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THE EFFECTS OF ZEBRA MUSSELS (*DREISSENA POLYMORPHA*) ON INLAND LAKE ECOSYSTEMS

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CARRIE ELIZABETH HULT SCHEELE

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THE EFFECTS OF ZEBRA MUSSELS (*DREISSENA POLYMORPHA*) ON INLAND LAKE ECOSYSTEMS

By

Carrie Elizabeth Hult Scheele

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ABSTRACT

THE EFFECTS OF ZEBRA MUSSELS (*DREISSENA POLYMORPHA*) ON INLAND LAKE ECOSYSTEMS

By

Carrie Elizabeth Hult Scheele

The zebra mussel (*Dreissena polymorpha*) has drastically transformed large freshwater ecosystems since its invasion of the Laurentian Great Lakes in 1988. Zebra mussels are now invading small inland lakes, but less is known about their effects on these systems. Previous studies in well-mixed, shallow systems have shown that zebra mussels negatively affect primary producers and small primary consumers through predation. However zebra mussel effects on larger primary and secondary consumers have varied greatly, likely due to resource competition, and other indirect pathways through the food web.

I conducted a survey of 50 thermally stratified lakes with similar nutrient concentrations and morphometries in southern Michigan to examine the direct and indirect impacts of zebra mussels on the biomass of microzooplankton, the biomass and species composition of macrozooplankton, and the growth rates and diet composition of bluegill sunfish (*Lepomis macrochirus*). Twenty-five lakes were infested with zebra mussels (invaded), while 25 lakes were zebra mussel free (uninvaded).

Phytoplankton biomass was 24% lower in lakes with zebra mussels, and water clarity was 21% greater in invaded lakes. Total microzooplankton biomass was 44% lower, with ciliate and rotifer biomass 39% and 45% lower, respectively, in invaded lakes. Total macrozooplankton biomass was 33% lower, cladoceran biomass was 43% lower, yet, copepod biomass was not significantly different. *Daphnia* spp., a large

macrozooplankton and the preferred prey of bluegill sunfish, was 40% lower in invaded lakes. My study is the first to document significantly lower biomass of large macrozooplankton, including *Daphnia* spp. in invaded lakes. Although macrozooplankton biomass was significantly lower, macrozooplankton community composition did not change in invaded lakes. Zebra mussels are most likely affecting zooplankton directly through predation and indirectly through resource competition.

Because zooplankton biomass was significantly reduced in invaded lakes, I expected bluegill sunfish growth to be lower. Surprisingly, only growth in first year bluegill was lower, while juvenile and adult growth was greater by 1.8-4.2 mm per year in invaded lakes. Contemporary and historical bluegill mean length at age studies confirm that zebra mussels are affecting bluegill, as there were no differences in mean length at age prior to 1988, the zebra mussel invasion in North America, yet after the invasion adults were significantly larger in invaded lakes. Stomach content and stable isotope analyses show that adult bluegill may have switched their diet in invaded lakes to include more benthic macroinvertebrates, providing an important potential mechanism for the unexpected growth patterns. I attribute lower first year growth to low microzooplankton abundance while in the larval growth stage, and the inability for growth to catch up once they move back into the littoral zone later in the summer. Higher juvenile growth likely results from increased benthos promoted by zebra mussels. Finally, higher adult growth most likely results from diet shifts from *Daphnia* spp. to benthos. This study indicates that zebra mussels are not contributing to bluegill sunfish stunting.

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

CHAPTER 2

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 1

THE EFFECTS OF ZEBRA MUSSELS (*DREISSENA POLYMORPHA*) ON MICROZOOPLANKTON AND MACROZOOPLANKTON IN INLAND MICHIGAN LAKES

Carrie E.H. Scheele[1], Lesley B. Knoll[2, 3], and Orlando Sarnelle[2]

[1]Department of Zoology, Michigan State University, East Lansing, MI 48824-1222

[2]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824-1222

[3]Current address, Department of Zoology, Miami University, Oxford, OH 45056

Abstract

The zebra mussel (*Dreissena polymorpha*) has drastically transformed large freshwater ecosystems since its invasion of the Laurentian Great Lakes in the late 1980s. Zebra mussels are now invading smaller inland lakes, but less is known about their effects on these systems. We conducted a survey of 50 thermally stratified lakes in Michigan with similar nutrient concentrations and morphometries to examine the direct and indirect impacts of zebra mussels on the biomass of microzooplankton and the biomass and community composition of macrozooplankton. Twenty-five lakes were infested with zebra mussels (invaded), while 25 lakes were zebra mussel free (uninvaded). In zebra mussel invaded lakes, phytoplankton biomass was 24% lower, and water clarity was 21% greater. Total microzooplankton biomass was 44% lower, with ciliate and rotifer biomass lower by 39% and 45%, respectively, in invaded lakes. Total macrozooplankton biomass was 33% lower, cladoceran biomass was 43% lower, and *Daphnia* spp. biomass was 40% lower in invaded lakes. Copepod biomass, calanoid copepod biomass and cyclopoid copepod biomass were not significantly different. We also observed no difference in macrozooplankton relative biomass, indicating that macrozooplankton community structure did not differ in invaded lakes. Our microzooplankton results are similar to previous studies conducted in shallow well-mixed systems, although the magnitude of the zebra mussel effects in our study was smaller. On the other hand, we are the first study to document lower biomass of large macrozooplankton, including *Daphnia* spp., in invaded lakes. We suggest that zebra mussels affected both microzooplankton and macrozooplankton biomass directly through predation and indirectly through resource competition. Zebra mussels have a bottom-up effect on inland lake ecosystems, and this

effect may be observed in higher trophic levels. Understanding how zebra mussels affect both microzooplankton and macrozooplankton will identify potential mechanisms by which fish are influenced by this invader.

Introduction

The zebra mussel (*Dreissena polymorpha* Pallas), an exotic species native to the Ponto-Caspian region of Eastern Europe, has invaded the United States and is rapidly spreading throughout freshwater systems. First detected in Lake St. Clair, Michigan in 1988 (Herbert et al. 1989), zebra mussels quickly established populations in all five of the Great Lakes and several major river systems (e.g., Hudson, Mississippi, and Ohio Rivers) (Ludyanskiy et al. 1993). Zebra mussels have also been inadvertently spread by recreational boat traffic and are colonizing smaller inland lakes (Kraft and Johnson 2000). Although most zebra mussel invasions are concentrated in the Midwestern United States, they have been transported to water bodies as far west as Washington and California (USGS 2007). Zebra mussels colonize hard substrates in lakes and rivers and can clog water-intake pipes and screens of municipal water supply facilities, industrial facilities, electric power plants, irrigation pipes and boat engine cooling systems, and they foul boat hulls and docks. Economic losses in the Great Lakes basin due to damage and control costs at power plants and water supply units are estimated at $500 million (US) each year, but there are no estimates available for the economic costs resulting from damage to beaches, fishing or boating (Pimentel 2005).

Zebra mussels are efficient filter feeders that represent a new component in the food webs of North American lakes. They filter particles as small as 1 μm in diameter but most efficiently feed on particles between 5 and 45 μm in diameter (MacIsaac and Rocha 1995, Sprung and Rose 1988, Ten Winkel and Davids 1982). Zebra mussel filtering leads to decreased phytoplankton abundance and chlorophyll *a* (Makarewicz et al. 1999, Caraco et al. 1997, Fahnenstiel et al. 1995a, b, Heath et al. 1995, Nicholls and Hopkins

1993), increased water clarity (Caraco et al. 1997, Fahnenstiel et al. 1995a, b, Heath et al. 1995), and altered phytoplankton community composition (Jack and Thorp 2000, Bastviken et al. 1998). Through selective feeding, zebra mussels can promote blooms of the toxic colonial cyanobacterium, *Microcystis aeruginosa*, in lakes with low to moderate nutrient levels (Sarnelle et al. 2005, Knoll 2004, Raikow et al. 2004, Vanderploeg et al. 2001).

Zooplankton dynamics can be affected both directly and indirectly by zebra mussels. Some microzooplankton (ciliates and rotifers) are small enough to be directly consumed by zebra mussels, and their abundance usually declines in invaded systems (Pace et al. 1998, MacIsaac 1996, MacIsaac et al. 1995, MacIsaac et al. 1991). Zebra mussels can also indirectly affect microzooplankton through resource competition for phytoplankton (Idrisi et al. 2001, Caraco et al. 1997, Fahnenstiel et al. 1995 a, Heath et al. 1995). Given these multiple interaction pathways, zebra mussel filtering has the potential to affect ciliate and rotifer biomass differently. Because zebra mussels prefer food particle sizes of 5-45 μm (MacIsaac and Rocha 1995, Sprung and Rose 1988, Ten Winkel and Davids 1982), they should inflict greater mortality on ciliates than rotifers, since ciliate cell sizes are commonly within the preferred range, while rotifers are generally larger (often > 100 μm). Bacteria are also an important food source for microzooplankton. However due to the small size of bacteria (< 1 μm), its abundance is typically not affected by zebra mussel presence (Findlay et al. 1998, Cotner et al. 1995). Ciliates generally consume bacteria more effectively than rotifers. Thus, the relative magnitude of zebra mussels' predatory effect may be larger for ciliates, while their

competitive effect may be larger for rotifers. Therefore, it is not obvious whether mussel invasion will have a greater overall impact on ciliates or rotifers.

Most macrozooplankton are too large to be consumed by zebra mussels (MacIsaac et al. 1995, MacIsaac et al. 1991; but see Shevtsova et al. 1986), and therefore are only indirectly affected through resource competition for phytoplankton and microzooplankton. Studies documenting the effects of zebra mussels on macrozooplankton abundance in the Great Lakes, inland lakes, and rivers are few and are sometimes contradictory. In shallow well-mixed areas of the Great Lakes, Padilla et al. (1996) found no change in zooplankton biomass in L. Michigan, and MacIsaac et al. (1991, 1995) found no change in macrozooplankton biomass in western L. Erie, post invasion. Both Johannsson et al. (2000) and Mills et al. (2003) suspected decreased zooplankton production after invasion in L. Erie and L. Ontario respectively, but neither study found direct evidence for this claim. In Saginaw Bay of L. Huron, Bridgemen (1995) showed a decrease in macrozooplankton biomass that he attributed not only to changes in algal food quality following zebra mussel invasion, but also to changes in predation levels in the lake that were not related to zebra mussels. In shallow Oneida Lake, NY, *Daphnia* species biomass and production did not change following invasion (Idrisi et al. 2001). In well-mixed river systems, zebra mussels have negatively affected the biomass (Thorp and Casper 2003) and growth (Jack and Thorp 2000) of smaller macrozooplankton species such as *Bosmina* spp., *Diaphanasoma* spp. and *Diacyclops* spp. Additionally, Pace et al. (1998) showed a non-significant decline in macrozooplankton biomass in the Hudson River after invasion. Although these results are sometimes contradictory, the general trend in macrozooplankton biomass is either to not

change or to decrease after zebra mussel invasion. The disparities in these results are most likely due to many unquantified indirect zebra mussel effects (Figure 1).

Macrozooplankton are the major food source for planktivorous fish. If macrozooplankton biomass declines due to zebra mussel invasion, then the mussels may negatively affect species in higher trophic levels, such as planktivorous and piscivorous fish (Rutherford et al. 1999), and could potentially threaten the recreational fishing industry in the Midwestern US. Strayer et al. (2004) provided a brief review of zebra mussel effects on fish in six different lake and river systems. These studies showed increased, decreased, or unchanged fish growth rates or abundance at different sites, even though 66% of the study locations underwent a significant decline in phytoplankton and 50% of the study locations endured a decline in zooplankton biomass after invasion. The authors attributed the varying results to the three indirect pathways in which zebra mussels can affect fish: 1) reduced phytoplankton and edible consumers, 2) increased biodeposits and shelter in mussel beds, and 3) enhanced littoral production. It is clear that more research is required to untangle the importance and relative magnitude of each of the three indirect effects.

Most studies on the effects of zebra mussels on lower trophic levels compare communities before and after invasion in a single, shallow, well-mixed ecosystem. In a well-mixed lake or river, water is frequently circulating, allowing zebra mussels to filter the entire water column. This results in strong effects on the biota, such as large declines in phytoplankton (Idrisi et al. 2001, Makarewicz et al. 1999, Caraco et al. 1997, Fahnenstiel et al. 1995a, b, Heath et al. 1995, Nicholls and Hopkins 1993) and microzooplankton (Pace et al. 1998, MacIsaac 1996, MacIsaac et al. 1995, MacIsaac et

al. 1991). Alternatively, in deep, thermally stratified lakes, zebra mussels may not filter the entire water column during summer, and zebra mussels would be expected to have weaker effects on the biota in these lakes (Noonburg et al. 2003, MacIassac 1996, MacIsaac et al. 1991). Additionally, deeper, thermally stratified lakes have a smaller proportion of epilimnetic area relative to zebra mussel habitat, also resulting in weaker zebra mussel effects in these lakes. Our group has investigated the zebra mussel effect on phytoplankton in deep, thermally stratified inland lakes and found significantly lower chlorophyll *a* (30% and 50%, respectively) and phytoplankton biomass (30% and 45%, respectively) (Knoll et al. in press, Raikow et al. 2004), consistent with studies on shallow well-mixed systems. However, it is still unknown how zebra mussels will affect microzooplankton and macrozooplankton in thermally stratified inland lakes and whether these results will be consistent with studies from shallow well-mixed systems. At this time, no studies have investigated the effects of zebra mussels on microzooplankton and macrozooplankton in multiple inland lakes.

A survey of multiple thermally stratified lake ecosystems with and without zebra mussels is a more general approach to studying the effects of zebra mussels on inland lakes, compared to before and after zebra mussel invasion studies on single systems. The multi-lake survey approach provides additional statistical power to detect patterns associated with the zebra mussel invasion that may not be detectable in before and after invasion studies. Thus, a large-scale, multi-system study will provide important clues regarding the indirect effect of zebra mussels on higher trophic levels, specifically through the phytoplankton and edible microzooplankton consumer pathway.

We conducted an extensive survey of 50 thermally stratified inland Michigan lakes (25 invaded and 25 uninvaded) to examine the effects of zebra mussels on microzooplankton and macrozooplankton. We addressed four main questions. 1) Do zebra mussels reduce microzooplankton biomass in thermally stratified inland lakes, and will our results be consistent with results from well-mixed systems? 2) Do zebra mussels cause a larger decline in ciliate biomass than in rotifer biomass? 3) Do zebra mussels reduce macrozooplankton biomass in thermally stratified inland lakes? 4) Do zebra mussels alter macrozooplankton community structure? This is the first study to document the effects of zebra mussels on microzooplankton and macrozooplankton abundance and macrozooplankton species composition in multiple thermally stratified inland lakes. We show that zebra mussels significantly lowered microzooplankton biomass and that the magnitude of the zebra mussel effect was similar on both ciliates and rotifers. We are the first study to show significantly lower biomass of large macrozooplankton, including *Daphnia* spp. in invaded lakes. Additionally, we show macrozooplankton community structure did not change. The results presented in this manuscript are a compliment study to Knoll et al. (2007; in press) that details the effects of zebra mussels on phytoplankton biomass and community structure in these same lakes. A small portion of the phytoplankton data from Knoll et al. (2007; in press) are reproduced here to facilitate interpretation of the microzooplankton and macrozooplankton data.

Methods

Lake Selection Criteria

We selected 50 study lakes in Southern Michigan, USA, 25 invaded by zebra mussels and 25 uninvaded references. Invaded and uninvaded lakes were nearly equally balanced in the southwest and southeast regions of the state. All lakes had low to moderate total phosphorus (TP) concentrations (<22 $\mu g\ L^{-1}$, Knoll et al 2007 in press, Michigan Department of Environmental Quality). Lakes selected for this study were ≥ 9 m in maximum depth to ensure summer temperature stratification, in contrast to most previous studies investigating the *D. polymorpha* invasion that were conducted in shallow well-mixed systems (Thorp and Casper 2003, Vanderploeg et al. 2001, Idrisi et al. 2001, Pace et al. 1998, Caraco et al. 1997, Bridgeman 1995, MacIsaac et al. 1995). The uninvaded lakes were similar in pH and calcium concentrations to the invaded ones, and thus would support zebra mussels if invaded (Raikow et al. 2004, Raikow 2002). To ensure that treatment and control groups were of similar mean depths, we calculated mean depth of all lakes from digitized bathymetric maps (ESRI 1999). Where lake maps were unavailable, we obtained mean depth data from the Michigan Department of Environmental Quality (unpublished data). We acquired zebra mussel presence or absence data from the United States Geological Survey Nonindigenous Aquatic Species database (USGS 2002, 2003) and the Michigan Sea Grant Zebra Mussel Infestation Monitoring Program (Michigan Sea Grant 2002, 2003). Adult zebra mussel presence and absence was verified while sampling the lake, and larval veliger presence and absence was confirmed while counting zooplankton samples (see below).

Lake sampling

We sampled lakes once either between 3 August and 5 September 2002, or 16 July and 23 August 2003. In 2002, we sampled 26 lakes (N uninvaded = 14, N invaded = 12) and in 2003, we sampled 24 lakes (N uninvaded = 11, N invaded = 13). Lakes were sampled in late summer to ensure thermal stratification and sampled over a short time period to reduce the influence of seasonal variability among lakes. Zebra mussel presence or absence was confirmed visually by examining the boat launch and adjacent shallow areas along the shoreline for approximately 15-20 min, looking for zebra mussels in the sediment or attached to other organisms.

Physical and Biological Parameters

We measured temperature, dissolved oxygen, chlorophyll *a*, and total phosphorus (TP) at the deepest part of each lake, as determined from bathymetric maps and an echosounder. We measured temperature and dissolved oxygen at 1 m depth intervals using a Hydrolab Surveyor 4a equipped with a Datasonde 4a (HACH Environmental, Loveland CO). Photosynthetically active radiation (PAR) was measured at 0.5 m depth intervals using a LiCor model Li-1000 quantum photometer with an attached spherical quantum underwater sensor and corresponding deck sensor (LiCor Environmental, Lincoln, NE). Light extinction coefficients were determined as the slope of the linear regression between ln PAR and depth.

We collected an integrated epilimnetic water sample using a flexible plastic tube (5 cm internal diam., 10 m length). The tube was lowered to the bottom of the mixed layer, as determined by the temperature and dissolved oxygen profile, capped and hauled into the boat. Two to four mixed layer samples were collected and pooled in a large

container, and sub samples were taken for phytoplankton composition, microzooplankton composition, chlorophyll *a* and TP. Phytoplankton samples were preserved immediately in Lugol's solution (Hasle 1978). Microzooplankton were collected by passing a 10 L sub sample of the mixed layer water through a 35 μm mesh screen and rinsing organisms on the screen into sample bottles containing glutaraldehyde (final concentration: 2%). Water samples for chlorophyll *a* and TP were placed on ice until they were processed later the same day (~6 h). Chlorophyll *a* samples were filtered through Gelman A/E glass fiber filters (Gelman Sciences, Ann Arbor, MI) and frozen until laboratory analysis. TP samples were frozen until laboratory analysis. Macrozooplankton samples were also obtained from the deepest part of the lake. The zooplankton net (30 cm diameter, 100 μm mesh) was lowered to ~1 m above the lake bottom, and hauled through the water column. Four hauls were pooled from each lake and preserved with 95% ethanol.

