September 19 to November 6, 2014.

I manipulated P and zebra mussels in the mesocosms using a 4 x 2 factorial design for a total of eight treatments each replicated in quadruplicate (N=32). I manipulated P by adding KH_2PO_4 to the mesocosms to mimic four P concentrations: mesotrophic (~25µg/L [L=Low]), eutrophic (50µg/L [M=Medium]), and two levels of hypereutrophic (100µg/L [H=High] and 200µg/L [V= Very High]) systems (Nurnberg 1996). The P concentrations were maintained through weekly P additions assuming a daily loss rate of 5% (Lennon et al 2003) and by measuring and comparing P concentrations from previous sampling dates in each mesocosm treatment.

I manipulated the presence of zebra mussels, which were collected from docks at Lake McMurtry (36°10'15.60"N, 97°11'19.69"W) and Lake Carl Blackwell (36° 8'6.94"N, 97°13'0.72"W). Before mussels were introduced into the mesocosms, they were

kept in a 45.4l cooler with a filter airstone, and seston from source lakes. Approximately 175 zebra mussels (mean mass 20.41g) were added to +Z treatments (N=16) (0.35 mussels/l); (Dzialowski 2013). No zebra mussels were added to the remaining 16 mesocosms (-ZM).

I sampled phytoplankton and P weekly by collecting 1.0l water samples by submerging a plastic brown bottle to a depth of 0.5m. A Turner Trilogy Fluorimeter (Turner Designs, Mountain View California) was used to measure relative chlorophyll fluorescence using the blue module and relative phycocyanin fluorescence was measured using the orange module. The fluorometer provided a relatively quick method for estimating algal biomass that is highly correlated with laboratory extracted chlorophyll *a* concentrations (Dzialowski unpublished data). A 10.0ml cuvette was washed with the sample; the cuvette was then filled using a plastic disposable pipette and then placed in the fluorometer. RFU was measured <24 hours after collection. Generally the samples were run first with the blue module and then the orange module, within 1.0 hour of each other. TP was measured within 24 hours of collection. TP was measured using a spectrometer (Genesys 20, Thermo Scientific,Waltham MA) after persulfate digestion (APHA 2005).

I collected zooplankton samples bi-weekly using a depth-integrated PVC sampler. A different sampler was used for each nutrient treatment for a total of four individual samplers. The samples were taken from the center of each mesocosm and the sampler collected water from the entire water column of the mesocosm. The samplers had one-way valves that opened to collect water in the sampler when they were pushed down into the mesocosms, but closed when they were pulled up. Multiple samples were collected

from each mesocosm and transferred into a bucket until 11.0l of water was collected from each individual mesocosm. This sample was then poured through a 45.0µm mesh filter to collect zooplankton that were preserved in Lugols solution.

Zooplankton were identified and enumerated using a round plexiglass counting tray to suborder for copepods, species for cladocerans, and genus for rotifers using the University of New Hampshire online key (http://cfb.unh.edu/cfbkey/html/index.html). Zooplankton were subsampled as necessary.

Indoor Mesocosm Experiment

I set up sixteen 20Lmesocosms in the laboratory, filled them with19L of dechlorinated tap water, and added 45mm of a single species of green algae (*Selenastrum capricornutum*) Four P concentrations: 0µg/L (Low=L), 520µg/L (Medium=M), 2200µg/L (High=H), 5200µg/L (Very high=V) were established, each replicated in quadruplicate. Fluorescent shops lights were placed on the top of the mesocosms and left undisturbed for 24 hours for the algae to take up the P (Plath and Boersma 2001). I collected a 1L water sample to measure initial chlorophyll concentrations. Two zebra mussel treatments were then established with either zebra mussels present (+Z, N=5 mussels, mean mussel mass per mesocosm=1.51g) or absent (-Z). Water samples were collected after 12 hours of zebra mussel inoculation for chlorophyll analysis (RFU). A disposable plastic pipette was used to first stir each mesocosm, and then a sample was collected in a brown 1.0l bottle and analyzed using the blue module in the Turner Fluorometer as described above.

Data Analysis Outdoor Mesocosm Experiment

I used a two way Repeated Measures Analysis of Variance (RM-ANOVA) to determine how target P and zebra mussels affected chlorophyll (measured as RFU) on days 0-49, phycocyanin on days 14-49, and TP and days 0-49. All data were log transformed to meet the assumptions of normality and homogeneity of variance. Significant treatment and interaction terms were compared using Tukey's post-hoc comparison tests ($P<0.05$). The RM-ANOVAs were conducted using NCSS 2007.

I also used a RM-ANOVA to compare zooplankton abundance between the P and zebra mussel treatments. Zooplankton were summed according to order: Cladocera (*Daphnia*, *Cerodaphnia*, *Diaphansoma*, *Simsocephalus*, *Bosmina*, *Alona*, *Chydorus*) and Copepoda (*Calanoids* and *Cyclopoids*). Zooplankton data was log transformed and Tukey's Post-Hoc comparison tests were used when significance were found ($P<0.05$). The RM-ANOVAs were conducted using NCSS 2007

Data Analysis Indoor Mesocosm Experiment

Zebra mussel feeding rates (RFU/hour) were determined by subtracting the 12 hour RFU reading from the starting RFU reading (time=0) in each mesocosm with zebra mussels and dividing by 12. Feeding rates were corrected for change in algal biomass resulting from P additions by subtracting the average RFU change over the 12 hour period observed in the non-mussel mesocosms with the corresponding P levels. Filtering rate data were log transformed to meet the assumptions of normality and homogeneity of variance. A one-way ANOVA was used to compare filtering rates between the different phosphorous treatments and Tukey's Post-Hoc comparison tests were used to compare

individual treatments when significance was found ($P<0.05$) . The one-way ANOVA was conducted using sigmaplot 10.0.

