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Vectors, Biology, and Impacts

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16 Impacts of the Zebra Mussel (*Dreissena polymorpha*) on Water Quality: A Case Study in Saginaw Bay, Lake Huron

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Thomas H. Johengen

INTRODUCTION

Impacts of benthic, suspension-feeders on pelagic measures of water quality (i.e., phytoplankton, water clarity, nutrients) have been well-documented in both freshwater and marine environments (Cloern 1982; Officer et al. 1982; Wright et al. 1982; Cohen et al. 1984; Dame et al. 1991). These organisms filter particles from the water and ingest material that is either assimilated and incorporated into biomass, or rejected and deposited as feces and pseudofeces. As a result, energy is shifted from the pelagic region to the benthic region, and changes occur in the normal pathways by which nutrients are utilized and cycled. Impacts of these feeding activities depend on the characteristics of the particular system, and on the density of the suspension-feeding population. Greatest impacts generally occur in productive, shallow water systems with high population densities. Under these conditions, the population can be capable of filtering water at a time rate constant that is much greater than the water residence time within the system, and at a rate greater than, or comparable to, phytoplankton growth.

After the suspension-feeding bivalve *Dreissena polymorpha* (zebra mussel) became established in the Great Lakes, changes in water quality parameters immediately became apparent in bays and nearshore regions where this species was most abundant. Water clarity increased (Hebert et al. 1991; Marsden et al. 1993; Leach 1993), chlorophyll and phytoplankton abundances declined (Leach 1993; Nicholls and Hopkins 1993; Holland 1993), and nutrient cycles were altered (Holland et al. 1995; Arnott and Vanni 1996; Mellina et al. 1995). While suspension feeders were present in the Great Lakes prior to *D. polymorpha* (i.e., bivalves of the families Unionidae, Sphaeriidae, and Corbiculidae), populations were too low and filtration capacity too limited to have any significant impact on water quality. Because of recent changes resulting from the filtering activities of *D. polymorpha*, responses of water quality variables to nutrient abatement programs are no longer predictable, and management approaches to water quality issues must be completely reevaluated.

In this paper, we examine impacts of *D. polymorpha* on the Saginaw Bay, Lake Huron ecosystem, emphasizing changes in pelagic measures of water quality. We focus primarily on summarizing changes during the early years of the invasion (1991–93), but also include preliminary results of water quality changes observed in 1994 and 1995. Specific details of changes during the 1991–93 period are given in a series of papers published in Volume 21 (4) of the *Journal of Great Lakes Research*. For sake of brevity and purpose, results given herein will emphasize changes occurring within the eutrophic inner portion of the bay. Changes in the outer bay were minimal and/or more local in nature and details can be found in the journal volume.

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JUSTIFICATION OF STUDY SITE

Soon after the zebra mussel was discovered in the Great Lakes in 1988, we identified Saginaw Bay as an ideal location to assess ecological changes that might result from the filtering activities of this organism. Specific considerations that led to the decision to initiate a monitoring program in the bay were as follows: (1) at the time, zebra mussels were not yet established in the bay, thus baseline conditions immediately prior to the mussel's invasion could be documented; further, previous surveys of water quality parameters in 1974–80 (Smith et al., 1977; Bierman et al., 1984) could provide a longer term perspective to assess potential changes; (2) the bay had extensive areas of hard bottom, along with ideal temperature and food regimes, and thus large populations of mussels were expected to develop; (3) there existed an important commercial and sport fishery that could be affected; (4) the natural gradient between the eutrophic inner bay and the more oligotrophic outer bay provided an opportunity to assess impacts over a wide range of trophic conditions; and (5) the bay is an Area of Concern as designated by the International Joint Commission and the subject of remedial action to reduce nutrient inputs (Richardson and Kreis 1987). After a decade of little or no monitoring in the bay, surveys of water quality parameters initiated as part of this study not only provide information to assess impacts of the zebra mussel, but also provide information to assess the bay's response to continued efforts to improve water quality.

DESCRIPTION OF STUDY SITE

Saginaw Bay is a shallow, well-mixed extension of the western shoreline of Lake Huron (Figure 16.1). The bay is 21–42 km wide, about 82 km long , and has a drainage basin of about 21,000 km^2. Total area of the bay is 2.77×10^9 m^2, and total water volume is 24.54×10^9 m^3 (Table 16.1). The bay can be functionally divided into an inner and outer region by a line extending along its narrowest width (21 km) from Sand Point to Point Lookout (Figure 16.1). A broad shoal and several islands (Charity Islands) along this line provide a natural demarcation between the two regions. Differences in physical and chemical features of the inner and outer bay regions are distinct (Beeton et al. 1967; Smith et al. 1977). The inner bay has a mean depth of 5.1 m, is nutrient-rich, and is heavily influenced by input from the Saginaw River, which accounts for over 70% of the total tributary flow into the bay. The outer bay has a mean depth of 13.7 m and is more influenced by the colder, nutrient-poor waters of Lake Huron.

Circulation within the inner bay is generally weak; currents average about 7 cm s^{-1} (Danek and Saylor 1977). Exchange and flushing of water in the inner bay occurs when winds blow along the long axis of the bay (southwest/northeast). Dominant winds in the summer are from the southwest. Little exchange occurs when winds are perpendicular to the long axis (west/east). Most water exchange/flushing between the inner and outer bay occurs on the northern side of the bay within the deep channel located between Point Lookout and Charity Island and that continues into the inner bay. Although some water may exit the inner bay along the southern shoreline, it is of minor significance because of the shallowness of the region (Danek and Saylor 1977). Furthermore, preliminary results of Lagrangian current measurements in the outer bay during the summers of 1992 and 1993 suggest that the flushing of inner bay waters into Lake Huron is episodic in nature (M. McCormick, unpublished data). Water residence times are about 120 days for the inner bay and 60 days for the outer bay (Bratzel et al. 1977).

