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Effects of the Zebra Mussel (*Dreissena polymorpha* Pallas) on Protozoa and Phytoplankton from Saginaw Bay, Lake Huron

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ABSTRACT. *Direct effects of the grazing activities of the zebra mussel,* Dreissena polymorpha, *on the natural assemblage of planktonic protozoa and algae from Saginaw Bay, Lake Huron, were studied in September and October 1994. Water and mussels collected from two eutrophic sites were incubated in an outdoor "natural light" incubator at ambient temperature for 24 hours. Experiments were conducted in 4-L bottles with screened (40 or 53-μm net) or unscreened water and with and without mussels. Despite relatively high growth rates of protozoa on both dates, mussels lowered protozoan numbers by 70–80% and reduced the species richness of the protozoan community by 30–50%. Large heterotrophic flagellates were reduced up to 100% while peritrichous ciliates attached to the colonies of blue-greens were reduced only by 50%.* Dreissena *selectively removed nanoplanktonic* Cryptomonas *and* Cyclotella, *but had no significant effect on the predominant phytoplankton species,* Microcystis. *Overall,* Dreissena *clearance rates were low in the presence of this cyanophyte species. We conclude that zebra mussels, in regions where they are abundant, can cause significant changes in composition of both the protozoan and phytoplankton communities.*

KEY WORDS: *Zebra mussels, Lake Huron, protozoa, phytoplankton populations.*

INTRODUCTION

After its introduction in the mid-1980s, the zebra mussel (*Dreissena polymorpha* Pallas) has spread throughout the Great Lakes and into other water bodies in North America. As voracious filter feeders, with a typical clearance rate of ca. 16 mL/mg ash free dry weight/h (Fanslow *et al.* 1995), and high densities, up to 350,000/ m^2 (Griffiths 1993), the mussels are profoundly altering planktonic food webs by removing large amounts of particles from the lake water. For example, in some parts of western Lake Erie where mussels are abundant, the mussels are thought to be responsible for a 90% decrease in abundances of phytoplankton (Nicholls and Hopkins 1993).

Early studies indicate that *Dreissena* ingests particles between 80 and 450 μm, including microzooplankton (Mikheev 1967). Starved individuals ingested diatoms as large as 750 μm, but when they were well-fed they preferred algal food < 50 μm. More recent studies show that *Dreissena* can filter particles from 0.7 to 450 μm, but maximum retention occurs in the size range from 5 to 35 μm (Jorgensen *et al.* 1984, Sprung and Rose 1988). Besides algae, the mussels have been shown to graze down large bacteria (Cotner *et al.* 1995), rotifers, and crustaceans, as well as their own larvae (MacIsaac *et al.* 1991, Shevtsova *et al.* 1986).

Planktonic protozoa are an inherent and important component of the Great Lakes ecosystem (Carrick and Fahnenstiel 1989,1990; Carrick *et al.* 1991,1992; Taylor 1984; Taylor and Heynen 1987). Given that the size of most protozoa lie within the preferred range of *Dreissena,* it is reasonable to as-

sume that they would also be vulnerable to mussel grazing activities. Decreases in abundances of two benthic ciliates caused by *Dreissena* grazing (Shevstova *et al.* 1986) provides evidence for the above assumption.

In this paper, we assess the effects of *Dreissena* on natural communities of planktonic protozoa and algae from Saginaw Bay, Lake Huron and examine the possible significance of these effects to the ecosystem. Specifically, we attempt to answer the following questions: (1) Are planktonic protozoa susceptible to *Dreissena* grazing? (2) Are there any size- or species-related differences in protozoan and algal vulnerability? (3) What are *Dreissena* clearance rates upon natural populations of protozoa and algae?

MATERIAL AND METHODS

Study Sites and Sampling

We examined the effects of zebra mussel filtering on protozoa and phytoplankton in a set of bottle experiments conducted on water collected from Saginaw Bay in September and October 1994. Saginaw Bay is a large (about 82 km long and 42 km wide) bay extending off the western edge of Lake Huron. The inner bay receives large inflows of enriched waters from the Saginaw River and is considered to be eutrophic (Bierman and Dolan 1981). Water and mussels were collected from two sites in the inner bay (Fig. 1). The plan was to sample at the same site (Station 5; see Nalepa *et al.* 1995) on both dates, but severe weather in September prevented sample collection at this site. Water depth was 3.5 m at both sites. Water was collected just below the surface by submerging acid-washed and distilled water-rinsed 20-L polyethylene carboys. Zebra mussels were collected with a benthic sled towed behind a small boat. Water and mussels were kept in closed coolers during transport to the shore laboratory to maintain temperatures at near-ambient conditions. Bottle experiments were initiated within 3 to 4 h after water and mussels were collected.

