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ABSTRACT. *A large-scale study of Saginaw Bay was initiated in 1990 and continued through 1993 to examine the effects of the zebra mussel colonization which began in summer/fall 1991. Saginaw Bay responded quickly to the zebra mussel colonization, as fall 1991 values of chlorophyll were similar to 1992 and 1993 values. In inner Saginaw Bay, where most zebra mussels were found, chlorophyll, kPAR, and total phosphorus values decreased, and Secchi disk depth increased during the study period, regardless of the presence or absence of zebra mussels at a specific station. At outer bay control stations no significant differences were found for chlorophyll, kPAR, and Secchi disk values. In order to examine longer-term trends, water quality data from 1979–1980 (STORET) were combined with our 1990 data (pre-zebra mussel period) and compared to values from the post zebra mussel period (fall 1991, all 1992 and 1993). At stations with high densities of zebra mussels, chlorophyll and total P decreased by 66% and 48%, respectively, and Secchi disk values increased 88%. At outer bay control stations no significant differences were found for chlorophyll or Secchi disk. When parameters were averaged throughout inner Saginaw Bay, zebra mussels caused a 59% and 43% decrease in chlorophyll and in total phosphorus and a 60% increase in Secchi disk transparency. Although zebra mussels significantly altered water quality parameters in the pelagic region of Saginaw Bay, they did not necessarily change system trophic state; rather they altered the spatial partitioning of resources.*

INDEX WORDS: *Zebra mussels, water quality, Saginaw Bay.*

INTRODUCTION

Saginaw Bay is one of the most heavily impacted areas in the Great Lakes (Stoermer and Theriot 1985) with some of the highest recorded standing stocks of phytoplankton and productivity (Vollenweider *et al.* 1974). Major deterioration of Saginaw Bay has occurred within the last 100 years due to degradation of water quality and invasion by non-indigenous species (Freedman 1974). In the mid-1970s phosphorus abatement controls were initiated throughout the basin. During the same period a large multidiscipinary research program, as part of the Upper Great Lakes Reference Study, was initiated to assess the water quality of Saginaw Bay (Bierman *et al.* 1984). This study, along with smaller studies in the 1970s and 1980, became the basis for assessing the response of the bay to phosphorus load reductions. Between 1974 and 1980, a 56% reduction in phosphorus load produced a 50% decrease in chlorophyll and a slight increase (<20%) in light transparency (Bierman *et al.* 1984).

One of the more significant non-indigenous species to become established in the Great Lakes is the zebra mussel, *Dreissena polymorpha*. The zebra mussel was first introduced to the Great Lakes around 1986 and established abundant populations in Lake St. Clair and Lake Erie by 1990 (Hebert *et al.* 1991, Leach 1993). In both Lake Erie and Lake St. Clair significant changes in water quality were noted after this species became established. Phytoplankton abundance and chlorophyll decreased dramatically with a concurrent increase in water clarity (Holland 1993, Leach 1993, Nichols and Hopkins 1993, Nalepa *et al.* 1993).

With the likelihood that the zebra mussel would spread throughout the Great Lakes and establish large populations in other shallow eutrophic bays, we initiated a large ecosystem study of Saginaw Bay in 1990. Large populations of zebra mussels did become established in Saginaw Bay in 1991 (Nalepa *et al.* 1995). In this paper we specifically examine trends in pelagic water quality parameters, chlorophyll, total phosphorus, Secchi disk transparency, and the underwater extinction coefficient of photosynthetically active irradiation (kPAR) from 1990 through 1993. We also reanalyzed water quality data collected in Saginaw Bay from 1974–1980 to put more recent trends into a longer-term perspective.

METHODS

Sampling was conducted at ten stations on three occasions (May, July, and September) in 1990, at 26 stations on nine occasions from 11 April through 12 November in 1991; at 26 stations on eight occasions from 13 April through 14 October in 1992, and at 13 stations on seven occasions from 27 April through 14 October in 1993 (Fig. 1). On a few occasions in 1993, additional stations (2–7), corresponding to 1991–1992 stations, were sampled. The sampling protocol was similar throughout the study period (1990–1993) except that nutrient samples and Secchi disk measurements were not collected in 1990.

We used the same differentiation between inner and outer regions of Saginaw as Bierman *et al.* (1984), which corresponds roughly to a line from Sand Point to Point Lookout (Fig. 1). The inner bay is a relatively shallow region (mean depth 5 m) directly influenced by the Saginaw River and considered eutrophic. The Saginaw River accounts for over 70% of the total tributary flow to the bay (F. Quinn, personal communication, Great Lakes Environmental Research Laboratory) and drains nearly 80% of the total drainage basin (Freedman 1974). The outer bay, on the other hand, is deeper (mean depth 14 m), more influenced by Lake Huron, and considered oligotrophic. The inner and outer regions of Saginaw Bay are approximately equal in surface area, but the inner bay possesses only 30% of volume of the entire bay. Seven stations were sampled in the inner bay in 1990, eighteen stations in 1991 and 1992, and eight in 1993. Three stations were

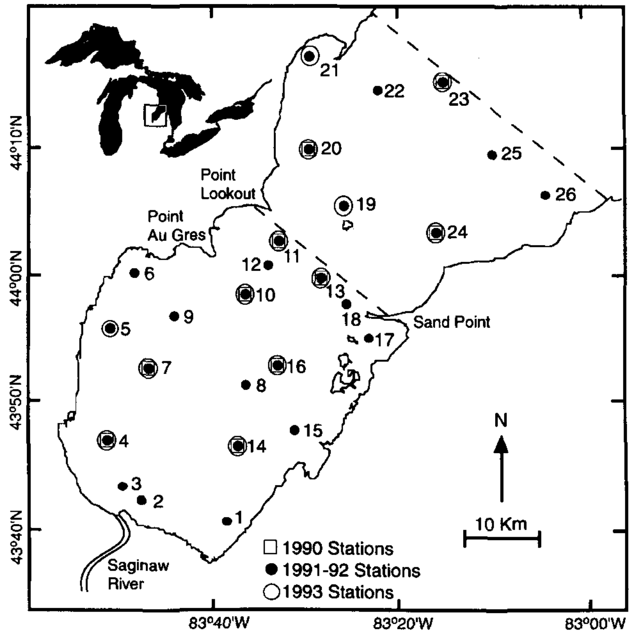

FIG. 1. Location of sampling sites in Saginaw Bay, Lake Huron, 1990–93. Dashed lines differentiate the inner bay from the outer bay and the outer bay from Lake Huron.

sampled in the outer bay in 1990, eight stations in 1991 and 1992, and five stations in 1993.

At each station a Sea-Bird CTD with fluorometer and transmissometer (25-cm beam path) was lowered from the surface to just above bottom. All data were sampled twice each second. Secchi disk transparency was measured with a 25-cm black/white disk. Underwater light extinction of photosynthetically active irradiation (kPAR) was measured with a LI-COR 193SB spherical (4 π) light sensor and LI-COR 1000 data logger.

Water samples were collected at 1 m at all stations and also at mid-depth for stations deeper than 9 m using a 5-l Niskin bottle. Samples for chlorophyll concentrations were filtered onto GF/F Whatman Glass Fiber filters and extracted and ground in 90% acetone (Strickland and Parsons 1972). Total phosphorus samples were analyzed by a modified persulfate oxidation method (Davis and Simmons 1979). Samples were digested with potassium persulfate for 30 min. at 120°C and 15 psi. Digested samples were analyzed by the molybdate/ascorbic acid method.