Results

Outdoor Mesocosm Experiment

Chlorophyll *a* responded to the P treatment (RM-ANOVA, P=0.003, Figure 1) and increased in the H treatment which had the highest concentrations. Chlorophyll *a* concentrations in the V treatment were similar to the concentrations that were observed in the M treatment. The zebra mussel treatment did not have a significant effect on chlorophyll *a* (RM-ANOVA, zebra mussel effect, P=0.919, Figure 1). P additions also affected phycocyanin (RM-ANOVA, P=0.002). Phycocyanin concentrations were higher in the H and V treatments than they were in the L and M treatments, especially on the first and second sampling dates (Figure 2). Phycocyanin increased from the start of the experiment, reaching a maximum on day 36 and then declining to concentrations below the starting values by the end of the experiment in all treatments. The presence of zebra mussels did affect phycocyanin (RM-ANOVA, zebra mussel effect, P=0.995). Phycocyanin was higher in H mesocosms with zebra mussels compared to H mesocosms without zebra mussel (RM-ANOVA, P x zebra mussel interaction, P=0.0497, Table 2). P additions resulted in a significant P gradient in the mesocosms where all four of the P treatments differed in TP concentrations over the course of the experiment (RM-ANOVA, P effect $P<0.001$, Figure 3). Zebra mussel treatment did not affect P concentrations and there were no differences between mesocosms with and without zebra mussels for any of the nutrient treatments (RM-ANOVA, zebra mussel effect, P=0.644).

Source Term	Degrees of Freedom	Sum of Squares	Mean Square	F-Ratio	Probability Level	Power
ZM	1	0.002	0.003	0.01	0.919	0.051
P	3	4.520	1.507	6.07	**0.003**	0.923
ZM X P	3	1.271	0.424	1.71	0.194	0.386
Tank	23	5.713	0.248			
Date	6	1.201	0.201	8.27	<**0.001**	0.999
ZM X Date	6	0.302	0.050	2.07	0.061	0.733
P X Date	18	1.860	0.103	4.25	<**0.001**	0.999
ZM X P X Date	18	0.568	0.003	1.30	0.197	0.825
(Tank X Date) X (ZM X P)	138	3.354	0.002			

Table 1. Chlorophyll *a* repeated measures ANOVA table (alpha = 0.05). Significant factors are bolded. ZM=zebra mussels, P=total phosphorous, X= interaction of variables, Tank=mesocosm tank, Date=date of sampling.

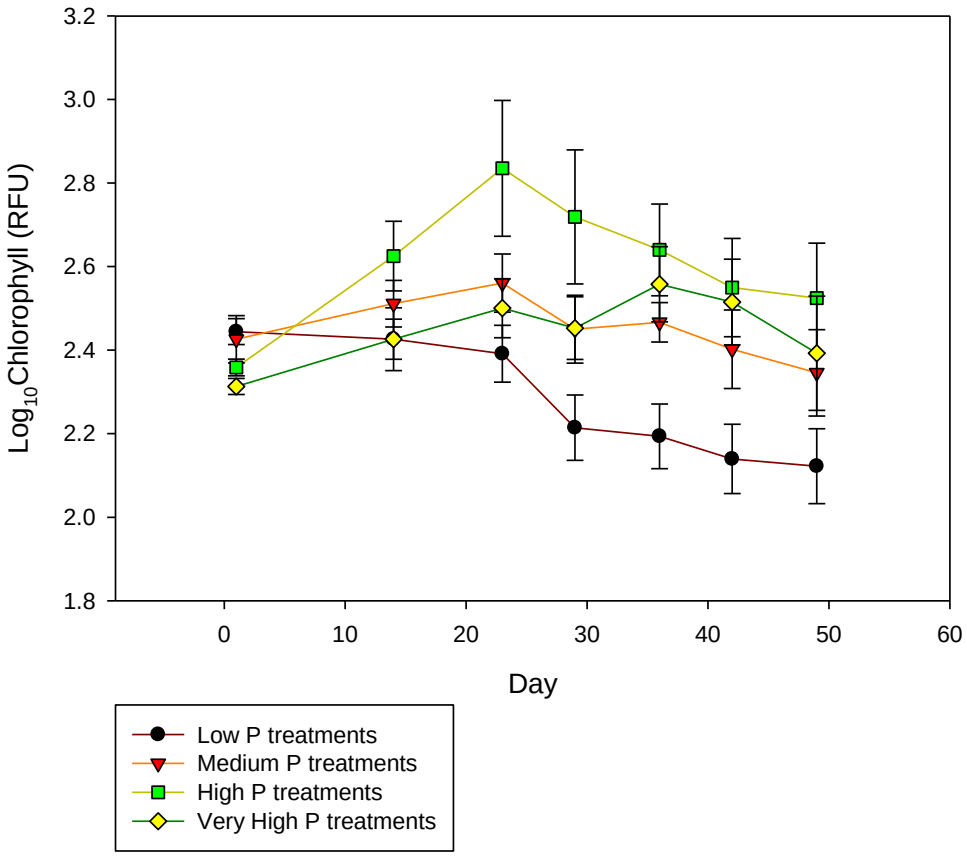

Figure 1. Log_{10} Chlorophyll *(*RFU) in the outdoor experiment over time. Days are from the start of the experiment (Day 1= September 19th). Circles are low (L) treatments (25µg/L), Triangles are medium (M) treatments (50µg/L), squares are high (H) treatments (100µg/L), diamonds are very high treatments (V) (200µg/L).