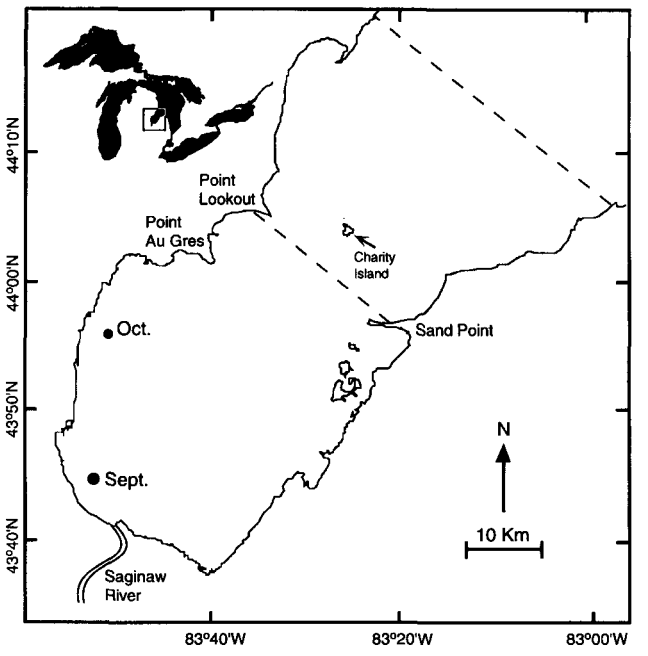

FIG. 1. Location of sampling sites in Saginaw Bay, Lake Huron.

Treatments

The experimental design consisted of four bottle treatments: unscreened water with mussels, unscreened water without mussels, screened water with mussels, and screened water without mussels. Four-liter aliquots of ambient water, that were either passed through a 40-μm nitex net (September), a 53-μm net (October), or left unscreened, were gently mixed and placed in acid-washed and distilled water-rinsed clear polycarbonate bottles. On the second date, the screening process removed zooplankton predators without significantly altering phytoplankton composition. Mussels were removed from their natural substrate by cutting the byssal threads with a razor blade and 15 individuals (based on zebra mussel abundances in this area in 1991 and 1992; Nalepa *et al.* 1995) were placed into one bottle with screened water and another bottle with unscreened water. Before they were placed in an experimental bottle, mussels were rinsed with bay water to remove periphyton, and preincubated three times (20 min per incubation) in 1-L portions of unscreened lake water from the sampling site.

Bottles were incubated at ambient temperature in outdoor incubators. On the September date, experiments were conducted in conjunction with other studies examining zebra mussel effects on nutrient cycling. Therefore, several other treatments were performed in addition to screening. Bottles were incubated either in the dark or at 75% of incident solar radiation to simulate in situ light conditions. Also, two bottles were fortified with the addition of an amino acid mixture (algal hydrolysate). Because we found no significant differences in abundances

and composition of protozoa and phytoplankton in light, dark, and amino acid treatments, we pooled the results from these treatments and only compared those treatments with screened and unscreened water, and with and without zebra mussels. In October, duplicate treatments of screened and unscreened water were incubated in the light with and without mussels.

Sample Processing

Samples were removed from the bottles initially and at 24 h for measurements of chlorophyll "a" concentrations as well as phytoplankton and protozoan abundances. To determine ciliate numbers, 100-mL aliquots were preserved with 1% (final concentration) acid Lugol's iodine and stored at 4°C. Ciliates were enumerated under a Wild inverted microscope, equipped with a phase contrast (255× magnification), after overnight settling onto coverslips in 50–mL columns. Because of the uneven settling patterns in Utermohl chambers, the entire area of a settling chamber was scanned. To determine large and colonial protozoa, 500-mL aliquots were passed through a 20-μm nitex net and the material retained was settled in 100-mL columns. Zooplankton were collected by passing a 3-L aliquot through a 53-μm net. For qualitative purposes, ciliates also were examined alive and after staining with acetic carmine, under a Wild compound microscope (125× to 600× magnification). In addition, an integrated 500 mL sample from each bottle was preserved with saturated mercury chloride solution (Pace 1982), as this technique allowed more accurate taxonomic resolution for ciliates compared to Lugol's.

Heterotrophic nanoflagellates were enumerated from slides prepared immediately after sampling and stored at –20°C. Subsamples (15 mL) of water, preserved with 1% (final concentration) glutaraldehyde buffered with 0.1 M sodium cacodylate, were filtered onto 0.8 μm prestained (Irgalan Black) Poretics filters and stained consequently with DAPI (Porter and Feig 1980) and primulin (Caron 1983). Slides were scanned under a Leitz Labour Lux microscope equipped for autofluorescence (450–490 excitation, > 515 emission) and UV light (320–380 excitation, > 420 emission).

