

## Ecosystem-Level Effects of Zebra Mussels (*Dreissena polymorpha*): An Enclosure Experiment in Saginaw Bay, Lake Huron

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**ABSTRACT.** We examined the short-term effects of zebra mussels (*Dreissena polymorpha*) on ecosystem processes in late August 1991 in Saginaw Bay, Lake Huron. Four 1,600-L enclosures, made of Fabreen with a diameter of 1 m, a depth of 2 m, and closed at the bottom, were used to enclose natural plankton communities. These communities were dominated by diatoms with some chlorophytes, chrysophytes, and cyanophytes. Phytoplankton growth was limited by P-availability. Two enclosures were held as controls, and zebra mussels encrusting unionid shells were suspended in two of the enclosures: one enclosure (HZ) contained approximately four-fold greater numbers of mussels than the other (LZ). The concentration of suspended particles, chlorophyll, and algal biomass in HZ and LZ declined over a 6-day interval. Diatom numbers declined more than other taxa. Phytoplankton growth rates in HZ and LZ increased to near  $\mu_{max}$ ; there was no apparent change in photosynthetic parameters  $\alpha$  or  $P_{max}$  scaled for chlorophyll. Soluble reactive P (SRP) increased significantly ( $p < 0.05$ ) in HZ but not LZ. Dissolved organic P (DOP) and ammonium ion were elevated; dissolved organic carbon (DOC) was unchanged in HZ and LZ. The rate of phosphate uptake by bacteria and algae declined to less than 2% of controls; this rate decrease could not be explained simply by grazing losses or isotope dilution. The rate of ammonium regeneration by the plankton and the potential rate of ammonium uptake by the plankton did not differ significantly in HZ or LZ from the control enclosures. Our findings indicate that the zebra mussel can have significant short-term effects on phytoplankton abundance, water transparency, water chemistry and phosphorus dynamics. We propose a model of zebra mussel effects that suggests high densities of zebra mussels may indirectly alter and control those processes that are rate-limited or concentration-limited by nutrient availability.

**INDEX WORDS:** Zebra mussels, enclosures, nutrients, nitrogen, phosphorus, phytoplankton, bacteria, Lake Huron.

### INTRODUCTION

The influence of zebra mussels (*Dreissena polymorpha*) on Great Lakes ecosystem functions is incompletely known. Life history of the zebra mussel suggests that the plankton community may be heavily grazed and mussel fecal and pseudofecal material may stimulate benthic community activity (Leech 1993, Griffiths 1993). Such activities conceivably could alter both the patterns of energy

flow and nutrient dynamics in Great Lakes communities. Understanding these effects is confounded by their complexity and by the fact that other factors may coincidentally impact ecosystem function. Recent studies indicate that declines in phosphorus inputs and introduction of zebra mussels may have a cumulative impact on these ecosystems (Nichols and Hopkins 1993).

Understanding the influence of this non-indigenous mollusc on Great Lakes ecosystem-level

processes requires direct comparison of communities affected and unaffected by zebra mussels. Comparative studies in open landscape-scale ecosystems having the complexity of the Great Lakes presents the evident problem that differences observed may result from factors other than the one of interest. At the other extreme, conducting controlled experiments in a laboratory environment may not always provide conditions sufficiently complex and similar to those in the field to provide reliable estimates of the effects that zebra mussels may have on natural communities. In this study we examined the effects of two densities of *D. polymorpha* on natural plankton communities enclosed in 1,600-L enclosures in Saginaw Bay during late August 1991. Over a 6-day interval we examined the influence of zebra mussels on photosynthetic rates, and on phosphorus and nitrogen dynamics as well as observed alterations in phytoplankton community composition and in water chemistry.

## MATERIALS AND METHODS

### Site Description

This experiment was conducted from 28 August 1991 until 3 September 1991. Enclosures were anchored about 20 m from the U.S. Coast Guard dock in East Tawas on the northwestern shore of Saginaw Bay (44°15.8' N; 83°26.7' W). This site was near Station 21 as given in Fahnenstiel *et al.* (1995). Water depth was 2.5 to 3 m; ambient temperature was 24°C.

### Experimental Design

Four 1,600-L enclosures were constructed from Fabreen material, similar to those of McCauley and Kalff (1987). They were 1 m in diameter, 2 m deep, and closed at the bottom with high density polyethylene, without sediment contact. Enclosures were filled with a column of water containing natural communities by raising them from the bottom and tying them to floatation collars. Two enclosures were kept as controls and compared with the surrounding bay water to provide an estimate of "enclosure effects." An alewife (*Alosa pseudoharengus*) about 10 cm long was introduced into one of the control enclosures (C-2) either at the beginning of the experiment or during a storm on Day 3.

Unionid shells encrusted with zebra mussels were collected from Lake St. Clair and immediately transported to the site in insulated containers. Holes were drilled in the unionid shells, and they were hung on nylon ropes in the center of the remaining

two enclosures. Unionid shells encrusted with a low zebra mussel density (892 individuals, 4.2 g AFDW, mean = 4.71 mg indiv.<sup>-1</sup>), or with a high zebra mussel density (2,928 individuals, 16.1 g AFDW, mean = 5.50 mg indiv.<sup>-1</sup>), were suspended in two of the enclosures, termed LZ and HZ, respectively; the other two enclosures were used as controls. Our experiments began shortly after zebra mussels invaded Saginaw Bay and populations in the bay were not yet large enough for these experiments (Nalepa *et al.* 1995). After completion of the experiment, zebra mussels were removed from their substrate, counted and sized using a computer graphics pad. Length measurements were converted to biomass using an empirically determined regression equation:  $\ln(\text{AFDW}) = -5.6733 + 2.7688 (\ln L)$ , where the ash-free dry weight (AFDW) is in milligrams and the shell length (L) is in millimeters (Thomas Nalepa, personal communication, Great Lakes Environmental Research Laboratory)

The enclosures were filled with water and the zebra mussels were suspended in them at 1600 on 28 August (Day 0). Limnological variables were measured and the enclosures were sampled with a 7-L Niskin bottle each morning between 0700 and 0800. The "Day 1" sample was taken 16 hours after the beginning of the experiment, the last sample ("Day 6") was taken at 0800 on 3 September.

### Limnological Variables

Percent light transmittance, chlorophyll fluorescence, and temperature were measured using a SeaBird CTD with fluorometer and transmissometer. Chlorophyll and transparency measurements were taken *in situ* from each enclosure immediately after being filled with water and daily between 0700 and 0800.

### Water Chemistry

Chlorophyll concentrations corrected for phaeophytin were determined fluorometrically on extracts in 90% acetone (Strickland and Parsons 1972). Triplicate 100-mL samples were filtered through 47-mm Whatman GF/F glass fiber filters and frozen until extraction.

Soluble reactive phosphorus (SRP), total soluble phosphorus (TSP), and total phosphorus (TP) were determined on samples collected each morning from the enclosures and the surrounding water. Samples were filtered through Whatman GF/F glass fiber filters under a vacuum not greater than 5 p.s.i., portions were frozen for later analysis with a Tech-

nicon AutoAnalyzer II using the standard molybdenum blue procedure (Murphy and Riley 1962). TP and TSP were determined after digestion with potassium persulfate in an autoclave for 30 min. at 120°C, 15 psi. Ammonium was determined on site using high-performance cation-exchange chromatography (HPLC) (Gardner and St. John 1991).

### Community Composition

Samples for phytoplankton community composition were collected daily from each enclosure and Saginaw Bay and fixed in 1% Lugol's fixative (AWWA 1991). Aliquots of 20 or 25 mL were filtered onto 0.45- $\mu\text{m}$  Millipore cellulose ester filters and made permanent using the procedure of Crumpton (1987). Algae were identified and enumerated at 400 $\times$  using differential interference contrast optics (Zeiss Axioskop). At least 300 cells were counted per slide and the cell density was determined from the relative proportion of the area counted. We measured lengths and widths of at least 10 individuals of each species, and biovolume was estimated from the average dimensions and the approximate geometric shape (Wetzel and Likens 1991).