We quantified chlorophyll *a* by first extracting it from the glass fiber filters with 90% ethanol and then analyzing the extract with a Turner Model 10-AU fluorometer (Welschmeyer 1994) calibrated to commercial chlorophyll *a* standards (*Anacystis*; Sigma-Aldrich Chemical Company, St. Louis, MO). TP samples were oxidized via persulfate digestion in an autoclave and then analyzed using the colorimetric molybdate blue method (Langner and Hendrix 1982).

Phytoplankton Biomass

Phytoplankton biomass was assessed in a randomly-chosen subset of the surveyed lakes (N uninvaded = 20, N invaded = 22; Knoll et al. 2007 in press). Phytoplankton were identified to species in most cases and enumerated via the inverted microscope technique (Hasle 1978). Biovolume was determined from measurements of cell

dimensions of at least ten individuals of common species in each sample at 1000x magnification using a NIKON model TE2000-S inverted microscope (NIKON, Melville NY), a SPOT insight QE model 4.2 digital camera, and SPOT Advanced version 4.0.9 image-analysis software (Diagnostic Instruments Inc., Sterling Heights, MI). Biovolume was converted to dry biomass assuming a specific gravity of 1 g cm^{-3} and a dry mass to wet mass ratio of 0.10.

Microzooplankton Biomass

Ciliates were assessed in all 50 study lakes (N uninvaded = 25, N invaded = 25). Ciliates were enumerated with the inverted microscope technique using a NIKON model TE2000-S inverted microscope. Sub samples (sub sample volume 30-100 ml) were settled in tubular chambers (Hydro-Bios, Kiel-Holtenau, Germany), the bottoms of which were divided into inner and outer zones of equal area (Sandgren and Robinson 1984). Within each zone, at least 20 random fields were counted at 100x magnification. Ciliate cell volume was determined by measuring at least five individuals per taxon at 400x magnification using the imaging system described above. Biovolume was converted to dry biomass assuming a specific gravity of 1 g cm^{-3} and a dry mass to wet mass ratio of 0.10.

Rotifers were assessed in all 50 study lakes. Rotifers were identified to species using a Nikon model E600 compound microscope at 100x magnification using a SPOT insight Color model 3.2.0 digital camera and SPOT Advanced version 4.0.9 image-analysis software (Diagnostic Instruments Inc., Sterling Heights, MI), and a Sedgwick-Rafter counting chamber. For each lake, approximately 400 individuals (average = 394,

range = 341-475) were counted in a minimum of 2 sub samples. Individual dry biomass for each species was estimated from established literature values (Pauli 1989).

Macrozooplankton Biomass

Macrozooplankton were assessed in all 50 study lakes. Macrozooplankton were counted and identified to genus or species using a 10 ml clear PVC zooplankton counting wheel and a Leica model MZ8 dissecting microscope (Leica Microsystems, Inc., Bannockburn, IL). Samples were diluted to a known volume and two to three 5 ml sub samples were counted. A minimum of 450 individuals were tallied per lake. Measurements of individuals were made at a magnification of 10x, using a Summa Sketch III digitizing pad and ZoopBiom software (Roff & Hopcroft 1986). For each sample, up to 50 individuals were measured for each large (> 1.0 mm) genus or species (*Daphnia galeata, D. pulicaria, D. retrocurva, Epischura* spp., *Leptadora* spp., and *Mesocyclops* spp.) and up to 25 individuals were measured for each small (< 1.0 mm) genus or species (*Alonella* spp., *Bosmina* spp., *Ceriodaphnia* spp., *Cyclops* spp., *Diaphanasoma* spp., *Diaptomus* spp., *Dreissena polymorpha* veligers, *Moina* spp., and nauplii). Biomass was calculated using published length-weight regressions for individual species (Culver et al. 1985, Dumont et al. 1975).

Statistical Analyses

Student's t-tests and Mann-Whitney U-tests were used to evaluate the effect of the presence or absence of zebra mussels on lake physical and biological parameters, and on phytoplankton, microzooplankton and macrozooplankton biomass. When data failed the Kolmogorov-Smirmov and Shapiro-Wilk tests for normality ($p > 0.05$), data were log transformed. If the log transformed data passed the tests for normality ($p < 0.05$),

Student's t-tests were employed. When log transformed data failed normality tests, the Mann-Whitney U non-parametric test was employed.

To determine the effect of zebra mussels on macrozooplankton community composition, we used a principal component analysis (PCA) on macrozooplankton relative biomass. To reduce the influence of zero values, only common taxa were included in the analysis (*Cyclops* spp., *Daphnia* spp., *Diaphanasoma* spp., *Diaptomus* spp., and *Mesocyclops* spp.). PCA taxa data were arcsine square root transformed to achieve normality of the residuals. Factor scores were then compared for zebra mussel invaded and univaded lakes with a Student's t-test. All data were analyzed using Systat version 11.0 (Wilkinson, 1989).

Results

Mean depth and TP in invaded and uninvaded lakes were not significantly different ($U_{25,25} = 241$, $p = 0.17$; $t_{48} = -0.32$, $p = 0.75$; respectively) (Table 1), indicating no bias in the selection of sample lakes with respect to these parameters. Light extinction coefficients were significantly higher ($t_{48} = -2.93$, $p = 0.01$) in invaded lakes, indicating increased penetration of PAR in the water column and increased water clarity. Although chlorophyll *a* did not differ significantly between the lake groups ($t_{48} = 1.68$, $p = 0.10$), total phytoplankton, total microzooplankton and total macrozooplankton biomass were significantly lower in invaded lakes by 24%, 44% and 33%, respectively ($t_{40} = 2.30$, $p = 0.03$; $t_{48} = 3.31$, $p = 0.002$; $t_{48} = 2.22$, $p = 0.03$; respectively) (Table 1). Within the microzooplankton and macrozooplankton categories, ciliate, rotifer and cladoceran biomass were 39%, 45% and 43% lower, respectively, in invaded lakes ($t_{48} = 2.16$, $p =$

0.04; $t_{48} = 3.06$, $p = 0.004$; $t_{48} = 2.79$, $p = 0.008$; respectively), while copepod biomass did not differ ($U_{25,25} = 365$, $p = 0.31$) (Figure 2). The magnitude of the effect of zebra mussel on ciliates and rotifers was similar; ciliate biomass decreased by 39% and rotifer biomass decreased by 45%. Within the cladoceran and copepod categories, *Daphnia* spp. biomass was significantly lower by 40% in invaded lakes ($U_{25,25} = 422$, $p = 0.03$), and calanoid and cyclopoid copepod biomass were not significantly different ($t_{48} = -0.75$, $p = 0.94$; $U_{24,25} = 387$, $p = 0.08$; respectively) (Figure 3).

Relative biomass of the most abundant macrozooplankton taxa was similar in both zebra mussel uninvaded and invaded lakes (Figure 4). The PCA of macrozooplankton relative biomass reduced the five taxa categories into two factors that explained 71% of the overall variance. However, factors 1 and 2 were not significantly related to zebra mussel presence or absence ($t_{48} = -0.77$, $p = 0.45$; $t_{48} = -1.18$, $p = 0.25$; respectively) (Figure 5), providing no evidence of a shift in macrozooplankton community composition in invaded lakes.

Discussion

Microzooplankton

Our results suggest that zebra mussels have a strong negative effect on microzooplankton in thermally stratified inland lakes (Table 1, Figure 2). However, the magnitude of effect zebra mussels exert on microzooplankton is lower in stratified lakes compared to shallow well-mixed systems. We found 39% lower ciliate biomass and 45% lower rotifer biomass in invaded lakes. Experimental studies have shown that zebra mussels reduce ciliate biovolume by 77% (Wilson 2003) and protozoan abundance by 70-

80% (Lavrentyev et al. 1995). In the Hudson River, total zooplankton biomass declined by 70% (Pace et. al 1998) and mean total zooplankton density (excluding ciliates) was 55-71% lower in Lake Erie following zebra mussel invasion (MacIsaac et al. 1995). Reductions of zooplankton in both the Hudson River and Lake Erie were mainly attributed to negative effects of zebra mussels on rotifers. The lesser reduction in our study compared to the Hudson River and Lake Erie studies could result from differences in mixing regime. The plankton in shallow, well-mixed systems may experience greater zebra mussel impacts than in deep, stratified systems (Noonburg et al. 2003, MacIassac 1996, MacIsaac et al. 1991). In a shallow well-mixed system, pelagic organisms are more likely to come into contact with benthic populations of zebra mussels because mussels are able to colonize a greater proportion of the lake bottom and because frequent water column mixing allows the entire benthic and pelagic zones of the lake to intermix. It was unclear whether zebra mussels would have a greater impact on rotifers and ciliates, because zebra mussels should inflict greater predatory effects on ciliates than rotifers, and greater competitive effects on rotifers. Overall, we found that the magnitude of the reduction for both groups was remarkably similar (39% vs. 45%), even though theory suggests that zebra mussels should filter ciliates more effectively than rotifers due to their smaller size (MacIsaac and Rocha 1995, Sprung and Rose 1988, Ten Winkel and Davids 1982).

The similar effect of zebra mussels on ciliates and rotifers may be explained by the fact that bacteria are not a primary food source of zebra mussels. Typically, zebra mussels do not reduce the total abundance of bacteria in systems they invade (Findlay et al. 1998, Cotner et al. 1995) because zebra mussels are not efficient at eating naturally

occurring bacteria due to their small size (< 0.1 μm). Planktonic ciliates feed primarily on phytoplankton (Fenchel 1987) and bacteria, and sometimes rely on bacteria as a key resource (Christoffersen et al. 1990). In contrast, rotifers have difficulty consuming bacteria (Arndt 1993), and primarily consume phytoplankton between 4-17 μm (Bogdan and Gilbert 1984, Bogdan et al. 1980). Thus, in invaded lakes, ciliates may be able to take advantage of bacteria more easily than rotifers, allowing ciliates to compensate for greater predation losses and phytoplankton reductions.

The relative importance of direct (predation) or indirect (competition) mechanisms in the negative impacts of zebra mussels on microzooplankton cannot be determined from this study. As discussed above, predation is likely an important factor. Yet, phytoplankton biomass was significantly lower in invaded lakes (Table 1), as found in previous studies (Idrisi et al. 2001, Caraco et al. 1997, Fahnenstiel et al. 1995b). By consuming phytoplankton, zebra mussels are competing with microzooplankton for resources. Thus, it is reasonable to assume that reductions in phytoplankton, mediated through zebra mussels, could indirectly affect microzooplankton abundance (Figure 1). Previous experiments concluded that zebra mussel predation may be more important than resource competition in reducing microzooplankton abundance (Thorp and Casper 2002, MacIsaac et al. 1995, MacIsaac et al. 1991). In these studies, small-bodied zooplankton were primarily reduced while large-bodied zooplankton were not, even though both compete for resources with zebra mussels. However, these experiments were either conducted in small containers (MacIsaac et al. 1995, MacIsaac et al. 1991), or were short-term (Thorp and Casper 2002). In small-scale experiments, predators and prey may experience greater spatial overlap than in thermally stratified lakes, which may

exaggerate the importance of predation over resource competition, particularly on smaller organisms (Sarnelle 1997). Short-term experiments may also overstate the importance of predation on microzooplankton because the effects of resource competition often take longer to observe than those of predation (Sarnelle 1997).

Macrozooplankton

Zebra mussels also negatively affected macrozooplankton biomass. Total macrozooplankton biomass was 33% lower, cladoceran biomass was 43% lower, and *Daphnia* spp. biomass was 40% lower in invaded lakes (Table 1, Figures 2 and 3). Copepod biomass, calanoid copepod biomass and cyclopoid copepod biomass were not significantly different between uninvaded and invaded lakes (Figures 2 and 3). Our study is the first to document significantly lower biomass of large macrozooplankton species, including *Daphnia* spp., in invaded lakes. The two most comprehensive studies that investigated the effects of zebra mussels on macrozooplankton were conducted before and after invasion in Oneida Lake, NY, (Idrisi et al. 2000) and the Hudson River (Pace et al. 1998). The authors documented no difference in *Daphnia* biomass and production, and mean abundance of post-naupliar copepods and cladocerans, respectively. Idrisi et al. (2000) attributed the lack of change in *Daphnia* spp. biomass and production to the lack of change in primary production in the lake due to increased water clarity. Pace et al. (1998) attributed the lack of change in cladocerans to high amounts of variation over time, the ability of cladocerans to change their diet to bacteria, and to abundant residual phytoplankton. These authors also attribute the lack of change in copepods to the ability to change their diet to protozoa, and to abundant residual phytoplankton. Therefore, our study shows a much greater effect of zebra mussels on macrozooplankton biomass

(33%), including *Daphnia* spp. (40%) in thermally stratified lakes, compared to shallow well-mixed systems.

It is interesting that copepod biomass was not lower, given 24% lower phytoplankton and 44% lower microzooplankton biomass. Copepods in the Hudson River did not decline after invasion (Pace et al.1998). Yet, Thorp and Casper (2002) documented a significant increase of the calanoid copepod *Eurytemora affinis* density (150%) in the presence of zebra mussels. These studies suggest that zebra mussels affect macrozooplankton groups through multiple indirect pathways that may vary across taxa and ecosystems (Figure 1).

Decreased macrozooplankton biomass in zebra mussel invaded lakes is most likely a result of resource competition. Zebra mussels significantly lowered phytoplankton and microzooplankton biomass (Table 1, Figure 2), thereby lowering food resources for macrozooplankton. Additionally, Knoll (2004) reported a shift in the phytoplankton community towards dominance by *Microcysis aeruginosa*, a toxic cyanobacterium, in a subset of the lakes used in our current study. Her results suggest that zebra mussels have not only lowered the overall abundance of both phytoplankton and microzooplankton in invaded lakes, but also they have potentially made the remaining food resources less edible for macrozooplankton. As a result of these altered food resources in invaded lakes, it is highly probable that zebra mussels are outcompeting macrozooplankton and negatively affecting macrozooplankton abundance. Resource competition was also suggested to explain mortality in unionid bivalve mollusks (Unionidae) (Schloesser et al. 1996), another primary consumer negatively affected by zebra mussels.

Finally, we found that although zebra mussels negatively affected the biomass of most macrozooplankton groups, macrozooplankton community structure (as defined by relative biomass) did not differ between invaded and uninvaded lakes (Figures 4 and 5). It is possible that through resource competition, zebra mussels have reduced population sizes of macrozooplankton, yet not shifted the relative biomass of species.

Overall, our study shows significant negative zebra mussel effects on phytoplankton, microzooplankton and macrozooplankton in thermally stratified lakes. The effects of zebra mussels on microzooplankton were somewhat smaller compared to those in shallow well-mixed systems. On the other hand, the effects of zebra mussels on macrozooplankton, including *Daphnia* spp., were much greater in our study compared to shallow well-mixed systems. Ciliates and rotifers were similarly affected by zebra mussels. Cladoceran biomass, including *Daphnia* spp. biomass was greatly lower, but macrozooplankton community structure did not change. These striking changes to the lower trophic levels resulting from zebra mussel invasions of lakes may have consequences for planktivorous and piscivorous fish (Rutherford et al. 1999).

Lower zooplankton biomass, especially lower *Daphnia* spp. biomass, has the potential to greatly affect higher trophic levels in lakes. Planktivorous fish, such as bluegill sunfish (*Lepomis macrochirus*), rely almost entirely on microzooplankton as larvae (Bremigan and Stein 1994, Barkoh and Modde 1987, Siefert 1972, Werner 1967), and *Daphnia* spp. are a major food resource for adults (Werner and Hall 1988; Mittelbach 1984, 1981). By reducing microzooplankton and macrozooplankton biomass, zebra mussels may indirectly affect the survival, growth and fitness of planktivorous fishes. In turn, decreases in planktivorous fish populations may negatively affect piscivorous fishes

and threaten recreational fishing in these lakes. Our study confirms that zebra mussels affect the phytoplankton and edible consumer pathway in a lake foodweb (Strayer et al. 2004) through predation and resource competition, because we saw lower phytoplankton and zooplankton biomass. Thus, it is possible that zebra mussels can negatively affect fish that rely on these resources.

Table 1. Average, range and standard error of physical and biological variables in zebra mussel invaded and uninvaded lakes in 2002-2003. * indicates significance at $\alpha = 0.05$.

Parameter	Uninvaded		Invaded		Test Statistic	P-value
	Average (range)	SE	Average (range)	SE		
Mean Depth (m)	5.28 (2.31-8.80)	0.43	6.28 (2.13-12.41)	0.55	$U_{25,25} = 241$	0.17
Total Phosphorus ($\mu g\ L^{-1}$)	10.56 (4.76-20.76)	0.84	10.95 (5.26-21.04)	0.85	$t_{48} = -0.32$	0.75
Light Extinction Coefficient (m^{-1})	-0.28 ((-0.43)-(-0.16))	0.01	-0.22 ((-0.33)-(-0.06))	0.01	$t_{48} = -2.93$	0.01*
Chlorophyll *a* ($\mu g\ L^{-1}$)	4.23 (1.08-9.29)	0.37	3.33 (0.89-6.2)	0.23	$t_{48} = 1.68$	0.10
Total Phytoplankton Biomass ($\mu g\ L^{-1}$)	49.39 (18.71-95.08)	4.45	37.69 (12.88-115.83)	5.44	$t_{40} = 2.30$	0.03*

Table 1 Continued.

Parameter	Uninvaded		Invaded		Test Statistic	P-value
	Average (range)	SE	Average (range)	SE		
Total Microzooplankton Biomass ($\mu g\ L^{-1}$)	46.40 (13.88-172.78)	6.9	26.16 (5.81-83.14)	3.83	$t_{48} = 3.31$	0.002*
Total Macrozooplankton Biomass ($\mu g\ L^{-1}$)	152.94 (36.26-327.94)	16.72	102.68 (18.17-280.19)	11.37	$t_{48} = 2.22$	0.03*

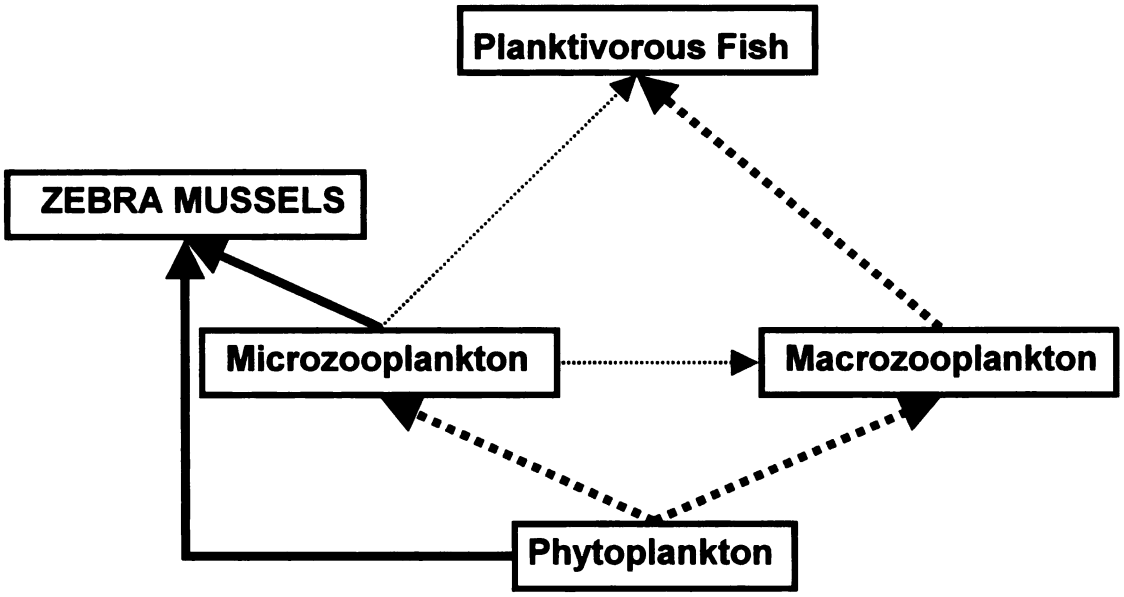

Figure 1. Simplified diagram of an inland lake food web including zebra mussels. Solid lines indicate the direct effects of zebra mussels on other compartments in terms of energy flow. Dotted lines indicate indirect zebra mussel effects. Line weight represents the strength of interactions between compartments. Note that microzooplankton and macrozooplankton can be affected by zebra mussels through multiple pathways in the food web. Other potential indirect pathways not included are the effects of zebra mussels on light, nutrients, dissolved organic carbon and bacteria, all of which may in turn affect micro- and macrozooplankton.