Source Term	Degree of Freedom	Sum of Squares	Mean Square	F-Ratio	Probability Level	Power
ZM	1	<0.000	<0.000	0.00	0.995	0.050
P	3	0.051	0.017	7.04	**0.002**	0.957
ZM X P	3	0.022	0.007	3.03	**0.0497**	0.635
Tank	23	0.056	0.002			
Date	5	5.721	1.144	1183.68	**<0.000**	1.000
ZM X Date	5	0.012	0.002	2.45	**0.038**	0.756
P X Date	15	0.013	0.001	0.88	0.587	0.548
ZM X P X Date	15	0.025	0.002	1.73	0.054	0.897
Tank X Date by ZM by P	185	0.111	0.001			

Table 2.Phycocyanin repeated measures ANOVA table (alpha = 0.05). Significant factors are bolded. ZM=zebra mussels, P=total phosphorous, X= interaction of variables, Tank=mesocosm tank, Date=date of sampling.

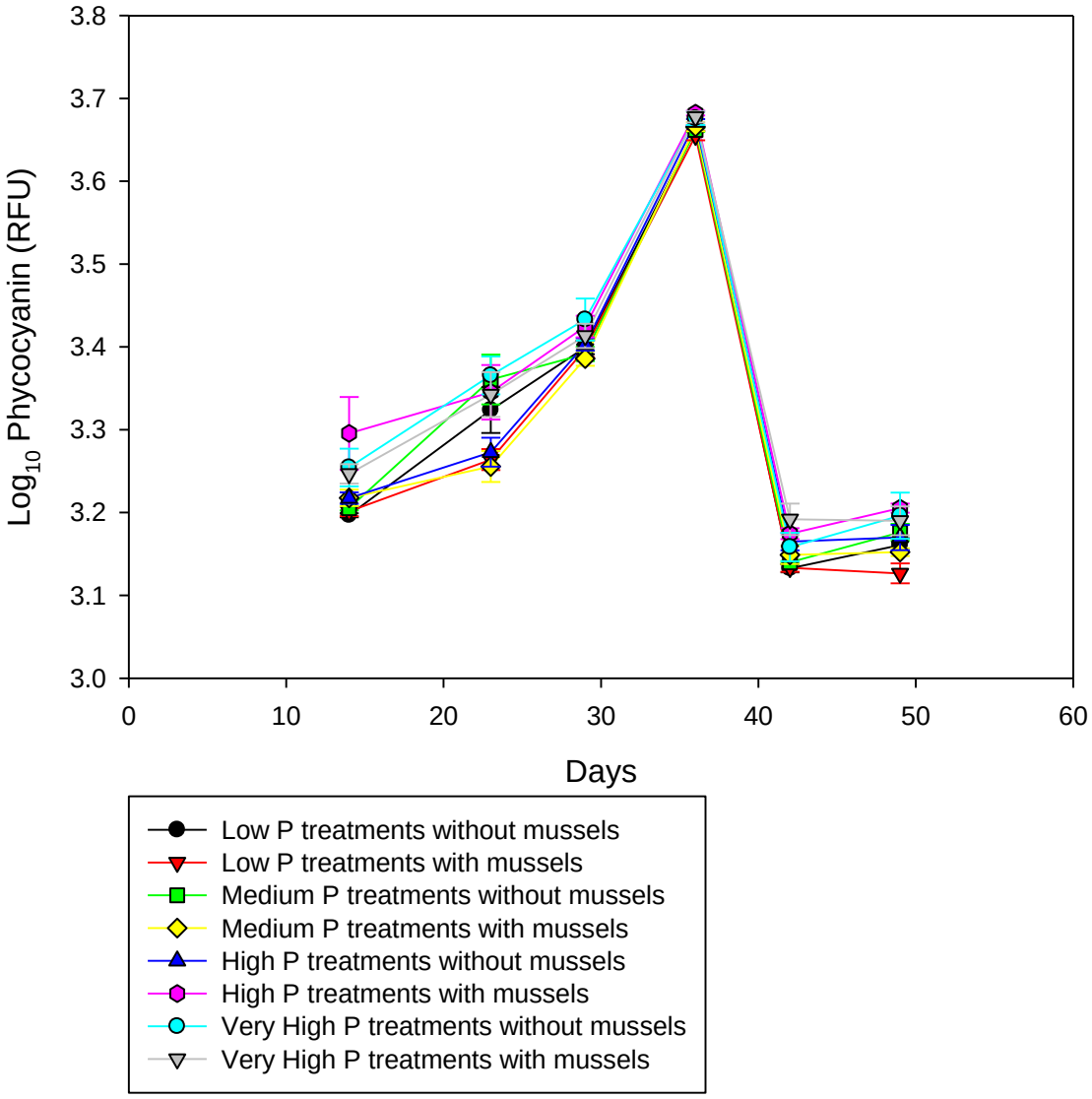

Figure 2. Phycocyanin (RFU) from the outdoor experiment. Days are from the start of the experiment (Day 0 = Sep 19th), although phycocyanin was not measured until Day 14. In descending order black circles are low (L) P treatments (25µg/L) without mussels, red downward facing triangles are low (L) treatments (25µg/L) with mussels, green squares are medium (M) treatments (50µg/L) without mussels, yellow diamonds are medium (M) treatments (50µg/L) with mussels, blue upward facing triangles are high (H) treatments (100µg/L) without mussels, purple hexagons are high (H) treatments (100µg/L) with mussels, teal hexagons are very high (V) treatments (200µg/L) without mussels, grey downward facing triangles are very high (V) treatments (200µg/L) with mussels.

Source Term	Degree of Freedom	Sum of Squares	Mean Square	F-Ratio	Probability Level	Power
ZM	1	0.034	0.034	0.22	0.644	0.073
P	3	19.787	6.596	42.10	**<0.001**	1.000
ZM X P	3	0.024	0.008	0.05	0.984	0.058
Tank	23	3.603	0.157			
Date	6	2.752	0.459	15.93	**<0.001**	1.000
ZM X Date	6	0.198	0.033	1.15	0.338	0.441
P X Date	18	0.336	0.019	0.65	0.854	0.449
ZM X P X Date	18	0.287	0.016	0.55	0.926	0.379
Tank X Date by ZM by P	138	3.973	0.029			

Table 3.Total phosphorous repeated measures ANOVA table
(alpha = 0.05). Significant factors are bolded. ZM=zebra mussels, P=total phosphorous, X= interaction of variables, Tank=mesocosm tank, Date=date of sampling.

