

Trends in nutrient concentrations in Hatchery Bay, western Lake Erie, before and after *Dreissena polymorpha*¹

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Abstract: Concentrations of soluble reactive phosphorus, ammonium-nitrogen, nitrate-nitrogen, silica, and chloride have all increased since the establishment of the zebra mussel (*Dreissena polymorpha*) in Hatchery Bay, western Lake Erie, in 1988. Total phosphorus concentrations have changed little. These results are from 188 samples collected weekly and year round before the establishment of *Dreissena* (1984-1987) and 192 samples post-*Dreissena* (1990-1993). The mean annual total phosphorus concentration for the three complete post-*Dreissena* years was $35 \mu\text{g}\cdot\text{L}^{-1}$, strikingly similar to the concentration of $36 \mu\text{g}\cdot\text{L}^{-1}$, which in 1959 helped to define the waters of Lake Erie as eutrophic. The relative steadiness in total phosphorus may reflect sediment reflux, because Hatchery Bay is a polymictic system. The slight increase in the biologically conservative ion, chloride, in the 1990s, is probably due to the increased precipitation and runoff in the western Lake Erie watershed. Decreased phytoplankton and associated increased water clarity caused by efficient filtering by *D. polymorpha*, have lessened symptoms of eutrophication and produced a situation where nutrients are not fully utilized. i.e., biological oligotrophy.

Résumé : Les concentrations de phosphore réactif soluble, d'azote sous forme d'ammoniac ou de nitrate, de silice et de chlorure ont augmenté depuis l'implication de la moule zébrée (*Dreissena polymorpha*) dans la baie Hatchery, partie ouest du lac Érie, en 1988. Les concentrations de phosphore total ont peu varié. Les résultats obtenus proviennent de 188 échantillons prélevés à chaque semaine tout au long de l'année avant l'implication de *Dreissena* (1984-1987) et de 192 échantillons prélevés après son implantation (1990-1993). La concentration totale annuelle moyenne au cours des trois années complètes suivant l'implantation était de $35 \mu\text{g}\cdot\text{L}^{-1}$. Cette valeur est fortement semblable à la concentration de $36 \mu\text{g}\cdot\text{L}^{-1}$ qui, en 1959, a contribué à faire qualifier les eaux du lac Érie d'eutrophes. La constance relative du phosphore total pourrait s'expliquer par un reflux sédimentaire, la baie Hatchery étant polymictique. La légère augmentation de l'ion chlorure biologiquement stable notée au cours des années 1990 s'explique sans doute par un accroissement des précipitations et du ruissellement dans le bassin versant de la partie ouest du lac Érie. La raréfaction du phytoplancton, et la plus grande transparence de l'eau qui en découle, due au filtrage des eaux par *D. polymorpha* ont donné lieu à une réduction des symptômes d'eutrophisation mais à une utilisation incomplète des matières nutritives par oligotrophie biologique.

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Introduction

The establishment of viable populations of the zebra mussel (*Dreissena polymorpha*), in North America has been viewed with alarm, because of its prolific reproductive and dispersive capacity. Since its introduction into the St. Lawrence Great Lakes in 1986, *D. polymorpha* has quickly spread into a diversity of aquatic ecosystems in

the eastern United States and Canada (National Fisheries Research Center 1994), where large populations are established in some parts of the Great Lakes, e.g., western Lake Erie, Lake St. Clair, and Saginaw Bay, Lake Huron (Griffiths et al. 1991). Despite the negative aspects of this nonindigenous species, there has been some suggestion that *D. polymorpha* enhance water quality by filtering large

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quantities of suspended particles, i.e., plankton and abiotic material, thereby increasing transparency of the water (Reeders et al. 1989). However, water transparency is merely one of many criteria used to quantify water quality in terms of its physical, chemical, biological, and aesthetic characteristics (National Academy of Sciences 1972). Of these criteria, nutrients, especially nitrogen, phosphorus, and silica, have been of special interest in the Great Lakes because of accelerated cultural eutrophication and the measures adopted to mitigate nutrient loading (Beeton 1969; Great Lakes Water Quality Board 1985). Research on Polish lakes has shown that *D. polymorpha* can affect concentrations and cycling of nitrogen and phosphorus through their filtering of seston (Stanczykowska and Planter 1985; Stanczykowska and Lewandowski 1992). These authors found between 50 and 80% of the nitrogen and about 40% of the phosphorus *D. polymorpha* filtered was directed to the sediments as feces and pseudofeces, while a smaller proportion was incorporated into *D. polymorpha* itself.

Previous research has shown that the planktonic diatom community has been greatly reduced and water transparency greatly increased in Hatchery Bay since *Dreissena* populations became established in western Lake Erie (Holland 1993). The decreased phytoplankton abundance (Nichols and Hopkins 1993) and increased water clarity suggest oligotrophication, especially if nutrients are removed and deposited in the sediments as in the Polish lakes. This paper presents data for major nutrients and chloride from water collected concurrently with the diatom samples 1984–1987 and 1990–1993, and examines the current trophic status of Hatchery Bay as it is defined by its nutrient chemistry and the possible contribution of *D. polymorpha* to that status.