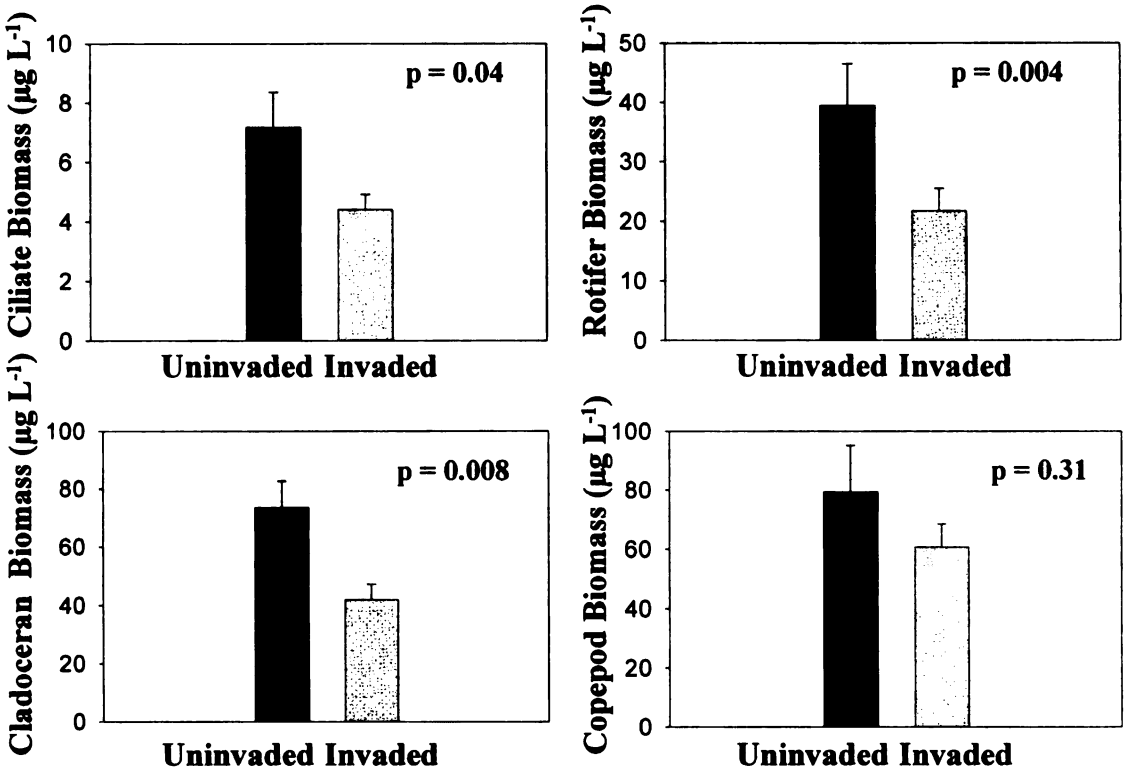

Figure 2. Ciliate, rotifer, cladoceran and copepod dry biomass (µg L^{-1}) in zebra mussel uninvaded and invaded lakes. P- values are from t-tests for ciliates, rotifers and cladocerans, and the Mann-Whitney U test for copepods. Error bars represent standard error.

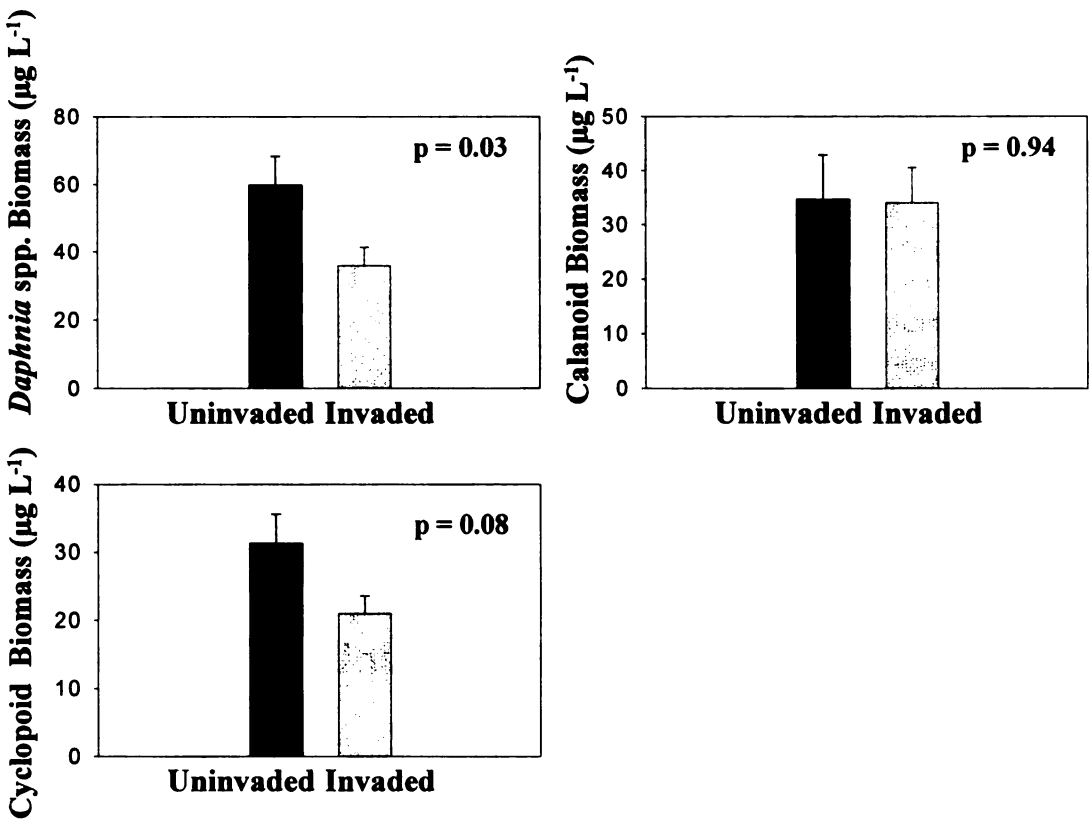

Figure 3. *Daphnia* spp., calanoid copepod, and cyclopoid copepod dry biomass (µg L^{-1}) in zebra mussel uninvaded and invaded lakes. P-values are from a t-test for calanoid copepods, and Mann-Whitney U tests for *Daphnia* spp. and cyclopoid copepods. Error bars represent standard error.

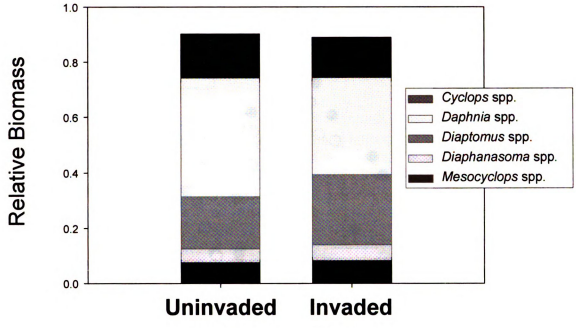

Figure 4. Mean relative biomass of the five most abundant macrozooplankton taxa in zebra mussel uninvaded and invaded lakes.

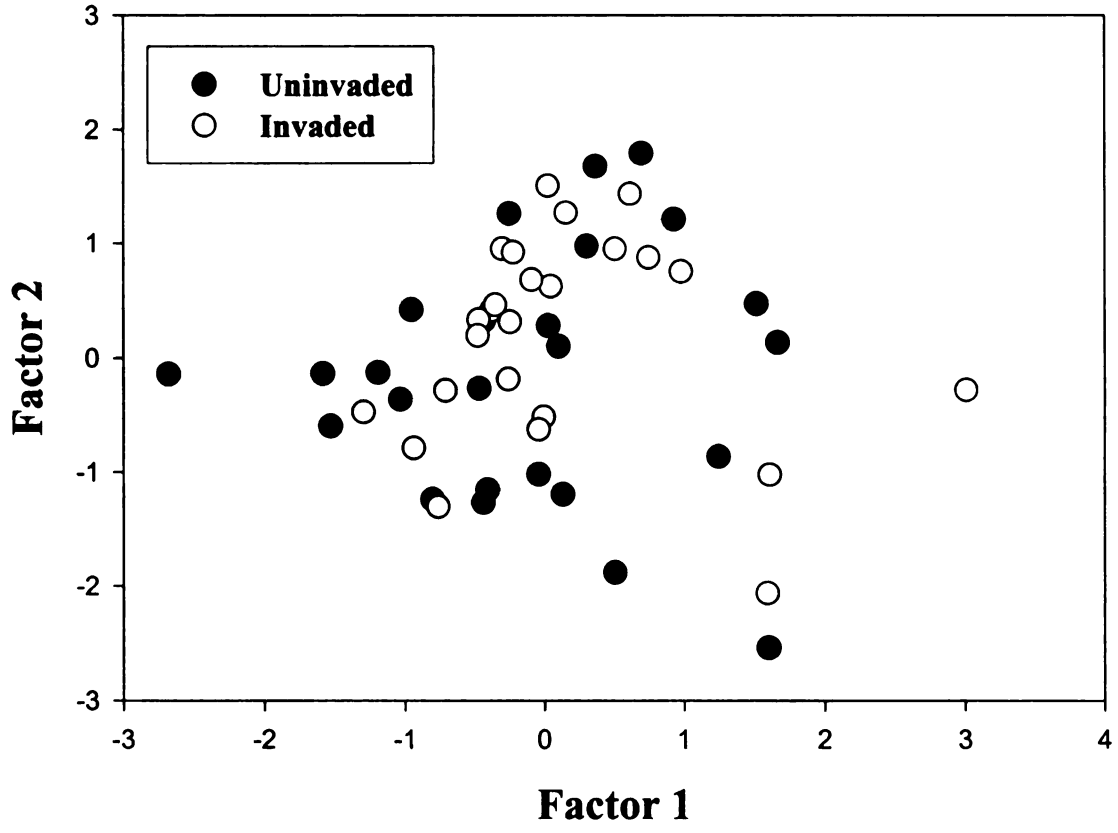

Figure 5. Macrozooplankton relative biomass PCA factor scores for zebra mussel invaded and uninvaded lakes. Factor 1 ($t_{48} = -0.77$, $p = 0.45$) and Factor 2 ($t_{48} = -1.18$, $p = 0.25$).

Literature Cited

Arndt, H.. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 255/256: 231-246.

Barkoh, A., and T. Modde. 1987. Feeding behavior of intensely cultured bluegill fry. Progressive Fish-Culturist 49: 204-207.

Bastviken, D.T.E., N.F. Caraco, and J.J. Cole. 1998. Experimental measurements of zebra mussel (*Dreissena polymorpha*) impacts on phytoplankton community composition. Freshwater Biology 39: 375-386.

Bogdan, K.G., and J.J. Gilbert. 1984. Body size and food size in freshwater zooplankton. Proceedings of the National Academy of Sciences (USA) 81: 6427-6431.

Bogdan, K.G., J.J. Gilbert and P.L. Starkweather. 1980. *In situ* clearance rates of planktonic rotifers. Hydrobiologia 73:73-77.

Bremigan, M.T., and R.A. Stein. 1994. Gape-dependant larval foraging and zooplankton size: implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences 51: 913-922.

Bridgeman, T.B., G.L. Fahnenstiel, G.A. Lang, and T.F. Nalepa. 1995. Zooplankton grazing during the zebra mussel (*Dreissena polymorpha*) colonization of Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21(4): 567-573.

Caraco, N.F., J.J. Cole, P.A. Raymond, D.L. Strayer, M.L. Pace, S.E.G. Findlay, and D.T. Fischer. 1997. Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. Ecology 78: 588-602.

Christoffersen, K., B. Riemann, L.R. Hansen, A. Klysner, and H.B. Sorensen. 1990. Qualitative importance of the microbial loop and plankton community structure in a eutrophic lake during a bloom of cyanobacteria. Microbial Ecology 20: 253-272.

Cotner, J.B., W.S. Gardner, J.R. Johnson, R.H. Sada, J.F. Cavaletto, and R.T. Heath. 1995. Effects of zebra mussels (Dreissena polymorpha) on bacterioplankton: evidence for both size-selective consumption and growth stimulation. Journal of Great Lakes Research 21: 517-528.

Culver, D.A., M.M. Boucherle, D.J. Bean, and J.W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Canadian Journal of Fisheries and Aquatic Sciences 42: 1380-1390.

Dumont, H.J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of

biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75-97.

ESRI 1999. Arc View. Version 3.2. ESRI, Redland, CA.

Fahnenstiel, G.L, G.A. Lang, T.F. Nalepa, and T.H. Johengen. 1995 a. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21: 435-448.

Fahnenstiel, G.L., T.B. Bridgeman, G.A. Lang, M.J. McCormick, and T.F. Nalepa. 1995 b. Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel (*Dreissena polymorpha*) colonization. Journal of Great Lakes Research 21: 465-475.

Fenchel, T.. 1987. Ecology of protozoa: the biology of free-living phagotrophic protists. Springer-Verlag, Berlin.

Findlay, S., M.L. Pace, and D.T. Fischer. 1998. Response of heterotrophic planktonic bacteria to the zebra mussel invasion of the tidal freshwater Hudson River. Microbial Ecology 36: 131-140.

Hasle, G.R.. 1978. The inverted-microscope method, p. 88-96 *in* A. Sournia, editor. Phytoplankton manual. UNESCO, Paris, France.

Heath, R.T., G.L. Fahnenstiel, W.S. Gardner, J.F. Cavaletto, and S.J. Hwang. 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*): an enclosure experiment in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21: 501-516.

Herbert, P.D., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusk in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 1587-1591.

Idrisi, N., E.L. Mills, L.G. Rudstam, and D.J. Stewart. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences. 58: 1430-1441.

Jack, J.D., and Thorp, J.H. 2000. Effects of the benthic suspension feeder *Dreissena polymorpha* on zooplankton in a large river. Freshwater Biology 44: 569-579.

Johannsson, O.E., R. Dermott, D.M. Graham, J.A. Dahl, E.S. Millard, D.D. Myles, and J. LeBlanc. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. Journal of Great Lakes Research 26 (1): 31-54.

Knoll, L.B.. 2004. Understanding zebra mussel (*Dreissena polymorpha*) impacts on

autotrophic and heterotrophic plankton of inland lake ecosystems. M.Sc. Thesis. Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI.

Knoll, L.B., O. Sarnelle, S.K. Hamilton, C.E.H. Scheele, A.E. Wilson, J.B. Rose and M.R. Morgan. 2007. Invasive zebra mussels (*Dreissena polymorpha*) increase cyanobacterial toxin concentrations in low-nutrient lakes. Limnology and Oceanography. In press.

Kraft, C.E., and L.E. Johnson. 2000. Regional differences in rates and patterns of North American inland lake invasions by zebra mussels (*Dreissena polymorpha*). Canadian Journal of Fisheries and Aquatic Sciences 57: 993-1001.

Langner, C.L., and P.F. Hendrix. 1982. Evaluation of a persulfate digestion method for particulate nitrogen and phosphorus. Water Research 16: 1451-1454.

Lavrentyev, P.J., W.S. Gardner, J.F. Cavaletto and J.R. Beaver. 1995. Effects of the zebra mussel (Dreissena polymorpha) on protozoa and the phytoplankton from Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21: 545-557.

Ludyanskiy, M.L., D. MacDonald, and D. MacNeill. 1993. Impact of the zebra mussel, a bivalve invader. BioScience 43: 533-544.

MacIsaac, H.J.. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist 36:287-299.

MacIsaac, H.J., and R. Rocha. 1995. Effects of suspended clay on zebra mussel (*Dreissena polymorpha*) faeces and pseudofaeces production. Archiv fur Hydrobiologie 135: 53-64.

MacIsaac, H.J., C.J. Lonnee, and J.H. Leach. 1995. Suppression of microzooplankton by zebra mussels: importance of mussel size. Freshwater Biology 34: 379-387.

MacIsaac, H.J., W.G. Sprules, and J.H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 48: 2051-2060.

Makarewicz, J.C., T.W. Lewis, and P. Bertram. 1999. Phytoplankton composition and biomass in offshore waters of Lake Erie: pre- and post-*Dreissena* introduction (1983-1993). Journal of Great Lakes Research 25: 135-148.

Michigan Sea Grant 2002, 2003. Michigan Sea Grant Zebra Mussel Infestation Monitoring Program. (http://www.miseagrant.umich.edu/ais/lakes.html)

Mills, E.L., J.M. Casselman, R. Dermott, J.D. Fitzsimons, G. Gal, K.T. Holeck, J.A.

Hoyle, O.E. Johannsson, B.F. Lantry, J.C. Makarewicz, E.S. Millard, I.F. Munawar, M. Munawar, R. O'Gorman, R.W. Owens, L.G. Rudstam, T. Schaner, and T.J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem. (1970-2000). Canadian Journal of Fisheries and Aquatic Sciences 60: 471-490.

Mittelbach G.G.. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499-513.

Mittelbach G.G.. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

Nicholls, K.H., and G.J. Hopkins. 1993. Recent changes in Lake Erie (North Shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. Journal of Great Lakes Research 19: 637-647.

Noonburg, E.G., B.J. Shuter, and P.A Abrams. 2003. Indirect effect of zebra mussels (*Dreissena polymorpha*) on the planktonic food web. Canadian Journal of Fisheries and Aquatic Sciences 60: 1353-1368.

Pace, M.L., S.E.G. Findlay, and D. Fischer. 1998. Effects of an invasive bivalve on the zooplankton community of the Hudson River. Freshwater Biology 39: 103-116.

Padilla, D.K., S.C. Adolph, K.L. Cottingham and D.W. Schneider. 1996. Predicting the consequences of dreissenid mussels on a pelagic food web. Ecological Modeling 85: 129-144.

Pauli, H.R.. 1989. A new method to estimate individual dry weights of rotifers. Hydrobiologia 186: 355-361.

Pimental, D.. 2005. Aquatic nuisance species in the New York State canal and Hudson River system and the Great Lakes basin: an economic and environmental assessment. Environmental Management 35: 692-701.