At sampling stations where two depths were sampled, chlorophyll and total phosphorus data were depth weighted and then averaged to provide a station mean value. At stations where only a single depth was sampled, this value was used as the water column mean.

Continuous profiles of chlorophyll fluorescence and transmissometry were used to interpret data between discrete sampling depths and to provide a check for possible outliers. Overall, good agreement was noted between water column depth-weighted values of chlorophyll concentration based on extracted values and continuous profiles of chlorophyll fluorescence using the CTD profiler ($r = 0.90$, $p = <0.0001$, $n = 80$). Thus, our water column averages, whether from one or two discrete depths, are accurate estimates of water column concentrations.

Prior to our sampling in 1990, an extensive study was conducted in Saginaw Bay from 1974–1980 as reported in Bierman *et al.* (1984). Sampling was conducted at 16 stations on an approximately monthly basis from February–December in 1974–1976 and from April–December 1977–1980. Spatially, these 16 stations were located in close proximity to the following stations sampled in this study: Stations 2, 3, 7, 8, 9, 12–17, 19, 22, 23, 25, 26. Data from this earlier study were provided by STORET and were analyzed in the same manner as data collected in 1990–1993 to provide a historical perspective on water quality trends.

Cruise average temperatures revealed a distinct and consistent cycle which allowed separation between spring (<15°C), summer (>15°C) and fall (<15°C) periods for all 4 years of sampling (Fig. 2). Using this differentiation, the spring period included samples taken in April and May, the summer period included samples taken in June through September, and the fall period included samples taken in October and November. In 1991 through 1993 samples were collected during all three periods; in 1990, however, samples were collected only in the spring and summer periods.

Most analyses from this study involve comparisons of various parameter values (chlorophyll, total P, Secchi, kPAR) from distinct spatial and temporal periods, i.e., spring, summer, fall, control stations, zebra mussel stations, etc. Figures display annual or seasonal mean values, whereas all data were used for statistical analyses. The figures are for illustrative purposes and therefore error bars are included only where they will not confuse the illustration. The statistical analyses of all data associated with each figure are reported in the results section. To examine the usefulness of parametric statistics the Lilliefors test (Lilliefors 1967) for normality was applied to the four parameters from three distinct

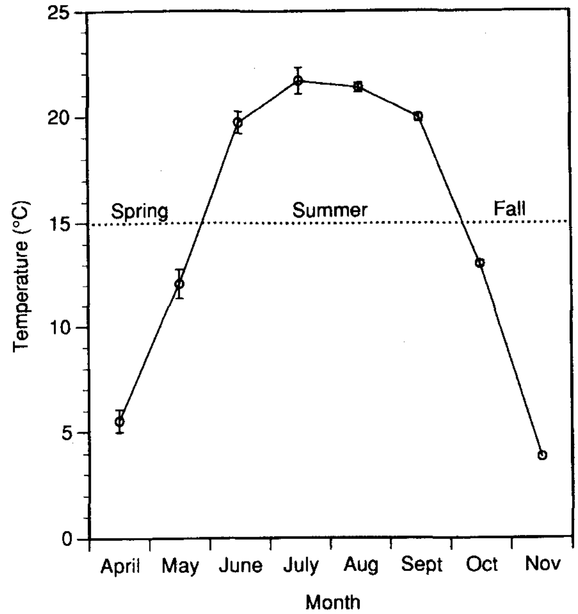

FIG. 2. Mean surface-mixed layer temperatures during monthly sampling from 1990–1993. Dashed line at 15°C is used to separate spring, summer, and fall periods. Error bar is one standard error.

seasons of 3 years and for two groups of stations. Despite limited data for some cases, in 54 of the 72 cases (75%) distributions were not significantly different from normal ($p > 0.05$). Thus, parametric statistics are justified. ANOVA and regression analyses were used to analyze overall trends among groups, and individual comparisons in specific temporal or spatial periods were analyzed with t-test or Tukey-Kramer HSD test when ANOVA was used.

Zebra mussels became widespread and abundant in Saginaw Bay in summer 1991, and abundant populations were found throughout 1992 and 1993 (Nalepa *et al.* 1995). Thus, all 1990 data should be indicative of pre-mussel conditions, whereas all 1992 and 1993 data should reflect conditions impacted by zebra mussels. Because 1991 was a transition year, data from this year should be interpreted with caution.

RESULTS

1990–93 Period

Several measurements of water clarity were made in this investigation including Secchi disk transparency, underwater light extinction (kPAR), and light transmission. Although all three measurements characterize water clarity, they may not exhibit similar values or trends due to differences in what is measured and in the optical properties of the water (Kirk 1983). In Saginaw Bay we found good agreement between all three measures of water clarity. Values of kPAR, which have the most biological relevance, were strongly correlated with Secchi disk values ($R^2 = 0.92$, Fig. 3a) and light transmission readings ($R^2 = 0.89$, Fig. 3b).

Trends in all water quality parameters, chlorophyll, total P, kPAR, and Secchi disk transparency, were very different in inner and outer Saginaw Bay (Figs. 4–7). Overall for the 1990–1993 period, significant differences were noted for all water quality parameters in both inner and outer bay ($p < 0.01$); however, more consistent and distinct trends were noted for water quality parameters from the inner bay (Figs. 4–7). In the inner bay, chlorophyll, kPAR, and total P values decreased significantly, whereas Secchi disk values increased significantly (individual regression analysis, all $p < 0.003$; Figs. 4a–7a). Chlorophyll and kPAR values decreased by approximately 50% and 25%, respectively, for the 1990–1993 period. It is important to note that chlorophyll and kPAR were measured all 4 years, while Secchi disk and total P were not measured in 1990. On a seasonal basis, chlorophyll, kPAR, and total P values all decreased significantly during spring and summer periods from 1990 or 1991 though 1993, whereas Secchi values increased significantly ($p < 0.01$; Figs. 4b–7b).

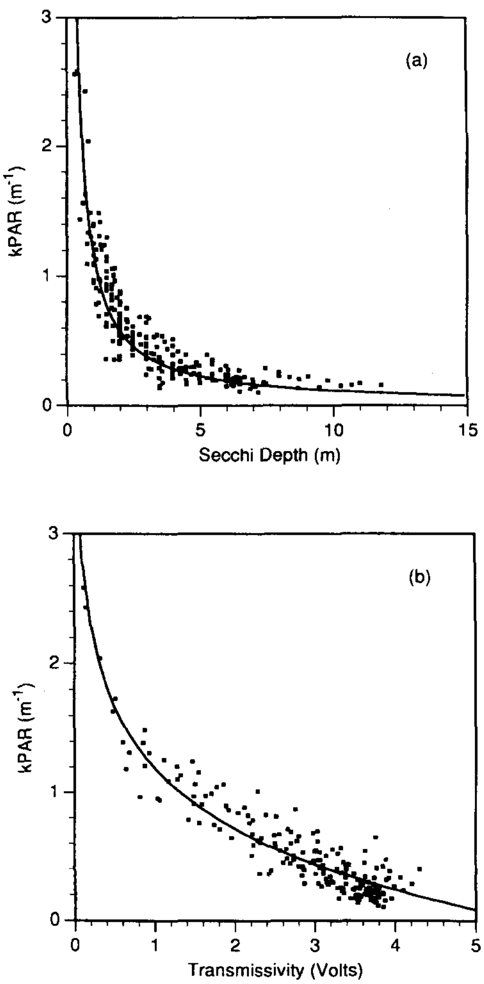

*FIG. 3. Comparison of three measures of the underwater light field from Saginaw Bay: a) kPAR vs. Secchi disk depth (kPAR= 1.16 (Secchi)$^{-1}$, R^2= 0.92, n = 231); b) kPAR vs. light transmittance (kPAR = 1.19 –0.698*ln (trans),R^2= 0.89,n = 190).*

