EPA Public Access

Author manuscript

J Great Lakes Res. Author manuscript; available in PMC 2019 August 01.

About author manuscripts

Submit a manuscript

Published in final edited form as:

J Great Lakes Res. 2018 August ; 44(4): 639–649. doi:10.1016/j.jglr.2017.08.001.

Biomonitoring Using Invasive Species in a Large Lake: *Dreissena* Distribution Maps Hypoxic Zones

ALEXANDER Y. KARATAYEV^{1,*}, LYUBOV E. BURLAKOVA¹, KNUT MEHLER¹, SERGHEI A. BOCANIOV², PARIS D. COLLINGSWORTH³, GLENN WARREN⁴, RICHARD T. KRAUS⁵, and ELIZABETH K. HINCHEY⁴

¹Great Lakes Center, Buffalo State College, 1300 Elmwood Ave., Buffalo, NY 14222, USA. Phone: 716-878-4504, Fax: 716-878-6644, karataay@buffalostate.edu. burlakle@buffalostate.edu mehlerk@buffalostate.edu

²Graham Sustainability Institute, University of Michigan, Ann Arbor, 625 E Liberty St, MI 48103, USA. Phone: 734-763-2646, bocaniov@umich.edu, serghei.bocaniov@gmail.com

³Illinois–Indiana Sea Grant and Department of Forestry and Natural Resources, Purdue University, 195 Marsteller Street, West Lafayette, IN 47907, USA. Phone. 317-886-7449, pcolling@purdue.edu

⁴United States Environmental Protection Agency, Great Lakes National Program Office, Chicago, Illinois, USA. Phone: 312-886-3451, 312-886-2405, warren.glenn@epa.gov; hinchey.elizabeth@epa.gov

⁵Lake Erie Biological Station, Great Lakes Science Center, US Geological Survey, 6100 Columbus Avenue, Sandusky, OH 44870, USA. Phone: 419-625-1976, rkraus@usgs.gov

Abstract

Due to cultural eutrophication and global climate change, an exponential increase in the number and extent of hypoxic zones in marine and freshwater ecosystems has been observed in the last few decades. Hypoxia, or low dissolved oxygen (DO) concentrations, can produce strong negative ecological impacts and, therefore, is a management concern. We measured biomass and densities of *Dreissena* in Lake Erie, as well as bottom DO in 2014 using 19 high frequency data loggers distributed throughout the central basin to validate a three-dimensional hydrodynamic-ecological lake model. We found that a deep, offshore hypoxic zone was formed by early August, restricting the *Dreissena* population to shallow areas of the central basin. Deeper than 20 m, where bottom hypoxia routinely develops, only young of the year mussels were found in small numbers, indicating restricted recruitment and survival of young *Dreissena*. We suggest that monitoring *Dreissena* distribution can be an effective tool for mapping the extent and frequency of hypoxia in freshwater. In addition, our results suggest that an anticipated decrease in the spatial extent of hypoxia resulting from nutrient management has the potential to increase the spatial extent of profundal habitat in the central basin available for *Dreissena* expansion.

*Corresponding author.

Keywords

ELCOM-CAEDYM; mapping hypoxia; Dreissena rostriformis bugensis; Lake Erie; oxygen dynamics

Introduction

Hypoxia (bottom oxygen concentration $< 2 \text{ mg L}^{-1}$) and anoxia (bottom oxygen concentration $< 1 \text{ mg L}^{-1}$) are the manifestations of combined effects of two major processes, decomposition of elevated autochthonous and/or allochthonous production, and increased water column stability, and are commonly linked to cultural eutrophication and global climate change (Diaz, 2001; Diaz and Rosenberg, 2008; Scavia et al., 2014; Altieri and Gedan, 2015). Over the past few decades there has been an exponential increase in the number and areal extent of hypoxic zones observed in freshwater, marine, and coastal ecosystems that has resulted in strong negative impacts on aquatic communities including fish and benthic and planktonic invertebrates (Diaz and Rosenberg, 2008; Stramma et al., 2008; Turner et al., 2008; Vaquer-Sunyer and Duarte, 2008).

Many government efforts worldwide, including recently established U.S. and Canadian binational targets for reducing nutrient inputs to the Laurentian Great Lakes (GLWQA, 2012), are focused on the development of nutrient abatement strategies to reduce external nutrient loads to control eutrophication and hypoxia (Mississippi River Gulf of Mexico Watershed Nutrient Task Force 2008; Backer et al., 2010; GLWQA, 2012; Chesapeake Bay Watershed Agreement, 2014). Key to tracking success of these efforts will be the ability to monitor the ecosystem response to reduced nutrient loads, which includes monitoring the extent of Great Lakes hypoxic zones. Hypoxia is a widespread phenomenon in the Great Lakes that occurs seasonally in the bottom layer (hypolimnion) of some productive basins and embayments in Lakes Michigan (e.g. Green Bay), Ontario (e.g. Hamilton Harbor) and in Lake Erie (central basin) (Dermott et al., 2007; Scavia et al., 2014; Hamidi et al., 2015). These zones are dynamic in time and space, and are affected by physical processes including mesoscale meteorological forcing events (Bocaniov and Scavia, 2016). The hypoxic zone can extend into nearshore zones during upwelling events, shrink or even disappear during severe storms, and then become re-established later, making the spatial and temporal extent of hypoxia difficult to quantify via hypoxia monitoring surveys currently conducted every three weeks by U.S. Environmental Protection Agency Great Lakes National Program Office (U.S. EPA GLNPO). Alternatively, the deployment of stationary oxygen loggers may increase our temporal coverage but misrepresent the spatial extent of the basin-wide hypoxic zone and hypolimnion thickness. Therefore, resource managers need alternative methods of monitoring that are able to provide more sensitive and time-integrated measures of hypoxia, especially its spatial extent. One such time-integrated method to monitor low-oxygen events is biological monitoring. This method is based on the assumption that changes in water quality are accompanied by the changes in certain species sensitive to the environmental condition of interest (e.g. dissolved oxygen concentration) (Merritt et al., 2008; Wiederholm, 1980). Benthic organisms, especially sessile species that live more than one year, are most vulnerable to hypoxia, thus the presence of robust benthic communities containing sensitive

species indicates normal oxygen conditions and can be used to monitor progress toward ecosystem restoration (Mandaville, 2002; Merritt et al., 2008). In the Laurentian Great Lakes, benthic communities are dominated by invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels (Watkins et al., 2007; Nalepa et al., 2010; Karatayev et al., 2014). Both dreissenid species are known to be sensitive to low oxygen (reviewed in McMahon and Bogan, 2001; Karatayev et al., 2007) and have a long life span, usually > 3 years (reviewed in Karatayev et al., 2006), which suggests that their presence can be used to assess past habitat conditions that were unfavorable for their survival. Here, we investigated interactions between hypoxia and invasive mussels at a system-wide scale in Lake Erie where hypoxia is a key issue for water resource management.

In Lake Erie, bottom hypoxia regularly occurs in the central basin (Vanderploeg et al., 2009; Kraus et al., 2015; Bocaniov and Scavia, 2016) and occasionally in the western basin (Ackerman et al., 2001; Bridgeman et al., 2006). The central basin has always experienced seasonal hypoxic conditions (Beeton, 1961; Delorme, 1982), but the extent of hypoxia substantially increased during the cultural eutrophication of the 1950s - 1960s. After the implementation of phosphorus reduction programs in the 1970s the extent of the hypoxic zone shrank (Makarewicz and Bertram, 1991; Bertram, 1993), but it then rebounded in the late 1990s and 2000s to previously reported levels (Scavia et al., 2014), driven by increases in dissolved reactive phosphorus (Richards et al., 2010; Scavia et al., 2014) and climate change (Michalak et al., 2013). As a result, a large portion (up to 10,000 km²) of the central basin now becomes severely hypoxic during August and September and remains hypoxic until fall overturn (Vanderploeg et al., 2009; Kraus et al., 2015; Bocaniov and Scavia, 2016).