Bottom substrates in Saginaw Bay range from silt to mostly cobble and rock. The inner bay has a wide sand-gravel bar that extends along the eastern side of the bay from the Saginaw River to the Charity Islands. Another sand-gravel bar extends along the western shoreline to Point Au Gres. Both sand bars have irregular areas of cobble along with patches of sand, gravel, and pebbles. The bars extend into the shorelines as extensive flats grade into marshes. Between the two sand bars is an area of maximum depth where sediment deposition occurs; the substrate in this region consists of fine-grained sediments (silt/mud). Based on areal estimates of substrate type by Wood

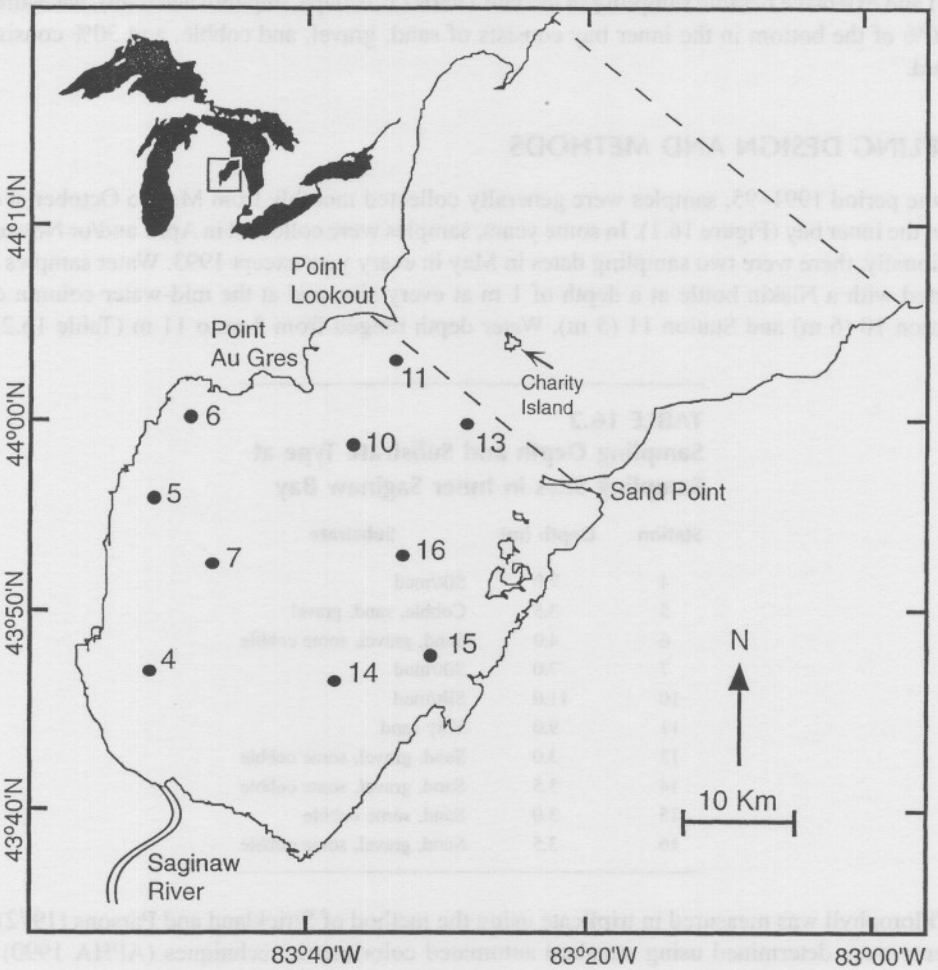

FIGURE 16.1 Location of sampling sites in inner Saginaw Bay, 1990–95. Dashed lines differentiate the inner bay from the outer bay, and the outer bay from Lake Huron.

TABLE 16.1
Mean Depth, Surface Area, and Water Volume of the Inner Bay, the Outer Bay, and the Bay as a Whole

	Mean Depth (m)	Surface Area (m^2)	Volume (m^3)
Inner Bay	5.09	1.55×10^9	7.91×10^9
Outer Bay	13.66	1.22×10^9	16.63×10^9
Whole Bay	8.86	2.77×10^9	24.54×10^9

Note: Values were computed from digitized NOAA chart no. 14863. A 0.66 m offset was used to account for low water datum.

(1964) and extensive benthic sampling in the late 1980s (T. Nalepa, unpublished data), we estimated that 70% of the bottom in the inner bay consists of sand, gravel, and cobble, and 30% consists of silt/mud.

SAMPLING DESIGN AND METHODS

Over the period 1991–95, samples were generally collected monthly from May to October at eight sites in the inner bay (Figure 16.1). In some years, samples were collected in April and/or November. Additionally, there were two sampling dates in May in every year except 1993. Water samples were collected with a Niskin bottle at a depth of 1 m at every site, and at the mid-water column depth at Station 10 (6 m) and Station 11 (5 m). Water depth ranged from 3 m to 11 m (Table 16.2).

TABLE 16.2
Sampling Depth and Substrate Type at Sampling Sites in Inner Saginaw Bay

Station	Depth (m)	Substrate
4	7.0	Silt/mud
5	3.5	Cobble, sand, gravel
6	4.0	Sand, gravel, some cobble
7	7.0	Silt/mud
10	11.0	Silt/mud
11	9.0	Silty sand
13	3.0	Sand, gravel, some cobble
14	3.5	Sand, gravel, some cobble
15	3.0	Sand, some cobble
16	3.5	Sand, gravel, some cobble

Chlorophyll was measured in triplicate using the method of Strickland and Parsons (1972), and nutrients were determined using standard automated colorimetric techniques (APHA 1990) on a Technicon Auto Analyzer II as detailed in Davis and Simmons (1979). Water clarity was measured with a 25-cm secchi disk. Analytical techniques, sampling dates, site locations, quality control, and values of all measured variables for each date and site can be found in Nalepa et al. (1996a).

Densities of zebra mussels were estimated in the fall of each year at each of the eight sampling sites and at two additional sites (Stations 6 and 15; Figure 16.1). The collection method depended upon substrate type. At sites with a hard substrate (sand, gravel, cobble; Table 16.2), divers randomly placed a 0.25 or 0.5 m^2 frame on the bottom and hand-collected all material within the frame area. Triplicate samples were collected at each site with divers moving about 2–3 m between replicates. At sites where the bottom consisted of silt, samples were collected using a Ponar grab. Triplicate samples were washed into an elutriation device fitted with a Nitex sleeve having 0.5-mm openings (Nalepa 1987). Details of counting and sizing procedures, as well as methods to estimate ash-free dry weight (AFDW) biomass, are given in Nalepa et al. (1995).

