

Effects of invasive zebra mussels on phytoplankton, turbidity, and dissolved nutrients in reservoirs

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Abstract Few experiments have quantified the effects of invasive zebra mussels (*Dreissena polymorpha*) on man-made reservoirs relative to other aquatic habitats. Reservoirs, however, are the dominate water body type in many of the states that are at the current front of the zebra mussel invasion into the western United States. The objective of this research, therefore, was to determine how zebra mussels affected phytoplankton, turbidity, and dissolved nutrients in water that was collected from three Kansas reservoirs that varied in trophic state (mesotrophic to hypereutrophic), but all experienced frequent cyanobacterial blooms. Laboratory mesocosm experiments were conducted to document the effects of zebra mussels on cyanobacteria and general water quality characteristics in the reservoir water. Zebra mussels significantly reduced algal biomass, and the total biovolume of cyanobacteria (communities were dominated by

Anabaena) in each reservoir experiment. The effects of zebra mussels on other major algal groups (diatoms, flagellates, and green algae) and algal diversity were less consistent and varied between the three reservoir experiments. Similarly, the effects of zebra mussels on nutrient concentrations varied between experiments. Zebra mussels increased dissolved phosphorus concentrations in two of the reservoir experiments, but there was no effect of zebra mussels on dissolved phosphorus in the mesotrophic reservoir experiment. Combined, our results strongly suggest that zebra mussels have the potential to significantly impact reservoirs as they continue to expand throughout the western United States. Moreover, the magnitude of these effects may be context dependent and vary depending on the trophic state and/or resident phytoplankton communities of individual reservoirs as has similarly been reported for natural lakes.

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Introduction

Invasive species have impacted virtually every ecosystem in the world. As cited by Langkilde (2009), over 205 nonnative species have been introduced into the United States since 1980, and 30% are estimated to have negative environmental and/or economic impacts. Aquatic ecosystems are especially sensitive

to invasive species with the establishment of invaders occurring more frequently in recent years, in part due to alterations of these ecosystems by humans (Holeck et al., 2004; Strayer, 2010). The zebra mussel (*Dreissena polymorpha*) illustrates the significant ecological and economic impacts that can be associated with an aggressive biological invader (Strayer, 2009). Since its invasion into the United States in the 1980s, zebra mussels have expanded their range to include water bodies in at least 30 states (Benson, 2011).

One of the most important impacts of zebra mussels has been on the biomass and community composition of phytoplankton. In a recent meta-analysis, Higgins & Vander Zanden (2010) showed that zebra mussels have reduced water column phytoplankton biomass by 35%–78% in invaded lakes and rivers. In contrast, the effects of zebra mussels on individual taxa have been more variable. While Higgins & Vander Zanden (2010) reported a mean 58.1% decrease in cyanobacteria in invaded systems, several individual studies have shown that zebra mussels can actually promote the growth of nuisance cyanobacteria (MacIsaac, 1996; Vanderploeg et al., 2001; Raikow et al., 2004; Sarnelle et al., 2005; Bykova et al., 2006; Knoll et al., 2008). Zebra mussels directly facilitate cyanobacteria through selective grazing as unwanted algal cells are covered in mucus and then rejected through the inhalant siphon as pseudofeces (Juhel et al., 2006). The algal cells that are rejected through this process can then remain viable and accumulate in the water column and continue to grow (Dionisio Pires & Van Donk, 2002). Cyanobacteria can also depress zebra mussel feeding rates (Vanderploeg et al., 2009) and cause zebra mussels to avoid cyanobacteria (Naddafi et al., 2007). These effects combined with consumption of non-cyanobacterial phytoplankton that are more palatable to zebra mussels have resulted in increases in cyanobacteria following zebra mussel invasions in at least some systems (Dionisio Pires et al., 2005; Juhel et al., 2006; Vanderploeg et al., 2009). It is important to note, however, that the increasing effects of zebra mussels on cyanobacteria appear to be taxa and/or system specific. For example, several studies have shown that the biovolume of *Microcystis* was greater in systems with zebra mussels than it was in non-invaded systems (Raikow et al., 2004; Knoll et al., 2008) or that *Microcystis* increased within individual systems following invasion by zebra mussels (Vanderploeg et al., 2001). The colonial

cyanobacterium *Aphanizomenon* also bloomed in the late summer in Lake Oneida, NY following invasion by zebra mussels (Horgan & Mills, 1997). In contrast, however, other studies have shown or suggested that zebra mussels can have negative effects on *Microcystis* (Baker et al., 1998; Smith et al., 1998; Dionisio Pires et al., 2004) or *Anabaena* (Knoll et al., 2008).