The return of severe hypoxia in the central basin of Lake Erie has had strong impacts on the spatial distribution and migration of a number of aquatic organisms including fish, zooplankton, and phytoplankton communities (Vanderploeg et al., 2009; Scavia et al., 2014; Kraus et al., 2015). Less information is available on the effect of hypoxia on benthos in the central basin, although evidence suggests hypoxia limits the distribution of *Dreissena*, especially in deep stratified areas (Patterson et al., 2005; Karatayev et al., 2014). However, it is unknown to what degree the populations of *Dreissena* spp. in a large lake can be affected by hypolimnetic hypoxia and to what extent mussel distribution reflects the spatial extent of the hypoxic zone.

In contrast to the deeper central basin, the shallow western basin rarely stratifies and historically (before 1960s) was not hypoxic, as it supported extremely large populations of mayflies *Hexagenia*, which are intolerant to low oxygen (Shelford and Boesel, 1942; Britt, 1955). Similarly to the central basin, cultural eutrophication resulted in significant large-scale depletion of dissolved oxygen in the western basin, causing a reduction of *Hexagenia* almost to the point of extirpation in the 1960s (Beeton, 1961; Carr and Hiltunen, 1965). Water quality improvements by the mid-1980s, coupled with the introduction of dreissenids in the basin, temporarily halted eutrophication (Makarewicz and Bertram, 1991; Leach, 1993) and subsequently brought about the restoration of *Hexagenia* to pre-extirpation levels by 1999 (Schloesser et al., 2000). Since the reappearance of eutrophication, however, *Hexagenia* have suffered occasional recruitment failures, most likely due to episodes of

severe oxygen depletion following temporary thermal stratification (Ackerman et al., 2001; Bridgeman et al., 2006).

Regular extended periods of hypoxia in the central basin and occasional episodes of hypoxic conditions in the western basin should have a strong impact on *Dreissena* spp. population dynamics, making these species useful indicators of the near bottom hypoxic conditions. We hypothesized that: 1) mussel density will be lowest at sites with more frequent hypoxia, reflecting impaired recruitment and higher mortality; and 2) mussels in areas with hypoxia will be smaller, reflecting a younger local population comprised only of recent recruits. To test these hypotheses and the ability of using *Dreissena* spp. abundance to map hypoxic zone extent we 1) measured bottom dissolved oxygen using data loggers distributed throughout the central basin to validate a three-dimensional hydrodynamic-ecological model simulating dissolved oxygen distribution, 2) carried out a lake-wide survey of *Dreissena* spp. in Lake Erie in 2014; 3) used a three-dimensional coupled hydrodynamic-ecological lake model calibrated and validated for Lake Erie in previous applications to simulate the spatial extent of hypoxia and the amount of days with hypoxia at each site sampled during 2014 survey, and 4) compared predicted values with the spatial distribution, abundance and size structure of *Dreissena*.

Materials and methods

Study Area and Hypoxia Description

Lake Erie is divided into three basins: the shallow western basin (average depth 7.4 m), the intermediate central basin (18.3 m), and the deepest eastern basin (average depth 24.4 m) (Bolsenga and Herdendorf, 1993) (Fig. 1a). The western basin is the most productive and turbid due to large inputs of nutrients and suspended sediments (Mortimer, 1987; Barbiero and Tuchman, 2004). Although the western basin stratifies only intermittently during the summer, it may periodically experience short-term episodes of severe hypoxia (Ackerman et al., 2001; Bridgeman et al., 2006). In contrast to the central basin, which requires several months to become hypoxic, the near bottom water in the western basin may rapidly become hypoxic following periods of calm weather and development of brief episodes of stable temporal stratification (Bridgeman et al., 2006). Though these hypoxic events are short-lived and the basin will turn-over, re-oxygenating the bottom layer during the next wind event. The central basin is deeper and has a large offshore area that typically stratifies during the summer. The basin receives nutrients and sediments from the western basin and is susceptible to sediment resuspension and seasonal hypoxia (Delorme, 1982; Mortimer, 1987; Scavia et al., 2014; Bocaniov and Scavia, 2016; Bocaniov et al., 2016). Finally, the eastern basin is the least eutrophic, develops stable stratification during summer with a large thick hypolimnion that never goes hypoxic, and has the lowest inputs of suspended solids and nutrients (Kemp et al., 1977; Mortimer, 1987).

Dreissena sampling protocol

As part of the Lake Erie Cooperative Science and Monitoring Initiative field year (CSMI, Richardson et al., 2012), the distribution, density, wet biomass, and length-frequency distribution of *Dreissena* spp. were measured in Lake Erie at 107 sites (Fig. 1b). Offshore

sites were sampled aboard the U.S. EPA R/V *Lake Guardian* using a regular PONAR grab sampler (sampling area 0.052 m²), while nearshore sites (<10 m depth) were sampled aboard Buffalo State R/V *John J. Freidoff* using a petite PONAR grab sampler (sampling area 0.023 m²). Sites were stratified based on depth zones and lake basins. Samples from rock/bedrock at 5 and 10 m depths in the eastern basin were collected by SCUBA divers (0.25 m² quadrat). A total of 294 PONAR and 27 quadrat samples were collected in July and August of 2014.

Dreissena mussels from all samples were identified to species, measured to the nearest mm with a caliper, counted, and the whole sample was weighed to the nearest 0.01 g after being blotted dry on absorbent paper (total wet weight, tissue with shell). If the sample was too large to process, it was split into n equal parts, one part was randomly selected for analysis and mussel density and weight from this part was adjusted (multiplied by n) to obtain sample totals.

Field measurements of dissolved oxygen in 2014

We measured bottom dissolved oxygen using an array of data loggers distributed throughout the central basin of Lake Erie (Fig. 1a). At each site in the array, we deployed HOBO data loggers (model U26) equipped with optical oxygen sensors that were moored approximately 0.5 m from the bottom. Data loggers were calibrated prior to deployment using a 2 point calibration. In 2014, the logger array was deployed from June 25 through October 8, a period shortly after the beginning of the lake overturn, and during this time temperature and dissolved oxygen were measured at 10 minute intervals.

Hydrodynamic and Ecological model to simulate oxygen dynamics

We used a three-dimensional (3D) hydrodynamic-ecological model of Lake Erie (ELCOM-CAEDYM) consisting of two coupled models, the 3D hydrodynamic Estuary and Lake Computer Model (ELCOM; Hodges et al., 2000), and the ecological Computational Aquatic Ecosystem Dynamics Model (CAEDYM; Hipsey and Hamilton, 2008). ELCOM simulates the velocity, transport, mixing, temperature, and salinity distribution in stratified aquatic ecosystems subjected to external environmental forcing such as inflows and outflows, wind stress, surface heating and cooling. Through coupling with CAEDYM, ELCOM simulates the 3D transport and interactions among physical, chemical, and biological processes. CAEDYM can simulate dissolved oxygen (DO), suspended sediments, particulate and dissolved organic matter, organic and inorganic nutrients and their fractions, and multiple phytoplankton and zooplankton groups. This version of ELCOM-CAEDYM (or ELCD) was calibrated and validated through several previous applications to Lake Erie, including predictions of thermal structure, DO, nutrients, phytoplankton biomass, as well as ice cover and thickness (Bocaniov et al., 2014a; Liu et al., 2014; Oveisy et al., 2014; Bocaniov and Scavia, 2016). Because of the relatively long life span of *Dreissena* (> 3 years, reviewed in Karatayev et al., 2006), settlement of their young-of-the-year during summer, and development of hypoxia in the central basin by the end of the growing season, mussel distribution and size structure in July 2014 was determined by the dissolved oxygen dynamics in 2012–2013 and recruitment in the current year. Therefore, we applied ELCD to simulate the oxygen dynamics for the year with high temporal and spatial resolution of the

bottom DO observations and in which mussels were collected (2014) as well as two preceding years, 2012 and 2013. The simulated spatial and temporal DO dynamics for 2012 and 2013 were used to explain mussel biomass and densities observed in 2014, as functions of the model-predicted number of hypoxic days for each location of the 2014 sampling stations at various DO thresholds (1, 2 and 3 mg L⁻¹).

