Evidence of recovery from phosphorus enrichment in Lake Michigan

Richard P. Barbiero, Marc L. Tuchman, Glenn J. Warren, and David C. Rockwell

Abstract: During the last century, diatom production responses to increased phosphorus loading in Lake Michigan resulted in increased silica sedimentation losses and a consequent decline in the silica content of the lake. In light of recent reductions in phosphorus loading to the lake, we examined long-term monitoring data to determine if this trend might be reversing. Spring total phosphorus concentrations, although highly variable, declined approximately 1 $\mu g \cdot L^{-1}$ throughout the lake between 1983 and 2000. Spring soluble silica concentrations, an indicator of total in-lake reserves, increased from 1.1 to 1.6 $mg \cdot L^{-1}$ during this period. Summer epilimnetic silica concentrations in the southern basin were at apparently limiting levels of approximately 0.15 $mg \cdot L^{-1}$ until 1991 and then increased sharply. A similar trend was seen in the northern basin. Summer diatom populations increased in both basins after 1991, and ordination analyses suggest that the species composition of both spring and summer communities has responded to these silica increases. These results document for the first time a reversal of the silica depletion sequence and provide the most compelling evidence to date that phosphorus load reductions are having an impact on the Lake Michigan ecosystem.

Résumé : Au cours du siècle dernier, la production de diatomées en réaction à la charge accrue de phosphore au lac Michigan a eu pour conséquence d'augmenter les pertes de silice par sédimentation, réduisant ainsi le contenu de silice du lac. Les chutes récentes de la charge de phosphore du lac nous ont incités à examiner les données de surveillance à long terme du lac pour voir si cette tendance était en train de se renverser. Les concentrations de phosphore total au printemps, bien que très variables, ont baissé d'environ 1 $\mu g \cdot L^{-1}$ dans l'ensemble du lac de 1983 à 2000. Les concentrations de silice soluble au printemps, un indicateur des réserves totales du lac, ont augmenté de 1,1 à 1,6 $mg \cdot L^{-1}$ durant la même période. Les concentrations de silice dans l'épilimnion en été dans le bassin sud étaient, semble-t-il, au niveau limitant d'environ 0,15 $mg \cdot L^{-1}$ jusqu'en 1991, pour ensuite augmenter fortement. Une tendance semblable s'est produite dans le bassin nord. Les populations estivales de diatomées ont crû dans les deux bassins après 1991 et des ordinations montrent que la composition spécifique des communautés de printemps et d'été a réagi aux augmentations de silice. Nos résultats démontrent pour la première fois un renversement dans la séquence d'épuisement de la silice; ils présentent aussi la preuve la plus convaincante à ce jour que les réductions des charges de phosphore ont un impact sur l'écosystème du lac Michigan.

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Introduction

Unlike smaller lakes, the silica (Si) budget of Lake Michigan, with its great depth and long hydraulic residence time, is dominated to a large extent by internal processes. Because external loads are so small relative to the volume of the lake, the reservoir of Si in the water mass constitutes the main source for seasonal diatom growth (Conway et al. 1977). An estimated 90–99% of the Si used for diatom production is recycled on an annual basis (Parker et al. 1977*a*; Schelske 1985), although most of this recycling takes place well below the photic zone (Conway et al. 1977) and is therefore unavailable during most of the growing season once it settles out of the upper waters. The remaining 1–10% is lost permanently to the sediments through burial of diatom cell walls. Even with such a high annual recycling rate, changes in annual diatom production, and thus the amount of biogenic Si sedimented and permanently lost to the sediments, can substantially alter in-lake concentrations on a long-term basis (Schelske 1985).

Such an alteration occurred during the last century, when increased diatom production caused by anthropogenic increases in phosphorus (P) loading resulted in increases in Si uptake and subsequent sedimentation, and led ultimately to long-term reductions in the reservoir of Si stored in the water column of the lake (Schelske and Stoermer 1971). This phenomenon of long-term Si decrease in response to P enrichment has been termed the silica-depletion sequence

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(Schelske et al. 1983) and is generally applicable to lakes in which long retention times cause internal processes to dominate nutrient dynamics. Schelske (1988) showed that between 1954 and 1969, offshore winter maximum Si concentrations in Lake Michigan decreased by about 3 mg $SiO_2 \cdot L^{-1}$. On a seasonal basis, the increases in diatom Si uptake combined with the declines in the overall Si reservoir and the lack of appreciable recycling, relative to other nutrients, within the upper waters during the growing season led to progressive reductions in epilimnetic Si concentrations over the course of the stratified period. This ultimately resulted in Si limitation of diatoms in the summer. Because diatoms had historically dominated the phytoplankton assemblage at all times (Davis 1966), seasonal Si limitation and the resulting shift in summer dominance to non-silica requiring forms, such as green and blue-green algae (Bartone and Schelske 1982; Chang and Rossmann 1988), constituted a substantial alteration in the community structure of the lake.

