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Long-term and recent changes in southern Lake Michigan water quality with implications for present trophic status

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ABSTRACT

Southern Lake Michigan has changed in response to alterations in nutrients and invasive species. NOAA and EPA monitoring results are used to examine those changes. NOAA provides detailed seasonal resolution, but limited spatial coverage, whereas the EPA provides more spatial coverage, but limited seasonal resolution. We compare changes in total phosphorus (TP), silica, nitrate plus nitrite, and chlorophyll concentrations from before and after the invasion by the quagga mussel (*Dreissena rostriformis bugensis*). Although TP at NOAA stations was consistently higher than at EPA stations, both confirm declines in spring and summer surface mixed layer (SML) conditions. Chlorophyll differed at EPA and NOAA stations before quagga mussel invasion, but not after the invasion. Spring chlorophyll decreased at NOAA stations after the invasion, but summer conditions did not change at either set of stations. Pre-invasion silica at NOAA stations was slightly higher than at EPA stations, and the lake's Si reservoir increased over the study period. Basin-scale spring Si increased gradually, whereas summer SML Si increased dramatically after 2003, likely reflecting reduced diatom production. Basin-scale nitrate increased significantly from pre- to post-invasion in both spring and summer. Summer nitrate utilization declined drastically in recent years, likely reflecting reduced phytoplankton production. TP loads decreased; however, the timing of changes in chlorophyll and Si and nitrate utilization suggest the recent increase in dreissenid filtering dramatically reduced spring phytoplankton abundance and production across the entire southern basin. The offshore pelagic zone of the historically mesotrophic southern Lake Michigan is now similar to oligotrophic Lake Superior.

Introduction

The Lake Michigan ecosystem has changed significantly over the past several decades. Reduced phosphorus loads lowered offshore total phosphorus (TP) concentrations (Warren and Horvatin, 2003; Environment Canada and US EPA, 2007), and although the response of phytoplankton community composition has been unclear (DePinto et al., 1986; Scavia et al., 1986; Johengen et al., 1994), recent evidence suggests that phytoplankton biomass and chlorophyll concentrations are declining (Carrick et al., 2001). Non-indigenous species introductions have dramatically and rapidly altered phytoplankton, zooplankton, benthos, and fish communities (Madenjian et al., 2002), with perhaps no invasive organism having as much impact as quagga (*Dreissena rostriformis bugensis*) and zebra (*D. polymorpha*) (hereafter dreissenid) mussels (Vanderploeg et al., 2002). With the expansion of quagga populations, dreissenids have only recently begun to increase in abundance offshore (Nalepa et al., 2009), so their impacts may not have been apparent until the last several years.

The US EPA Great Lakes National Program (GLNPO) Office has conducted offshore surveys in all five Great Lakes annually since 1983. NOAA's Great Lakes Environmental Research Laboratory has conducted offshore surveys in southern Lake Michigan on and off since 1983, with greater seasonal resolution. In this paper, we use these long-term datasets to explore temporal and spatial trends in TP, chlorophyll *a*, soluble silica (Si), and nitrate plus nitrite (hereafter nitrate), as well as recently updated estimates of TP loads. We compare changes in nutrient concentrations between 1983-1999 (pre-quagga influence) and 2000-2008 (post-quagga), as well as between the two agencies. We show significant declines in productivity in the last decade, and suggest these changes are largely attributable to dreissenid mussel filtering.

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Methods

EPA field and laboratory methods

EPA's TP, chlorophyll *a*, Si, and nitrate data come from samples collected during annual surveys from 1983 to 2008, except 1994-1995. From 1983 to 1991, stations were sampled three to seven times per year. From 1992 to 2008, there were only two cruises per year; a spring cruise in April-May after ice-out when the water column was isothermal, and a summer cruise in July-August during mid-stratification. For our analysis, we used data collected from the five southern basin stations: MI11, MI17, MI18M, MI19, and MI23 (Fig. 1). Station MI19 was not sampled in 1983 or 1984. MI18M was the only station sampled in spring 1993. Temperature profiles were measured at each station using various CTD systems. Data were retrieved from EPA's Great Lakes Environmental Database (GLENDA) (US EPA Great lakes National Program Office, 2009a).

The following description of field and laboratory methods comes from GLNPO's most recent Standard Operating Procedures (US EPA Great lakes National Program Office, 2009b). Historical methods are noted where relevant. Discrete water samples were collected at various depths throughout the water column in Niskin bottles. Sample depths were determined based upon several factors, including the season of the survey and the thermal structure of the lake. In all years, samples for chlorophyll *a* were vacuum filtered in the field. The filters were frozen, protected from exposure to light, and shipped to the