### Photosynthesis

We estimated algal growth rates from the rate of incorporation of  $^{14}\text{C}$ - $\text{HCO}_3$  into chlorophyll *a*, subsequently isolated by HPLC, collected and counted by liquid scintillation. The determined specific activity of Chl *a* was used to estimate the growth rates and the phytoplankton carbon content of the water (Redalje 1993, Goericke and Welschmeyer 1993). Photosynthesis-irradiance (P-I) experiments were conducted to determine the photosynthetic efficiency at low light intensities ( $\alpha$ ,  $\text{mg C} [\text{mg Chl } a]^{-1} \text{Einst}^{-1} \cdot \text{m}^2$ ) and photosynthetic capacity,  $P_{\text{max}}$ , the specific production rate at optimal light intensity ( $\text{mg C} [\text{mg Chl } a]^{-1} \text{h}^{-1}$ ). For P-I experiments, 3-mL samples inoculated with  $^{14}\text{C}$ -bicarbonate were incubated for 40 minutes at ambient temperature in a "photosyntheson," a temperature-controlled apparatus that provided 18 light intensities ranging from 0 to approximately  $1,200 \mu\text{E m}^{-2} \text{sec}^{-1}$  (Lewis and Smith 1983). After incubation, samples were acidified and bubbled with air for 15 minutes. Time zero blanks were taken and subtracted from all light values. Total available  $\text{CO}_2$  was determined from alkalinity and pH measurements (AWWA 1991). Photosynthetic rates, normalized to chlorophyll,

were used to construct a single P-I curve (Fahnenstiel *et al.* 1989).

### Phosphate Uptake

Samples were taken from each enclosure and the surrounding water on Days 1, 2, 4, 5, and 6. Each treatment was examined in duplicate, plus a control fixed with a tenth-volume of formalin (4% formaldehyde, final concentration). Carrier-free  $^{32}\text{P}$ -orthophosphate (17 kBq, i.e., 0.45  $\mu\text{Ci}$ , DuPont NEN) was added to each 10-mL aliquot, and the solution was incubated at ambient temperature. At 1-minute intervals, 1-mL portions were filtered through 0.2- $\mu\text{m}$  or 1.0- $\mu\text{m}$  filters. Filters were dried and counted by liquid scintillation spectrometry. Phosphate uptake rate constants were determined according to Heath (1986). Total particulate uptake rate constant was determined from cpm on 0.2- $\mu\text{m}$  filters above a formalin fixed control; "algal" uptake was determined from cpm above a formalin-fixed control on 1.0- $\mu\text{m}$  filters; "bacterial" uptake rate constant was determined as the difference between "total particulate" and "algal" rate constants; units of all rate constants were  $\text{min}^{-1}$ . Velocity of phosphate uptake was determined by multiplying the rate constant by SRP and reported as  $\text{nmol L}^{-1} \text{min}^{-1}$  (Heath 1986).

### Nitrogen Dynamics

Samples (500 mL) were collected in duplicate from enclosures on Days 1, 2, 4, and 5 and placed into clean polycarbonate bottles and fortified with  $^{15}\text{N}$ -ammonium chloride; 4  $\mu\text{M}$ , final concentration. Aliquots were removed after 0, 8, and 24 hours of incubation in nylon mesh bags hung in near-surface lakewater near the enclosures. Bottles were mixed and an 11-mL aliquot was filtered through a 0.2- $\mu\text{m}$  nylon filter (Rainin); the first 3 mL were used to wash the filter, a portion of the remaining 8 mL was used for ammonium determination on site, and the remaining portion was frozen and returned to the lab for isotope dilution determination later. Isotope ratios,  $[\text{NH}_4^+ \text{ } ^{15}\text{N}]:[\text{total NH}_4^+]$ , were determined directly on thawed filtrates by HPLC (Gardner *et al.* 1991, 1993). Potential ammonium uptake and ammonium regeneration rates were calculated from changes in ammonium concentration and isotope ratios over the first incubation interval using the model of Blackburn (1979).

### Dissolved and Particulate Carbon

Particulate organic carbon (POC) and dissolved organic carbon (DOC) were determined from the

same aliquot of water from the enclosure. Triplicate 50-mL samples were filtered through 2.5-cm Whatman GF/F glass fiber filters, pre-combusted at 500°C for 4 hours. Filters were frozen until analysis, and the filtrate was collected in pre-combusted ampoules and sealed. Immediately before analysis the filtrate was acidified to pH 2 and sparged for 6 minutes. Samples were analyzed with a Shimadzu TOC 5000, using the high-temperature catalytic oxidation technique (Sugimura and Suzuki 1988). POC was determined from the material collected on filters, thawed, acidified and dried immediately before analysis with a Perkin-Elmer 2400 CHN elemental analyzer.

### Statistical Analysis

We examined whether the replicate control enclosures significantly varied from the surrounding waters by a comparison of the means using Student's

t-test (Mendenhall 1971). Except where noted,  $p < 0.05$  was the confidence interval that we considered as "significant." To compare the means of the unreplicated zebra mussel amendments, we assumed that the variance of each treatment was the same as that for the controls and compared the mean of each treatment with the mean of the controls and the surrounding water ( $n = 3$ ,  $v = 2$ ) for each variable of interest, using Student's t-test, as above. Standard errors in tables provide information on the precision of the measurement procedure used.

### RESULTS

Immediately after the enclosures were filled with water, transparency in the enclosures and the surrounding water had a mean of 67 percent light transmittance ( $\pm 2$ , S.E.) at 1 m, and a mean chlorophyll concentration of 1.54 ( $\pm 0.11$ , S.E.)  $\mu\text{g L}^{-1}$  (Table 1, Day 0). The similarity of observations

**TABLE 1.** *Phytoplankton characteristics in enclosures and the water immediately surrounding the enclosures (Saginaw Bay), all readings taken from the 1-m depth, %T, percent transmittance of incident light; Chl a, chlorophyll a ( $\mu\text{g L}^{-1}$ ) as determined by extraction from filtered samples or from fluorescence detected by the CTD fluorometer. Photosynthetic parameters reported as mean  $\pm$  standard error,  $\alpha$ , ( $\mu\text{g C} \cdot \mu\text{g Chl}^{-1} \cdot \text{Einst}^{-1} \cdot \text{m}^2$ ),  $P_{\text{max}}$  ( $\mu\text{g C} \cdot \mu\text{g Chl}^{-1} \cdot \text{h}^{-1}$ ). Algal growth rate ( $\mu \text{d}^{-1}$ ); algal biomass ( $\mu\text{g C L}^{-1}$ ); algal biovolume ( $\mu\text{L L}^{-1}$ ).*

	% T	Extracted Chl a ( $\mu\text{g L}^{-1}$ )	CTD Chl a ( $\mu\text{g L}^{-1}$ )	Photosynthetic Parameters		Algal $\mu$ ( $\text{day}^{-1}$ )	Algal Biomass ( $\mu\text{g C L}^{-1}$ )	Algal Biovolume ( $\mu\text{L L}^{-1}$ )
				$\alpha$	$P_{\text{max}}$			
<b>Day 0</b>								
High ZM	64.4	—	1.69	—	—	—	—	—
Low ZM	66.1	—	1.61	—	—	—	—	—
Control 1	69.1	—	1.44	—	—	—	—	—
Control 2	69.1	—	1.51	—	—	—	—	—
Saginaw Bay	66.9	—	1.44	—	—	—	—	—
<b>Day 1</b>								
High ZM	87.8	0.46	0.40	15.30 $\pm$ 2.36	5.78 $\pm$ 0.44	0.89	34	0.37
Low ZM	82.3	0.71	0.49	17.40 $\pm$ 2.53	5.73 $\pm$ 0.25	0.81	45	0.56
Control 1	76.0	1.00	0.82	15.30 $\pm$ 2.70	6.84 $\pm$ 0.45	0.44	83	0.66
Control 2	75.8	1.37	0.96	11.82 $\pm$ 2.70	5.32 $\pm$ 0.23	0.55	86	0.73
Saginaw Bay	69.5	2.02	1.24	19.09 $\pm$ 3.04	5.11 $\pm$ 0.25	0.71	124	0.69
<b>Day 6</b>								
High ZM	84.2	0.36	0.53	11.82 $\pm$ 2.03	6.12 $\pm$ 0.45	1.05	17	0.38
Low ZM	88.4	0.39	0.57	21.11 $\pm$ 5.40	7.10 $\pm$ 0.54	1.36	19	0.35
Control 1	69.5	1.65	1.69	21.45 $\pm$ 5.24	5.52 $\pm$ 0.37	—	—	0.96
Control 2	65.3	2.00	2.07	12.33 $\pm$ 2.03	6.41 $\pm$ 0.49	0.39	96	—
Saginaw Bay	69.5	1.24	1.03	11.49 $\pm$ 1.69	5.92 $\pm$ 0.38	0.56	76	0.81

taken in each enclosure with those taken in the surrounding water indicated that the bags enclosed similar samples of Saginaw Bay water and that the enclosures were similar at the start of the experiment.

