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Chemistry of the Offshore Surface Waters of Lake Erie: Pre- and Post-*Dreissena* Introduction (1983–1993)

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ABSTRACT. *Major changes in ambient surface nutrient chemistry were observed after the introduction of* Dreissena *to Lake Erie. For example, statistically significant increases in spring soluble reactive phosphorus (SRP) (180%, 1.0 to 2.8 µg P/L), nitrate+nitrite (40%, 0.57 to 0.80 mg N/L), ammonia (131%, 15.1 to 34.9 µg N/L), silica (75%, 0.8 to 1.4 mg/L), N:P ratio and turbidity and a significant decrease in total Kjeldahl nitrogen (TKN) (25%, 0.24 to 0.18 µg N/L) were observed in the western basin from the 1983 to 1987 pre-*Dreissena *baseline period to the 1989 to 1993 post-*Dreissena *period. In the summer, total phosphorus (TP) (13%, 20.1 to 17.5 µg P/L) and TKN (27%, 0.30 to 0.22 µg N/L) decreased, while nitrate+nitrite (122%, 0.18 to 0.40 mg N/L) and the N:P ratio increased significantly. Fewer chemical parameters changed significantly in the central and eastern basins, but major changes were observed. For example, spring SRP concentrations in the central and eastern basins increased 250% (0.8 to 2.8 µg P/L) and 92% (2.4 to 4.6 µg P/L), respectively. Silica in these basins increased 300% (0.1 to 0.4 mg/L) and 250% (0.2 to 0.7 mg/L), respectively. TKN decreased in all basins in both the spring and summer (range = 22 to 27%), while TP decreased in all basins in the summer (range = 13 to 24%) but not in the spring.*

*Spatially, spring post-*Dreissena *(1989 to 1993) ammonia, TP, and nitrate+nitrite concentrations were high in the western basin and decreased easterly, while chloride concentrations were variable with no downward or upward trend. In the central basin and eastward through the eastern basin, concentrations of ammonia, chloride, nitrate+nitrite, and total phosphorus were remarkably consistent during and between the pre- and post-*Dreissena *periods. After the* Dreissena *invasion, a different spatial pattern of SRP, silica and phytoplankton biomass was observed. SRP and silica concentrations were high in the western basin and decreased into the central basin as in the pre-*Dreissena *period. Similarly, post-*Dreissena *SRP and silica concentrations were low in the western portion of the central basin but then unexpectedly increased easterly by > 250% and > 1,000%, respectively, over the pre-*Dreissena *period. Phytoplankton biomass increased from within the west end of the western basin to a peak about halfway into the central basin, after which biomass decreased into the eastern basin.*

The increase in the dissolved fraction of nutrients in the western basin can be attributed to the excretion of dissolved fractions by Dreissena *spp. after digestion of particulate matter, the remineralization of surficial organic sediments containing nitrogen and phosphorus-rich feces and pseudofeces and to a decrease in uptake of SRP by less abundant populations of phytoplankton in the western basin. In the western portion of the central basin, it is possible that SRP is being carried by the prevailing westerly current into the central basin stimulating phytoplankton population growth combined with minimal* Dreissena *grazing causing a peak in phytoplankton abundance. There does not appear to be a satisfactory explanation for the simultaneous increase in SRP and the lack of any change in phytoplankton pre- and post-*Dreissena *in the eastern portion of Lake Erie.*

INDEX WORDS: *Nutrient chemistry, phytoplankton,* Dreissena, *Lake Erie.*

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INTRODUCTION

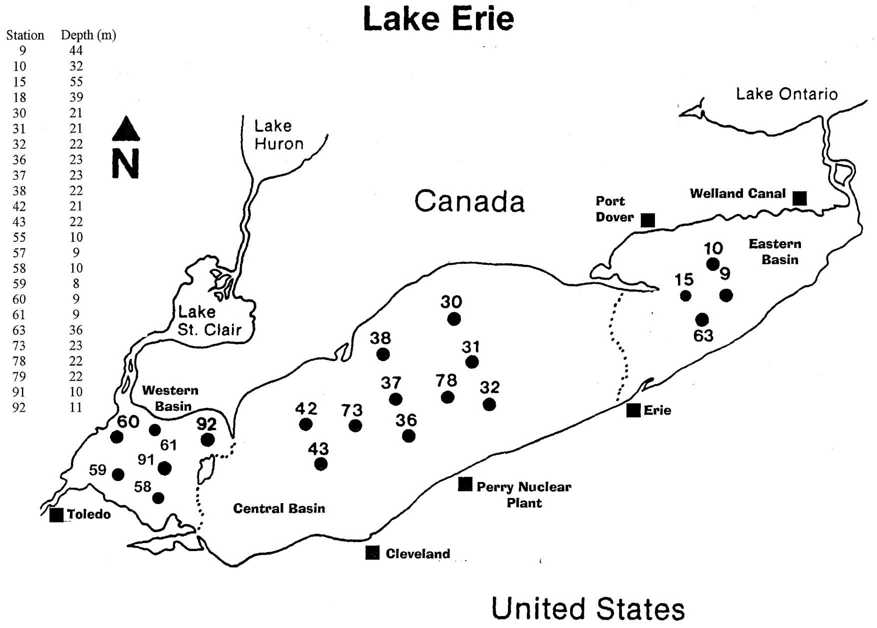
A considerable body of field and laboratory research has suggested that *Dreissena* consumption of phytoplankton is likely (MacIsaac 1996, Reeders and Bij de Vaate 1990, Ten Winkle and Davids 1982, MacIsaac *et al*. 1992, Silvermann *et al*. 1996, Roditi *et al*. 1996, Leach 1993, Nicholls and Hopkins 1993, James *et al*. 1997, Fanslow *et al*. 1995, Holland 1993, Madenjian 1995, Makarewicz *et al*. 1999). In general, *Dreissena* removes suspended material (as high as 30% of the suspended matter from the entire water column per day, Klerks *et al*. 1996) accelerating the flux of particles from the water column to the lake bottom through deposition of feces and pseudofeces. Excretion of soluble forms of phosphorus and nitrogen (nitrate and ammonium) by *Dreissena* (Heath *et al*. 1995, Quigley *et al*. 1992, Mellina *et al*. 1995, James *et al*. 1997) potentially will return nutrients back into the water column and make them available to phytoplankton. On a basin-wide scale, comparison of potential *Dreissena* phosphorus cycling rates with other phosphorus sources suggests that mussels are a major factor in the recycling and flux of phosphorus in the western basin of Lake Erie (Arnott and Vanni 1996).

