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COMPLEX INTERACTIONS BETWEEN ZEBRA MUSSELS
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COMPLEX INTERACTIONS BETWEEN ZEBRA MUSSELS AND THEIR PLANKTONIC PREY

By

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ABSTRACT

COMPLEX INTERACTIONS BETWEEN ZEBRA MUSSELS AND THEIR PLANKTONIC PREY

By

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Many studies in North American lakes have documented decreases in phytoplankton and ciliate abundance after the invasion of the zebra mussel (*Dreissena polymorpha*). However, fewer studies have examined the effect of zebra mussels on phytoplankton species composition or investigated the effects at a scale appropriate to phytoplankton. In Chapter 1, I derived an equation that predicts zebra mussel dry tissue biomass from total phosphorus concentration to estimate a reasonable stocking density of mussels for my experiment. Chapter 2 describes a five-week replicated *in situ* mesocosm experiment I conducted to evaluate the impact of zebra mussels on phytoplankton and ciliate communities in a pond that lacked mussels. Within one week, zebra mussels non-selectively reduced phytoplankton biomass by 53%. The effect of zebra mussels on total phytoplankton biomass gradually declined over the remaining four weeks of the experiment. By the end of the experiment, no algal groups were statistically different between treatments. This waning effect of zebra mussels on algal abundance could not be explained by a shift towards less edible algal species and may have been due to the deteriorating condition of the zebra mussels. The algal data suggested that the zebra mussels suffered from food limitation after the first week. In contrast, the mussels reduced ciliate abundance by 70% or greater throughout the entire study.

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Introduction

The following two chapters represent part of the work I completed as part of my Master's degree requirements in Fisheries and Wildlife. I wanted to perform an ecologically sound mesocosm experiment aimed at examining the effect of zebra mussels on phytoplankton and ciliates. To do this correctly, I needed to determine a suitable amount of zebra mussels to stock into my enclosures. Since the pond where the experiment was conducted was mussel-free, I was unable to determine a zebra mussel biomass estimate for the pond. Chapter 1 describes an analysis of published data on zebra mussel biomass and limnological variables. From this data, a predictive equation was developed for calculating zebra mussel biomass from total phosphorus concentration. At the time when this thesis was submitted, a manuscript based on Chapter 1 was submitted to Archiv für Hydrobiologie. I used this equation from Chapter 1 to stock my experimental enclosures with a realistic, naturally occurring amount of zebra mussels. In Chapter 2, I describe an experiment I conducted to determine how zebra mussels affect phytoplankton and ciliates in a newly invaded system. A manuscript based on Chapter 2 is currently being prepared for submission to Canadian Journal of Fisheries and Aquatic Sciences.

Chapter 1: Relationship between zebra mussel biomass and total phosphorus in European and North American lakes

Introduction

Since its invasion from Europe in the mid-1980's, the zebra mussel (*Dreissena polymorpha*) has spread rapidly into freshwater systems throughout eastern North America (Hebert et al. 1991; Ludyanskiy et al. 1993), with often dramatic effects on community structure and ecosystem processes (Gillis and Mackie 1994; Johengen et al. 1995; Lavrentyev et al. 1995; MacIsaac et al. 1995; Nalepa et al. 1996; Bastviken et al. 1998; Pace et al. 1998). Forecasting the effects of zebra mussels on ecosystems yet to be invaded is currently limited by, among other things, the ability to predict the eventual abundance of *Dreissena*. Ramcharan et al. (1992a, b) were successful in building empirical models of steady-state (i. e., long-term average) abundance and population fluctuations based on lake characteristics, but these models only predict the density of mussels (number • m^{-2}). Many ecosystem impacts of invading species should be more closely linked to population biomass (g • m^{-2}) than to density (Mellina et al. 1995; Arnott and Vanni 1996; Young et al. 1996), so it would also be useful to develop empirical models that can predict zebra mussel biomass from easily-measured lake characteristics. For example, the relationship between zebra mussel body mass and the rate at which particles are filtered is only weakly nonlinear (log:log slope ~0.9, Kryger and Riisgard 1988), so biomass predictions can be used to roughly predict potential filtration rates by future mussel populations. A predictive model for zebra mussel biomass would also be helpful in the selection of mussel stocking levels for manipulative experiments, especially in habitats where no estimates of natural abundance are available.

A number of lake characteristics may potentially influence the biomass of zebra mussels in freshwater lakes, including: lake depth, bottom slope, substrate type, degree of mixing, turbidity, nutrient concentrations, and phytoplankton biomass (Hanson and Peters 1984; Rasmussen and Kalff 1987; Ramcharan et al. 1992b; Mellina and Rasmussen 1994). We expected mussel biomass to be positively related to TP, as seen for zoobenthic biomass in general (Hanson and Peters 1984; Rasmussen and Kalff 1987), because of the strong influence of phosphorus in limiting lake, and in particular, phytoplankton productivity (Schindler 1977; 1978). However, Stanczykowska (1984) reported a tendency for mussel density to be reduced in lakes with very high TP (> 300 $mg \bullet m^{-3}$) and Ramcharan et al. (1992b) found a negative relationship between mussel density and orthophosphate concentration.

Materials and Methods

Literature data

We found published data on zebra mussel biomass (reported here as dry tissue biomass) and one or more predictor variables, including; total phosphorus concentration (TP; summer and spring), calcium concentration (Ca^{+2}), lake area and depth (mean and maximum), Secchi depth, and chlorophyll concentration (summer and spring). We were only able to find sufficient literature data for three of these potential predictors; depth, Ca^{+2}, and TP. Of these three predictors, we did not expect there to be a strong influence of depth or calcium in the data set. Shallow lakes might be expected to have higher areal biomass than deep lakes, since a greater fraction of phytoplankton production should be available to benthic filter feeders, and there should be less oxygen depletion near the bottom in shallow well-mixed systems. However, most literature data on zebra mussel abundance refer to biomass in the depth zone of mussel occurrence, so deep areas with no mussels would presumably not affect the average biomass reported for deeper lakes. This makes it less likely that lake depth, independent of lake productivity, will influence zebra mussel biomass as typically reported in the literature. In addition, we limited our analyses to lakes that contain zebra mussels, so presumably all lakes in the data set should have sufficient calcium for mussel growth. Consequently, we did not expect Ca^{+2} to be an important factor influencing zebra mussel biomass (Sprung 1987; Ramcharan et al. 1992b). The data set comprised 32 lakes in Poland and six lakes in North America (Tables 1, 2). Note that the set of studies that report mussel biomass is only a small fraction of all studies that have estimated zebra mussel density.

Several of the Polish lakes were part of three lake systems: Beldany-Mikolajskie-Sniardwy; Bozcne-Niegocin; and Dargin-Dobskie-Kisajno-Mamry. We followed Ramcharan et al. (1992a) and considered each of these lakes as an independent observation, since there was considerable variation in mussel biomass and both stable and unstable mussel populations (Ramcharan et al. 1992a) among lakes within the same system. Treating these lakes as independent observations did not influence our conclusions with respect to the statistical significance (at $P < 0.05$) of the two relationships between mussel biomass and predictor variables that we report.

We excluded data from studies in which we judged that the lake bottom was sampled in a biased manner; as in studies that collected samples only from hard substrates or reefs (e. g., Hamilton et al. 1994; Kornobis 1977). We limited our data set to include only those studies that presented zebra mussel biomass as dry tissue weight, and in most cases, we relied on mean biomass values reported by the authors (all Polish lakes, Saginaw Bay, Lake St. Clair, Lake Erie). For the remaining lakes we made our own determinations of lake-wide mean biomass, as described below.

For Oneida Lake, we extracted size distribution data from Figure 7 of Mellina et al. (1995) with a digitizer, and applied their tissue mass to shell length relationship (dry mass = $0.00622\text{length}^{2.61}$) to determine biomass. For Lake Ontario, we relied on depth-specific biomass estimates (reported as kg • 10 min trawl^{-1}) from Figure 2 of Mills et al. (1999) and their estimate of 0.73 ha swept per 10 min trawl. Mills et al. (1999) reported dreissenid biomass for 8 depth strata ranging from 15 m to 85 m. We converted their depth-specific biomass estimates to an area-weighted lake average by determining the proportion of lake bottom within each of the sampled depth strata from a digitized bathymetric map (NOAA, National Geophysical Data Center).

Gull Lake sampling

We estimated zebra mussel biomass in Gull Lake (42°24'N, 85°24'W) on 8 - 9 July, 1999, 5 years after *Dreissena* was first sighted in this lake (see Moss 1972 for a description of the lake). Four sampling sites were selected randomly from each of four depths: 2.5, 5, 7.5, and 10 m. SCUBA divers collected all mussels and macrophytes by hand within a 1 m^2 quadrat from each site. Samples were frozen for a few days before sorting. We counted and measured all mussels larger than 15 mm, and subsampled smaller mussels. Some sites had large numbers of very small mussels attached to macrophytes. In these cases, macrophytes were subsampled by measuring the total wet weight of the macrophytes, then weighing out subsamples from which mussels were counted and measured. We developed a dry tissue mass (g) versus shell length (mm) relationship for fresh Gull Lake mussels: (log dry tissue mass = 2.5429 * log length – 4.9396, $R^2 = 0.93$, $N = 50$) to convert size distributions to biomass.

The epilimnion of Gull Lake was sampled four times from June to August, 1998, with a depth integrating tube sampler. Water samples were filtered through Whatman GF/F glass fiber filters on the day of collection. Total phosphorus (the sum of dissolved and particulate fractions) was measured via persulfate digestion (Valderrama 1981) followed by molybdate blue colorimetry (Murphy and Riley 1962).

Data analysis

Much of the mussel biomass data represented single-year estimates, and most of the measurements of Ca^{+2} and TP (summer averages for the epilimnion) in the Polish data set were made many years after zebra mussel biomass was estimated (Table 1). Although Ca^{+2} should not change drastically from year to year, large temporal changes in TP are possible due to human influence. These factors should increase the unexplained error of a predictive relationship, especially given that zebra mussel abundance can vary greatly from year to year (Ramcharan et al. 1992a; Stanczykowska 1984; Stanczykowska and Lewandowski 1993). Restricting the data set to lakes in which mussel biomass and TP were measured within three years of each other did not improve fit ($N = 6$). We log-transformed the TP data which greatly reduced skewness in this variable.