Methods

Our station (41°39'30"N, 82°49'23"W, corrected from Holland 1993) is in Hatchery Bay (also known as Fishery Bay), a U-shaped embayment in western Lake Erie defined by South Bass Island on the west, Gibraltar Island on the east, and Alligator Bar on the south. It opens from the northeast to waters between South and Middle Bass Islands and has a surface area of approximately 160600 m². Depths range from 0.3 m near Alligator Bar to 6.7 m at its mouth. Like western Lake Erie in general, it is a polymictic system driven by wind, storm surges, and seiches (Chandler 1944; Bolsenga and Ladewski 1993). The depth at our station is approximately 4 m, but varies annually, seasonally, and owing to seiches (Holland 1993). On days when ice was unstable owing to onset of formation or spring thaw, samples were collected approximately 250 m west of the station, from the end of a dock, where water depth is 3.5 m. Since the establishment of *Dreissena* in the bay, submersed macrophytes have become abundant in the shallower areas from late May into October. The macrophytes support growths of epiphytic diatoms (R. E. Holland, personal observation).

Water samples were collected year round, approximately weekly, from 6 March 1984 to 29 September 1987 (pre-*Dreissena* period) and 3 April 1990 to 28 December 1993 (post-*Dreissena* period). Our data are based upon

188 samples from the 1980s and 192 samples from the 1990s. Although we have extensive continuous weekly data sets spanning almost four pre-*Dreissena* and four post-*Dreissena* years, they do not include January and February 1984, October–December 1987, and January–March 1990. Ammonium values are also missing for mid-July through October 1991.

Water was collected by personnel of Ohio State University at a depth of 1 m with a 1-L Kemmerer bottle and poured into a 1-L polyethylene bottle for transport to the Stone Laboratory at Put-in-Bay, Ohio. Subsequently, 15 mL of raw water were poured into an acid-cleaned Pyrex test tube and refrigerated for analysis of total phosphorus content. Water for chemicals in solution was filtered through a 0.45 µm HA Millipore filter and the filtrate split between two chemically clean polyethylene bottles. One sample was immediately frozen for subsequent determination of nitrate-nitrogen, soluble reactive phosphorus, and ammonium-nitrogen. The unfrozen samples were mailed weekly to Ann Arbor, Mich., for chloride and silica analyses. Frozen and refrigerated samples were shipped periodically to Ann Arbor for analyses.

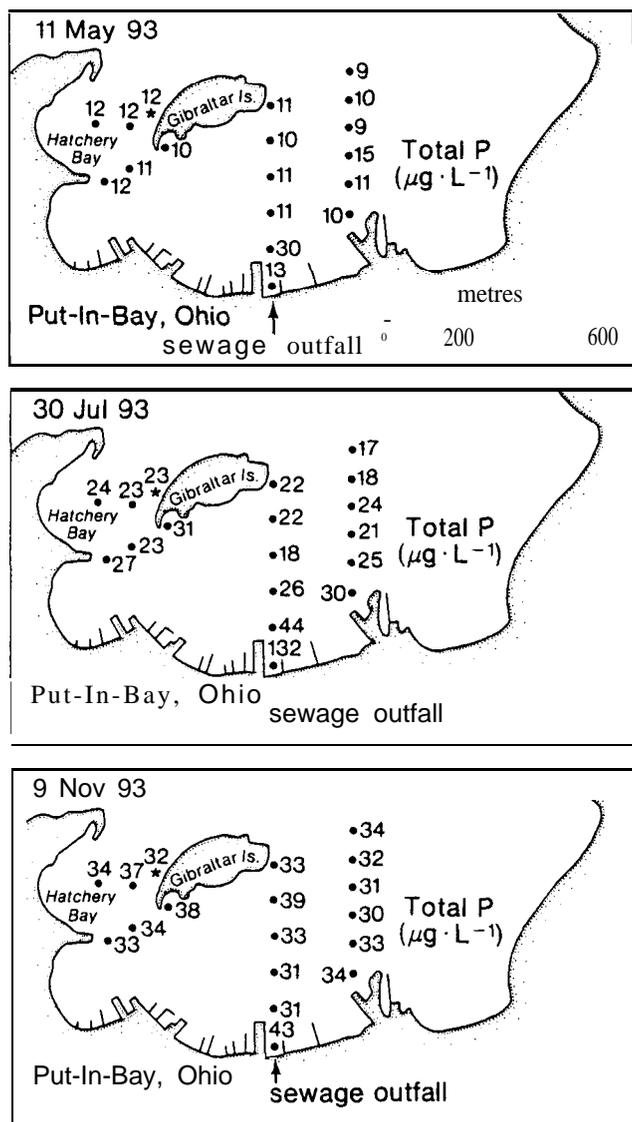
Nutrients were analyzed on a Technicon auto analyzer II using standard calorimetric techniques as modified by Davis and Simmons (1979). Ammonium-nitrogen was determined by the phenate method, nitrate-nitrogen by the cadmium reduction method, soluble reactive phosphorus by the molybdate – ascorbic acid method, and silica by the molybdate – oxalic acid and heteropoly blue method. Chloride concentrations were measured as an adjunct to the nutrient data because this anion is considered biologically conservative; however, it did increase in Lake Erie during the years of accelerated eutrophication (Beeton 1969). Chloride was analyzed by the ferric thiocyanate method. Total phosphorus was determined calorimetrically after sample digestion with potassium persulfate in an autoclave for 30 min (Menzel and Corwin 1965). Elemental concentrations are reported for C, N, and P, whereas silicon is presented as SiO₂. Silica depletion rates were generated from linear regressions of weekly concentrations in April and May for individual years for the period of record. Samples were analyzed in the laboratory of the Great Lakes Research Division, University of Michigan, Ann Arbor, until 1992 when they were analyzed at the Great Lakes Environmental Research Laboratory, Ann Arbor, Mich. The same procedures and techniques were used in both laboratories: T.H. Johengen analyzed samples in both laboratories, further enhancing consistency.

