Phytoplankton Productivity in Saginaw Bay, Lake Huron: Effects of Zebra Mussel (*Dreissena polymorpha*) Colonization

**Gary L. Fahnenstiel,[1] Thomas B. Bridgeman,[2,3] Gregory A. Lang,[2]
Michael J. McCormick,[2] and Thomas F. Nalepa[2]**

[1] *Lake Michigan Field Station*
Great Lakes Environmental Research Lab/NOAA
1431 Beach St.
Muskegon, Michigan 49441

[2] *Great Lakes Environmental Research Lab/NOAA*
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105

ABSTRACT. *Phytoplankton photosynthesis-irradiance parameters, chlorophyll concentrations, underwater extinction coefficients (kPAR), and surface irradiance were determined at 8–10 sites on 27 occasions in Saginaw Bay from spring 1990 through fall 1993 corresponding to a period before and after the establishment of large zebra mussel populations (began in summer 1991). Similar measurements, with the exception of the photosynthetic parameter, α, had also been made in 1974/75 at eight sites on nine occasions. In inner Saginaw Bay where zebra mussels were primarily found, chlorophyll and kPAR values decreased, while the photosynthetic parameters, P_{max} and α, increased after zebra mussel colonization. At sites in the outer bay where no zebra mussels were found, chlorophyll and kPAR values did not change after zebra mussel colonization, whereas photosynthetic parameters increased. Decreases in chlorophyll and kPAR in the inner bay were related to the zebra mussel, but increases in photosynthetic parameters in both the inner and outer bay were not. Areal-integrated and volumetric phytoplankton productivity decreased by 38% and 37%, respectively, in inner Saginaw Bay after the establishment of zebra mussels; phytoplankton productivity at outer bay control sites was similar during the same period. Decreased phytoplankton productivity in the inner bay was attributable to the large decrease in chlorophyll as increases in underwater irradiance (increased kPAR) and photosynthetic parameters could not compensate for the chlorophyll effect. Increase in underwater irradiance produced a significant increase in light to the benthic region and contributed to increased benthic primary productivity; ratio of photic zone to station depth increased in inner Saginaw Bay, from 0.6–0.8 before the zebra mussel colonization (1974–1990) to 1.1–1.3 after colonization (1992–1993). Overall, primary productivity in the inner bay did not exhibit a notable change after zebra mussel colonization as decreases in phytoplankton productivity were accompanied by increases in benthic primary productivity. Thus, zebra mussels altered inner Saginaw Bay from a pelagic-dominated system to a benthic/pelagic system which will have long-term effects on food web structure and productivity at higher trophic levels.*

INDEX WORDS: Lake Huron, productivity, zebra mussels, phytoplankton, photosynthesis.

INTRODUCTION

The initial colonization of zebra mussels (*Dreissena polymorpha*) in the Laurentian Great Lakes occurred sometime in 1986 (Griffiths *et al.* 1991). By 1989, large populations were noted in both Lake Erie and Lake St. Clair. With the establishment of

these populations, significant changes in water column phytoplankton abundance and water transparency were noted (Hebert *et al.* 1991, Leach 1993, Holland 1993, Nicholls and Hopkins 1993). Similar changes in water quality parameters were noted in Saginaw Bay after zebra mussels became established (Fahnenstiel *et al.* 1995). However, the effects of these colonizations on rates of phytoplankton productivity were not examined. One might predict decreases in volumetric and areal in-

tegrated production given the large decreases in phytoplankton abundance, but the compensating effect of increases in light transmittance and other parameters may complicate the response.

Saginaw Bay is a shallow, eutrophic bay with some of the highest reported rates of primary productivity in the entire Great Lakes (Vollenweider *et al.* 1974). With the likely establishment of zebra mussels in the bay, we initiated a large ecosystem study to examine the response of the bay to the zebra mussel colonization. Specifically, in this paper we examine phytoplankton photosynthesis before and after the establishment of large populations of zebra mussel with consideration of overall system primary productivity and trophic state.

METHODS

Samples were collected at ten stations in 1990, eight stations in 1991, and nine stations in 1992 and 1993 (Fig. 1). Sampling was conducted on three occasions in 1990 (May, July, September), on nine occasions in 1991 (April–November), on eight occasions in 1992 (April–October), and on seven occasions in 1993 (May–November). The stations sampled for this study were a subsample of those

FIG. 1. Location of sampling stations in Saginaw Bay, Lake Huron. Dashed lines differntiate the inner bay form the outer bay and the outer bay from Lake Huron. Note: Station 21 was only sampled in 1992 and 1993.

from the larger water quality study (Fahnenstiel *et al.* 1995). At each station a Sea-Bird CTD with fluorometer and transmissometer was lowered from the surface to the bottom. Underwater light extinction of photosynthetically active irradiation (kPAR) was measured using a LI-COR 193 SB spherical (4π) light sensor and LI-COR 1000 data logger.

Discrete water samples were collected at one or two depths using a clean 5-L Niskin bottle. Samples for chlorophyll analyses were filtered onto GF/F Whatman filters, extracted and ground in 90% acetone, and analyzed fluorometrically (Strickland and Parsons 1972).

Phytoplankton photosynthesis was measured with the ^{14}C-technique in a photosynthetron (Lewis and Smith 1983). Water samples were inoculated with ^{14}C, and subsamples of 3 ml were incubated in acid-rinsed scintillation vials for 40 min. Eighteen light levels from <1 to 1,800 μEin $\cdot$ m^{-2} $\cdot$ s^{-1} were used. After incubation subsamples were acidified and bubbled for 15 min. Time zero blanks were taken and subtracted from all light values. Total CO_2 was determined from alkalinity and pH measurements (Vollenweider 1974).

