



## Recent change in summer chlorophyll *a* dynamics of southeastern Lake Michigan

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### ABSTRACT

Six offshore stations in southeastern Lake Michigan were sampled during a pre quagga mussel *Dreissena rostriformis bugensis* period (1995–2000) and a post quagga mussel period (2007–2011). Chlorophyll *a* fluorescence profiles were used to characterize chlorophyll *a* concentrations during early (June–July) and late (August–September) summer stratification. During the early summer period the average whole water column chlorophyll *a*, the deep chlorophyll maximum, and the size of deep chlorophyll layer decreased 50%, 55%, and 92%, respectively, between 1995–2000 and 2007–2011. By contrast, in late summer there were no changes in these metrics between periods. Surface mixed layer chlorophyll *a* in early and late summer did not differ between time periods. On the other hand, chlorophyll *a* in the near bottom zone (bottom 20 m) declined 63% and 54% between 1995–2000 and 2007–2011 in early and late summer respectively. Changes in total phosphorus between 1995–2000 and 2007–2011 were less dramatic, with declines of 22–27% in early summer and 11–30% in late summer. Changes in the chlorophyll *a* conditions were attributed to dreissenid mussels which reduced material available from the spring bloom and disrupted the horizontal transport of nutrients to the offshore. Although light availability increased (i.e., increased secchi depths), reduced nutrient availability and spring diatom abundance resulted in a much smaller deep chlorophyll layer in 2007–2011.

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### Introduction

Recent work in offshore Lake Michigan has documented dramatic changes in the offshore phytoplankton community during the winter–spring isothermal period in 2007–2008 compared to the 1980s and 1990s (Fahnenstiel et al., 2010; Mida et al., 2010). In particular, the spring phytoplankton bloom, an important feature of the ecosystem, was reported to have disappeared based on a 66% decline in chlorophyll *a* concentrations between 1995–1998 and 2007–2008 (Fahnenstiel et al., 2010). This change during the isothermal period was attributed primarily to the filtering activities of the quagga mussel (*Dreissena rostriformis bugensis*) (Fahnenstiel et al., 2010; Pothoven and Fahnenstiel, in press).

The spring bloom historically influenced stratified period phytoplankton dynamics (Fahnenstiel and Scavia, 1987a; Moll and Stoermer, 1982). Following stratification, a deep chlorophyll layer (DCL) developed which was attributable to in situ growth, shade adaptation and to a lesser degree the settling of the spring diatom bloom (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987a; Moll and Stoermer, 1982). The DCL represents a broad band of increased chlorophyll *a* concentration in sub-epilimnetic waters that historically accounted

for much of the water column chlorophyll *a* and primary production in Lake Michigan (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987b). This layer can represent an important area of food for macroinvertebrates such as *Mysis diluviana* (Bowers and Grossnickle, 1978) and can enhance zooplankton biomass based on studies in oceans (Ortner et al., 1980) and lakes (Williamson et al., 1996).

As the summer progresses, material continues to settle near the lake bottom in the benthic nepheloid region, whose formation depends on a combination of horizontal transport from nearshore areas, settling of material, and re-suspension of bottom material (Chambers and Eadie, 1981; Hawley and Muzzi, 2003). The settling of spring bloom plankton to the lake bottom historically provided an important link between pelagic and benthic food webs as material was assimilated by the macroinvertebrates *Diporeia* (Fitzgerald and Gardner, 1993) and *Mysis* (Sierszen et al., 2011).

Despite the expectation that summer phytoplankton conditions would follow those changes observed in the spring period, preliminary observations indicated that summer chlorophyll *a* concentrations in the surface mixed layer (SML) had not changed in 2007–2008 compared to the 1980s and 1990s (Fahnenstiel et al., 2010; Mida et al., 2010). Also, the size of the DCL and the maximum sub-epilimnetic chlorophyll *a* concentration (DCM) did not show any apparent increasing or decreasing trend between the 1980s–1990s and 2007–2008 owing to high variability between the latter two years (Fahnenstiel et al., 2010). On the other hand, daily integral primary production during the summer was about 20% lower in 2007–2008 than in the 1980s and 1990s. Therefore,

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because of limited sampling (2007–2008), it is difficult to know the full extent of changes, if any, in the summer stratified period.

Given the ecological importance of the summer period, we expanded on the previously limited observations available during the summer in Fahnenstiel et al. (2010) and evaluated whether changes in summer water quality parameters were occurring as had been observed during spring. We hypothesized that the size of the DCL and the DCM and nepheloid zone chlorophyll *a* concentrations would be decreasing because of their historical linkage to the spring phytoplankton bloom, which had essentially disappeared. To accomplish our objective, we used whole water column profiles of chlorophyll *a* that were derived from fluorometer voltage profiles for 1995–2000 and 2007–2011. Besides three additional years of data, this approach provided a much more complete analysis of summer water column structure than in Fahnenstiel et al. (2010), which relied on limited discrete water samples. Data on phosphorus and carbon were collected to provide insight into trophic status and phytoplankton nutritional condition over the course of the study. Finally, zooplankton were collected to provide insight into the potential role of grazers on the phytoplankton community.