### Phytoplankton and Bacterioplankton Community Composition

The phytoplankton community of Saginaw Bay at the time of this experiment was dominated by diatoms with lower densities of green algae, chrysophytes, cyanophytes and dinoflagellates (Fig. 1). Taxa accounting for the majority of the biovolume in each class were diatoms *Cyclotella* spp. and *Fragilaria crotonensis*, chlorophytes *Selanastrum* sp., cryptophytes *Cryptomonas erosa*, chrysophytes *Dinobryon* sp. and *Synura* sp., cyanophytes *Aphanocapsa* sp., and dinoflagellates *Ceratium hirundinella* and *Glenodinium*. By the end of the first day algal biovolume declined in both enclosures containing zebra mussels (Fig. 1). Algal biovolume in HZ was 50% that of the mean of the control enclosures, and the biovolume in LZ was 80% that of the controls (Table 1). Mean of the biovolume in the control enclosures did not differ significantly from the mean of the surrounding water column.

By the end of Day 5, algal biovolume in both LZ and HZ differed significantly from that of the mean of the control enclosures but not from each other (Fig. 1); the biovolume in each was 50% that of the control enclosures. Biovolume in the control enclou-

tures did not differ from the biovolume in the ambient waters of Saginaw Bay surrounding the enclosures. The major difference between control enclosures and enclosures with zebra mussels was a 60% decrease in diatom biovolume and a 40% decrease of green algal biovolume in the enclosures with zebra mussels. Within classes, some taxa were more affected than others: the greatest declines in diatoms in both HZ and LZ were in *Fragilaria* and *Tabellaria* sp., in HZ *Dinobryon* sp. was nearly absent, but *Synura* increased in biovolume. Losses of *Cryptomonas erosa* in LZ were compensated by a great increase in *Rhodomonas* sp. Biovolume of cyanophytes was essentially unchanged in the enclosures containing zebra mussels over the duration of this experiment.

On Day 1 bacterial numbers were lower in HZ than in LZ and control enclosures, but the difference of the means was not significantly different from the mean of the control enclosures. Means and standard errors we observed were HZ,  $1.98 \pm 0.71 \times 10^6 \text{ mL}^{-1}$ ; LZ,  $2.49 \pm 0.04 \times 10^6 \text{ mL}^{-1}$ ; C-1,  $2.19 \pm 0.03 \times 10^6 \text{ mL}^{-1}$ ; C-2,  $2.61 \pm 0.51 \times 10^6 \text{ mL}^{-1}$ , and  $3.00 \pm 0.71 \times 10^6 \text{ mL}^{-1}$  in the surrounding water. On Day 6 bacterial numbers were lower in HZ ( $2.6 \pm 0.8 \times 10^6 \text{ mL}^{-1}$ ) compared with  $3.3 \pm 0.5 \times 10^6 \text{ mL}^{-1}$  in LZ,  $3.4 \pm 0.2 \times 10^6 \text{ mL}^{-1}$  in C-1,  $3.7 \pm 0.9 \times 10^6 \text{ mL}^{-1}$  in C-2, and  $3.7 \pm 0.3 \times 10^6 \text{ mL}^{-1}$  in the surrounding water. A companion study to this reports that bacterial numbers were significantly lower ( $p < 0.05$ ) in the HZ treatment through preferential loss of the larger bacteria (Cotner *et al.* 1995).

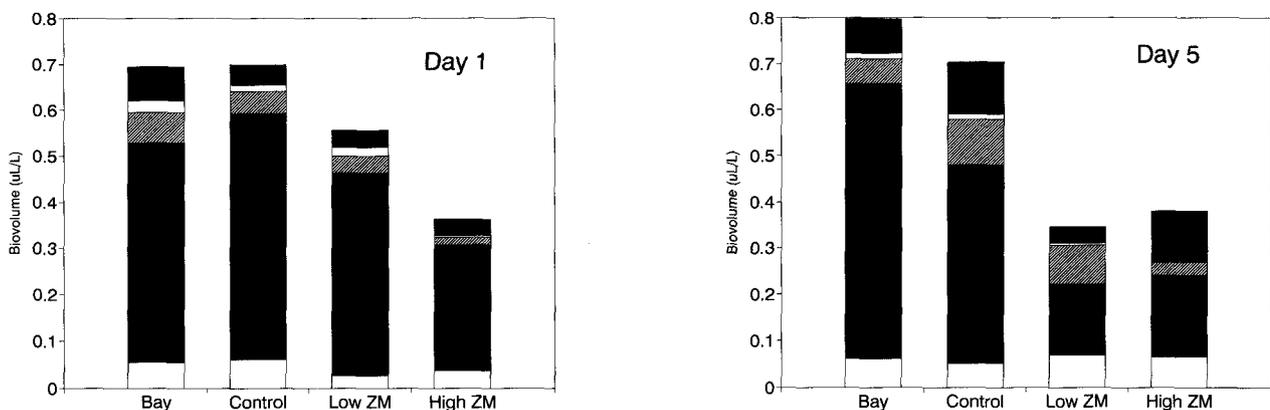


FIG. 1. Phytoplankton community composition, reported as biovolume ( $\mu\text{L L}^{-1}$ ), on Day 1 and Day 5. Algal classes: open, cyanophytes; closed, diatoms; heavy lines, chlorophytes; stippled, dinoflagellates; gray, chrysophytes. Note: control was C-1.

### Phytoplankton Biomass and Productivity

Concentrations of suspended particles, chlorophyll, and algal biomass rapidly declined in the enclosures containing zebra mussels. After 16 hours ("Day 1") phytoplankton biomass in HZ had declined to about 50% that of the control enclosures. Enclosures with zebra mussels had a transparency of 85 percent light transmittance, chlorophyll concentration of  $0.58 \pm 0.18 \mu\text{g L}^{-1}$ , and an estimated phytoplankton carbon content of  $39.5 \pm 7.79 \mu\text{g C L}^{-1}$ . Transparency of the LZ and HZ treatments did not differ from each other but was higher than the control enclosures, which had a transparency of 75 percent transmittance ( $\pm 1$ ), chlorophyll concentration of  $0.89 \pm 0.10 \mu\text{g L}^{-1}$ , and phytoplankton carbon content of  $84.5 \pm 2.1 \mu\text{g C L}^{-1}$ .

On Day 6, transparency in the LZ and HZ enclosures remained essentially the same as on Day 1 (transmittance = 86 percent  $\pm 3$ ), while chlorophyll ( $0.38 \pm 0.02 \mu\text{g L}^{-1}$ ) and estimated phytoplankton carbon content ( $18.0 \pm 1.4 \mu\text{g C L}^{-1}$ ) were lower than on Day 1. Control enclosures had virtually the same transparency as the surrounding water column, but had elevated chlorophyll and phytoplankton carbon. Control enclosures had a transparency of 67 percent transmittance ( $\pm 3$ ) and a chlorophyll content of  $1.82 \pm 0.25 \mu\text{g L}^{-1}$ .

Phytoplankton growth rates increased in enclosures with zebra mussels, but there was no apparent change in the photosynthetic physiological characteristics of the phytoplankton (Table 1). Algal growth rates in LZ and HZ were more than double the growth rates in the control enclosures, and they were significantly ( $p < 0.10$ ) elevated over the growth rates in the controls and the surrounding water. At the end of the experiment (Day 6), the mean phytoplankton growth rate in enclosures with zebra mussels was  $1.2 \pm 0.16 \text{ d}^{-1}$ , compared with a phytoplankton growth rate in the control enclosures of  $0.39 \pm 0.06 \text{ d}^{-1}$ . Despite this increase in growth rate, neither  $\alpha$  nor the  $P_{\text{max}}$  in the control enclosures differed significantly from values observed in the surrounding water and in the LZ and HZ enclosures.

