



Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: [www.elsevier.com/locate/jglr](http://www.elsevier.com/locate/jglr)

## The benthic community of the Laurentian Great Lakes: Analysis of spatial gradients and temporal trends from 1998 to 2014

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### ARTICLE INFO

#### Article history:

Received 13 July 2017

14 March 2018

Accepted 9 April 2018

Available online xxx

Communicated by Lars Rudstam

#### Keywords:

Benthic invertebrates

Biomonitoring

Great Lakes

Exotic species

Community analysis

### ABSTRACT

We used the results of seventeen years of Great Lakes benthic monitoring conducted by the U.S. EPA's Great Lakes National Program Office to describe the spatial and temporal patterns of benthic communities, assess their status, trends, and main drivers, and to infer the potential impact of these community changes on ecosystem functioning. Benthic abundance and diversity were higher at shallow (<70 m in depth) stations with chlorophyll concentrations above 3 µg/L than at deeper sites (<1 µg/L). We infer that lake productivity, measured by chlorophyll was likely the major driver of benthic abundance and diversity across lakes. Consequently, benthic diversity and abundance were the highest in the most productive Lake Erie, followed by lakes Ontario, Michigan, Huron, and Superior. Multivariate analysis distinguished three major communities shared among lakes (littoral, sublittoral, and profundal) that differed in species composition and abundance, functional group diversity, and tolerance to organic pollution. Analysis of temporal trends revealed that the largest changes occurred in profundal communities, apparent in significant shifts in dominant taxa across all lakes except Lake Superior. In lakes Michigan, Huron, and Ontario, the former dominant *Diporeia* was replaced with *Dreissena* and *Oligochaeta*. Profundal species, with the exception of dreissenids, became less abundant, and their depth distribution has shifted. In contrast, density and diversity of native littoral and sublittoral communities increased. The invasion of dreissenids was among the most important drivers of changes in benthic communities. Continued monitoring is critical for tracking unprecedented changes occurring in the Great Lakes ecosystem.

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### Introduction

Observation of trends or spatial patterns in long-term ecosystem data can reveal emerging environmental problems and advance environmental science in new directions (Lovett et al., 2007). The ability to adequately assess ecosystem changes however is often hindered because studies are conducted over relatively short time periods and over small spatial scales (Magnuson, 1990). Monitoring ecosystem trends over time can help distinguish between natural variability in the ecosystem versus long-term changes, including those occurring due to human activity, and can help to adaptively manage the ecosystems, providing crucial information for environmental policy (Lovett et al., 2007).

Although limnology has traditionally focused on processes occurring in the pelagic zone, lake benthic habitats can be a major contributor to whole-lake productivity (Vadeboncoeur et al., 2002, 2011) and

biodiversity (Hutchinson, 1993). Benthic organisms provide important ecosystem services including bioturbation of sediment, nutrient cycling and channeling of energy to higher trophic levels (Covich et al., 1999; Vander Zanden and Vadeboncoeur, 2002). Zoobenthic species are sensitive to ecological and environmental change because they live longer than most planktonic organisms, and thus can integrate the effects of environmental conditions over longer periods of time, and can be more sensitive to environmental changes than the pelagic community (Karatayev et al., 2013). Benthic invertebrates live associated with bottom sediments where most of the organic and pollution load ultimately deposits (Rosenberg et al., 2004), integrating water and sediment qualities. Many benthic invertebrates are detritivores, feeding on organic material produced in the pelagic zone. Benthic organisms are often important components of fish diets, and thus provide an important link between pelagic production and higher trophic levels. Finally, benthic organisms are relatively sedentary and are therefore easier to sample than nektonic organisms, such as fish. As a result, benthic invertebrate community assessment has long been a tool of choice in both

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<https://doi.org/10.1016/j.jglr.2018.04.008>

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classifying and monitoring the impacts of anthropogenic stress in aquatic systems (Hilsenhoff, 1988; Howmiller and Scott, 1977; Milbrink, 1973; Resh et al., 1995).

The Laurentian Great Lakes, located on the Canada–United States border, form the largest group of inland water bodies in North America. Anthropogenic alteration of the watershed and the lakes began >200 years ago with watershed deforestation and pollution, wetland dewatering, overfishing, and culminated in strong eutrophication of Lake Erie in mid-1900s when Lake Erie was called “America’s Dead Sea” (Beeton, 1965; Sweeney, 1995). Under the Great Lakes Water Quality Agreement (GLWQA) of 1972 signed by Canada and the United States, a binational effort was undertaken to restore and maintain the chemical, physical and biological integrity of the Great Lakes. As a result, one of the world’s largest freshwater ecosystem monitoring programs (in geographic scale) was initiated.

The U.S. EPA Great Lakes National Program Office (GLNPO) Biology Monitoring Program assesses the long-term status and trends of the lower food web in the open waters of the Great Lakes. The Program’s annual monitoring of the Great Lakes began in 1983 for lakes Michigan, Huron, and Erie, in 1986 for Ontario, and in 1992 for Superior and was initially focused on chemical eutrophication and whole lake response to changes in phosphorous loadings (Barbiero et al., *this issue*). The lower trophic level monitoring included collection of phytoplankton, zooplankton, and chlorophyll *a*. Recognizing the importance of the benthic community in the evaluation and management of the Great Lakes, GLNPO added a benthic invertebrate monitoring program in 1997. A unique aspect of GLNPO’s benthic monitoring program is the extent of coverage, which includes all five lakes and collects data from 58 permanent stations on an annual basis.

