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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 that dreissenid-related shifts in water quality of

invaded waterbodies are 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.

Keywords

ecosystem impacts; hypoxia; *Dreissena rostriformis bugensis*; Lake Erie; long-term changes

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 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, 2015a; McMahon and Bogan, 2001). Thus during the industrial revolution, zebra mussels disappeared from several polluted European lakes and rivers and were 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⁻¹, 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 (Howell et al., 1996; 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), Ciborowski et al., in preparation), 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: $\text{AFDW (g)} = 0.0274 \times \text{TWW (g)}$; to convert SFDTW into AFDW, we used the relationship: $\text{AFDW (g)} = 0.8711 \times \text{SFDTW (g)}$ (both equations estimated for *Dreissena* in Lake Michigan by Ashley Elgin, NOAA, Ann Arbor, personal communication).

Dreissenid clearance rate

To accommodate the differences in bathymetry, retention times, and nutrient dynamics between Lake Erie basins, we calculated the fraction of the water column cleared per day during the spring (FC, Vanderploeg et al., 2010) for each basin during the years when dreissenid density and biomass were measured to provide an objective comparison between the effects of dreissenid mussels on water quality variables. Whole basin FC was calculated as net clearance rate (FA) $\times$ biomass per $\text{m}^2 \div$ mean water depth (m) in each depth zone. Spring net clearance rate (FA), was first calculated according to the equation $\text{FA} = 0.93 \times \text{temperature} + 4.53$ (mg/ml/h, Vanderploeg et al., 2010), then used in the calculations for season FC (Fig. 2), with water temperature at 4°C. During the spring, when the water column was not stratified, we assumed that dreissenid mussels have access to the entire water column in all basins at all depths. During summer stratification in the central and eastern basins, we made the assumption that dreissenids only have access to epilimnetic waters. No summer stratification was assumed in the western basin. Depth zones were defined as 0 – 16 and 16 – 24 m in the central basin and 0 – 19 and 19 – 64 m in the eastern basin. Two central basin profundal stations (#946 at 24 m depth, and # 944 at 18 m), located on the eastern edge of the basin (Fig. 1) were excluded from the profundal density calculation. This area of the central basin is unique as it receives well oxygenated water from the eastern basin thermocline keeping the eastern part of the central basin hypolimnion better oxygenated than other parts of the central basin (Boyce et al., 1980) and thus allowing higher *Dreissena* densities to colonize. Since the western basin is shallow (<19 m) and it stratifies only periodically and for a very short time, depth zones were not defined there.

Environmental parameters

Environmental parameters analyzed in this paper as response variables (potentially affected by *Dreissena*) to compare differences among the three periods of *Dreissena* invasion in Lake Erie included transparency (as estimated by Secchi depth), turbidity, total phosphorus (TP), total soluble phosphorous (TSP) and spring dissolved silica concentration in the water column. These data were collected from 6 stations in the western basin (depth range 9 – 12 m), 10 stations in the central basin (depths range 19 – 24 m), and 4 stations in the eastern basin (depths range 32 – 62 m) aboard R/V *Lake Guardian* as part of the U.S. EPA spring and summer surveys (Fig. 1). The same stations were sampled each year. To standardize sampling time across years, we used data collected during the spring isothermal period (March – April) and the summer stratified period (July – August) cruises only. When stations were resampled more than once during the same year and season, data were averaged. Since our results are observations rather than direct manipulations, we advise that the relationships we found imply correlation rather than causation.

Turbidity at each station was determined onboard R/V *Lake Guardian* using a nephelometer and reported in Nephelometric Turbidity Units (NTU) (Barbiero and Tuchman, 2004). TP and TSP were measured by the ascorbic acid method after acid persulfate digestion and reported in $\mu\text{gP L}^{-1}$. Soluble silica (mg L^{-1}) was determined as SiO_2 by the molybdate method (American Public Health Association, 1985; Barbiero et al., 2006). Samples for turbidity and dissolved silica were collected from the surface layer of the water column (in the epilimnion, 10 m in the central and western basins, and 12 m in the eastern basin) and near the bottom (approximately 1 m above the bottom). Only surface water total phosphorous data were used in this study.

