1995

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ABSTRACT. *Concentrations of particulate and dissolved nutrients in Saginaw Bay, Lake Huron, were examined relative to zebra mussel colonization which occurred summer 1991. The magnitude and spatial pattern of changes indicate that mussels had a significant impact on nutrients in Saginaw Bay. Annual means for total suspended solids, particulate organic carbon, particulate phosphorus, and particulate silica in the inner bay were significantly lower in 1992 and 1993 (post-zebra mussel) than in 1991 (pre-zebra mussel). Annual means decreased from 11.5 mg L^{-1}, 1.45 mg C L^{-1} (121 µM), 20.4 µg P L^{-1}(0.66 µM), and 1.52 mg SiO_2 L^{-1} (24 µM) respectively in 1991 to 4.4 mg L^{-1}, 0.79 mg C L^{-1}(66 µM), 11.2 µg P L^{-1} (0.36 µM), and 0.77 mg SiO_2 L^{-1} (12 µM) in 1993. In contrast, there were no significant differences among years for these parameters at control stations, which were located in the outer bay and had no known populations of mussels. Annual means for nitrate, ammonium, and silica were significantly higher in the inner bay in 1992 than in 1991, but not significantly different in 1993. Means increased from 0.39 mg N L^{-1}, 21.0 µg N L^{-1}, and 1.11 mg SiO_2 L^{-1} respectively in 1991 to 0.47 mg N L^{-1}, 30.9 µg N L^{-1}, and 1.71 mg SiO_2 L^{-1} in 1992. No significant differences were observed for these parameters in the control group. Differences between 1992 and 1993 may reflect differences in the amount of runoff and circulation between Saginaw Bay and Lake Huron.*

A phosphorus budget indicated that zebra mussels were a significant sink for phosphorus. Mussels from the inner bay accumulated 108, 682, and 52 t respectively in 1991, 1992, and 1993. Comparatively, the annual pool of phosphorus in the water column of the inner bay decreased from a pre-zebra mussel (1979–1980) average of 712 t to 421 and 382 t in 1992 and 1993 respectively.

INDEX WORDS: *Nutrients, silica, zebra mussels, Lake Huron.*

INTRODUCTION

The introduction of the zebra mussel, *Dreissena polymorpha*, into the Laurentian Great Lakes (Hebert *et al.* 1989) has caused major changes in the structure and function of the lower food web in regions where they have become abundant. Zebra mussels impact ecosystems through their ability to establish high densities, to filter large volumes of water, and to filter particles ranging in size from 0.7 µM (Sprung and Rose 1988) up to 750 µm (Ten Winkel and Davids 1982). Zebra mussels are relatively indiscriminate filter feeders that selectively ingest particles and reject unwanted material as pseudofeces (Ten Winkel and Davids 1982). The amount of material filtered and ingested is a function of both the quality and quantity of the seston

(Walz 1978, Reeders *et al.* 1989). In a study of zebra mussels in Polish lakes, a carbon budget indicated that 30% of the seston filtered was rejected as pseudofeces and only 12% was used in the production of biomass and gametes (Stanczykowska and Planter 1985). Consequently, zebra mussels affect carbon and nutrient cycling not only in terms of the amounts utilized for growth, but more significantly in terms of the overall amount of material they filter (Stanczykowska 1984). The quantitative removal of phytoplankton and zooplankton, and the transport of these carbon and nutrient pools to the sediment, could have a major effect on the nutrient cycling within the pelagic food web.

Zebra mussels have greatly decreased standing crops of phytoplankton and increased water clarity in western Lake Erie (Holland 1993, Leach 1993, Nicholls and Hopkins 1993) and in Saginaw Bay (Fahnenstiel *et al.* 1995a), however, less is known about how their filtering activity affects nutrient cycling. The filtering activity of zebra mussels will have the direct effect of reducing nutrients which are associated with particles and plankton. Depleting the standing crop of phytoplankton could result in a secondary effect of reducing the rate at which nutrients are used within the water column. Additionally, zebra mussels have been shown to excrete significant amounts of ammonium (Quigley *et al.* 1993, Gardner *et al.* 1995) and phosphorus (Johengen, unpubl. data). These two processes would lead to increased amounts of dissolved nutrients in the water. In Hatchery Bay, western Lake Erie annual mean nitrate, ammonium, silica, and soluble reactive phosphorus concentrations increased by 38, 20, 51, and 17% respectively, after zebra mussels heavily colonized the region (Holland *et al.* 1995), suggesting these processes can be quantitatively significant. It is not, however, well understood how the combination of these direct and indirect effects will alter pelagic nutrient cycling, or how consistent the response will be across different ecosystems.

Zebra mussels were first observed in Saginaw Bay in 1990, and the first large recruitment occurred in late summer 1991 (Nalepa *et al.* 1995). Population densities increased dramatically in 1992 and then declined somewhat in 1993. At their observed densities and filtering rates, zebra mussels were processing volumes of water equivalent to the entire inner region of Saginaw Bay between 1.3 and 0.2 times per day in 1992 and 1993 respectively (Fanslow *et al.* 1995). An intensive monitoring program was conducted during 1991 to 1993 to evaluate the impact of the zebra mussel on the Saginaw

Bay ecosystem. In this paper, we document changes in total suspended solids (TSS), particulate organic carbon (POC), particulate silica (PSi), particulate phosphorus (PP), total dissolved phosphorus (TDP), dissolved organic carbon (DOC), silica (SiO_2), soluble reactive phosphorus (SRP), nitrate+nitrite (NO_3), ammonium (NH_4), and chloride (Cl). Results of concurrently collected data for total phosphorus (TP), chlorophyll, and water transparency are described by Fahnenstiel *et al.* (1995a). We also examine the role of zebra mussels in a total phosphorus budget for Saginaw Bay. The amount of phosphorus accumulated in standing stocks of zebra mussels is compared to changes in standing stocks of phosphorus within the water column, as well as to total loadings to the bay.

STUDY AREA

Saginaw Bay is a shallow extension of Lake Huron approximately 40 km wide by 80 km long and receives inputs from a drainage area of 21,000 km^2 (Smith *et al.* 1977). The bay is often functionally divided into inner and outer regions on the basis of topography and trophic gradients. Most of the nutrient load to the bay is derived from the Saginaw River (Canale and Squire 1976) and, consequently, the inner bay is characterized by higher levels of nutrients, suspended solids, and phytoplankton biomass (Dolan *et al.* 1978).

For this study, the inner bay is defined as the area within a line connecting Point Lookout on the west to the tip of Wild Fowl Bay on the east (Fig. 1). The inner bay has a surface area of 1,554 km^2, a mean depth of 5.1 m, and a volume of 7.9 km^3 (Nalepa *et al.* in press). The boundary of the outer bay is defined by a line between Au Sable Point on the west and Pointe aux Barques on the east. The outer bay has a surface area of 1,217 km^2, a mean depth of 13.7 m, and a volume of 16.6 km^3 (Nalepa *et al.* in press). Water movement in the bay has been previously described to follow a general counterclockwise pattern (Danek and Saylor 1977), flowing in from Lake Huron along the north shore, mixing with Saginaw River water, and flowing out of the bay along the south shore. However, this general circulation pattern is frequently altered by changes in wind direction (Schelske *et al.* 1980).

