

Food web interactions between larval bluegill (*Lepomis macrochirus*) and exotic zebra mussels (*Dreissena polymorpha*)

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Abstract: Food web interactions between native larval bluegill (*Lepomis macrochirus*), exotic invasive zebra mussels (*Dreissena polymorpha*), and zooplankton were examined with a mesocosm experiment. Hatchling larval bluegill collected from nests were reared in the presence of size-structured populations of zebra mussels in 1500-L limnocoralls suspended in an artificial pond for 2 weeks. Chlorophyll *a*, other limnological variables, and zooplankton abundance and biomass (including copepod nauplii and rotifers) were monitored over time. During their first 2 weeks of life, larval fish reared in the presence of mussels grew 24% more slowly than fish reared alone. Differential growth rates can be explained by competition between mussels and bluegill for food in the form of microzooplankton. Also likely was an indirect competition via starvation of the zooplankton community as zebra mussels consumed phytoplankton. Either direct or indirect trophic competition between zebra mussels and obligate planktivores may result in ecological harm as zebra mussels spread throughout inland lakes of North America.

Résumé : Une expérience en mésocosme a servi à étudier les relations trophiques entre les larves de crapets arlequins (*Lepomis macrochirus*) indigènes, les moules zébrées (*Dreissena polymorpha*) envahissantes et le zooplancton. Des larves néonates de crapets récoltées sur les nids ont été élevées pendant deux semaines en présence de populations de moules zébrées de structure en taille déterminée dans des enceintes de 1500 L suspendues dans un étang artificiel. La chlorophylle *a*, des variables limnologiques, ainsi que l'abondance et la biomasse du zooplancton (incluant les nauplii de copépodes et les rotifères) ont été mesurées au cours de la période. Durant leurs deux premières semaines de vie, les larves de poissons élevées en présence des moules ont crû 24 % plus lentement que les poissons élevés seuls. Les différences de taux de croissance peuvent s'expliquer par la compétition entre les moules et les crapets pour le microzooplancton qui leur sert de nourriture. Il est aussi probable qu'il y ait une compétition indirecte par manque de nourriture pour la communauté zooplanctonique, alors que les moules zébrées consomment du phytoplancton. Tant la compétition directe qu'indirecte entre les moules zébrées et les groupes obligatoirement planctonophages peuvent causer des dommages écologiques à mesure que la répartition des moules zébrées s'étend parmi les lacs de l'intérieur du continent nord-américain.

[Traduit par la Rédaction]

Introduction

As zebra mussels (*Dreissena polymorpha*) expand their range in North America, new ecosystems become invaded. Beginning with the Great Lakes and continuing through the Mississippi River drainage network, the zebra mussel invasion is currently spreading among small inland lakes (Klepinger 2000). The southern peninsula of the State of Michigan is at the forefront of this invasion because of its

proximity to the Great Lakes, its high density of inland lakes, and its high rate of interlake recreational boat traffic (Buchan and Padilla 1999). Over 150 of Michigan's inland lakes are known to have zebra mussels, and over 75% of Michigan's thousands of inland lakes possess suitable pH and calcium to support zebra mussels (Ramcharan et al. 1992; Klepinger 2000).

Among the ecological concerns of zebra mussel invasion are food web interactions. Zooplankton communities, for example, have been negatively affected by the invasion of zebra mussels in the Great Lakes and Hudson River. Zooplankton abundance dropped 55–71% after mussel invasion in Lake Erie, with the smallest of these animals more heavily affected (MacIsaac et al. 1995). The total biomass of zooplankton in the Hudson River declined 70% after mussel invasion because of both a reduction in large zooplankton body size and a reduction in small zooplankton abundance (Pace et al. 1998). These effects can be attributed to competition with zebra mussels for available food (phytoplankton) and direct predation on microzooplankton such as copepod nauplii and rotifers (Pace et al. 1998). Interactions between zebra mussels and higher trophic levels, e.g., fish, are of particular interest.