All three Lake Erie basins were colonized by *Dreissena* in the 1980s and densities initially increased rapidly. Subsequently, the mussel population in the central basin declined sharply after 1998, while *Dreissena* density in the western and eastern basins was relatively high during the entire period of observation. To evaluate the potential impact of *Dreissena* colonization and subsequent population decline on environmental parameters, comparisons were performed among Lake Erie basins. As the central and the eastern basins become stratified during summer but differ in susceptibility to hypoxia and in sizes of resident *Dreissena* populations, we used the eastern basin as a natural control to test for the effect of *Dreissena* population decline on water quality. Alternatively, since at least some of the observed recent changes in the central basin environmental parameters may be due to the possible re-eutrophication of the basin associated with the increase in dissolved reactive phosphorous loading (Richards et al., 2010; Scavia et al., 2014) not seen in the eastern basin, we compared the changes in the central and eastern basins with the western basin. Time periods compared were: before *Dreissena* invasion (1983 – 1988); high *Dreissena* density in all basins (1989 – 1998); low *Dreissena* density in central basin, but high density in western and eastern basins (1999 – 2014).

To compare *Dreissena* densities between basins in the same year we used *t*-tests on log-transformed densities. To compare water quality parameters among time periods (1983 – 1988, 1989 – 1998, and 1999 – 2013) we used one-way ANOVA with post-hoc unequal *n* Tukey HSD test if ANOVA was significant. Water quality parameters were log-transformed, with the exception of Secchi depth, which was normally distributed. Due to a limited number of stations per basin, it was not possible to conduct a repeated-measures ANOVA; however, due to a relatively short water residence time in Lake Erie (2 years) when compared to the length of this study, station effect may be relatively minor. Analyses were done using Statistica 13 (TIBCO Software Inc., Tulsa, OK) and R (version 3.3.2; R Core Team 2016). All tests effects were considered significant at $P < 0.05$.

Results

Dreissena spp. long-term dynamics

Dreissena polymorpha and *D. r. bugensis* colonized Lake Erie in the late 1980s. At the time of the first lake-wide study of dreissenid populations in Lake Erie in 1992, mussels were already distributed across the entire lake, and their densities in the western, central, and eastern basins were already high ($842 \pm 620 \text{ m}^{-2}$, $1131 \pm 679 \text{ m}^{-2}$, and $6003 \pm 2093 \text{ m}^{-2}$, respectively) (average $\pm$ standard error here and elsewhere) (Fig. 2). *Dreissena* density in the

western basin during the first ten years of observation (1992–2002) was substantially lower than in the central and eastern basin, but, after 2002, mussel density in the western and eastern basins were similar and both were higher than in the central basin (Fig. 2). By 1993, the central basin average mussel density increased to $2746 \pm 806 \text{ m}^{-2}$ and remained at this level until 1998, then declined almost 5-fold by 2002 and had not recovered as of 2014. *Dreissena* density in 1998 in the eastern basin did not differ significantly from that in the central basin ($P = 0.56$, t -test), but then increased by 2002. Two years later, when the eastern basin was surveyed again (Ciborowski et al., in preparation), basin-wide *Dreissena* density was more than 6-fold lower than in 2002, and did not change substantially during the next ten years. The density differences between the central and eastern basins were even more dramatic when comparing *Dreissena* populations in the profundal zone (Fig. 2). In 2014, the average profundal mussel density in the central basin was 14 times lower than in the eastern basin ($84 \pm 59 \text{ m}^{-2}$ vs. $1193 \pm 217 \text{ m}^{-2}$ respectively, $P < 0.0001$, t -test). Mussels in the central basin were largely limited to the shallow nearshore area, while in the western and eastern basins they were distributed across the whole basin.

Dramatic differences in *Dreissena* density and biomass between time periods and basins are reflected in mussel clearance rates (Fig. 2). During the initial phase of the invasion in 1992 – 1998, when *Dreissena* density and biomass were high, the calculated percent of the water column cleared per day in spring in the central basin was higher ($5.22 \pm 2.28\%$) than in the eastern ($3.06 \pm 0.70\%$) and western ($2.88 \pm 1.86\%$) basins. At that time, the mussel population in the central basin was able to filter the volume of water equivalent to that of the central basin in 19 days, whereas it would take 33 and 35 days for mussels to filter the volume of water equivalent to that of the eastern and western basins respectively.