METHODS

Samples for dissolved and particulate nutrients were collected in Saginaw Bay at approximately
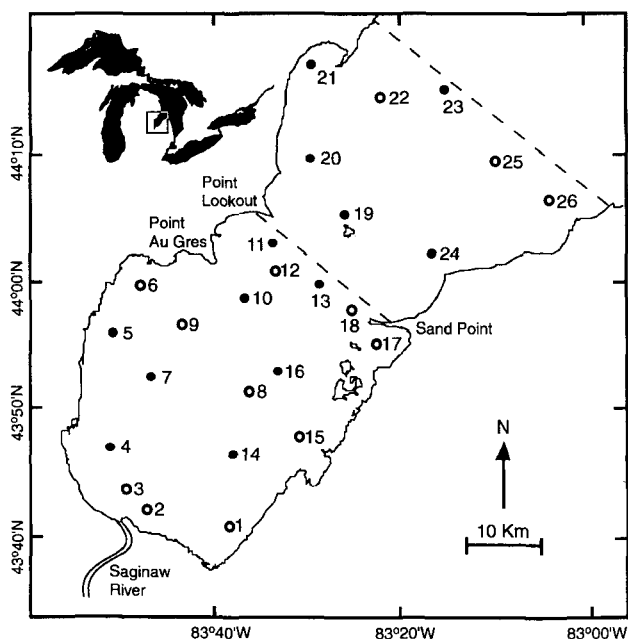
FIG. 1.   Location of sampling sites in Saginaw Bay, Lake Huron. All 26 sites were sampled in 1991 and 1992, and solid circles denote the 13 sites sampled in 1993. The dotted lines indicate inner and outer regions of the bay. The outermost sites (Stations 21, 22, 23, 25, and 26) represent a control group for comparing zebra mussel effects.

monthly intervals from April through November in 1991 and April through October in 1992 and 1993 (Table 1). In 1991 and 1992, samples were collected at 26 sites, while in 1993 the number of sites was reduced to 13. Cluster analysis was used to se-

lect sites to omit based on their similarity to adjacent sites. An analysis of variance on means from the original and subset sites for the years 1991 or 1992 indicated no significant differences ($p < 0.05$), therefore, the reduction in sampling sites should not affect comparisons to data for 1993.

Water samples were collected with a 5-L Niskin bottle at a depth of 1 m and at the mid-water column depth for stations deeper than 10 m. Samples were stored in the dark at 4°C and processed within 24 hours of collection. Nutrient concentrations were determined using standard automated colorimetric techniques (APHA 1990) on a Technicon Auto Analyzer II, as detailed in Davis and Simmons (1979). Nitrate + nitrite was determined using the cadmium reduction method and hereafter will be referred to simply as NO_3. NH_4 concentrations were determined by the Bertholet reaction, phosphorus concentrations by the molybdate/ascorbic acid method, and silica concentrations by the heteropoly blue method. TP and TDP were determined after digesting 50 mL of unfiltered and filtered sample respectively with potassium persulfate in an autoclave for 30 min (Menzel and Corwin 1965). PP was calculated from the difference between TP and TDP. PSi was determined on 100-mL aliquots of water filtered through a 0.45 m Nucleopore filter and then extracted with 1N NaOH at 95°C for 30 minutes (Krausse et al. 1983). Samples for POC and DOC were processed in triplicate by filtering 100 mL of sample through pre-combusted GFF filters. POC was determined on the filtered material using a Perkin Elmer (model 2400) CHN elemental analyzer. DOC was determined on the filtrate using a Shimadzu total organic carbon analyzer (model

TABLE 1.   Sampling dates and mean surface water temperatures (°C) for Saginaw Bay, Lake Huron. Samples were collected at 26 stations during 1991–1992, and 13 stations in 1993.

	1991		1992		1993	
Dates	Temperatures	Dates	Temperatures	Dates	Temperatures
11–18 April	8.2	14–15 April	3.8	29–30 April	7.8
1–3 May	10.4	4–6 May	10.1	17 May	13.7
20–27 May	16.8	27 May –2 June	15.1	—	—
15–18 June	22.9	15–23 June	19.0	21 June	19.5
22–26 July	23.6	20–23 July	20.2	12 July	23.6
19 -23 August	22.8	10–12 August	21.9	10 August	21.0
9 -12 September	22.1	9–15 September	19.0	8 September	19.9
7–22 October	12.2	4–7 October	14.5	5–14 October	11.9
*8–12 November					

* November 1991 was not used in any of the present analyses.

TOC-5000). TSS was determined gravimetrically after filtering between 500–2,000 mL of sample through a pre-dried, pre-weighed Whatman GFC 47-mm filter. All mass concentration units for POC, DOC, NO_3, NH_4, PP, TDP, SRP, and Cl are given for the respective element C, N, P, or Cl, whereas PSi and SiO_2 are reported as mg SiO_2/L. Further details of sampling techniques and laboratory methods are given in Nalepa et al. in press.

The phosphorus content of zebra mussels was determined using a modification of the combustion/ hot HCl procedure of Andersen (1976). Determinations were made on mussels collected at Station 5 from the inner bay during April–September of 1992. Ten to 15 mussels from each month were shucked, dried for 48 h at 90°C, and ground with a mortar and pestle. Three 10-mg aliquots were weighed for each monthly sample, placed into Pyrex test-tubes, and combusted at 450°C for 4 h. After combustion, 10 mL of 1N HCl were added to each tube and the samples boiled for 1 h. Samples were then diluted to 50 mL with distilled, deionized water and the phosphorus content determined colorimetrically.

For the purpose of trend analysis, data were aggregated into three seasons: spring (April–May), summer (June–September), and fall (October). Seasonal groupings were based on similarities in the thermal structure of the water column. The mean water temperature observed within the three seasons was 10.7, 21.3, and 12.9°C respectively (Table 1). Data collected in November 1991 were not included in the present analyses because samples were not collected for this month in 1992 or 1993. Consequently, annual means were calculated using only data collected between April–October. To simplify spatial and temporal comparisons, all analyses were made on data from the 1-m depth. These data should be representative of overall conditions within the bay because most of the bay never stratified completely, and nutrient concentrations generally exhibited minimal differences with depth (Nalepa et al. in press).

Data were also aggregated into three separate spatial groups. The inner bay consisted of Stations 1–18 and the outer bay consisted of Stations 19–26 (Fig. 1). A third control group was constructed from a subset of outer bay sites (Stations 21, 22, 23, 25, and 26) which were considered to have been minimally influenced by zebra mussels (Fahnenstiel et al. 1995a). The control group was used to compare against sites known to be affected by zebra mussels. The control group did not include Station 19, because this site

had a high abundance of zebra mussels (Nalepa et al. 1995), and the two adjacent sites (Stations 20 and 24), which were likely to be the most influenced by mixing with Station 19 water. A fourth group consisting of only sites with high zebra mussel abundances was also analyzed, but will not be discussed here because results were essentially the same as those for the inner-bay group. This finding is consistent with results for TP, chlorophyll, and secchi depths reported by Fahnenstiel et al. (1995a), who also used the same site groupings.

The presence of zebra mussels in late summer 1991 precludes this year from being a complete pre-zebra mussel year, therefore differences in the annual means between 1991 and post-mussel years are probably somewhat conservative. For comparing seasonal means, spring and summer 1991 were considered to be pre-zebra mussel periods. Current results are also compared to data collected from 1974 to 1980 as part of the Upper Lakes Reference Study (USEPA STORET). These data were collected under similar temporal and spatial scales and provide the best historical comparison to the current data. Details of the historical data set are given in Smith et al. (1977) and Bierman et al. (1984).