### Phosphorus Dynamics

Zebra mussels had a profound acute effect on phosphorus dynamics of enclosed communities. By the time the sample was drawn on Day 1, SRP and TSP were significantly elevated in the HZ enclosure (Table 2). SRP concentration continued to increase through Day 2, when it reached  $330 \pm 10$

nM ( $10.2 \mu\text{g P L}^{-1}$ ) compared with SRP in the control enclosures of  $60 \pm 8 \text{ nM}$  ( $1.9 \mu\text{g L}^{-1}$ ). SRP in HZ declined after Day 2, but it was still significantly elevated over the controls on Day 6. SRP in the LZ and control enclosures remained at  $60 \pm 8 \text{ nM}$  throughout the experiment. Concentration of total soluble P (TSP) was significantly elevated in the HZ enclosure on Day 1, in comparison with the mean of the controls and the surrounding water. By the end of the experiment on Day 6, there were no significant differences in TSP concentration among the enclosures ( $200 \pm 29 \text{ nM}$ ), and they did not differ significantly from the TSP concentration in the surrounding water.

Biotic phosphate uptake was significantly slowed following the introduction of zebra mussels. Using  $^{32}\text{P}$ -labelled phosphate in tracer quantities coupled with SRP as a measure of ambient phosphate concentration we determined the velocity of phosphate uptake and the phosphate turnover rate in the water column (Table 3). The plankton community in Saginaw Bay water surrounding the enclosures took up phosphate at a rate of 2.5 to 3  $\text{nmol L}^{-1} \text{ min}^{-1}$  with a turnover time (inverse of the overall uptake rate constant) of about 18 min. Using size-selective filtration, we determined that about one-third of the phosphate was taken up by particles greater than 1.0  $\mu\text{m}$  (presumably algae and very large bacteria), and the remainder of the material was taken up by bacterial-sized particles in the size range of 0.2–1.0  $\mu\text{m}$ . Because formalin-killed and CCCP-killed controls showed an uptake rate less than 4% that of the unkilld samples, we concluded that most of the uptake was by living bacteria and algae, rather than abiotic sorption to surfaces of clays.

Plankton in the control enclosures took up phosphate at a rate that did not differ significantly from that of the external community (Fig. 2). Phosphate uptake by plankton in LZ and HZ differed significantly ( $p < 0.10$ ) from that of the control enclosures at the end of the experiment. Plankton in the LZ enclosure took up phosphate at about half the rate of plankton in the controls on Day 1 and less than 2% that of controls on Day 6. Phosphate uptake by plankton in the HZ enclosure was at a rate less than 2% that of controls on Day 1 and less than 1% of controls on Day 6.

### Nitrogen Dynamics

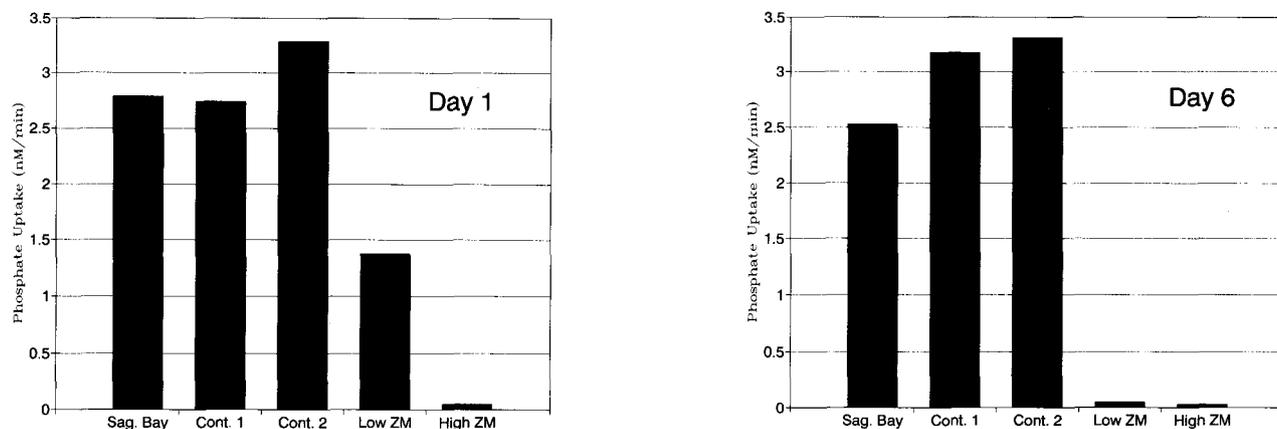
Ammonium concentrations in Saginaw Bay water surrounding the enclosures remained at  $2.24 \pm 0.50 \mu\text{M}$  throughout the experiment. Ammonium in-

**TABLE 2.** Dissolved materials in enclosures and the water immediately surrounding the enclosures (Saginaw Bay). SRP, soluble reactive P (nmol L<sup>-1</sup>); TSP, total soluble P (nmol L<sup>-1</sup>); NH<sub>4</sub><sup>+</sup> ammonium (μmol L<sup>-1</sup>); DOC, dissolved organic C (mg C L<sup>-1</sup>); POC, particulate organic carbon (mg C L<sup>-1</sup>).

	SRP (nM)	TSP (nM)	NH <sub>4</sub> <sup>+</sup> (μM)	DOC (mg C L <sup>-1</sup> )	POC (mg C L <sup>-1</sup> )
<b>Day 1</b>					
High ZM	110	274	5.68	2.66	0.50
Low ZM	52	136	2.66	2.51	0.49
Control 1	48	87	1.00	2.71	0.65
Control 2	52	201	1.45	2.56	0.72
Saginaw Bay	52	112	1.84	2.37	0.65
<b>Day 2</b>					
High ZM	330	—	11.85	—	—
Low ZM	65	—	3.84	—	—
Control 1	55	—	0.61	—	—
Control 2	60	—	1.35	—	—
Saginaw Bay	61	—	1.84	—	—
<b>Day 6</b>					
High ZM	94	225	4.97	2.33	0.38
Low ZM	58	168	4.03	2.57	0.38
Control 1	58	185	1.49	2.61	0.77
Control 2	74	225	2.78	2.30	0.79
Saginaw Bay	58	185	3.01	2.12	0.49

**TABLE 3.** Phosphate uptake rate by algal- and bacterial-sized particles. SRP, soluble reactive P (nmol L<sup>-1</sup>); *k*, active phosphate proportional uptake constant (min<sup>-1</sup>) for bacterial-sized particles (0.2–1.0 μm) and algal-sized particles (> 1.0 μm). Phosphate uptake velocity, *k* • (SRP), (nmol L<sup>-1</sup> min<sup>-1</sup>).

	SRP (nM)	Uptake Rate Const.		Phosphate Turnover Time (min)	Phosphate Uptake Rate	
		Bacterial (min <sup>-1</sup> )	Algal (min <sup>-1</sup> )		Bacterial (nM min <sup>-1</sup> )	Algal (nM min <sup>-1</sup> )
<b>Day 1</b>						
High ZM	110±12	0.0003	0.0002	2,000	0.03	0.02
Low ZM	52±10	0.020	0.006	38	1.05	0.33
Control 1	48±10	0.043	0.013	18	2.10	0.64
Control 2	52±10	0.051	0.013	16	2.62	0.67
Saginaw Bay	52± 8	0.037	0.018	18	1.89	0.90
<b>Day 6</b>						
High ZM	94±12	0.0001	0.0002	3,300	0.01	0.02
Low ZM	58±10	0.0005	0.0004	1,100	0.03	0.02
Control 1	58±10	0.040	0.015	18	2.32	0.86
Control 2	74± 8	0.027	0.018	22	1.99	1.32
Saginaw Bay	58± 8	0.27	0.017	23	1.54	0.99



**FIG. 2.** Phosphate uptake velocity by size fractionated particles, reported in units of  $nM\ min^{-1}$  above formalin-killed controls. Enclosures were sampled on Day 1 and Day 6. Closed, represents uptake by bacterial-sized particles (particles that pass through a  $1.0\ \mu m$  filter but are retained on  $0.2\ \mu m$  filters); open, "algal" uptake (i.e., phosphate uptake by particles greater than  $1\ \mu m$ ).

creased in the HZ enclosure to  $11.9\ \mu M$  during the first 36 hours of the experiment then declined over the next 48 hours and remained at  $4.97 \pm 0.51\ \mu M$  until the end of the experiment (Table 2). Ammonium concentration in the LZ increased during the first 36 hours then remained constant at  $3.91 \pm 0.12\ \mu M$ . Ammonium in the C-1 control enclosure was virtually unchanged during the course of the experiment at  $1.21 \pm 0.24\ \mu M$ ; ammonium continued to increase slowly in the C-2 enclosure (i.e., the one containing the fish) to  $2.44 \pm 0.19\ \mu M$  on Day 6.