## Methods

Sampling took place in offshore (>100 m depth) southeastern Lake Michigan at two primary stations, Station A and B located at 43° 01.16'N,

086° 37.91'W and 43° 11.99'N, 086° 34.19'W respectively (Fig. 1). Average water column chlorophyll *a*, surface chlorophyll *a* and integrated DCL chlorophyll *a* concentrations did not differ between these two sites based on sampling that took place at each station on nine dates in 1995 (paired *t*-test:  $p > 0.55$ ). Limited additional sampling at 4 offshore sites located near these two stations was also done (Fig. 1). Sampling took place during two time periods, 1995–2000 (excluding 1997) and 2007–2011. Sampling took place during the summer stratified period (June–September) with varying amounts of effort at stations/months among years (see Table 1). To adequately characterize summer stratification conditions, we only used data from samples collected when surface water temperatures exceeded 10 °C (Fahnenstiel et al., 2010).

Temperature was measured from the surface to just above the bottom and binned into 1-m depth increments using a Seabird CTD (conductivity, temperature, and depth) equipped with a Sea-Tech, Turner, or Wet Labs fluorometer. Secchi depth transparency was measured with a black/white or white 25-cm diameter disk. Discrete samples of water were taken from 3 to 6 depths in the water column with a modified Niskin bottle (Fahnenstiel et al., 2002) and poured into acid-cleaned polycarbonate carboys (1-carboy for each depth) from which all water samples were taken. Water samples were not taken every time a CTD was used.

Water for chlorophyll *a* analysis was filtered under low vacuum onto Whatman GF/F filters, extracted with N, N-dimethylformamide

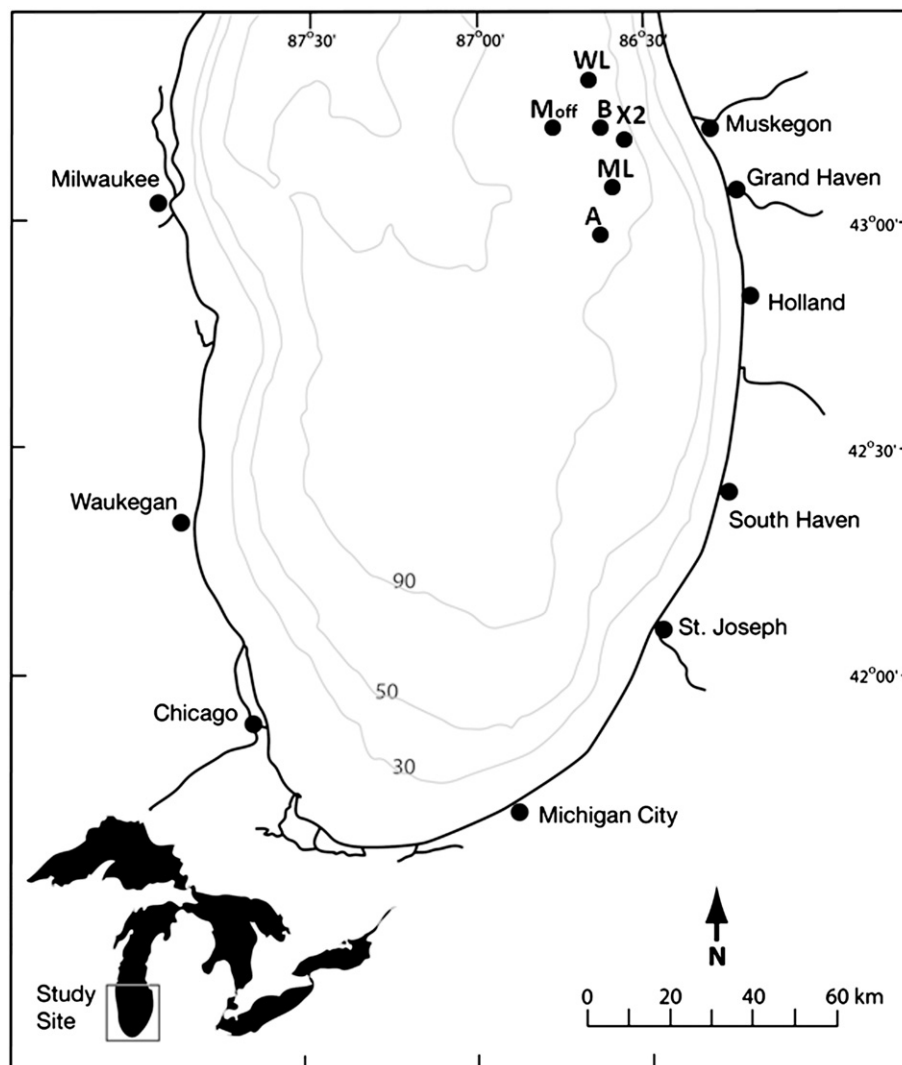


Fig. 1. Map showing locations of sampling locations in southeastern Lake Michigan.

**Table 1**

Number of sampling events at each site in early summer (June–July) and late summer (August–September) for each year of the study.

Year	Site	June–July	Aug–Sept
1995	A	6	4
1995	B	7	4
1996	A	1	1
1996	B	3	2
1998	A	1	0
1998	B	4	4
1999	B	2	2
2000	A	2	0
2000	B	4	1
2000	ML	1	0
2000	WL	1	0
2007	B	3	3
2008	A	1	2
2008	B	3	4
2008	X2	0	2
2009	B	3	6
2010	B	13	4
2010	X2	0	1
2010	Moff	0	1
2011	B	4	4
2011	Moff	2	0

(Speziale et al., 1984) and analyzed fluorometrically. Total phosphorus (TP) was measured using standard automatic colorimetric procedures on an autoanalyzer (Davis and Simmons, 1979; Laird et al., 1987). 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. Particulate phosphorus (PP) samples were filtered onto 0.4  $\mu\text{m}$  Nuclepore filters and these filters were digested and analyzed with procedures used for total phosphorus (Millie et al., 2003). Particulate carbon (PC) samples were filtered onto pre-combusted Whatman GF/F filters and these filters were analyzed on a Model 1110 CHN analyzer (Millie et al., 2003).