Cell volumes of protozoa were calculated for each abundant taxon by measuring the cellular dimensions of at least 30 cells and approximating simple geometric solids. The conversion factor of 0.15 pg C μm^{-3} was used to estimate protozoan biomass (Ohman and Synder 1991, Putt and Stoecker 1989), and biomass estimates were corrected for cell shrinkage due to preservation with the factor of 1.25 (Choi and Stoecker 1989, Muller and Geller 1993). Protozoa were determined to the species level whenever possible without the use of silver staining, consulting Foissner *et al.* (1991,1992), Krainer (1995), Patterson and Larsen (1991), Skuja (1956), Small and Lynn (1985), and Starmach (1985).

Phytoplankton taxa (autotrophic eukaryotes and cyanobacteria) were quantified using the Utermohl method (Lund *et al.* 1958). Cells were settled for at least 24 h in 50-mL columns in the dark. Homogeneity in settling was checked to determine the minimum number of fields necessary to obtain consistency in enumerating abundant taxa (> 5% of the total biovolume) per unit chamber area. The abundance of common taxa were estimated by random field counts. At least 400 cells were enumerated from each sample. Rarer taxa were quantified by scanning a strip of the Utermohl chamber. Large, rare taxa were quantified by scanning one-half of the chamber at 300×. In colonies with extremely small cells (e.g., *Microcystis*), cells were enumerated from a small representative area of the colony containing at least 100 cells. Counts were performed on a Wilovert inverted microscope equipped with phase-contrast at a magnification of 600×.

Cells were measured and their biovolumes were estimated by assuming solid geometric shapes (Vollenweider 1974). For taxa with substantial size variation (such as diatoms), size classes were designated arbitrarily to determine average cell size and 25 cells were measured from each size class for each taxon. Mean biovolumes within each size class were used to calculate the total biovolume contributed by the taxon to its particular sample. Carbon was assumed to be 10% of wet weight. Major taxonomic sources included Prescott (1982), Whitford and Schumacher (1968), and Patrick and Reimer (1966, 1975).

For chlorophyll analysis, phytoplankton were collected by filtering water through Whatman GF/F filters. Chlorophyll was extracted by grinding and holding the filters in cold 90% acetone for 24 h, and measured fluorometrically (Strickland and Parsons 1972). Chlorophyll extraction and measurements were performed in triplicate. Here we present only those data on chlorophyll that were obtained from the light incubations.

Protozoan and algal specific growth rates were estimated assuming exponential growth as

$$r = \ln (Nt / No) / t$$

where:

r was the rate of population growth (d^{-1}),
No and Nt were initial and final abundances,
and t was duration of incubation.

Zebra mussel shell lengths were measured and converted to ash free dry weight (AFDW) using empirical equations obtained for mussels collected from Station 5 in September and October 1994 (T.F. Nalepa, personal communication, Great Lakes Environmental Research Laboratory).

Zebra mussels prey-based clearance rates (CR) for the most abundant protozoan and algal species, total protozoan and phytoplankton biomass, and chlorophyll were calculated for each experiment as

$$CR = [\, V \ln (C/E)] / tn$$

where :

V was the experimental volume,
E and C – the final concentrations of prey in bottles with and without mussels respectively,
t – the duration of experiment, and
n – the number of mussels.

Differences between treatments were tested with ANOVA.

RESULTS

Initial chlorophyll concentrations were 17 and 7.5 μg L^{-1} , and surface temperatures were 19°C and 13.5°C at the study sites in September and October, respectively. The zooplankton were mostly represented by *Bosmina longirostris*, *Acanthocyclops* sp., and *Polyarthra* sp. In October, their densities were 15, 4, and 40 individuals L^{-1}. A relatively diverse assemblage of planktonic ciliates and flagellates (also *Actinophys sol* belonging to Heliozoa, and *Difflugia* sp. belonging to Testacea), was present at the study sites at the time of sampling (Table 1). The main difference in composition between the two sampling dates was the presence of tintinnids, *Katablepharis ovalis*, and *Difflugia* sp., and the absence of *Histobalantium* sp., *Nassula ornata*, and *Disematostoma* sp. in October compared to September. In unscreened treatments without mussels, the number of species declined the least during the experimental period (Table 1), followed by screened treatments without mussels. In comparison, the number of species declined the most in treatments with mussels (screened or unscreened).

Although abundances of the major protozoan groups [ciliates, heterotrophic microflagellates (HMICRO) and heterotrophic nanoflagellates (HNANO)] were twice as high in September as in October (Figs. 2 and 3), significant differences ($p < 0.01$) between treatments with and without mussels were observed on both dates. These differences were greater in screened treatments, due to increases in protozoan abundance over time. Similar patterns were observed for protozoan biomass (Fig.4).