Dreissena occur on soft and hard bottom substrates of Lake Erie. Dermott and Munawar (1993) suggest that 80% of the total bottom area of Lake Erie had been invaded by *Dreissena* by 1992. Distribution was clumped and abundance in 1992 was variable (range = 0 to 26,595/m^2). With *Dreissena bugensis* prevalent in the profundal zone and *Dreissena polymorpha* prevalent in the littoral zone (Dermott and Munawar 1993), filtering activies of *Dreissena* impact both the littoral and profundal zones of the lake. Apparently, the only region of Lake Erie that has not been colonized by *D. polymorph*a or *D. bugensis* is the central basin which undergoes periodic summer anoxia (Dermott and Munawar 1993, Roe and MacIsaac 1997). Deposition of feces and pseudofeces on the sediment surface and excretion of soluble nutrients can potentially affect sediment chemistry and nutrient dynamics at the sediment water interface (James *et al*. 1997, Klerks *et al*. 1996, Arnott and Vanni 1996). However, the impact on the overlying water column is not clear. Theoretically, the water column chemistry of the entire Lake Erie basin could be affected by *Dreissena*. At a minimum, the cycling of nutrients from the sediment water interface into the water column would be a function of abundance of *Dreissena*, concentration of nutrients at the interface, depth of the water column, and vertical mixing of the water column. In Hatchery Bay, a small continuously mixed bay in the western basin of Lake Erie, concentrations of soluble reactive phosphorus, nitrate+nitrite, ammonium, silica, and chloride increased in the water column after the invasion of *Dreissena* (Holland *et al*. 1995). Thus it would be expected that levels of soluble nutrients would increase in the wind-mixed, non-stratified waters of the western basin. However, the existence of deeper, thermally stratified waters of the central and eastern basin suggests that an increase in soluble nutrients in the upper water column generated from *Dreissena* is not likely during the summer and perhaps not the spring.

Makarewicz *et al*. (1999) observed a significant decrease in phytoplankton in the western basin from 1983 to 1993. This decrease was attributed to *Dreissena* grazing. A similar reduction in phytoplankton biomass did not occur in the central or eastern basins: a fact attributed to the depth of the basins and thermal stratification. In fact, phytoplankton biomass increased in the western portion of the central basin (Makarewicz *et al*. 1999). In this study, pre-*Dreissena* (1983 to 1988) and post-*Dreissena* (1989 to 1993) water chemistry trends in all basins of Lake Erie were examined in an attempt to answer the question of whether there are changes in offshore water chemistry that may be related to the *Dreissena* invasion.

METHODS

With the exception of spring 1989 when ship problems precluded collection, water and phytoplankton samples were collected during 42 cruises from 1983 to 1993 during the spring and summer. Sampling schedules, station locations (Fig. 1) and protocols were selected and implemented to provide information useful for the evaluation of long-term trends in water quality and to assess attainment of general and specific objectives of the Great Lakes Water Quality Agreement (GLWQA). The field sampling design was conducted according to the Lake Erie Surveillance Plan (LESP) of the Great Lakes International Surveillance Plan (IJC 1986a), which was prepared by the Lake Erie Task Force for the Water Quality Board of the Great Lakes Regional Office of the International Joint Commission. The LESP was modified in 1986 by sampling an additional three stations (stations 61, 91, and 92) in the western basin to define a representative off-



Station	Depth (m)
9	44
10	32
15	55
18	39
30	21
31	21
32	22
36	23
37	23
38	22
42	21
43	22
55	10
57	9
58	10
59	8
60	9
61	9
63	36
73	23
78	22
79	22
91	10
92	11

FIG. 1. Lake Erie showing sampling stations in the western, central, and eastern basins.

shore region (Fay and Rathke 1986). In 1996, the U.S. Environmental Protection Agency sought another external review of the sampling design. The participants confirmed that the design was appropriate for assessing year-to-year variations and long-term trends. Nevertheless, the data presented are seasonally limited because of the lack of any sampling during the biologically active periods of May, June, and July. This is unfortunate because significant changes in nutrient concentrations and phytoplankton biomass may occur between April and August.