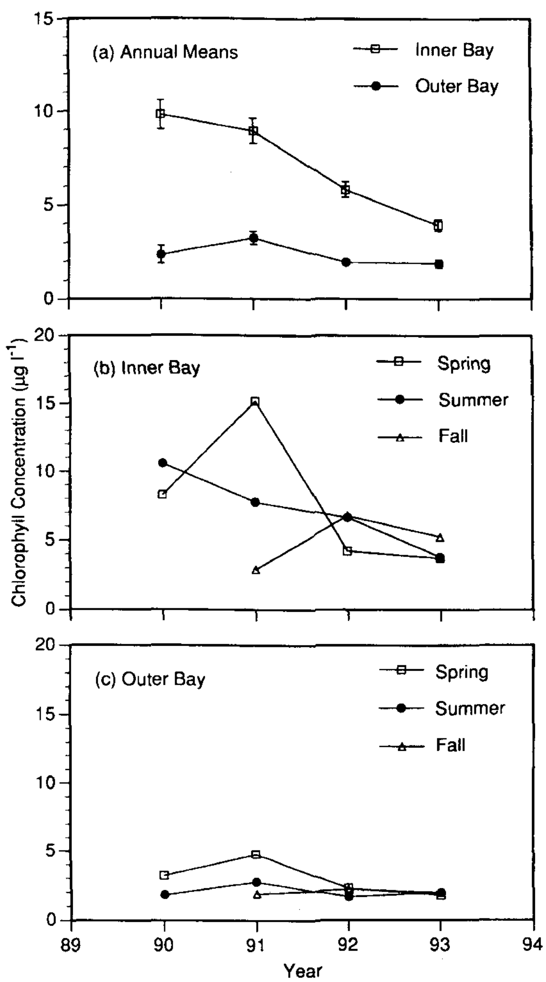

FIG. 4. Seasonal and annual mean chlorophyll concentrations in inner and outer Saginaw Bay from 1990–1993: a) annual means, b) seasonal means for inner bay, c) seasonal means for outer bay. Error bar is one standard error.

In the outer bay water quality parameters were very similar in the 1990–1993 period as fewer significant trends were noted (Figs. 4a–7a). On a seasonal basis, significant decreases were noted only for spring chlorophyll and summer kPAR ($p < 0.02$).

While trends in water quality parameters of the inner and outer bays are important, they may not display the effects of zebra mussels due to the patchiness of zebra mussel populations in Saginaw Bay (Nalepa *et al.* 1995). Of the ten stations sampled for zebra mussels in the inner bay only six had significant populations (Fig. 8). On at least one occasion, each of these six stations had recorded densities of >4,000/m^2. At the other four inner bay stations zebra mussels were either absent or present at low abundances (<20/m^2). In the outer bay zebra mussels were abundant at only one station (Station 19), but some of the highest recorded zebra mussel densities (on one occasion >50,000/m^2) were found at this station.

To more specifically examine the possible effect of zebra mussels on water quality parameters from 1990–1993, we grouped the stations based on relative densities of zebra mussels (Nalepa *et al.* 1995) and then compared values of water quality values from the three groups. The first group (termed zebra 2) consisted of seven stations with high densities of zebra mussels (Stations 5, 6, 13, 14, 15, 16, and 19); the second group (termed zebra 1) consisted of twelve inner bay stations where zebra

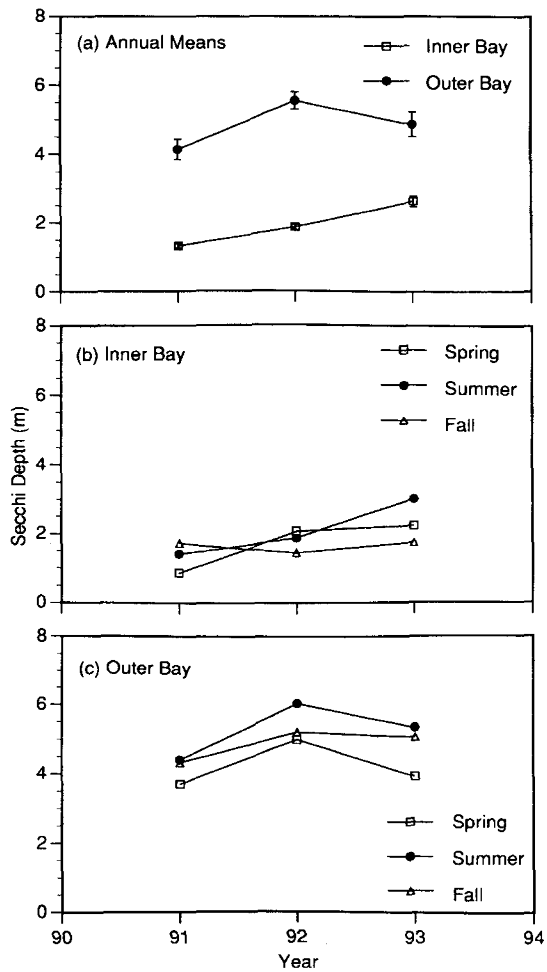

FIG. 5. Seasonal and annual mean values for Secchi disk depth in inner and outer Saginaw Bay from 1991–1993: a) annual means, b) seasonal means for inner bay, c) seasonal means for outer bay. Error bar is one standard error.

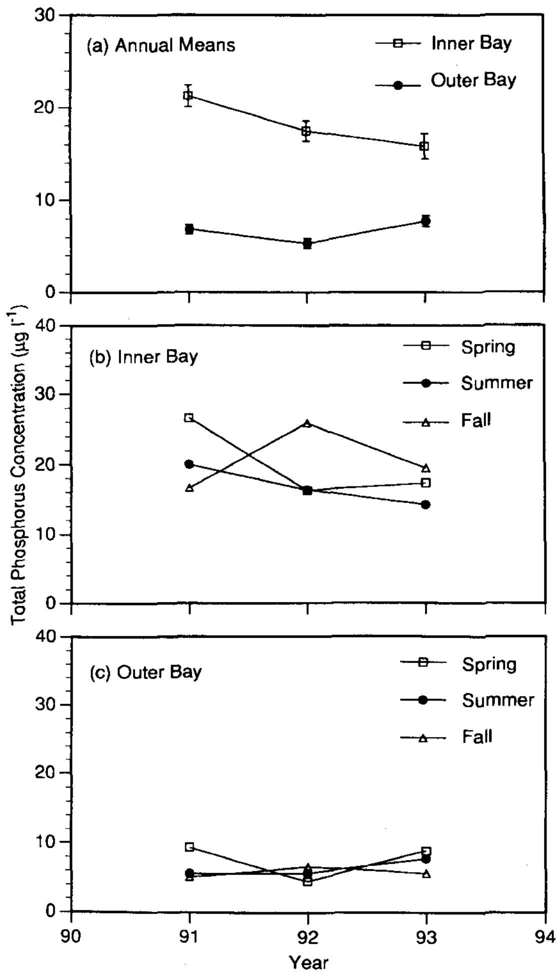

FIG. 6. Seasonal and annual mean total phosphorus concentrations in inner and outer Saginaw Bay from 1991–1993: a) annual means, b) seasonal means for inner bay, c) seasonal means for outer bay. Error bar is one standard error.

