

## Effects of the Zebra Mussel, *Dreissena polymorpha*, on Community Nitrogen Dynamics in Saginaw Bay, Lake Huron

Wayne S. Gardner,<sup>1</sup> Joann F. Cavaletto,<sup>1</sup> Thomas H. Johengen,<sup>1,2</sup>  
Jeffrey R. Johnson,<sup>1,2</sup> Robert T. Heath,<sup>3</sup> and James B. Cotner, Jr.<sup>4</sup>

<sup>1</sup>NOAA Great Lakes Environmental Research Laboratory  
2205 Commonwealth Blvd.  
Ann Arbor, Michigan 48105

<sup>2</sup>Cooperative Institute for Limnology and Ecosystem Research  
University of Michigan  
Ann Arbor, Michigan 48104

<sup>3</sup>Department of Biological Sciences  
Kent State University  
Kent, Ohio 44240

<sup>4</sup>Department of Wildlife and Fisheries  
Texas A&M University  
College Station, Texas 77843

**ABSTRACT.** *The effects of the zebra mussel, Dreissena polymorpha, on chlorophyll and nutrient concentration changes and community ammonium uptake and regeneration rates were determined in bottle experiments on waters collected from a eutrophic site and an oligotrophic site in Saginaw Bay, Lake Huron in 1992. Our objectives were to estimate nitrogen cycling rates and to determine the direct (excretion) and indirect (foodweb) effects of the zebra mussel on these rates. Isotope labeling experiments with added <sup>15</sup>NH<sub>4</sub><sup>+</sup> were conducted on waters collected on five sampling dates between April and October. Direct effects of zebra mussels on ammonium regeneration and potential uptake were examined by comparing results from bottles incubated with (15 individuals in 4 L lake water) and without added zebra mussels. Indirect foodweb effects were examined by measuring regeneration and potential uptake rates in subsamples of water that had previously been incubated in the presence or absence of zebra mussels.*

*Zebra mussels removed a large fraction of chlorophyll from the oligotrophic site on all sampling dates and from the eutrophic site in October, but had a negligible effect on chlorophyll levels in waters from the eutrophic site in June, July, August, and September when cyanophytes were abundant. Community ammonium regeneration rates and uptake rates both followed seasonal patterns resembling those for chlorophyll concentrations in control treatments at the eutrophic site. Rates for water from the oligotrophic site were low (usually not significantly different from zero) and are not reported here. Community ammonium regeneration rates were consistently enhanced in the presence of zebra mussels, indicating that zebra mussel excretion could have a dominant effect on nitrogen regeneration in regions where it is abundant. Zebra mussels appeared to decrease community uptake rates of ammonium in August and September but did not predictably affect nitrogen remineralization rates by other lower foodweb organisms (e.g. bacteria, protozoans, zooplankton).*

**INDEX WORDS:** *Zebra mussels, Saginaw Bay, Lake Huron, nitrogen cycling, nutrients.*

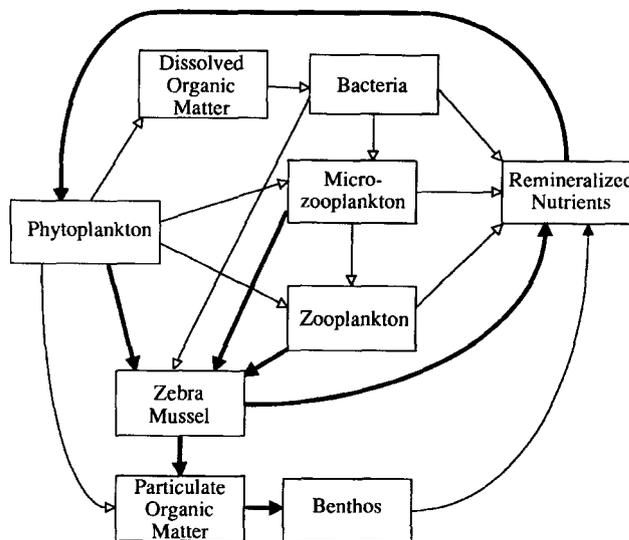
### INTRODUCTION

Nutrient concentrations, ratios, and cycling rates, in combination with physical characteristics such as light availability and temperature, are important factors controlling phytoplankton production and

lower foodweb dynamics in aquatic ecosystems (Scavia and Fahnenstiel 1987). Information about concentrations, cycling rates, pathways, and fates of nutrients (nitrogen, phosphorus, and silicate) in coastal ecosystems such as Saginaw Bay are needed to develop accurate ecosystem models and to make

reasonable predictions about seasonal succession patterns of phytoplankton and other lower food web organisms in these environments. Nutrient concentration data are commonly used in mass balance models to help determine the nutrient status (i.e., the degree of eutrophication) and trends of nutrients in aquatic ecosystems (e.g., Bierman and Dolan 1981, 1986). In contrast, nutrient-cycling rates are often not measured and, therefore, can only be estimated in ecosystem models. Nutrient regeneration is commonly the dominant mechanism supplying nutrients for primary production in coastal environments where rates have been measured (e.g., Selmer 1988, Selmer *et al.* 1993). Although nutrient recycling is recognized to be an important process driving phytoplankton dynamics in Saginaw Bay (Bierman and Dolan 1981), regeneration rates have not been previously measured in the bay.

The zebra mussel, *Dreissena polymorpha*, that has recently invaded the Laurentian Great Lakes (Griffiths *et al.* 1991, Leach 1993, Nicholls and Hopkins 1993), could potentially have major effects on the biogeochemistry of nutrients in regions of the lakes where they have become dominant organisms. For example, in Polish lakes with large populations of macrophytes, zebra mussels contain and process quantities of N and P comparable to the macrophytes (Stanczykowska 1984, Stanczykowska and Planter 1985). Zebra mussels could change the dynamics of nutrient cycling and biochemical energy flow by selectively affecting different components of the foodweb (Fig. 1) based on organism size and composition. The high filtering capacity of zebra mussels (Sprung and Rose 1988, Reeders and bij de Vaate 1990, Fanslow *et al.* 1995) allows them to quantitatively remove particles from large volumes of water. Retained particles are either ingested and metabolized (Quigley *et al.* 1993) or incorporated into pseudofeces that may be deposited in benthic regions and/or processed by other organisms (Griffiths 1993, Stanczykowski and Planter 1985). The size range of particles quantitatively filtered by zebra mussels (ca 1  $\mu\text{m}$  to 450  $\mu\text{m}$ ; Jørgensen *et al.* 1984, Sprung and Rose 1988) includes most phytoplankton and many small invertebrates, including protozoans and rotifers, but tends to be larger than the size of many bacteria in natural waters (<1 $\mu\text{m}$ ; Cotner *et al.* 1995). The ability of zebra mussels to quantitatively remove phytoplankton and small zooplankton but not all bacteria (the primary consumers of dissolved organic matter) from the water could cause zebra mussels to have major ef-



**FIG. 1.** Conceptual model showing potential direct (bold line) and indirect (thin line) effects of zebra mussels on nutrient cycling by lower food web components.

fects on organic matter production and degradation and associated nutrient cycling processes.

