Lake Erie and Lake Michigan Benthos: Cooperative Science and Monitoring Initiative

Final Report

U.S. Geological Survey
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U.S. GEOLOGICAL SURVEY

OAG DENVER ACQUISITION BRANCH

FINAL TECHNICAL REPORT

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CHAPTER 1. LAKE ERIE SURVEY WITHIN COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2014

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INTRODUCTION

As part of the Coordinated Science and Monitoring Initiative (CSMI) in Lake Erie in 2014, a lake-wide benthic survey was conducted to assess the status of the benthic macroinvertebrate community, with a primary focus on the invasive mussels *Dreissena rostriformis bugensis* and *D. polymorpha,* and to compare current benthic community with historic data.

Lake Erie is perhaps the most severely impacted of all the Great Lakes. Impacts from nutrient loadings from the watershed and the introduction of non-indigenous species continue to drive large-scale trophic changes today. 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 abatement programs was then followed by major ecosystem changes resulting from 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; Karatayev et al. 2014).

Lake Erie was the first waterbody in North America colonized by both *Dreissena polymorpha* (zebra mussel) and *D. r. bugensis* (quagga mussel). 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 zebra mussels, but by late 1990s zebra mussels remained common only in the shallow western basin, while in the central and eastern basins it was almost completely replaced by quagga mussels (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 declined dramatically, while densities in the western and eastern basins densities remained at high levels (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., 2017). Large declines were also observed in *Dreissena* population densities in the eastern basin, and the reason for these changes could be a potential bias in sampling conducted in different years, as well as various extrinsic and intrinsic factors (Karatayev et al., 2014).

This report provides an assessment of benthic community structure, density and biomass across different basins and depths, as well as a comparison of recent data with previous studies. To a large extent, the report is focused on the analysis of 2014 *Dreissena* spatial distribution and long-term dynamics in different basins. In addition, we tested the ability of using *Dreissena* spp. abundance and length-frequency distribution to map hypoxic zone extent in the central basin of Lake Erie. More detailed analyses and discussion of spatial and temporal trends in Lake Erie benthic community could be found in paper recently accepted in the Journal of Great Lakes Research "Biomonitoring Using Invasive Species in a Large Lake: *Dreissena* Distribution Maps Hypoxic Zones" (Appendix 1.1, Karatayev et al. 2017), as well as in other publications that are currently in preparation.

METHODS

Inter-basin comparison

Samples for benthic macroinvertebrates were collected in July and August of 2014 in triplicate at 107 stations located throughout the western, central, and eastern basins (Figure 1.1, Table 1.1). Sites were stratified based on depth zones and lake basins. Sample locations included the historical stations sampled in 1978-1979, 1992, 1993, 2002, 2009, 2011-2012 (Burlakova et al., 2014; Karatayev et al., 2014). Ninety stations (269 samples) were sampled aboard the U.S. EPA R/V *Lake Guardian* using a regular Ponar grab (sampling area 0.052 m^2). Seventeen of the nearshore stations were sampled aboard Buffalo State R/V *John J. Freidhoff* using a petite Ponar grab (sampling area 0.023 m^{-2}, at 8 stations) or by SCUBA divers (at 9 stations using 0.25 m^2 quadrat). A total of 293 Ponar and 27 quadrat samples were collected in July and August of 2014. We were not able to collect samples at an additional 5 stations (950, CCW10, CCW5 (179), ERI5 (174), O35) due to hard substrates, and one replicate was discarded at station 956.

All benthos (including *Dreissena*) was identified from 239 samples collected at 80 stations (termed as "Benthic survey" in Table 1.3). An additional 82 samples at 27 stations were processed for *Dreissena* only (no other benthic invertebrates were processed from these samples). Therefore, together with data from benthic survey, *Dreissena* density and biomass was recorded from a total of 107 stations ("*Dreissena* survey" in Table 1.3).

Dreissena (*D. polymorpha* and *D. r. bugensis*) from all samples were identified to species, measured to the nearest millimeter with a caliper, counted, and the whole sample was weighed to the nearest 0.001 g after being blotted dry on absorbent paper (total wet weight, tissue with shell). If the sample was too large to process, it was split into *n* equal parts, one part was randomly selected for analysis and mussel density and weight from this part was adjusted (multiplied by *n*) to obtain sample totals. At stations where we collected only dreissenids, mussels were removed from the substrate, counted, measured and weighed onboard.

Table 1.1. Number of stations sampled and samples collected (in parentheses) at each basin and lake-wide in 2014.

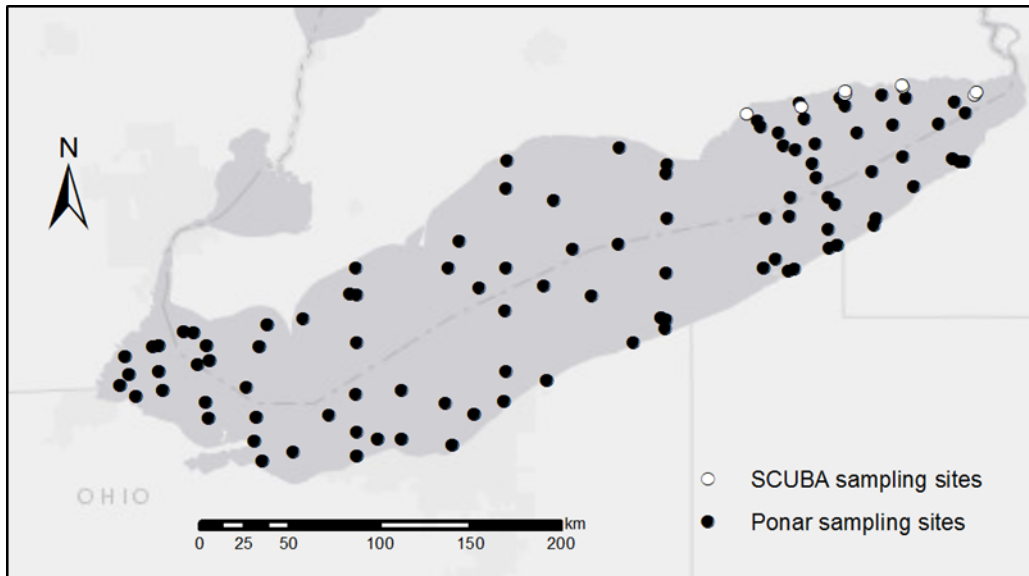| Sampling method	Western	Central	Eastern	Total
SCUBA diving (*Dreissena* only)	0	0	9 (27)	9 (27)
Ponars for *Dreissena* only	1 (3)	11 (33)	6 (18)	18 (54)
Ponars for all benthos	21 (63)	31 (93)	28 (84)	80 (240)

Figure 1.1. Location of Ponar (black circles) and SCUBA (open circles) *Dreissena* spp. sites sampled in Lake Erie in 2014.

At 80 benthic stations, the entire benthic macroinvertebrate community was collected using three replicate samples at each station with a Ponar grab. Each sample was placed separately into an elutriation device and then washed through a 500-um mesh screen. All retained organisms and sediments were placed into a collection jar and preserved with neutral buffered formalin with Rose Bengal stain to a final concentration of 5 – 10%. Details are described in Standard Operating Procedure for Benthic Invertebrate Field Sampling (SOP LG406, Revision 11, June 2016).

The entire benthic macroinvertebrate community found at these 80 stations was sorted, identified, counted, and weighted (total wet weight). Organisms were picked out of samples under low magnification using a dissecting microscope. Oligochaetes and chironomids were mounted on slides and identified under a compound microscope; other organisms were identified under a dissecting microscope. Adult oligochaetes were identified to species; immatures were taken to the lowest taxonomic level possible, usually family, and included in abundance estimates. Taxonomic identification of oligochaetes from slides was done by Jacob Boehler (Heidelberg University). Oligochaete fragments, though counted, were excluded from analyses. Fragment weight, however, was considered in calculation of biomass. Chironomids were identified to the lowest practical taxonomic level, usually genus. Other invertebrates were identified to species, when possible. Taxonomy followed Kathman and Brinkhurst (1998) (oligochaetes); Holsinger (1972) and Bousfield (1958) (amphipods); Epler (2001) and Wiederholm (1983) (chironomids); and Smith (2001), Merritt et al. (2008), and Thorp and Covitch (2001) (for other groups). Details are described in Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis (SOP LG407, Revision 09, April 2015).

Hypoxia study (Central Basin)

Field measurements of dissolved oxygen in 2014 and hydrodynamic and ecological modeling to simulate oxygen dynamics

This study was done in collaboration with Serghei Bocaniov (Graham Sustainability Institute, University of Michigan, Ann Arbor), Paris Collingsworth (Illinois–Indiana Sea Grant, Department of Forestry and Natural Resources, Purdue University), Glenn Warren and Elizabeth Hinchey (U.S. Environmental Protection Agency, Great Lakes National Program Office), and Richard Kraus (Lake Erie Biological

Station, Great Lakes Science Center, U.S. Geological Survey). Please find additional details of this study in attached manuscript accepted in the Journal of Great Lakes Research (Karatayev et al., 2017, Appendix 1.1).

To elucidate the relationship between hypoxia and dreissenid abundance in this study, we measured bottom dissolved oxygen using an array of data loggers distributed throughout the central basin of Lake Erie (Figure 1.2A).

Our collaborator Dr. Bocaniov used a three-dimensional (3D) hydrodynamic-ecological model of Lake Erie (ELCOM-CAEDYM) consisting of two coupled models; the 3D hydrodynamic Estuary and Lake Computer Model (ELCOM; Hodges et al., 2000), and the ecological Computational Aquatic Ecosystem Dynamics Model (CAEDYM; Hipsey and Hamilton, 2008). This version of ELCOM-CAEDYM (or ELCD) was calibrated and validated through several previous applications to Lake Erie, including predictions of thermal structure, DO, nutrients, phytoplankton biomass, as well as ice cover and thickness (Bocaniov et al., 2014a; Liu et al., 2014; Oveisy et al., 2014; Bocaniov and Scavia, 2016). Because of the relatively long life span of *Dreissena* (> 3 years, reviewed in Karatayev et al., 2006), settlement of their young-of-the-year during summer, and development of hypoxia in the central basin by the end of the growing season, mussel distribution and size structure in July 2014 was determined by the dissolved oxygen dynamics in 2012-2013 and recruitment in the current year. Therefore, we applied ELCD to simulate the oxygen dynamics for the year with high temporal and spatial resolution of the bottom DO observations and in which mussels were collected (2014), as well as two preceding years, 2012 and 2013. The simulated spatial and temporal DO dynamics for 2012 and 2013 were used to explain mussel biomass and densities observed in 2014, as functions of the model-predicted number of hypoxic days for each location of the 2014 sampling stations at various DO thresholds (1, 2 and 3 mg L^{-1}).

To estimate the ELCD model performance, we used a combination of graphical and statistical techniques. We used visual comparisons, model evaluation statistical tests (e.g. independent two-sample *t*-test) and measures of model performance such as Root Mean Square Error (RMSE). To compare mussel densities between three basins and depth zones within basin, we used Kruskal-Wallis ANOVA by Ranks. To compare the average length of mussels within and among basins and depth zones, we used a Generalized Linear Model with subsequent post-hoc unequal-*n* Tukey's Honestly Significant Difference (HSD) tests. To find relationships between log-transformed ($\log_{10}(x+1)$) mussel density and biomass recorded in 2014 and hypoxic duration of different DO thresholds (< 1, 2 and 3 mg L^{-1}) for 2012 and 2013, we used linear regressions. These analyses were done using STATISTICA software (*STATISTICA* for Windows version 12, StatSoft, Inc. 1984-2014). Effects were considered statistically significant at $P < 0.05$).
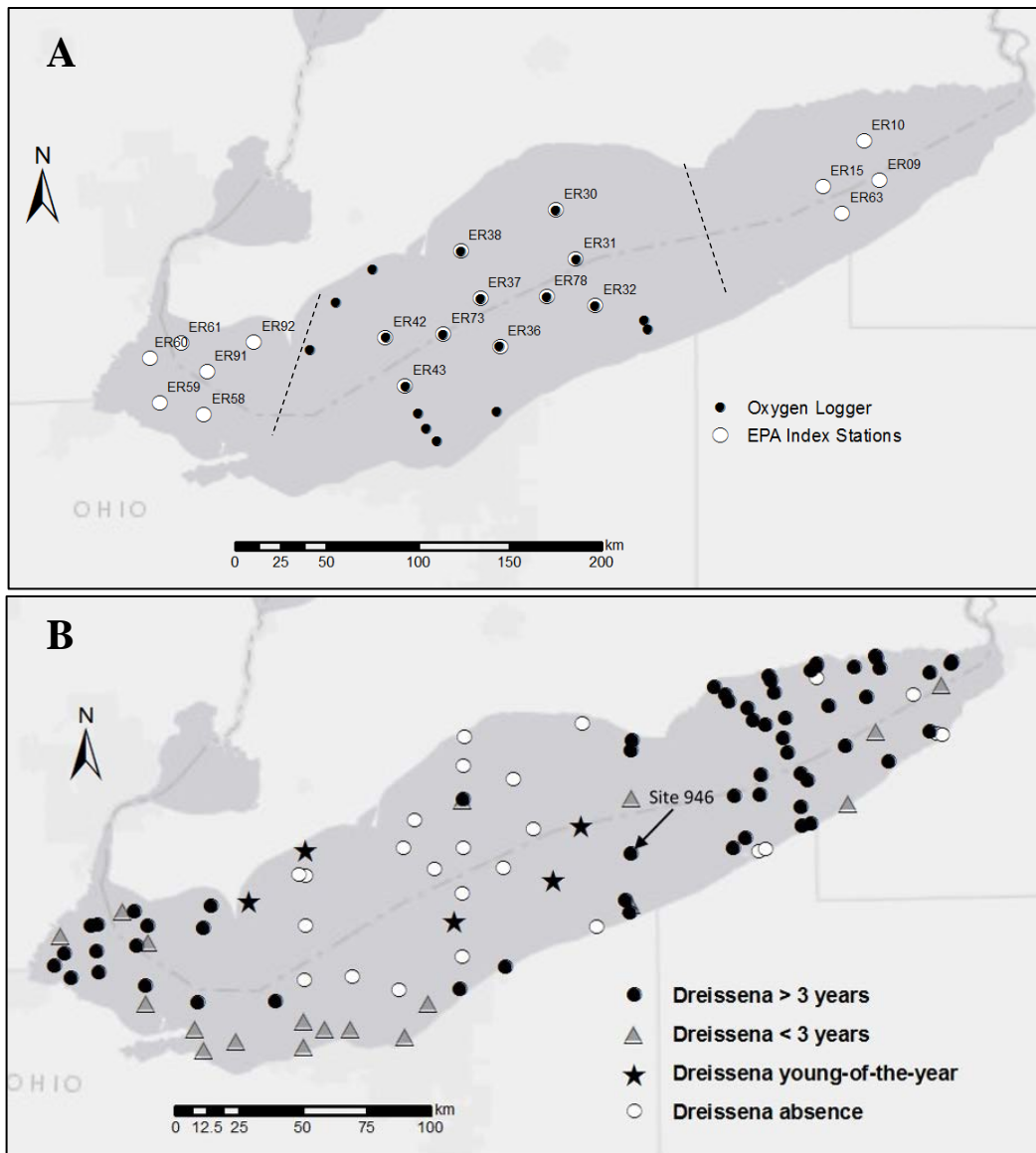
Figure 1.2. A: Location of oxygen data logger (black circles) and U.S. EPA GLNPO central basin of Lake Erie Dissolved Oxygen Monitoring Program stations (open circles) in 2014. Dashed lines indicate borders between western, central, and eastern basins (A). B: distribution of *Dreissena* spp. in Lake Erie in 2014 by age group.

Dreissena long-term-dynamics

To compare *Dreissena* dynamics in the western, central and eastern basins we compiled a dataset of *Dreissena* spp. densities and biomass by stations 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). All historic and current data on *Dreissena* biomass were converted into TWW. To convert AFDW into TWW, we

used the relationship: TWW (g) = 36.4964 × AFDW (g) (estimated for *Dreissena* in Lake Michigan, Ashley Elgin, NOAA, Ann Arbor, personal communication).

To calculate the weighted average (± standard error) of *Dreissena* spp. density and biomass per basin, we calculated the average density and biomass in each depth zone (0 – 4, 4 – 8, 8 – 15, 15 – 24, and > 24 m, Patterson et al. 2005), and then calculated the average density and biomass across the depth zones, weighted by the area of each depth zone relative to the total area of the basin. The weighted lake-wide average is the sum of the weighted average densities and biomass of *Dreissena* per each basin, multiplied by the proportion of each basin from the total area of the lake. Please find details in Karatayev et al. (2014).

Historical comparison: 1978-1979 and 2014

In July 2014 we sampled 25 stations that were previously studied in October 1978-1979 (Dermott, 1994, Table 1.2). During 1978-1979 survey, one Shipek sample was collected at each station and sieved aboard research ship *C.S.S. Limnos* using Nitex screening with a mesh size of 153 µm. The samples were fixed in 10% buffered formalin solution and kept for 3 years before sorting and identification. To sort out the invertebrates the samples were either elutriated or washed through a series of sieves from 2 mm to 153 µm. The coarse residues were examined in a white enamel tray, and the finer residues were examined under a dissecting microscope. At most stations, up to 50 oligochaetes were mounted on microscope slides in Canada balsam after dehydration in 2 baths of absolute ethyl alcohol. These were examined for specific determination and the species composition of the sample based on the percent composition of the worms mounted. Due to the length of time the samples remained in formalin, most of the mollusc shells in the samples from the central and east basins were dissolved too much to allow identification beyond genus. In addition to macrozoobenthos, Harpacticoida, Nematoda and Ostracoda were counted, but not considered for comparison with our study. The number and biomass of the animals per square meter in 1978-1979 were adjusted by Dermott (1994) by multiplying the actual organisms counted in the samples by 30, to take into consideration the relative inefficiency of the Shipek grab (jaw area 0.0416 m^{-2}). Data from Shipek-Ponar comparisons indicated that the Shipek collected an average of 954.0 invertebrates, while the more efficient Ponar grab collected an average of 1216.6 m^{-2} (Dermott, 1994).

We used non-parametric Wilcoxon matched pairs test to compare station data in 1978-79 (1 replicate) with average of 3 replicates (2014) to test densities of different taxa by basin and lake-wide. To compare the species richness in 2014 with 1978-1979 data we first calculated the number of species per each replicate collected at each station and then averaged the number of species per station.

Table 1.2. Location and depth of the 25 Lake Erie stations sampled in 1978-79 and in 2014.

Station	Depth, m	Basin	Latitude	Longitude
D02	5	Western	41.42.4	83.16.9
E03	7	Western	41.48.1	83.09.9
F03	7	Western	41.48.1	83.09.9
W42	10	Western	41.56.7	82.59.5
C05	8	Western	41.37.5	82.55.3
F05	11	Western	41.53.8	82.55.7
B07	11	Western	41.32.5	82.41.6
C07	14	Western	41.37.8	82.40.9

Station	Depth, m	Basin	Latitude	Longitude
G09	14	Central	41.59.7	82.27.0
C10	14	Central	41.38.2	82.19.2
H11	19	Central	42.05.2	82.12.9
B12	15	Central	41.32.9	82.04.8
B13	15	Central	41.32.9	81.57.6
D13	21	Central	41.43.8	81.57.7
I15	22	Central	42.10.9	81.43.6
C16	14	Central	41.38.5	81.35.9
J22	14	Central	41.54.8	80.52.8
N22	10	Central	42.38.0	80.52.5
I28	13	Eastern	42.10.9	80.09.4
K28	33	Eastern	42.22.0	80.09.0
K29	38	Eastern	42.22.3	80.01.7
L29	45	Eastern	42.26.5	80.01.5
N30	42	Eastern	42.38.3	79.54.1
J31	12	Eastern	42.16.1	79.47.4
P31	13	Eastern	42.48.4	79.46.6

RESULTS

Inter-Basin Comparison

A total of 118 species and higher taxa of benthic aquatic invertebrates were recorded in Lake Erie in 2014 (Appendix 1.2). The most diverse were Oligochaeta (41 species and higher taxa), Chironomidae (35), Gastropoda (16), Bivalvia (6), Hirudinea (6), and Amphipoda (4). Other classes were represented by less than 3 taxa, or were not identified to species level (e.g., Enchytraeidae, Hydra, Nemertea).