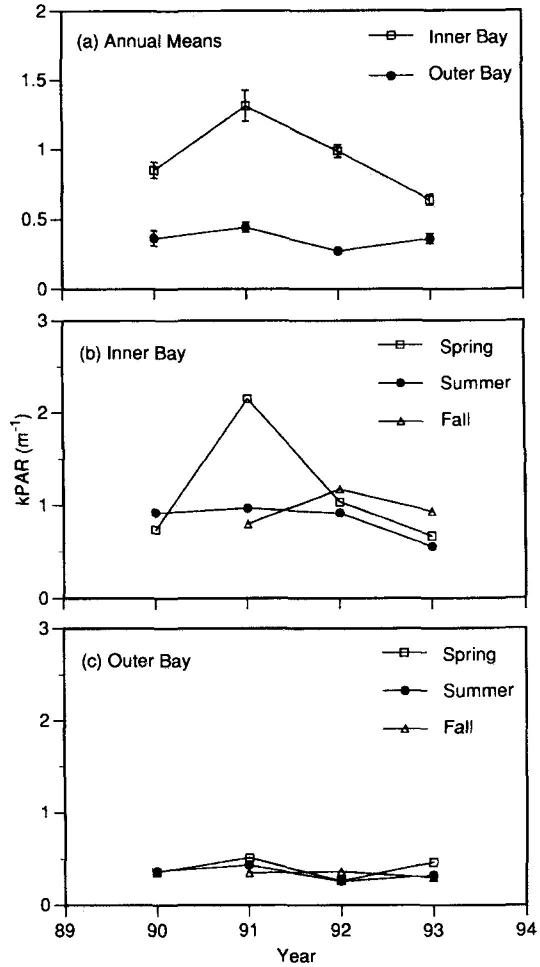

FIG. 7. Seasonal and annual mean kPAR values for inner and outer Saginaw Bay from 1990–1993: a) annual means, b) seasonal means for inner bay, c) seasonal means for outer bay. Error bar is one standard.

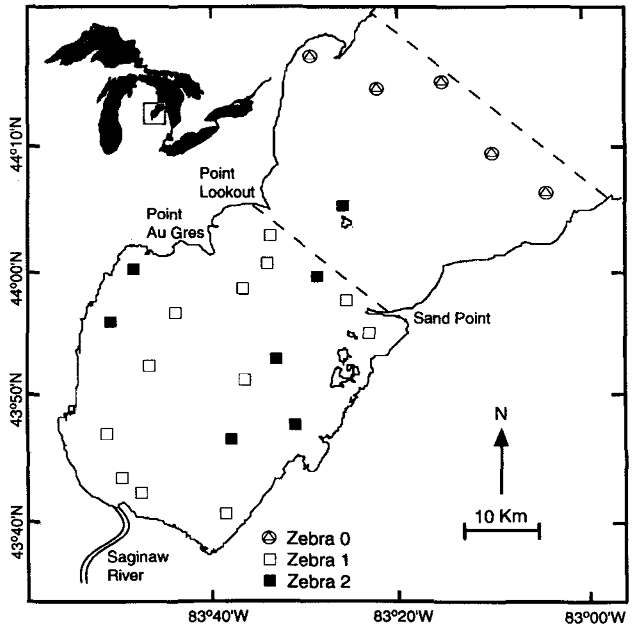

FIG. 8. Map of Saginaw Bay showing designation of zebra mussel stations. Zebra 2 are stations with high densities of zebra mussels (>4,000/m² on at least one occasion). Zebra 1 are inner bay stations where zebra mussel densities were zero, low, or unknown. Zebra 0 are outer bay control stations where zebra mussel densities were zero, or unknown but had a substrate not conducive for mussel colonization and were removed from stations with mussels.

mussel densities were low, zero, or unknown, but where the effects may be evident due to the well-mixed nature of the inner bay (Stations 1, 2, 3, 4, 7, 8, 9, 10, 11, 12, 17, and 18); the third group (termed zebra 0) consisted of five stations in the outer bay (Stations 21, 22, 23, 25, and 26) where mussel densities were zero, or unknown, but had a substrate not conducive for mussel colonization and were removed from stations with mussels (Figs. 1 and 8).

Significant differences in values of chlorophyll, total phosphorus, kPAR, and Secchi disk were noted for zebra mussel stations (zebra 2) for the study period (all $p < 0.001$ except total phosphorus with $p = 0.02$; Fig. 9). At these stations, mean values for chlorophyll, kPAR, and total phosphorus decreased by 69%, 35%, and 24%, respectively, while Secchi disk values approximately doubled (Fig. 9). During the same period significant differences were also noted at other inner bay stations (zebra 1) for chlorophyll, Secchi disk, and kPAR values (all $p < 0.003$, Fig. 9a–c), but not total P values ($p = 0.12$, Fig. 9d). Chlorophyll, kPar, and total P mean values decreased by approximately, 57%, 22%, and 25%, respectively, while mean Secchi disk values approximately doubled.

Comparisons of mean values for individual years for zebra mussel stations (zebra 2) suggest that the major changes occurred between 1991 and 1992. Mean chlorophyll concentrations in 1992 (4.0 $\mu g \cdot L^{-1}$) and 1993 (2.8 $\mu g \cdot L^{-1}$) were not significantly different from each other ($p = 0.7$), but were significantly different from values in 1990 (9.0 $\mu g \cdot L^{-1}$) and 1991 (8.0 $\mu g \cdot L^{-1}$)($p < 0.05$). Similarly, Secchi disk values in 1992 (2.7 m) and 1993 (3.0 m) were not sig-

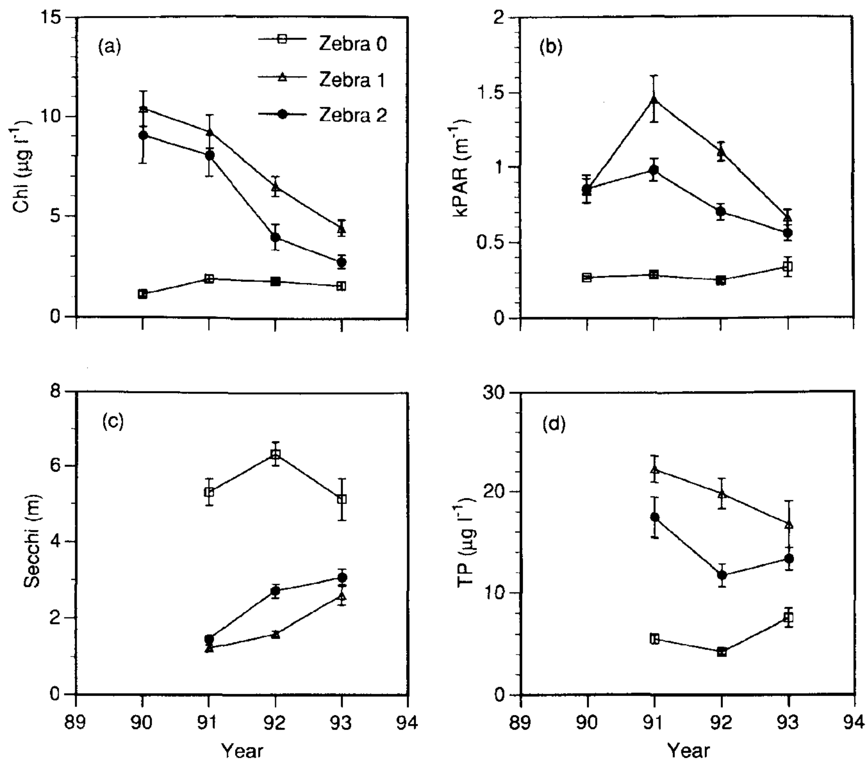

FIG. 9. Annual means of various water quality parameters: a)chlorophyll, b) kPAR, c) Secchi disk depth, d) total phosphorus at three groupings of stations: zebra 2, zebra 1 and zebra 0. See Figure 8 for an explanation of these station groupings. Error bar is one standard error.

nificantly different from each other (p = 0.33), but were significantly different from values in 1991 (1.5 m; both p <0.001). For zebra mussel stations, the most dramatic changes in water quality parameters were found during the spring and summer periods; little change was detected in fall values (Fig. 10a–d), which was probably related to the lack of sample collection in fall 1990. Significant seasonal differences were noted for spring and summer values of chlorophyll, Secchi disk, and kPar (all p <0.002). Fall values for the same parameters did not exhibit significant differences (all p >0.1, Fig. 10).