Photosynthetic rates, normalized to chlorophyll, were used to construct a single photosynthesis-irradiance (P-I) curve (Platt *et al.* 1980) using the methods outlined in Fahnenstiel *et al.* (1989). Three parameters were determined from this model: P_{max} or P_M^B = maximum photosynthetic rate at light saturation (mg C $\cdot$ mg Chl^{-1} $\cdot$ h^{-1}), α = initial linear slope at low irradiances (mg C $\cdot$ mg Chl^{-1} $\cdot$ Einst^{-1} $\cdot$ m^2), and β = negative slope at high irradiance (same units as α). In cases where the 95% confidence interval of β included zero, we used a simple two-parameter model (Fahnenstiel *et al.* 1989). In this paper we use the terms photosynthesis and productivity interchangeably; both refer to the rate of carbon fixation by phytoplankton.

We modeled depth-specific and areal-integrated phytoplankton photosynthesis using a modified version of the model developed by Fee (1973) and described in detail in Lang and Fahnenstiel (1995). This model integrates P-I curves over time and depth by prescribing temporal and spatial variations in light. Model input includes hourly values of surface PAR, and depth-specific values of chlorophyll, kPAR, and P-I parameters. Linear interpolation was used to estimate P-I parameters and chlorophyll concentrations at depths for which measurements were not available. Because incident irradiance was measured in air subject to reflectance at the water surface, Fresnel's equation and Snell's law were used to estimate the proportion of light transmission
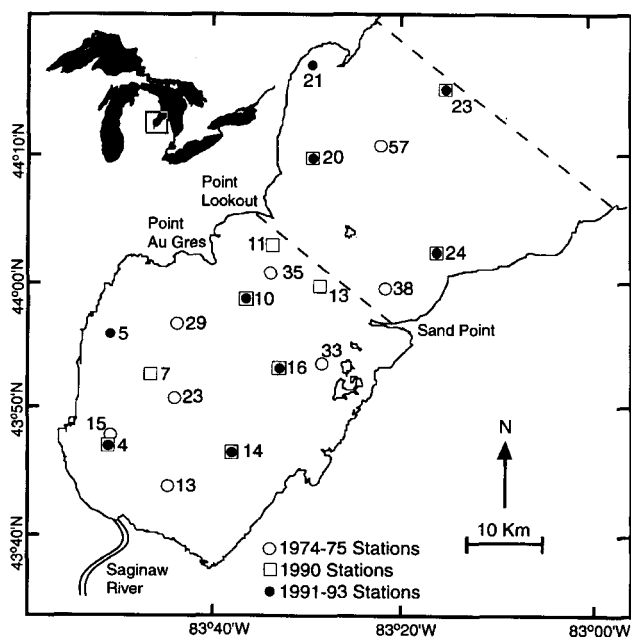
across the air-water interface as a function of the zenith angle (Kirk 1983). The model's numerical integration scheme uses a time step of 1 h and a depth step of 0.1 m. Model output includes a profile of the volumetric rate of photosynthesis (mgC $\cdot$ m^{-3} $\cdot$ h^{-1}) vs. depth and integrated areal production (mg C $\cdot$ m^{-2} $\cdot$ d^{-1}) for specific depth intervals and for the entire water column. Model estimates of primary productivity compare favorably with *in situ* measurements (Fahnenstiel and Scavia 1987). We have used this model on several occasions in the past and it has been referred to as the Great Lakes Production Model (GLPM) (Lohrenz *et al.* 1992).

As part of the IJC Upper Great Lakes Reference Group Study in Saginaw Bay, chlorophyll, Secchi disk, incident irradiance, and the photosynthetic rate at light saturation were measured in 1974 and 1975 (Canale *et al.* 1976). Sampling was conducted on nine occasions from the fall of 1974 through the summer of 1975. These data will be referred to as 1975 data to simplify discussion. We used these data as input for our model and for comparison to our parameter values from 1990–1993. Because α was not measured in 1974 or 1975, we used a mean value from the pre-zebra mussel period (1990) as an estimate for model input.

Temporal trends in the data were analyzed using ANOVA and year-to-year variation was analyzed using a Tukey HSD Multiple Comparison Test (Wilkinson 1990). Pre- and post-zebra mussel comparisons were analyzed with a t-test. All data were used for statistical analyses whereas only mean values from specific periods were included in figures. The statistical analysis of all data associated with each figure is discussed in the results section. Error bars were presented on figures only when they did not confuse the illustration.

In this paper we will focus on changes in values from specific regions and time periods. These regions represent large areas of Saginaw Bay and therefore can be used for assessing the bay-wide response. Moreover, comparisons from specific time periods, spring, summer, fall, annual, also provide for a more integrative analysis. Based on surface temperatures as defined in Fahnenstiel *et al.* (1995), the spring period includes April and May, the summer period is from June through September, and the fall period includes October and November. While our approach is useful for assessing large-scale trends, some statistical power is lost due to the large variability in values between sites and sampling dates. For example, the coefficient of variation of areal integrated productivity from individual sites in inner and outer bay ranged from 60–80% and 50–63%, respectively.

To place the results in a broader persective, we compared trends in the inner and outer bay and at sites with varying densities of zebra mussels. The rationale and complete description of this approach is described in detail in Fahnenstiel *et al.* (1995). We used the same differentiation between inner and outer regions of Saginaw Bay as Bierman *et al.* (1984) and Fahnenstiel *et al.* (1995) (Fig. 1). The inner bay is relatively shallow (mean depth = 5 m), directly influenced by the Saginaw River, and considered eutrophic. The outer bay, on the other hand, is deeper (mean depth = 14 m), more influenced by Lake Huron, and considered oligotrophic.

