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Changes in Lake Erie benthos over the last 50 years: Historical perspectives, current status, and main drivers

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ABSTRACT

During the last 50 years the ecosystem of Lake Erie has experienced major environmental changes, from anthropogenic eutrophication in 1930–1960s, to nutrient and pollution abatement in the 1970s, and then the introduction of exotic dreissenids in the 1980s. We used multivariate statistical techniques to examine long-term changes in the zoobenthic community, comparing contemporary collections (2009, 2011–2012) and historical data (1963–1965, 1978–1979, 1993, and 1998). The Lake Erie benthic community underwent significant changes during each decade examined, showing signs of recovery following ecosystem restoration in the 1970s, but then experiencing major structural and functional changes after dreissenid (*Dreissena polymorpha* and *D. r. bugensis*) introductions. There was a significant temporal trend in community composition changes from 1963 to 2012, and the largest difference was found between pre- and post-dreissenid invasion communities. Currently the lake-wide benthic community is dominated by dreissenids both in density (41%) and total wet biomass (97%), followed by oligochaetes and chironomids. The largest benthic density was found in the central basin, and the greatest biomass in the eastern basin. The number of exotic species found in benthic surveys increased every decade, from 1 in 1963 to 10 in 2009–2012, and the majority of the invaders were molluscs. Whereas the role of benthic invaders in community diversity is still low, their impact has had enormous consequences for the whole ecosystem.

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Introduction

The story of Lake Erie is a classic example of how profoundly human activity can affect the structure and function of an ecosystem. Further, this case study illustrates the difficulty in predicting the intentional and unintentional consequences of human actions. Lake Erie experienced anthropogenic eutrophication in 1930–1960s, followed by a successful bi-national effort in nutrient and pollution abatement in the 1970s (Sweeney, 1995). The ecosystem recovery initiated by planned abatement programs was then followed by major ecosystem changes after the accidental introduction of natural “ecosystem engineers”—exotic dreissenids (Conroy and Culver, 2005; Conroy et al., 2005b; Hecky et al., 2004; Mills et al., 1993, 1998). The recovery of the benthic

invertebrate community of Lake Erie has not been complete; the history of this community demonstrates how planned actions such as abatement may aide recovery, but unplanned actions such as species invasions will continue to make the trajectory of recovering systems unpredictable.

The degradation of Lake Erie started perhaps in the early 1800s with massive forest cutting, construction of sawmills and dams and the draining of wetlands (Sweeney, 1995). The first report on deterioration of water quality was issued in 1918 by the International Joint Commission on the Pollution of Boundary Waters Reference stating that the “... situation along the frontier is generally chaotic, everywhere perilous and in some cases, disgraceful” (International Joint Commission, 1918). The most dramatic growth in watershed population and economy occurred from early 1900 to 1950s; by 1930, the Great Lakes basin population increased one third in 20 years and became close to 23 million. In 1940s high demands for chemicals, rubber, steel, etc. for the Second World War Allied effort led to a major industrial expansion in the Great Lakes basin, resulting in large-scale chemical and heavy metal discharges to the lakes. The heaviest pollution appears to have occurred in the 1960s and 1970s when Lake Erie was called “America’s Dead Sea” (Beeton, 1965; Sweeney, 1995).

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The best indicators of the deteriorating conditions, the “canaries in the coal mine”, were the mayflies *Hexagenia* in western Lake Erie (Britt, 1955a, 1955b). Prior to human-driven eutrophication, mayflies were abundant: for example in the 1920s in Cleveland “the horse-drawn dump wagons [were not] adequate for the loads of Mayflies which piled up overnight under the lamp posts during a warm summer evening” (Dambach, 1969). In the 1930s, the benthic community of the western basin was dominated by *Hexagenia* and trichoptera *Oecetis* with average mayfly densities of 300–500 m⁻², and a maximum average to up to 1000 m⁻² (Britt, 1955a, 1955b; Shelford and Boesel, 1942). These extensive *Hexagenia* populations were devastated in September 1953 as a result of the first recorded significant large-scale depletion of dissolved oxygen in the western basin. Densities of mayflies somewhat recovered in 1954 (Britt, 1955a, 1955b), but then were reduced again almost to extirpation in 1960s (Beeton, 1961; Carr and Hiltunen, 1965). Due to the shallow depth of the western basin (average depth 7.4 m), the discharge of the major tributaries (the Detroit and Maumee rivers that account for > 90% of the organic loading and 84% of the water volume entering the lake), and its proximity to large urban centers such as Detroit and Toledo, this basin is highly vulnerable to changes caused by human activities and was the first to suffer from anthropogenic eutrophication (Hartman, 1972; Makarewicz and Bertram, 1991). Extensive changes have occurred in other groups of benthos, including a sharp decline in the density of *Oecetis*, and a large increase in the taxa tolerant to organic enrichment (e.g., tubificids and midges) (Carr and Hiltunen, 1965). Historically, the dramatic degradation of the benthic community in the western basin has provided the strongest evidence of the magnitude of change in the Great Lakes (Brinkhurst, 1969).

Under the Great Lakes Water Quality Agreement of 1972 signed by Canada and the U.S., an extensive binational effort was undertaken to reduce and eliminate sources of pollution to Lake Erie, including bans on the sale of phosphate detergents, improvements in organic waste collection and treatment systems, and reductions in industry discharges (Sweeney, 1995). The results were dramatic and in some cases occurred more rapidly than expected (Sweeney, 1995). Water quality in the lake responded to those measures; open-lake concentrations of total phosphorus, chlorophyll *a*, phytoplankton abundance and biomass were reduced by the mid-1980s, and the pelagic ecosystem became less eutrophic (Makarewicz and Bertram, 1991). The abundance and dominance of oligochaetes in the western basin in the 1970s decreased compared to the 1960s (Dermott, 1994). Reduction in the number of oligochaetes in nearshore zones and at the mouths of the large tributaries in late 1970s–early 1980s was consistent with the reduced eutrophication (Dermott, 1994; Schloesser et al., 1995).

Recently Lake Erie has become a “hot spot” for the introduction of exotic species. Both of the most well-known aquatic invaders in North America were first detected in Lake Erie: *Dreissena polymorpha*, the zebra mussel, in 1986 (Carlton, 2008), and *Dreissena rostriformis bugensis*, the quagga mussel, in 1989 (Mills et al., 1993). Both *Dreissena* species are ecosystem engineers (Karatayev et al., 1997, 2002, 2007b) that fundamentally change the flow of energy and nutrients through lake ecosystem and affect both the benthic and pelagic communities in ways that are not entirely predictable (Arnott and Vanni, 1996; Bunt et al., 1993; Conroy and Culver, 2005; Conroy et al., 2005a, 2005b; Howell et al., 1996; MacIsaac et al., 1992; Makarewicz et al., 2000; Mellina et al., 1995; Nicholls and Hopkins, 1993). Benthic freshwater systems are often detritus dominated and have little influence on planktonic systems (Hutchinson, 1993). Dreissenids are able to control pelagic processes by removing particulate matter, increasing water transparency and hence the volume of the photic zone, impacting phytoplankton standing stock, and therefore, influencing planktonic trophic interactions (Higgins and Vander Zanden, 2010; Karatayev et al., 1997, 2002, 2007b; Mills et al., 1993, 1998). As a result, the role of the benthic community in lakes populated by dreissenids increases tremendously and the benthos become capable of controlling processes

and dynamics in the planktonic system and affecting the whole ecosystem. Dreissenids also have strong local impacts by physically changing benthic substrates, and providing shelter and food for other benthic invertebrates (Burlakova et al., 2005, 2012; Higgins and Vander Zanden, 2010; Karatayev and Burlakova, 1992; Karatayev et al., 1997, 2002, 2007b; Mayer et al., 2002; Ward and Ricciardi, 2007). Dreissenids have strong interactions with many species and facilitate certain functional groups (Burlakova et al., 2012; DeVanna et al., 2011b); and thus some of their effects in particular systems have run contrary to original predictions, adding further uncertainty to understanding the trajectory of the benthic community in Lake Erie.

We used historical data on benthic community composition from Lake Erie covering the last 50 years, in combination with three years of contemporary sampling to examine the long-term changes in the zoobenthic community. We used multivariate community analysis to test the temporal changes in community composition, and to assess whether invasive species played a role in altering the benthos.

Materials and methods

To determine the species composition, abundance, distribution, and year-to-year variability of the Lake Erie zoobenthos community, a total of 500 benthic samples were collected in western, central, and eastern basins in 2009, 2011, and 2012. We used transects running perpendicular to the shore with fixed sample stations at 2, 5, 10, and 20 m (Pennuto et al., in this issue). In 2009, sampling was done along six transects located near the major lake tributaries (Sandusky and Grand Rivers in central basin, and Cattaraugus Creek in eastern basin) within the Nearshore and Offshore Lake Erie Nutrient Study (NOLENS) (Fig. 1). In 2011–2012 samples were collected from eight transects spaced approximately equidistant along the southern Lake Erie shoreline (two in eastern and western basins, and four in central basin, Fig. 1) within the Lake Erie Nearshore and Offshore Nutrient Study (LENONS). Two of these transects (Grand River east (GRE) and Cattaraugus Creek west (CCW)) also were sampled as part of the 2009 NOLENS project. Samples were collected twice a year—in June and in August or September, and the data were averaged for each station. For each transect in the central and eastern basins, samples were collected from the same depths as in 2009. In the western basin, the deepest site was at 15 m depth. As the majority of 2-m samples in the central and eastern basins in 2011 yielded no animals, we excluded them from the survey in 2012. Three or more replicate samples were taken at each depth and processed separately, and then the data were pooled during analysis. All samples were collected with a petite Ponar grab (area 0.0231 m⁻²) or Ekman grab (area 0.0225 m⁻²), with the exception of 9 samples in 2009, which were collected by SCUBA divers from 2 and 5 m (GRE transect) and 10 m (CCW) using an air-lift sampler (area 0.0625 m⁻², Pennuto et al., 2012a). In addition, 55 samples were collected with a Ponar grab (area 0.0529 m⁻²) in June 2009 aboard of EPA R/V *Lake Guardian* at 22 routine EPA stations in all 3 basins (ER 09, 10, 15 M, 30, 31, 32, 36, 37, 38, 42, 43, 58, 59, 60, 61, 63, 73, 78, 91 M, 92, 93B, 95B, the coordinates and depths info at http://www.epa.gov/glnpo/monitoring/sop/appendix_b.pdf, accessed February 12, 2014). Samples were washed through a 500- μ m mesh net. All macroinvertebrates collected were fixed with 10% neutral buffered formalin, and identified to the lowest possible taxonomic level (usually species, genus or family), counted, blotted dry on absorbent paper and weighed to the nearest 0.0001 g (total wet mass). We did not attempt to count ostracods and nematodes. The oligochaete, *Branchiura sowerbyi*, was identified to species, but all others were categorized as oligochaetes.