Raikow, D.F., 2002. How the feeding ecology of native and exotic mussels affects freshwater ecosystems. Ph.D. Thesis. Department of Zoology, Michigan State University, East Lansing, MI.

Raikow, D.F., O. Sarnelle, A.E. Wilson, and S.K. Hamilton. 2004. Dominance of the noxious cyanobacterium *Microcystis aeruginosa* in low-nutrient lakes is associated with exotic zebra mussels. Limnology and Oceanography 49(2): 482-487.

Roff, J.C., and R.R. Hopcroft. 1986. High precision microcomputer based measuring system for ecological research. Canadian Journal of Fisheries and Aquatic Sciences 43: 2044-2048.

Rutherford, E.S., K.A. Rose, E.L. Mills, J.L. Forney, C.M. Mayer and L.G. Rudstam. 1999. Individual-based model simulations of zebra mussel (*Dreissena polymorpha*) induced energy shunt on walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) populations in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 56: 2148-2160.

Sandgren, C.D., and J.V. Robinson. 1984. A stratified sampling approach to compensating for non-random sedimentation of phytoplankton cells in inverted microscope settling chambers. British Phycological Journal 19: 67-72.

Sarnelle, O.. 1997. Daphnia effects on microzooplankton: comparisons of enclosure and whole-lake responses. Ecology 78: 913-927.

Sarnelle, O., A.E. Wilson, S.K. Hamilton, L.B. Knoll, and D.F. Raikow. 2005. Complex interactions between the zebra mussel, *Dreissena polymorpha*, and the harmful phytoplankter, *Microcystis aeruginosa*. Limnology and Oceanography 50(3): 896-904.

Schloesser, D.W., T.F. Nalepa, and G.L. Mackie. 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. American Zoologist 36: 300-310.

Shevtsova, L.V., G.A. Zhdanova, V.A. Movchan, and A.B. Primak. 1986. Experimental interrelationship between *Dreissena* and planktonic invertebrates. Hydrobiological Journal 22(6): 36-39.

Siefert, R.E.. 1972. First food of the larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt. Transactions of the American Fisheries Society 101: 219-225.

Sprung, M., and U. Rose. 1988. Influence of food size and food quality on the feeding of the mussel *Dreissena polymorpha*. Oecologia 77: 526-532

Strayer, D.L., K.A. Hattala, and A.W. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 61: 924-941.

Ten Winkel, E.H., and C. Davids. 1982. Food selection by *Dreissena polymorpha* Pallas (mollusca: bivalvia). Freshwater Biology 12: 553-558.

Thorp, J.H., and A.F. Casper 2003. Importance of biotic interactions in large rivers: an experiment with planktivorous fishes, dreissenid mussels and zooplankton in the St. Laurence River. River Research and Applications 19: 265-279.

Thorp, J.H., and A.F. Casper 2002. Potential effects on zooplankton from species shifts in

planktivorous mussels: a field experiment in the St. Lawrence River. Freshwater Biology 47: 107-119.

USGS 2007. United States Geological Survey Nonindigenous Aquatic Species Database. (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/maps/current_zm_quag_map.jpg)

USGS 2002, 2003. United States Geological Survey Nonindigenous Aquatic Species Database. (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/)

Vanderploeg, H.A., J.R. Liebig, W.W. Carmichael, M.A. Agy, T.H. Johengen, G.L. Fahnenstiel, and T.F. Nalepa. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 58: 1208-1221.

Welschmeyer, N.A.. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography 39:1985-1992.

Werner, E.E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

Werner, G.H.. 1967. Intralacustrine movements of bluegill fry in Crane Lake, Indiana. Transactions of the American Fisheries Society 96: 416-420.

Wilkinson, L.. 1989. Systat: the system for statistics. Evanston, 822 pp.

Wilson A.E.. 2003. Effects of zebra mussels on phytoplankton and ciliates: a field mesocosm experiment. Journal of Plankton Research 25(8): 905-915.

CHAPTER 2

THE EFFECT OF ZEBRA MUSSELS (*DREISSENA POLYMORPHA*) ON THE GROWTH RATE AND DIET COMPOSITION OF BLUEGILL SUNFISH (*LEPOMIS MACROCHIRUS*) IN INLAND MICHIGAN LAKES

Carrie E.H. Scheele[1], Lesley B. Knoll[2, 5], Alan E. Wilson[3], Orlando Sarnelle[2], and Stephen K. Hamilton[4]

[1]Department of Zoology, Michigan State University, East Lansing, MI 48824-1222

[2]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824-1222

[3] Cooperative Institute for Limnology and Ecosystems Research, Ann Arbor, Michigan 48105

[4]W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060-9516

[5]Current address, Department of Zoology, Miami University, Oxford, OH 45056

Abstract

The zebra mussel (*Dreissena polymorpha*) has drastically transformed large freshwater ecosystems since its invasion of the Laurentian Great Lakes in 1988. Zebra mussels are now invading small inland lakes, but less is known about their effects on these systems. We conducted a survey of 50 southern Michigan lakes with similar nutrient concentrations and morphometries to examine the indirect impacts of zebra mussels on the growth rate and diet composition of bluegill sunfish (*Lepomis macrochirus*). Twenty-five lakes contained zebra mussels (invaded), and 25 lakes did not (uninvaded). Light extinction coefficients were 21% higher in invaded lakes, while phytoplankton, microzooplankton, and macrozooplankton biomass were significantly lower (24%, 44%, and 40%, respectively) in the presence of zebra mussels. Zebra mussels significantly affected growth rates of bluegill sunfish, and the effect changed depending on the life history stage of the fish. The growth of first year bluegill was lower in invaded lakes likely due to low microzooplankton abundance while in the larval growth stage, and the inability for growth to catch up once they move back into the littoral zone later that summer. In contrast, juveniles and adults grew an additional 1.8-4.2 mm per year in invaded lakes. Higher growth of juveniles and adults in invaded lakes was unexpected. Through stomach content and stable isotope analyses, we show evidence that adult bluegill may have switched their diet in invaded lakes to include more benthic macroinvertebrates. Juveniles most likely took advantage of increased benthic invertebrate biomass promoted by zebra mussels in invaded lakes. The most likely mechanism for higher adult growth rates was diet supplementation with benthic invertebrates that are promoted by zebra mussel presence in lakes. We also observed a

significant positive effect of zebra mussels on adult bluegill mean length at age in a subset of 24 lakes (11 invaded, 13 uninvaded) in 2002-2003, yet no effect was detected in these same lakes and treatment groups prior to invasion (< 1988). These pre- and post-invasion data support the zebra mussel effect on bluegill growth in 2002-2003. Overall, our results provide no evidence of a negative zebra mussel effect on juvenile and adult bluegill growth, even though we do show evidence that bluegills may have switched their diet. Thus, zebra mussels do not contribute to bluegill stunting.

Introduction

The zebra mussel (*Dreissena polymorpha* Pallas) has invaded the United States and is rapidly spreading throughout freshwater systems. Economic losses in the Great Lakes basin due to damage and control costs are estimated at $500 million (US) each year (Pimentel 2005). First detected in Lake St. Clair, Michigan, USA, in 1988 (Herbert et al. 1989), zebra mussels quickly established populations in all five of the Great Lakes and several major river systems (e.g. Hudson, Mississippi, and Ohio Rivers) (Ludyanskiy et al. 1993), and soon began to invade smaller inland lakes (Kraft and Johnson 2000).

Zebra mussels are efficient filter feeders that consume large quantities of algae and small zooplankton. Phytoplankton biomass usually declines following zebra mussel invasion and water clarity increases (Idrisi et al. 2001, Caraco et al. 1997, Nicholls and Hopkins 1993). At the same time, zebra mussels can promote blooms of the toxic colonial cyanobacterium, *Microcystis aeruginosa*, in low nutrient lakes (Knoll et al. 2007 in press, Sarnelle et al. 2005, Knoll 2004, Raikow et al. 2004, Vanderploeg et al. 2001).

Due to their efficient filtering and production of feces and pseudofeces, zebra mussels can divert energy from pelagic to benthic communities (MacIsaac 1996), enhancing nutrient fluxes to the benthos (Conroy et al. 2005), and increasing benthic algae and benthic primary productivity (Fahnenstiel et al. 1995, Lowe and Pillsbury 1995). Additionally, the increased habitat heterogeneity created from their colonies coupled with the production of nutrient rich feces and pseudofeces results in increased biomass of benthic macroinvertebrates (Stewart et al. 1998a, b, Ricciardi et al. 1997, Thayer et al. 1997, Stewart and Haynes 1994).

Zooplankton dynamics can be affected both directly and indirectly by zebra mussels. Microzooplankton are directly consumed by zebra mussels resulting in decreased biomass of this trophic level (Pace et al. 1998). Most macrozooplankton are too large to be consumed by zebra mussels (MacIsaac et al. 1995, MacIsaac et al. 1991; but see Shevtsova et al. 1986), but zebra mussels indirectly affect abundance (Thorp and Casper 2003, Bridgeman et al. 1995), and fecundity (Horgan and Mills 1999) of small macrozooplankton species by reducing food availability. Decreased macrozooplankton abundance, in turn, affects species in higher trophic levels in the food web, including fish (Rutherford et al. 1999).

Studies of the effects of zebra mussels on fish growth in lakes, rivers, and experimental enclosures are few and often contradict each other. Fish growth in the presence of zebra mussels decreased, increased, or remained the same for species in different life stages and ecosystems (Table 1). This variation may also result from the multitude of indirect pathways through which fish may be affected by zebra mussels in complex aquatic food webs (Strayer et al. 2004).

Bluegill sunfish (*Lepomis macrochirus*) is the dominant fish species in southern Michigan inland lakes (Werner et al. 1978). Bluegills undergo ontogenetic niche shifts twice during their life histories (Werner and Hall 1988). As larvae [< 14 mm standard length (SL)], they forage on small zooplankton in the pelagic zone. Juveniles (20-79 mm SL) forage in the vegetation of the littoral zone to avoid predation from largemouth bass (*Micropterus salmoides*) and feed mainly on invertebrates. Adults (> 80 mm SL) are large enough to avoid predation and feed extensively on macrozooplankton (*Daphnia*) that are abundant in the water column in the pelagic zone (Werner and Hall 1988;

Mittelbach 1984, 1981). Reduction of macrozooplankton abundance by zebra mussels could limit food for bluegills, substantially decrease adult growth (Osenberg et al. 1988), and lead to lake populations dominated by stunted adults (Gerking 1962, Swingle and Smith 1942). Bluegill population size structures skewed toward adults < 150 mm are considered a primary management concern in the Midwestern U.S. (Drake et al. 1997). Recently, Raikow (2004) found that zebra mussels reduced the growth rates of larval bluegills in experimental enclosures. He attributed this to fewer microzooplankton in the presence of zebra mussels and to competition between zebra mussels and larval bluegills for food. Thus, if zebra mussels negatively affect larval bluegill growth, it is possible that they could affect the growth of juveniles and adults.

We conducted an extensive survey of inland Michigan lakes and addressed 3 main questions. 1) Are there differences in bluegill growth rates in inland Michigan lakes with and without zebra mussels? 2) Is there a detectable change in bluegill mean length at age in lakes containing zebra mussels compared to historical data from the same lakes prior to zebra mussel infestation? 3) Do adult bluegill sunfish alter their diet in the presence of zebra mussels?

Methods

Lake Selection Criteria

We selected 50 lakes for study, 25 invaded by zebra mussels and 25 uninvaded reference lakes. Lakes were located in the glacial terrain of southern Michigan, USA. Invaded and uninvaded lakes were nearly equally balanced in the southwest and southeast regions of the state. The lakes had low to moderate total phosphorus (TP) concentrations

(<22 μgL^{-1}; Knoll et al. 2007 in press, Michigan Department of Environmental Quality). All lakes selected for this study were $\geq$ 9 m in maximum depth, to ensure summer temperature stratification. We calculated mean depth of all lakes from digitized bathymetric maps (ESRI 1999) to ensure that treatment and control groups were of similar depths. Where lake maps were unavailable, we obtained mean depth data from the Michigan Department of Environmental Quality (unpublished data). We acquired zebra mussel presence or absence data from the United States Geological Survey Nonindigenous Aquatic Species database (USGS 2002, 2003) and the Michigan Sea Grant Zebra Mussel Infestation Monitoring Program (Michigan Sea Grant 2002, 2003).

Lake sampling 2002-2003

Lakes were sampled once between either 3 August and 5 September 2002, or 16 July and 23 August 2003. In 2002, we sampled 26 lakes (N uninvaded = 14, N invaded = 12) and in 2003, we sampled 24 lakes (N uninvaded = 11, N invaded = 13). Zebra mussel presence or absence was confirmed during sampling by wading near the boat launch and adjacent shallow areas along the shoreline for approximately 15-20 min, looking for zebra mussels in the sediment or attached to other organisms.

Physical and Biological Parameters 2002-2003

We sampled from the deepest part of each lake, as determined from bathymetric maps and an echosounder. We measured temperature and dissolved oxygen from the water column at 1 m depth intervals using a Hydrolab Surveyor 4a equipped with a Datasonde 4a (HACH Environmental, Loveland, CO). Photosynthetically active radiation [PAR] was measured at 0.5 m depth intervals using a LiCor model Li-1000 quantum photometer with an attached spherical quantum underwater sensor and

corresponding deck sensor (LiCor Environmental, Lincoln, NE). Light extinction coefficients were determined as the slope of the linear regression between ln PAR and depth. We collected an integrated epilimnetic water sample from the surface to the bottom of the mixed layer, using a flexible plastic tube (5 cm inner diameter, 10 m length). Two to four mixed layer samples were collected and pooled in a large container, and sub samples were taken for phytoplankton biomass and stable isotope analysis, chlorophyll *a*, TP and microzooplankton. Phytoplankton biomass samples were preserved immediately in Lugol's solution (Hasle 1978). Mixed-layer water for phytoplankton stable isotope samples, chlorophyll *a*, and TP was put on ice and processed later in the same day (~6 h). Seston for analysis of stable isotopes, and chlorophyll *a* was collected on Gelman A/E glass fiber filters (Gelman Sciences, Ann Arbor, MI), that were frozen until laboratory analysis. Microzooplankton were collected by passing a 10 L sub sample of the mixed-layer water through a 35 μm mesh screen and rinsing organisms on the screen into sample bottles containing glutaraldehyde (final concentration: 2%). Macrozooplankton samples were also obtained from the deepest part of the lake. The zooplankton net (30 cm diameter, 100 μm mesh) was lowered to ~1 m above the lake bottom and hauled through water column. Four hauls were pooled from each lake and preserved with 95% ethanol for macrozooplankton biomass analysis. An additional two tows were pooled from each lake, put on ice, and brought back to the lab for stable isotope analysis. Zebra mussels, snails and sediment samples for stable isotope analysis were collected from the littoral zone and frozen until analysis.

We measured chlorophyll *a* by first extracting it from the glass fiber filters with 90% ethanol and then analyzing the extract with a Turner Model 10-AU fluorometer

(Welschmeyer 1994) calibrated to commercial chlorophyll *a* standards (*Anacystis*; Sigma-Aldrich Chemical Company, St. Louis, MO). Total phosphorus samples were oxidized via persulfate digestion in an autoclave and then analyzed using the molybdate blue colorimetric method (Langner and Hendrix 1982).

Phytoplankton Biomass 2002-2003

Phytoplankton biomass was assessed in a randomly chosen subset of survey lakes (N uninvaded = 20, N invaded = 22; Knoll et al. 2007 in press). Phytoplankton were identified to species in most cases and enumerated via the inverted microscope technique (Hasle 1978). Biovolume was determined from measurements of cell dimensions of at least ten individuals of common species in each sample at 1000x magnification using a NIKON model TE2000-S inverted microscope (NIKON, Melville NY), a SPOT insight QE model 4.2 digital camera and SPOT Advanced version 4.0.9 image-analysis software (Diagnostic Instruments Inc., Sterling Heights, MI). Biovolume was converted to dry biomass assuming a specific gravity of 1 g cm^{-3} and a dry mass to wet mass ratio of 0.10.

Microzooplankton Biomass 2002-2003

Ciliate biomass was assessed in all 50 study lakes (N uninvaded = 25, N invaded = 25). Ciliates were enumerated with the inverted microscope technique using a NIKON model TE2000-S inverted microscope. Sub samples (sub sample volume 30-100 ml) were settled in tubular chambers (Hydro-Bios, Kiel-Holtenau, Germany), the bottoms of which were divided into inner and outer zones of equal area (Sandgren and Robinson 1984). Within each zone, at least 20 random fields were counted at 100x magnification. Ciliate cell volume was determined by measuring at least five individuals per taxon at 400x magnification using the imagine system described above. Biovolume was converted to

dry biomass assuming a specific gravity of 1 g cm^{-3} and a dry mass to wet mass ratio of 0.10.

Rotifer biomass was assessed in all 50 study lakes. Rotifers were identified to species using a Nikon model E600 compound microscope (NIKON, Melville NY) at 100x magnification using a SPOT insight Color model 3.2.0 digital camera and SPOT Advanced version 4.0.9 image-analysis software (Diagnostic Instruments Inc., Sterling Heights, MI), and a Sedgwick-Rafter counting chamber. For each lake, approximately 400 individuals (average = 394, range = 341-475) were counted in a minimum of 2 sub samples. Individual dry biomass for each species was estimated from established literature values (Pauli 1989).

Macrozooplankton Biomass 2002-2003

Macrozooplankton biomass was assessed in all 50 study lakes. Macrozooplankton were counted and identified to genus or species using a 10 ml clear PVC zooplankton counting wheel and a Leica model MZ8 dissecting microscope (Leica Microsystems, Inc., Bannockburn, IL). Samples were diluted to a known volume and two to three 5 ml sub samples were counted. A minimum of 450 individuals were tallied per lake. Measurements of individuals were made at a magnification of 10x, using a Summa Sketch III digitizing pad and ZoopBiom software (Roff & Hopcroft 1986). For each sample, up to 50 individuals were measured for each large (> 1.0 mm) genus or species (*Daphnia galeata, D. pulicaria, D. retrocurva, Epischura* spp., *Leptadora* spp., and *Mesocyclops* spp.) and up to 25 individuals were measured for each small (< 1.0 mm) genus or species (*Alonella* spp., *Bosmina* spp., *Ceriodaphnia* spp., *Cyclops* spp., *Diaphanasoma* spp., *Diaptomus* spp., *Dreissena polymorpha* veligers, *Moina* spp., and

nauplii). Biomass was calculated using published length-weight regressions for individual species (Culver et al. 1985, Dumont et al. 1975).

Bluegill Growth 2002-2003

We collected bluegill sunfish from several sites in the littoral zone of each lake using a beach seine, a cast net, or angling. We weighed and measured approximately 100 bluegill per lake, including adults [≥ 90 mm total length (TL)], juveniles (40 - 90 mm TL) and first year (< 40 mm TL). For age and growth determination, we obtained 5 to 10 scales from each of the first 50 bluegills sampled. We removed the scales from the left side of the body, just posterior of the tip of the depressed pectoral fin.

To determine fish age, we pressed 6 to 10 scales from each of the 50 bluegills sampled per lake between two microscope slides. We counted the number of annuli present on one randomly selected scale per slide and measured the distances from the focus to each annulus and the scale margin using a Nikon Eclipse E600 dissecting microscope (NIKON, Melville, NY), and Optimus 6.0 software (Media Cybernetics, Silver Spring, MD).