The most widely occurred species throughout the lake was oligochaete *Limnodrilus hoffmesiteri* (found in 94% of all benthic samples), followed by chironomid *Procladius* sp. (80%), exotic bivalve *Dreissena r. bugensis* (76%), chironomids *Chironomus* sp. (75%), *Tanytarsus* sp. (65%), tubificids *Ilyodrilus templetoni* (63%) and *Aulodrilus limnobius* (51%), bivalve *Pisidium* sp. (54%), Hydra (51%) and flatworm *Hydrolimax grisea* (50%). All other species were found in less than 50% of the samples (Appendix 1.2).

Oligochaeta comprised a large part of lake-wide benthos densities (57%), followed by *D. r. bugensis* (18%), and by Chironomida (8%) (Appendix 1.1, Figure 1.3). Contribution of other groups (Amphipoda, Gastropoda, Hirudinea, etc) into total benthos density was less than 2% each. Among Oligochaeta, the most numerous were Tubificidae (48%).

Dreissena r. bugensis dominated lake-wide benthos by biomass (96% of total wet biomass) (Table 1.3, Figure 1.3). The rest of the benthic biomass was mainly represented by *D. polymorpha* (1.8%), Oligochaeta (1.1%), Chironomida (0.4%) and *Hexagenia* sp. (0.4%) (Table 1.3).

The distribution of lake-wide diversity, densities and biomass of benthic invertebrates varied with depth (Table 1.4). Species richness was the highest at shallow (< 20 m) depths (in average 25.4 ± 1.1 species/sample, mean ± standard error here and elsewhere unless noted) and decreased to 19.1 ± 1.1 at 20 – 40 m, and to 11.8 ± 0.7 species/sample at depths > 40 m. The highest densities and biomass of Amphipoda, Hirudinea, Hexagenia, Gastropoda and Naididae (Oligochaeta) were also found at shallow (< 20 m) depths. Taxa prevalent at depth interval from 20 to 40 m included Chironomida, Oligochaeta (mostly Tubificidae), and Bivalvia (mostly *Pisidium* sp.). The deepest zone (> 40 m) was dominated by *Dreissena* and Lumbriculidae. While the highest densities of *Dreissena* were found at shallow depths (< 20 m), the highest biomass was found at > 40 m depth, largely due to different size structure (see Figure 1.6 in subchapter "Length-frequency distribution" in "2014 *Dreissena* spp. distribution and hypoxia" below).

Lake Erie basins are very different in terms of morphometry, nutrient load, and benthic species composition (Burlakova et al., 2014). Basin-wise, the highest total average benthos density in 2014 was found in the central basin, followed by the eastern and western basins (Table 1.3). *Dreissena* spp. dominated benthos densities only in the western basin (41%), while oligochaetes were the most dominant group in both eastern (63%) and especially central (67%) basins. The lowest densities of *Dreissena* were found in the central basin (6% from total benthos density) where its population is limited by periodic hypoxia (please find details in subchapter "2014 *Dreissena* spp. distribution and hypoxia"). *Dreissena*, however, was the dominant species in terms of biomass (measured in total wet weight) in all basins, where its percentage increased from 80% in western basin to 99.6% in the eastern basin. Without consideration of dreissenids, density of benthos was the lowest in the western basin. The total wet biomass in this basin, however, was almost three times higher than in the eastern basin, and was comparable to the central basin due to presence of large-bodied *Hexagenia* sp. and abundance of molluscs (Table 1.3, Figure 1.4). Species richness was the highest in the shallowest and the most productive western basin (on average 27.1±1.5 species per sample), intermediate in the central (21.9±1.3), and the lowest in the least productive eastern basin (18.8±1.4). As a result, Shannon diversity was higher in the western basin (H' = 3.85) compared to the central (3.75) and eastern (3.72) basins. Pielou's evenness of benthic community in the western basin was also higher (J' = 0.873) that in both the central (0.850) and eastern basins (0.846).

Figure 1.3. Percentage of lake-wide density (left) and wet biomass (right) of major benthic taxa calculated with (upper) and without (lower) *Dreissena* in Lake Erie in 2014. Oligochaete fragments were not included in calculation of oligochaete densities, but were considered for calculation of biomass.

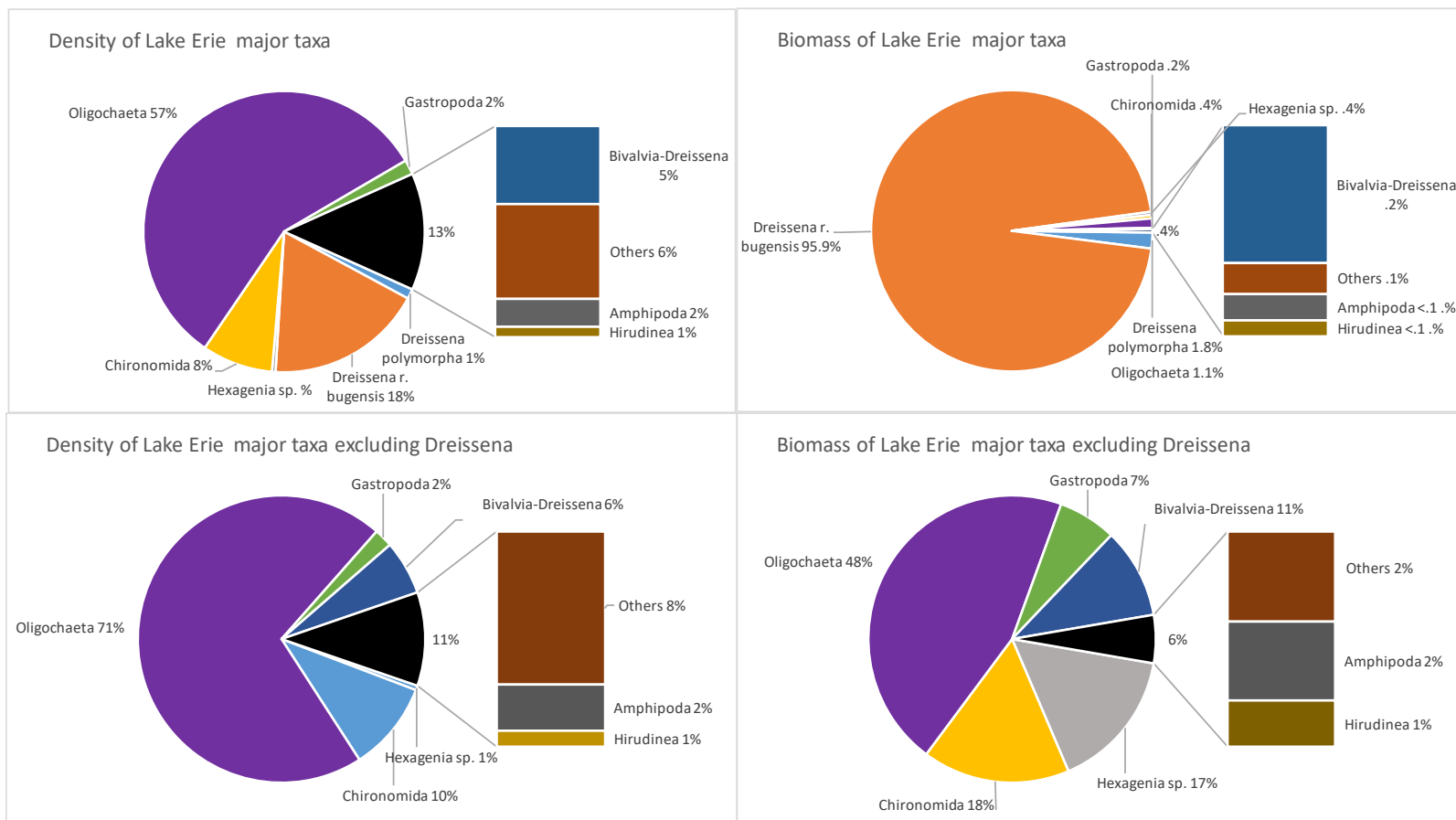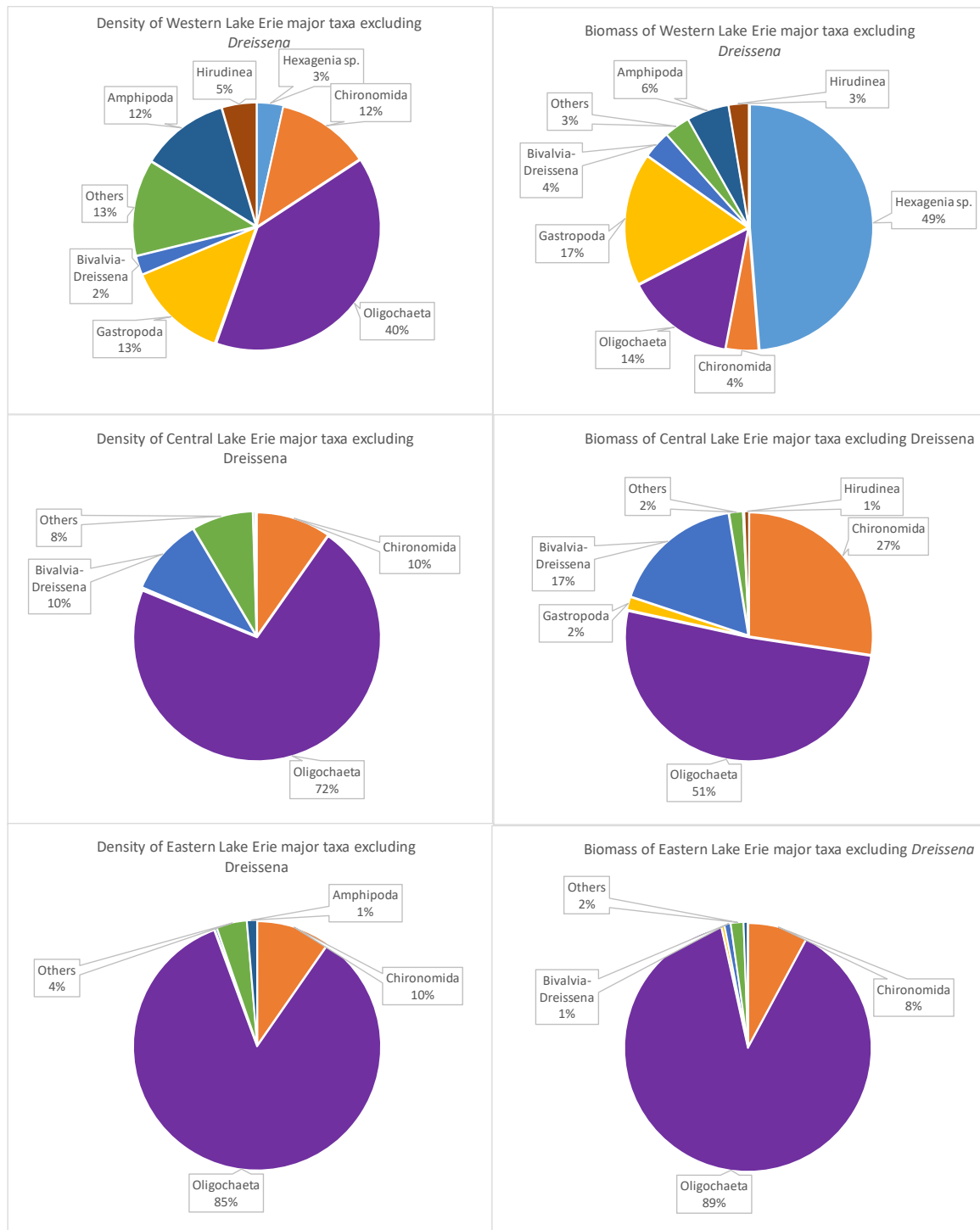**Figure 1.4.** Percentage of basin-wide density (left) and wet biomass (right) of major benthic taxa calculated without *Dreissena* in Lake Erie in 2014. Taxa that were < 1% of total benthic density are not shown.

Table 1.3. Density (ind. m^{-2}) and wet biomass (g m^{-2}) of major taxonomic groups of benthic invertebrates collected in Lake Erie in 2014 (inter-basin comparison) and averaged by basin and lake-wide. In 2014 benthos was collected at 80 stations, and data on *Dreissena* were collected from 80 benthic and additional 27 "*Dreissena* only" stations. Therefore *Dreissena* density and biomass are provided separately from *Dreissena* survey (107 stations total) and for benthic survey (80 stations). Densities are also calculated as percentage from basin-wide and lake-wide total densities (for both benthos and *Dreissena* surveys). Oligochaete fragments were not considered for calculation of oligochaete densities, but were considered for biomass calculation.

Taxa	Western basin	%	Central basin	%	Eastern basin	%	Lake-wide	%
Dreissena **survey** (*n*)	**22**		**42**		**43**		**107**	
Dreissena polymorpha (m^{-2})	368.5	*13.0*	15.4	*2.5*	4.4	*0.19*	83.6	*4.8*
Dreissena polymorpha (g m^{-2})	39.29	*15.0*	0.48	*0.5*	0.60	*0.04*	8.51	*1.1*
Dreissena r. bugensis (m^{-2})	2475.0	*87.0*	592.9	*97.5*	2282.9	*99.8*	1659.0	*95.2*
Dreissena r. bugensis (g m^{-2})	222.12	*85.0*	92.28	*99.5*	1623.89	*99.9*	734.48	*98.9*
All *Dreissena* (m^{-2})	2843.6	*100*	608.3	*100*	2287.4	*100*	1742.7	*100*
All *Dreissena* (g m^{-2})	261.41	*100*	92.75	*100*	1624.49	*100*	742.99	*100*
Benthic survey (*n*)	**21**		**31**		**28**		**80**	
Dreissena polymorpha (m^{-2})	386.1	*5.2*	20.9	*0.2*	6.8	*0.1*	111.8	*1.2*
Dreissena polymorpha (g m^{-2})	41.16	*14.1*	0.64	*0.6*	0.92	*0.1*	11.38	*1.8*
Dreissena r. bugensis (m^{-2})	2592.9	*35.2*	675.8	*5.6*	2325.6	*26.2*	1756.4	*18.1*
Dreissena r. bugensis (g m^{-2})	232.70	*79.8*	80.50	*80.8*	1432.56	*99.6*	593.67	*95.9*
Total *Dreissena* (m^{-2})	2979.0	*40.5*	696.7	*5.8*	2332.4	*26.2*	1868.3	*19.2*
Total *Dreissena* (g m^{-2})	273.86	*93.9*	81.15	*81.5*	1433.48	*99.6*	605.05	*97.8*
Mollusca (m^{-2})	3584.0	*48.7*	2116.0	*17.6*	2385.5	*26.8*	2595.7	*26.7*
Mollusca (g m^{-2})	277.53	*95.1*	84.93	*85.3*	1433.58	*99.6*	607.52	*98.2*
Bivalvia (m^{-2})	3087.0	*41.9*	1845.5	*15.3*	2352.0	*26.5*	2348.6	*24.2*
Bivalvia (g m^{-2})	274.52	*94.1*	84.48	*84.8*	1433.54	*99.6*	606.54	*98.0*
Bivalvia without *Dreissena* (m^{-2})	108.0	*1.5*	1148.8	*9.5*	19.6	*0.2*	480.3	*4.9*
Bivalvia without *Dreissena* (g m^{-2})	0.66	*0.2*	3.34	*3.4*	0.06	*<0.1*	1.49	*0.2*
Gastropoda (m^{-2})	581.5	*7.9*	26.2	*0.2*	3.2	*<0.1*	163.9	*1.7*
Gastropoda (g m^{-2})	3.16	*1.1*	0.32	*0.3*	0.03	*<0.1*	0.96	*0.2*
Chironomida (m^{-2})	538.2	*7.3*	1107.2	*9.2*	633.4	*7.1*	792.0	*8.2*
Chironomida (g m^{-2})	0.77	*0.3*	5.26	*5.3*	0.55	*<0.1*	2.43	*0.4*
Amphipoda (m^{-2})	509.2	*6.9*	29.5	*0.2*	86.0	*1.0*	175.2	*1.8*
Amphipoda (g m^{-2})	1.00	*0.3*	0.04	*<0.1*	0.04	*<0.1*	0.29	*0.0*
Hexagenia sp. (m^{-2})	152.2	*2.1*	0.8	*<0.1*	0.0	*<0.1*	40.3	*0.4*
Hexagenia sp. (g m^{-2})	8.84	*3.0*	0.01	*<0.1*	0.00	*<0.1*	2.32	*0.4*
Hirudinea (m^{-2})	199.3	*2.7*	25.2	*0.2*	0.9	*<0.1*	62.4	*0.6*
Hirudinea (g m^{-2})	0.48	*0.2*	0.11	*0.1*	0.00	*<0.1*	0.17	*<0.1*
Oligochaeta (m^{-2})	1740.4	*23.6*	8109.0	*67.3*	5552.1	*62.5*	5542.4	*57.1*

Taxa	Western basin	%	Central basin	%	Eastern basin	%	Lake-wide	%
Oligochaeta (g m^{-2})	2.61	0.9	9.82	9.9	6.16	0.4	6.64	1.1
Lumbriculidae (m^{-2})	0.0	0.0	0.0	0.0	215.8	2.4	75.5	0.8
Lumbriculidae (g m^{-2})	0.00	0.0	0.00	0.0	0.92	0.1	0.32	0.1
Naididae (m^{-2})	290.6	3.9	1432.9	11.9	293.0	3.3	734.1	7.6
Naididae (g m^{-2})	0.05	<0.1	0.31	0.3	0.24	<0.1	0.22	<0.1
Tubificidae (m^{-2})	1446.9	19.7	6674.1	55.4	4873.3	54.8	4671.7	48.1
Tubificidae (g m^{-2})	2.29	0.8	8.93	9.0	4.04	0.3	5.48	0.9
Others (m^{-2})	555.1	7.5	909.8	7.5	259.5	2.9	589.1	6.1
Others (g m^{-2})	0.61	0.2	0.34	0.3	0.12	<0.1	0.33	0.1
Benthos total density (m^{-2})	7362.9	100	12053.3	100	8887.2	100	9713.9	100
Benthos total biomass (g m^{-2})	291.70	100	99.58	100	1438.88	100	618.77	100
Benthos total density without *Dreissena* (m^{-2})	4383.9	59.5	11356.6	94.2	6554.8	73.8	7845.6	80.8
Benthos total biomass without *Dreissena* (g m^{-2})	17.84	6.1	18.44	18.5	5.40	0.4	13.72	2.2

Table 1.4. Lake-wide density (m^{-2}) and biomass (total wet weight, g m^{-2}) of major taxonomic groups of benthic invertebrates collected in Lake Erie in 2014 and averaged by depth zones. Data for *Dreissena* (combined *D. polymorpha* and *D. r. bugensis*) are provided separately from *Dreissena* survey (all 107 stations total) and from benthic survey (80 stations). Fragments were not considered for calculation of oligochaete densities, but were considered for biomass calculation. Colors highlight the depth intervals with lowest and highest densities and biomass increasing in intensity from green (low values) to yellow (middle range) to red (high values).