Five species were present in all treatments and accounted for ca 75% of the protozoan abundance and biomass: *Rimostrombidium* (formerly *Strobilidium*) *humile*, *Urotricha ristoi*, *Vorticella* sp., *Chromulina* sp., and *Paraphysomonas* sp. Quantitative differences observed between treatments with and without zebra mussels were primarily attributed to changes in concentrations of the above species. Specific growth rates of these five species, except for *Paraphysomonas* sp.(Table 2), were higher in September than in October, and higher in the screened than in the unscreened water. Differences between screened and unscreened treatments was especially pronounced for *Chromulina* sp. The proportion of each species removed after the 24 h period in the unscreened treatments ranged from 50.0% to 99.1% (Table 2). Despite no growth being observed for *Vorticella* sp. attached to blue-green colonies, this species had the lowest proportion of individuals removed by zebra mussels. In contrast, the heterotrophic flagellate, *Paraphysomonas* sp., had relatively high growth rates, but had the highest proportion of individuals removed. There was no apparent relationship between the cell volume of the species and the proportion removed.

On both dates, phytoplankton community at the sampling sites was dominated by cyanophytes, mostly by *Microcystis aeruginosa* (up to 40% of the total phytoplankton biomass) that formed large gelatinous colonies. Screening reduced this species by 90% and 30% on the first and the second dates, respectively. Chlorophytes were subdominant in September and diatoms were subdominant in October (Table 3). Two species, *Cryptomonas erosa* and *Cyclotella operculata*, decreased significantly ($p < 0.01$) in treatments with zebra mussels (Table 2). For phytoplankton biomass and chlorophyll (Figs. 5 and 6), significant differences ($p < 0.05$) were found only between screened treatments with and without zebra mussels in September. Clearance rates of zebra mussels (Table 4) that were based on the number of *Microcycstis* and *Paraphysomonas* represented extreme values in the range between 0 and 18.9 mL mg AFDW $^{-1}$ h^{-1} (4.09 ± 0.32; mean ± SE).

TABLE 1. Composition of protozoa at the beginning and end of the 24-h experimental period. Int = Initial; S = screened; U = unscreened; ZM = treatments with zebra mussels added. Asterisks denote species present. HMICRO = Heterotrophic microflagellates; HNANO = Heterotrophic nanoflagellates

				September					October	
Taxon	Int	S	S+ZM	U	U+ZM	Int	S	S+ZM	U	U+ZM
CILIATES										
Askenasia sp.	*					*				
Codonella cratera						*			*	
Cyclidium sp.	*	*		*						
Disematostoma sp.	*			*						
Enchelydon sp.	*									
Histobalantium sp.	*			*	*					
Litonotus sp.				*	*					
Mesodinium sp.						*				
Monodinium vorax	*									
Nassula ornata	*			*	*					
Pelagohalteria viride	*									
Pelagostrombidium sp.						*	*			
Pseudobalanion planktonicum						*	*		*	
Rimostrombidium humile	*	*		*	*	*	*	*	*	*
R. lacustris						*				
Strombidium viride	*	*		*		*	*		*	*
Tintinnidium sp.						*				
Urotricha furcata	*	*		*		*	*			
U. pelagica	*	*	*	*		*	*		*	
U. ristoi	*	*	*	*	*	*	*	*	*	*
Vaginicola sp.	*	*	*	*	*	*	*		*	
Vorticella sp.	*			*	*	*			*	*
HMICRO										
Katablepharis ovalis						*			*	
Paraphysomonas sp.	*	*	*	*	*	*	*	*	*	*
Spumella sp.	*	*							*	
HNANO										
Bodo sp.	*	*		*						
Chromulina sp.	*	*	*	*	*	*	*	*	*	*
Ochromononas sp.	*			*						
OTHER										
Actinophrys sol (Heliozoa)	*			*						
Difflugia sp. (Testacea)						*			*	*
TOTAL TAXON:	21	11	5	17	9	18	10	4	13	7
Proportional reduction (%)		45	75	20	55		45	78	28	61

DISCUSSION

Our findings are consistent with the data published on other Great Lakes plankton (Cotner *et al.* 1995, Holland 1993, MacIsaac *et al.* 1991) in that they indicate dramatic effects of *Dreissena* on the qualitative and quantitative characteristics of communities in regions of the Great Lakes with large populations of mussels. Zebra mussel clearance rates based on changes in protozoan biomass in unscreened water in September and abundances of the mussels leads to a conclusion that they should clear the entire water column of protozoa within less than one day under idealized mixing conditions. Despite the fact that planktonic communities in Saginaw Bay have been exposed to *Dreissena* impacts since fall 1991 (Nalepa *et al.* 1995), we observed relatively dense populations of planktonic protozoa at these sites, even though their concentrations were