Other important impacts of zebra mussels include increases in water clarity (Higgins & Vander Zanden, 2010) and alterations in the concentrations of dissolved nutrients, such as ammonia, nitrate, and soluble reactive phosphorous (Makarewicz et al., 2000; Bykova et al., 2006; Miller & Watzin, 2007; Strayer, 2009). Zebra mussels have also reduced the ratios of total nitrogen to total phosphorus (TN:TP) in some systems (Miller & Watzin, 2007). Lower TN:TP ratios could in turn further favor cyanobacteria that are able to fix nitrogen from the atmosphere and do well under nitrogen-limiting conditions (Smith & Bennett, 1999). Combined, these impacts have helped primary production to be shifted from pelagic to benthic regions (e.g. macrophytes and/or attached algae) in a number of invaded systems (Higgins & Vander Zanden, 2010).

Few experiments to date have been conducted to quantify the effects of zebra mussels on man-made reservoirs relative to other aquatic habitats in the United States. However, reservoirs are the dominant water body type in many of the states that are at the current western front of the zebra mussel invasion (see Benson, 2011 for a recent distribution map). Reservoirs differ from natural lakes in many ways including size, shape, shoreline development, and water flushing rates (Thornton et al., 1990). Reservoirs also often have larger watersheds, are more eutrophic, and turbid (Thornton et al., 1990), and at least in some instances, produce more cyanobacteria per unit total phosphorus than natural lakes (Dzialowski et al., 2011). With respect to invasive species, reservoirs tend to support multiple invaders, and they are more likely to be invaded than natural lakes (Johnson et al., 2008). Based on these differences between natural lakes and reservoirs, therefore, it is likely that the effects of zebra mussels on water quality may be significantly different in these two types of water bodies as well.

Limited research suggests that zebra mussels have the ability to significantly impact reservoirs. Wojtal-Frankiewicz & Frankiewicz (2011) recently conducted a laboratory mesocosm study using water that was collected from a Polish reservoir to document

zebra mussel impacts. They found that zebra mussels were able to significantly alter nutrient concentrations and algal community structure in the reservoir water. Several studies also showed that zebra mussels can significantly impact pond ecosystems (Noordhuis et al., 1992; Reeders et al., 1993). For example, Noordhuis et al. (1992) observed that cyanobacteria disappeared from an experimental pond following zebra mussel invasion. In order to further study how zebra mussels impact reservoir ecosystems, we conducted several short-term laboratory mesocosm studies using water that was collected from three Kansas reservoirs that varied in trophic state from mesotrophic to hypereutrophic. Specifically, we were interested in determining how zebra mussels impacted the biomass and community structure of phytoplankton and several important water quality parameters (e.g., turbidity and dissolved nutrient concentrations) in the reservoir water, and if these impacts were context dependent and varied based on the trophic state of the reservoirs.

Methods

Laboratory mesocosm experiments were conducted using water that was collected from three Kansas reservoirs: Big Hill (mesotrophic, TP = 23.4 µg/l, 8.4–35.1), Cheney (eutrophic, TP = 85.2 µg/l, 57.9–209.0), and Marion (hypereutrophic, TP = 206.7 µg/l, 121.0–384.0) (average, range from Dzialowski et al., 2009).

Surface water samples were collected from each reservoir and returned to the laboratory at Oklahoma State University. Water was collected from Cheney on August 5, 2010, Marion on August 13, 2010, and Big Hill on August 23, 2010; experiments were staggered, and each was initiated within 12 h of collecting the water from the respective reservoir. To begin each experiment, the reservoir water was first filtered through an 80-µm mesh net to remove macrozooplankton and then added to twelve 18-l mesocosms. Zebra mussels for each experiment were collected from Sooner Reservoir located near Stillwater, OK. They were collected from the field and within 6 h were added to six randomly selected mesocosms, where they attached to the bottom and sides of the mesocosms shortly after addition. The remaining six mesocosms were used as zebra mussel-free controls.

Zebra mussels were added to the mesocosms at a density of 1/l, which is consistent with densities used in previous experiments and with volumetric densities found in nature (Mellina et al., 1995). The mussels ranged in size between 12 and 20 mm in length (Naddafi et al., 2007). Full spectrum lights were placed on top of the mesocosms on a 16-h light/8-h dark schedule, and each mesocosm was gently aerated with an air stone. Once the zebra mussels were added to the mesocosms, each experiment was maintained for 96 h (Miller & Watzin, 2007).

Time 0 water samples were collected immediately before zebra mussels were added to the assigned mesocosms using clear 275-ml bottles. Water samples were then collected every 12 h over the course of the 96-h experiment for measurements of chlorophyll *a* (Miller & Watzin, 2007). Before the collection of samples, the mesocosms were gently stirred to resuspend settled material. Concentrations of chlorophyll *a* were determined on samples that were collected onto Whatman GF/F glass fiber filters and frozen until analysis. Chlorophyll *a* was then extracted in 90% basic (10% saturated MgCO₃) methanol for 20–24 h in the dark at 4°C (Cleceri et al., 2005) and then measured with a Turner Fluorometer. Turbidity was measured in the center of each mesocosm using a Horiba multi-probe, after the mesocosms were gently stirred.