Bluegill growth was back calculated using the Scale Proportional Method (Whitney and Carlander 1956):

$$TL_i = (-a/b) + (TL_c + (a/b))(S_i/S_c)$$

TL_i = estimated total length of a fish (mm) at the formation of the i^{th} scale mark, for i = 1, 2...n; TL_c = total fish length (mm) at the time of capture; S_i = scale radius (mm) at the formation of the i^{th} scale mark, for i = 1, 2...n; and S_c = scale radius (mm) at time of capture. We determined the intercept (a) and slope (b) from the linear function describing the relationship between S_c and TL_c:

$S_c = 0.0228 (TL_c) - 0.4266$, $n = 3168$, $R^2 = 0.938$.

Annual growth rates, or the change in length from one annulus to the next, were expressed as:

$$\Delta TL = TL_{x+1} - TL_x$$

Growth rates were expressed as a function of the total fish length (mm) at the start of the year's growth stanza (TL_x) in the year before capture. Bluegill were then placed into 3 life history categories according to their length (mm) at the start of the year's growth stanza: adults (≥ 90 mm TL), juveniles (40 - 90 mm TL) and first year (< 40 mm TL) (Werner and Hall 1988; Mittelbach 1984, 1981). Note that first year bluegill (age 1 + at capture) encompass both the larval open water stage where they feed on small zooplankton, and a small juvenile stage that includes feeding on macroinvertebrates in the littoral zone.

Historical vs. Contemporary Bluegill Mean Length at Age

Historical data on bluegill growth was not available for the study lakes. However, we examined historical bluegill mean length at age data for 24 of the lakes in our study (N uninvaded = 13, N invaded = 11) (Michigan Department of Natural Resources Fisheries Division, unpublished data). These data were used as a baseline to determine if mean length at age in the lake groups changed after zebra mussel infestation. We compared mean length at age of juvenile (ages 1-2) and adult bluegill (ages 3-6) between lake groups and within individual time periods (< 1988 and 2002-2003) to be consistent with the 2002-2003 growth analyses. Historical first year bluegill data were not available and therefore we were unable to make comparisons for that life history category. Because actual zebra mussel infestation dates for our study lakes are not available, all historical

data used in our comparisons were from June-September (1956-1987), prior to the first zebra mussel sightings in the US in 1988. The methods and gear used to collect the bluegill for the historical data varied from electrofishing, encircling gill nets, gill nets, trap nets, fyke nets, seines, and angling. Many scientists from the MI-DNR were involved in collecting and analyzing the historical data. In cases when there were historical data from more than one year from the same lake, these data were averaged to make one overall historical mean length at each age for that lake.

Contemporary bluegill mean length at age data were obtained for the same 24 lakes using the 2002-2003 bluegill dataset. The contemporary data were arranged in the same manner as the historical mean length at age data and allowed for comparison between the two lake groups in both the historical and contemporary time periods.

Bluegill Diet 2002-2003

Thirty adult bluegills (> 90 mm TL) were sacrificed per lake for stomach content analyses. In the field, sacrificed adults were killed using a 1g/L water dose of MS-222 and then put on ice to slow down digestion. In the laboratory, the fish were thawed, and the stomachs removed and preserved in 95% ethanol. Stomach content analyses were performed for 26 of the 50 study lakes (N uninvaded = 13, N invaded = 13). Ten randomly chosen adult bluegill stomachs were examined per lake.

We employed two different methods for determining the biomass of prey items in bluegill stomachs. For both biomass methods, stomach contents were counted using a Leica model MS5 dissecting microscope (Leica Microsystems, Inc., Bannockburn, IL). The prey were identified to family or genus [*Daphnia* spp., cladocerans (without *Daphnia* spp.), copepods, snails, clams, zebra mussels, mites, ostracods, beetles, true bugs,

caddisfly larvae, *Chironomus* larvae, amphipods, springtails, damselfly larvae, dragonfly larvae, stonefly larvae, mayfly larvae, small worms, earthworms, moth larvae, *Chaoborous* spp., mosquito larvae, and wasps]. In the first method, measurements of up to 50 individuals of each prey were taken under a magnification of 10x, using a Summa Sketch III digitizing pad and ZoopBiom software (Roff & Hopcroft 1986). Biomass was calculated using published length-weight regressions for bluegill prey items found in three lakes habitats: 1) open water [*Daphnia* spp., cladocerans (without *Daphnia* spp.), and copepods], 2) bare sediment (*Chiromomus* larvae) and 3) vegetation (all other taxa) (Mittelbach 1981). This direct method of determining stomach content biomass was employed for 6 of the 26 lakes.

The second method we was used was a multiple-regression technique to estimate the mean weight of prey taxa in fish stomachs, developed by Hayes and Taylor (1991). Stomach contents were removed from the stomach, weighed, and abundance of each prey taxon was recorded. The multiple-regression technique regressed the total weight of the stomach contents against the counts of the individual prey taxon present, where:

$$SW_i = a_1 x_{i1} + a_2 x_{i2} + \ldots + a_j x_{ij} + e_i$$

SW_i = total weight of stomach contents from fish i; a_j = regression coefficient that becomes an estimate of the mean weight per individual of prey taxon j; x_{ij} = number of prey j in stomach i; and e_i = random error for stomach i. The mean weight attributable to each taxon for the entire sample was determined by multiplying the mean count of each taxon by the regression coefficient (a_j) for that group:

$$W_j = a_j \bar{x}_j;$$

W_j = mean weight attributable to prey *j*; and $\bar{x}_j$ = mean number of prey item *j* per stomach.

The variance of estimates of W_j was determined by:

$$var(ab) = [a^2 var(b)] + [b^2 var(a)],$$

assuming that $\bar{x}_j$ and a_j are independent variables. The 24 prey taxa were reduced into 11 categories based on similar organism size to reduce zeros in the dataset [1. *Daphnia* spp., 2. snails, clams and zebra mussels, 3. mites and ostracods, 4. beetles and true bugs, 5. amphipods and springtails, 6. damselfly larvae, dragonfly larvae, stonefly larvae and mayfly larvae, 7. small worms, moth larvae, *Chaoborous* spp. and wasps, 8. caddisfly larvae and *Chironomus* larvae, 9. cladocerans (without *Daphnia* spp.) and copepods, 10. mosquito larvae and 11. earthworm]. The multiple-regression successfully estimated the average weight of the 11 stomach content taxa ($R^2 = 0.85$, $F_{11,189} = 100.95$, $p < 0.001$) (Figure 1). Estimates for each taxon are reported in Table 2. The regression method was used for 20 of the 26 lakes that were analyzed for stomach contents.

Carbon and nitrogen stable isotope analyses were performed on select food web compartments in 29 of the 50 study lakes (N uninvaded = 12, N invaded = 19) to determine if bluegill diet changed in invaded lakes. Twenty of these lakes (N uninvaded = 10, N invaded = 10) were also analyzed for bluegill stomach contents. Approximately 1 cm^3 of muscle tissue was removed from 3 adult bluegill (size range of 100 - 110 mm TL), per lake. The tissue was removed from the left side of the body, just adjacent to the dorsal fin and placed into a folded weighing tin. Zooplankton was concentrated onto Gelman A/E glass fiber filters (Gelman Sciences, Ann Arbor, MI) and non zooplankton species were removed manually. Phytoplankton samples were filtered onto A/E glass

fiber filters until the filter clogged and the volume filtered was recorded. Zebra mussel and snail tissue was removed from the shell and placed into a folded weighing tin. Sediment samples were also placed into a folded weighing tin. All samples were dried at 55 °C for two days.

Phytoplankton and zooplankton samples on filters were placed into tin capsules and ground. Muscle tissues from bluegill, zebra mussels and snails, and the dried sediment samples were also placed into tins and ground. Each ground sample was split in half for replicate analysis, with one replicate treated with dilute HCl to remove carbonates. Isotope measurements were made by continuous-flow isotope-ratio mass spectrometry using a Micromass Optima interfaced to a Carlo Erba NC 2500 elemental analyzer for on-line combustion and purification of sample nitrogen and carbon. All isotope abundances are expressed as $\delta^{15}N$ or $\delta^{13}C$ values relative to atmospheric nitrogen and Pee Dee Belemnite carbon standards, respectively. We compared the acidified $\delta^{15}N$ and $\delta^{13}C$ values to those that were not acidified from a subset of the 29 lakes and determined that all animal values were similar (A.E. Wilson unpublished data). Additionally it has been shown that acidifying animal tissues can alter $\delta^{15}N$ and $\delta^{13}C$ values, potentially confounding interpretations of food webs (Bunn et al. 1995). Thus, all stable isotope values presented in this study were unacidifed, except for the phytoplankton and sediment samples, which potentially contain inorganic carbonates (Jackson et al 1986, Rau et al. 1983). Bluegill and zooplankton samples were analyzed from all 29 lakes, sediment and phytoplankton were analyzed from 6 lakes (N uninvaded = 1, N invaded = 5) and snails and zebra mussels were only analyzed from 5 lakes (N uninvaded = 0, N invaded = 5).

Statistical Analyses

We compared physical and biological parameters for zebra mussel invaded and uninvaded lakes using the Student's t-test, when data were normal and had equal variances between treatments. Whenever data did not meet the assumption of normality (Kolmogorov-Smirmov and Shapiro-Wilk tests for normality $p < 0.05$), the data were log transformed. If the log transformation was successful to meet the normality assumption, the log transformed data were t-tested. If the log transformation was not successful, the untransformed data were tested using the Mann-Whitney U test (Systat®11, Wilkinson, 1989).

We used analysis of covariance (lme, R Version 2.4.1, R Development Core Team 2007) to compare bluegill growth during the year prior to sampling between invaded and uninvaded lakes. Length at the start of the year's growth stanza in the year before capture was the covariate in the model, lake was a random effect, and zebra mussel treatment (invaded vs. uninvaded) was the fixed effect of interest. We compared contemporary and historical bluegill mean length at age using analysis of covariance (PROC MIXED, SAS 2001) with age as the covariate, lake as a random effect, and zebra mussel treatment and time period (< 1988 or 2002-2003) as the fixed effects.

To compare the percent zooplankton found in bluegill stomachs in invaded and uninvaded lakes, we used a linear mixed effects model (lme, R Version 2.4.1, R Development Core Team 2007) with lake as the random factor and zebra mussel treatment as the fixed effect. In order to meet the assumptions of the model, the variable percent zooplankton was arcsin square root transformed. We used analysis of covariance (lme, R Version 2.4.1, R Development Core Team 2007) to compare bluegill stomach

weight between invaded and uninvaded lakes. Length at capture was the covariate in the model, lake was a random effect, and zebra mussel treatment was the fixed effect. To meet the assumptions of the model, the variable stomach weight was log transformed. To determine if the changes between zooplankton and bluegill $\delta^{15}N$ or $\delta^{13}C$ values were different between treatments, we used linear mixed effects models (lme, R Version 2.4.1, R Development Core Team 2007) with lake as the random factor and zebra mussel treatment as the fixed effect. All assumptions of mixed effect models were satisfied in all analyses.

Results

Physical and Biological Parameters 2002-2003

Mean depths and TP concentration in invaded and uninvaded lakes were not significantly different ($U_{25,25} = 241$, $p = 0.17$; $t_{48} = -0.32$, $p = 0.75$, respectively) (Table 3), indicating no bias in the selection of sample lakes with respect to these parameters. Light extinction coefficients were significantly higher ($t_{48} = -2.93$, $p = 0.01$) in invaded lakes, indicating greater penetration of PAR in the water column and greater water clarity. Interestingly, chlorophyll *a* did not differ between the lake groups ($t_{48} = 1.68$, $p = 0.10$) (Table 3). Total phytoplankton, total microzooplankton, total macrozooplankton, and *Daphnia* spp. biomass all were significantly lower in invaded lakes ($t_{40} = 2.30$, $p = 0.03$; $t_{48} = 3.31$, $p = 0.002$; $t_{48} = 2.22$, $p = 0.03$; $U_{25,25} = 422$, $p = 0.03$; respectively) (Table 3).

Bluegill Growth in 2002-2003

A frequency distribution of bluegill length at the beginning of the final year of growth in invaded and uninvaded lakes revealed similar numbers of bluegill in each 10 mm size class (Figure 2). We then divided the bluegill into three life history categories based on ontogenetic diet shifts (first year < 40 mm, juvenile = 40 - 89 mm, and adult ≥ 90 mm) (Werner and Hall 1988; Mittelbach 1984, 1981). Note that first year bluegill (age 1 + at capture) encompass both the larval open water stage where they feed on small zooplankton, and a small juvenile stage that includes feeding on macroinvertebrates in the littoral zone. Zebra mussels significantly affected bluegill growth ($F_{1,48} = 5.74$, $p = 0.02$), but the direction of this effect changed depending on the life history category ($F_{2,2413} = 5.52$, $p = 0.004$) (Table 4). First year growth was lower, yet juvenile and adult growth was higher in zebra mussel lakes (Figure 3).

Historical vs. Contemporary Bluegill Mean Length at Age

Mean length at age of juvenile bluegills (ages 1-2) in the two lake groups was not significantly different before zebra mussel invasion ($F_{1,14} = 0.33$, $p = 0.57$) (Figure 4, Table 6). Juvenile mean length at age in 2002-2003 was also not significantly different between invaded and uninvaded lakes ($F_{1,21} = 2.76$, $p = 0.11$) (Figure 4, Table 7). However, mean length at age was significantly greater in juvenile bluegill prior to 1988, indicating that juveniles were historically larger at both ages 1 and 2 compared to contemporary juveniles ($F_{1,56} = 53.37$, $p < 0.001$) (Figure 4, Table 5). Prior to zebra mussel invasion, adult bluegill mean length at age (ages 3-6) did not differ significantly in the two lake groups ($F_{1,62} = 0.69$, $p = 0.41$) (Figure 4, Table 9). Mean length at age of adults was significantly greater in invaded lakes in 2002-2003 ($F_{1,37} = 6.37$, $p = 0.02$)

(Figure 4, Table 10). Mean length at age was significantly greater in adults prior to 1988, indicating that before 1988, adults were larger at all ages compared to 2002-2003 ($F_{1,122}$ = 253.2, $p < 0.001$) (Figure 4, Table 8).

Bluegill Diet 2002-2003

Stomach content analyses from 26 lakes revealed a non-significant pattern that bluegill in invaded lakes had 65% less zooplankton in their diets ($F_{1,24} = 2.24$, $p = 0.15$) (Figure 5, Table 11). Stomach content weight did not differ between invaded and uninvaded lakes, indicating that bluegill are eating similar quantities of food ($F_{1,24} = 0.60$, $p = 0.44$) (Figure 6, Table 12). Stable isotopes of $\delta^{15}N$ and $\delta^{13}C$ from the food webs of 29 lakes show that bluegill have different carbon and nitrogen signatures in invaded and uninvaded lakes (Figure 7). The ^{15}N trophic enrichment (as determined by the change in $\delta^{15}N$) from zooplankton to bluegill in invaded lakes was significantly lower ($F_{1,27} = 6.70$ $p = 0.02$) (Figure 8, Table 13), indicating that bluegill in invaded lakes eat organisms from an isotopically distinct basal food resource. The distance from zooplankton to bluegill in terms of $\delta^{13}C$ is greater, yet not-significant, suggesting that bluegill in invaded lakes may be incorporating less ^{13}C from zooplankton and more from benthic macroinvertebrates ($F_{1,27} = 2.19$, $p = 0.15$) (Figure 9, Table 14).

Discussion

Bluegill Growth in 2002-2003

Higher juvenile and adult bluegill growth in zebra mussel invaded lakes was unexpected. We postulated that zebra mussels, because they are efficient filter feeders, would have a bottom-up effect on lake ecosystems. We predicted this would lead to

lower phytoplankton and zooplankton biomass (as seen in Table 3), and ultimately, slower bluegill growth. Our results only supported this prediction for first year bluegill; growth of juvenile and adult bluegills was slightly higher in lakes with zebra mussels.

Even though our bluegill growth results were surprising, prey abundance and bluegill feeding behavior may be responsible for the detected patterns. First year bluegill feed on microzooplankton (copepod nauplii, rotifers, and small-bodied cladocerans) in the pelagic zone of the lake (Bremigan and Stein 1994, Barkoh and Modde 1987, Siefert 1972, Werner 1967) for the first portion of the summer, and then switch littoral benthic macroinvertebrates by late summer. Because zebra mussels reduced the abundance of microzooplankton by 44% and macrozooplankton by 33% (Table 3), first year bluegill would be expected to grow slower due to resource competition for the first portion of summer. Our first year results are consistent with Raikow (2004) who found a 24% decline in larval bluegill growth in the presence of zebra mussels. However, once first year bluegill become vulnerable to predation by bass, they move back to the littoral zone and feed on a variety of benthic invertebrates (Turner and Mittelbach 1990, Werner and Hall 1988, Werner et al. 1983, Mittelbach 1981). We did not sample the benthos; however, it has been shown that zebra mussels increase benthic invertebrate biomass (Beekey et al. 2004, Stewart et al. 1998a, b, Ricciardi et al. 1997, Thayer et al. 1997, Stewart and Haynes 1994) and productivity (Johannsson et al. 2000). Thayer et al. (1997) found that adult yellow perch, which are primarily benthivores during this life history stage, grew significantly larger in the presence of zebra mussels due to elevated benthic invertebrate biomass. Therefore, it is likely that first year bluegill growth is depressed in the beginning of the summer due to resource competition with zebra mussels for small

zooplankton, but after they move back to the littoral zone, their growth would be greater due to increased benthic macroinvertebrate biomass. We still saw lower growth in first year bluegill in invaded lakes, which suggests that growth may have been much lower while first year bluegill were still in the larval stage, and the higher growth while in the littoral zone did not completely make up for the initial slow growth.

Juveniles also feed on a variety of benthic macroinvertebrates in the littoral zone (Turner and Mittelbach 1990, Werner and Hall 1988, Werner et al. 1983, Mittelbach 1981). Because zebra mussels promote benthic macroinvertebrate biomass and benthic production, juvenile bluegill growth should also be greater in the presence of zebra mussels. Thus our result of higher juvenile growth in invaded lakes due to increased benthos is a reasonable conclusion.

Adult bluegill return to the pelagic zone of the lake once they are large enough to avoid predation, and may feed primarily on *Daphnia* spp. (Mittelbach and Osenberg 1993, Werner and Hall 1988; Mittelbach 1984, 1981). We found significantly lower *Daphnia* spp. (40%) and macrozooplankton biomass (33%) in invaded lakes (Table 3) and expected the growth of adults to be lower. Thus, the higher growth of adults in invaded lakes was surprising. Potential reasons for higher adult bluegill growth in invaded lakes include increased water clarity and diet shifts.

Bluegill sunfish are visual predators that actively seek their prey in the water column (Breck and Gitter 1983, Vinyard and O'Brien 1976). In dense vegetation where their vision is limited, bluegill foraging efficiency declines (Harrel and Dibble 2001). Therefore it is possible that bluegill were better able to see their zooplankton prey because the water clarity of invaded lakes was 21% higher (Table 3); thus, swimming

effort needed to search for prey may decrease and prey encounter rates and foraging efficiency should increase, thereby increasing energy available for growth (Werner and Hall 1988; Mittelbach 1984, 1981; Vineyard and O'Brien 1976; but see O'Brien et al. 1976). However, because we did not see increased biomass of zooplankton in the stomach contents of adults in invaded lakes (Figure 5), it is unlikely that water clarity is the mechanism for higher adult growth.