Unlike values at the station group with high mussel densities (zebra 2) and the station group of other inner bay stations (zebra 1), values of chlorophyll, Secchi disk, and kPAR at the control station group (zebra 0) were very similar throughout the study period and exhibited no significant differences, either overall or on a seasonal basis (all p >0.05, Fig. 9). Mean values for chlorophyll, Secchi disk and kPAR ranged from 1.1–1.9 μg • L^{-1}, 5.1–6.3 m, and 0.25–0.33 m^{-1}, respectively. Significant differences for total phosphorus concentrations were noted, however, for this control station group (p <0.001, Fig. 9d).

1974–1993 Period

Water quality measurements made in Saginaw Bay in 1974–1980 are useful to examine the more long–term trends in values before and after zebra mussel colonization (Figs. 11–13). Values in 1979 and 1980 are particularly useful since this was the period after major phosphorus load reductions (Bierman *et al.* 1984). Mean chlorophyll values in 1979, 1980, and 1990 were not significantly different for stations with high mussel densities (zebra 2; p >0.5) and control stations (zebra 0; p >0.15) (Fig. 11). Thus, we include data from 1990 with those of 1979 and 1980 as pre-zebra mussel conditions. Similarly, data from fall 1991 can be combined with data from 1992 and 1993 to represent conditions after the establishment of zebra mussels in Saginaw Bay. Chlorophyll values from fall 1991, 1992, and 1993 were not significantly different for

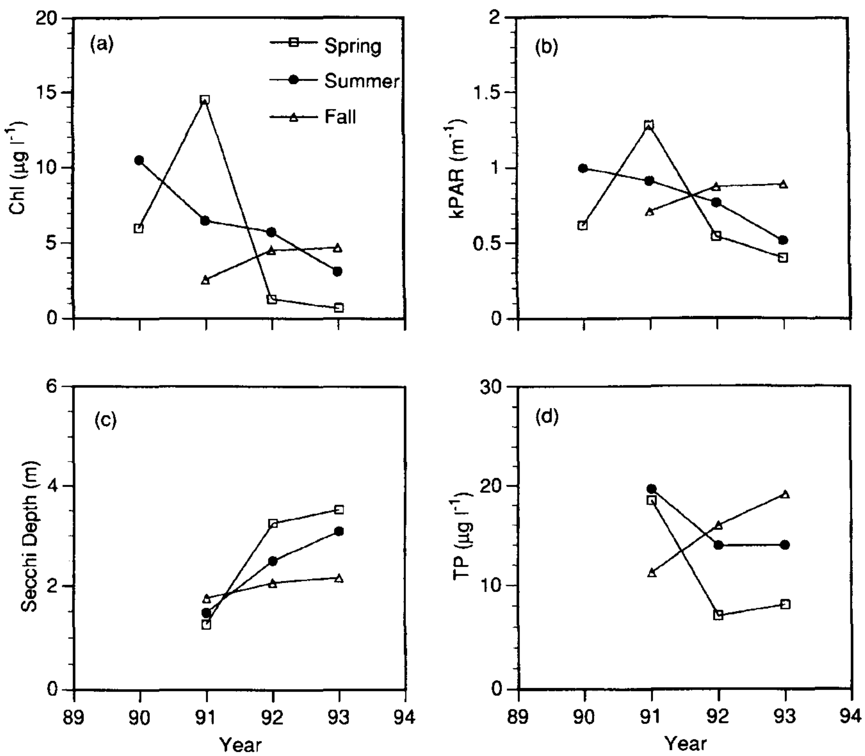

FIG. 10. Seasonal means of water quality parameters: a) chlorophyll, b) kPAR, c) Secchi disk depth, d) total phosphorus (TP) at stations with high densities of zebra mussels (zebra 2).

the high zebra mussel density stations ($p > 0.1$) and control stations ($p > 0.8$). Thus, to assess the effects of zebra mussels on water quality parameters, we compared data collected in 1979, 1980, and 1990 to data collected from fall 1991 through 1992 and 1993. Data collected during spring and summer 1991 are considered transitory and are not included in this analysis. We confined our comparisons to chlorophyll, Secchi disk transparency, and total phosphorus concentrations. Measurements of kPAR were not made prior to 1990.

For zebra mussel stations (zebra 2), significant differences in chlorophyll, Secchi disk, and total phosphorus values were noted between the 1979–1990 and the 1991–1993 periods ($p < 0.001$, Fig. 11). Chlorophyll and total P decreased 66% and 48%, respectively, whereas Secchi disk values increased 88% (Fig. 11). The consistent changes among all three water quality parameters are noteworthy. For this same station group, significant decreases were noted during all seasons for chlorophyll and total P ($p < 0.005$). Most of these decreases were in the range of 40–60%. For Secchi disk, significant differences were only noted in spring and summer ($p < 0.001$), but values increased during all seasons by at least 50%.

At the other inner bay stations (zebra 1), significant differences also were noted for all three parameters ($p < 0.001$; Fig. 11). The overall and seasonal trends for these stations were very similar to those observed for the zebra mussel stations (zebra 2). Chlorophyll and total P values decreased 57% and 42% respectively, for the 1979–1990 vs. 1991–1993 study period, and Secchi disk values increased 53%. All seasonal trends were significant with the exception of fall Secchi disk values ($p = 0.06$) and fall total P ($p = 0.11$). Thus, even though zebra mussels are confined to specific sites, their effects were noted throughout the inner bay.

At the control stations (zebra 0), chlorophyll and Secchi disk values were very similar for the two time periods, with no significant differences noted ($p > 0.06$, Fig. 11). For these parameters significant seasonal differences were noted only for summer Secchi disk values ($p = 0.005$). Total phosphorus values were significantly different overall