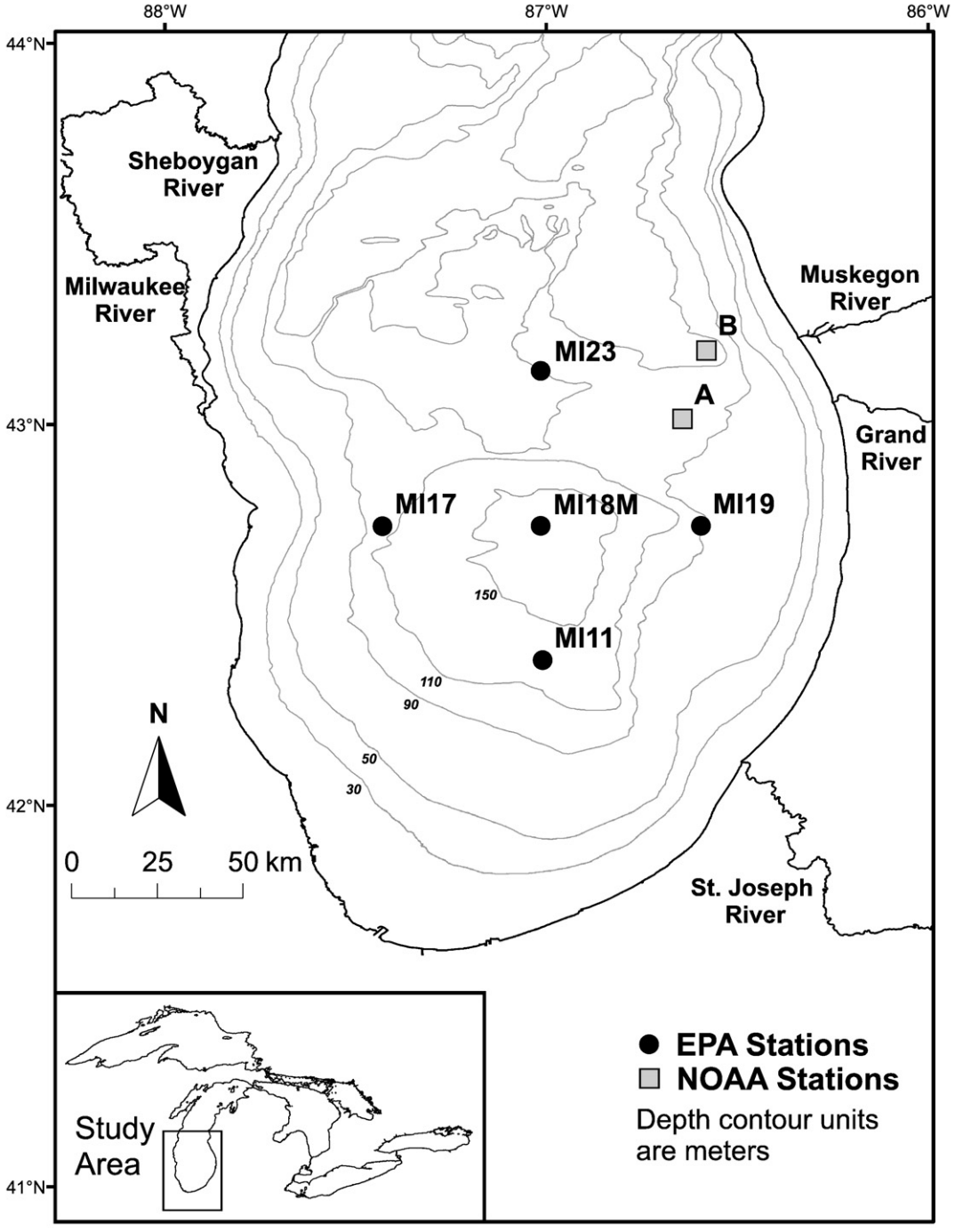

Fig. 1. Map of southern Lake Michigan showing locations of two NOAA sampling stations and five EPA sampling stations.

laboratory for extraction. Prior to 1998, chlorophyll *a* was corrected for phaeophytin concentrations determined using the APHA (1985) method. Post-1998, chlorophyll *a* concentrations were determined on a Turner Designs Digital Fluorometer using the narrow-band filter method described in Welschmeyer (1994). During early cruises, nutrients were analyzed on a Technicon Autoanalyzer System using procedures outlined in Lesht and Rockwell (1985); later, a Lachat QuickChem FIA 8000 was used. Samples for TP analysis were preserved in the field by adding 1 mL of H_2SO_4 per liter of sample. TP samples were digested in sulfuric acid and persulfate, and concentrations were measured on the Lachat QuickChem Flow Injection Analyzer (FIA) 8000 using Lachat Method #10-115-01-1-F. Samples collected for silica were stored at 4 °C before being analyzed on the Lachat QuickChem FIA 8000 using Lachat Method #10-114-27-1-A. Silica values in 1983-1993 were reported in GLENDA as mg $SiO_2 \cdot L^{-1}$, whereas values from 1996-2007 were reported as mg $Si \cdot L^{-1}$. In this paper, soluble silica (hereafter Si) refers to mg $Si \cdot L^{-1}$. Samples for nitrate (reported as mg N (as $NO_3 + NO_2$) $\cdot L^1$) were preserved by adding 1 mL of concentrated sulfuric acid per liter of sample. In the lab, nitrate was reduced to nitrite by passing the sample through a column containing copper-coated cadmium. Nitrate concentration was then measured on the Lachat QuickChem FIA 8000 using Lachat Method #10-107-04-1-C.

NOAA field and laboratory methods

NOAA sampling was conducted at two offshore stations (≥100 m depth; 43° 11.99′ N, 86° 34.19′ W and 43° 01.16′ N, 86° 37.91′ W) in southeastern Lake Michigan (Fig. 1) during 1983-2000, 2002, and 2007-2008. These stations were sampled approximately biweekly from March/April through November/December, except in 1983 and 1984, which were sampled from May through August. In 1983-1990, temperature at depth was measured with an electronic bathythermograph. Starting in 1991, a Seabird CTD (conductivity, temperature, and depth) was used.

Water samples were taken with a Niskin bottle. Typically, 6-12 depths were sampled during the thermally stratified period. Chlorophyll *a* samples were filtered onto Whatman GF/F filters, extracted with either 90% acetone (1983-1990s; Strickland and Parsons, 1972) or N, N-dimethylformamide (1991- 2008; Speziale et al., 1984) and analyzed fluorometrically.

Nutrients were measured using standard automatic colorimetric procedures on an autoanalyzer (Davis and Simmons, 1979; Laird et al., 1987). Si samples were filtered through a 0.2 µm Nuclepore filter and then analyzed. Total phosphorus samples were digested in an autoclave after the addition of potassium persulfate (5% final concentration, Menzel and Corwin, 1965) and then measured as soluble reactive phosphorus.

Total phosphorus load estimation update methods

All data used to estimate southern Lake Michigan TP loads come from government (federal and state) databases. Estimates for major tributaries made during the Lake Michigan Mass Balance Study (1994-1995) were obtained directly from the U.S. EPA (Russell Kreis, *pers. comm.*). Most of the rest of the tributary data came from the U.S. Geological Survey, the Wisconsin Department of Natural Resources, and the Michigan Department of Environmental Quality. Most of the point source data came from the U.S. EPA's Permit Compliance System (PCS). Additional data sources are discussed below.