Zebra mussels promoted increased abundance of benthic organisms in Lake Ontario, Western Lake Erie, Lake Champlain, NY, USA, and enclosures in an experimental pond adjacent to Lake St. Clair, MI, USA (Stewart and Haynes 1994, Stewart et al. 1998a, b, Beekey et al. 2004, Thayer et al. 1997, respectively), increased density of macrozoobenthic organisms in the shallow areas of the Hudson River (Strayer et al. 1998), and increased benthic production in Lake Erie (Johannsson et al. 2000). Adult bluegills are not obligate planktivores and will feed on many different food items (Werner and Hall 1988; Mittelbach 1984, 1983, 1981). However, when it is not energetically profitable to eat large *Daphnia*, bluegill will switch to more profitable items (Mittelbach 1983). We show that zebra mussels significantly lowered macrozooplankton and *Daphnia*, the preferred food items of adult bluegill. Thus, it is possible that bluegill were forced to switch their diets to the more abundant benthic organisms when zooplankton prey was scarce.

Stable isotope evidence suggests that adult bluegill in invaded lakes have changed their diet. Stable isotope analyses have been used to characterize various aquatic food webs (Vander Zanden and Rasmussen 1999, Hamilton et al. 1992, Kling et al. 1992, Sholto-Douglas et al. 1991). More recently, they have been used to determine food web

responses to exotic species invasions (Maguire and Grey 2006, Vander Zanden et al. 1999, Mitchell et al. 1996). Stable isotopes of nitrogen reflect the trophic position of organisms because ^{15}N accumulates in tissues by approximately 3.5‰ per trophic transfer, while the lighter ^{14}N is preferentially excreted (Cabana and Rasmussen 1994, Peterson and Fry 1987). The difference in $\delta^{15}N$ from zooplankton to bluegill in our study was significantly less in invaded lakes (Figure 8, Table 13). Thus, in invaded lakes, bluegills ate organisms that were less enriched in ^{15}N. Bluegill prey items in invaded lakes (e.g. benthic macroinvertebrates) may therefore reflect a dependence on bacteria, which have low $\delta^{15}N$ (~ 0‰, Goericke et al. 1994) compared to phytoplankton (3.7-5.7‰, Gu et al. 1996), and would result in higher trophic levels having depressed $\delta^{15}N$. Carbon isotopes of consumers tend to correspond closely to their food sources, as $\delta^{13}C$ generally changes less than 1‰ per trophic transfer (Peterson and Fry 1987). Due to the distinct $\delta^{13}C$ isotopic ratios between aquatic and terrestrial systems, it is also possible to determine if the food source is of allochthonous or autochthonous origin (Peterson et al. 1994, Hamilton et al. 1992). The average benthic algae $\delta^{13}C$ value in lakes is enriched compared to planktonic algae (-26‰ vs. -32‰) and this difference can be reflected in the $\delta^{13}C$ of consumers (France 1995). The greater change in $\delta^{13}C$ from zooplankton to bluegill in invaded lakes, although not significant, also shows potential evidence of a diet shift to organisms that are enriched in ^{13}C. Thus, bluegill in invaded lakes may potentially be feeding on organisms that are more associated with the benthos, because of the enriched $\delta^{13}C$ values that were incorporated in their tissues. The shifting of zebra mussel-invaded food webs towards enriched $\delta^{13}C$ values and thus a system more reliant on the benthos, is consistent with the changes in $\delta^{13}C$ values noted in Oneida Lake (NY, USA)

and Lough Erne (Ireland), post-invasion (Mitchell et al. 1996 and Maguire and Grey 2006, respectively).

We also show potential evidence of a diet shift in adult bluegill in invaded lakes, based on stomach content analyses. Percent zooplankton in the stomach, although not significant, was 65% lower in invaded lakes (Figure 5, Table 11). In addition, overall weight of stomach contents did not differ between lake treatments (Figure 6, Table 12). Thus, bluegills ate similar amounts of food in invaded and uninvaded lakes, yet diets may have consisted of more benthic macroinvertebrates in invaded lakes. Trometer and Busch (1999) proposed prey switching from less abundant zooplankton to more abundant benthic invertebrates as a mechanism to describe growth for age 0 fish in Lake Erie after zebra mussel invasion. It is possible that higher adult bluegill growth in invaded lakes is due to heightened abundance of benthos which would be consistent with the effects of zebra mussels on adult yellow perch growth in enclosures (Thayer et al. 1997, Rautio 1995).

Although we were surprised by the increased growth of juvenile and adult bluegill in invaded lakes, increased growth is advantageous for bluegill populations. We show that juveniles and adults grew approximately 1.8-4.2 mm more per year in invaded lakes (Figure 3). This additional growth is cumulative over time, as reflected by the increased difference in growth between lake groups as bluegill change from juveniles to adults. Therefore, if a juvenile grows faster each year in an invaded lake, it should reach the threshold size to escape bass predation sooner. In turn, faster growing bluegills will have higher survival rates, because predation risk also declines as bluegills grow. Increased survival will then result in populations with increased reproductive output because they

reach reproductive maturity sooner. Overall, these positive changes due to zebra mussels will translate into increased fitness (Werner and Gilliam 1984).

Contemporary vs. Historical Bluegill Mean Length at Age

Comparing mean length at age of bluegill prior to 1988 and data from 2002-2003 allowed us to look at the effects of zebra mussels on Michigan lakes before and after invasion, and validated our contemporary growth analyses. We observed no differences in the mean length at age of juvenile and adult bluegill in the two lake groups prior to invasion (Figure 4; Tables 6 and 9). However, adult bluegill mean length at age in 2002-2003 was significantly greater in invaded lakes (Figure 4, Table 10). Even though using mean length at age to examine growth may have limitations, our results were consistent with our contemporary bluegill growth analyses (Figure 3).

The mean length at age data prior to 1988 that we obtained from the Michigan Department of Natural Resources Fisheries Division did not include enough information to determine size specific growth. Rather, we were limited to determining growth from mean length at age analyses. It is possible to determine if bluegill reach a particular size earlier or later in life from analyses of mean length at age, but it is difficult to determine if an environmental factor (i.e. presence of zebra mussels) affects all ages of bluegill in the same way. Growth rate is derived from the slope of the line for mean length at age. Therefore it is challenging to determine if growth rates change at different times during the lifespan of fish because each length at age value is incorporated into the overall slope calculation (Osenberg et al. 1988). Size specific growth is the most rigorous and accurate way to determine fish growth, as it can distinguish between the responses of fish to environmental factors over multiple life history stages (Osenberg et al. 1988). While

comparisons of mean length at age are less rigorous growth analyses and may be difficult to interpret, we still see a significant positive zebra mussel effect on adult bluegills in 2002-2003.

An interesting result of the pre- and post-invasion analysis was that juvenile and adult bluegill mean length at age in all lakes, whether or not they were later invaded, was significantly greater prior to invasion compared to 2002-2003 (Figure 4; Tables 5 and 8). These results indicate that bluegills were either all larger prior to invasion due to productivity differences between time periods, or that a potential measurement bias existed. TP was not greater in the 24 lakes prior to invasion ($U_{24,24} = 344.5$, $p = 0.24$) and does not explain this pattern. An alternative explanation may be measurement variation introduced by the many scientists who analyzed the pre-invasion fish scale data. Pre-invasion samples were collected and analyzed between 1956-1987 by multiple scientists from the Michigan Department of Natural Resources, while CEHS was the only scientist to analyze all of the 2002-2003 bluegill scales. Determining the age of bluegills is a subjective skill that requires much practice and can vary from one scientist to another. Consistent scale reading within a time period by one person allows valid comparison. Therefore, this source of potential variation does not affect our comparisons of mean length at age between invaded and uninvaded lakes within the pre- or post-invasion time period (i.e. Tables 6, 7, 9 and 10), it does only in the comparison across time periods (i.e. Tables 5 and 8), analyses that were not paramount to our study goal.

Overall, our study shows strong negative zebra mussel effects on the primary producers and the primary consumers (Table 3). In addition, there is a positive effect on secondary consumer growth (Figures 3 and 4), even though we document a potential diet

change (Figures 5, 8 and 9). These results are consistent with the food web effects of zebra mussels in Lake Erie. Johannsson et al. (2000) reported that zebra mussels in Lake Erie suppressed primary production of phytoplankton and secondary production of zooplankton in the pelagic zone, while promoting benthic production. The increased benthic production was estimated to support increased fish biomass, and therefore the authors found no negative zebra mussel effect on fish biomass.

Our study used a survey to search for broad-scale zebra mussel effects on bluegill in inland Michigan lakes. The results provide no evidence of a negative zebra mussel effect on juvenile and adult bluegill growth or bluegill mean length at age. Moreover, we show evidence that adult bluegill have switched their diets in invaded lakes, with positive effects on growth. Therefore, zebra mussels are not contributing to bluegill stunting.

Table 1. Effects of zebra mussels on fish growth in several lakes, rivers, and experimental enclosures. (- = decrease, 0 = no change, + = increase).

Fish Species	Life Stage	Location	Growth Response	Reference
Bluegill sunfish (*Lepomis macrochirus*)	Larval	Exp. enclosures	-	Raikow 2004
	Age 1 and 2	Rice Lake, ON	0	Mercer et al. 1999
	Juvenile	Exp. enclosures	0	Richardson and Bartsch 1997
Fathead minnows (*Pimephales promelas*)	Juvenile	Exp. enclosures	-	Jennings 1996
Lake white fish (*Coregonus clupeaformis*)	Ages 2-10	SE Lake Michigan	-	Pothoven et al. 2001
Pumpkinseed sunfish (*Lepomis gibbosus*)	Age 1 and 2	Rice Lake, ON	+	Mercer et al. 1999
Spottail shiner (*Notropis hudsonius*)	0+ Juvenile	Hudson River, NY	+	Strayer et al. 2004
Yellow perch (*Perca flavescens*)	YOY	Oneida Lake, NY	+	Mayer et al. 2000
	YOY	Lake Erie	-/+	Graham et al. 1999
	Age 1 and 2	Rice Lake, ON	0	Mercer et al. 1999
	Adult	Pond Enclosures	+	Thayer et al. 1997, Rautio 1995
	Adult	Oneida Lake, NY	0	Mayer et al. 2000

Table 1. Continued

Fish Species	Life Stage	Location	Growth Response	Reference
White perch (*Morone americana*)	YOY	Lake Erie	0	Graham et al. 1999
Pelagic fish	0+ Juvenile	Hudson River, NY	-	Strayer et al. 2004
	Age 0	W. basin Lake Erie	0	Trometer and Busch 1999

Table 2. Multiple-regression estimates for average weight per prey item (g wet weight) in bluegill sunfish stomachs from 20 of the study lakes (N uninvaded = 10, N invaded = 10) in 2002-2003.

Parameter	Weight Estimate (g)	SE	t-value	P-value
Daphnia spp.	0.00010	0.000013	7.70	< 0.001
Snails, Clams, Zebra Mussels	0.0022	0.0018	1.22	0.22
Mites, Ostracods	0.00020	0.00083	0.24	0.81
Beetles, True Bugs	0.0040	0.0012	3.35	0.001
Amphipods, Springtails	0.001	0.00018	5.71	< 0.001
Damselfly, Dragonfly, Mayfly and Stonefly Larvae	0.0059	0.0017	3.44	0.001
Worms, Moth larvae, *Chaoborus* spp.	0.0000070	0.00058	0.01	0.99
Caddisfly and *Chironomus* Larvae	0.00084	0.00018	4.69	< 0.001
Cladocerans (without *Daphnia* spp.) and Copepods	0.000013	0.000018	0.71	0.48
Mosquito Larvae	0.00043	0.00014	3.00	0.003
Earthworm	1.59	0.71	22.27	< 0.001

Table 3. Average, range and standard error of physical and biological variables in zebra mussel invaded and uninvaded lakes in 2002-2003. * indicates significance at $\alpha = 0.05$.

Parameter	Uninvaded		Invaded		Test Statistic	P-value
	Average (range)	SE	Average (range)	SE		
Mean Depth (m)	5.28 (2.31-8.80)	0.43	6.28 (2.13-12.41)	0.55	$U_{25,25} = 241$	0.17
Total Phosphorus ($\mu g\ L^{-1}$)	10.56 (4.76-20.76)	0.84	10.95 (5.26-21.04)	0.85	$t_{48} = -0.32$	0.75
Light Extinction Coefficient (m^{-1})	-0.28 ((-0.43)-(-0.16))	0.01	-0.22 ((-0.33)-(-0.06))	0.01	$t_{48} = -2.93$	0.01*
Chlorophyll *a* ($\mu g\ L^{-1}$)	4.23 (1.08-9.29)	0.37	3.33 (0.89-6.2)	0.23	$t_{48} = 1.68$	0.10
Total Phytoplankton Biomass ($\mu g\ L^{-1}$)	49.39 (18.71-95.08)	4.45	37.69 (12.88-115.83)	5.44	$t_{40} = 2.30$	0.03*

Table 3 Continued.

Parameter	Uninvaded		Invaded		Test Statistic	P-value
	Average (range)	SE	Average (range)	SE		
Total Microzooplankton Biomass ($\mu g\ L^{-1}$)	46.40 (13.88-172.78)	6.9	26.16 (5.81-83.14)	3.83	$t_{48} = 3.31$	0.002*
Total Macrozooplankton Biomass ($\mu g\ L^{-1}$)	152.94 (36.26-327.94)	16.72	102.68 (18.17-280.19)	11.37	$t_{48} = 2.22$	0.03*
Daphnia spp. Biomass ($\mu g\ L^{-1}$)	59.74 (2.51-154.43)	8.55	35.92 (0.83-88.73)	5.40	$U_{25,25} = 422$	0.03*

Table 4. Fixed effects from a linear mixed-effects model of 2467 observations of individual bluegill growth in the final year from 50 lakes (25 uninvaded, 25 invaded) in the years 2002-2003.

Effect	Num df	Den df	F-value	P-value
Intercept	1	2413	2593	< 0.001
Zebra Mussel Treatment	1	48	5.74	0.02
Life History Stage	2	2413	1038	< 0.001
Interaction: Zebra Mussel*Life History Stage	2	2413	5.52	0.004

Table 5. Fixed effects from a linear mixed-effects model comparing 83 observations of juvenile bluegill mean length at age (ages 1-2) in 24 lakes in the survey with both historical (prior to 1988) and contemporary (2002-2003) data. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Age	1	56	80.02	< 0.001
Time Period (Historical or Contemporary)	1	56	53.37	< 0.001
Zebra Mussel Treatment	1	56	2.48	0.12
Interaction: Age*Zebra Mussel Treatment	1	56	4.26	0.04

Table 6. Fixed effects from a linear mixed-effects model comparing 37 observations of juvenile bluegill mean length at age (ages 1-2) in 24 lakes only using historical (prior to 1988) data. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Age	1	14	65.78	< 0.001
Zebra Mussel Treatment	1	14	0.33	0.57

Table 7. Fixed effects from a linear mixed-effects model comparing 46 observations of juvenile bluegill mean length at age (ages 1-2) in 24 lakes only using contemporary (2002-2003) data. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Age	1	21	370.1	< 0.001
Zebra Mussel Treatment	1	21	2.76	0.11

Table 8. Fixed effects from a linear mixed-effects model comparing 148 observations of adult bluegill mean length at age (ages 3-6) in 24 lakes in the survey with both historical (prior to 1988) and contemporary (2002-2003) data. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Age	1	122	430.9	< 0.001
Time Period (Historical or Contemporary)	1	122	253.2	< 0.001
Zebra Mussel Treatment	1	122	2.04	0.16

Table 9. Fixed effects from a linear mixed-effects model comparing 86 observations of adult bluegill mean length at age (ages 3-6) in 24 lakes only using historical (prior to 1988) data. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Age	1	62	525.0	< 0.001
Zebra Mussel Treatment	1	62	0.69	0.41

Table 10. Fixed effects from a linear mixed-effects model comparing 62 observations of adult bluegill mean length at age (ages 3-6) in 24 lakes only using contemporary (2002-2003) data. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Age	1	37	238.5	< 0.001
Zebra Mussel Treatment	1	37	6.37	0.02

Table 11. Fixed effects from a linear mixed-effects model comparing 260 observations of percent zooplankton in the stomach of adult bluegill in 26 lakes in 2002-2003.

Effect	Num DF	Den DF	F-value	P-value
Intercept	1	234	15.56	< 0.001
Zebra Mussel Treatment	1	24	2.24	0.15

Table 12. Fixed effects from a linear mixed-effects model comparing 260 observations of adult bluegill stomach weight in 26 lakes from 2002-2003. Non-significant interaction terms were removed from the model.

Effect	Num DF	Den DF	F-value	P-value
Intercept	1	232	2375.44	< 0.001
Length	1	232	28.64	< 0.001
Zebra Mussel Treatment	1	24	0.60	0.44

Table 13. Fixed effects from a linear mixed-effects model comparing 81 observations of the change in $\delta^{15}N$ between zooplankton and adult bluegill in 29 lakes in 2002-2003.

Effect	Num DF	Den DF	F-value	P-value
Intercept	1	52	46.59	< 0.001
Zebra Mussel Treatment	1	27	6.70	0.02

Table 14. Fixed effects from a linear mixed-effects model comparing 81 observations of the change in $\delta^{13}C$ between zooplankton and adult bluegill in 29 lakes in 2002-2003.