Reported here are data from 730 samples from the unstratified "spring" period (23 March to 7 May) and the stratified "summer" period (August). An 8-L PVC Niskin bottle mounted on a General Oceanics^{TM} Rossette sampler with a Guildline electrobathythermograph (EBT) was used to collect water samples at a depth of 1 m. Dissolved fractions for analysis were obtained by filtration through 0.45-µm cellulose membrane filters within 60 minutes of collection. The following analyses were performed on board the R.V. *Roger Simons* or the R.V. *Lake Guardian*: chlorophyll (fluorometry, APHA 1985), turbidity (Turner Nephelometer), sulfate (autoanalyzer, Technicon Industrial Method #118-71W), chloride (autoanalyzer, Technicon Industrial Method #99-70W), soluble reactive phosphorus (stannous chloride, autoanalyzer, Technicon Industrial Method #155-71W), total phosphorus (persulfate digestion, autoanalyzer, Technicon Industrial Method #155-71W), ammonia (autoanalyzer, Technicon Industrial Method 154-71W), nitate+nitrite (autoanalyzer, Technicon Industrial Method #154-71W) and dissolved reactive silica (autoanalyzer, Technicon Industrial Method #186-72W). Total Kjeldahl nitrogen (Jirka *et al.* 1976) analysis was performed in the laboratory after preservation on the ship to a pH of 1.5. Nitrogen to phosphorus ratios (N/P) were calculated based on weight (nitrate+nitrite+TKN/TP). Methodology for phytoplankton enumeration and biomass calculations were presented in Makarewicz *et al.* (1999). Chemistry QA/QC procedures followed EPA (1997).

Ambient water chemistry (1-m depth) in the central and western basins was compared between the 1983 to 1988 (pre-invasion) and the 1989 to 1993 (post-invasion) periods. These periods were consistent with the impact of zebra mussels on nearshore phytoplankton communities in Lake Erie observed by Nicholls and Hopkins (1993). In the eastern basin, 1983 to 1989 was compared to 1990 to 1993. In general, the selection of these periods was based on the known occurrence of adult and larval *Dreis-*

sena in Lake Erie and followed Makarewicz *et al.* (1999).

Data manipulations were conducted within the Doric INFO data management system (16816 35th Ave. N.E., Seattle, WA.). The data were grouped and analyzed by basin as a 2 by "n" unbalanced factorial design (western basin, n = 6; central basin, n = 10; eastern basin, n = 4) where the chemical parameter was the dependent variable and time (pre- and post-invasion) and stations were the independent variables. Post hoc multiple range tests on the independent variable stations included Least Significant Difference (LSD) and Bonferroni tests. When the data were organized by station from a west to east orientation, graphical comparisons were made using the mean and one standard error.

RESULTS

Basin Comparisons—Spring (Table 1)

In all three basins of Lake Erie, a highly significant increase in soluble reactive phosphorus (SRP) and dissolved reactive silica, a significant decrease in total Kjeldahl nitrogen (TKN), and no significant changes in total phosphorus (TP) and chloride concentrations were observed from the pre- to the post-*Dreissena* period. In the western and central basins, a significant increase in nitrate+nitrite was observed. In the western basin, a significant increase in ammonia and in the N:P ratio and a significant decrease in phytoplankton biomass and chlorophyll occurred. In the central basin, phytoplankton biomass and chlorophyll increased significantly; these did not change in the eastern basin. Turbidity increased significantly in the western basin after the *Dreissena* invasion and decreased in the eastern basin, but there was no change in the central basin. An inverse relationship between SRP and phytoplankton biomass existed for the entire lake post-*Dreissena* (Fig. 2) that was not evident prior to the *Dreissena* invasion. During the spring, average temperatures (1 m depth) in all basins were below 6°C (western basin= 6.0°C, central basin = 3.4°C, eastern basin = 1.8°C).

TABLE 1. Selected average chemical and biological parameters at a depth of 1m in the western, central and eastern basins of Lake Erie pre- (1983-1988) and post- (1989-1993) **Dreissena** ***invasion. SRP = Soluble Reactive Phosphorus, TP = Total Phosphorus, NO$_3$ = Nitrate+Nitrite, N:P = Nitrogen:Phosphorus ratio, Silica = Dissolved reactive SiO$_2$, TOT = Total phytoplankton biomass, Chl a = Chlorophyll*** **a**, ***Turb = Turbidity. $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.***

	SRP µgP/L	TP µgP/L	NO$_3$ mgN/L	TKN mgN/L	NH$_3$ µgN/L	N:P	Silica mg/L	Cl mg/L	Turb NTU	TOT g/m^3	Chl a µg/L
Western Basin											
Spring											
Pre	1.0^{***}	17.9	0.57^{**}	0.24^{**}	15.1^{**}	50.7^{**}	0.8^{**}	13.0	6.14^{**}	1.97^{*}	7.5^{***}
Post	2.8	20.3	0.80	0.18	34.9	72.1	1.4	14.6	10.60	1.27	3.1
Summer											
Pre	1.2	20.1^{*}	0.18^{***}	0.30^{**}	12.9	31.7^{**}	1.0	10.0	3.10	2.51^{**}	10.2
Post	1.7	17.5	0.40	0.22	15.4	40.1	1.1	11.0	2.70	1.79	9.2
Central Basin											
Spring											
Pre	0.8^{***}	13.2	0.21^{*}	0.22^{***}	8.4	40.3	0.1^{***}	14.5	1.86	1.37^{*}	3.3^{*}
Post	2.8	10.7	0.28	0.16	6.6	43.3	0.4	14.5	2.02	1.79	4.2
Summer											
Pre	0.6	7.7^{**}	0.17^{**}	0.25^{***}	6.2	62.1	0.2	14.2	0.55^{*}	0.86	3.5
Post	0.5	6.5	0.14	0.19	5.7	55.5	0.2	14.2	0.48	0.85	2.7
Eastern Basin											
Spring											
Pre	2.4^{***}	12.5	0.25	0.18^{*}	4.1	38.5	0.2^{***}	15.2	2.09^{**}	0.80	1.3
Post	4.6	10.3	0.28	0.14	4.3	41.5	0.7	14.9	1.30	0.60	1.3
Summer											
Pre	0.5	6.7^{*}	0.13	0.26^{**}	5.0	64.8	0.2	15.1	0.76^{**}	0.63	2.4
Post	0.6	5.1	0.14	0.19	6.2	77.8	0.2	14.5	0.51	0.52	2.0

