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Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan ☆

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ABSTRACT

Phytoplankton abundance, composition, and productivity were monitored on a bi-weekly basis from March/April through November/December at two offshore stations in southeastern Lake Michigan in 1983–1987, 1995–1998 and 2007–2008 (exception 1983–1984 which were sampled from May to August). During the spring isothermal mixing period, surface-mixed layer (SML) chlorophyll *a* and phytoplankton biomass (carbon) and water column primary productivity decreased substantially in 2007–2008 as compared to 1995–1998 (66%, 87%, and 70% decrease, respectively). Smaller or no decreases were noted between 1983–1987 and 1995–1998 (chlorophyll *a* 23% decrease, phytoplankton biomass 5% increase, and production 22% decrease). Phytoplankton composition also changed during the spring isothermal mixing period in 2007–2008 as compared to 1983–1987 and 1995–1998; all phytoplankton groups with the exception of cyanobacteria and chlorophytes exhibited dramatic reductions in 2007–2008. The pronounced changes in phytoplankton properties during spring mixing in 2007–2008 were attributed to the filtering activities of the quagga mussel (*Dreissena rostriformis bugensis*). During mid- and late thermal stratification periods, SML phytoplankton chlorophyll *a* and phytoplankton carbon and water column primary production exhibited only one significant change across all decades (mid-stratification production in 2007–2008 as compared to 1995–1998 and 1983–1987). Phytoplankton compositional changes in the SML also were limited during thermal stratification. The size of the deep chlorophyll layer (DCL) in 2007–2008 was similar to or smaller than those in 1983–1987 and 1995–1998. However, phytoplankton composition in the DCL changed as net diatoms constituted <5% of total phytoplankton in the 2007–2008 DCL but over 50% in 1983–1987 and 1995–1998.

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Introduction

In the 1980s the Lake Michigan lower food-web exhibited large changes, and these changes contributed to debate over top-down and bottom-up control of food-webs (Kitchell et al., 1988; Scavia et al., 1988). Because of large reductions in nutrient inputs and significant fish stocking, these discussions had important management implications (Kitchell et al., 1988). The debate about control of food-webs extended to phytoplankton communities in the 1980s. During thermal stratification, phytoplankton community composition in the surface mixed layer shifted from cyanobacteria and chlorophytes in the 1970s to phytoflagellates in the 1980s (Fahnenstiel and Scavia, 1987a). The cause of this shift was unclear, but top-down (zooplankton grazing) control of phytoplankton growth rates was evident during mid summer in Lake Michigan (Dorazio et al., 1987). With the invasion of *Bythotrephes* in the late 1980s, Lehman (1998) suggested that phytoplankton communities in Lake Michigan were not controlled by zooplankton, but that abiotic factors controlled phytoplankton abundance. Subsurface phytoplankton communities also changed in the 1980s. The deep chlorophyll layer (DCL) became much larger in the 1980s due to increases in light penetration attributed to increased zooplankton grazing pressure (Fahnenstiel and Scavia, 1987b).

Much of this work on Lake Michigan phytoplankton in the 1980s was completed before zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) became established in the Great Lakes and Lake Michigan. Zebra mussels first appeared in Lake Michigan in 1989, and their populations expanded in the 1990s (Nalepa et al., 1998, 2009). Zebra mussels were mostly confined to the nearshore region of Lake Michigan and by 2005 were replaced by quagga mussels. Quagga mussels became much more abundant throughout the lake, including the offshore region by 2007 (T. Nalepa, unpubl. data). The effects of zebra mussels on phytoplankton populations were studied in

☆ This paper is dedicated to Dr. Claire L. Schelske, an outstanding gentleman, mentor and scientist.

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the 1990s in other regions of the Great Lakes, and it was clear that zebra mussels had the potential to control phytoplankton abundance and composition (Holland, 1993; Nicholls and Hopkins, 1993; Fahnenstiel et al., 1995a,b); much less was known about quagga mussel impacts. Despite the presence of large mussel populations, and their impact on benthic algal communities (Bootsma et al., 2005), there was little work done to determine their effect on phytoplankton communities in Lake Michigan. Moreover, nutrient load reductions continued in Lake Michigan into the 1990s (Johengen et al., 1994) possibly altering phytoplankton communities. The investigations of phytoplankton in the 1990s were limited to the period prior to the mussel invasion and found that communities were similar to those in the 1980s (Makarewicz et al., 1999; DeStasio and Richman, 1998).

In this study, we report on trends in phytoplankton abundance, composition, and productivity from the early 1980s through 2008. The data collected in this study were part of an offshore monitoring program at NOAA's Great Lakes Environmental Research Laboratory. Analysis of data collected as part of this monitoring program allowed us to determine changes in phytoplankton in the last three decades and examine the factors controlling phytoplankton dynamics in Lake Michigan. The senior author had the privilege of being involved in the collection and analysis of almost all of these samples, and this continuity contributed to the value of these data.

Methods

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 the 1980s (1983, 1984, 1986, and 1987), 1990s (1995, 1996, 1997, and 1998) and 2007 and 2008. These stations were sampled approximately biweekly from March/April through November/December, except 1983 and 1984 which were sampled from May through August.

In 1983–1987, temperature at depth was measured with an electronic bathythermograph. Starting in 1995, a Seabird CTD (conductivity, temperature, and depth) equipped with a Sea-Tech fluorometer and transmissometer (25 cm beam path) was lowered from the surface to just above the bottom. Secchi disk transparency was measured with a black/white or white 25-cm disk. Underwater light extinction of photosynthetically active irradiation (kPAR) was measured with a LICOR 193SB scalar (4π) light sensor and LICOR 1000 data logger and/or a Biospherical integrating natural fluorometer (INF-3000). Surface incident irradiance was measured with a LICOR sensor and data logger. During night sampling or when kPAR values were not measured, transmissometer and Secchi disk measurements were converted to kPAR values using the conversions of Fahnenstiel et al. (1995a) for the same transmissometer or a Lake Michigan empirically-derived conversion for Secchi (kPAR = 1.53 (1/Secchi)).

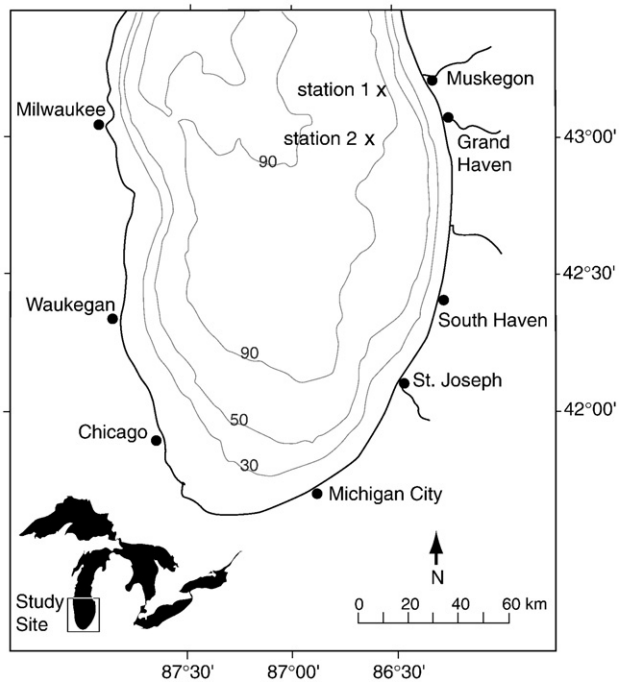

Fig. 1. Map of southern Lake Michigan showing location of two sampling stations.

Discrete samples were taken with a modified Niskin bottle (Fahnenstiel et al., 2002) and poured into carboys (1-carboy for each depth) from which all water samples were taken. 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 (1980s; Strickland and Parsons, 1972) or *N,N*-dimethylformamide (1990s and 2007–2008; Speziale et al., 1984) and analyzed fluorometrically.