Historical sampling

To examine the effect of the *Dreissena* spp. invasion on the benthic community we compared pre- (prior to 1986) and post-invasion historic information with the results of recent sampling. We used the Great

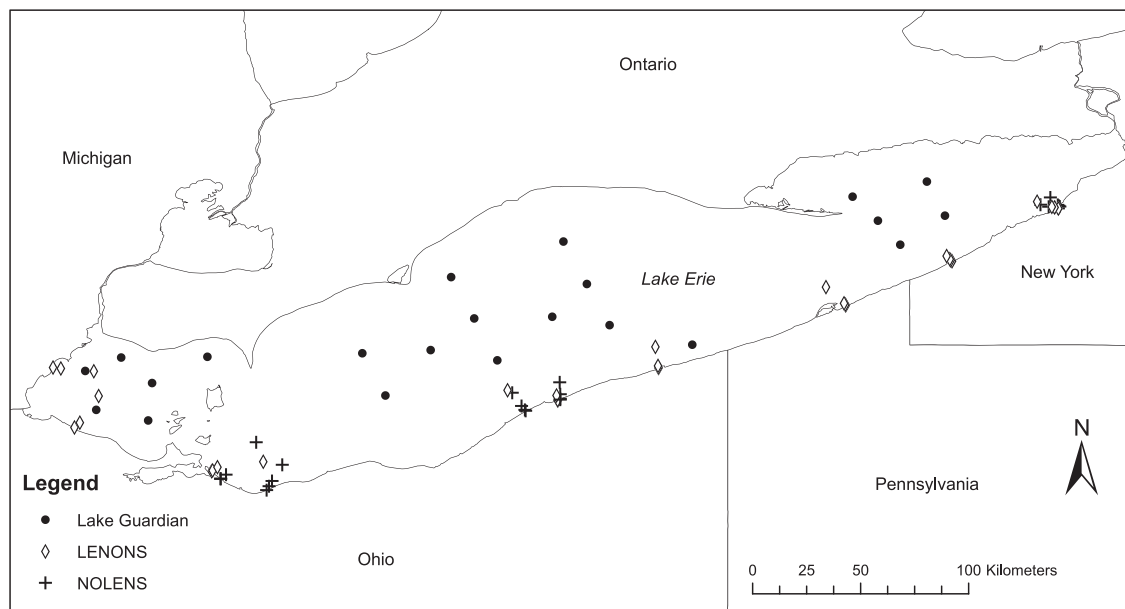


Fig. 1. Locations of sites on Lake Erie that were sampled as part of the Nearshore and Offshore Lake Erie Nutrient Study (NOLENS, 2009), aboard the R/V *Lake Guardian* (2009), and the Lake Erie Nearshore and Offshore Nutrient Study (LENONS, 2011–2012).

Lakes Institute Cruise's benthic density data from a total of 1168 samples collected with a Franklin–Anderson grab (area 0.028 m^{-2}) from 83 sites sampled from 1 to 8 times a year during April–November in 1963–1965 (Barton, 1988). Data from the 1970s were collected using SHIPEK grabs (area 0.0417 m^{-2}) in October from 89 sites in 1978 (central and eastern basins), and 69 sites in the western and central basins in 1979 (Dermott, 1994). Average data from Dermott and Dow (2008) for two depths ranges (<16 and >16 m) and among basins, collected with a petite Ponar grab (area 0.0223 m^{-2}) were used for 1993 and 1998.

To minimize the effects of changes in taxonomic designations (Metzeling et al., 2002), we used a similar, common level of taxonomic resolution to analyze all historic and recent data, and synonymized historic and current species names. For some taxa, to avoid possible species confusion, we used the lowest common taxon for analysis. For example, all oligochaetes species identified in the 1970s and the oligochaete families found in the 1990s, but not identified in our study, were reduced to *Oligochaeta* spp. (except for *B. sowerbyi*). We also combined all species of *Pisidium* found in 2009–2012 (e.g., *P. idahoense*, *P. compressum*, and *P. variable*) into *Pisidium* spp., except for the exotic *P. amnicum*. Likewise, different chironomids identified to genus and species level in our study, were aggregated to Chironomidae spp. for historical comparison. Similarly we combined all *Sphaerium* species and all *Musculium* species into one group *Sphaerium* spp., except for the exotic *S. corneum*.

Data analysis

We used a non-parametric Kruskal–Wallis test (as no transformation was able to normalize the species abundance data due the large number of zero values) to test whether the total combined density and biomass of all species in the zoobenthos differed among years in 2009, 2011 and 2012. These analyses were performed on data collected from permanent transects (NOLENS and LENONS data) and excluded samples from EPA sites collected in 2009 in the offshore zone of the lake (as they were not resampled in 2011–2012) using Statistica software (STATISTICA data analysis software system, version 10.0, StatSoft, Inc. 1984–2011, www.statsoft.com).

We tested for differences in community structure through time with nonparametric multivariate statistical techniques on data matrices of all species and their abundances found in the community in PRIMER 6 (Plymouth Routines In Multivariate Ecological Research, Version 6.1.6, Primer E-Ltd. 2006). A fourth-root transformation was used to normalize the data for analysis. The similarity of the community composition was summarized by calculating Bray–Curtis similarity indices (BC) ranging from 0 (no species in common) to 1 (identical samples) (Bray and Curtis, 1957; Clarke, 1993). To visualize the differences among assemblages we used Non-metric Multi-Dimensional Scaling (NM-MDS), which calculates a set of metric coordinates for samples, most closely approximating their nonmetric distances. NM-MDS was found to be consistently reliable in a comparative study of ordination methods for community data (Kenkel and Orlóci, 1986). In this analysis we excluded sites where less than two species were collected. For complete description of the tests used please see Clarke and Green (1988) and Clarke (1993).

We tested for differences in community composition among different transects, lake zones and years with Analysis of Similarities (ANOSIM), a resampling technique that uses permutation/randomization methods on BC similarity matrices to identify differences among groups of samples, after which pairwise comparisons are conducted (Clarke, 1993). Large values of the test statistic (R) indicate complete separation of groups, and small values (close to 0), little or no separation. Thus, R is a useful comparative measure of the degree of separation, and its value is at least as important as its statistical significance which is limited by the number of available permutations (Clarke and Warwick, 2001).

Community changes could be related to a temporal trend, and the PRIMER RELATE algorithm was used to find the Spearman rank correlation between the biotic resemblance matrix (BC of fourth-root transformed benthos density data from 1963 to 2012) and the seriation resemblance matrix of sampled years (Euclidian distances) (Clarke et al., 1993).

We used “Similarity Percentage” (SIMPER) analysis to examine the contribution of each species to the average BC similarity among communities within each level of factors tested. In addition, we determined the contribution of each species to the average BC dissimilarity between these groups. When we tested for differences in communities with and

without *Dreissena*, we excluded *Dreissena* densities. “Similarity profile” permutation tests (SIMPROF routine) were used to test for structure in the data (Clarke and Gorley, 2006). To distinguish communities among years, we used Cluster analysis followed by SUMPROF to find significant difference among clusters. All tests effects were considered significant if $p < 0.05$.

Results

2009–2012 community structure

We found 63 taxa (species, genera or higher taxa) of benthic macroinvertebrates in Lake Erie, including 26 taxa of chironomids, and 22 mollusc species. The most abundant invertebrates in the lake, excluding unidentified oligochaetes, were *D. r. bugensis* (35% of total density), *Chironomus* spp., *Pisidium* spp., and *D. polymorpha* (Table 1; Fig. 2; Electronic Supplementary Material SI 1). Exotic molluscs also dominated in terms of biomass: *D. r. bugensis* represented 95% of total community wet biomass, followed by *D. polymorpha* (Table 1; Fig. 2).

The highest total benthic density in 2009–2012 was found in the central basin ($2883 \pm 320 \text{ m}^{-2}$, mean \pm standard error here and elsewhere) (SI 2), and was dominated by unidentified oligochaetes (35% of total density, Fig. 3), followed by *Dreissena* spp. and chironomids (mostly *Chironomus* spp. and *Procladius* sp.).

In contrast to the central basin, oligochaetes formed only 7% of the total benthic invertebrate density in the western basin (average combined basin density $2377 \pm 437 \text{ m}^{-2}$) (Fig. 3). Sixty seven percent of the benthic community in this basin was comprised of *Dreissena* spp., followed by chironomids (mostly *Chironomus* spp. and *Coelotanyus tricolor*). Other common taxa were non-dreissenid molluscs, isopods *Caecidotea* sp. (syn. *Asellus* of earlier authors) and the exotic amphipod *Echinogammarus ischnus*. The mayfly *Hexagenia* was mainly found in this basin and constituted 6% of total non-dreissenid benthic density.