Extracted chlorophyll *a* concentrations from specific depths were regressed against the fluorescence voltage value from the fluorometer at the same depth to correct chlorophyll fluorescence values to extracted chlorophyll *a* concentration. Values from near surface taken during the day were not used due to surface quenching (Cullen, 1982). Equations of extracted chlorophyll *a* as a function of fluorometer voltage were developed for each fluorometer used in the study and were developed for each year the instrument was used, except in a few instances, when data from multiple years was combined due to small sample size. The regressions were used to convert fluorometer voltage profiles into whole water column profiles of chlorophyll *a* concentrations. These derived chlorophyll *a* concentrations are hereafter simply referred to as chlorophyll *a*.

To evaluate SML chlorophyll *a* concentrations, we used the actual extracted chlorophyll *a* values from discrete water samples because fluorometric chlorophyll *a* values near surface may be biased low (Cullen, 1982). For all other chlorophyll concentrations (i.e., DCL, DCM, near bottom), we used the derived chlorophyll *a* concentrations from fluorescence profiles. To evaluate the DCM, we determined the maximum chlorophyll *a* concentration in the sub-epilimnetic region for each profile. The depth of the maximum chlorophyll *a* concentration was also determined. To evaluate the DCL, we defined the DCL as the sub-epilimnetic region where chlorophyll *a* concentration exceeded  $2 \text{ mg}\cdot\text{m}^{-3}$  (Fahnenstiel and Scavia, 1987a; Fahnenstiel et al., 2010). We determined the integrated chlorophyll *a* concentration within this region (i.e., the size of the DCL) using an image analysis system (Image-Pro V7.0). This approach of evaluating the size of the DCL incorporates both the concentration (e.g., DCM) and the width of the region and provides a DCL value that is not relative to SML chlorophyll concentrations. To evaluate the near-bottom hypolimnetic waters that

would include the nepheloid zone, we calculated the average chlorophyll *a* concentration in the bottom 20 m. To determine average water column chlorophyll *a*, we first replaced near surface values (approx. top 10–15 m) in the chlorophyll *a* corrected fluorescence profile with the corresponding extracted chlorophyll *a* concentration. In cases where no extracted chlorophyll *a* was available, we used the value from approximately 10–15 m below the surface where surface quenching appeared minimal. Although sampling took place in 1997, no CTD cast data were available, so 1997 was excluded from analysis. Multiple profiles during a day at a given site were combined into a single average value for each metric of interest.

To evaluate trends in phosphorus, we determined concentrations from discrete samples in the SML, in the 20–60 m depth zone, and below 70 m. The 20–60 m depth zone was used to characterize the area where the DCL and DCM would historically occur (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987a) because too few depths were sampled to adequately determine nutrient concentrations in the actual DCL. Nutrient concentrations below 70 m were used to determine near bottom values. We calculated PP:TP and PC:PP ratios to provide information on cycling of P and phytoplankton nutritional condition.

We collected zooplankton to evaluate the potential role of grazers on the phytoplankton community. Zooplankton were collected using duplicate, whole water column tows with a 50-cm diameter, 2.5-m long, 153- $\mu\text{m}$  mesh, conical net. Zooplankton were narcotized with Alka-Seltzer and preserved in a 2–4% sugar formalin solution. For counting an aliquot was removed with a Hensen–Stempel pipette and a minimum of 600 zooplankton were identified for each sample taken. Zooplankton were classified as cyclopoid copepods, calanoid copepods, and herbivorous cladocerans. Analysis focused on herbivorous zooplankton, e.g., calanoid copepods and herbivorous cladocerans. More details on zooplankton sampling are available in Vanderploeg et al. (2012).

For analysis, we separated data into two time periods, a pre quagga mussel period (1995–2000) and a post quagga mussel period (2007–2011; Nalepa et al., 2010). Within each time period, data were separated into early (June and July) and late (August and September) summer. The DCL has historically been at its peak in early summer (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987a; Fahnenstiel et al., 2010). Comparisons between time periods were done using a two sample *t*-test. A Bonferroni correction was applied to *t*-tests because summer data had been separated into early and late summer for each time period, so a *p*-value of 0.025 was considered significant.

## Results

A total of 125 CTD casts at a total of 106 site/day combinations were analyzed (Table 1). Representative examples of early summer and late summer chlorophyll *a* profiles from the two periods (1995–2000 and 2007–2011) are shown in Fig. 2.

Secchi depth differed between 1995–2000 and 2007–2011 in both early ( $p = 0.02$ ) and late summer ( $p < 0.001$ ). Mean secchi depth was 9.3 and 11.1 m in early summer in 1995–2000 and 2007–2011, respectively. Mean secchi depth was 6.1 and 13.6 m in late summer in 1995–2000 and 2007–2011, respectively.

