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Patterns of long-term dynamics of aquatic communities and water quality parameters in the Great Lakes: Are they synchronized?

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ABSTRACT

Long time series data can provide insights into dynamics of large lakes. We use the USEPA-GLNPO biological monitoring dataset (phytoplankton, benthos, zooplankton and water quality), collected from 1996 through 2016, to identify whether there is evidence of concordant linear or non-linear trends in community composition, density/biomass/biovolume and major environmental parameters. We show changes in biotic assemblages and water quality variables, particularly in Lakes Michigan and Huron. These include changes in phytoplankton biovolume and zooplankton biomass, increasing invasive *Dreissena* abundance and decreasing densities of other benthos. Biotic changes are accompanied by pronounced changes in water quality and nutrient ratios. Species change-points, identified using threshold indicator taxon analysis, are often less abrupt, but there are clear shifts in a large proportion of species in each assemblage. The concordance of breakpoints among assemblages or lack thereof provides valuable insight into potential drivers of ecosystem change.

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Introduction

The Laurentian Great Lakes are changing rapidly due to multiple anthropogenic factors (Mills et al., 2003; Reavie and Allinger, 2011; Shaw Chraïbi et al., 2011; Bunnell et al., 2014; Madenjian et al., 2015), many of which are intertwined and interact directly or indirectly. Among the >50 anthropogenic stressors affecting the Great Lakes (GL), invasive zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*, hereafter we refer to both species as *Dreissena*) and climate change ranked as the highest-impact stressors based on surveys of expert opinion (Smith et al., 2015). Both *Dreissena* species were first found in Lake Erie: zebra mussels in 1986 (Carlton, 2008) and quagga mussels in 1989 (Mills et al., 1993). In four years after the initial discovery, zebra mussels spread across all Great Lakes (except Lake Superior), where they quickly colonized all available substrates in shallow (usually <30 m) areas. It took twice as long for quagga mussels to spread from Lake Erie into lakes Ontario (1991), Michigan, and Huron (both 1997) than for zebra mussels (Table 1), but by late 1990s – mid 2000s, quagga mussels dominated in most of the Great Lakes (Patterson et al., 2005; Watkins et al., 2007; Nalepa et al., 2007, 2010; Karatayev et al., 2014). Other invasive species such as alewife (*Alosa*

pseudoharengus) and spiny water flea (*Bythotrephes longimanus*) have also left their mark on the pelagic Great Lakes (reviewed in Barbiero et al., 2018a, this issue; Bunnell et al., 2014). Concurrently with the spread of invasive species, other stressors such as nutrient loading (and abatement) and warming/ice period changes (e.g. Mason et al., 2016) are also thought to have affected the biota (e.g. Reavie et al., 2017).

Long-term sampling provides a unique opportunity to observe community and ecosystem changes in these large lakes, where experimental manipulation is not possible. One of the longest-running Great Lakes monitoring programs is administered by the U.S. Environmental Protection Agency (US EPA) Great Lakes National Program Office (GLNPO). GLNPO's mission is to 'restore and maintain the chemical, physical and biological integrity of the Great Lakes Basin Ecosystem' in accordance with the Great Lakes Water Quality Agreement. This program includes monitoring of environmental parameters and biotic assemblages of the GL across a set of annually sampled pelagic stations, which has generated decades of high-resolution biotic and abiotic data (Barbiero et al., 2018a, this issue). Based on these data, previous studies reported on significant changes in biotic assemblages, including phytoplankton (Reavie et al., 2014), benthic invertebrates (Burlakova et al., this issue), and zooplankton (Barbiero et al., 2012) across the GL basin. Although these assemblages and the abiotic variables are well-known to be related, it is not straightforward to predict whether changes in some could cause

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Table 1
Years of the first report of invasion and lake-wide population maximum (observed so far) of *Dreissena polymorpha* and *D. r. bugensis* in Great Lakes and years of *Dreissena* spp. lake-wide studies.

Lake	<i>D. polymorpha</i>		<i>D. r. bugensis</i>		<i>D. polymorpha</i> outcompeted by <i>D. r. bugensis</i>
	First record	Year with maximum density	First record	Year with maximum density	
Erie	1986 (Carlton, 2008)	1990 (Dermott et al., 1993; Fitzsimons et al., 1995)	1989 (Mills et al., 1993)	1998 (Patterson et al., 2005; Karatayev et al., 2014)	1998 (Patterson et al., 2005; Karatayev et al., 2014)
Ontario	1989 (Griffiths et al., 1991)	1995 (Watkins et al., 2007)	1991 (Griffiths et al., 1991)	2003 (Watkins et al., 2007)	1998 (Watkins et al., 2007)
Michigan	1989 (Nalepa et al., 2010)	2000 (Nalepa et al., 2014)	1997 (Nalepa et al., 2001)	2010 (Nalepa et al., 2014)	2005 (Nalepa et al., 2014)
Huron, Main basin	1990 (Nalepa et al., 1995)	2000 (Nalepa et al., 2007)	1997 (Nalepa et al., 2001)	2012 (Nalepa unpublished)	2003 (Nalepa et al., 2007)

concurrent shifts in others on the scale of the entire basin. Some of the biotic trends could be caused, or mediated, by water quality changes. Other water quality parameters, particularly nutrient ratios, are likely to be at least partially driven by the biota (e.g. Ozersky et al., 2015). Even though cause-effect mechanisms may be unclear, or driven by hierarchically superior forcing factors, it is enlightening to examine such patterns from a multi-assemblage perspective, which has rarely been applied across all five of the Laurentian Great Lakes simultaneously (but see Bunnell et al., 2014).