The main goals of this paper are to use the results of seventeen years of the GLNPO benthic monitoring program to: 1) provide a general description of benthic communities of all five Great Lakes; 2) identify spatial and temporal patterns of distribution of these communities; 3) identify the potential environmental factors controlling the species makeup of these communities, 4) provide an assessment of status and

trends in the benthic community over the last two decades, and to infer the potential impact of these changes on the functioning of Great Lakes ecosystems.

## Methods

U.S. EPA GLNPO’s sampling of the benthos was initiated in 1997 at 39 stations, with coverage gradually increasing to a total of 58 fixed summer survey benthos sampling stations in 2000 (Fig. 1, Electronic Supplementary Material (ESM) Table S1). The summer survey typically spans the month of August of each year. Benthic samples are also collected during the GLNPO spring (April) survey at five stations (for the mayfly *Hexagenia* spp. only), but are not included in our study. Triplicate samples for benthic invertebrates were collected from each station using a Ponar grab (sampling area 0.0523 m<sup>2</sup>). Samples for invertebrates were washed through a 500 μm mesh sieve and preserved with neutral buffered formaldehyde with Rose Bengal stain to a final formalin concentration of 5–10%. Details are described in Standard Operating Procedure for Benthic Invertebrate Field Sampling (SOP LG406, Revision 11, June 2016).

Organisms were picked out of samples under low magnification using a dissecting microscope. *Dreissena* (*D. polymorpha* and *D. rostriformis bugensis*) were counted in samples beginning in 2003. Oligochaetes and chironomids were mounted on slides and identified under a compound microscope; other organisms were identified under a dissecting microscope. Adult oligochaetes were identified to species; immatures were taken to the lowest taxonomic level possible, usually family, and included in abundance estimates. Fragments, though counted, were excluded from all analyses. Chironomids were identified to the lowest practical taxonomic level, usually genus. Other invertebrates were identified to species, when possible. Sample sorting and taxonomical identification was carried out in 1997–2000 by Grace Analytical, Inc.; in 2001–2006 by the Lake Superior Research Institute, University of Wisconsin at Superior; in 2007–2011 by University of Michigan, and since 2012 by the Great Lakes Center at Buffalo State

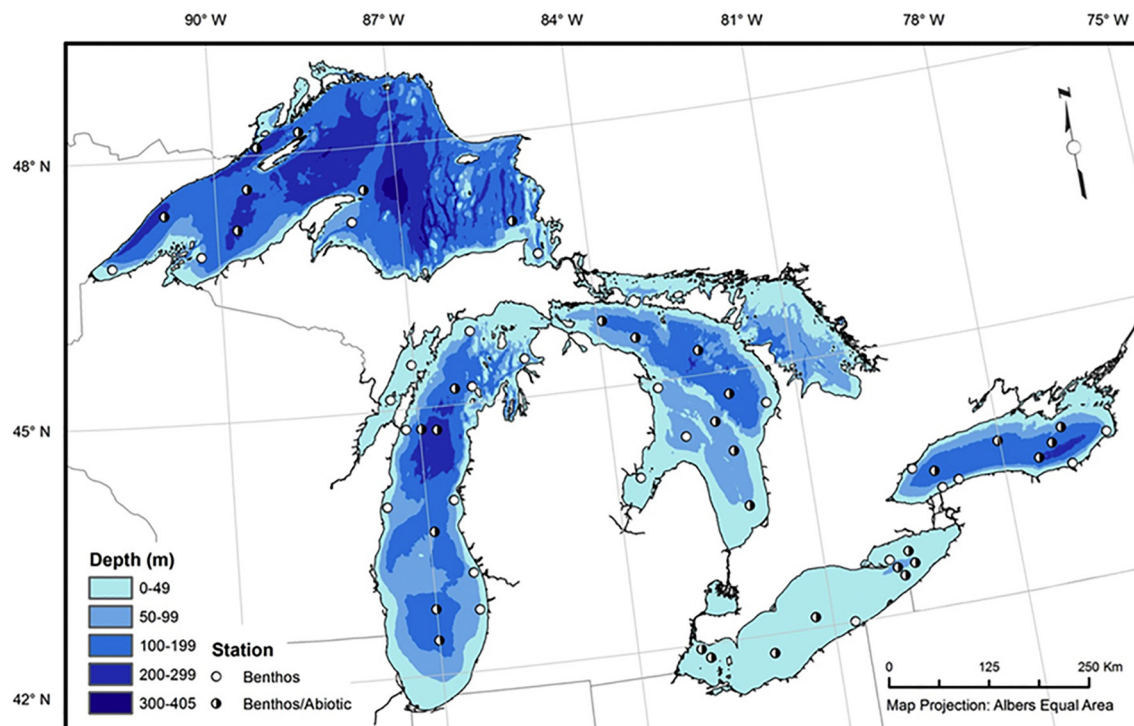


Fig. 1. Map of GLNPO permanent benthic sampling stations in the Great Lakes. Not all stations were sampled in all years. Stations where abiotic variables (chlorophyll *a* and water chemistry) were collected in addition to benthos are indicated.

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