Initial statistical analyses indicated the presence of two very large outliers (Lake Olow and Lake Stregiel, Table 1) in the Polish data set. For example, when we regressed mussel biomass against TP, Ca^{+2} and mean depth, the standardized residual for Lake Olow was 6.1, indicating an extreme outlier. There were no TP data for Lake Stregiel, so inclusion/exclusion of this lake was inconsequential to analyses involving TP. These two lakes had unusually high biomass (> 40 g • m^{-2}) and were responsible for strong skewness in the mussel data that could not be alleviated via transformation. Consequently, we excluded these two lakes from all subsequent statistical analyses. We strongly suspect that values of mussel biomass greater than 40 g • m^{-2} represent transient, nonsustainable excursions from long-term average biomass (see Discussion). For this reason, we also restricted the data from Saginaw Bay, Lake Huron to data collected in 1993. Mussel biomass in Saginaw Bay increased from 10 g • m^{-2} in 1991 (first year after invasion) to 62 g • m^{-2} in 1992, then declined to 4.5 g • m^{-2} in 1993 (Nalepa et al. 1995), suggesting that zebra mussel biomass was far above long-term sustainable levels in 1992.

Results

The Polish data consisted of mesotrophic to hyper-eutrophic lakes (mean and range of TP: 70, 19 - 233 mg • m^{-3}) with mean depths from 1 - 14 m, and Ca^{+2} concentrations from 32 - 75 mg • L^{-1} (Table 1). Not surprisingly, mean depth and maximum depth were highly intercorrelated ($r = 0.81$, $P < 0.0001$, $N = 25$), so we only used mean depth in regression analyses. There was only a marginally significant correlation between Ca^{+2} and logTP ($r = 0.43$, $P = 0.09$, $N = 16$) and no significant correlation between mean depth and logTP ($r = -0.32$, $P = 0.13$, $N = 24$) in the Polish data. Stepwise multiple regression indicated that Ca^{+2} and mean depth had no statistically significant influence on mussel biomass in these data ($P > 0.3$). The latter result was robust to the order in which variables were entered and whether variables were forced into the model. Multiple regression indicated that logTP was the only potentially influential variable (Table 3). Based on these results, we calculated a predictive equation for the Polish data (Figure 1): mussel biomass = -10.8 (±8.8) + 11.0 (±4.9) $\log_{10}$TP, $R^2 = 0.19$, $P = 0.04$, $N = 24$ (standard errors in parentheses).

The TP range of the six North American lakes (Table 2, mean and range of TP: 15.9, 9.3 - 22.5 mg • m^{-3}) was much smaller and extended lower than the range of TP in the Polish data. With the exception of Oneida Lake, biomass estimates in these recently-invaded North American lakes fit within the 95% confidence limits of predictions from the equation above (Figure 1). The data for Oneida Lake were collected from within two years of initial invasion, and so probably represent a transient, nonsustainable biomass, as seen in Saginaw Bay (see Discussion).

Combining the Polish and North American data and excluding Lake Olow and Oneida Lake (not near steady-state), we calculated the following predictive equation: mussel biomass = -6.5 (±5.4) + 8.7 (±3.2) $\log_{10}$TP, $R^2 = 0.22$, $P = 0.01$, $N = 29$ (standard errors in parentheses).

Discussion

Total phosphorus was the only variable that significantly predicted zebra mussel biomass in the Polish data set. Lack of Ca^{+2} influence was expected, since Ca^{+2}

concentrations were above 30 mg • L^{-1} in every lake (Table 1), a level that is above minimum thresholds for successful *Dreissena* growth and reproduction (Ramcharan et al. 1992b). Likewise, mean and maximum depth should have little direct influence given that mussel biomass is generally reported from Polish lakes for the restricted depth zone of mussel occurrence.

The amount of variation in mussel biomass explained by TP ($R^2 = 0.19, 0.22$) was low but comparable to that reported for total zoobenthic biomass by Rasmussen and Kalff (1987) ($R^2 = 0.20, 0.26$). In contrast, Hanson and Peters (1984) found a stronger relationship between zoobenthic biomass and TP (1984; $R^2 = 0.48$), which may be related to the lower TP range in their study (3 - 117 mg • m^{-3}) relative to the range in Rasmussen and Kalff (4 - 390 mg • m^{-3}) and our study (9 - 233 mg • m^{-3}). The response of lake productivity (as indexed by phytoplankton biomass) to increases in TP tends to be weaker for lakes with TP greater than ~200 mg • m^{-3} (Sarnelle et al. 1998). At high levels of TP other factors begin to limit lake productivity (Smith 1982, McCauley et al. 1989), so the influence of increased phosphorus on benthic biomass should weaken.

Given that the response of a single species to enrichment is likely to be much more variable than the response of total zoobenthic biomass, the statistical significance of the TP:zebra mussel relationship is encouraging. However, we were only able to establish a TP influence after excluding lakes with mussel biomass > 40 g • m^{-2}. The status of these excluded lakes is thus critical to our analysis.

Based on both Polish and North American data, we propose that a dreissenid biomass in excess of ~40 g • m^{-2} is not sustainable (i. e., much higher than steady-state biomass) in lakes. This hypothesis is supported by evidence suggesting that mussel populations in outlier lakes were unstable at the time that biomass was measured. One of the three high-biomass lakes (Lake Stregiel, Table 1) was classified as having an unstable mussel population by Ramcharan et al. (1992a), based on the magnitude of interannual density fluctuations. Lake Olow, a second high-biomass lake, was not explicitly classified as unstable by Ramcharan et al. (1992a), but we note that mussel density was reported as 1830 • m^{-2} in 1978 (the year in which biomass was estimated, Lewandowski 1991) and as 514 • m^{-2} (year unspecified) by Stanczykowska and Lewandowski (1993). Thus, the mussel population in Lake Olow may have been at a transient high biomass level in 1978. Biomass data for Oneida Lake, the third high-biomass lake, were limited to the first two years after invasion (Mellina et al. 1995), and thus may represent an initial overshoot of steady-state biomass, as documented in Saginaw Bay (Nalepa et al. 1995). Based on our empirical relationship, we would expect that zebra mussel biomass in Oneida Lake should be about five times lower than that observed in 1992 and 1993. This prediction can be readily tested as a way of evaluating our contention that a zebra mussel biomass in excess of ~40 g • m^{-2} is far above steady-state levels.

To more rigorously examine population instability as a factor producing residual variation in the TP:mussel biomass relationship, we restricted the Polish data to lakes classified as stable by Ramcharan et al. (1992a), and recalculated the logTP:biomass regression. This restriction greatly improved the fit: mussel biomass = -33.5 (±16.3) + 23.2 (±8.4) $\log_{10}$TP, $R^2 = 0.60$, $P = 0.04$, $N = 7$ (standard errors in parentheses). We caution against using this equation for prediction because it is based on very few lakes, but the improvement in fit suggests that population instability may be a major source of residual variation in the TP-mussel biomass relationship. Additional factors that may account for residual variation are: substrate quality (Mellina and Rasmussen 1994), the temporal mismatch between measurements of TP and mussel biomass for most of the Polish lakes, and within-lake spatial variation in mussel biomass estimates. Standard deviations of single-year biomass estimates for North American lakes vary from 65% (Gull Lake) to >>100% (Lake Erie, Lake St. Clair, Saginaw Bay) of the mean (Nalepa et al. 1995; Nalepa et al. 1996; Dermott and Kerec 1997), so this source of residual variation may be important.

With the exception of the first two years after invasion, we found no evidence to suggest that time since colonization influences steady-state dreissenid biomass. North American lakes three years after invasion do not seem to support detectably higher biomass of zebra mussels than Polish lakes in which mussels have existed for >50 years. The limited data available on population dynamics immediately after invasion (Saginaw Bay, Nalepa et al. 1995) support the suggestion that dreissenid populations in North America require only about three years to approach steady-state biomass. Ironically, mussel populations in some recently invaded North American lakes may be closer to steady-state biomass than populations in some European lakes. Long-term presence is no guarantee that a mussel population will be near steady-state biomass in any given year, especially when one considers the precipitous declines and rapid recoveries that characterize some long-established populations (Stanczykowska et al. 1975). Clearly, more study of *Dreissena* population dynamics is needed.

To compare the response of dreissenid biomass to TP enrichment with the response of total zoobenthic biomass reported in previous studies requires conversion of the data to common scales. To this end, we calculated $\log_{10}$TP vs. $\log_{10}$biomass and lnTP vs. $(\text{biomass})^{0.1}$ regressions for the combined Polish and North American data to enable comparison with the relationships reported by Hanson and Peters (1984) for profundal benthos, and Rasmussen and Kalff (1987) for profundal and sublittoral benthos, respectively. For both of these comparisons, the slope of the zebra mussel response to TP enrichment (log:log slope:0.55, ln:tenth root slope: 0.06) was roughly similar to the slope for total zoobenthic biomass (log:log slope: 0.71, ln:tenth root slope: 0.08-0.09). These comparisons suggest that dreissenid biomass increases at a roughly similar rate with enrichment as total zoobenthic biomass. The elevation of the dreissenid regression was similar to those reported by Rasmussen and Kalff (1987), but somewhat lower than that reported by Hanson and Peters (1984) (-0.22 versus -0.09). A lower elevation is expected for the response of a single taxon relative to total zoobenthic biomass.

The positive relationship that we found between dreissenid biomass and TP is not surprising given that zoobenthic biomass responds positively to nutrient enrichment, but contrasts with the negative correlation found between mussel density and orthophosphate concentration by Ramcharan et al. (1992b). It is difficult to compare these contrasting results because of the difference in independent variables employed, but we can suggest that the data set analyzed by Ramcharan et al. (1992b) included lakes with much higher levels of phosphorus loading than the lakes that we analyzed. Their data set included 15 lakes with orthophosphate concentrations in excess of 100 mg • m^{-3}. Many of these lakes probably had TP in excess of 233 mg • m^{-3}, the maximum in our data set. In extremely eutrophic waters, anoxia and toxic cyanobacteria may lead to reduced zebra mussel biomass, as suggested by Stanczykowska (1984). In any case, orthophosphate concentration is a poorer surrogate variable for lake productivity than TP, because the former is subject to much greater seasonal variation and is under much greater control by the biota (via uptake and excretion) than is TP.