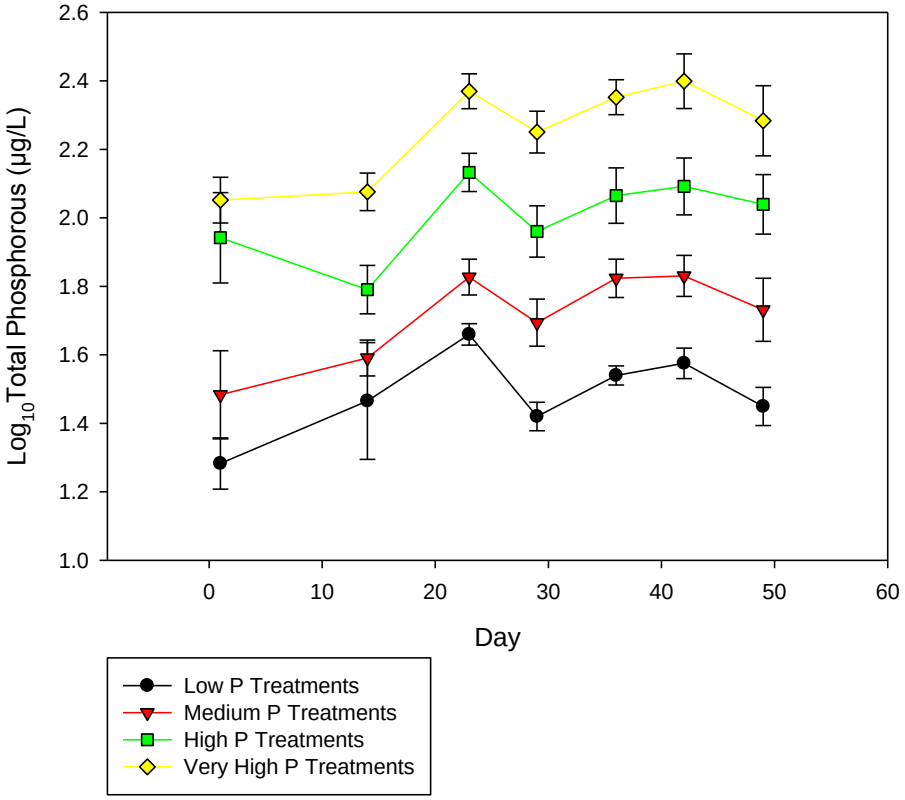

Figure 3.Log_{10} total phosphorous (µg/L) in the outdoor experiment over time. Days are from the start of the experiment (Day 0 = Sep 19th).circles are low (L) treatments (25µg/L),triangles are medium (M) treatments (50µg/L), squares are high (H) treatments (100µg/L), diamonds are very high (V) treatments (200µg/L).

Zooplankton were affected by the P and zebra mussel treatments. Cladoceran abundance increased with P and was highest in the V treatment (RM-ANOVA, phosphorus effect, P=0.022) (Figure 5). In contrast, cladoceran abundance decreased in the presence of the mussels, as it was lower in zebra mussel treatments across all P treatments (RM-ANOVA, zebra mussel effect, P=0.001) (Table 4). Copepod abundance also increased with P (RM-ANOVA, P effect, P=0.004), but there was no effect from zebra mussels (RM-ANOVA, zebra mussel effect, P=0.501) (Figure 6).

Source Term	Degree of Freedom	Sum of Squares	Mean Square	F-Ratio	Probability Level	Power
ZM	3	1.841	0.614	3.86	**0.022**	0.754
P	1	2.372	2.372	14.93	**0.001**	0.960
ZM X P	3	0.694	0.231	1.46	0.251	0.335
Tank	24	3.812	0.159			
Date	3	46.473	15.491	199.88	<**0.001**	1.000
ZM X Date	9	1.045	0.116	1.50	0.165	0.663
P X Date	3	0.205	0.068	0.88	0.454	0.234
ZM X P X Date	9	0.417	0.046	0.60	0.795	0.270
Tank X Date by ZM by P	72	5.580	0.078			

Table 4.Sum cladocerans repeated measures ANOVA table
(alpha = 0.05). Significant factors are bolded. ZM=zebra mussels, P=total phosphorous, X= interaction of variables, Tank=mesocosm tank, Date=date of sampling.