Zebra mussels were first noted in Saginaw Bay in 1990 at a few sites, but the first large recruitment did not occur until summer 1991 (Nalepa *et al.* 1995). Thus, 1975 and 1990 are considered pre-zebra mussel years and 1992 and 1993 are considered post-zebra mussel years. Data from 1991 must be interpreted with caution and should be regarded as a transition year because this was the year of initial heavy colonization. For the sites sampled in this study, zebra mussels were found only at some stations in the inner bay and not at any stations in the outer bay.

To assess the effect of zebra mussels we assigned specific stations (Fig. 1) to the following groups for the 1990–1993 period based on mussel densities reported in Nalepa *et al.* (1995). Sites in outer Saginaw Bay where no zebra mussels have been found (Station 23) or where their abundance was unknown (Station 21) were designated as controls. Because water quality parameters were very similar at Stations 21 and 23 and because Station 21 was also used as a control station in Fahnenstiel *et al.* (1995), it was classified as a control station. Inner bay sites where zebra mussel densities are unknown, zero, or low were designated as other inner bay stations (Stations 4, 7, 10, and 11). Finally, inner bay sites with high densities of zebra mussels (densities on at least one occasion > 4,000 m^2; Stations 5, 13, 14 and 16) were designated as zebra mussel stations. These three designations for sampling stations, control (Zebra 0), other inner bay (Zebra 1), and high density zebra mussels (Zebra 2), are similar to the designations used in Fahnenstiel *et al.* (1995) to examine changes in water quality parameters.

The location of stations was relatively similar in 1990 through 1993 (Fig. 1; however, the station locations in 1975 were different. Because different stations were sampled in 1975 and 1990–1993, and because of the heterogeneous distribution of zebra mussels in Saginaw Bay (Nalepa *et al.* 1995), the designation of specific zebra mussel stations (Zebra 0–2) is questionable for 1975 and therefore will not be used.

RESULTS

Trends and differences in chlorophyll and kPAR have already been described in detail by Fahnenstiel *et al.* (1995). Because the productivity experiments involved a subsample of the stations described therein, we will only briefly describe the data from these specific stations. For inner bay stations, regardless of zebra mussel density (Zebra 1 and 2), a significant change in chlorophyll was noted for the 1990–1993 period (p <0.05) with a dramatic decrease between 1991 and 1992 (Figs. 2a and 2b). Chlorophyll values from outer bay control stations were not significantly different for the 1990–1993 period (p =0.24; Figs. 2a and 2b). For all of inner bay, chlorophyll concentrations from 1992–1993 were approximately 50% lower than values from

1975 and 1990 (Fig. 2a). Mean kPAR values at high density zebra mussel stations and in the inner bay overall also exhibited a decrease during the 1990–1993 period, but the trends were not significant (p = 0.06 for all of inner bay and p = 0.1 for high zebra mussel stations, Figs. 2c and 2d). Even though these changes were not significant, the approximate 28% decrease noted between the 1990–1991 and the 1992–1993 sampling periods is similar to the significant decrease noted in Fahnenstiel *et al.* (1995) from a larger sample of stations. kPAR values from outer bay control stations remained relatively constant during the same period (p = 0.38, Fig. 2d). For all of the inner bay, the mean kPAR from post-zebra mussel years (1992 and 1993) was 29% lower than the mean value from pre-zebra mussel years (1975 and 1990; p <0.001, Fig. 2c).
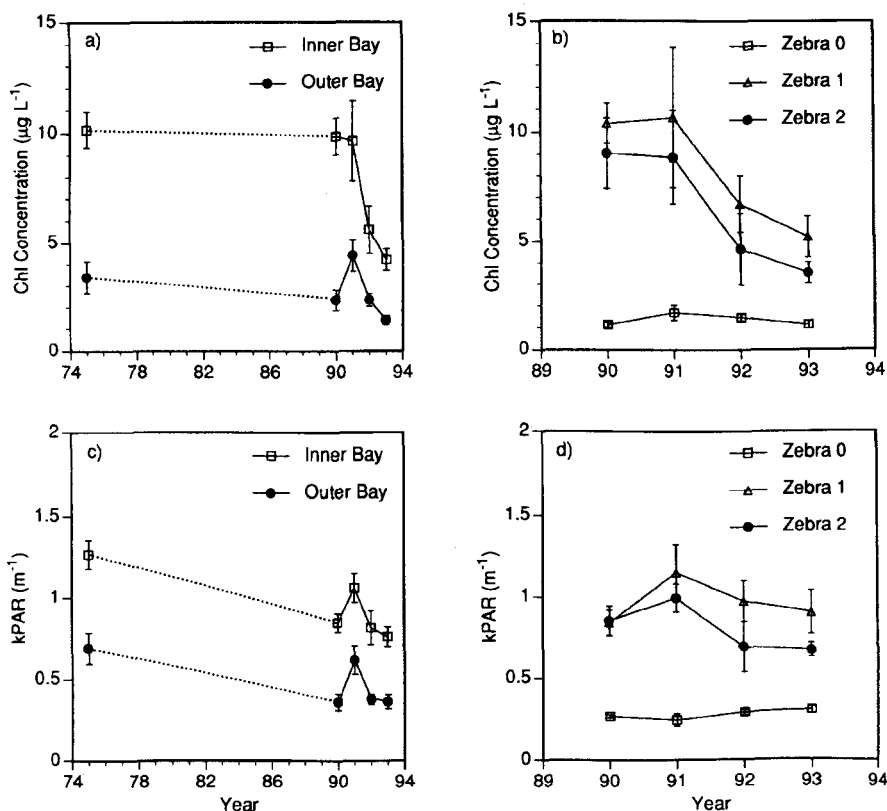