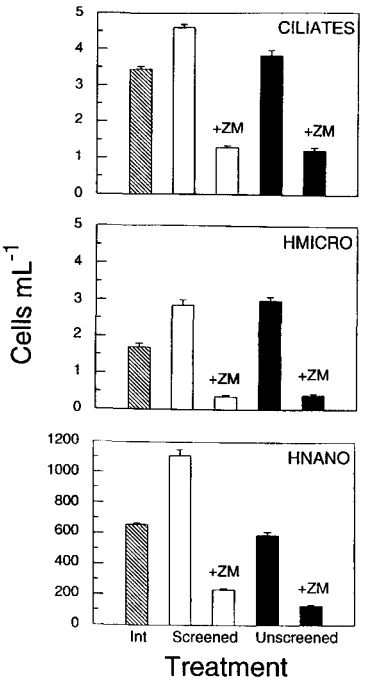

FIG. 2. Mean (± SE) abundance of ciliates, heterotrophic microflagellates (HMICRO), and nanoflagellates (HNANO) in treatments with and without zebra mussels and in screened (40 μm) and unscreened water in the September experiment. Int = Initial sample.

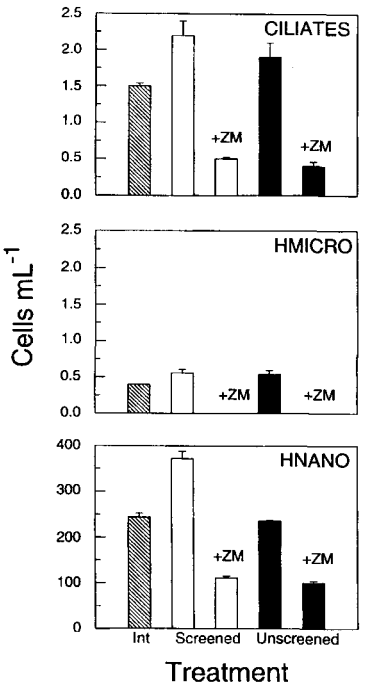

FIG. 3. Mean (± SE) abundance of ciliates, heterotrophic microflagellates (HMICRO), and nanoflagellates (HNANO) in treatments with and without zebra mussels and in screened (53 μm) and unscreened water in the October experiment. Int = Initial sample.

lower than might be expected from chlorophyll concentrations in the absence of zebra mussels (Pace 1986). Vertical separation in the water column may only partially explain this observation, because the water should often be quite well-mixed at these shallow sites.

The specific growth rates of predominant ciliates and flagellates in screened water were similar to those observed in the same or relative species in offshore regions of the Great Lakes (Carrick *et al.* 1992), but were a little lower than those obtained in laboratory cultures (Muller and Geller 1993). Although trophic interactions within the protozoan community might result in a certain underestimation of real growth rates (Taylor and Johannsson 1991), the observed rates appeared to be sufficient to sustain population densities above a threshold level. In contrast, *Cryptomonas* was nearly eliminated by mussels in screened treatments in September despite its high growth rates. Among protozoa, higher growth rates in September than in October can be explained by both higher temperature and a higher chlorophyll

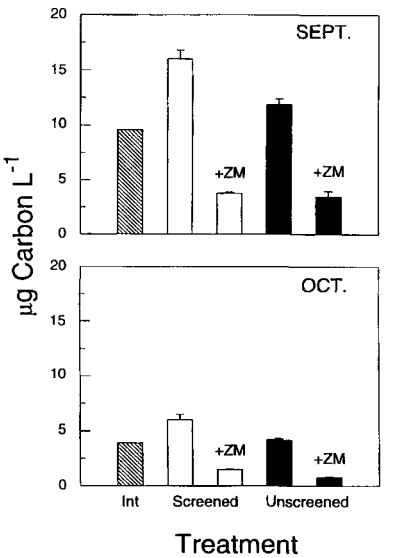

FIG. 4. Mean (± SE) biomass of planktonic protozoa in treatments with and without zebra mussels and in screened and unscreened water. Int = Initial sample.

TABLE 2. Cell volumes (V, μm³) and specific growth rates (r, day⁻¹) of abundant protozoan and nanophytoplankton species in treatments without zebra mussels, and their proportional grazing losses (GL, %) in treatments with zebra mussels added. S = screened; U = unscreened.

		September				October			
		S		U		S		U	
Taxon	V	r	GL	r	GL	r	GL	r	GL
PROTOZOAN									
Chromulina sp.	10	0.71	80	0.05	76	0.61	82	0.13	77
Paraphysomonas sp.	750	0.48	87	0.53	86	0.35	99	0.3	98
Rimostrombidium humile	10,000	0.68	69	0.59	69	0.59	69	0.38	71
Urotricha ristoi	2,250	0.72	88	0.36	85	0.53	86	0.39	84
Vorticella sp.	18,000	na	na	0.03	50	na	na	0	54
PHYTOPLANKTON									
Cryptomonas erosa	12	2.03	80	1.12	67	0.05	63	0.0	15
Cyclotella operculata	143	0.2	52	0.15	34	0	16	0	12

TABLE 3. Composition of phytoplankton at the beginning and end of the 24-h experimental period. Int = Initial; S = screened; U = unscreened; ZM = treatments with zebra mussels added. Asterisks denote species present.

