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Life after *Dreissena*: The decline of exotic suspension feeder may have significant impacts on lake ecosystems

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ABSTRACT

It is well documented that the introduction of dreissenid bivalves in eutrophic lakes is usually associated with decreases in turbidity and total phosphorus concentrations in the water column, concomitant increases in water clarity, as well as other physical changes to habitat that may have cascading effects on other species in the invaded waterbody. In contrast, there is a paucity of data on the ecological ramifications of the elimination or decline of dreissenids due to pollution, bottom hypoxia, or other mechanisms. Using data collected by the U.S. Environmental Protection Agency Great Lakes National Program Office's Long-Term Biology and Water Quality Monitoring Programs, we analyzed the impacts of the hypoxia-induced declines in *Dreissena* densities in the central basin of Lake Erie on major water chemistry and physical parameters. Our analysis revealed that the decline in *Dreissena* density in the central basin was concomitant with a decrease in spring dissolved silica concentrations and an increase in total phosphorus and near bottom turbidity not seen in the western or eastern basins. In contrast, opposite patterns in water quality were observed in the eastern basin which was characterized by a high and relatively stable *Dreissena* population. We are the first to report on observations suggesting that dreissenid-related shifts in water quality may be reversible by documenting that the sharp decline of *Dreissena* in the central basin of Lake Erie was concomitant with a shift from clear to turbid water.

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Introduction

Exotic dreissenids *Dreissena polymorpha*, the zebra mussel, and its congener *D. rostriformis bugensis*, the quagga mussel, are considered the most aggressive freshwater invaders in the Northern hemisphere (reviewed in Nalepa and Schloesser, 1993, 2014; Karatayev et al., 1997, 2002, 2007, 2015; Higgins and Vander Zanden, 2010). Both species cause multi-million dollars of damages annually to industries that use raw water supplies (Pimentel et al., 2005) and profoundly alter freshwater ecosystems (Karatayev et al., 1997, 2002, 2015; Higgins and Vander Zanden, 2010). By moving large amounts of seston from pelagic to benthic habitats, dreissenids increase water clarity (reviewed in Karatayev et al., 1997, 2002, 2015) and increase the rates of mineralization of nutrients (James et al., 2000; Mosley and Bootsma, 2015), oxygen consumption (Tyner et al., 2015), and sedimentation. Dreissenids are thought to have suppressed the spring diatom bloom in Lake Michigan by filtering out large amounts of algae (Fahnenstiel et al., 2010),

which could in turn explain increased silica concentrations in the lake (Reavie et al., 2014). These impacts on the environment may have cascading effects on other species that interact with or are directly impacted by dreissenids. Profound changes in waterbodies invaded by dreissenids are well known and have been reported multiple times both in Europe and in North America (reviewed in Nalepa and Schloesser, 1993, 2014; Karatayev et al., 1997, 2002, 2007, 2015; Higgins and Vander Zanden, 2010). In contrast, there is a lack of data on the ecological consequences of the elimination of dreissenids from invaded waterbodies as a result of pollution, bottom hypoxia, or other factors. While there is evidence that the introduction of zebra and quagga mussels may cause or contribute to an increase in transparency in eutrophic lakes (Ibelings et al., 2007; Karatayev et al., 2014a; Mayer et al., 2014), it is unknown whether this process reverses after the elimination of *Dreissena* from an invaded waterbody.

Although distributed widely across Europe and North America, dreissenids are quite sensitive to pollution and low oxygen concentrations (reviewed in Karatayev et al., 1998, 2007, 2015; McMahon and Bogan, 2001). Thus during the industrial revolution, zebra mussels disappeared from several polluted European lakes and rivers and were

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only able to recolonize waterbodies after water quality was substantially improved (bij de Vaate et al., 1992; Jantz and Neumann, 1992; Burlakova, 1998). Bottom hypoxia (reduction of oxygen concentration below 2 mg/L, Diaz, 2001) associated with cultural eutrophication recently became a major stressor both in freshwaters and coastal marine ecosystems (reviewed in Diaz, 2001; Diaz and Rosenberg, 2008), including the Laurentian Great Lakes (Hamidi et al., 2015; Scavia et al., 2014; Bocaniov and Scavia, 2016). In waterbodies populated with *Dreissena* spp., hypoxia may cause massive mussel mortality and restrict their distribution to well oxygenated nearshore waters (Karatayev et al., 2018).