FIG. 2. Mean annual chlorophyll and kPAR values from different regions of Saginaw Bay: a) chlorophyll from inner and outer bay; b) chlorophyll from outer bay control stations (Zebra 0), other inner bay stations (Zebra 1), and inner bay stations with high densities of zebra mussels (Zebra 2); c) kPAR from inner and outer bay; d) kPAR from stations with varying densities of zebra mussels (see b). Error bars are one standard error.

Photosynthetic parameters did not display the same changes as chlorophyll and kPAR, and no clear response to the colonization of zebra mussels was noted (Figs. 3a–3d). We will focus on P_{max} and α values, because significant β values were found in only 13% of the experiments. These significant

β values were primarily confined to the spring and fall periods; only one significant value was noted during summer. The general trend of increasing P_{max} and α values for the 1990–1993 period was relatively similar for all station groupings including outer bay control stations (Figs. 3a–3d), but signifi-
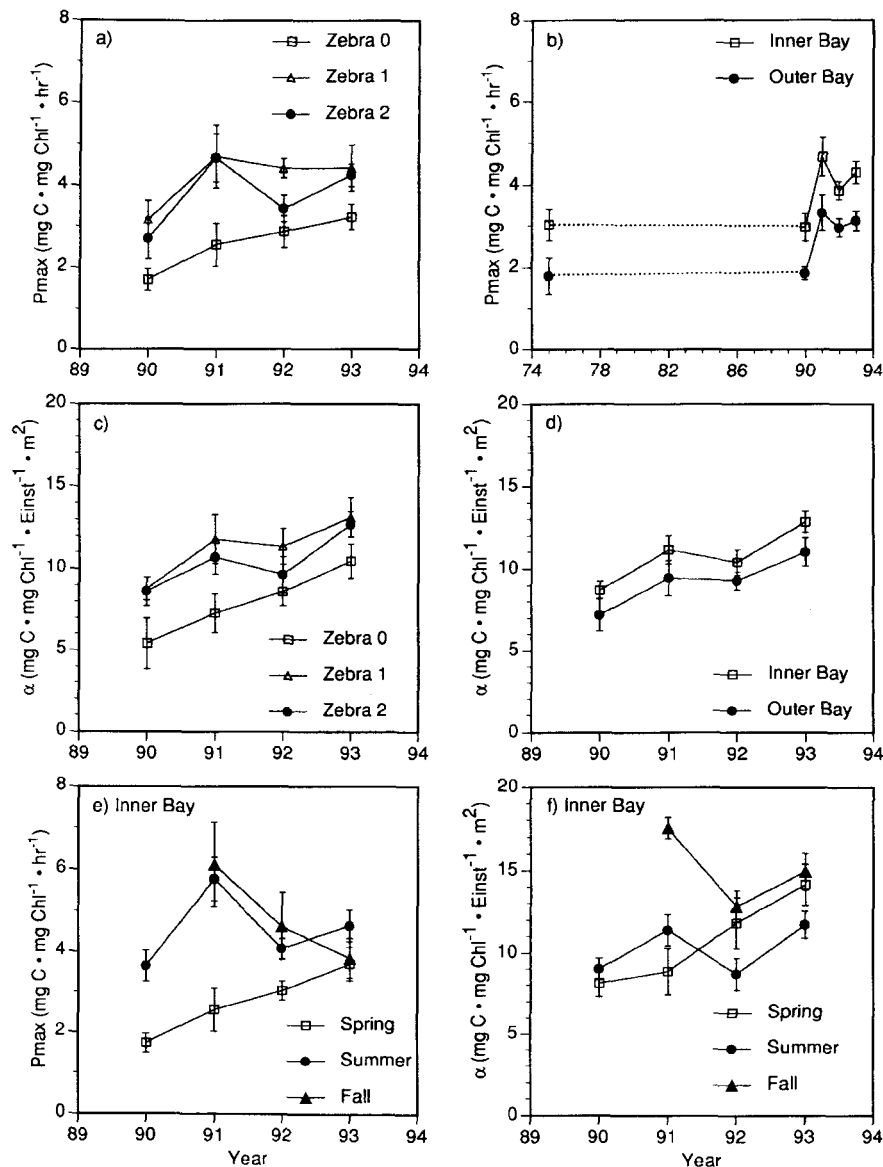

FIG. 3. *Mean annual and seasonal values of the photosynthetic parameters (P_{max} and α) from specific regions of Saginaw Bay: a) annual P_{max} from outer bay control stations (Zebra 0), other inner bay stations (Zebra 1), and inner bay stations with high densities of zebra mussels (Zebra 2); b) annual P_{max} from inner and outer bay; c) annual α from stations with varying densities of zebra mussels (see a); d) annual α from inner and outer bay; e) seasonal P_{max} from inner bay; f) seasonal α from inner bay. Error bars are one standard error.*

cant differences were observed only for all of inner bay (P_{max} and α, $p < 0.05$) and high zebra mussel stations (P_{max} only, $p < 0.05$). P_{max} values from high zebra mussel stations (Zebra 2), other inner bay stations (Zebra 1), and control outer bay stations (Zebra 0) increased 57%, 39%, and 89%, respectively, for the 1990 to 1993 period (Fig. 3a). P_{max} values from the post-zebra mussel years (1992 and 1993) for both inner and outer bay were significantly higher than values from pre-zebra mussel years (1975 and 1990; inner bay 35% higher, outer bay 67% higher, both $p < 0.001$).