In conclusion, we found that dreissenid biomass can be predicted from TP for lakes with TP less than 233 mg • m^{-3}, and that steady-state biomass in recently invaded North American lakes generally fits the positive TP:biomass relationship for Polish lakes. The latter fit, however, is at least in part a function of the low R^2 of the Polish relationship. The TP:biomass relationship for Polish and North American lakes combined can be used to predict future zebra mussel biomass in uninfested lakes, and to suggest reasonable biomass stocking levels for experiments in habitats for which biomass estimates are lacking. These predictions, however, carry a large degree of uncertainty, much of which may stem from large interannual and spatial variation in mussel abundance for individual lakes. To refine these predictions, more unbiased estimates of dreissenid biomass over multiple years are needed. We strongly recommend that dry tissue mass (rather than total or shell-free wet mass) be determined in future studies given that most existing studies report dry tissue mass and that dry mass estimates are more generally reliable and reproducible.

Chapter 2: Effects of zebra mussels on phytoplankton and ciliates: a mesocosm experiment

Introduction

Since their introduction into North America in the mid-1980's, zebra mussels have been implicated in drastic ecosystem-level changes, including a shift in energy flow from the pelagic to the benthic zone (Fahnenstiel et al. 1995; Johengen et al. 1995; Arnott and Vanni 1996; Lavrentyev et al. 2000), declines in microzooplankton and phytoplankton biomass (Holland 1993; Heath et al. 1995; Lavrentvey et al. 1995; MacIsaac et al. 1995; Bastviken et al. 1998; Pace et al. 1998; Jack and Thorp 2000; James et al. 2000; Yu and Culver 2000), and shifts in phytoplankton species composition from communities dominated by palatable species, like diatoms, to inedible blue-greens (Lowe and Pillsbury 1995) and vice versa (Reeders and bij de Vaate 1990; Caraco et al. 1997; Smith et al. 1998; Yu and Culver 2000).

Several manipulative studies have been performed to assess the effects of zebra mussels on phytoplankton and ciliates (Reeders and bij de Vaate 1990; Heath et al. 1995; Lavrentyev et al. 1995; Mellina et al. 1995; Klerks et al. 1996; Roditi et al. 1996; James et al. 1997; Bastviken et al. 1998; Jack and Thorp 2000; James et al. 2000). Of these, laboratory experiments have documented zebra mussel feeding preferences for particular groups of protozoans and algae (Lavrentyev et al. 1995; Bastviken et al. 1998), as well as decoupling of a well-established total phosphorus-chlorophyll relationship (Mellina et al. 1995). Although laboratory studies can be useful for examining small-scale effects on individual species and populations, they are inappropriate for studying community processes such as shifts in species composition. For questions of this type, larger-scaled experiments are needed. Of those experiments aimed at examining the effects of zebra mussels on phytoplankton communities in the field, only three were large-scale field experiments (Reeders and bij de Vaate 1990; Heath et al. 1995; Jack and Thorp 2000). The first of these was unreplicated and the latter two studies lasted less than a week. Because phytoplankton and ciliates can take several weeks to establish a new community equilibrium after a disturbance, studies aimed at examining the effect of a newly introduced grazer on these guilds should allow enough time for populations to reach a new equilibrium. In this paper, I examine the effect of zebra mussels on the phytoplankton and ciliate community with a five-week replicated field experiment. Specifically, I address the following questions:

1. Do zebra mussels negatively affect phytoplankton, and if so, over what time scale?
2. Do zebra mussels cause a shift in phytoplankton species composition from palatable to unpalatable species?
3. How does the effect of zebra mussels on ciliates compare to their effects on phytoplankton?

Materials and Methods

Experimental Setup

This experiment was performed in an experimental pond at the Kellogg Biological Station (Michigan State University, Hickory Corners, Michigan). The pond was 30 m in diameter and 1.8 m in depth and almost completely surrounded by cattails. The pond contained abundant macrophytes, sunfish (*Lepomis* spp.), and macroinvertebrates, but no zebra mussels.

Two treatments with four replicates each were used in the experiment: zebra mussels present and zebra mussels absent (control). Eight experimental enclosures were constructed out of clear polyethylene (1.13 m in diameter by 1.5 m in depth and heat sealed at the bottom) that was stapled to 1.0 m x 1.0 m Styrofoam-supported wooden frames. Enclosures were covered by plastic window screen to prevent pond organisms from entering the enclosures.

The enclosures were filled on 15 June 1999 with pond water pumped through a 149 μm mesh net to remove all macrozooplankton. Zooplankton were then collected with a 102 μm mesh net from the pond and stocked into each enclosure on two occasions (22 June and 9 July) to achieve a natural zooplankton density. The second stocking was performed because zooplankton densities were much lower in both sets of enclosures relative to the pond during the first two weeks. Despite the additional stocking, zooplankton densities remained low in the enclosures relative to the pond throughout the entire experiment.

In order to prevent large zooplankton from dominating in the enclosures, one juvenile bluegill (*Lepomis macrochirus;* 40±1 mm total length) was added to each enclosure. Stocking density was below the natural density of bluegill for local lakes (Mittelbach 1988) because the pond was less productive than local lakes. The fish were seined from a local lake on 27 May and held in aquaria until they were transferred to the enclosures on 18 June. The enclosures were checked daily for fish mortality. Dead fish were removed and immediately replaced with a similar-sized fish. A total of five fish were replaced during the course of the experiment, but fish mortality did not have a significant impact on any measured responses (ANOVA; $p > 0.35$)

I used an equation that predicts zebra mussel dry tissue biomass ($g \bullet m^{-2}$) from total phosphorus concentration ($\mu g \bullet L^{-1}$) to estimate a reasonable stocking density ($\approx 1 g \bullet m^{-2}$) for the experiment (dry tissue biomass = -10.8 + 11.0 * logTP, $R^2 = 0.19$, $P < 0.04$, $N = 24$; Wilson and Sarnelle submitted). On 20 May, zebra mussels were collected from Gull Lake and quickly transported directly to the lab where druses were separated with a razor and all detritus was gently scraped from each mussel with a coarse scouring pad. Next, all mussels between 10 and 20 mm were placed into a flow-through tank (2.5 m x 0.3 m x 0.3 m) where they were allowed to attach to one of eight substrates made from PVC pipe (0.1 m in diameter, 0.5 m in length, and 0.05 m thick) cut lengthwise to create symmetrical pipe halves. Fresh water was pumped from Gull Lake ($19 L \bullet min^{-1}$) and filtered for large debris with a 1-mm-mesh net before entering the tank. Settled detritus and feces were siphoned from the tank twice daily.

To determine the relative condition of the mussels before and after the experiment, length-weight relationships were derived from randomly chosen mussels. On the same day that the mussels were collected and added to the flow-through tank, 50 fresh mussels (mean length = 13.9 mm, length ranging from 6.3 – 24.4 mm) were measured with calipers to the nearest 0.1 mm, and the soft body tissue was removed with a scalpel. The tissue was then placed into a drying oven at 55 °C for 22 hours until a constant weight was observed. Dried mussel tissues were weighed to the nearest ± 0.01 mg. Post-experimental mussels were removed from the experimental substrates on 7

August and frozen for later analysis. Twenty-five post-experimental mussels from each enclosure (for all post-experimental mussels: mean length =13.7 mm, range 9.0 – 21.0 mm) were later thawed and a length-weight relationship for post-experimental mussels was derived following the same protocol used for pre-experimental mussels. Because dry weight can be lost through freezing (J. Chiotti, A. E. Wilson, and T. Toda, unpublished data), a correction factor was used to adjust the dry weight of frozen samples. To determine the correction factor, additional mussels were collected from Gull Lake and the length-weight protocol was repeated using a set of fresh mussels versus a matched set that had been frozen. The correction factor derived from a linear regression of frozen dry tissue mass on fresh dry tissue mass was: Frozen (g) = 1.3406 * Fresh (g) - 0.0003 (R^2 = 0.997, $P < 0.001$).

On Day 1 (21 June), one substrate was hung into each of the eight enclosures from a 0.5 m nylon rope attached to a PVC pipe (30 mm in diameter and 1.2 m in length) secured across the tops of each enclosure. This allowed each substrate to be hung directly in the middle of each enclosure. All zebra mussels were removed from four of the eight mussel substrates and these substrates were placed into the control enclosures. All mussels on the remaining four treatment substrates were counted and measured before being deployed. Mussels used in the experiment averaged 12.2±2.7 mm in length (mean ± standard error), and the average initial dry tissue biomass used in each enclosure was 1.2±0.1 g (dry tissue, mean ± standard error). This biomass is within the bounds of the 95% confidence intervals predicted for the total phosphorus concentration of the pond (13 $\mu g \bullet L^{-1}$). Mussel density averaged 162±10 mussels (mean ± standard error) per treatment enclosure. Zebra mussels were monitored at each sampling date for mortality.

Sampling and laboratory analyses

The enclosures and the pond were sampled on 20 June (Day 0), 21 June (Day 1), and at seven day intervals for the next five weeks (N = 37 days). All sampling was conducted from a small boat.

A YSI multisensor (model 600XL) was used to measure temperature (°C), pH, and dissolved oxygen (mg • L^{-1}) at three depths (surface, 0.5 m, and 1.0 m) in each enclosure and the pond. Readings were averaged over all depths for all analyses.

A clear plastic tube (5 cm in diameter and 1 m in length) was used to take integrated water samples (≈2 L • $tube^{-1}$) from the enclosures and the pond. The contents of two tubes were placed into 10 L plastic cubitainers and stored in the dark on ice. At the lab, each cubitainer was poured into a bucket and the sample was thoroughly mixed.