The eastern basin had the lowest total density of benthic invertebrates relative to the other basins ($2016 \pm 342 \text{ m}^{-2}$, SI 2), and was dominated by *Dreissena* spp., oligochaetes, and chironomids (Fig. 3). Non-dreissenid molluscs were very rare in eastern basin (only 0.5% of total density) compared to the western (9%) and central (13%) basins.

Dreissena spp. dominated benthic biomass in all basins, comprising 99.8% of the total wet biomass in the eastern basin, 96% in the central, and 88% in the western basin (Fig. 3, SI 2). In the eastern and central basins oligochaetes and chironomids together were responsible for the majority of non-dreissenid biomass (Fig. 3). In contrast, in the western basin both *Pisidium* and *Hexagenia* contributed eight times more to the

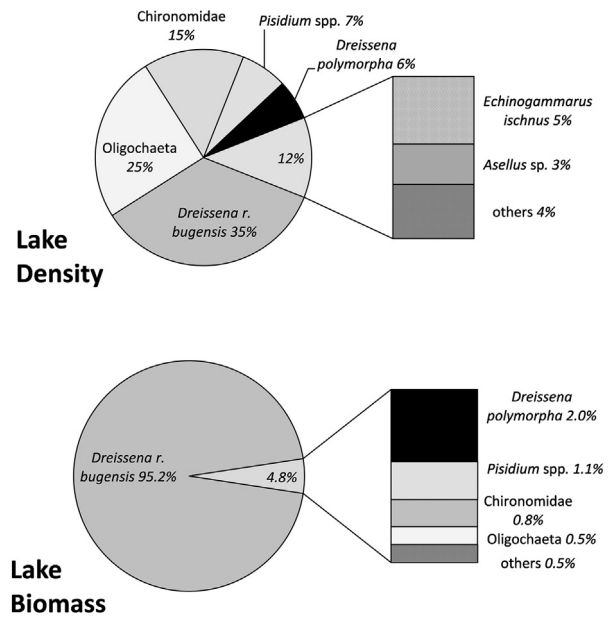


Fig. 2. Contribution (percent from total) of major taxa to the density (upper plot) and biomass (lower plot) of Lake Erie benthic communities in 2009–2012.

total benthic biomass than oligochaetes and chironomids combined (Fig. 3).

The total density and biomass of benthos collected in transects in 2009, 2011 and 2012 (excluding profundal sites sampled from R/V Lake Guardian in 2009 and not repeated in following years) were significantly different among years (density: $p = 0.005$; biomass: $p = 0.0148$, Kruskal–Wallis test) (Table 1). Most of the variation, however, was due to *Dreissena* abundance (Karatayev et al., in this issue), and the difference among years became insignificant after *Dreissena* was excluded from the analysis (density: $p = 0.19$; biomass: $p = 0.20$).

Community structure based on the density of all macroinvertebrate taxa collected from transects sampled in 2009, 2011 and 2012, did not differ significantly among the years ($R = 0.024$, $p = 0.122$; 1-way ANOSIM), and there were no significant temporal trends in the community (Spearman $\rho = 0.046$, $p = 0.088$). There was a significant difference in communities among the basins when we considered both basin and depth factors simultaneously (basin: $R = 0.226$, $p = 0.001$; depth: $R = 0.397$, $p = 0.001$, two-way crossed ANOSIM). The largest differences were found between eastern and western basins ($R =$

Table 1
Density (N, ind. m^{-2}) and biomass (B, g m^{-2}) of major benthic groups and selected species^a found in Lake Erie in 2009–2012 surveys (mean \pm standard error, n —number of sampling sites). In 2009 samples were taken from EPA routine sites aboard R/V Lake Guardian, and from NOLENS transects; in 2011–2012—from LENONS transects only.

Taxa	2009 (n = 46)		2011 (n = 30)		2012 (n = 24)	
	N	B	N	B	N	B
Mollusca	1119 \pm 233	349.2 \pm 103.5	1025 \pm 254	198 \pm 62.7	1835 \pm 343	448.9 \pm 105.9
<i>Dreissena r. bugensis</i>	828 \pm 218	337.3 \pm 102.8	834 \pm 238	193.2 \pm 62.8	1062 \pm 213	430.7 \pm 106.5
<i>Dreissena polymorpha</i>	53 \pm 22	3.8 \pm 1.9	77 \pm 51	4.0 \pm 2.8	399 \pm 221	15.6 \pm 6.2
Mollusca without <i>Dreissena</i>	237 \pm 54	8.2 \pm 6.8	114 \pm 39	0.9 \pm 0.3	373 \pm 150	2.6 \pm 1.1
<i>Hexagenia</i> sp.	17 \pm 10	0.9 \pm 0.7	12 \pm 6	0.1 \pm 0.1	7 \pm 4	0.2 \pm 0.1
Oligochaeta	550 \pm 102	2.3 \pm 0.5	785 \pm 176	1.1 \pm 0.3	616 \pm 157	1.2 \pm 0.3
Chironomidae	271 \pm 44	3.4 \pm 1.3	381 \pm 80	1.2 \pm 0.4	578 \pm 156	2.4 \pm 1.0
Hirudinea	10 \pm 3	0.06 \pm 0.02	16 \pm 7	0.08 \pm 0.04	20 \pm 6	0.12 \pm 0.03
Amphipoda	107 \pm 55	0.3 \pm 0.1	117 \pm 74	0.2 \pm 0.1	158 \pm 60	0.3 \pm 0.1
Total benthos	2091 \pm 266 ^b	356.2 \pm 103.2 ^b	2364 \pm 373	200.9 \pm 62.6	3488 \pm 499	453.6 \pm 105.4
Total benthos without <i>Dreissena</i>	1209 \pm 156	15.2 \pm 6.9	1453 \pm 275	3.8 \pm 1.0	2026 \pm 485	7.2 \pm 1.9
Total exotic species	1004 \pm 249	341.9 \pm 103.8	1038 \pm 310	197.7 \pm 62.8	1646 \pm 379	448.2 \pm 106.1
Total native species	1087 \pm 153	14.3 \pm 6.8	1327 \pm 275	3.2 \pm 0.9	1842 \pm 493	5.4 \pm 1.7

^a The detailed information on all taxa identified in this study can be found in SI 1, 2.

^b NOLENS transect data only ($n = 24$): $N = 1598 \pm 398 \text{ m}^{-2}$, $B = 330.2 \pm 147.9 \text{ g m}^{-2}$.

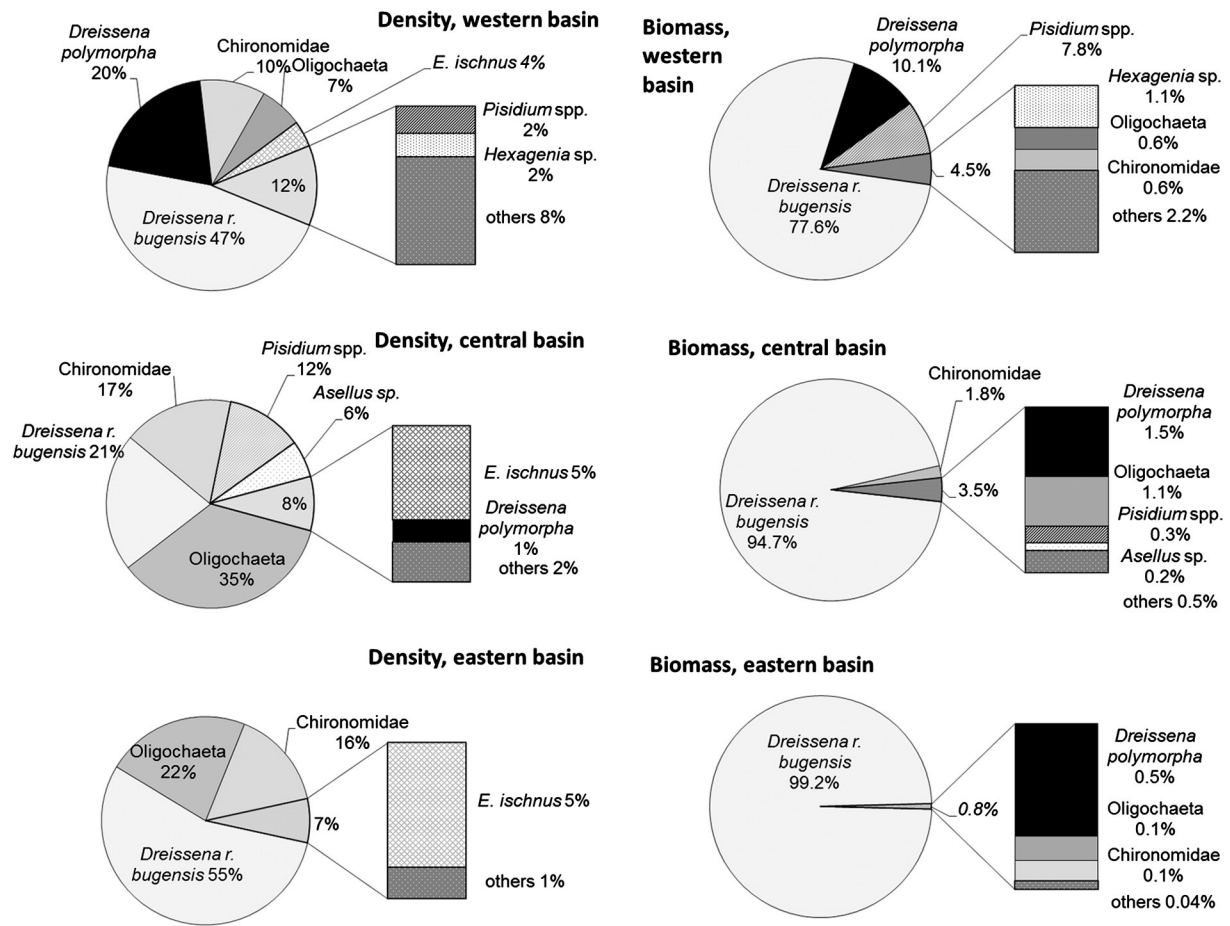


Fig. 3. Contribution (percent from total) of major taxa to the density (left panel plots) and biomass (right panel plots) of Lake Erie benthic communities in western, central and eastern basins in 2009–2012.