With the creation of the Great Lakes Water Quality Act in 1972, binational efforts have focused on controlling P inputs to the Great Lakes. Given the strong P limitation of the phytoplankton community in the lake (Schelske et al. 1986), we hypothesized that reductions in P loading would result in reduced annual diatom productivity, consequent reduced deposition of Si to the sediments via diatom sedimentation, and a decrease in the annual loss of Si from the water column. Therefore, reductions in P loads should ultimately be apparent in increases in the Si reservoir of the lake, an easing of summer Si limitation, and an increase in summer diatom populations. With increases in Si and Si–P ratios, we also expected shifts in diatom species composition. Kilham (1971) recognized that species with lower Si requirements are favored at lower ambient Si concentrations. Differences in supply ratios of P and Si, where both are potentially limiting, also lead to differences in competitive outcomes and, ultimately, species composition (Titman 1976; Tilman 1977). The importance of Si and Si:P has previously been shown in determining diatom dominance patterns in Lake Michigan (Barbiero et al. 2001).

The U.S. Environmental Protection Agency's (U.S. EPA) Great Lakes National Program Office has been conducting regular annual surveillance monitoring of Lake Michigan since 1983. Here we make use of this unique 18-year dataset of nutrient concentrations, diatom abundances, and species composition to test these hypotheses. Specifically, we were interested in assessing whether recent decreases in phosphorus loading to Lake Michigan have brought about increases in total in-lake silica content, easing of summer silica limitation, increases in summer diatom populations, and shifts in diatom species composition.

Materials and methods

Spring sampling was conducted on Lake Michigan from 1983 to 2000, and summer sampling from 1983 to 1999. Spring surveys were conducted as early as possible after ice-out conditions in the Straits of Mackinac to provide estimates of initial growing season concentrations of nutrients, and summer surveys were conducted during the period of stable thermal stratification to assess the extent of epilimnetic nutrient depletion. Although both stations and sampling dates remained relatively consistent during the course of the study period, some stations in the extreme north and extreme south of the lake were only sampled during the first 2 years of the program, and these stations were excluded from our analyses (Fig. 1). Also, from 1983 to 1995, multiple sampling runs were often undertaken for one or both of the seasonal cruises. Because these runs were sometimes nearly a month apart, to maximize comparability, only those runs most closely approaching the average dates for each seasonal survey were used.

At each station, water column profiles for temperature were taken using a Seabird STE-911 conductivity–temperature–depth (CTD) multisensor unit (Sea-Bird Electronics, Inc., Bellevue, Wash.). Samples for nutrients were taken at discrete depths throughout the entire water column, although data reported here are station means of all samples ≤20 m. Integrated samples for phytoplankton enumeration were created from a composite of equal aliquots of water samples taken at discrete depths (spring: surface, 5 m, 10 m, and 20 m; summer: surface, 5 m, 10 m, and lower epilimnion) with Niskin bottles mounted on a SeaBird carousel water sampler.

Samples for total soluble phosphorus (TSP) and soluble Si were filtered in the field through 0.45-μm Sartorius filters. Samples for TSP and total phosphorus (TP) were preserved with H_2SO_4 for later analysis in the lab. Samples for soluble Si were stored at 4°C. Samples for phytoplankton analysis were preserved in the field with Lugol's solution and with formalin upon return to the laboratory.

TSP and TP were measured on a Lachat QuikChem AE autoanalyzer (Lachat Instruments, Milwaukee, Wis.) by the ascorbic acid method after acid persulfate digestion (APHA 1985). Soluble Si was determined as SiO_2 by the molybdate method on a Lachat QuikChem AE autoanalyzer (APHA 1985). Before 1991, chemical analyses were conducted on board ship; after this date, analyses were performed in a land-based laboratory. Internal comparisons have shown no difference and confirmed the comparability of data from the two periods (G. Warren, unpublished data). Diatom abundances were determined using the Utermöhl technique (Lund et al. 1958) at a magnification of 500×, with only species of *Urosolenia* identified at this stage. Identification of all other diatoms was done from permanent slide mounts at 1250×, with approximately 500 frustules identified per sample. Relative proportions of each taxon of centrics and pennates were then multiplied by the appropriate Utermöhl counts. Primary taxonomic keys used were Krammer and Lange-Bertalot (1991, 1997), Patrick and Reimer (1966, 1975), and Germain (1981). Further details on methods are available elsewhere (Barbiero and Tuchman 2001).

As an indication of the timing of thermal development in different years, data were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Data Buoy Center (http://www.ndbc.noaa.gov) for the northern basin (buoy 45002) and the southern basin (buoy 45007), and the first date at which lake surface temperature remained above 4°C was determined. This is referred to here as the first date of stratification, although well-developed thermal structure probably did not occur until somewhat later.

Before assessing trends, differences between the northern

Fig. 1. Map of sampling stations in Lake Michigan showing location of the lake in the Great Lakes region of North America. Not all stations were sampled in all years. Line indicates division between northern and southern basin stations.