A 250 ml aliquot of water was filtered through a Gelman A/E filter for particulate phosphorus analysis (PP). After the filters were dried for 24 hours at 30 °C, they were stored in a closed container with desiccant until further analysis. Filtrate was collected in 60 ml Nalgene bottles for analyses of total dissolved phosphorus (TDP) and ammonium (NH_4^+). PP and TDP were determined spectrophotometrically (Lambda 20, Perkin Elmer) after potassium persulfate digestion (Menzel and Corwin 1965). NH_4^+ was measured by indophenol blue colorimetry (Wetzel and Likens 1991). Total phosphorus (TP) was calculated as the sum of PP and TDP.

A 500 ml aliquot of water was filtered through a Gelman A/E filter for chlorophyll analysis. After filtration, the filter was placed into a tightly-sealed film canister and frozen. Chlorophyll a (µg • L^{-1}) was determined fluorometrically (Turner Designs 10A) after dark extraction in 95% ethanol for 30 hours.

A 100 ml sample was preserved with 1% Lugol's solution for phytoplankton counting. Phytoplankton samples from each enclosure and the pond were counted for Days 8, 22, and 36. Depending on the chlorophyll concentration, 10 - 100 ml aliquots from each enclosure were settled in Utermohl settling chambers, and sufficient time (≥ 10 hours per cm of chamber height) was allowed for complete settling. Each chamber was divided into circular inner and outer halves and an equal number of visual fields were counted in each half (Sandgren and Robinson 1984). At least 15 fields per chamber half were counted for the most abundant species and at most 100 fields from each half were counted for most species. Phytoplankton were identified and enumerated to genus or species with an inverted microscope at 400x and 1000x.

Phytoplankton were grouped into six categories according to morphological and functional characteristics, as well as abundance. These groups consisted of small greens < 10 μm (*Elakothrix* spp., *Nannochloris* spp., *Oocystis* spp.), dinoflagellates (*Ceratium* spp., *Peridinium* spp.), cryptomonads (*Cryptomonas erosa*, *Cryptomonas pusilla*, *Rhodomonas spp.*), miscellaneous flagellates < 10 μm (*Dinobryon* spp., *Trachlemonas* spp.), colonials (*Uroglenopsis* spp.), and others (desmids {*Closterium* spp., *Cosmarium* spp., *Staurastrum* spp.}, diatoms {*Nitzschia* spp., *Synedra* spp.}, and filamentous greens). For each sample, 10 randomly selected individuals of each common species were measured with a micrometer. Formulas for simple geometric volumes that most resembled particular species were used to calculate phytoplankton biovolume ($\mu m^3 \bullet ml^{-1}$). Average phytoplankton biovolume per cell for each algal species did not vary among treatments or dates so a single average (across treatment and dates) cell volume was calculated for each species.

Ciliates were counted and measured in the same manner as the phytoplankton, although ciliates were not identified into specific categories. Unlike phytoplankton biovolume, average ciliate biovolume differed significantly ($p < 0.05$) between treatments, so I used separate average cell volumes for ciliates from zebra mussel enclosures, control enclosures, and the pond for each sampling date. Ciliate and phytoplankton biovolumes were converted to dry biomass ($\mu g \bullet L^{-1}$) assuming a specific gravity of 1 and a dry mass to wet mass ratio of 0.10.

Macrozooplankton were sampled by pouring the contents of seven integrated tubes (≈ 14 L) through a 102 µm mesh net, and preserved in 95% ethanol. For most dates, the entire sample was counted and measured, otherwise 2 ml subsamples were taken with a Henson-Stempel pipette and counted until 50 individuals of each species were measured. Zooplankton subsamples were counted with a Ward zooplankton counting wheel at magnifications between 20x and 80x. Cladoceran taxa included: *Bosmina* spp., *Ceriodaphnia* spp., *Chydorus* spp, *Daphnia retrocurva*, and *Diaphanosoma* spp. The copepod taxa measured were calanoid juveniles, cyclopoid juveniles, *Diacyclops* spp., *Diaptomus*, *Mesocyclops* spp., *Tropocyclops* spp., and nauplii. Dry biomass ($\mu g \bullet L^{-1}$) of each species was estimated from measured lengths using length-weight regressions derived by Culver et al. (1985).

Data analyses

I used one-way analysis of variance (ANOVA) to assess treatment effects for most parameters on Days 0, 1, 8, and 36 and on time-averaged data (Days 8 – 36). If no statistically significant treatment effects were detected for time-averaged data ($P > 0.05$), I performed repeated-measures ANOVA on all data from Day 8 through Day 36 to determine if any time x treatment interactions were present. None were found, so results from the repeated-measures ANOVA are not shown. Effect sizes were calculated from treatment means using the following formula: (100 * [(zebra mussel – control)/control]). Linear regression was used to determine zebra mussel dry body weight (g) from length (mm), and analysis of covariance was used to compare length-weight regressions for mussels analyzed at the beginning of the experiment and for zebra mussels in each of the four treatment enclosures at the end of the study. To determine if TP:chlorophyll decoupling had occurred on Day 8, a two-sample t-test assuming unknown variance (Welch test) was used. The observed chlorophyll concentrations for the two treatments and the pond were compared to the predicted chlorophyll concentrations from the TP:chlorophyll regression provided in Dillon and Rigler (1974). Log transformations were applied to data if they were skewed or their variances were heterogeneous. Arcsine transformations were applied to relative algal biomass estimates. All statistical analyses were performed with Systat 8.0 (SPSS 1998). Rejection criterion was set at $\alpha < 0.05$.

Results

Physical and chemical parameters

Although no measured parameters differed significantly between treatments on Day 0 (the day before mussels were added), three variables (temperature, TDP, and TP) were statistically different four hours after the addition of the zebra mussels on Day 1 (Table 4).

Temperature varied from 22 to 27 °C for all enclosures for all days, and the average temperature throughout the experiment was approximately 25.7 °C (Table 4). The pH in the enclosures ranged from 7.4 to 7.8 and was similar between treatments (Table 4). Similarly, dissolved oxygen concentrations in the enclosures were comparable and averaged approximately 6 mg • L^{-1} in the enclosures (Table 4).

Total dissolved phosphorus tended to decline over the course of the experiment and averaged 3.5 μg • L^{-1} for all enclosures (Table 4). As expected, mean PP and NH_4^+ differed significantly between treatments ($p = 0.01$ and $p = 0.02$, respectively, Table 4). Particulate phosphorus averaged < 3 μg • L^{-1} in the enclosures and was consistently higher in the control enclosures. A similar trend was observed for TP (treatments averaged < 6.5 μg • L^{-1}). As early as Day 8, NH_4^+ was higher in the zebra mussel enclosures, and this effect was maintained throughout the remainder of the experiment (except for Day 36). Ammonium ranged from 7.0 to 14.5 μg • L^{-1} in zebra mussel enclosures and from 7.5 to 11.4 μg • L^{-1} in the control enclosures.

Biological parameters

Zebra mussels had a dramatic but ephemeral effect on phytoplankton abundance. Chlorophyll concentrations differed significantly between treatments (5-week average, $p = 0.001$; Table 4) and averaged 1.1 μg • L^{-1} in the control enclosures and 0.6 μg • L^{-1} in the zebra mussel enclosures. Although a large negative effect on chlorophyll concentration was observed early in the experiment in the zebra mussel enclosures (71.4% less chlorophyll in the zebra mussel enclosures when compared to the control enclosures; Day 8), chlorophyll in the zebra mussel enclosures consistently increased throughout the remainder of the study to eventually reach a concentration no different than the control enclosures on Day 0 ($p = 0.57$; Figures 2, 3). The response of total phytoplankton biomass (from microscope counts) paralleled that observed for chlorophyll concentration (Table 4).

The Dillon-Rigler TP:chlorophyll equation (from Dillon and Rigler 1974) predicted the chlorophyll concentrations observed in the control enclosures and the pond, however the observed chlorophyll concentration for the zebra mussel enclosures on Day 8 was significantly lower than predicted ($p < 0.0001$; Figure 4). Thus, the negative effects of zebra mussels on phytoplankton biomass was not driven by a negative effect on total phosphorus.

The effect of zebra mussels on phytoplankton species composition was modest. Two algal groups were significantly greater in the control enclosures (cryptomonads $p = 0.003$ and small greens $p = 0.01$, Table 4). When examining phytoplankton species composition on individual days, all groups except colonials were significantly lower in the zebra mussel enclosures when compared to the control enclosures on Day 8 (Table 5). However, the effect of zebra mussels on the phytoplankton community composition was not maintained after Day 8. By Day 22, only one group significantly differed between treatments (small greens), and by the end of the study, no groups differed (Table 5). The relative phytoplankton biomass data suggest that the mussels were predominantly non-selective in their filtering of the phytoplankton throughout the entire study, with no groups being different by Day 8 (Table 6, Figure 5) and only one algal group's relative biomass being significantly different between treatments (5-week average, misc. flagellates $p = 0.03$; Table 6).

Ciliates significantly declined throughout the entire study in the zebra mussel enclosures. Ciliate biomass in the zebra mussel enclosures averaged 77.5% lower than the control enclosures throughout the entire study ($p < 0.0001$, Table 4). Ciliate biomass in the zebra mussel enclosures was reduced by 70.6% by Day 8 and was maintained at these reduced levels (or greater) until the end of the study (Figure 6).

Bosmina spp. and *Diaphanosoma* spp. accounted for > 99% of all cladocerans, and calanoid and cyclopoid juveniles accounted for > 73% of all copepods for both treatments. Copepods were almost 3 times more abundant than cladocerans in the zebra mussel enclosures, and both groups were equally abundant in the control enclosures. Zebra mussels had a significant effect on total zooplankton biomass averaged over all dates ($p = 0.048$, Table 4). Zebra mussels significantly reduced total cladocerans throughout the study (time-averaged, $p = 0.035$), but had no effect on copepods.