All statistics were performed with *Systat* ver. 5.0 (Wilkinson et al. 1992). Differences among annual and seasonal means were tested using analysis of variance. When significant differences were found, a post-hoc Tukey HSD multiple comparison was used to test for differences between specific years. All reported cases of significant differences were attained at a significance level of 5% or less.

RESULTS

Annual Means

Particulate Nutrients

In the inner bay, concentrations of TSS, POC, PP, and PSi were all significantly correlated (ANOVA, $p < 0.05$), and each parameter exhibited similar decreasing trends after zebra mussels became established. Annual means for TSS, PP, and PSi were significantly lower in both 1992 and 1993 than in 1991 (Table 2). Additionally, the annual mean for POC in 1993 was significantly lower than in 1991. Annual means for TSS, POC, PP, and PSi decreased from 11.5 mg L^{-1}, 1.45 mg L^{-1}, 20.4 µg L^{-1}, and 1.52 mg L^{-1} respectively in 1991 to 7.6 mg L^{-1}, 1.22 mg L^{-1}, 12.8 µg L^{-1}, and 0.96 mg L^{-1} in 1992. Annual means decreased further in 1993 to 4.4 mg L^{-1}, 0.79 mg L^{-1}, 11.2 µg L^{-1}, and 0.77 mg L^{-1}.

TABLE 2. *Annual mean concentrations for station groups in the inner, outer, and control regions of Saginaw Bay, Lake Huron during 1991–1993. Means are computed from monthly sampling cruises conducted during April–October (see Table 1).*

Year	TSS (mg L⁻¹)	POC (mg L⁻¹)	PP (ug L⁻¹)	PSi (mg L⁻¹)	NO₃ (mg L⁻¹)	NH₄ (μg L⁻¹)	SiO₂ (mg L⁻¹)	TDP (μg L⁻¹)	SRP (μg L⁻¹)	DOC (mg L⁻¹)	Cl (mg L⁻¹)
Inner Bay											
1991	11.5	1.45	20.4	1.52	0.39	21.0	1.11	4.2	1.9	4.2	17.9
1992	7.6	1.22	12.8	0.96	0.55	30.9	1.71	5.0	1.5	3.8	21.0
1993	4.4	0.79	11.2	0.77	0.47	19.9	1.12	5.0	0.8	3.2	13.8
Outer Bay											
1991	2.6	0.49	4.1	0.68	0.29	19.4	0.96	3.3	1.2	2.3	8.8
1992	1.3	0.39	2.7	0.41	0.32	20.3	0.94	2.8	0.8	2.4	9.7
1993	1.9	0.41	4.4	0.42	0.35	19.6	1.04	3.8	0.5	2.3	8.4
Control											
1991	1.3	0.28	2.1	0.41	0.29	18.4	1.13	3.7	1.0	2.1	7.1
1992	1.0	0.31	1.7	0.38	0.30	18.3	0.90	2.8	0.8	2.3	8.6
1993	1.8	0.35	4.5	0.37	0.33	19.9	1.09	3.2	0.5	2.2	7.0

In the outer bay, annual means for TSS, POC, PP, and PSi were initially only 20–40% of those in the inner bay, and concentrations decreased much less during the study period. Annual means for TSS, POC, PP, and PSi decreased from 2.6 mg L⁻¹, 0.49 mg L⁻¹, 4.1 μg L⁻¹, and 0.68 mg L⁻¹ respectively in 1991 to 1.3 mg L⁻¹, 0.39 mg L⁻¹, 2.7 μg L⁻¹, and 0.41 mg L⁻¹ in 1992, but differences were significant only for TSS and PSi. In 1993, annual means of particulate nutrients in the outer bay increased again and only the annual mean for PSi remained significantly less than in 1991 (Table 2).

For the control group, there were no significant differences in annual means for TSS, POC, PP, and PSi between 1991 and 1992, and the amount of change in annual means was much less than observed in the inner bay (Table 2). The only significant change in annual means for the control group was that PP was significantly higher in 1993 than in 1991. In general, changes for the control group contrast sharply with those for the inner bay, where annual means for particulate nutrient concentrations decreased between 45–62%.

Dissolved Nutrients

Annual means for dissolved nutrients were more variable than for particulate nutrients. In the inner bay, annual means for NO₃, NH₄, and SiO₂ increased significantly between 1991 and 1992, but then decreased again in 1993. Annual means increased from 0.39 mg L⁻¹, 21.0 μg L⁻¹, and 1.11

mg L⁻¹ respectively in 1991 to 0.55 mg L⁻¹, 30.9 μg L⁻¹, and 0.96 mg L⁻¹ in 1992. Annual means in 1993 were significantly less than in 1992, but were not significantly different from those in 1991 (Table 2). The annual mean for Cl, a biologically conservative element, showed a similar pattern to these nutrients but the magnitude of change was not as great. Annual means for Cl were 17% higher in 1992, and 23% lower in 1993, than the mean for 1991. The 1992 mean was significantly different from both years. The annual mean for TDP increased as did the other dissolved nutrients in 1992, but then remained the same in 1993. Annual means increased from 4.2 μg L⁻¹ in 1991 to 5.0 μg L⁻¹ in 1992 and 1993, but differences were not statistically significant. In contrast, annual means for SRP and DOC decreased continuously during the study period. Annual means for SRP concentrations decreased from 1.9 to 0.8 μg L⁻¹ between 1991 and 1993, but differences were not statistically significant. Similarly, the annual mean for DOC decreased from 4.19 to 3.21 mg L⁻¹ during the study, and the mean for 1993 was significantly less than for 1991 and 1992.

In the outer bay, changes in annual means of dissolved nutrients, with the exception of SRP, were much less than for the inner bay. Annual means for NO₃, NH₄, SiO₂, TDP, and DOC were not significantly different between 1991 and 1992. The annual mean for Cl was significantly higher in 1992, but the change was only 10%. Changes in SRP levels in

the outer bay were similar to those for the inner bay. Annual means for SRP decreased from 1.2 to 0.5 μg L^{-1} during the study, and the means for both 1992 and 1993 were significantly less than for 1991 (Table 2). The magnitude of these changes was again, however, quite small and concentrations were close to analytical detection limits most of the time. The only other significant change in the outer bay was that the annual mean for NO_3 in 1993 was significantly higher than in 1991, going from 0.30 to 0.35 mg L^{-1}.