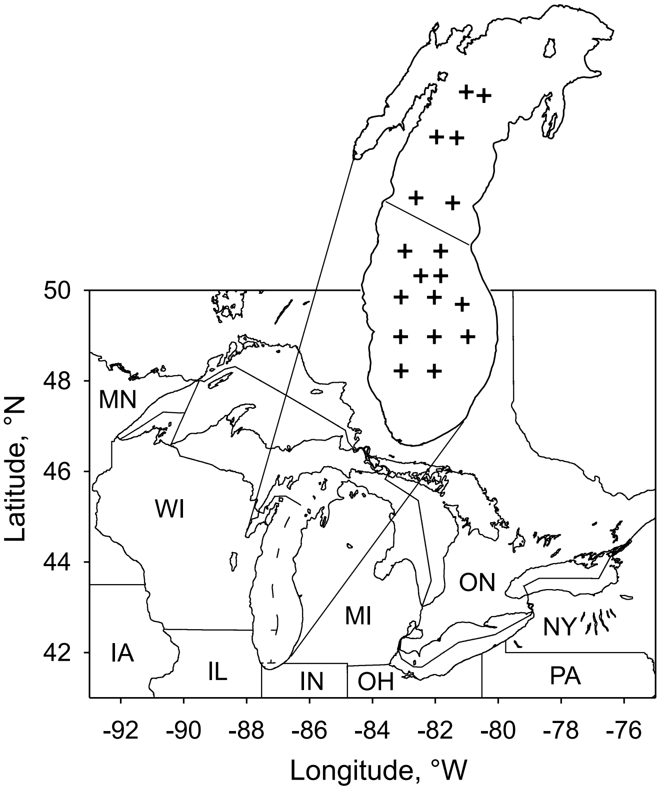
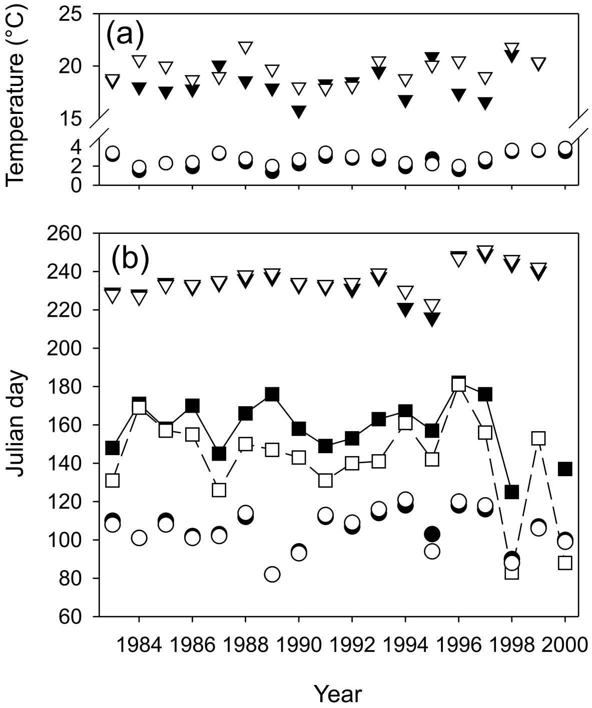


Fig. 2. (*a*) Average surface water temperature during spring (○) and summer (▽) cruises. (*b*) Julian day of start of spring (○) and summer (▽) cruises and date of first stratification (□) as defined in text. Solid symbols, northern basin; open symbols, southern basin.



and southern basins (see Fig. 1) were tested for using a two-way analysis of variance (ANOVA), with basin and year as factors, transforming when necessary to satisfy assumptions of normality and homoscedasticity. If significant ($\alpha = 0.05$) differences were not found, data from the two basins were pooled. Trends over time were assessed using the nonparametric Spearman's rank correlation. Where appropriate, rate of change was estimated using Sen's nonparametric slope estimator (Gilbert 1987).

To test for changes in diatom community composition over time, detrended correspondence analysis (DCA; Hill and Gauch 1980) was employed using the program CANOCO (Ter Braak 1988). Phytoplankton abundances were converted to natural logarithms before analysis to reduce effects of differences in abundances. Environmental gradients associated with the two main DCA axes were identified by correlating environmental variables and sample axis scores using the Spearman's rank correlation procedure, and when significant, these correlation coefficients were plotted against the respective axes after appropriate rescaling.

Results

Dates of spring surveys spanned a range of 40 days, with no systematic changes during the course of the study (Fig. 2). Average temperatures during spring surveys remained within the relatively narrow range of 1.4–3.9°C, and although temperatures tended to be higher in the southern basin, differences were extremely slight. Temperatures were higher than usual during the last 3 years examined (1998–2000), and in two of those years, the spring survey coincided with the warming of surface waters above 4°C. Estimated dates of first stratification were relatively constant from 1983 through 1995, but became increasingly erratic after that, and 1998 and 2000 appeared to be years during which surface water warming occurred quite a bit earlier than usual. Summer surveys were conducted within a range of 35 days, with 1994 and 1995 surveys occurring particularly early, and subsequent ones particularly late (Fig. 2). Timing of surveys, however, was not reflected in differences in temperatures, which showed little systematic change during the course of the study. Temperatures in the northern basin were almost always lower than those in the southern basin, as would be expected. The length of the summer season before sampling (estimated as the difference between Julian day of first stratification and Julian day of the summer survey in Fig. 2) was always shorter in the north and was quite consistent from year to year with the notable exception of 1998, when a combination of early warming and a later than usual cruise resulted in a relatively longer sampling interval. The longer interval preceding summer sampling in 1998 would have resulted in a greater probability of Si limitation having been achieved by the time of the survey.

Estimates of P loads to the lake show dramatic declines from the mid-1970s to the mid-1990s (Fig. 3). Although highly variable, loads appear to have been reduced by at least 50% during this time. The most dramatic reductions seem to have taken place during the early 1980s, although reductions have apparently continued into the mid-1990s, at which point the data record ends.