The first sign of zebra mussel mortality was observed on 12 July (Day 22). I continued to observe dead mussels throughout the experiment, however the average total mortality observed in the zebra mussel enclosures over the entire experiment accounted for only 7.6±3.6% (mean ± standard error) of the total density. The mussels that survived were shown to have lost 56% of their initial weight by the completion of the study (Figure 7). No differences were observed for post-experimental weights between replicates of the zebra mussel treatment (ANCOVA; $p = 0.71$), but there was a highly significant difference between length-weight relationships for pre-experimental mussels [log dry tissue mass (g) = 2.5429 * log length (mm) – 4.9396, $R^2 = 0.93$, N = 50] and post-experimental mussels [log dry tissue mass (g) = 2.1455 * log length (mm) – 4.8135,

$R^2 = 0.76$, N = 100) (Tukey-Kramer test of slopes, $p < 0.0001$), after correcting for the weight lost due to freezing.

Pond Conditions

The pond was similar to the control enclosures for several parameters (i.e., temperature, pH, and NH_4^+), but chlorophyll, PP, TDP, and TP were almost twice as high in the pond as the control enclosures throughout the entire experiment (five-week treatment averages, Table 4). Only on Day 8 were algal assemblages in the control enclosures similar to that observed in the pond (Figure 5). Ciliate abundance in the pond was similar to the control enclosures until Day 22, but by Day 36 the control enclosures had 4 times greater ciliate biomass than the zebra mussel enclosures and the pond (Table 4). In addition, after two zooplankton inoculations, total zooplankton biomass measured in the enclosures averaged 6.2 times lower than that observed in the pond (Table 4). Finally, the zooplankton assemblage in the pond was very similar to that observed in the control enclosures.

Discussion

As expected, zebra mussels had a dramatic negative impact on algal abundance early in the experiment. By the end of the first week, the mussels reduced algal biomass and chlorophyll concentrations by 53% and 71%, respectively. Similar but less steep declines in chlorophyll occurred in the control enclosures shortly after zooplankton were inoculated in all enclosures on Days 8 and 22. Although zebra mussels removed a majority of the algae from the enclosures early in the study, their effect on algal abundance was not maintained throughout the experiment. After Day 8, chlorophyll concentrations continued to increase until the completion of the experiment, at which time concentrations were similar to the control enclosures. The inability of the mussels to maintain the phytoplankton at a low level could be a result of an algal species shift to inedible species, altered algal size structure, nutrient enrichment via zebra mussel mortality, and/or to the declining health of the mussels.

Although the zebra mussels significantly reduced most algal groups (except colonials) by Day 8, a shift in phytoplankton species composition was not observed because abundances of all algal groups were similar between treatments by Day 36. Additionally, I did not encounter "inedible" algal species, such as colonial blue-greens, thus it is unreasonable to conclude that a shift to less palatable species occurred. It also is not likely that the size-structure of the algal assemblages affected mussel grazing because all algal species were well within the size range mussels have been shown to consume (range 1 – 150 μm; Ten Winkel and Davids 1982; Sprung and Rose 1988; Horgan and Mills 1997) and all algal groups have been shown to be grazed by mussels in other studies (Heath et al. 1995; Lavrentyev et al. 1995; Bastviken et al 1998; Smith et al. 1998).

Zebra mussels immediately reduced and maintained low levels of ciliates throughout the experiment (Figure 6), while phytoplankton abundance continued to increase after Day 8 (Figure 2). This result is not surprising given that phytoplankton were capable of acquiring available nutrients created via mussel excretion and mortality, while ciliates competed with and were preyed upon by zebra mussels. Others have shown similar impacts of zebra mussels on protozoan abundances. For example, Lavrentyev et al. (1995) conducted laboratory experiments where they showed that zebra mussels reduced protozoan abundance by > 70%, while the mussels had less of an impact on phytoplankton abundance (≈ 45% decline). Additonally, competition between zebra mussels and ciliates for small edible algae, like small greens, could help explain the observed effects on ciliate and algal abundances. A positive correlation between ciliates and small green algae for the enclosures (Figure 8) suggests that although the zebra mussels reduced all algal groups equally, the large absolute reduction of small green algae (68%, Table 5) could have aided in keeping ciliate numbers low. Thus, zebra mussels are extremely effective at controlling ciliates, however the importance of competition and predation in zebra mussels' ability to control ciliates is currently unresolved. Thus, further research directed at understanding the competitive and predative interactions between protozoans and zebra mussels will aid in developing more complete and accurate food-web models.

The deteriorating health of the mussels could also help explain the lack of effect on algal concentration observed later in this experiment. Several studies have examined the role of physical and chemical parameters in regulating zebra mussels in lakes (Ramcharan et al. 1992; Ludyanskiy et al. 1993; Mackie and Schloesser 1996; Karatayev et al. 1998). Specifically, calcium provides the material for mussel shell construction and mussels require at least 20 mg • L^{-1} Ca^{+2} to establish populations (Ludyanskiy et al. 1993). The pond used in this study had calcium concentrations above 50 mg • L^{-1} Ca^{+2} (S. Hamilton and D. Raikow, personal communication), thus calcium limitation likely did not affect mussel growth and maintenance. Ramcharan et al. (1992) demonstrated that mussels are sensitive to pH and found mussels to be absent from lakes with pH < 7.3.

The pH in the enclosures ranged from 7.4 to 7.8; therefore, it is not likely that pH significantly affected zebra mussel health.

Most temperate species are adapted to seasonally changing thermal environments, however extremely high (or low) temperatures can be lethal. Karatayev et al. (1998) suggest that zebra mussels thrive in temperatures below 27°C and have difficulty surviving in temperatures greater than 32 °C. Although the enclosures reached 27 °C, the average measured temperature experienced by the mussels throughout the entire study was 25 °C. Thus it seems unlikely that temperature by itself affected mussel health and grazing, however, higher temperatures could have made routine physiological maintenance more difficult due to higher food requirements at higher temperatures (Walz 1978; Aldridge et al. 1995; Fanslow et al. 1995; Horgan and Mills 1997).

An individual zebra mussel's growth rate is dependent on body size and temperature, among other factors (Walz 1978). Walz (1978) indicates that higher temperatures severely restrict zebra mussel growth rates due to a greater demand for food and that larger mussels require less food per gram of mussel than smaller mussels (Walz 1978; James et al. 2000). Comparisons of length-weight relationships performed on the mussels before and after the study show that the mussels lost 56% of their weight during the experiment (Figure 7). Average available daily rations were calculated by converting measured chlorophyll concentrations into carbon (µg) (carbon:chlorophyll = 67:1; Riemann et al. 1989) and then calculating filtration rates based on the size distribution and density of mussels used in the study (Kryger and Riisgård 1988). The average daily ration on Day 8 of the experiment was 31 µg carbon • day^{-1} in the mussel enclosures. Walz (1978) used *Nitzschia*, a high-quality laboratory cultured diatom, to show that a 5 mg (dry tissue mass) mussel requires 42.5 μg carbon • day^{-1} for routine maintenance at 20 °C. Although this size is slightly larger than the average mussel used in this study (3.7 mg dry tissue mass), smaller mussels typically require more food per unit body weight than larger mussels (Walz 1978). Additionally, given the lower quality pond water, which contained a considerable amount of detritus, the zebra mussels would have needed to filter more enclosure water when compared to a similar amount of cultured *Nitzschia* medium to acquire the carbon needed for basic maintenance. My calculations indicated that food abundance in the zebra mussel enclosures was below that required for basic maintenance on Day 8 (Figure 9). Thus, it is reasonable to conclude that the mussels lost weight due to insufficient food availability soon after they were added to the enclosures. Although I attempted to predict a reasonable stocking density of zebra mussels for my enclosures based on the TP concentration of the pond (13 μg • L^{-1}), the enclosures were half as productive as the pond (Table 4), and, consequently, I over-estimated the amount of mussels required. With this in mind, careful consideration of the mussels' food availability must be accounted for when designing field experiments with zebra mussels in enclosed, previously mussel-free systems. Given that many earlier experimental studies involving zebra mussels used excessively high amounts of zebra mussels, presumably to see a grazing effect, my study clearly shows how critical determining a natural density of zebra mussels can be to outcome of the study. Also, this is first study to compare length-weight relationships to monitor the health of zebra mussels during an experiment. Without this type of data, conclusions based on the health of the mussels would only be conjecture. Thus, future experiments using zebra mussels should; 1) take precautions to not overstock their zebra mussel treatments by either taking benthic samples to determine a biomass estimate for water bodies where mussels have already invaded or by measuring total phosphorus concentration of the experimental units for mussel-less systems and then calculating dry tissue biomass, 2) monitor total phosphorus levels in enclosures related to the natural system, and 3) monitor the health of the mussels throughout the experiment.

In conclusion, zebra mussels have been shown to quickly reduce algae and ciliates soon after entering a new water body. However, their impact on phytoplankton biomass was shown to diminish within two weeks of their introduction. The deteriorating health of the mussels has been proposed to help explain this effect. Future work incorporating a long-term, large-scale, controlled field experiment aimed at examining the gradual development of a zebra mussel founder population and its effects on the community will elucidate the important complex interactions between zebra mussels and other food web components.

Table 1. Lake characteristics and dreissenid abundance for Polish lakes. Mussel biomass expressed as dry tissue mass. Year of sampling (when known) in parentheses.