Taxa	Density			Biomass		
	< 20 m	20-40 m	> 40 m	< 20 m	20-40 m	> 40 m
Amphipoda	291.9	0.3	0.0	0.48	0.00	0.00
Chironomidae	314.2	1161.0	12.0	1.91	4.49	0.02
Hexagenia sp.	67.1	0.0	0.0	3.87	0.00	0.00
Hirudinea	89.2	11.7	1.6	0.23	0.13	0.00
Mollusca	3076.7	1899.8	1797.3	561.18	228.76	2021.75
Dreissena from benthic survey	2643.9	342.0	1793.3	559.10	224.71	2021.75
Dreissena from all sites	2500.1	346.0	1793.3	843.17	267.50	2021.75
Dreissena %	21	6	33	62	29	100
Bivalvia - *Dreissena*	154.3	1292.5	0.0	0.62	3.71	0.00
Gastropoda	315.3	265.3	4.0	1.52	0.34	0.00
Total Oligochaeta	5002.2	7276.0	3582.6	3.69	12.23	7.57
Oligochaeta %	45	71	66	10	37	0
Lumbriculidae	0.0	106.2	436.6	0.00	0.38	2.09
Naididae	968.5	498.4	35.9	0.26	0.19	0.04
Tubificidae	4019.7	6598.5	2802.7	2.98	10.95	4.01
Others	798.4	75.2	12.0	4.24	0.07	0.04

Taxa	Density			Biomass		
	< 20 m	20-40 m	> 40 m	< 20 m	20-40 m	> 40 m
Total benthos	10500.5	9577.0	5405.4	571.15	244.47	2027.36
Total benthos - *Dreissena*	7856.6	9235.0	3612.1	12.05	19.76	5.61

Community analysis

There was a significant difference in benthic communities among basins both with and without consideration of *Dreissena* (R = 0.67, P = 0.001; 1-way ANOSIM, Figure 1.5). The largest differences were found between communities in the eastern and western basins (R = 0.89, P = 0.001, pairwise tests after ANOSIM), but differences between central and western basins (R = 0.70) and eastern and central basins (R = 0.45) were significant as well (P = 0.001).
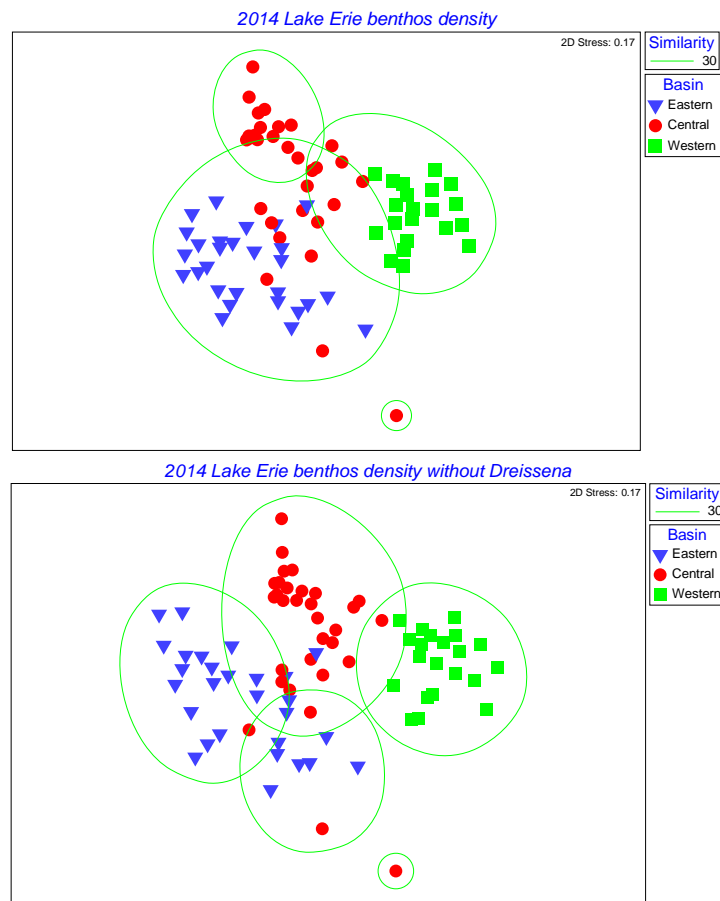

Figure 1.5. NMDS ordination plots of the benthic community structure of Lake Erie based on Bray-Curtis similarities (using 4th root transformed density) in 2014. Stress = 0.17. There were significant differences in community structure among basins (ANOSIM, P = 0.001). Analysis was done with consideration of *Dreissena* (upper) and excluding *Dreissena* densities (lower).

To understand the differences in community composition of the three basins and identify species responsible for dissimilarity of these communities, we examined the contribution of each species (based on density) to the average Bray-Curtis similarity in each community.

The benthic community of western basin was dominated by *D. r. bugensis* (8% contribution to the similarity within community), *Hexagenia* sp. (7%), chironomid *Coelotanypus* sp. (7%), oligochaeta *Limnodrilus hoffmeisteri* (6%), and *D. polymorpha* (6%). In contrast, benthic community of the central basin was dominated by hypoxia-tolerant species *Chironomus* sp. (12%), *Pisidium* sp. (10%), oligochaetes *L. hoffmeisteri* (8%), *Quistadrilus multisetosus* (6%) and *Spirosperma ferox* (6%), and chironomids *Procladius* sp. and *Tanytarsus* sp. Benthos of the eastern basin was largely defined by *D. r. bugensis* (20% contribution to the similarity within community), oligochaeta *Potamothrix vejdovskyi* (16%), *L. hoffmeisteri* (11%) and *Tubifex tubifex* (7%). These species determined the largest dissimilarities among communities (western and central: 75%; western and eastern: 79%; central and eastern: 70%).

2014 *Dreissena* spp. distribution and hypoxia

In 2014, dreissenid biomass was higher in the eastern basin, mostly due to larger sizes of *Dreissena* (Table 1.4 & 1.5, Figure 1.6). Dreissenids comprised anywhere from 38% of all benthic density in the central basin, to 45% in the eastern, and to 70% in the western basin, and from 97.5 to 99% of the total benthic biomass. Almost 40% of all dreissenid density and 17% of biomass was represented by *D. polymorpha* in the western basin. This species was almost absent from the central basin and was not found in the eastern basin (Table 1.4, Figure 1.2B). The highest density and biomass of dreissenids were found at 5 and 10 m depth in all basins (Table 1.4). Without dreissenids, the abundance of benthos in the western basin was higher at 2 and 10 m, and in the central and eastern basins – at 20 m depth (Table 1.5). *Dreissena* distribution varied dramatically among lake basins. While *Dreissena* spp. in the western and eastern basins mussels were found on almost all sites sampled, a large portion of the central basin was free of adult *Dreissena* (Figure 1.2B). Average *Dreissena* spp. densities and biomass were also different among basins (density: P < 0.001; biomass: P < 0.001, Kruskal-Wallis ANOVA by Ranks; Table 1.4). Maximum average basin wide density of *Dreissena* was found in the western basin followed by the eastern basin. However, *Dreissena* biomass was by far the highest in the eastern basin. While in the western basin dreissenid density and biomass were distributed fairly equally among two depth zones (density: P = 0.84; biomass: P = 0.54), in the central and eastern basins these parameters differed significantly among depth zones (central basin density: P < 0.001, biomass: P < 0.001; eastern basin density: P = 0.0195, biomass: P = 0.0349, Table 1.4).

In the central basin, both *Dreissena* density and biomass declined dramatically with depth. Deeper than 20 m we found only one site (#946) with high quagga mussels density and biomass which was located on the eastern edge of the basin (Fig. 1.2 B). This part of the central basin receives well-oxygenated water from the east basin thermocline keeping the eastern part of the central basin hypolimnion better oxygenated than other parts of the central basin (Boyce et al. 1980). Excluding this site, *Dreissena* average density at depths > 20 m was only 2 ± 1 m^{-2} and wet biomass was 0.3 ± 0.3 mg m^{-2}. In contrast to the central basin, mussel density and biomass were two to three orders of magnitude higher in the same depth zone of the eastern basin. In the eastern basin, *Dreissena* spp. density and biomass was highest at the 10 – 20 m depth interval, then declined at the 20 – 40 m depth zone and then increased again at depths over 40 m.

Length-frequency distribution

Dreissena length-frequency distribution was different among basins (Figure 1.6). In the western and central basins it was mostly unimodal, positively skewed due to the dominance of small (younger) mussels, and negatively truncated due to the lack of large mussels. As a result, 96% of all mussels in these basins were < 18 mm, a distribution indicating successful population recruitment but failed survival in older size classes. This distribution was also consistent with depth, since *Dreissena* spp. average length was not significantly different among depth zones in both basins (all P > 0.89, Turkey HSD tests).

In contrast, the length-frequency distribution of *Dreissena* in the eastern basin at depths < 40 m was bimodal, suggesting both good recruitment and survival. At deeper (> 40 m) depths, however, the length-frequency distribution was unimodal again, with > 98% of all mussels being > 18 mm, and the average mussel length in this depth zone was higher than in other depth zones (P < 0.012, Turkey HSD test). The size structure of *Dreissena* in this deep zone may indicate strong population survival of adult mussels but consistent recruitment failures or high mortality of smaller/younger mussels. As a result, the average dreissenid length varied significantly among both lake basins and depths zones (basin: P < 0.001, depth zone: P < 0.001, Generalized Linear Model, Figure 1.6), with the average mussel length in eastern basin being significantly larger than in other basins (average length 15.5 ± 0.6 mm vs. 6.8 ± 0.7 mm in central and 7.6 ± 0.6 mm in wester basins, P < 0.0001, Turkey HSD test). In addition, maximum mussel lengths were always higher in the eastern basin and often exceeded 30 mm.

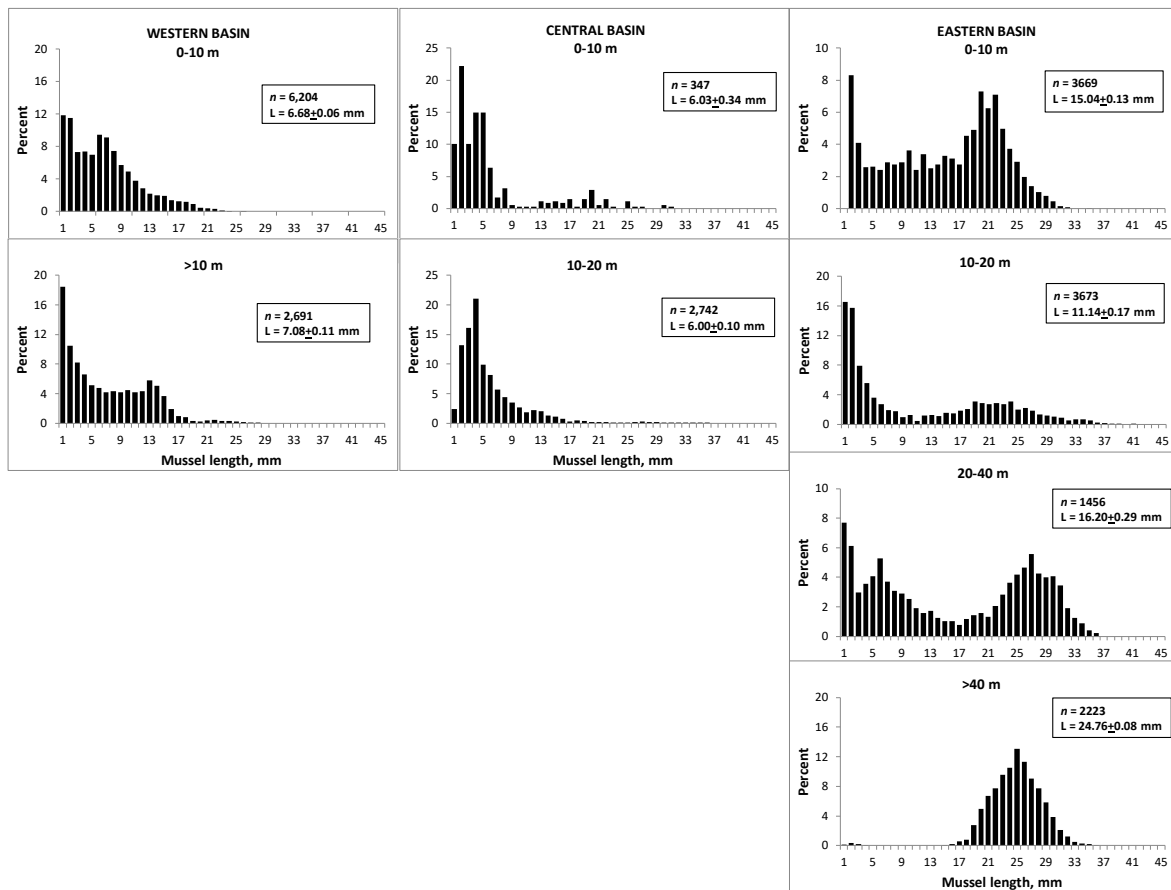**Figure 1.6.** Length-frequency distributions of *Dreissena* spp. in Lake Erie in 2014 presented by depth intervals. Inserts: sample size (n) and the average length of mussels in the samples (L, mm ± standard error).

Table 1.5. Density (N, average ± standard error here and elsewhere in the table, m^{-2}), wet biomass (B, shell plus tissue g m^{-2}) of *Dreissena* spp., and the total number of sites sampled (N) in Lake Erie in 2014.   n.r. – not recorded.

Basin, depth, m	N	*D. polymorpha*		*D. r. bugensis*		All *Dreissena*	
		N	B	N	B	N	B
Western							
0-10	14	398±150	36.7±14.4	2846±2004	243.1±147.8	3243±2009	279.8±150.4
>10	8	318±218	43.8±29.8	1826±1074	185.5±86.7	2144±1108	229.3±107.2
Average	22	369±122	39.3±13.8	2475±1317	222.1±97.8	2844±1324	261.4±01.7
Central							
0-10	4	50±32	1.6±0.9	1199±1015	233.5±231.7	1249±1012	235.2±231.9
10-20	16	28±14	0.8±0.6	1082±481	123.9±56.8	1110±484	124.8±56.7
> 20	22	*n.r.*	*n.r.*	127±126	43.6±43.3	127±126	43.6±43.3
Average	42	15±7	0.5±0.3	593±223	92.3±37.6	608±224	71.8±32.0
Eastern							
0-10	10	*n.r.*	*n.r.*	2645±908	1897.4 ±616.6	2645±908	1897.4±616.6
10-20	12	16±11	2.2±1.7	4005±1337	2189.6±554.7	4021±1338	2191.8±555.8
20-40	13	*n.r.*	*n.r.*	716±281	646.5±237.1	716±281	649.0±236.6
>40	8	*n.r.*	*n.r.*	1793±214	2021.8±183.3	1793±214	2021.8±183.3
Average	43	4±3	0.6±0.5	2283±468	1623.9±239.7	2287±469	1625.3±239.8
Lake average	107	84±28	8.5±3.2	1659±346	734.5±121.6	1743±350	741.3±122.6

Dreissena long-term-dynamics

Dreissena polymorpha and *D. r. bugensis* colonized Lake Erie in the late 1980s. By the time of the first lake-wide study of dreissenid populations in Lake Erie in 1992, the combined densities of these species in all basins were already high (842±620 m^{-2} in the western, 1131±679 m^{-2} in the central, and 6003±2093 m^{-2} in the eastern basins, Figure 1.7).

In the western basin *Dreissena* spp. population was relatively stable compared to other basins. After the initial peak, zebra mussel density declined and was stable since 1998 (Figure 1.8). In contrast, quagga mussel density was constantly increasing and reached maximum in 2014. In 2014 zebra mussels were still common in western basin, where their occurrences were only slightly lower than that of quagga mussels (91% vs. 86% quagga and zebra mussels respectively). The small increase in *Dreissena* spp. density we found in 2014 was likely due to the recent spawning, since the biomass has not changed.

In the central basin *D. polymorpha* density was constantly declining since the first lake-wide study (1992). By 1998 *D. polymorpha* has virtually disappeared from the basin. In contrast, *D. r. bugensis* density in 1990s was climbing until it reached the maximum in 1998, but then declined almost 5-fold by 2002 and had not recovered since (Figure 1.8).

Similar to the central basin, *D. polymorpha* densities declined since 1992 in the eastern basin. *D. r. bugensis* reached their maximum in the basin in 2002 and then declined. *Dreissena* spp. 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. This large increase, however, could be explained as an artifact of the sampling design. In 2002, the nearshore (< 15 m) part of the eastern basin was sampled at 10 stations located on the northern shoreline

and represented largely by bedrock with very high *Dreissena* densities (Patterson et al., 2005; Karatayev et al., 2014). Two years later, when the eastern basin was surveyed again in a more comprehensive study with over 35 stations sampled (Ciborowski et al., in preparation), the average basin-wide density was more than 6 fold lower and did not change substantially during the next 10 years. Nevertheless, even excluding 2002 data, the average basin-wide *Dreissena* density after 1998 (2004 - 2014) in the eastern basin was almost 5-fold higher than in the central basin (1572 *vs.* 348 m^{-2}).
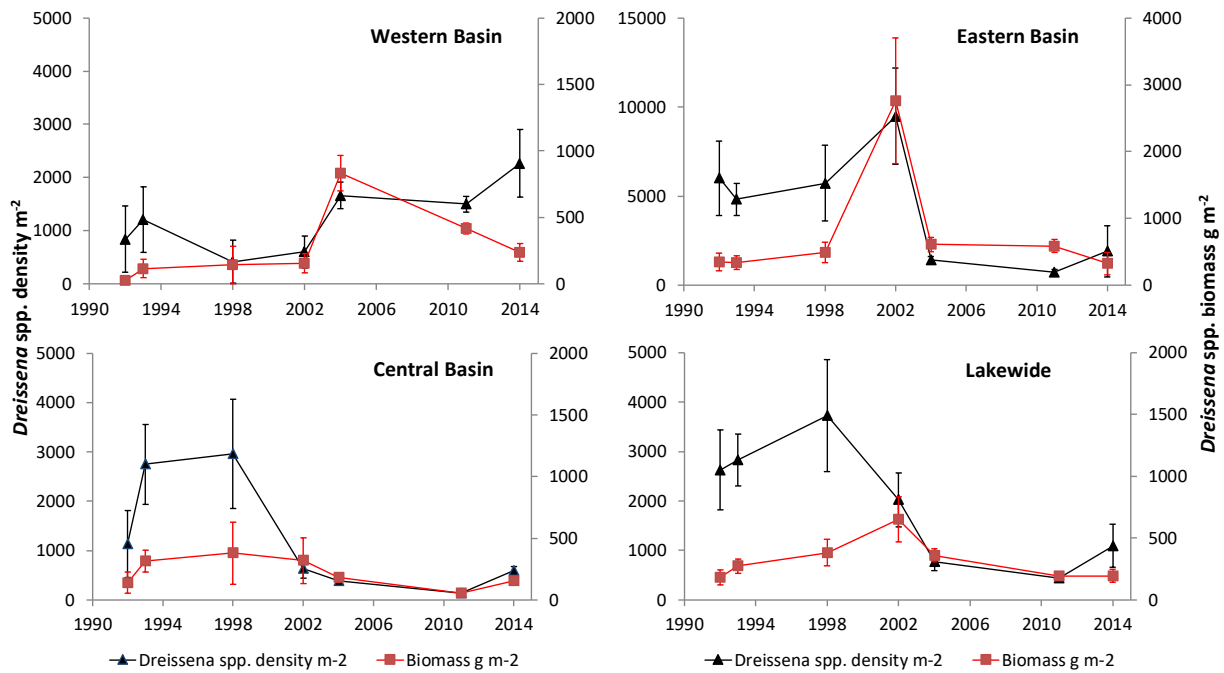
Figure 1.7. Long-term dynamics of *Dreissena* spp. density and wet biomass in Lake Erie (vertical bars are standard errors). Data represent a variety of non-randomly selected sampling stations and differing sampling methods over the years. For 1992-1998 (Jarvis et al., 2000), data are presented as averages for all survey sites. Data collected in 2002 (Patterson et al., 2005), 2004 (Ciborowski et al., in preparation), 2009-2011 (average for 2009, 2011, 2012, Karatayev et al. 2014), and in 2014 are presented as weighted averages.