The southern Lake Michigan TP load estimates for 1980-1993 (historic) were derived from the total Lake Michigan estimates reported to the International Joint Commission (IJC) by the Great Lakes Water Quality Board (1981, 1983, 1987, 1989). These loads were summarized in an Access database and provided to the authors by the IJC (John Gannon, *pers. comm.*). Using codes available in the database, loads to the southern basin were separated from the totals and calculated using the rivers discussed below.

The updated (1994-2008) load estimates were made as part of a U.S. EPA-GLNPO grant for improving nutrient mass balances for Lake Michigan. The methodology was similar to previous work on Lake Erie (Dolan and McGunagle, 2005). Since these methods have been reported in detail elsewhere, this discussion will focus on departures from standard methodology that were sometimes necessary to complete the 15-year update.

The major southern Lake Michigan tributaries are the Sheboygan and Milwaukee Rivers in Wisconsin and the St. Joseph, Kalamazoo, Grand, and Muskegon Rivers in Michigan. With the exception of the Michigan rivers in 1997 and 1998, flow and TP samples were available for every year. For these six major monitored tributaries, the Stratified Beale's Ratio Estimator (Beale, 1962; Tin, 1965; Dolan et al., 1981) was used to obtain a load estimate. In addition, when data were available for other, smaller tributaries, a ratio estimate was made. When these minor tributaries had no TP load estimate for a particular year, the size of the unmonitored area (see below) was increased and a unit area estimate was made.

Procedures for estimating loads from unmonitored tributaries were similar to those of Rathke and McCrae (1989). For unmonitored tributaries, a unit area load (UAL) was estimated from nearby monitored tributaries and applied to the unmonitored basin area. The Lake Michigan Mass Balance study included a pairing of monitored and unmonitored tributaries for estimation purposes and this was used wherever possible. The only departure from this approach occurred in 1997 and 1998 for all Michigan tributaries. For these cases, UALs were estimated from years (usually 1999) when more sampling was conducted.

We used the method of Dolan (1993) to estimate point source loads from data available in the PCS database. However, this system is being phased out by the EPA and therefore, depending on the state, point source data were not available for the whole study period. In particular, Indiana data were retrieved from a new system (ICIS) by the U.S. EPA (James Coleman, *pers. comm.*). Also, additional Wisconsin data were provided by the Wisconsin DNR (Jim Schmidt, *pers. comm.*).

Spatially detailed atmospheric loads for 1994–1995 were provided as part of the LMMB study (Miller et al., 2000). However, it appears that no precipitation sampling for total phosphorus in Lake Michigan has occurred since 1995. NOAA rainfall data were available for the study period and so fluxes observed by Miller, et al. were applied to subsequent years with adjustments for differing precipitation amounts. Given the lack of data, this approach seemed reasonable, especially since Miller et al. reported no temporal trend in phosphorus fluxes from the atmosphere but did note a north/south gradient that was due mainly to differing rainfall amounts.

Data analysis

Spring samples from EPA and NOAA data sets were those taken while the temperature of the entire water column was ≤4 °C. Sampling dates for this period were generally from late March to early or late May. Typically, NOAA stations were sampled 4 to 6 times during this period; before 1992, EPA stations were also sampled several times during the isothermal period, but after 1992 were sampled only once each spring. To facilitate analyses, all samples from an individual station from this period for a given year were averaged to obtain a spring isothermal water column mean value.

During stratified conditions, the surface mixed layer (SML) was defined as the portion of the water column above the metalimnion. All comparisons were limited to the SML. The mid-stratification period is defined as the period during which surface temperatures are >15 °C and typically occurs during July, August, and September. After 1992, EPA stations were sampled only once in summer, during August in most years. In contrast, NOAA stations were typically sampled 6 times

between July and September. As with spring data, averages for each set of stations during the entire mid-stratification period were used for comparisons.

Zebra mussels primarily affect nearshore areas in southern Lake Michigan, so we focused on quagga mussels because they are more likely to influence water quality at our offshore stations. Therefore, we chose years prior to 2000 to represent the pre-invasion period based on Nalepa et al. (2009).

Differences among EPA southern basin stations were not significant, so they were pooled to obtain basin-wide means (Barbiero et al., 2002). Data from the two NOAA stations were also pooled (Fahnenstiel et al., 2010). When appropriate assumptions were met Student's t-tests were used to compare means and the significance is reported as (t, p). When the assumptions were not met, non-parametric Mann-Whitney U tests were performed and the significance is reported as (U, p). Linear regressions were used to analyze long-term changes in TP loads and their relationship to spring and summer chlorophyll *a*. Data were log transformed, when necessary, to meet assumptions. A significance level of $\alpha = 0.05$ was used in all tests.

Results and Discussion

Phosphorus loads

Southern basin TP loads (Fig. 2) ranged between 1,193 and 2,870 metric tonnes per year (MT yr^{-1}). Despite substantial interannual variability, there was a significant overall decrease ($R^2 = 0.28$, $p = 0.003$) from 1980 to 2008, with a rate of change of 31 MT yr^{-1} (SE = 9.67). The eastern side of the southern basin (including the Michigan and northern Indiana shores up to but not including the Indiana Harbor Ship Canal) receives a relatively constant 70% of the southern basin load. No significant relationships were found between annual TP loads and spring chlorophyll *a* at EPA (Pearson's $r = 0.073$, $p = 0.736$) or NOAA stations ($r = 0.324$, $p = 0.152$), or summer SML chlorophyll *a* concentrations (EPA: $r = 0.323$, $p = 0.132$; NOAA: $r = -0.088$, $p = 0.703$). Similarly, annual TP loads were not correlated with TP concentrations in spring (EPA: $r = 0.336$, $p = 0.117$; NOAA: $r = 0.337$, $p = 0.136$) or summer (EPA: $r = 0.204$, $p = 0.349$; NOAA: $r = 0.077$, $p = 0.740$).

Phosphorus

Spring TP concentrations prior to 2000 were significantly higher than those after 1999 at both EPA (U, $p < 0.001$) and NOAA (t, $p = 0.025$) stations (Fig. 3a, Table 1). NOAA TP concentrations were also significantly higher than EPA throughout the time period (pre-2000: U, $p < 0.001$; post-1999: U, $p < 0.001$). Pre-quagga mean summer SML TP concentrations were significantly higher than post-quagga means at both EPA (U, $p < 0.001$) and NOAA (t, $p = 0.045$) stations (Fig. 3b, Table 1). Summer TP at NOAA stations was significantly higher than at EPA stations during both periods (pre-2000: t, $p < 0.001$; post-1999: U, $p < 0.001$).