Phytoplankton photosynthesis was measured with the clean C-14 technique in a photosynthesis–irradiance incubator (Fahnenstiel et al., 1989; Fahnenstiel, 2000). In 1983–1987, experiments were conducted in a large volume (2-L samples) incubator for 1–2 h with 8–12 light levels (Fahnenstiel et al., 1989). In 1995–1998 and 2007–2008, experiments were conducted in a small volume (3 ml samples) incubator for 1 h with 18 light levels (Fahnenstiel, 2000). After incubation, samples were filtered onto 0.45-μm Millipore filters, decontaminated with 0.5 ml of 0.5 N HCL for 4–6 h, placed in scintillation vials with scintillation cocktail, and counted with a liquid scintillation counter. Time-zero blanks were taken and subtracted from all light values. Total carbon dioxide was determined from alkalinity and pH measurements.

Photosynthetic rates, normalized to chlorophyll *a*, were used to construct a photosynthesis–irradiance curve using the methods outlined in Fahnenstiel et al. (1989). Three parameters were determined from this model: P_{max}, maximum photosynthetic rate at light saturation; α, initial linear slope at low irradiances; and β, negative slope at high irradiances. If the 95% confidence interval of β included zero, then a simple two-parameter model was used (Fahnenstiel, 2000).

Integral daily primary production was determined using the Great Lakes Production Model (Lang and Fahnenstiel, 1996), which is based on the model of Fee (1973). This model accounts for diel variations in surface irradiance, and depth variations in photosynthetic–irradiance parameters, chlorophyll *a* concentrations, and light extinction coefficient to estimate daily integrated primary production. Daily integral production was calculated for the 4 days preceding and following each sampling day to factor out unusual surface irradiance on the sampling day and to provide a more representative estimate for the sampling period.

Phytoplankton samples were preserved in amber bottles with 0.5% Lugol's solution. These samples were then either filtered (Dozier and Richerson, 1975) or settled (Wetzel and Likens, 2000) onto microscope slides. A minimum of 300 phytoplankton entities were enumerated under high (>600×) and low magnification (200×). Phytoplankton were identified to the lowest taxonomic group. Cell volumes were estimated by determining average cell dimensions of a minimum of 100 cells for each dominant taxa and at least 10 cells for rare taxa, and then applying these dimensions to appropriate geometric shapes. Phytoplankton volumes were converted to carbon units using the equations from Strathman (1966) for diatoms and Verity et al. (1992) for non-diatoms. Phytoplankton were placed into five broad taxonomic groups (Bacillariophyceae, Chrysophyceae and similar small flagellates, Cryptophyceae, cyanobacteria and chlorophytes, and others) to facilitate comparisons (Fahnenstiel and Scavia, 1987a). Mean abundance (mg/m^3) in the various vertical layers were compared among time periods.

All data were analyzed using standard parametric statistics (SYSTAT 8.0). If data did not meet parametric assumptions, they were transformed as needed (log, square root, etc.). ANOVA (mostly

one-way across time periods), Tukey test (individual mean comparisons), paired *t*-test, and regression were used to evaluate trends among the data.

To facilitate comparisons among years, sampling was divided into four periods based on surface mixed-layer (SML) temperatures (Fahnenstiel and Scavia, 1987c). The first period was the spring isothermal period, which typically lasted from first sampling in March/April until early May/early June. This period included all sampling where the SML temperature was ≤4 °C. The second period was early stratification and was defined as the period where SML temperatures were >4 °C but ≤15 °C. This period typically was very short, lasting for approximately one month or less due to the rapid heating of the shallow surface mixed-layer. Because of the short transitory nature of this period, no comparisons were made for this period. The third period was mid-stratification and was defined as the period where surface temperatures were >15 °C. This period typically lasted from July through September. The final period was late stratification and was defined as the period where SML temperatures were ≤15 °C but >4 °C. This period typically lasted from October through late December.

Results

All methods for primary productivity, chlorophyll *a* and phytoplankton were similar between 1995 and 2008, and thus, comparisons between 1995–1998 and 2007–2008 were robust. A few changes did occur between 1983–1987 and 1995–1998 but they did not significantly affect comparisons among years. For primary productivity measurements, the volume of sample incubated and the type of incubator changed between 1983–1987 and 1995–1998. In 1983–1987 large sample volumes were used (2-L) whereas in 1995–2008 small volumes were used (3 mL). In 1995, experiments were conducted to examine the effect of these changes on photosynthetic rate and no significant difference was noted in 1-h incubations ($p>0.05$). For chlorophyll *a*, the solvent was changed from 90% acetone to *N*,*N*-dimethylformamide prior to sampling in the 1990s. Again, comparisons were made between these two techniques and no significant differences were noted in spring chlorophyll *a* concentrations ($p>0.05$). For phytoplankton enumeration the settling technique (Wetzel and Likens, 2000) replaced a filtering technique (Dozier and Richerson, 1975) prior to sampling in the 1990s. Comparisons in 1995 revealed no significant differences in total phytoplankton biomass between techniques ($p>0.05$), although occasional differences in abundance of small flagellates were noted. The filtering technique may underestimate small flagellate abundance, particularly the Chrysophyte and similar small flagellate group. Thus, comparisons of this minor group (Chrysophytes and similar small flagellates) between 1983–1987 and other sampling years should be interpreted with caution.

Primary production

Significant differences in estimates of mean daily integral water-column primary production were noted among years and months at both stations (Fig. 2, $p<0.05$). Similar differences were noted for volumetric production estimates. Because estimates of mean daily integral primary production at the two stations did not differ significantly among months, years, or overall (paired t, $p>0.05$), estimates from the two stations were combined to provide an indication of offshore values. In the 1980s, mean values were low in March (<500 mgC/m^2/day) and increased through May/July (Fig. 2a). The highest daily integral values in 1983, 1984, 1986, and 1987 were 951 mg C/m^2/day (July) 1202 mgC/m^2/day (July), 1168 mgC/m^2/day (May), and 1327 mgC/m^2/day (May), respectively. Values decreased after July in all four years, and lowest values were found in November 1987 (320 mgC/m^2/day). The trend in daily integral primary production was similar in the 1990s. Values were low in March (<400 mgC/m^2/day) and increased during

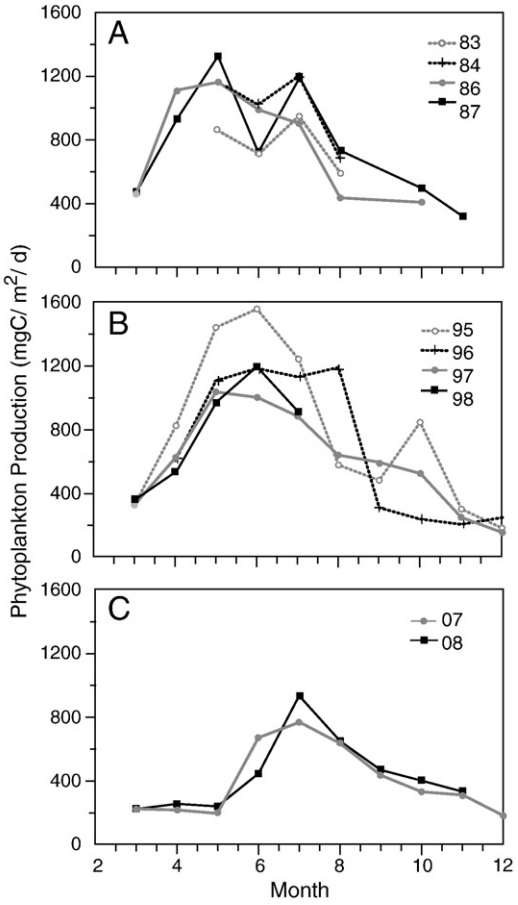

Fig. 2. Mean estimates of daily areal integrated primary production (mgC/m2/day) for months in (a) 1983–1987, (b) 1995–1998, and (c) 2007/08.

