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Variation in the abundance of pico, nano, and microplankton in Lake Michigan: Historic and basin-wide comparisons

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ABSTRACT

The Lake Michigan ecosystem has undergone numerous, systemic changes (reduced nutrient, changing climate, invasive mussels) that have altered portions of the food web and thus, appear to have changed the lake's trophic state. That said, little is known about the components of the microbial food web (MFW, heterotrophic and phototrophic pico, nano, and micro-plankton), which we hypothesized have compensated as a food source for crustacean zooplankton given the recent declines in the biomass of large phytoplankton (mainly diatoms). Therefore, we measured the abundance of the entire MFW using complementary microscopic techniques, flow cytometry, and size fractionated chlorophyll concentrations at sites in northern and southern Lake Michigan, and one site in Lake Superior; the latter site served as a benchmark for oligotrophic conditions. In addition, a historic comparison was made between 1987 and 2013 for the southern Lake Michigan site. Ppico numbers (i.e., picocyanobacteria) in 2013 were lower compared with those in the 1980s; however, the percent contribution of the <2 μm fraction increased 2-fold (>50% of total chlorophyll). The abundance of small, pigmented chrysomonads and cryptomonads (Pnano size category) was not significantly different between 1987 and 2013 at the same time Pmicro did decline; this shift towards Ppico and Pnano dominance may be related to the recent oligotrophication of Lake Michigan. The abundance of ciliated protists (Hmicro size class) was 3-fold lower in 2013 compared with levels in 1987, while the abundance of both Hpico (eubacteria, range 0.24–1.36 × 10^6 cells mL^{-1}) and Hnano (mainly colorless chrysomonads; range 0.11–6.4 × 10^3 cells mL^{-1}) remained stable and reflected the resilience of bacteria–flagellate trophic linkage.

Introduction

The Lake Michigan ecosystem has undergone numerous, systemic changes that appear to have altered its trophic state (reduced nutrient loading, changing climate, proliferation of invasive mussels). Among these changes, there has been a conspicuous decline in the typical, winter–spring phytoplankton bloom (mainly diatoms), now largely absent from the water column. The large decline (66–87%) in phytoplankton abundance and productivity was observed in 2007–08 as compared with the 1995–98 and 1983–87 time periods (Fahnenstiel et al., 2010). Loss of the bloom is alarming, because the spring diatom bloom sustained a large fraction of animal production (invertebrates and fish) in the lake (e.g., Gardner et al., 1990). Moreover, the winter–spring zooplankton assemblage also changed dramatically during the same time period, as native cyclopoids, cladocerans, and small copepod species declined by 50–90% in 2007–08 (Vanderploeg et al., 2012).

While the mechanism(s) driving these changes are difficult to ascertain, few human influences have had as large an impact on aquatic ecosystems over the short term as the introduction of dreissenid mussels in North America (Strayer et al., 2004). The quagga mussel expansion into mid-depth regions of Lake Michigan coincided with a shift towards smaller phytoplankton species in both surface and subsurface assemblages (Vanderploeg et al., 2010) with an overall decline in the magnitude of the subsurface chlorophyll layer (Pothoven and Fahnenstiel, 2013). Because changes in phytoplankton were mirrored by shifts in other elements of the food web, salmon stocking was reduced in 2013. While the re-engineering by non-indigenous bivalves in the Great Lakes has received much attention in terms of effects on larger conspicuous changes such as these (e.g., Hecky et al., 2004), our knowledge of pelagic food web structure and dynamics in Lake Michigan after the recent zebra–quagga mussel shift remains unknown.

Given declines in phytoplankton biomass and primary production in the lake, we hypothesized that the abundance and size-specific composition of less conspicuous plankton has compensated for the decline in larger diatoms in Lake Michigan. Components of the microbial food

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web (MFW), namely bacteria, pico-sized algae, and flagellated and ciliated protist predators, have constituted alternative trophic pathways in other pelagic food webs (Calbet and Landry, 2004). Moreover, previous studies have shown the MFW to be represented throughout the Great Lakes prior to many of the systemic changes cited above (see Fahnenstiel et al., 1998). More recently, phototrophic picoplankton (Ppico) abundance in the western half of southern Lake Michigan appeared to decline below historic estimates in the 1980s, although their contribution to total pelagic chlorophyll concentrations has doubled since 2005 (Cuhel and Aguilar, 2013). The results were important, because they suggest that Ppico are now major contributors to carbon fixation and its subsequent transfer to higher trophic levels. Given this, the specific objectives of this study were:

1. Assess spatio-temporal variation in size-specific phytoplankton biomass in Lake Michigan, particularly to determine if long term changes observed for the phytoplankton were limited to specific locations in the lake (north–south, and near-offshore) and/or thermal periods (mixing, periods of stratification).
2. Assess historic differences in the abundance of key heterotrophic plankton components in Lake Michigan by comparing our data collected here (2013) against identical measurements made in southern Lake Michigan (1987).
3. Discuss the possible factors that might account for the current abundance and size specific composition of phototrophic and heterotrophic plankton in Lake Michigan.