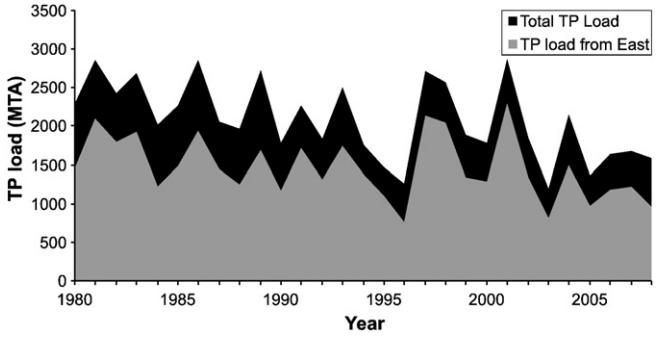

Fig. 2. Estimates of total annual phosphorus loads to the southern basin of Lake Michigan. Dark fill represents total loads; light fill represents loads from the eastern side of the lake.

Barbiero et al. (2002) also observed significant decreases in spring TP for the entire lake between 1983 and 2000, noting that spring values declined at an average of 0.07 $\mu g \cdot L^{-1}$ per year, resulting in an overall decrease of 1.2 $\mu g \cdot L^{-1}$. Our results show this trend continued throughout the 2000s, with an additional decrease of about 0.43 $\mu g \cdot L^{-1}$ since 2000 in the southern basin.

The higher spring and summer TP concentrations at NOAA stations compared to EPA stations potentially reflect an offshore gradient. Higher nearshore TP concentrations have also been observed in Lake Michigan in the past (Rousar, 1973, Bartone and Schelske, 1982), although more recent studies indicate that the nearshore and offshore may be becoming more similar (Carrick et al., 2001). With the exception of one station (MI19), EPA stations are farther offshore than NOAA stations (Fig. 1) and higher TP concentrations at NOAA stations may reflect their relative proximity to river inputs; about 70% of the TP loads to the southern basin come from the east (Fig. 2). Higher nearshore TP values may also be a consequence of the dreissenid-driven phosphorus "shunt" proposed by Hecky et al. (2004), whereby dreissenids sequester P in the nearshore, preventing it from being exported offshore. However, this effect would not have been seen until more recently when dreissenids became abundant, likely around 2005 (Nalepa et al., 2009; Vanderploeg et al., 2010).

If either of these spatial phenomena was responsible for the differences in TP concentrations, we would expect to see similar large gradients in chlorophyll and silica, but we do not. This suggests that differences in TP values could be the result of methodological differences between the two agencies. It is difficult to determine what is causing this discrepancy, and to what degree spatial variation or methodological differences are important. Both datasets show a similar decrease over time, however, and we conclude with confidence that TP concentrations in southern Lake Michigan decreased over the course of the study period.

Chlorophyll

Mean spring chlorophyll *a* concentrations at EPA stations (Fig. 3c, Table 1) did not differ significantly between the two time periods (U, $p = 0.482$), whereas post-quagga chlorophyll concentrations at NOAA stations were significantly lower that pre-quagga concentrations (t, $p < 0.001$). Concentrations at the two agencies' stations were significantly different prior to quagga mussels (t, $p < 0.001$), but not post-quagga (t, $p = 0.580$). Mean summer SML chlorophyll *a* concentrations did not differ between the two periods at either EPA (U, $p = 0.268$) or NOAA stations (t, $p = 0.401$) (Fig. 3d, Table 1). EPA and NOAA SML chlorophyll concentrations differed significantly pre-quagga (U, $p < 0.001$), but not post-quagga (t, $p = 0.066$).

It appears the difference between the two agencies is because the decline at EPA stations occurred much earlier than at NOAA stations (Fig. 3). However, this earlier decline at EPA stations is inconsistent with the seasonal nutrient utilization analysis (see below) and we believe it is due to limitations in the temporal resolution of EPA's program. As Fahnenstiel et al., (2010) show, spring chlorophyll *a* concentrations typically do not peak until May. We therefore suspect that the temporally-limited sampling by EPA missed the 1990s peak, biasing values low. In contrast, spring chlorophyll *a* concentrations from the two agencies in the 1980s are similar, and this is likely because during those years, EPA stations were sampled several times during spring, more closely matching NOAA's sampling regime, and because chlorophyll *a* peaked in April during this period (Fahnenstiel et al., 2010). After 2000, EPA and NOAA spring chlorophyll *a* concentrations both become low, reflecting the drastic overall