Samples were collected at the completion of each experiment (time 96 h) for measurements of soluble reactive phosphorus (SRP) and ammonia. SRP was analyzed within 24 h of sample collection using a Genesys 20 Spectrophotometer (Cleceri et al., 2005). Water samples for ammonia were frozen until analyses were performed at a later date using an Accumet Excel XL 25 dual channel pH/ion meter as NH₄-N (Cleceri et al., 2005).

Phytoplankton samples (250 ml) were also collected at the end of each experiment from the center of the mesocosms in amber glass bottles. Phytoplankton samples were preserved in Lugol's solution and identified using the Utermohl technique (Utermohl, 1958; Cleceri et al., 2005). In brief, a 10 ml aliquot was taken from each sample and placed in a settling chamber for 24 h. The settled phytoplankton were then identified using a Zeiss inverted microscope at 400× magnification, and the biovolume of each taxon was determined using approximate geometric shapes. Phytoplankton were identified to corresponding genus

or species whenever possible and organized into four broad groups: diatoms, flagellates, cyanobacteria, and green algae. Data are reported as biovolume (mm^3/l). Shannon Diversity, a measure of biodiversity that accounts for both taxa richness and evenness, was calculated for the phytoplankton in each sample based on biovolume measurements (Cadotte et al., 2010).

Repeated Measure Analysis of Variance (RM-ANOVA) was used to determine if zebra mussels had significant effects on turbidity and chlorophyll *a* concentrations in the mesocosms over the course of each 96-h experiment. Individual RM-ANOVAs were used for each reservoir experiment where zebra mussels and time were the independent variables, and turbidity and chlorophyll *a* were the dependent variables. When significant differences were detected with RM-ANOVA, Holm-Sidak tests ($P < 0.05$) were used to identify differences between individual treatments at the individual sampling times.

T-tests or Mann–Whitney tests (when data were not normally distributed) were used to determine if zebra mussels affected the concentrations of dissolved nutrients (SRP and ammonia) at the end of each experiment (time 96 h). With respect to phytoplankton, comparisons were made using time 96-h data between mesocosms with and without zebra mussels for total phytoplankton biovolume, the biovolume of the major phytoplankton groupings, and the most abundant cyanobacteria taxa individually using *t*-tests or Mann–Whitney tests.

Results

Zebra mussels had significant negative effects on turbidity (RM-ANOVA, zebra mussel effect, $F_{(1,10)} \geq 71.45$, $P < 0.001$ for each experiment; Fig. 1) and chlorophyll *a* (RM-ANOVA, zebra mussel effect, $F_{(1,10)} \geq 19.42$, $P < 0.001$ for each experiment; Fig. 2) in each of the three experiments. There were also significant zebra mussel \times time interactions for turbidity (RM-ANOVA, zebra mussel effect, $F_{(8,80)} \geq 9.60$, $P < 0.001$ for each experiment) and chlorophyll *a* (RM-ANOVA, zebra mussel effect, $F_{(8,80)} \geq 7.89$, $P < 0.001$ for each experiment) in each experiment. Specifically, turbidity was lower ($P < 0.05$, Holm-Sidak tests) in water that was collected from the zebra mussel mesocosms during each 12 h sampling event in the Big Hill experiment and for each 12-h sampling

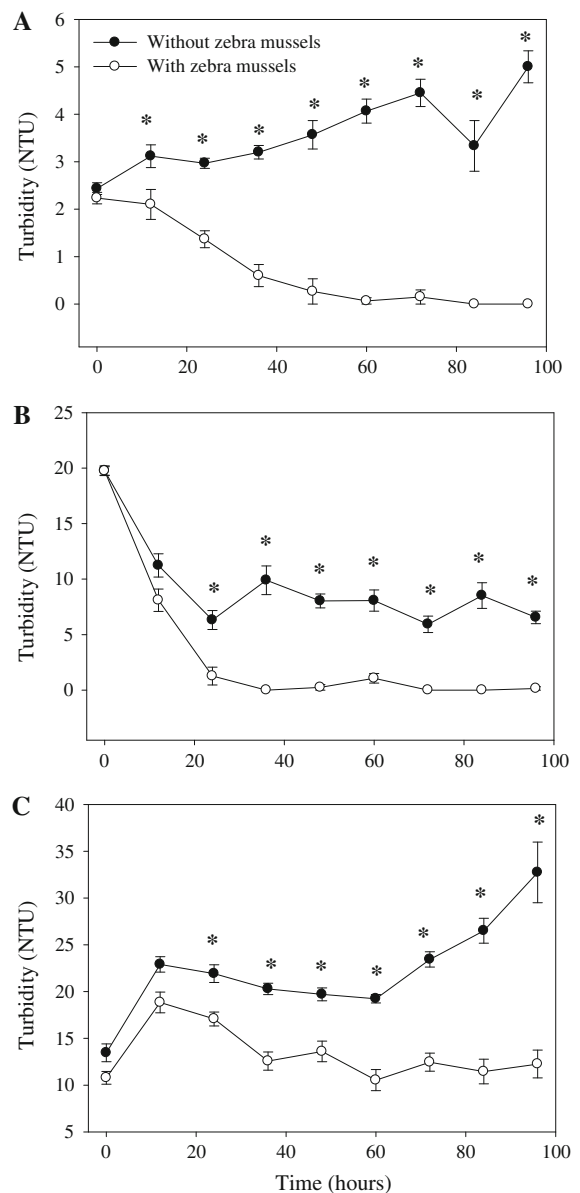


Fig. 1 Effects of zebra mussels on turbidity concentrations in the experimental mesocosms. Zebra mussels significantly lowered turbidity in each experiment. Significant differences between treatments for individual sampling times based on Holm-Sidak tests (* $P < 0.05$). **A** Big Hill, **B** Cheney, **C** Marion