Lake	Mean depth (m)	Maximum depth (m)	TP ($mg \bullet m^{-3}$)	Calcium ($mg \bullet L^{-1}$)	Mussel Biomass ($g \bullet m^{-2}$)
Beldany	10.0	31.0	55.0[k] ('76)	33.0[l]	0.2[l] ('62)
Boczne	8.7	15.0	157.0[k] ('76)	54.0[a]	19.6[l] ('62)
Dargin	10.6	37.0	63.0[k] ('76)	63.1[a,l]	7.7[l] ('62)
Dobskie	7.8	21.0	60.0[k] ('76)	53.2[a,l]	5.4[l] ('62)
Glebokie	11.8	34.3	62.5[b,f]	.....	5.0[j] ('76)
Goldopiwo	.....	24.5	.....	46.5[e]	9.7[l] ('62)
Inulec	4.6	10.1	147.0[b,f]	.....	6.7[j] ('76)
Jagodno	8.7	34.0	92.0[k] ('76)	64.0[a]	18.4[l] ('62)
Jorzek	5.5	11.6	111.0[b,f]	.....	7.0[j] ('76)
Kierzlinski	11.7	44.0	38.0[k] ('77)	45.0[g]	2.5[d] ('77)
Kisajno	8.4	24.0	54.4[h,k] ('76)	54.0[a]	7.4[l] ('62)
Kolowin	4.0	7.2	53.0[k] ('78)	.....	15.1[d] ('78)
Kotek	1.0	2.5	103.0[k] ('76)	50.0[a]	4.7[l] ('62)
Kuc	8.0	28.0	40.0[k] ('77)	.....	1.1[d] ('78)
Majcz Wielki	6.0	16.4	18.5[f]	.....	12.0[d,j] ('76)
Mamry	11.7	40.0	43.4[h,k] ('76)	34.5[e,l]	13.4[l] ('62)
Mikolajskie	11.1	27.8	60.0[k] ('76)	36.0[l]	0.6[l] ('62)

Table 1. (cont'd)

Niegocin	10.0	40.0	233.0[k] ('76)	66.1[a,I]	17.7[I] ('62)
Olow	12.9	40.1	29.5[c,k] ('77)	46.0[g]	43.2[d] ('78)
Pilakno	13.0	56.6	20.0[k] ('77)	38.0[g]	0.8[d] ('77)
Probarskie	9.2	31.0	38.0[k] ('77)	.....	8.8[d] ('77)
Ros	.....	29.0	.....	.....	13.9[I] ('62)
Sniardwy	5.9	25.0	38.0[k] ('76)	32.0[i]	5.2[I] ('62)
Stregiel	.....	12.5	.....	49.0[e]	51.3[I] ('62)
Szymon	1.1	2.9	87.0[k] ('76)	.....	21.0[I] ('62)
Tajty	7.6	34.0	55.0[k] ('76)	54.0[a]	17.1[I] ('62)
Taltowisko	14.0	38.4	54.0[k] ('76)	75.0[a]	12.6[I] ('62)
Talty	13.6	37.5	36.0[k] ('76)	64.0[a]	0.6[I] ('62)
Wilkus	.....	5.5	.....	44.0[e]	25.8[I] ('62)
Zabinska	.....	42.5	.....	.....	32.2[I] ('62)
Zelwazek	3.7	7.4	.....	.....	5.5[j] ('76)
Mean	8.5	26.2	69.9	50.1	12.7

Data sources: [a]Gieysztor and Odechowska 1958; [b]Hillbricht-Ilkowska et al. 1984; [c]Kajak and Zdanowski 1983; [d]Lewandowski 1991; [e]Patalas 1960; [f]Planter and Wisniewski 1985; [g]Prusik et al. 1989; [h]Spodniewska 1978; [i]Stanczykowska 1977; [j]Stanczykowska et al. 1983; [k]Zdanowski 1982.

Table 2. Total phosphorus, mean depth and dreissenid abundance for North American lakes. Mussel biomass expressed as dry tissue mass.

Lake	TP ($mg \bullet m^{-3}$)	Year invaded	Year sampled	Mean Depth (m)	Mussel biomass ($g \bullet m^{-2}$)
Erie (eastern basin)	11.7[a]	1988	'92-'93	25.0	7.7[b]
Gull	14.0[i]	1994	'99	12.5	6.1[I]
Oneida	19.0[e]	1991	'92-'93	6.8	44.0[e]
Ontario	9.3[d]	1990	'95	86.0	0.9[f]
Saginaw Bay, Lake Huron (inner bay)	19.0[c]	1990	'93	7.2	4.5[g]
St. Clair	22.5[c]	1986	'90-'94	3.8	3.8[h]

Data sources: [a]Bertram 1993; [b]Dermott and Kerec 1997 [c]Fahnenstiel et al. 1995; [d]Johengen et al. 1994; [e]Mellina et al. 1995; [f]Mills et al. 1999; [g]Nalepa et al. 1995; [h]Nalepa et al. 1996; [i]this study.

Table 3. Multiple regression statistics for the influence of mean depth (m), calcium ($mg \bullet L^{-1}$) and log total phosphorus ($mg \bullet m^{-3}$) on zebra mussel biomass in Polish lakes. N = 16.

Variable	Slope	Standard error	P
Log mean depth	5.5	5.8	0.36
Log calcium	11.7	13.9	0.42
Log total phosphorus	16.9	6.8	0.03
Full model			0.04

Table 4. Treatment and pond averages (Days 8-36), ranges (Days 1- 36), p-values, and treatment effects (100 * [(zebra mussel – control)/control]) for chemical, physical, and biological parameters. On July 19, pH was not recorded due to a malfunction with the electrode. NA = not available

	Treatment averages (range: Days 1 - 36)			Significance of Treatment Effects (zebra mussels vs. controls) P-values (treatment effects)				
Variables	Pond	Control	ZM+	5-week average	Day 0	Day 1	Day 8	Day 36
Temperature (°C)	25.86 (22.04-27.21)	25.73 (22.06-26.95)	25.71 (22.31-26.95)	0.32 (-0.08%)	0.05 (-0.76%)	0.01 (1.13%)	0.68 (0.00%)	0.69 (0.00%)
pH	7.35 (7.19-7.44)	7.67 (7.38-7.77)	7.66 (7.36-7.81)	0.83 (-0.13%)	0.93 (0.03%)	0.17 (-0.27%)	0.52 (0.00%)	0.59 (0.55%)
Dissolved Oxygen (mg L^{-1})	3.63 (3.07-4.61)	5.57 (4.91-6.93)	5.52 (4.59-7.11)	0.81 (-0.90%)	0.41 (-1.45%)	0.80 (0.66%)	0.10 (-6.52%)	0.63 (2.63%)
Particulate Phosphorus (μg L^{-1})	7.55 (2.43-14.61)	2.84 (2.36-3.47)	2.13 (1.60-3.40)	0.01 (-25.12%)	0.15 (-9.22%)	0.22 (-6.82%)	0.02 (-42.77%)	0.21 (-17.23%)
Total Dissolved Phosphorus (μg L^{-1})	5.52 (3.01-8.26)	3.50 (1.74-7.61)	3.48 (2.11-4.82)	0.84 (-0.63%)	0.12 (17.63%)	0.05 (-41.24%)	0.11 (52.34%)	0.51 (20.87%)
Total Phosphorus (μg L^{-1})	13.07 (5.44-19.26)	6.34 (4.10-10.80)	5.60 (4.06-7.45)	0.27 (-11.60%)	0.21 (11.05%)	0.03 (-31.07%)	0.75 (7.72%)	0.84 (-1.05%)
Ammonium (μg L^{-1})	7.89 (4.78-16.71)	9.26 (7.50-11.43)	10.79 (6.95-14.49)	0.02 (16.52%)	0.55 (17.43%)	0.18 (-18.44%)	0.53 (11.78%)	0.99 (-9.51%)

Table 4. (cont'd)

	Treatment averages (range: Days 1 - 36)			Significance of Treatment Effects (zebra mussels vs. controls) P-values (treatment effects)				
Variables	Pond	Control	ZM+	5-week average	Day 0	Day 1	Day 8	Day 36
Chlorophyll ($\mu g\ L^{-1}$)	2.67 (2.35-2.98)	1.11 (0.76-1.40)	0.59 (0.22-1.07)	0.00 (-46.85%)	0.10 (-15.30%)	0.26 (-16.60%)	0.00 (-71.43%)	0.57 (-23.23%)
Phytoplankton Dry Biomass ($\mu g\ L^{-1}$)	35.30	15.17	9.87	0.03 (-34.91%)	NA	NA	0.00 (-53.11%)	0.69 (-24.33%)
Ciliate Dry Biomass ($\mu g\ L^{-1}$)	2.40	4.23	0.95	0.00 (-77.50%)	NA	NA	0.01 (-70.55%)	0.02 (-80.53%)
Zooplankton Dry Biomass ($\mu g\ L^{-1}$)	6.95	1.48	0.74	0.05 (-50.13%)	NA	NA	0.59 (-81.43%)	0.35 (-63.32%)

Table 5. Absolute observed treatment differences (zm+ vs. control) in algal groups throughout the study. All groups are measured as total algal dry biomass ($\mu g \bullet L^{-1}$) and "Other" denotes desmids, diatoms, and filamentous algae.

	Treatment Averages (Days 8, 22, and 36)		Day 8		Day 22		Day 36	
Algal group	Treatment difference	p-values	Treatment difference	p-values	Treatment difference	p-values	Treatment difference	p-values
Dinoflagellates	-38%	0.44	-51%	0.05	47%	0.24	-46%	0.61
Misc Flagellates (< 10 μm)	17%	0.69	-49%	0.00	-2%	0.81	204%	0.20
Cryptomonads	-65%	0.00	-83%	0.00	-33%	0.68	-51%	0.10
Small Greens (< 10 μm)	-68%	0.01	-41%	0.02	-61%	0.00	-87%	0.08
Colonial	-37%	0.24	133%	0.54	-47%	0.16	-18%	0.54
Other	-32%	0.18	-64%	0.00	-34%	0.32	1%	0.91
Total	-35%	0.03	-53%	0.00	-30%	0.02	-24%	0.69

Table 6: Relative observed treatment differences (zm+ vs. control) in algal groups throughout the study. All groups are measured as relative dry biomass (% of total biomass) and "Other" denotes desmids, diatoms, and filamentous algae.

