



Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

A comparative examination of recent changes in nutrients and lower food web structure in Lake Michigan and Lake Huron

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ARTICLE INFO

Article history:

Received 31 January 2018

Received in revised form 15 May 2018

Accepted 21 May 2018

Available online xxxx

Communicated by Elizabeth K. Hinchey

Keywords:

Phosphorus

Chlorophyll

Zooplankton

Diporeia

Lake Huron

Lake Michigan

ABSTRACT

The lower food webs of Lake Huron and Lake Michigan have experienced similar reductions in the spring phytoplankton bloom and summer populations of *Diporeia* and cladocerans since the early 2000s. At the same time phosphorus concentrations have decreased and water clarity and silica concentrations have increased. Key periods of change, identified by using a method based on sequential *t*-tests, were 2003–2005 (Huron) and 2004–2006 (Michigan). Estimated filtration capacity suggests that dreissenid grazing would have been insufficient to directly impact phytoplankton in the deeper waters of either lake by this time (mid 2000s). Despite some evidence of decreased chlorophyll:TP ratios, consistent with grazing limitation of phytoplankton, the main impact of dreissenids on the offshore waters was probably remote, e.g., through interception of nutrients by nearshore populations. A mass balance model indicates that decreased phosphorus loading could not account for observed in-lake phosphorus declines. However, model-inferred internal phosphorus dynamics were strongly correlated between the lakes, with periods of increased internal loading in the 1990s, and increased phosphorus loss starting in 2000 in Lake Michigan and 2003 in Lake Huron, prior to dreissenid expansion into deep water of both lakes. This suggests a limited role for deep populations of dreissenids in the initial phosphorus declines in the lakes, and also suggests a role for meteorological influence on phosphorus dynamics. The high synchrony in lower trophic level changes between Lake Michigan and Lake Huron suggests that both lakes should be considered when investigating underlying causal factors of these changes.

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Introduction

Lake Huron and Lake Michigan are arguably the two most similar of the five Laurentian Great Lakes. Connected by the 8 km wide Straits of Mackinac, through which water flows in either direction, albeit primarily east (Saylor and Sloss, 1976), and with the same surface elevation, hydrologically the two water bodies can be considered a single lake (Beeton and Saylor, 1995). Differences do exist between the two lakes; most notably, the human population of the Lake Michigan basin is several times that of Lake Huron, making the former more susceptible to anthropogenic influences, while the dilutive influence of inputs from Lake Superior to Lake Huron has contributed to lower concentrations of many dissolved constituents in the latter lake (Beeton, 1965; Hough, 1958). Consequently, Lake Michigan has historically been the more

productive of the two lakes, with higher chlorophyll *a* and primary productivity, and lower water clarity (Schelske and Roth, 1973). Several notable physical differences also exist between the two lakes, most importantly the greater residence time of Lake Michigan (62 years compared to 22 years; Quinn, 1992) and its greater average depth (85 m compared to 59 m).

The two lakes share largely congruent histories of biological invasions. Invasions and introductions of non-native fish have occurred in parallel in the two lakes, with the parasitic sea lamprey (*Petromyzon marinus*) becoming widespread in both lakes by the 1940s, and the non-native planktivore alewife (*Alosa pseudoharengus*) reaching substantial numbers slightly later (Berst and Spangler, 1972; Wells and McLain, 1972). Both species have had dramatic impacts on the food webs of the two lakes (Berst and Spangler, 1972; Wells and McLain, 1972). Similarly, invasions of non-native invertebrates have largely coincided in the two lakes. The predatory cladoceran *Bythotrephes longimanus* (hereafter *Bythotrephes*) established populations in both

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lakes in the mid 1980s (Bur et al., 1986; Evans, 1988), resulting in marked shifts in the crustacean zooplankton communities (Barbiero and Tuchman, 2004; Lehman and Cáceres, 1993). By 1990, zebra mussels (*Dreissena polymorpha*) had been found in both lakes (Griffiths et al., 1991), and the congeneric *Dreissena rostriformis bugensis*, or quagga mussel, was first found in the Straits of Mackinac region in 1997 and in the main bodies of both lakes by 2000 (Nalepa et al., 2001, 2007).

Since the 2000s, the food webs of both Lake Huron and Lake Michigan have experienced substantial changes at multiple trophic levels. Both lakes have undergone declines in spring total phosphorus (TP) concentrations (Barbiero et al., 2011a, 2012), dramatic reductions in the size of the spring phytoplankton bloom (Barbiero et al., 2011a; Fahnenstiel et al., 2010b), increases in water clarity (Barbiero et al., 2009b, 2011a; Vanderploeg et al., 2012), declines in the abundance of the benthic amphipod *Diporeia* (Barbiero et al., 2011b; Nalepa et al., 2007, 2009) and a biomass reduction and relative shift in summer crustacean communities away from cladocerans and cyclopoid copepods towards calanoid copepods (Barbiero et al., 2009a, 2009b, 2012; Vanderploeg et al., 2012).

In Lake Michigan, the changes in water quality, primary production and phytoplankton community structure, at least in the southern basin, have been largely ascribed to direct filtration impacts by dreissenid mussels (Fahnenstiel et al., 2010a; Kerfoot et al., 2010; Vanderploeg et al., 2010; Yousef et al., 2014; see, though, Warner and Lesht, 2015), due at least in part to the rapid expansion of *D. r. bugensis* into the profundal zone of that lake in the 2000s (Nalepa et al., 2010), a period during which the production declines were observed. While some of the changes seen in Lake Huron have been more pronounced than those in Lake Michigan, e.g., the near complete collapse of cladocerans in 2003 (Barbiero et al., 2009a), dreissenid expansion in Lake Huron has lagged substantially behind that in Lake Michigan (Nalepa et al., 2007, 2009), raising questions about the adequacy of dreissenid filtration as the main causal mechanism behind these changes (Barbiero et al., 2012; Bunnell et al., 2014).