The average whole water column chlorophyll *a* over the entire summer ranged between 1.02 and  $2.22 \text{ mg}\cdot\text{m}^{-3}$  during 1995–2000, and between 0.70 and  $1.05 \text{ mg}\cdot\text{m}^{-3}$  during 2007–2011 (Fig. 3). In early summer, there was a significant difference in mean whole water column chlorophyll *a* between the pre and post quagga mussel establishment time periods ( $p < 0.001$ ), but not in late summer ( $p = 0.32$ ) (Table 2). In early summer, mean whole water column chlorophyll *a* declined 50% between 1995–2000 and 2007–2010.

Mean SML chlorophyll *a* did not differ between 1995–2000 and 2007–2011 in either early or late summer ( $p > 0.26$ ) (Table 2). By contrast, mean near bottom chlorophyll *a* declined 63% in early summer

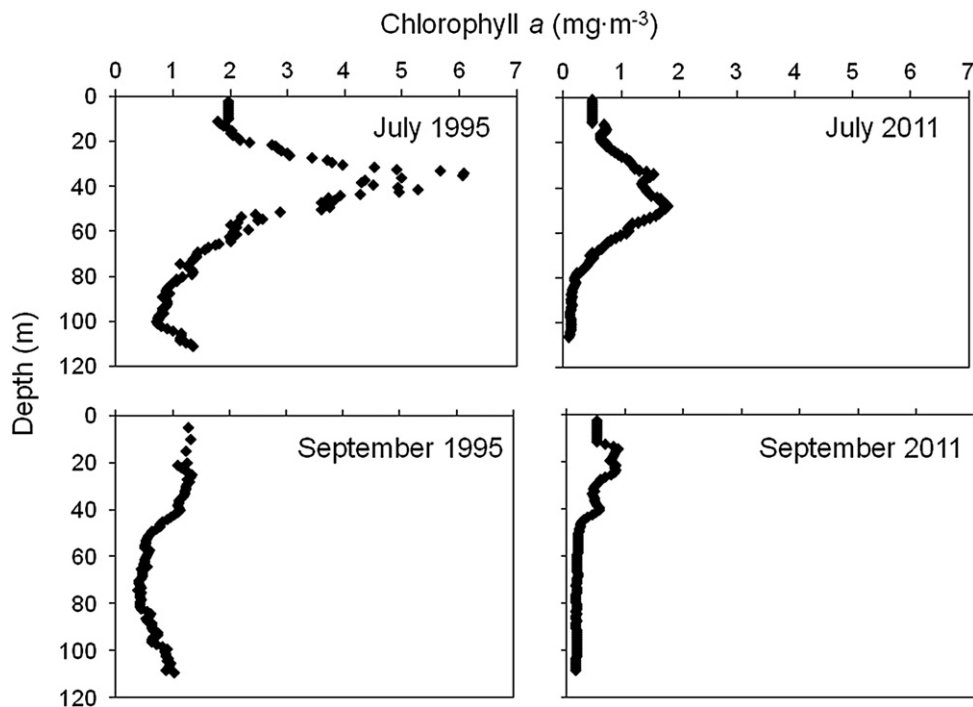


Fig. 2. Examples of chlorophyll *a* profiles in early summer (July) and late summer (September) in southeastern Lake Michigan during 1995 and 2011.

and 54% in late summer between 1995–2000 and 2007–2010 ( $p < 0.01$ ) (Table 2).

Mean DCM chlorophyll *a* concentrations differed between pre and post quagga establishment time periods in early summer ( $p < 0.001$ ), but did not differ between time periods in late summer ( $p = 0.45$ ) (Table 2). The DCM in both early and late summer was found deeper in the water column in 2007–2010 compared to 1995–2000 ( $p < 0.01$ ) (Table 2).

Mean size of the DCL (i.e., integrated chlorophyll *a* concentrations; includes zero values) ranged between 17 and 46  $\text{mg}\cdot\text{m}^{-2}$  in 1995–2000, and between 1 and 9  $\text{mg}\cdot\text{m}^{-2}$  in 2007–2011 (Fig. 4). Similar to the pattern for the DCM, the size of the DCL region differed between 1995–2000 and 2007–2011 in early summer ( $p < 0.001$ ), decreasing 93% between periods (Table 2). In late summer the size of the DCL region did not differ between 1995–2000 and 2007–2011 ( $p = 0.40$ ).

In early summer, TP concentrations decreased 22–27% between 1995–2000 and 2007–2011 in all depth zones, but the changes were only statistically significant in the DCL region (20–60 m) and near bottom regions ( $p < 0.02$ ) (Table 3). In late summer, TP declines in the SML and DCL regions were small (11–14%) and were not significant

( $p > 0.06$ ). By contrast, there was a significant difference in TP concentrations in late summer between 1995–2000 and 2007–2011 in the near bottom region ( $p = 0.001$ ), with a decline of 30% noted between periods.

In all depth regions, the PP:TP ratio demonstrated a downward trend in both early and late summer between 1995–2000 and 2007–2010 (Table 3). The PC:PP ratio demonstrated an increasing trend between 1995–2000 and 2007–2011 in early and late summer in the SML, mid depth zone, and the near bottom zone (Table 3).