Materials and methods

Lake sampling

We sampled six sites distributed among three lake regions (northern Lake Michigan, southern Lake Michigan, and Lake Superior) to evaluate variation in the abundance of the entire microbial food web (Table 1). First, long-term trends in chlorophyll concentrations at the offshore station in southern Lake Michigan were evaluated using monthly data collected from 1987 to 2013 (see Pothoven and Fahnenstiel, 2013). Second, variation in the MFW components (MFW, heterotrophic and phototrophic pico, nano and microplankton) was evaluated among all three lake-regions and against data collected previously in 1987 (southern Lake Michigan) that served as a historical benchmark. This comparison was made on data collected using identical methodologies for the two time periods (see Fahnenstiel and Carrick, 1992; Carrick and Fahnenstiel, 1989, 1990). Third, variation in the phytoplankton assemblage in Lake Michigan was evaluated by assessing potential differences in size-fractionated chlorophyll among near and offshore locations and temporal periods (2013 data only).

In terms of logistics, near and offshore waters (locations) in Lake Superior (LS), northern Lake Michigan (LMN), and southern Lake Michigan (LMS) were sampled in 2013 (Table 1). Lake Superior was sampled from a small research vessel (R/V Agassiz,) on four dates at an offshore station north of the Keweenaw peninsula within the 300 m contour (LS1) and on one date (July) in Keweenaw Bay near Houghton, MI at a nearshore station (LS6). On four dates, near and offshore stations in northern Lake Michigan were sampled from a small research vessel (M/V Chippewa) in the vicinity of Beaver Island west of the Straits of Mackinaw; the nearshore station was located eastward off the north shore of the island (LMN1) and the offshore sites were located within the 100 m contour eastward off the south shore (LMN8). Southern Lake Michigan was sampled from the research vessel R/V Laurentian on four dates along a historic transect from Muskegon within the 15 m contour (LMS15) and 100 m contour (LMS110). Finally, the offshore LMS110 station was previously sampled on four dates in 1987 aboard the R/V Shennehon.

At all stations (including LMS in 1987), the water column was sampled during four major thermal periods that included: mixing (April–May), early (June), mid (July), and late (August, September) stratification (see Scavia and Fahnenstiel, 1987). The early June sample at the northern Lake Michigan sites served as the mixing period, because the water column had not stratified there. Water column conditions were measured for key physical–chemical parameters (e.g., temperature, conductivity, PAR) using either a Seabird CTD or a handheld YSI-8800 m along with an underwater PAR sensor (Li-cor LI-1000). Whole water samples were retrieved from 5 m depth in the surface mixed layer (5 m depth, except LMN1, 1 m depth). This depth was chosen because it is a mid-depth in the surface mixed layer for Lake Michigan and was the same depth sampled in previous studies (see Carrick and Fahnenstiel, 1989, 1990). All water samples were collected using a trace metal clean, modified 5-L Niskin bottles poured into 10-L carboys and then dispensed into a dark 4-L bottles (polycarbonate). Two subsamples were removed and preserved (1% Lugol's solution, 1% glutaraldehyde) to enumerate plankton and for flow cytometry analysis, while the remaining water was placed in coolers and transported back to the laboratory for subsequent analysis (see below).

Size-specific chlorophyll

In 2013 only, size-specific plankton biomass was estimated from duplicate chlorophyll-a measurements made on water collected (seasonally, 4 thermal periods) at near and offshore locations in both LMN and LMS (2 regions, 2 locations, 4 periods, 2 replicates, $n = 32$). Duplicate water samples were passed separately through three screens with specific pore sizes (2.0-μm Nucleopore filters, 20-μm Nitex mesh, and raw unfiltered water, see Fahnenstiel and Carrick, 1992). The filtrate was subsequently concentrated onto filter membranes (Whatman GFF, 0.7 μm pore size) and the pigments extracted for 1 h in a 50:50 mixture of Acetone:DMSO (Shoaf and Lium, 1976) without grinding (Carrick et al., 1993). Chlorophyll-a concentrations were corrected for phaeopigments and chlorophyll-b interference (Welschmeyer, 1994) and coefficients of variation among samples were typically <5%. Chlorophyll concentrations were estimated for three major plankton size categories (picoplankton 2-μm; nanoplankton 2–20 μm; microplankton >20 μm).

Plankton abundance and taxonomic composition

The abundance and taxonomic composition of the entire microbial food web were measured using a series of complementary enumeration techniques (see Carrick and Schelske, 1997). The abundance

Table 1
A summary of locations and dates sampled during the present study in 2013. Previous data collected at the offshore station in southern Lake Michigan was reanalyzed herein and served as a historic benchmark (offshore, 1987).

Lake region	Location station ID	Longitude	Latitude	Depth (m)	Dates sampled
Northern Lake Michigan	Nearshore LMN1	85.44712	45.75000	10	12-June, 26-June, 22-July, 5-August (2013)
	Offshore LMN8	85.47470	45.55817	100	12-June, 26-June, 22-July, 5-August (2013)
Southern Lake Michigan	Nearshore LMS15	86.34972	43.19139	15	24-April, 15-May, 16-July, 23-September (2013)
	Offshore LMS110	86.53778	43.19139	110	24-April, 15-May, 16-July, 23-September (2013)
	Offshore LMS110	86.53778	43.19139	110	7-April, 1-May, 21-July, 9-September (1987)
Central Lake Superior	Nearshore LS6	88.57537	47.46459	80	26-July (2013)
	Offshore LS1	88.47073	46.80396	150	24-May, 25-June, 26-July, 6-September (2013)