Three synoptic surveys were conducted in 1993 (11 May, 30 July, and 9 November) to determine if a small sewage outfall from Put-in-Bay affected total phosphorus concentrations at the sampling site. Water was collected with a Kemmerer bottle at a depth of 1 m at 18 stations. Total phosphorus was measured on all three dates.

Statistical methods

Monthly mean concentrations were computed for the pre- and post-*Dreissena* periods. For graphical presentations, means and standard errors represent all weekly data collected within a given month during the respective period.

Fig. 1. Total phosphorus concentrations during three synoptic surveys in the vicinity of Hatchery Bay and Put-in-Bay, Ohio, 1993. Asterisk indicates regular sampling station.



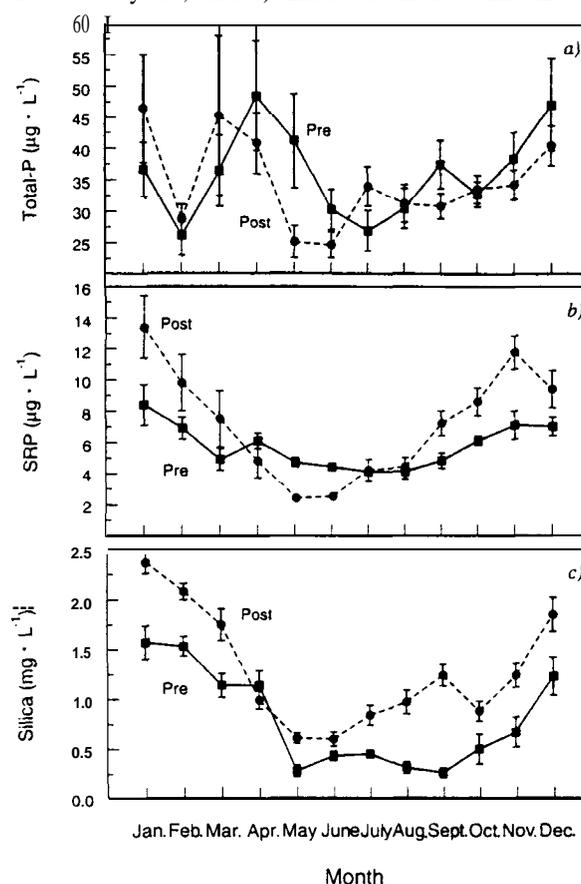
For statistical testing, weekly data were first averaged into monthly means, and then analyzed by month, to avoid the bias of correlation. Testing by month also avoided the effects of seasonal variation within years. Monthly means between any given year were considered to be independent, and differences between periods were tested using both a parametric *t*-test, and the nonparametric Mann-Whitney *U*-test when data did not appear to be normally distributed. All reported cases of significant differences were attained at a significance level of 5% or less. All statistics were performed with SYSTAT version 5.0 (Wilkinson et al. 1992).

Results

Synoptic surveys

The three synoptic surveys indicated that the sewage outfall did not significantly affect water quality at the sampling

Fig. 2. Monthly mean concentrations of (a) total phosphorus, (b) soluble reactive phosphorus, and (c) silica (SiO_2) in Hatchery Bay, western Lake Erie, for 1984-1987 (pre-*Dreissena* years; squares), and 1990-1993 (post-*Dreissena* years; circles). Error bars indicate ± 1 SE.



site in Hatchery Bay (Fig. 1). Two of the surveys, May and November, were conducted when sewage plant operation was low. The July survey was carried out when the plant was in full operation because of the large increase in tourist population. On 11 May 1993, total phosphorus at the outfall was only $13 \mu\text{g} \cdot \text{L}^{-1}$, about the same as elsewhere in the bay, but total phosphorus concentration was $132 \mu\text{g} \cdot \text{L}^{-1}$ near the outfall on 30 July 1993, about 5.5 times greater than in the bay. Concentrations of total phosphorus were about 23% greater at the outfall than in the bay in November. Because in all three surveys total phosphorus at the sampling site in Hatchery Bay was closely similar to concentrations found in adjacent waters, there is no indication of flow of sewage water into the site. The effect of the sewage outfall appears to be limited to the vicinity of the outfall.

Total phosphorus

Total phosphorus concentrations fluctuated much more widely than those of any other variable. The variance in monthly means was large from December through May in the 1980s and from December through April in the 1990s. For the period of record, 19 of 24 monthly mean concentrations were higher than $30 \mu\text{g} \cdot \text{L}^{-1}$ (Fig. 2). The annual mean concentration for 1985-1986 was $39 \mu\text{g} \cdot \text{L}^{-1}$, while

Table 1. Major nutrients and chloride in Hatchery Bay, western Lake Erie, for two full pre- *Dreissena* years, 1985-1986 (105 observations), and three full post-*Dreissena* years, 1991-1993 (total P and soluble reactive P from 152 observations; silica, nitrate-N, and chloride from 153 observations; ammonium from 137 observations).