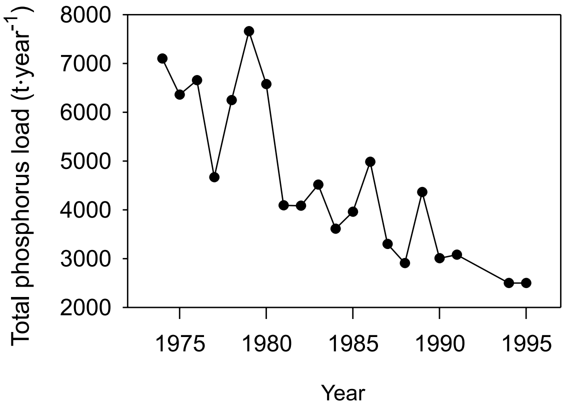


Fig. 3. Estimated annual total phosphorus loading to Lake Michigan from 1974 to 1995. Data are from the International Joint Commission (1974–1991) and U.S. Environmental Protection Agency (1994–1995).

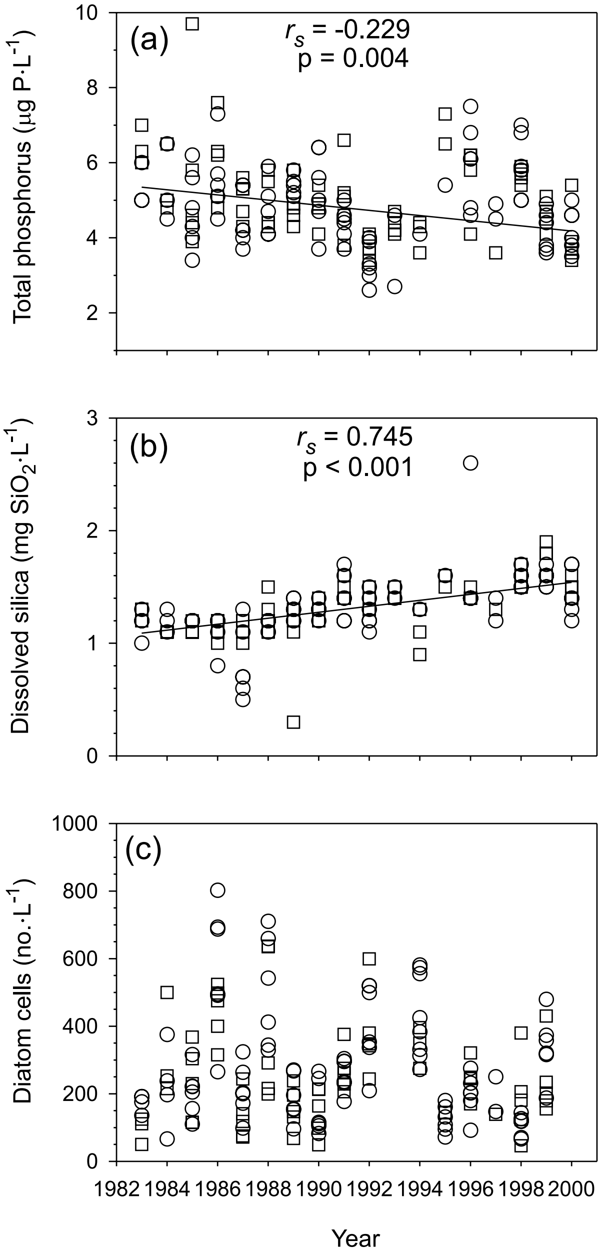


Fig. 4. Spring northern (□) and southern (○) basin mean station values of (*a*) total phosphorus, (*b*) dissolved silica, and (*c*) diatom cell counts. Where significant, Spearman's rank correlation coefficients (r_s) and probabilities (p) are shown; trend lines were estimated using Sen's nonparametric slope estimator.

Spring

To determine if significant differences existed between basins during the spring for TP, Si, and diatom counts, after accounting for year-to-year differences, a two-way ANOVA was conducted on ln-transformed values for each variable, with year and basin as factors. Significant interbasin differences were not found for any variable ($\alpha = 0.05$), and spring data were therefore pooled with respect to basin.

TP concentrations in the spring were highly variable over the course of the study, ranging from 2.6 to 9.7 $\mu g \cdot L^{-1}$ and averaging 4.2 $\mu g \cdot L^{-1}$ (Fig. 4). Spearman's rank correlations of TP against year showed a statistically significant decrease. The annual rate of change was estimated using Sen's nonparametric slope estimator, and this indicated that TP was decreasing, on average, by 0.07 $\mu g \cdot L^{-1} \cdot year^{-1}$, representing a total decrease of approximately 1.2 $\mu g \cdot L^{-1}$ over the course of the study period. Although TP concentrations exhibited an overall downward trend, interannual variability was very high, and some of the highest TP values occurred during the mid- and late 1990s.

We used spring SiO_2 concentrations as an indication of the total reservoir of Si in the lake. It should be noted that these concentrations do not represent annual maximum values; it has been shown that approximately 0.1–0.2 mg $SiO_2 \cdot L^{-1}$ is removed by biological uptake by the time of the spring survey (Lesht and Rockwell 1985). Although these samples are expected to be somewhat less than the annual maximum, they are still comparable over the long term and can therefore provide an indication of changes in the total Si reservoir of the lake. Spring station mean SiO_2 concentrations ranged between 0.3 and 2.6 $mg \cdot L^{-1}$, although 90% of values occupied a much narrower range (1.0–1.7 $mg \cdot L^{-1}$). A steady and highly significant rise in SiO_2 concentration occurred between 1983 and 2000, increasing from approximately 1.1 to 1.5 $mg \cdot L^{-1}$ during that time (Fig. 4). In most years, variability was slight, indicating fairly uniform concentrations throughout the lake.