April and May, with maximum values found in May/July (Fig. 2b). Maximum daily integral values in 1995, 1996, 1997, and 1998 were 1554 mgC/m^2/day (June), 1185 mgC/m^2/day (June), 1036 mgC/m^2/day (May), and 1190 mgC/m^2/day (June), respectively. After July/August, values decreased, and lowest values were found during November/December (<300 mgC/m^2/day). The one exception was 1995 where high values (841 mgC/m^2/day) were found during October.

The trend in monthly primary production in 2007–2008 was significantly different (Fig. 2c). During March to May, production values were similar ($p>0.05$), unlike the increasing values found in the 1980s and 1990s. March, April, and May values from 2007 to 2008 were significantly different than March, April, and May values from 1983 to 1987 and 1995 to 1998 ($p<0.05$ for both comparisons). In 2007–2008 production estimates increased in June, and by July were not significantly different from July values in 1983, 1987, 1997, and 1998 ($p>0.05$; Fig. 2). By August, values from 2007 to 2008 were very comparable to those in August in the 1980s and 1990s with the exception of 1996 (all except 1996 $p>0.05$). For the rest of the year (September-December), values in 2007–2008 were comparable to those in 1983–1987 and 1995–1998 (Fig. 2).

Significant differences in mean daily integral production were noted during thermal periods. During the spring isothermal mixing period, production decreased approximately 78% from 1983–1987 to 2007–2008 (993 vs. 221 mgC/m^2/day; $p<0.05$, Fig. 3A). The 2007–2008 values were also significantly lower (70%, 221 vs. 772 mgC/m^2/day) than values from 1995 to 1998, and the 1995 to 1998 values were significantly lower (23%, 772 vs. 993 mgC/m^2/day) than 1983–1987 values ($p<0.05$). Because only half the years in the 1980s were sampled in March and April, a comparison of spring isothermal values

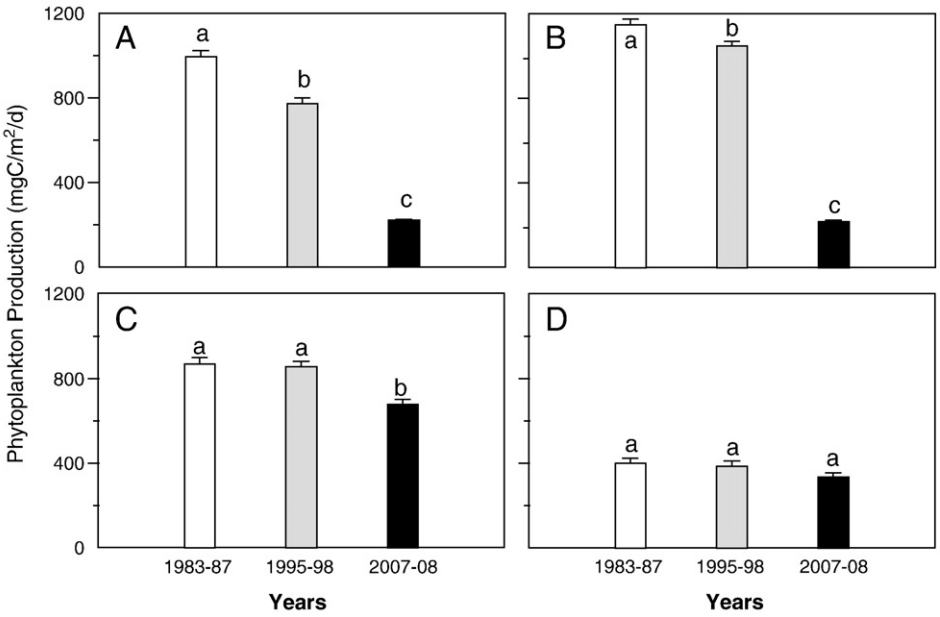

Fig. 3. Mean estimates of daily areal integrated primary production (mgC/m^2/day) by decade in thermal periods, (A) spring isothermal mixing, (B) May isothermal mixing, (C) mid stratification, (D) late stratification. Data are means ± 1 standard error. Means with different letters (a, b, c) indicate significant difference ($p<0.05$).

from only May was also made (Fig. 3B). Comparisons across decades were similar to the spring isothermal period, except differences between the 1980s and 1990s were smaller (<10%).

During mid-stratification, production values from 2007 to 2008 (677 mgC/m^2/day) were significantly less than values from 1983 to 1987 (867 mgC/m^2/day) and the 1995 to 1998 (855 mgC/m^2/day; $p<0.05$), but the differences (22% and 21%, respectively) were much smaller than those noted for the spring isothermal period (Fig. 3C). Production values from 1983 to 1987 and 1995 to 1998 were similar ($p>0.05$, Fig. 3C).

For the late stratification period, daily integral production did not vary across decades ($p>0.05$, Fig. 3D). Mean daily values for 1983–1987, 1995–1998, and 2007–2008 were 400, 386, and 335 mgC/m^2/day, respectively.

Chlorophyll

Mean SML chlorophyll *a* concentrations were similar at both stations (paired *t*-test, $p>0.05$, $r=0.97$), and thus, concentrations were combined for further analysis. In 1983–1987 and 1995–1998, monthly trends in mean SML chlorophyll *a* exhibited an April/May peak with another smaller peak in October (Fig. 4). Highest chlorophyll *a* concentrations for 1983–1987 and 1995–1998 were found in April (3.4 mg/m^3) and May (3.2 mg/m^3), respectively. After the spring chlorophyll *a* peak, concentrations decreased through September, and then increased again in October/November (Fig. 4). The high November 1987 value was associated with one sampling.

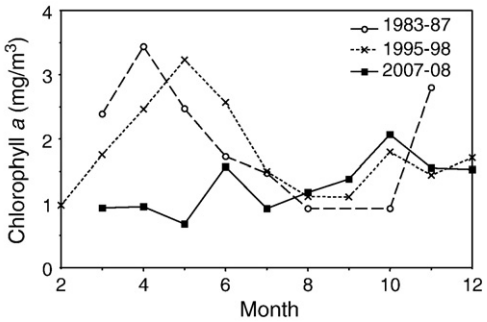

Fig. 4. Mean surface mixed-layer chlorophyll *a* concentrations (mg/m^3) for months in 1983–1987 (○),1995–1998 (x), and 2007/08 (■).

In 2007–2008, the seasonal trend in SML chlorophyll *a* was significantly different from 1983 to 1987 and the 1995 to 1998 (Fig. 4). In 2007–2008, chlorophyll *a* concentrations from April and May were significantly less than those from in 1983–1987 and 1995–1998 ($p<0.05$, 71% and 75% decrease, respectively), and maximum concentrations were not found in April/May but rather in October (Fig. 4). By June, SML chlorophyll *a* concentrations in 2007–2008 were similar to those from 1983–1987 and 1995–1998, and this pattern continued for the rest of the year ($p>0.05$, for all monthly comparisons from June through December, Fig. 4).

SML chlorophyll *a* concentrations varied significantly during the spring isothermal period across the decades (Fig. 5A). Chlorophyll *a* concentrations from 2007 to 2008 were significantly lower than those from 1983 to 1987 ($p<0.05$, 74% decrease) and 1995 to 1998 ($p<0.05$, 66% decrease). Chlorophyll *a* concentrations from 1995 to 1998 were also significantly lower than 1983–1987 values ($p<0.05$, 22% decrease); however May isothermal chlorophyll *a* concentrations were not significantly different in 1983–1987 as compared to 1995–1998 ($p>0.05$; Fig. 5B). May isothermal concentrations from 2007 to 2008 were significantly lower than both 1983–1987 ($p<0.05$, 79% decrease) and 1995–1998 ($p<0.05$, 77% decrease).

