

## Dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) reduce microzooplankton and macrozooplankton biomass in thermally stratified lakes

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### Abstract

We conducted a survey of 50 thermally stratified lakes with similar nutrient concentrations and morphometries in Michigan to examine the direct and indirect effects of dreissenid mussels on the biomass and community composition of microzooplankton and macrozooplankton. Twenty-five lakes were infested with dreissenid mussels (invaded), while 25 lakes were dreissenid free (uninvaded). In invaded lakes, phytoplankton biomass was 24% lower, and water clarity was 21% greater. 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, largely driven by a 40% lower biomass of *Daphnia* spp. in invaded lakes. In contrast, dreissenid status had no significant influence on total copepod biomass, calanoid biomass, or cyclopoid biomass. Our microzooplankton results are similar to those of previous studies conducted in shallow, well-mixed systems, although the magnitude of the dreissenid influence in our study was smaller, as might be expected in thermally stratified systems. On the other hand, ours is the first study to document lower biomass of *Daphnia* spp. and reduced rotifer diversity in invaded lakes. In contrast, we found no difference in macrozooplankton community structure. Dreissenids likely affected zooplankton directly through predation (microzooplankton) and indirectly through resource competition (micro- and macrozooplankton). Understanding how dreissenid mussels affect both micro- and macrozooplankton will help us to identify the potential mechanisms by which higher trophic levels (e.g., fish) are influenced by these invaders.

Dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*), exotic species native to the Ponto–Caspian region of Eastern Europe, have invaded North America and are rapidly spreading throughout freshwater systems with suitable alkalinity (Ramcharan et al. 1992). First detected in Lake St. Clair, Michigan, in 1988 (Herbert et al. 1989), dreissenids 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). Dreissenids have also been inadvertently spread by recreational boat traffic and are colonizing smaller inland lakes.

Dreissenids are efficient benthic filter feeders that represent a new component in the food webs of North American lakes. Dreissenid invasion usually leads to decreased phytoplankton abundance and chlorophyll *a* (Chl *a*) (Fahnenstiel et al. 1995; Knoll et al. 2008a), increased water clarity (Fahnenstiel et al. 1995; Idrisi et al. 2001), and altered phytoplankton community composition (Smith et al. 1998). Dreissenids also promote blooms of the toxic colonial cyanobacterium *Microcystis aeruginosa* in lakes with low to moderate nutrient levels (Vanderploeg et al. 2001; Raikow et al. 2004; Sarnelle et al. 2005) and increase concentrations of the associated toxin, microcystin (Knoll et al. 2008a).

Zooplankton dynamics can be affected both directly and indirectly by dreissenids (Fig. 1). Some microzooplankton

(ciliates and rotifers) are small enough to be directly consumed by dreissenids, and their abundance usually declines in invaded systems (MacIsaac et al. 1991; Pace et al. 1998). Dreissenids can also indirectly affect microzooplankton through resource competition for phytoplankton (Heath et al. 1995; Idrisi et al. 2001). Given these multiple interaction pathways, dreissenid filtering has the potential to affect ciliate and rotifer biomass differently. Because dreissenids generally prefer food particle sizes of 5–45  $\mu\text{m}$  (Ten Winkel and Davids 1982), they should inflict greater mortality on ciliates than on rotifers, since ciliate cell sizes are commonly within the preferred range, while rotifers are generally larger (often  $> 100 \mu\text{m}$ ). Bacteria are also an important food source for microzooplankton. However, as a result of the small size of planktonic bacteria ( $< 1 \mu\text{m}$ ), their abundance is typically not greatly affected by dreissenid presence (Cotner et al. 1995). Ciliates generally consume bacteria more effectively than do rotifers. Thus, the size-selective nature of dreissenid feeding may result in a larger predatory effect on ciliates but a larger competitive effect on rotifers (via phytoplankton consumption). Therefore, it is not obvious whether mussel invasion will have a greater overall effect on ciliates or on rotifers.

Macrozooplankton are generally too large to be consumed by dreissenids (MacIsaac et al. 1991, 1995) and, therefore, are only indirectly affected through resource competition for phytoplankton and small microzooplankton. Studies documenting the influence of dreissenids on macrozooplankton abundance in North America are few and somewhat contradictory. In shallow, well-mixed areas of western Lake Erie, MacIsaac et al. (1991, 1995) found no change in macrozooplankton biomass postinvasion. In

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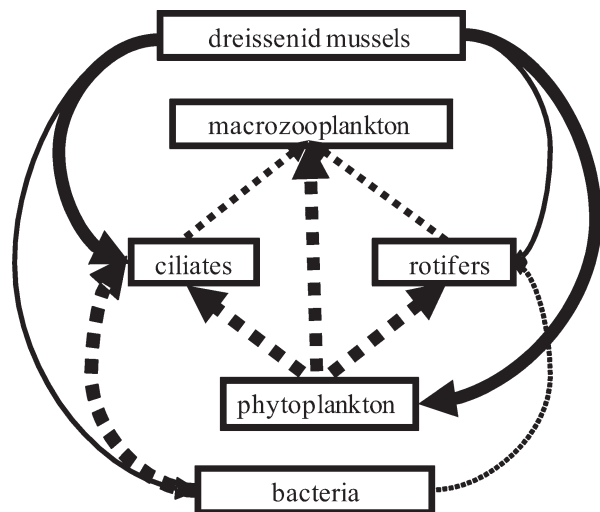