Differences in trends for ammonium regeneration by lower food web organisms in the experimental and control treatments were not apparent. Ammonium uptake in the enclosures was lower than in the external community in each of the enclosures on Days 2, 4, and 5 (Fig. 3). On Day 5, ammonium uptake rate in the LZ enclosure was higher than that in C-1 but lower than that in C-2. Potential ammonium uptake in HZ enclosure did not differ from that of LZ. Ammonium regeneration by the plankton was similar in C-2 to that of the external Saginaw Bay community, but ammonium regeneration rate in C-1 was lower than C-2 on Days 4 and 5 (Fig. 4). Regeneration rates in LZ and HZ did not differ significantly from the controls on Days 1 and 2. On Day 4, LZ regeneration rate was lower than both control enclosures and did not differ from HZ. On Day 5, ammonium regeneration rate in LZ was higher than C-1 but lower than C-2; the regeneration rate in HZ did not differ significantly from C-1, but it was lower than C-2. We did not measure the regeneration rate of ammonium by zebra mus-

sels, but they were likely responsible for much of it, as seen by the transitory increases of ammonium in the enclosures with zebra mussels.

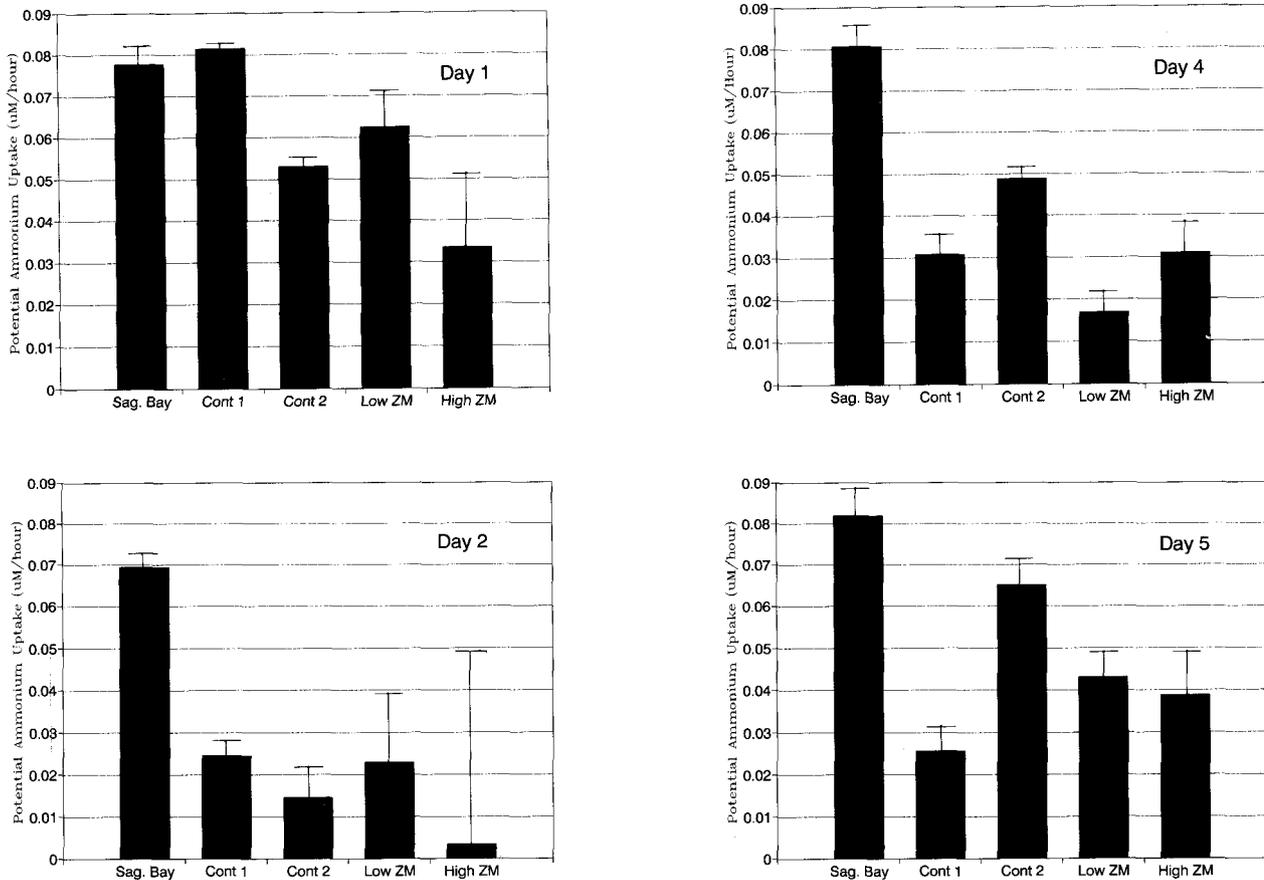
#### Dissolved and Particulate Organic Carbon

DOC content of Saginaw Bay water was  $2.14 \pm 0.16\ mg\ C\ L^{-1}$ . We saw no significant difference between the means of the control enclosures and Saginaw Bay waters surrounding the enclosures, and we observed no significant difference between the means of DOC in LZ or HZ compared with the mean of the control enclosures (Table 2). On Day 6, POC content in the LZ and HZ enclosures was one-half that of the control enclosures. Phytoplankton C, estimated by the method of Redalje (1993) apparently represented only a small portion of the POC content of the water (compare Table 1 phytoplankton C and Table 2 POC). The water surrounding the enclosures showed variations in POC from day to day, probably due to turbulent mixing and a storm on Day 3.

## DISCUSSION

### Experimental Design and Statistical Inference

Our experimental design included duplicate control enclosures and unreplicated treatment enclosures with two densities of zebra mussels, LZ and HZ. With this design we were able to use inferential statistics based on replicate determinations to look for "enclosure effects" by comparing the means of samples from the control enclosures to one another