RESULTS

ZEBRA MUSSEL POPULATION TRENDS

Zebra mussels were first discovered in Saginaw Bay in 1990, but the population did not become widespread and abundant until 1991 (Nalepa et al. 1995). Yearly trends in densities in 1991–95 at sites with hard substrates are given in Table 16.3. Mean densities in the inner bay increased between

TABLE 16.3
Mean Density (Individuals m^{-2}) of *D. polymorpha* at Each Hard-Substrate Site Sampled in Inner Saginaw Bay, 1991–95

	Year				
Station	**1991**	**1992**	**1993**	**1994**	**1995**
5	28,244	75,296	237	2,959	1,018
6	4,453	3,620	3,557	10,724	2,291
13		8,956	376	854	211
14	208	63,242	7,506	3,900	2,564
15	43,117	5,556	7,341	9,725	6,728
16	26	46,360	4,830	1,727	60
Mean	10,130	33,838	3,975	4,982	2,145

1991 and 1992 to reach a peak of 33,800 m^{-2}. Densities declined after 1992; mean yearly densities varied between 2,000–5,000 m^{-2} in 1993–95. These results indicate that the population apparently reached an equilibrium on hard substrates by fall 1993, just a few years after the first major recruitment. Factors that likely limited population growth were lack of suitable substrate, adults filtering the larvae before settling occurred, and a decline in food availability (Nalepa et al. 1995). Such a dramatic increase and decline within just a few years of the initial colonization is not unusual. A similar trend was noted when zebra mussels colonized the freshwater portion of the Hudson River estuary (Strayer et al. 1996).

Variation in densities between individual sites was large for any given year, with densities often differing by an order of magnitude (Table 16.3). However, no individual site had densities that were consistently higher or lower than the other sites over the entire 5-year sampling period. Site variation was likely related to the nature of "hard" substrate within the inner bay. As noted, the substrate at stations designated as "hard-substrate sites" consisted of a patchy mixture of cobble, sand, and gravel. Most mussels were found on cobble, and the amount of cobble at some sites varied from 5% to 50% between years. Thus, while the navigation system (Loran C) provided accurate positioning, even slight variation in sampling location between years could lead to large differences in density estimates.

To examine the extent of spatial variation at individual sites, we conducted a high-frequency sampling program at two sites (Stations 5 and 14) in spring 1994. Nine replicate quadrat samples were collected at the designated site location, and at locations that were 0.4 and 0.8 km from the designated site on north, south, east, and west transects (nine replicates per nine sampling sites). Mean densities at the nine sampling locations varied from 410 to 7,690 m^{-2} at Station 5, and from 840 to 4,760 m^{-2} at Station 14 (Nalepa et al. 1995). Coefficients of variation of the mean densities at the nine sampling locations were 64% and 63% at the two sites, respectively. In comparison, coefficients of variation for the means for all six sites with hard substrate in 1993, 1994, and 1995 were 81%, 84%, and 115%. Thus, variation within 1.6 km of an individual site was only slightly lower than variation between all sites within a given year. This further indicates that densities on hard substrates were generally similar within the bay by 1993, and that year-to-year differences thereafter were primarily a function of substrate variability. Densities at "soft" substrate sites (mud/silt) were minimal and insignificant over the entire sampling period (Nalepa et al. 1995; Nalepa, unpublished data).

Yearly trends in AFDW biomass at the hard-substrate sites were similar to trends in densities. Mean biomass peaked in 1992 at 61.9 g m^{-2} and then declined; mean biomass in 1993–1995 varied from 3.1 to 4.5 g m^{-2} (Table 16.4).

TABLE 16.4
Mean Biomass (g AFDW m^{-2}) of *D. polymorpha* at Each Hard-Substrate Site in Inner Saginaw Bay, 1991–95

	Year				
Station	1991	1992	1993	1994	1995
5	10.5	106.9	0.2	5.6	2.1
6	4.4	8.9	6.7	6.9	6.3
13		24.7	0.8	1.2	0.7
14	0.1	144.0	11.6	1.7	6.1
15	34.1	8.6	3.4	1.9	9.4
16	<0.1	78.3	4.4	1.1	0.1
Mean	9.8	61.9	4.5	3.1	4.1

IMPACTS ON CHLOROPHYLL, TOTAL PHOSPHORUS, AND WATER CLARITY

The impact of mussel filtering activities were apparent soon after the first large population recruitment occurred in summer 1991. For example, mean chlorophyll in late summer/fall 1991 was 51% lower than mean chlorophyll in late summer/fall 1990 (Table 16.5). To put subsequent changes into a long-term perspective, mean seasonal values of chlorophyll, total phosphorus, and secchi-disk transparency were determined for spring (April–June) and fall (August–October) of each year over

TABLE 16.5
Mean Values of Total Phosphorus, Chlorophyll, and Secchi Depth in Inner Saginaw Bay

	Total Phosphorus (μg/L)		Chlorophyll a (μg/L)		Secchi Depth (m)	
Year	Spring	Late Summer/Fall	Spring	Late Summer/Fall	Spring	Late Summer/Fall
1974	32.5	27.0	21.5	29.7	1.20	0.93
1975	33.5	33.5	17.3	21.3	1.50	1.20
1976	46.7	39.3	20.0	27.2	0.90	1.04
1977	—	—	—	—	1.53	0.93
1978	47.5	33.1	18.9	14.7	1.31	1.09
1979	39.6	30.2	9.8	13.6	1.20	0.92
1980	26.1	24.5	10.2	11.1	1.52	1.39
1990	—	—	8.2	10.9	—	—
1991	24.9	21.7	13.3	5.3	1.29	1.61
1992	14.1	17.2	3.7	7.6	2.48	1.73
1993	13.2	17.4	3.1	4.9	2.92	2.18
1994	14.7	25.8	4.9	11.2	2.73	1.70
1995	7.4	21.1	3.1	6.8	2.69	1.33

Note: Values of total phosphorus and chlorophyll are from the 1-m depth interval. 1974–80 values were calculated from data taken from STORET (U.S. EPA) as defined by Bierman et al. (1984) and 1990–95 values are from this study. Monthly data were aggregated into spring (April–June) and late summer/fall (August–October) (Bierman 1984).

the sampling period and compared to corresponding seasonal means in 1974–80. The 1974–80 data were taken from STORET (U.S. EPA), and means were calculated from values at sites that were in close proximity to our sampling locations. Rational for these seasonal categories is given in Bierman et al. (1984).