Mean abundance of herbivorous zooplankton (i.e., calanoid copepods + herbivorous cladocerans) was 29% (early summer) and 24% (late summer) lower in 2007–2011 than in 1995–2000, including a 52% decline of late summer herbivorous cladoceran abundance (Fig. 5). Despite these downward trends, there was no statistical difference in herbivorous zooplankton abundance for either early ( $p = 0.06$ ) or late ( $p = 0.26$ ) summer between 1995–2000 and 2007–2011.

## Discussion

The results for this study are an extension of those presented in Fahnenstiel et al. (2010) which focused on the dramatic loss of the spring phytoplankton bloom (i.e., decreased primary production and chlorophyll *a*) in offshore Lake Michigan in 2007–2008 relative to the 1980s and 1990s. Fahnenstiel et al. (2010) presented limited data on the stratified period based on discrete water samples that indicated less dramatic or no changes in phytoplankton production and chlorophyll *a* concentration in the SML, and equivocal changes in the DCL and DCM. Herein we provide additional years of data (2009–2011) along with continuous whole water column profiles of chlorophyll *a* from fluorometer casts to provide greater insight into the summer period in offshore Lake Michigan. Furthermore, the use of whole water column chlorophyll *a* profiles enables us to more fully explore the important aspects of the summer plankton community, including the SML, DCL, DCM and near bottom zone than can be done with discrete water samples alone.

The whole water column chlorophyll *a* concentrations decreased 50% between 1995–2000 and 2007–2011 in early summer, but did not change during late summer. The changes in whole water column

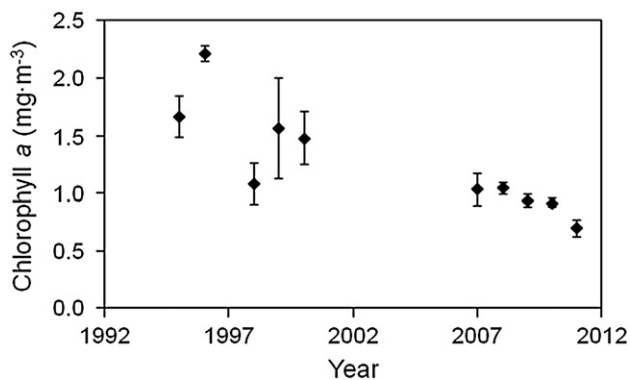


Fig. 3. Mean ( $\pm 1$  SE) whole water column chlorophyll *a* concentrations over the entire summer (June–September) in the offshore of southeastern Lake Michigan during 1995–2011.

**Table 2**

Average ( $\pm 1$  SE) whole water column chlorophyll *a* concentration, surface mixed layer chlorophyll *a* concentration (SML), deep chlorophyll *a* maximum (DCM), depth of DCM, integrated deep chlorophyll *a* concentration (DCL), and near bottom chlorophyll *a* concentration in 1995–2000 and 2007–2011 for June–July and August–September.

Years	Months	Average mg · m <sup>-3</sup>	SML mg · m <sup>-3</sup>	DCM mg · m <sup>-3</sup>	DCM depth m	DCL mg · m <sup>-2</sup>	Near bottom mg · m <sup>-3</sup>
<i>Early summer</i>							
1995–2000	June–July	1.94 $\pm$ 0.11*	1.49 $\pm$ 0.22	5.09 $\pm$ 0.49*	28 $\pm$ 1*	48.77 $\pm$ 6.70*	1.06 $\pm$ 0.08*
2007–2011	June–July	0.97 $\pm$ 0.04	1.27 $\pm$ 0.20	2.26 $\pm$ 0.13	33 $\pm$ 2	3.51 $\pm$ 1.10	0.39 $\pm$ 0.04
<i>Late summer</i>							
1995–2000	Aug–Sept	0.99 $\pm$ 0.13	1.03 $\pm$ 0.06	2.20 $\pm$ 0.36	25 $\pm$ 1*	7.98 $\pm$ 3.60	0.70 $\pm$ 0.12*
2007–2011	Aug–Sept	0.85 $\pm$ 0.04	1.14 $\pm$ 0.17	2.52 $\pm$ 0.21	33 $\pm$ 2	4.67 $\pm$ 1.30	0.32 $\pm$ 0.02

An asterisk indicates a significant difference between year periods within each pair of months ( $p < 0.025$ ).

chlorophyll *a* were not related to changes in the SML, because SML chlorophyll *a* concentrations did not differ between 1995–2000 and 2007–2011. This observation is consistent with previous results that also found little change in SML chlorophyll *a* concentrations since the 1980s in the offshore of southern Lake Michigan during the stratified period (Fahnenstiel et al., 2010; Mida et al., 2010).

In contrast to the SML, chlorophyll *a* concentrations in the near bottom zone declined 63% in early summer and 54% in late summer. Chlorophyll *a* in the near bottom zone is part of the benthic nepheloid layer, which consists of a combination of biogenic and fine sediment material (Hawley and Muzzi, 2003; Sanilands and Murdoch, 1983). The settling of spring bloom plankton to the lake bottom historically provided an important link between pelagic and benthic food webs as material was assimilated by the macroinvertebrate *Diporeia* (Fitzgerald and Gardner, 1993). Furthermore, detrital material in the near bottom zone is an important food source for *Mysis* in Lake Superior and likely was in Lake Michigan as well (Sierszen et al., 2011). Therefore, the drastic decline of chlorophyll *a* in this region represents a major loss of material available for macroinvertebrate production in the lake and can be related to the decline in the spring bloom.