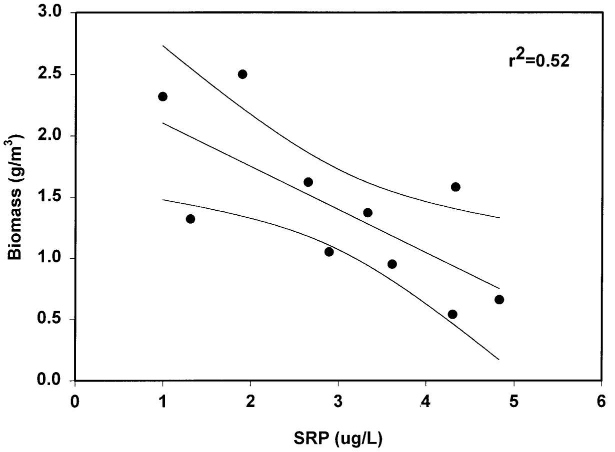


FIG. 2. Relationship between spring phytoplankton biomass and soluble reactive phosphorus after the **Dreissena** *introduction. Shown are the mean and the 95% confidence interval. Spring station data are averaged along a north/south transect (60, 59; 61,91,58; 92; 42,43; 73; 38, 37, 36; 78; 15, 63; 10, 9) to form 10 plotted points.*

Significant differences among stations within basins were observed for several analytes. Within the western basin, there were significant differences in concentrations between some stations for ammonia (stations 91 and 92 from 60 and 59, Fig. 3A), TP (stations 92 from 58, Fig. 4B) and silica (station 60 and 59 from 92, Fig. 4D) for the entire study period. These significant differences among stations within the western basin probably reflect the influence of the plumes of the Maumee and the Detroit rivers and possibly the Sandusky River. Significant interactions between the independent variables, stations and time, were observed with the dependent variables ammonia and silica. Significant differences in post-*Dreissena* concentrations between stations for ammonia (stations 60, 55, 61, and 58 from 91 and 92) and silica (stations 60, 59, 61, and 58 from 91 and 92, Fig. 4D) were observed.

Within the central basin, there were significant differences in silica concentrations between some stations (stations 42, 43, and 78 from 30, 31, 36,

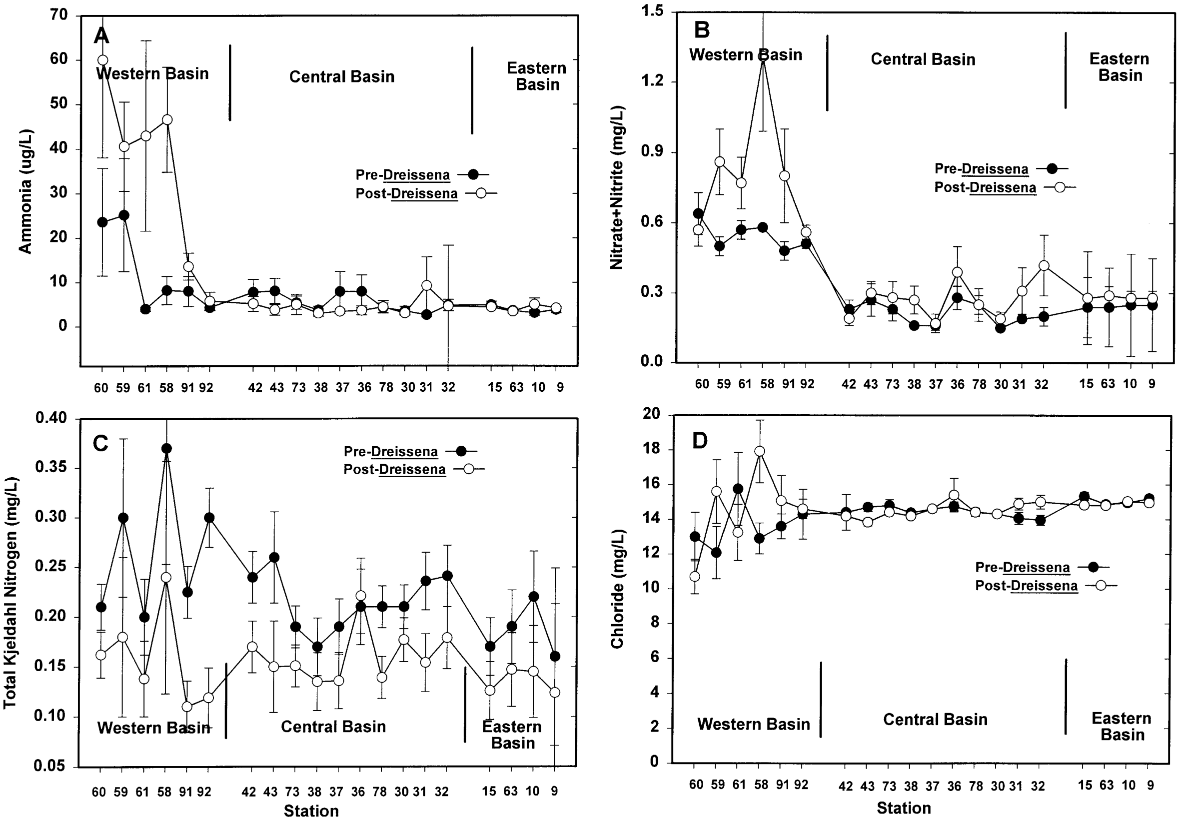


FIG. 3. Lake Erie spring surface (1 m) chemistry: A. ammonia, B. nitrate+nitrite, C. total Kjeldahl nitrogen, D. chloride. Values are the mean ± S.E.