The applied in this study model of ELCOM-CAEDYM was previously calibrated for 2002 (Leon et al., 2011; Bocaniov et al., 2014a) and then validated with the data from 2008 (Liu et al., 2014; Bocaniov and Scavia, 2016; Bocaniov et al., 2016). The current work builds on the previous work and provides a further validation of the capability of the model to predict water temperatures and dissolved oxygen concentrations for an additional year, 2014, without any recalibration. Model configuration was similar to its previous applications (e. g. Bocaniov et al., 2014a; Liu et al., 2014) but with a larger number of tributaries (19 vs. 11) and meteorological forcing zones (13 vs. 3) as in Bocaniov and Scavia (2016) and Bocaniov et al. (2016). The bathymetric data for Lake Erie used in this study was obtained from the NOAA Geophysical Data Center. The model domain was represented by 2 × 2 km horizontal cells with 45 unevenly spaced vertical layers with different thicknesses varying from 0.5 to 1 m in west and central basins, and from 0.5 to 5 m in the east basin. The vertical resolution of the computational model domain in the metalimnion and hypolimnion was 0.5 m in the central basin. Overall, the computational domain was represented by 755,595 cells (193 × 87 × 45) but only about 20% (147,061) were used in actual computations. The 3D model employed in this study is able to predict and output the water quality variables, including temperatures and dissolved oxygen, for each water cell of the computational domain at the user-specified format. The latter represents a set of points (cells) at which the output data (e.g. dissolved oxygen, water temperature, etc.) are required. In this study we specified the model output in two major formats, as vertical columns of points (profiles) at the locations of the 10 EPA GLNPO stations in the central basin (Fig. 1a) and a two dimensional surface consisting of water cells at a specified distance/height above the bottom (bottom sheet). The simulated data for both profiles and bottom sheets were outputted at the intervals of one hour for the entire simulation period. We used data from the simulated vertical profiles for model validation purposes to compare the simulated results against the measured DO and water temperature data, while the data from the bottom sheet of the DO concentrations were used to estimate the basin-wide spatial extent of hypoxia and its duration as well as to calculate the total duration of hypoxic conditions for different DO thresholds at the location of each station sampled for mussel densities and biomass in 2014. Model runs were 191 days (2012, 2014) and 211 days (2013). In-lake conditions were obtained from the observations of water quality parameters at twenty U.S. EPA GLNPO long-term water quality monitoring program stations (Fig. 1a) during the spring cruises in the modeled years. Boundary conditions included nineteen tributary inflows and one outflow, the Niagara River, which included the daily discharge through the Welland Canal. Daily flow rates, water temperatures and concentrations of water quality parameters were gathered from a variety of data sources (e.g. Bocaniov et al., 2014a, 2016; Bocaniov and Scavia, 2016). The meteorological forcing was represented by 13 approximately equal-sized zones and based on hourly observations of wind speed and direction, air temperature, relative humidity, cloud cover and solar radiation (shortwave) at 21 coastal and 3 in-lake

weather stations. All observed data from the land based meteorological stations were corrected for the over-lake conditions using empirical relationships developed for Lake Erie (Schwab and Morton, 1984; Schertzer et al., 1987), which were extrapolated to 13 meteorological forcing zones following Sambridge et al. (1995).

To estimate the ELCD model performance we used a combination of graphical and statistical techniques. We used visual comparisons, model evaluation statistical tests (e.g. independent two-sample *t*-test) and measures of model performance such as Root Mean Square Error (RMSE). To compare mussel densities between three basins and depth zones within basin we used Kruskal-Wallis ANOVA by Ranks. To compare the average length of mussels within and among basins and depth zones, we used a Generalized Linear Model with subsequent post-hoc unequal-*n* Tukey's Honestly Significant Difference (HSD) tests. To find relationships between log-transformed ($\log_{10}(x+1)$) mussel density and biomass recorded in 2014 and hypoxic duration of different DO thresholds ($< 1, 2$ and 3 mg L^{-1}) for 2012 and 2013 we used linear regressions. These analyses were done using STATISTICA software (*STATISTICA* for Windows version 12, StatSoft, Inc. 1984–2014). Effects were considered statistically significant at $P < 0.05$.

Results

2014 *Dreissena* spp. distribution

Dreissena distribution varied dramatically among lake basins. While in the western and eastern basins mussels were found on almost all sites sampled, large portion of the central basin was free of adult *Dreissena* (Fig. 2). Average *Dreissena* spp. densities and biomass were also different among basins (density: $P < 0.001$; biomass: $P < 0.001$, Kruskal-Wallis ANOVA by Ranks; Table 1). Maximum average basin wide density of *Dreissena* was found in the western basin followed by the eastern basin. However, *Dreissena* biomass was by far the highest in the eastern basin. While in the western basin dreissenid density and biomass were distributed fairly equally among two depth zones (density: $P = 0.84$; biomass: $P = 0.54$), in the central and eastern basins these parameters differed significantly among depth zones (central basin density: $P < 0.001$, biomass: $P < 0.001$; eastern basin density: $P = 0.0195$, biomass: $P = 0.0349$, Table 1). In the central basin, both *Dreissena* density and biomass declined dramatically with depth. Deeper than 20 m we found only one site (#946) with high quagga mussels density and biomass which was located on the eastern edge of the basin. This part of central basin receives well-oxygenated water from the east basin thermocline keeping the eastern part of the central basin hypolimnion better oxygenated than other parts of the central basin (Boyce et al., 1980). Excluding this site, *Dreissena* average density at depths $> 20 \text{ m}$ was only $2 \pm 1 \text{ m}^{-2}$ and wet biomass was $0.3 \pm 0.3 \text{ g m}^{-2}$. In contrast to the central basin, mussel density and biomass were two to three orders of magnitude higher in the same depth zone of the eastern basin. In the eastern basin *Dreissena* spp. density and biomass was highest at the 10 – 20 m depth interval, then declined at the 20–40 m depth zone and then increased again at depths over 40 m.

Length-frequency distribution

Dreissena size structure was different among basins (Fig. 3). In the western and central basins it was mostly unimodal, positively skewed due to the dominance of small (younger) mussels, and negatively truncated due to the lack of large mussels. As a result, 96% of all mussels in these basins were <18 mm, a distribution indicating successful population recruitment but failed survival in older size classes. This distribution was also consistent with depth, since *Dreissena* spp. average length was not significantly different among depth zones in both basins (all $P > 0.89$, Turkey HSD tests).

In contrast, the distribution of *Dreissena* in eastern basin at depths < 40 m was bimodal, suggesting both good recruitment and survival. At deeper (> 40 m) depths, however, the size distribution was unimodal again, with > 98% of all mussels being > 18 mm, and the average mussel length in this depth zone was higher than in other depth zones ($P < 0.012$, Turkey HSD test). The size structure of *Dreissena* in this deep zone may indicate strong population survival of adult mussels but consistent recruitment failures or high mortality of smaller/younger mussels. As a result, the average dreissenid length varied significantly among both lake basins and depths zones (basin: $P < 0.001$, depth zone: $P < 0.001$, Generalized Linear Model, Fig. 3), with the average mussel length in eastern basin being significantly larger than in other basins (average length 15.5 ± 0.6 mm vs. 6.8 ± 0.7 mm in central and 7.6 ± 0.6 mm in western basins, $P < 0.0001$, Turkey HSD test). In addition, maximum mussel lengths were always higher in the eastern basin and often exceeded 30 mm.