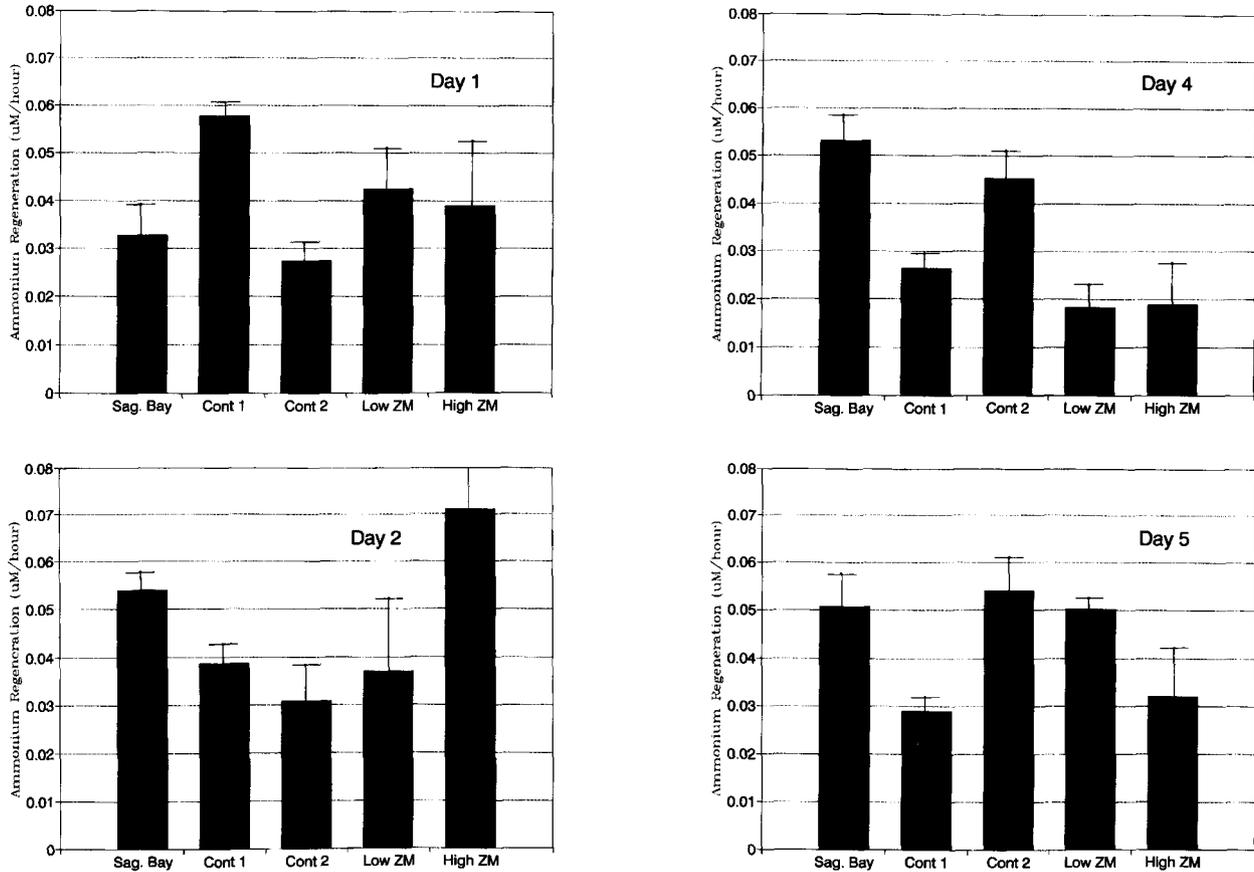
**FIG. 3.** Potential rate of ammonium uptake by plankton samples removed from the enclosures, reported in units of  $\mu\text{M h}^{-1}$ . Bars are the means of duplicates, lines indicate the standard error.

and to the means of replicate samples from Saginaw Bay waters surrounding the enclosures. Our LZ and HZ treatment enclosures were unreplicated so it would be inappropriate to use inferential statistics based only on replicate laboratory determinations to examine differences between the means (Hurlbert 1984). By assuming that the variance of the treatment enclosure means was no greater than the variance taken directly from the means of two control enclosures and surrounding waters, we determined that the means of certain variables in LZ and HZ differed significantly from the means of the control enclosures, within stated confidence intervals. It should also be noted that common sense, biological knowledge, and intuition were applied to the task of appraising whether differences were due to treatment effects (Hurlbert 1984). From the consistency of our observations including dose and time-dependent effects, with implications of zebra mussel life history and reported effects of mussels on commu-

nities elsewhere, we felt confident in concluding that our results could represent short-term effects that zebra mussels may exert on nearshore Great Lakes communities.

### Enclosure Effects

We saw few "enclosure effects" in our experiment, as evidenced by the similarity between control enclosures and the surrounding water throughout the experiment. We enclosed large volumes to avoid sampling errors and to minimize the surface:volume ratio. By conducting the experiment for only 6 days, the effects of periphyton growth were minimized. Algal and bacterial community composition was virtually the same in control enclosures and the surrounding water, although the chlorophyll content of the controls was significantly greater than in the surrounding water, possibly indicating compensation for some shading in the enclosures. Water chemistry in control enclo-



**FIG. 4.** Rate of ammonium regeneration by plankton samples removed from the enclosures, reported in units of  $\mu\text{M h}^{-1}$ . Bars are the means of duplicates, lines indicate the standard error. Note: the Standard error of the estimate of the ammonium regeneration rate on Day 2 in the High ZM treatment was  $\pm 0.0469 \mu\text{M h}^{-1}$ , and is off-scale on this graph.

tures was virtually unchanged from the surroundings waters, except for significantly lower concentrations of ammonium. Potential ammonium uptake rate was also significantly lower in the two control enclosures. Significant differences between C-1 and C-2 in ammonium regeneration rate and in SRP may have arisen from enclosing slightly different communities at the beginning of the experiment, e.g., the alewife inadvertently introduced in C-2.

#### Community was Typical of Nearshore Great Lakes Communities

Plankton composition and water chemistry of the site used in Saginaw Bay were within ranges often reported for Great Lakes communities, indicating that the findings of this study may be useful in anticipating effects of zebra mussels broadly over this re-

gion. The phytoplankton community at this site was typical of mesotrophic regions of the Great Lakes, with 1-2  $\mu\text{g}$  chlorophyll *a* per liter, dominated by diatoms, with lesser amounts of chlorophytes, cryptophytes, chrysophytes and cyanophytes. With a measured algal biovolume of about  $1 \mu\text{L L}^{-1}$ , the community examined compared well with the 5-year average (1983-88) for the central basin of Lake Erie before invasion of the zebra mussel (Makarewicz 1993). The algal C:Chl ratio ( $61 \pm 12$ ) was within the range reported in the epilimnion of other Great Lakes communities (Fahnenstiel and Scavia 1987). Observed bacterioplankton densities were similar to values reported for a nearshore community in Lake Michigan (Moll and Brahe 1986).

Concentrations of dissolved nutrients in Saginaw Bay water surrounding the enclosures were similar to

values reported elsewhere in the nearshore regions of the Great Lakes. The low concentrations of SRP (average of 60 nM = 1.9  $\mu\text{g P L}^{-1}$ ) we observed were similar to values reported in nearshore Lake Michigan stations using the same analytic procedures (Moll and Brahce 1986), and ammonium concentrations (2–3  $\mu\text{M}$ ) were about 4–6 fold greater than those reported in samples taken from 5 m depth in an offshore station in Lake Michigan (Gardner *et al.* 1989). We expected that zebra mussels would rapidly release pseudofeces that could potentially dissolve and increase the DOC content in the water. We noted large amounts of material at the bottom of the enclosures containing zebra mussels that were presumed to be fecal and pseudofecal material. The lack of differences between control and experimental enclosures indicated either that measurable DOC was not rapidly released from feces or pseudofeces or that if released it was rapidly assimilated. DOC concentrations (2–2.5  $\text{mg C L}^{-1}$ ) compared well with values reported for surface water (2.22  $\pm$  0.35  $\text{mg C L}^{-1}$ ) at an offshore station of Lake Michigan (Laird and Scavia 1990). Typically, nutrients are in higher concentration nearshore (Moll and Brahce 1986), and we believe that the nutrient concentrations observed indicate that this site can be viewed as “typical” of many of the nearshore regions of the Great Lakes likely to be affected by zebra mussels.

#### Phytoplankton were P-limited

Many of our findings are consistent with the view that communities in the surrounding lakewater and in the control enclosures were growth-limited by P-availability. SRP concentrations, phosphate turnover times, and the relationship between phosphate uptake rate and optimum photosynthetic fixation rate indicated that the community we studied was P-limited at the start of the experiment. SRP concentrations below 65 nM (i.e., less than 2  $\mu\text{g P L}^{-1}$ ), such as those observed in Saginaw Bay, are characteristic but not diagnostic of P-limited communities (Lean *et al.* 1983). Both the phosphate uptake rate constant and the phosphorus deficiency index, PDI, are strong indicators of phosphorus deficiency (Currie 1990). Turnover rates greater than 0.02  $\text{min}^{-1}$  (i.e., phosphate turnover times less than 1 hour) and PDI values less than 30 are indicative of P-limitation (Lean *et al.* 1983). The phosphate uptake rates in Saginaw Bay of 0.05  $\pm$  0.01  $\text{min}^{-1}$  (i.e., phosphate turnover times of about 20 min) indicate moderate P-limitation.