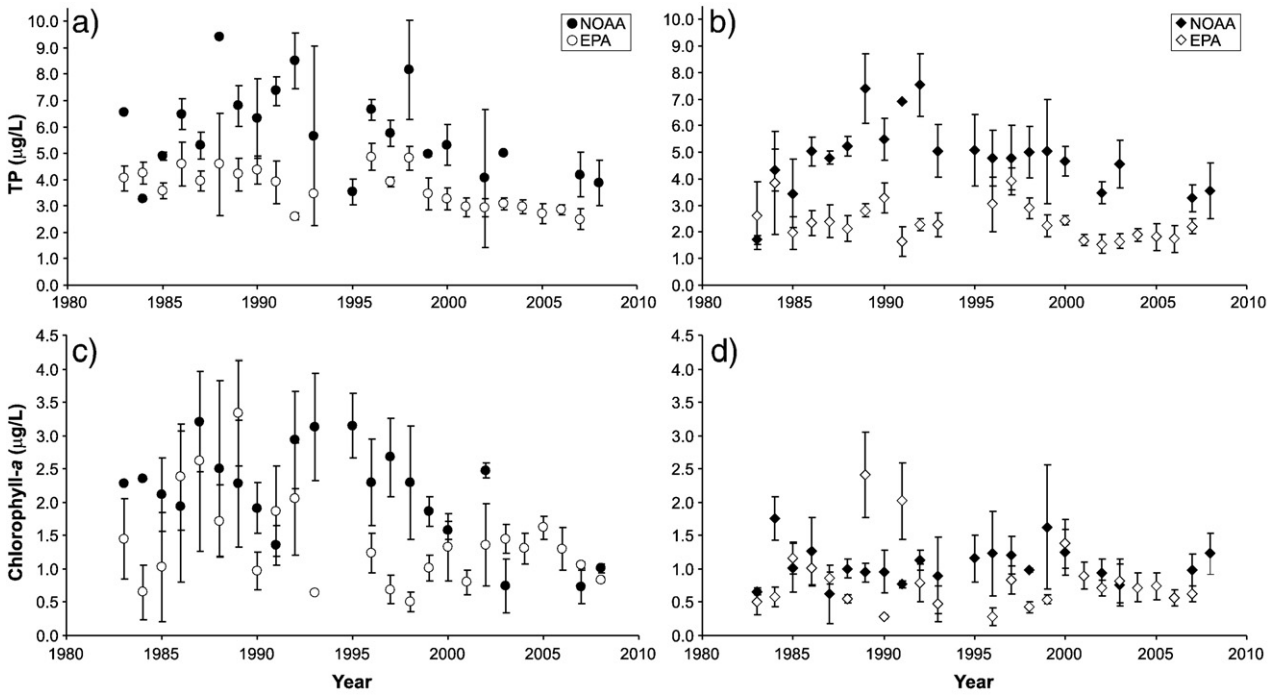

Fig. 3. Average a) spring isothermal and b) mid-stratification surface mixed layer TP concentrations and average c) spring isothermal and d) mid-stratification surface mixed layer chlorophyll *a* concentrations. Error bars are mean ± 1 SD. Open symbols are EPA data, closed symbols are NOAA data.

reduction in spring production and consistently low chlorophyll concentrations throughout the spring (Fahnenstiel et al., 2010).

Because methods and analysts changed across the course of the study for both agencies, it is possible that methodological differences play a role in observed chlorophyll *a* differences. It is also possible that differences in chlorophyll *a* are due to spatial variation in the lake, which would be consistent with potential spatial patterns in TP. However, if methodological differences were mostly to blame, we would expect to see comparably higher SML chlorophyll *a* at NOAA stations during the 1990s. While there were statistically significant differences in EPA and NOAA chlorophyll *a* values during the pre-quagga summer period (Fig. 3), differences were small and there was no consistent pattern of higher NOAA values as observed in spring. Because chlorophyll *a* concentrations tend to be less variable in summer (Fahnenstiel et al., 2010), it is not surprising that EPA data are similar to NOAA's despite limited temporal EPA sampling . This supports the argument that limited spring sampling at EPA stations results in a failure to capture the spring bloom, with methodological and spatial differences likely only playing a small role, if any.

Silica and Nitrogen

Spring Si concentrations (Fig. 4, Table 1) were significantly lower in the pre-quagga vs. post-quagga period at EPA stations (t, $p<0.001$). Si concentration at NOAA stations were slightly higher than EPA stations in both spring (t, $p=0.017$) and summer (t, $p=0.002$). Mean summer Si concentrations at EPA stations was significantly higher in the post-quagga vs. pre-quagga period (U, $p<0.001$) (Fig. 4a, Table 1). Nitrate concentrations at EPA stations were significantly higher during the post-quagga period in both spring (t, $p<0.001$) and summer (U, $p<0.001$) (Fig. 4b, Table 1). NOAA did not report nitrate data or any Si data after 2000.

Significant increases in spring Si from 1983 to 2007 (Fig. 4a) represent a reversal of the Si depletion described by Schelske and Stoermer (1971), and a dramatic increase in the lake's silica reservoir (Schelske, 1988). Because the Si depletion reported in the 1971 study was attributed to increasing TP loads, it is not unexpected that the decrease in TP loading to southern Lake Michigan observed since the early 1980s (Fig. 2) should result in a rebound in Si concentrations. Barbiero et al. (2002) noted significant increases in spring Si between 1983 and 2000, with an overall spring silica increase of about 0.19 mg $Si \cdot L^{-1}$. We found an additional increase of 0.15 mg $Si \cdot L^{-1}$ in the southern basin in only the last 6 years (2001-2007).

Summer Si concentrations were generally much lower than in spring, as reported previously (Rousar, 1973; Bartone and Schelske, 1982; Johengen et al., 1994), reflecting a seasonal Si utilization and subsequent deposition by phytoplankton. However, there was a sharp increase in summer SML Si concentrations after 2004 to an average of 0.62 mg $Si \cdot L^{-1}$ during the last 4 years of the study period, which is only slightly lower than the mean spring concentration of 0.84 mg $Si \cdot L^{-1}$ during the same period. This drastic reduction in seasonal Si utilization likely reflects a dramatic decrease in basin-wide diatom production. While utilization rates are also affected by temperatures,

Table 1
Mean (standard deviation) of total phosphorus, chlorophyll *a*, silica, and nitrate concentrations at NOAA and EPA stations during spring and summer for periods before and after the quagga mussel invasion.

		Total Phosphorus		Chlorophyll		Silica		Nitrate
		NOAA	EPA	NOAA	EPA	NOAA	EPA	EPA
Spring	Pre-quagga	6.08(1.65)	4.04(0.74)	2.36(0.54)	1.70(0.09)	0.70(0.13)	0.62(0.11)	0.29(0.02)
	Post-quagga	4.41(0.61)	2.91(0.37)	1.31(0.62)	1.21(0.39)	ND	0.80(0.09)	0.33(0.01)
Summer	Pre-quagga	5.08(1.30)	2.63(0.91)	1.15(0.30)	0.85(0.65)	0.19(0.07)	0.11(0.08)	0.18(0.02)
	Post-quagga	3.96(0.80)	1.88(0.42)	1.04(0.20)	0.81(0.32)	ND	0.39(0.24)	0.24(0.03)