Spring diatom counts ranged between 46 and 802 $cells \cdot L^{-1}$ ($\bar{x}$ = 266 $cells \cdot L^{-1}$), and showed no clear trends during the course of the study (Fig. 4). Variability was high both within and between years, with the latter most likely reflecting differences in the timing of spring bloom development, the height of which generally occurs at least a month after our spring survey, in May or June (Parker et al. 1977*b*; Bartone and Schelske 1982; Johengen et al. 1994).

Summer

TP concentrations were somewhat more variable in the summer (range 0.9–10.3 $\mu g \cdot L^{-1}$), with the northern basin showing significantly (two-way ANOVA, $p < 0.001$) greater

Fig. 5. Summer mean station values in northern basin of (*a*) total phosphorus, (*b*) dissolved silica, and (*c*) diatom cell counts. Where significant, Spearman's rank correlation coefficients (r_s) and probabilities (p) are shown.

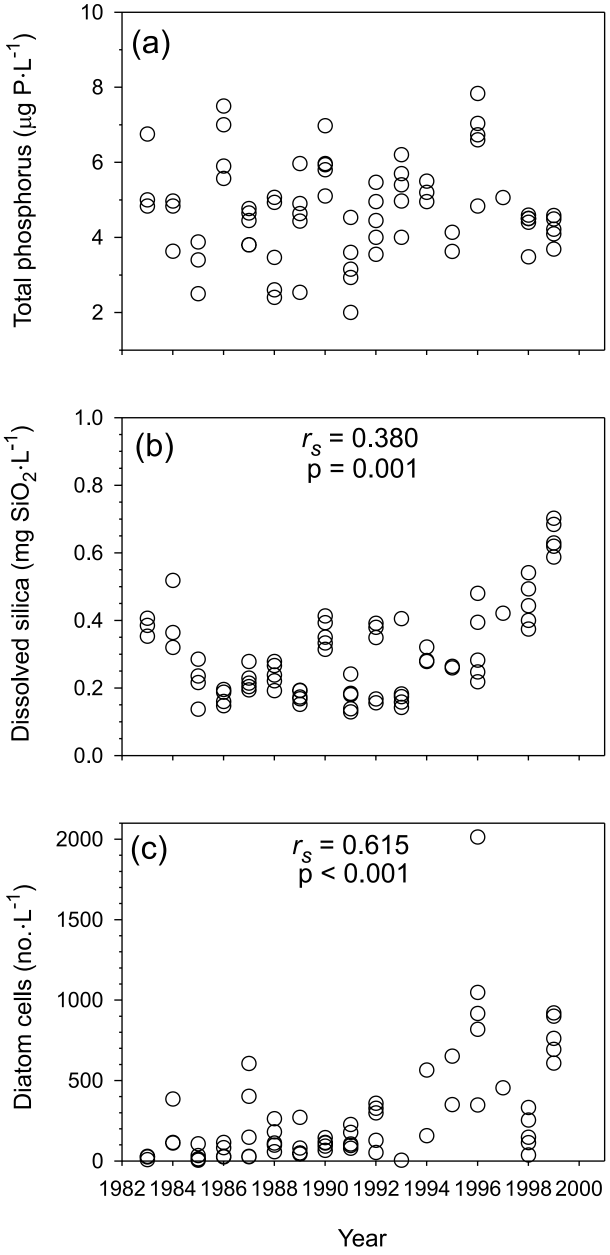
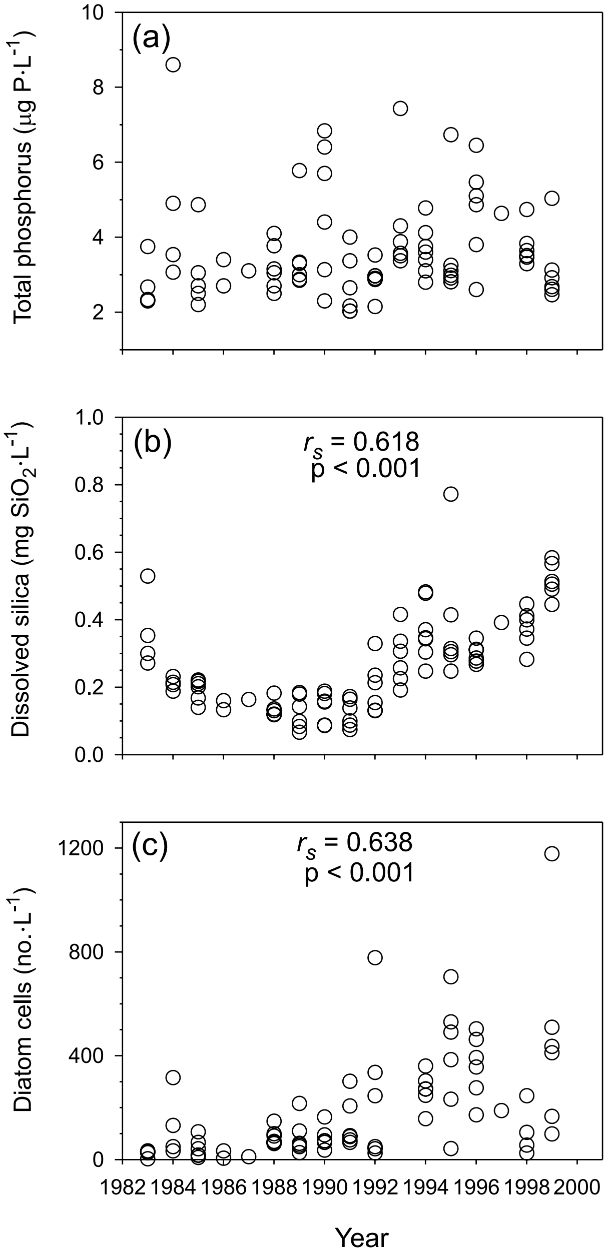