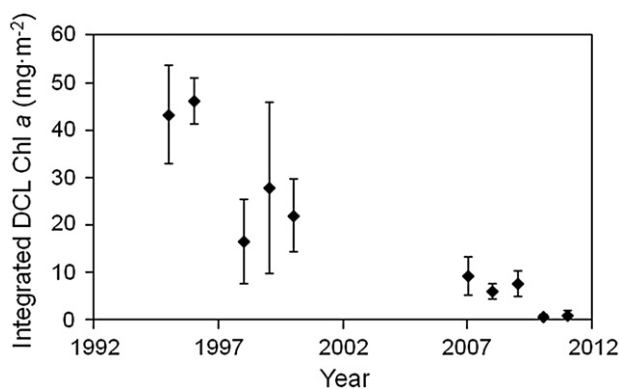
During early summer, we documented dramatic declines between 1995–2000 and 2007–2011 in the integrated DCL (92%) and DCM (56%) chlorophyll *a* concentrations. Historically, the DCL was a dominant feature of the summer water column profile in Lake Michigan (Brooks and Torke, 1977). This region contains a large fraction of water column chlorophyll *a* and primary production during the stratified period (Brooks and Torke, 1977; Fahnenstiel and Scavia, 1987b; Moll and Stoermer, 1982). Historically, the early summer (June or July) was when DCL chlorophyll *a* concentrations were at their maximum (Brooks and Torke, 1977; Fahnenstiel et al., 2010). Thus, the decline we noted in early summer occurred when the DCL should have been at its peak. By contrast, in late summer, when the DCL is declining

(Brooks and Torke, 1977; Fahnenstiel et al., 2010), we found no significant difference in the size of the DCL or DCM chlorophyll *a* concentration between 1995–2000 and 2007–2011. Interestingly, owing to low values in early summer, there was no apparent decrease in the size of the DCL between early and late summer in 2007–2011 in contrast to the 84% decrease observed in 1995–2000.

The conditions in Lake Michigan during the summer have been linked to chlorophyll *a* concentrations during the isothermal period in Lake Michigan (Scavia and Fahnenstiel, 1987; Scavia et al., 1986). In particular, the formation of the DCL is linked to the spring bloom as spring plankton move downward where in situ growth, shade adaptation and to a lesser degree, continued plankton settling, combine to produce the DCL (Fahnenstiel and Scavia, 1987a; Moll and Stoermer, 1982). The relationship between spring chlorophyll *a* and the DCL can be seen by the high correlation ( $R^2 = 0.87$ ) of maximum size of the DCL as a function of the corresponding maximum spring chlorophyll *a* value (G. Fahnenstiel, unpublished data) for that year (Fig. 6). The former importance of spring diatoms such as *Aulacoseira islandica* in the July DCM demonstrated the link between the spring bloom and the DCL, but after the disappearance of the spring bloom, these diatoms were no longer found in the DCM (Fahnenstiel et al., 2010).

The declines in water column, DCM, DCL, and near bottom chlorophyll *a* concentrations in offshore southeastern Lake Michigan during the summer appear to be driven by the invasion of dreissenid mussels. Similarly, dreissenids were implicated in the dramatic declines in chlorophyll *a* during the spring isothermal period (Fahnenstiel et al., 2010; Pothoven and Fahnenstiel, in press). Dreissenids have continued to increase in abundance in the offshore between 2007–2008 and 2011 (T. Nalepa, unpubl. data). During the spring, the fully mixed water column provides direct contact between mussels and phytoplankton throughout the water column which allows mussel filtering to have a large impact (Fahnenstiel et al., 2010). Although dreissenids are not in direct contact with the entire water column during the stratified period, there are a number of reasons why dreissenids can still be associated with the changes in summer chlorophyll *a* conditions. First, dreissenid mussels are responsible for the loss of spring bloom (Fahnenstiel et al., 2010) and as noted previously, there is a clear connection between spring and summer chlorophyll *a* concentrations throughout water column (Fig. 6; Moll and Stoermer, 1982; Scavia et al., 1986).

Second, dreissenids have altered the flow of nutrients to the offshore. Dreissenids in rocky nearshore areas intercept and retain nutrients, depriving the offshore of nutrients through a “nearshore shunt” (Hecky et al., 2004). Dreissenids can also create conditions favorable for *Cladophora* growth, further sequestering nutrients in the nearshore (Hecky et al., 2004). Similarly, after the establishment of dreissenid mussels, the proportion of P retained in the shallow embayment Saginaw Bay increased 46–70%, reducing P export to the offshore regions of Lake Huron (Cha et al., 2011). In Lake Ontario, mussels in the littoral zone depleted the available seston during the spring when the DCM intercepted the lake bottom (Malkin et al., 2012). In areas where



**Fig. 4.** Mean ( $\pm 1$  SE) integrated DCL chlorophyll *a* concentrations over the entire summer (June–September) in the offshore of southeastern Lake Michigan during 1995–2011. The DCL is defined as the sub-epilimnetic region where chlorophyll *a* concentration exceeded 2 mg·m<sup>-3</sup>.

**Table 3**  
Mean total phosphorus (TP;  $\text{mg} \cdot \text{m}^{-3}$ ), PC:PP molar ratio, and PP:TP ratio in the SML (surface mixed layer), mid depth region (20–60 m; where the DCL historically was found), and near-bottom zone during June–July and August–September in 1995–2000 and 2007–2011.