For the control group, there were very few differences in annual means for dissolved nutrients during the study. None of the annual means were significantly different between 1991 and 1992, and only the mean for SRP was significantly different between 1991 and 1993 (Table 2). Between 1991 and 1992, annual means for TDP, NH4, and SiO2 in the control group decreased between 1 and 24%, in contrast to annual means for the inner bay which increased between 19 and 54%.
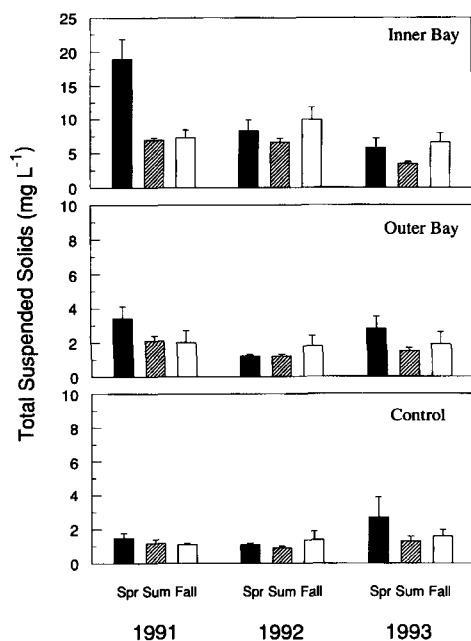
Seasonal Means

Particulate Nutrients

Concentrations of particulate nutrients and suspended solids were highly variable within years, and differences among years varied according to season (Figs. 2–5). The greatest change in particulate nutrient concentrations between years occurred in spring. In 1991, particulate nutrient concentrations peaked in spring and decreased throughout summer and fall. After 1991, however, concentrations were much lower in the spring and tended to peak in the fall. It should be noted that because zebra mussels were well established by fall 1991, it is not clear to what extent differences in fall means resulted from the effect of zebra mussels.

In the inner bay, spring means for TSS, POC, PP, and PSi decreased from 18.9 mg L^{-1}, 1.57 mg L^{-1}, 20.9 μg L^{-1}, and 2.51 mg L^{-1} respectively in 1991 to 8.3 mg L^{-1}, 0.74 mg L^{-1}, 10.6 μg L^{-1}, and 1.11 mg L^{-1} in 1992, and all differences were significant. In

FIG. 2. *Seasonal means for total suspended solids concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.*
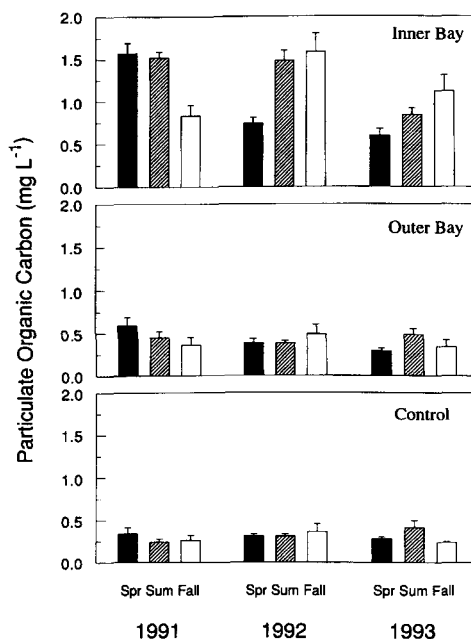

FIG. 3. *Seasonal means for particulate organic carbon concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.*

1993, spring means for TSS, POC, and PSi further decreased to 5.8 mg L^{-1}, 0.59 mg L^{-1}, and 0.77 mg L^{-1} and all means were again significantly less than for 1991. The spring mean for PP increased to 11.2 μg L^{-1} in 1993 and was no longer significantly different from 1991. In the outer bay, the spring means for TSS, PP, and PSi in 1992 were also significantly less than in 1991, however, the amount of change was again much lower than observed for the inner bay (Figs. 3–6). Spring means declined from 3.4 mg L^{-1}, 5.5 μg L^{-1}, and 0.90 mg L^{-1} respectively in 1991 to 1.2 mg L^{-1}, 1.6 μg L^{-1}, and 0.44 mg L^{-1} in 1992. Spring means for TSS and PP increased to 2.8 mg L^{-1} and 4.0 μg L^{-1} in 1993 and were no longer significantly different from 1991. There were no significant changes in spring means for any of the particulate nutrients in the control group.

Differences in summer means of particulate nutrient concentrations were not as large as those for spring means, and the greatest change occurred in 1993 instead of 1992 (Figs. 2–5). In the inner bay,

only the summer means for PP and PSi were significantly lower in 1992 than in 1991. PP decreased from 20.2 to 12.0 μg L^{-1} and PSi decreased from 0.94 to 0.74 mg L^{-1}. In 1993, summer means for TSS, POC, PP, and PSi in the inner bay decreased to 3.4 mg L^{-1}, 0.84 mg L^{-1}, 9.9 μg L^{-1}, and 0.68 mg L^{-1} respectively, and all means were significantly lower than in 1991. In the outer bay, summer means for TSS and PSi were also significantly lower in 1992 than in 1991 and declined by 0.9 and 0.17 mg L^{-1} respectively. For this period only, the change in TSS in the outer bay was actually greater than that for the inner bay. In 1993, the summer mean for TSS was again significantly less than in 1991 in the outer bay, but the decrease of 3.5 mg L^{-1} was only 17% of that for the inner bay between these years. For the control group, summer means for PP and POC were significantly higher in 1993 than in 1991.

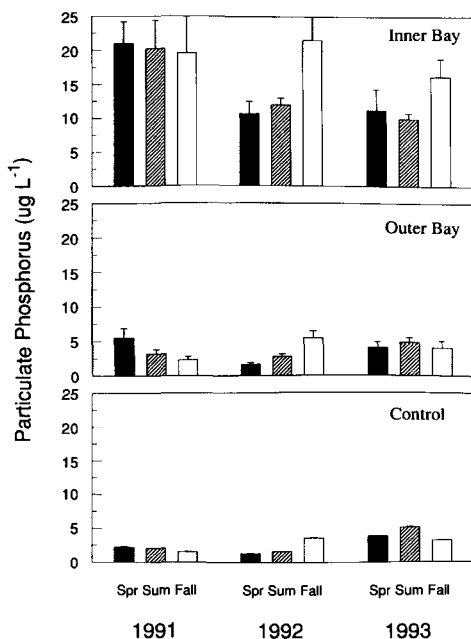Fall means did not change appreciably for any of the three site groups. The only significant change

FIG. 4. *Seasonal means for particulate phosphorus for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.*
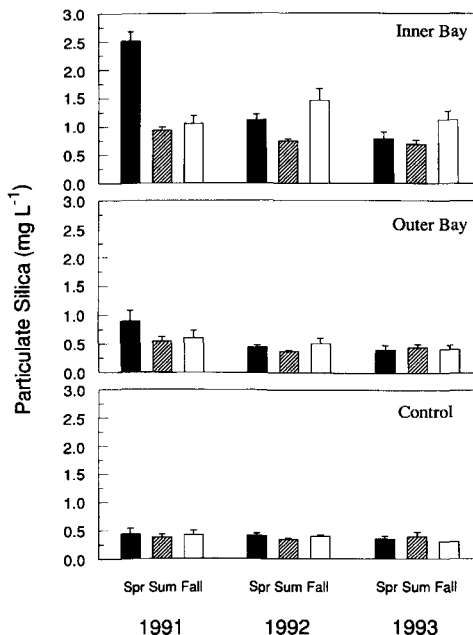

FIG. 5. *Seasonal means for particulate silica concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.*

was an increase in POC in the inner bay from 0.83 to 1.58 mg L^{-1} between 1991 and 1992.

Dissolved Nutrients

Seasonal means for inner and outer bay dissolved nutrient and chloride concentrations are presented in Figures 6–12. In general, nutrient concentrations in the inner bay exhibited a much greater range within the year than concentrations in the outer bay. This pattern reflects both the higher loading rates and higher nutrient demand within the inner bay. Seasonal patterns also varied considerably for different nutrients with respect to when concentrations were at maximum and minimum levels during the year.