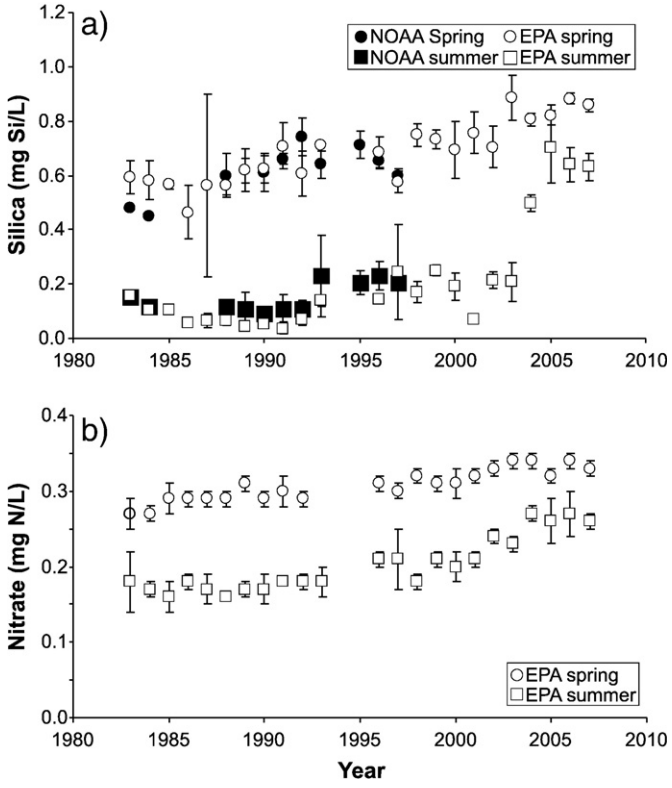

Fig. 4. a) Average spring isothermal and summer surface mixed layer silica concentrations. b) Average spring isothermal and summer surface mixed layer nitrate concentrations (EPA only). Filled symbols represent NOAA data; open symbols represent EPA data; circles represent spring and diamonds represent mid-stratification Error bars are mean ± 1 SD.

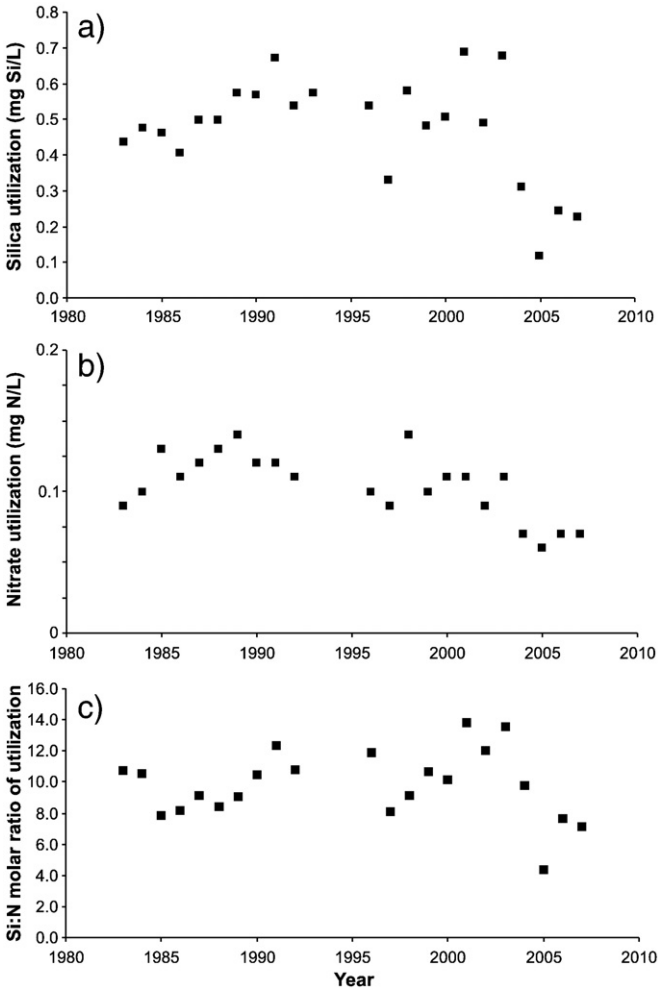

Fig. 5. a) Seasonal silica utilization (difference between spring and summer means). b) Seasonal nitrate utilization (difference between spring and summer means). c) Si:N molar ratio of seasonal utilization. All data are from EPA stations only.

data from NOAA's southern Lake Michigan buoy (NDBC #45007) show that the onset of thermal stratification (warming of water column above 4 ° C) varied widely during 2004-2007, the period of low Si utilization. The water column was warmer and stratification began in mid-April in 2005 and 2006, but it was colder and stratification did not set up until early to mid-May 2004. Therefore, reductions in Si utilization are not likely due to spring temperature differences.

Current (2004-2007) seasonal Si utilization (Fig. 5a) averaged 0.22 mg $Si \cdot L^{-1}$, a 57% decrease from the historical average of 0.52 mg $Si \cdot L^{-1}$ (1983-1993). The seasonal nitrate utilization (Fig. 5b) decreased 42% from the 1983–1992 mean of 0.12 mg $N \cdot L^{-1}$ to a 2004–2007 mean of 0.07 mg $N \cdot L^{-1}$. The greater reduction in Silica utilization is likely due at least in part to the fact that nitrogen cycles more rapidly than silica. It also suggests that not only has overall phytoplankton production decreased, but also that the proportion of that production as diatoms decreased. Fahnenstiel et al., (2010) report dramatic reductions in spring phytoplankton biomass and particularly in the abundance of diatoms between 1995-1998 and 2007-2008 at the NOAA stations, and the sharp decrease in the Si:N utilization ratio at EPA stations beginning in about 2005 (Fig. 5c) supports the notion that this was a basin-wide phenomenon.