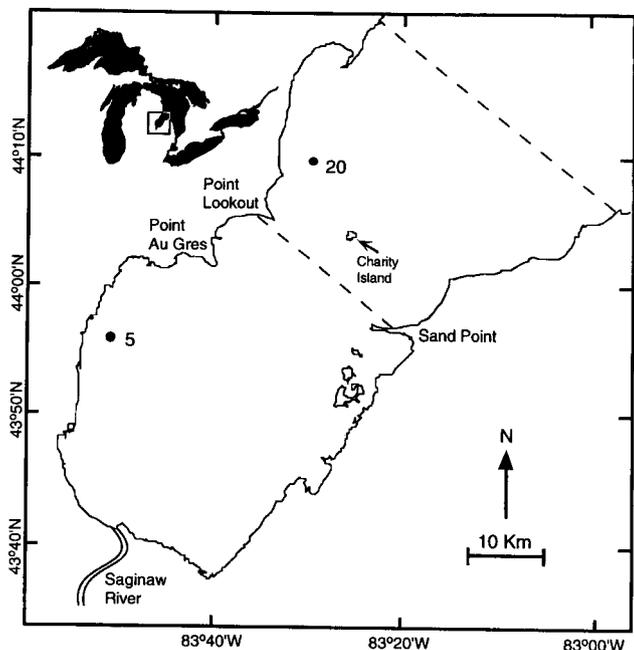
We hypothesized that zebra mussels would directly affect community nutrient cycling processes in the water column by excreting inorganic (or organic) forms of nutrients and would indirectly affect cycling processes by changing the composition and dynamics of organisms such as phytoplankton, protozoans, and small zooplankton that normally recycle nutrients in the Great Lakes foodweb (Fig. 1).

In this paper, we report nitrogen cycling rates in Saginaw Bay and estimate how they are directly and indirectly affected by the presence of zebra mussels. Specifically, we address the following questions: (1) What are the seasonal rates of community ammonium uptake and regeneration in Saginaw Bay water? (2) Do seasonal nitrogen turnover rates relate to chlorophyll concentrations? (3) How does the presence of zebra mussels affect nitrogen turnover rates, directly by excretion and indirectly through foodweb changes?

## METHODS

### Study Sites and Sampling Design

Saginaw Bay is a large (about 82 km long and 42 km wide) bay extending off the western edge of Lake Huron (Fig. 2). Water movement is generally



**FIG. 2.** Location of the two sampling sites in Saginaw Bay, Lake Huron. Dashed lines differentiate the inner bay from the outer bay and the outer bay from Lake Huron.

counterclockwise, flowing in from Lake Huron along the north shore, mixing with Saginaw River water in the lower portion of the bay, and flowing out of the bay along the south shore (Danek and Saylor 1977). The inner bay, mean depth of about 5 m, receives large inflows of enriched waters from the Saginaw River, and is generally considered to be eutrophic. The Saginaw River accounts for about 70% of total tributary flow into the bay (Frank Quinn, personal communication, Great Lakes Environmental Research Laboratory) The outer bay has a mean depth of about 14 m, is influenced strongly by Lake Huron water, and has lower nutrient levels than the inner bay (Bierman and Dolan 1981). Our sampling sites (Stations 5 and 20; Fig. 2) were selected as "typical" inner-bay and outer-bay sites and were chosen to represent 2 out of the 26 sites that were examined in the Saginaw Bay monitoring program (Fahnenstiel *et al.* 1995, Johengen *et al.* 1995). Zebra mussels were abundant at Station 5 but were not found at Station 20 (Nalepa *et al.* 1995). The water depths at Stations 5 and 20 are ca 3.5 and 17 m, respectively.

Water was collected just below the water surface at the two sites by submerging acid-washed and dis-

tilled water-rinsed polyethylene carboys. Zebra mussels were collected from Station 5 with an epibenthic sled. Water from Station 5 was collected monthly from June to October, 1992, and water from Station 20 was collected monthly from August to October, 1992. Water and zebra mussels were kept in closed coolers during transport to the shore laboratory to maintain temperatures near-ambient.

### Community Remineralization and Potential Uptake Rates ( $^{15}\text{N}$ Studies)

Four-liter aliquots of mixed unfiltered near-surface water from the sites were placed in acid-washed and distilled water-rinsed clear polycarbonate bottles for isotope labeling experiments. Fifteen zebra mussels per bottle (equivalent to 52,500 individuals  $\text{m}^{-2}$  at the Station-5 depth) were placed into the zebra mussel-treatment bottles after individuals were separated from their substrates by razor blade and pre-incubated three times (20 min each) in 1-L portions of unfiltered lakewater. Direct effects of zebra mussels on community ammonium regeneration and potential uptake rates were examined by adding  $^{15}\text{NH}_4\text{Cl}$  (4  $\mu\text{M}$ , 56  $\mu\text{g N/L}$ ) to the treatment bottles with and without zebra mussels and monitoring the changes in ammonium concentrations and isotope ratios over time. The calculated uptake rates should be considered to be "potential" rather than "actual" rates because more than tracer levels of ammonium were added. However, the presence of measurable ammonium (0.2 to 2.67  $\mu\text{M}$ ), and nitrate (8.3 to 33.8  $\mu\text{M}$ ), on all sampling dates suggests that nitrogen availability probably did not limit phytoplankton growth in these waters. A companion study of the effects of zebra mussels on phosphorus dynamics at the same sites indicated that phosphorus was likely the most limiting nutrient (R. Heath, unpublished data). In August, for example, immediately available phosphorus concentrations (10–15 nM; 0.3–0.48  $\mu\text{gP/l}$ , Rigler bioassay) and soluble reactive phosphorus concentrations (10–20 nM) were both very low, and phosphate turnover times were rapid (3–6 min) at both stations. Similar observations were made in June through September. Therefore, we felt that the experimental additions did not greatly affect the nitrogen turnover rates.

Indirect effects of the zebra mussels were examined by doing  $^{15}\text{NH}_4^+$  isotope labeling experiments on 60-ml subsamples of site water that had previously been incubated for 25–38 h in 4-L bottles in the presence and absence of zebra mussels. In addi-

tion to the 4-L treatments, control isotope labeling experiments were done on 60-ml water samples. These results were combined with those from the large bottles without zebra mussels to increase replication for control treatments.

Treatment bottles were incubated under artificial light in an indoor Percival incubator equipped with fluorescent lights (ca 100 Einsteins  $m^{-2} h^{-1}$ ). In some experiments (indirect-effect treatments of July, August, and September), treatment bottles were also incubated in outdoor incubators (after Lohrenz *et al.* 1988) to simulate natural light (i.e., about 75 % of incident radiation) and temperature conditions.

Samples for isotope dilution experiments were taken at the beginning of each experiment and at 2–3 intervals of 6–20 h as the experiments progressed. Total incubation times were always less than 40 h. At each sampling time, the bottles were gently mixed, and 10-mL samples were collected by syringe with a clean needle and passed through a 0.2  $\mu m$  pore-size nylon filter. The first 3 mL of sample were used to rinse the filter and discarded. The remaining 7 mL were placed into clean vials (Wheaton No. 224884) and frozen for later analysis of ammonium concentrations and isotope ratios.