Fig. 1. Simplified diagram of the lower trophic levels of an inland lake food web including dreissenids. Solid lines indicate the direct negative predatory influence of dreissenids on other food web compartments. Dotted lines indicate indirect dreissenid influences. Line weight represents the strength of interactions between compartments. Note that ciliates, rotifers, and macrozooplankton can be affected by dreissenids through multiple pathways in the food web. Other potential indirect pathways not included are the influence of dreissenids on light, nutrients, and dissolved organic carbon, all of which may in turn affect ciliates, rotifers, and macrozooplankton.

shallow Oneida Lake, New York, *Daphnia* species biomass and production did not change following invasion (Idrisi et al. 2001). In well-mixed river systems, dreissenids have negatively affected the growth of smaller macrozooplankton species such as *Bosmina* spp., *Diaphanosoma* spp., and *Diacyclops* spp. (Jack and Thorp 2000). Additionally, Pace et al. (1998) showed a non-significant decline in macrozooplankton biomass in the Hudson River after invasion. The disparities in these results are most likely due to many unquantified indirect zebra mussel effects (Fig. 1). Although changes in macrozooplankton biomass have been documented in some systems, the community structure of macrozooplankton did not change in the St. Lawrence River after invasion (Winkler et al. 2005).

Macrozooplankton are the major food source for planktivorous fish. If macrozooplankton biomass declines as a result of dreissenid invasion, this may negatively affect species at higher trophic levels (e.g., planktivorous and piscivorous fish; Rutherford et al. 1999) and could potentially degrade recreational fishing. In their review of dreissenid effects on fish species, Strayer et al. (2004) reported variable responses in fish growth or abundance after dreissenid infestation in six river or lake systems. They attributed these results to three indirect pathways by which dreissenids can affect fish: (1) reduced phytoplankton and edible consumers (i.e., zooplankton and zoobenthos), (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 these indirect effects.

Most studies on the influence of dreissenids on lower trophic levels compare communities before and after invasion in a single, well-mixed ecosystem. In a well-mixed lake or river, dreissenids on the bottom are able to filter the entire water column. This should result in relatively strong influences on the biota, such as large declines in phytoplankton (Fahnenstiel et al. 1995; Idrisi et al. 2001) and microzooplankton (MacIsaac et al. 1991; Pace et al. 1998). In contrast, dreissenids in thermally stratified lakes do not have access to the entire water column during summer and thus would be expected to have weaker influences on the biota (MacIsaac et al. 1991; Noonburg et al. 2003). Our group has conducted two studies that investigated the dreissenid influence on phytoplankton in thermally stratified inland lakes and found significantly lower Chl *a* (50% and 30%, respectively) and phytoplankton biomass (45% and 30%, respectively) (Raikow et al. 2004; Knoll et al. 2008a). However, it is still unknown how dreissenids will affect microzooplankton and macrozooplankton in stratified lakes relative to well-mixed systems. We know of no studies that have investigated the influence of dreissenids on both microzooplankton and macrozooplankton in thermally stratified lakes.

Multi-lake surveys offer a powerful tool for assessing the effects of environmental variables (Pace 1993), including invasion (Raikow et al. 2004; Knoll et al. 2008a), on lake biota, and these surveys provide an alternative to the before-after approach for examining the influence of dreissenid establishment. We conducted an extensive survey of thermally stratified lakes in Michigan to address the following two main questions: (1) Do dreissenids reduce microzooplankton and macrozooplankton biomass in thermally stratified inland lakes and are there different responses within each zooplankton group?; (2) Do dreissenids alter microzooplankton and macrozooplankton community structure? Our results compliment a previous article (Knoll et al. 2008a) on the influence of dreissenids on phytoplankton biomass and community structure in these same lakes. Most notably, we show that dreissenid invasion leads to significantly lower biomass of *Daphnia* spp. and a decrease in species richness and evenness of rotifers, the first clear evidence for these effects.

## Methods

**Lake selection criteria**—We selected 50 study lakes in Southern Michigan, 25 of which were invaded by dreissenids and 25 of which were uninvaded reference lakes. 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 ( $< 22 \mu\text{g L}^{-1}$ ; Knoll et al. 2008a; Michigan Department of Environmental Quality). Lakes selected for this study were  $\geq 9$  m in maximum depth to ensure summer temperature stratification. Invaded and uninvaded lakes were similar in pH and calcium concentrations, and, thus, all could support dreissenids (Ramcharan et al. 1992; Raikow et al. 2004). To ensure that treatment and control groups were of similar mean depths,

mean depths were calculated using a Geographic Information System. Where lake maps were unavailable, we obtained mean depth data from the Michigan Department of Environmental Quality (unpubl.). We acquired dreissenid presence or absence information from the U.S. Geological Survey Nonindigenous Aquatic Species database (<http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/>). Adult dreissenid presence or absence was further verified by searching the littoral zone of each lake for 1 h and by noting the presence or absence of veligers (planktonic *Dreissena* larvae) in zooplankton samples (see below).