Fig. 6. Summer mean station values in southern basin of (*a*) total phosphorus, (*b*) dissolved silica, and (*c*) diatom cell counts. Where significant, Spearman's rank correlation coefficients (r_s) and probabilities (p) are shown.



values than the southern basin ($\bar{x}$ 4.8 µg·L^{-1} and 3.6 µg·L^{-1}, respectively). Values in the southern basin were notably lower in the summer than in the spring; no seasonal difference was noted in the northern basin. There was no statistically significant correlation between TP and year in either basin (Figs. 5, 6).

Summer epilimnetic concentrations of SiO$_2$ were substantially lower than spring values, never exceeding 0.77 mg·L^{-1}. Concentrations were significantly (two-way ANOVA, p < 0.001) lower in the southern basin than in the northern basin, with the most pronounced differences in the first 10 years of the dataset. Both basins showed strong, statistically significant increases from 1983 to 1999 (Figs. 5, 6). In the southern basin, concentrations during most of the first 10 years of the study period were uniformly low, in most cases less than 0.2 mg·L^{-1}, and had probably been driven to minima by biological uptake at the time of sampling. Concentrations were relatively higher in the northern basin during this time. After about 1991, concentrations increased notably in both basins. As pointed out earlier, during these years, surveys tended to occur somewhat later in the season when Si limitation should be more severe.

Total diatom counts showed marked increases in both basins corresponding to the increases in Si (Figs. 5, 6). As with

Fig. 7. Results of detrended correspondence analysis (DCA) ordination of diatom communities in spring samples for 1983–1991 (shaded triangles) and 1992–1999 (○). Environmental variables are graphed with the angle of the line indicating the degree of correlation with the two axes and the length of the line indicating the relative strength of that correlation. Chl, chlorophyll *a*; °C, temperature; Si, dissolved silica; NO_3, nitrate + nitrite.

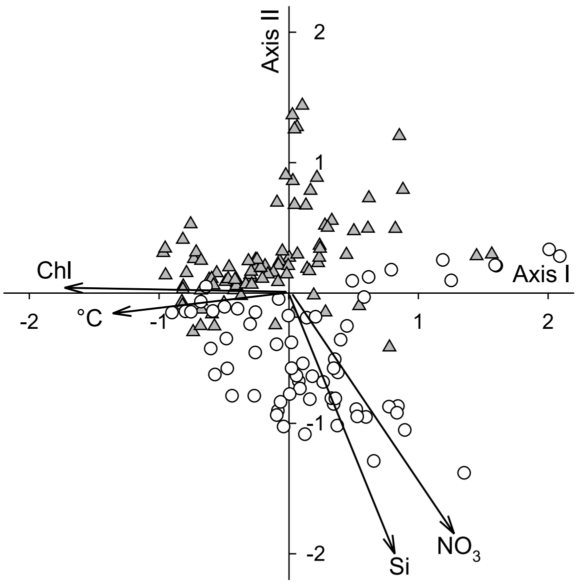


Table 1. Results of detrended correspondence analysis of spring diatom communities in Lake Michigan, 1983–1999.

	Axis 1	Axis 2
Eigenvalue	0.285	0.239
Cumulative % variance	12.5	23.1
Correlations		
Chlorophyll	–0.35	0.01
Temperature	–0.28	–0.03
Silica	0.17	–0.40
Nitrate–nitrite	0.26	–0.37

Fig. 8. Results of detrended correspondence analysis (DCA) ordination of diatom communities in summer samples for 1983–1991 (shaded triangles) and 1992–1999 (○). Environmental variables are graphed with the angle of the line indicating the degree of correlation with the two axes and the length of the line indicating the relative strength of that correlation. TP, total phosphorus; Si, dissolved silica; Si:P, ratio of dissolved silica to total dissolved phosphorus; °C, temperature.

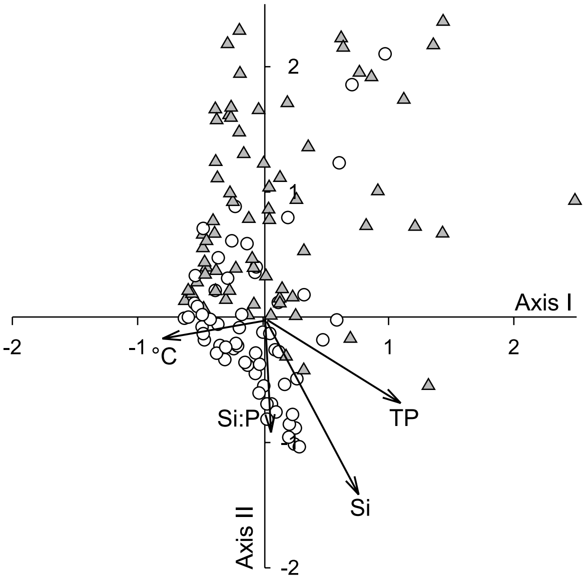


Table 2. Results of detrended correspondence analysis of summer diatom communities in Lake Michigan, 1983–1999.