Years	Months	TP SML	TP Mid	TP Bottom	PC:PP SML	PC:PP Mid	PC:PP Bottom	PP:TP SML	PP:TP Mid	PP:TP Bottom
<i>Early summer</i>										
1995–2000	June–July	5.9	5.8*	4.8*	225	185	61	0.61	0.67	0.59
2007–2011	June–July	4.4	4.5	3.5	307	259	258	0.50	0.52	0.31
<i>Late summer</i>										
1995–2000	Aug–Sept	4.3	5.8	4.9*	171	156	130	0.74	0.67	0.60
2007–2011	Aug–Sept	3.8	5.0	3.4	364	261	250	0.42	0.54	0.33

An asterisk indicates a significant difference between year periods within each pair of months for TP ( $p < 0.025$ ).

the nearshore substrate is sandy and not favorable for stable dreissenid colonization, such as in our sampling region, large numbers of mussels can be found in a transitional region (30–50 m) where a “mid-depth sink” operates to capture P and C and disrupt the flow of nutrients from the nearshore to the offshore (Vanderploeg et al., 2010). Therefore dreissenid mussels in nearshore and mid-depth regions are able to remotely affect nutrient and chlorophyll dynamics in offshore regions without direct contact with the entire offshore water column.

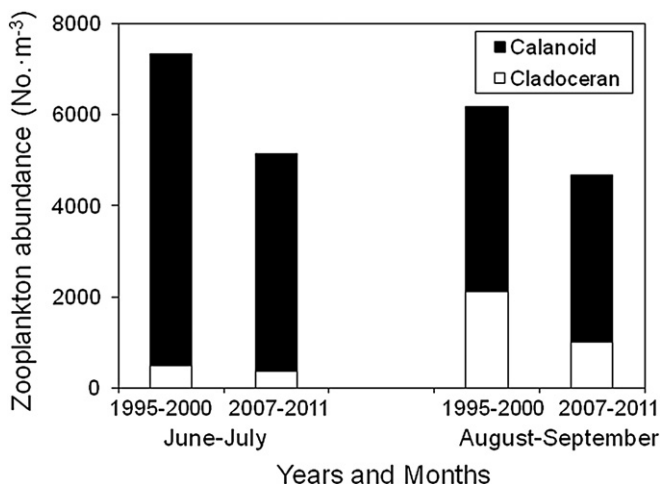
The most likely alternative to dreissenids to explain the changes in chlorophyll *a* in the summer is reductions in P loading and subsequent declines in P concentrations. Phosphorus loading has decreased gradually since the 1980s with concurrent declines in P concentrations in the lake (Mida et al., 2010). However it should be noted that separating the effects of declines in P loading from the filtering effects of mussels is not easy because mussels alter the cross depth transport of nutrients from nearshore to the offshore (Hecky et al., 2004; North et al., 2012; Vanderploeg et al., 2010). Therefore, changes in nutrient loading simply cannot be examined in isolation from nearshore and mid-depth dreissenid dynamics when considering the offshore.

Furthermore, it is unlikely that decreases in P loading can explain the dramatic decreases in chlorophyll *a* over the relatively short time period (<1 decade) observed in this study. The declines in P loading and concentrations have been gradual from the 1980s through the present (Mida et al., 2010) whereas chlorophyll *a* concentrations declined precipitously within the last decade concurrent with the colonization of large populations of mussels. For example, the integrated DCL chlorophyll *a* concentrations averaged 31 and  $27 \text{ mg} \cdot \text{m}^{-2}$  in 1983 and 1984 (June–August) based on extracted values (Fahnenstiel et al., 2010) and  $49 \text{ mg} \cdot \text{m}^{-2}$  in 1995–2000, followed by a nine-fold decrease to  $4 \text{ mg} \cdot \text{m}^{-2}$  in 2007–2011. The more rapid decrease in chlorophyll

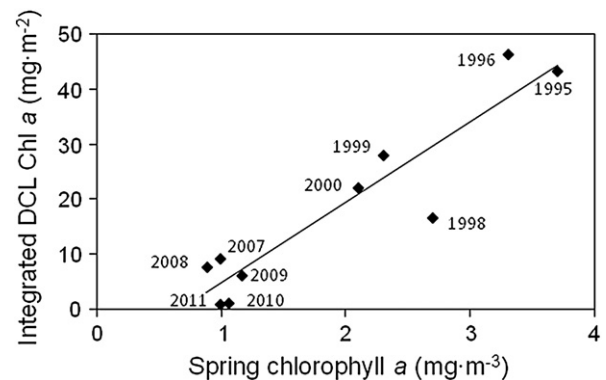
relative to TP resulted in an overall 33–55% decrease in the Chl:TP ratio in the regions where mussel impacts were most evident (i.e., early summer DCL region and near bottom region). The decrease in Chl:TP ratios is entirely consistent with a dreissenid effect (Higgins et al., 2011; North et al., 2012).

The DCL can enhance zooplankton biomass in oceans (Ortner et al., 1980) and lakes (Williamson et al., 1996), although cooler temperatures may limit the value of this region for zooplankton compared to the SML (Lampert and Grey, 2003). In Lake Michigan, large diatoms in the DCL were considered an important food source for the vertically migrating macroinvertebrate *M. diluviana* (Bowers and Grossnickle, 1978). Thus, the nearly complete disappearance of the DCL could lead to changes in secondary production or behavior of herbivores in Lake Michigan.