0.311, $p = 0.001$, pairwise tests after ANOSIM). There was a significant correlation between changes in community structure with depths (Spearman $\rho = 0.25$, $p = 0.001$), and all sampled depths (2, 5, 10, 15 and 20) were significantly different ($R = 0.22$ – 0.85 , $p < 0.05$, pairwise tests) except for depths 5 and 10 m ($R = 0.063$, $p = 0.12$). Similar patterns were found in community analyses based on biomass: there were no differences in macroinvertebrate communities collected from transects sampled in 2009, 2011 and 2012 among the years ($R = 0.021$, $p = 0.149$; 1-way ANOSIM), and no temporal trends (Spearman $\rho = 0.029$, $p = 0.188$).

The presence of *Dreissena* in samples had a large effect on the structure of benthic community (density: $R = 0.486$, $p = 0.001$, Fig. 4A; biomass: $R = 0.703$, $p = 0.001$, 1-way ANOSIM). The effect of *Dreissena* presence was smaller, but still significant, when we excluded *Dreissena* density and biomass from the analysis (density: $R = 0.107$, $p = 0.038$, Fig. 4B; biomass: $R = 0.146$, $p = 0.007$, 1-way ANOSIM).

To understand the differences in the composition of communities with and without *Dreissena* and to identify species responsible for dissimilarity of these communities, we examined the contribution of each species to the average BC similarity in each community. Samples with and without *Dreissena* (dissimilarity 68%) differed in oligochaetes density, which were 1.8 times more abundant in samples without *Dreissena*. This difference in oligochaetes density had the largest contribution (8.4%) to the dissimilarity between these groups. Likewise, densities of filter-feeding molluscs *Pisidium*, predatory chironomid larvae *Procladius* and *Cryptochironomus* were twice those of non-*Dreissena* samples, contributing further to the dissimilarity between samples with and without *Dreissena*. Species that were more abundant in the

presence of *Dreissena* included the exotic amphipod *E. ischnus* (densities 226.5 vs 0.7 m^{-2}), chironomids *Chironomus* (244.6 vs 93.9 m^{-2}), *Coelotanyus tricolor* (18.9 vs 3.9 m^{-2}), *Dicrotendipes tritonus* (18.7 vs 0.3 m^{-2}), and isopods *Caecidotea* (135.7 vs 1.7 m^{-2}).

Historical comparison

There was a significant difference among benthic communities in each decade from the 1960s to the 2010s ($R = 0.351$, $p = 0.001$; 1-way ANOSIM, Fig. 5, SI 3). The largest differences were found between communities before and after *Dreissena* invasion: between the 1960s and 1990s ($R = 0.640$, $p = 0.001$, pairwise tests after ANOSIM), and the 1970s and 1990s ($R = 0.509$, $p = 0.001$). The differences between pre-invasion decades and recent communities (2009–2012) were smaller ($R < 0.460$, $p = 0.001$) (SI 3). In contrast, pre-invasion communities were much more similar ($R = 0.24$, $p = 0.001$), and there was no significant differences between communities in the last two decades after *Dreissena* invasion ($R = 0.062$, $p = 0.185$). The difference was still significant (in most cases) when we excluded *Dreissena* from the analysis (SI 3).

Cluster analysis on average yearly densities showed significant differences ($p < 0.003$, SIMPROF test) among these time periods, and same clusters were still significant ($p = 0.001$) with and without consideration of *Dreissena* (Fig. 5B, D). Pre-invasion years clustered significantly by decades and were similar at 69% level ($p = 0.001$). This pre-invasion cluster was, however, more similar to 2009–2012 than the community in 1993–1998 (similarity 64 vs. 56%, $p = 0.001$).

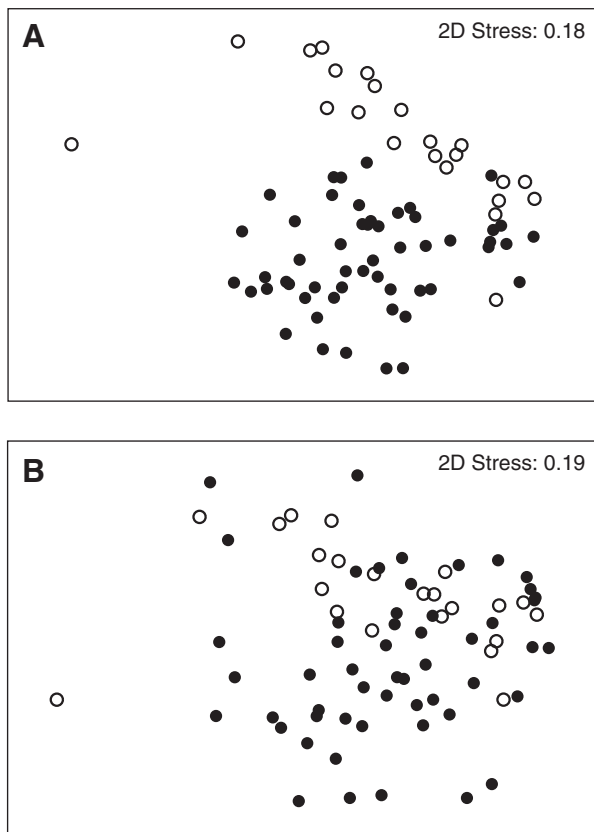


Fig. 4. NM-MDS ordination plots of the benthic community structure of Lake Erie based on Bray–Curtis similarities (by density) for samples collected from transects in 2009, 2011, and 2012. Stress = 0.18. There were significant differences in community structure between samples with (filled circles) and without (open circles) *Dreissena*. Analysis was done with consideration of *Dreissena* (A) and excluding *Dreissena* densities (B).

To follow the changes in benthic community structure among decades, we made pairwise comparisons excluding *Dreissena* from the analysis.

1963–65 vs 1978–79: During this decade, densities of most dominant taxa increased dramatically: oligochaetes—6-fold, contributing the largest part (20%) to the dissimilarity between communities, *Pisidium*—10-fold, chironomids—3-fold, *Sphaerium*—4-fold, *Diporeia*—3-fold, and *Caecidotea*—8-fold (SI 4; Fig. 6). Density of the polychaeta *Manayunkia speciosa* increased 65 times, and the exotic oligochaete *B. sowerbyi* was found in the samples. The exotic gastropod *Bithynia tentaculata* decreased in abundance and was not found alive in the subsequent surveys (Table 3; SI 1).

1978–79 vs. 1993, 1998: During the first decade of *Dreissena* invasion the densities of native oligochaetes and chironomids increased further (~3- and 2-fold), contributing the largest share (16% and 9%, respectively) to dissimilarities between communities (SI 4). Density of molluscs *Pisidium* and *Sphaerium*, decreased ~2- and 3-fold, and *Diporeia* declined to levels below detection. However, in the same decade the density of *Hexagenia* increased 10-fold (Fig. 6), and the density of native *Gammarus*—6-fold (SI 1).

1993, 1998 vs 2009–2012: after two decades of *Dreissena* presence in the lake, the densities of oligochaetes and chironomids declined dramatically (13- and 2-fold) for the first time in the previous 50 years, contributing the largest share (23 and 7%) to dissimilarities between communities (SI 4). Native filter-feeding molluscs *Pisidium* and *Sphaerium* continued to decline (1.8 and 3 times, correspondingly). The exotic *E. ischnus* was established and became one of the dominant species, while native *Gammarus* was found rarely in our surveys. The densities of Hirudinea, Trichoptera, and native *Valvata*

declined as well (3, 5, and 53-fold respectively), while *Hexagenia* maintained its abundance (Fig. 6; SI 1, 2). The dominance of exotic species in the community was further augmented by increased density of *Valvata piscinalis*, *B. sowerbyi*, *Potamopyrgus antipodarum*, *Corbicula fluminea*, *Sphaerium corneum*, and *P. amnicum* (Table 3; SI 1).

Changes in benthic communities after *Dreissena* invasion

Using a common level of taxonomic resolution, we compared the benthic community composition (species presence and density) before (1963–1965, 1978–1979) and after *Dreissena* invasion (1993, 1998, 2009, 2011–2012). We found that the benthic community (all taxa included) was significantly different between these two periods ($R = 0.41$, $p = 0.001$; 1-way ANOSIM, Fig. 5A), and the difference was significant even when we excluded *Dreissena* from the analysis ($R = 0.24$, $p = 0.001$; 1-way ANOSIM).

We found a significant temporal trend in benthic community from 1963 to 2012: there was a correlation between the seriation similarity matrix built on temporal distances in samples among years, and the biotic matrix of the samples (Spearman $\rho = 0.350$, $p = 0.001$) (Fig. 5C). However, a large part of this relationship was due to *Dreissena* invasion, as the correlation coefficient was similar when we considered time since *D. polymorpha* invasion (Spearman $\rho = 0.345$, $p = 0.001$) or *D. r. bugensis* invasion (Spearman $\rho = 0.344$, $p = 0.001$). The correlation was lower but still significant when we repeated the analysis excluding *Dreissena* (years: $\rho = 0.241$, $p = 0.001$; time since *D. polymorpha* invasion: $\rho = 0.216$, $p = 0.001$; time since *D. r. bugensis* invasion: $\rho = 0.217$, $p = 0.001$).