In 1999 – 2013, spring clearance rates in the central basin declined almost 5-fold compared to 1992 – 1998, while the eastern basin clearance rates increased by 2.5-fold (to $7.57 \pm 1.84\%$), and 3.7-fold in the western basin (Fig. 2). In spring 2014, mussel populations in the eastern basin were able to filter the whole basin in 13 days and in 7 days in the western basin, while approximately 90 days was required to filter the whole central basin.

Environmental parameters

To examine the impact of central basin *Dreissena* population declines on Lake Erie water quality parameters, we analyzed data grouped by the same three time periods: before *Dreissena* invasion (1983 – 1988), during high *Dreissena* densities in all basins (1989 – 1998), and during very low *Dreissena* density in the central basin, but high *Dreissena* density in the eastern and western basins (1999 – 2013) (Figures 3–6). We found that the period of introduction of *Dreissena* coincided with different, sometimes opposite changes in water transparency (Secchi depth) in different basins and seasons (Fig. 3). *Dreissena* introduction coincided with a 20% decrease in spring water transparency in 1989 – 1998 in the central basin ($P = 0.035$, Tukey HSD test) and a 2-fold increase in the eastern basin ($P = 0.019$), whereas no significant changes were observed in the well-mixed western basin compared to the pre-invasion period. The sharp decline in *Dreissena* density in the central basin in 1999 – 2014 coincided with a small insignificant decline in spring and summer transparency compared to 1989 – 1998, although spring transparency during this period was still

significantly lower ($P = 0.0003$) than that during the pre-invasion period. In contrast to the central basin, during the same time period, there was a further significant increase in spring transparency in the eastern basin, where *Dreissena* biomass remained high. In the western basin with similarly relatively stable *Dreissena* population, spring Secchi depth was significantly lower in 1999 – 2014 compared to the pre-invasion time. There were no significant changes in summer transparency in any of the basins or time periods.

Similar to changes in transparency, colonization of Lake Erie by *Dreissena* was accompanied by different patterns in water turbidity in different basins (Fig. 4). Compared to the pre-invasion period, spring surface turbidity from 1989 – 1998 did not change significantly in the western basin ($P = 0.487$), slightly but significantly increased in the central basin ($P = 0.014$), and decreased in the eastern basin ($P = 0.0004$). No significant changes were found in spring bottom turbidity between first and second time periods in any of the three basins (Fig. 4). The decline in *Dreissena* population in the central basin was concomitant with a strong significant increase in spring bottom and surface turbidity: 68% (equivalent to 1.6 NTU absolute increase) and 82% (1.7 NTU) increase for bottom and surface, respectively ($P < 0.0001$). In contrast, spring surface and bottom turbidity declined from 1989 – 1998 to 1999 – 2013 ($P = 0.010$ and $P < 0.0001$, respectively) in the eastern basin. No significant changes were found in spring surface western basin turbidity among any of the three time periods.

In contrast to the spring mixing period, the introduction of *Dreissena* was concomitant with significant decreases in summer bottom turbidity in the stratified central ($P = 0.015$) and eastern ($P < 0.0001$) basins, but not in the well-mixed western basin (Fig. 4). For summer surface turbidity, changes between 1983 – 1988 and 1989 – 1998 were similar in all three basins. Decline of *Dreissena* density was concomitant with increases in summer turbidity in the central basin both at the surface and near the bottom ($P < 0.001$). In the eastern basin, no changes were found in surface turbidity, while summer bottom turbidity further declined between second and third period of observation ($P < 0.0001$). In the western basin there was a significant increase in the summer surface ($P < 0.001$), but not bottom turbidity between 1989 – 1998 and 1999 – 2014.