Maximum NO_3 concentrations occurred in the spring, and spring means exhibited the largest amount of change among years (Fig. 6). In the inner bay, mean NO_3 concentration in spring increased from 0.76 mg L^{-1} in 1991 to 0.93 and 1.09 mg L^{-1} in 1992 and 1993 respectively, but differences were not

statistically significant. In the outer bay, spring means were similar in 1991 and 1992 (0.39 and 0.38 mg L^{-1}), but increased significantly to 0.52 mg L^{-1} in 1993. Although changes in spring means for 1993 were significant in the outer bay but not in the inner bay, the actual amount of change in the outer bay was only about 40% of that observed in the inner bay. For the control group, the spring mean for NO_3 was also significantly greater in 1993 than in 1991, but again, the increase (0.45 vs. 0.34 mg L^{-1}) was only 30% of that for the inner bay. In summer, the inner–bay mean for 1992 was significantly higher than in 1991, increasing from 0.17 to 0.36 mg L^{-1}. In the outer bay, summer means for both 1992 (0.30 mg L^{-1}) and 1993 (0.28 mg L^{-1}) were significantly higher than in 1991 (0.24 mg L^{-1}), however the amount of change was again only 30 and 40% respectively of that in the inner bay (Fig. 6). There were no significant differences among summer means for NO_3 in the control group. In fall, there were no significant differences in NO_3 in the inner
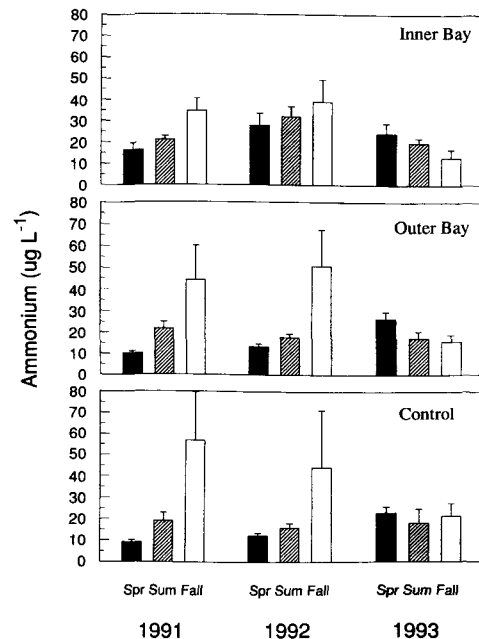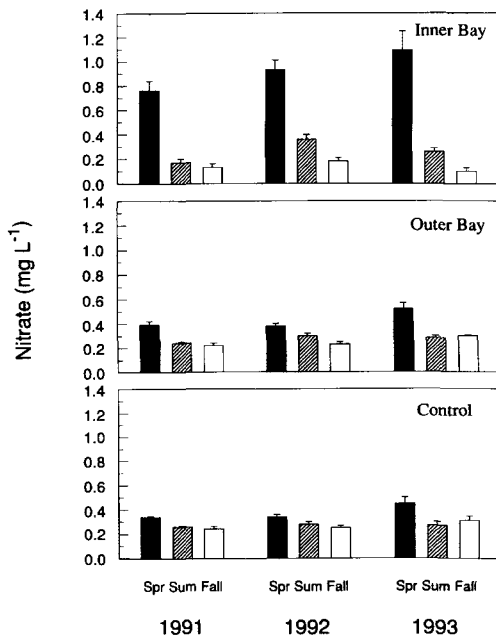

FIG. 6. Seasonal means for nitrate+nitrite concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.

FIG. 7. Seasonal means for ammonium concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.

bay, but the outer bay mean was significantly greater in 1993 (0.30 mg L^{-1}) than in 1991 (0.22 mg L^{-1}).

Seasonal patterns of NH$_4$ concentrations were very different from those for NO$_3$ concentrations. In 1991 and 1992, concentrations were lowest in the spring and increased throughout the year to maximum values in the fall. In 1993, however, there was a complete reversal in this pattern, and concentrations decreased from spring to fall (Fig. 7). In the inner bay, NH$_4$ increased between 1991 and 1992 for all three seasons, however, differences were not significant due to high spatial variability. The only significant difference among inner bay means was that the fall mean in 1993 (12.8 μg L^{-1}) was significantly less than in 1991 (34.6 μg L^{-1}). In the outer bay, the fall mean in 1993 (15.7 μg L^{-1}) was also significantly less than for 1991 (44.1 μg L^{-1}) and the amount of change was actually greater than for the inner bay. The spring means for 1993 were significantly higher than for 1991 in both the outer bay and control group.

Of the dissolved nutrients, SiO$_2$ concentrations exhibited the greatest amount of change between years (Fig. 8). In the inner bay, the spring mean for SiO$_2$ increased from 1.07 mg L^{-1} in 1991 to 1.15 and 1.55 mg L^{-1} in 1992 and 1993 respectively, and both differences were statistically significant. The summer and fall means for 1992 (1.90 and 2.59 mg L^{-1}) were also significantly higher than in 1991 (1.40 and 1.69 mg L^{-1}). In 1993, the direction of change was reversed, and summer and fall means (0.87 and 0.89 mg L^{-1}) were significantly less than in 1992, and lower also than in 1991. In the outer bay, the only significant change in SiO$_2$ was that the mean for fall 1993 (1.01 mg L^{-1}) was less than for fall 1992 (1.16 mg L^{-1}). There were no significant changes in seasonal means for SiO$_2$ in the control group.

Seasonal patterns in TDP were similar in the inner and outer bay and overall, concentrations in the two regions tended to be more similar than for the other dissolved nutrients (Fig. 9). Although none of the
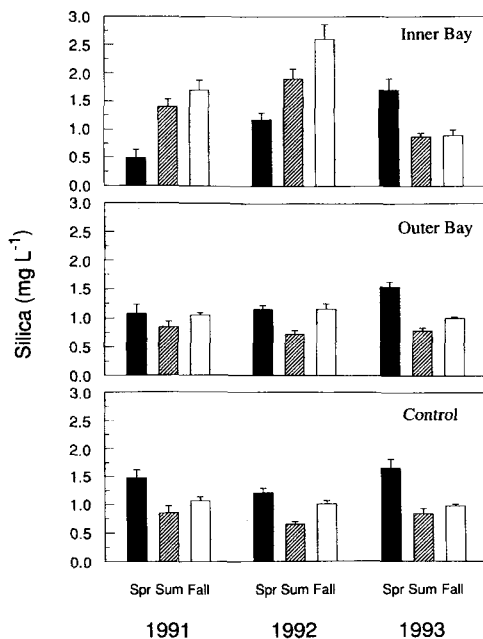

FIG. 8. *Seasonal means for dissolved silica concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.*

FIG. 9. *Seasonal means for total dissolved phosphorus concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.*
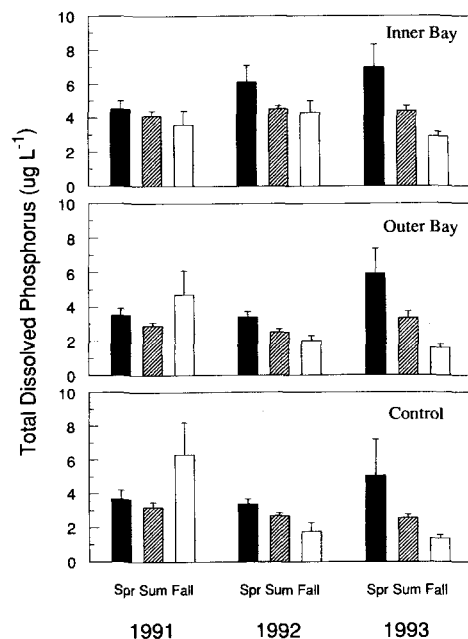
inner bay seasonal means were significantly different between years, spring means increased from 4.5 μg L^{-1} in 1991 to 6.1 and 7.0 μg L^{-1} in 1992 and 1993, respectively. In the outer bay, significant differences occurred in all seasons, but the changes were not consistent with results for other nutrients. In the control group, the fall means for 1992 and 1993 were significantly lower than in 1991.