To identify the changes in benthic community structure after the *Dreissena* invasion, we compared the pre- and post-invasion community (excluding *Dreissena*). In pre-*Dreissena* years, the most abundant and wide-spread taxonomic group was Oligochaeta, which contributed 47% to the similarity of samples in the pre-invasion community. The next most abundant groups were Chironomidae (27%) and *Pisidium* (15%). Other important taxa were *Sphaerium*, Hirudinea, the isopod *Caecidotea*, and amphipods *Diporeia* and *Gammarus*. Collectively, these animals comprised 99% of community similarity.

After the *Dreissena* invasion, the dominant complex of the community (excluding *Dreissena* spp.) remained the same: chironomids (42%), oligochaetes (42%), and *Pisidium* (5%). However, exotic amphipods *E. ischnus*, and oligochaete *B. sowerbyi* become more important in the community (4% and 1%, respectively).

The major contributors to the dissimilarity between pre- and post-invasion communities were the native oligochaetes, *Pisidium*, and *Sphaerium* that decreased in density, and the disappearance of *Diporeia* (Table 2). However, some groups (e.g., chironomids, *Caecidotea*, *Valvata tricarinata*, Turbellaria) increased in abundance in the last two decades. *Hexagenia* became common in the western basin of the lake. A number of exotic species increased in their abundance (*B. sowerbyi*, *P. antipodarum*, *V. piscinalis*, *S. corneum*, *C. fluminea*, and *P. amnicum*, Table 3), while *B. tentaculata* decreased in density and distribution in the last two decades.

When dreissenids were included in community analysis, *D. r. bugensis* became the third co-dominant in the post-invasion community, contributing 19% to the community similarity (while *D. polymorpha*—only 2%). *Dreissena r. bugensis* was also contributing the most to the dissimilarity between pre- and post-invasion communities (16.5%)—more than the main co-dominants, oligochaetes (13%) and chironomids (11%), combined.

Exotic species

The number of exotic species found in benthic surveys increased every decade, from 1 in 1963 to 10 in 2009–2012 (Table 3). Their proportion in the total benthic density increased from 0.6% in 1963–1965

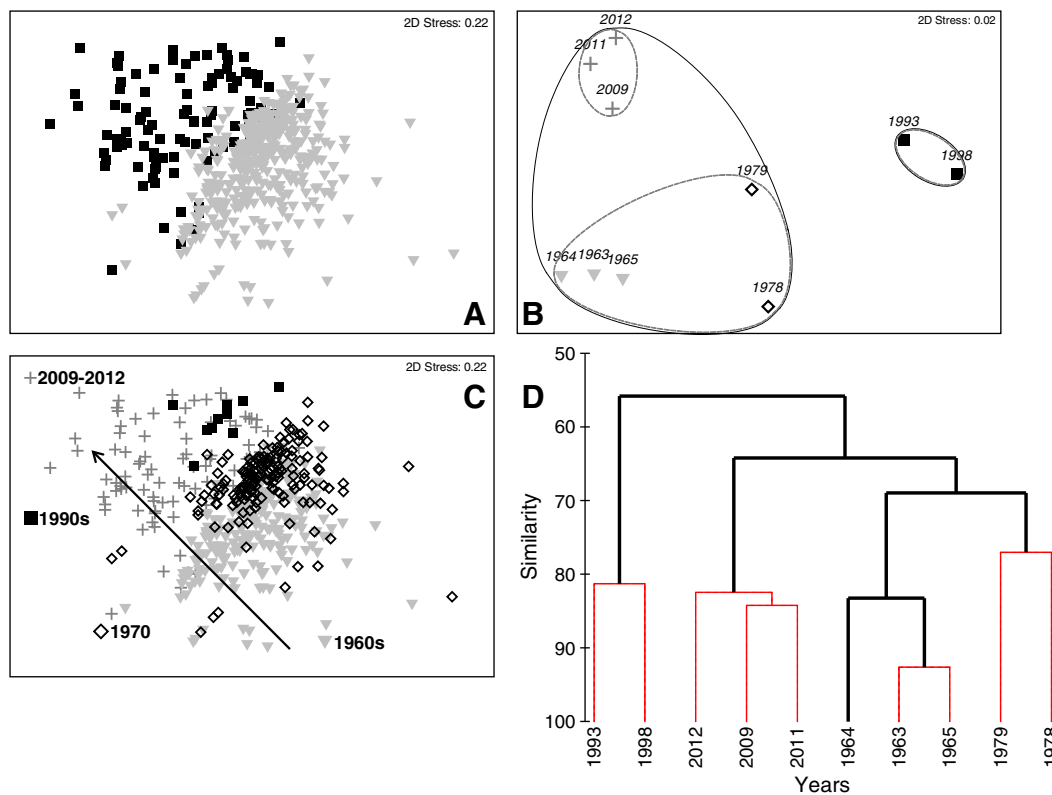


Fig. 5. A: NM-MDS ordination plot of the benthic community structure (including *Dreissena*) of Lake Erie based on Bray–Curtis similarities (by density) for samples collected before (1963–1965, 1978–1979, gray triangles) and after *Dreissena* invasion (1993, 1998, 2009, 2011–2012, filled squares). Stress = 0.22. B: NM-MDS ordination plot of the benthic community structure (excluding *Dreissena*) built on average densities per sampled year. Groups are distinct at 64% (solid line) and 68% (dashed line) similarities, and are significant ($P = 0.001$, SIMPROF test). C: There were significant differences in community structure (including *Dreissena*) among the decades (1963–1965—gray triangles; 1978–1979—open rhombuses, 1993 and 1998—filled squares, and 2009–2012—gray crosses; years and symbols indicated), and a significant temporal trend from 1963 to 2012 indicated by an arrow. D: Cluster analysis (group average) built on Bray–Curtis similarity matrix of average yearly densities of benthic macroinvertebrates excluding *Dreissena*. Black solid lines are significant at $p \leq 0.003$ (SIMPROF test).

to 53% in 2012 (Table 3; SI 1). The regression between the years and the proportion of exotic species from the total benthic density was significant (raw data: $R = 0.63$, $p = 0.0004$; average data: $R = 0.92$, $p = 0.0002$). Similarly, there was a significant regression between the

years and the total number of exotic species per year ($R = 0.90$, $p = 0.0005$). The number of exotic species was not significantly different among basins in 1963–1998 ($p = 0.45$, Kruskal–Wallis test), but was different in 2009–2012 ($p = 0.04$), and higher in the western basin.

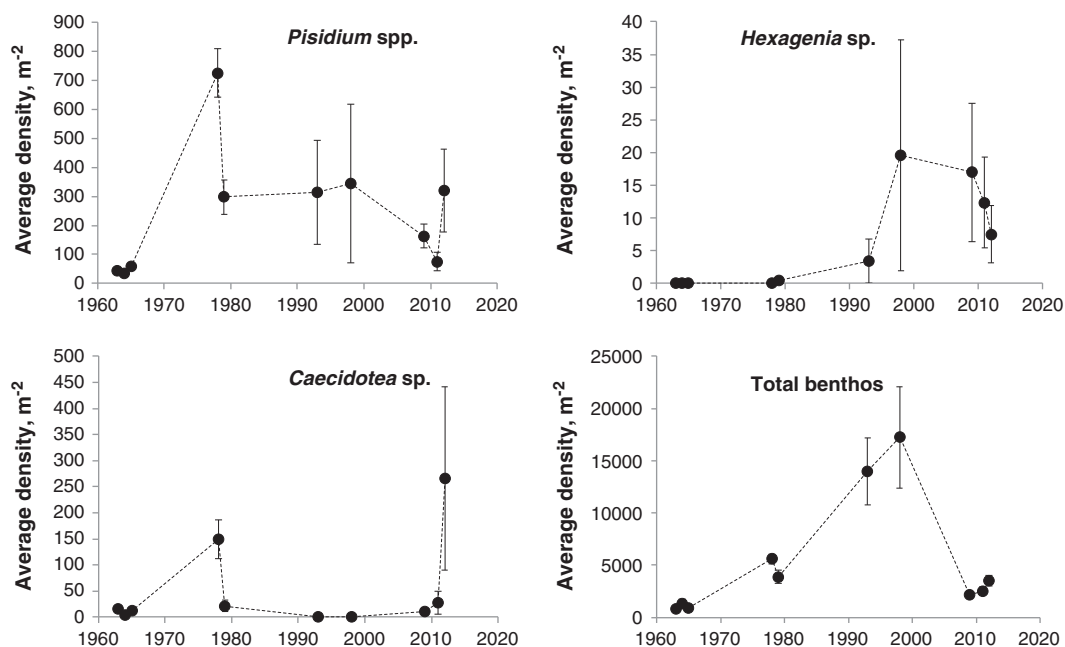


Fig. 6. Changes in mean density (\pm standard error) of different benthic taxa and total benthic density from 1963 to 2012 with moving average trendlines (2 periods). The changes of density with time were significant (Kruskal–Wallis tests, $p < 0.001$).

Table 2
Results of multivariate SIMPER (“Similarity Percentages - species contributions”) analyses on species relative densities in benthic communities before (1963–1965, 1978–1979) and after *Dreissena* invasion (1993, 1998, 2009, 2011–2012). Species average densities (ind. m⁻²) where densities were fourth-root transformed for the analysis, but are presented in the table as original, and their contribution to the dissimilarity of pre- and post-invasion communities (with a 96.2% contribution cut-off) are given. *Dreissena* spp. densities were excluded from the post-invasion group. Mean dissimilarity between the groups—55.25. *Caecidotea* sp. is the same as *Asellus* sp. of earlier authors.