The time period corresponding to *Dreissena* introduction did not coincide with a significant change in spring surface TP concentration in any of the basins (i.e. no change from 1983 – 1988 to 1989 – 1998) (Fig. 5). Summer TP decreased significantly only in the central basin ($P < 0.0001$). The period corresponding with the decline in *Dreissena* density in the central basin was concomitant with a significant increase in surface TP concentrations both in spring ($P = 0.008$) and summer ($P = 0.001$). In contrast, in the eastern basin which supported a large *Dreissena* population, there was no significant difference in TP concentration in either spring or summer between the 1989 – 1998 and 1999 – 2013 periods ($P = 0.14$ spring, $P = 0.10$ summer). In the western basin, there were no differences in TP among periods in either spring or summer.

The introduction of *Dreissena* was concomitant with nearly a 50% increase in spring TSP mean values in the central (absolute increase 1.8 $\mu\text{g/L}$, $P = 0.0027$) and eastern basins (absolute increase 2.4 $\mu\text{g/L}$, $P = 0.0047$) (Fig. 5). During summer, however, there was a

significant decline in central basin TSP following the introduction of *Dreissena* ($P = 0.010$). No changes were observed in the TSP concentration in the central basin concomitant with the decline of *Dreissena* in either season. In the eastern basin, spring TSP increased from the first to the second period, whereas summer TSP did not change from 1983 – 1988 to 1989 – 1998, but declined significantly thereafter. TSP dynamics was more variable in the western basin, but overall there was no significant change in summer TSP and a significant increase in spring TSP only from 1983 – 1988 to 1999 – 2013.

Following the introduction of *Dreissena*, there was a highly significant increase in spring dissolved silica concentration both at the surface and near the bottom in all basins ($P = 0.015$ for bottom silica in western basin, $P < 0.0001$ for other basins) (Fig. 6). Effect sizes ranged from a moderate 50% (from 0.36 to 0.54 mg/L) increase in bottom silica in the western basin to 3-fold and 6-fold (from nearly undetectable to 0.2 mg/L) increases in the eastern and central basins, respectively (note that raw values were used to calculate effect sizes, whereas analyses were done on log-transformed data). After the *Dreissena* population collapsed in the central basin, spring dissolved silica concentration significantly declined (surface: $P = 0.005$, near-bottom $P = 0.008$, approximately 40% or 0.08 mg/L decline in both cases) (Fig. 6). In contrast, in the eastern basin where the *Dreissena* population has maintained high densities, there were no significant changes in spring dissolved silica concentration between 1989 – 1998 and 1999 – 2013, with concentrations remaining elevated compared to the pre-invasion period ($P = 0.86$ surface, $P = 0.98$ bottom). In the western basin, dissolved silica continued to increase both near the surface and near the bottom between 1989 – 1998 and 1999 – 2013, though this increase was significant only at the surface ($P = 0.032$).

Discussion

Our analysis revealed that the decline in *Dreissena* density in the central basin was concomitant with a significant decrease in spring dissolved silica concentrations and an increase in total phosphorus and near bottom turbidity not seen in the western or eastern basins. We are the first to report that dreissenid-related shifts in water quality of invaded waterbodies are 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. Alternatively, at least some of the observed recent changes in the central basin environmental parameters may be due to the possible re-eutrophication of the basin associated with the increase in dissolved reactive phosphorous loading (Richards et al., 2010; Scavia et al., 2014).

The three basins of Lake Erie clearly show different, often opposite responses to the *Dreissena* invasion, suggesting that different environmental factors may govern ecosystem processes in the different basins. In the eastern basin, previous studies documented both short- and long-term increases in transparency, increases in dissolved silica concentration and a decrease in phytoplankton and turbidity after the establishment of *Dreissena* (Howell et al., 1996; Makarewicz et al., 2000; Barbiero and Tuchman, 2004; Barbiero et al., 2006). Using a longer dataset (1983 – 2014 vs. 1983 – 2004) we confirm earlier observed trends in the water quality parameters in this basin and in many cases document further changes, including a significant increase in spring transparency and decrease in turbidity between