	Axis 1	Axis 2
Eigenvalue	0.385	0.330
Cumulative % variance	13.2	24.6
Correlations		
Total phosphorus	0.23	–0.13
Silica	0.15	–0.27
Si:P	0.01	–0.17
Temperature	–0.17	–0.02

Note: Si:P, ratio of silica to total dissolved phosphorous.

Si, these were highly significant ($p < 0.001$) and were most pronounced after 1991. Overall counts were higher in the northern basin than in the southern basin ($p = 0.001$), reflecting the higher Si concentrations there.

Ordination analyses

Results from ordination analyses suggest that the species composition of both spring and summer diatom communities have changed over the course of our study period. Ordination of spring samples resulted in a marked, though not absolute, separation of communities from the earlier (1983–1991) and the later (1992–1999) portions of the dataset (Fig. 7), indicating differences in diatom community composition between these two periods. Of the environmental variables examined, ordination scores exhibited statistically significant ($\alpha = 0.05$) correlations with temperature, chlorophyll *a*, Si, and nitrate + nitrite (NO_3) (Table 1). The implied gradient of Si on the ordination plot (Si concentrations increasing with increases in axis I scores and decreases in axis II scores) corresponded very closely with the distinction between earlier and later samples, with later samples associated with higher Si concentrations. Although not proving cause and effect, this does suggest a role of Si concentration in determining the differences in diatom community composition indicated by the ordination. NO_3 concentrations showed a similar relationship to the change in diatom community composition.

As in spring, ordination of summer communities resulted in a separation of earlier and later communities (Fig. 8), again pointing to differences in diatom community composition between the two periods. A preponderance of later samples was seen in the lower portion of the ordination plot, whereas earlier communities were highly dispersed in the upper portion of the ordination. Significant correlations were found between axis scores and Si, TP, the ratio between dissolved silica and total dissolved phosphorus (Si:P), and temperature (Table 2). In general, lower scores for axis II were associated with both increased Si concentration and increased Si:P and diatom communities from later samples. Again, this suggests a potential role of changes in Si and (or) Si:P in structuring the diatom communities.

Discussion

The increases in spring soluble silica seen here, amounting to 0.45 mg·L^{-1} over the 18 years of our study, indicate that the trend of silica depletion seen during the last century has been reversed. Historic winter Si maxima in Lake Michigan have been estimated to be approximately 4.4 mg·L^{-1}, and this concentration had dropped to 1.4 mg·L^{-1} by about 1970 (Schelske 1988). Although the most recent spring concentrations reported here are only marginally higher than that latter value, as pointed out earlier, concentrations of our spring samples, taken in March or April, underestimate the true winter maximum by approximately 0.1–0.2 mg·L^{-1}. Comparable seasonal data do exist for 1976, when April Si concentrations recorded at stations corresponding to our northern basin stations averaged 1.1 mg·L^{-1} (Schelske 1988), a value similar to that recorded at the beginning of our study. Johengen et al. (1994) reported an average April Si concentration for 1981–1992 of 1.3 mg·L^{-1}, which corresponds exactly to our 1983–1992 average concentration. Those authors did not note any interannual differences, presumably because of the brevity of their dataset. Schelske (1988) has pointed out that winter maximum concentrations changed little between 1970 and 1978, and our results further suggest that concentrations probably remained fairly stable into the early 1980s. It thus seems that the increase in spring Si concentration is probably a relatively recent occurrence.

Interannual increases in the Si reservoir of the lake are a consequence of a change in the mass balance of that element, specifically a reduction in the annual sedimentation loss from the system. A more immediate consequence of reduced P loads would come about from decreased diatom growth, and hence Si uptake, during the spring mixed period before the development of thermal stratification. If Si concentrations are sufficiently reduced during spring uptake, further uptake by summer diatom communities could eventually result in silica limitation in the epilimnion, as was the case during much of the 1980s. It is important to bear in mind that in a lake with an average epilimnetic depth of 20 m and an average depth of 85 m, most of the Si reservoir will in fact be unavailable to summer epilimnetic growth and that epilimnetic depletion and long-term reductions in the total Si mass in the lake are two different, albeit related, phenomena.

In our study, summer epilimnetic concentrations of Si showed distinct increases during the 1990s, indicating a lessening of Si limitation over the course of the study period. Our samples were taken during August and early September, a period that previous studies have shown to coincide with the seasonal Si minimum (Beeton and Moffett 1964; Rousar 1973; Johengen et al. 1994). Minimum epilimnetic concentrations during the mid-1950s were in the range of 2.0 to 2.2 mg·L^{-1} (Beeton and Moffett 1964) and dropped to 0.2 mg·L^{-1} or less by around 1970 (Schelske and Callender 1970; Rousar 1973; Tarapchak and Stoermer 1976). A more recent report has shown that August epilimnetic Si concentrations in the southern basin of Lake Michigan have remained below 0.2·mg L^{-1} from 1981 through 1992 (Johengen et al. 1994). These concentrations correspond closely to our averages for the southern basin for the same time period. After 1992, concentrations in the southern basin increased to more than double that value, and a similar trend was seen in the north. Parker et al. (1977*b*) found that a Si concentration of 0.4 mg·L^{-1} was associated with declines in diatom biomass accumulation rate in Lake Michigan and suggested this as threshold concentration for the onset of Si limitation. This concentration was exceeded much more frequently in our dataset during the 1990s than during the 1980s. Diatom growth, however, can continue at Si concentrations down to 0.04 mg·L^{-1} (Jörgensen 1953; Lund 1969; LaZerte 1980), a value only occasionally approached in our study.