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Although the feeding habits of the larval stages of many fish species are not well understood, larvae are most often visually oriented predators of zooplankton during the earliest life stage (Gerking 1994). Larval fish also experience high mortality rates (Gerking 1994). Body size is generally believed to affect survival because larger size confers advantages in starvation resistance (Miller et al. 1988), swimming ability (Werner and Gilliam 1984), predation avoidance (Blaxter 1986), foraging ability (Crowder et al. 1987), and overwinter survival (Adams et al. 1982; Pepin 1991; Schindler 1999). Prey availability can also affect larval size development (Mills et al. 1989; Rettig and Mittelbach 2002). If zebra mussels change zooplankton abundance and population size structure, larval fish growth or survival could be diminished (Richardson and Bartsch 1997; Thayer et al. 1997; Trometer and Busch 1999).

One fish species that might compete for food with zebra mussels in inland lakes is bluegill (*Lepomis macrochirus*). In early summer, bluegill hatch from eggs in nests built in the littoral zone, migrate to the limnetic zone, and then return to the littoral zone in the fall (Faber 1967; Werner 1967, 1969). Larval bluegill feed on microzooplankton such as copepod nauplii and rotifers, as well as small-bodied cladocerans, while in the limnetic zone (Siefert 1972; Barkoh and Modde 1987; Bremigan and Stein 1994). The purpose of this study was to determine whether the presence of zebra mussels affected larval bluegill growth and survival. I tested whether zebra mussels negatively impact the growth and survival of larval bluegill using a mesocosm experiment. A negative impact of zebra mussels on larval bluegill could occur by several mechanisms: (i) the entire zooplankton community might decline because of starvation if algal biomass declines in the presence of zebra mussels, (ii) microzooplankton might differentially decline relative to macrozooplankton dynamics if zebra mussels consumed microzooplankton heavily and thus competed directly with larval bluegill for food (and if microzooplankton were less tolerant of lower algal concentrations), and (iii) toxic conditions such as oxygen depletion might be produced by zebra mussels.

Materials and methods

Twelve 1.5-m-deep, 1-m² limnocorrals holding 1500 L of water each were installed in an artificial pond at the Experimental Pond Facility of the W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, Mich. The artificial pond measured 29 m in diameter and 1.8 m deep; it did not have zebra mussels but contained redear sunfish (*Lepomis microlophus*) that maintained a zooplankton community dominated by small-bodied cladocerans and copepods. A balanced factorial design of zebra mussels (ZM) × bluegill (BG) with three replicates each of the four treatments (ZM, BG, ZM + BG, control (no ZM or BG)) was used. Limnocorrals were arranged in two parallel rows and treatments assigned in a stratified random fashion with one replicate of each treatment at the end of a row. The limnocorrals were filled with pond water screened through 100- μ m mesh. Zooplankton was collected from the pond with a 100- μ m net, held and mixed in a large container, and distributed in several aliquots to stock mesocosms to densities found in the pond.

Zebra mussels were collected from nearby Gull Lake (Kalamazoo County) and then held in a tank with continuous flow-through of Gull Lake water and allowed to attach to Plexiglas sheets for 2 weeks. Size-structured populations of 200 mussels per treatment were created: 25 of 20–30 mm, 75 of 10–20 mm, and 100 of <10 mm for a total of approximately 2 g ash-free dry mass mussel soft tissue·m⁻² (Young et al. 1996). The Plexiglas sheets with attached zebra mussels were suspended vertically 50 cm below the water surface in the center of the limnocorrals. Sediment traps were attached to the Plexiglas sheets to collect zebra mussel feces and pseudofeces. Control treatments received Plexiglas sheets without any attached mussels. Dead mussels were removed from the experiment when detected, but any change in mussel abundance within a replicate was disregarded during data analysis because of low mortality.

Hatchling bluegill were collected directly from nests in nearby Warner Lake (Barry County) and reared in the laboratory for several days. When the fish reached the swimming stage, they were fed brine shrimp nauplii. Fish that had fed upon nauplii were then selected from a single cohort in one tank for use in limnocorrals. The standard length of larval fish from the cohort used for the experiment was 5.5 mm (SD \pm 0.16) estimated by measuring 20 fish not used in the experiment but from the same cohort. Twenty larval fish were used per treatment. Control treatments had no fish. Bluegill and zebra mussels were added to the mesocosms at the same time 3 days after zooplankton had been added.