In Lake Erie, a large portion of the central basin has always experienced seasonal hypoxic events, but the extent of hypoxia substantially increased during the cultural eutrophication of the 1950s–1960s, ultimately reaching 11,000 km² (Beeton, 1961, 1963; Delorme, 1982; Scavia et al., 2014). After the implementation of phosphorus reduction programs in the 1970s, the extent of the hypoxic zone shrank and remained relatively small (Makarewicz and Bertram, 1991; Bertram, 1993). From the late 1980s to the mid-1990s the estimated areal extent of central basin hypoxia declined from about 10,000 km² to almost zero (Scavia et al., 2014). Since the mid-1990s, however, the extent of the hypoxic zone increased to the 1970s levels (Zhou et al., 2013; Scavia et al., 2014), most likely due to increases in dissolved reactive phosphorous loading that drives phytoplankton biomass (Richards et al., 2010; Scavia et al., 2014). Alternatively increase in silica export from Lake Huron that, according to Reavie et al. (2016) drives winter-spring diatom bloom in the central basin of Lake Erie, maybe another reason for the increase of algal biomass. Sedimentation of algae and fecal material drives dissolved oxygen depletion in the hypolimnion by stimulating bacterial respiration. Currently, by the end of the growing season, a large portion (up to 10,000 km²) of the central basin becomes hypoxic and remains hypoxic until fall overturn (Vanderploeg et al., 2009a, 2009b; Kraus et al., 2015; Bocaniov and Scavia, 2016; Karatayev et al., 2018). The hypolimnion of the eastern basin receives a lesser amount of suspended solids and nutrients than the central basin and never goes hypoxic (Kemp et al., 1977; Mortimer, 1987; Karatayev et al., 2018).

Lake Erie was the first waterbody in North America colonized by both *D. polymorpha* and *D. r. bugensis*. The first *D. polymorpha* was found in the lake in 1986 (Carlton, 2008) and the first *D. r. bugensis* was documented in 1989 (Mills et al., 1993). By the end of 1989 the entire lake was completely colonized by *Dreissena* (Griffiths et al., 1991). During the initial stage of colonization, all three Lake Erie basins were dominated by *D. polymorpha*; but, by the late 1990s, *D. polymorpha* remained common only in the shallow western basin, while in the central and eastern basins it was almost completely replaced by *D. r. bugensis* (Patterson et al., 2005; Karatayev et al., 2014b). During the 1990s, *Dreissena* spp. density was high in all three Lake Erie basins, but after 1998, dreissenid density in the central basin dramatically declined, while in the western and eastern basins densities were still high (Karatayev et al., 2014b). The decline of *Dreissena* density in the central basin coincided with and was likely caused by the return of widespread and persistent hypoxia (Karatayev et al., 2018). This sharp decline in the *Dreissena* population in the central basin may be driving decreases in water clarity and silica concentrations, increases in turbidity and phytoplankton density, and other chemical and biological changes in the ecosystem. Alternatively, these observed chemical and biological changes in the central basins of Lake Erie may be the result of recent increases in non-point source nutrient loading (especially dissolved reactive phosphorous) resulting in phytoplankton blooms (Richards et al., 2010; Scavia et al., 2014).