Observed late summer thermal stratification in 2012 and 2013

The late summer stratification is a time integrated measure of all in-lake internal and external physical processes. Stratification is driven, to a large degree by meteorological conditions and hydrology, which affect the thickness of the hypolimnion and, therefore, determine the internal pool of the dissolved oxygen available for the hypolimnetic water column and sediment oxygen demands. The thermal stratification defined here as the depths of epilimnion, hypolimnion and thermocline (the depth of the greatest change in temperature with depth) were calculated from the late summer profiles (August through mid-September, Table 2) measured at 10 U.S. EPA GLNPO stations in the central basin (Fig. 1a). Though there are some differences between years, such as a thinner hypolimnion in 2013 than in 2012, the two-sample Student's *t*-test showed no significant differences in the depths of epilimnion ($P = 0.553$), thermocline ($P = 0.211$) and hypolimnion ($P = 0.171$) between 2012 and 2013, meaning that these two years were similar in respect to the late summer thermal structure.

Observed Lake Erie hypoxia in 2014

Lake Erie central basin near bottom oxygen concentrations were fairly high at the beginning of the 2014 growing season. However, later in the season near bottom oxygen concentration dropped below 2 and even 1 mg L⁻¹ forming hypoxic and anoxic zones respectively (Fig. 4). Although the exact chronology differed at each site, near bottom dissolved oxygen declined throughout the growing season at all sites. A deep, offshore hypoxic zone was formed by early August, and expanded into nearshore waters throughout the summer, reaching a maximum spatial extent by late September. On October 4, a strong storm caused a complete

overturn of the central basin and subsequently returned the near bottom waters to normoxic conditions.

3D lake model application to Lake Erie

We validated the 3D ELCD model using continuous and high-frequency observations of water temperatures and dissolved oxygen collected via data loggers in 2014, and then used it for predictions of DO dynamics and spatial distribution in 2012 and 2013, years in which we do not have fine-scale temporal data on DO. The model results were compared to continuous and high-frequency data logger measurements of the bottom temperature and DO in 2014 at the locations of 10 U.S. EPA GLNPO stations in the central basin of Lake Erie (Fig. 1a). The agreement between observed (2014 data logger data) and model results for the same year was good and the calculated RMSE values were within the range of values reported in similar 3D modeling studies in Lake Erie (Liu et al., 2014; Oveisy et al., 2014; Bocaniov et al., 2014a, 2016; Bocaniov and Scavia, 2016) as well as in other lakes and reservoirs (e.g. Bocaniov et al., 2014b). The values of RMSE between daily simulated and measured near-bottom temperatures in 2014 were from 0.9 to 1.4°C, while for DO they were between 0.83 and 1.26 mg L⁻¹ (Fig. 5). Overall, comparing the simulated results with measured values for a pooled dataset of all 10 U.S. EPA GLNPO stations in the central basin for 2014, the grand total RMSEs for daily-averaged values were 1.2°C and 1.13 mg L⁻¹ for daily bottom temperatures (N = 1023) and bottom DO (N = 1019), respectively.

In both 2012, and 2013 simulated years, the model predicted the occurrence of large hypoxic areas, usually developing in August and extending in time towards the lake overturn in early/mid October. Hypoxic extent was very large in 2012 occupying a significant portion of the central basin and smaller in 2013 with maximum daily extents of 11600 and 9400 km², respectively (Fig. 6). However, the temporal and spatial dynamics revealed more contrasting inter-annual differences. For example, the durations of the hypoxic extents exceeding 6000 and 8000 km² were 37 and 31 days (2012), and 35 and 13 days (2013), respectively. The average daily hypoxic extents per one hypoxic day (arbitrary defined here as a day with the daily hypoxic extent exceeding 1000 km² corresponding to about 6% of the basin area) were 6800 km² (2012) and 5700 km² (2013). The spatial pattern of time-integrated hypoxia varied by year (Fig. 6). In 2012, the western part of the central basin was an area with the longest duration of hypoxia, while the duration of hypoxia was longer in the eastern part of the central basin in 2013. The maximum total seasonal duration of hypoxia in both years was about 60 days for hypoxic conditions with DO < 2 mg L⁻¹. Hypoxia was also present in the western basin but only in 2012 and negligible in 2013. Across all 41 sites, we found a significant relationship between *Dreissena* density and biomass and the number of hypoxic days predicted by the model for both 2012 and 2013 (Fig. 7). Regression coefficients between *Dreissena* densities recorded in 2014 and near bottom oxygen concentrations were negative for both years (2012: <1 mg L⁻¹: b = -0.76; <2 mg L⁻¹: b = -0.77, and <3 mg L⁻¹: b = -0.75; 0.56 < R² < 0.59 for all regressions; 2013: b = -0.62; -0.74; -0.80, 0.37 < R² < 0.65). Similarly, the relationship between near bottom oxygen concentrations and *Dreissena* biomass in 2014 was negative (2012: oxygen <1 mg L⁻¹: b = -0.68; <2 mg L⁻¹: b = -0.71; <3 mg L⁻¹: b = -0.73; 0.45 < R² < 0.53; 2013: b = -0.54; -0.63 and -0.73, respectively, 0.29 < R² < 0.53). In all cases regressions were highly significant (P < 0.001).

Discussion

We believe that near-bottom hypoxia is an important environmental factor that governs the spatial distribution of dreissenids in the central basin of Lake Erie where persistent summer hypoxia results in almost complete elimination of mussels at depths over 20 m. Periodic hypoxia may also be an important factor that limits long-term survival of dreissenids in the western basin. Densities and size frequency distribution of *Dreissena* spp. in Lake Erie revealed that multi-year-class populations largely occurred only in the deep eastern basin, an area not affected by hypoxia. Dreissenid populations in both western and central basin were largely represented by small (young) individuals, indicating that survival beyond 2 years was limited, most likely by hypoxia. Therefore we suggest that monitoring of *Dreissena* spp. distribution can be an effective tool in mapping of the extent and frequency of hypoxia in a large waterbody.

Western basin: occasional hypoxia reduces *Dreissena* longevity

In the western basin of Lake Erie dreissenids were distributed rather evenly across the whole basin and exhibited densities equal to those in the eastern basin. Basin-wide average biomass, however, was over six times lower than in the eastern basin (Table 1). Over 98% of all *Dreissena* spp. found in the western basin were <18 mm in length (Fig. 3), which corresponds to mussels younger than 3 years old. The observed smaller sizes of mussels in the western basin in 2014 compared to the eastern basin are consistent with our previous observations (Karatayev et al., 2014). Smaller mussel length in the western basin suggested that *Dreissena* there do not live as long as mussels in the eastern basin, and this is indicative of periodic mortality events that affect the entire population. We hypothesize that these events are due to occasional episodes of severe oxygen depletion following temporary thermal stratification typical for western basin (Ackerman et al., 2001; Bridgeman et al., 2006). For example, our 3D hydrodynamic-ecological model predicted the occurrence of brief episodes of hypoxia in 2012 (< 10 days) and the absence of hypoxia in 2013 (Fig. 6) and 2014. Such hypoxic episodes could cause mass mortality of *Dreissena* spp. of all sizes. Both dreissenid species are sensitive to the lack of oxygen with zebra mussels being less tolerant to low oxygen than quagga mussels (reviewed in Karatayev et al., 1998, 2007, 2015; McMahon and Bogan, 2001). Under anoxic conditions (those with DO < 1 mg L⁻¹) mussels will die after 3 to 6 days, depending on temperature (reviewed in Karatayev et al., 1998). Since almost all mussels in the western basin were < 3 years old, our data suggest that these die-offs occur once every 2 – 3 years. Rapid recolonization is likely from adjacent shallow areas in Lake Erie that are unaffected by hypoxia, or from upstream colonies, e.g., in the St. Clair – Detroit River system. These data are also consistent with the observed periodic failures of *Hexagenia* spp. recruitment in the western basin (Bridgeman et al., 2006). *Hexagenia* spp. are more sensitive to low oxygen than *Dreissena* spp., dying after one or two days of exposure to anoxic conditions (Eriksen, 1963; Nebeker, 1972). Physical habitat disturbance, including ice scour may be among the other factors potentially limiting *Dreissena* population survival in the shallow depths of western Lake Erie (MacIsaac, 1996).