Taxa	Pre-invasion average abundance	Post-invasion average abundance	Mean dissimilarity	Contribution (%)	Cumulative contribution (%)
Oligochaeta	1835.60	1387.50	8.81	15.95	15.95
<i>Pisidium</i> spp.	269.39	90.75	7.54	13.65	29.60
Chironomidae	243.41	409.65	6.06	10.97	40.57
<i>Echinogammarus ischnus</i>	0.00	110.19	3.86	6.99	47.55
<i>Sphaerium</i> spp.	64.01	15.40	3.82	6.91	54.46
Hirudinea	17.08	17.14	3.49	6.31	60.77
<i>Caecidotea</i> sp.	49.10	71.47	3.13	5.67	66.44
<i>Diporeia</i> sp.	119.18	0.00	2.44	4.42	70.86
<i>Branchiura sowerbyi</i>	4.57	4.80	1.53	2.76	73.62
<i>Valvata sincera</i>	4.06	6.27	1.41	2.56	76.18
<i>Gammarus</i> sp.	7.00	8.20	1.25	2.26	78.44
<i>Hexagenia</i> sp.	0.09	13.13	1.25	2.25	80.69
<i>Valvata tricarinata</i>	2.15	10.70	1.23	2.22	82.91
Trichoptera	0.69	1.88	0.88	1.60	84.52
<i>Potamopyrgus antipodarum</i>	0.00	2.55	0.75	1.36	85.87
<i>Ammicola</i> sp.	4.51	0.00	0.71	1.29	87.17
<i>Turbellaria</i> sp.	1.79	22.56	0.70	1.27	88.44
<i>Valvata piscinalis</i>	0.00	2.49	0.69	1.24	89.68
<i>Probythinella lacustris</i>	0.00	8.91	0.68	1.23	90.91
<i>Manayunkia speciosa</i>	60.28	5.64	0.66	1.20	92.11
<i>Sphaerium corneum</i>	0.00	4.97	0.57	1.03	93.14
<i>Culicoides</i> sp.	0.00	0.95	0.45	0.82	93.96
<i>Physella</i> sp.	1.28	1.16	0.42	0.75	94.71
<i>Caenis</i> sp.	0.00	0.98	0.41	0.75	95.46
<i>Valvata</i> spp.	0.00	3.57	0.39	0.71	96.17

Asellus sp. of earlier authors.

Exotic species in benthos were taxonomically disproportionately represented among molluscs (8 species, 80% of all non-native species), comprising 36% of all current mollusc diversity (22 species), 45% of all bivalves (5 exotic species, *D. r. bugensis*, *D. polymorpha*, *P. amnicum*, *S. corneum*, and *C. fluminea*, of total 11 Bivalvia), and 27% of gastropods (3 exotic species, *Cipangopaludina chinensis*, *P. antipodarum*, and *V. piscinalis* of 11 total Gastropoda). Other exotic species found in the lake were the amphipod *E. ischnus*, and the oligochaete *B. sowerbyi*. In total, in 2009–2012 exotic species comprised 46.7% of total benthic density, and 97.3% of total biomass.

Discussion

Our historical analysis of Lake Erie revealed major benthic community changes in the last 50 years, coincident with dramatic planned and unplanned environmental changes from anthropogenic eutrophication in 1930–1960s, nutrient and pollution abatement in 1970s, and then the introduction of exotic dreissenids. We found that the dreissenid invasion likely had a larger effect on the benthic community compared to

all other environmental changes in the lake over the last 50 years. While differences in sampling leave some questions unanswered, Lake Erie now has a benthic community dominated by dreissenids and fundamentally changed from its past.

1960s: benthos during anthropogenic eutrophication

The shift in the benthic community since the 1930s was well described in the western basin where large increases in taxa tolerant to organic enrichment (e.g., tubificids and midges) were found in habitats previously dominated by mayflies and trichoptera (Carr and Hiltunen, 1965). Being the most dominant taxa in 1930s, *Hexagenia* populations were reduced almost to extirpation in 1960s (Barton, 1988; Beeton, 1961; Carr and Hiltunen, 1965). In the 1960s, during the peak of anthropogenic eutrophication, the benthic community was dominated by oligochaetes and chironomids. Their distribution was characterized by the west–east gradient, representing three different trophic levels, from more eutrophic in the western basin represented by species more tolerant of organic enrichment, to mesotrophic in the central

Table 3
Invasive species found in Lake Erie in 1963–2012 surveys (Barton, 1988; Dermott, 1994; Dermott and Dow, 2008; author’s data), their mean (\pm standard error) reported densities, and the mean (\pm standard error) percentage of their densities from the total benthic density. Only exotic species for which densities were reported in the surveys are presented.

Year	# invasive species	Invasive species mean density	% from total density	Invasive species
1963	1	4.12 \pm 1.72	0.6 \pm 0.2	<i>Bithynia tentaculata</i>
1964	1	3.33 \pm 1.96	0.5 \pm 0.4	<i>B. tentaculata</i>
1965	1	2.48 \pm 0.8	0.3 \pm 0.1	<i>B. tentaculata</i>
1978	1	1.35 \pm 1.35	0.02 \pm 0.02	<i>B. tentaculata</i>
1979	1	23.32 \pm 9.70	1.1 \pm 0.3	<i>Branchiura sowerbyi</i>
1993	2	6289 \pm 2182	37.2 \pm 12.4	<i>Dreissena r. bugensis</i> , <i>D. polymorpha</i>
1998	3	4997 \pm 2487	25.9 \pm 12.4	<i>D. r. bugensis</i> , <i>D. polymorpha</i> , <i>Echinogammarus ischnus</i>
2009	8	1029 \pm 256	37.1 \pm 5.8	<i>D. r. bugensis</i> , <i>D. polymorpha</i> , <i>Sphaerium corneum</i> , <i>Cipangopaludina chinensis</i> , <i>Potamopyrgus antipodarum</i> , <i>Valvata piscinalis</i> , <i>B. sowerbyi</i> , <i>E. ischnus</i>
2011	8	1114 \pm 329	34.6 \pm 7.1	<i>D. r. bugensis</i> , <i>D. polymorpha</i> , <i>Pisidium amnicum</i> , <i>Corbicula fluminea</i> , <i>P. antipodarum</i> , <i>V. piscinalis</i> , <i>B. sowerbyi</i> , <i>E. ischnus</i>
2012	8	1654 \pm 380	52.8 \pm 8.3	<i>D. r. bugensis</i> , <i>D. polymorpha</i> , <i>S. corneum</i> , <i>C. fluminea</i> , <i>P. antipodarum</i> , <i>V. piscinalis</i> , <i>B. sowerbyi</i> , <i>E. ischnus</i>

and oligotrophic conditions in the eastern basin, where the dominant species were taxa sensitive to organic enrichment (Brinkhurst, 1969). The relative abundances of the native amphipod *Diporeia* in 1960s were the highest in the more oligotrophic deepwater eastern basin compared to central basin (Barton, 1988).

Both abundance and diversity of benthic invertebrates tended to decline from east to west and from nearshore to offshore (Barton, 1988). In 1963–1965 species diversity was lowest in the western basin where tubificids dominated (Barton, 1988), and where only five most pollution tolerant chironomid genera were found compared to 14 in the eastern basin (Brinkhurst, 1969). About 20–30% of the samples collected from the central and western basins during the months of June through August in the 1960s contained no living animals. Molluscs were more abundant in the west part of the western basin during 1951–1952 and in early 1960s, and exotic *S. corneum* and *B. tentaculata* were the most common species (Barton, 1988). Thus, the benthic community underwent significant degradation from 1930s to 1960s, and changes were especially pronounced in the shallow western basin located near the sources of pollution.

1970s: The first evidence of recovery following nutrient and pollution abatement

The first positive changes in the community were found 15 years later, after the Great Lakes Water Quality Agreement of 1972 was put in action. In less than six months after the phosphorus bans took effect, average phosphorus concentration in municipal treatment plant discharges in the impacted areas decreased to 25% of previous values (Sweeney, 1995). The first signs of improvement were evident in the abundance and dominance of oligochaetes in the western basin in 1970s. Oligochaetes decreased in abundance compared to the 1960s along with the reduced eutrophication and nutrient levels, especially near the river mouths (Carr and Hiltunen, 1965; Dermott, 1994; Wright, 1955). *Limnodrilus hoffmeisteri*, a pollution-tolerant species dominated the oligochaete fauna in 1961, but was not dominant in 1982, along with other eutrophic taxa, indicating that heavy pollution substantially decreased near shore and moderate pollution increased in open waters (Schloesser et al., 1995). The decline in eutrophication of nearshore substrates between 1961 and 1982 was likely a result of pollution abatement programs (Schloesser et al., 1995). Although the overall increase in benthic density in the 1970s compared to the 1960s (Fig. 6; SI 1A) should be treated with caution (as it could partially be attributed to the different gear and preservation techniques used in 1970s, Barton, 1989, 1988), similar increases were found in lakes Huron and Michigan between the 1960s and late 1970s–early 1980s (Johnson and McNeil, 1986; Nalepa, 1987; Nalepa et al., 2007). These elevated densities could be explained by the high sediment nutrient loads that carried over from previous decades, and benthic populations had not yet fully responded to nutrient abatement programs initiated in the 1970s (Nalepa et al., 2007). While it is difficult to interpret changes occurring shortly after implementation of the Clean Water Act and Great Lakes Water Quality Agreement, it is clear that along with the positive signs of recovery (e.g. reduced dominance by oligochaetes), increase in benthic densities likely reflected the lingering effect of years of eutrophication.