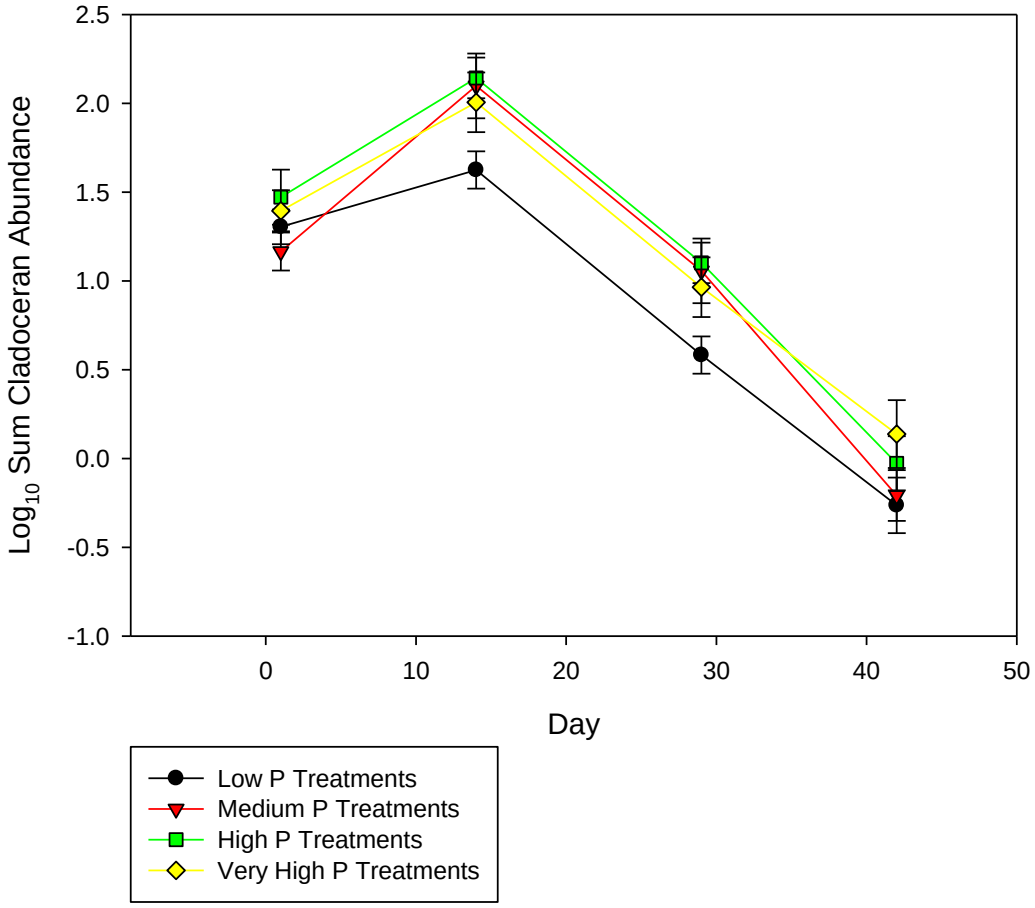

Figure 4. Log_{10} sum cladoceran abundance in phosphorous treatments over time. Days are from the start of the experiment (Day 0 = Sep 19th). circles are Low (L) treatments (25µg/L), triangles are medium (M) treatments (50µg/L), squares are high (H) treatments (100µg/L), and diamonds are very high (V) treatments (200µg/L).

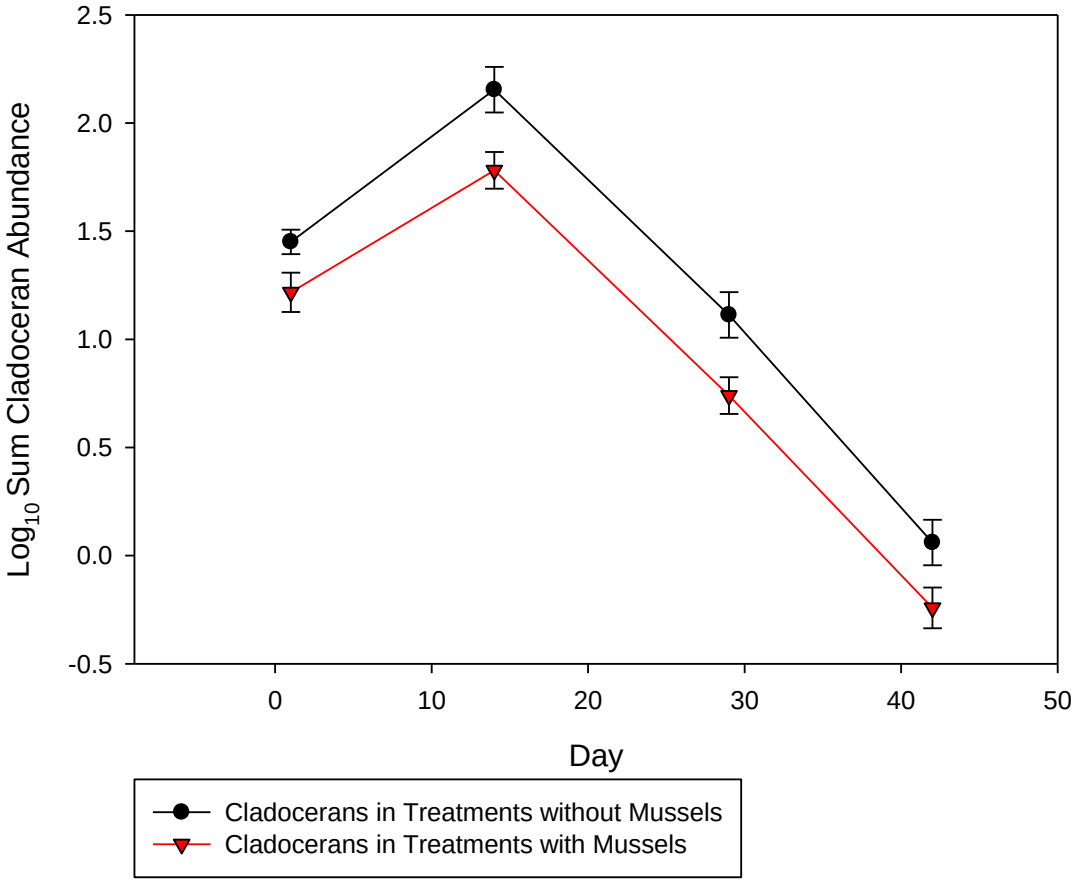

Figure 5-Log_{10} sum cladoceran abundance in zebra mussel treatments over time. Days are from the start of the experiment (Day 0=Sep 19th). Circles are treatments without zebra mussels, triangles are treatments with zebra mussels.