Central basin: regular hypoxia restricts *Dreissena* to nearshore areas

In the central basin *Dreissena* spp. occurred at high densities at shallow depths and then sharply declined to virtually zero at depths greater than 20 m, where bottom hypoxia routinely develops in August – September (Table 1, Figs. 4, 6). In most of the hypoxic zone, *Dreissena* were either absent or represented by young of the year (< 5 mm in length) mussels that likely settled at the beginning of the growing season before the development of hypoxia (Fig. 2). This effect was evident in the trends of both density and biomass (Fig. 7). Even in shallower areas (10 – 20 m) of the central basin where mussels were abundant, *Dreissena* populations were mostly comprised of small, young individuals, supporting model inferences that hypoxia occurs infrequently in these areas.

Eastern basin: multiyear *Dreissena* classes indicate lack of hypoxia

The eastern basin supported the largest dreissenid population. In contrast to western and central basins, in the eastern basin dreissenids were represented by mussels of various sizes, from recently settled 1 mm individuals to old mussels (greater than 3 years) > 30 mm in length across almost all depth zones (Fig. 3). Presence of old mussels across the whole eastern basin suggests a lack of hypoxia and an environment supportive of stable dreissenid populations.

It should be noted that successful recruitment was recorded at all depths except the deepest zone (> 40 m) of the eastern basin where virtually no mussels smaller than 17 mm were found. Likewise, no mussels smaller than 16 mm were found previously at these sites sampled in 2009 (Karatayev et al., 2014). A plausible hypothesis is that this lack of successful recruitment is likely due to the competition of juveniles with large mussels. The food resources in the deep part of the eastern basin of Lake Erie may now be depleted to the point where only large mussels with powerful filtration apparatus can survive, preventing the establishment of young-of-the-year mussels. The long-term presence of adult mussels without recruitment in this more stable, colder profundal environment may be an indication of slower growth of *D. r. bugensis* (Karatayev et al., 2010) and longer life spans, thus contributing to their larger sizes relative to shallower areas. In contrast, in profundal zone of Lake Michigan in 2015, 1 – 5 mm quagga mussels were dominated among dreissenids in 31 – 100 m and >100 m depth intervals (Karatayev et al. 2018 this issue), indicating favorable conditions for successful recruitment.

Dreissena distribution as a tool for mapping hypoxia

The role of benthic invertebrates as indicators of environmental condition has been long recognized (reviewed in Merritt et al., 2008; Wiederholm, 1980). The benthic community is often used to monitor organic pollution that causes decline in oxygen concentrations, resulting in replacement of highly oxyphilic species (e.g. mayflies, caddisflies) by species tolerant to hypoxia (e.g. oligochaetes, midges) (Mandaville, 2002; Merritt et al., 2008). Nevertheless, benthos have almost never been used to map hypoxic areas in freshwater lakes (but see Delorme, 1978), most likely due to the complex and time consuming procedures of collecting and processing a large number of benthic samples. In this study, we found that monitoring *Dreissena* occurrence and length-frequency distribution can be an effective tool in mapping the extent and frequency of hypoxia in freshwater. Both *Dreissena* species are

quite sensitive to low oxygen concentration (reviewed in Karatayev et al., 2007). In contrast to plankton, fish, and some motile benthic species, dreissenids cannot migrate to escape hypoxia. Their life span is much longer than majority of other benthic organisms and their populations usually consists of multiyear cohorts. Therefore, analysis of *Dreissena* size/age structure can reveal even rare hypoxic events, such as those in the western basin. Dreissenids also have unusually high fecundity for freshwater benthos and are able to quickly disperse through planktonic larvae and recolonize substrates. Finally, due to their large body size and high density, they can be detected using remote sensing (e.g. underwater video), allowing for rapid collection and processing of information on their distribution, in lieu of time consuming collections and processing of a large number of benthic samples (Lietz et al., 2015; Mehler et al., 2016).

Management implications of *Dreissena*/hypoxia relationship

The relationship between the *Dreissena* distribution and near-bottom hypoxic conditions has important management implications for the lower Great Lakes. With the introduction of quagga mussels in the 1990's, *Dreissena* populations gained access to the extensive profundal zone of the Great Lakes (Watkins et al., 2007; Nalepa et al., 2010; Karatayev et al., 2015). The rapid expansion of quagga mussel populations into habitats that were previously uninhabited by zebra mussels has been tremendously damaging, particularly in the upper Great Lakes. For example, *Dreissena* populations have been implicated in the disappearance of springtime diatom blooms (Fahnenstiel et al., 2010; Vanderploeg et al., 2010) and the benthic invertebrate *Diporeia* (Watkins et al., 2007; Nalepa et al., 2010), along with changes in zooplankton community structure (Barbiero et al., 2012; Vanderploeg et al., 2012). Further inshore, *Dreissena* have been linked to increases in the abundance of the benthic green alga *Cladophora* (Bootsma et al., 2015; Brooks et al., 2015) and shifting lake food webs increasingly from offshore pelagic to nearshore benthic energy pathways (Karatayev et al., 2015; Turschak et al., 2014). Given the negative impacts that have been documented thus far, it should come as no surprise that *Dreissena* is considered the most aggressive freshwater invader in the northern hemisphere (reviewed in Karatayev et al., 2007, 2015), and one of the major environmental stressors across the entire Great Lakes Basin (Burlakova et al., 2014; Smith et al., 2015).

We demonstrated how persistent hypoxia effectively excludes *Dreissena* populations in the profundal zone of the central basin of Lake Erie. Management programs in Lake Erie focus on limiting nutrient loading, particularly in the western basin, where phosphorus loading from agricultural watersheds causes persistent harmful algal blooms during the summer in the western basin (Bridgeman et al., 2012; Michalak et al., 2013). Excessive phosphorus loads from western basin tributaries have cascading negative impacts on the Lake Erie ecosystem as well, and have been linked to seasonal hypoxia in the central basin (Scavia et al., 2014; Bocaniov et al., 2016). To address this problem, the 2012 Great Lakes Water Quality Agreement suggests a 40% reduction in total phosphorus loads relative to 2008 loads entering the western and central basins of Lake Erie as a way of reducing harmful algal growth and minimizing the extent of hypoxic zones (GLWQA Annex 4 Objectives and Targets Task Team, 2015). For example, a recommended 40% reduction in total phosphorus load to Lake Erie relative to the GLWQA 1978 load target of 11000 MTA (metric tons per

annum) is predicted to increase the mean (August – September) hypolimnetic DO concentration and significantly reduce both the maximum and mean summer (August – September) areal spatial extent of hypoxia ($\text{DO} < 2 \text{ mg L}^{-1}$) by about 20% (1700 km^2) and 43% (2000 km^2), respectively (Bocaniov et al., 2016). While the GLWQA 2012 phosphorus load targets are designed to raise the average August and September hypolimnetic dissolved oxygen to 2.0 mg L^{-1} or higher, thus decreasing the spatial extent of hypoxia (GLWQA Annex 4 Objectives and Targets Task Team, 2015), our results suggest that a decrease in hypoxia may render more profundal zone habitat of the central basin available for *Dreissena* expansion. We believe this hypothetical scenario needs to be further evaluated using detailed hydrodynamic and food web models to fully assess the effects of potential *Dreissena* expansion in the central basin on water quality and food web dynamics.