Effect	Num DF	Den DF	F-value	P-value
Intercept	1	52	8.57	0.005
Zebra Mussel Treatment	1	27	2.19	0.15

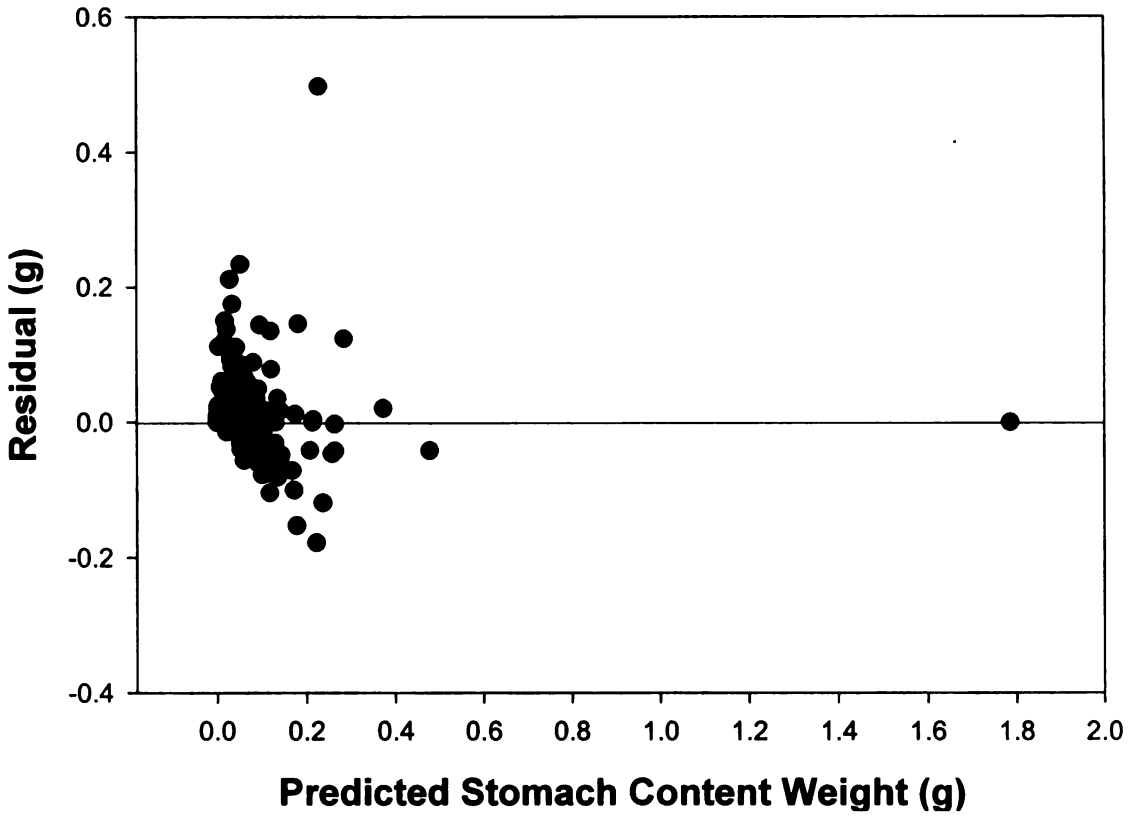

Figure 1. Residual plot for the multiple-regression model used to estimate the average weight of prey items in bluegill sunfish guts from 20 of the study lakes (N uninvaded = 10, N invaded = 10) in 2002-2003. $R^2 = 0.85$, $F_{11,189} = 100.95$, $p < 0.001$.

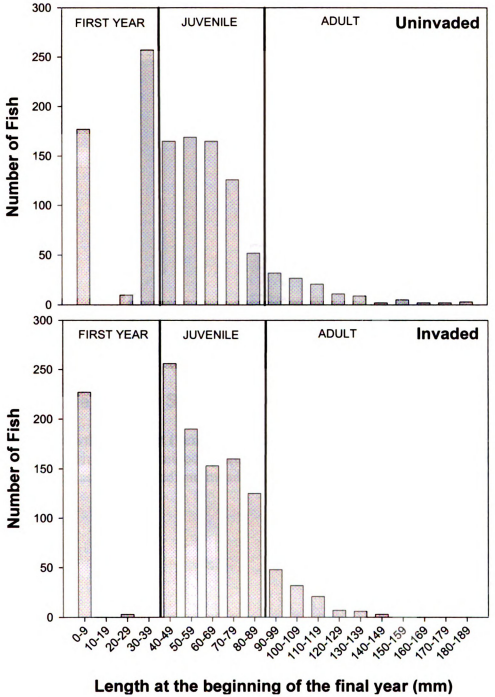

Figure 2. Frequency distribution and approximate life history category of bluegill sunfish placed into 10 mm size classes in uninvaded and invaded lakes in 2002-2003. Life history categories are separated by the bold vertical lines.

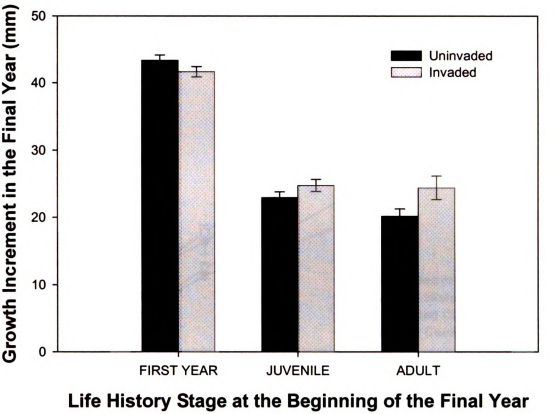

Figure 3. Growth increment (mm) ± SE in the final year for bluegill sunfish in three life history categories (as determined by length at the beginning of the final year from Figure 2) in zebra mussel uninvaded and invaded lakes in 2002-2003. $F_{1,48} = 5.74$, $p = 0.02$.

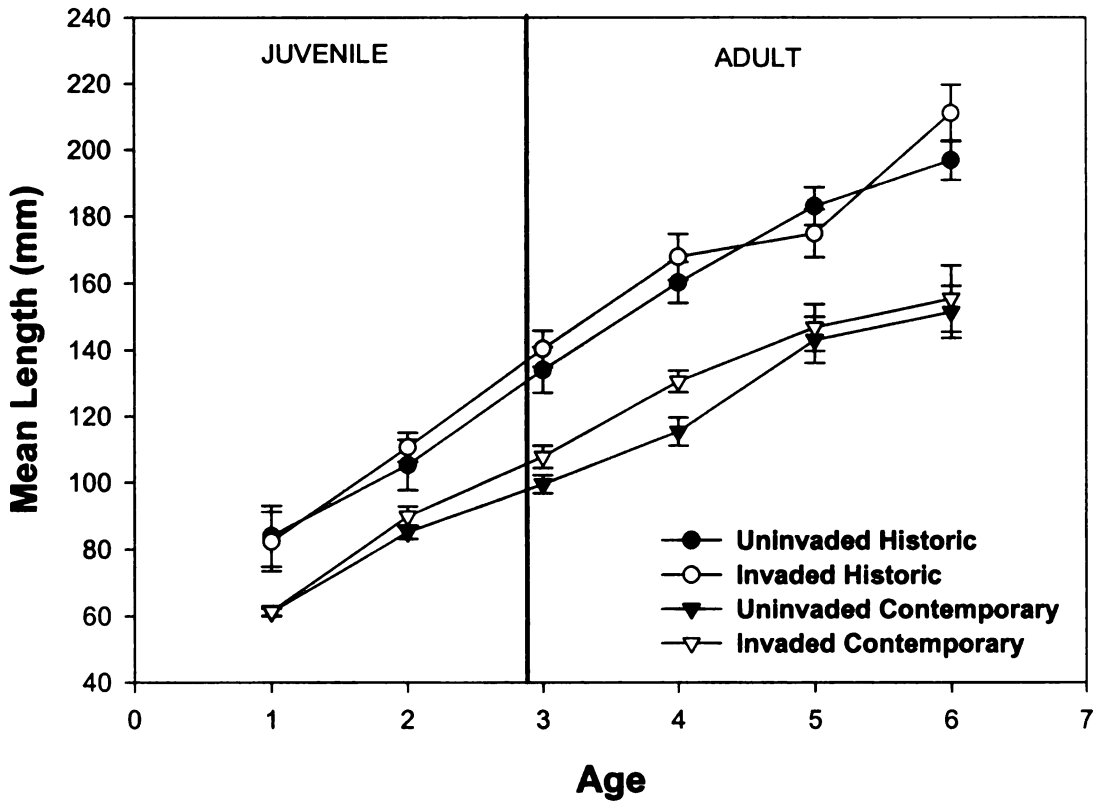

Figure 4. Comparison between historical (prior to 1988) and contemporary (2002-2003) data of bluegill mean length at age (mm) ± SE in 24 of our study lakes (N uninvaded = 13, N invaded = 11). Life history categories are separated by the bold vertical line. Juvenile Historical $F_{1,14} = 0.33$, $p = 0.57$; Juvenile Contemporary $F_{1,21} = 2.76$, $p = 0.11$; Adult Historical $F_{1,62} = 0.69$, $p = 0.41$; Adult Contemporary $F_{1,37} = 6.37$, $p = 0.02$.

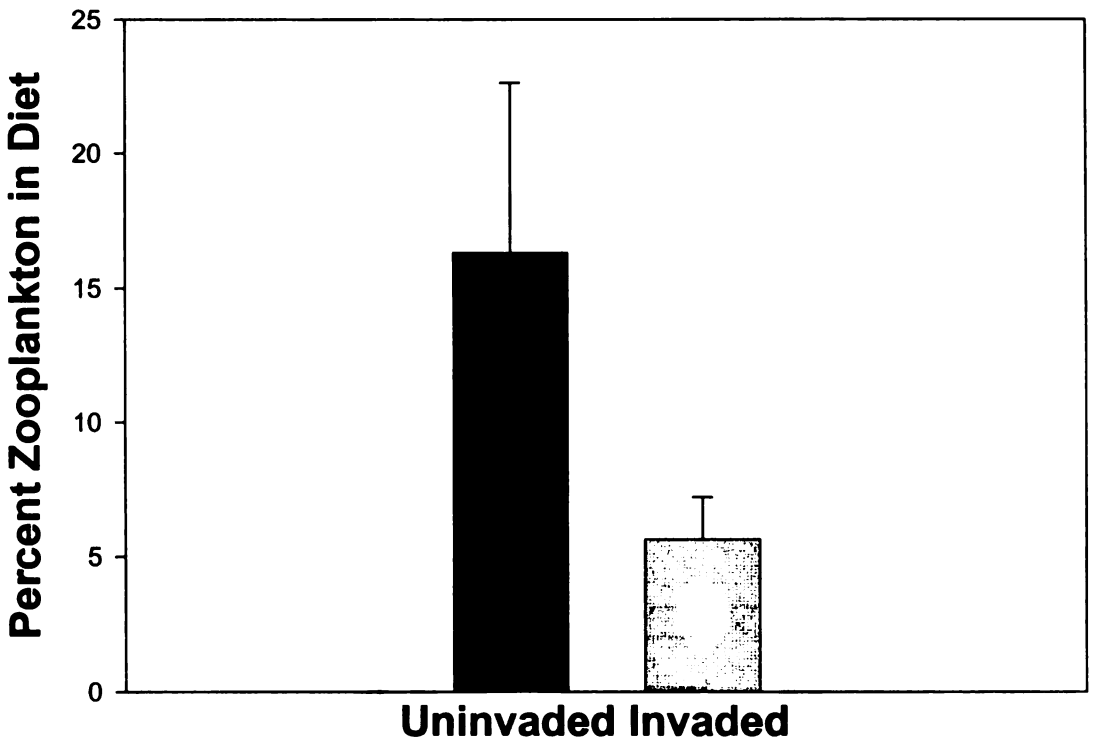

Figure 5. Percent zooplankton ± SE in the diet of adult bluegill sunfish from invaded and uninvaded lakes in 2002-2003 (N uninvaded = 13, N invaded = 13). $F_{1,24} = 2.24$, $p = 0.15$.

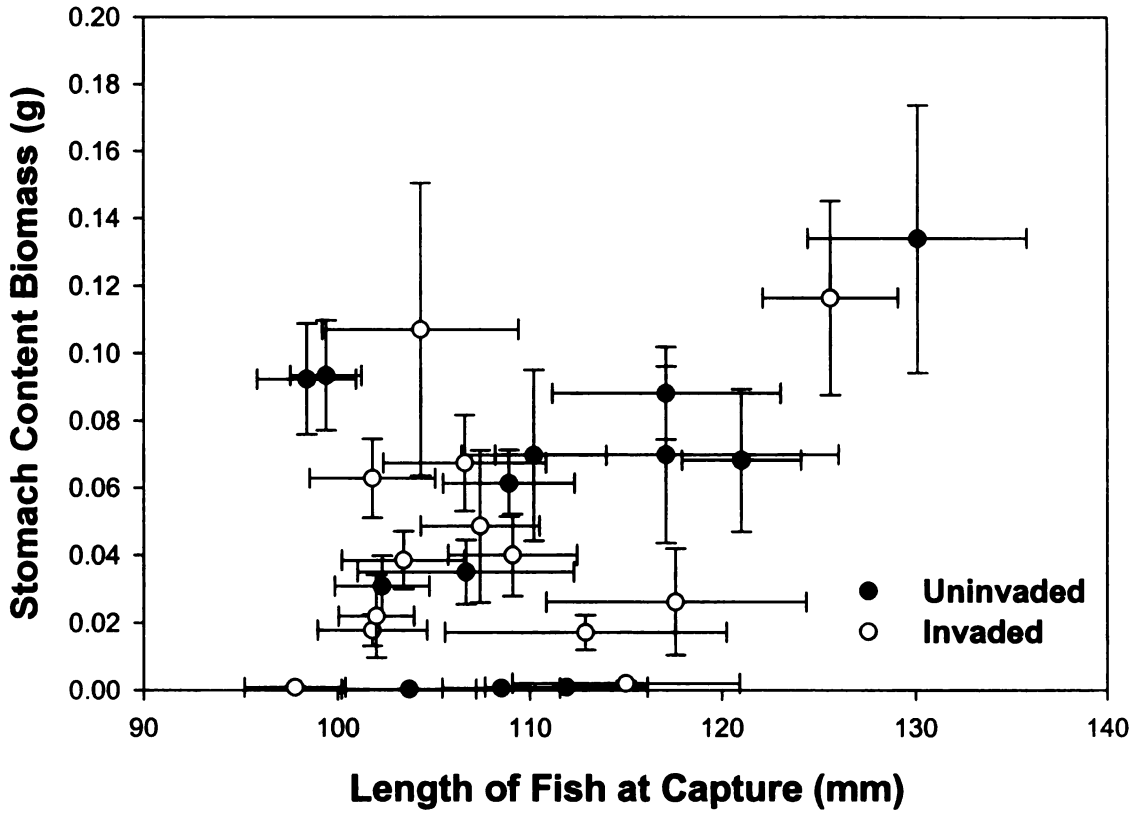

Figure 6. Adult bluegill sunfish stomach content biomass (g) ± SE as a function of the length of fish at capture (mm) ± SE in invaded and uninvaded lakes in 2002-2003 (N uninvaded = 13, N invaded = 13). $F_{1,24} = 0.60$, $p = 0.44$.

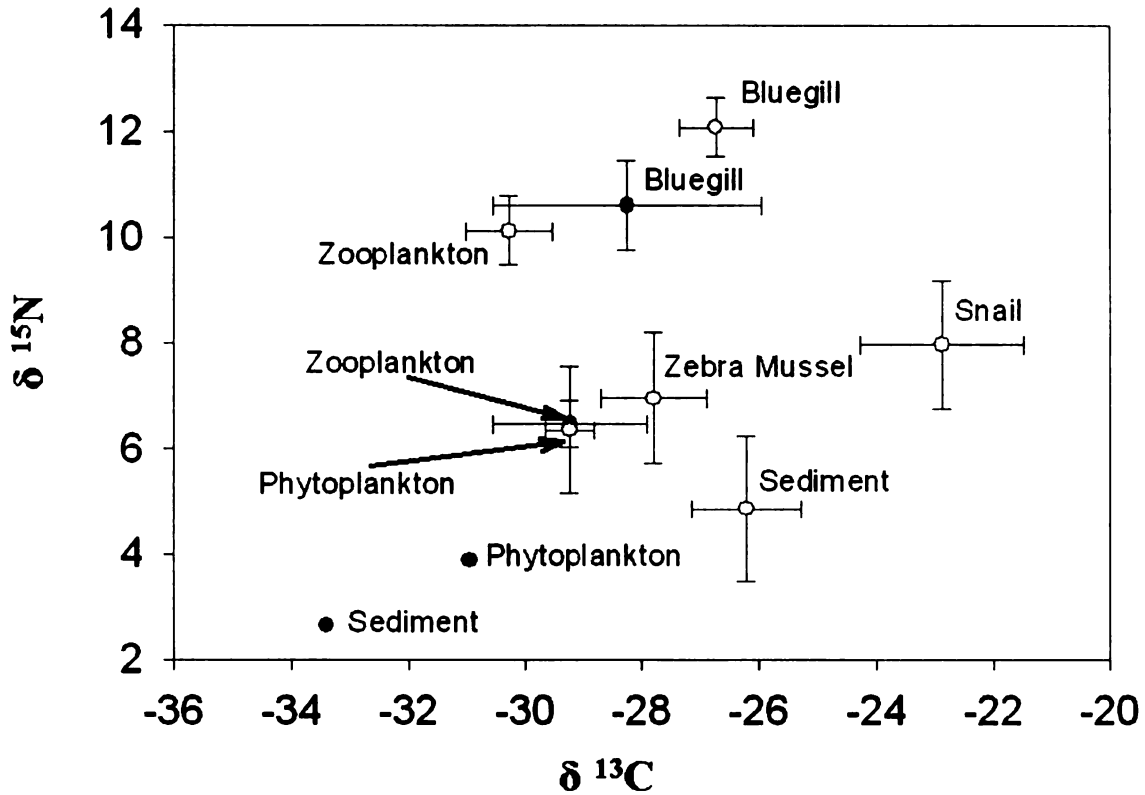

Figure 7. Average isotopic composition ($\delta^{13}C \pm SE$ and $\delta\ ^{15}N \pm SE$) of select food web compartments in invaded (open circles) and uninvaded lakes (closed circles) in 2002-2003. For the bluegill and zooplankton compartments (N uninvaded = 12, N invaded = 17), for the sediment and phytoplankton compartments (N uninvaded = 1, N invaded = 5) and for the snail and zebra mussel compartments (N uninvaded = 0, N invaded = 5).

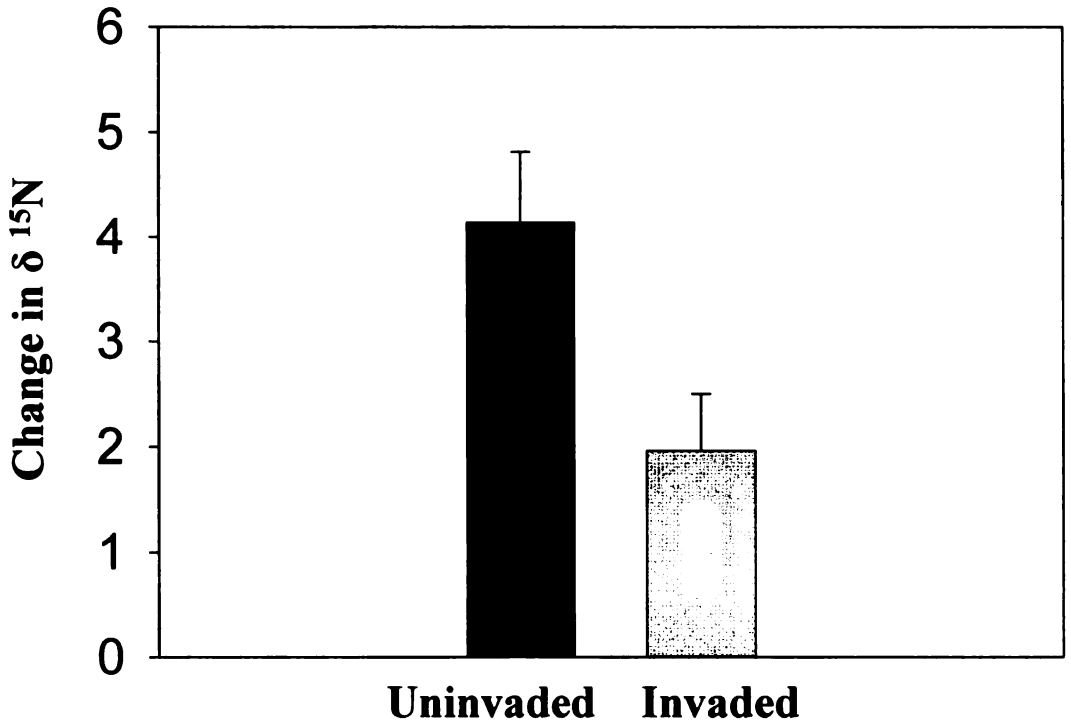

Figure 8. The change in $\delta\ ^{15}N \pm$ SE between zooplankton and bluegill sunfish compartments in invaded and uninvaded lakes in 2002-2003 (N uninvaded = 12, N invaded = 17). $F_{1,27} = 6.70$, $p = 0.02$.