**Lake sampling**—We sampled lakes once between 03 August and 05 September 2002 or between 16 July and 23 August 2003. In 2002, we sampled 26 lakes (uninvaded lakes = 14, invaded lakes = 12), and in 2003, we sampled 24 lakes (uninvaded lakes = 11, invaded lakes = 13). Lakes were sampled in late summer to ensure thermal stratification. We avoided a confound between date of sampling and mussel presence by alternating between sampling uninvaded and invaded lakes several times each summer. All pelagic sampling was conducted at the deepest part of the lake, as determined from bathymetric maps and an echo sounder.

**Physical and biological parameters**—We measured temperature and dissolved oxygen at 1-m depth intervals using a Hydrolab Surveyor 4a equipped with a Datasonde 4a (HACH Environmental). 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). Light extinction coefficients were determined as the slope of the linear regression between  $\ln$  PAR and depth ( $r^2$  values ranged between 0.89 and 0.99).

We collected an integrated epilimnetic water sample using a flexible plastic tube (5-cm internal diameter). 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 subsamples were taken for phytoplankton composition, microzooplankton composition, Chl *a*, and TP. Phytoplankton and ciliate samples were preserved immediately in Lugol's solution. Rotifers were collected by passing a 10-liter subsample of the mixed-layer water through a 35- $\mu$ m mesh screen and rinsing organisms on the screen into sample bottles containing glutaraldehyde (final concentration: 2%). Water samples for Chl *a* and TP were placed on ice until they were processed later the same day (~ 6 h). Chl *a* samples were filtered through Gelman A/E glass-fiber filters (Gelman Sciences) and frozen until laboratory analysis. TP samples were frozen until laboratory analysis.

Macrozooplankton samples were collected with vertical hauls of a zooplankton net (30-cm diameter, 100- $\mu$ m mesh) from ~ 1 m above the lake bottom to the surface. Four hauls were pooled from each lake and preserved with 95% ethanol.

We quantified Chl *a* by extracting filters with 90% ethanol and analyzing the extract with a Turner Model 10-AU fluorometer (Welschmeyer 1994) calibrated to a commercial Chl *a* standard (*Anacystis*; Sigma-Aldrich Chemical Company). 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 (uninvaded lakes = 20, invaded lakes = 22; Knoll et al. 2008a). Phytoplankton identification and biomass calculations were performed according to the method of Knoll et al. (2008a,b).

**Microzooplankton biomass**—Ciliates were assessed in all 50 study lakes (uninvaded lakes = 25, invaded lakes = 25). Ciliates were identified to the Family level and measured using a NIKON model TE2000-S inverted microscope, a SPOT insight Color model 3.2.0 digital camera, and SPOT Advanced version 4.0.9 image-analysis software (Diagnostic Instruments). Subsamples (volume, 30–100 mL) were settled in tubular chambers (Hydro-Bios), the bottoms of which were divided into inner and outer zones of equal area. Within each zone, at least 20 random fields were counted at 100 $\times$  magnification. Ciliate cell volume was determined by measuring at least five individuals per taxon at 400 $\times$  magnification. Biovolume was converted to dry biomass assuming a specific gravity of 1 g cm<sup>-3</sup> and a dry mass to wet mass ratio of 0.40.

Rotifers were assessed in all 50 study lakes. Rotifers were identified to the species level using a Nikon model E600 compound microscope at 100 $\times$  magnification and a Sedgwick–Rafter counting chamber. For each lake, a total of approximately 400 individuals (average = 394, range = 341–475) were counted in a minimum of two subsamples. 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 the genus or species level using a 10-mL clear polyvinyl chloride zooplankton counting wheel and a Leica model MZ8 dissecting microscope (Leica Microsystems). Samples were diluted to a known volume, and two to three 5-mL subsamples were counted. A minimum of 450 individuals were tallied per lake. Measurements of individuals were made at a magnification of 10 $\times$  using a Summa Sketch III digitizing pad and ZoopBiom software. For each sample, up to 50 individuals were measured for each large (> 1.0-mm) genus or species (*Daphnia galeata*, *Daphnia pulicaria*, *Daphnia retrocurva*, *Epischura* spp., *Leptodora* 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., *Diaphanosoma* spp., *Diaptomus* spp., *Dreissena* spp. veligers, *Moina* spp., and nauplii). Biomass was calculated using published length–weight regressions for individual species (Culver et al. 1985).

Table 1. Average, range, and standard error (SE) of physical and biological parameters in dreissenid invaded and uninvaded lakes in 2002–2003. Mean depth and total macrozooplankton biomass were analyzed with ANOVA, chlorophyll *a* was analyzed with ANCOVA, and all others were analyzed with Student's *t*-tests. Degrees of freedom are given in subscript.