Acknowledgments

Research supported by U.S. Geological Survey, Department of the Interior, under USGS Agreement No. G14AC000263, “Lake Erie and Lake Michigan Benthos: Cooperative Science and Monitoring Initiative”. This publication was also supported by an agreement with Cornell University, Department of Natural Resources under Prime Agreement Award GL 00E01184 from the U.S. EPA “Great Lakes Long-Term Biological Monitoring of Zooplankton, Benthos, and Chlorophyll a”. The lake ecosystem modeling component of this work was funded in part by the University of Michigan Graham Sustainability Institute and by the USEPA under contract EP-R5-11-07, Task Order 21. We appreciate the assistance of the Captain and crew of the U.S. EPA R/V *Lake Guardian*, and Susan Daniel, Joshua Fisher, Wendy Paterson, Brianne Tulumello, and Keith Pawlowski (SUNY Buffalo State, Great Lakes Center) for help with sample collection and sorting. We also would like to thank Vadim Karatayev (UC Davis) for valuable comments for the data analysis and David Schwab (University of Michigan) for his help with the interpolation of the meteorological data. The views and conclusions contained in this document are those of the authors and should not be interpreted as necessarily representing the official policies, either express or implied, of the U.S. Government. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

References

- Ackerman JD, Loewen MR, Hamblin PF, 2001 Benthic–pelagic coupling over a zebra mussel reef in western Lake Erie. *Limnol. Oceanogr* 46, 892–904.
- Altieri AH, Gedan KB, 2015 Climate change and dead zones. *Global Change Biol.* 21, 1395–1405.
- Backer H, Leppänen J-M, Brusendorff AC, Forsius K, Stankiewicz M, Mehtonen J Pyhälä M, Laamanen M, Paulomäki H, Vlasov N, Haaranen T, 2010 HELCOM Baltic Sea Action Plan - A regional programme of measures for the marine environment based on the Ecosystem Approach. *Marine Poll. Bull* 60, 642–649.
- Barbiero RP, Tuchman ML, 2004 Long-term dreissenid impacts on water clarity in Lake Erie. *J. Great Lakes Res* 30, 557–565.
- Barbiero RP, Lesht BM, Warren GJ, 2012 Convergence of trophic state and the lower food web in Lakes Huron, Michigan and Superior. *J. Great Lakes Res* 38, 368–380.
- Beeton AM, 1961 Environmental changes in Lake Erie. *Trans. Am. Fish. Soc* 90, 153–159.
- Bertram PE, 1993 Total phosphorus and dissolved oxygen trends in the central basin of Lake Erie, 1970–1991. *J. Great Lakes Res* 19, 224–236.
- Bocaniov SA, Smith REH, Spillman CM, Hipsey MR, Leon LF, 2014a The nearshore shunt and the decline of the phytoplankton spring bloom in the Laurentian Great Lakes: Insights from a three-dimensional lake model. *Hydrobiologia* 731, 151–172.
- Bocaniov SA, Ullmann C, Rinke K, Lamb KG, Boehrer B, 2014b Internal waves and mixing in a stratified reservoir: insights from three-dimensional modeling. *Limnologia* 49, 52–67.
- Bocaniov SA, Scavia D, 2016 Temporal and spatial dynamics of large lake hypoxia: Integrating statistical and three-dimensional dynamic models to enhance lake management criteria. *Water Resour. Res* 52, 4247–4263.

- Bocaniov SA, Leon LF, Rao YR, Schwab DJ, Scavia D, 2016 Simulating the effect of nutrient reduction on hypoxia in central Lake Erie with a three-dimensional lake model. *J. Great Lakes Res* 42, 1228–1240. 10.1016/j.jglr.2016.06.001
- Bolsenga S, Herdendorf C, 1993 Lake Erie and Lake St. Clair handbook. Wayne State University Press, Detroit, MI, USA.
- Bootsma HA, Rowe MD, Brooks CN, Vanderploeg HA, 2015, Commentary: The need for model development related to *Cladophora* and nutrient management in Lake Michigan. *J. Great Lakes Res* 41(Suppl. 3), 7–15.
- Boyce FM, Chiocchio F, Eid B, Penicka F, Rosa F, 1980 Hypolimnion flow between the central and eastern basins of Lake Erie during 1977 (inter-basin hypolimnion flows). *J. Great Lakes Res* 6, 290–306.
- Bridgeman TB, Schloesser DW, Krause AE, 2006 Recruitment of *Hexagenia* mayfly nymphs in western Lake Erie linked to environmental variability. *Ecol. Appl* 16, 601–611. [PubMed: 16711047]
- Bridgeman TB, Chaffin JD, Kane DD, Conroy JD, Panek SE, Armenio PM, 2012 From river to lake: phosphorus partitioning and algal community compositional changes in Western Lake Erie. *J. Great Lakes Res* 38, 90–97.
- Britt NW, 1955 *Hexagenia* (Ephemeroptera) population recovery in western Lake Erie following the 1953 catastrophe. *Ecology*, 36, 520–522.
- Brooks C, Grimm A, Shuchman R, Sayers M, Jessee N, 2015 A satellite-based multi-temporal assessment of the extent of nuisance *Cladophora* and related submerged aquatic vegetation for the Laurentian Great Lakes. *Remote Sens. Environ* 57, 58–71.
- Burlakova LE, Karatayev AY, Pennuto C, Mayer C, 2014 Changes in Lake Erie benthos over the 1 last 50 years: historical perspectives, current status, and main drivers. *J. Great Lakes Res* 40, 560–573.
- Carr JF, Hiltunen JK, 1965 Changes in the bottom fauna of western Lake Erie from 1930 to 1961. *Limnol. Oceanogr* 10, 551–569.
- Chesapeake Bay Watershed Agreement, 2014 http://www.chesapeakebay.net/documents/FINAL_Ches_Bay_Watershed_Agreement.withsignatures-Hires.pdf
- Delorme LD, 1978 Distribution of freshwater ostracodes in Lake Erie. *J. Great Lakes Res* 4, 216–220.
- Delorme LD, 1982 Lake Erie oxygen: the prehistoric record. *Can. J. Fish. Aquat. Sci* 39, 1021–1029.
- Dermott R, Johannsson O, Munawar M, Bonnell R, Bowen K, Burley M Fitzpatrick M, Gerlofsma J, Niblock H, 2007 Assessment of lower food web in Hamilton Harbour, Lake Ontario, 2002 – 2004. *Can. Tech. Rep. Fish. Aquat. Sci* 2729.
- Diaz RJ, 2001 Overview of hypoxia around the world. *Journal of Environmental Quality* 30:275–281. [PubMed: 11285887]
- Diaz RJ, and Rosenberg R 2008 Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929. [PubMed: 18703733]
- Eriksen CE, 1963 Respiratory regulation in *Ephemera simulans* Walker and *Hexagenia limbata* (Serville) (Ephem-eroptera). *J. Exp. Biol* 40, 455–467.
- GLWQA, 2012 Great Lakes Water Quality Agreement Protocol Amending the Agreement Between the United States of America and Canada on Great Lakes Water Quality, 1978, as amended on October 16, 1983, and on November 18, 1987. Signed September 7, 2012.
- GLWQA Annex 4 Objectives and Targets Task Team, 2015 Recommended Phosphorus Load Targets for Lake Erie. Final Report to the Nutrients Annex Subcommittee. Available online: <https://binational.net/wp-content/uploads/2015/06/nutrients-TT-report-en-sm.pdf>
- Fahnenstiel GL, Pothoven SA, Nalepa TF, Vanderploeg HA, Klarer DM, Scavia D, 2010 Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *J. Great Lakes Res* 36, 20–29.
- Hamidi SA, Bravo HR, Klump JV, Waples JT, 2015 The role of circulation and heat fluxes in the formation of stratification leading to hypoxia in Green Bay, Lake Michigan. *J. Great Lakes Res* 41, 1024–036.
- Hipsey MR, Hamilton DP, 2008 Computational aquatic ecosystems dynamics model: CAEDYM v3 Science Manual. Centre for Water Research Report, University of Western Australia.