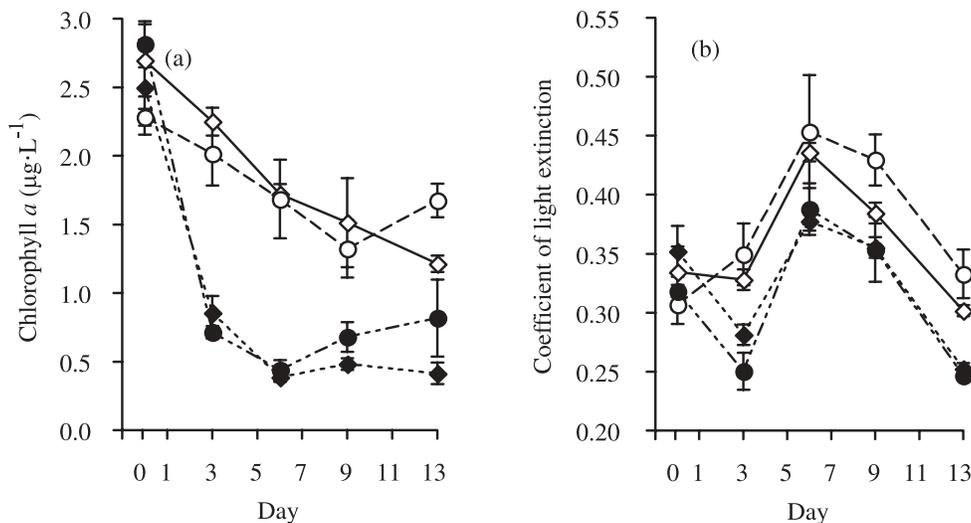
Larval fish were collected only at the end of the experiment to prevent such a disturbance causing death before the conclusion of the experiment. To collect the larval bluegill, a 1-m-diameter, 500- μ m net was lowered with its opening on its side and allowed to flatten out on the floor of the limnocorrals. The net, with a diameter as wide as the width of the limnocorral interior, was then pulled through each limnocorral until three consecutive tows yielded no fish. Fish were placed into containers, put on ice, and measured the day of collection. The experiment was terminated after 2 weeks to focus on the period when larval fish and zebra mussel diets overlap.

My primary interest was determining effects on bluegill growth and survival. Standard length of surviving fish was compared with standard length of fish from the original cohort using a two-sample *t* test for the means. The number of surviving fish was compared with the initial population size also with a *t* test. Results for unequal variances are reported (note the different standard deviations; Table 1).

Also of interest were temporal patterns in ecosystem components. Physical parameters, water, and zooplankton could be sampled during the course of the experiment because such a disturbance was minor and not expected to kill fish. Samples were taken approximately every 3 days from 9 July to 22 July 1999. Temperature, oxygen, pH, and specific conductance were measured with a YSI multisensor. Sestonic chlorophyll *a* was measured by fluorometry (Welschmeyer 1994). Limnological measurements and water sampling were performed in the space between the wall and center (where Plexiglas sheets were suspended) of the limnocorral before collecting sediment to prevent sediment from being resuspended and thereby contaminating the water column and samples. Transparency was measured with a light meter. A

Table 1. *t* test for unequal variances of zebra mussel (ZM) effects on larval bluegill (BG) growth and survival.

	Treatment	<i>N</i>	Mean	SD	SE	df	<i>t</i>	<i>P</i>
Bluegill length (mm)	ZM + BG	3	8.5	0.06	0.03	2.2	5.330	0.0274
	BG	3	9.3	0.26	0.15			
Bluegill survival (count)	ZM + BG	3	10.7	2.9	1.7	3.4	0.426	0.6956
	BG	3	12.0	4.6	2.6			

Fig. 1. Phytoplankton and transparency response over the course of the experiment in the presence of zebra mussels and larval bluegill. Shown are means \pm SE. \diamond , control treatments; \blacklozenge , zebra mussel treatments; \circ , larval bluegill treatments; \bullet , zebra mussel plus larval bluegill treatments. (a) Chlorophyll *a*; (b) coefficient of light extinction. Transparency decreases with an increasing coefficient of light extinction.

two-tiered regime was used to sample zooplankton: two 1-m tows using a 10-cm-diameter, 100- μ m net for macrozooplankton and the filtration of 4 L of water through 30- μ m mesh for microzooplankton. All zooplankton were stored in 95% ethanol. Zooplankton were enumerated with a dissecting microscope. Body size was measured for macrozooplankton only using a digitizing pad. Entire zooplankton samples were enumerated, but up to 50 individuals of a species were measured for calculation of biomass using published length–mass regressions (McCauley 1984).