Ammonium concentrations and [ $^{15}NH_4^+$ ]:[Total  $NH_4^+$ ] ratios of the thawed samples for the isotope labeling experiments were measured by high performance cation exchange liquid chromatography (Gardner *et al.* 1991, 1993). Ammonium concentrations were determined by comparing the area for the sample-ammonium peak to the area for the standard-ammonium peak in mobile phase buffer that was injected 5.0 min before each lake water sample (Gardner *et al.* 1993). Corrections were made for sample matrix differences between the lake water and mobile phase buffer. Ammonium regeneration rates and potential uptake rates for the respective intervals between sampling times were calculated from ammonium concentrations and isotope ratios using the Blackburn-Caperon model (Blackburn 1979, Caperon *et al.* 1979). In these experiments, both ammonium isotopes are assumed to be taken up at the same rates by organisms but previously fixed nitrogen with a natural isotope ratio ( $^{14}NH_4^+$ :Total  $NH_4^+$  = 0.9963) is assumed to account for all ammonium released by mineralization processes during short incubation intervals (hours). Seasonal comparisons were made using only the initial interval of 7–13 h for each experiment to minimize differences in rates that could be caused

by bottle or incubation effects or by recycling of the isotopic label over longer incubation times.

### Chlorophyll Analysis

On each sampling date, initial chlorophyll concentration was measured on a portion of the bay water that was collected for experimental treatments. Upon termination of the bottle experiments, a final sample was taken for chlorophyll analysis from each treatment bottle. Water was filtered through a Whatman GF/F filter and chlorophyll was extracted by grinding the filter in cold 90% acetone and measured fluorometrically after the extracts were held at 4°C for ca 24 h (Strickland and Parsons 1972). Chlorophyll extractions and measurements were done in triplicate.

To determine phytoplankton composition in initial and final-experimental waters, 100-mL aliquots of water were collected, fixed in 1% Lugol's fixative (final concentration), and stored at 4°C for phytoplankton identification and enumeration by differential interference contrast microscopy.

### Nutrient Measurements in Bottle Experiments

Nutrients were measured in experimental bottles without added  $^{15}NH_4^+$  at the beginning and after ca 24 h for each treatment. In the September experiment, concentrations were also determined over a time course of 0, 2, 4, 7, 16, and 23 h. At each sampling point, approximately 20 mL of sample were withdrawn from each treatment bottle, with a chemically-clean needle and syringe, and immediately filtered through a prerinsed 0.4  $\mu m$  cellulose filter. The first 5 mL of filtrate was used to rinse the filter and culture tube and discarded. The rest of the filtrate was collected in an acid-washed polyethylene culture tube and frozen for later analysis.

Nutrient concentrations for these experiments were determined using standard colorimetric techniques on a Technicon Auto Analyzer II (U.S. E.P.A. 1974, A.P.H.A. 1990). Nitrate + nitrite was determined using the cadmium reduction method and hereafter will be referred to simply as nitrate. Ammonium was determined by the Bertholet reaction, soluble reactive phosphorus (SRP) by the molybdate/ascorbic acid method, and silica by the heteropoly blue method, respectively.

Seasonal data for nutrient and chlorophyll concentrations and process rates are presented in figures and tables below as mean values  $\pm$  SE. For the purpose of discussion, mean values that differ by

more than  $2 \times \text{SE}$  are considered to be significantly different, whereas those with overlapping SE are considered to be not significantly different.

## RESULTS

### Temperature and Nutrient Concentrations at Sampling Sites

Temperature at Station 5 increased from 19°C in June to 24°C in August and then decreased to 14°C in October, the last sampling month (Table 1). Similar water temperatures were observed at Station 20 except for August when the water temperature was 17°C (Table 2).

Initial nutrient concentrations in the bottles at the beginning of the experiments at Stations 5 and 20 are presented in Tables 1 and 2. Nitrate was the dominant form of inorganic nitrogen at both sites (Tables 1, 2). At Station 5, initial nitrate concentrations ranged from 34  $\mu\text{M}$  in June to about 8  $\mu\text{M}$  in September but at Station 20 concentrations were relatively constant (19–24  $\mu\text{M}$ ) over the sampling period (Tables 1 and 2). Initial ammonium concentrations at Station 5 ranged from about 0.6 to 2.5  $\mu\text{M}$  whereas at Station 20, initial ammonium concentrations ranged from 0.2 to 1.2  $\mu\text{M}$ . Concentrations of soluble reactive phosphorus, the only form of phosphorus that was measured, remained low (<0.060  $\mu\text{M}$  at Station 5 and < 0.025  $\mu\text{M}$  at Station 20) at all sampling times. In October, initial phosphorus concentrations at Station 5 were high (ca 0.055  $\mu\text{M}$ ) relative to concentrations on the other sampling dates. Silicate levels at Station 5 ranged from 7  $\mu\text{M}$  in June to 60–70  $\mu\text{M}$  in August, September, and October (Table 1), as compared to a progressive increase from 6  $\mu\text{M}$  in August to about 20  $\mu\text{M}$  in October at Station 20 (Table 2).

Except for ammonium, nutrient concentrations were not predictably affected by the presence of zebra mussels in the experimental bottles over incubation intervals of about 24 hours (Tables 1 and 2). Nitrate, SRP, and  $\text{SiO}_2$  showed only relatively small percentage changes in concentrations, that were generally similar in treatments with and without zebra mussels. In contrast, ammonium showed only small net changes in the absence of zebra mussels but consistently increased several-fold over initial concentrations in the treatments with zebra mussels. Of course, net concentration changes do not reveal the actual fluxes of nutrients through the biota because regeneration and uptake process occur simultaneously.

In September, ammonium concentrations were monitored at several time intervals between about 2 and 23 h to observe the patterns of ammonium accumulation in the bottles without  $^{15}\text{NH}_4^+$  additions (Fig. 3). Ammonium concentrations progressively increased over time in the treatments with zebra mussels, in water from both Station 5 and Station 20, but did not increase extensively in either of the treatments without zebra mussels. Net accumulation rates in the zebra mussel treatments were more rapid during the first 7 h of the incubation (ca 0.34  $\mu\text{M h}^{-1}$ ) than during the remaining 16 h (ca 0.15  $\mu\text{M h}^{-1}$ ; Fig. 3).

Annual and seasonal means of field measurements of dissolved nutrient concentrations at Station 5 in 1991, before or during the zebra mussel invasion, and in 1992, are given in Nalepa *et al.* (in press) and summarized in Johengen *et al.* (1995). Field concentrations of the dissolved inorganic nutrients at Station 5 either did not change significantly or increased after the invasion of the zebra mussel. Observed increases in nutrient levels from 1991 to 1992, corresponding to the arrival of the zebra mussel, could have resulted from decreased community uptake rates, and/or from increased rates of nutrient inputs either from outside sources or internal regeneration processes. For example, inner bay spring silicate concentrations increased from about 8  $\mu\text{M}$  in 1991 to 20 in 1992 (Johengen *et al.* 1995). This change was probably caused by a large decrease in community silicate uptake rates as a result of zebra mussels reducing the abundances of diatoms after the invasion. Spring diatom abundances were much lower in 1992 than in 1991 (G. Fahnenstiel, personal communication, Great Lakes Environmental Research Laboratory).

### Chlorophyll

Initial chlorophyll concentrations in our 1992 field season, that did not include spring values, were highest in September at both Stations 5 and 20 (Fig. 4). At this time, concentrations were about 8 times greater in water from Station 5 than from Station 20, 18 and 2.2  $\mu\text{g L}^{-1}$ , respectively. Following bottle incubations, chlorophyll concentrations in treatments without zebra mussels with Station 5 water increased, relative to initial concentrations, in July and October (Fig. 4). During the other three months, chlorophyll concentrations decreased slightly or did not change in treatments without mussels. Chlorophyll concentrations in treatments

**TABLE 1.** Initial (T-0) and final (T-F) concentrations and net changes of nutrients for bottle experiments conducted without (Cont) and with (ZM) added zebra mussels for water collected from Station 5 in Saginaw Bay, Lake Huron. SRP = soluble reactive phosphorus. "In" and "out" refer to indoor and outdoor incubators.