Parameter	Uninvaded		Invaded		Test statistic	<i>p</i> -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	$F_{1,46}=1.41$	0.24
Total phosphorus ( $\mu\text{g L}^{-1}$ )	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 ( $\text{m}^{-1}$ )	0.28(0.16–0.43)	0.01	0.22(0.06–0.33)	0.01	$t_{48}=-2.93$	0.01
Chlorophyll <i>a</i> ( $\mu\text{g L}^{-1}$ )	4.23(1.08–9.29)	0.37	3.33(0.89–6.2)	0.23	$F_{1,47}=5.70$	0.02
Total phytoplankton biomass ( $\mu\text{g L}^{-1}$ )	197.57(74.83–380.30)	17.80	150.76(51.54–463.31)	21.76	$t_{40}=2.30$	0.03
Total microzooplankton biomass ( $\mu\text{g L}^{-1}$ )	68.10(18.35–178.54)	7.71	39.39(8.27–101.14)	4.62	$t_{48}=3.46$	0.001
Total macrozooplankton biomass ( $\mu\text{g L}^{-1}$ )	152.94(36.26–327.94)	16.72	102.68(18.17–280.19)	11.37	$F_{1,46}=11.07$	0.002

*Statistical analyses*—We first examined the influence of dreissenids on the biomass of the four zooplankton groups: ciliates, rotifers, cladocerans, and copepods. We also further divided the copepod group into calanoids and cyclopoids. Within the cladocerans, we separately assessed *Daphnia* biomass because this genus is a major driver of food web effects in lakes and a major food source for zooplanktivores (Mittelbach 1981).

To test for the influence of sample day on response variables, we used linear regression with day after 01 July as the independent variable. If a response variable had a significant day effect ( $p < 0.05$ ; Chl *a* and calanoid copepod biomass), it was further analyzed using an analysis of covariance (ANCOVA) with dreissenid presence or absence as a fixed effect and day after 01 July as a covariate. Similarly, Student's *t*-tests were used to determine if there was a year effect (2002 vs. 2003) on all response variables. If a response variable had a significant year effect ( $p < 0.05$ ; mean depth and total macrozooplankton [cladoceran, *Daphnia* spp., copepod, and calanoid copepod biomass]), it was further analyzed using an ANOVA with dreissenid presence or absence and year (2002 or 2003) as fixed effects. For response variables that did not have a sample day or year effect, Student's *t*-tests were used to evaluate the influence of dreissenids. When data failed the Kolmogorov–Smirnov and Shapiro–Wilks tests for normality ( $p < 0.05$ ), data were log or square root transformed to achieve normality.

Rotifer richness was quantified as the total number of species in each sample. Evenness was assessed using the reciprocal of the Berger–Parker Index,  $d = N_{\text{max}}/N$ , where  $N_{\text{max}}$  is the number of individuals of the most abundant species and  $N$  is the total number of individuals (Berger and Parker 1970). To examine the influence of dreissenids on rotifer and crustacean species composition, we subjected the relative abundances (as proportions of total biomass) of individual genera in each group to a principal component analysis (PCA). To reduce the influence of zero values, only common genera were included in the PCA (for rotifers, *Ascomorpha* spp., *Colletheca* spp., *Conochilus* spp., *Keratella* spp., *Polyarthra* spp., *Synchaeta* spp., and *Trichocerca* spp.; for crustaceans, *Cyclops* spp., *Daphnia* spp., *Diaphanosoma* spp., *Diatomus* spp., and *Mesocyclops* spp.). Proportional data were arcsine square root transformed to achieve normality of the residuals. Factor scores were

then compared in invaded and uninvaded lakes with a Student's *t*-test. All data were analyzed using Systat version 11.0.

## Results

Mean depth and TP in invaded and uninvaded lakes were not significantly different ( $F_{1,46} = 1.41$ ,  $p < 0.24$ ;  $t$ -test =  $-0.32$ ,  $\text{df} = 48$ ,  $p < 0.74$ ; respectively) (Table 1), indicating no bias in the selection of sample lakes with respect to these parameters. Light extinction coefficients were significantly lower ( $t$ -test =  $-2.93$ ,  $\text{df} = 48$ ,  $p < 0.01$ ), indicating increased water clarity, in invaded lakes. Chl *a*, total phytoplankton, total microzooplankton, and total macrozooplankton biomass were significantly lower in invaded lakes, by 21%, 24%, 44%, and 33%, respectively ( $F_{1,47} = 5.70$ ,  $p < 0.02$ ;  $t$ -test =  $2.30$ ,  $\text{df} = 40$ ,  $p < 0.03$ ;  $t$ -test =  $3.46$ ,  $\text{df} = 48$ ,  $p < 0.001$ ;  $F_{1,46} = 11.07$ ,  $p < 0.002$ ; respectively) (Table 1). Within the zooplankton, ciliate, rotifer, and cladoceran biomass were 39%, 45%, and 43% lower, respectively, in invaded lakes ( $t$ -test =  $2.16$ ,  $\text{df} = 48$ ,  $p < 0.04$ ;  $t$ -test =  $3.06$ ,  $\text{df} = 48$ ,  $p < 0.004$ ;  $F_{1,46} = 10.88$ ,  $p < 0.002$ ; respectively), while copepod biomass did not differ significantly ( $F_{1,46} = 1.76$ ,  $p < 0.191$ ) (Figs. 2, 3). *Daphnia* spp. biomass was 40% lower in invaded lakes ( $F_{1,46} = 7.23$ ,  $p < 0.01$ ), whereas there was no significant dreissenid influence on calanoid or cyclopoid biomass ( $F_{1,46} = 0.001$ ,  $p < 0.98$ ;  $t$ -test =  $1.87$ ,  $\text{df} = 48$ ,  $p < 0.07$ ; respectively) (Fig. 3).