For the mid-stratification and late stratification thermal periods, there were no significant differences in SML chlorophyll *a* concentrations across decades ($p>0.05$; Fig. 5C and D). For mid-stratification, chlorophyll *a* concentrations averaged 1.2, 1.3, and 1.1 mg/m^3 in 1983–1987, 1995–1998, and 2007–2008, respectively. Similarly, for the late stratification period, chlorophyll *a* concentrations averaged 1.4, 1.7, and 1.8 mg/m^3 for 1983–1987, 1995–1998, and 2007–2008, respectively.

During early and mid-stratification (June–August) maximum chlorophyll *a* concentrations were typically found below the SML in all sampling years, and are referred to here as the deep chlorophyll maximum (DCM). In all sampling years, the DCM developed in June and reached maximum concentrations in late June/July at depths of 20–40 m. Chlorophyll *a* concentrations in the DCM during July were 2–16× SML concentrations. DCM concentrations decreased in August, and the DCM usually disappeared in September. Due to limited vertical sampling in 1986–1987 (some June and July dates only had one sample deeper than 15 m) and the lack of CTD profiling to adequately locate the DCM,

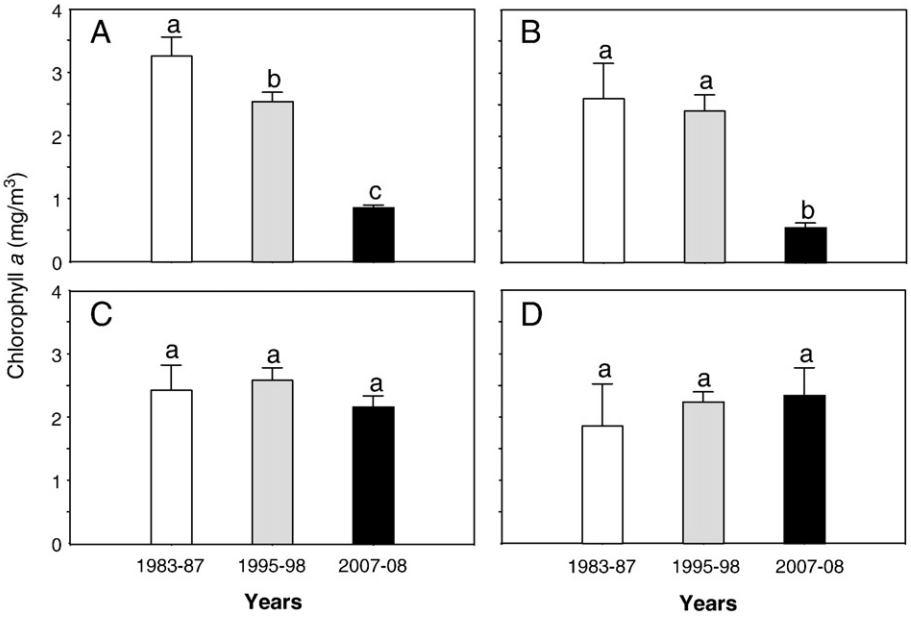

Fig. 5. Mean surface mixed-layer chlorophyll *a* concentrations (mg/m3) by decade in thermal periods, (A) spring isothermal mixing, (B) May isothermal mixing, (C) mid stratification, and (D) late stratification. Data are means ± 1 standard error. Means with different letters (a, b, c) indicate significant difference ($p<0.05$).

only 1983–1984 data were used to characterize the DCM in the 1980s. Intensive vertical sampling was conducted in 1983–1984 to characterize the DCM (Fahnenstiel and Scavia, 1987b). Maximum chlorophyll *a* concentrations in the DCM were 7.1 mg/m^3 in 1983 (July) and 5.5 mg/m^3 in 1984 (July). Starting in 1995 the use of a CTD with fluorometer allowed us to better locate and characterize the DCM. Maximum chlorophyll *a* concentrations in the DCM were 6.1 mg/m^3 in 1995 (late June), 4.2 mg/m^3 in 1996 (July), 4.1 mg/m^3 in 1997 (late June), and 4.2 mg/m^3 in 1998 (late June). In 2007–2008 maximum chlorophyll *a* concentrations in the DCM were 5.6 mg/m^3 in 2007 (July) and 3.0 mg/m^3 in 2008 (July).

The DCM contributes to a large region of subsurface chlorophyll *a* often referred to as the deep chlorophyll layer (DCL). To characterize the DCL, we defined the DCL as the subsurface region where chlorophyll *a* concentrations were ≥2.0 mg/m^3 (Fahnenstiel and Scavia, 1987b). Integral chlorophyll *a* concentrations in the DCL from June-August (surface temperatures ≥ 10 °C) were determined. Within any given year and decade, there was considerable variability in DCL size, which contributed to the lack of a clear trend across sampling periods (Fig. 6). In 1983 and 1984, the average areal DCL chlorophyll *a* concentrations were 31 and 27 mg/m^2, respectively (range: 9–51 in 1983, 20–39 in 1984). In 1995 and 1996, DCL average concentrations were high, averaging 47 and 36 mg/m^2 respectively (range: 0–124 in 1995, 24–48 in 1996), but in 1997 and 1998 average concentrations decreased to 13 and 19 mg/m^2, respectively (range: 0–24 in 1997, 0–49 in 1998). The smallest DCL was found in 2008 with average concentrations of 6 mg/m^2 (range: 1–20), but the 2007 DCL was similar to those from 1995 to 1998 with average concentrations of 21 mg/m^2 (range: 0–60).

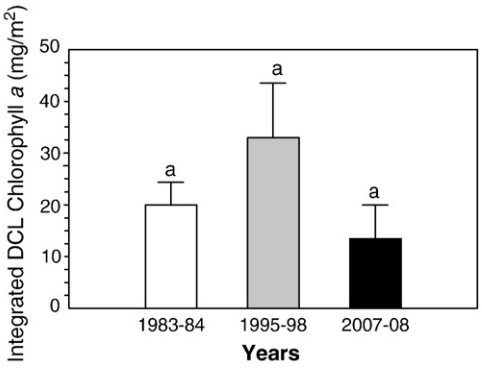

Fig. 6. Average summer DCL integrated chlorophyll *a* concentrations in different sampling years. Data are means ± 1 standard error. Means with different letters (a, b, c) indicate significant difference ($p<0.05$). DCL was defined as area where chlorophyll *a* concentrations were ≥2 mg/m^3 for the period June–August (surface temperatures ≥ 10 °C).

Phytoplankton biomass

Phytoplankton biomass (mgC/m^3) trends in the SML were similar to chlorophyll *a*. During the spring isothermal and May isothermal mixing periods, phytoplankton biomass in 2007–2008 was significantly lower than biomass in 1983–1987 and 1995–1998 ($p<0.05$, 84% and 87% decrease, respectively) but no significant difference was noted between 1983–1987 and 1995–1998 ($p>0.05$, Fig. 7A). For the mid-stratification and late stratification thermal periods, no significant differences were noted across time periods ($p>0.05$, Fig. 7B, C).