Figure 1.8. Long-term dynamics of *Dreissena polymorpha* and *D. r. bugensis* density in Lake Erie (vertical bars are standard errors). Data represent a variety of non-randomly selected sampling stations and differing sampling methods over the years. For 1992-1998 (Jarvis et al., 2000), data are presented as averages for all survey sites. Data collected in 2002 (Patterson et al., 2005), 2004 (Ciborowski et al., in preparation), 2009-2011 (average for 2009, 2011, 2012, Karatayev et al. 2014), and in 2014 are presented as weighted averages.
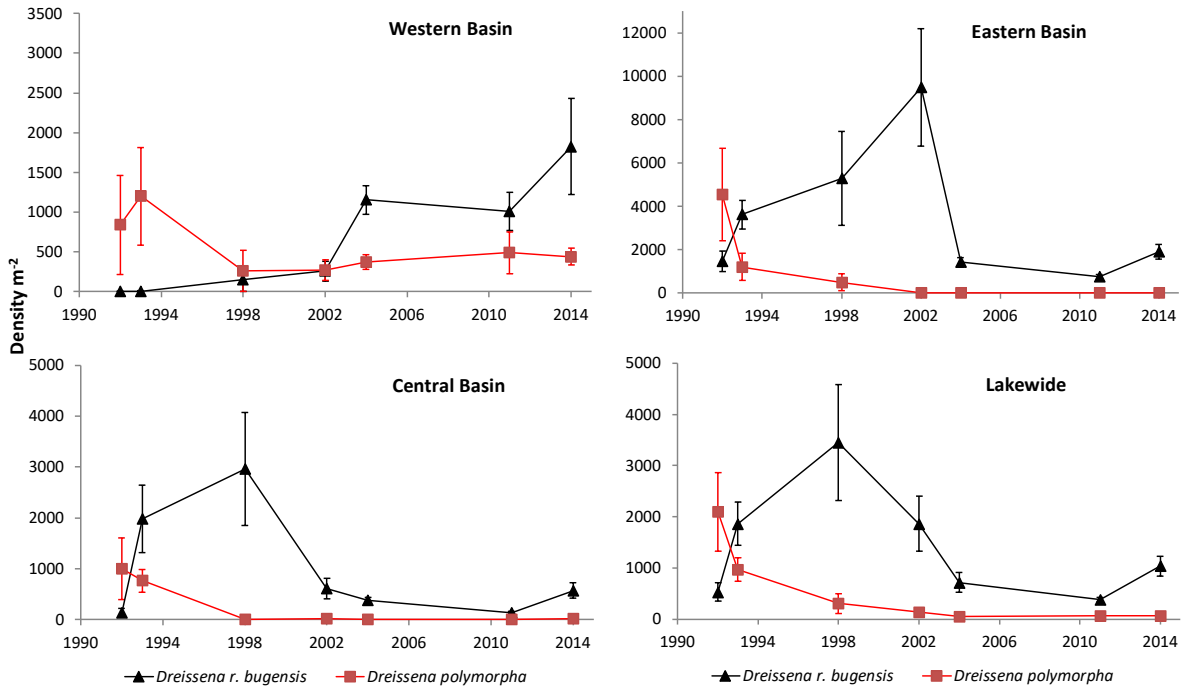
The density differences between the central and eastern basins were even more dramatic when comparing *Dreissena* populations in the profundal zone. In 2014, the average profundal mussel density in the central basin was 14 times lower than in the eastern basin (84 ± 59 m^{-2} *vs.* 1193 ± 217 m^{-2} respectively, $P < 0.0001$, *t*-test). Mussels in the central basin were largely limited to the shallow nearshore area.

Historical comparison: 1978-79 and 2014

In total, we found 94 species of benthic macroinvertebrates, compared to 68 species found at the same stations in 1978-79 (Table 1.6). In part, the increase in the total number of species maybe due to a larger sampling area since in 2014 we collected more replicates at each station than in 1978-79 (3 vs. 1), that effected the total number of species reported per station.

Species diversity, however, was higher in 2014 even when we compensated for the larger sampling area by calculating the number of species (excluding *Dreissena*) per each replicate, and averaging them per sampling station. We found that species richness increased from 10 to 17 species per station between 1978-79 and 2014 ($P = 0.0004$, Wilcoxon matched pairs test, Figure 1.9, Table 1.6). The largest increase (from 9 to 19 species) was found in the western basin, mostly due to the increase in diversity of Gastropoda and Hirudinea (Table 1.6).
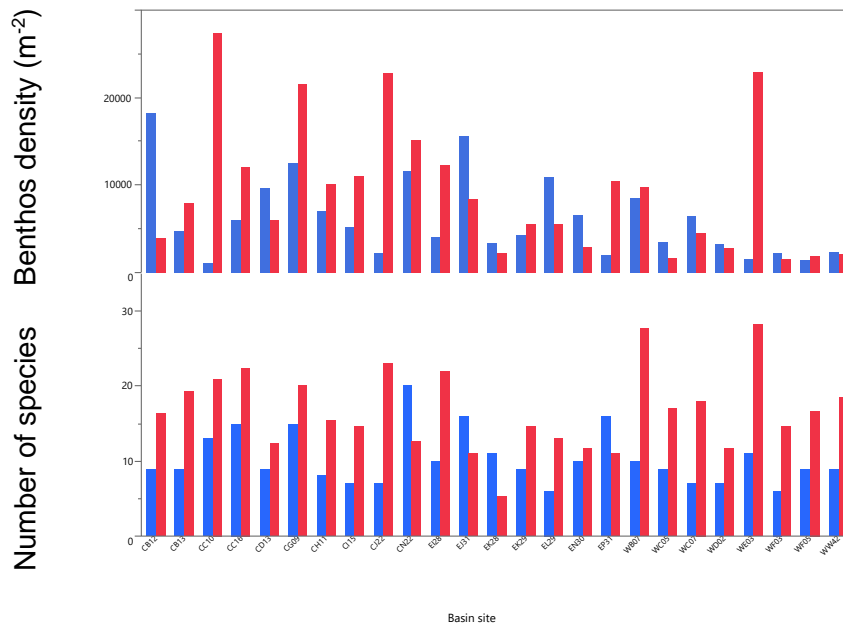
Figure 1.9. Species richness and density of benthos collected from the same 25 stations in 1978-79 (blue, 1 replicate per site) and 2014 (red, average of 3 replicates per site). Stations are labeled by basin (C – central, E – eastern, and W – western) and station number. Benthos density and diversity in 2014 was calculated without consideration of *Dreissena*.

Table 1.6. Number of species and higher taxa in major benthic groups found in Lake Erie at the same 25 stations sampled in 1978-79 and 2014 (with consideration of *Dreissena*).

Taxa	1979	2014
Bivalvia	2	5
Gastropoda	3	12
Chironomidae	16	24
Amphipoda	2	4
Ephemeroptera	0	1
Isopoda	1	1
Trichoptera	0	1
Hirudinea	3	5
Oligochaeta	39	38
Polychaeta	1	1
Platyhelminthes	1	2
Total	**68**	**94**

The increase in benthos density was not significant within basins, due to large variability among stations and small number of replicates (Figure 1.9). Densities of oligochaetes increased in the central basin (Figure 1.8), and densities of non-dreissenid bivalves decreased in the eastern basin. The largest changes were found in the western basin where, along with increased diversity, the densities of Amphipoda, Gastropoda, Trichoptera and other taxa increased, and mayfly *Hexagenia* spp. re-established (Table 1.7, Figure 1.10 & 1.11). The densities of Isopoda, Turbellaria, Nemertea, and Hydra increased significantly lake-wide, while the abundance of polychaeta *Manayunkia speciosa* decreased in the western basin. Densities of Chironomida have not changed significantly in any of the basins (Figure 1.12, Table 1.7).
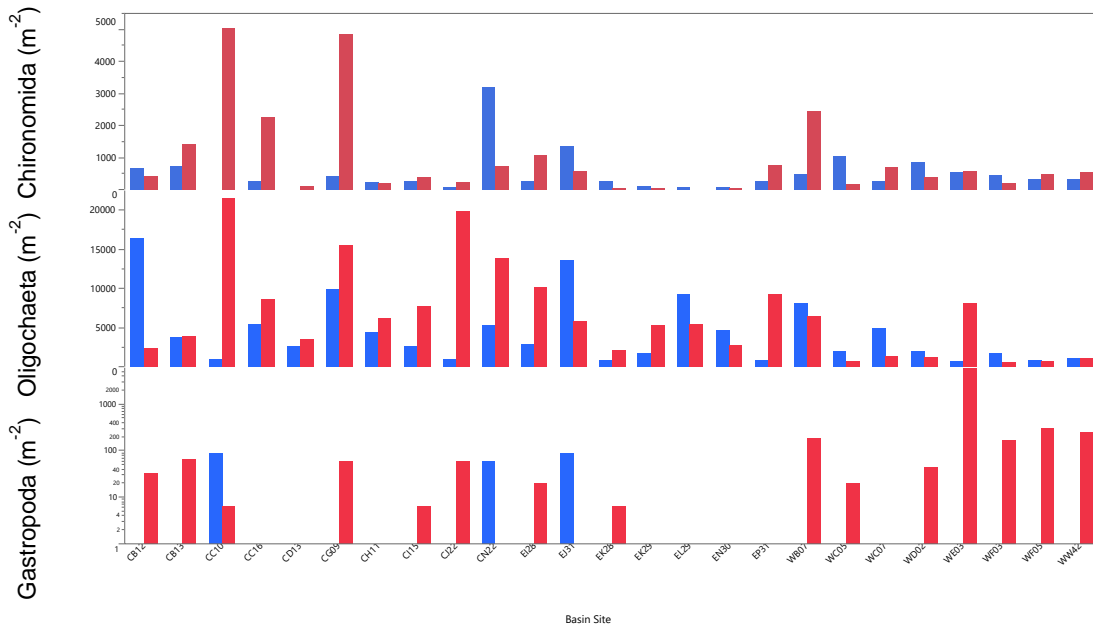

Figure 1.10. Density of Gastropoda, Oligochaeta and Chironomidae in 1979 (blue, 1 replicate per site) and 2014 (red, average of 3 replicates per site). Stations are labeled by basin (C – central, E – eastern, and W – western) and station number.

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Figure 1.11. Density of Amphipoda, Hirudinea and Bivalvia (excluding *Dreissena* spp. in 2014) in 1979 (blue, 1 replicate per site) and 2014 (red, average of 3 replicates per site). Stations are labeled by basin (C – central, E – eastern, and W – western) and station number.
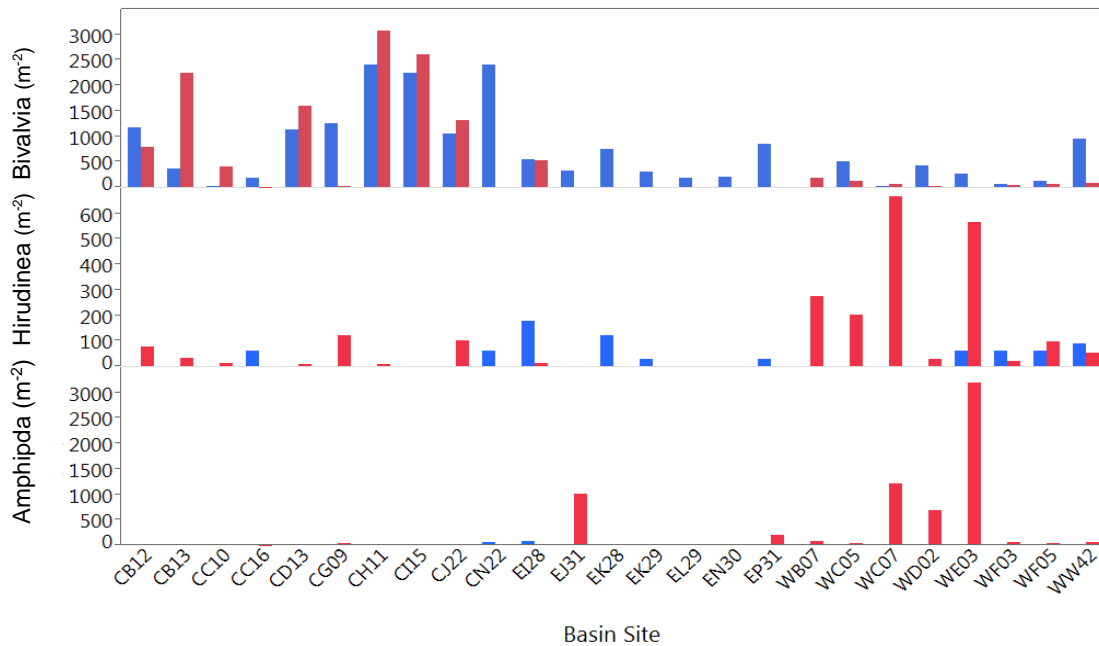
Table 1.7. Average density of major taxa and species richness of benthos collected from same stations of Lake Erie sampled in 1978-1979 and in 2014. Since in 2014 we collected three replicates per station (vs. one in 1978-79), we calculated the number of species per replicate (excluding *Dreissena*) and then averaged per station. Average of station means by basin and lake-wide, standard errors and P-values (P) of Wilcoxon matched pairs test are given (*significant differences). The group "Others" include Polychaeta (*Manayunkia speciosa*), Isopoda, Turbellaria, Nemertea, *Mysis* sp. and Hydra.

Taxa	Year	Western	Central	Eastern	Lakewide
Number of stations		8	10	7	25
Total benthos density with *Dreissena*	1978-79	3677±897	7832±1645	6660±1839	6174±922
	2014	10729±5958	14400±2482	10608±2067	12163±2162
	P	0.161	0.114	0.176	0.007*
Total benthos density without *Dreissena*	1978-79	3677±897	7832±1645	6660±1839	6174±922
	2014	5898±2622	13800±2463	6773±1438	9304±1504
	P	0.674	0.114	0.866	0.174
Gastropoda	1978-79	0	15±10	13±13	10±5
	2014	834±699	22±9	4±3	277±227
	P	0.018*	0.735	1.00	0.035*
Oligochaeta	1978-79	2650±911	5211±1495	4817±1850	4281±840
	2014	2461±1054	10306±2204	5859±1128	6551±1177
	P	0.164	0.047*	0.735	0.166

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Taxa	Year	Western	Central	Eastern	Lakewide
Chironomidae	1978-79	536±100	579±303	334±178	497±132
	2014	689±260	1567±605	361±170	948±273
	P	0.889	0.169	0.735	0.300
Amphipoda	1978-79	0	6±6	21±13	8±4
	2014	670±391	5±4	175±141	266±138
	P	0.012*	1.00	0.285	0.019*
Hexagenia spp.	1978-79	0	0	0	0
	2014	134±55	2.5±1.4	0	44±25
	P	0.012*	0.109		0.003*
Hirudinea	1978-79	34±13	12±8	51±27	30±9
	2014	239±89	36±15	2±2	91±35
	P	0.123	0.173	0.068	0.289
Others	1978-79	0	27±27	9±9	13±11
	2014	723±581	654±122	297±146	576±191
	P	0.012*	0.005*	0.018*	<0.001*
Bivalvia excluding *Dreissena*	1978-79	296±116	1224±281	450±100	710±146
	2014	74±21	1205±363	76±76	527±182
	P	0.092	0.721	0.018*	0.135
Trichoptera	1978-79	0.0	0.0	0.0	0.0
	2014	73.7±20.1	1.9±1.4	0.0	24.4±9.3
	P	0.012*	0.180		0.005*
Total species (in 2014 calculated as the mean number of species per station excluding *Dreissena*)	1978-79	8.5±0.8	11.2±1.2	11.1±1.2	10.3±0.8
	2014	19.1±2.1	17.7±1.2	12.7±1.9	16.7±1.1
	P	0.012*	0.024*	0.50	<0.001*

The structure of dominant species in Lake Erie benthic community changed in the last 40 years (Figure 1.12). The largest changes were again found in the western basin where the share of previously dominant Oligochaeta (75% of total density in 1978-1979) decreased to 23% (considering *Dreissena* spp. densities) or to 42% (without *Dreissena*). These changes were due to increased percentage of Amphipoda, Gastropoda, and other taxa. In contrast, in central basin where *Dreissena* is limited due to hypoxia, no changes were found in percentage of Oligochaeta densities (75% in 1970s vs. 75% in 2014) from total benthos, but there was a decline in non-dreissenid bivalves. In the eastern basin *Dreissena*, the role of Oligochaeta declined from 85% to 56% mainly due to the increase in densities of bivalves (largely *Dreissena* spp.) from 8% to 36%. However, no change in Oligochaeta dominance (85% vs. 87%) was found when we excluded *Dreissena* from the analysis. The relative contribution of bivalves (excluding *Dreissena*) in the eastern basin decreased from 8% to 1% (Figure 1.12).
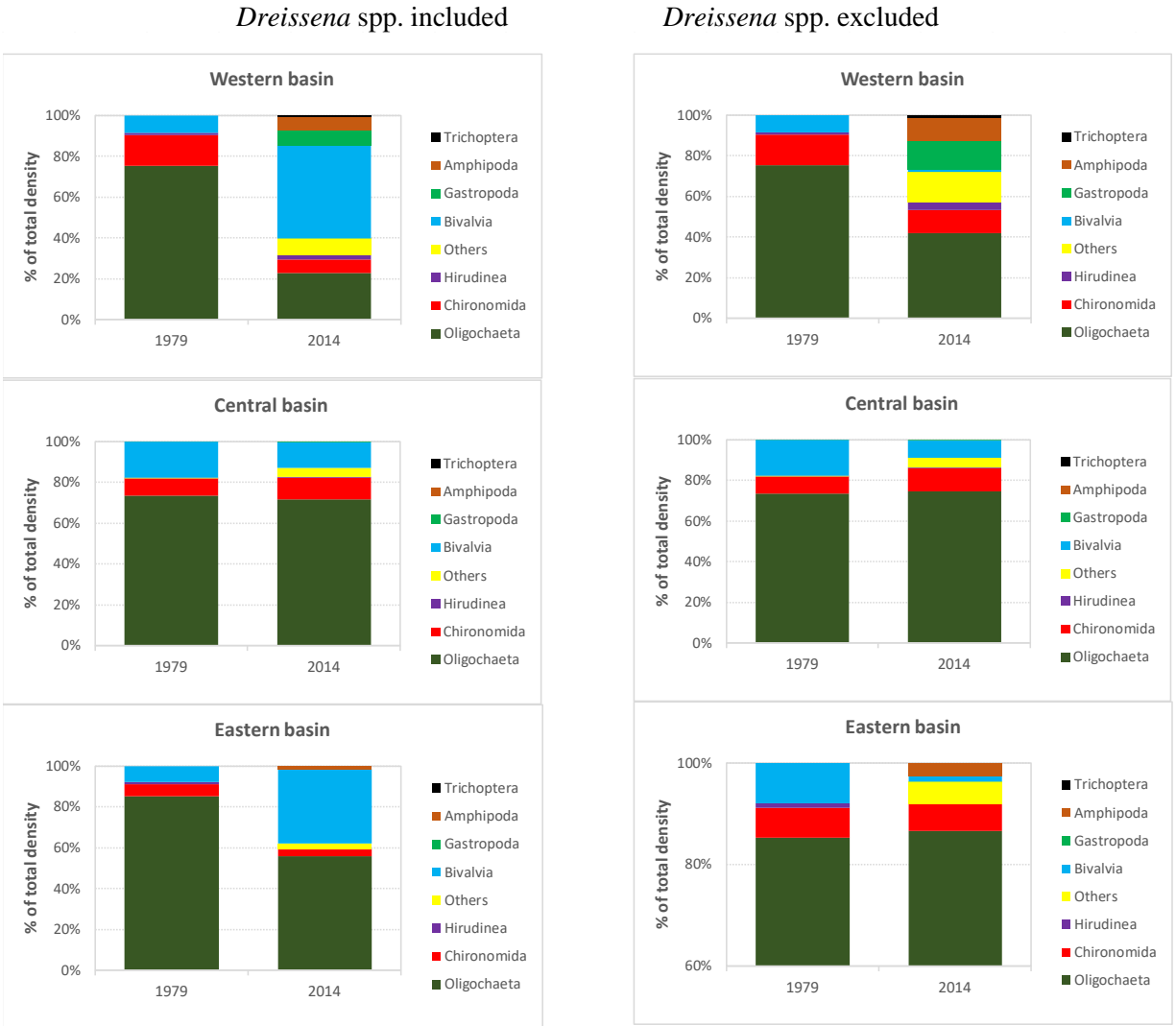
Figure 1.12. Major dominant taxa (in percentage of total benthos density) in Lake Erie basins in 1978-79 and 2014. Left column: benthic densities including *Dreissena* spp., right column – benthic densities excluding *Dreissena* spp.