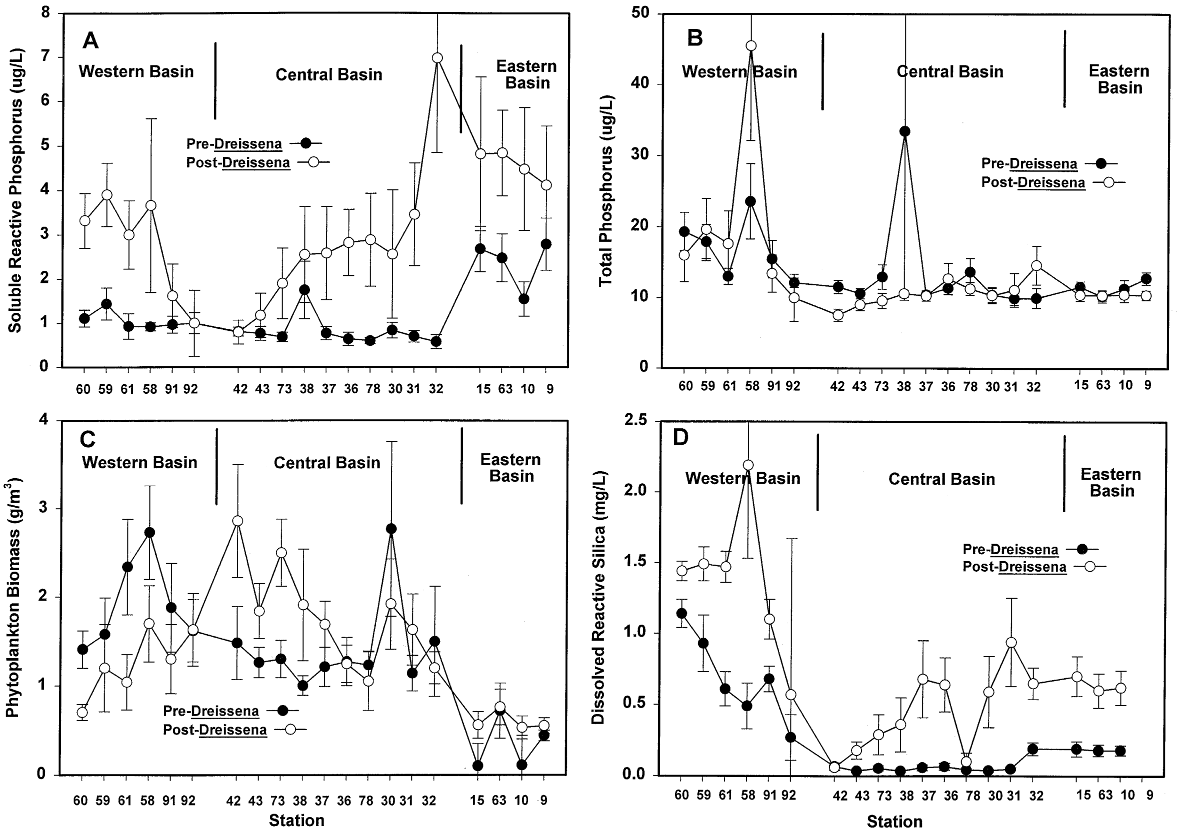


FIG. 4. Lake Erie spring surface (1m) chemistry: A. soluble reactive phosphorus B. total phosphorus C. phytoplankton biomass D. dissolved reactive silica. Values are the mean ± S.E.

and 37; Fig. 4D). Significant interactions between the independent variables, stations and time, were observed with the dependent variables SRP, ammonia and silica. In the post-*Dreissena* period, significant differences in concentrations of SRP (station 32 from 42, 43, 73, 38, 37, 36, and 78; Fig. 4A), and silica (stations 42 and 78 from 30, 31, 32, 36, and 37; Fig. 4D) were observed. In the pre-*Dreissena* period, significant differences in concentrations of ammonia (stations 31, 32, and 38 from 36, 37, 42, and 43) were observed.

Within the eastern basin, there were no significant differences in analyte concentrations between stations and there were no significant interactions between the independent variables, stations and time.

Basin Comparisons—Summer (Table 1)

Comparing the pre- to post-*Dreissena* period, there were no significant changes in summer concentrations of SRP, ammonia, chloride, or silica in any of the three basins. However, TP and TKN decreased significantly in all three basins. Nitrate+nitrite increased significantly in the western basin, decreased significantly in the central basin and did not change in the eastern basin. In the western basin, a significant increase in the N:P ratio, a significant decrease in phytoplankton biomass, and no significant change in chlorophyll concentrations was observed between the pre-and post-*Dreissena* periods. A small but significant decrease in turbidity in the central and eastern basins was also observed. No other significant changes were observed from the pre- to the post-*Dreissena* period in the central and eastern basins during the summer. Average summer water temperatures (1m depth) for the eleven-year period varied little between basins (western = 21.0°C, central = 20.1°C, eastern = 20.1°C).

Significant differences among stations within basins were observed for a few stations. Within the western basin, there were significant differences in