Phytoplankton composition in the SML varied by season and decade with most significant differences noted during the spring isothermal period ($p<0.05$). During the spring isothermal mixing period, four of the five phytoplankton groups exhibited significant decreases in abundance in 2007–2008 as compared to 1983–1987 and 1995–1998 ($p<0.05$, Fig. 8A, B). Diatoms (Bacillariophyceae) were the most abundant phytoplankton group in 1983–1987 and 1995–1998, comprising 50–67% of total spring isothermal period abundance, but they exhibited one of the largest percentage decreases in 2007–2008. Diatom abundance decreased from 29 and 22 mgC/m^3 in 1983–1987 and 1995–1998, respectively, to 1.6 mgC/m^3 in 2007–2008 ($p<0.05$, Fig. 8A). The next most abundant phytoplankton group in the spring period, Cryptophyceae, decreased from 9 and 17 mgC/m^3 in 1983/87 and 1995/98, respectively, to 1.7 mgC/m^3 in 2007–2008 ($p<0.05$, Fig 8B). Two groups that were not particularly abundant during the spring isothermal mixing period, Chrysophyceae and small flagellates and the others group (low abundance group comprised of Dinophyceae and Euglenoidea), also exhibited significantly lower abundance in 2007–2008 as compared to 1983–1987 and 1995–1998 ($p<0.05$, Fig. 8bB). The abundance of Chrysophyceae and small flagellates and the others groups was lower in 2007/2008 (94%, and 77%, respectively) than in 1983–1987 and 1995–1998.

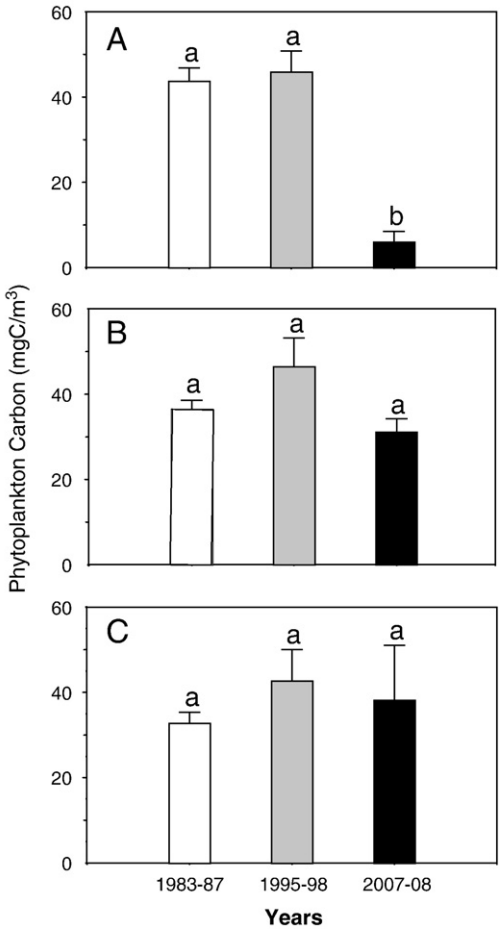

Fig. 7. Mean surface mixed-layer phytoplankton carbon concentrations (mg/m3) by decade in thermal periods, (A) spring isothermal mixing, (B) mid-stratification, and (C) late stratification. Data are means ± 1 standard error. Means with different letters (a, b, c) indicate significant difference ($p<0.05$).

The only phytoplankton group that did not exhibit a significant decrease across years during the spring isothermal period was cyanobacteria and chlorophytes ($p>0.05$, Fig. 8B). Because of the dramatic reduction of all other major groups, cyanobacteria and chlorophytes became more much important in the spring isothermal mixing period. During the spring isothermal mixing period, cyanobacteria and chlorophyte were not a dominant phytoplankton group during 1983–1987 and 1995–1998 with absolute abundance of 1.5 and 0.8 mgC/m^3, respectively, and relative abundances of 3 and 2%, respectively; however, in 2007–2008 their absolute abundance remained similar at 1.6 mgC/m^3, but their relative abundance increased to 27%. The cyanobacteria and chlorophyte group was dominated by cyanobacteria, most notably *Pseudoanabeana catenata/limnetica, Planktolyngbya limnetica*, *Anabaena circinalis*, *Limnothrix redekei*, *Oscillatoria tenuis*, *O. limnosa*, *Aphanocapsa delicitissima*, and *Microcystis smithii*.

During mid-stratification the responses of phytoplankton groups in the SML were more variable (Fig. 8C, D). Diatom abundance varied among all three decades, with 2007–2008 values significantly lower than 1983–1987 and 1995–1998 ($p<0.05$, Fig. 8C). Diatom abundance decreased from 5.7 and 11.9 mgC/m^3 in 1983–1987 and 1995–1998, respectively, to 1.9 mgC/m^3 in 2007–2008. Cyanobacteria and chlorophytes exhibited a significant increase in abundance in 2007–2008 (6.1 mgC/m^3) as compared to 1983–1987 (2.9 mgC/m^3) and 1995–1998 (2.5 mgC/m^3, $p<0.05$, Fig. 8D). The other three groups, Cryptophyceae, Chrysophyceae and small flagellates, and others, exhibited no significant changes across the three decades ($p>0.05$; Fig. 8C, D). It should be noted that Cryptophyceae abundance did decrease in 2007–2008 as compared to 1983–1987 and 1995–1998 (43% decrease), but the decrease was not significant ($p=0.13$ for 1983–1987 and $p=0.10$ for 1995–1998 comparisons).

For the late stratification period, only one group exhibited a significant change across decades in the SML, and that was for the 2007–2008 period only (Fig. 8E, F). Chrysophyceae and small flagellates abundance decreased in 2007–2008 as compared to 1983–1987 and 1995–1998 ($p<0.05$, Fig. 8F). Diatoms, Cryptophyceae, cyanobacteria and chlorophytes, and others abundances were similar for all decades during the late stratification period ($p>0.05$).