Invaded lakes had significantly lower rotifer richness ( $t$ -test =  $2.49$ ,  $\text{df} = 48$ ,  $p < 0.016$ ) and significantly lower evenness, as measured by the reciprocal of the Berger–Parker Index ( $F_{1,46} = 4.47$ ,  $p < 0.04$ ) (Fig. 2). The PCA on rotifer community structure reduced the taxon-specific data to two factors that explained 43% of the total variance. Factor 1 scores were significantly lower in invaded lakes ( $t$ -test =  $3.48$ ,  $\text{df} = 48$ ,  $p < 0.001$ ), but no influence was found for Factor 2 scores ( $t$ -test =  $0.60$ ,  $\text{df} = 48$ ,  $p < 0.55$ ) (Fig. 4). Taxa with the highest loadings on Factor 1 were *Polyarthra* spp., *Trichocerca* spp., and *Keratella* spp. Based on these results, we examined the dreissenid influence on each of these taxa. We found that in invaded lakes, *Polyarthra* spp. was significantly more abundant ( $t$ -test =  $-2.47$ ,  $\text{df} = 48$ ,  $p < 0.017$ ), whereas *Trichocerca* spp. was significantly lower ( $t$ -test =  $2.98$ ,  $\text{df} = 48$ ,  $p < 0.005$ ) (Fig. 2).