Given the similarities in changes in so many lower trophic level variables in lakes Michigan and Huron within the past twenty years, we believe that a comparative examination of the magnitude and timing of these changes in the two lakes, particularly in the context of differences in dreissenid population development, can give additional insights into potential causal mechanisms. Up to now there have been few comparative assessments of recent ecosystem changes in the two lakes (see, though, Bunnell et al., 2014; Dove and Chapra, 2015; Warner and Lesht, 2015), primarily because research activities conducted by most institutions are generally limited to one lake, or indeed to geographically restricted portions of one lake. The US EPA's Great Lakes Water Quality Survey, on the other hand, generates comparable data from Lake Huron and Lake Michigan on a range of lower food web variables, thus permitting comparative studies.

In this study we make use of GLNPO's unique dataset to compare the magnitude and timing of changes in a suite of key lower trophic level variables from the open water of the two lakes. These include a suite of spring water quality variables as well as summer crustacean zooplankton composition and *Diporeia* abundances. We were specifically interested first in quantifying the degree of synchrony of lower trophic level changes between the two lakes, and in objectively determining the timing of those changes. We assess the possibility of bottom-up impacts on invertebrate populations through correlations with chlorophyll *a* and both crustacean zooplankton and *Diporeia*, and assess the possibility of more direct dreissenid impacts on *Diporeia* by comparing temporal and spatial distributions of the two species. To evaluate the potential impact of direct filtration by *Dreissena* on offshore phytoplankton, we compare *Dreissena* filtration rates and chlorophyll/TP ratios between the two lakes. Reductions in chlorophyll/TP ratios are indicative of control of phytoplankton by grazing, rather than nutrient limitation (Mazumder, 1994a, 1994b), and such reductions have been seen in nearshore areas of the Great Lakes in association with the establishment

of dreissenids (Nicholls et al., 1999). We distinguish here between direct filtration, i.e. direct removal of phytoplankton by dreissenid grazing, from other potential dreissenid impacts, such as remote interception and sequestration of nutrients. Finally, we utilize a mass balance model to assess the extent to which changes in phosphorus loading might have contributed to reductions in offshore phosphorus concentrations in the two lakes, and by extension, to what extent changes in internal processes, including phosphorus sequestration by dreissenids, might have impacted in-lake phosphorus concentrations.

Methods

Field sampling

Most of the data used for this study were drawn from the U.S. EPA's Great Lakes National Program Office (GLNPO) biannual off-shore monitoring program, which began sampling lakes Huron and Michigan in 1983. A total of 35 stations were initially visited in the main basins of the lakes for water column sampling, although from 1996 onward this was reduced to 25. Benthos sampling was initiated in 1997 and has been conducted at 19 stations, some of which coincide with plankton sampling sites. Further details on locations and characteristics of stations are available in Barbiero et al. (2018) and Lesht et al. (2018).

Sampling surveys were conducted during the spring isothermal period and summer stratified period. Spring surveys were conducted as early as possible after ice out (typically April) to provide estimates of initial growing season concentrations of nutrients, while summer surveys were conducted during the period of stable thermal stratification (generally August). From 1983 to 1991 multiple sampling runs were often undertaken for one or both of the seasonal surveys. While sometimes separated by several weeks, no consistent differences were found in the data generated by multiple runs (Rockwell et al., 1989), so data from all runs were included in annual survey averages.

At each water column station, samples for nutrients were taken at discrete depths throughout the water column with Niskin bottles mounted on a SeaBird Carousel Water Sampler. For the present study, station averages were calculated from all water column samples except the deepest sample to avoid contamination from sediments or the benthic nepheloid layer. Spring phytoplankton samples were composited from discrete samples taken from the surface, 5 m, 10 m and 20 m. Crustacean zooplankton were collected by vertical tows taken from depths of 100 m or 2 m from the bottom, whichever was shallower, using a 0.5-m diameter, 153- μ m mesh conical net (D:L = 1:3) equipped with a calibrated Tsurumi-Seiki Co. (TSK) flow meter. Prior to 1997, zooplankton tows were taken to a depth of 20 m, which would miss a substantial portion of the zooplankton community. Only data from deeper tows collected during August surveys were used in this study, therefore our zooplankton time series begins in 1997. Triplicate samples for benthos density estimates were collected using a Ponar grab during August surveys from 1997 to 2015 except in 2004 when four replicates were taken. Secchi depth readings were taken at all stations visited between 1 h after sunrise and 1 h before sunset.

Analytical methods

Samples for soluble silica (Si) were filtered in the field through 0.45 μ m Sartorius filters and stored at 4 °C. Samples for total dissolved phosphorus (TDP) were filtered in the field through a 0.45 μ m membrane filter and along with samples for TP were preserved with H₂SO₄ for later analysis in the lab. TDP and TP were measured on a Lachat QuikChem AE autoanalyzer by the ascorbic acid method after acid persulfate digestion (APHA, 1985). Soluble Si was determined as SiO₂ by the molybdate method on a Lachat QuikChem AE autoanalyzer (APHA, 1985). Samples for particulate nutrients were collected from three representative 'master' stations (see Barbiero et al., 2018) in each of the two lakes. Samples for particulate organic carbon (POC) were filtered in the field onto 0.7-

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