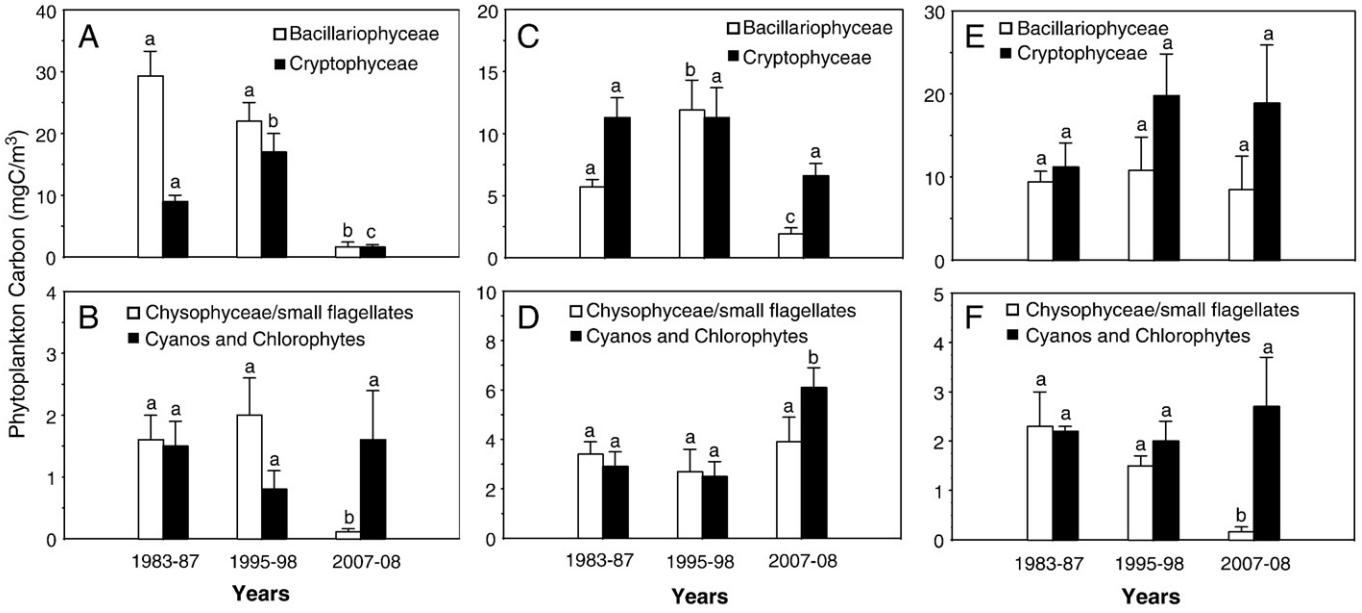

Fig. 8. Mean surface mixed-layer phytoplankton carbon (mg C/m^3) for specific phytoplankton groups by decade in thermal periods. (A) diatoms (open) and Cryptophyceae (solid) during spring isothermal mixing, (B) Chrysophyceae and small flagellates (open) and cyanobacteria and chlorophytes (solid) during spring isothermal mixing, (C) diatoms (open) and Cryptophyceae (solid) during mid stratification, (D) Chrysophyceae and small flagellates (open) and cyanobacteria and chlorophytes (solid) during mid stratification, (E) diatoms (open) and Cryptophyceae (solid) during late stratification, and (F) Chrysophyceae and small flagellates (open) and cyanobacteria and chlorophytes (solid) during late stratification. Data are means ± 1 standard error. Means with different letters (a, b, c) indicate significant difference ($p<0.05$).

The DCM represented a deep phytoplankton biomass maximum. During July, phytoplankton biomass at the DCM ranged from 2 to 11× surface mixed-layer concentrations. Average phytoplankton carbon concentrations in the DCM were 74 mgC/m^3 in 1983–1984, 65 mgC/m^3 in 1995–1998 and 52 mgC/m^3 in 2007–2008. Phytoplankton composition in the DCM did change from 1983–1987 to 2007–2008. In 1983–1987 and 1995–1998, diatoms (notably *Asterionella formosa*, *Aulacoseira islandica*, and *Fragilaria crotonensis*) dominated the July DCM, typically constituting over 50% of total biomass. Also abundant in the DCM were cyanobacteria (notably *Oscillatoria* spp.) and Cryptophyceae. The abundant spring diatom *Aulacoseira islandica* was an important component of the July DCM in 1983–1987 and 1995–1998 often reaching abundances of >100 cell/ml. In 2007–2008 the July DCM was dominated by Cryptophyceae (43–57% of total biomass), mostly *Rhodomonas minuta*, with lesser amounts of Chrysophyceae and small flagellates (notably *Dinobryon* spp.), cyanobacteria (notably *Anabeana*), and diatoms (notably *Fragilaria crotonensis* and *Asterionella formosa*). The spring diatom, *Aulacoseira* was not found in the DCM in July 2007–2008.

Discussion

The declines in primary production and phytoplankton abundance noted in this study are some of the more remarkable changes that have occurred in any offshore region of a Great Lake within a decade. These changes are remarkable not only for the magnitude and consistency of the changes in all measured parameters, but also for the seasonal-specific nature of these changes. These large changes were noted exclusively during the spring isothermal mixing period when phytoplankton primary production, abundance, and chlorophyll *a* decreased approximately 70, 87, and 66%, respectively, from 1995–1998 to 2007–2008. During the mid- and late stratification periods, only one significant change was noted for phytoplankton primary production, abundance, and chlorophyll *a*, and that change was much smaller (21%) than those noted during the spring isothermal mixing period.

Relatively rapid changes (within one decade) in phytoplankton abundance, chlorophyll *a*, and primary production have been noted with establishment of large dreissenid populations in the Great Lakes and in a much more limited scale with nutrient abatement controls, but typically these occurred within two or more seasonal periods. In the shallow, periodically well-mixed regions of the Great Lakes (e.g., Saginaw Bay, north shore of Lake Erie, western Lake Erie), phytoplankton abundance decreases of >60% have been noted to occur within a few years of establishment of large populations of zebra mussels (Holland, 1993; Nicholls and Hopkins, 1993; Fahnenstiel et al., 1995a), and these changes were found across several seasons (Holland, 1993; Fahnenstiel et al., 1995a). Large changes in primary productivity during spring and summer periods were also noted after the arrival of zebra mussels in Saginaw Bay (Fahnenstiel et al, 1995b). In the offshore region of western Lake Erie, Makarewicz et al. (1999) noted significant changes in phytoplankton abundance during spring and summer after establishment of large zebra mussel populations.

Phosphorus abatement program can also produce large changes in phytoplankton abundance in short time periods, although the results are more ambiguous for the offshore regions of the Great Lakes. When significant changes in phytoplankton abundance and chlorophyll *a* have been noted, they also typically occurred in more than one season. In Saginaw Bay, and the nearshore region of western Lake Erie, significant decreases (50–80%) in phytoplankton abundance have been associated with phosphorus abatement programs within a decade (Bierman et al, 1984; Nicholls and Hopkins, 1993). However, similar phytoplankton reductions were not found in the nearshore region of the central and eastern basins of Lake Erie (Nicholls and Hopkins, 1993). Phosphorus load reductions have produced more limited or unclear results in the offshore regions of lakes Erie, Michigan, and Ontario. In the offshore regions of Lake Erie when total phosphorus concentrations decreased in the 1980s prior to the arrival of zebra mussels, phytoplankton biomass decreased approximately 50% (Conroy et al., 2005), but chlorophyll *a* concentration changes were more mixed, and possibly even increased in some basins (Rockwell et al., 2005; Conroy et al., 2005). In Lake Michigan, phosphorus concentrations decreased in the 1980s and early 1990s as a result of phosphorus loading reductions, but no significant differences in chlorophyll *a* concentrations were noted (Scavia et al., 1986; Johengen et al., 1994). In Lake Ontario, Gray (1987) noted significant changes in phytoplankton abundance but not chlorophyll *a* concentrations from 1970–1972 to 1982; however, by the early 1990s Johengen et al. (1994) noted significant reductions in chlorophyll *a*.

The large changes noted in all measured parameters of this study during the spring isothermal mixing period are due primarily to the filtering impacts of dreissenid mussels, particularly the quagga mussel (*Dreissena rostriformis bugensis*). This conclusion is based on evidence from the following: (1) temporal coherence of documented changes and establishment of large populations of dreissenid mussels, (2) seasonal-specific nature of documented changes and direct filtering effects of mussels (spring isothermal mixing period only), and (3) calculated quagga mussel clearance rate based on abundance and filtering rates compared to phytoplankton growth and turnover rates.

Large populations of quagga mussels (*Dreissena rostriformis bugensis*) became established in Lake Michigan after 2000 (Nalepa et al., 2009). By 2005, quagga mussel populations had exploded nearshore, and their abundance was increasing offshore (stations >90 m). This increase in quagga mussels was noted in the vicinity of our sampling stations. Prior to the quagga mussel invasion, dreissenids were either not found in Lake Michigan (1983–1987) or limited populations of the zebra mussel, *Dreissena polymorpha*, were found in the nearshore region (depths <50 m) (1994–1995, Nalepa et al., 2009). Thus, the effects of dreissenid filtering would likely not have been noticed in the offshore region of Lake Michigan until after 2000, and most likely after 2005. This is consistent with the large changes found in 2007–2008 as compared to 1983–1987 and 1995–1998. Also, the filtering activities of quagga mussels are only directly linked to phytoplankton in the surface-layer waters when the water column is thoroughly mixed. The one time of the year when the offshore water column is completely mixed is when water temperatures are ≤4 °C, corresponding typically to the period from January to mid/late May (our spring isothermal mixing sampling period). When surface waters are near the temperature of maximum density (4 °C) the surface wind stress is effectively communicated throughout the water column, thus maintaining a well mixed water column. At colder surface temperatures (1–4 °C), observations suggest that the potential for reverse stratification to exist and to inhibit vertical mixing is minimal to non-existent, and a well-mixed water column has been observed (Beletsky et al., 2006; M. McCormick, pers. comm.). Once the lake is thermally stratified, the SML is isolated from direct effects of mussel filtering. Thus, mussel filtering impacts would be expected to be greatest during this spring mixing period, and that was observed. Finally, calculated filtering effects are in the range of phytoplankton growth and turnover rates during this spring mixing period suggesting that quagga mussels can reduce/control phytoplankton abundance. Mean quagga mussel biomass in the vicinity of our stations was approximately 30 g/m^2 (T. Nalepa, unpubl. data) and assuming a mean filtering rate of 12 ml/mg/h (H. Vanderploeg, unpubl. data), quagga mussels had the potential to clear the water column of phytoplankton in 12 days (fractional clearance rate of 0.08/day). Average water-column average phytoplankton growth rates during the spring isothermal period were approximately 0.06/day (Fahnenstiel, 2000), which corresponds to a doubling every 11 days. Also, calculated phytoplankton turnover rates (biomass/production) during the spring isothermal period ranged from 2 to 20 days.