To visualize the changes in the structure and abundance of Lake Erie benthic communities in the last 40 years, we averaged benthic densities by basin and year, and aggregated species to phyla that are depicted as vectors on the NMDS plot (Figure 1.13). Community changes were more pronounced in the western basin resulting in the increase in flatworms (Platyhelminthes, Turbellaria), Mollusca (Gastropoda), and Arthropoda (Trichoptera, *Hexagenia*). At the same time, oligochaetes (Annelida) declined. Large changes were also found in benthic community of the eastern basin associated with the decrease in Sphaeriidae, and with the increase in Platyhelminthes, Annelida (Oligochaetes), and Arthropoda (Amphipoda and Isopoda). Changes in the central basin profundal were less pronounced and were mostly due to the significant increase in Oligochaeta and Turbellaria.
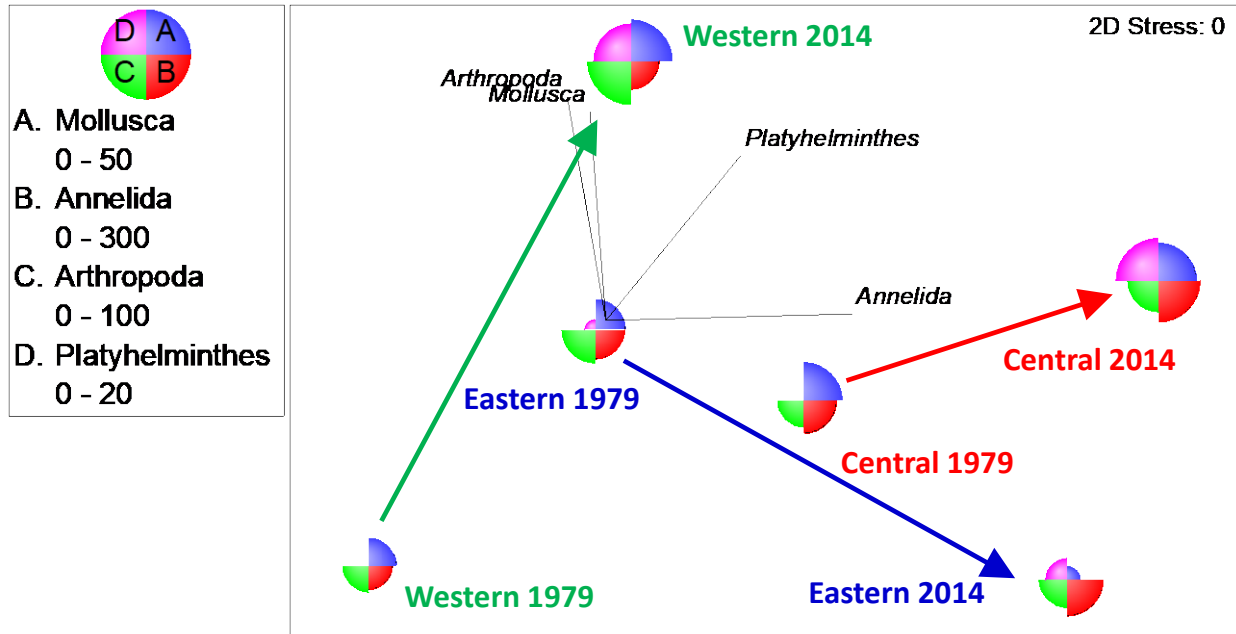
Figure 1.13. NMDS bubble plot of changes in benthic communities after *Dreissena* invasion of three basins of Lake Erie from 1978-79 to 2014. Density data (excluding *Dreissena*) from all stations were averaged by year and basin, and species were aggregated to major phyla. The size and directions of vectors (phyla) correspond to values and sign of Pearson correlations of the phyla densities with NMDS axes, and highlight the directions of changes.

DISCUSSION

Inter-Basin Comparison

A total of 118 species and higher taxa of benthic aquatic invertebrates were recorded in Lake Erie in 2014, and Oligochaeta and Chironomidae were the most diverse taxonomic groups. Oligochaeta comprised a large part of lake-wide benthos densities, followed by *D. r. bugensis* and Chironomidae. Among Oligochaeta, the most numerous were tolerant to organic enrichment Tubificidae. *Dreissena r. bugensis* dominated lake-wide benthos by biomass.

We found that benthic species diversity, density and biomass varied with depth. Species richness was the highest at shallow depths (< 20 m, 25 species/sample), declined to 19 species/sample at 20 – 40 m, and further declined to 12 species/sample at depths > 40 m. The highest densities and biomass of Amphipoda, Hirudinea, Hexagenia, Gastropoda and Naididae (Oligochaeta) were found at shallow (< 20 m) depths. Taxa prevalent at 20 - 40 m depth interval included Chironomidae, Oligochaeta (mostly Tubificidae), and Bivalvia (mostly *Pisidium* sp.). The deep zone (> 40 m) was dominated by *Dreissena* and Lumbriculidae. While the highest densities of *Dreissena* were found at shallow depths (< 20 m), the highest biomass was found at > 40 m depth, largely due to the prevalence of large mussels.

Species richness was the highest in the shallowest and most productive western basin, intermediate in the central, and was the lowest in the least productive eastern basin. The highest total average benthos density was found in the central basin due to a high density of Oligochaeta and Chironomidae, followed by the eastern basin with high densities of both *Dreissena* and Oligochaeta, and western basin where *Dreissena* spp. dominated benthos densities. In all other basins Oligochaeta were the most dominant group. The

lowest densities of *Dreissena* were found in the central basin where its population is limited by periodic hypoxia. Dreissenids continue to be the dominant taxa in term of biomass (measured in total wet weight) in all basins.

Benthic community structure was significantly different among basins, with the largest differences found between the eastern and western basins. Species with the largest contribution to the similarity of benthic communities within the western basin included *Dreissena* spp., *Hexagenia* sp., chironomid *Coelotanypus* sp., and oligochaeta *Limnodrilus hoffmeisteri*. In contrast, benthic community of the central basin was dominated by hypoxia-tolerant species *Chironomus* sp., *Pisidium* sp., pollution-tolerant oligochaetes (*L. hoffmeisteri*, *Quistadrilus multisetosus* and *Spirosperma ferox*), and chironomids *Procladius* sp. and *Tanytarsus* sp. Benthos of the eastern basin was largely defined by *D. r. bugensis*, and Tubificida (*P. vejdovskyi*, *L. hoffmeisteri* and *Tubifex tubifex*).

In 2009-2012 Lake Erie survey we found that benthos density was the highest in the central basin, but it was the lowest in the eastern basin (Burlakova et al., 2014). Our sampling design in 2009-2012, however, was somewhat different; therefore instead of direct comparison of densities we assessed the dominant structure of benthos by basin among years. The percentage of *D. r. bugensis* density from the total benthos density in the central basin decreased in 2014 compared to 2009-2012, and the role of Oligochaeta increased (2009-2012 vs. 2014: Oligochaeta - 35% vs. 67%, *D. r. bugensis* - 21% vs. 7% from total). Periodic hypoxia in the central basin that prevents establishment of stable *Dreissena* population is likely the main reason for these changes (see the subchapter "*Hypoxia and Dreissena distribution*" below). The same changes, however were seen in the eastern basin where the dominance of *Dreissena* declined (from 55 to 26% from total) and the share of Oligochaeta increased (22 vs. 63%), and in the western basin (2009-2012 vs. 2014: Oligochaeta - 7% vs. 24%, *Dreissena* - 67% vs. 40%, respectively). In addition, we found a 5 – 20% increase in the Oligochaete Trophic Index (OTI) in all Lake Erie basins between 1998-2002 and 2009-2013 (Burlakova et al., 2017), confirming these trends. Therefore, although the data are not directly comparable, there is some indication of a decline in *Dreissena* dominance along with an increase in the share of Oligochaetes in the lake, in agreement with the recent findings from the western Lake Erie (Schloesser et al., Chapter 2).

Hypoxia and *Dreissena* distribution

Western basin: Occasional hypoxia reduces *Dreissena* longevity

In 2014, in the western basin of Lake Erie, dreissenids were distributed rather evenly across the whole basin and exhibited densities equal to those in the eastern basin. Basin-wide average biomass, however, was over six times lower than in the eastern basin (Table 1.5). Over 98% of all *Dreissena* spp. found in the western basin were < 18 mm in length (Figure 1.6), which corresponds to mussels younger than 3 years old. The observed smaller sizes of mussels in the western basin in 2014 compared to the eastern basin are consistent with our previous observations (Karatayev et al., 2014). Smaller mussel length in the western basin suggested that *Dreissena* there do not live as long as mussels in the eastern basin, and this is indicative of periodic mortality events that affect the entire population. We hypothesize that these events are due to occasional episodes of severe oxygen depletion following temporary thermal stratification typical for western basin (Ackerman et al., 2001; Bridgeman et al., 2006). For example, our 3D hydrodynamic-ecological model predicted the occurrence of brief episodes of hypoxia in 2012 (< 10 days) and the absence of hypoxia in 2013 and 2014. Such hypoxic episodes could cause mass mortality of *Dreissena* spp. of all sizes. Both dreissenid species are sensitive to the lack of oxygen with zebra mussels being less tolerant to low oxygen than quagga mussels (reviewed in Karatayev et al., 1998, 2007, 2015; McMahon and Bogan, 2001). Under anoxic conditions (DO < 1 mg L^{-1}) mussels will die after 3 to 6 days, depending on temperature (reviewed in Karatayev et al., 1998). Since almost all mussels in the western basin were < 3 years old, our data suggest that these die-offs occur once every 2 to 3 years. Rapid recolonization is likely

from adjacent shallow areas in Lake Erie that are unaffected by hypoxia, or from upstream colonies, e.g., in the St. Clair-Detroit River system. These data are also consistent with the observed periodic failures of *Hexagenia* spp. recruitment in the western basin (Bridgeman et al., 2006). *Hexagenia* spp. are more sensitive to low oxygen than *Dreissena* spp., dying after one or two days of exposure to anoxic conditions (Eriksen, 1963; Nebeker, 1972). Physical habitat disturbance, including ice scour, may be among the other factors potentially limiting *Dreissena* population survival in the shallow depths of western Lake Erie (MacIsaac, 1996).

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

In the central basin *Dreissena* spp. occurred at high densities at shallow depths and then sharply declined to virtually zero at depths greater than 18 m, where bottom hypoxia routinely develops in August – September. In most of the hypoxic zone, *Dreissena* were either absent or represented by young of the year (< 5 mm in length) mussels that likely settled at the beginning of the growing season before the development of hypoxia. This effect was evident in the trends of both density and biomass. Even in shallower areas (10 – 20 m) of the central basin where mussels were abundant, *Dreissena* populations were mostly comprised of small, young individuals, supporting model inferences that hypoxia occurs infrequently in these areas.

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

The eastern basin supported the largest dreissenid population. In contrast to western and central basins, the eastern basin dreissenids were represented by mussels of various sizes, from recently settled 1 mm individuals to old mussels (greater than 3 years) > 30 mm in length across almost all depth zones (Figure 1.6). Presence of old mussels across the whole eastern basin suggests a lack of hypoxia and an environment supportive of stable dreissenid populations.

It should be noted that successful recruitment was recorded at all depths except the deepest zone (> 40 m) of the eastern basin where virtually no mussels smaller than 18 mm were found. Likewise, no mussels smaller than 16 mm were found previously at these sites sampled in 2009 (Karatayev et al., 2014). A plausible hypothesis is that this lack of successful recruitment is likely due to the competition of juveniles with large mussels. The food resources in the deep part of the eastern basin of Lake Erie may now be depleted to the point where only large mussels with powerful filtration apparatus can survive, preventing the establishment of young-of-the-year mussels. The long-term presence of adult mussels without recruitment in this more stable, colder profundal environment may be an indication of slower growth of *D. r. bugensis* (Karatayev et al., 2010) and longer life spans, thus contributing to their larger sizes relative to shallower areas. In contrast, in profundal zone of Lake Michigan in 2015, 1 – 5 mm quagga mussels were dominated among dreissenids in 31 – 100 m and >100 m depth intervals (Karatayev et al., 2017, Appendix 1.1), indicating favorable conditions for successful recruitment potentially due to a better hydrodynamics, large size and openness of the profundal zone.

Dreissena distribution as a tool for mapping hypoxia

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

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

Management implications of *Dreissena*/hypoxia relationship

The relationship between the *Dreissena* distribution and near-bottom hypoxic conditions has important management implications for the lower Great Lakes. With the introduction of quagga mussels in the 1990's, *Dreissena* populations gained access to the extensive profundal zone of the Great Lakes (Watkins et al., 2007; Nalepa et al., 2010; Karatayev et al., 2015). The rapid expansion of quagga mussel populations into habitats that were previously uninhabited by zebra mussels had a large impact, particularly in the upper Great Lakes. For example, *Dreissena* populations have been implicated in the disappearance of springtime diatom blooms (Fahnenstiel et al., 2010; Vanderploeg et al. 2010) and the benthic amphipod *Diporeia* (Watkins et al., 2007; Nalepa et al., 2010), along with changes in zooplankton community structure (Barbiero et al., 2012; Vanderploeg et al., 2012). Further inshore, *Dreissena* have been linked to increases in the abundance of the benthic green alga *Cladophora* (Bootsma et al., 2015; Brooks et al., 2015), promotion of toxic *Microcystis* blooms (Vanderploeg et al. 2001), and shifting lake food webs increasingly from offshore pelagic to nearshore benthic energy pathways (Karatayev et al., 2015; Turschak et al., 2014). Given the negative impacts that have been documented thus far, it should come as no surprise that *Dreissena* is considered the most aggressive freshwater invader in the northern hemisphere (reviewed in Karatayev et al., 2007, 2015), and one of the major environmental stressors across the entire Great Lakes Basin (Burlakova et al., 2014; Smith et al., 2015).

We demonstrated how persistent hypoxia effectively excludes *Dreissena* populations in the profundal zone of the central basin of Lake Erie. Management programs in Lake Erie focus on limiting nutrient loading, particularly in the western basin, where phosphorus loading from agricultural watersheds causes persistent harmful algal blooms during the summer in the western basin (Bridgeman et al., 2012; Michalak et al., 2013). Excessive phosphorus loads from western basin tributaries have cascading negative impacts on the Lake Erie ecosystem as well, and have been linked to seasonal hypoxia in the central basin (Scavia et al., 2014; Bocaniov et al., 2016). To address this problem, the 2012 Great Lakes Water Quality Agreement developed a target of 40% reduction in total phosphorus loads relative to 2008 loads entering the western and central basins of Lake Erie as a way of reducing harmful algal growth and minimizing the extent of hypoxic zones (GLWQA Annex 4 Objectives and Targets Task Team, 2015). Similarly, a 40% reduction in total phosphorus load to Lake Erie relative to the GLWQA 1978 load target of 11000 MTA (metric tons per annum) is predicted to increase the mean (August – September) hypolimnetic DO concentration and significantly reduce both the maximum and mean summer (August – September) areal spatial extent of hypoxia (DO < 2 mg L^{-1}) by about 20% (1700 km^2) and 43% (2000 km^2), respectively (Bocaniov et al., 2016). While the GLWQA 2012 phosphorus load targets are designed to raise the average August and September hypolimnetic dissolved oxygen to 2.0 mgL^{-1} or higher, thus decreasing the spatial extent of hypoxia (GLWQA Annex 4 Objectives and Targets Task Team, 2015), our results suggest that a decrease in hypoxia may render more profundal zone habitat of the central basin available for *Dreissena* expansion. We believe this hypothetical scenario needs to be further evaluated using detailed hydrodynamic and food web models to fully assess the effects of potential *Dreissena* expansion in the central basin on water quality and food web dynamics.

Dreissena **long-term-dynamics**

We found that while in the western basin *Dreissena* spp. population is relatively stable, in the central and eastern basins dreissenid densities and biomass declined since late 1990s – early 2000s.

Typically, *D. polymorpha* reaches its population maximum in about 2 – 4 years (average 2.5 ± 0.2 y) after it is first detected in an invaded waterbody (reviewed in Karatayev et al., 2011). Initially, populations of *D. polymorpha* attain very high densities, but because of density-dependent processes, total sustainable biomass declines as the system is altered by zebra mussel presence, and densities well below the maximum achieved persist, but populations do not stabilize, and densities can fluctuate widely (Karatayev et al., 1997, 2002; Burlakova et al., 2006; Nalepa et al., 2010). As *D. polymorpha* was first found in Lake Erie in 1986 (Carlton, 2008), zebra mussels likely reached their maximum around 1989, when they colonized most of the hard substrates in the nearshore areas (Griffiths et al., 1991). Therefore, during the first lake-wide study of *Dreissena* spp. distribution in 1992, *D. polymorpha* may have already passed its maximum population density, and had already been in decline. Although this decline was evident in the central and eastern basins, as well as lake-wide, it was less pronounced and not statistically significant in the western basin.

In contrast to the zebra mussels, quagga mussels are characterized by a much longer lag time between the initial introduction and large population sizes. Usually, the maximum *D. r. bugensis* population density is not achieved until 6 to 19 years (average 12.2 ± 1.5 y) after their first detection in a waterbody (Karatayev et al., 2011). In Lake Erie, quagga mussels were found for the first time in 1989 (Mills et al., 1993), and the population peaked somewhere between 1998 (central basin) and 2002 (eastern basin).

Combined dreissenid density in Lake Erie was high during the first 12 years of observation, but then sharply declined by 2009-2012, while the average wet biomass peaked with some delay in 2004, and then declined as well (Figure 1.7). In most cases, biomass was less variable than density. The biomass data for the assessment of population dynamics is more important for monitoring mussels than density as it takes into account both number and size, which ultimately impact the filtering role of mussels in the lake (Karatayev et al., 1997; Burlakova et al., 2006; Nalepa et al., 2010).

Zebra and quagga mussels had clearly opposite trends in their dynamics in the central and eastern basins, as well as lake-wide, resulting in an almost complete replacement of *D. polymorpha* with *D. r. bugensis*. Similar trends in *D. polymorpha* and *D. r. bugensis* dynamics were found in 16-30 m and 31-50 m depth zones in southern Lake Michigan, where the constant increase in quagga mussel population density from 2001 to 2008 was also accompanied by a replacement of zebra mussels (Nalepa et al., 2010). Similar to our findings, Nalepa et al. (Chapter 3) reported a decline in densities of *D. r. bugensis* at depths < 90 m in Lake Michigan since 2010.

Historical comparison: 1978-79 and 2014

Our analysis of changes in benthic community of Lake Erie in the last four decades indicated both positive and negative trends depending on lake basins. The most remarkable changes were connected to the significant increase in biodiversity which can't be explained by the sample bias (different sampling or identification methods used). While we identified all oligochaetes in 2014 compared to a just a portion (50 oligochaetes) collected in 1978-79 (Dermott, 1994), the taxonomic expertise of the author (R. Dermott) and his familiarity with Great Lakes taxa was excellent, and he identified several taxa to lower taxonomic level (species and genera, e.g., *Kincaidiana hexatheca*, *Lumbriculus* sp.) that we currently identify (SOP LG407). Nevertheless, we found the same amount of Oligochaeta species in 2014 as Dermott did in samples

collected in 1978-79. Dermott's expertise with Chironomidae was exceptional as well. Although we found a larger number of Chironomidae species (16 vs. 24), we believe that was not due to the lack of expertize in previous years, since 30 total Chironomidae species was found by Dermott (1994) in 1978-1979 samples. We also found higher diversity of Gastropoda (12 species in 2014 vs. 3 in 1978-79), Huridinea (5 vs. 3) and Amphipoda (4 vs. 2). These all are large conspicuous taxa unlikely to be missed or misidentified; in total 9 species of gastropods were found in 1978-1979 at all 159 stations (Dermott, 1994). In addition, the mesh size used to sieve samples (153 µm used in 1978-79 compared to 500 µm used in 2014) preclude the possibility of overlooking a large number of Turbellaria, Hydra and Nemertea that we found in 2014. In 2014 we sampled in July compared to 1978-79 sampling done in October, but the two month difference should not affect much the presence of benthic species that live for over a year. Finally, the smaller mesh size used in 1978-1979 has likely retained more oligochaetes and chironomids than the 500- um mesh screen we used. Therefore, we believe that the increase in species diversity we found in 2014 was not an artefact of taxonomic expertise or the methods used.