Analyses of major environmental parameters collected by the U.S. Environmental Protection Agency (EPA), Great Lakes National Program Office (GLNPO) Biology and Water Quality Monitoring Programs since 1983 provide a unique opportunity to examine the impact of the decline of a large population of suspension feeders on water quality in the central basin of Lake Erie. The eastern basin, similar to the central basin,

stratifies during summer and still supports a large population of *Dreissena*, and thus represents a natural “control”. Previous studies have documented post-dreissenid decreases in spring phytoplankton and chlorophyll *a* in Lake Erie, most notably in the western basin (Holland, 1993; Makarewicz et al., 1999; Makarewicz et al., 2000; Barbiero and Tuchman, 2004), and increases in spring silica (Makarewicz et al., 2000; Barbiero et al., 2006; Reavie et al., 2014). Post-dreissenid changes in spring transparency have not been consistent between the basins, decreasing in the western basin and increasing in the eastern basin (Makarewicz et al., 2000; Barbiero and Tuchman, 2004; see though Leach, 1993; Holland, 1993). We hypothesize that the decline of *Dreissena* in the late 1990s in the central basin should have reversed these trends, which would not be the case in the eastern or western basins, where *Dreissena* densities remain high.

Methods

Study area

Lake Erie's three basins include: the shallow western basin (average depth 7.4 m, maximum depth 19 m), the most productive and turbid basin due to large inputs of nutrients and suspended sediments; the intermediate depth, mesotrophic central basin (average depth 18.3 m, maximum depth 25 m); and the deepest and more oligotrophic eastern basin (average depth 24.4 m, maximum depth 64 m) (Mortimer, 1987; Barbiero and Tuchman, 2004; Conroy et al., 2005) (Fig. 1). The western basin is usually well-mixed in summer, although during calm weather it may stratify intermittently, resulting in short-term episodes of severe hypoxia (Ackerman et al., 2001; Bridgeman et al., 2006). Most of the central basin's offshore area stratifies during summer and is susceptible to periodic hypoxia that usually develops by the end of the growing season in August–September, before the fall overturn (Vanderploeg et al., 2009a, 2009b; Kraus et al., 2015; Bocaniov and Scavia, 2016; Karatayev et al., 2018). The eastern basin also develops stable stratification during summer with a large hypolimnion that never goes hypoxic due to its large volume and low inputs of suspended solids and nutrients (Kemp et al., 1977; Mortimer, 1987).

Dreissena long-term-dynamics

To compare the pattern of population dynamics of *Dreissena* in Lake Erie, we compiled a dataset of *Dreissena* spp. densities and biomass by station and depth for 1992, 1993, and 1998 (biomass reported in total wet weight including shell (TWW), Jarvis et al., 2000), 2002 (reported only by depths intervals and lake basins, biomass reported in shell free dry tissue weight (SFDTW), Patterson et al., 2005), 2004 (biomass reported in ash free dry tissue weight (AFDW), J. Ciborowski (University of Windsor, personal communication)), 2009–2011 (biomass reported in TWW, Karatayev et al., 2014b), and 2014 (biomass reported in TWW, Karatayev et al., 2018). The 2014 data were collected in support of the Lake Erie Cooperative Science and Monitoring Initiative (CSMI). During this 2014 intensive sampling event, the distribution, density, biomass, and length-frequency distribution of *Dreissena* spp. were studied in Lake Erie at 107 stations, including 22 stations in the western basin, 42 stations in the central basin and 43 stations in the eastern basin (Fig. 1). Offshore stations were sampled aboard the U.S. EPA R/V *Lake Guardian* using a regular Ponar (surface area 0.0529 m²), while nearshore stations (<10 m depth) were sampled aboard Buffalo State R/V *John J. Freidoff* using a petite Ponar (surface area 0.023 m²). We used SCUBA to collect samples (0.25 m² quadrat) from rock/bedrock at 5 and 10 m depths. All historic and current data on *Dreissena* biomass were converted into AFDW. To convert TWW into AFDW, we used the relationship: AFDW (g) = 0.0274 × TWW (g); to convert SFDTW into AFDW, we used the relationship: AFDW (g) = 0.8711 × SFDTW (g) (both equations estimated for *Dreissena* in Lake Michigan by Ashley Elgin, NOAA, Ann Arbor, personal communication).

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