If we accept that the EPA chlorophyll *a* data in the 1990s are biased low because temporally limited sampling failed to capture the spring bloom, then it is likely that the decline in biomass and production in the early 2000s was linked to the spread and increasing abundance of dreissenid mussels. In a 1999 survey, zebra mussels were found at 9-82 m stations, but peaked in abundance at stations in the 27-46 m depth range (Fleischer et al., 2001). Quagga mussel populations were not significant in the southern basin at 51-90 m depths until 2005, and densities were just beginning to increase at stations deeper than 90 m in 2007 (Nalepa et al., 2009). Based on these observations, we would expect the mussel impact to begin to be apparent in 2000 and likely not significant until the middle of the decade, consistent with the largest changes in chlorophyll concentrations and nutrient utilization. We chose the year 2000 as a breakpoint in our analyses because of the relatively small amount of data available after 2005; however, the timing of quagga mussel offshore expansion and our observations of silica utilization dynamics suggest that comparisons of pre- vs. post-2005 data may show even stronger dreissenid filtering effects.

Observations at both EPA and NOAA stations show significant decreases in spring chlorophyll *a* concentrations after 2000, but no significant declines in summer (Fig. 3). Because dreissenid mussel filtering can only affect the bottom water mass, it can only cause significant declines in phytoplankton production during spring mixing. Vanderploeg et al. (2010) measured clearance rates of Lake Michigan quagga mussels at low temperatures, and using size frequency data on mussel abundance from Nalepa et al. (2010), demonstrated that mussels cleared the water column at a rate sufficient to overcome phytoplankton growth rates throughout the isothermal period in depth zones out to ~80 m. In shallower areas, mussel filtering greatly exceeded growth rate, suggesting they may have intercepted offshore transport of phytoplankton and particulate P trapping it nearshore in recent years. Our findings are consistent with Fahnenstiel et al., (2010) conclusion that observed declines in primary production and phytoplankton abundance at NOAA stations are primarily a result of the filtering effects of dreissinid mussels, and

we suggest that they are now affecting the entire southern basin of Lake Michigan.

If declines in production were caused by the gradual decrease in phosphorus loads, we would expect also to see significant gradual declines in summer SML chlorophyll and our production proxy, seasonal Si and nitrate utilization. However, SML chlorophyll has not changed and the utilization rates changed rather abruptly in recent years. In addition, we found no significant relationship between TP loads and spring or summer chlorophyll concentrations at either NOAA or EPA stations.

It appears that the filtering activities of quagga mussels have resulted in nutrient dynamics and production in southern Lake Michigan similar to the more oligotrophic Lake Superior, particularly in the last 4-5 years. SML TP and chlorophyll concentrations in Lake Superior are typically 3.0-4.0 $\mu g \cdot L^{-1}$ and 0.5-1.2 $\mu g \cdot L^{-1}$ respectively (Weiler, 1978; El-Shaarawi and Munawar, 1978; Fahnenstiel and Glime, 1983; Barbiero and Tuchman, 2001). In Lake Michigan in the post-quagga period, total phosphorus and chlorophyll concentrations averaged 2.9 $\mu g \cdot L^{-1}$ and 0.9 $\mu g \cdot L^{-1}$, respectively. Recent values of phytoplankton primary production in Lake Michigan are also similar to historical Lake Superior values. In Lake Michigan during 2007-2008, average daily production values were 440 mg C/m^2/day (Fahnenstiel et al., 2010), similar to the Lake Superior mean value of 330-350 C/m^2/day (Vollenweider et al., 1974). Silica utilization rates are similar to, or even less than, those in Lake Superior (Schelske et al., 2006).

Summary

Our analysis suggests that spring production across the entire southern basin of Lake Michigan decreased significantly after the invasion of quagga mussels, particularly after their offshore expansion in 2005, and nutrient dynamics, chlorophyll concentrations, and primary production now resemble Lake Superior. These changes will likely have important implications for the base of the fishery food web, as the pelagic region of this historically mesotrophic system becomes more oligotrophic and less able to support secondary production. The present management goals of salmonid/trout stocking and phosphorus load reductions may need to be re-evaluated in light of this dramatic oligotrophication of the Lake Michigan water column. However, present conditions are dependent on large quagga mussel populations that may not be sustainable. Nearshore populations of quagga mussels are already declining (Nalepa et al., 2009) and we may expect quagga mussel densities to be lower in the future (Strayer and Malcom, 2006).

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References

APHA (American Public Health Association), 1985. Standard Methods for the Examination of Water and Wastewater, 16th ed. American Public Health Association, Washington, D.C.

Barbiero, R.P., Tuchman, M.L., 2001. Results from the U.S. EPA's biological open water surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results. J Great Lakes Res 27, 134–154.

Barbiero, R.P., Tuchman, M.L., Warren, G.J., Rockwell, D.C., 2002. Evidence of recovery from phosphorus enrichment in Lake Michigan. Can J Fish Aquat Sci 59, 1639–1647.

Bartone, C.R., Schelske, C.L., 1982. Lake-wide seasonal changes in limnological conditions in Lake Michigan in 1976. J Great Lakes Res 8, 413–427.

Beale, E.M.L., 1962. Some uses of computers in operational research. Industrielle Organisation 31, 51–52.

Carrick, H., Barbiero, R.P., Tuchman, M., 2001. Variation in Lake Michigan plankton: temporal, spatial, and historical trends. J Great Lakes Res 27, 467–485.

Davis, C.O., Simmons, M.S., 1979. Water Chemistry and Phytoplankton Field and Laboratory Procedures. Special Report 70. Great Lakes Research Division, Univ. Michigan, Ann Arbor.

DePinto, J.V., Young, T.C., McIlroy, L.M., 1986. Great Lakes water quality improvements: the strategy of phosphorus discharge control is evaluated. Environ Sci Technol 20, 752–759.

Dolan, D.M., 1993. Point source loadings of phosphorus to Lake Erie: 1986-1990. J Great Lakes Res 19 (2), 212–223.

Dolan, D.M., McGunagle, K.P., 2005. Lake Erie Total Phosphorus Loading Analysis and Update: 1996–2002. J Great Lakes Res 31 (Suppl. 2), 11–22.

Dolan, D.M., Yui, A.K., Geist, R.D., 1981. Evaluation of river load estimation methods for total phosphorus. J Great Lakes Res 7 (3), 207–214.

El-Shaarawi, A., Munawar, M., 1978. Statistical evaluation of the relationships between phytoplankton biomass, chlorophyll a, and primary production in Lake Superior. J Great Lakes Res 4, 443–455.