SRP concentrations were generally quite low throughout the study period (< 2 μg L^{-1}), but concentrations in the inner bay were about twice as high as in the outer bay (Fig. 10). In both regions, concentrations tended to be highest in the spring followed by a decline throughout the year. In the inner bay, SRP decreased between 1991 and 1993 in each of the seasons, however, only the summer means for 1992 and 1993 (1.0 and 0.8 μg L^{-1}) were significantly different from 1991 (1.7 μg L^{-1}). In the outer bay, concentrations also decreased during the study, and the summer and fall means in 1992 (0.7 and 0.3 μg L^{-1}) and in 1993 (0.5 and 0.3 μg L^{-1}) were both significantly less than in 1991 (1.6

and 1.0 μg L^{-1}). There were no significant differences among seasonal means in the control group.

Temporal and spatial variations in DOC were similar to SRP although the relative amount of change among years was somewhat less. In the inner-bay, DOC concentrations were about twice as high as in the outer bay, and concentrations tended to be highest in spring and decrease throughout the year (Fig. 11). In the inner bay, the spring mean for 1993 (3.48 mg L^{-1}) was significantly less than for 1991 (5.20 mg L^{-1}). The summer and fall means for 1993 (0.84 and 2.52 mg L^{-1}) were also significantly less than for 1991 (3.80 and 2.95 mg L^{-1}). There were no significant differences among seasonal means in either the outer bay or the control group.

Chloride

Seasonal patterns in Cl varied greatly among the three years of this study. Spring means for Cl were not significantly different among years for any of the three station groupings, however, summer and
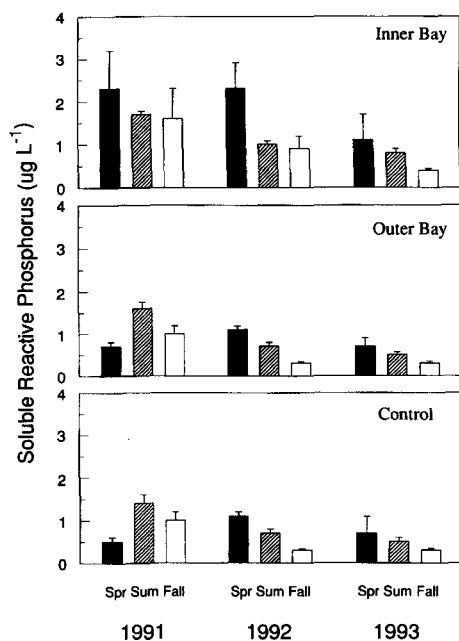

FIG. 10.   Seasonal means for soluble reactive phosphorus concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.
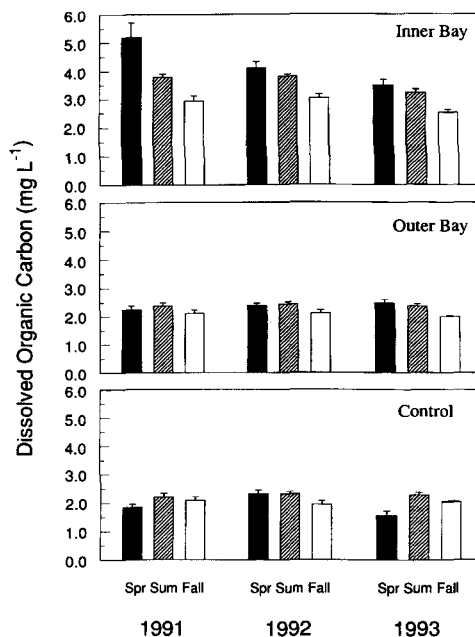
FIG. 11.   Seasonal means for dissolved organic carbon concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.

fall means were significantly different among all years in both the inner and outer regions of the bay (Fig. 12). In 1991, Cl concentrations peaked in spring and decreased throughout the year. The fall mean was 24 and 15% lower than the spring mean in the inner and outer bay, respectively. In 1992, the pattern was reversed and Cl concentrations increased throughout the year in both the inner and outer bay. Fall means were 5 and 27% higher than spring means for the inner and outer bay respectively. In 1993, Cl concentrations decreased from spring to fall, and the amount of change was approximately twice as large as in 1991. Fall means were 43 and 34% lower than spring means for the inner and outer bay, respectively.

Zebra Mussel Phosphorus Budget

The amount of phosphorus contained in the soft-tissue of zebra mussels was examined to evaluate whether zebra mussel biomass could account for a significant portion of the observed loss of phospho-
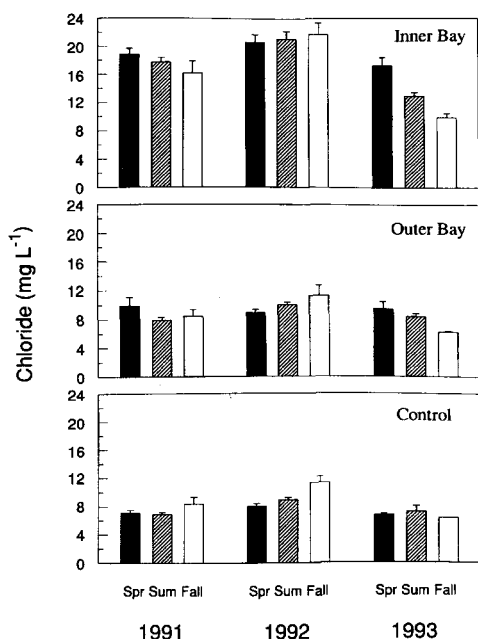

FIG. 12. Seasonal means for chloride concentrations for inner bay, outer bay, and control station groups during 1991–1993 in Saginaw Bay, Lake Huron. Spring means are computed for samples from April–May, summer means for samples from June–September, and fall means for samples from October. Error bars denote the standard error of the mean.