event beginning at 24 h through the completion of the experiment for the Cheney and Marion experiments. Similarly, chlorophyll *a* was lower ($P < 0.05$, Holm-Sidak tests) in water that was collected from the zebra mussel mesocosms for each of the 12-h sampling events in each experiment except for the

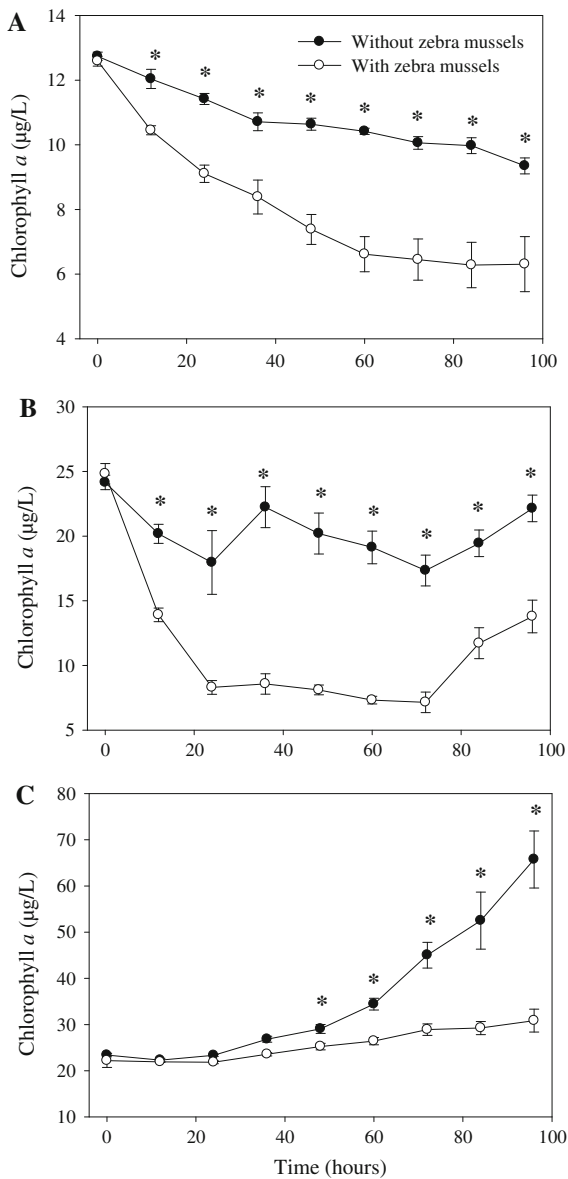


Fig. 2 Effects of zebra mussels on chlorophyll *a* concentrations in the experimental mesocosms. Zebra mussels significantly lowered chlorophyll *a* in each experiment. Significant differences between treatments for individual sampling times based on Holm-Sidak tests ($*P < 0.05$). **A** Big Hill, **B** Cheney, **C** Marion

Marion experiment where differences were first detected at 48 h and then throughout the remainder of the experiment (Fig. 2).

Cyanobacteria accounted for 92.2, 47.0, and 86.7% of the total algal biovolume in Big Hill, Cheney, and Marion reservoirs (based on the data from the control mesocosms at time = 96 h), respectively.

Table 1 Relative abundances (% based on biovolume) of the major cyanobacterial taxa in each of the three reservoirs

	Big Hill (%)	Cheney (%)	Marion (%)
<i>Anabaena</i>	59.9	97.5	90.7
<i>Chroococcus</i>	<1	<1	<1
<i>Cylindrospermopsis</i>	22.3	0	6.3
<i>Lyngbya</i>	13.5	<1	<1
<i>Oscillatoria</i>	<1	0	1.4

Values are based on measurements taken at the end of each experiment in control mesocosms (no mussels, time = 96 h). Other taxa were present, but at levels below 1% of the total cyanobacterial biovolume