1990s: the peak of *Dreissena* invasion

In contrast to the gradual changes seen after planned nutrient abatement programs were implemented (Dermott, 1994; Schloesser et al., 1995, our analysis), the unplanned introduction of *Dreissena* had rapid, dramatic, and probably indelible effects on the benthic community. Dreissenid densities peaked in 1990s (Karatayev et al., in this issue; Patterson et al., 2005), and *D. polymorpha* was displaced by *D. r. bugensis* by 1998 in all but the shallowest and western most region of the lake (Dermott and Dow, 2008; Jarvis et al., 2000; Karatayev et al., in this

issue). However, *Dreissena*-induced change was not operating in isolation, as nutrient concentrations were also dropping. As a result, in the early 1990s the western and west central basins became mesotrophic and the eastern basin oligotrophic, an improvement from the 1980s when the western basin was classified as highly eutrophic and the eastern-mesotrophic (Bartish, 1987). This move toward oligotrophy was initiated by the phosphorus control in the early 1970s, but most of the changes were assumed to be due to the filtration activity of *Dreissena* that probably interacted with changing nutrient concentrations to relocate nutrients to the nearshore (Hecky et al., 2004). All local and system-wide changes induced by *Dreissena* made a profound impact on the benthic community (Figs. 5, 6).

The first indicators of changes were again the *Hexagenia* mayflies that followed the ecosystem degradation and recovery for the last 100 years (Britt, 1955a, 1955b; Carr and Hiltunen, 1965; Krieger et al., 2007; Schloesser et al., 2000; Soster et al., 2011). The recovery of *Hexagenia* populations in Lake Erie that started in the 1990s was considered a historic event in the Great Lakes, likely attributable to pollution-abatement programs and rapid ecological changes brought about by *D. polymorpha*, which may have contributed to the speed at which nymphs recolonized sediments (Griffiths et al., 1991; Hebert et al., 1989; Krieger et al., 1996, 2007; Nalepa and Schloesser, 1993; Schloesser et al., 1991, 2000). The effect of dreissenid mussels on the survival and condition of *Hexagenia* is complex: while dreissenid shells degrade the quality of soft sediments for *Hexagenia*, some of the negative effect is offset by the presence of live dreissenids, which add food resources by their filtering activity (Freeman et al., 2011). *Hexagenia* was shown to actively select *Dreissena* aggregations as refuge from fish predation and to escape anoxic burrows during hypoxic conditions (DeVanna et al., 2011a).

During the first decade of the *Dreissena* invasion, the densities of chironomids, oligochaetes, and native *Gammarus* increased, while the abundance of native *Pisidium* and *Sphaerium* declined compared to the previous decade. Most of the changes in the benthic community in the 1990s can be explained by the role of *Dreissena* as an ecosystem engineer that physically changes benthic substrates, providing shelter and food for other benthic invertebrates, resulting in a significant increase in the biomass of the majority of native invertebrates (reviewed in Burlakova et al., 2012; Higgins and Vander Zanden, 2010; Karatayev et al., 1997, 2002, 2007b; Ward and Ricciardi, 2007). The functional feeding group approach is a key to understanding the taxonomic shifts in the benthic community as a result of *Dreissena* invasion (reviewed in Burlakova et al., 2005, 2012; Karatayev and Burlakova, 1992; Ward and Ricciardi, 2007). Native filter feeders were out-competed by *Dreissena*, and decreased in abundance; thus, both native Unionidae and Sphaeriidae were reduced in abundance after the introduction of *Dreissena* in the western basin (Table 2). The wet (shell-free) weight of Unionidae alone in this basin was 112 g m⁻² in 1979 (Dermott, 1994), in contrast to their absence in 1993 (Dahl et al., 1995). The dramatic decline in native Unionidae after *Dreissena* invasion in Lake Erie has been very well documented (Haag et al., 1993; Schloesser and Nalepa, 1994; Schloesser et al., 1996). Similarly, filter-feeding *Tanytarsus* and *Micropsectra*, *Chironomus* spp., and Sphaeriidae in the profundal community of Lake Erie declined in abundance post *Dreissena* invasion (Dermott and Kerec, 1997). The densities of filter-feeding molluscs *Pisidium*, predatory chironomid larvae *Procladius* and *Cryptochironomus* were two times higher in non-*Dreissena* samples collected in 2009–2012. The competition for food after *Dreissena* invasion and pollution-abatement programs perhaps contributed to the decline of the filter-feeding polychaeta *M. speciosa* (Howell et al., 1996; Schloesser, 2013).

Diporeia was last recorded in 1993; in 1998, no specimens were found in any of the profundal samples from Lake Erie (Dermott and Dow, 2008). No individuals of *Diporeia* were found between 1997 and 2009 at any of the EPA sites confirming that it is now effectively absent from the lake (Barbiero et al., 2011). The dramatic decline of *Diporeia*

spp. in all the Great Lakes colonized by *Dreissena* was attributed to the reduction in its original food source (diatoms) due to *Dreissena* filtration (Dermott, 2001; Dermott et al., 2005, 2012; Dermott and Kerec, 1997; Lozano et al., 2001; Nalepa, 2009, 2010; Nalepa et al., 2006, 2007, 2009; Watkins et al., 2007). However, the exact mechanisms underlying decreasing *Diporeia* densities are still unclear (Barbiero et al., 2011; Ryan et al., 2012) as not all *Diporeia* populations that coexist with dreissenids are declining (Dermott et al., 2005; Watkins et al., 2012) and multiple stressors may be involved in addition to food limitation, including pathogenic viruses (Hewson et al., 2013).

Feces and pseudofeces, organic matter deposited actively and passively by *Dreissena*, and the phyto-, zooperiphyton and bacteria thriving on their shells provide food for collectors and scrapers, which increase in density. This explains the dominance of isopods, amphipods, gastropods, mayflies, some species of trichopterans, oligochaetes, and chironomids, especially in *D. polymorpha* aggregations (reviewed in Burlakova et al., 2005, 2012; Karatayev et al., 2002; Ward and Ricciardi, 2007). The native amphipod *G. fasciatus*, not collected in the deepwater samples from eastern basin in 1979, was found after *Dreissena* colonized the basin, and from 1979 to 1993 *Gammarus* populations increased over 300-fold due to the increased substrate heterogeneity and scavenging opportunities among the mussel colonies (Dahl et al., 1995; Dermott and Kerec, 1997). Other taxa benefiting from the changing substrate heterogeneity in the deep-water zone of Lake Erie were gastropods, tardigrades, and hydra (Dermott and Kerec, 1997). Species more abundant in the presence of *Dreissena* in 2009–2012 included the exotic amphipod *E. ischnus* (gathering collector and predator), chironomids *Chironomus* (filtering gathering collectors), *Coelotanytus tricolor* (predator), and gathering collectors (e.g., chironomid *Dicrotendipes tritonus* and isopods *Caecidotea* sp.). Therefore, the first decade after *Dreissena* invasion saw the largest increase in benthic community abundance, but it's important to note that the overall increase in the total benthic biomass was probably not a result of the replacement by *D. polymorpha* as the total wet weight of native benthos (excluding unionids) in all three basins did not change in 1993 (Dahl et al., 1995).

2010s: twenty five years after *Dreissena* invasion

In recent years (2009–2012) the density of non-dreissenid benthic community is more similar to the pre-invasion density (SI 1; Figs. 5, 6), but it is structurally different. Densities of certain groups continue to decline (e.g., *Pisidium*, *Shaerium*, Hirudinea, Trichoptera, and native *Valvata*); native *Gammarus* are very rare, while the exotic amphipod *E. ischnus* has become one of the dominant species (Table 2). *Hexagenia* has maintained its abundance in the western and west-central parts of Lake Erie, and although it was not found in the eastern basin during our survey, it was detected in 2009 and 2011 at the Great Lakes Center's permanent monitoring sites at 13 and 10 m depth (coordinates: 42°50.04'N and 78°55.44'W; 42°51.84'N and 78°54.42'W correspondingly, K. Hastings, 2013, SUNY Buffalo State, personal communications).

Due to several shortcomings in data available for our historical comparison (e.g., most of the historical samplings covered just a part of the lake; surveys differed in sampling design, gear and preservation techniques; authors used different taxonomic resolution during sample identification or reporting) we were not able to statistically compare benthic densities among years, and to follow structural changes in two major taxa, oligochaetes and chironomids in the past 50 years. However we found a reduction in the abundance of both oligochaetes and chironomids during the most recent decade, as well as a decline in their role in community. Thus, the contribution of oligochaetes to total community density in the western basin decreased from 61% in 1973–1974 (Britt et al., 1980) to 20% from non-dreissenid benthic density in 2009–2011 (7% of total density and <1% from biomass). If Wright's (1955) pollution index is applied to the current data, most of the basin would be considered lightly polluted, compared to moderately-polluted in 1970s.

Although we need to treat this decline cautiously due to the difficulties inherent in assessing historical data, and interannual variability in taxa abundance, the same trends have been found by Soster et al. (2011) that analyzed samples collected from permanent sites in western Lake Erie using the same sampling techniques over the years. The authors tested the effects of physical environmental stressors and changes in organic loadings, and found them insufficient to explain the significant declines in the densities of Tubificidae (mostly due to the dramatic decline in the former dominant, tolerant of organic enrichment *Limnodrilus* spp.), Naididae, ostracods, and some species of chironomids from 1980s to 2000s (Soster et al., 2011). The major driver of these declines, according to Soster et al. (2011), was the invasion of dreissenids, and these offshore infaunal changes could be caused by the “nearshore shunt” (Hecky et al., 2004) due to interception of nutrients by the littoral community. Likewise, the greatest change to the benthic community of the Bay of Quinte (Lake Ontario) over the 40-years period was the major regime shifts created by the arrival of *Dreissena* (Dermott et al., 2012). Declines in oligochaete abundance after dreissenid invasion in other Great Lakes have been explained by reductions in phosphorus loads and the filtering activities of dreissenids (Lozano et al., 2001; Nalepa et al., 2007, 2003, 1998).