As noted by Fahnenstiel et al. (1995a), three distinct periods are readily distinguished based on chlorophyll values: the period before phosphorus control (prior to 1976), the period after phosphorus control but before zebra mussel (1978 to spring 1991), and the period after zebra mussel (late summer/fall 1991 to present). Prior to 1976, mean chlorophyll levels varied between 17–30 $\mu g\ l^{-1}$ (Table 5); such values were considered among the highest within the Great Lakes (Vollenweider et al. 1974). During the mid-1970s, municipal treatment plants were upgraded and phosphorus was banned from detergents by the State of Michigan. As a result of these remedial efforts, annual phosphorus loads declined 55% between 1974–76 and 1978–80 and, over the same period, chlorophyll declined 53% in spring and 61% in late summer/fall (Bierman et al. 1984). In the period immediately after phosphorus control (1978–80), mean chlorophyll levels declined to 10–19 $\mu g\ l^{-1}$ (Table 16.5). After 1980, there was no monitoring of water quality parameters in the bay until our study was initiated in 1990. Chlorophyll levels in 1990 and in spring 1991 were very similar to values found in 1978–80 (Table 16.5). However, after the zebra mussel became established, mean chlorophyll declined further, varying from 3–11 μg/l in late summer/fall 1991 through 1995. Chlorophyll levels declined 54% between 1978 and spring 1991 and late summer/fall 1991–95. Thus, the decline in chlorophyll after mussels became established was comparable to the decline observed after phosphorus control measures were initiated.

A comparison of mean values of total phosphorus and secchi-disk transparency between the pre-phosphorus control and post-phosphorus control periods (1974–76 vs. 1978 to spring 1991) showed that total phosphorus tended to decline, but the decline was far less than the decline in chlorophyll over the period (Table 16.5). Also, there was no apparent change in secchi-disk transparency. Bierman et al. (1984) suggested that the relatively minor change in total phosphorus was a result of sediment resuspension. Phosphorus associated with resuspended material can contribute to concentrations in the water column, but not in a form readily available for use by phytoplankton. However, after zebra mussel became established, both total phosphorus and secchi-disk transparency changed dramatically. A comparison of means between the post-phosphorus control period and the post-zebra mussel period (1978 to spring 1991 vs. late summer/fall 1991–95) showed that total phosphorus declined 47% and secchi-disk transparency increased 72%.

IMPACTS ON PRIMARY PRODUCTION

While chlorophyll is an important measure of phytoplankton biomass, primary production is a measure of the photosynthetic rate of carbon fixation. Primary production thus more accurately reflects a system's trophic status. Water column primary production is a function of both phytoplankton biomass (e.g.,chlorophyll) and the amount of available light (e.g., underwater extinction and surface irradiance). As shown, chlorophyll levels in the bay declined after zebra mussel became established, which would lead to a decline in production. On the other hand, water clarity increased, which would lead to greater light penetration in the water column, a condition more favorable to production. Fahnenstiel et al. (1995b) measured primary production in 1990–93 using the C^{14} method within a photosynthetron. Photosynthetic rates were used to construct a photosynthesis-irradiance (P-I) curve and resulting output was then modeled to determine the areal and volumetric rate of primary production. Mean areal production was 942 $mgC\ m^{-2}\ d^{-1}$ in 1990 (pre-zebra mussel year) and 912 $mgC\ m^{-2}\ d^{-1}$ in 1991 (transition year). Areal production was 483 $mgC\ m^{-2}\ d^{-1}$ and 536 $mgC\ m^{-2}\ d^{-1}$ in 1992 and 1993 (post-zebra mussel years), respectively. Thus, excluding the transitional year 1991, production declined 38% after zebra mussel became established. Based on input data from Canale et al. (1976), areal production in 1974/75 was calculated to be 753 mgC $m^{-2}\ d^{-1}$. A sensitivity analysis indicated that the decline in production was solely a result of the decline in chlorophyll as other components of model input, such as the underwater light extinction coefficient (kPar), the maximum photosynthetic rate at light saturation (P_{max}), and the initial linear slope at low irradiances (α), actually increased production by 32-35%.

In a light-limited system such as pre-zebra mussel Saginaw Bay, any increase in water clarity would be favorable to benthic primary production since more light would reach the bottom. Fahnenstiel et al. (1995b) made the assumption that the 1% light level was the lower limit for photosynthesis and then compared the ratio of the 1% light level in the water to the bottom depth. Prior to the zebra mussel infestation (1975 and 1990), the ratio in the inner bay was 0.6–0.8. After infestation (1992 and 1993), the ratio increased to 1.1–1.3, indicating a shift to light conditions that favor benthic production. Indeed, although the extent of the light increase was variable depending upon the site location, the overall abundance, depth of colonization, and areal coverage of both submersed vascular macrophytes and benthic macrophytic algae were greater in 1992 and 1993 than in 1991 (Skubinna et al. 1995; Lowe and Pillsbury 1995). Taxa that increased to the greatest extent were the vascular hydrophyte *Chara gobularis* and the following benthic macrophytic algae: *Cladophora*, *Spirogyra*, *Zygnema*, *Hydrodictyon*, and *Oedogonium* (Figure 16.2). Macrophytic algae have high growth rates, high nutrient absorption efficiency, and low light adaptations, making them especially well-adapted for a rapid response to any changes in light availability. To put changes in system productivity in perspective, primary production estimates of mostly benthic macrophytic algae (Lowe and Pillsbury 1995) were compared to estimates of primary production of phytoplankton for the years after the zebra mussel infestation (Fahnenstiel et al. 1995b). The decrease in pelagic primary production was nearly compensated for by the increase in benthic production, without even considering production associated with vascular macrophytes. This finding indicates that zebra mussel did not change the overall productivity of the bay, but only changed how this productivity was distributed between the pelagic and benthic regions.