Time series data was analyzed with repeated-measures analysis of variance (ANOVA) to account for correlation between measurements. In repeated-measures ANOVA terminology, “between-subjects effects” refer to differences between the means of treatments for the time period and “within-subject effects” refer to differences between treatments in the temporal pattern of response (i.e., the time \times treatment interactions). Univariate tests of within-subject effects require covariance matrices that are circular (von Ende 1993). Circularity can be evaluated with a sphericity test on orthogonal components using Mauchly’s criterion (SAS institute Inc. 1999). As Mauchly’s criterion approaches zero, the data depart from sphericity and therefore circularity, necessitating the use of multivariate repeated-measures ANOVA (MANOVA), which has no assumption of circularity (von Ende 1993). Only days 3–13 were used for time series analysis because day 0 represented initial conditions, i.e., those measurements were taken before treatment factors were in place.

Several measures were undertaken to ensure that zebra mussels did not escape from the experiment (Reid et al. 1993). The tops of mesocosms were covered with gray fiberglass window screen to prevent animals from entering the limnocorrals and transporting water potentially infested with zebra mussel veligers to other experimental ponds. After the experiment, the limnocorrals were treated with Rotenone and chlorine before the bags were cut away from their frames. Lastly, the entire pond was drained (with the water infiltrating nearby soil) and allowed to dry completely before being refilled.

Results

Larval bluegill reared in the presence of zebra mussels were shorter at the end of the experiment than larval bluegill reared alone (Table 1) (initial standard lengths were 5.5 ± 0.16 mm). Thus, bluegill growth rates were about 24% lower in the ZM + BG treatments compared with the BG treatments (0.22 and 0.29 mm·day⁻¹, respectively). There was no significant difference in survival among treatments (Table 1) (initial count was 20 fish). Toxic conditions were not produced by zebra mussels.

Within the control treatment, chlorophyll *a* fell steadily from a mean of 2.70 μ g·L⁻¹ to a mean of 1.21 μ g·L⁻¹ (Fig. 1a). Zebra mussels decreased the concentration of chlorophyll *a* (between subjects: $P < 0.0001$, $F = 415.39$). Zebra mussels increased the transparency of the water column (between subjects: $P = 0.0001$, $F = 46.27$) (Fig. 1b).

Most of the impact of zebra mussels occurred within the first 3 days. Transparency decreased in all treatments between days 3 and 6. Specific conductance (corrected to 25 °C) fell from an initial experiment-wide mean (\pm SD) of $315 \pm 1.3 \mu\text{S}\cdot\text{cm}^{-1}$ to $311 \pm 1.7 \mu\text{S}\cdot\text{cm}^{-1}$ on day 3 and then remained level. Dissolved oxygen fell from an initial experiment-wide mean (\pm SD) of $75 \pm 4\%$ saturation to $54 \pm 7\%$ saturation and then remained level. The pH of all treatments rose from an experiment-wide mean (\pm SD) of 7.67 ± 0.03 to 7.75 ± 0.05 by day 9 (day 13 pH data were not available). Temperature did not vary among treatments and ranged between 23 and 26 °C during the experiment.

Macrozooplankton included calanoid and cyclopoid copepods, as well as the cladocerans *Daphnia ambigua*, *Bosmina longirostris*, *Diaphanosoma* spp., *Scaphloberis* spp., *Simocephalus* spp., *Chydorus* spp., and *Sida* spp. Greater initial densities of *Bosmina*, *Diaphanosoma*, and adult copepods were present in control treatments in spite of attempts to equalize densities across all enclosures (Figs. 2a–2c). Other macrozooplankton species were not plentiful enough to allow individual analysis but were included in sums of total macrozooplankton biomass, which fell over time during the experiment (Fig. 2d). Although significant between-subjects effects of zebra mussels and bluegill were found for total macrozooplankton biomass ($P = 0.0021$, $F = 19.82$ and $P = 0.0076$, $F = 12.53$, respectively), the difference in initial conditions confounds interpretation of zebra mussel effects on both individual macrozooplankton species and total macrozooplankton biomass (i.e., for between-subjects effects). Within-subject effects, however, can be compared.