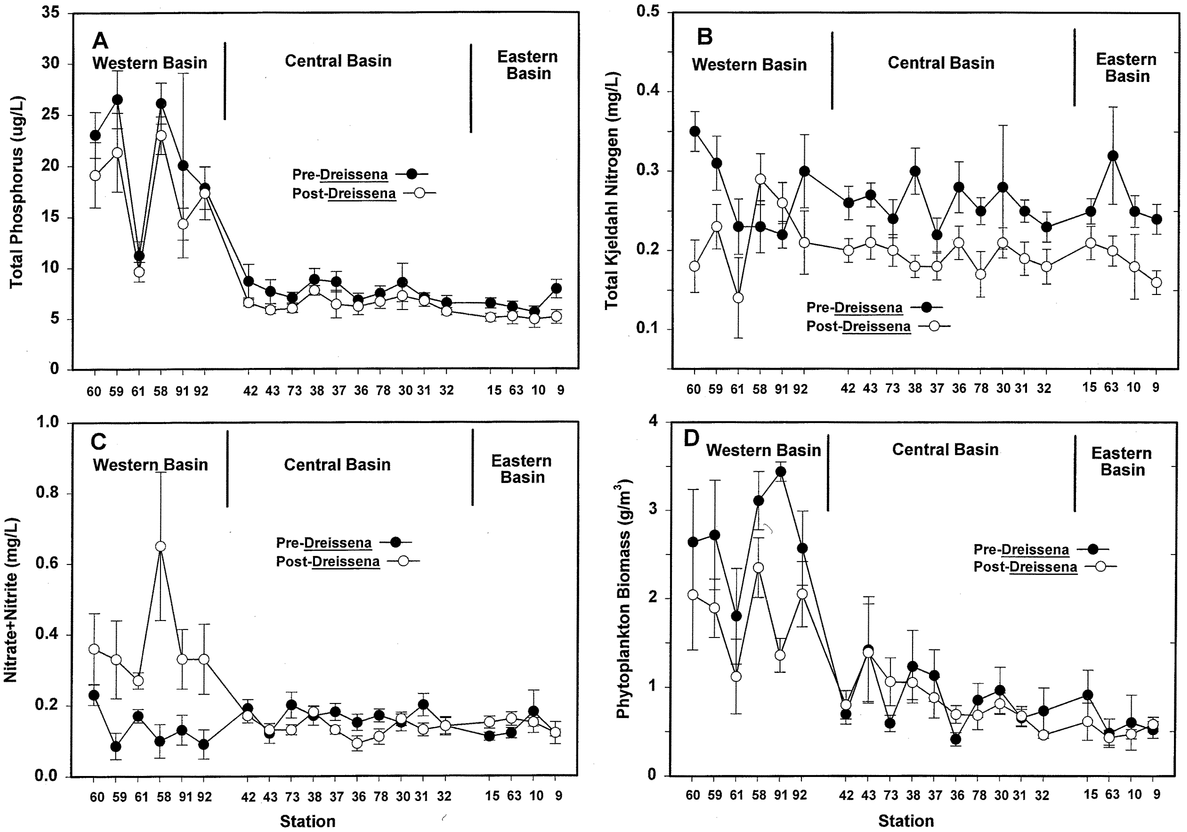


FIG. 5. Lake Erie summer surface (1m) chemistry: A. total phosphorus, B. total Kjeldahl nitrogen, C. nitrate+nitrite, D. phytoplankton biomass. Values are the mean ± S.E.

concentrations between some stations for TP (station 61 from other stations, Fig. 5A) and silica (station 60 from 59, 61, 91, and 92) which most likely reflect the influence of the Detroit River plume on this basin during the summer. Within the central basin, there were significant differences in concentrations between some stations for silica (station 38 from all other stations). Within the eastern basin, no significant difference in concentration between stations were observed. In each of the three basins, no significant interactions between the independent variables, stations and time, were observed with any of the dependent variables reported during the summer.

Spring Spatial Nutrient and Phytoplankton Distributions

In both the pre- and post-*Dreissena* periods, concentrations of ammonia (Fig. 3A), total phosphorus (Fig. 4B), and nitrate+nitrite (Fig. 3B) were higher in the western basin than in other basins. Pre- and post-*Dreissena* chloride concentrations were more variable in the western basin but similar to the central and eastern basins (Fig. 3D). From the western edge of the central basin and eastward through the eastern basin, concentrations of ammonia, chloride, nitrate+nitrite, and total phosphorus (with the exception of a few outliers, e.g., station 38) were remarkably consistent during and between the pre- and post-*Dreissena* periods (Figs. 3 and 4). Similarly, no obvious post-*Dreissena* west to east pattern was observed for TKN except that post-*Dreissena* levels were significantly lower than pre-*Dreissena* concentrations for all basins in the spring (range = 22–27%, Fig. 3C). This was not the case for SRP and silica.

Spatial variation in concentrations of silica (Fig. 4D) and SRP (Fig. 4A), along with total phytoplankton biomass (Fig. 4C), were considerable along the west to east axis of Lake Erie during the pre- and post-*Dreissena* periods. Spring pre-*Dreissena* spatial distribution of SRP and silica was not dissimilar from spring 1970 (Burns 1976) as concentrations were slightly higher in the western basin, decreased into the central basin, and had a small increase in the eastern basin. During the post-*Dreissena* period, a very different spring spatial distribution patterns for SRP and silica were evident. The concentration gradient from the western basin into the central basin (Figs. 4A and D) observed during the pre-*Dreissena* period was still evident, but significantly greater after the *Dreissena* invasion. What was different was the spatial pattern of SRP and silica east of the western basin after the *Dreissena* invasion. Post-*Dreissena* SRP and silica concentrations were low in the western portion of the central basin and then increased easterly by > 250% and > 1,000%, respectively, over pre-*Dreissena* concentrations (comparing stations 38, 37, 36, 78, 30, 31, and 32).

The spring spatial phytoplankton biomass differed considerably between the pre- and post-*Dreissena* period also (Fig. 4C). During the pre-*Dreissena* period, phytoplankton biomass reached a biomass peak in the western basin, decreased into the central basin and then decreased further into the eastern basin. During the post-*Dreissena* period, phytoplankton biomass increased from west to east reaching a peak biomass in the western half of the central basin before generally declining into the eastern basin.