Source Term	Degree of Freedom	Sum of Squares	Mean Square	F-Ratio	Probability Level	Power
ZM	3	1.169	0.390	5.90	**0.004**	0.917
P	1	0.031	0.031	0.47	0.501	0.101
ZM X P	3	0.313	0.104	1.58	0.221	0.361
Tank	24	1.585	0.066			
Date	3	44.122	14.707	239.96	<**0.001**	1.000
ZM X Date	9	0.366	0.041	0.66	0.739	0.301
P X Date	3	0.252	0.084	1.37	0.258	0.350
ZM X P X Date	9	0.244	0.027	0.44	0.908	0.201
Tank X Date by ZM by P	72	4.413	0.061			

Table 5.Sum copepods repeated measures ANOVA table (alpha = 0.05). Significant factors are bolded. ZM=zebra mussels, P=total phosphorous, X= interaction of variables, Tank=mesocosm tank, Date=date of sampling.

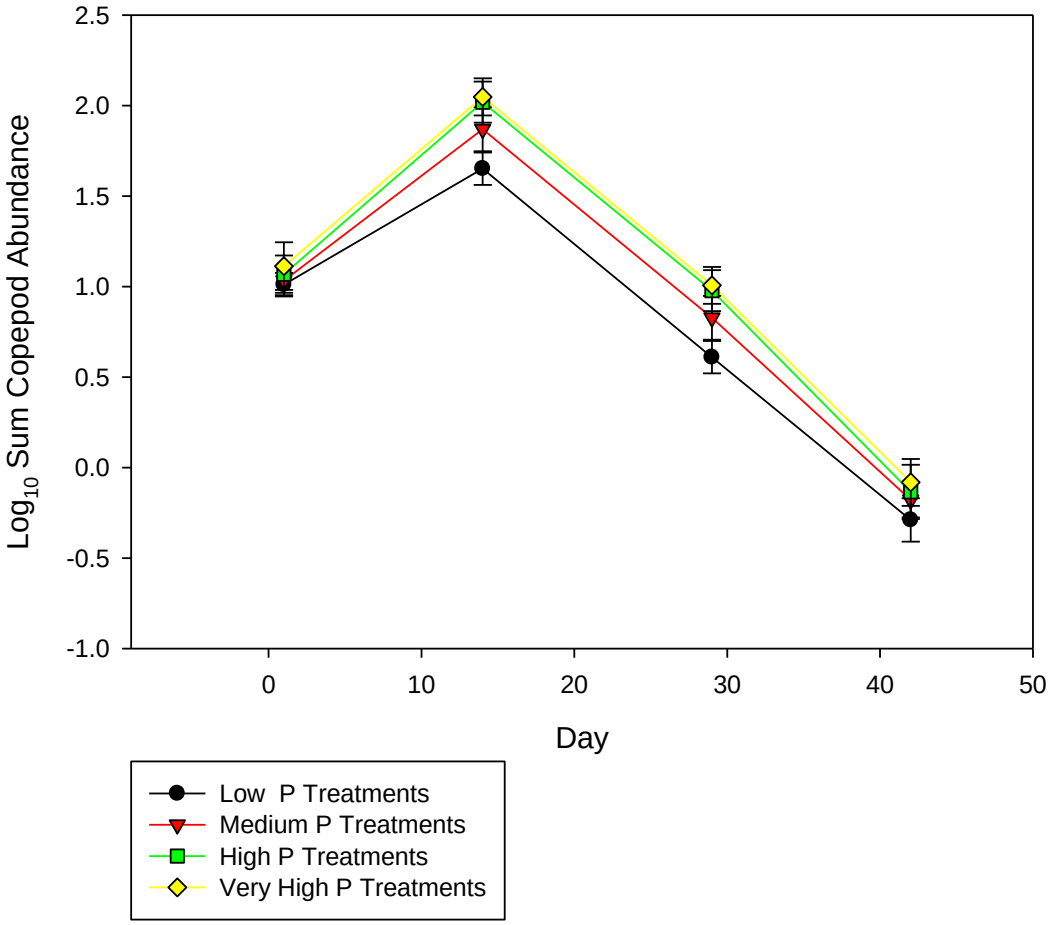

Figure 6. Log_{10} sum copepod abundance in phosphorus treatments over time. Days are from the start of the experiment (Day 0=Sep 19th). Circles are low (L) treatments (25µg/L), triangles are medium (M) treatments (50µg/L), squares are high (H) treatments (50µg/L), and diamonds are very high (V) treatments (200µg/L).

Indoor Mesocosm Experiment

There was a significant effect of the P treatment on zebra mussel filtering rates (ANOVA, P=0.018, Table 6). The low treatment and medium treatment filtering rate both differed from the very high treatments (P=0.023, P=0.04, table 7), both had an average higher filtering rate than the very high treatment (Figure 7).

Source Term	Degrees of Freedom	Sum of Squares	Mean Squares	F-Ratio	Probability Level
Between Groups	3	0.0859	0.0286	12.155	**0.018**
Residual	4	0.009	0.002		
Total	7				

Table 6.Filtering rate one-way ANOVA table (alpha = 0.05).Significant factors are bolded.