We set out to look for signs of concordance among temporal patterns of multiple Great Lakes biotic assemblages using taxonomically-detailed time series. We identify whether there is evidence for linear or non-linear temporal trends in phytoplankton, benthos, and zooplankton based on multi-year GLNPO station data, with particular focus on within-lake concordance of community change-points. Furthermore, we determine the degree to which temporal trends are associated with major water quality (WQ) variables using machine learning approaches. Presence of multi-assemblage breakpoints in the offshore areas of the Great Lakes may indicate changing ecosystem responses to anthropogenic impacts, which may lead in turn to unexpected outcomes for societally and economically important endpoints, such as key fishery species.

Materials and methods

GLNPO datasets

We use phytoplankton count data from 2001 to 2014 collected as part of the US EPA Great Lakes Biology and Water Quality Monitoring Programs (SOP LG401, 2010; <https://www.epa.gov/great-lakes-monitoring>). These data are collected during spring and summer at 72 stations throughout the Great Lakes (see map in Barbiero et al., 2018a, *this issue*) and have been previously used to diagnose long-term phytoplankton trends (Reavie et al., 2014). Briefly, from each station equal volumes of water were collected by a rosette sampler from multiple depths representing the isothermal water column (spring) or the epilimnion (summer) (Reavie et al., 2014). Four equal-volume samples (isothermal: 0, 5, 10, 20 m; summer: 0, 5, 10 m, and lower epilimnion) were composited and preserved with Lugol's iodine solution. Soft-bodied algal analyses were performed using the Utermöhl (1958) method and subsamples were processed for detailed diatom assessment by acid digestion, slide mounting and high-resolution microscopy. Algae were identified to the lowest possible taxonomic level. Algal specimens were also measured to allow for biovolume calculations (Reavie et al., 2010). All of these methods followed standard GLNPO phytoplankton techniques (SOP LG401, 2010; Reavie et al., 2014).

Crustacean zooplankton were collected by vertical tows taken from depths of 100 m, or 2 m from the bottom if station depth was <100 m, using a 0.5-m diameter, 153- μ m mesh conical net (D:L = 1–3) equipped with a calibrated Tsurumi-Seiki flow meter, at the same time and stations as the phytoplankton data. Samples were identified to the smallest practical taxonomic unit (in most cases species) and up to 20 individuals in each group were measured. Biomass was calculated from group-specific length-weight regressions, and reported as units of

μ g dry weight/ m^3 (a single set of length-weight coefficients were used to generate the entire time series). Juveniles and adults were merged by species when possible. When juvenile identification was only possible to genus level, that juvenile densities were apportioned to species following the relative proportion of adults that were identified to species. This study used zooplankton data available in September 2017: 1997–2016 for summer, 1998–2016 for spring in lakes Ontario, Michigan and Erie and 1998–2014 for spring in lakes Huron and Superior. Detailed methods and length weight regressions used are described in standard operating procedures (SOP LG403, 2017).

Benthos samples were collected using Ponar grabs (sampling area 0.0523 m^2) at permanent GLNPO benthic sampling stations in August of each year, starting in 1997 (SOP LG406, 2016). We used benthic data from 1998 to 2015, as the taxonomic resolution in the first year of monitoring (1997) was inconsistent with that used in subsequent years. There were 39 stations in 1998 and 1999 and 58 stations beginning in 2000. Samples were washed through a 500 μ m mesh sieve and preserved with neutral buffered formaldehyde with Rose Bengal stain to a final concentration of 5–10%. Triplicate samples were collected at each station, and organism densities were averaged for analyses. Organisms were picked out of samples under low magnification using a dissecting microscope. *Dreissena* were counted in samples beginning in 2003. Oligochaetes and chironomids were identified under a compound microscope to species and genus, respectively, whereas other organisms were identified under a dissecting microscope to species, when possible. Identification details and keys are listed in Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis (SOP LG407, 2015) and Burlakova et al. (*this issue*). Data were reported as average densities/ m^2 .

Water quality data collected from spring and summer cruises in 1996–2013 were analyzed in this study. Predictors analyzed here included chloride, nitrate + nitrite (NO_x), silica (Si), total dissolved phosphorus (TDP), total phosphorus (TP), TP/TDP ratio, pH, N/P (nitrogen/phosphorus, calculated as the ratio of NO_x to TP), and N/Si ratio; all ratios were mass-based. Detailed description of protocols is available in standard operating procedures (QAPP, 2017; SOP LG200, 2017). Remote-sensed data based on SeaWiFS (1998–2007) and MODIS (2008–2016) were used for estimating surface chlorophyll concentrations (see Lesht et al., 2013; Barbiero et al., 2018b, *this issue*, for details). Briefly, chlorophyll estimates were extracted from 5 pixel by 5 pixel (roughly 5 km \times 5 km) boxes centered on each of the stations and the average of the individual pixel values was used to represent the concentration at each station. Only values obtained from boxes with a majority (>12) of cloud-free pixels were used. For zooplankton analyses, we used an average of monthly averages (based on daily values) from April through July of each year, whereas for benthos, we used pre-stratification averages of March through April.

Statistical analyses

To determine whether there is evidence for linear or non-linear temporal trends in phytoplankton, benthos, and zooplankton and whether there are community change-points, we performed lake-specific analyses as: linear/non-linear individual temporal trends in composite

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