Summer Spatial Nutrient and Phytoplankton Distributions

Spatial distribution patterns of total phosphorus (Fig. 5A) and phytoplankton biomass (Fig. 5D) were similar between the pre- and post-*Dreissena* period. Phytoplankton biomass and total phosphorus concentration were higher in the western basin than in the central and eastern basin. This was not the case for nitrate+nitrite (Fig. 5C) and TKN (Fig. 5B). Compared to the pre-*Dreissena* period, post-*Dreissena* nitrate+nitrite concentrations were higher in the western basin than the central and eastern basins. As with the spring, no obvious post-*Dreissena* west to east pattern was observed for TKN except that post-*Dreissena* levels were significantly lower than pre-*Dreissena* concentrations for all basins in the summer (Fig. 5B).

DISCUSSION

Western Basin

Major changes in ambient water chemistry were observed after the introduction of *Dreissena* to Lake Erie. Most of the significant changes in chemistry and phytoplankton occurred during the spring (nine parameters in the western basin) compared to the summer (five in the western basin) and more changes were observed in the western basin compared to the other basins (spring: 9 in the western basin, 6 in the central basin, 4 in the eastern basin). Potential causes for an increase in ambient concentrations of nutrients in the western basin include increased nutrient loading from the Detroit River, resuspension and remineralization of sediments, excretion of nutrients by *Dreissena* and a reduction in uptake by phytoplankton. Historically, the Detroit River has been a major source of nutrients to the western basin of Lake Erie (Makarewicz and Bertram 1991). However, loading of nutrients, especially phosphorus, from the Detroit River, as well as the Maumee, Sandusky and Cuyahoga rivers has decreased during the period of this study, not increased (R.D. Richards, Heidelberg College personal communication 1999; Dolan 1993; Richards and Baker 1993; Fraser 1987; IJC 1986b).

Resuspension and recycling of nutrients from bottom sediments in the well-mixed non-stratified waters of the western basin (Bartish 1987) is another possible source. Factors that affect mixing of the water column and sediments in the western basin include wind speed, wind direction, and the shallow depth of the basin. Significant differences in these physical factors between the two, 5-year pre-*Dreissena* and post-*Dreissena* periods are unlikely. What has changed is the nature of the sediments and the bottom fauna from the addition of *Dreissena*, a species well known to excrete soluble nutrient fractions and deposit large amounts of feces and pseudofeces. A further observation consistent with a biological cause for the changes in ambient chemistry is the lack of any significant difference in the concentration of the biologically inactive chloride ion between the pre- and post-*Dreissena* periods in all basins.

Ammonia

Quigley *et al.* (1992) and Arnott and Vanni (1996) experimentally determined that *D. polymorpha* excreted ammonia. Similarly, Gardner *et al.* (1995) and Heath *et al.* (1995) have found that the primary excretory product of *Dreissena* was ammonium nitrogen although James *et al.* (1997) observed no change in ammonium nitrogen in laboratory microcosm studies with differing densities of *Dreissena*. Others have observed an increase in ambient ammonium concentrations after the

Dreissena invasion in Saginaw Bay (Johengen *et al.* 1995), Hatchery Bay (Holland *et al.* 1995), and the Seneca River (Effler *et al.* 1996). The increase in ambient concentrations of ammonia observed here and the experimentally determined excretion of ammonia support the hypothesis that excretion of ammonium by *Dreissena* is an important direct effect of *Dreissena* on affected ecosystems (Gardner *et al.* 1995).

Nitrate+Nitrite and Total Kjeldahl Nitrogen (TKN)

In a series of microcosm experiments, James *et al.* (1997) found density-dependent increases in nitrate+nitrite nitrogen accompanied by declines in organic nitrogen with increased *Dreissena* density. In this 11-year study, TKN concentrations decreased significantly in the spring and summer (25 and 27% decrease, respectively) while nitrate+nitrite increased significantly in the western basin in the spring and summer (40% and 122% increase, respectively). A similar increase in ambient nitrate+nitrite concentrations was observed in Hatchery Bay (Lake Erie) and Saginaw Bay (Lake Huron) after the *Dreissena* invasion (Holland *et al.* 1995, Johengen *et al.* 1995). Experimental work, before and after field studies from other sites, and the results reported in this study support the hypothesis that *Dreissena* has had a major effect on TKN and nitrate+nitrite chemistry of the western basin.

Phosphorus

In a series of *Dreissena* microcosm experiments, declines in total phosphorus coincided with density-dependent increases in the concentration of soluble reactive phosphorus (James *et al.* 1997). Numerous workers (Arnott and Vanni 1996, James *et al.* 1997, Heath *et al.* 1995, Effler *et al.* 1996, Mellina *et al.* 1995) have demonstrated that *Dreissena* can play an important role as a nutrient source by excreting nutrients, such as SRP, back into the water column. Marked increases in SRP have been reported in lakes and rivers at high population densities of *Dreissena* in Hatchery Bay, Lake Erie (Holland *et al.* 1995), Lake St. Clair (Mellina *et al.* 1995) and the Seneca River in New York (Effler *et al.* 1996). Only in Saginaw Bay did a small but consistent decline in SRP occur after *Dreissena* introduction (Johengen *et al.* 1995), which was attributed to low initial ambient concentrations of SRP. The significant increase in ambient spring concentrations of SRP and the significant decrease in summer TP reported here, the numerous field studies demonstrating an increase in SRP after *Dreissena* introduction, and the experimental evidence of excretion of SRP by *Dreissena* support the hypothesis that the excretion of SRP by *Dreissena* can have an important direct effect on aquatic ecosystems.