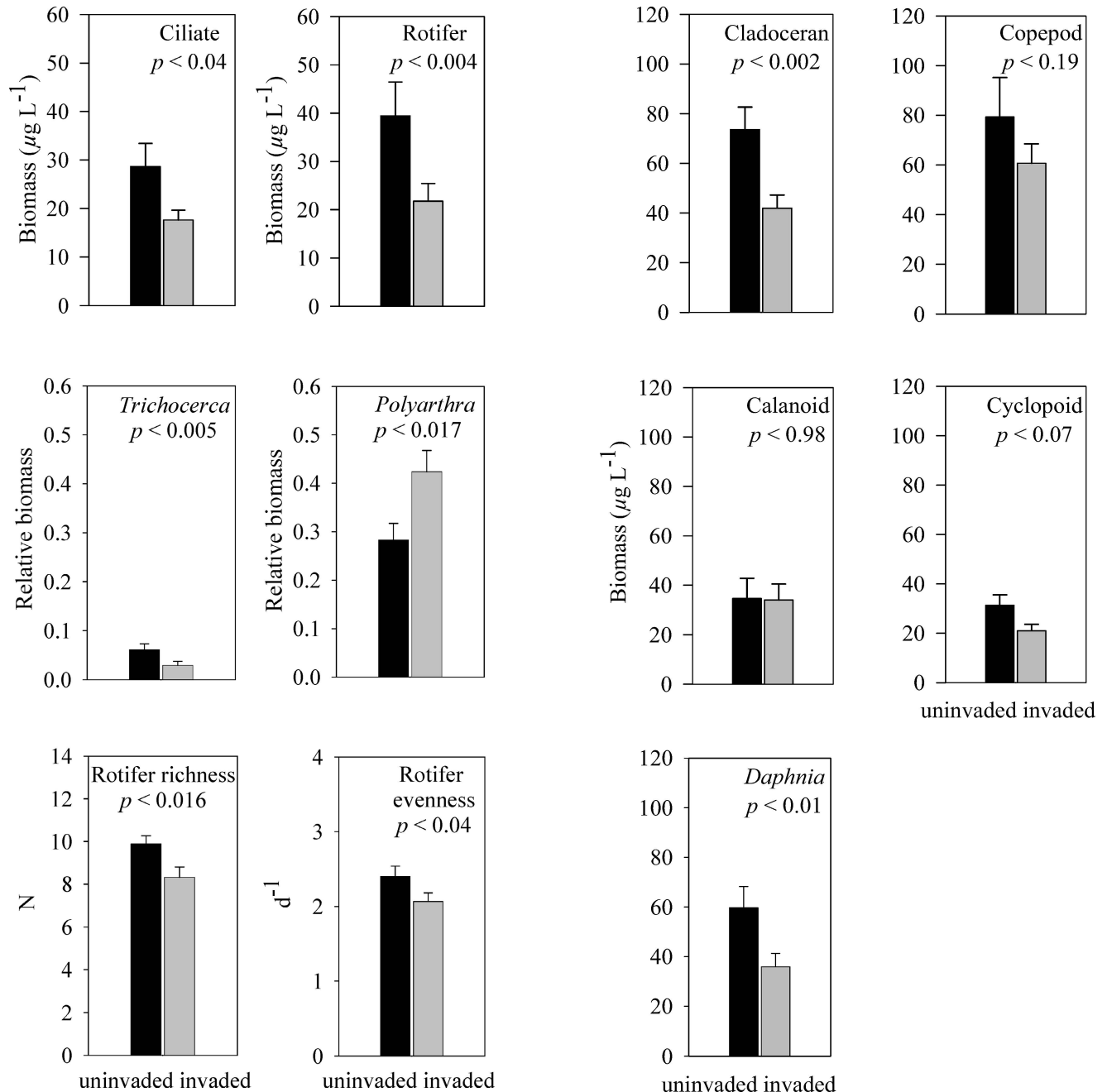


Fig. 2. Ciliate and rotifer dry biomass ( $\mu\text{g L}^{-1}$ ); *Trichocerca* spp. and *Polyarthra* spp. relative biomass; and rotifer species richness (N) and evenness ( $d^{-1}$ ) in dreissenid uninvaded and invaded lakes. *p*-Values are from Student's *t*-tests. Error bars represent standard error.

Fig. 3. Cladoceran, copepod, calanoid copepod, cyclopoid copepod, and *Daphnia* spp. dry biomass ( $\mu\text{g L}^{-1}$ ) in dreissenid uninvaded and invaded lakes. *p*-Values are from Student's *t*-tests for cyclopoid copepod biomass and from ANOVA tests for cladoceran, copepod, calanoid copepod, and *Daphnia* spp. biomass. Error bars represent standard error.

Macrozooplankton community structure was similar in uninvaded and invaded lakes. The PCA of macrozooplankton relative biomass reduced the five taxonomic variables into two factors that explained 71% of the overall variance. However, neither factor was significantly related to dreissenid presence or absence (*t*-test =  $-0.77$ ,  $df = 48$ ,  $p < 0.45$ ; *t*-test =  $-1.18$ ,  $df = 48$ ,  $p < 0.25$ ; respectively) (Fig. 5).

## Discussion

*Microzooplankton and macrozooplankton biomass*—Our results indicate that dreissenids have a strong negative influence on both microzooplankton and macrozooplankton in thermally stratified inland lakes (Table 1; Figs. 2, 3). Within the microzooplankton groups, the negative influence of dreissenids on ciliates and rotifers was similar.

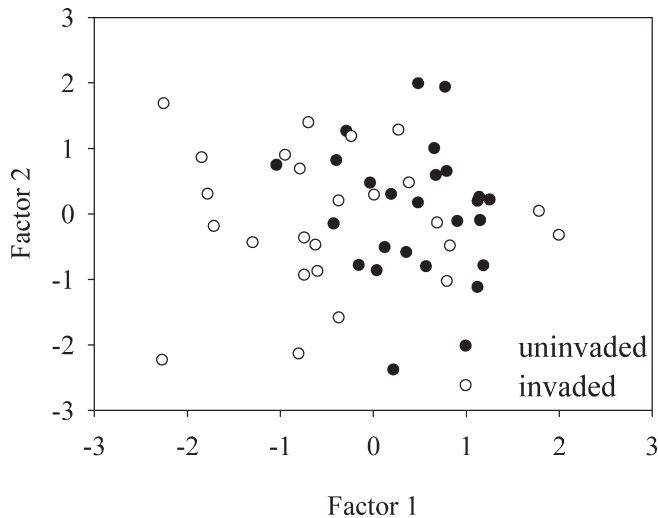


Fig. 4. Rotifer relative biomass PCA factor scores for dreissenid invaded and uninvaded lakes. Factor 1 ( $t$ -test = 3.48,  $df = 48$ ,  $p < 0.001$ ) and Factor 2 ( $t$ -test = 0.60,  $df = 48$ ,  $p < 0.55$ ).

Within the macrozooplankton, *Daphnia* spp. biomass was negatively affected, while copepods were not affected.

We found 39% lower ciliate biomass and 45% lower rotifer biomass in invaded lakes. Experimental studies have shown that dreissenids 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 dreissenid invasion (MacIsaac et al. 1995). Reductions of zooplankton in both the Hudson River and Lake Erie were mainly attributed to negative effects of dreissenids on rotifers. The lesser reduction in our study compared to reductions noted in the Hudson River and Lake Erie studies could be the result of differences in mixing regime. In a shallow, well-mixed system, pelagic organisms are more likely to come into contact with benthic populations of dreissenids (MacIsaac et al. 1991; Noonburg et al. 2003) because mussels are able to colonize a greater proportion of the lake bottom and because frequent water-column mixing allows the entirety of the benthic and pelagic zones of the lake to intermix.