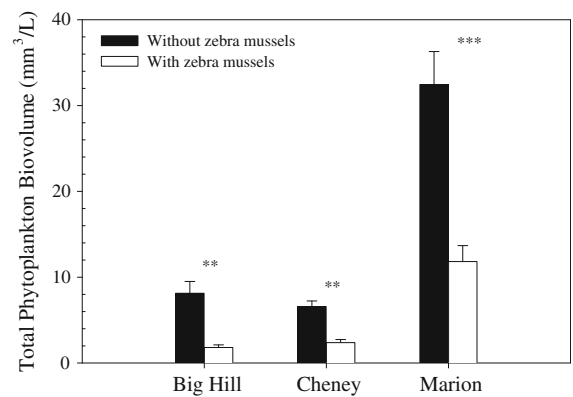


Fig. 3 Effects of zebra mussels on total phytoplankton biovolume in the experimental mesocosms at the end of the 96-h experiments. Significant differences were observed in each experiment. *P* values were determined using *t*-tests ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns = $P > 0.05$)

Furthermore, *Anabaena* was the dominant cyanobacterium in each reservoir accounting for 59.9, 97.5, and 90.7% of the total cyanobacterial biovolume in Big Hill, Cheney, and Marion reservoirs, respectively (Table 1). The major groupings of cyanobacteria that were found in at least one of the experiments included: *Anabaena*, *Chroococcus*, *Cylindrospermopsis*, *Lyngbya*, and *Oscillatoria*; additional genera were also present, but at lower biovolumes. Total phytoplankton biovolume (Fig. 3) and the total biovolume of cyanobacteria (Fig. 4) were both significantly lower in zebra mussel mesocosms than they were in control mesocosms in the three experiments. Zebra mussels significantly reduced the biovolume of *Anabaena* in each experiment, while the effects on other genera varied (Table 2). Zebra mussels significantly reduced the

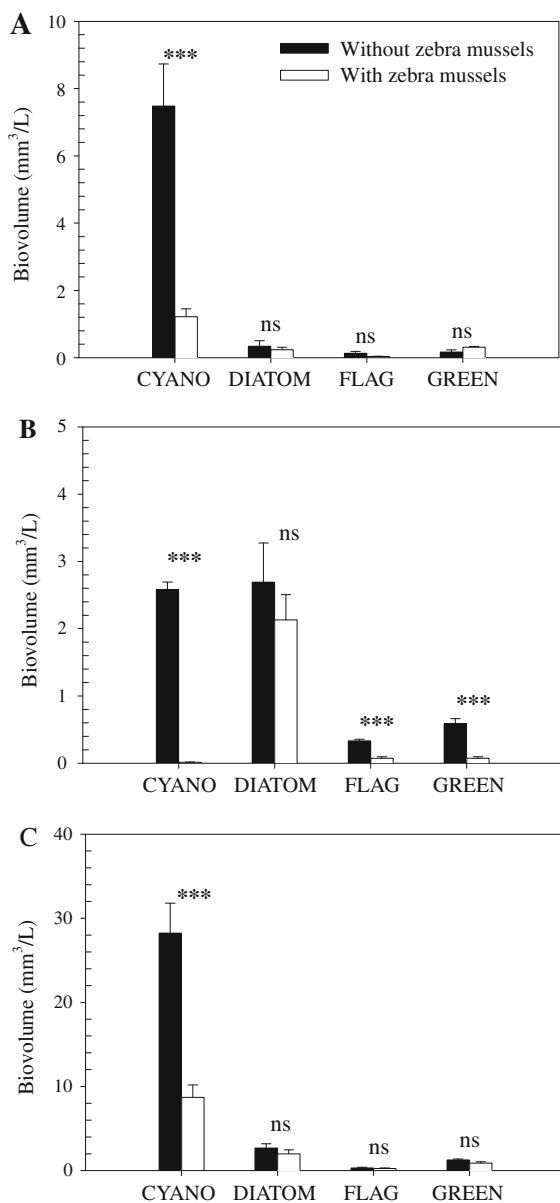


Fig. 4 Effects of zebra mussels on the biovolume of the four major phytoplankton groupings in the experimental mesocosms at the end of the 96-h experiments. **A** Big Hill, **B** Cheney, **C** Marion. Significant differences were observed in each experiment. *P* values were determined for Big Hill using Mann–Whitney tests for each group except green algae; for Marion using *t*-tests for each group; and for Cheney using *t*-tests for cyanobacteria and flagellates, and Mann–Whitney tests for diatoms and green algae (**P* < 0.05, ***P* < 0.01, ****P* < 0.001, ns = *P* > 0.05)

biovolume of *Cylindrospermopsis* and *Lyngbya* in the Big Hill experiment and *Cylindrospermopsis* in the Marion experiment (Table 2).