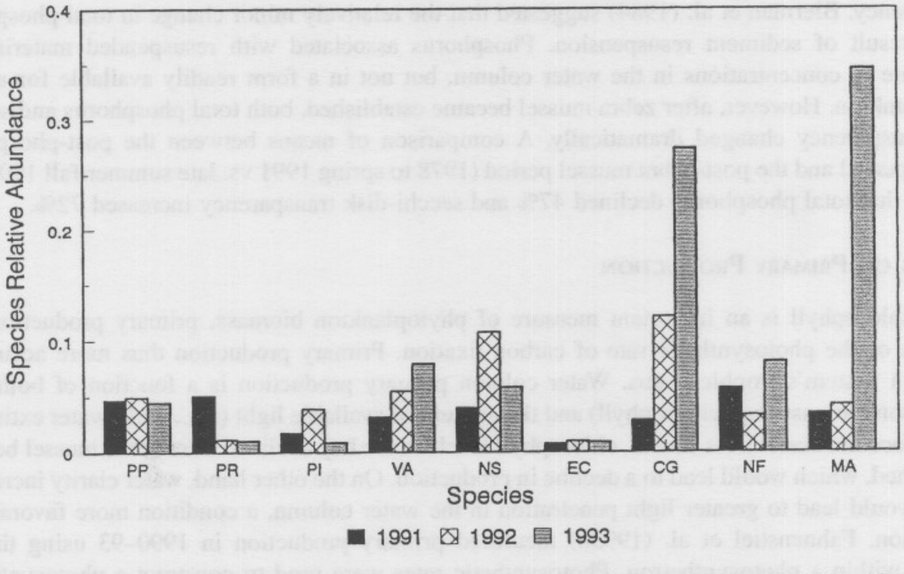

FIGURE 16.2 Relative abundance of the most abundant taxa in inner Saginaw Bay in July 1991–93. Relative abundance is defined as the proportion of the total number of samples containing the particular taxa. PP = *Potamogeton pectinatus*, PR = *Potamogeton richardsoni*, PI = *Potamogeton illinoensis*, VA = *Vallisneria americana*, NS = *Najas sp*., EC = *Elodea canadiensis*, CG = *Chara globularis*, NF = *Nitella flexilis*; MA = macrophytic algae. From Skubinna et al., *J. Great Lakes Res.* 21, 476–488, 1995. With permission.

DID ZEBRA MUSSELS CAUSE THESE CHANGES?

The evidence clearly suggests that zebra mussels were the cause of changes in water clarity, chlorophyll, and total phosphorus in the inner bay beginning in late 1991. Yet to further establish mussels as the cause, it must be shown that the filtering capacity of the mussel population was high enough to initiate the observed changes, and also that other potential causes were insignificant. Filtration capacity can be determined from estimates of population biomass and filtration rates. Population biomass in the inner bay was estimated by first multiplying mean biomass on the two dominant substrates (sand/cobble, silt) by the total bottom area covered by the two substrates, and then summing the two values. Seasonal filtration rates on natural seston from the inner bay were measured in both 1992 and 1993 (Fanslow et al. 1995). Mean filtration rates were 8.6 and 15.6 ml mg^{-1} h^{-1} in the 2 years, respectively. Assuming mussels filter 17 h per day (Walz 1978), the population filtered 6.4 m^3 m^{-2} d^{-1} and 0.9 m^3 m^{-2} d^{-1} in the two years. With an inner bay water volume of 7.9×10^9 m^3, the population theoretically filtered the entire volume of the inner bay at a rate of 0.8 d^{-1} in 1992, and 0.2 d^{-1} in 1993. For the mussel population to cause a decline in chlorophyll levels, filtration turnover times must equal or exceed algal growth rates. Algal growth rates in the inner bay were 0. 25 d^{-1} in 1992 and 0.20 d^{-1} in 1993 (Fahnenstiel et al. 1995a). Thus, the filtering activities of the mussel population could certainly account for the changes observed.

Other variables that could potentially cause changes in water quality variables are phosphorus loading and zooplankton grazing. While there was a decline in phosphorus loads after control measures were initiated in the mid-1970s (Bierman et al. 1984), there was no significant trend in loadings between 1978 and 1994 (Limno-Tech 1995; Limno-Tech, unpublished data). The mean (± SD) yearly phosphorus load for the 1978–89 period was 781 ± 464 t (metric tons). In the 1990–93 period, when dramatic changes occurred in chlorophyll, total phosphorus, and water clarity, phosphorus loads were 506, 1150, 611, and 724 t in each of the four years, respectively. Note that, over this period, the phosphorus load was highest in 1991, the year chlorophyll declines were first observed. Also, note that the phosphorus load in 1990 was somewhat lower than loads in 1992 and 1993, but mean chlorophyll levles were higher (Table 16.5). Since it has been previously shown that chlorophyll is directly correlated with phosphorus loads in the inner bay (Bierman et al. 1984), it seems improbable that variation in annual loads were the cause of the observed changes over this period.

During the early years of the zebra mussel invasion in the western basin of Lake Erie, it was argued that zooplankton grazing could account for declines in phytoplankton and increases in water clarity (Wu and Culver 1991). While these findings have since been discounted for the western basin (MacIsaac et al. 1992; Nicholls and Hopkins 1993), zooplankton grazing in Saginaw Bay was examined in 1991 and 1992 to determine if zooplankton played a role in the observed changes in water quality (Bridgeman et al. 1995). For the seasonal period when zooplankton biomass was the greatest (May/June), biomass-specific grazing rates were similar in both years. However, because of a decrease in biomass in 1992 compared to 1991, total community grazing rates were actually 58% lower in the later year. It is not clear why biomass was lower in 1992, but certainly the decrease in grazing pressure would indicate zooplankton did not play a major role in the decline in chlorophyll and increase in water clarity in that year. Based on maximum community grazing estimates in May/June, zooplankton could theoretically filter the volume of the inner bay in 17 days in 1991 and 37 days in 1992 (Bridgeman et al. 1995). Given these theoretical rates, which were far lower than those for the zebra mussel population, grazing by zooplankton was not likely a cause of the changes observed.