Dreissenids also negatively affected macrozooplankton biomass, with this influence being driven primarily by a reduction in *Daphnia* spp. in invaded lakes (Fig. 3). This is the first study to document significantly lower biomass of *Daphnia* spp. in dreissenid-invaded lakes. The most comprehensive study (Idrisi et al. 2001) that investigated the effect of dreissenids on macrozooplankton (including *Daphnia* spp.) was conducted before and after invasion in shallow, well-mixed Oneida Lake, New York. The authors did not observe significant declines in macrozooplankton biomass postinvasion and attributed the lack of change in *Daphnia* spp. biomass and production to the lack of change in phytoplankton primary production in the lake due to increased water clarity. Thus, the significant decline in *Daphnia* spp. (40%) we observed in our study differs greatly

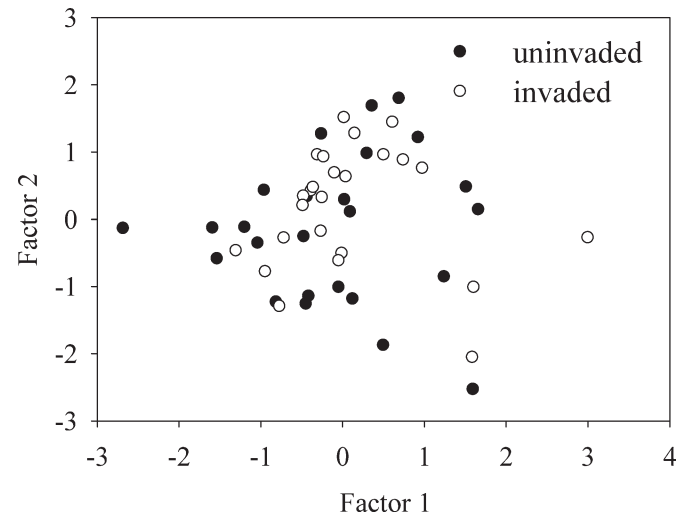


Fig. 5. Macrozooplankton relative biomass PCA factor scores for dreissenid invaded and uninvaded lakes. Factor 1 ( $t$ -test =  $-0.77$ ,  $df = 48$ ,  $p < 0.45$ ) and Factor 2 ( $t$ -test =  $-1.18$ ,  $df = 48$ ,  $p < 0.25$ ).

from the findings in Oneida Lake, despite the fact that we also noted an increase in water clarity.

It was unclear whether dreissenids would have a greater effect on rotifers and ciliates, because dreissenids may inflict a greater predatory effect on ciliates (Ten Winkel and Davids 1982) but exert a greater competitive effect on rotifers (Fig. 1). Overall, we found that the magnitude of the reduction for both groups was remarkably similar (39% vs. 45%). This similarity might be explained by the fact that dreissenids are effective consumers of phytoplankton (Idrisi et al. 2001) but much less effective consumers of bacteria (Cotner et al. 1995). Depending on species, planktonic ciliates feed on both bacteria and phytoplankton (Fenchel 1987) and sometimes rely on bacteria as a major resource (Christoffersen et al. 1990). In contrast, rotifers are much less effective at consuming bacteria (Arndt 1993) and primarily rely on phytoplankton measuring between 4  $\mu\text{m}$  and 17  $\mu\text{m}$  (Bogdan et al. 1980). Thus, in invaded lakes, ciliates may experience greater predation losses because they are within the preferred size range of dreissenids, whereas rotifers experience more food depletion as a result of reductions in phytoplankton biomass, their primary food source.

It is interesting that copepod biomass was not lower, given 24% lower phytoplankton and 44% lower microzooplankton biomass in invaded lakes. Our results are congruent with the fact that copepods did not decline after invasion in the Hudson River (Pace et al. 1998). Thorp and Casper (2002) also documented a significant increase in the calanoid copepod *Eurytemora affinis* (150%) in the presence of dreissenids. Copepods tend to have an advantage over non-selective cladocerans when exposed to conditions of low food quality (Richman and Dodson 1983). As a result of their selective feeding, copepods might be expected to be less negatively affected by the increase in low-quality, toxic cyanobacteria that results from dreissenid invasions in low-nutrient lakes (Vanderploeg et al.

2001; Raikow et al. 2004; Sarnelle et al. 2005). The results of Pace et al. (1998) and Thorp and Casper (2002) also indicate that dreissenids affect macrozooplankton groups through multiple indirect pathways that may vary across taxa and ecosystems (Fig. 1).