Even though the increases in P_{max} and α coincided with the colonization of zebra mussels, they are not easily attributable to zebra mussels because they occurred in all regions. Similarly, α values from inner and outer bay increased from 1990 to 1992–1993 (inner 32% higher, $p = 0.004$; outer 39% higher, $p = 0.03$; Fig. 3d). Although α values from outer bay control, other inner bay and high zebra mussel stations increased from 1990–1993 by 94%, 50%, and 41% respectively, these increases were not significant ($p > 0.05$; Fig. 3c). The increase in annual values of P_{max} and α was driven by the large increase in spring values (Figs. 3e and 3f), where values approximately doubled between 1990 and 1993.

The final parameter for model input is incident irradiation and values were similar for the study period ($p > 0.05$).

Areal-integrated primary production in both inner and outer Saginaw Bay, as calculated from the Great Lakes Production model, was highly variable during the 1990–1993 period ($p < 0.002$; Fig. 4), but not necessarily similar in the two regions. For the inner bay trends in areal productivity coincided with the establishment of the zebra mussel. Rates in 1992 and 1993 were significantly lower than rates in 1990 with an overall decrease of 45% for the 1990–1993 period ($p < 0.001$; Fig. 4a). Trends in areal productivity in the outer bay did not reflect the establishment of zebra mussels. Outer bay values from 1991 were much higher than values from all other years (Fig. 4a; $p < 0.05$); however, values from 1990, a pre-zebra mussel year, were not significantly different from those in 1992 and 1993, which were both post-zebra mussel years ($p = 0.66$).

Similar changes in areal-integrated productivity were noted for stations categorized by zebra mussels (Zebra 0–2; Fig. 4b). A large decrease in productivity was noted at high zebra mussel stations ($p = <0.01$; Fig. 4b), with values decreasing by approximately 41% by 1993. At these stations, areal-integrated production was significantly higher in the pre-zebra mussel year (1990; 738 mg $C \cdot m^{-2} \cdot d^{-1}$) than in post-zebra mussel years (1992 and 1993; 342 mg $C \cdot m^{-2} \cdot d^{-1}$; $p < 0.001$). Although the decrease for other inner bay stations was not significant for the 1990–1993 period ($p = 0.18$), the values from 1992 and 1993 were 32% lower than 1990 values ($p = 0.02$). Outer bay control stations exhibited a trend similar to that in the outer bay, although this trend was not significant ($p > 0.05$, Fig. 4b). Areal-integrated production from 1990 (195 mg $C \cdot m^{-2} \cdot m^{-1}$) was relatively similar to the mean value from 1992 and 1993 (268 mg $C \cdot m^{-2} \cdot d^{-1}$; $p = 0.66$).

Due to more limited sampling, seasonal trends in areal productivity exhibited more variation than annual trends (Figs. 4 and 5). At outer bay control stations, trends for all seasons were not significant ($p > 0.05$), although 1991 values were noticeably higher (Fig. 5a). At high density zebra mussel stations, significant trends were noted only for the summer period (Fig. 5b, $p = 0.02$). The lack of significance in fall values is not surprising, given the lack of fall 1990 data. The trend for spring values is biased by one extremely high value in 1993, which contributed over 50% of the increase in the 1993 mean.

To better assess the effect of the zebra mussel colonization, areal-integrated production from pre-zebra mussel years (1975 and 1990) was compared to rates from post-zebra mussel years (1992 and 1993). In inner Saginaw Bay production rates from the post-zebra mussel period were 38% lower than rates from the pre-zebra mussel period ($p = 0.001$; Fig. 4a). Outer bay production rates were not significantly different ($p = 0.51$), and even exhibited a slight increase (12%) in the post-zebra mussel years.