	Total P ($\mu\text{g}\cdot\text{L}^{-1}$)	Soluble reactive P ($\mu\text{g}\cdot\text{L}^{-1}$)	Silica ($\text{mg}\cdot\text{L}^{-1}$)	Nitrate-N ($\text{mg}\cdot\text{L}^{-1}$)	Ammonium-N ($\mu\text{g}\cdot\text{L}^{-1}$)	Chloride ($\text{mg}\cdot\text{L}^{-1}$)
Mean						
Pre	39	6	0.88	0.52	55	13.4
Post	35	7	1.33	0.72	66	13.9
Median						
Pre	34	5	0.68	0.46	43	12.8
Post	31	5	1.20	0.70	56	13.8
Minimum						
Pre	10	2	0.07	0.01	10	9.1
Post	9	1	0.20	0.20	11	9.4
Maximum						
Pre	168	22	2.55	1.52	245	24.7
Post	188	28	3.60	1.65	220	24.0
Date of maximum						
Pre	9 Apr 85	14 Jan 86	28 Jan 86	9 Apr 85	18 Nov 86	19 Mar 85
Post	9 Mar 93	20 Jan 93	29 Dec 92	1 Jun 93	13 Apr 93	5 Feb 91
SD						
Pre	25.2	3.0	0.70	0.36	40.5	2.5
Post	20.3	5.3	0.70	0.31	40.7	2.5
SE						
Pre	2.5	0.3	0.07	0.04	4.0	0.2
Post	1.6	0.4	0.06	0.03	3.5	0.2

that for 1991-1993 was $35 \mu\text{g}\cdot\text{L}^{-1}$, a reduction of 10% (Table 1). Monthly mean concentrations of total phosphorus for both pre- and post- *Dreissena* periods were highest in winter and spring except for February when they dropped conspicuously. Of the 12 pairs of monthly mean concentrations of total phosphorus (Fig. 2), six from the pre- *Dreissena* period were greater than, and six less than, from the post- *Dreissena* period.

Soluble reactive phosphorus

Monthly mean concentrations of soluble reactive phosphorus for both the pre- and post- *Dreissena* periods declined from January to March and rose in autumn (Fig. 2). They were greater for all months in 1990-1993 than in 1984-1987 except April, May, and June. Monthly means were significantly different only in May. The annual mean concentration for 1985-1986 was $6 \mu\text{g}\cdot\text{L}^{-1}$, whereas for 1991-1993, it was $7 \mu\text{g}\cdot\text{L}^{-1}$, an increase of 17% (Table 1).

Silica (measured as SiO_2)

Monthly mean concentrations of silica for both the 1980s and the 1990s were highest in winter and declined into May (Fig. 2). During the pre- *Dreissena* years, concentrations of silica remained relatively low into September when they began a steady rise into January. Except for a drop in October, concentrations of silica in the post-*Dreissena* years rose steadily during the summer, autumn, and winter to also reach a peak in January. Post-*Dreissena* means were greater than pre- *Dreissena* means in all months except April, and were significantly different in February, March,

and May-September. The annual mean concentration was a $0.88 \text{ mg}\cdot\text{L}^{-1}$, for 1985-1986, whereas for 1991-1993, it was $1.33 \text{ mg}\cdot\text{L}^{-1}$, an increase of 51% (Table 1). The mean springtime April-May depletion rate for silica in the pre-*Dreissena* period was $0.04 \text{ mg}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, whereas in the post-*Dreissena* period it was only $0.02 \text{ mg}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ (Fig. 3); this difference was significant at $P < 0.01$ (r-test). The decrease in silica January-April was greater in the post-*Dreissena* period.

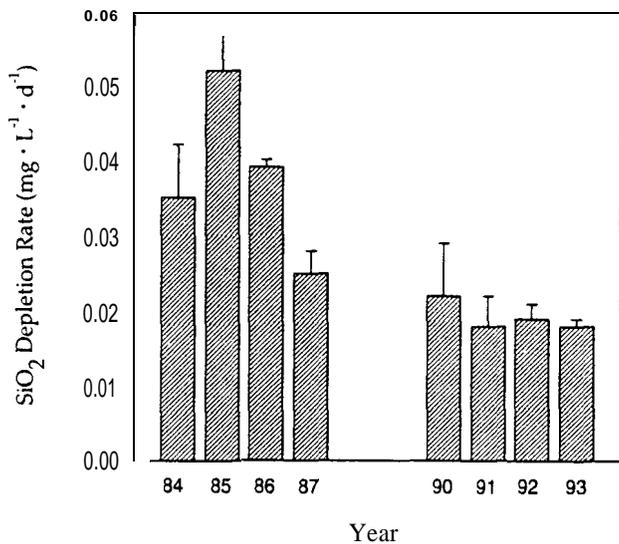
Nitrate-nitrogen

Nitrate was highest in winter and spring, declined throughout the summer and increased again in autumn (Fig. 4). Monthly mean concentrations of nitrate-nitrogen for 1990-1993 were greater than those for 1984-1987 except for April and December, and were significantly different during the warmer months, June-October. The other striking change in monthly mean concentration patterns was the shift from a minimum level of $0.07 \text{ mg}\cdot\text{L}^{-1}$ in the pre-*Dreissena* years to a minimum level of $0.44 \text{ mg}\cdot\text{L}^{-1}$ in the post-*Dreissena* years, both in September. The annual mean for 1985-1986 was $0.52 \text{ mg}\cdot\text{L}^{-1}$, whereas for 1991-1993, it was $0.72 \text{ mg}\cdot\text{L}^{-1}$, an increase of 38% (Table 1).

