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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

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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)).

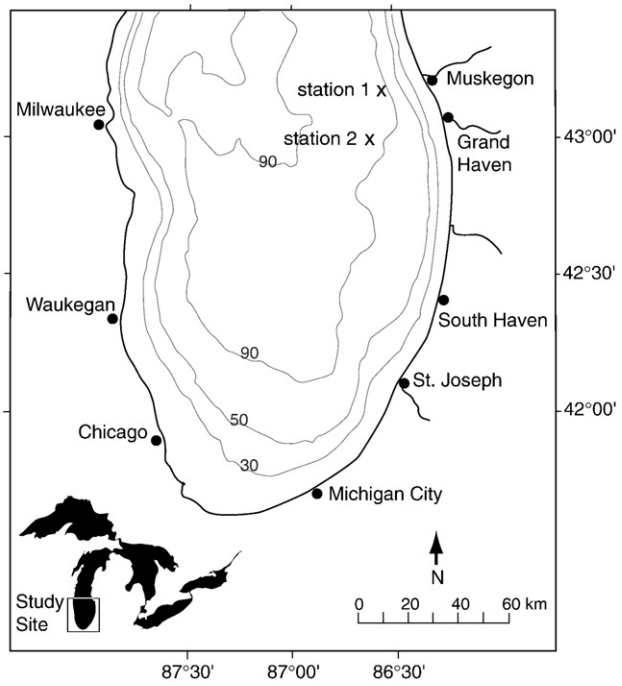

Fig. 1. Map of southern Lake Michigan showing location of two sampling stations.

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