Month (Temp)	Treatment	Nutrient	Concentration ( $\mu\text{M}$ )		
			T-O	T-F	Change
June (19°C)	Cont-In	$\text{NO}_3^-$	33.6	35.5	+1.90
		$\text{NH}_4^+$	1.24	1.10	-0.14
		SRP	0.024	0.032	+0.08
		$\text{SiO}_2$	6.90	5.60	-1.30
	ZM-In	$\text{NO}_3^-$	33.80	35.70	+1.90
		$\text{NH}_4^+$	0.87	4.07	+3.20
		SRP	0.03	0.06	+0.03
		$\text{SiO}_2$	6.50	6.20	-0.30
July (21°C)	Cont-In	$\text{NO}_3^-$	22.30	20.90	-1.40
		$\text{NH}_4^+$	1.64	0.93	-0.71
		SRP	Not measured		
		$\text{SiO}_2$	11.20	8.90	-2.30
	ZM-In	$\text{NO}_3^-$	22.30	21.90	-0.40
		$\text{NH}_4^+$	1.25	5.07	+3.82
		SRP	0.03	0.04	+0.01
		$\text{SiO}_2$	11.00	10.60	-0.40
August (24°C)	Cont-In	$\text{NO}_3^-$	19.20	19.00	-0.20
		$\text{NH}_4^+$	1.54	0.89	-0.65
		SRP	0.04	0.02	-0.02
		$\text{SiO}_2$	64.10	68.30	+4.20
	ZM-In	$\text{NO}_3^-$	19.70	19.30	-0.40
		$\text{NH}_4^+$	1.65	6.08	+4.43
		SRP	0.05	0.02	-0.03
		$\text{SiO}_2$	61.90	66.10	+4.20
September (19°C)	Cont-In	$\text{NO}_3^-$	8.30	7.50	-0.80
		$\text{NH}_4^+$	0.60	1.40	+0.80
		SRP	0.03	0.03	0
		$\text{SiO}_2$	70.00	72.00	+2.00
	ZM-In	$\text{NO}_3^-$	8.30	8.30	0
		$\text{NH}_4^+$	0.60	4.60	+4.00
		SRP	0.03	0.03	0
		$\text{SiO}_2$	68.00	73.00	+5.00
October (14°C)	Cont-In	$\text{NO}_3^-$	11.70	11.70	0
		$\text{NH}_4^+$	2.48	1.98	-0.50
		SRP	0.06	0.05	-0.01
		$\text{SiO}_2$	68.60	65.10	-3.50
	ZM-In	$\text{NO}_3^-$	12.10	12.10	0
		$\text{NH}_4^+$	2.55	3.99	+1.44
		SRP	0.05	0.05	0
		$\text{SiO}_2$	62.60	61.40	-1.20
	Cont-Out	$\text{NO}_3^-$	11.40	11.40	0
		$\text{NH}_4^+$	2.67	1.82	-0.85
		SRP	0.05	0.04	-0.01
		$\text{SiO}_2$	62.60	65.00	+2.40
ZM-Out	$\text{NO}_3^-$	11.70	11.70	0	
	$\text{NH}_4^+$	2.56	4.17	+1.61	
	SRP	0.06	0.09	+0.03	
	$\text{SiO}_2$	61.70	66.40	4.70	

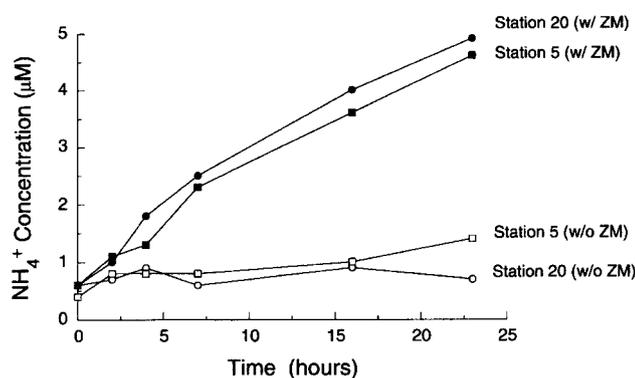
**TABLE 2.** Initial (T-O) and final (T-F) concentrations and net changes of nutrients for bottle experiments conducted without (Cont) and with (ZM) added zebra mussels for water collected from Station 20 in Saginaw Bay, Lake Huron. SRP = soluble reactive phosphorus. "In" and "out" refer to indoor and outdoor incubators.

Month (Temp)	Treatment	Nutrient	Concentration ( $\mu\text{M}$ )		
			T-O	T-F	Change
August (17°C)	Cont-In	$\text{NO}_3^-$	23.40	23.60	+0.20
		$\text{NH}_4^+$	1.20	0.93	-0.27
		SRP	0.02	0.01	0
		$\text{SiO}_2$	6.10	6.10	0
	ZM-In	$\text{NO}_3^-$	23.60	23.20	-0.40
		$\text{NH}_4^+$	1.20	6.10	+4.90
		SRP	0.02	0.02	0
		$\text{SiO}_2$	5.60	6.20	+0.60
September (18°C)	Cont-In	$\text{NO}_3^-$	18.60	18.20	-0.40
		$\text{NH}_4^+$	0.60	0.70	+0.10
		SRP	0.03	0.02	-0.01
		$\text{SiO}_2$	14.00	15.00	+1.00
	ZM-In	$\text{NO}_3^-$	19.50	19.50	0
		$\text{NH}_4^+$	0.60	4.90	+4.30
		SRP	0.02	0.03	+0.01
		$\text{SiO}_2$	14.00	17.00	+3.00
October (14°C)	Cont-In	$\text{NO}_3^-$	20.60	20.60	0
		$\text{NH}_4^+$	0.26	0.29	+0.03
		SRP	0.01	0.01	0
		$\text{SiO}_2$	16.80	14.30	-2.50
	ZM-In	$\text{NO}_3^-$	20.60	21.60	+1.00
		$\text{NH}_4^+$	0.20	1.73	+1.53
		SRP	0.01	0.01	0
		$\text{SiO}_2$	16.30	17.10	+0.8
October (14°C)	Cont-Out	$\text{NO}_3^-$	19.90	19.90	0
		$\text{NH}_4^+$	0.31	0.33	+0.02
		SRP	0.01	0.01	0
		$\text{SiO}_2$	20.30	19.30	-1.00
	ZM-Out	$\text{NO}_3^-$	20.00	19.90	-0.10
		$\text{NH}_4^+$	0.21	2.49	+2.28
		SRP	0.01	0.01	0
		$\text{SiO}_2$	21.90	18.30	-3.60

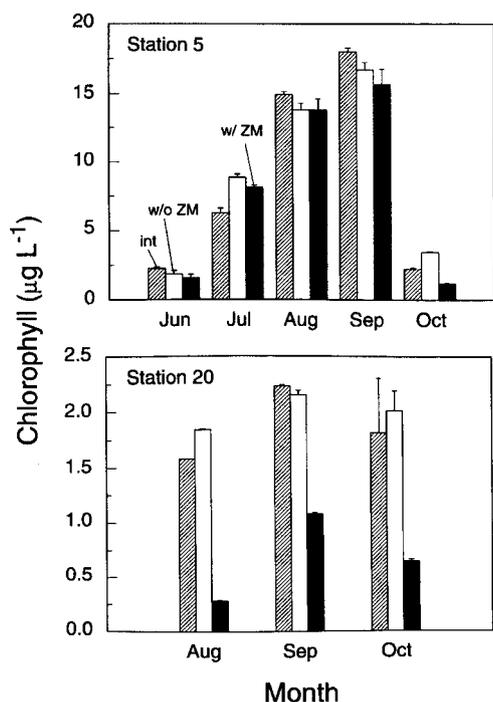
without mussels in Station 20 water were generally similar to initial concentrations (Fig. 4).