Table 2 Average biovolume (mm³/l) measurements for the major cyanobacterial taxa in mesocosms with and without zebra mussels in each of the three experiments (time = 96 h)

Reservoir	Taxa	Without zebra mussels	With zebra mussels	<i>P</i> values
Big Hill	<i>Anabaena</i>	4.45	0.75	0.002
	<i>Cylindrospermopsis</i>	1.83	0.11	0.002
	<i>Lyngbya</i>	1.02	0.16	0.004
Cheney	<i>Anabaena</i>	2.51	0.00	0.015
Marion	<i>Anabaena</i>	25.59	8.07	<0.001
	<i>Cylindrospermopsis</i>	1.78	0.08	0.002
	<i>Oscillatoria</i>	0.38	0.12	0.065

Comparisons were only made for those taxa that accounted for more than 1% of the total cyanobacterial biovolume (see Table 1). *P* values were determined using *t*-tests or Mann–Whitney *U* tests

The effects of zebra mussels on the other major groups of phytoplankton (diatoms, flagellates, and green algae) also varied between experiments. There were no significant differences in the biovolume of diatoms between zebra mussel and control mesocosms in any of the three experiments (Fig. 4). The total biovolume of flagellates and green algae were significantly lower in zebra mussel mesocosms in the Cheney experiment only (Fig. 4). Zebra mussels also had significant effects on Shannon Diversity in all the three experiments; however, the direction of these effects varied. Zebra mussels increased diversity in the Big Hill and Marion experiments, while they decreased diversity in the Cheney experiments (Fig. 5).

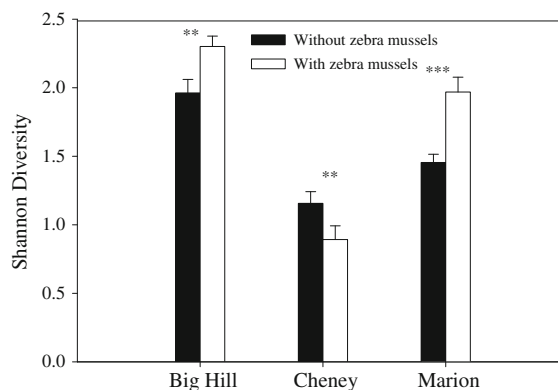


Fig. 5 Effects of zebra mussels on phytoplankton Shannon Diversity in mesocosms with and without zebra mussels at the end of each 96 h experiment. Significant differences were observed in each experiment. *P* values were determined using *t*-tests (**P* < 0.05, ***P* < 0.01, ****P* < 0.001, ns = *P* > 0.05)

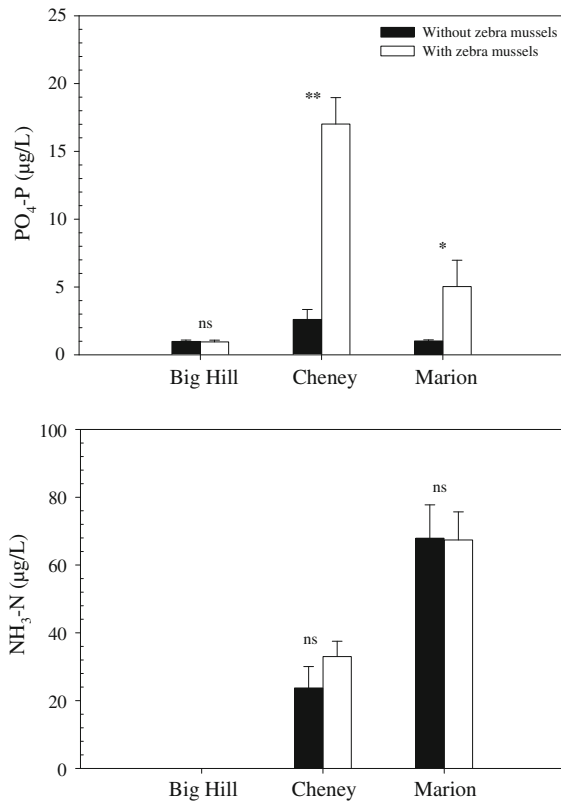


Fig. 6 Effects of zebra mussels on total soluble reactive phosphorus (SRP) and ammonia in mesocosms with and without zebra mussels at the end of each 96-h experiment. *P* values were determined using *t*-tests for SRP and Mann–Whitney *U* tests for ammonia ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns = $P > 0.05$). Note. ammonia concentrations were below detection in Big Hill

Concentrations of SRP were significantly higher in zebra mussel mesocosms than they were in control mesocosms in the Cheney and Marion experiments. There were no significant effects of zebra mussels on ammonia in the Cheney and Marion experiments, or on either dissolved nutrient in the Big Hill experiment (Fig. 6).

Discussion

Zebra mussels significantly reduced both total algal biomass (measured as chlorophyll *a*) and the biovolume of cyanobacteria. In each of the three reservoirs, cyanobacterial communities were dominated by species within the genus *Anabaena* (the dominant species were *Anabaena affinis* in Big Hill and Marion, and

Anabaena spiroides in Cheney). Interestingly, previous studies documenting the impacts of zebra mussels on *Anabaena* have varied. Bastviken et al. (1998) showed that zebra mussels did not reduce the relative abundance of *Anabaena* in experimental mesocosms, while Knoll et al. (2008) reported a negative association between *Anabaena* and zebra mussels in Michigan lakes. Our results clearly show that zebra mussels were able to graze *Anabaena* from the three reservoirs. *Anabaena* typically dominate cyanobacterial communities in Kansas reservoirs (Dzialowski et al., 2009); therefore, cyanobacterial blooms may be less frequent and/or of reduced magnitude in invaded reservoirs. In order to test this hypothesis under more natural conditions, however, we suggest that biovolumes of *Anabaena* be compared in reservoirs with and without zebra mussels similar to those surveys that were conducted for natural lakes in other parts of the country (e.g., Knoll et al., 2008; Kissman et al., 2010). Furthermore, monitoring changes in phytoplankton community composition over time following zebra mussel invasion in newly invaded reservoirs could also be used to test this hypothesis.