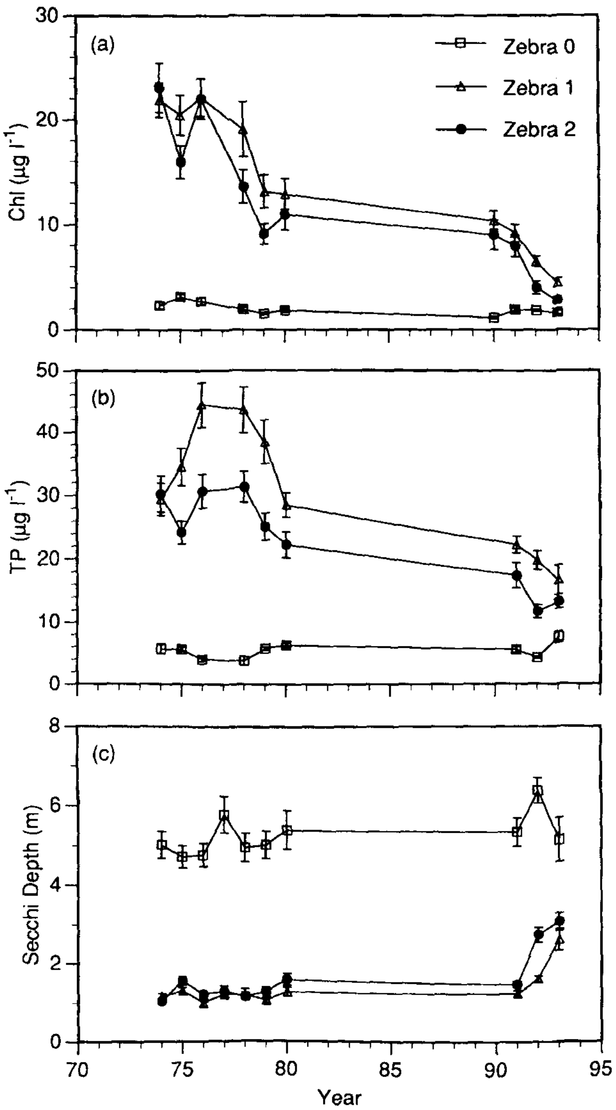

FIG. 11. Annual means of water quality parameters from 1974–1993: a) chlorophyll, b) total phosphorus (TP), c) Secchi disk depth. Stations were grouped into three categories: zebra 2, zebra 1, and zebra 0; see Figure 8 for an explanation of these groupings. Error bar is one standard error.

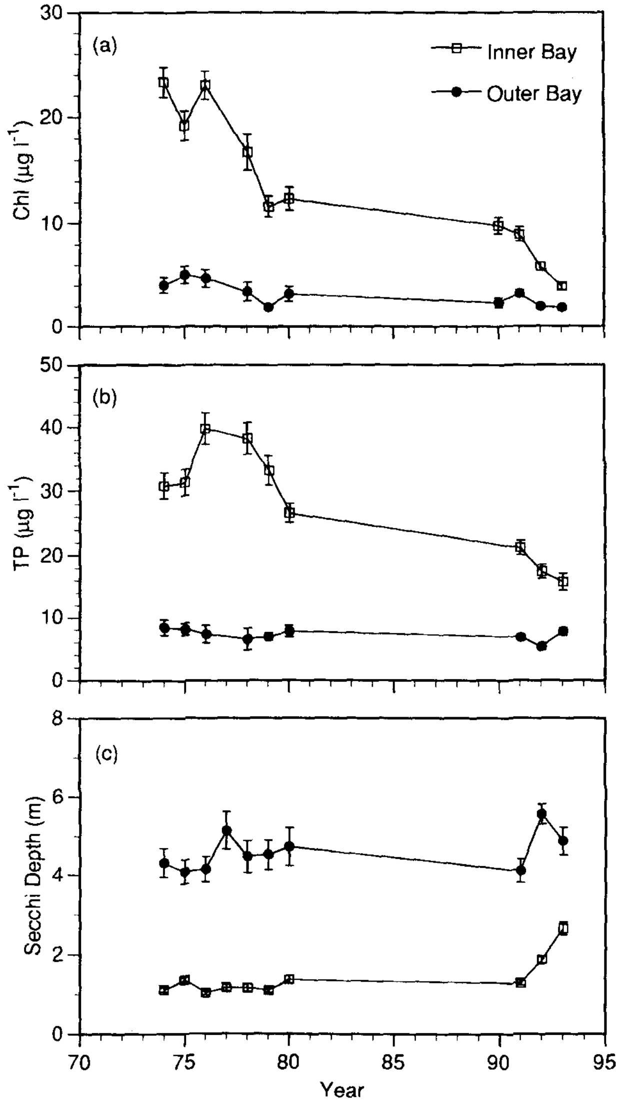

FIG. 12. Annual means of water quality parameters from inner and outer Saginaw Bay: a) chlorophyll, b) total phosphorus, c) Secchi disk depth. Error bar is one standard error.

($p < 0.03$), with lower values in the 1991–1993 period, but all seasonal values were not significantly different ($p > 0.1$).

When these same comparisons are made for all stations in inner and outer bay, the overall impact of zebra mussels on Saginaw Bay is evident. For inner bay stations, chlorophyll, Secchi disk, and total phosphorus values were significantly different overall and for all seasons (spring, summer, and fall) between the 1979–1990 and 1991–1993 periods (all $p < 0.03$, Fig. 12). Chlorophyll and total phopshorus decreased by 59% and 43%, respectively, and Secchi disk values increased 60%. For outer bay stations, chlorophyll, total phosphorus, and Secchi disk values were relatively similar for the two period (all $p > 0.05$, Fig. 12). Although the values were not significant, chlorophyll and total phosphorus values did decrease by 24% and 17%, respectively, while Secchi disk values increased by 13%. However, these changes were small compared to those in the inner bay. All

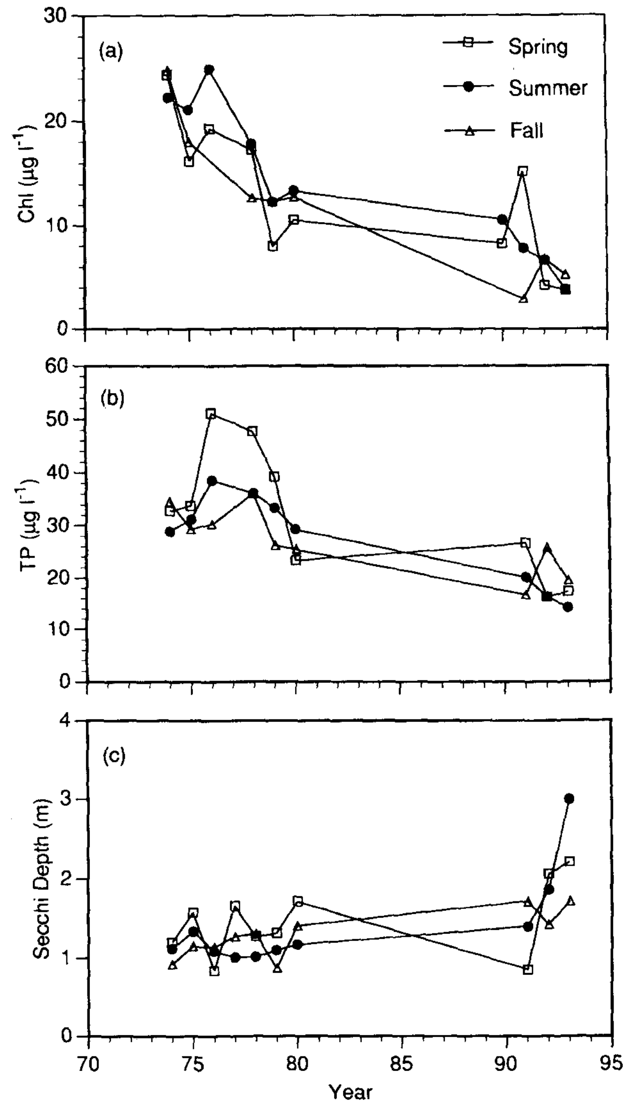

FIG. 13. Seasonal means of water quality parameters from inner Saginaw Bay: a) chlorophyll, b) total phosphorus, and c) Secchi disk depth

outer bay seasonal comparisons with one exception (summer Secchi disk) also were not significantly ($p > 0.1$) different between the periods.

It is interesting to note that inner Saginaw Bay has occupied three distinct trophic states in the past 20 years which can be easily seen from long-term chlorophyll data (Figs. 11 and 12). In 1974 and 1975 and likely as early as 1960, chlorophyll concentrations were approximately 18–22 $\mu g \cdot L^{-1}$. In the 1979–1990 period, mean chlorophyll values were approximately 8–12 $\mu g \cdot L^{-1}$ and by 1992 and 1993 they had further decreased to 4–6 $\mu g \cdot L^{-1}$.