Because many biological processes function on a volumetric rather than an areal basis, we calculated volumetric production by dividing areal-integrated rates by the photic zone depth (1% light level). Where photic zone depth was greater than station depth, station depth was used. For the 1990–1993 period trends in volumetric production were similar to those for areal rates (Fig. 6a). Significant trends were noted for both inner and outer bay ($p < 0.002$). Outer bay rates from 1991 were significantly different from all other years ($p < 0.05$), whereas in the inner bay volumetric rates decreased in 1992 and 1993 by approximately 49% from 1990 values ($p < 0.01$). For stations categorized by zebra mussels, the trends at high density zebra mussel ($p = 0.01$) and other inner bay stations ($p = 0.13$) were very similar to trends in the inner bay, but distinctly different from control stations ($p = 0.46$, Fig. 6b).
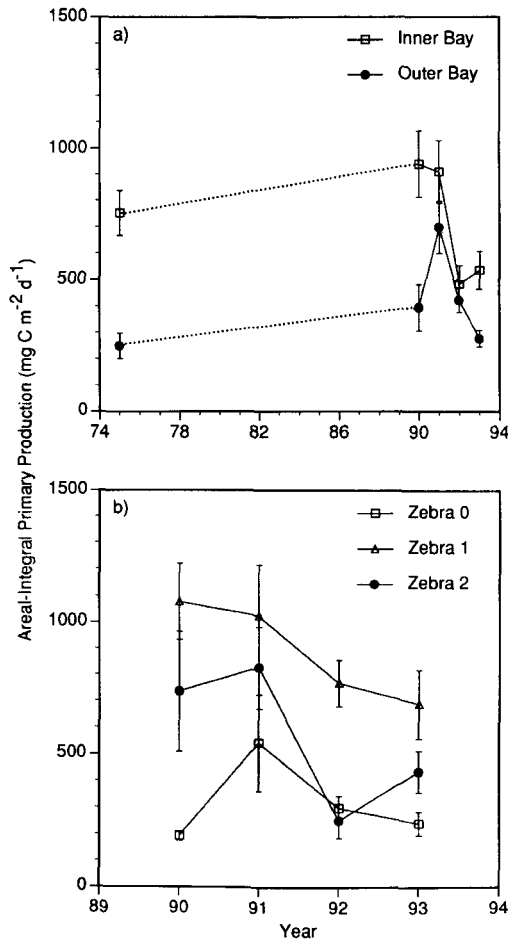
FIG. 4. *Mean areal-integrated phytoplankton productivity calculated with the Great Lakes Production Model for: a) inner and outer bay; b) outer bay control stations (Zebra 0), other inner bay stations (Zebra 1), and inner bay stations with high densities of zebra mussels (Zebra 2). Error bars are one standard error.*
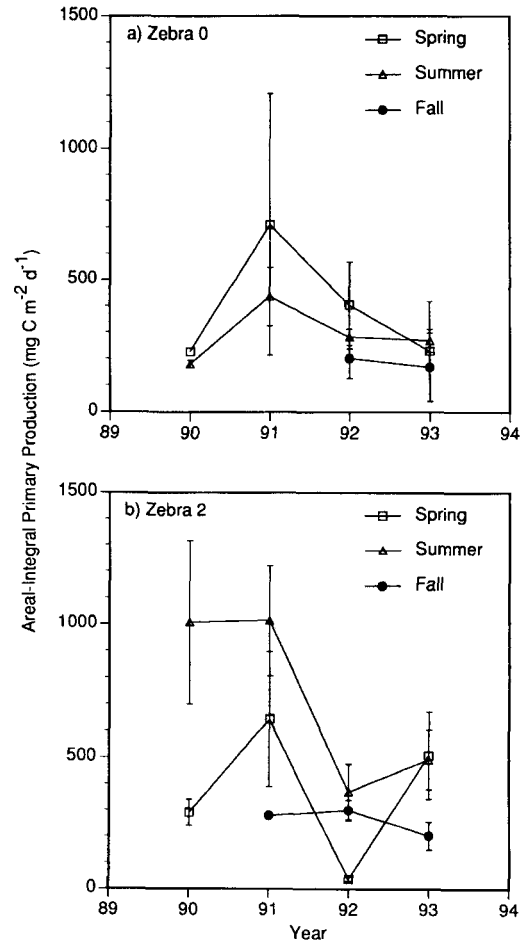
FIG. 5. *Seasonal means of areal-integrated phytoplankton productivity calculated with Great Lakes Production Model for: a) outer bay control stations (Zebra 0), b) inner bay stations with high densities of zebra mussels (Zebra 2). Error bars are one standard error.*

By including the 1975 data we can assess the effect of zebra mussels on volumetric production. In the inner bay volumetric rates from post-zebra mussel years (1992 and 1993) were 37% lower than values from pre-zebra mussel years (1975 and 1990; p = 0.001) whereas outer bay values did not exhibit any significant difference between the pre- and post-zebra mussel years (p = 0.97).

DISCUSSION

Major decreases in phytoplankton production occurred as a result of the zebra mussel colonization. In inner Saginaw Bay where most zebra mussels

were found, relatively similar decreases were noted for both volumetric and areal integrated productivity, 38% and 37%, respectively. These results may be surprising given the variable responses of the input parameters (chl., kPAR, P_{max}, α) to the zebra mussel colonization. Because all of the input parameters changed with the exception of incident irradiation, the role of each parameter in contributing to the observed changes in areal-integrated phytoplankton productivity is not readily apparent.

To examine the relative roles of input parameters on phytoplankton productivity during the zebra mussel colonization in Saginaw Bay, a variably-scaled sensitivity analysis was used. Previous sensi-
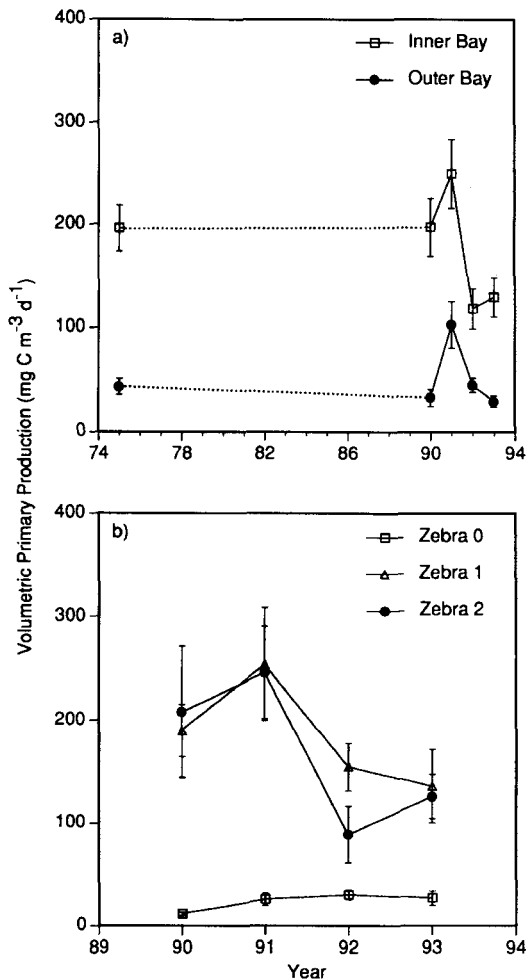
FIG. 6. *Annual means of volumetric photoplankton productivity calculated from Great Lakes Production Model and photic zone depth for: a) inner and outer bay; b) outer bay control stations (Zebra 0), other inner bay stations (Zebra 1), and inner bay stations with high densities of zebra mussels (Zebra 2). Error bars are one standard error.*