1989 – 1998 and 1999 – 2014 (Figures 3–4). While early in the invasion there was a significant increase in spring TSP in the eastern basin (from $5.3 \mu\text{gP L}^{-1}$ in 1983 – 1988 to $7.7 \mu\text{gP L}^{-1}$ in 1989 – 1998), later in the invasion we found a significant decrease in summer TSP (from $2.8 \mu\text{gP L}^{-1}$ in 1989 – 1998 to $2.3 \mu\text{gP L}^{-1}$ 1999 – 2013) (Fig. 5). In 1999 – 2013, decreases in turbidity in the entire water column in spring and at the bottom in summer were observed. In addition, transparency increased dramatically in the spring. These changes coincided with an increase in estimated filtration capacity of mussels in the eastern basin. Taken together, they suggest that an increase in mussel filtration since 1999 has resulted in further increases in water clarity. Overall, the observed changes in the eastern basin water quality parameters were very similar to commonly observed changes in other waterbodies invaded by *Dreissena*, including increases in water clarity and decreases in phytoplankton, turbidity, and TP concentrations in the water column (reviewed in Karatayev et al., 1997, 2002, 2007, 2015; Higgins and Vander Zanden 2010; Mayer et al., 2014) and most likely were caused by mussel activity.

Although localized increases in water clarity were also seen in the western basin immediately after the appearance of *Dreissena* (Leach, 1993; Holland, 1993), more extensive longer-term analyses have indicated that spring turbidity actually increased in this basin (Makarewicz et al., 2000; Barbiero and Tuchman, 2004). Decreases in spring phytoplankton and chlorophyll have been observed (Holland, 1993; Makarewicz et al., 1999; Makarewicz et al., 2000; Barbiero and Tuchman, 2004), and were accompanied by increases in spring silica (Makarewicz et al., 2000), presumably due to reduced diatom uptake. The discrepancy in responses of chlorophyll and turbidity in the western basin was thought to be due to the high sediment loads entering the basin and resuspension of unassimilated non-algal particulates in the shallow basin. Again, our analysis of a longer dataset in most cases confirmed earlier observations of changes in the water quality parameters and for some parameters documented further changes, including a further decline in transparency and increase in spring TSP and dissolved silica concentration between 1989 – 1998 and 1999 – 2014, perhaps indicating ongoing re-eutrophication in the western basin (Figures 3, 5, 6). While early in the invasion there was a significant decrease in summer western basin surface turbidity (from 3.2 NTU in 1983 – 1988 to 2.3 NTU in 1989 – 1998), later in the invasion we found a significant increase in summer surface turbidity (to 4.2 NTU in 1999 – 2013) (Fig. 4). Overall, observed changes in the western basin are very different from changes documented in the eastern basin, as well as changes in other waterbodies invaded with *Dreissena*. Barbiero and Tuchman (2004) suggested that the external load of suspended solids to the western basin and sediment resuspension overwhelmed *Dreissena* filtering capacity and was the major reasons why no increase in spring water clarity was noticed after the introduction of mussels.

In the central basin, dynamics of some water quality parameters resemble patterns of the western basin (e.g., transparency, turbidity, and TP), while the changes in TSP and dissolved silica are very similar to the eastern basin (Figures 3–6). Previous studies reported changes in the water quality parameters in the central basin after the introduction of *Dreissena*, including decline in transparency in 1989 – 2004 compared to 1983 – 1988 (Barbiero and Tuchman, 2004) and increase in SRP, dissolved silica, turbidity, and chlorophyll in 1989 – 1993 compared to 1983 – 1988 (Makarewicz et al., 2000). These studies, however, did not

address the possible impacts of the sharp decline of *Dreissena* in the central basin on water quality parameters after 1998.

We found that decreasing *Dreissena* densities in the central basin were concomitant with a significant increase from 1989 – 1998 to 1999 – 2013 in spring surface turbidity (82% increase), spring bottom turbidity (68% increase) and TP (20% increase); changes not observed in the eastern and western basins (Figures 4, 5a). Significant increase in surface TP in the central basin after the decline of *Dreissena*, especially evident in summer (21% increase in 1999 – 2013 vs. 1989 – 1998), at least to some extent may be associated with the collapse of the mussel population, as there was only nonsignificant decrease in TP concentration in the same time period in the eastern basin where *Dreissena* density remained high in 2014. In addition, since a decline in TP concentration following *Dreissena* invasion has been recorded in many waterbodies (reviewed in Higgins and Vander Zanden, 2010; Mayer et al., 2014), we suggest that the decline of mussels may result in an increase in TP. It is well known that *Dreissena* spp. introduction may cause, or contribute to, the shift from a turbid to clear water in eutrophic lakes (Ibelings et al., 2007; Karatayev et al., 2014a; Mayer et al., 2014). Here we report for the first time that the decline of *Dreissena* in the invaded waterbody may cause a shift from a clear to turbid water state.