As previously mentioned, prior research from natural lakes suggests that zebra mussels can promote dominance by *Microcystis* in at least some systems (e.g., MacIsaac, 1996; Vanderploeg et al., 2001). In the current study, *Microcystis* was only present in four of the replicates in the Big Hill experiment; previously collected data from these three reservoirs also confirms that *Microcystis* are rare in these reservoirs (Dzialowski et al., 2009). In the Big Hill mesocosms in which *Microcystis* was detected, the relative biovolume ranged from only 1.3 to 5.9%, and there were no differences between mesocosms with and without zebra mussels (data not shown). It is also important to note that the effects of zebra mussels on *Microcystis* in natural lakes appear to be nutrient dependent (Raikow et al., 2004; Sarnelle et al., 2005; Knoll et al., 2008). For example, Raikow et al. (2004) reported that zebra mussels increased *Microcystis* sp. in low nutrient lakes in Michigan (TP < 25 µg/l), but not in high nutrient lakes (TP > 25 µg/l). While low nutrient lakes (e.g., TP < 25 µg/l) are rare in Kansas and other Central Plains states, Big Hill does exhibit average TP concentrations less than 25 µg/l (Dzialowski et al., 2009). Therefore, it is possible that if zebra mussels invade Big Hill and other relatively low nutrient reservoirs in the region that it could provide a

competitive advantage to *Microcystis* leading to increases in its relative abundance. In contrast, both Cheney and Marion (e.g., Cheney average TP = 85.2 µg/l; Marion average TP = 206.7 µg/l; Dzialowski et al., 2009) and most of the reservoirs in the region have average TP concentrations that are greater than 25 µg/l. As noted by Dzialowski & Jessie (2009), therefore, there may not be a high risk of zebra mussel mediated *Microcystis* blooms in reservoirs in this region because they tend to be eutrophic or hypereutrophic.

Relative to cyanobacteria, the effects of zebra mussel on other major groups of phytoplankton varied between experiments. Zebra mussels did not impact diatoms in any of the three experiments contrasting with the results of Heath et al. (1995) who found a 60% decrease in diatoms when zebra mussels were present in experimental enclosures. Flagellates and green algae were significantly reduced in the Cheney experiment only. Heath et al. (1995) similarly found a 40% decrease of green algae when zebra mussels were present in enclosures, while Vanderploeg et al. (2009) found that flagellates stimulated feeding in zebra mussels. Naddafi et al. (2007) showed that zebra mussels avoided chlorophytes (green algae) and preferred cryptophytes (e.g., *Cryptomonas* sp.—a flagellate) which were present in the Big Hill and Cheney experiments. Therefore, while previous research has shown that zebra mussels are able to reduce diatoms (Heath et al., 1995), green algae (Heath et al., 1995), and flagellates (Naddafi et al., 2007), similar effects were not consistently observed in the current study. However, these groups had low biovolumes relative to cyanobacteria in each reservoir experiment except Cheney (Fig. 4), which may have affected grazing rates in the current experiments.

Zebra mussels also had significant effects on phytoplankton diversity. Zebra mussels increased Shannon Diversity in the Big Hill and Marion experiments, but decreased Shannon Diversity in the Cheney experiment. In both the Big Hill and Marion experiments, phytoplankton communities were dominated by cyanobacteria. As described above, zebra mussels were able to significantly reduce the biovolume of cyanobacteria thus increasing evenness and Shannon Diversity of the communities in the mesocosms from these two studies. In the Cheney experiment, however, both cyanobacteria and diatoms were abundant. Although zebra mussels effectively grazed

cyanobacteria in Cheney experiment, they did not have the same effect on diatoms which led to an increase in the relative abundance of diatoms and an overall reduction in Shannon Diversity. Therefore, the starting community of phytoplankton (e.g., what species are present and which are dominant) should help us determine how zebra mussels affect the diversity of phytoplankton within individual reservoirs.

Zebra mussels reduced turbidity in each of the three experiments. Skubinna et al. (1995) similarly showed that turbidity declined from 9.2 NTU to 3.7 NTU in the three years following invasion in the Hudson Bay and Higgins & Vander Zanden (2010) also reported that water clarity increased in nearly all of the studies that they included in their meta-analysis following invasion. While our data clearly indicate that zebra mussels can reduce turbidity caused by phytoplankton, we do not know if zebra mussels were able to reduce non-algal turbidity in the reservoir water. Research suggests that zebra mussels can filter at least some suspended sediment particles from the water column (Higgins & Vander Zanden, 2010). Alternatively, zebra mussels may filter sediment particles from the water column, but then expel them as pseudofeces where they could be resuspended (Roditi et al., 1996). Reservoirs in Kansas and surrounding states tend to have high levels of non-algal turbidity (Dzialowski et al., 2011). Therefore, it is important to expand the current research to better understand how zebra mussels will impact suspended sediment concentrations and ultimately water clarity in turbid reservoirs.