With consideration of *Dreissena*, the dominance of Oligochaeta in the eastern basin declined from 85% to 56% mainly due to the increase in densities of exotic bivalves (*Dreissena* spp.) from 8% to 36%. Without consideration of *Dreissena*, there was no change in the percentage of Oligochaeta (85% in 1970s vs. 87% in 2014) and Chironomidae (5.9% vs. 5.3%), while the share of non-dreissenid bivalves decreased from 8% to 1%.

In contrast, in the central basin where *Dreissena* is largely lacking due to periodic hypoxia, there was no change in percentage of Oligochaeta (75% in 1978-79 and 2014) or in the overall dominant structure of benthic community. The regular occurrence of hypoxia in the central basin produces the greatest restriction on the distribution of the benthic invertebrates in Lake Erie (Davis, 1966; Burns 1976; Charlton 1987). The periodic hypoxia limits the benthic fauna to species that can survive on stored hemoglobin bound oxygen (i.e. *Chironomus*), reduce their respiration (*Pisidium*), or undergo anaerobic fermentation (*Tubifex*) for several weeks (Holopainen and Jonasson 1989).

In the western basin, in addition to increased diversity, we found higher densities of Amphipoda, Gastropoda, Trichoptera and other taxa, along with the re-establishment of mayfly *Hexagenia* spp. These changes may indicate recovery in benthic community of the western basin likely due to watershed improvements implemented in the 1970s and 1980s and the impacts of *Dreissena* in early 1990s.
The densities of Isopoda, Turbellaria, Nemertea, and Hydra increased significantly lake-wide, while the abundance of polychaeta *Manayunkia speciosa* decreased in the western basin. Densities of oligochaetes increased in the central basin, likely due to increased organic enrichment. Densities of Sphaeriidae decreased in the eastern basin, probably as a result of food competition with filter-feeding Dreissena spp. that are very abundant in that basin. While we found higher species richness of Chironomidae in 2014, their densities have not changed significantly in any of the basins.

As a result, the dominant structure of Lake Erie benthic community has changed in the last 40 years, with the largest changes found in the western basin. With the reduction of phosphate levels, water quality in the basin has greatly improved since the 1960's (Nicholls and Hopkins 1993). The densities of oligochaetes in the western basin have decreased from 83% of the benthic macroinvertebrate fauna in 1961 (Carr and Hiltunen, 1965) to 66% in 1979 (Dermott, 1994). In 2014, the share of Oligochaetes decreased further to 23% (considering *Dreissena* spp. densities) or to 42% (without *Dreissena*) along with increased percentage of Amphipoda, Gastropoda, and other taxa.

Analysis of long-term data collected from USGS monitoring stations in the western basin of Lake Erie (Chapter 2) provide much stronger evidence for the changes we found in our snapshot comparison of sites sampled in 1978-79 and 2014. Although the patterns of de-eutrophication, that occurred in the basin since

late 1980s as reflected in benthic community structure were similar in both the long-term and snapshot studies, the long-term monitoring also detected the warning signals of re-eutrophication in early 2000 (Chapter 2). 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). Therefore, it is imperative to continue monitoring of the historical stations in the western basin to be aware of rapid changes in Lake Erie environmental conditions.

More detailed analyses and discussion of trends, spatial patterns, and community composition, including comparisons to previous lake-wide benthic surveys in Lake Erie and other Great Lakes are ongoing and will be provided in future publications.

SUMMARY

As part of the Coordinated Science and Monitoring Initiative in Lake Erie in 2014, a lake-wide survey was conducted to assess the status of the benthic macroinvertebrate community, with a primary focus on the invasive quagga mussel *Dreissena rostriformis bugensis* and zebra mussel *D. polymorpha*, and to compare the current benthic community with historical data. Samples for benthic macroinvertebrates were collected in July and August of 2014 in triplicate at 80 stations located throughout the western, central, and eastern basins, with an additional 27 stations where only *Dreissena* spp. were processed. A total of 118 species and higher taxa of benthic invertebrates were recorded in Lake Erie in 2014, and Oligochaeta and Chironomidae were the most diverse taxonomic groups. The highest benthic diversity (27 species/sample) was found in the western basin, the highest benthic density (12,053 m^{-2}) in the central basin, and the highest wet biomass (1,439 g m^{-2}) in the eastern basin. A comparison with historical data (1978-1979) revealed an increase in species diversity lake-wide, with the largest changes found in the western basin where densities of amphipods, gastropods and caddisflies increased, along with the re-establishment of mayfly *Hexagenia* spp. As a result, the dominant structure of the Lake Erie benthic community has changed in the last 40 years, indicating some recovery in the benthic community of the western basin likely due to watershed improvements implemented in the 1970s and 1980s and the impacts of *Dreissena*. However, a comparison with more recent (2009-2012) benthic surveys indicated an escalating dominance of tolerant to organic pollution Oligochaeta in Lake Erie benthos, which was especially pronounced in the central basin with periodic hypoxia. As a result, lake trophic status, assessed by the Oligochaete Trophic Index, is increasing, indicating highly eutrophic conditions.

Dreissenid densities and biomass in the central and eastern basins of Lake Erie were high during the first 15 years since invasion (late 1980s), but then declined. *Dreissena* spp. populations in these basins are represented almost exclusively by quagga mussels, while in the western basin *D. polymorpha* still maintains a relatively stable population. As of 2014 *D. r. bugensis* density was still increasing in the western basin. *Dreissena* distribution across depths varied within and among basins. While in the western basin mussels are distributed relatively evenly, a substantial part of the bottom at over 20 m depth in the central basin is largely free of *Dreissena* due to periodic hypoxia. In contrast, in the eastern basin *D. r. bugensis* forms high densities and biomass in the deep profundal zone that never goes hypoxic. We found that monitoring *Dreissena* occurrence and length-frequency distribution can be an effective tool in mapping the extent and frequency of hypoxia in freshwater and can reveal even rare hypoxic events, such as those in the western basin.

ACKNOWLEDGEMENTS

APPENDICES

Appendix 1.1. Karatayev, A. Y., L. E. Burlakova, K. Mehler, S. A. Bocaniov, P. D. Collingsworth, G. Warren, Kraus, R. T., and E. K. Hinchey. Biomonitoring using invasive species in a large lake: *Dreissena* distribution maps hypoxic zones. Journal of the Great Lakes Research. Published on-line DOI 10.1016/j.jglr.2017.08.001.

Appendix 1.2. Taxa recorded from 80 benthic stations sampled in Lake Erie in 2014. The information is provided for the lowest identified taxa, in most cases species or genus. In cases where taxa was identified only to a family or higher taxonomic level, it was listed at the level it was identified. Species occurrence (P, in percent of all 80 stations samples, for *Dreissena*: from 107 stations), average density (N, ind./m^2), average wet biomass (B, g/m^2).

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CHAPTER 2. BENTHOS IN WESTERN LAKE ERIE 2014; ABUNDANCES AND DISTRIBUTION AT 9 STATIONS IN 1929-30, 1961, 1982, 1993, 2003, 2010, AND 2014

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This study comprises one portion of a larger program to evaluate the status of the benthos of Lake Erie. It was performed as part of a comprehensive study of the benthos of Lake Erie and Lake Michigan associated with the Cooperative Science and Monitoring Initiative. This larger study sampled 107 stations in the western, central and eastern basins of Lake Erie. In 2014, 31 additional stations were sampled in the western basin to obtain a more complete assessment of this basin than provided by the lake-wide survey.

Information from the 31 stations in 2014 are part of an eight-four year historical-data base obtained by studies in 1929-30, 1961, 1982, 1993, 2003, and 2010. As such, these data provide the most comprehensive information on benthos in the Great Lakes. In the present study, analysis of changes of benthos was performed for only nine consistently-sampled stations between 1930 and 2014. Future statistical analysis of all information from all stations (n = 40-80) will be possible once historical information become available.

INTRODUCTION

Dreissenid mussels invaded the Great Lakes in the mid-1980s and have become a dominate component of ecosystems in many areas (Nalepa and Schloesser 1993, 2011). In addition to nearshore colonization, mussels have covered many substrates in profundal areas of the Great Lakes where they would not have been expected to occur based on extensive literature records of dreissenid mussels in Europe and Russia (Schloesser et al., 1994; Schloesser and Schmuckal 2012). In the Great Lakes, mussels have often covered a large proportion of hard surfaces. As a result, large numbers of mussels near shore have created a nearshore-shunt of nutrients that previously would have traveled to off-shore waters and been available for profundal productivity that forms the basis of fisheries productivity in the Great Lakes.

As a result of concern for near-shore and off-shore ecosystem changes associated with dreissenid mussels, many benthic studies performed previous to dreissenid colonizations of the Great Lakes have been 'repeated' to allow temporal comparisons (e.g., Schloesser et. al., 1998; Schloesser et al., 2000; Nalepa et. al., 2003; Ratti and Barton 2003; Dermott 2012;). This is especially true for western Lake Erie which has become a 'poster-child' example of how an invasive species can cause ecosystem change in a short period of time (Nalepa and Schloesser 1993, 2013). Fortunately, Lake Erie, and especially western Lake Erie, has the most historically complete, albeit not geographically consistent, temporal series of benthic studies in the Great Lakes (e.g., Wright and Tidd 1933; Carr and Hiltunen 1965; Schloesser et. al., 1995; Manny and Schloesser 1999). Starting in 1929-30, these studies were conducted by the Great Lakes Science Center, U.S. Geological Survey (predecessors of Bureau of Commercial Fisheries and U.S. Fish & Wildlife Service). Portions of these historical studies have been summarized for: taxa of general benthos by Wright and Tidd (1933), Wright (1955a), Carr and Hiltunen (1965), Manny and Schloesser (1999), Schloesser (2013), and Schloesser et al. (2016); for oligochaetes by Hiltunen (1969) and Schloesser et al. (1995); and, for mayflies by Britt (1955), Reynoldson et al. (1989), Kolar et al. (1997), Madenjian et al. (1998), Krieger et al. (1996), Schloesser (et. al. 2000), Devanna et al. (2014).

Studies of the overall benthos of western Lake Erie were conducted in 1993, 2003 and 2010 to add to historical comparisons and assess one and two decadal responses of benthos to exotic dreissenid mussels.

The present overall benthic study was conducted in 2014. Although conducted to provide supplemental information of benthos populations to aid interpretation of a benthic study of the western, central, and eastern basins of Lake Erie (Chapter 1), the present study adds to unpublished decadal studies (1982, 1993, and 2003) of western Lake Erie. This report places the 2014 study in context of the historical time-series of other benthic studies in western Lake Erie.

METHODS

CSMI Study

Sediment samples containing benthos were collected at 31 stations located by GPS (Appendix 2.1) between April 4 and May 28, 2014 (Figure 2.1). A standard Ponar sampler (484-cm^2 sampling area) was used to collect three replicate samples at each station. Sediment samples were individually washed through a U.S. Standard No. 30 sieve (ca. 0.6-mm openings, Clesceri et al., 1998) and retained debris and benthos were individually placed in a 5-10% formalin solution.
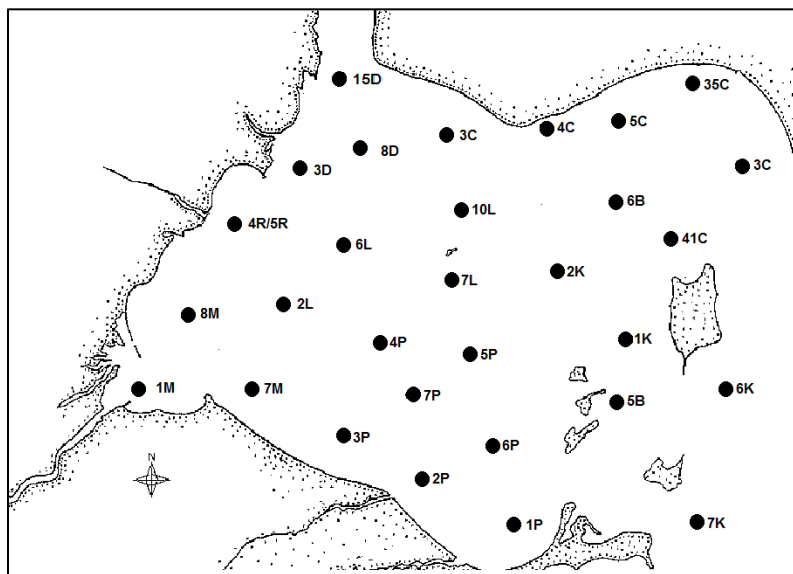
Figure 2.1. Locations of 31 stations sampled for benthos in western Lake Erie 2014. Nine stations (3D, 8D, 15D, 2L, 6L, 1M, 7M, 8M, and 4R) were sampled for comparative benthos analysis 1930, 1961, 1982, 1993, 2003, 2010, and 2014.

In the laboratory, individual samples of debris and benthos were washed through a U.S. Standard No. 60 sieve (ca. 0.25-mm openings) and benthos were separated and enumerated (i.e., picked) from debris under 7X magnification. Some identifications of benthos were made when a sample was picked if positive identifications were known. Other identifications and enumerations of benthos were made at various magnifications by taxonomic experts familiar with benthos of the Great Lakes (e.g., Ron Griffiths, Oregon

State University). Identifications and enumerations were compiled (Appendices 2.2-2.5, available upon request); general benthos, mollusks, Chironomidae, and Oligochaeta, respectively). In addition, individual dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) were measured to the nearest whole mm (Appendix 2.6, available upon request).

Historical Studies

Comparisons of studies performed over large periods of time have many sources of error, some of which can be identified and some of which cannot. Fortunately, comparison of the present 2014 study and previous studies (1929-30, 1961, 1982, 1993, 2003, and 2010) is likely to have lower sources of errors than other comparative studies of benthos because the first author has had indirect involvement (e.g., 1929-1930 and 1961 studies, through personal communications with J. K. Hiltunen and original laboratory identification records) and direct involvement (1982, 1993, 2003, 2010, and 2014 studies, principal and co-principal investigator) in the subject studies. Undoubtedly, consistency of investigators and availability of original data sets (including laboratory bench sheets for 1961, 1982, and 1993) and electronic bench files (2003, 2010 and 2014) at one laboratory (primarily Great Lakes Science Center and its predecessors) has yielded the best comparable time-series of benthic data in the western Lake Erie and, probably, in the Great Lakes. Availability of original data and personal knowledge of studies allowed construction of a table with respective methods for each study (Table 2.1). These records and knowledge have also been used to document historical changes in mayflies in western Lake Erie (Schloesser et al., 2000).

The 1929-30 studies were conducted to assess the 'status' of benthic and water resources of western Lake Erie and a comparison of these studies to subsequent surveys is the most difficult and challenging. The 1929-1930 study was performed under restrictions of where fishery investigations were being conducted (i.e., and where boat went). In addition, since little was known about benthos at the time (ca. 1920s) sampling lacked a systematic and purposeful goal. As a result samples were collected with different gear (e.g., Eckman, Peterson), at different stations and times of season/year, and different numbers of replicate samples were obtained at individual stations and sampling periods. In addition, laboratory methods for analysis of benthos were varied and rapidly changing at the time of study (i.e., much emphasis was placed on impressions/conclusions of investigators). None the less, the 1929-30 study was one of the first and most extensive benthic studies in the early-20th century.

1961

The 1961 study was performed to assess pollution. Although a senior author (J.K. Hiltunen, USFWS, Great Lakes Fishery Laboratory, Ann Arbor, MI) of this study had personal contact with investigators and obtained paper files of methods and data of the 1929-30 study, comparisons and analysis between the 1929-30 studies and the 1961 study was limited. The 1961 study was designed to assess impacts of nutrient pollution primarily from rivers that carried wastes away from population centers of Detroit, Michigan and Toledo, Ohio. As such, the 1961 study was systematic in that it included samples primarily from around river mouths (also included open water sites primarily for reference benthos), collected in a short period of time in spring before most insects emerge from the water (May-June), consistently collected an equal number of replicates at each site (n = 3), and followed detailed sample laboratory methodology. The 1961 study set the stage for most successive studies of benthos in western Lake Erie for the next 50 years.

1982

The 1982 was performed to assess progress of pollution-abatement programs that were initiated in the early 1970s. J. K. Hiltunen (USFWS, Great Lakes Fishery Laboratory, Ann Arbor, MI) performed both the 1961

and 1982 studies and provided field and laboratory guidance to maintain continuity of study comparisons. In addition, Hiltunen mentored the present investigator (1976-1985) to provide continuity between successive studies 1993-2014.

1993

The 1993 study was conducted primarily to assess impacts of pollution-abatement programs. However, additional stations were added to assess impacts associated with introduced dreissenid mussels which heavily colonized western Lake Erie in 1989. All 40 stations sampled in 1961 and 1982 were included, as well as an additional 7 stations in 1993.

2003-2014

These studies were strongly influenced by the study goals of assessing impacts of dreissenid mussels as well as pollution abatement. In 2003, a total of 60 stations were sampled throughout the entire basin and was the most extensive study performed to date in the western basin. By 2003, impacts of pollution on benthos near river mouths (previous sampling designs 1961-1993) had become localized to immediate river-mouth areas of the Detroit, Raisin, and Maumee rivers. In effect, pollution-abatement programs had achieved major improvements in water/benthic quality and impacts of pollution were becoming difficult to assess, especially in open-waters of the basin. Therefore, some previously sampled stations near river mouths were excluded in subsequent studies of 2010 and 2014 primarily to assess impacts of dreissenid mussels on basin-wide productivity.

Although it is unknown to what extent differences in methodologies of the present study and comparisons to previous studies affected data interpretation, the author assumes the differences are minimized compared to other historical-comparative studies and likely represent the best time-series of benthic data in the Great Lakes.

Table 2.1. Summary of methods of benthic surveys in western Lake Erie 1929-2014. Latitude and longitude coordinates in Schloesser et al. 2000.

	1929	1930	1961	1982	1993	2003	2010	2014
Data source	Wright (1955)	Wright (1955)	Carr and Hiltunen (1961)	Manny and Schloesser (1999); Unpublished	Unpublished	Unpublished	Unpublished	Present study
Dates	15 June-15 September	15 June - 15 September	31 May - 16 June	7-10 June	1-17 June	29 April - 28 May	30 March-15 April	9 April - 21 May
Number of stations	14	80	40	40	47	60	31	31
Location method	time and distance of moving boat	time and distance of moving boat	time and distance of moving boat	Loran	Loran	GPS	GPS	GPS
Sampler type	Peterson	Peterson	Peterson	Ponar	Ponar	Ponar	Ponar	Ponar
Number of samples/visit	varied	varied	3	3	3	3	3	3
Surface area of sampled substrate	0.073	0.073	0.073	0.046	0.052	0.046	0.046	0.046
Multification factor to obtain number/m2	13.51	13.51	13.51	20.66	19.23	20.66	20.66	20.66
Sieve size to remove debris	no. 36 grit bag (0.5 mm)	no. 36 grit bag (0.5 mm)	0.6 mm sieve then 0.250 mm sieve	0.6 mm sieve then 0.250 mm sieve	0.6 mm sieve then 0.250 mm sieve	0.6 mm sieve then 0.250 mm sieve	0.6 mm sieve then 0.250 mm sieve	0.6 mm sieve then 0.250 mm sieve
Separation of debris from benthos	unaided eye	unaided eye	15X magnification	10X magnification	10X magnification	10X magnification	10X magnification	10X magnification
Identification of general benthos	7X magnification	7X magnification	15X magnification	10X magnification	10X magnification	10X magnification	10X magnification	10X magnification

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	1929	1930	1961	1982	1993	2003	2010	2014
Data source	Wright (1955)	Wright (1955)	Carr and Hiltunen (1961)	Manny and Schloesser (1999); Unpublished	Unpublished	Unpublished	Unpublished	Present study
Identification of mollusks	7X magnification	7X magnification	15X magnification	10X magnification	10X magnification	10X magnification	10X magnification	10X magnification
Identification of chironomids	7X magnification	7X magnification	>100X magnification	>200X magnification	>200X magnification	>200X magnification	>200X magnification	>200X magnification
Identification of oligochaetes	7X magnification	7X magnification	>100X magnification	>200X magnification	>200X magnification	>200X magnification	>200X magnification	>200X magnification

In addition to lake- and laboratory- methodological changes over the past 85 years, changes in levels of taxonomic identifications and nomenclature also have the potential to affect analyses (Tables 2.2-2.5). Therefore, efforts to standardize taxonomic names and examine nomenclatural differences between studies included notes in files from original study investigators, internet searches of identifications, solicitation of benthic experts, personal knowledge, and reference to published taxonomic check-lists (e.g., Spencer 1980; Spencer and Hudson 2003). In addition, a few 'spot-identifications' of organisms collected in 1982, 1993, 2010, and 2014 were obtained to verify consistency of 'modern' nomenclature and identifications. When reasonable doubt about consistent identifications and/or use of consistent nomenclature occurred, inclusion of alternatives (i.e., conservative) were included in the present study. However, some changes to original bench identifications were noted and not possible to correct because original identifications were deleted from bench sheets; this occurred when nomenclature changes occurred in the time authors/users were working with data. In some cases, data compilation took many years and nomenclature updates were made to original data to keep them current. The extent to which updates of nomenclature covered earlier nomenclature is not known but is believed to have affected comparisons little since few changes for individual taxa rarely occurred more than once, if at all. Current nomenclature in Tables 2.2-2.5 are as precise as possible with current known information.