The declines in the densities of oligochaetes and chironomids coincided with a large reduction in densities and biomass of *D. r. bugensis* since the end of 1990s (SI 1). Typically, *D. polymorpha* reaches its population maximum in 2–4 years, and *D. r. bugensis* in 6 to 19 years after it is first detected in an invaded waterbody (Karatayev et al., 2011). Therefore, *D. polymorpha* likely reached their maximum in Lake Erie around 1989, and *D. r. bugensis* population peaked between 1998 and 2002 (Karatayev et al., in this issue). The following falloff could result from density-dependent processes as the system was altered by dreissenid presence, and densities well below the maximum persist (Karatayev et al., 2002, 1997), or can be in part an artifact of different methods and station locations used that is warranted further investigation. At any rate, this decline in *Dreissena* density can potentially cause the decline in other benthic groups, as a response to the reduction in substrate complexity and the rate of organic matter deposition to the benthos caused by dreissenid colonies.

However, the decline in benthos in the early 2000s (Fig. 6; SI 1) could be caused by other factors. For example, the population explosion of another invader, the round goby (*Neogobius melanostomus*) occurred near 2002 when an estimated 9.9 billion gobies were found in the western part of the lake alone (Johnson et al., 2005). Round goby voraciously prey on selected benthic groups (e.g., amphipods, dreissenids, ostracods, chironomids; Campbell et al., 2009; Dermott et al., 2012; Diggins et al., 2002; French and Jude, 2001; Kornis et al., 2012; Walsh et al., 2007) and thus could strongly impact the community. A 94% reduction in the density of quagga mussels in the eastern basin between 2001 and 2004 and the disappearance of small *Dreissena* spp. in the lake in 2002 were explained by round goby predation (Barton et al., 2005; Patterson et al., 2005). The decline in non-dreissenid benthos may also be an indirect effect of round gobies altering dreissenid colonies (Kuhns and Berg, 1999). However, the predation effect of gobies on *Dreissena* is spatially heterogeneous (Ruetz et al., 2012) depending on substratum and water clarity/visibility (Diggins et al., 2002); and the consumption rates may not be high enough to effect dreissenid populations on a system-wide scale (Johnson et al., 2005; Kornis et al., 2012; Pennuto et al., 2012b). In addition, this predation alone cannot explain the large decline in oligochaetes, which is not a preferred food for round goby (Copp et al., 2008).

Another source of uncertainty in explaining the decline in oligochaetes and chironomids in the last decade is the lack of data on the effect of *D. r. bugensis* on benthic invertebrates, particularly from the profundal zone, as most of the studies of the direct effect of *Dreissena* on benthic communities were done on *D. polymorpha* in littoral habitats. We found that samples with and without *Dreissena* in 2009–2012 differed primarily in the density of oligochaetes and chironomids which

were more abundant in the absence of *Dreissena* (mainly *D. r. bugensis*). The discrepancy between the positive effect of *Dreissena* on deposit feeders in druses and the recent decline in oligochaetes on soft offshore sediments of Lake Erie may perhaps be explained by the difference in *Dreissena* impact on infaunal versus epifaunal species in littoral versus profundal zones. Druse inhabitants are predominantly epifaunal organisms which are likely to take advantage of both the resources and structural complexity provided by druses. Infaunal invertebrates (e.g., burrowing oligochaetes) may avoid druses due to the oxygen depletion associated with the large amounts of organic matter derived from the mussels' feces and pseudofeces (Caraco et al., 2000; Efler and Siegfried, 1994) that inhibits their development. In contrast to highly mobile epifaunal organisms that may rapidly colonize druses (Mörtl and Rothhaupt, 2003), many infaunal species are less mobile (Merritt et al., 1984). On soft substrates in deep profundal zone there are no epifaunal species and dreissenid do not form large multilayer aggregations (Dermott and Kerec, 1997). It was shown that the presence of individual *D. polymorpha* even on shallow sandy bottom does not change the qualitative and quantitative composition of the benthic community (Karatayev et al., 1994, 1983). In contrast to the well mixed littoral zone with abundant food supply, benthic invertebrates may be food limited in the deep profundal zone, especially during summer stratification. Available food sources in deep profundal zone include the benthic nepheloid layer rich in organic matter (Urban et al., 2004) that develops in Great Lakes above profundal sediments during summer stratification (Hawley and Muzzi, 2003; Mudroch and Mudroch, 1992) or the deep chlorophyll layer below the thermocline (Barbiero and Tuchman, 2001; Pothoven and Fahnenstiel, 2013). Since dreissenids invaded the Great Lakes, the deep chlorophyll maximum and spring phytoplankton blooms have been reduced (Barbiero et al., 2011; Nalepa, 2009). Therefore, *D. r. bugensis* in profundal zone may be in direct competition with infaunal species for space and food (Karatayev et al., in review; Nalepa et al., 2007). For example, no increases in Lumbriculidae and Tubificidae, which feed 5–10 cm below the surface, were found in the deep-water eastern basin after 10 years of *D. r. bugensis* invasion (Dermott and Kerec, 1997), and significant reduction in the densities of deposit-feeding oligochaetes (particularly the deep-dwelling Tubificidae) was recorded in western basin recently (Soster et al., 2011). More data on the effect of *D. r. bugensis* on benthic species in profundal versus littoral zone is needed before we can fully understand their impact on benthic communities.

Dynamics of exotic species in Lake Erie

Implementation of strict environmental measures resulted in rapid improvements in water quality in the Laurentian Great Lakes and associated rivers and has been correlated with a dramatic increase in the number of successful invasions by a wide range of taxa. In particular, dreissenid mussels are now important ecological factors driving dramatic changes in these systems, preventing restoration of the native communities (Mills et al., 1993, 1994). The number and the proportion of exotic species in benthic community increased significantly in the last 50 years, with 10 exotic species found in Lake Erie during our recent surveys. All exotic species combined comprised 47% of total density, and 97% of total benthic biomass in 2009–2012. Shell-free *Dreissena* (considering that wet tissue comprises 40% of the total wet weight, P. Juette, SUNY Buffalo State, 2013, personal communication) currently represents 93% of the total benthic biomass in the lake.

The density of *Dreissena* was lowest in the central basin, where large parts of the bottom were completely devoid of the species, likely due to frequent hypoxia and anoxia events (Conroy et al., 2011; Matzinger et al., 2010). *Dreissena polymorpha* is intolerant of even moderate hypoxia and has a critical threshold of 25% oxygenation, while *D. r. bugensis* appears to be somewhat more tolerant (lower oxygen limit at 20 °C 1.8–2.4 mg L⁻¹ for *D. polymorpha* and 1.5 mg L⁻¹ for *D. r. bugensis*, reviewed in Karatayev et al., 1998, 2007a). The absence of snails in some parts of

the central basin was linked to prolonged anoxia (Krieger, 1985), in contrast to other taxa which are either more tolerant of oxygen depletion, or can readily repopulate the areas (oligochaetes, sphaeriid clams and midges; Krieger, 1984). We suggest that *Dreissena* distribution can potentially be used as an indicator of oxygen conditions at the bottom of this basin.

Some exotic species (oligochaete *B. sowerbyi*, molluscs *C. chinensis*, *P. antipodarum*, *V. piscinalis*, *S. corneum*, *C. fluminea*, and *P. amnicum*) have either increased their abundance, or their densities have simply not been found (or reported quantitatively) in previous routine benthic surveys. For example, gastropod *V. piscinalis* invaded Lake Erie in 1897 (Grigorovich et al., 2005), *S. corneum* in 1900 (Kipp et al., 2013; Mills et al., 1993), and *C. chinensis* between 1931 and 1942 (Mills et al., 1993). *Sphaerium corneum* was one of the most abundant sphaeriids in the lake in 1960s (Brinkhurst, 1969), but unfortunately, the results of 1960s survey were reported with taxonomic resolution to the genus level (Barton, 1988), limiting our ability to make comparisons. Other invaders like the gastropod *B. tentaculata* (likely introduced in 1870, Mills et al. (1993)) decreased in density and distribution in the last two decades and were not found in our surveys. The invasive amphipod *E. ischnus* colonized the lake in 1993 (Nalepa et al., 2001) and spread rapidly by 1998 (Dermott and Dow, 2008). Although the native amphipod *G. fasciatus* increased in the deeper areas of eastern basin in 1998, after *Dreissena* invasion, its displacement by *E. ischnus* had already begun in 2001 (Ratti and Barton, 2003); very few native *Gammarus* were found in 2009–2012 (SI 1, 2).

The number of exotic species was different among lake basins. The western basin, with its proximity to large ports, urban centers, and the major tributaries, had the highest number of invaders. Exotic species were disproportionately represented among taxonomic groups, with 80% of all recently found benthic exotic species represented by molluscs. This is a common pattern for aquatic invasive species in general. Karatayev et al. (2009) found that exotic molluscs and crustaceans are disproportionately over-represented among aquatic invaders (>50% and 38% of the invaders, respectively). Collector-filterers (including suspension feeders) and collector-gatherers are the two dominant feeding modes of macroinvertebrate invaders, indicating that suspension feeders are much more likely to become established in new waterbodies. This is in sharp contrast with the feeding structure of native assemblage, where collector-gatherers, predators and scrapers are the most abundant feeding groups (Karatayev et al., 2009).

While the number of benthic invaders in community is still low compared to the diversity of native species, their functional role, due to extremely high density and biomass, far exceeds the role of all native species combined. Therefore, the introduction of a handful of species had enormous consequences and changed dramatically the whole ecosystem.

Conclusions

Despite of all the shortcomings in data available for our historical comparison (e.g., difference in sampling design, gear and preservation techniques, taxonomic resolution) we found that Lake Erie benthic community underwent significant changes during each decade of the last half-century. During this time the community showed signs of recovery following the ecosystem restoration as a result of the pollution and nutrient abatement program, and then experienced major structural and functional changes after dreissenid introduction. Our analysis revealed that there was a significant temporal trend in the benthic community structure from 1963 to 2012, and a large part of this relationship was due to *Dreissena* invasion. Therefore, the impact of *Dreissena* invasion seems to have had a larger effect on the benthic community compared to all other environmental changes in the lake over the last 50 years.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2014.02.008>.

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