rus within the water column. The phosphorus content of soft tissue ranged from 0.97% (± 0.03 SE) to 1.10% (± 0.07 SE) of dry weight for mussels analyzed at monthly intervals from May–October 1992. The mean phosphorus content for all samples was 1.01% (0.02 SE) of dry weight. As a result of large changes in the biomass of adult populations, the total amount of phosphorus accumulated in standing stocks of zebra mussels varied substantially from year to year during the study. The shell-free dry weights of zebra mussel standing stocks in the inner bay were estimated at 10,700, 67,500, and 5,200 t in 1991, 1992, and 1993 respectively (Nalepa *et al.* 1995). Using a mean phosphorus content of 1.01%, the mass of phosphorus contained within the soft tissue of zebra mussels in inner bay was 108, 682, and 52 t respectively. To evaluate whether these accumulations of phosphorus were quantitatively important we compared them against estimates of the annual exchange of phosphorus through the inner bay and the annual phosphorus load to the bay. Monitoring data from 1979 and 1980 (USEPA STORET) indicate that the annual mean standing stock of phosphorus in the water column of the inner bay averaged 234 t before zebra mussels. Assuming the average water residence time within the inner bay is 120 d (Bratzel *et al.* 1977), the annual exchange of phosphorus would be 712 t. This estimate represents a net exchange of phosphorus through the inner bay and the actual flux of phosphorus would be much greater if you considered recycling between the water and sediment pools. This estimate is, however, similar to the mean annual phosphorus load to the whole bay, which averaged approximately 1,200 t for the years 1981–1992 (David Dolan, International Joint Commission, personal communication). In the present study, the phosphorus content of water in the inner bay averaged 195, 139, and 127 t in 1991, 1992, and 1993 respectively. As compared to the annual phosphorus pool of 712 t prior to the establishment of zebra mussels, these values represent a decline in annual phosphorus pools of 200, 291, and 330 t in each of the 3 years, respectively. Although the decline in phosphorus from the water column does not follow the same annual pattern as the amount sequestered by zebra mussels, the magnitude of the two estimates is similar.

DISCUSSION

Concentrations and seasonal cycles of nutrients in Saginaw Bay can be affected by a variety of physical and biological processes. The interaction

of these processes makes it difficult to evaluate the effects of any single factor, such as the establishment of zebra mussels. However, the magnitude, direction, and spatial segregation of changes in nutrient concentrations strongly suggests that zebra mussels had a significant impact on nutrient dynamics in Saginaw Bay. In general, we observed a decrease in particulate nutrient concentrations and an increase in dissolved nutrient concentrations after zebra mussels colonized the bay. This pattern is consistent with the expectation that zebra mussels would filter a significant portion of the seston from the water column, as has been observed in other regions of the Great Lakes where they are abundant (Holland 1993, Leach 1993, Nicholls and Hopkins 1993). Zebra mussels reduce concentrations of particulate nutrients by removing seston from the water and either assimilating the nutrients or depositing them onto the sediment in the form of feces and pseudofeces. Because zebra mussels filter much more material than they consume (Walz 1978, Stanczykowska and Planter 1985) their effect on standing stocks of nutrients is much greater than that needed to simply maintain growth and reproduction. As evidenced by a 59% decline in mean chlorophyll concentrations in the inner bay after zebra mussels became established (Fahnenstiel *et al.* 1995a), there has been a dramatic reduction in the standing crop of phytoplankton in Saginaw Bay. This reduction in phytoplankton abundance may in part have reduced the demand for dissolved nutrients, except SRP, within the water column. Concentrations of NO_3, NH_4, and SiO_2 tended to remain higher throughout the year and there were significant increases in spring, summer, and annual means in 1992 and 1993. Zebra mussels can also increase dissolved nutrient concentrations directly, by excreting significant amounts of ammonium and phosphorus. Net rates of ammonium and phosphorus accumulation measured in benthic chambers containing natural populations of zebra mussels reached up to 20 and 1.2 μg L^{-1} h^{-1} respectively for the inner bay (Johengen, T. H. and Cotner, J. B., Texas A&M University, unpublished data). Increased concentrations of NH_4 and SRP were also noted in a mesocosm study of zebra mussels in Saginaw Bay after 16 h of incubation (Heath *et al.* 1995). During the next 5 days, however, concentrations decreased to levels near those for control mesocosms and bacterial phosphorus demands became satiated and phytoplankton growth rates approached maximum levels in mesocosms containing zebra mussels. The authors concluded that the por-

tion of the planktonic community which was not grazed by the mussels was able to efficiently utilize the new source of NH_4 and SRP. This type of response could help explain why SRP concentrations actually declined in the bay after zebra mussel colonization, despite possible excretion of phosphorus by mussels. While SRP concentrations declined, NH_4 concentrations increased significantly during the study period. This result may partly be explained by the tendency of zebra mussels to excrete nutrients at much higher N:P ratio than utilized by phytoplankton and bacteria. Preliminary results from bottle and *in situ* chamber experiments with Saginaw Bay zebra mussels indicate that nutrients are excreted at mass ratios of greater than 40 (Johengen, T. H., unpublished data), which is much greater than the 7.2 Redfield ratio. These results indicate that phosphorus is efficiently retained within zebra mussels and the benthic region, and is not rapidly recycled into the water column. Consequently, zebra mussels may alter the N:P ratio of dissolved nutrients available to the microbial community and hence potentially alter species abundance and composition (Hecky and Kilham 1988).

The hypothesis that observed changes in nutrient concentrations resulted from the filtering activity of zebra mussels is further supported by comparing changes at inner-bay sites, where zebra mussels were most abundant, against changes at control sites where mussels were rare. Annual means for TSS, POC, PP, and PSi in the inner bay were all significantly lower in 1992 and 1993 when compared to 1991. In contrast, none of the annual means for particulate nutrients were significantly lower in 1992 or 1993 in the control group. Annual means for TSS and PSi also declined significantly in the outer bay, however, the amount of change was less than half of that found in the inner bay. The finding that some significant changes also occurred in the outer bay, even though only one site had high abundances of mussels (Nalepa *et al.* 1995a), is not surprising given the well mixed nature of the bay and the monthly sampling frequency. The same spatial segregation also existed for changes in dissolved nutrient concentrations. Annual means for NO_3, NH_4, and SiO_2 in the inner bay were all significantly higher in 1992 than in 1991, but there were no significant changes in these nutrients in the control group.

The amount of change in annual means in the inner bay was probably a conservative estimate of the effects of zebra mussels. Benthic surveys of Saginaw Bay indicated that zebra mussels were abun-

dant in September 1991 (Nalepa *et al.* 1995), and it is probable that nutrient concentrations were already affected by fall 1991. This conclusion is consistent with the result that differences in spring means for 1991 versus 1992 and 1993 were greater than those for annual means and that there were no significant differences in nutrient concentrations in the fall. Although large numbers of mussels began to settle in summer 1991 the increase in zebra mussel biomass and filtering impacts between summer 1991 and 1992 was large enough to produce significant changes in nutrient concentrations for this season.

There have been very few studies which assess the impacts of zebra mussels on nutrient concentrations. Most of the earlier work in the Great Lakes has focused on changes in water clarity and phytoplankton standing crops (Holland 1993, Leach 1993, Nicholls and Hopkins 1993). Holland (1993) reported that the total number of planktonic diatoms in Hatchery Bay, western Lake Erie declined by 86% after zebra mussels became established in the region. In the present study, we measured a 50% decrease in the annual mean of PSi in the inner bay, which in the Great Lakes is a reasonable estimate of diatom abundance (Conley *et al.* 1986). Thus, reduction in diatom abundance appears to be proportionately less in Saginaw Bay than in western Lake Erie. These results may reflect differences in both the densities of zebra mussels and the morphologies of the regions. The volume of water in Hatchery Bay is four orders of magnitude less than in inner Saginaw Bay but there is no direct information on residence times or zebra mussel abundances that would allow a comparison of the expected impact of zebra mussel filtering. In a concurrent study at this same site, Holland *et al.* (1995) reported that annual means for TP decreased by only 10% after zebra mussels became established. The lack of change was attributed to the fact that total phosphorus concentrations were probably being controlled by sediment resuspension and did not necessarily represent changes in trophic dynamics within the water column. In the present study, we saw a much greater change in phosphorus concentrations after zebra mussels became established. In the inner bay, annual means for PP decreased significantly by 45% between 1991 and 1993 and annual means for TP in Saginaw Bay decreased significantly by 48% between 1979–80 (pre-zebra mussel) and 1991–93 (post-zebra mussel) (Fahnenstiel *et al.* 1995a). Changes in SRP concentrations were also different in the two ecosystems. In contrast to an 11% increase in the annual mean for SRP in post mussel