Within-subjects effects on macrozooplankton varied. *Bosmina* declined in zebra mussel treatments earlier than in non-zebra-mussel treatments (MANOVA: $P = 0.0044$, $F = 13.57$) (Fig. 2a). Zebra mussels had no statistically significant effect on *Diaphanosoma*, whereas bluegills did, reducing the zooplankton's abundance to near zero by the end of the experiment ($P = 0.0006$, $F = 11.22$, univariate comparison) (Fig. 2b). Zebra mussels and bluegill had no statistically significant effect on adult copepods (Fig. 2c). The abundance of all macrozooplankton species fell during the course of the experiment with the exception of *Diaphanosoma*, which increased in abundance in the presence of zebra mussels after day 6 (Fig. 2b). Most importantly, zebra mussels and bluegill had no within-subject effect on total macrozooplankton biomass (Table 2; Fig. 2d).

Microzooplankton included copepod nauplii and the rotifers *Keratella cochlearis* and *Polyarthra vulgaris*. Initial microzooplankton densities were similar among all treatments (Fig. 3). Temporal dynamics varied between microzooplankton taxa. Copepod nauplii dominated the microzooplankton count and drove the temporal pattern of total microzooplankton abundance. Nauplii abundance dropped initially in all treatments, then increased over time in control treatments, declined quickly in ZM and ZM + BG treatments, and declined late in the experiment in BG treatments (Fig. 3a) (between-subjects effects, mussels: $P = 0.0016$, $F = 21.76$, fish: $P = 0.0327$, $F = 6.65$; within-subject effects, MANOVA, mussels: $P = 0.0017$, $F = 19.66$, fish: $P = 0.0017$, $F = 19.58$). *Keratella* abundance quickly dropped and reached levels below detection in all treatments

by the end of the experiment showing no statistically significant between- or within-subject effects (Fig. 3b). *Polyarthra* was reduced to low levels by day 3 and held at low and relatively constant levels in ZM and ZM + BG treatments (Fig. 3c) (between-subjects effects of mussels: $P = 0.0066$, $F = 13.21$). *Polyarthra* abundance increased in control treatments and remained relatively stable in BG treatments (Fig. 3c) (MANOVA, within-subject effects of mussels: $P = 0.0219$, $F = 7.87$). Fish had no statistically significant effects on *Polyarthra*. Most importantly, both zebra mussels and bluegill caused significant between-subjects effects, reducing the abundance of total microzooplankton (Table 3; Fig. 3d).

Discussion

Zebra mussels substantially reduced the growth of bluegill during the critical larval stage. This effect can be explained by a reduction in microzooplankton abundance. Two likely mechanisms caused by zebra mussels exist to explain observed declines in microzooplankton abundance: (i) consumption of microzooplankton and thus competition with fish for food and (ii) starvation of microzooplankton through reduction in the abundance of phytoplankton. Although the mechanism of zebra mussel consumption of microzooplankton was supported, the relative importance of predator limitation versus resource limitation on microzooplankton by zebra mussels could not be evaluated in this experiment.

The hypothesized mechanism of zebra mussels consuming microzooplankton and slowing larval fish growth rates was supported by temporal patterns in both total microzooplankton and total macrozooplankton abundance. Specifically, this empirical support existed in the observed decline in microzooplankton abundance without a comparable decline in macrozooplankton abundance (i.e., in the presence of zebra mussels). This observed pattern is possible because macrozooplankton, as opposed to microzooplankton, are generally too large to fit in the inhalant siphon. Additionally, susceptibility of microzooplankton including the rotifers *Keratella* and *Polyarthra* to zebra mussel predation has been demonstrated by others (Shevtsova et al. 1986; MacIsaac et al. 1991, 1995). It is possible, however, that macrozooplankton may have tolerated reduced food availability longer than microzooplankton because of larger body sizes.

A decline in *Bosmina* abundance occurred earlier in zebra mussel treatments but did not greatly influence temporal patterns of total macrozooplankton. The early decline of *Bosmina* may be due to starvation, since *Bosmina* were among the smaller macrozooplankton. Because of the short duration of the experiment, the effects of reduced food availability on other macrozooplankton might not yet have been observable. Thus, although the overall results observed in the experiment are consistent with predator limitation of microzooplankton, they are not inconsistent with resource limitation of all zooplankton.