Alternatively, at least some of the observed recent changes in the central basin may be driven by the re-eutrophication which is especially evident in the western basin and associated with the increase in dissolved reactive phosphorous loading (Richards et al., 2010; Scavia et al., 2014). Indeed, in the western basin we found a consistent increase in spring TSP and a weak increasing trend in TP (Fig. 5), consistent with the ongoing eutrophication of the basin. Not surprisingly, increases in the TP and TSP in the western basin coincided with the decline in spring Secchi depth (Fig. 3). Trends in both turbidity and TP in the central basin closely matched those seen in the western basin. Therefore, it is possible that conditions in the western basin also contributed to the changes seen in the central basin, particularly given the markedly higher levels of turbidity and TP in the western basin and the lake's high flushing rate.

However, because of the re-eutrophication processes are by far stronger in the western basin, we may also expect more pronounced changes in the water quality parameters here, compare to the central basin. In contrary, in the western basin we observed only small nonsignificant increase in spring turbidity and TP between 1989 – 1998 and 1999–2013, while in the central basin these increases were more pronounced and significant, suggesting that these processes were associated with the decline in *Dreissena* population, rather than re-eutrophication of the basin. The impact of reduced filtration activity of *Dreissena* in the central basin is especially evident in changes in dissolved silica concentrations (Fig. 6). It is well known that dreissenids may suppress the diatom bloom (Fahnenstiel et al., 2010), which could in turn explain increase in silica concentrations (Higgins and Vander Zanden, 2010; Reavie et al., 2014). The sharp decline in *Dreissena* density may reduce mussels grazing impact on diatoms, allowing them to create high density, consuming large amount of silica. The highly significant increases in spring dissolved silica found in this study (in 1989 – 1998 compare to 1983 – 1988) following the introduction of *Dreissena* in all basins (Fig. 6) are consistent with previous reports from our program of post-dreissenid increases in

spring dissolved silica concentrations in the central and eastern basins (Makarewicz et al., 2000; Rockwell et al., 2005; Barbiero et al., 2006). The post-dreissenid spring dissolved silica increases in the eastern basin coincided with dramatic declines in total phytoplankton biomass and a shift towards a limited number of centric diatoms (Barbiero et al., 2006). After the *Dreissena* population in the central basin collapsed, spring dissolved silica concentrations significantly declined. This decline was observed in the central basin only, coincided with, and was likely caused by the increase in spring diatoms during the last 15 years in Lake Erie (Reavie et al., 2014, 2016). Reavie et al. (2016) hypothesized that the increase in diatoms was due to an increase in dissolved silica inputs from Lake Huron where silica has been increasing simultaneously with decreasing spring phytoplankton populations (Barbiero et al., 2012). Consistent increase in dissolved silica concentration in the western basin during all periods of observation may support the Reavie et al. (2016) hypothesis of external origin of dissolved silica. However, in contrast to the western basin, in the central basin there was a significant decline in dissolved silica concentration after the decline in *Dreissena* density. The decline in dissolved silica concentration and increase in diatoms in the central basin could be, at least partially, linked to the decline in the central basin *Dreissena* density. In contrast, in the eastern basin, there was no large change in spring dissolved silica concentration between the 1989 – 1998 and 1999 – 2013 time periods. The insignificant declines in spring dissolved silica concentration in the eastern basin (surface: 10%, $P = 0.86$, bottom: 13% $P = 0.98$) may have been influenced by the decline of silica in the central basin.