Chlorophyll concentrations in Station 5 treatments with zebra mussels did not change except in October when a decrease was observed. Excluding October, changes in treatments with mussels generally resembled those for treatments without mussels (Fig. 4). In Station 20 treatments, chlorophyll concentrations consistently decreased to a greater extent in treatments with mussels than in treatments without mussels. The maximum difference between sites occurred in August when chlorophyll concen-

trations declined 84% between treatments with and without mussels in Station 20 water, but did not decline in either treatment with Station 5 water. In October, chlorophyll concentrations in Station 5 treatments with mussels were reduced to about the same extent as they were for Station 20 treatments with mussels on all sampling dates (Fig. 4). The absence of chlorophyll removal in Station 5 treatments with mussels on other dates was probably related to the composition of the phytoplankton at those times. Phytoplankton composition information was not available for June, but the phytoplank-



**FIG. 3.** Mean changes in ammonium concentrations in water from the two sites without added  $^{15}\text{NH}_4^+$  during the experimental period (24 h) in treatments with and without zebra mussels added (15 individuals per 4 L water) in September 1992.



**FIG. 4.** Mean seasonal chlorophyll concentrations at the beginning and end of the experimental period on treatments with and without zebra mussels at Stations 5 and 20.

ton community at Station 5 was dominated by chlorophytes (*Gleocystis* and *Scenedesmus*) with some cyanophytes (*Microcystis* and *Chroococcus*) and diatoms (*Cyclotella* with some *Flagellaria*) in July, cyanophytes (predominantly *Merismopedia*,

*Microcystis* and *Chroococcus*) in August, and by chlorophytes (*Gleocystis* and several species of *Scenedesmus*) and diatoms (*Cyclotella*) in October. The phytoplankton community at Station 20 consisted largely of chlorophytes and/or diatoms (Soon-Jin Hwang, personal communication, Kent State University).

### Seasonal Nitrogen Turnover Rates

#### Direct Effects

Different patterns in ammonium concentration and isotope ratio changes over time of incubation were observed for treatments with and without mussels in water from Station 5 (Fig. 5). Concentrations of added ammonium decreased over time in all treatments without mussels whereas ammonium concentrations progressively increased over time in all treatments with zebra mussels (Fig. 5). Except for the June treatment without mussels, where the isotope ratio remained approximately constant over time,  $^{15}\text{N}/^{14}\text{N}$  isotope ratios decreased in all treatments due to dilution with  $^{14}\text{NH}_4^+$ , as a result of heterotrophic mineralization of organic nitrogen. More ammonium production and isotope dilution of the  $^{15}\text{N}$  was consistently observed in the mussel treatments than in those without mussels, likely because ammonium was excreted by the zebra mussels. Higher nitrogen transformation rates were observed in July, August, and September than in June or October.

Calculated uptake rates for ammonium in Station 5 water without zebra mussel additions ranged from about  $0.02 \mu\text{M h}^{-1}$  in June up to  $0.37 \mu\text{M h}^{-1}$  in September (Fig. 6). Except for some minor discrepancies in July and August, the seasonal pattern of uptake rates generally corresponded ( $r$ , correlation coefficient = 0.95) to the patterns of chlorophyll concentrations in the water (Fig. 4), a result that would be expected if phytoplankton abundance was the major factor controlling community uptake rates of ammonium. The presence of zebra mussels did not measurably affect community uptake rates in June, July, or October when rates were low, but appeared to decrease uptake rates in August and September when initial chlorophyll levels and uptake rates were highest (Fig. 6). Nitrogen uptake and regeneration rates at oligotrophic Station 20 are not presented because rates in control treatments were too low (i.e., usually not significantly different from zero) to be effectively measured by our  $^{15}\text{N}$  isotope labeling technique.

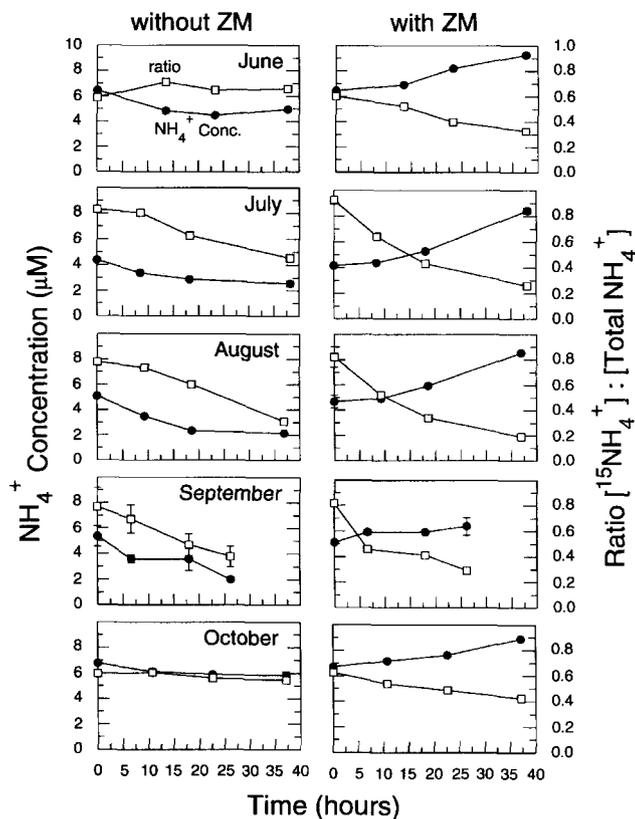


FIG. 5. Mean ( $\pm$  SE) concentrations of ammonium (dots) and isotope ratios (squares) in water from Station 5 over the experimental period. The water was spiked with  $4 \mu\text{M } ^{15}\text{NH}_4^+$  in 4-L bottles and incubated without and with zebra mussels (15 individuals per bottle).

Calculated ammonium regeneration rates for Station 5 treatments without mussels ranged from less than 0 in June up to about  $0.1\text{--}0.2 \mu\text{M h}^{-1}$  in September (Fig. 7). As was the case for uptake results, seasonal regeneration rate patterns for treatments without mussels resembled the patterns observed for chlorophyll concentrations ( $r = 0.98$ ), suggesting a relationship, probably indirect, between phytoplankton abundance and ammonium regeneration rates. The presence of zebra mussels consistently enhanced community ammonium regeneration rates (Fig. 7). Thus, excretion by zebra mussels appeared to be an important contributor to community ammonium regeneration.