The mechanism of toxic conditions was not supported, and other potential mechanisms were not likely. In theory, selective consumption of phytoplankton by zebra mussels could have caused selective suppression of microzooplankton. Zebra mussels, however, preferentially feed on

Fig. 2. Macrozooplankton response over the course of the experiment in the presence of zebra mussels and larval bluegill. Shown are means \pm SE. \diamond , control treatments; \blacklozenge , zebra mussel treatments; \circ , larval bluegill treatments; \bullet , zebra mussels plus larval bluegill treatments. (a) *Bosmina longirostris*; (b) *Diaphanosoma* spp.; (c) adult copepods (calanoids and cyclopoids); (d) sum of all macrozooplankton.

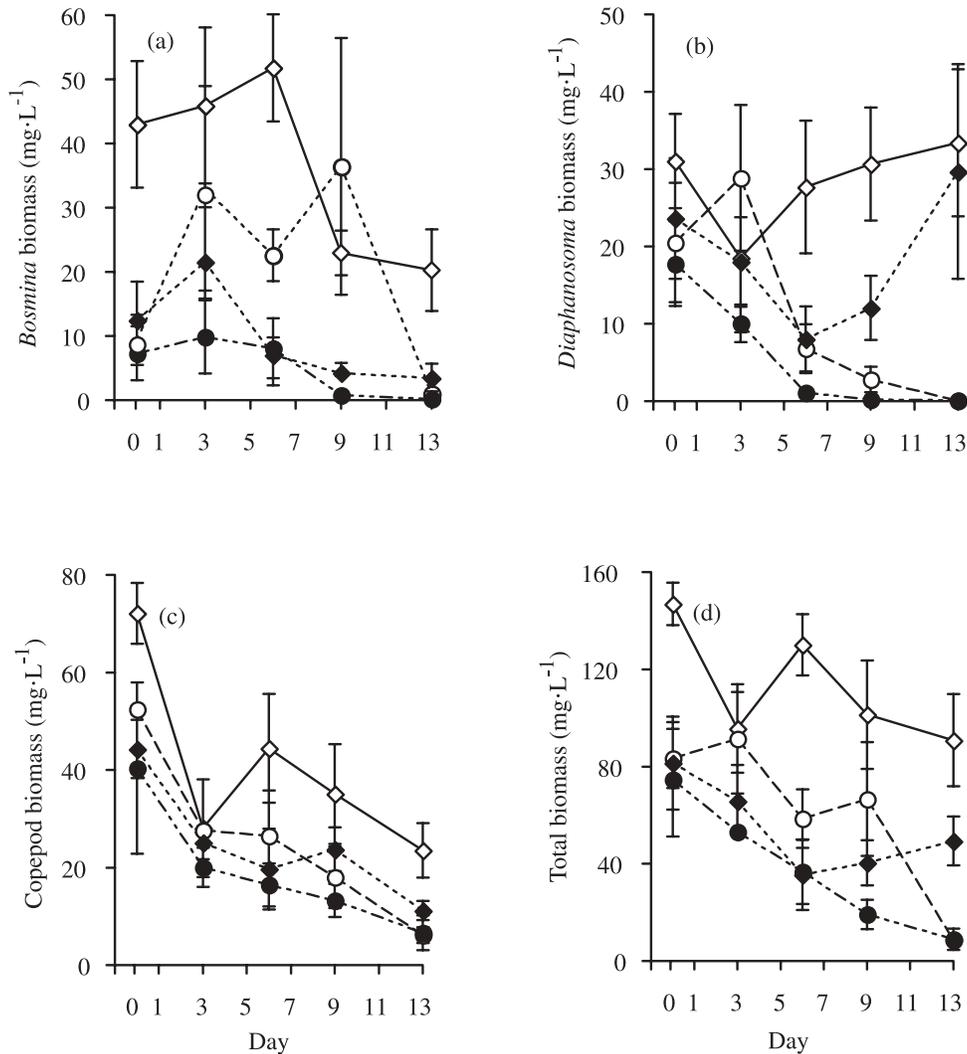


Table 2. Univariate repeated-measures ANOVA test for effects of zebra mussels (ZM) and larval bluegill (BG) on macrozooplankton biomass over the course of the experiment (days 3–13).