PDI is defined as the quotient of ( $P_{\text{opt}}/V_{\text{max}}$ ), where  $P_{\text{opt}}$  is the optimum photosynthetic uptake rate

( $\mu\text{g C L}^{-1} \text{h}^{-1}$ ) and  $V_{\text{max}}$  is the maximum phosphate uptake rate ( $\mu\text{g P L}^{-1} \text{h}^{-1}$ ). Given our data, we were able to calculate an upper bound for PDI. Our average photosynthetic maximum (5.5  $\mu\text{g C } \mu\text{g chl}^{-1} \text{h}^{-1}$ ) was scaled for chlorophyll (average 1.8  $\mu\text{g chl L}^{-1}$ ), giving an estimated  $P_{\text{opt}} = 9.9 \mu\text{g C L}^{-1} \text{h}^{-1}$ . We did not observe  $V_{\text{max}}$ ; our phosphate uptake values (1.7  $\text{nmol L}^{-1} \text{min}^{-1} = 3.2 \mu\text{g P L}^{-1} \text{h}^{-1}$ ) underestimated  $V_{\text{max}}$  and therefore overestimated PDI. Even so, our estimate of PDI = 3.1 indicates “extreme” P-limitation (Lean and Pick 1981).

Additionally, a trophic state index (TSI) value of a community can be estimated from concentrations of chlorophyll or TP (Carlson 1977). If the phytoplankton community is P-limited, TSI values calculated from TP will equal the TSI values calculated from chlorophyll concentrations. From our observations of the community surrounding the enclosures we calculate a  $\text{TSI}_{\text{chl}} = 40 \pm 3$  and a  $\text{TSI}_{\text{TP}} = 42 \pm 7$ , indicating that Saginaw Bay phytoplankton were P-limited. A value of 40 is indicative of mesotrophic communities (Carlson 1977). Similar values were obtained for Lake Erie prior to the zebra mussel invasion. For example, we calculated  $\text{TSI}_{\text{chl}} = \text{TSI}_{\text{TP}} = 40 \pm 3$  for data collected in early September 1983–85 from the central basin of Lake Erie and reported by Charlton *et al.* (1993).

#### Community and Ecosystem Effects of Zebra Mussels

Conceivably, zebra mussels can exert direct and indirect effects on communities and ecosystems. Direct effects are those that result from the activities of the mussels (e.g., grazing and excretion); indirect effects are those that result from the disruption of the regular patterns and processes of the ecosystem, present before the zebra mussel. Most of the observed effects of zebra mussels in our experiment can be regarded as direct effects resulting from their grazing of algae and mineralization of nutrients. Their alteration of P-dynamics represents an important indirect effect.

Our observation of rapid decline of phytoplankton and rapid increase in transparency is explained by the known rapid filtration of the water by the zebra mussel. Dramatic declines in chlorophyll *a* and phytoplankton biomass have been noted in natural populations, declining 54% in Lake Erie offshore (Leach 1993), 90% in Lake Erie nearshore environments (Nicholls and Hopkins 1993), and 60% in Saginaw Bay (Fahnenstiel *et al.* 1995). Although individual zebra mussels may filter 1 L  $\text{d}^{-1}$

(Reeders and bij de Vaate 1990), it is unlikely that filtering rates per mussel will be so high in nature. Because zebra mussels occur in druses, much of the water filtered by each individual has also been filtered by its nearest neighbors. A more reasonable estimate can be made from an experiment such as ours, in which natural druses of zebra mussels graze natural communities in a nearshore setting, yet under controlled conditions.

We assumed a simple first-order model of grazing, that an average grazing rate could be observed assuming a completely mixed reactor (i.e., negligible sinking loss) within the enclosures over the initial 16-hour interval. The change in algal biovolume ( $N$ ) would be the net result of grazing losses and growth increases:

$$\frac{d(N)}{dt} = -g(N) + \mu(N),$$

where  $g$  is average grazing loss rate of biovolume and  $\mu$  is the growth rate. We assumed that differences in growth rates between controls and those to which zebra mussels were added were negligible because this was a short interval at the beginning of the experiment. We used the loss rate of phytoplankton biovolume during the first 16 hours (i.e., "Day 1" sample) to estimate zebra mussel grazing rates from the solution of the integrated form of the above model:

$$\ln \frac{(N)}{(N_0)} = -g(t),$$

where  $N$  was the phytoplankton biovolume in LZ ( $0.58 \mu\text{L L}^{-1}$ ) or HZ ( $0.38 \mu\text{L L}^{-1}$ ),  $N_0$  was the phytoplankton biovolume in the controls ( $0.70 \mu\text{L L}^{-1}$ ) (cf. Fig. 1), and  $t$ , the time interval in days (0.67 d). We calculated the grazing loss constants, multiplied by 1,600 L to express the rate in L filtered per day, to be  $450 \text{ L d}^{-1}$  in LZ and  $1,460 \text{ L d}^{-1}$  in HZ. When each value was scaled for the number of mussels in each enclosure, we calculated an identical effective filtration rate of  $0.50 \text{ L d}^{-1}$  per zebra mussel from both LZ and HZ under these conditions, and  $4.46 \text{ mL h}^{-1} \text{ mg}^{-1}$  in LZ and  $3.78 \text{ mL h}^{-1} \text{ mg}^{-1}$  in HZ. Our calculated filtration rate per mussel was midrange in the values reported by Stanczykowska (1975), who reported  $0.19\text{--}0.96 \text{ L d}^{-1}$  per individual at the low end of the range of filtration rates and ( $4.0\text{--}41 \text{ mL h}^{-1} \text{ mg}^{-1}$ , mean =  $16 \text{ mL h}^{-1} \text{ mg}^{-1}$ ) observed in Saginaw Bay (Fanslow *et al.* 1995). The zebra mussel filtration rate that we estimated, scaled for tissue mass, was about 10-fold greater

than the filtration rate ( $0.46 \text{ mL h}^{-1} \text{ mg}^{-1}$ ) observed for *Lampsilis radiata siliquoidea*, a unionid mussel that was abundant in Lake St. Clair before displacement by *D. polymorpha* (Vanderploeg *et al.* 1995, in press).

The standing crop of phytoplankton at the end of the experiment showed that not all algal classes and populations were affected equally by the zebra mussel, unlike the community effects noted in a seasonal investigation of Lake Erie nearshore communities where all classes of algae declined equally (Nicholls and Hopkins 1993). In our short-term study, diatoms and chlorophytes showed the greatest declines, while cyanophyte and chrysophyte biovolumes were relatively unaltered in the experimental enclosures. It is not certain whether this was a direct or an indirect effect of the zebra mussel. Zebra mussels indiscriminately filter a large but variable size range and select their food from the material that is filtered; material that is not ingested is removed from the water column by incorporation into pseudofeces (Dorgelo 1993). Phytoplankton species that were relatively unaffected were large colonial cyanophytes (e.g., *Microcystis*) and chrysophytes (e.g., *Synura*), and so may have been excluded from filtration.

An alternative, "indirect" effect may have been that nutrients released by zebra mussels, especially phosphate, may have stimulated growth, and those species that responded most rapidly may have been those that showed the least alteration in standing crop. Many algae known to grow fast in response to nutrient inputs are those that thrive in relatively high nutrient concentrations, whereas those most efficient at obtaining nutrients are able to adapt to low nutrient conditions but do not respond with rapid growth (Lee 1980). Although species displacements may be possible over a long term, it seems unlikely that significant alteration of species composition of the phytoplankton community could occur over the short duration of this experiment.

The great increase in growth rate of the phytoplankton assemblage in the enclosures with zebra mussels likely was caused by an increase in the supply rate of available nutrients, especially phosphate, allowing P-limited phytoplankton to grow near their maximum growth rate. Growth rates in HZ ( $1.05 \text{ d}^{-1}$ ) and LZ ( $1.36 \text{ d}^{-1}$ ) were greater than rates in C-2 ( $0.39 \text{ d}^{-1}$ ) and in Saginaw Bay water surrounding the enclosures ( $0.56 \text{ d}^{-1}$ ). The value determined for the phytoplankton assemblage in LZ was near the maximum growth rate ( $\mu_{\text{max}}$ ) expected from laboratory and field studies elsewhere. Values

for  $\mu_{\max}$  are species specific and although we do not have information on the  $\mu_{\max}$  of the species of this community, general values in the literature place it around  $1 \text{ d}^{-1}$  for many freshwater species at temperatures between 20 and  $30^\circ\text{C}$  (Reynolds 1984). Using the  $^{14}\text{C}$ -chlorophyll labelling method of determining  $\mu$ , Redalje and Laws (1981) observed  $\mu$  as high as  $1.17 \text{ d}^{-1}$  in a culture of the marine diatom *Thalassiosira weissflogii*. Growth rates of  $1.44 \text{ d}^{-1}$  were observed for a natural phytoplankton assemblage in nearshore surface ocean waters (Welschmeyer and Lorenzen 1984). The maximum growth rate,  $\mu_{\max}$ , was estimated for natural surface phytoplankton assemblages in the North Pacific subtropical gyre at  $25^\circ\text{C}$  to be  $1.49 \pm 0.44 \text{ d}^{-1}$  (Laws *et al.* 1987).