Ammonium-nitrogen

Monthly mean concentrations of ammonium were highest in late autumn and winter and low from late spring into early autumn during the pre- *Dreissena* years. Sustained high concentrations of ammonium were found from winter through April of the post-*Dreissena* years (Fig. 4). Post-*Dreissena*

Fig. 3. Silica depletion rates for April-May in Hatchery Bay, western Lake Erie, for 1984–1987 (pre- *Dreissena* years) and 1990–1993 (post- *Dreissena* years). Error bars indicate ± 1 SE.



means were greater than pre- *Dreissena* means for every month except November, and significantly different in February. The annual mean for 1985–1986 was $55 \mu\text{g}\cdot\text{L}^{-1}$, whereas for 1991–1993, it was $66 \mu\text{g}\cdot\text{L}^{-1}$, an increase of 20% (Table 1).

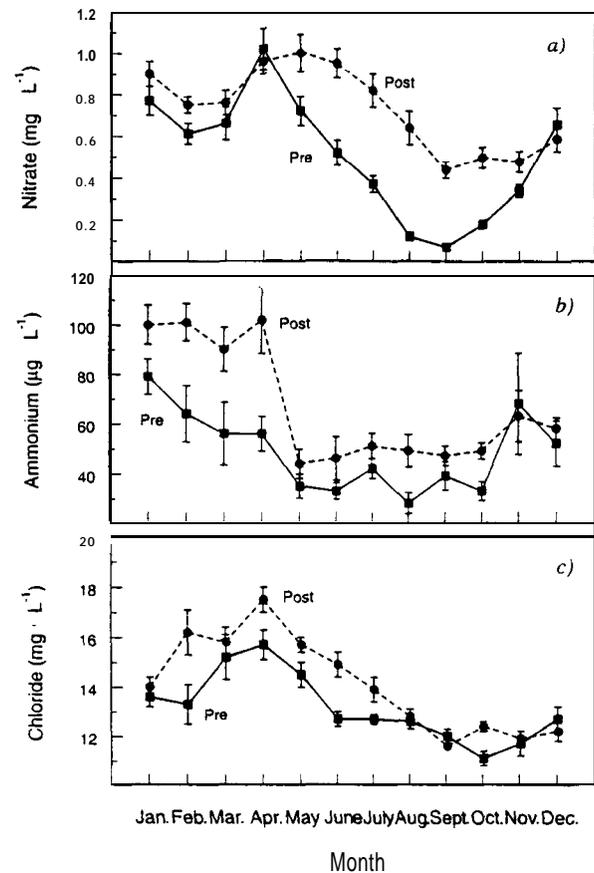
Chloride

Monthly mean concentrations of chloride for both pre- and post- *Dreissena* periods rose during winter and early spring. Pre- *Dreissena* concentrations declined in late spring to a summer plateau while post-*Dreissena* concentrations declined April–September (Fig. 4). Mean concentrations of chloride were greater for all months in 1990–1993 except for September and December and were significantly different in February, April, June, and October. The annual mean for 1985–1986 was $13.4 \text{ mg}\cdot\text{L}^{-1}$, whereas the annual mean for 1991–1993 was $13.9 \text{ mg}\cdot\text{L}^{-1}$, an increase of 5% (Table 1).

Discussion

Our data indicate that after the establishment of *D. polymorpha*, the waters of Hatchery Bay in western Lake Erie remain eutrophic as defined by their nutrient chemistry. All soluble nutrients have increased and total phosphorus has changed little. Although there was a 33% reduction in total phosphorus loadings to Lake Erie between 1972 and 1982 (Great Lakes Water Quality Board 1985), the mean concentration for 1991–1993, the post-*Dreissena* years for which we have complete data, was $35 \mu\text{g}\cdot\text{L}^{-1}$, strikingly similar to the concentration of $36 \mu\text{g}\cdot\text{L}^{-1}$ found by Beeton (1961) in 1959 to indicate accelerated eutrophication in the island region of western Lake Erie. The high levels of total phosphorus and other nutrients that we find in post-*Dreissena* Hatchery Bay may seem curious in light of the perception that *Dreissena* enhances water quality by removing large quantities of suspended particles, thereby

Fig. 4. Monthly mean concentrations of (a) nitrate-N, (b) ammonium-N, and (c) chloride in Hatchery Bay, western Lake Erie for 1984–1987 (pre- *Dreissena* years; squares), and 1990–1993 (post-*Dreissena* years; circles). Error bars indicate ± 1 SE.



increasing water clarity. While it is true that the filtering activity of the zebra mussel does increase water transparency (Holland 1993), and transparency is one of several criteria used to quantify water quality, the word eutrophic pertains most specifically to nutrients. We use it in this paper in the original limnological sense, i.e., well provided with nutrients (Hutchinson 1975).

Stanczykowska (1984) and Stanczykowska and Planter (1985) found that *D. polymorpha* play an important role in the nutrient cycling of some Polish lakes by accumulating nitrogen and phosphorus in their shells and soft tissues in amounts similar to those stored by macrophytes or fishes in the same lakes. A much larger proportion of the nitrogen and phosphorus processed by *Dreissena* is expelled into the water as feces and pseudofeces. Death and reproduction are additional means of release. In a dimictic lake, extruded material of sufficient density would tend to sink to the sediments. All but one (Imulec) of the Polish lakes studied was dimictic. In a polymictic system, such as Hatchery Bay, biodeposits not utilized by the benthos would be recurrently suspended. This material, in aggregates of feces and pseudofeces, would have a diminished impact on water clarity while at the same time contributing to the total nutrient pool.

Table 2. Periods of ice cover for Hatchery Bay, western Lake Erie, for three pre- *Dreissena* winters (1983-1986) and three post-*Dreissena* winters (1990-1993).