		September						October			
Taxon	Int	S	S+ZM	U	U+ZM	Int	Int S	S	S+ZM	U	U+ZM
BACILLARIOPHYTA											
Achnanthes spp.	*	*	*	*		*	*				*
Amphora ovalis	*				*		*		*		
Aulacoseira distans		*		*	*	*				*	
Aulacoseira italica										*	
Cocconeis placentula	*	*	*	*	*	*	*	*	*	*	*
Cyclotella glomerata	*	*	*	*	*	*	*	*		*	*
Cyclotella kuetzingiana	*	*	*	*	*	*	*	*	*	*	*
Cyclotella operculata	*	*	*	*	*	*	*	*	*	*	*
Cyclotella stelligera		*	*	*	*				*		
Cymatopleura elliptica	*	*	*	*	*						
Cymbella spp.	*	*			*			*	*		*
Flagilaria construens	*		*	*	*	*	*				*
Gomphonema constrictum						*			*	*	*
Gomphonema olivaceum		*				*					*
Melosira binderana											*
Melosira varians	*										
Meridion circulare	*			*			*				
Navicula cryptocephala	*	*	*	*	*	*	*	*	*	*	*
Navicula radiosa					*		*				
Navicula spp.	*	*	*			*			*	*	*
Nitzschia linearis	*		*	*	*	*	*	*	*	*	
Nitzschia spp.	*	*		*				*	*		*
Rhoicosphenia spp.			*		*						
Stephanodiscus hantzschii	*				*	*	*	*	*	*	
Synedra ulna		*							*		
Tabellaria fenestra	*	*		*	*			*		*	

Continued

TABLE 3. Continued.

Taxon	September					October					
	Int	S	S+ZM	U	U+ZM	Int	Int S	S	S+ZM	U	U+ZM
CHLOROPHYTA											
Coelastrum spp.		*									*
Gloecystis gigas						*					
Kirchneriella lunaris	*										
Mougeotia spp.				*							
Pediastrum duplex	*	*	*	*	*	*	*	*	*	*	*
Pediastrum simplex	*		*		*					*	
Quadrigula lacustris		*	*		*	*		*	*		
Scenedesmus bijuga	*	*	*	*	*	*	*	*	*	*	*
Scenedesmus quadricauda	*	*	*	*	*	*	*	*	*		*
Scenedesmus spp.										*	
Sphaerocystis schroeteri	*	*	*	*		*	*	*	*	*	*
Staurastum spp.							*				
Tetrastrum heterocanthum		*					*				
CHRYSOPHYTA											
Dinobryon sertularia								*			
Mallomonas spp.					*						*
CRYPTOPHYTA											
Cryptomonas erosa	*	*	*	*	*	*	*	*	*	*	*
Rhodomonas spp.		*	*								
CYANOPHYTA											
Anabaena spp.	*										
Aphanocapsa spp.					*						
Chroococcus limneticus	*	*	*	*	*	*	*	*	*	*	
Chroococcus turgidus	*										
Merismopedia elegans	*		*	*	*	*	*	*			*
Microcystis aeruginosa	*	*	*	*	*	*	*	*	*	*	*
Oscillatoria spp.	*	*	*	*	*	*			*	*	*
DINOPHYTA											
Glenodinium spp.		*									
TOTAL TAXON:	30	28	24	24	28	24	22	20	22	21	23
Proportional reduction (%)		7	20	20	7		8	17	8	13	4

concentration. Also, a finer net was used to screen the water in September than in October.

Significant differences ($p < 0.001$) in HNANO growth rates between screened and unscreened treatments without mussels indicate that zooplankton also exerted grazing pressure on protozoa. Large, potentially carnivorous ciliates, that also might be responsible for the observed difference, were rare even in unscreened treatments (< 30 cells L^{-1}). The ability of copepods (Burns and Gilbert 1993, Hartmann *et al.* 1993) and cladocerans (Jack and Gilbert 1994, DeBiase *et al.* 1990) to prey on protozoa is well documented. The importance of flagellate-crustacean trophic link in the Great Lakes has been stressed (Carrick *et al.* 1991). However, in our experiments, grazing by the zooplankton neither suppressed the protozoan populations nor changed the protozoan community composition to the same extent as was observed for zebra mussel treatments. We did not attempt to separate grazing losses due to zooplankton from those due to mussels because trophic conditions for *Dreissena* were significantly altered by screening.