Analyses

Analyses of benthic data in the present study (2014) include determination of density estimates and comparison to data obtained in recent studies of western Lake Erie (e.g., Soster et. al., 1990; Burlakova et. al., 2014). Evaluation of 2014 study relative to historical studies (1929-30, 1961, 1993, 2003, and 2010) was done for nine consistently sampled stations in each time period (Figure 2.1; 3D, 8D, 15D, 4R/5R, 2L, 6L, 1M, 7M, and 8M). Trend analysis of changes over time was the primary tool for analysis along with observed changes found in other studies.

Future Analyses

Rigorous statistical analysis of changes in successive time periods, at all stations, and of individual benthic taxa is a logical goal that is beyond available resources and time. However, continued compilation of available benthic data at the Great Lakes Science Center for all stations (n = 31 to 80 stations/time-period) will allow evaluations of de-eutrophication attributed to decades of pollution-abatement programs, initiated primarily in the early-1970s, and impacts of exotic species, primarily dreissenid mussels, that colonized western Lake Erie in the late-1980s. Expectations of additional intensive analysis of the 85 years of benthic data in the present study is likely to yield results similar to studies of western Lake Erie in the past few decades (McCall and Soster 1990; Soster and McCall 1990; Soster et. al., 2011; Burlakova et. al., 2014).

Future analyses of oligochaete taxa and abundances are likely to yield the most information of ecosystem changes over the 85 years of comparison because this taxa group was the most dominate group in western Lake Erie for decades. In addition, interpretation of changes in species has yielded valuable information about the major man-made disruption (i.e., nutrient eutrophication) in the Great Lakes, and many other water bodies throughout the world (e.g., Milbrink 1983; Reynoldson et. al., 1989; Schloesser et. al., 1995). However, at the present time, trophic indices assembled through species of oligochaete are currently being evaluated and developed (National Coastal Condition Assessment Great Lakes Benthic Indicator Development Workshop, 2016).

Table 2.2. Taxa identifications and corresponding nomenclature of general-benthic taxa in western Lake Erie 2014, 2010, 2003, 1993, 1982, 1961, and 1929-30. A total of 49 taxa were identified with current nomenclature. Not all taxa quantified in 1929-30.

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Amphipoda	Amphipoda	Amphipoda						*Hyalella knickerbockeri*
Amphipoda	*Echinogammarus* spp.	*Echinogammarus* spp.	*Echinogammarus* spp.	*Echinogammarus* spp.				
Amphipoda	*Gammarus* spp.			*Gammarus* spp.	*Gammarus* spp.	*Gammarus* spp.	*Gammarus* spp.	*Gammarus* spp.
Amphipoda	*Gammarus fasciatus*	*Gammarus fasciatus*	Gammarus fasciatus					
Amphipoda	*Hyalella* spp.	*Hyalella* spp.		*Hyalella* sp.				
Ceratopogonidae	Ceratopogonidae			Ceratopogonidae	Ceratopogonidae	Ceratopogonidae	Ceratopogonidae	
Chaoboridae	*Chaoborous* spp.					*Chaoborous* spp.	*Chaoborous* spp.	
Coleoptera	Coleoptera						Coleoptera	
Coleoptera	*Dubiraphia* spp.	*Dubiraphia* spp.	*Dubiraphia* spp.		*Dubiraphia* spp.			
Coleoptera	Elmidae			Elmidae	Elmidae	Elmidae		
Cnidaria	Cnidaria	Cnidaria		Cnidaria	Cnidaria	Cnidaria	Cnidaria [a/]	
Decapoda	*Orconectes propinquus*							*Cambarus propinquus*
Ephemeroptera	*Caenis* spp.	*Caenis* spp.	*Caenis* spp.		*Caenis* spp.	*Caenis* spp.	*Caenis* spp.	
Ephemeroptera	*Hexagenia* spp.	*Hexagenia* spp.	*Hexagenia* spp.	*Hexagenia* spp.	*Hexagenia* spp.	*Hexagenia* spp.	*Hexagenia* spp.	*Hexagenia* spp.
Hemiptera	Corixidae				Corixidae			
Hirudinea	Hirudinea	Hirudinea		Hirudinea	Hirudinea		Hirudinea	

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Hirudinea	*Erpobdella* spp.	*Mooreobdella* spp.	*Mooreobdella microstoma*					*Dina fervida*
Hirudinea	*Erpobdella obscura*					*Nephelopsis obscura*		
Hirudinea	*Helobdella elongata*	*Helobdella elongata*	*Helobdella elongata*			*Helobdella elongata*		
Hirudinea	*Helobdella stagnalis*	*Helobdella stagnalis*	*Helobdella stagnalis*			*Helobdella stagnalis*		*Glossiphonia fusca*
Hirudinea	*Helobdella stagnalis*							*Glossiphonia nepheloidea*
Hirudinea	*Helobdella stagnalis*							*Glossiphonia stagnalis*
Hirudinea	*Herpodella pinctata*							*Herpodella pinctata*
Hirudinea	*Placobdella montifera*	*Placobdella montifera*						
Hydracarina	Hydracarina				Acarina	Acarina	Acarina	
Hydracarina	*Hygrobates* spp.	*Hygrobates* spp.						
Hydracarina	*Lebertia* spp.		*Lebertia* spp.					
Hydracarina	*Limnaecia* spp.	*Limnaecia* spp.	*Limnaecia* spp.					
Isopoda	*Caecidotea* spp.				*Asellus* spp.	*Asellus* spp.		
Lepidoptera	Pyralidae					Pyralidae		
Lepidoptera	*Acentria ephemerella*	*Acentria ephemerella*						

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Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Nematoda	Nematoda	Nematoda	Nematoda	Nematoda	Nematoda	Nematoda	Nematoda	Nematoda
Nemertinea	Nemertinea		Nemertinea	Nemertinea	Nemertinea	Nemertinea		
Platyhelminthes	*Hydrolimax* sp.		*Hydrolimax* sp.					
Platyhelminthes	Schmidtea polychoroa	Schmidtea polychoroa	*Dugesia trigrina*					
Platyhelminthes	Rhabdocoela	Rhabdocoela	Rhabdocoela	Rhabdocoela	Rhabdocoela	Rhabdocoela	Rhabdocoela	
Platyhelminthes	Tricladida			Tricladida	Tricladida	Tricladida	Tricladida	
Platyhelminthes	Turbellaria				Turbellaria			
Polychaeta	*Manayunkia speciosa*	*Manayunkia speciosa*	*Manayunkia speciosa*	*Manayunkia speciosa*	*Manayunkia speciosa*	*Manayunkia speciosa*	*Manayunkia speciosa*	
Porifera	Porifera				Porifera	Porifera		
Trichoptera	Trichoptera					Trichoptera		Trichoptera
Trichoptera	*Agraylea* spp.	*Agraylea* spp.						
Trichoptera	*Ceraclea* spp.	*Anthripsodes* spp.						
Trichoptera	Hydroptilidae				Hydroptilidae			
Trichoptera	Leptoceridae				Leptoceridae		Leptoceridae	
Trichoptera	*Oecetis* spp.	*Oecetis* spp.	*Oecetis* spp.	*Oecetis* spp.	*Oecetis* spp.	*Oecetis* spp.	*Oecetis* spp.	
Trichoptera	*Phylocentropus* spp.						*Phylocentropus* spp.	
Trichoptera	Psychomyiidae						Psychomyiidae	

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Trichoptera	*Triaenodes* spp.	*Triaenodes* spp.						
Number stations		31	31	60	47	40	40	14-80
Number taxa	47	24	17	14	21	21	17	11

Cnidaria [a/] = not quantified 1961

Table 2.3. Taxonomic identifications and corresponding nomenclature of mollusk taxa in western Lake Erie 2014, 2010, 2003, 1993, 1982, 1961, and 1929-30. A total of 63 taxa were identified with current nomenclature. Not all taxa quantified in 1929-30.

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Bivalvia	*Amblema costata*					*Amblema costata*		
Bivalvia	*Anodonta grandis*					*Anodonta grandis*	*Anodonta grandis*	*Anodonta grandis*
Bivalvia	*Amblema plicata*					*Amblema plicata*		
Bivalvia	*Amblema plicata*					*Amblema costata*		
Bivalvia	*Cyclocalx* spp.	*Pisidium* spp.	*Pisidium* spp.	*Pisidium* spp.	*Pisidium* spp.	*Pisidium* spp.	*Pisidium* spp.	
Bivalvia	*Cyclocalx casertanum*						*Pisidium casertanum*	
Bivalvia	*Cyclocalx compressum*						*Pisidium compressum*	*Pisidium compressum*

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Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Bivalvia	*Cyclocalx concinnulum*							*Pisidium concinnulum*
Bivalvia	*Cyclocalx amnicum*						*Pisidium amnicana*	
Bivalvia	*Cyclocalx fallax*						*Pisidium fallax*	
Bivalvia	*Cyclocalx henslowanum*						*Pisidium henslowanum*	
Bivalvia	*Cyclocalx nitidum*						*Pisidium nitidum*	
Bivalvia	*Cyclocalx scutellatum*							*Pisidium scutellatum*
Bivalvia	*Cyclocalx subtruncatum*						*Pisidium subtruncatum*	
Bivalvia	*Cyclocalx variabile*						*Pisidium variabile*	
Bivalvia	*Cyclocalx walkeri*						*Pisidium walkeri*	
Bivalvia	*Dreissena bugensis*	*Dreissena bugensis*	*Dreissena bugensis*	*Dreissena bugensis*				
Bivalvia	*Dreissena polymorpha*	*Dreissena polymorpha*	*Dreissena polymorpha*	*Dreissena polymorpha*	*Dreissena polymorpha*			
Bivalvia	*Elliptio dilatata*						*Elliptio dilatata*	
Bivalvia	*Elliptio dilatata*							*Elliptio dilatatus sterkii*
Bivalvia	*Fusconaia flava*						Fusconaia flava	
Bivalvia	*Fusconaia flava*							*Fusconaia flava parvula*

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Bivalvia	Lampsilis cardium						Lampsilis cardium	*Lampsilis ventricosa canadensis*
Bivalvia	*Lampsilis cardium*						*Lampsilis ventricosa*	
Bivalvia	*Leptodea fragilis*						*Leptodea fragilis*	*Leptodea fragilus*
Bivalvia	*Lampsilus radiata*					*Lampsilus radiata*		
Bivalvia	*Lampsilis siliquoidea*						*Lampsilus radiata siliquodia*	
Bivalvia	*Lampsilis siliquoidea*					*Lampsilis siliquoidea*	*Lampsilis siliquoidea*	*Lampsilis siliquoidea rosacea*
Bivalvia	*Ligumia nasuta*						*Ligumia nasuta*	*Eurynia nasuta*
Bivalvia	*Obovaria leibii*							*Obovaria leibii*
Bivalvia	Pelecypoda	Pelecypoda						
Bivalvia	*Proptera alata*						*Proptera alata*	*Proptera alata*
Bivalvia	Sphaeridae				Sphaeridae		Sphaeridae	
Bivalvia	*Sphaerium* spp.	*Sphaerium* spp.		*Sphaerium* spp.	*Sphaerium* spp.		*Sphaerium* spp.	
Bivalvia	*Sphaerium corneum*						*Sphaerium corneum*	
Bivalvia	*Sphaerium lacustre*					*Sphaerium lacustre*	*Sphaerium lacustre*	
Bivalvia	*Spaherium securis*		*Spaherium securis*					

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Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Bivalvia	*Sphaerium simile*		*Sphaerium simile*					
Bivalvia	*Sphaerium solidulum*							*Sphaerium solidulum*
Bivalvia	*Sphaerium striatinum*					*Sphaerium striatinum*	*Sphaerium striatinum*	
Bivalvia	*Sphaerium transversum*					*Sphaerium transversum*	*Sphaerium transversum*	
Bivalvia	*Sphaerium transversum*							*Musculium transversum*
Bivalvia	*Strophitus rugosus*							*Strophitus rugosus*
Bivalvia	*Truncilla donaciformis*						*Truncilla donaciformis*	*Truncilla donaciformis*
Bivalvia	*Truncilla donaciformis*							*Truncilla truncilla*
Bivalvia	Unionidae					Unionidae	Unionidae	
Gastropoda	*Amnicola* spp.	*Amnicola* spp.	*Amnicola* spp.	*Amnicola* spp.	*Amnicola* spp.	*Amnicola* spp.	*Amnicola* spp.	
Gastropoda	*Birgella subglobosus*	*Birgella subglobosus*	*Birgella subglobosus*	*Birgella subglobosus*				
Gastropoda	*Bithynia spp.*					*Bithynia spp.*		
Gastropoda	*Bithynia tentaculata*	*Bithynia tentaculata*	*Bithynia tentaculata*	*Bithynia tentaculata*	*Bithynia tentaculata*		*Bithynia tentaculata*	*Bithynia tentaculata*
Gastropoda	*Bulimus tentaculata*						*Bulimus tentaculata*	
Gastropoda	*Campeloma* spp.	*Campeloma* spp.		*Campeloma* spp.				
Gastropoda	*Capoloma descisum*		*Capoloma descisum*		*Capoloma descisum*	*Capoloma descisum*	*Capoloma descisum*	*Capoloma descisum*

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Gastropoda	*Cincinnatia cincinnatiensis*	*Cincinnatia cincinnatiensis*						
Gastropoda	*Ferrissia spp.*				Ferrissia spp.			
Gastropoda	Gastropoda	Gastropoda			Gastropoda			
Gastropoda	*Helisoma* spp.						*Helisoma* spp.	
Gastropoda	Hydrobiidae	Hydrobiidae						
Gastropoda	*Physa* spp.				*Physa* spp.		*Physa* spp.	
Gastropoda	*Physa* spp.							*Physa sayii*
Gastropoda	*Physa* spp.	*Physella* spp.	*Physella* spp.					
Gastropoda	*Physella integra*						*Amnicola integra*	
Gastropoda	*Physella integra*						*Amnicola limosa*	*Amnicola limosa parva*
Gastropoda	*Planorbella trivolvis*							*Helisoma trivolvis*
Gastropoda	*Pleurocera* spp.	*Pleurocera* spp.		*Goniobasis* spp.				
Gastropoda	*Pleurocera canaliculata*		*Pleurocera acuta*					*Pleurocera acuta*
Gastropoda	*Pleurocera semicarinata*		*Elimia livescens*		*Goniobasis livescens*			*Goniobasis livescens*
Gastropoda	*Probythinella protera*	*Probythinella lacustris*	*Probythinella lacustris*					
Gastropoda	*Somatogyrus subglobosus*					*Somatogyrus subglobosus*	*Somatogyrus subglobosus*	*Somatogyrus subglobosus*
Gastropoda	*Valvata* spp.	*Valvata* spp.						
Gastropoda	*Valvata piscinalis*	*Valvata piscinalis*	*Valvata piscinalis*	*Valvata piscinalis*	*Valvata piscinalis*			

Grouping	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Gastropoda	*Valvata sincera*	*Valvata sincera*	*Valvata sincera*	*Valvata sincera*	*Valvata sincera*		*Valvata sincera*	
Gastropoda	*Valvata tricarinata*	*Valvata tricarinata*	*Valvata tricarinata*	*Valvata tricarinata*	*Valvata tricarinata*	*Valvata tricarinata*	*Valvata tricarinata*	*Valvata tricarinata*
Gastropoda	*Viviparidae*				*Viviparidae*	*Viviparidae*		
Number stations		31	31	60	47	40	40	14-80
Number taxa	63	19	16	13	15	17	37	26

Table 2.4. Taxonomic identifications and corresponding nomenclature of Chironomidae taxa in western Lake Erie 2014, 2010, 2003, 1993, 1982, 1961, and 1929-30. A total of 45 taxa were identified with current nomenclature. Not all taxa quantified in 1929-30.

Current nonemclature	2014	2010	2003	1993	1982	1961	1929-30
Chironomidae							Chironomidae
Ablabesmyia spp.			*Ablabesmyia* spp.	*Ablabesmyia* spp.			
Ablabesmyia annulata	*Ablabesmyia annulata*	*Ablabesmyia annulata*					
Acalcarella spp.				*Acalcarella* spp.			
Axarus spp.			*Axarus* spp				
Chironomus spp.	*Chironomus spp.*	*Chironomus spp.*	*Chironomus* spp.	*Chironomus* spp.	*Chironomus* spp.	*Chironomus spp.*	
Cladopelma spp.	*Cladopelma spp.*						
Cladotanytarsus spp.	*Cladotanytarsus spp.*			*Cladotanytarsus spp.*	*Cladotanytarsus spp.*		
Clinotanypus spp.				*Clinotanypus* spp.			
Coelotanypus spp.	*Coelotanypus spp.*	*Coelotanypus spp.*	*Coelotanypus spp.*	*Coelotanypus* spp.	*Coelotanypus* spp.	*Coelotanypus spp.*	
Conchapelopia spp.		*Conchapelopia spp.*	*Conchapelopia spp.*				

Current nonemclature	2014	2010	2003	1993	1982	1961	1929-30
Cricotopus spp.				*Cricotopus* spp.	*Cricotopus* spp.		
Cryptochiron-omus spp.	*Cryptochiron-omus* spp.	*Cryptochiron-omus* spp.	*Cryptochiron-omus* spp.	*Cryptochiron-omus* spp.	*Cryptochiron-omus* spp.	*Cryptochiron-omus* spp.	
Demicryptochiron-omus spp.				*Demicryptochiron-omus* spp.			
Dicrotendipes spp.	*Dicrotendipes* spp.	*Dicrotendipes* spp.	*Dicrotendipes* spp.	*Dicrotendipes* spp.	*Dicrotendipes* spp.		
Epoicocladius spp.	*Epoicocladius* spp.	*Epoicocladius* spp.	*Epoicocladius* spp.				
Eukiefferiella spp.				*Eukiefferiella* spp.			
Glyptotendipes spp.	*Glyptotendipes* spp.						
Harnischia spp.				*Harnischia* spp.	*Harnischia* spp.		
Hydrobaenus spp.	*Hydrobaenus* spp.	*Hydrobaenus* spp.					
Macropelopia spp.				*Macropelopia* spp.			
Microchironomus spp.			*Microchironomus* spp.	*Microchironomus* spp.			
Orthocladimae					Orthocladimae		
Orthocladius spp.				*Orthocladius* spp.			
Parachironomus spp.					*Parachironomus* spp.		
Paracladius spp.				*Paracladius* spp.			
Paracladopelma spp.		*Paracladopelma* spp.	*Paracladopelma* spp.				
Parakieferiella spp.	*Parakieferiella* spp.	*Parakiefferiella* spp.		*Parakiefferiella* spp.			
Paralauterborniella spp.				*Paralauterborniella* spp.	*Paralauterborniella* spp.		
Paratanytarsus spp.	*Paratanytarsus* spp.	*Paratanytarsus* spp.	*Paratanytarsus* spp.	*Paratanytarsus* spp.			
Pentaneurini					Pentaneurini	Pentaneurini	

Current nonemclature	2014	2010	2003	1993	1982	1961	1929-30
Polypedilum spp.				*Polypedilum* spp.	*Polypedilum* spp.		
Polypedilum flavum		*Polypedilum flavum*	*Polypedilum flavum*				
Polypedilum halterale	*Polypedilum halterale*	*Polypedilum halterale*	*Polypedilum halterale*			*Polypedilum halterale (group)*	
Polypedilum scalaenum			*Polypedilum scalaenum*				
Potthastia spp.	*Potthastia* spp.	*Potthastia* spp.					
Procladius spp.	*Procladius* spp.	*Procladius* spp.	*Procladius* spp.	*Procladius* spp.	*Procladius* spp.	*Procladius* spp.	
Pseudochironomus spp.	*Pseudochiron-omus* spp.	*Pseudochiron-omus* spp.	*Pseudochiron-omus* spp.				
Rheotanytarsus spp.					*Rheotanytarsus* spp.		
Stictochironomus spp.	*Stictochironomus* spp.	*Stictochironomus* spp.	*Stictochironomus* spp.	*Stictochironomus* spp.			
Tanytarsus spp.	*Tanytarsus* spp.		*Tanytarsus* spp.	*Tanytarsus* spp.	*Tanytarsus* spp.		
Tribelos spp.	*Tribelos* spp.	*Tribelos* spp.	*Tribelos* spp.				
Tanytarsini						Tanytarsini	
Unknown				Unknown			
Number stations	31	31	60	47	40	40	14-80
Number taxa	19	18	19	24	15	7	1

Table 2.5. Taxonomic identifications and corresponding nomenclature of Oligochaeta taxa in western Lake Erie 2014, 2010, 2003, 1993, 1982, 1961, and 1929-30. A total of 54 taxa were identified with current nomenclature. Not all taxa quantified in 1929-30.