Conclusion

Usually *Dreissena* colonization is associated with the oligotrophication of an invaded waterbody, characterized by an increase in water clarity and a decrease in chlorophyll and TP concentrations (reviewed in Karatayev et al., 1997, 2002, 2007, 2015; Higgins and Vander Zanden, 2010; Mayer et al., 2014). We documented changes in water quality trends coinciding with dramatic declines in *Dreissena* populations in Lake Erie's central basin, including an increase in turbidity and TP. The binational effort to reduce TP loads entering the western and central basins of Lake Erie by 40% as a way of reducing harmful algal growth and minimizing the extent of hypoxic zones (GLWQA Annex 4 Objectives and Targets Task Team., 2015) may favor re-establishment of *Dreissena* population in the profundal zone of the central basin if hypoxia severity is successfully reduced. Recovery of *Dreissena* in the central basin may in turn contribute to a decrease in TP and an increase in water clarity, but may also contribute to the decline of spring diatom blooms (Fahnenstiel et al., 2010; Vanderploeg et al., 2010) and changes in zooplankton community structure (Barbiero et al., 2012; Vanderploeg et al., 2012) that have been observed in other Great Lakes. Finally, our results suggest that control or elimination of suspension feeders may have wide-ranging and sometimes unanticipated effects on the ecosystem.

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Figure 1.
Location of benthos stations (black triangles) sampled in 2014 and U.S. EPA GLNPO stations (open circles) in Lake Erie. Dashed lines indicate borders between lake basins.

Figure 2.

Dreissena spp. basin-wide densities (mean $\pm$ standard error) (a) and profundal densities (mean $\pm$ standard error) (c) in the western (grey solid line), central (black solid line) and eastern (dashed line) basins of Lake Erie. Area-weighted biomass and clearance rate (FC) calculated as the percentage of the water column cleared per day in the western (b), central (d), and eastern (e) basins in Lake Erie.

Figure 3.

Secchi depths for the three basins measured during spring and summer cruises. Boxes indicate standard error; horizontal lines indicate mean; whiskers indicate 95% confidence interval. Time periods: 1983 – 1988 - pre-*Dreissena* invasion; 1989 – 1998 - high *Dreissena* density in all basins; 1999 – 2013 - low density in central basin, high in eastern/western basin. Different letters indicate significant differences among means ($P < 0.05$, Tukey HSD test).

Figure 4.

Surface and near-bottom turbidity (NTU) in the three basins of Lake Erie measured during spring and summer cruises. Boxes indicate standard error; horizontal lines indicate mean; whiskers indicate 95% confidence interval. Time periods: 1983 – 1988 - pre-*Dreissena* invasion; 1989 – 1998 - high *Dreissena* density in all basins; 1999 – 2013 - low density in central basin, high in eastern/western basin. Different letters indicate significant differences among means ($P < 0.05$, Tukey HSD test). Analyses were done on log-transformed data but raw data are presented in the figure. Note different scales for surface and bottom turbidity in spring and summer.

Figure 5.

Surface total phosphorus (TP) and total dissolved phosphorus (TSP) concentrations for the three basins of Lake Erie measured during spring and summer cruises. Boxes indicate standard error; horizontal lines indicate mean; whiskers indicate 95% confidence interval. Time periods: 1983 – 1988 - pre-*Dreissena* invasion; 1989 – 1998 - high *Dreissena* density in all basins; 1999 – 2013 - low density in central basin, high in eastern/western basin. Analyses were done on log-transformed data but raw data are presented in the figure. Different letters indicate significant differences among means ($P < 0.05$, Tukey HSD test).

Figure 6.

Surface dissolved silica concentrations for the three basins of Lake Erie measured during spring cruises (only surface data are presented as patterns of silica changes at the surface and near the bottom were almost identical). Boxes indicate standard error; horizontal lines indicate mean; whiskers indicate 95% confidence interval. Time periods: 1983 – 1988 - pre-*Dreissena* invasion; 1989 – 1998 - high *Dreissena* density in all basins; 1999 – 2013 - low density in central basin, high in eastern/western basin. Analyses were performed on log-transformed data but raw data are presented in the figure. Different letters above boxes indicate significant differences among means ($P < 0.05$, Tukey HSD test).