tivity work with the GLPM demonstrated that model output is most sensitive to changes in chlorophyll and kPAR (Lohrenz *et al.* 1995), which are the parameters most affected by the zebra mussel colonization (Fahnenstiel *et al.* 1995). By performing additional sensitivity analyses using the observed percent change in each model parameter after zebra mussel colonization to define the sensitivity scales (Table 1), we were able to assess the specific role of zebra mussels on phytoplankton photosynthesis.

The results of our sensitivity analyses demonstrate that the large decrease in areal-integrated phy-

TABLE 1. *Results of sensitivity analyses to examine the individual effects of each parameter on model output of areal-integrated phytoplankton productivity in inner Saginaw Bay. The percentage change in each parameter during colonization by zebra mussels (post-zm period) and the resultant change in modeled productivity expressed as a ratio of productivity during the post-zebra mussel period(post-zm): productivity during pre-zebra mussel period (pre-zm) are presented.*

Parameter	Percent Change After Zebra Mussel[1]	Resultant Change in Productivity as ratio (post-zm:pre-zm)
Chlorophyll	−66%	0.34
kPAR	+35%	1.36
P_{max}	+35%	1.20
α	+32%	1.11
Cumulative Effect		0.62

[1]Chlorophyll and kPAR values taken from Fahnenstiel *et al.* (1995); P_{max} and α values taken form this paper.

toplankton productivity after the establishment of zebra mussel populations is the result of the large decrease in chlorophyll concentrations (Table 1). Increases in the other input parameters, P_{max}, α, and kPAR, could not compensate for the substantial chlorophyll decrease, but they did buffer the effect. The changes in these other parameters would have had to increase productivity by approximately 300% to compensate for the chlorophyll decrease; yet, they increased production by only 81%.

Because the phytoplankton productivity decrease was the result of decreased chlorophyll, we can conclude that zebra mussels caused the productivity decrease. As discussed in Fahnenstiel *et al.* (1995), the large decrease in chlorophyll after the zebra mussel colonization in Saginaw Bay can be attributed to zebra mussels based on the following: 1) simultaneous decrease in chlorophyll with colonization of zebra mussels, 2) similar results from enclosure experiments manipulated with zebra mussels, 3) calculations of filtering impacts of zebra mussels, and 4) the most likely alternative explanations, increased zooplankton grazing or decreased phosphorus loadings, were not supported by available data.

Although both photosynthetic parameters, P_{max} and α, increased during the study period, these trends do not appear to be related to the colonization of zebra mussels, because P_{max} and α increased at both inner (zebra mussel-influenced) and outer (control) bay stations. Since photosynthetic parameters

are sensitive to many factors such as temperature, light and nutrient availability, and species composition (Dunstan 1973, Harris and Piccinin 1977, Senft 1978) which might have changed during the zebra mussel colonization, it is difficult to determine the cause of P_{max} and α increases and whether they could have been related either directly or indirectly to zebra mussels. However, the lack of a clear zebra mussel effect on these photosynthetic parameters is consistent with the results from short-term enclosure experiments performed in Saginaw Bay (Heath *et al.* 1995). Four enclosures with varying densities of zebra mussels were deployed in Saginaw Bay in 1991. Although there were large changes in phytoplankton abundance, light transparency, and even phytoplankton growth rates in enclosures with zebra mussels, P_{max} and α values remained similar to controls (p >0.25).

The decrease in phytoplankton productivity noted during zebra mussel colonization in Saginaw Bay cannot be used alone to infer a change in trophic state of Saginaw Bay. The production of organic matter by all primary producers, i.e., phytoplankton, periphyton, macrophytes, etc., must be considered in determining trophic state. Most of the input parameters for our model are specific for phytoplankton; however, one parameter, kPAR, can also be important in non-phytoplankton productivity.

Increases in kPAR not only increase phytoplankton productivity, but also may affect benthic primary productivity, either algal or macrophytic. A simple increase in light penetration does not necessarily produce an increase in benthic productivity, unless light levels exceed a critical value for benthic productivity. If we make a simple assumption that the depth of the 1% light level is the lower limit for photosynthesis, then we can compare the ratio of the 1% light level to bottom (station) depth to determine if light levels change enough to allow for a significant shift in the ratio of pelagic/benthic productivity. If the ratio was much less than one, we would expect phytoplankton to be the dominant primary producers; but as this ratio increases to one or more, then benthic primary producers become more important.