	1983-1984	1984-1985	1985-1986	1990-1991	1991-1992	1992-1993
Ice in	20 Dec	14 Jan	16 Dec	8 Jan	21 Jan	12 Jan
Ice out	7 Apr	4 Mar	20 Mar	27 Feb	25 Feb	23 Mar

Dreissena polymorpha appears to have had minimal effect on levels of total phosphorus in Hatchery Bay when average values are considered. At the same time, concentrations of total phosphorus fluctuated more than those of any other chemical studied (Fig. 2). Hutchinson (1941) attributed considerable variation in the total phosphorus of Linsley Pond, during the period of summer stratification, to relative rates of diffusion from the mud and sedimentation from the water. In a polymictic system, repetitive turbulence should heighten variability. At the same time, turbulence may contribute to the relative stability of mean concentrations. In the shallow, well-mixed waters of western Lake Erie, resuspension flux appears to be a significant factor in retarding the rate of decline in total phosphorus even as loading to the basin has been reduced (De Pinto et al. 1986). Relative stability may also be enhanced by the presence of nonavailable phosphorus derived from the watershed. Phosphorus associated with clays enters Lake Erie through shoreline erosion (John Robbins, Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, Mich., personal communication). Some of this particulate phosphorus may not be available to the plankton; however, it is included in total phosphorus measurements, and may limit the extent to which total phosphorus concentrations may be reduced in western Lake Erie. Leaching of phosphorus from the drainage basin is enhanced by snowmelt and severe storms, which are prevalent in spring and autumn but may occur during any season (National Oceanic and Atmospheric Administration 1984-1987, 1990-1992). The effect of storms on total phosphorus concentrations in Hatchery Bay can be observed in 1985 when on four out of five sampling days unusually high values were associated with greatly increased turbidity and high winds: 12 Mar ($101 \mu\text{g}\cdot\text{L}^{-1}$), 2 Apr ($103 \mu\text{g}\cdot\text{L}^{-1}$), 9 Apr ($168 \mu\text{g}\cdot\text{L}^{-1}$), and 31 Dec ($130 \mu\text{g}\cdot\text{L}^{-1}$). Conversely, concentrations were depressed in February from both pre- and post-*Dreissena* periods, coincident with ice cover (Table 2, Fig. 2).

Bottle experiments indicate that a large proportion of the phosphorus and nitrogen processed by *Dreissena* is excreted as phosphate, detectable as soluble reactive phosphorus (R.T. Heath, Kent State University, Kent, Ohio, personal communication) and ammonium (Quigley et al. 1992). All of the major dissolved nutrients, i.e., soluble reactive phosphorus, silica, ammonium, and nitrate have increased since the establishment of the *D. polymorpha*, suggesting excretion of soluble reactive phosphorus and ammonium by *Dreissena* as well as a diminished need by the plankton, which is not counterbalanced by the nutritional needs of increased macrophytes and the periphyton.

Soluble reactive phosphorus concentrations were higher in the post- *Dreissena* years except for April-June, which

incorporates the periods of fastest growth for diatoms and macrophytes. The decrease during April-June is probably attributable to uptake by periphytic diatoms, macrophytes, and perhaps by nondiatom algae. Filamentous members of the *Zygnematales* classically respond to increased light penetration by proliferating in the benthos; they are abundant in Saginaw Bay, Lake Huron, since the establishment of the *D. polymorpha* there, and may be phosphorus limited (R.L. Lowe and R.W. Pillsbury, Bowling Green State University, Bowling Green, Ohio, personal communication). The post-*Dreissena* increase of such benthic algae in Hatchery Bay is probable and might help explain why, in the 1990s, the winter-spring decrease in soluble reactive phosphorus preceded the decline in silica by about a month.

Changes in the silica content of the water are likely to follow diatom growth and abundance rather closely because few other freshwater organisms use it in quantity (Hutchinson 1975; Round 1981); however, large cells tend to take up more of the nutrient than do small cells (Round 1981). Therefore, the continued decline of silica during the pre-*Dreissena* period into early autumn, may be due to its assimilation by large-celled species which were abundant during that time, in particular, the very robust *Actinocyclus normanii* (R.E. Holland, unpublished data). Although annual mean silica concentrations were higher in the 1990s (Table 1), there was a greater absolute loss from winter to spring than in the pre- *Dreissena* years. Uptake by several groups more abundant in the 1990s may have contributed to this. In addition to diatoms, which are epiphytic on macrophytes, there are diatoms which are epizoic on *D. polymorpha* (R.G. Kreis, U.S. Environmental Protection Agency, Grosse Ile, Mich., personal communication). There is also a perception that sponges may have increased in Hatchery Bay during post-*Dreissena* years (D.W. Garton, Indiana University, Kokomo, personal communication), and because freshwater sponges incorporate silica in their skeletons, the spring decrease of silica may reflect uptake by both sponges and diatoms during their peak growth periods. Nevertheless, the development of diatom blooms, as in the spring in Hatchery Bay, constitutes the most important mechanism by which silica is removed from lake waters (Hutchinson 1975). Evidently there was sufficient diatom growth in the spring to decrease silica, but most of the planktonic diatoms were probably soon filtered out by *Dreissena*. Perhaps the factors that contributed most significantly to the more dramatic decline in silica January-April of the post- *Dreissena* years were increased water clarity, earlier ice out (Table 2), and warmer temperatures.