Environment Canada and US Environmental Protection Agency, 2007. State of the Great Lakes 2007. http://www.epa.gov/glnpo/solec/sogl2007/SOGL2007.pdf2007.

Fahnenstiel, G.L., Glime, J.M., 1983. Subsurface chlorophyll maximum and associated *Cyclotella* pulse in Lake Superior. Int Rev Gesamten Hydrobiol 68, 605–616.

Fahnenstiel, G.L., Pothoven, S., Nalepa, T., Vanderploeg, H., Klarer, D., Scavia, JD., 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. J. Great Lakes Res. 36 (Supplement 3), 20–29.

Fleischer, G.W., DeSorcie, T.J., Holuszko, J.D., 2001. Lake-wide distribution of *Dreissena* in Lake Michigan, 1999. J Great Lakes Res 27, 252–257.

Great Lakes Water Quality Board, 1981. Report on Great Lakes Water Quality. International Joint Commission, Windsor, Ontario.

Great Lakes Water Quality Board, 1983. Report on Great Lakes Water Quality. International Joint Commission, Windsor, Ontario.

Great Lakes Water Quality Board, 1987. Report on Great Lakes Water Quality. International Joint Commission, Windsor, Ontario.

Great Lakes Water Quality Board, 1989. Report on Great Lakes Water Quality. International Joint Commission, Windsor, Ontario.

Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., et al., 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can J Fish Aquat Sci 61, 1285–1293.

Johengen, T.H., Johannsson, O.E., Pernie, G.L., Millard, E.S., 1994. Temporal and seasonal trends in nutrient dynamics and biomass measures in Lakes Michigan and Ontario in response to phosphorus control. Can J Fish Aquat Sci 51, 2570–2578.

Laird, G.A., Scavia, D., Fahnenstiel, G.L., Strong, L.A., Malczyk, J.M., Lang, G.A., et al., 1987. Southern Lake Michigan nutrients, temperature, chlorophyll, plankton and water movement during 1983 and 1984. NOAA Tech. Memo. ERL GLER-67. Great Lakes Environmental Research Lab, Ann Arbor, MI. 27 pp.

Lesht, B.M., Rockwell, D.C., 1985. The state of the Middle Great Lakes: results of the 1983 water quality survey of Lakes Erie, Huron, and Michigan. Report No. ANL/ER-85-2. Argonne National Laboratory, Argonne, IL.

Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., et al., 2002. Dynamics of the Lake Michigan food web, 1970-2000. Can J Fish Aquat Sci 59, 736–753.

Menzel, D.W., Corwin, N., 1965. The measurement of total phosphorus liberated in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol Oceanogr 10, 280–282.

Miller, S.M., Sweet, C.W., DePinto, J.V., Hornbuckle, K.C., 2000. Atrazine and Nutrients in Precipitation: Results from the Lake Michigan Mass Balance Study. Environ Sci Technol 34, 55–61.

Nalepa, T.F., Fanslow, D.L., Lang, G.A., 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshw Biol 54, 466–479.

Nalepa, T.F., Fanslow, D.L., Pothoven, S.A., 2010. Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena* populations in Southern Lake Michigan. J. Great Lakes Res. 36 (Supplement 3), 5–19.

Rathke, D.E., McCrae, G., 1989. Appendix B, Volume III, Report of the Great Lakes Water Quality Board. International Joint Commission, Windsor, Ontario.

Rousar, D.C., 1973. Seasonal and spatial changes in primary production and nutrients in Lake Michigan. Water Air Soil Pollut 2, 497–514.

Scavia, D.S., Fahnenstiel, G.L., Evans, M.S., Jude, D.J., Lehman, J.T., 1986. Influence of salmonine predation and weather on long-term water quality trends in Lake Michigan. Can J Fish Aquat Sci 43, 435–443.

Schelske, C.L., 1988. Historic trends in Lake Michigan silica concentrations. Int. Revue ges. Hydrobiol. 73, 559–591.

Schelske, C.L., Stoermer, E.F., 1971. Eutrophication, silica depletion, and predicted changes in algal quality in Lake Michigan. Science 173, 423–424.
Schelske, C.L., Stoermer, E.F., Kenney, W.F., 2006. Historic low-level phosphorus enrichment in the Great Lakes inferred from biogenic silica accumulation in sediments. Limnol Oceanogr 51, 728–748.
Speziale, B.J., Schreiner, S.P., Giammatteo, P.A., Schindler, J.E., 1984. Comparison of N, N-dimethylformamide, dimethyl sulfoxide, and acetone for extraction of phytoplankton chlorophyll. Can J Fish Aquat Sci 41, 1519–1522.
Strayer, D.L., Malcom, H.M., 2006. Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. Freshw Biol 51, 117–130.
Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of seawater analysis. 2nd ed. Bull. Fish. Res. Bd. Can., 167. 310 pp.
Tin, M., 1965. Comparison of some ratio estimators. J Am Statist Assoc 60, 294–307.
US EPA Great Lakes National Program Office, 2009a. Great Lakes Environmental Database. http://www.epa.gov/glnpo/monitoring/data_proj/glenda/glenda_query_index.html. Accessed 5 Aug.
US EPA Great Lakes National Program Office, 2009b. Sampling and Analytical Procedures for GLNPO's Open Lake Water Quality Survey of the Great Lakes. http://www.epa.gov/glnpo/monitoring/sop/index.html. Accessed 23 July.
Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., et al., 2002. Dispersal and emerging ecological impacts of Ponto-caspian species in the Laurentian Great Lakes. Can J Fish Aquat Sci 59, 1209–1228.
Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., Pothoven, S.A., 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. 36 (Supplement 3), 50–59.
Vollenweider, R.A., Munawar, M., Stadelmann, P., 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J Fish Res Bd Can 31, 739–762.
Warren, G.J., Horvatin, P.J., 2003. Great Lakes monitoring results: comparison of probability based and deterministic sampling grids. Environ Monit Assess 81, 63–71.
Weiler, R.R., 1978. Chemistry of Lake Superior. J Great Lakes Res 4, 370–385.
Welschmeyer, N., 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnol Oceanogr 39, 1985–1992.