It is interesting to compare estimates of zebra mussel ammonium production rates obtained by measuring accumulation rates of ammonium in

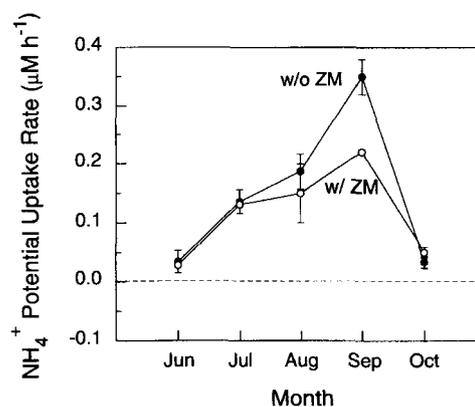


FIG. 6. Mean ( $\pm$  SE) community ammonium uptake rates in water from Station 5 for treatments without (dots) and with (circles) zebra mussels. Initial volume of water in bottles was 4 L. Incubations were conducted in an indoor Percival Incubator. Treatments with zebra mussels were not replicated in June or July.

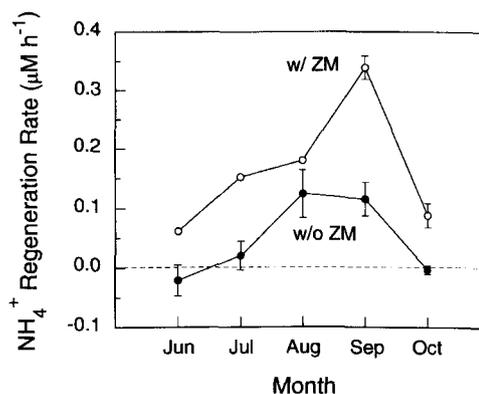


FIG. 7. Mean ( $\pm$  SE) community ammonium regeneration rates in water from Station 5 for treatments without (dots) and with (circles) zebra mussels. Initial volume of water in bottles was 4 L. Incubations were conducted in an indoor Percival Incubator. Treatments with zebra mussels were not replicated in June or July.

treatments without added  $^{15}\text{NH}_4^+$  (e.g., Fig. 3) to those obtained in isotope labeling experiments containing  $4 \mu\text{M}$  of added  $^{15}\text{NH}_4^+$  (September zebra mussel results, Fig. 7). Although the net rates of ammonium accumulation were different in the treatments with (Fig. 5) and without (Fig. 3) added

$^{15}\text{NH}_4^+$ , the calculated ammonium regeneration rates in the presence of zebra mussels during the first several hours of the incubation were the same (ca  $0.34 \mu\text{M h}^{-1}$ ) for the two measurement approaches.

### Indirect Effects

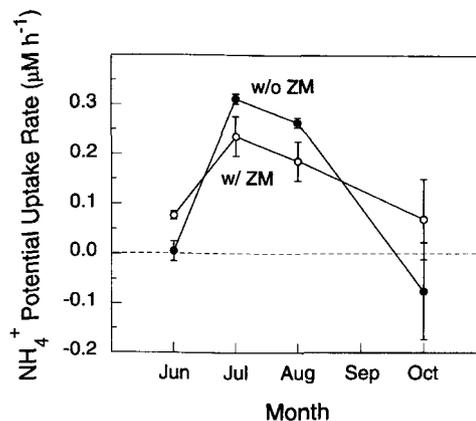
Indirect effects of zebra mussels on nitrogen uptake (Fig. 8) and regeneration (Fig. 9) were examined on four sampling dates in indoor incubators and on three dates in the outdoor incubators (Figs. 10 and 11). In July and August, community uptake rates in water that had previously been exposed to zebra mussels for about 40 h showed lower ammonium uptake rates than did those without exposure to zebra mussels in both indoor and outdoor experiments (Figs. 8 and 10). However, in June (indoor), treatments without mussels had lower rates than those with mussels (Fig. 8), and in October the results were not significantly different (overlapping SE; Figs. 8 and 10). Overall, final uptake rates were higher in outdoor incubators (Fig. 10) than in indoor incubators (Fig. 8) likely because phytoplankton growth rates were higher under natural light than under the reduced light conditions in the indoor incubators.

Our data did not yield consistent trends concerning the indirect effects of the zebra mussels on community ammonium regeneration rates. In the indoor experiments, water from treatments with mussels had higher regeneration rates than did water from treatments without mussels in three out of four experiments (Fig. 9). However in the outdoor experiments, regeneration rates were comparable in treatments with and without mussels (Fig. 11). Thus, consistent differences between final ammonium regeneration rates in water from treatments with and without zebra mussels were not apparent.

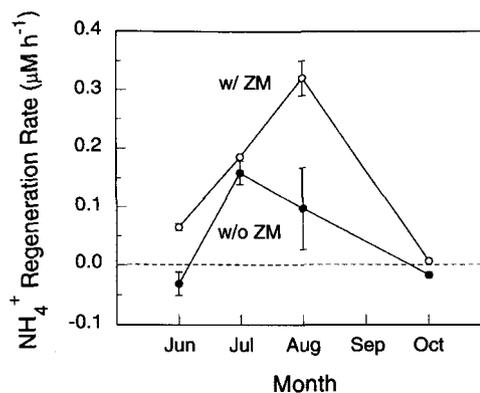
## DISCUSSION

### Seasonal Rates of Ammonium Uptake and Regeneration in Saginaw Bay and their Relationships to Chlorophyll Concentrations

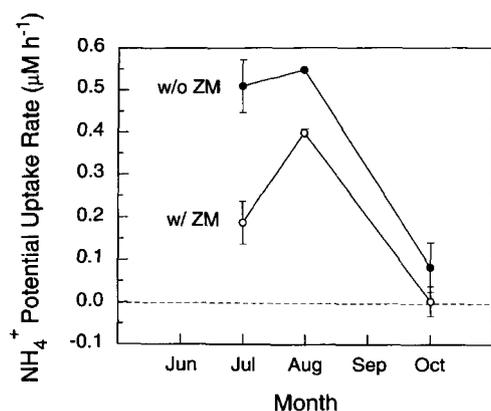
Assessment of ambient inorganic nutrient concentrations in coastal regions such as Saginaw Bay provides information about the steady state balance between production and uptake rates, but gives incomplete insights into the interactions between nutrients and organisms in these ecosystems. An



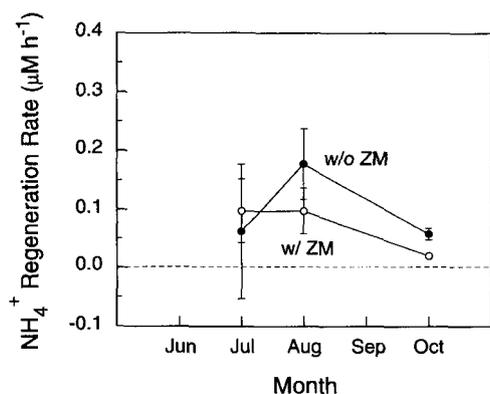
**FIG. 8.** Mean ( $\pm$  SE) community ammonium uptake rates in small bottles for Station 5 water that had been sampled from 4-L treatment bottles at the end of incubations from treatments without (dots) and with (circles) zebra mussels. Incubations were conducted in an indoor Percival Incubator. Treatments with zebra mussels were not replicated in June or July.



**FIG. 9.** Mean ( $\pm$  SE) community ammonium regeneration rates in small bottles for Station 5 water that had been sampled from 4-L treatment bottles at the end of incubations from treatments without (dots) and with (circles) zebra mussels. Incubations were conducted in an indoor Percival Incubator.