	Source	df	MS	F	P
Between subjects	ZM	1	0.021	19.82	0.0021
	BG	1	0.013	12.53	0.0076
	ZM \times BG	1	0.002	2.54	0.1493
	Error	8	0.001		
Within subjects*	Time	3	0.002	6.51	0.0022
	Time \times ZM	3	0.000	2.08	0.1300
	Time \times BG	3	0.001	3.21	0.0409
	Time \times ZM \times BG	3	0.000	2.06	0.1321
	Error	24	0.000		

*Sphericity test of orthogonal components: Mauchly's criterion = 0.31, $\chi^2 = 7.9$, $P = 0.1596$.

particles 5–45 μm in size, a range that overlaps that which rotifers consume (4–17 μm) and that which copepods consume (<1 μm – 1 mm) (Gilbert 1985; Sprung and Rose 1988; Williamson 1991). Zebra mussels can also feed on a

larger range of particles, from <1 to 750 μm , including bacterioplankton, *Ankistrodesmus* cells, and cyanobacterial filaments (Ten Winkel and Davids 1982; Cotner et al. 1995; Horgan and Mills 1997). Zebra mussels were thus unlikely

Fig. 3. Microzooplankton response over the course of the experiment in the presence of zebra mussels and larval bluegill. Shown are means \pm SE. ind., individuals; \diamond , control treatments; \blacklozenge , zebra mussel treatments; \circ , larval bluegill treatments; \bullet , zebra mussels plus larval bluegill treatments. (a) Copepod nauplii; (b) *K. cochlearis*; (c) *P. vulgaris*; (d) sum of all microzooplankton.