Our data suggest that underwater light levels in the inner bay increased enough during the zebra mussel colonization to allow for a significant increase in benthic primary productivity (Fig. 7). Prior to the establishment of large populations of zebra mussels (1975 and 1990) and during the first year of heavy colonization (1991), the ratio of photic zone depth:station depth ranged from 0.6–0.8, suggesting that most of the primary productivity was associated with phytoplankton. How-
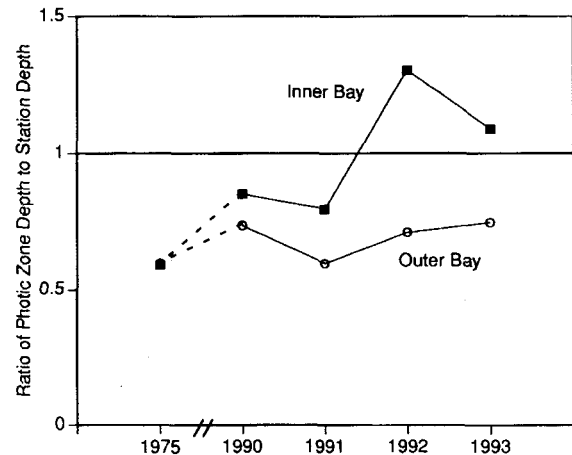

FIG. 7. Mean ratio of photic zone depth (1% isolume): station depth for inner and outer Saginaw Bay.

ever, after zebra mussels became abundant, this ratio increased to 1.1–1.3 in 1992 and 1993, suggesting that benthic productivity might increase if light were limiting their productivity. This is indeed what happened. Large increases in benthic algal biomass and productivity were noted during the zebra mussel colonization in 1992 and 1993 (Lowe and Pillsbury 1995, Skubinna *et al.* 1995).

It should also be noted that our evaluation of the changes of critical irradiance levels for benthic productivity is simplistic. The light environments and requirements of benthic algae and macrophytes can be very different (Wetzel 1983). However, our analyses are useful for demonstrating the marked potential for increases in benthic productivity in the post-zebra mussel period in Saginaw Bay.

While benthic primary productivity increased and phytoplankton productivity decreased during the zebra mussel colonization, it is difficult at present to accurately balance all forms of primary production because limited information is available on the bay-wide response of other forms of primary productivity, i.e., benthic and metaphytonic algae, vascular hydrophytes, etc., to the zebra mussel colonization. However, a preliminary examination of the available data does suggest that system-wide productivity changed little during the study period.

The most significant increase in benthic plant biomass after zebra musssel colonization in Saginaw Bay was associated with filamentous algae (Skubina and Coon 1995). Large increases in benthic algal biomass and productivity were noted be-

tween 1991 and 1993 (Lowe and Pillsbury 1995), whereas vascular hydrophytes exhibited little or no increase in distribution or relative abundance during the same time period (Skubina and Coon 1995). Using the hourly productivity rates from Lowe and Pillsbury and the GLPM to estimate daily production, we estimate that benthic algal productivity increased by about 460 mg C $\cdot$ m^{-2} $\cdot$ d^{-1} from 1991–1993. Because the Lowe and Pillsbury site had high densities of zebra mussels, and because benthic algal distribution is likely to be very patchy in the bay, their estimate of benthic production is best compared to our estimates of phytoplankton productivity from summer periods of 1991–1993 at our stations with high densities of zebra mussels. Phytoplankton productivity at these stations decreased by approximately 600 mg C $\cdot$ m^{-2} $\cdot$ d^{-1} from 1991–1993. Thus, the large decrease in phytoplankton productivity is almost compensated for by the increase in benthic algal production, without considering any increase in productivity associated with vascular hydrophytes or metaphytonic algae. Moreover, benthic algal production at the one site of Lowe and Pillsbury (1995) in 1993 was approximately 700 mg C $\cdot$ m^{-2} $\cdot$ d^{-1}, which is slightly greater than phytoplankton productivity during the summer at high zebra mussel stations (ca. 500 mg C $\cdot$ m^{-2} $\cdot$ d^{-1}). These data for benthic algae productivity suggest that Saginaw Bay has moved from a pelagic-dominated system to a pelagic/benthic system.

With additional data on benthic algal and vascular hydrophyte production in Saginaw Bay, we should be able to assess the impact of zebra mussels on bay-wide primary productivity. If the definition of trophic state is the organic production of the entire system, then it is clear that little information exists to suggest that the trophic state of Saginaw Bay has changed. The trophic state, and therefore primary productivity of any body of water, is controlled by the amount of limiting nutrient and the recycling rate of that nutrient. We have little evidence to suggest that the total amount of phosphorus in the system changed in the 1990s (Fahnenstiel *et al.* 1995, Johengen *et al.* 1995). Moreover, it is indeed possible that given utilization of sediment phosphorus by vascular hydrophytes (Carignan and Kalff 1980), coupled with increases in light and nutrient recycling (Heath *et al.* 1995), that biomass of primary producers over the entire system may even increase in the post-zebra mussel period. Increased nutrient supply rates may increase growth rates of both benthic and pelagic algae (Heath *et al.* 1995).

Even though there is little evidence to suggest

that system-wide primary productivity changed after the zebra mussel colonization, the spatial shift in primary productivity from pelagic-dominated to a pelagic/benthic system will have a profound effect on productivity at other trophic levels. In other regions of the Great Lakes zebra mussels have caused significant increases in abundance and diversity of benthic invertebrates (Griffiths 1993, Stewart and Haynes 1994). This zebra mussel effect on benthic secondary production was attributed to increased carbon and energy flow to the benthic region (Stewart and Haynes 1994). Similar increases in the abundance and diversity of benthic invertebrates are likely to occur in Saginaw Bay. Moreover, fish species that are dependent on pelagic productivity for recruitment success and year-class strength will likely be negatively affected in the post-zebra mussel years, whereas secondary producers that are dependent on benthic productivity will benefit from this energy shift. These changes will have ramifications for long-term restructuring of both the pelagic and benthic food webs in regions of the Great Lakes where zebra mussels are abundant.

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