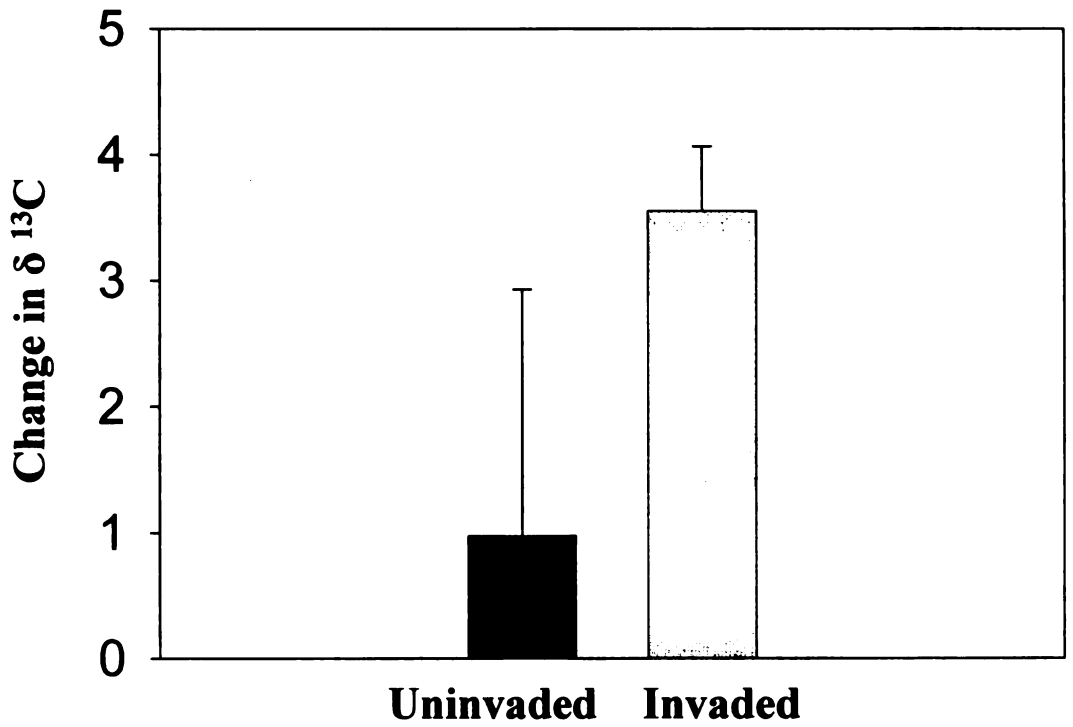

Figure 9. The change in $\delta\ ^{13}C \pm$ SE between zooplankton and bluegill sunfish compartments in invaded and uninvaded lakes in 2002-2003 (N uninvaded = 12, N invaded = 17). $F_{1,27} = 2.19$, $p = 0.15$.

Literature Cited

Barkoh, A., and T. Modde. 1987. Feeding behavior of intensely cultured bluegill fry. Progressive Fish-Culturist 49: 204-207.

Beekey, M.A., D.J. McCabe and J.E. Marsden. 2004. Zebra mussel colonization of soft sediments facilitates invertebrate communities. Freshwater Biology 49: 535-545.

Breck, J.E., and M.J. Gitter. 1983. Effect of fish size on the reactive distance of bluegill (Lepomis macrochirus) sunfish. Canadian Journal of Fisheries and Aquatic Sciences 40: 162–167.

Bremigan, M.T., and R.A. Stein. 1994. Gape-dependant larval foraging and zooplankton size: implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences 51: 913-922.

Bridgeman, T.B., G.L. Fahnenstiel, G.A. Lang, and T.F. Nalepa. 1995. Zooplankton grazing during the zebra mussel (*Dreissena polymorpha*) colonization of Saginaw Bay, Lake Huron. Journal of Great Lakes Research 21(4): 567-573.

Bunn, S.E., N.R. Loneragan, and M.A. Kempster 1995. Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: Implications for food-web studies using multiple stable isotopes. Limnology and Oceanography 40(3): 622-625.

Cabana, G., and J.B. Rasmussen. 1994. Modeling food chain structure and containment bioaccumulation using stable nitrogen isotopes. Nature 372: 255-257.

Caraco, N.F., J.J. Cole, P.A. Raymond, D.L. Strayer, M.L. Pace, S.E.G. Findlay, and D.T. Fischer. 1997. Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. Ecology 78: 588-602.

Conroy, J.D., W.J. Edwards, R.A. Pontius, D.D. Kane, H. Zhang, J.F. Shea, J.N. Richey and D.A. Culver. 2005. Soluble nitrogen and phosphorous excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. Freshwater Biology 50: 1146-1162.

Culver, D.A., M.M. Boucherle, D.J. Bean, and J.W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Canadian Journal of Fisheries and Aquatic Sciences 42: 1380-1390.

Drake, M.T., J.E. Claussen, D.P. Philipp and D.L. Pereira. 1997. A comparison of bluegill reproductive strategies and growth among lakes with different fishing intensities. North American Journal of Fisheries Management 17: 496-507.

Dumont, H.J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of

biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75-97.

ESRI 1999. Arc View. Version 3.2. ESRI, Redland, CA.

Fahnenstiel, G.L., T.B. Bridgeman, G.A. Lang, M.J. McCormick, and T.F. Nalepa. 1995. Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel (*Dreissena polymorpha*) colonization. Journal of Great Lakes Research 21: 465-475.

France, R.L.. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnology and Oceanography 40(7): 1310-1313.

Gerking, S.D.. 1962. Production of food utilization in a population of bluegill sunfish. Ecological Monographs 32:31-78.

Graham, D.M., Sprules, W.G., and S.J. Nepszy. 1999. Growth and condition of juvenile yellow perch (*Perca flavescens*) and white perch (*Morone americana*) during zebra mussel establishment in western Lake Erie (1988-1991). Pages 337-349, in M. Munawar, T. Edsall and I.F. Munawar editors. State of Lake Erie (SOLE) – past, present and future. Backhuys Publishers, Leiden, The Netherlands.

Goericke, R., J.P. Montoya, and B. Fry. 1994. Physiology of isotopic fractionation in algae and cyanobacteria, pp. 187-221 *in* K. Lajtha and R.H. Michener editors. Stable isotopes in ecology and environmental science. Blackwell Scientific Publications, London.

Gu, B., C.L. Schelske, and M.V. Hoyer. 1996. Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake. Journal of Fish Biology 49: 1233-1243.

Hamilton, S.K., W.M. Lewis Jr., and S.J. Sippel. 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia 89(3): 324-330.

Harrel, S.L., and E.D. Dribble. 2001. Foraging efficiency of juvenile bluegill, *Lepomis macrochirus*, among different vegetated habitats. Environmental Biology of Fishes 62(4): 441-453.

Hasle, G.R.. 1978. The inverted-microscope method, p. 88-96 *in* A. Sournia, editor. Phytoplankton manual. UNESCO, Paris, France.

Hayes, D.B., and W.W. Taylor. 1991. A multiple-regression technique for analyzing stomach contents of fish. Transactions of the American Fisheries Society 120: 396-400.

Herbert, P.D., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusk in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 1587-1591.

Horgan, M.J., and E.L. Mills. 1999. Zebra mussel filter-feeding and food-limited production of *Daphnia*: recent changes in lower trophic level dynamics of Oneida Lake, New York, U.S.A. Hydrobiologia 411: 79-88.

Idrisi, N., E.L. Mills, L.G. Rudstam, and D.J. Stewart. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences. 58: 1430-1441.

Jackson, D., D.D. Harkness, C.F. Mason and S.P. Long. 1986. Spartina angelica as a carbon source for salt-marsh invertebrates: a study using $\delta^{13}C$ values. Oikos 46(2): 163-170.

Jennings, C.A.. 1996. Effects of zebra mussel (*Dreissena polymorpha*) density on the survival and growth of juvenile fathead minnows (*Pimephales promelas*): implications for North American river fishes. Hydrobiologia 324: 157-161.

Johannsson, O.E., R. Dermott, D.M. Graham, J.A. Dahl, E.S. Millard, D.D. Myles, and J. LeBlanc. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. Journal of Great Lakes Research 26 (1): 31-54.

Kling, G.W., B. Fry, and W.J. O'Brien. 1992. Stable isotopes and planktonic trophic structure in Arctic lakes. Ecology 73(2): 561-566.

Knoll, L.B.. 2004. Understanding zebra mussel (*Dreissena polymorpha*) impacts on autotrophic and heterotrophic plankton of inland lake ecosystems. M.Sc. Thesis. Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI.

Knoll, L.B., O. Sarnelle, S.K. Hamilton, C.E.H. Scheele, A.E. Wilson, J.B. Rose and M.R. Morgan. 2007. Invasive zebra mussels (*Dreissena polymorpha*) increase cyanobacterial toxin concentrations in low-nutrient lakes. Limnology and Oceanography. In press.

Kraft, C.E., and L.E. Johnson. 2000. Regional differences in rates and patterns of North American inland lake invasions by zebra mussels (*Dreissena polymorpha*). Canadian Journal of Fisheries and Aquatic Sciences 57: 993-1001.

Langner, C.L., and P.F. Hendrix. 1982. Evaluation of a persulfate digestion method for particulate nitrogen and phosphorus. Water Research 16: 1451-1454.

Lowe, R.L., and R.W. Pillsbury. 1995. Shifts in benthic algal community structure and

function following the appearance of zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 51(4): 558-566.

Ludyanskiy, M.L., D. MacDonald, and D. MacNeill. 1993. Impact of the zebra mussel, a bivalve invader. BioScience 43: 533-544.

MacIsaac, H.J.. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist 36:287-299.

MacIsaac, H.J., C.J. Lonnee, and J.H. Leach. 1995. Suppression of microzooplankton by zebra mussels: importance of mussel size. Freshwater Biology 34: 379-387.

MacIsaac, H.J., W.G. Sprules, and J.H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 48: 2051-2060.

Maguire, C.M., and J. Grey. 2006. Determination of zooplankton dietary shift following a zebra mussel invasion, as indicated by stable isotope analysis. Freshwater Biology 51: 1310-1319.

Mayer, C.M., A.J. VanDerValk, J.L. Forney, L.G. Rudstam, and E.L. Mills. 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the establishment of zebra mussels (*Dreissena polymorpha*). Canadian Journal of Fisheries and Aquatic Sciences 57: 742-754.

Mercer, J.L., M.G. Fox, and C.D. Metcalfe. 1999. Changes in benthos and three littoral zone fishes in a shallow, eutrophic Ontario Lake following the invasion of the zebra mussel (*Dreissena polymorpha*). Journal of Lake and Reservoir Management 15: 310-323.

Michigan Sea Grant 2002, 2003. Michigan Sea Grant Zebra Mussel Infestation Monitoring Program. (http://www.miseagrant.umich.edu/ais/lakes.html)

Mitchell, M.J., E.L. Mills, N. Idrisi and R. Michener. 1996. Stable Isotopes of nitrogen and carbon in an aquatic food web recently invaded by *Dreissena polymorpha* (Pallas). Canadian Journal of Fisheries and Aquatic Sciences 53: 1445-1450.

Mittelbach G.G.. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499-513.

Mittelbach G.G.. 1983. Optimal foraging and growth in bluegills. Oecologia 59: 157-162.

Mittelbach G.G.. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

Mittelbach G.G., and C.W. Osenberg. 1993. Stage-structured interactions in bluegill: consequences of adult resource variation. Ecology 74: 2381-2394.

Nicholls, K.H., and G.J. Hopkins. 1993. Recent changes in Lake Erie (North Shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. Journal of Great Lakes Research 19: 637-647.

O'Brien, W.J., N.A. Slade and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57: 1304-1310.

Osenberg, C.W., E.E. Werner, G.G. Mittelbach, and D.J. Hall. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. Canadian Journal of Fisheries and Aquatic Sciences 45: 17-26.

Pace, M.L., S.E.G. Findlay, and D. Fischer. 1998. Effects of an invasive bivalve on the zooplankton community of the Hudson River. Freshwater Biology 39: 103-116.

Pauli, H.R.. 1989. A new method to estimate individual dry weights of rotifers. Hydrobiologia 186: 355-361.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18: 293-320.

Peterson, B., B. Fry, M. Hullar, S. Saupe, and R. Wright. 1994. The distribution and stable isotopic composition of dissolved organic carbon in estuaries. Estuaries 17: 111-121.

Pimental, D.. 2005. Aquatic nuisance species in the New York State canal and Hudson River system and the Great Lakes basin: an economic and environmental assessment. Environmental Management 35: 692-701.

Pothoven S.A., T.F. Nalepa, P.J. Schneeberger and S.B. Brandt. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. North American Journal of Fisheries Management 21(4): 876-883.

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raikow, D.F.. 2004. Food web interactions between larval bluegill (*Lepomis macrochirus*) and exotic zebra mussels (*Dreissena polymorpha*). Canadian Journal of Fisheries and Aquatic Sciences 61: 924-941.

Raikow, D.F., O. Sarnelle, A.E. Wilson, and S.K. Hamilton. 2004. Dominance of the noxious cyanobacterium *Microcystis aeruginosa* in low-nutrient lakes is associated with exotic zebra mussels. Limnology and Oceanography 49(2): 482-487.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olson, H.A. Schafer and I.R. Kaplan. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. Ecology 64(5): 1314-1318.

Rautio, S.A.. 1995. Zebra mussel effects on diet and growth of adult yellow perch and predatory impact of freshwater drum on zebra mussels in pond enclosures. Michigan Department of Natural Resources Fisheries Division Research Report No.2015.

Ricciardi, A., F.G. Whoriskey, and J.B. Rasmussen. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences 54: 2596-2608.

Richardson, W.B., and L.A. Bartsch. 1997. Effects of zebra mussels on food webs: interactions with juvenile bluegill and water residence time. Hydrobiologia 354:141-150.

Roff, J.C., and R.R. Hopcroft. 1986. High precision microcomputer based measuring system for ecological research. Canadian Journal of Fisheries and Aquatic Sciences 43: 2044-2048.

Rutherford, E.S., K.A. Rose, E.L. Mills, J.L. Forney, C.M. Mayer and L.G. Rudstam. 1999. Individual-based model simulations of zebra mussel (*Dreissena polymorpha*) induced energy shunt on walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) populations in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 56: 2148-2160.

Sandgren, C.D., and J.V. Robinson. 1984. A stratified sampling approach to compensating for non-random sedimentation of phytoplankton cells in inverted microscope settling chambers. British Phycological Journal 19: 67-72.

Sarnelle, O., A.E. Wilson, S.K. Hamilton, L.B. Knoll, and D.F. Raikow. 2005. Complex interactions between the zebra mussel, *Dreissena polymorpha*, and the harmful phytoplankter, *Microcystis aeruginosa*. Limnology and Oceanography 50(3): 896-904.

SAS Institute. 2001. The SAS System Inc., Cary, NC.

Shevtsova, L.V., G.A. Zhdanova, V.A. Movchan, and A.B. Primak. 1986. Experimental interrelationship between *Dreissena* and planktonic invertebrates. Hydrobiological Journal 22(6): 36-39.

Siefert, R.E.. 1972. First food of the larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt. Transactions of the American Fisheries Society 101: 219-225.

Sholto-Douglas, A.D., J.G. Field, A.G. James, and N.J. van der Merwe. 1991. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratios in the Southern Benguela Ecosystem: indicators of food web relationships among different size-classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. Marine Ecology Progress Series 78: 23-31.

Stewart, T.W., and J.M. Haynes. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. Journal of Great Lakes Research 20: 479-493.

Stewart, T.W., J.G. Miner and R.L. Lowe. 1998a. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. Journal of the North American Benthological Society 17(1): 81-94.

Stewart, T.W., J.G. Miner and R.L. Lowe. 1998b. Macroinvertebrate communities on hard substrates in Western Lake Erie: structuring effects of *Dreissena*. Journal of Great Lakes Research 24(4): 868-879.

Strayer, D.L., K.A. Hattala, and A.W. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 61: 924-941.

Strayer, D.L., L.C. Smith, and D.C. Hunter. 1998. Effects of the zebra mussel (Dreissena polymorpha) invasion on the macrobenthos of the freshwater tidal Hudson River. Canadian Journal of Zoology 76: 419-425.

Swingle, H.S., and E.V. Smith. 1941. The management of ponds with stunted fish populations. Transactions of the American Fisheries Society 71: 102-105.

Thayer, S.A., R.C. Hass, R.D. Hunter, and R.H. Kushler. 1997. Zebra mussel (*Dreissena polymorpha*) effects on sediment, other zoobenthos, and the diet and growth of adult yellow perch (*Perca flavescens*) in pond enclosures. Canadian Journal of Fisheries and Aquatic Sciences 54: 1903-1915.

Thorp, J.H., and A.F. Casper 2003. Importance of biotic interactions in large rivers: an experiment with planktivorous fishes, dreissenid mussels and zooplankton in the St. Laurence River. River Research and Applications 19: 265-279.

Trometer, E.S., and W.D.W. Busch. 1999. Changes in age-0 fish growth and abundance

following the introduction of zebra mussels *Dreissena polymorpha* in the western basin of Lake Erie. North American Journal of Fisheries Management 19: 604-609.

Turner, A.M., and G.G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. Ecology 71: 2241-2254.

USGS 2002, 2003. United States Geological Survey Nonindigenous Aquatic Species Database. (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/)

Vanderploeg, H.A., J.R. Liebig, W.W. Carmichael, M.A. Agy, T.H. Johengen, G.L. Fahnenstiel, and T.F. Nalepa. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 58: 1208-1221.

Vander Zanden, M.J., and J.B. Rasmussen. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80(4): 1395-1404.

Vander Zanden, M.J., J.M. Casselman, and J.B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464-467.

Vinyard, G.L., and W.J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). Journal of the Fisheries Research Board of Canada 33, 2845–2849.

Welschmeyer, N.A.. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography 39:1985-1992.

Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393-425.

Werner, E.E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69: 1352-1366.

Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 62: 1540-1548.

Werner, E.E., D.J. Hall, and M.D. Werner. 1978. Littoral zone fish communities of two Florida lakes and a comparison with Michigan Lakes. Environmental Biology of Fishes 3:163-172.

Werner, R.G.. 1967. Intralacustrine movements of bluegill fry in Crane Lake, Indiana.

Transactions of the American Fisheries Society 96: 416-420.

Whitney, R.R., and K.D. Carlander. 1956. Interpretation of body-scale regression for computing body length of fish. Journal of Wildlife Management 20:21-27.

Wilkinson, L.. 1989. Systat: the system for statistics. Evanston, 822 pp.

APPENDIX

Appendix A. Individual lake survey data. An electronic file containing: lake name, county, keycode, year sampled, mean depth, total phosphorus (TP), chlorophyll *a*, total microzooplankton biomass, total macrozooplankton biomass, and average bluegill growth can be obtained by emailing C.E.H. Scheele at scheelec@msu.edu.