years in Lake Erie (Holland *et al.* 1995), we observed a small, but consistent decline in SRP concentrations in both the inner and outer regions of the bay from 1991 to 1993. The different response may in part result from SRP concentrations in Lake Erie being 3–4 times higher than in Saginaw Bay, and therefore not as severely limiting. Consequently, the phosphorus supplied by zebra mussel excretion would have a greater chance of accumulating in the water column. The observed changes in NO_3, NH_4, and SiO_2 in Saginaw Bay were, however, similar to results for western Lake Erie. Annual means for NO_3, NH_4, and SiO_2 increased by 38, 20, and 51% respectively in Hatchery Bay after zebra mussels became established (Holland *et al.* 1995). The magnitude and direction of these changes was similar to those observed in the present study. The 49% decrease in annual means of PSi between 1991 and 1993 (Table 2), indicates that the increase in SiO_2 (and presumably the other dissolved nutrients) resulted in part from a dramatic reduction in the standing crop of planktonic diatoms.

Trends in Cl concentration indicate that there may have been substantial differences in the amount of runoff and in the amount of mixing between Lake Huron and Saginaw Bay between years during the study period. For example, in 1993, Cl concentrations declined by 43 and 34% respectively in the inner and outer bay between spring and fall. Spring means for Cl concentrations were not significantly different between years, however, summer and fall means for 1993 were significantly lower than in comparable seasons in both 1991 and 1992. Two factors can influence Cl concentrations in Saginaw Bay: relative inputs from tributaries and relative exchange rates between bay water and Lake Huron. Tributaries of the watershed have Cl concentrations 2–10 fold higher than in the bay (MDNR 1994) and would act as a source of Cl. Conversely, Cl concentrations in open Lake Huron are typically 5.5 mg L^{-1} (Lesht and Rockwell 1987) as compared to annual means of 18 and 10 mg L^{-1} in the inner and outer bay respectively, and any increase in mixing into the bay should reduce Cl levels. Both factors are likely important, although a comparison of monthly and seasonal runoff volumes within the watershed (Frank Quinn, Great Lakes Environmental Research Laboratory, personal communication) and monthly and seasonal chloride concentrations in the bay showed no significant correlations. This finding, along with observed yearly differences in Cl gradients along the axis of the bay, indicates that mixing patterns are

quite complex and strongly affect the distribution of Cl within the bay. In 1992, the distribution of Cl appeared to be heavily influenced by runoff. Increased Cl levels in summer and fall of 1992 presumably resulted from the amount of runoff during June–September being 2.8 and 2.0 times higher in 1992 than in 1991 and 1993 respectively (Frank Quinn, Great Lakes Environmental Research Laboratory, personal communication). The higher amount of runoff in summer 1992 may partly explain why particulate nutrient concentrations declined less in 1992 than in 1993. In contrast, Cl concentrations in the inner bay in summer and fall 1993 were 27 and 39% lower than in summer and fall 1991 despite similar amounts of runoff in the 2 years. This result, coupled with the finding that there was very little gradient in concentration along the axis of the bay, indicate that water was well mixed within the bay and that there was an increased contribution of water from Lake Huron in 1993. Reasons for this pattern in 1993 are presently unclear. Skubinna *et al.* (1995) reported that there were no significant shifts in wind speed and direction in Saginaw Bay during 1991–1993, and concluded that there should not have been any major shifts in circulation patterns.

Even though there might have been substantial differences in circulation patterns and runoff, it is not known to what extent these factors might affect our measurements of nutrient concentrations. Water in the inner bay has an average residence time of around 120 d (Bratzel *et al.* 1977). In contrast, zebra mussels filtered an equivalent volume of the inner bay every 1–5 d (Fanslow *et al.* 1995), and algal growth rates were on the order of 0.2–0.3 d^{-1} (Fahnenstiel *et al.* 1995b). Thus, it seems logical that biological processes should still exert the most influence on dissolved and particulate nutrient concentrations. It is, however, important to consider the possible effects of loading and circulation when working in such physically dynamic ecosystems such as Saginaw Bay.

There is evidence to suggest that particulate and dissolved nutrient concentrations in spring 1991 were higher than normal, leading to greater differences between pre- and post-mussel years for this season. To partially address this question, the current data set was compared to data collected from 1974 to 1980 as part of the Upper Lakes Reference Study (USEPA STORET). For the inner bay, the spring mean for TSS was 40% higher in 1991 than in 1980, however, means were not significantly different. TP and chlorophyll data from spring 1991

(Fahnenstiel *et al.* 1995a) were 14 and 44% greater respectively than for spring 1980, but again, differences were not statistically significant. For dissolved nutrients, spring means for Cl and NO_3 were 8 and 19% higher respectively in 1991 versus 1980, but again, these differences were not statistically significant. Spring means for SiO_2 were 25% lower in 1991 than in 1980 and spring means for TSS, PP, NO_3 and SiO_2 in 1980 were also significantly lower than spring means in 1992.

Zebra mussels appear to be a significant sink for phosphorus in Saginaw Bay, although it is not certain what the long-term fate of this material might be. The percentage of phosphorus in the soft tissue of mussels was slightly higher in Saginaw Bay (0.97–1.10% dry weight) than reported for mussels from Polish lakes (0.84–0.92% dry weight; Stanczykowska and Planter 1985). In the present study, phosphorus content of the shells was not measured, but Stanczykowska and Planter (1985) estimated that the amount of phosphorus in the shell was approximately 20% of that in soft tissue. Thus, our estimates of phosphorus in mussel standing stocks are somewhat conservative. When mussels were most abundant in 1992, the population biomass contained 682 t of phosphorus. This standing stock is equivalent to 56% of the average annual phosphorus load from the Saginaw River to the entire bay over the last decade. Although yearly changes in phosphorus concentrations within the water column did not consistently follow yearly changes in mussel standing stocks, it seems clear that zebra mussels played a major role in reducing phosphorus levels within the water column. The amount of phosphorus contained in population standing stocks ranged from 20 to 200% of the observed decrease in the annual phosphorus pool in the inner bay. The large variation in these estimates is again a reflection of the large variability in standing stocks of mussels. Zebra mussels assimilate only a small fraction (< 20%) of the material that they process during filtration (Stanczykowska and Planter 1985), therefore, this estimate of a phosphorus sink should be quite conservative relative to their potential impact. The fact that zebra mussels could account for more than 100% of the water-column change in a given year (682 t vs. 291 t in 1992) is not surprising given that annual phosphorus loads vary by 2-fold between years and the potential for differences in the amount of phosphorus contributed from the sedimentary pool for any given year. Furthermore, the annual phosphorus load to the bay supplies a greater amount of phos-

phorus than is estimated for the annual exchange of phosphorus based on water column concentrations and could alone account for the ex*ra phosphorus found within the mussel standing stocks.

ACKNOWLEDGMENTS

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