Changes observed in the protozoan community structure in our experiments likely reflected the simultaneous effects and interactions of multiple fac-

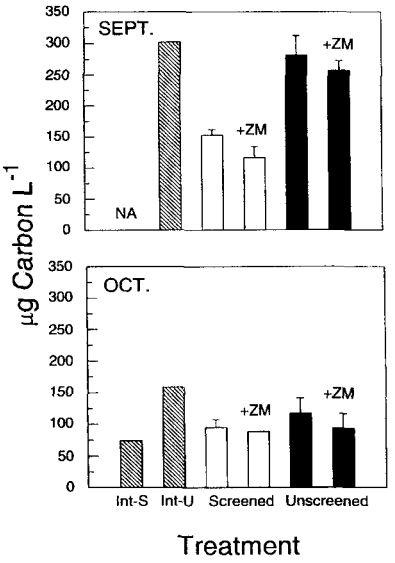

FIG. 5. Mean (± SE) biomass of phytoplankton in treatments with and without zebra mussels and in screened and unscreened water. INT-S = Initial screened sample. INT-U = Initial unscreened sample.

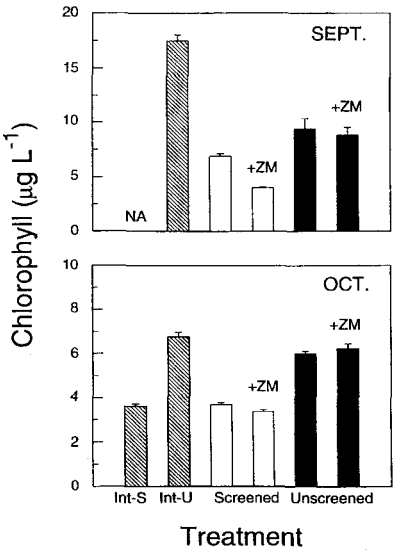

FIG. 6. Mean (± SE) concentrations of chlorophyll in treatments with and without zebra mussels and in screened and unscreened water. INT-S = Initial screened sample. INT-U = Initial unscreened sample.

tors in addition to the obvious effects of zebra mussels. Taxonomic differences in the initial bay water may be attributed to seasonal changes in phytoplankton, i.e., a shift from a complex associated with *Anabaena* (*Nassula, Histobalantium, Disematostoma*) in September to diatom-oriented oligotrichs, tintinnids, and *Katablepharis* in October. The absence of large-bodied species (e.g., *Litonotus, Difflugia, Codonella*) in the bottles with screened water may be explained by the screening effect. Furthermore, a decrease in protozoan diversity in treatments without mussels indicates that experimental manipulations involving containment and screening were an excluding factor for some fragile species such as *Mesodinium* sp. However, disappearance of small ciliates *Cyclidium*, *Pseudobalanion*, *Urotricha furcata*, and nanoflagellates *Bodo* and *Spumella* in treatments with zebra mussels, without corresponding decreases in bacterial densities (James B. Cotner, personal communication, Texas A & M University), suggests that mussel grazing directly eliminated these populations.

Previous work has indicated that small ciliates (< 30 µm) were suppressed by *Daphnia pulex* while larger ones (> 81 µm) were unaffected, but ciliates were not consistently more vulnerable to cladoceran suppression than similarly sized rotifers (Jack and Gilbert 1994). The suggestion that prey swimming abilities may influence predation efficiency of *Dreissena* (MacIsaak *et al.* 1991) is also consistent

TABLE 4. Zebra mussel clearance rates (mL mg AFDW^{-1}h^{-1}) S = screened water; U = unscreened water.

	September		October	
Taxa	S	U	S	U
Chromulina sp.	4.1	3.6	4.3	5.1
Paraphysomonas sp.	5.1	5.0	13.6	18.9
Rimostrombidium humile	3.0	3.0	3.6	3.5
Urotricha ristoi	5.4	4.8	5.4	5.9
Vorticella sp.	na	1.7	na	2.2
Total Protozoa	3.8	3.4	3.6	4.7
Cryptomonas erosa	5.8	2.8	2.9	0.5
Cyclotella operculata	1.8	1.1	0.5	0.4
Microcystis aeruginosa	0	0	0	0
Total phytoplankton	0.7	0.3	0.3	0.5
Chlorophyll *a*	1.1	0.2	0.3	0

with our findings. Behavioral differences among ciliates may be as important as their size in their susceptibility to predation (Burns and Gilbert 1993). In our study, the protozoan species strongly suppressed by zebra mussel predation did not possess strong swimming abilities and, therefore were unable to escape from the inhalant current of *Dreissena*. In contrast, resistant species were either strong swimmers (*Rimostrombidium*) or attached to larger particles (*Vorticella*).