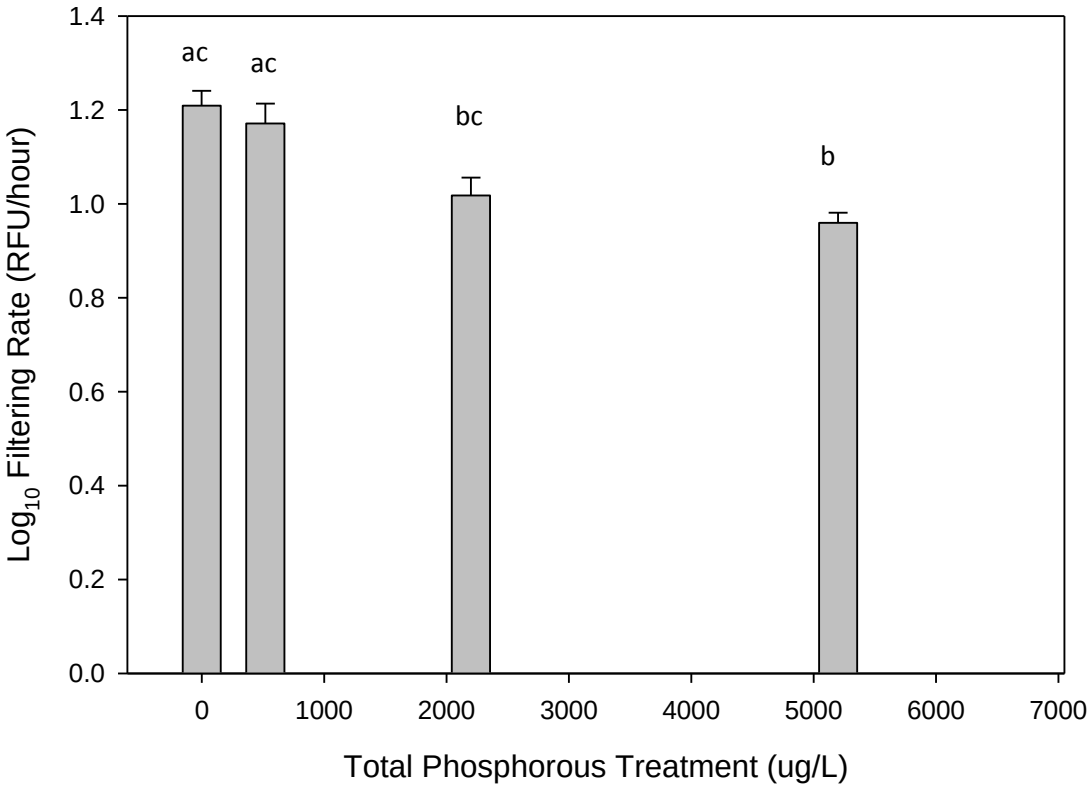

Figure 7**.** Log_{10} Zebra mussel filter rate measured in Relative Fluorescent Units per hour (RFU/hour). Treatment levels were low (0µg/L), medium (520µg/L), high (2200µg/L), and very high (5200µg/L). Different letters represent significant differences between treatments based on Tukey's post-hoc tests ($P<0.05$).

Discussion

Despite the importance of both eutrophication and zebra mussels, surprisingly little is known about the interactions between these two stressors. The objective of this research was to better understand the interactions between eutrophication and invasive zebra mussels to help better manage these important stressors. I predicted that treatments with higher P concentrations would have higher chlorophyll *a* levels due to reduced zebra mussel feeding rate compared to treatments with low P and mussels. I also hypothesized that increased P concentration would lead to a decline in zebra mussel feeding rates and increase phytoplankton growth as the zebra mussels would meet their dietary P requirements and reduce their feeding rate.

Outdoor Mesocosm Experiment

Both chlorophyll *a* and phycocyanin increased along the P gradient (Figure 1), which is consistent with a large body of research showing that phosphorus stimulates algal production (Smith 2003). However, my prediction that chlorophyll *a* would be higher in non-mussel treatments was incorrect, as zebra mussels did not decrease chlorophyll *a*. In contrast there was some indication that zebra mussels may have increased phycocyanin in the H treatment as indicated by a significant interaction between the P and the zebra mussel treatments. This result was somewhat surprising as one would expect algae abundance to be reduced due to the zebra mussels feeding. However, the literature is conflicting, as Higgins et al. (2011) found through an analysis of zebra mussel effects on multiple lakes that the chlorophyll *a*:TP ratio was reduced by zebra mussels because chlorophyll *a* decreased in invaded lakes. Knoll et al. (2008) and

Raikow et al. (2004) showed that there was a positive impact on cyanobacteria in the presence of zebra mussels but only at low P conditions (<25µg/L). Wojtal-Frankiewicz and Frankiewicz (2011) also observed the highest chlorophyll *a* levels in zebra mussel only treatments as opposed to their controls and *Daphnia* only treatments. They attributed this to P release by zebra mussels as phosphate concentrations were highest in zebra mussel treatments and could imply that P release from zebra mussels could contribute to algal blooms (Wojtal-Frankiewicz and Frankiewicz 2001). Although the P levels in the current experiment were highest in the V treatments, excess P in the H treatment may have been more optimal for mussels, phytoplankton, and/or cyanobacteria. Potentially as mussels were taking up phytoplankton in the H treatment they were releasing P as waste, and this excess P in turn led to increased phytoplankton and cyanobacteria growth. This is supported by Conroy et al. (2005) findings which showed an increase in P turnover in mesocosms with zebra mussels present versus those with only zooplankton, which could also lead to increased phytoplankton growth. Additionally, Hunt and Matveev (2005) found that in a mesocosm study comparing grazing effects of a zooplankton grazer (*Cerodaphnia*) on phytoplankton in the absence of small fish predators, phytoplankton abundance tended to increase despite grazing presence. They attributed this to nutrient release from zooplankton, which counteracted the grazing pressure.

The lack of significant effects of mussels on chlorophyll *a* or interactions between P and mussels in the current experiment may be due to the size of mussels that I used in the experiment. Mussel size and mass play a role in filter and feeding capacity of zebra mussels. Conroy et al. (2005) looked at *Dressena* remineralization in Lake Eire and

found that phosphate release was highest in mussels 15-25mm in shell length, with smaller mussels releasing less P into the water column. Due to the lack of readily available mussels of larger sizes at local sites when my experiment was established, the mussels used in the mesocosms were smaller than 15mm. Due to their size, the smaller mussels in this experiment could have less of an impact through filtering since mussels did not have a significant effect on P levels but P was observed to be slightly higher in mussel treatments. Larger mussels with increased filter effects may alter P concentrations and additional studies should focus on interactions between P and zebra mussels of varying sizes.