	Treatment Averages (Days 8, 22, and 36)		Day 8		Day 22		Day 36	
Algal group	Treatment difference	p-values	Treatment difference	p-values	Treatment difference	p-values	Treatment difference	p-values
Dinoflagellates	3%	0.94	7%	0.78	126%	0.12	-14%	0.59
Misc Flagellates (< 10 μm)	66%	0.03	9%	0.48	37%	0.22	190%	0.07
Cryptomonads	-47%	0.16	-64%	0.06	-8%	0.88	-37%	0.44
Small Greens (< 10 μm)	-49%	0.10	25%	0.26	-44%	0.01	-76%	0.19
Colonial	-8%	0.84	365%	0.14	-32%	0.37	53%	0.58
Other	8%	0.65	-24%	0.16	-3%	0.91	29%	0.57

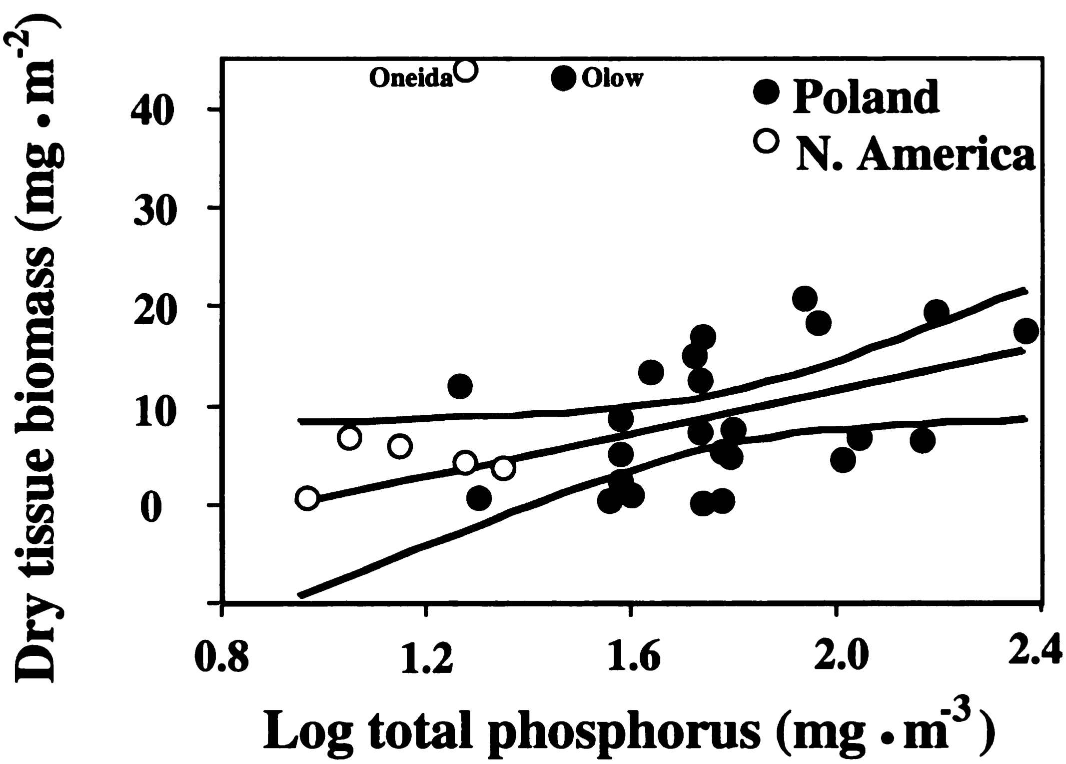

Figure 1. Relationship between total phosphorus and dreissenid biomass for Polish and North American lakes. Data from Tables 1 & 2. Regression line and 95% confidence bands for equation estimates were calculated for Polish lakes after excluding the outlier (Lake Olow).

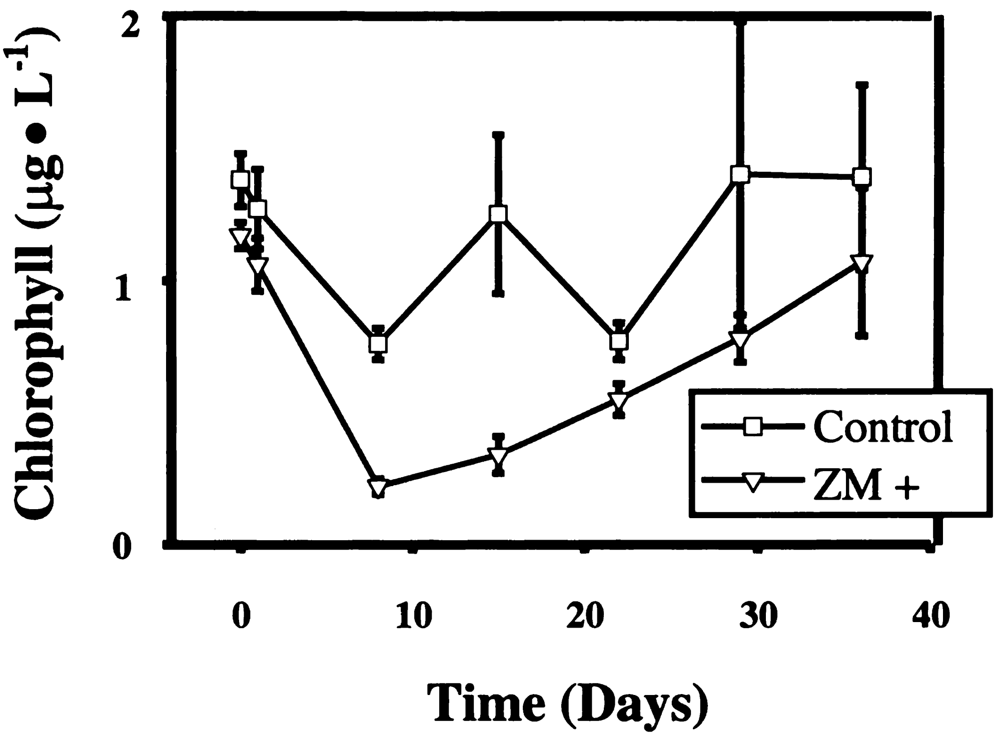

Figure 2: Chlorophyll concentration in the control and zebra mussel enclosures (daily treatment averages ± 1 standard error).

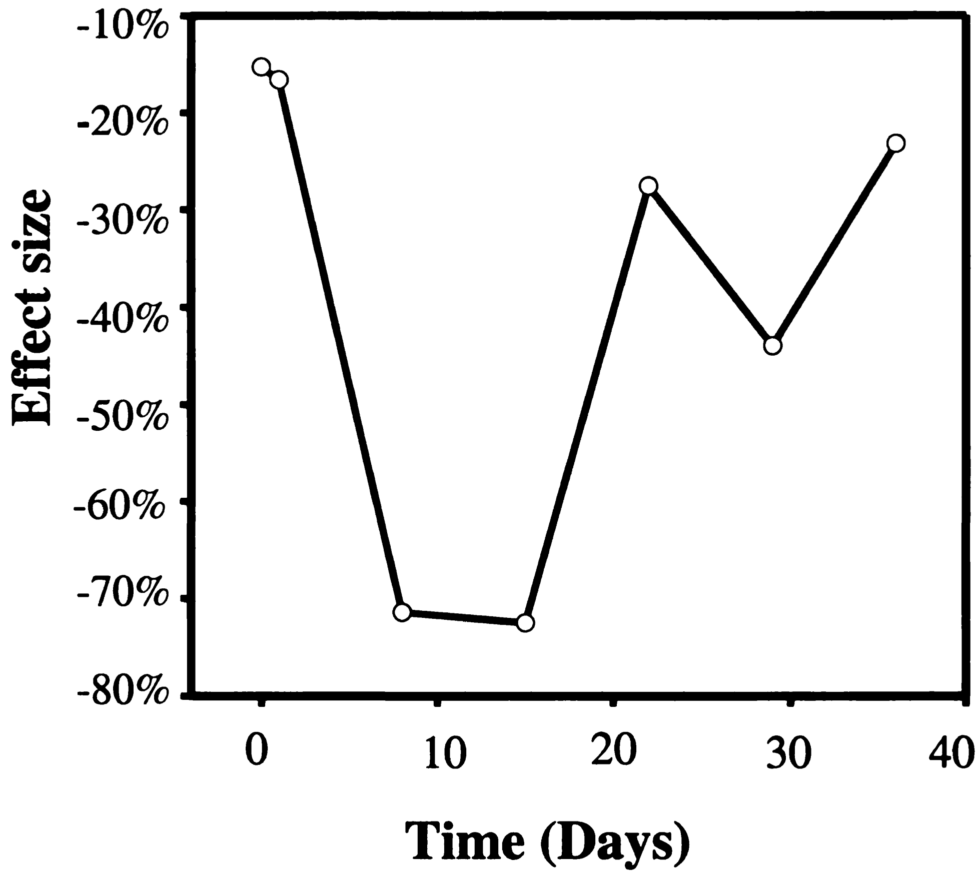

Figure 3. Measured effect size (100 * [(zebra mussel – control) / control]) of zebra mussels on phytoplankton abundance (measured as chlorophyll a) over the 37 days of the experiment.

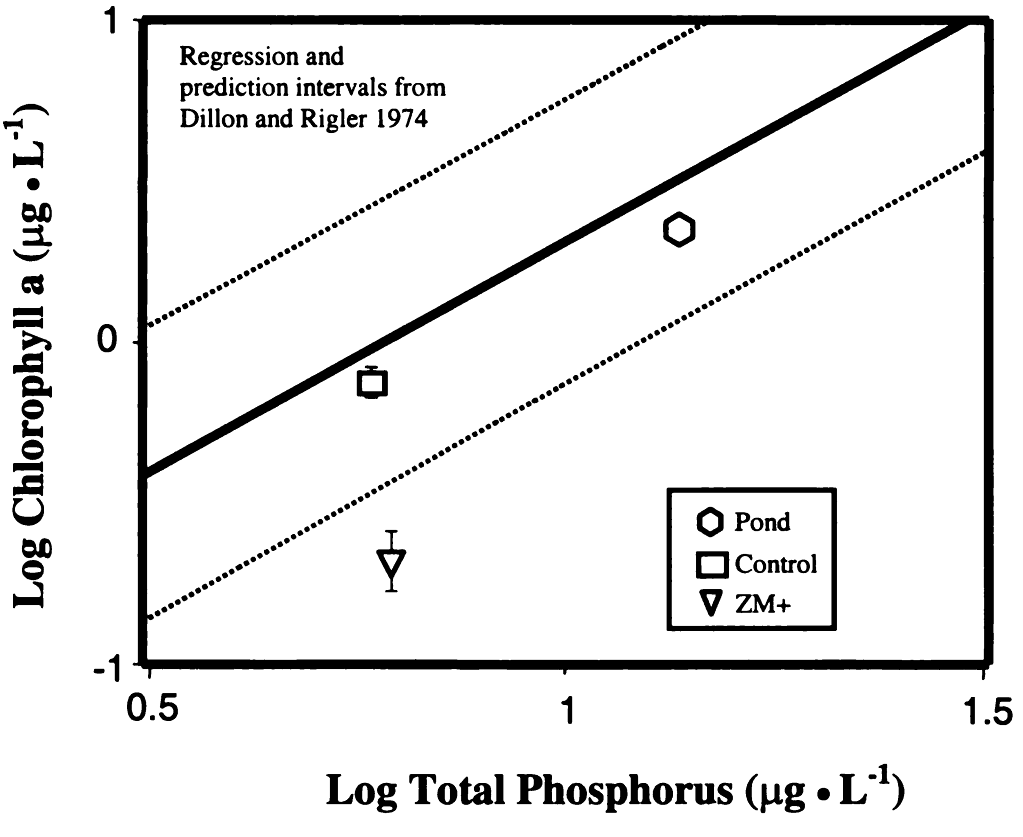

Figure 4. Observed chlorophyll a concentrations for Day 8 plotted in relation to the Dillon-Rigler TP – chlorophyll relationship (logChl a = 1.449 * logTP – 1.136). 95% prediction intervals for Dillon-Rigler are provided. Error bars represent ± 1 standard error.