**FIG. 10.** Mean ( $\pm$  SE) community ammonium uptake rates in small bottles for Station 5 water that had been sampled from 4-L treatment bottles at the end of incubations from treatments without (dots) and with (circles) zebra mussels. Incubations were conducted under natural light in an outdoor incubator.



**FIG. 11.** Mean ( $\pm$  SE) community ammonium regeneration rates in small bottles for Station 5 water that had been sampled from 4-L treatment bottles at the end of incubations from treatments without (dots) and with (circles) zebra mussels. Incubations were conducted under natural light in an outdoor incubator.

understanding of cycling rates in combination with standing-stock concentrations of nutrients is needed to interpret ecosystem dynamics and the effects of perturbations, such as the zebra mussel invasion, on these dynamics. A problem associated with determining nitrogen cycling rates, however, is that their measurement requires time-consuming bottle incubations, a factor that limits the number of measurements that can be made in given time and space scales. For this reason, we limited our investigation of nutrient cycling rates to two sites. In this paper, we emphasize results from the relatively eutrophic Station 5 because rates at oligotrophic Station 20 were often not significantly different from zero using our measurement technique.

The ranges of ammonium uptake rates ( $0.05$  to  $0.34 \mu\text{M h}^{-1}$ ; Fig. 7) and regeneration rates ( $0$ – $0.12 \mu\text{M h}^{-1}$ ; Fig. 7) measured at Station 5 are similar to values observed in other nutrient-rich ecosystems. For example, in the Delaware River, ammonium regeneration rates ranged from  $< 0.02$  to  $0.46 \mu\text{M h}^{-1}$  (Lipshultz *et al.* 1986). In estuarine and coastal regions of Georgia, ammonium assimilation rates ranged from ca  $0$  to  $0.18 \mu\text{M h}^{-1}$  and regeneration rates ranged from  $0.02$  to  $0.35 \mu\text{M h}^{-1}$  in July (Hansen *et al.* 1990). In the Gulf of Mexico, ammonium regeneration rates in waters of the Mississippi River plume ranged from zero to ca  $0.44 \mu\text{M h}^{-1}$  with much higher rates observed in September than in February (Cotner and Gardner 1993). Lower uptake ( $0.003$  to  $0.018 \mu\text{M h}^{-1}$ ) and regeneration ( $0.001$  to  $0.015 \mu\text{M h}^{-1}$ ) rates were observed in meso-oligotrophic surface waters of Castle Lake (Axler *et al.* 1981). A summary of earlier published rates of ammonium regeneration and uptake indicated that ammonium regeneration values ranged from  $0$  to  $0.3 \mu\text{M h}^{-1}$ , and uptake rates ranged from  $0.01$  to  $0.22 \mu\text{M h}^{-1}$  with uptake to regeneration ratios ranging from  $0$  to  $9.2$  (Selmer 1988). In most of these studies, ammonium uptake rates were comparable or exceeded regeneration rates in surface waters, but regeneration rates exceeded uptake rates in bottom waters where absence of light minimized uptake by autotrophs (Hansen *et al.* 1990). Our results indicate that the presence of zebra mussels can strongly affect the ratios of community ammonium uptake to regeneration rates. In treatments without mussels, ammonium uptake rates were consistently higher than ammonium regeneration rates, whereas in treatments with mussels, regeneration rates always exceeded uptake rates (Figs. 6 and 7).

Nitrogen turnover rates at Station 5 showed a

strong seasonal signal (Figs. 6 and 7) as may be expected from corresponding changes in temperature (Tables 1 and 2) and chlorophyll concentrations (Fig. 4). The correlation ( $r = 0.95$ ) between mean ammonium uptake rates in the treatments without mussels (Fig. 7) and ambient chlorophyll levels (Fig. 4) suggests that rates were predominantly controlled by phytoplankton. Community ammonium regeneration rates were also correlated with chlorophyll concentrations ( $r = 0.98$ ). Ammonium regeneration rates were higher in August and September than in the other months (Fig. 7). The high correlation between heterotrophic ammonium regeneration rates and chlorophyll concentrations was not necessarily expected because, in contrast to uptake, the relationship between autotrophic processes and ammonium regeneration is expected to be indirect. The relationship that was observed likely resulted from the autotrophic production of labile organic nitrogen substrates that can be mineralized by heterotrophic lower food web organisms (bacteria, protozoans, and zooplankton) in the water column (Gardner *et al.* 1987).

In direct-effect experiments, uptake rates of ammonium in Station 5 water were not significantly affected by the presence of zebra mussels except in September when uptake rates were lower in the treatments with mussels than in those without mussels (Fig. 6). The relatively small effect of zebra mussels on ammonium uptake rates for Station 5 waters is not totally surprising because, in contrast to our expectations, chlorophyll levels were not greatly affected by the presence of mussels in most of our experiments at that Station (Fig. 4). In September, mean chlorophyll levels were lower in treatments with mussels than in those without mussels, but SE overlapped. In October, chlorophyll levels were decreased in the zebra mussel treatments relative to controls (Fig. 4); however, uptake rates were not significantly affected by zebra mussels (Fig. 6). One possible explanation for this result is that bacterial uptake of ammonium became more important relative to phytoplankton uptake in waters where phytoplankton were depleted by the zebra mussel. Although large bacteria can potentially be removed by zebra mussels, bacterial activities may be enhanced in the presence of zebra mussels under some circumstances (Cotner *et al.* 1995). Zebra mussels may indirectly affect bacterial abundances and activities both by changing the composition and turnover rates of dissolved organic matter, a principal substrate for heterotrophic bacte-

ria, and by removing protozoans, the predominant grazers of bacteria. For example, we have observed that removal rates of added dissolved amino acids were often greatly increased by the presence of zebra mussels relative to control treatments in Saginaw Bay (unpublished data). In recent bottle experiments with water from Station 5, zebra mussels removed a large portion of protozoans (Lavrentyev *et al.* 1995).

In contrast to the results for community ammonium uptake rates, community ammonium regeneration rates were consistently enhanced by the presence of zebra mussels (Fig. 7). This increase in regeneration rate can be reasonably attributed to the excretion of ammonium by the zebra mussels (Quigley *et al.* 1993). Ammonium regeneration rates, measured as the accumulation in ammonium concentrations over time in September zebra mussel treatments without added  $^{15}\text{NH}_4^+$  (Fig. 3), were about  $0.34 \mu\text{M h}^{-1}$  during the first 8 h. The same rate was obtained by the isotope dilution approach during the first measurement interval of about 7 h (see September result on Fig. 7).

In both cases, measured regeneration rates decreased with increased time of bottle incubation. These decreases may have been caused in part by depletion of food supplies in the bottles under conditions of diminished light. Community nitrogen cycling rates tended to decrease over time of incubation more often in the indoor incubators than in the outdoor natural-light incubators (data not shown). Net ammonium accumulation rates decreased to about one half of initial values after about 7 h in the bottle without added  $^{15}\text{NH}_4^+$  (Fig. 3). This change in accumulation rate may have resulted from changes in zebra mussel activity or food supply, or may have represented a foodweb-feedback effect caused by elevated levels of ammonium that accumulated in the bottle. In agreement with the second hypothesis, net ammonium accumulation rates were lower in bottles spiked with  $4 \mu\text{M } ^{15}\text{NH}_4^+$  (see Fig. 5) than for control treatments (Fig. 3) even though the calculated ammonium regeneration rates during the first interval were virtually identical by both approaches.

