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Phytoplankton trends in the Great Lakes, 2001–2011

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ABSTRACT

We describe recent trends in phytoplankton composition and abundance in the Laurentian Great Lakes using synoptic spring (April) and summer (August) sampling events from 2001 through 2011, a period of rapid shifts in pelagic food webs and water quality. Data analysis identified qualitative and quantitative changes in algal densities, biovolume, and taxonomic composition of assemblages. Since 2001, Lake Superior has changed subtly with an increase in small-celled blue-green algae in spring and a recent decline in summer centric diatoms, possibly a result of lake warming and changes in water quality. Spring phytoplankton declines mainly attributed to diatoms occurred in Lakes Huron and Michigan, a probable result of invasions by non-native dreissenids that have reduced pelagic nutrients and selectively consumed certain taxa. The decline in Lake Huron's spring phytoplankton biovolume was earlier and more severe than that in Lake Michigan, despite a faster and more abundant dreissenid invasion in Lake Michigan. Lake Erie's central basin had a notable increase in spring centric diatoms (largely Aulacoseira), while the whole of Lake Erie shows a summer increase in cyanobacteria, complementing that found in coastal regions. The composition of Lake Ontario's species assemblage shifted, but little overall change in algal abundance was observed with the exception of higher summer densities of cyanophytes. Additional mechanisms for shifts in the pelagic primary producers are described or hypothesized in the context of concurrent shifts in water quality and invertebrate populations. Tracking these trends and explaining driving factors will be critical to the management of lake conditions.

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Introduction

Recent observations from the pelagic Laurentian Great Lakes have revealed rapid qualitative and quantitative changes in lake biology and water quality. Some of these rapid shifts include increases in chloride (all lakes; Chapra et al., 2009), declines (Lakes Huron and Michigan; Barbiero et al., 2011a) and blooms (uniquely in Lake Erie; Twiss et al., 2012) of phytoplankton, rapid propagation of non-native mussels (e.g. Lake Michigan; Nalepa et al., 2009), declines in zooplankton populations (e.g. Lake Huron; Barbiero et al., 2009), and changes in fish populations (e.g. Lake Huron; Schaeffer et al., 2006). In some cases these changes have apparent causation, such as the probable links between proliferation of profundal quagga mussels and the decline in spring phytoplankton (Vanderploeg et al., 2010) and zooplankton (Vanderploeg et al., 2012) populations in Lake Michigan. The unprecedented oligotrophication of Lakes Huron and Michigan has resulted in a convergence of the lower food webs of those lakes with Lake Superior (Barbiero et al., 2012). Lake Erie is experiencing increasing algal biovolume, and blooms of the blue-green alga *Microcystis* (Millie et al., 2009) and the diatom *Aulacoseira* (Twiss et al., 2012) in the lake are under study. No major shifts in algal abundance were observed in oligotrophic Lake Superior within a few decades prior to the 2000s (Barbiero and Tuchman, 2001), but the known warming of the atmosphere and lake (Austin and Colman, 2007) may be affecting the food web. Lake Ontario experienced a significant decline in phytoplankton biomass from the 1970s through the 1990s due to nutrient reductions and filtration by dreissenids (e.g. Millard et al., 2003), and a significant drop in the late 1990s. In the last decade, any effects of continuing food web changes on Lake Ontario phytoplankton are poorly known. In many cases throughout the Great Lakes, linkages between human activities and these ecological shifts need resolution.

Anthropogenic activities often cause changes in phytoplankton abundance and community composition. For example, pelagic phytoplankton data from Lake Michigan were used to track shifts in algal abundance resulting from the mussel invasion (Fahnenstiel et al., 2010), but there has been no recent, comprehensive assessment of phytoplankton across the Great Lakes basin, and there has been little use of taxonomic information to provide potentially more refined reconstructions of community dynamics. Taxonomic details have provided robust

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environmental information, such as the increasing power of diatomnutrient predictive models when refining from sub-division to species resolution (Rimet and Bouchez, 2012). Details of the phytoplankton assemblages and their temporal characteristics are particularly needed to monitor the impacts of human activities that are changing nutrient supplies, introducing non-native species, and altering climate. As a primary goal of the USEPA's biological monitoring program (USEPA, 2010), tracking long-term changes should be strongly supported by phytoplankton data because they are often the first group of organisms in the lower food web to respond to perturbations in pelagic ecosystems (Willen, 2000). Use of the latest biological collections may be beneficial in tracking changes and predicting trajectories of lake conditions for guiding management.

This study evaluated an 11-year record of algal assemblages in each of the Great Lakes. Major aims were to describe trends in biovolumes and cell densities and likely mechanisms for changes. Further, to clarify structural changes in the assemblages and possibly support mechanistic explanations, we evaluated changes in taxonomic composition of the phytoplankton over time using multivariate analyses. These analyses revealed lake-specific trends in pelagic primary producers; and where notable changes occurred, causes are described or suggested.

Materials and methods

We employed the most recently available 11 years of phytoplankton data collected as part of the Great Lakes monitoring program. The standard operating procedure for phytoplankton collection and analysis is described in detail in the published procedures (USEPA, 2010), but abbreviated details were as follows. The EPA data were based on twiceannual synoptic sampling ("spring" = typically the month of April, "summer" = typically the month of August) from standard stations throughout the Great Lakes basin (Fig. 1). Our analyses focused on samples collected from 2001 through 2011. Although additional data were available, data used in this report were analyzed by one team of taxonomists, and the data underwent identical quality assessment procedures for taxonomic and quantitative consistency. Some sampling stations had 11 years of data (the 14 "master stations") while all 72 stations had the most recent five years (2007 through 2011).

Whole water samples were collected from the rosette sampler onboard the Research Vessel Lake Guardian. Phytoplankton samples were composites of water sampled at discrete depths from the euphotic zone of the water column. For isothermal spring samples, the sample integrated equal volumes of water from 1, 5, 10, and 20 m. In shallower locations in Lake Erie, the 20-m sample was replaced by an abovebottom collection. If the total depth was less than 15 m, equal volumes were integrated from surface, mid-depth, and above-bottom samples. For the stratified (summer) water column, equal volumes were taken from 1 m, 5 m, 10 m, and the lower epilimnion and integrated. If the epilimnion was very shallow, equal volumes were integrated from a maximum of four and a minimum of two sampling depths. Samples were split and analyzed separately for the whole phytoplankton assemblage (i.e., "soft" algae) and diatoms. Analysis of soft algae used the quantitative Utermöhl method of counting preserved specimens in a settling chamber on an inverted microscope (Utermöhl, 1958). During soft algal analyses, diatoms containing cytoplasm were identified as centric or pennate forms. The second split sample was digested in nitric acid and subsequently in peroxide to isolate the diatom valves which were then plated on slides and counted using oil immersion ($1000 \times$ or higher) to identify taxa. All counting included measurements of cell dimensions so that algal biovolumes could be calculated. Ultimately, analyses afforded detailed taxonomic resolution, and data were available in quantitative data formats [cell density (cells/ml) and biovolume $(\mu m^3/ml)].$

Because each lake has specific physical, chemical, and biological considerations, assessments were grouped according to nine major basins in the lakes: Superior, Michigan north, Michigan south, Huron north,



Fig. 1. Map of Great Lakes sample stations with master stations underlined. Lake regions within lakes used for data compilations are identified.

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