The relative importance of direct (predation) or indirect (exploitative competition) mechanisms in the negative influence of dreissenids on microzooplankton cannot be determined from this study, and both mechanisms may have played a role. Phytoplankton biomass was significantly lower in invaded lakes (Table 1), as found in previous studies (Fahnenstiel et al. 1995; Idrisi et al. 2001). By consuming phytoplankton, dreissenids are competing with microzooplankton and macrozooplankton for resources. Thus, it is reasonable to assume that reductions in phytoplankton, mediated through dreissenids, could indirectly affect microzooplankton and macrozooplankton abundance (Fig. 1). Previous experiments (MacIsaac et al. 1991, 1995; Thorp and Casper 2002) concluded that dreissenid predation may be more important than resource competition in reducing microzooplankton abundance. In these studies, small-bodied zooplankton were primarily reduced, while large-bodied zooplankton were not, even though both compete for resources with dreissenids. However, these experiments were conducted at small spatial (MacIsaac et al. 1991, 1995) or temporal (Thorp and Casper 2002) scales. In small containers, predators and prey may experience greater spatial overlap than in thermally stratified lakes, which may increase the importance of predation over resource competition, particularly for smaller microzooplankton (Sarnelle 1997). Short-term experiments may also emphasize the importance of predation over resource competition because the effects of the latter often take longer to observe than do those of predation (Sarnelle 1997).

Decreased *Daphnia* spp. biomass in dreissenid invaded lakes is most likely a result of resource competition. Dreissenids significantly reduced phytoplankton and microzooplankton biomass (Table 1; Fig. 2) and increased toxic *Microcystis* (Knoll et al. 2008a), thereby decreasing the quantity and quality of food resources for macrozooplankton. As a result of these altered food resources in invaded lakes, it seems likely that dreissenids are outcompeting macrozooplankton and negatively influencing 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 dreissenids.

*Microzooplankton and macrozooplankton community structure*—Although evidence indicates that dreissenids increase benthic invertebrate diversity (Stewart and Haynes 1994) but decrease native unionid diversity (Herbert et al. 1991), no studies have investigated possible diversity changes in pelagic organisms. Both rotifer richness and evenness were lower in invaded lakes (Fig. 2). Lower richness might be attributed to dreissenids' ability to filter large quantities of suspended particles that span a wide size range (Ten Winkel and Davids 1982), including some rotifers and rotifer food resources. Despite lower richness,

one rotifer taxa, *Polyarthra*, appeared to take advantage of invasion, comprising a larger fraction of total rotifer biomass in invaded lakes (Fig. 2). Two potential mechanisms that may account for *Polyarthra*'s success in invaded lakes relate to defense mechanisms and available food resources. Rotifer species with effective defense mechanisms (e.g., spines, large size, escape mechanisms) may be able to avoid ingestion and so be less affected by dreissenids. For example, faster-swimming species may be able to escape *D. polymorpha*-filtering currents (MacIsaac et al. 1991). Unlike most rotifers, *Polyarthra* is able to avoid predators (e.g., *Asplanchna*, *Chaoborus*, *Daphnia*) using a jump mechanism (Gilbert 1987). This mechanism may allow *Polyarthra* to escape predation by *D. polymorpha*. In contrast to our results, however, *Polyarthra* abundance was dramatically reduced by *D. polymorpha* in experiments (MacIsaac et al. 1991, 1995; Thorp and Casper 2002), in the Hudson River (Pace et al. 1998), and in Lake Erie (MacIsaac et al. 1995). In these prior studies, which were conducted in experimental containers or well-mixed systems, *Polyarthra* may have come into such close proximity with *D. polymorpha* that its jump mechanism could not facilitate escape. Since the lakes in this survey were thermally stratified and a jump mechanism may provide little advantage in this environment, it is possible that another mechanism may have contributed to *Polyarthra*'s success. *Polyarthra* is known to feed selectively on cryptophyte phytoplankton (Gilbert and Bogdan 1984). In the survey lakes, the cryptophyte *Cryptomonas* had higher biomass in invaded lakes (Knoll et al. 2008a), possibly allowing *Polyarthra* to withstand increased predation rates.

Overall, our study shows significant negative influences of the dreissenid invasion on phytoplankton, microzooplankton, and macrozooplankton in thermally stratified lakes. The influence of dreissenids on microzooplankton were somewhat smaller compared to that noted in shallow, well-mixed systems. In contrast, the influence of dreissenids on *Daphnia* spp. was much more apparent in our study compared to a before-and-after study of Oneida Lake. Ciliates and rotifers were similarly affected by dreissenids, and rotifer species richness and evenness declined. These striking changes to the lower trophic levels, resulting from dreissenid invasions of lakes, may have consequences for planktivorous and piscivorous fish (Rutherford et al. 1999).

Reduced zooplankton biomass, in particular *Daphnia* biomass, has the potential to affect higher trophic levels. Planktivorous fish, such as bluegill sunfish (*Lepomis macrochirus*), rely almost entirely on microzooplankton as larvae (Siefert 1972), whereas *Daphnia* are a major food resource for adults (Mittelbach 1981). By reducing microzooplankton and macrozooplankton biomass, dreissenids 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. Previous studies on the effects of dreissenids on fish growth and abundance show varied responses (Strayer et al. 2004). These studies were conducted in shallow, well-mixed systems (Strayer et al. 2004) or in experimental enclosures

(Thayer et al. 1997). Our study confirms that dreissenids can negatively affect the phytoplankton and edible consumer pathway in stratified lake food webs (Strayer et al. 2004) through predation and resource competition. Thus, it is conceivable that dreissenids may negatively affect fishes that rely on this pathway.

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