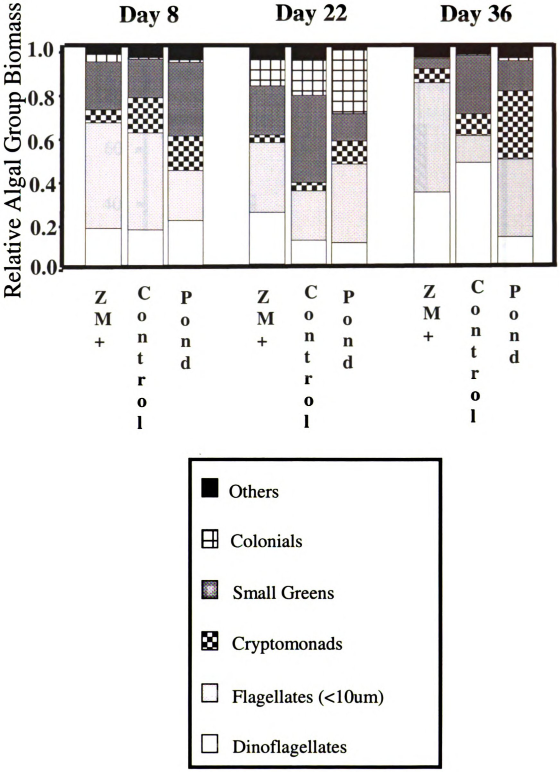

Figure 5. Relative algal group dry biomass (%) for zebra mussel enclosures, control enclosures, and the pond for Day 8, Day 22, and Day 36.

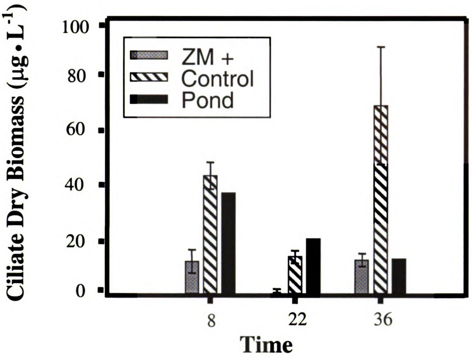

Figure 6. Mean ciliate dry biomass (µg • L^{-1}, ± 1 standard error) for zebra mussel and control enclosures and pond for Days 8, 22, and 36.

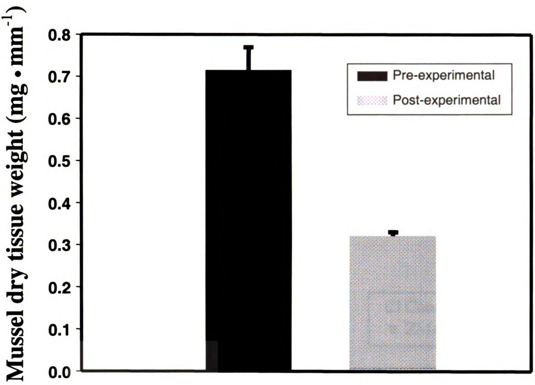

Figure 7. Dry tissue biomass (mg • mm^{-1}) for average mussel length (12mm) for pre- and post-experimental zebra mussels. A correction factor for the effect of freezing as a preservative technique was used to determine the post-experimental mussel weights. Error bars represent 1 standard error.

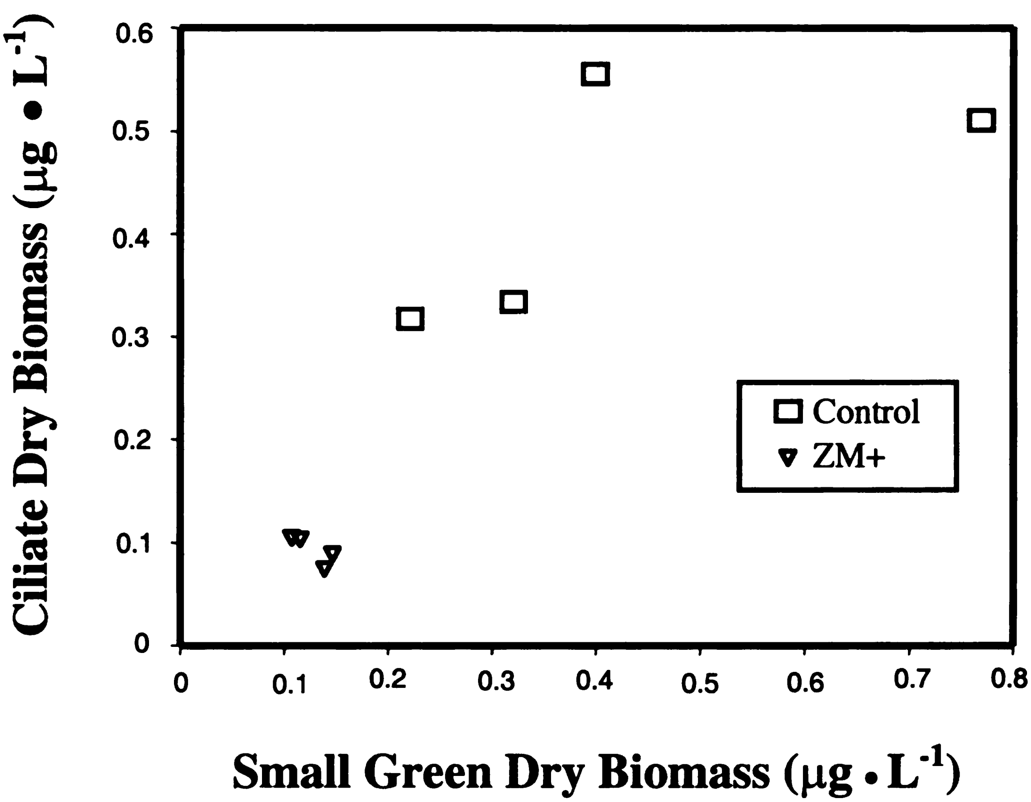

Figure 8. Time-averaged (Days 8, 22, and 36) data on small green algal group Dry biomass (μg • L^{-1}) vs. ciliate dry biomass (μg • L^{-1}) for the four replicates of both treatments.

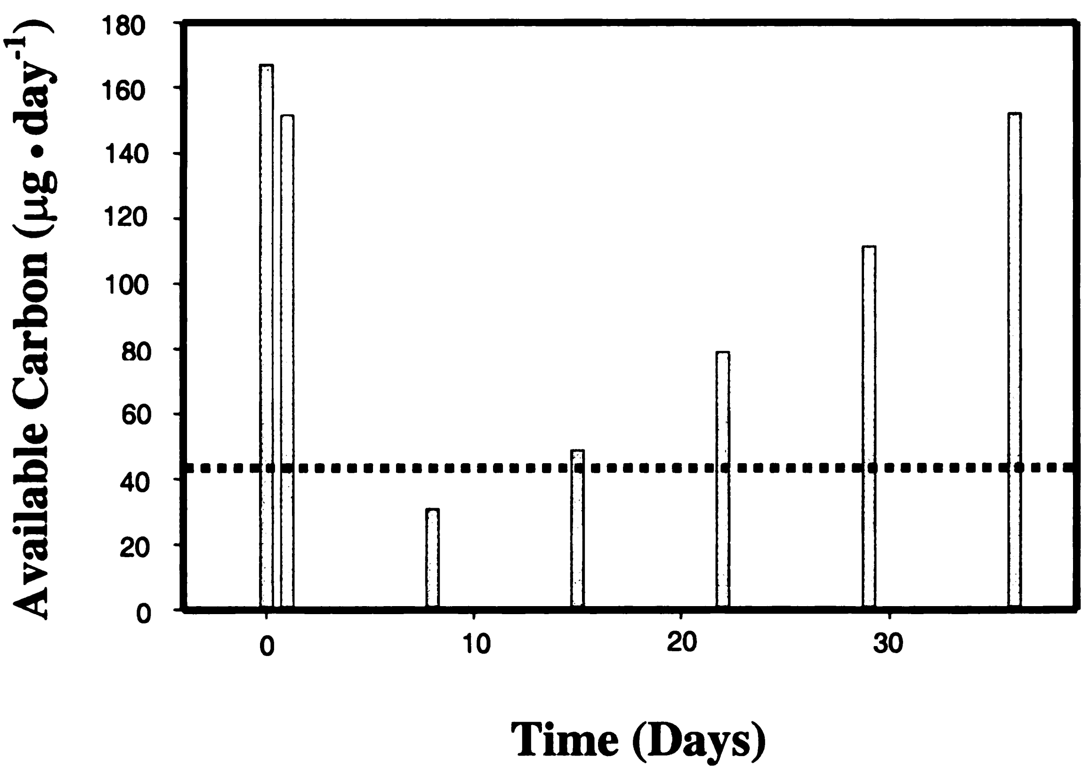

Figure 9. Average available carbon (μm^{-3} • day) in the zebra mussel enclosures. Horizontal dotted line indicates minimum amount of carbon necessary for routine maintenance without growth based on mussels fed *Nitzschia* (from Walz 1978).

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