Recent changes in phytoplankton composition during the spring isothermal period are also consistent with the role of quagga mussel

filtering. Selective filtering by dreissenid mussels can promote or sustain the abundance of colonial cyanobacteria relative to other more edible phytoplankton groups (Vanderploeg et al., 2001). During spring mixing in 2007–2008, all major phytoplankton groups with the exception of cyanobacteria and chlorophyte, exhibited dramatic abundance declines. The cyanobacteria and chlorophyte group was dominated by colonial and filamentous cyanobacteria that are not effectively grazed by dreissenid mussels (H. Vanderploeg, pers. comm.).

The most likely alternative explanation for the dramatic reductions in phytoplankton production and abundance in 2007–2008 would be reductions in phosphorus loadings and phosphorus concentrations due to phosphorus abatement program initiated in the 1970s. Phosphorus loading to Lake Michigan has exhibited a gradual decrease from 1976 through 2008 (Pauer et al., 2007, D. Dolan unpubl. data). Phosphorus loadings to the main lake averaged slightly more than 3000 MT/year in the 1980s, approximately 2500 MT/year in the 1990s, and approximately 1900 in 2005–2008 (D. Dolan, unpubl. data). Consistent with these load reductions were gradual declines in total phosphorus concentrations in Lake Michigan (Johengen et al., 1994; Mida et al., 2010). In response to these load and concentration reductions, phytoplankton and chlorophyll *a* should have exhibited a gradual decrease during all seasons (Pauer et al., 2007). This was not observed, rather, no significant decrease in phytoplankton carbon or chlorophyll *a* was noted during thermal stratification (mid- or late periods) from 1983–1987 to 2007–2008, and a dramatic decline (70–90%) during the spring isothermal period was noted only between 1995–1998 and 2007–2008.

The lack of a clear phytoplankton response to documented deductions in phosphorus load reductions may be a little surprising. The gradual decline in phytoplankton parameters during the spring isothermal mixing period from 1983–1987 to 1995–1998 does suggest a role for phosphorus load reductions, and any possible further reduction in 2007–2008 was likely masked by the observed dreissenid effect. But why was there no decrease in phytoplankton abundance during the stratified period, July–November, a period when mussel impacts are reduced or even eliminated and phosphorus load reductions should have produced reduced phytoplankton carbon and chlorophyll? There are two likely explanations. The first is that total phosphorus concentrations did not decrease as much during the thermal stratification periods as they did during the spring isothermal period and thus, smaller changes in phytoplankton concentrations would have been observed. Total phosphorus concentrations in the surface-mixed layer during mid stratification decreased 20% from 1983–1987 to 2007–2008, and 25% during late stratification (G. Fahnenstiel, unpubl. data). Second, and maybe more important, is the possibility that phosphorus recycling and utilization in Lake Michigan have been altered due to recent food-web changes. Not only have large populations of dreissenid mussels become established with documented effects on phosphorus recycling and transport (Hecky et al., 2004), but significant changes in cyclopoid copepods, *Daphnia* spp., *Diporeia* and possibly *Mysis relicta* populations have also been noted in Lake Michigan since 2000 (Nalepa et al., 2009; Pothoven et al., 2010; S. Pothoven, unpubl. data). Large changes in the abundance of key invertebrates would likely affect phosphorus recycling and utilization, and the assumed relationships between phosphorus loading and phytoplankton abundance. Pronounced differences in the ratio of phytoplankton carbon to total phosphorus provide evidence for changes in phosphorus recycling and utilization from 1983–1987 to 2007–2008. In 2007–2008 the spring isothermal ratio (molar ratio = 3.9) was approximately 20% of the ratio during the same periods in 1983–1987 (ratio = 17.5) and 1995–1998 (ratio = 20.3) ($p<0.05$) suggesting the importance of dreissenids in altering the phosphorus cycle in 2007–2008 (Nichols et al., 1999). Also, during late stratification the phytoplankton carbon to total phosphorus ratio was higher in 2007–2008 (ratio = 20) than in 1983–1987 (ratio = 14) and in 1995–1998 (ratio = 16, $p<0.05$). The higher ratios found during thermal stratification in 2007–2008 suggests that invertebrates other than dreissenids were responsible for altering phosphorus cycling (Nichols et al., 1999).

Spring phytoplankton production and biomass can also be influenced by other factors such as zooplankton grazing and even climate change, but neither factor is a significant contributor to recent changes in spring phytoplankton parameters. Spring zooplankton biomass in 2007–2008 (18 μg/L) was similar to biomass in 1986 (17 μg/L; only year in 1980s with consistent numbers) but slightly higher than zooplankton biomass in 1995–1998 (13 μg/L; S. Pothoven, unpubl. data). However, zooplankton grazing during the spring isothermal period in the 1980s was relatively low and did not exhibit significant control over phytoplankton abundance (Scavia and Fahnenstiel, 1987). Thus, zooplankton grazing pressure in 2007–2008 did not cause the dramatic decrease in spring phytoplankton abundance, but may be contributing to the maintenance of low spring phytoplankton biomass in 2007–2008 as the ratio of zooplankton biomass/phytoplankton biomass is greater in 2007–2008 as compared to the 1980s and 1990s. It is more difficult to see a role for climate change. Because the spring isothermal period is defined by temperature, the effect of global climate change would be to decrease the length of the spring isothermal period, or the timing of thermal stratification (4 °C isotherm) which may affect phytoplankton parameters. Studying temperature at water intakes around the Great Lakes, McCormick and Fahnenstiel (1999) noted an increase in the period of thermal stratification (period between 4 °C isotherms) of 4–6 h/year, thus, over our 25 year study, we would expect the spring period to be shortened by only 2–3 days. The change in timing of thermal stratification (first week when temperatures >4 °C) during our study period can be assessed by examining NOAA buoy data from southern Lake Michigan (NDBC #45007). In 2007–2008 thermal stratification occurred during the first full week of May (May 6–12). In three of the prior sampling years (1983, 1987 and 1998) thermal stratification occurred earlier than 2007–2008, and in the other 5 years thermal stratification occurred later. Given this variability among years and the short time period of our study, it is highly unlikely that global climate change was a significant factor contributing to the dramatic changes in phytoplankton parameters in 2007–2008.

The low phytoplankton abundance and productivity noted in the spring isothermal period in 2007–2008 is not limited to our stations in southeastern Lake Michigan but extends to the entire offshore region of southern Lake Michigan. Our mean chlorophyll *a* concentrations during spring isothermal mixing period in 2007–2008 were similar to those found at other offshore stations in the southern basin of Lake Michigan. Mean chlorophyll *a* concentrations at the mid lake NOAA buoy station (#NDBC45007) averaged 0.97 mg/m^3 for April/May in 2008 which is similar to our mean value of 0.95 mg/m^3 for April/May 2008 (G. Fahnenstiel, unpubl. data). Furthermore, the mean chlorophyll *a* concentration for offshore stations sampled in the southern basin of Lake Michigan during the spring EPA surveillance cruises in 2007–2008 was 0.92 mg/m^3 (T. Johengen, unpubl. data) which is similar to our mean value of 0.86 mg/m^3 for the spring isothermal period in 2007–2008.