Although nanoplanktonic *Chromulina* is not a "strong swimmer" and was strongly reduced by zooplankton in our treatments, its high growth rate allowed this genus to survive grazing pressure by mussels. Zebra mussels, like other bivalves whose gills have latero-frontal cirri, should retain particles of at least 1 μm or even less (Mohlenberg and Riisgard 1978). They were, in fact, able to remove large bacterial cells from the water column in Saginaw Bay (Cotner *et al.* 1995). However, the preferred prey size range for zebra mussels lies between 5 and 35 μm (Sprung and Rose 1988). *Chromulina* cells were typically < 3 μm in diameter, a factor that may contribute to their relatively high survival in zebra mussel treatments. Thus, our findings indicate that zebra-mussel grazing primarily eliminated weak-swimming and slow-growing protozoan species falling within the preferred prey-size range.

The observed zebra mussel effects on nanoplanktonic algae are in agreement with the results of earlier experiments in Saginaw Bay (Gardner *et al.* 1995) where mussels significantly reduced chlorophyll concentrations in the water taken from an outer bay site that was dominated by diatoms, but had little effect on chlorophyll concentrations in the water from the inner bay that was dominated by blue-green algae. It seems to contradict Nicholls and Hopkins (1993) work showing a proportional effect on all groups of the phytoplankton in Lake Erie where blue-green algae were found at very low concentrations.

Estimates of *Dreissena* clearance rates based on density changes of protozoa (excluding those based on *Vorticella*) and *Cryptomonas* are within the range reported for *Dreissena* feeding on natural seston (Kondratyev 1963, Reeders and bij de Vaate 1990, Fanslow *et al.* 1995), *Chlorella* (Kryger and Riisgard 1988), and clay particles (Alimov 1969). However, clearance rates based on density changes in other phytoplankton in our study are lower than the lowest rates reported for natural seston.

Dissolved compounds released by *Microcystis* can have inhibitory effects on zooplankton (Haney *et al.* 1994). Similarly, a mass development of this alga in Saginaw Bay, Lake Huron, reportedly coincided with lower filtration rates of mussels (Fanslow *et al.* 1995). These results provide insights about why zebra mussel clearance rates upon nanophytoplankton were low in unscreened water and also why the September and October results were different. Moreover, recent video-microscopic observations (Vanderploeg *et al.* 1995) have revealed that zebra mussels do not stop pumping in the presence of *Microcycstis* but expel filtered algae as loosely consolidated pseudofeces. Algae possessing strong cellulose walls may withstand this pressure but fragile protozoan cells may be destroyed.

The ecological effects of zebra mussel protozoan grazing are complex and have several major implications. By removing small heterotrophic organisms that would normally channel bacterial production to the higher trophic levels, mussels can change planktonic food web structure and affect mineralization rates in the water column (Gardner *et al.* 1995). The most suppressed protozoan species in this study graze on bacteria and small algae (e.g., Fenchel 1987, Finlay *et al.* 1988). Increases in bacterial abundance and productivity in mesocosm experiments (Cotner at al. 1995), suggest that mussels may stimulate bacterioplankton abundances by removing micrograzers and thereby compensate in part for their direct grazing effect on large bacteria.

At the same time, mussels can potentially create favorable conditions for mass development of cyanophytes , that are an undesirable food source, by selectively removing nanoplanktonic algae and excreting large amounts of nutrients. Enhanced importance of planktonic ciliates as trophic intermediaries following blooms of cyanophytes has been reported for temperate (Christoffersen *et al.* 1990), African (Finaly *et al.* 1987), and arctic lakes (Lavrentyev 1994). Species of protozoa that would likely proliferate in the presence of zebra mussel would be expected to have high growth rates and/or to possess other features (e.g., association with algal colonies) that allow them to survive pressure from mussels.

Another impact of zebra mussels on the Great Lakes ecosystem is that they have caused a shift in production from the plankton to the benthos in regions where they are abundant (Griffiths 1993, Stewart and Haynes 1994). Agglutinates and metabolites of *Dreissena* can be a food source for benthic ciliates, in particular *Paramecium* sp. (Shevtsova *et al.* 1986), and may indirectly affect the microbial food web by providing an organic carbon substrate for bacteria (Wayne S. Gardner,

unpublished data). However, it is not yet clear how zebra mussel activities are affecting benthic microbial food webs in the Great Lakes.

In conclusion, our results suggest: (1) where they are abundant, *Dreissena* can drastically reduce abundances of planktonic protozoa, (2) weak-swimming and slow-growing protozoa are the most susceptible to grazing by mussels, (3) *Dreissena* can selectively remove some types of nanophytoplankton, and (4) mass development of *Microcystis* results in lower *Dreissena* clearance rates. Thus, the zebra mussel can potentially cause major changes in the protozoan and phytoplankton communities in the Great Lakes. More studies are needed to determine the extent that these changes will affect overall foodweb dynamics in Saginaw Bay and other Great Lakes ecosystems.

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