IMPACTS ON NUTRIENT DYNAMICS

There are several different ways in which the zebra mussel affects nutrient concentrations and cycling. First, by its filtering activities, the zebra mussel removes particles from the water column, thereby reducing the pool of nutrients associated with these particles. Second, the zebra mussel excretes dissolved nutrients (phosphate and ammonia) as part of the digestive process and thus changes supply rates to phytoplankton. In a phosphorus-limited system such as Saginaw Bay (Heath et al. 1995), phosphate excretion increases phosphorus availability for growth in species (algae or bacteria) that are not heavily grazed by the mussels. Also, since less phytoplankton are present because of mussel filtering, there is less demand for dissolved nutrients. Third, the zebra mussel affects nutrients directly by accumulating nutrients in soft-tissue biomass.

In Saginaw Bay, all measured particulate nutrients (total suspended solids, particulate organic carbon, particulate phosphorus, and particulate silica) declined significantly after the zebra mussel became established (Johengen et al. 1995). These particulate nutrients were likely either incorporated into mussel biomass, or tied up in biodeposits of feces and pseudofeces. The relative significance of phosphorus incorporated into mussel biomass was examined by comparing phosphorus in soft-tissue biomass to phosphorus loads and to changes in amounts in the water column (Johengen et al. 1995). Phosphorus in biomass was determined by multiplying the mean annual biomass in the inner bay by a measured phosphorus content of 1.0%. Thus determined, the mass of phosphorus contained in the soft-tissue of the zebra mussel population in the inner bay was 108, 682, and 52 t in 1991, 1992, and 1993, respectively. From annual loads given previously, phosphorus in mussel biomass accounted for 9%, 111%, and 7% of the load in each of the three years. Additional data for biomass and loads in 1994 and 1995 (loads of 941 t in 1994 and 578 t in 1995; Limnotech, Inc., unpublished data) indicated that phosphorus in soft-tissue biomass accounted for 4% and 8% of the loads in these two years. The extremely high percentage in 1992 might be considered atypical since it was directly related to the unsustainably high biomass found in that year.

In theory, mussels can increase dissolved nutrients both by direct excretion and by decreasing algal demand. In the inner bay, nitrate (NO_3), ammonia (NH_4), and silica (SiO_2) increased between 1991 and 1993, but soluble reactive phosphorus (SRP) decreased (Johengen et al. 1995). Reasons for the contrary trend in SRP are not immediately apparent, and explanations are particularly difficult given that all observed concentrations over the period were very low and near the detection limit. However, a potential explanation may be found in results of controlled mesocosm experiments in the bay (Heath et al. 1995). Zebra mussels were placed at two different densities in enclosures containing 1600 l of water, while other enclosures without mussels served as controls. Over the short time period of the experiments (6 days), SRP concentrations in the mesocosms with zebra mussels initially increased but then declined. In the same mesocosms, phytoplankton abundance declined but growth rates increased. These results were interpreted in terms of the dynamic relationship between nutrient supply rates and phytoplankton uptake kinetics. As P-limited phytoplankton were grazed by zebra mussels, the concentration of SRP initially increased because of lower demand by phytoplankton and excretion by the mussels. Over time, the remaining, ungrazed phytoplankton rapidly adjusted to the increase in available phosphorus with increased rates of growth, leading to a decrease in SRP levels. Growth rates of phytoplankton in mesocosms with mussels were over two times greater than control mesocosms without mussels. Extending these mesocosm results to *in situ* changes in the bay, the decrease in SRP in the inner bay between 1991 and 1993 may indeed be related to increased uptake by phytoplankton that were ungrazed by the mussels. However, phytoplankton growth rates did not change between 1992 and 1993, which may indicate that other factors were also involved. Most likely, the decrease in SRP was related to increased uptake by the more extensive benthic algae community. Also, both bacteria and protozoa can influence the dynamics of nutrient supply rates to phytoplankton; the dynamics and community structure of both of these groups were affected by mussel grazing and excretion activities (Cotner et al. 1995; Lavrentyev et al. 1995).

Besides phosphate, mussels also excrete ammonia. In the above-mentioned mesocosm experiments (Heath et al. 1995), and also in short-term bottle experiments using bay water (Gardner et al. 1995), concentrations of ammonia increased in treatments with mussels as compared to controls without mussels, which is consistent with increases in both nitrate and ammonia in the inner bay between 1991 and 1993 (Johengen et al. 1995).

IMPACT ON PHYTOPLANKTON COMPOSITION

While detailed accounts of changes in phytoplankton community composition are not yet available, there is enough evidence to suggest that zebra mussel filtering and/or excretion activities have likely contributed to major changes in relative abundances of phytoplankton species. The most apparent change is the occurrence of a summer bloom of the cyanophyte (blue-green algae) *Microcystis*; intense blooms have occurred in the inner bay in late summer/fall 1994 and 1995 (Lavrentyev et al. 1995; Vanderploeg et al. 1996). Cyanophyte blooms have not been reported in the bay since phosphorus control measures were initiated in the mid-1970s (Richardson and Kreis 1987). The exact role of zebra mussels in initiating and sustaining these blooms is not clear. One likely theory is that mussels create favorable conditions for mass blooms of cyanophytes by selectively removing more desirable algae species and rejecting the less-palatable cyanophytes. Such activities would favor cyanophytes by decreasing competition for nutrients and allowing cyanophytes to rapidly grow when conditions are favorable (i.e., warm water temperature in late summer). Evidence for selective filtration/rejection by mussels is derived from both experimental results and direct observation. In the previously mentioned mesocosm experiments, not all algal classes were equally affected by the zebra mussel — diatoms and chlorophytes declined, but biovolumes of cyanophytes (*Microcystis*) and chryosphytes *(Synura)* remained unchanged (Heath et al. 1995). Further, during the intense bloom in 1994, zebra mussels selectively removed *Cyclotella* and *Cryptomonas*, but had no affect on abundances of *Microcystis* (Lavrentyev et al. 1995). Other studies using bay water showed that zebra mussels had little effect on chlorophyll when cyanophytes were abundant (Fanslow et al. 1995; Gardner et al. 1995). Recent observations using microcinematography showed that zebra mussels do not stop pumping water in the presence of *Microcystis*, but rather continued pumping while rejecting this species as unconsolidated pseudofeces (Vanderploeg et al. 1996).