Data from every year over the 1974–93 period, with one exception (1991), are consistent with the pattern described above. In 1991, water quality parameters from inner Saginaw Bay during the three seasons (spring, summer, and fall) were similar to annual values from three different time periods. Chlorophyll values in spring 1991 were more similar to values from 1974–1978 period than to values from the 1979–1990 or 1992–1993 periods (Fig. 13). Similarly, mean Secchi disk values in spring 1991 (0.8 m) were as low as any spring value from 1974 through 1993. The only year with a comparably low value was 1976. Values of water quality parameters in summer 1991, however, were more similar to values from the 1979–1990 period. In fall 1991, values of all water quality parameters were similar to values from 1992 and 1993, reflecting values in the period after zebra mussel colonization. Thus, water quality parameters in the transitory year of 1991 exhibited pronounced changes over the spring, summer, and fall seasons which were comparable to relative changes noted between the periods 1974–78, 1979–90, and 1992–93, respectively.

DISCUSSION

Dramatic changes in the water quality of Saginaw Bay occurred coincident with the colonization of the zebra mussel. For the period from 1979 through 1990, which is prior to the initial zebra mussel colonization (Nalepa *et al.* 1995), mean annual values for all water quality parameters in inner Saginaw Bay were similar (Figs. 11 and 12). However, after the initial colonization of zebra mussels in 1991 and continuing through 1992 and 1993, significant decreases in chlorophyll (59–66%) and total phosphorus (43–50%) and significant increases in Secchi disk transparency (60–100%) were observed at stations with zebra mussels and throughout inner Saginaw Bay. Similar changes in water quality parameters were not observed at several outer Saginaw Bay control stations (Fig. 11). Thus, the coherence between water quality changes and zebra mussel colonization strongly suggests that these recent changes were caused by the zebra mussel.

Large changes in water quality, similar to those reported herein, have been noted in other regions of the Great Lakes after the establishment of zebra mussel populations. In the western basin of Lake Erie, a region that is limnologically similar (shallow, eutrophic) to Saginaw Bay, chlorophyll concentrations decreased by approximately 43%, and Secchi disk transparency increased by 85–100% after colonization by zebra mussels (Leach 1993, Holland 1993). In Lake St. Clair significant decreases in turbidity (Hebert *et al.* 1991) and chlorophyll (Nalepa *et al.* 1993) were noted after the establishment of the zebra mussel.

It should be emphasized that other information besides the coincidental relationship between water quality changes and zebra mussel colonization is needed to verify that zebra mussels were the contributing factor to recent water quality changes in Saginaw Bay. Zebra mussels may not have been the sole cause of the recent water quality changes in western Lake Erie. After the establishment of zebra mussels in Lake Erie, Wu and Culver (1991) concluded that *Daphnia* grazing still controlled edible algal density and water transparency. More recently, several investigators have evaluated the relative roles of zebra mussels and zooplankton in causing recent water quality changes in Lake Erie and have concluded that, while zooplankton change may have contributed to some changes, zebra mussels were likely the primary cause (Holland 1993, Nicholls and Hopkins 1993).

In Saginaw Bay, however, all available data clearly point to the role of zebra mussels in causing recent changes in water quality parameters. In summer 1991, mesocosm experiments were conducted to examine the possible impact of zebra mussels on Saginaw Bay (Heath *et al.* 1995). The results from these mesocosms were similar to those observed in Saginaw Bay in 1992 and 1993 after zebra mussel colonization. Four mesocosms (ca. volume 1.6 m^3) were deployed, two controls and two with zebra mussel densities of 1,000–4,000/m^2, which is similar to the mean density of zebra mussels in inner Saginaw Bay in 1992 and 1993 expressed on a volumetric basis (Nalepa *et al.* 1995). In the mesocosms with zebra mussels, chlorophyll concentrations decreased approximately 70%, and light transmittance increased 35% (Heath *et al.* 1995). In the control treatments no significant differences in chlorophyll or light transmittance were noted. The similarity of these results with those observed in the bay just one year later suggests that zebra mussels were the likely cause of the observed water quality changes.

A comparison of zebra mussel filtering impact and phytoplankton growth rates in Saginaw Bay also demonstrates the potential of zebra mussels to cause significant reductions in phytoplankton abundance and thereby water transparency. Fanslow *et al.* (1995) determined the filtering impact of zebra mussels in inner Saginaw Bay from measured filtering rates and population biomass. They estimated that zebra mussels could filter the entire volume of the inner bay on average every 0.8 d in 1992 and 5.0 d in 1993. Moreover, phytoplankton growth rates in inner Saginaw Bay averaged 0.25 d^{-1} in 1992 and 0.20 d^{-1} in 1993 (G. Fahnenstiel, unpubl. data) and thus, phytoplankton biomass would double every 2.8 to 3.5 d. The similarity of zebra mussel filtering impact and phytoplankton growth rates suggest that at least on an average basis, zebra mussels have the capability to cause a significant decrease in phytoplankton abundance similar to those observed in 1992 and 1993. It must be remembered that these bay-wide calculations have limited value in determining the relative importance of factors controlling actual phytoplankton abundance at a specific site, but they are useful in demonstrating the potential impact of zebra mussels in Saginaw Bay.

Unlike Lake Erie, where it is possible that recent changes in water quality parameters may have been partially caused by zooplankton, recent changes in Saginaw Bay were not caused by zooplankton. Zooplankton abundance and filtering rates were measured in Saginaw Bay immediately before and during colonization by zebra mussels. For the period 1990 through 1993, the abundance of all major groups of zooplankton either decreased or remained constant after zebra mussel colonization (Bridgeman *et al.* 1995, T. Nalepa unpublished data). Likewise, mean zooplankton filtering rates measured at several stations in June 1991 (pre-zebra mussel) and June 1992 (post-zebra mussel) were very similar 0.8 $mL \cdot ind^{-1} \cdot d^{-1}$ and 0.6 $mL \cdot ind^{-1} \cdot d^{-1}$, respectively (Bridgeman *et al.* 1995). Thus, the filtering impact of zooplankton likely decreased after the colonization of zebra mussels in Saginaw Bay. Moreover, based on filtering rates and abundance, zooplankton cleared the water volume of the inner bay approximately every 37 days in 1992 (Bridgeman *et al.* 1995). Because filtering rates of zooplankton and zebra mussels were both calculated by changes in chlorophyll, the filtering impacts of these two groups are directly comparable. Thus, not only did zooplankton grazing decrease at the time of the large chlorophyll decrease (1992 and 1993), but zooplankton grazing was a small loss compared to zebra mussel grazing.

Another possible explanation for the the marked changes in water quality parameters in Saginaw Bay may be decreased phosphorus loading; however, the available data do not support this possibility. Reductions in phosphorus loadings to Saginaw Bay from 1974–1980 caused a significant decrease in water column concentrations of phosphorus and chlorophyll and a slight increase in Secchi disk transparency by 1980 (Bierman *et al.* 1984). For our study period, however, the same correlative relationships between phosphorus loadings and water column concentrations do not exist. Phosphorus loadings to Saginaw Bay did not exhibit any significant trend from 1979–1992 ($p = 0.41$), and loadings from 1991 (2,158 mt) and 1992 (946 mt) were higher than loadings from 1990 (512 mt) and the mean for the 1979–1990 period (775 mt; MDNR 1994). Thus, during the zebra mussel colonization phosphorus loadings to Saginaw Bay increased while water column concentrations of total phosphorus and chlorophyll decreased.