Deep chlorophyll layers are regulated by light and nutrient availability (Moll and Stoermer, 1982). Thus, increased light (i.e., increased secchi depth) observed in 2007–2011 might be expected to produce a larger DCL. A large increase in the Lake Michigan DCL in the late 1980s was related to increased subsurface light availability (Fahnenstiel and Scavia, 1987c). More recently, Barbiero et al. (2009) suggested that the late summer DCM in Lake Michigan was increasing due to increased light penetration after the dreissenid mussel invasion. However, Fahnenstiel et al. (2010) suggested that the DCL and DCM were either similar or smaller in 2007–2008 than in the 1980s and 1990s due to decreased nutrient availability. With our extensive sampling during the summers of 2007–2011 we demonstrated that the DCL and DCM are significantly smaller than they were in the 1990s due to decreased nutrient availability. Total phosphorus in the region where the DCL occurs declined in 2007–2011 and PC:PP ratios indicated a shift from moderate P limitation (see Hecky et al., 1993) in 1995–2000 to severe P limitation in 2007–2011. Similarly, nutrient deficiency increased in offshore eastern Lake Erie following dreissenid invasion (North et al., 2012). Moll and Stoermer (1982) noted that the size of the DCL is related to trophic status with a nutrient-poor lake (Lake Superior) having a smaller DCL



**Fig. 5.** Mean herbivorous (calanoid copepods + herbivorous cladocerans) zooplankton abundance during early (June–July) and late (August–September) summer for 1995–2000 and 2007–2011 in southeastern Lake Michigan.



**Fig. 6.** Maximum integrated summer DCL chlorophyll *a* concentration for a given year as a function of the maximum spring isothermal period chlorophyll *a* concentration for the same year during 1995–2011 in southeastern Lake Michigan.

than a moderate-nutrient lake (Lake Michigan). Therefore, it is not surprising that as Lake Michigan becomes more oligotrophic and similar to Lake Superior (Evans et al., 2011) the DCL would shrink.

As is the case for most sub-epilimnetic regions, chlorophyll *a* concentrations in the near bottom zone depend on a number of sources of material (Chambers and Eadie, 1981; Hawley and Muzzi, 2003), all of which were greatly altered by dreissenid mussels. First, settling of material from the spring bloom was greatly reduced by dreissenids (Fahnenstiel et al., 2010). Second, offshore transport of material was reduced as material was intercepted by mussels in the nearshore and mid-depth regions (Hecky et al., 2004; Malkin et al., 2012; Vanderploeg et al., 2010). Finally, material in the near bottom zone was in direct contact with the filtering activities of quagga mussels which were increasing in offshore areas (Nalepa et al., 2010).

Zooplankton grazing can reduce phytoplankton abundance in the sub-epilimnetic regions (e.g., DCL and bottom) (Fahnenstiel and Scavia, 1987a; Scavia et al., 1986) or enhance concentrations through nutrient transport and subsequent recycling (Pilati and Wurtsbaugh, 2003). However, we did not find any evidence that overall herbivorous zooplankton grazing demands were driving the changes we observed in chlorophyll *a* concentrations. Furthermore, although the changes were not significant, there was a downward trend in herbivorous zooplankton abundance, especially for cladocerans. It is likely that declines in phytoplankton abundance are playing a role in this downward trend in cladoceran abundance (Vanderploeg et al., 2012). Declines in cladocerans could lead to a decrease in nutrient transport from the SML into deeper layers through vertical migrations of herbivores, which in turn could cause phytoplankton to become even more nutrient starved in deeper layers.

Phosphorus declined in deep layers more than in the SML because the concentrations of chlorophyll *a* and TP were more linked to the spring bloom in the deep layers as phytoplankton (mostly large diatoms) quickly settle through the shallow mixed layer once thermal stratification occurs (Fahnenstiel and Scavia, 1987a). Moreover, the summer SML is a very active region that functions primarily on the fast recycling of nutrients within the layer (Scavia and Fahnenstiel, 1987) unlike the deeper layers of thermal stratification where processes proceed more slowly and retention rates are greater (Fahnenstiel and Scavia, 1987a,b; Scavia and Fahnenstiel, 1987). The significant decline in nutrient ratios documented in this study is somewhat paradoxical. On the one hand, soluble P concentrations probably increased as the result of increased nutrient recycling due to mussel filtration, but the P deficiency of the phytoplankton populations appeared to increase as indicated by the increased PC:PP ratios. A similar trend was noted in nutrient ratios during the spring mixing period (Pothoven and Fahnenstiel, in press) and an additional nutrient indicator (Vmax: Pmax) also suggested that the phytoplankton were more P deficient after dreissenid mussel populations were established. Thus, our understanding of nutrient dynamics and linkages between phytoplankton processes and nutrient availability likely have changed markedly after the establishment of large populations of mussels, and these linkages merit further investigation.

The summer chlorophyll *a* dynamics of offshore Lake Michigan have been greatly altered by dreissenid mussel invasion, including the nearly complete loss of the deep chlorophyll layer and near bottom chlorophyll. These changes are likely to affect other aspects of the food web, including zooplankton and macroinvertebrate production. As dreissenid mussels stabilize within the lake, it will be important to continue to monitor summer chlorophyll and other lower food web parameters to understand the future state of the offshore pelagic food web in Lake Michigan.

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