It is interesting to compare our measurements of uptake and regeneration rates to measurements of ambient nutrient concentrations before and after the invasion of the zebra mussel (Holland *et al.* 1995, Johengen *et al.* 1995). As mentioned above, field measurements of nutrients represent the net effects of community nutrient inputs, recycling dynamics,

and removal mechanisms but do not provide information about the magnitude of the rates. On the other hand, bottle experiments can provide nutrient cycling-rate estimates but do not provide as much detailed field information. In agreement with our observed increased ammonium regeneration rates for mussel treatments relative to those without mussels (Fig. 7), and some decreases in uptake rates in the presence of mussels (Fig. 6), mean *in situ* ammonium concentrations at Station 5 were on average higher in 1992 than in 1991. However, differences were not significant (overlapping SE) except for spring (Johengen *et al.* 1995). Mussels were rare at Station 5 in spring 1991 but had become abundant by late summer of that year. Similarly, at a site in western Lake Erie, ammonium concentrations increased after the zebra mussel invasion and the increase was particularly pronounced in January through April (Holland *et al.* 1995). Also ambient concentrations of  $\text{SiO}_2$  and nitrate usually increased after the invasion at both Station 5 (Johengen *et al.* 1995) and at the site in western Lake Erie. Soluble reactive phosphorus concentrations did not change following the zebra mussel invasion at Station 5 but some seasonally-dependent changes were observed following the invasion in western Lake Erie (Holland *et al.* 1995). We did not observe consistent changes in SRP or silica during the course of the bottle experiments either in the presence or absence of zebra mussels (Tables 1 and 2). The lack of SRP concentration changes in the bottle experiments does not necessarily imply that the zebra mussels were not excreting phosphate, but probably indicates that regenerated phosphate was immediately removed by the phytoplankton or bacterioplankton (Heath *et al.* 1995).

The comparison of Station 5 treatments with and without mussels may provide conservative estimates of the potential effects of zebra mussels on nutrient cycling dynamics in Great Lakes waters because zebra mussels did not significantly reduce chlorophyll levels, relative to controls, on most of the sampling dates (Fig. 5). We attribute this unexpected result to the dominant presence of cyanophytes that are not a preferred food for the zebra mussel (Lavrentyev *et al.* 1995). A study of seasonal changes in filtering rates indicated that chlorophyll levels in Station 5 water were reduced by the filtering activities of mussels, but the removal rate was diminished in late summer (Fanslow *et al.* 1995). In contrast, chlorophyll concentrations were consistently and substantially reduced in zebra

mussel treatments over controls when diatoms and chlorophytes were the dominant species, e.g. at Station 20 (Fig. 4). We did not conduct bottle experiments in April and May, but the diminished spring diatom abundances in 1992 relative to 1991 (G. Fahnenstiel, personal communication, Great Lakes Environmental Research Laboratory) and large increases in spring dissolved  $\text{SiO}_2$  concentrations after the invasion of the zebra mussel (Johengen *et al.* 1995) suggest that the zebra mussels may have maintained diatoms at much lower levels in 1992 than in 1991. Likewise, reductions in chlorophyll were consistently found after the zebra mussel invasion in western Lake Erie (Holland 1993, Leach 1993) and during the course of mesocosm experiments at a site in outer Saginaw Bay (Heath *et al.* 1995).

A second reason that our measurements may have given conservative estimates of the effects of zebra mussel excretion on community ammonium regeneration rates was that the abundances of zebra mussels placed in the bottles were slightly lower than *in situ* abundances found in 1992. Based on the Station 5 water-column depth of ca 3.5 m, our experimental density of 15 individuals per 4 L in the experimental bottles was calculated to be 52,500 per  $\text{m}^2$ , as compared to *in situ* abundances of 28,000 and 75,000 individuals  $\text{m}^{-2}$  at Station 5 in 1991 and 1992, respectively (Nalepa *et al.* 1995). Also, zebra mussels at Station 5 may have been physiologically stressed in 1992, relative to 1991. The mean zebra mussel ash free dry weight per shell length dropped substantially in 1992 and did not recover the following spring in 1993 (Nalepa *et al.* 1995).

Potential uptake rates for ammonium were lower in waters that had been subsampled from treatments with mussels than in waters from treatments without mussels during the first incubation intervals in July and August. This result occurred even though chlorophyll levels were not appreciably affected by the presence of zebra mussels. These data indicate that the zebra mussels could have selectively removed species of phytoplankton or bacteria that preferentially took up ammonium. In agreement with the phytoplankton uptake hypothesis, the differences in uptake rates between the zebra mussel and control treatments in July and August appeared to be enhanced in the presence of natural light (Fig. 10 vs. Fig. 8). In the June indoor experiment, ammonium uptake appeared to be higher in the mussel-water treatment than in one without mussels whereas in

October, differences between the two treatments were not detectable (SE bars overlapped; Fig. 8).

Indirect effects of the zebra mussel on community ammonium regeneration rates were inconsistent in the indoor and outdoor experiments. In the indoor treatments, regeneration rates were consistently higher in waters that had been exposed to zebra mussels than in control waters (Fig. 9), whereas in outdoor experiments, differences were not obvious (Fig. 11). In agreement with these outdoor results, ammonium regeneration rates were generally not significantly different in treatments with and without mussels in mesocosm experiments (Heath *et al.* 1995).

The most important effect of zebra mussels on community nitrogen dynamics appears to be their direct excretion of ammonium. The direct enhancement of ammonium regeneration rates caused by the zebra mussels in our experiments and the increase in ambient ammonium concentrations after the zebra mussel invasion (Johengen *et al.* 1995, Holland *et al.* 1995) both agree with the idea that ammonium excretion by zebra mussel (Quigley *et al.* 1993) is an important direct effect of the zebra mussel on nitrogen dynamics in affected ecosystems. Likewise, the zebra mussel should substantially decrease the rate and amount of community ammonium uptake in these environments, a process that would also contribute to a net increase in ammonium concentrations as has been observed in western Lake Erie and at Station 5 in the spring. By ingesting phytoplankton as well as small heterotrophic animals, mussels likely affect rates of organic mineralization in the water column. By removing heterotrophic animals (e.g., protozoans and small zooplankton) that would normally mineralize organic material and by removing a large fraction of the desirable food supplies for large zooplankton, they appear to divert the mediation of nutrient regeneration from these animals to themselves.

The complexity of foodweb interactions in both the absence and presence of zebra mussels (Fig. 1) complicates the interpretation of indirect zebra mussel effects on nutrient dynamics. For example, zebra mussels can decrease community nutrient uptake rates by directly removing phytoplankton and bacteria, but at the same time they may increase growth and nutrient uptake rates of the ones that remain by regenerating inorganic nutrients for them to use. The net indirect effects of zebra mussels on community regeneration rates is dampened by the fact that they remove small zooplankton, such as rotifers

(MacIsaac *et al.* 1991) and protozoans (Lavrentyev *et al.* 1995) that otherwise account for a quantitatively large fraction of nutrient regeneration in coastal ecosystems (Selmer 1988, Selmer *et al.* 1993). More complete biological information on zebra mussel interactions with lower foodweb organisms and associated nutrient dynamics is needed to completely interpret their indirect effects on the mediation of nutrient cycling in Great Lakes ecosystems.

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