- Hodges B, Imberger J, Saggio A, Winters K, 2000 Modelling basin-scale internal waves in a stratified lake. *Limnol. Oceanogr* 45, 1603–1620.
- Karatayev AY, Burlakova LE Padilla DK, 1998 Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). *J. Shellfish Res* 7, 1219–1235.
- Karatayev AY, Burlakova LE, Padilla DK, 2006 Growth rate and longevity of *Dreissena polymorpha* (Pallas): a review and recommendations for future study. *J. Shellfish Res* 25, 23–32.
- Karatayev AY, Padilla DK, Minchin D, Boltovskoy D, Burlakova LE, 2007 Changes in global economies and trade: the potential spread of exotic freshwater bivalves. *Biol. Invasions* 9, 161–180.
- Karatayev AY, Mastitsky SE, Padilla DK, Burlakova LE, Hajduk MM, 2010 Differences in growth and survivorship of zebra and quagga mussels: size matters. *Hydrobiologia* 668, 183–194.
- Karatayev AY, Burlakova LE, Pennuto C, Ciborowski J, Karatayev VA, Juette P, Clapsadle M, 2014 Twenty five years of changes in *Dreissena* spp. populations in Lake Erie. *J. Great Lakes Res* 40, 550–559.
- Karatayev AY, Burlakova LE, Padilla DK, 2015 Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia* 746, 97–12.
- Karatayev AY, Mehler K, Burlakova LE, Hinchey EK, Warren GJ, 2018 You can count them, if you can see them: Underwater video image analysis can greatly improve monitoring of *Dreissena* populations. *J. Great Lakes Res* 44, 628–638.
- Kemp ALW, MacInnis GA, Harper NS, 1977 Sedimentation rates and a revised sediment budget for Lake Erie. *J. Great Lakes Res* 3, 221–233.
- Kraus RT, Knight CT, Farmer TM, Gorman AM, Collingsworth PD, Warren GJ Kocovsky PM, Conroy JD, 2015 Dynamic hypoxic zones in Lake Erie compress fish habitat, altering vulnerability to fishing gears. *Can. J. Fish. Aquat. Sci* 72, 797–806, 10.1139/cjfas-2014-0517.
- Leach JH, 1993 Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie In: Nalepa TF and Schloesser DW, (Eds.), *Zebra Mussels: Biology, Impacts, and Control*, Nalepa, 1993, Lewis Publishers/CRC Press; Boca Raton, Florida, 381–397.
- Leon LF, Smith REH, Hipsey MR, Bocaniov SA, Higgins SN, Hecky RE, Antenucci JP, Imberger JA, Guildford SJ, 2011 Application of a 3D hydrodynamic-biological model for seasonal and spatial dynamics of water quality and phytoplankton in Lake Erie. *J. Great Lakes Res* 37, 41–53.
- Lietz JE, Kelly JR, Scharold JV, Yurista PM, 2015 Can a rapid underwater video approach enhance the benthic assessment capability of the national coastal condition assessment in the Great Lakes? *Environ. Manage* 55, 1446–1456. [PubMed: 25832344]
- Liu W, Bocaniov SA, Lamb KG, Smith REH, 2014 Three dimensional modeling of the effects of changes in meteorological forcing on the thermal structure of Lake Erie. *J. Great Lakes Res* 40, 827–840.
- MacIsaac HJ, 1996 Population structure of an introduced species (*Dreissena polymorpha*) along a wave-swept disturbance gradient. *Oecologia* 105, 484–492. [PubMed: 28307141]
- McMahon RF, Bogan AF, 2001 Mollusca: Bivalvia. In: *Ecology and Classification of North American Freshwater Invertebrates*, Thorp JH, Covich AP, editors. pp. 331–430. 2nd Edition. New York Academic Press.
- Makarewicz JC, Bertram P, 1991 Evidence for the restoration of the Lake Erie ecosystem. *Bioscience*, 41, 216–223.
- Mandaville SM, 2002 Benthic Macroinvertebrates in Freshwaters - Taxa Tolerance Values, Metrics, and Protocols. Project H-1, Soil and Water Conservation Society of Metro Halifax.
- Mehler K, Burlakova LE, Karatayev AY, Biesinger Z, Valle-Lewinson A, Castiglione C, Gorsky D, 2016 Sonar technology and underwater video analysis can enhance invasive *Dreissena* distribution assessment in large rivers. *Hydrobiologia*. DOI 10.1007/s10750-016-3040-z
- Merritt RW, Cummins KW, Berg MB, 2008 An Introduction to the Aquatic Insects of North America. 4th Edition, Kendall Hunt Publishing, 1158 pp.
- Michalak AM, Anderson E, Beletsky D, Boland S, Bosch NS, Bridgeman TB, Chaffin JD, Cho KH, Confesor R, Dalo I, DePinto J, Evans MA, Fahnenstiel GL, He L, Ho JC, Jenkins L, Johengen T, Kuo KC, Laporte E, Liu X, McWilliams M, Moore MR, Posselt DJ, Richards RP, Scavia D,