All of the above information taken together, clearly establish zebra mussels as the causative agent in the major changes in water quality parameters in Saginaw Bay beginnning in late 1991 and through 1992 and 1993. Besides simultaneous change in water quality with colonization by zebra mussels, calculations of zebra mussel filtering impacts and similar mesocosm results substantiate the role of zebra mussels in causing recent water quality changes. Moreover, the most likely alternative explanations for the dramatic changes in water quality parameters in late 1991 and 1992–1993, increased zooplankton grazing or decreased phosphorus loadings, are not supported by available data.

Because of the extensive spatial and temporal sampling in Saginaw Bay before and during zebra mussel colonization, several observations into the response of the Saginaw Bay ecosystem to this colonization are noteworthy. First, the system responded quickly to the initial colonization. Within months after the first observations of settled veligers in Saginaw Bay, significant changes in chlorophyll, total phosphorus, and light transparency were noted (Fig. 10). Water quality changes in fall 1991 corresponded to the establishment of large populations of juvenile mussels (<5 mm) in Saginaw Bay (Nalepa *et al.* 1995). Similar abrupt changes in water quality parameters were noted in Lake Erie with the initial colonization of zebra mussels (Leach 1993, Nicholls and Hopkins 1993). These observations demonstrate the high filtering rates of juvenile mussels and their effect on water quality. These field observations are also consistent with laboratory measurements of pumping rates by juvenile zebra mussels and theoretical calculations of their potential filtering impact. Bunt *et al.* (1993) measured high pumping rates for juvenile mussels and noted that these individuals could theoretically pump between 39–96% of the water in the western basin of Lake Erie on a daily basis. These results suggest that studies designed to assess the ecological impacts of zebra mussels need to be in place well before their initial colonization.

Second, despite large declines in density and biomass of the zebra mussel population from the fall 1991 through the fall 1993 in Saginaw Bay (Nalepa *et al.* 1995), chlorophyll, total phosphorus, and light clarity values remained relatively constant (Figs. 9 and 11), demonstrating little density dependence and suggesting a possible threshold effect. Similar field results have been noted in western Lake Erie and in mesocosm studies in Saginaw Bay. In western Lake Erie, Nicholls and Hopkins (1993) noted an abrupt decline in phytoplankton abundance at a water plant intake in fall 1988, when juvenile/adult zebra mussels were first noted (Leach 1993). Even though zebra mussel density increased considerably in the next two years in the western Lake Erie (Leach 1993), phytoplankton abundance remained at relatively constant levels. In two mesocosms in Saginaw Bay, zebra mussel densities were 890 and 2,900/m^2, yet chlorophyll decreases in the two enclosures were generally similar (Heath *et al.* 1995). Thus, an important feedback mechanism exists between phytoplankton abundance and mussel filtration rates, as is evidenced by the strong relationship between seston concentrations and filtration rates found by Fanslow *et al.* (1995). The long-term effects of this feedback mechanism are unclear; however, it is likely that the recent water quality changes we noted are simply transitory and that the long-term response may be different.

Third, the physical nature of Saginaw Bay directly affects the response of the system. The effects of the zebra mussels were not confined to just stations with high densities of zebra mussels, but rather were found at all stations in the inner bay regardless of the mussel density (Fig. 9). This suggests that inner Saginaw Bay is relatively well-mixed on time periods less than our sampling intervals. Previous studies on the physical limnology in Saginaw Bay have also concluded that the bay is relatively well-mixed (Danek and Saylor 1977). Similar conclusions regarding the lack of strong spatial effect were noted in western Lake Erie, where large changes in phytoplankton abundance were noted regardless of the presence or absence of zebra mussels at the specific sampling site (Holland 1993, Leach 1993, Nicholls and Hopkins 1993).

The changes in water quality parameters reported herein are some of the largest documented in Saginaw Bay for at least the past 20 years, and the present values may be consistent with values from a much earlier period. Although work prior to the 1950s provided only limited information, it does suggest that the Saginaw Bay ecosystem was already heavily impacted in the 1930s (Freedman 1974). In the first limnological survey performed in 1956, Beeton *et al.* (1967) reported total phosphorus concentrations and Secchi disk values from 1956 that were similar to values from the early 1970s. Thus, present water quality indicators have changed dramatically and are consistent with values before at least the 1950s and likely earlier than the 1920s. Because water quality parameters have been used to assess trophic state or level, it is tempting to suggest that these trends represent a reversal of eutrophication.

However, recent water column changes do not appear to reflect a change in system productivity or trophic state, but rather a shift in partitioning or allocation of resources and productivity. Through their filtering activities, zebra mussels shift production and resources from the pelagic region to the benthic region. These changes can be seen by substantial decreases in phytoplankton productivity and increases in benthic algae productivity and macrophyte distibution (Fahnenstiel *et al.* 1995, Lowe and Pillsbury 1995, Skubinna *et al.* 1995). These changes in productivity are driven by changes in resources to the benthic region (i.e., light and nutrients). Increased light transmittance and the possible effect on benthic primary production have been noted (Fahnenstiel *et al.* 1995).

Similarly, marked increases in the limiting nutrient, phosphorus, have been noted in and near clumps of zebra mussels. During isothermal conditions total phosphorus concentrations in and near zebra mussel beds were 4–8× higher than concentrations just 0.5 m above the bed (Fahnenstiel, unpubl. data). Abundant populations of zebra mussels not only recycle large quantities of phosphorus, they also contain a large fraction of the phosphorus that used to be found in phytoplankton (Johengen *et al.* 1995). Thus, the present conditions in Saginaw Bay do not appear to represent a shift in trophic state, rather a transfer of pelagic productivity to the benthic region (Fahnenstiel *et al.* 1995). Unless phosphorus loading declines or phosphorus is permanently buried or removed from the system, however, there can be no real change in the trophic condition of Saginaw Bay, only the appearance of one.

Zebra mussels can alter nutrient recycling and supply rates without producing a shift in trophic state. Changes in nutrient supply rate need to be separated from changes in mass or concentration of the limiting nutrient. Alterations in nutrient supply ratios such as N:P can have a profound impact on algal species composition (Tilman *et al.* 1982).

Finally, it is important to note that the changes reported herein are only for the 2 years immediately after colonization, and it is difficult to predict future trends in water quality parameters. The very low levels of chlorophyll and particulate material observed in the bay in 1993 may limit zebra mussel fecundity and future population size (Nalepa *et al.* 1995), which will have obvious affects on chlorophyll, total phosphorus, and water clarity. It will be interesting to monitor the relationship between zebra mussel density and trends in water quality parameters during the next decade.

Given the dramatic effects of zebra mussels on water quality parameters in Saginaw Bay, it will be easy to attribute many future changes in shallow bay ecosytems to zebra mussels. However, in Saginaw Bay it is clear that other factors, i.e., nutrient loadings, continue to play an important role in controlling ecosystem processes in the post-zebra mussel era. A large increase in phosphorus loadings to Saginaw Bay in 1991 appeared to cause high chlorophyll concentrations and metaphytonic algal blooms in spring 1991 (Fig. 13; Fahnenstiel unpublished data). These metaphytonic algal blooms continued through 1992, but were substantially reduced when phosphorus loadings decreased. The roles of "top-down" and "bottom-up" control of food web structure and water quality of shallow bays will be interesting to examine with the introduction of a benthic indiscriminate filter feeder that occupies the "middle" of the food web. It is likely that zebra mussels will substantially change the system response to perturbations from both ends of the food web.

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