Seasonality may have also been an important component of this study. Most field and outdoor mesocosm studies are conducted during the summer when there is the greatest amount of photo activity and the warmest temperatures. While field studies measuring biotic and abiotic factors can continue throughout the entire year, (MacIsaac et al. 1992, Vanderploeg et al. 2009, Bowen and Johannsson 2011) resources in a mesocosm are inherently limited, thus a month during peak photo activity is preferred and tends to have the highest productivity (Sarnelle 2012). During sampling for my project in the fall the temperature maximum was 31.1^{o}C with a mean high of 26.7^{o}C, a minimum temperature of 6.1^{o}C with the mean low being 11.1^{o}C, and the daytime average temperature being 18.9^{o}C (https://www.mesonet.org/). As such, the effects of P and zebra mussels on algae may have been lower than observed in other summer experiments because of colder temperatures and shorter days in the current experiment, particularly at the end of the experiment in October.

I predicted that zooplankton communities in mussel treatments would decrease in abundance due to interspecific effects, namely predation and competition from zebra mussels (Dzialowski 2013). Cladoceran abundance was positively affected by P, but negatively affected by zebra mussels as the presence of zebra mussels caused cladocerans to decline. Total copepods were similarly affected by P, as abundances increased with increasing P. Both cladocerans and copepods had their highest abundances in V and H treatments, potentially as these treatments had the greatest available phytoplankton biomass for food. Previous studies have found that zebra mussel effects, both direct predation on smaller zooplankton taxa and competition for phytoplankton food resources, led to declines in zooplankton biomass (Higgins and Vander-Zanden 2010, Bowen and Johannsson 2011) explaining the observed decline in cladocerans in zebra mussel treatments. The most noticeable decline in zooplankton abundance was in the L treatments where lower P concentrations could have contributed to reduced phytoplankton biomass, so a decline could have been caused by limited food resources. In the mussel treatments this could have been compounded by not only reduced food resources but also the increased level of resource competition between mussels and cladocerans.

Indoor mesocosm experiment

Zebra mussel feeding rate declined with increasing P enrichment in the treatments, which I attributed to the excessive P that was added to the mesocosms. Although zebra mussels cannot directly take up P, algae can uptake P at very high concentrations (>500µg/L) over a relatively short period of time (15 minutes) (Plath and

Boersma 2001). Zebra mussels likely became satiated from feeding on the P rich algae leading to reduced filtering demands, which is consistent with other studies that looked at stoichiometric imbalances under high P conditions. Plath and Boersma (2001) showed that *Daphnia* exhibited reduced growth and feeding rates under high P conditions. More recently, Laspoumaderes et al. (2016) showed that three species of *Daphnia* exhibited increased metabolic costs as indicated by increased respiration rates when feeding on P-rich algae. Interestingly, the *Daphnia* also exhibited increased feeding rates on P-rich food although the rates were reduced compared to moderately P-rich food (Laspoumaderes et al. 2016).

There appears to be a cost for maintaining excess internal P. Under nutrient limited conditions, nutrients are held as consumers maintain homeostasis of body elements despite variability in their food source's elemental ratio (Urabe 1993). Morehouse et al. (2013) showed that the effects of a low C:P diet on zebra mussels growth rate had severe physiological effects on mussel condition (release of ammonia due to being internal C limited), which resulted in reduced growth rates. This would suggest that an increase in biologically-available P in a system would not result in a higher filtering rate, as the mussels would become limited by other elements (e.g., C) in their diet (Plath and Boersma 2001). Laspoumaderes et al. (2016) termed this as a "stoichiometric knife edge", in which an optimal internal elemental balance exists and diverting from this, either by ingesting food of a lower or higher nutrient:C ratio, has immediate detrimental effects. As with established freshwater plankton consumers (Plath and Boersma 2001) zebra mussels also seem to be effected by excess P in their diet (Morehouse et al. 2013).

Interestingly, there did not appear to be a difference in the feeding rate of zebra mussels in the L and M treatments despite the large difference in the P concentrations between these two treatments. Unlike the outdoor experiment where the total P gradient ranged from 25µg/L-200µg/L, the range of P enrichment in the indoor experiment was much greater with the difference between the L and M treatments being 15µg/L-520µg/L. Despite this substantial difference in P concentration between these two treatments, feeding rate did not decrease until P concentrations reached extremely high levels. These findings suggest that although there is a restriction for mussel feeding on P-rich algae, the restriction occurs at extremely high P concentration (5,200µg/L). My findings suggest that the negative effects of P on mussel feeding rates are not likely to occur in natural settings because P concentrations in excess of the H and V treatments are relatively rare as Laspoumaderes et al. (2016) noted that the P-rich conditions which he tested *Daphnia* in were also not ecologically relevant. It is also important to note that zebra mussel feeding rates (as well as other filter feeders) may respond differently under P-rich conditions when feeding on more complex algae assemblages and under different water quality conditions (e.g., increased turbidity) that occur in nature (Laspoumaderes et al. 2016). Additional experiments should use mesocosms that are filled with natural lake seston under different P conditions (Plath and Boersma 2001).

Conclusion

In summary, while P did play a role in phytoplankton and cyanobacteria growth in the mesocosms, it did not affect mussels, neither increasing their feeding rate at low P nor reducing it at high P in the mesocosm. However P was found to affect feeding rate for

mussels at much higher P concentrations, reducing it in very high P treatments, although these treatments are beyond what would normally occur in nature, including hypereutrophic reservoirs found in the United States. As a theoretical case this study provides a unique perspective on excess P in the environment. Although in most cases P is a limiting element and is in high demand by many species, it also seems that stoichiometric ratios are maintained by organisms (Laspoumaderes et al. 2016). Despite an abundance of P too much of this element can be detrimental to organismal function. More research is telling us that the stoichiometric balance is more important than environmental elemental abundance for proper organismal function. This gives us insight not only at an organismal level but also how this can affect communities and ecosystems and that the manipulation of elements both intentionally and unintentionally can lead to changes on multiple trophic levels.

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