Much of the concern regarding the effects of zebra mussels on nutrient dynamics has been directed toward their removal of N and P into feces and pseudofeces, in the short-term, and into tissues and shells over the long-term (e.g., Stanczykowska and Planter 1985), thereby removing nutrients from being available to plankton. Our interest was in nutrient release by zebra mussels and the recycling of N and P for phytoplankton growth. Ammonium excretion by zebra mussels increased with temperature in laboratory studies (Quigley *et al.* 1993), and was expected to be high under the ambient temperatures encountered in our experiment ( $24^\circ\text{C}$ ). Ammonium was high after the first 16 hour interval and then declined. A companion paper reports experimental findings that conclude zebra mussels in abundance could be a major source of ammonium regeneration (Gardner *et al.* 1995). Phosphate concentrations (detected as SRP) also increased in similar experimental situations (Heath, unpubl. obs.). Other mussels are known to release both phosphate and ammonium to the surrounding water (Nalepa *et al.* 1991). Both ammonium and SRP concentrations, but not TP, have increased in the western basin of Lake Erie since the establishment of large populations of zebra mussels, presumably as a combined result of the removal of phytoplankton and the remineralizing activities of the mussels (Holland *et al.* 1995, in press).

It is unlikely that the great decrease in phosphate uptake rate can be explained as a direct effect of zebra mussel grazing. Zebra mussels can filter bacterial-sized particles with a low efficiency. Tomson (1983) showed that bacteria less than  $1 \mu\text{m}$  were grazed at 1% of the efficiency of particles greater than  $5 \mu\text{m}$ . A companion study to ours reports that zebra mussels grazed bacterial-sized particles with an efficiency of 10 to 34% that of the efficiency of chlorophyll removal (Cotner *et al.* 1995). In com-

parison with the mean values in control enclosures on Day 6, the community in HZ showed 30% fewer bacterial cells and 50% less algal biomass than in the control enclosures; LZ showed about 10% fewer bacteria 50% less algal biomass than in the control enclosures. These differences alone cannot account for the observed 99% decline in phosphate uptake rate both by bacterial-sized particles (i.e., particles between 0.2 and  $1.0 \mu\text{m}$ ) and by particles greater than  $1 \mu\text{m}$ .

### Proposed Model of Indirect Zebra Mussel Effects

Our findings suggest that large populations of zebra mussels are able to control ecosystem functions indirectly by providing nutrients (e.g., phosphate and ammonium) at a rapid rate, altering those processes that are rate-limited or concentration-limited by nutrient availability. In both natural communities and laboratory studies, bacteria outcompete phytoplankton for very low concentrations of available phosphate ( $< 50 \text{ nM}$ ) by having receptors with a high affinity for phosphate (i.e., lower  $K_d$ ) (Rhee 1972, Currie and Kalf 1984). At higher phosphate concentrations many algae compete favorably by having higher potential phosphoryl transport rates ( $V_{\max}$ ) and by being able to store phosphate in luxury amounts (Healey and Hendzel 1980, Cotner and Wetzel 1992, Rothhaupt and Gude 1992). Whether bacterioplankton are growth limited by P-availability or the rate at which carbon is supplied to them is currently much debated. Even if bacteria are not P-limited their higher demand for phosphate can make them major consumers of inorganic P in many freshwater environments (Vadstein *et al.* 1988, 1993; Cotner and Wetzel 1992).

Zebra mussels also may affect the rate at which labile DOC (LDOC) is supplied to bacterioplankton from algal primary production. In a study in Lake Michigan, LDOC ranged from 40% of total DOC in offshore near-bottom water in late May to 14% of total DOC in nearshore surface water in July (Laird and Scavia 1990). The supply of LDOC is explained largely by the amount of primary productivity (Laird *et al.* 1986, Baines and Pace 1991). We did not measure LDOC in our enclosures, but it is reasonable to expect that as algal biomass was removed by zebra mussel grazing, the supply of LDOC diminished.

For communities that we examined in Saginaw Bay, phosphate and ammonium concentrations were low, phytoplankton growth rates were slow and apparently limited by the rate of phosphate supply, and bacteria were major consumers of phosphate. We

propose that zebra mussels disturbed this steady state by providing phosphate and ammonium rapidly. As P-limited phytoplankton were grazed by zebra mussels, TP was mineralized and released as phosphate that was taken up by bacteria and algae. Bacteria became P-satiated, and with decreased densities of phytoplankton to supply C-substrate, they may have become C-limited, further decreasing their P-demand. The increased concentrations of phosphate and decreased bacterial P-demand in the enclosures with the zebra mussels provided phosphate to phytoplankton at a high rate, yet phytoplankton biomass remained low because of continued filtration by zebra mussels. The remaining cells had more P available to them per cell, and phytoplankton grew rapidly in response to their release from P-limitation. By growing rapidly, phytoplankton utilized ammonium also released by the mussels.

We view that during the short interval of our experiment the community was in transition from one steady state to another in the presence of zebra mussels. The concentration "spikes" in SRP and ammonium that we observed represented the increased supply, provided by mussel re-mineralization activities, that was later consumed as phytoplankton grew in response to the new supply rate. The second steady state is one in which particles are grazed rapidly by zebra mussels, mineralized nutrients flow rapidly from the mussels, and phytoplankton growth rates increase. The rate at which materials move in this second steady state is a function of the rate at which limiting nutrients are released from zebra mussels.

Whether these findings are confined to the enclosures and the short interval we studied or are applicable to regions of the Great Lakes where large populations of zebra mussels develop and persist remains to be shown. Our model predicts that growth rates in P-limited phytoplankton communities would increase and be controlled by the rate of phosphate release by zebra mussels. Based on this model we predict that phytoplankton would not be as severely P-limited (e.g., the PDI values in communities heavily grazed by zebra mussels would increase). Inasmuch as phytoplankton growth in response to supply rates of limiting nutrients is species specific (Reynolds 1984), it is possible that phytoplankton community composition eventually may change in response to altered nutrient availability (Sommer 1989). Given this scenario, we would expect that communities may change from species that are competitively advantaged by having high affinity for low concentrations of P and by

having comparatively high  $\mu_{\max}/k_s$  (e.g., diatoms of the family Fragilariaceae) to those species competitively advantaged to grow rapidly in response to increased supply of nutrients by having relatively high  $\mu_{\max}$  (e.g., rapidly growing cyanophytes) (Kilham and Kilham 1980, Sommer 1989). We also would expect bacterial growth to slow, due to increased growth limitation by diminished LDOC availability, and that the amount of phosphate taken up by bacteria, relative to that taken up by algae, would decrease.

Evidence for our expectation of an elevated PDI is supported by our data from Day 6. To calculate an approximate PDI, as above, we divided our observed  $P_{\text{opt}}$  (2.20  $\mu\text{g C L}^{-1} \text{h}^{-1}$ , HZ; 2.77  $\mu\text{g C L}^{-1} \text{h}^{-1}$ , LZ) by the observed phosphate uptake rate for each enclosure (which is  $\leq V_{\max}$ ) (0.056  $\mu\text{g P L}^{-1} \text{h}^{-1}$ , HZ; 0.093  $\mu\text{g P L}^{-1} \text{h}^{-1}$ , LZ) to give maximum possible PDI values of 39.3 for HZ and 29.8 for LZ. These values are indicative of "low" phosphorus deficiency (Lean and Pick 1981). Examination of the other expectations of this model are on-going in field and laboratory studies.

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