The decline in spring phytoplankton abundance and primary production and in particular spring net diatoms (e.g., *Aulacoseira* spp.) may affect food-web dynamics and abundance of key invertebrates. *Diporeia* is an important benthic invertebrate which has been linked to the spring diatom bloom in Lake Michigan (Gardner et al., 1990; Fitzgerald and Gardner, 1993). *Diporeia* obtains a large portion of its energy from the spring diatom bloom (Gardner et al., 1990), and efficient transfer of energy from spring diatoms to *Diporeia* has been documented (Fitzgerald and Gardner, 1993). Recently, large declines in *Diporeia* have been noted throughout Lake Michigan, and the cause of the decline is unknown (Nalepa et al., 2009). While it is unlikely that the loss of the spring diatom bloom is the cause of the *Diporeia* decline (Nalepa et al., 2009), the loss of net diatoms would likely prevent a strong recovery in *Diporeia* populations.

Net diatoms were also an important component of the DCL in Lake Michigan (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987b). Historically, the DCL represented a large subsurface chlorophyll layer where many spring diatoms were abundant (Fahnenstiel and Scavia, 1987b). In Lake Michigan and in other environments this DCL serves as an important habitat and source of food for many invertebrates (Bowers and Grossnickle, 1978; Ortner et al., 1980; Barbiero et al., 2009). Recent changes in the Lake Michigan DCL may contribute to future changes in invertebrate populations in Lake Michigan. Phytoplankton composition, and possibly size, of the DCL has changed in 2007–2008 as compared to 1983–1984, and 1995–1998. Diatoms, and in particular large net diatoms, are now minor contributors to phytoplankton carbon in the DCL constituting <5% of phytoplankton carbon in the July DCL whereas in 1983–1984 and 1995–1998, diatoms were dominant contributors to phytoplankton carbon, constituting over 50% of phytoplankton carbon. These large net diatoms (*Aulacoseira*, *Tabellaria*, *Fragilaria*, *Asterionella*), an important food source for *Mysis relicta* (Bowers and Grossnickle, 1978), were unavailable in 2007–2008. In 2007–2008 smaller algae dominated the DCL, and these smaller algae (primarily Cryptophyceae) are not readily consumed by *Mysis relicta* (Bowers and Grossnickle, 1978). Present populations of *Mysis relicta* have declined since the 1990s, and changes in food supply may be a contributing factor for the decline of some size classes (Pothoven et al., 2010).

The size of the DCL and DCM may have changed recently as well, but further monitoring is needed to document the current size. Our results suggest the DCL and DCM in 2007–2008 were either similar to or smaller than those in 1983–1984 and 1995–1998 with significant variability in 2007–2008 likely obscuring a clear trend (Fig. 6). In 2007, the DCL and DCM were similar to those in previous years; however, in 2008, they were noticeably smaller than those in 1983–1984 and 1995–1998. The idea that the DCL and DCM are similar to or smaller than previous years is in contrast to the results of Barbiero et al. (2009). Studying the DCL in August of 1998–2006, Barbiero et al. (2009) noted DCL concentrations and the ratio of DCL:SML concentrations had increased in recent years. The difference in findings between ours and those of Barbiero et al. (2009) is likely a result of our more complete observations during the summer DCL (entire period of feature) compared to their limited characterization of only the August DCL (limited period of feature). In all sampling years, the summer DCL reached maximum concentrations in late June/July and decreased in August. A temporally transient event (summer DCL) cannot be adequately characterized with limited temporal sampling during the decline of the event (August). In 1998, the year we both have data, Barbiero et al. (2009) report low DCL concentrations, <1.0 mg/m^3, similar to our August concentrations of 1.0 mg/m^3. However, DCL concentrations in late June/July were 4.2 and 3.0 mg/m^3, respectively. Moreover, there is no clear relationship between August DCM concentrations and summer average DCL or DCM concentrations, and thus, August values cannot be used to predict average summer concentrations (Fig. 9). Finally, Barbiero et al. (2009) relate their increases in DCL size in recent years to increases in water transparency. While we agree that summer water transparency has increased in recent years, the size of the DCL and DCM is related to both light and nutrient availability (Moll and Stoermer, 1982; Fahnenstiel and Scavia, 1987b). Recent increases in light availability in the DCL have been accompanied by decreases in nutrient concentrations (G. Fahnenstiel, unpubl. data). Moll and Stoermer (1982) noted that low nutrient lakes (e.g. Lake Superior) have smaller DCL than moderate nutrient lakes (e.g. Lake Michigan) and as Lake Michigan nutrient concentrations become more similar to Lake Superior, we might expect the DCL in Lake Michigan to decrease in size even with increases in water transparency.

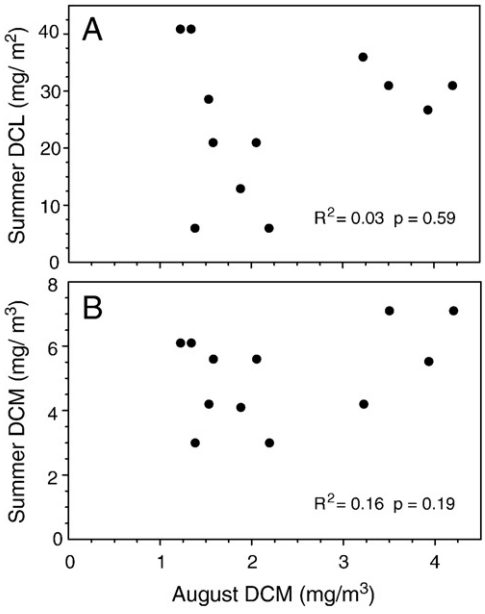

Fig. 9. The relationships between August DCM chlorophyll *a* concentrations (mgC/m^3) and (A) mean summer integrated DCL chlorophyll *a* concentrations (mgC/m^2) and (B) mean summer DCM chlorophyll *a* concentrations (mgC/m^3).

Future research in Lake Michigan should continue to monitor the phytoplankton community with intensive temporal sampling to characterize the long-term effect of quagga mussels. Given the large changes in all phytoplankton parameters within distinct temporal periods noted in this study and the large basin-wide changes documented by Lesht et al. (2002), it is clear that intensive temporal sampling is needed to characterize these trends. Using remote sensing, Lesht et al. (2002) documented a large early summer phytoplankton bloom throughout the southern basin of Lake Michigan that accounted for 25% of the lake's annual primary production. This bloom started in early June, peaked in mid/late June and was undetectable by mid July. Thus, sampling on times scales more frequent than monthly would have been needed to adequately describe this bloom, and many of the features we describe in this paper also support the need for sampling on weekly/bi-weekly scales.

Finally, the changes documented in this paper occurred during the initial colonization of quagga mussels in Lake Michigan (Nalepa et al., 2009). As quagga mussel populations stabilize in Lake Michigan, further changes in phytoplankton communities are likely to occur. During the initial stages of colonization, most dreissenid populations increase rapidly followed by a decline to more stable, sustainable levels (Strayer and Malcom, 2006). This trend has been seen in the Great Lakes (Nalepa et al., 2009) and is likely occurring in Lake Michigan. Quagga mussel populations in the nearshore region of Lake Michigan have appeared to stabilize, whereas populations in the offshore region have just started to increase (Nalepa et al., 2009). It is important to continue monitoring phytoplankton populations in Lake Michigan as quagga mussel populations stabilize and reach sustainable levels.

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