The seasonal cycles for both pre- and post- *Dreissena* nitrate-nitrogen monthly means followed the general pattern described by Hutchinson (1975), and were remarkably similar to that in Lake Windermere (Pearsall 1930). In

both periods, maximum concentrations occurred in spring and may be related to high ammonium values in winter. In ponds, an ammonium maximum in early winter may be succeeded by a nitrate maximum, which is not usually stoichiometrically equivalent to the simultaneous decline in ammonium (Nygaard 1938). Nitrate as well as ammonium concentrations were almost always greater in the 1990s than in the 1980s. This might be attributed to several factors. In addition to a reduced need by a diminished plankton community, and biodeposition and excretion by *Dreissena*, there is the decomposition of dead *Dreissena*. Every winter *D. polymorpha* succumb to harsh temperatures and ice scour in Hatchery Bay (J. Hageman, F.T. Stone Laboratory, Ohio State University, Put-in-Bay, personal communication). This decimation and subsequent decomposition may, in part, be reflected in the elevated concentrations of ammonium January–April of the *post-Dreissena* years. Between April and May, a period of accelerated growth of phytoplankton (Chandler 1942; Holland 1993), periphytic diatoms, and perhaps nondiatom benthic algae, this ion may have been assimilated in preference to nitrate (Brezonik 1972). Other ammonium ions were probably oxidized to nitrate as ice cover faded and spring storms mixed the water. Assuming that ammonium of the *post-Dreissena* years was present in quantities sufficient to meet the needs of the algae in spring, it is possible that the decline in nitrate from May to September of those years was due to uptake by summer algae and submersed macrophyte species as they successively developed. Low summer levels of soluble reactive phosphorus (Fig. 3) should not inhibit growth of macrophytes, which can absorb nutrients through their roots from the substratum as well as through their foliage from the water (Wetzel 1983). The striking difference between nitrate concentrations June–October of the pre- and *post-Dreissena* years may reflect the magnitude of ammonium excretion by *Dreissena* in warm months and its subsequent oxidation to nitrate in an environment where nitrogen-concentrations exceed the needs of the biota. Nitrogen excretion rates were relatively low in cool months and high during warm months in Lake St. Clair (Quigley et al. 1992). Direct excretion effects were much greater than indirect foodweb effects on community nitrogen regeneration in the water column of Saginaw Bay (W.S. Gardner, Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, Mich., personal communication).

The annual chloride load to Lake Erie is largely from diffuse sources (agricultural runoff, highway deicing, sheet and gully erosion, and streambank erosion). For example, the percentage of chloride load to Lake Erie from diffuse sources in 1975, 1977, and 1979, was respectively 90% (Sonzogni et al. 1978), 76% (U.S. Environmental Protection Agency 1980), and 79% (Lang 1984). Maximum loading to the lake occurs during spring runoff and episodically during severe storms (Yaksich et al. 1982). The seasonal pattern for chloride concentration that we observed in Hatchery Bay also reflects spring runoff. The slightly higher general levels of chloride during the *post-Dreissena* period are probably related to increased precipitation in the western Lake Erie watershed during the 1990s. The relative increases in the soluble nutrients are much greater than for chloride (Table 1). The annual mean precipitation for northwestern

Ohio and southeastern Michigan for 1984–1987 was 89.54 cm compared with 96.2 cm for 1990–1992; the annual precipitation summary for 1993 was not yet published at the time of this writing (National Oceanic and Atmospheric Administration 1984–1987, 1990–1992).

The perception that Hatchery Bay, and perhaps western Lake Erie, is less eutrophic since the invasion of *D. polymorpha* is due to reversal in symptoms of eutrophication (i.e., increased water clarity and decreased plankton abundance). Nevertheless, nutrient concentrations have increased thus, it is inappropriate to state the system is more oligotrophic. Apparently the mussel are filtering phytoplankton so rapidly and efficiently as to preclude full utilization of the nutrients by the plankton or the *post-Dreissena* periphyton and macrophytes. Consequently, we have what should be called biological oligotrophy, which is similar in concept to morphometric oligotrophy, where nutrients are not fully utilized by plankton in deep, cold large lakes (Rawson 1960). Meisner et al. (1992), concluded that the ultimate effect of *D. polymorpha* on water quality in the upper Bay of Quinte in Lake Ontario would be determined by processes of sedimentation and reflux of phosphorus at the sediment–water interface. In Hatchery Bay, we speculate that much of the phosphorus sedimented by *Dreissena* is being returned to the water by sediment reflux. Meisner et al. (1992) further concluded that remedial actions for the Bay of Quinte to reduce nutrient loadings may become more important as *D. polymorpha* invade that bay. Our data suggest that this may indeed also be the case for *post-Dreissena* Hatchery Bay.

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References

- Beeton, A.M. 1961. Environmental changes in Lake Erie. *Trans. Am. Fish. Soc.* 90: 153–159.
- Beeton, A.M. 1969. Changes in the environment and biota of the Great Lakes. *In* Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington, D.C. pp. 150–187.
- Bolsenga, S. J., and Ladewski, T.B. 1993. The hydrosphere. *In* Lake Erie and Lake St. Clair handbook. *Edited by* S.J. Bolsenga and C.E. Herdendorf. Wayne State University Press. Detroit, Mich. pp. 171–238.
- Brezonik, P.L. 1972. Nitrogen: sources and transformations in natural waters. *In* Nutrients in natural waters. H.E. *Edited by* H.E. Allen and J.R. Kramer. John Wiley & Sons, New York. pp. 1–50.
- Chandler, D.C. 1942. Limnological studies of western Lake Erie. III. Phytoplankton and physical-chemical data from November, 1939, to November, 1940. *Ohio J. Sci.* 42: 24–44.
- Chandler, D.C. 1944. Limnological studies of western Lake Erie. IV. Relationship of limnological and climatic factors to the phytoplankton of 1941. *Trans. Am. Microsc. Soc.* 63: 203–236.