Another theory is that zebra mussels may be affecting phytoplankton composition by altering N:P molar ratios. Many phytoplankton species growing at maximum rates will maintain a cell ratio of 16:1 (Redfield 1958); however, some species grow best at other ratios, and changes in species composition will occur depending upon how this ratio changes over time. Preliminary results indicate that mussels in the bay excrete nutrients at a ratio of greater than 40:1 (Johengen et al. 1995). This high ratio may explain the increase in nitrogen compared to phosphorus in the bay since the mussels became established. Yet, since *Microcystis* grows best at low N:P ratios (Rhee and Gotham 1980), it is unlikely that changes in the N:P ratio within the bay contributed to conditions that favor this species.

DISCUSSION

The impact that a suspension-feeding bivalve such as *D. polymorpha* will have on a given ecosystem will depend on a number of factors, including population densities, phytoplankton composition and growth rates, nutrient levels and dynamics, and physical factors such as water residence times and water column mixing. Since there have been a number of studies assessing the impacts of zebra mussels in North American waters over the past several years, particularly in western Lake Erie, changes observed in Saginaw Bay offer some interesting comparisons and contrasts.

Mean densities of the mussel population within inner Saginaw Bay are similar to, or lower than densities reported for other distinctly defined systems (Table 16.6). Relatively modest densities in the bay are likely a result of the limited amount of suitable hard substrate. Mussels are mostly found on cobble, and the proportion of cobble in a given area is highly variable and generally less than the total bottom area (Nalepa et al. 1995). Also, few mussels are found on soft sediments in the inner bay. In contrast, mussels are quite abundant in soft bottom regions of other systems such

TABLE 16.6
Densities of *Dreissena polymorpha* and Corresponding Declines in Chlorophyll and Total Phosphorus in Different Water Bodies after Mussels Became Established

Water Body	Density (individuals m^{-2})	Decline in Chlorophyll (%)	Decline in Total Phosphorus (%)	Filtration Turnover Rate (d^{-1})
Saginaw Bay	1,200–3,400[a]	54	47	0.2–0.8[e]
Western Lake Erie	10,500[b]	67[c]	10[c]	2.2–9.8[c]
Oneida Lake	36,800[c]	34[c]	13[c]	0.5–1.4[c]
Lake St. Clair	3,000[d]	68[f]	0[c]	0.25[d]

Note: The filtration turnover rate is the theoretical time (days) it would take for the mussel population to filter the entire water volume. Densities are derived from whole-system surveys or from calculations based on the proportion of suitable substrate.

[a] from Nalepa et al. (1995) and Nalepa (unpublished).

[b] from Arnott and Vanni (1996).

[c] from Mellina et al. (1995).

[d] from Nalepa et al. (1996b).

[e] from Fanslow et al. (1995).

[f] From Nalepa et al. (1993).

as Lake St. Clair and western Lake Erie (Dermott and Munawar 1993; Nalepa et al. 1996b). In these two systems, unionids (both live and dead) are found in soft sediments and the shells provide a substrate for mussel attachment, and a means for the population to further expand (Hunter and Bailey 1992). Unionid shells are not found in regions with soft sediment in Saginaw Bay.

Despite marked differences in the spatial distribution of mussels as related to substrate type, spatial differences in the extent of water quality changes based on mussel densities could not be readily discerned (Fahnenstiel et al. 1995a). This finding might be expected since water circulation patterns respond rapidly to wind changes in the inner bay, resulting in a well-mixed water column (Danek and Saylor 1977). Also, vertical profiles of algal fluorescence (a function of chlorophyll) showed that near-bottom values were not lower than values in the upper water column (Nalepa et al. 1996a). If the water column was not well-mixed, near-bottom depletion would have occurred. Overall, impacts of suspension feeders are most prominent in well-mixed systems (Officer et al. 1982).

A key consideration in assessing the impact of the zebra mussel population on water quality parameters is the relationship between filtration capacity and phytoplankton growth rates. In 1992, when the population in Saginaw Bay was at a peak, filtration turnover rate exceeded algal growth rates by threefold (0.8 d^{-1} vs. 0.25 d^{-1}), but mean densities decreased in 1993, and filtration turnover rates were lower and similar to algal growth rates (0.2 d^{-1} vs. 0.2 d^{-1}). Interestingly, despite the decline in filtration turnover rates between 1992 and 1993, corresponding mean values of chlorophyll, total phosphorus, and water clarity were similar for the two years. This suggests that the impact of mussel filtering activity on water quality parameters is not linear, and that impacts will be observed as long as filtration turnover rates are at, or above, some threshold level compared to algal growth rates. A comparison between changes observed in western Lake Erie and Saginaw Bay illustrate this point. In the western basin of Lake Erie, filtration turnover rates were estimated to be between 2.2 and 9.8 d^{-1} (Mellina et al. 1995). While algal growth rates in the western basin have not been measured, they were not likely greater than the general mean growth rate of 1.0 d^{-1} (Reynolds 1984). Thus, although filtration turnover rates were much lower relative to algal growth rates in Saginaw Bay than in western Lake Erie, changes in chlorophyll were generally similar, and changes in total phosphorus were greater (Table 16.6).