The effects of zebra mussels on dissolved nutrient concentrations were reservoir specific. SRP concentrations were significantly higher in mesocosms with zebra mussels than they were in mesocosms without zebra mussels in the Marion and Cheney experiments. Similarly, zebra mussels have increased SRP concentrations in a number of natural systems following invasion including Lake Erie, Seneca River, and Lake St. Clair (James et al., 1997; Makarewicz et al., 2000; Higgins & Vander Zanden, 2010). Zebra mussels excrete high concentrations of SRP in eutrophic systems because there are high levels of nutrients available for consumption through the phytoplankton (Arnott & Vanni, 1996); the nutrients are then assimilated, and subsequently stored in the mussel's tissues or released back into the water column in dissolved form (Naddafi et al., 2008). In contrast to the

results observed in the Marion and Cheney experiments; however, zebra mussels did not affect SRP concentrations in the Big Hill experiment. Interestingly, of the three reservoirs, Big Hill had the lowest initial SRP concentrations. Johengen et al. (1995) found that SRP actually declined after zebra mussel invasion in Saginaw Bay, which they attributed to low initial concentrations of SRP. They hypothesized that phytoplankton communities in phosphorus-limited environments were more likely to utilize the SRP that was excreted by zebra mussels so that there were no increases in SRP levels. Similarly, Higgins & Vander Zanden (2010) found that zebra mussels did not have consistent effects on SRP in littoral and pelagic habitats of lakes. Instead, they suggested that there was a coupling between the pelagic and benthic regions of invaded systems where increases in dissolved nutrients from zebra mussels were quickly taken up and stored by benthic biota. Obviously, the current experiment was not designed to assess benthic-pelagic coupling or the impacts of phytoplankton and/or bacteria on nutrient cycling in mesocosms with and without zebra mussels. Therefore, additional studies are needed to determine how these factors affect the magnitude of zebra mussel impacts on nutrients within individual reservoir ecosystems.

Ammonia concentrations did not differ between control and zebra mussel mesocosms in any of the three experiments. Similarly, James et al. (1997) and Bykova et al. (2006) reported that dissolved nitrogen concentrations did not differ between zebra mussel and control mesocosms. In their meta-analysis, Higgins & Vander Zanden (2010) found that the effects of zebra mussels on dissolved nitrogen were complex. While zebra mussels generally increased ammonia concentrations in enclosure experiments, they found no consistent effects of zebra mussels on ammonia in natural systems (Higgins & Vander Zanden, 2010). Furthermore, as noted above the current experiment did not account for the effects of phytoplankton and/or benthic bacteria on dissolved nutrient concentrations in the mesocosms.

Conclusion

Combined, the results from the three experiments show that zebra mussels can alter phytoplankton biomass and community structure and general water

quality conditions in water collected from three reservoirs. However, the effects of zebra mussels appear to be context dependent and vary between reservoirs. For example, while zebra mussels were able to reduce the biovolume of cyanobacteria in each of the three experiments, the effects on other groups of algae varied between reservoirs. The overall effects on phytoplankton may be dependent on the initial composition of taxa that are present including the presence or absence of less-palatable taxa such as *Microcystis* sp. The effects of zebra mussels on *Microcystis*, however, may not be as significant as previously reported in other parts of the country because most of the reservoirs in this region are eutrophic with TP concentrations $>25 \mu\text{g/l}$ (e.g., Raikow et al., 2004). Furthermore, the effects of zebra mussels on nutrient concentrations also appeared to be reservoir specific. Zebra mussels increased SRP concentrations in the two reservoirs with the highest initial nutrient concentrations; in contrast, they had no effect on SRP concentrations in the low nutrient reservoir.

We believe that our results provide an important step in determining how zebra mussels impact man-made reservoirs that are the dominant water body type in many of the states that are at the current western front of its invasion. However, as we have noted above, additional experiments are needed to verify our results under more natural conditions. For example, our mesocosms did not allow for the consideration of how important environmental factors may influence the ability of zebra mussels to impact phytoplankton and water quality in reservoir ecosystems (e.g., benthic-pelagic coupling, mixing regimes; see *Comment* by Conroy (2010) and *Reply* by Dzialowski & Jessie (2010)). Therefore, additional studies that compare conditions in reservoirs with and without zebra mussels are needed to test the hypotheses outlined above. Specifically, surveys of reservoirs such as those that have previously been conducted in Michigan lakes with and without zebra mussels (Raikow et al., 2004; Knoll et al., 2008; Kissman et al., 2010), will allow for a determination of zebra mussel impacts on the biological and chemical conditions of reservoir ecosystems.

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