- Steiner AL, Verhamme E, Wright DM, Zagorski MA, 2013 Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proc. Natl. Acad. Sci* 110, 6448–6452. [PubMed: 23576718]
- Mississippi River Gulf of Mexico Watershed Nutrient Task Force, 2008. Gulf Hypoxia Action Plan 2008 https://www.epa.gov/sites/production/files/2015-03/documents/2008_8_28_msbasin_ghap2008_update082608.pdf
- Mortimer CH, 1987 Fifty years of physical investigations and related limnological studies on Lake Erie, 1928–1977. *J. Great Lakes Res* 13, 407–435.
- Nalepa TF, Fanslow DL, Pothoven SA, 2010 Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena* populations in southern Lake Michigan. *J. Great Lakes Res* 36, 5–19.
- Nebeker AV, 1972 Effect of low oxygen on survival and emergence of aquatic insects. *Trans. Am. Fish. Soc* 4, 675–679.
- Oveisy A, Rao YR, Leon LF, Bocaniov SA, 2014 Three-dimensional winter modeling and the effects of ice cover on hydrodynamics, thermal structure and water quality in Lake Erie. *J. Great Lakes Res* 40, 19–28.
- Patterson MWR, Ciborowski JJH, Barton DR, 2005 The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. *J. Great Lakes Res* 31, 223–237.
- Richards RP, Baker DB, Crumrine JP, Stearns AM, 2010 Unusually large loads in 2007 from the Maumee and Sandusky Rivers, tributaries to Lake Erie. *J. Soil Water Conserv* 65, 450–462.
- Richardson V, Warren GJ, Nielson N, Horvatin PJ, 2012 Cooperative science and monitoring initiative (CSMI) for the Great Lakes - Lake Ontario 2008. *J. Great Lakes Res* 38, 10–13.
- Sambridge M, Braun J, McQueen H, 1995 Geophysical parametrization and interpolation of irregular data using natural neighbors. *Geophys. J. Int* 122, 837–857.
- Scavia D, Allan JD, Arend KK, Bartell S, Beletsky D, Bosch NS, Brandt SB, Briland RD, Daloglu I, DePinto JV, Dolan DM, Evans MA, Farner TM, Goto D, Han H, Hook TO, Knight R, Ludsin SA, Mason DM, Michalak AM, Richards RP, Roberts JJ, Rucinski DK, Rutherford ES, Schwab DJ, Sesterhenn T, Zhang H, Zhou Y, 2014 Assessing and addressing the re-eutrophication of Lake Erie: Central basin hypoxia. *J. Great Lakes Res* 40, 226–246.
- Shelford VE, Boesel MW, 1942 Bottom animal communities of the island area of western Lake Erie in the summer of 1937. *Ohio J. Sci* 42, 179–190.
- Schertzer WM, Saylor JH, Boyce FM, Robertson DG, Rosa F, 1987 Seasonal thermal cycle of Lake Erie. *J. Great Lakes Res* 13, 468–486.
- Schloesser DW, Krieger KA, Ciborowski JJH, Corkum LD, 2000 Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. *J. Aquat. Ecosyst. Stress Recovery* 8, 125–141.
- Schwab DJ, Morton JA, 1984 Estimation of over lake wind speed from overland wind speed: a comparison of three methods. *J. Great Lakes Res* 10, 68–72.
- Smith SDP, McIntyre PB, Halpern BS, Cooke RM, Marino AL, Boyer GL, Buchsbaum A, Burton GA, Campbell LM, Ciborowski JJH, Doran PJ, Infante DM, Johnson LB, Read JG, Rose JB, Rutherford ES, Steinman AD, Allan JD, 2015 Rating impacts in a multi-stressor world: a quantitative assessment of 50 stressors affecting the Great Lakes. *Ecol. Appl* 25, 717–728. doi: 10.1890/14-0366.1 [PubMed: 26214917]
- Stramma L, Johnson GC, Sprintall J, Mohrholz V, 2008 Expanding oxygen-minimum zones in the tropical oceans. *Science* 320, 655–658. [PubMed: 18451300]
- Turner RE, Rabalais NN, Justic D, 2008 Gulf of Mexico hypoxia: Alternate states and a legacy. *Environ. Sci. Technol* 42, 2323–2327. [PubMed: 18504960]
- Turschak BA, Bunnell D, Czesny S, Höök TO, Janssen J, Warner D, Bootsma HA, 2014 Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. *Ecology*, 95, 1243–1252. [PubMed: 25000756]
- Vaquer-Sunyer R, Duarte CM, 2008 Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci* 105, 15452–15457. [PubMed: 18824689]

- Vanderploeg HA, Ludsin SA, Ruberg SA, Höök TO, Pothoven SA, Brandt SB, Lang GA, Liebig JR, Cavaletto JF, 2009 Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *J. Exp. Mar. Biol. Ecol* 381, S92–S107.
- Vanderploeg HA, Liebig JR, Nalepa TF, Fahnenstiel GL, Pothoven SA, 2010 *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Res* 36 (Suppl. 3), 50–59.
- Vanderploeg HA, Pothoven SA, Fahnenstiel GL, Cavaletto JF, Liebig JR, Stow CA Nalepa TF, Madenjian CP, Bunnell DB, 2012 Seasonal zooplankton dynamics in Lake Michigan: disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *J. Great Lakes Res* 38, 336–352.
- Watkins JM, Dermott R, Lozano SJ, Mills EL, Rudstam LG, Scharold JV, 2007 Evidence for remote effects of dreissenids mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1997–2003. *J. Great Lakes Res* 33, 642–657.
- Wiederholm T, 1980 Use of benthos in lake monitoring. *J. Water Pollut. Control Fed* 52(3), 537–547.

Figure 1. Location of oxygen data logger (black circles) and U.S. EPA GLNPO Central Basin of Lake Erie Dissolved Oxygen Monitoring Program stations (open circles). Dashed lines indicate borders between western, central, and eastern basins (a). Location of PONAR (black circles) and SCUBA (open circles) *Dreissena* spp. sites sampled in 2014 (b).

Figure 2.
Distribution of *Dreissena* spp. in Lake Erie in 2014 by age group.

Figure 3.
Length-frequency distributions of *Dreissena* spp. in Lake Erie in 2014.

Figure 4.

Dissolved oxygen (solid line, mg L^{-1}) and temperature (dashed line, $^{\circ}\text{C}$) dynamics at two representative sites in the central basin of Lake Erie. These sites were chosen because they represented two distinct patterns that were observed during the study. At shallow sites (a), dissolved oxygen and temperature trends were dynamic throughout the study. At deeper sites (b), dissolved oxygen decreased throughout while temperature remained relatively stable, until a rapid overturn event late in the study increased both variables.

Figure 5.

Time series of the observed vs. simulated daily near-bottom dissolved oxygen (DO) concentrations (a, c, e) and water temperatures (b, d, f) at the locations of three selected stations in the central basin of Lake Erie: ER31 (a, b), ER42 (c, d) and ER78 (e, f). The lake-overturn conditions (October 5–10, 2014) were excluded from the statistical analysis (RMSE values). N is the number of the compared pairs.

Figure 6.

Maps of spatial time-integrated distribution of hypoxia for 2012 and 2013 with the locations of stations (open circles and triangles) sampled during 2014 field season. Open circles (black color) and triangles (white color) indicate stations with presence and absence of dreissenid mussels in 2014, respectively.

Figure 7. Relationship between *Dreissena* spp. density and biomass (2014) and the length of near bottom predicted oxygen concentration in the central basin based on the model below 2 mg L⁻¹ for 2012 (upper) and 2013 (lower). All regressions are highly significant ($P < 0.001$).

Table 1.

Frequency of occurrence (%), density (average $\pm$ standard error here and elsewhere in the table, m^{-2}), wet biomass (shell plus tissue g m^{-2}) of *Dreissena* spp., and the number of sites sampled (N) in Lake Erie in 2014.

Basin, depth, m	N	Frequency	Density	Biomass
Western				
0–10.0	14	100	3243 ± 2009	279.8 ± 150.4
>10.0	8	88	2144 ± 1108	229.3 ± 107.2
Average	22		2844 ± 1324	261.4 ± 101.7
Central				
0–10.0	4	75	1249 ± 1012	235.2 ± 231.9
10.1–20.0	16	81	1110 ± 484	124.8 ± 56.7
> 20.0	22	27	127 ± 126	43.6 ± 43.3
> 20.0 *	21 *		2 ± 1	0.3 ± 0.3
Average	41 *		556 ± 223	71.3 ± 31.9
Eastern				
0–10.0	10	80	2645 ± 908	1897.4 ± 616.6
10.1–20.0	12	100	4021 ± 1338	2191.8 ± 555.8
20.1–40.0	13	92	716 ± 281	646.5 ± 237.1
>40.0	8	100	1793 ± 214	2021.8 ± 183.3
Average	43		2287 ± 469	1624.5 ± 239.9
Lake average	106 *		1743 ± 350	741.0 ± 122.6

* Excluding site 946.

Table 2.

Characterization of Lake Erie central basin thermal structure in late summer 2012 and 2013 (August through mid-September) based on temperature profiles measured at the locations of 10 U.S. EPA GLNPO Central Basin of Lake Erie Dissolved Oxygen Monitoring Program stations (see Fig. 1a).

Thermal strata (layer)	2012 (<i>n</i> = 30)	2013 (<i>n</i> = 30)
Depth of epilimnion (upper boundary of metalimnion), m	16.7 ± 2.1	17.0 ± 2.2
Depth of thermocline, m	17.8 ± 2.0	18.5 ± 2.2
Depth of hypolimnion (lower boundary of metalimnion), m	18.7 ± 1.8	19.5 ± 2.1
Thickness of metalimnion, m	2.0 ± 0.6	2.4 ± 0.6