The decline in total phosphorus in Saginaw Bay was greater than observed in other lake systems invaded by zebra mussels (Table 16.6). Exact reasons for the greater relative decline in total phosphorus are not clear, but the magnitude of the decline appears consistent with other changes within the bay itself. Given that the mean steady-state biomass of the zebra mussel population in the inner bay is about 3.9 g m^{-2} (Table 16.4), and assuming phosphorus in soft tissue is about 1.0% (Johengen et al. 1995), the amount of phosphorus bound in mussel biomass is 39 mg m^{-2}. With a relative decline of total phosphorus of about 15 $\mu g\ l^{-1}$ (Table 16.5), and with a mean depth of 5 m in the inner bay, the decline in total phosphorus amounts to about 75 mg m^{-2}. The difference of 36 mg phosphorus between water column loss and that bound in mussel biomass can certainly be attributed to increased biomass of benthic algae and macrophytes (Skubinna et al. 1995), or perhaps to incorporation into biodeposited material such as feces and pseudofeces. However, it is unlikely that biodeposits significantly contributed to losses of total phosphorus in the water column. This material is readily resuspended (Haven and Morales-Alamo 1966), and mass balance models imply that this material does not represent permanent removal from the water column (Mellina et al. 1995). The lower decline in water column total phosphorus in western Lake Erie (from 39 $\mu g\ l^{-1}$ before mussels to 35 $\mu g\ l^{-1}$ after mussels) observed by Holland et al. (1995) was attributed to sediment resuspension. Yet sediment resuspension of phosphorus is also significant in Saginaw Bay (Bierman et al. 1984). Conceivably, differences in relative declines of total phosphorus between the various systems were a result of differences in phosphorus inputs and throughput rates in relation to population biomass. For example, total phosphorus apparently did not decline in Lake St. Clair after mussels became established (Table 16.6). Mean biomass of the zebra mussel population in Lake St. Clair in 1994 was about 3.1 g m^{-2} (Nalepa et al. 1996b). Assuming a phosphorus tissue content of 1.0%, the amount of phosphorus bound in soft tissue is 31 mg m^{-2}, or 34 t for the entire lake (lake area = $1.11 \times 10^9\ m^2$). Since the annual phosphorus load of Lake St. Clair is 3,100 t (mean of 1975–80 period; Lang et al. 1988), phosphorus bound in mussel tissue is only 1% of the annual load. Also, phosphorus throughput time is very rapid as water residence time in Lake St. Clair is only 9 days. Accurate basin-wide estimates of population biomass in western Lake Erie are not available. However, if overall densities are about four times greater in western Lake Erie than in Saginaw Bay (Table 16.6), and assuming all other factors are equal (size-frequency, length-weight), then the amount of phosphorus bound in mussel tissue in western Lake Erie would be four times that of Saginaw Bay, or 156 mg m^{-2}. This amount would be equivalent to 574 t (western basin area = $3.68 \times 10^9\ m^2$) or 12% of the annual load of 6,693 t (mean of 1984–91 period; Mellina et al. 1995). While the proportion of the phosphorus load bound in mussel tissue is less in Saginaw Bay (7% for 1993) than in western Lake Erie, throughput time is less since water residence time is longer (120 days for inner Saginaw Bay vs. 51 days for the western basin of Lake Erie).

Evidence that Saginaw Bay is more severely P-limited than western Lake Erie can be derived from relative concentrations of SRP in the water column. Values of SRP are three to four times lower in Saginaw Bay (Johengen et al. 1995) and, as such, any dissolved phosphate excreted by mussels would less likely accumulate in the water column. Hence, SRP levels were generally lower in Saginaw Bay after mussels became established, while SRP in western Lake Erie increased by 11% (Holland et al. 1995). Also, zebra mussels in Saginaw Bay excreted nutrients at a N:P ratio of greater than 40:1, while this ratio was less than 20:1 for mussels in western Lake Erie (Arnott and Vanni 1996), indicating that phosphorus in Saginaw Bay is more efficiently retained by mussels and not as rapidly recycled into the water column. Interestingly, despite different phosphorus levels and N:P ratios in the two systems, blooms of *Microcystis* have also recently appeared in western Lake Erie (Taylor 1995), which gives credence to the selection/rejection hypothesis of Vanderploeg et al. (1996).

Obviously, the invasion of *D. polymorpha* into North American waters has altered fundamental relationships between phosphorus loads, phosphorus cycling, and measures of water quality. For Saginaw Bay, reductions in loads may now be more reflected in corresponding reductions in benthic algae, a group far more difficult to measure and quantify. Also, there is no longer a simple, direct relationship between nutrient reductions and diminished probability of cyanophyte blooms. With the likely role of zebra mussel in creating conditions favorable for these blooms, efforts to reduce nutrient loads below target levels must be reassessed if blooms are to be prevented.

Eutrophication models are valuable tools in assessing and predicting responses of water quality variables to nutrient abatement efforts. Because of the zebra mussel, new assumptions will need to be validated with experimental data, and models will need to be recalibrated with long term data sets. Submodels of zebra mussel population dynamics need to be incorporated into such modeling efforts to not only evaluate mussel impacts, but also to assess interactive responses of the population to created changes. Such models are being developed (Meisner et al. 1993; Limno-Tech 1995), and early results have led to some interesting predictions. For example, the model of Meisner et al. (1993) for the Bay of Quinte, Ontario, predicted that declines in total phosphorus in the water column will be restricted to the short term. After full colonization (steady state), total phosphorus would return to preinvasion levels because of sediment resuspension and net flux out of the sediments. In Saginaw Bay, total phosphorus has remained lower for the entire post-zebra mussel period despite the importance of resuspension in influencing total phosphorus levels in the water (Bierman et al. 1984).

Models of estuarine systems have shown that suspension-feeding bivalves that form pseudofeces are the most important determinant of stability in water quality variables (Herman and Scholten 1990; Gerritsen et al. 1994). Suspension feeders contribute to functional stability by exerting continuous pressure on phytoplankton. These models predict that feeding influences are so great that even major increases in nutrient loads have little impact on phytoplankton biomass; on the other hand, only a minor decline in suspension-feeder biomass could lead to major increases in phytoplankton at the same nutrient level (Herman and Scholten 1990). The role of zebra mussel as a stabilizing influence on phytoplankton in Saginaw Bay remains questionable. Certainly, chlorophyll levels in both spring and late summer/fall are lower now than before mussels became established, but seasonal differences are more pronounced. Chlorophyll levels in late summer/fall averaged 1.15 times greater than spring levels in years prior to mussels (1978–90), but average 2.02 times greater in years after mussels (1992–95).

Have water quality parameters and zebra mussel populations reached a steady state in Saginaw Bay? Density and biomass of the mussel population have remained relatively constant over the past few years (1993–95), and distinct trends in chlorophyll have not been apparent over the same period. In addition, seasonal changes in 1994 and 1995 have followed a characteristic pattern — an intense clear-water phase in the spring followed by a late summer bloom of the cyanophyte *Microcystis*. Additional yearly data, particularly in years when phosphorus loadings are atypical, should provide valuable information in predicting the response of water quality parameters to nutrient abatement efforts in the post-zebra mussel era.

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