Spring Spatial Nutrient Distribution Pattern—All Basins

The increase in the dissolved fraction of nutrients and the decrease in particulate fractions (summer especially) observed in the western basin were most likely caused by the excretion of dissolved fractions by *Dreissena*, the remineralization and resuspension of surficial organic sediments containing nitrogen and phosphorus-rich feces and pseudofeces produced by *Dreissena*, a reduction in nutrient uptake by phytoplankton, and by *Dreissena* filtration of suspended particles including phytoplankton. The changes in water chemistry observed were consistent with the hypothesis that *Dreissena* excretion of nutrients and removal of particulate fractions were the causative agents. However, it is unlikely that the variability in chemistry along the entire west-east axis of Lake Erie (Figs. 3 and 4) was solely because of *Dreissena*, particularly in the deeper waters of the central and eastern basins. Variability in spring nutrient concentrations may be influenced by many factors, including *Dreissena* and zooplankton excretion of nutrients, resuspension and remineralization of sediments influenced by *Dreissena*, nitrification, and phytoplankton nutrient dynamics (uptake kinetics).

In order to consider the potential interactions between spring phytoplankton biomass and phosphorus and silica levels along the west/east axis of Lake Erie, their values averaged along the south-to-north transects (stations 30, 31, and 32 are averaged and plotted as station 31) for the years 1989 to 1992 are plotted (Fig. 6). Post-*Dreissena* phytoplankton biomass increased from the west (station 60) to the east reaching a peak at station 73 in the central basin, after which phytoplankton biomass generally decreased into the eastern basin. Using the pre-*Dreissena* phytoplankton biomass spatial distribution as a reference point, the proximal cause of the post-*Dreissena* spatial distribution was a significant decrease in phytoplankton biomass in the western basin and a significant increase in biomass in the central basin (Fig. 4C). This decrease in western basin phytoplankton biomass may be attributed to

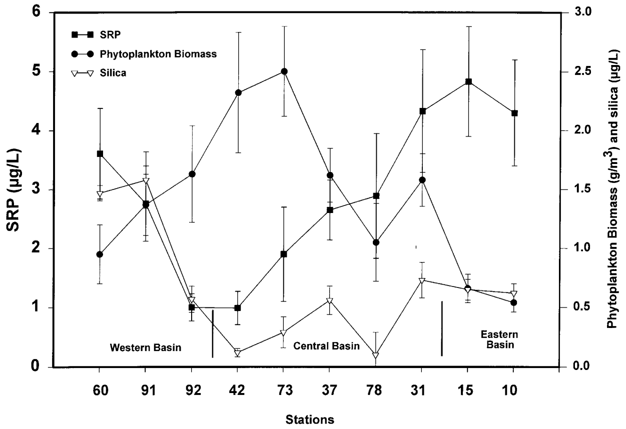


FIG. 6. Post-**Dreissena** ***spring spatial variation in soluble reactive phosphorus, dissolved reactive silica, and phytoplankton biomass. Plotted are the same data presented in Figure 2 with stations along the north south axis grouped and arranged along the west to east axis. For example, stations 9 and 10 are grouped and plotted as station 10. Stations 30, 31, and 32 are grouped and plotted as station 31. Values are the mean±S.E.***

Dreissena filtration in the shallower, well-mixed waters of the western basin (Makarewicz *et al.* 1999, Holland *et al.* 1995, Leach 1993). Because of the greater depth (in excess of 20 m) of the central and eastern basins, Makarewicz *et al.* (1999) suggested that *Dreissena* was not able to effectively graze down phytoplankton biomass in the upper portion of the water column of the central and eastern basins as it did in the western basin; thus the lack of effective grazing by *Dreissena* allowed phytoplankton biomass to be high. However, what was the ultimate cause of the increase in phytoplankton biomass in the western portion of the central basin? It is possible that SRP is being carried by the prevailing westerly current (Bartish 1987) into the central basin stimulating phytoplankton growth, that epilimnetic phytoplankton populations were released from grazing pressure from *Dreissena*, and thus the normally P-limited phytoplankton increased in biomass to levels typically observed only in the western basin prior to the arrival of *Dreissena*. Similarly, diatom biomass increased significantly in the central basin, especially in the western stations of the central basin (Makarewicz *et al.* 1999), and as would be expected, dissolved silica and nitrate levels decreased because of uptake by diatoms (Schelske *et al.* 1986)(Fig. 6, Fig. 4D) and phytoplankton uptake in general (Fig. 3B).

East of station 73 in the central basin, phytoplankton biomass generally decreased easterly from the central basin into the eastern basin (Fig. 6). No significant difference (station 38 to 9, paired T-test, $P < 0.05$) in phytoplankton biomass was observed between the pre- and the post-*Dreissena* periods (Fig. 4C) despite SRP levels being 2 to 3 times greater than the pre-*Dreissena* period from roughly station 73 eastward (Fig. 4A). It is possible that phytoplankton were being stimulated by the increase in SRP, but *Dreissena* grazing was roughly equal to the production rate, leaving no net change in biomass. This seems unlikely, but there are no data to disprove this hypothesis. Other factors that may be controlling phytoplankton biomass in the eastern half of the lake include another undefined nutrient or physical factor, such as light, or differential zooplankton grazing in the eastern portion of the lake.

Similarly, there is no satisfactory explanation for the increase in SRP east of station 73. If *Dreissena* impacted the pelagic waters of the eastern end of the lake, SRP, ammonia, and nitrate+nitrite should increase, and phytoplankton biomass should decrease as observed in the western basin. An increase in SRP was observed, but phytoplankton biomass and ammonia and nitrate+nitrite levels did not change from the pre- to the post-*Dreissena* period east of station 73. Also, the reduction of SRP levels in the central basin by station 42 made it impossible to infer P transport from the western basin into the eastern half as previously suggested for the western end of the central basin. Either an autochthonous source of nutrients, such as transport of P from the nearshore or upwellings, which is unlikely (Bartish 1987, Schertzer *et al.* 1987), zooplankton excretion of P, a new allochthonous source(s) or a yet undefined process was present in the eastern basin.

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