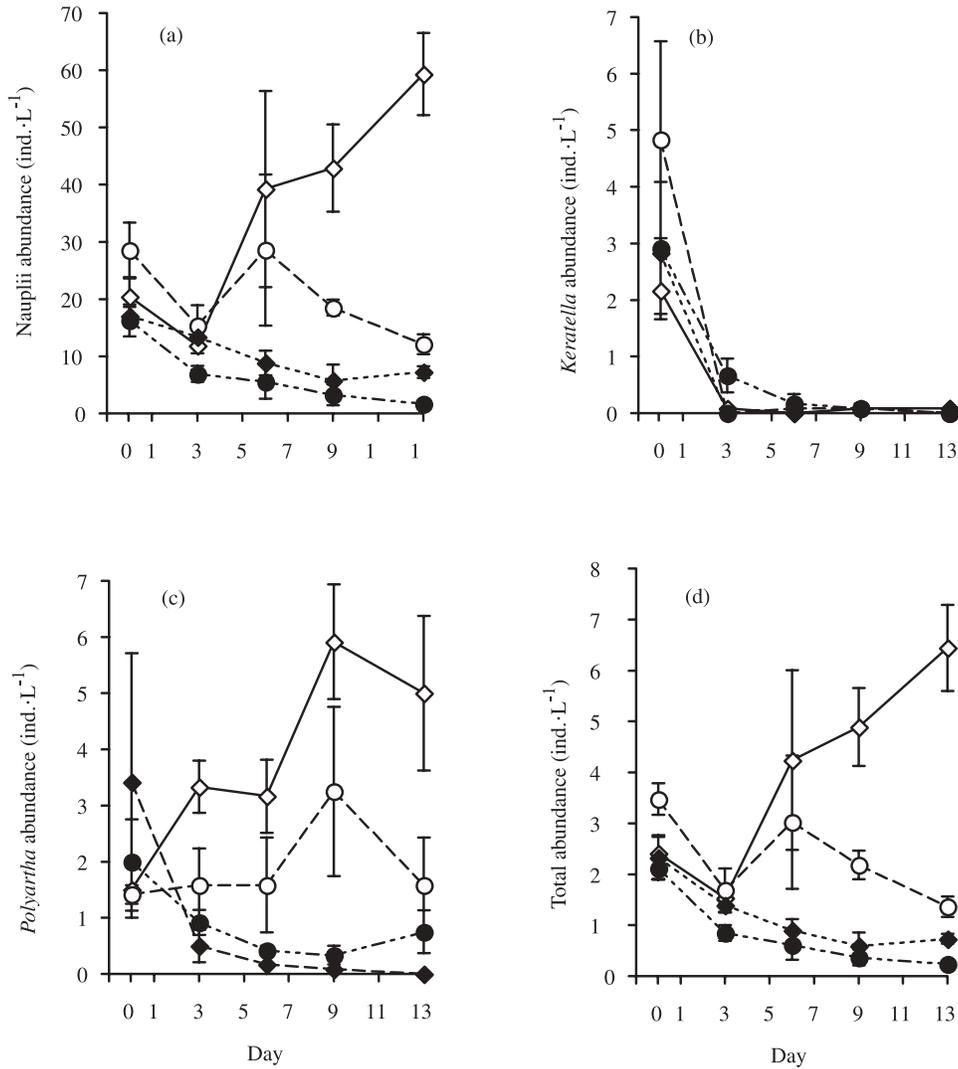


Table 3. Univariate repeated-measures ANOVA and MANOVA testing for effects of zebra mussels (ZM) and larval bluegill (BG) on microzooplankton abundance over the course of the experiment (days 3–13).

	Source	df	MS	F	P
Between subjects	ZM	1	116 328.5	24.91	0.0011
	BG	1	32 396.0	6.94	0.0300
	ZM \times BG	1	15 950.5	3.42	0.1018
	Error	8	4 670.6		
Within subjects*	Time	3		5.00	0.0452
	Time \times ZM	3		18.37	0.0020
	Time \times BG	3		19.92	0.0016
	Time \times ZM \times BG	3		18.57	0.0019

*Sphericity test of orthogonal components: Mauchly's criterion = 0.07, $\chi^2 = 17.8$, $P = 0.0032$, necessitating the use of MANOVA.

to have selected particles that would produce an effect simultaneously detrimental to microzooplankton and not detrimental to macrozooplankton.

The relative importance of predator limitation and resource limitation by zebra mussels on zooplankton can be addressed in future experiments. Reduced phytoplankton

abundance reduces available energy to zooplankton, which can be reflected in lower reproductive rates (Williamson 1991). Thus, examination of zooplankton reproductive rates by assessing egg ratios (number of eggs per individual) should accompany evaluation of zooplankton abundance in future experiments. For example, a mesocosm experiment could be installed in a lake already invaded by zebra mussels with some treatments containing no mussels. Released from the influence of mussels in those treatments, phytoplankton and microzooplankton abundance should increase. If egg ratios also increase, then resource limitation is suggested, as organisms allocate newly available energy to reproduction. If egg ratios do not increase, then predator limitation is suggested.

Richardson and Bartsch (1997) studied zebra mussel–bluegill food web interactions in mesocosms using omnivorous juvenile bluegill (34 mm long) that were not limited to microzooplankton and found that the growth of bluegill was not affected by the presence of zebra mussels. Thus, competition with zebra mussels should not occur during later life stages when bluegill display more omnivorous feeding behavior. The present study shows that the potential for zebra mussels in natural systems to affect bluegill growth occurs during the earliest life stages when bluegill are most restricted in their diet.

Several questions affect the potential for and biological significance of fish – zebra mussel interaction in natural systems. The first question is whether zebra mussels actually affect microzooplankton abundance in lakes. MacIsaac et al. (1991) speculated that vertical zonation of zooplankton and poor water column mixing might ameliorate the impact of microzooplankton predation by benthic zebra mussels in the Great Lakes, and the same could be true of small inland lakes. The epilimnion of a small inland lake, however, is arguably in greater contact with the benthos than the epilimnia of the Great Lakes. An exception would be where the Great Lakes are shallow, like the western basin of Lake Erie and Saginaw Bay.

Lastly, if obligatory feeding on microzooplankton is restricted to a short enough time period, then larval fish might survive long enough to outgrow reliance on the size class of zooplankton consumed by zebra mussels (Lazzaro 1987). This ontogenetic niche shift may include feeding on benthic or littoral invertebrates and may help to explain why detrimental impacts on fish populations have not yet been observed in lakes invaded by zebra mussels (Gopalan et al. 1998; Mayer et al. 2000; Idrisi et al. 2001). A slowed growth rate early in life, however, could produce a deficit that is never fully recovered and reduce the chance of overwinter survival.

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