- Davis, C.O. and Simons, M.S. 1979. Water Chemistry and phytoplankton field and laboratory procedures. Great Lakes Research Division, The University of Michigan, Ann Arbor. Spec. Rep. 70.
- DePinto, J. V., Young, T. C., and McIlroy, L.M. 1986. Great Lakes water quality improvement. Environ. Sci. Technol. 20:752-759.
- Great Lakes Water Quality Board. 1985. Report on Great Lakes water quality to the International Joint Commission. Great Lakes Water Quality Board, Windsor, Ont.
- Griffiths, R. W., Schloesser, D. W., Leach, J. H., and Kovalak, W.P. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48: 1381-1388.
- Holland, R.E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, western Lake Erie since the establishment of the zebra mussel. J. Great Lakes Res. 19:617-624.
- Hutchinson, G.E. 1941. Limnological studies in Connecticut. IV. The mechanism of intermediary metabolism in stratified lakes. Ecol. Monogr. 11:21-60.
- Hutchinson, G.E. 1975. A treatise on limnology. Vol. 1. Part 2. Chemistry of lakes. John Wiley & Sons, New York.
- Lang, G.A. 1984. Update of U.S. Great Lakes tributary loadings, 1979-80. Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan. NOAA Tech. Memo. ERL GLERL-54.
- Meisner, J. D., Kuc, M., and Wedeles, C.H.R. 1992. Effects of zebra mussels, *Dreissena polymorpha* on summer phosphorus and algae biomass of the upper Bay of Quinte: implications for remedial scenarios. Report prepared for Fisheries and Oceans Canada. Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, Ont.
- Menzel, D. W., and Corwin, N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10:280-281.
- National Academy of Sciences. 1972. Water quality criteria 1972. Committee on Water Quality Criteria, Environmental Studies Board, National Academy of Sciences, Washington, D.C. Ecol. Res. Ser. EPA R3.73.033.
- National Fisheries Research Center. 1994. Zebra mussel distribution in the United States (map). National Biological Survey, Gainesville, Fla.
- National Oceanic and Atmospheric Administration. 1984, 1985, 1986, 1987, 1990, 1991, 1992. Climatological data. Total precipitation and departures from normal for southeast lower Michigan and northwest Ohio. National Climatic Data Center, Asheville, N.C.
- Nichols, K. H., and Hopkins, G.J. 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. J. Great Lakes Res. 19:637-647.
- Nygaard, G. 1938. Hydrobiologische studien tiber Danische teiche and seen. I. Teil: Chemisch-physikalische untersuchungen and planktonwagungen. Arch. Hydrobiol. 32: 523-692.
- Pearsall, W.H. 1930. Phytoplankton in the English Lakes. I. The proportions in the waters of some dissolved substances of biological importance. J. Ecol. 18:306-320.
- Quigley, M. A., Gardner, W-S., and Gordon, W.M. 1992. Metabolism of the zebra mussel (*Dreissena polymorpha*) in Lake St. Clair of the Great Lakes. In Zebra mussels: biology, impacts, and control. Edited by T. Nalepa and D. Schloesser. Lewis Publishers, Chelsea, Mich. pp. 295-314.
- Rawson, D.S. 1960. A limnological comparison of twelve large lakes in northern Saskatchewan. Limnol. Oceanogr. 5: 195-211.
- Reeders, H. H., bij de Vaate, A., and Slim, F.J. 1989. The filtration rate of *Dreissena polymorpha* (Bivalvia) in three Dutch Lakes with reference to biological water quality management. Freshwater Biol. 22: 133-141.
- Round, F.E. 1981. The ecology of algae. Cambridge University Press, New York.
- Sonzogni, W. C., Monteith, T. J., Bach, W. N., and Hughes, V.G. 1978. United States Great Lakes tributary loadings. Technical report of the International Reference Group on Great Lakes pollution from land use activities of the International Joint Commission. Great Lakes Basin Commission, Ann Arbor, Mich.
- Stanczykowska, A. 1984. Role of bivalves in the phosphorus and nitrogen budget in lakes. Verb. Int. Ver. Theor. Angew. Limnol. 22. pp. 982-985.
- Stanczykowska, A., and Lewandowski, K. 1992. Effect of filtering activity of *Dreissena polymorpha* (Pall.) on the nutrient budget of the littoral of Lake Mikolajskie. Hydrobiologia, 251:73-79
- Stanczykowska, A., and Planter, M. 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian Lakeland, Poland). X. Role of the mussel *Dreissena polymorpha* (Pail.) in N and P cycles in a lake ecosystem. Ekol. Pol. 33:345-356.
- U.S. Environmental Protection Agency. 1980. Post-pluarg evaluation of Great Lakes water quality management studies and programs. Vol. 2. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago. 111.
- Wetzel, R.G. 1983. Limnology. Saunders College Publishing, New York.
- Wilkinson, L., Hill, M., Welna, J., Birkenbeuel, G. 1992. SYSTAT for windows: statistics, version 5 edition. SYSTAT, Inc., Evanston, Ill.
- Yaksich, S. M., Melfi, D. A., Baker, D. B., and Kramer, J.W. 1982. Lake Erie nutrient loads, 1970-1980. U.S. Army Corps of Engineers, Buffalo, NY. Publ. 14207.