It is unlikely that the increases we saw in the 1990s were due to systematic changes in sampling date between the two time periods, because samples were collected slightly later in the season after 1992. The observed increase in available silica during the 1990s would also be consistent with a decrease in Si demand resulting from increased grazing pressure by, for example, *Dreissena* spp., which were well established in the lake by this time. However, both summer diatom and total phytoplankton standing crop increased during this time (Barbiero and Tuchman 2003), so an increase in supply, rather than a decrease in demand, seems a more likely explanation for the increased Si.

Concomitant with the changes in Si concentration have been changes in diatom community structure, as indicated by ordination analysis. Although ordination analyses alone are not sufficient to establish a cause and effect relationship between changes in Si and (or) Si:P and changes in community composition, the implied role of both Si and Si:P in determining diatom species composition is consistent with previous findings for Lake Michigan phytoplankton (Tilman 1977, 1982; Barbiero et al. 2001). Shifts in diatom species composition in response to the decline in silica during the last century have been demonstrated by paleolimnological analyses (Stoermer et al. 1990). Further analyses will be required to determine individual species' responses to the recent increases in Si.

The trends seen here have occurred in both the northern and southern basins; however, consistent differences were seen between the two basins in the summer. Geographical differences in open-water Si concentration were noted as early as 1955 (Ayers et al. 1958), and Si depletion appears to have proceeded much more rapidly in the southern basin than the northern basin because of its relative shallowness, and hence smaller Si pool, and greater degree of anthropogenic P loading (Schelske 1988). That the southern basin remains more heavily impacted is indicated by the lower summer epilimnetic Si concentrations and smaller summer diatom populations in the southern basin compared with the northern basin. Spring TP concentrations did not differ between the two basins, whereas summer concentrations were generally lower, probably resulting from greater uptake and subsequent sedimentation in the south between the spring and summer samplings.

The decrease in spring TP, based on the overall trend for the study period, was just over 1 $\mu g \cdot L^{-1}$. Scavia et al. (1986) have shown a further decline of about 2 μg $P \cdot L^{-1}$ in spring TP in the southern basin for the period preceding our study (1976–1984). Johengen et al. (1994) have stated that if just the load reduction to the main body of Lake Michigan is considered, the phosphorus model of Chapra and Sonzogni (1979) predicts a decrease in in-lake concentrations of 2.6 $\mu g \cdot L^{-1}$, an amount similar to that documented by Scavia et al. (1986) and this study, with 90% of this change occurring within 14 years. In general, concentrations in the 1980s and 1990s, which averaged 3–7 μg $P \cdot L^{-1}$ in our study, seem to be lower than those recorded in the 1970s, which typically averaged 5–10 μg $P \cdot L^{-1}$ (Rousar and Beeton 1973; Rockwell et al. 1980; Bartone and Schelske 1982), by approximately this amount.

It is perhaps surprising that the changes seen in Si concentration should have occurred with such modest declines in open-water TP concentration. However, when first implemented, P load reductions were targeted at highly bioavailable forms, e.g., phosphates in detergents and sewage effluents, so it is likely that the lake has experienced a proportionately greater reduction in bioavailable phosphorus than in total phosphorus. Also, silica is required by diatoms in substantially greater amounts than phosphorus; the mass ratio of these two elements in diatom cells can be anywhere between 9:1 and 2240:1 Si:P (Schelske 1975). This means that relatively small changes in P availability should result in proportionately greater changes in Si uptake, assuming that P is the primary limiting nutrient for diatom populations annually. A precise stoichiometric relationship between TP reduction and Si increase should not be assumed, though, because the long-term Si mass balance in the lake is also determined to a large extent by Si dissolution dynamics (Parker et al. 1977*a*).

TP concentrations in Lake Michigan are typically subject to very high interannual variability (Bartone and Schelske 1982; Johengen et al. 1994) that makes it difficult to discern temporal trends. It is unclear why this is so, particularly in such a large lake with a long residence time, but it is likely that interannual differences in factors affecting internal processes, such as the period of ice cover (Rockwell et al. 1980) or sediment resuspension events, contribute to this variability. It seems likely that, given the variability of P measurements, Si concentrations might more effectively integrate annual changes in diatom productivity over a decadal range and may be a better indicator of Lake Michigan's response to decreases in P loading.

Our results provide strong evidence that reductions in P loading over the past 25 years have brought about significant changes in Si concentration and diatom population dynamics in Lake Michigan. Spring Si concentrations have shown clear increases since 1983, and Si limitation in August has eased substantially during the study period, leading to an increase in summer diatom populations and apparent shifts in diatom community composition. These changes represent a reversal of the Si declines seen in the past 50 years and indicate a trend towards phytoplankton community composition that is closer to the historical condition of year-round diatom dominance. We believe that these results offer the most compelling evidence to date that phosphorus load reductions are having an impact on the Lake Michigan ecosystem.

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