Group	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Aeolosomatidae	*Aeolosoma spp.*				*Aeolosoma spp.*			
Enchytraeidae	Enchytraeidae	Enchytraeidae	*Enchytraeidae*	Enchytraeidae	*Enchytraeidae*			

Group	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Tubificidae	*Aulodrilus americanus*	*Aulodrilus americanus*	*Aulodrilus americanus*	*Aulodrilus americanus*	*Aulodrilus americanus*	*Aulodrilus americanus*	*Aulodrilus americanus*	
Tubificidae	*Aulodrilus limnobius*	*Aulodrilus limnobius*	*Aulodrilus limnobius*	*Aulodrilus limnobius*	*Aulodrilus limnobius*	*Aulodrilus limnobius*	*Aulodrilus limnobius*	
Tubificidae	*Aulodrilus pigueti*	*Aulodrilus pigueti*	*Aulodrilus pigueti*	*Aulodrilus pigueti*	*Aulodrilus pigueti*	*Aulodrilus pigueti*	*Aulodrilus pigueti*	
Tubificidae	*Aulodrilus pluriseta*	*Aulodrilus pluriseta*	*Aulodrilus pluriseta*	*Aulodrilus pluriseta*	*Aulodrilus pluriseta*	*Aulodrilus pluriseta*	*Aulodrilus pluriseta*	
Tubificidae	*Bothrioneurum vejdovskyanum*			*Bothrioneurum vejdovskyanum*	*Bothrioneurum vejdovskyanum*	*Bothrioneurum vejdovskyanum*		
Tubificidae	*Branchiura sowerbyi*	*Branchiura sowerbyi*	*Branchiura sowerbyi*	*Branchiura sowerbyi*	*Branchiura sowerbyi*	*Branchiura sowerbyi*	*Branchiura sowerbyi*	
Tubificidae	*Ilyodrilus templetoni*	*Ilyodrilus templetoni*	*Ilyodrilus templetoni*	*Ilyodrilus templetoni*	*Ilyodrilus templetoni*	*Ilyodrilus templetoni*	*Ilyodrilus templetoni*	
Tubificidae	*Isochaetides freyi*			*Isochaetides freyi*	*Isochaetides freyi*	*Isochaetides freyi*		
Tubificidae	*Limnodrilus spp.*							*Limnodrilus spp.*
Tubificidae	*Limnodrilus cervix*	*Limnodrilus cervix*	*Limnodrilus cervix*	*Limnodrilus cervix*	*Limnodrilus cervix*	*Limnodrilus cervix*	*Limnodrilus cervix*	
Tubificidae	*Limnodrilus cervix*					*Limnodrilus cervix* varient	*Limnodrilus cervix* varient	
Tubificidae	*Limnodrilus claparedianus*		*Limnodrilus claparedianus*	*Limnodrilus claparedianus*	*Limnodrilus claparedianus*	*Limnodrilus claparedianus*	*Limnodrilus claparedianus*	
Tubificidae	*Limnodrilus hoffmeisteri*	*Limnodrilus hoffmeisteri*	*Limnodrilus hoffmeisteri*	*Limnodrilus hoffmeisteri*	*Limnodrilus hoffmeisteri*	*Limnodrilus hoffmeisteri*	*Limnodrilus hoffmeisteri*	
Tubificidae	*Limnodrilus maumeensis*	*Limnodrilus maumeensis*		*Limnodrilus maumeensis*	*Limnodrilus maumeensis*	*Limnodrilus maumeensis*	*Limnodrilus maumeensis*	
Tubificidae	*Limnodrilus spiralis*					*Limnodrilus spiralis*		
Tubificidae	*Limnodrilus udekemianus*	*Limnodrilus udekemianus*	*Limnodrilus udekemianus*	*Limnodrilus udekemianus*	*Limnodrilus udekemianus*	*Limnodrilus udekemianus*	*Limnodrilus udekemianus*	

Group	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Tubificidae	*Lumbricillis* spp.				*Lumbricillis* spp.			
Tubificidae	*Potamothrix moldaviensis*	*Potamothrix moldaviensis*	*Potamothrix moldaviensis*	*Potamothrix moldaviensis*	*Potamothrix moldaviensis*	*Potamothrix moldaviensis*	*Potamothrix moldaviensis*	
Tubificidae	*Potamothrix vejdovskyi*	*Potamothrix vejdovskyi*	*Potamothrix vejdovskyi*	*Potamothrix vejdovskyi*	*Potamothrix vejdovskyi*	*Potamothrix vejdovskyi*	*Potamothrix vejdovskyi*	
Tubificidae	*Quistadrilus multisetosus*			*Quistadrilus multisetosus*	*Quistadrilus multisetosus multisetosus*	*Quistadrilus multisetosus multisetosus*	*Pelescolex multisetosus*	
Tubificidae	*Quistadrilus multisetosus*					*Quistadrilus multisetosus longidentus*		
Tubificidae	*Spirosperma ferox*		*Spirosperma ferox*	*Spirosperma ferox*	*Spirosperma ferox*	*Spirosperma ferox*	Pelescolex ferox	
Tubificidae	*Tubifex* spp.							*Tubifex* spp.
Tubificidae	*Tubifex tubifex*	*Tubifex tubifex*	*Tubifex tubifex*	*Tubifex tubifex*			*Tubifex tubifex*	
Tubificidae	Tubificidae							Tubificidae
Tubificidae	Immature Tubificidae					Immature	Immature	
Tubificidae	Immature Tubificidae w/ capilliform chaetae	Immature Tubificidae w/ capilliform chaetae	Immature Tubificidae w/ capilliform chaetae	Immature Tubificidae w/ capilliform chaetae	Immature Tubificidae w/ capilliform chaetae	Immature Tubificidae w/ capilliform chaetae	Immature Tubificidae w/ capilliform chaetae	
Tubificidae	Immature Tubificidae w/o capilliform chaetae	Immature Tubificidae w/o capilliform chaetae	Immature Tubificidae w/o capilliform chaetae	Immature Tubificidae w/o capilliform chaetae	Immature Tubificidae w/o capilliform chaetae	Immature Tubificidae w/o capilliform chaetae	Immature Tubificidae w/o capilliform chaetae	
Naididae	*Amphichaeta leydigi*	*Amphichaeta leydigi*	*Amphichaeta leydigi*	*Amphichaeta leydigi*				

Group	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Naididae	*Arcteonais lomondi*	*Arcteonais lomondi*	*Arcteonais lomondi*	*Arcteonais lomondi*	*Arcteonais lomondi*	*Arcteonais lomondi*		
Naididae	*Chaetogaster diaphanus*		*Chaetogaster diaphanus*		*Chaetogaster diaphanus*	*Chaetogaster diaphanus*		
Naididae	*Chaetogaster limnaei*				*Chaetogaster limnaei*			
Naididae	*Dero digitata*	*Dero digitata*	*Dero digitata*	*Dero digitata*	*Dero digitata*	*Dero digitata*		
Naididae	*Dero obtusa*				*Nais obtusa*			
Naididae	*Nais* spp.				*Nais* spp.	*Nais* spp.	*Nais* spp.	
Naididae	*Nais bretscheri*			*Nais bretscheri*	*Nais bretscheri*			
Naididae	*Nais communis*	*Nais communis*	*Nais communis*	*Nais communis*	*Nais communis*			
Naididae	*Nais elinguis*		*Nais elinguis*	*Nais elinguis*	*Nais elinguis*		*Nais elinguis*	
Naididae	*Nais pardalis*				*Nais pardalis*	*Nais pardalis*		
Naididae	*Nais pseudobtusa*	*Nais pseudobtusa*	*Nais pseudobtusa*		*Nais pseudobtusa*			
Naididae	*Nais simplex*	*Nais simplex*		*Nais simplex*				
Naididae	*Nais variabilis*	*Nais variabilis*	*Nais variabilis*	*Nais variabilis*	*Nais variabilis*	*Nais variabilis*	*Nais variabilis complex*	
Naididae	*Ophidonais serpentina*	*Ophidonais serpentina*	*Ophidonais serpentina*	*Ophidonais serpentina*	*Ophidonais serpentina*	*Ophidonais serpentina*	*Ophidonais serpentina*	
Naididae	*Paranais frici*	*Paranais frici*	*Paranais frici*	*Paranais frici*	*Paranais frici*		*Paranais frici*	
Naididae	*Piguetilla blanci*	*Piguetilla blanci*						
Naididae	*Piguetiella michiganensis*	*Piguetiella michiganensis*		*Piguetiella michiganensis*	*Piguetiella michiganensis*	*Piguetiella michiganensis*		
Naididae	*Pristina* spp.					*Pristina spp.*		
Naididae	*Pristina acuminata*		*Pristina acuminata*		*Pristina acuminata*			

Group	Current nomenclature	2014	2010	2003	1993	1982	1961	1929-30
Naididae	*Pristina aequiseta*				*Pristina aequiseta*			
Naididae	*Pristina osborni*		*Pristina osborni*					
Naididae	*Slavina appendiculata*	*Slavina appendiculata*	*Slavina appendiculata*	*Slavina appendiculata*	*Slavina appendiculata*	*Slavina appendiculata*	*Slavina appendiculata*	
Naididae	*Specaria josinae*	*Specaria josinae*	*Specaria josinae*		*Specaria josinae*	*Specaria josinae*		
Naididae	*Stylaria fossularia*	*Stylaria fossularia*						
Naididae	*Stylaria lacustris*	*Stylaria lacustris*	*Stylaria lacustris*	*Stylaria lacustris*	*Stylaria lacustris*	*Stylaria lacustris*		
Naididae	*Uncinais uncinata*	*Uncinais uncinata*		*Uncinais uncinata*	*Uncinais uncinata*	*Uncinais uncinata*	*Uncinais uncinata*	
Naididae	*Vejdovskyella* spp.						*Vejdovskyella* spp.	
Naididae	*Vejdovskyella intermedia*	*Vejdovskyella intermedia*	*Vejdovskyella intermedia*	*Vejdovskyella intermedia*	*Vejdovskyella intermedia*	*Vejdovskyella intermedia*	*Vejdovskyella intermedia*	
Naididae	*Wapsa mobilis*					*Wapsa mobilis*		
Number stations sampled		31	31	60	47	40	40	?
Number taxa		33	33	36	44	36	27	3

RESULTS AND DISCUSSION

Survey 2014

In 2014, a total of 95 benthic taxa were identified with a total mean-station density of 9,478 individuals/m^2 in samples collected at 31 stations in western Lake Erie April 9 - May 28, 2014 (Table 2.6). This included 24 general-benthic taxa at a mean station density of 2,403/m^2, 19 mollusks at 3,336/m^2 (4 pelecypods at 3,110/m^2 and 16 gastropods at 223/m^2), 19 chironomids at 1,361/m^2, and 33 oligochaete taxa (15 tubificids at 2,209/m^2, 17 naidids at 183/m^2, and 1 enchytraeid at 1/m^2) at a mean station density of 2,393/m^2.

Distribution and abundance of individual benthic taxa indicate that, in general, few were widely distributed and few occurred at relatively high densities (Table 2.6). Of the total 95 taxa, only 6 were distributed at all 31 stations including; nematodes, mayflies (primarily *Hexagenia* spp.), caddisflies (primarily *Oecetis* spp.), midges (primarily *Chironomus* spp. and *Procladius* spp.), and immature tubificid worms without capilliform chaetae. Eighteen taxa were found at between 17 and 30 (55-97%) stations, 35 between 3 and 14 stations (10-45%), and 39 taxa were found at 1 or 2 stations (1-2%). Abundances of four taxa accounted for 64% (6,042/m^2) of the total mean-station density of 9,478/m^2: these taxa include; the exotic quagga mussel *Dreissenia bugensis* at 2,175 individuals/m^2 (23%), nematodes at 1,656/m^2 (17%), immature tubificid oligochaetes without capilliform chaetae at 1,427/m^2 (15%), and the exotic zebra mussel *D. polymorpha* at a mean station density of 784/m^2 (8%). Twelve other taxa accounted for 26% (2,475/m^2) and the remaining 82 taxa accounted for 10% of the total mean-station density.

Table 2.6. Mean density (number/m^2) and number of stations (n = 31) with individual benthic taxa in western Lake Erie April 9 - May 1, 2014.

Common name	Grouping	Taxa	Density	Number of stations
Mussels/clams	Pelecypoda	*Dreissena bugensis*	2,175.0	26
Nematodes	Nematoda	Nematoda	1,656.0	31
Tubuficid worms	Tubificidae	Immature Tubificidae	1,476.0	31
Mussels/clams	Pelecypoda	*Dreissena polymorpha*	784.0	27
Midges	Chironomidae	*Procladius* spp.	541.0	31
Midges	Chironomidae	*Coelotanypus* spp.	399.0	30
Mayflies	Ephemeroptera	*Hexagenia* spp.	298.0	31
Tubuficid worms	Tubificidae	*Ilyodrilus templetoni*	245.0	20
Midges	Chironomidae	*Chironomus* spp.	166.0	31
Tubuficid worms	Tubificidae	*Branchiura sowerbyi*	151.0	30
Tubuficid worms	Tubificidae	*Limnodrilus hoffmeisteri*	129.0	17
Naidid worms	Naididae	*Vejdovskyella intermedia*	127.0	5
Mussels/clams	Pelecypoda	*Cyclocalx* spp.	114.0	22
Flat/round worms	Platyhelminthes	Schmidtea polychoroa	105.5	23
Tubuficid worms	Tubificidae	*Aulodrilus pigueti*	105.0	28
Polychaetes	Polychaeta	*Manayunkia speciosa*	95.0	2
Snails	Gastropoda	*Valvata tricarinata*	75.0	20
Caddisflies	Trichoptera	*Oecetis* spp.	69.0	31
Snails	Gastropoda	*Amnicola* spp.	69.0	22
Scuds	Amphipoda	*Gammarus fasciatus*	62.0	18

Common name	Grouping	Taxa	Density	Number of stations
Tubuficid worms	Tubificidae	*Aulodrilus limnobius*	57.0	7
Midges	Chironomidae	*Cryptochironomus* spp.	56.0	26
Midges	Chironomidae	*Ablabesmyia annulata*	54.0	26
Midges	Chironomidae	*Stictochironomus* spp.	48.0	7
Midges	Chironomidae	*Polypedilum halterale*	38.0	26
Mussels/clams	Pelecypoda	*Sphaerium* spp.	36.0	8
Water mites	Hydracarina	*Limnaecia* spp.	32.0	13
Tubuficid worms	Tubificidae	*Aulodrilus pluriseta*	32.0	6
Leeches	Hirudinea	*Helobdella stagnalis*	30.0	20
Midges	Chironomidae	*Paratanytarsus* spp.	28.0	4
Leeches	Hirudinea	*Helobdella elongata*	23.0	20
Snails	Gastropoda	*Cincinnatia cincinnatiensis*	21.0	11
Naidid worms	Naididae	*Amphichaeta leydigi*	21.0	2
Snails	Gastropoda	*Birgella subglobosus*	18.0	13
Scuds	Amphipoda	*Echinogammarus* spp.	14.0	9
Snails	Gastropoda	*Physella* spp.	14.0	14
Midges	Chironomidae	*Glyptotendipes* spp.	14.0	2
Naidid worms	Naididae	*Dero digitata*	8.0	9
Snails	Gastropoda	*Valvata piscinalis*	7.0	6
Midges	Chironomidae	*Tribelos* spp.	6.0	5
Naidid worms	Naididae	*Nais communis*	6.0	4
Naidid worms	Naididae	*Slavina appendiculata*	6.0	2
Snails	Gastropoda	*Bithynia tentaculata*	5.0	5
Midges	Chironomidae	*Epoicocladius* spp.	5.0	1
Naidid worms	Naididae	*Specaria josinae*	5.0	4
Flat/round worms	Platyhelminthes	Rhabdocoela	4.0	8
Snails	Gastropoda	*Probythinella lacustris*	4.0	7
Tubuficid worms	Tubificidae	*Limnodrilus cervix*	4.0	1
Midges	Chironomidae	*Dicrotendipes* spp.	3.0	7
Tubuficid worms	Tubificidae	*Potamothrix moldaviensis*	3.0	2
Scuds	Amphipoda	Amphipoda	2.0	4
Hydras	Cnidaria	Cnidaria	2.0	4
Mayflies	Ephemeroptera	*Caenis* spp.	2.0	1
Leeches	Hirudinea	*Erpobdella* spp.	2.0	6
Snails	Gastropoda	Gastropoda	2.0	7
Snails	Gastropoda	Hydrobiidae	2.0	4
Snails	Gastropoda	*Valvata* spp.	2.0	5
Midges	Chironomidae	*Pseudochironomus* spp.	2.0	4
Midges	Chironomidae	*Tanytarsus* spp.	2.0	6
Tubuficid worms	Tubificidae	*Limnodrilus udekemianus*	2.0	2
Tubuficid worms	Tubificidae	*Potamothrix vejdovskyi*	2.0	3
Naidid worms	Naididae	*Arcteonais lomondi*	2.0	3

Common name	Grouping	Taxa	Density	Number of stations
Naidid worms	Naididae	*Paranais frici*	2.0	1
Naidid worms	Naididae	*Stylaria fossularia*	2.0	1
Naidid worms	Naididae	*Stylaria lacustris*	2.0	3
Scuds	Amphipoda	*Hyalella* spp.	1.0	2
Leeches	Hirudinea	Hirudinea	1.0	5
Water mites	Hydracarina	*Hygrobates* spp.	1.0	2
Mussels/clams	Pelecypoda	Pelecypoda	1.0	2
Snails	Gastropoda	*Campeloma* spp.	1.0	2
Snails	Gastropoda	*Pleurocera* spp.	1.0	1
Tubuficid worms	Tubificidae	*Aulodrilus americanus*	1.0	3
Naidid worms	Naididae	*Nais variabilis*	1.0	1
Naidid worms	Naididae	*Ophidonais serpentina*	1.0	1
Naidid worms	Naididae	*Piguetiella michiganensis*	1.0	1
Enchytid worms	Enchytraeidae	Enchytraeidae	1.0	3
Beetles	Coleoptera	*Dubiraphia* spp.	<1	1
Leeches	Hirudinea	*Placobdella montifera*	<1	2
Butterflies/moths	Lepidoptera	*Acentria ephemerella*	<1	1
Caddisflies	Trichoptera	*Agraylea* spp.	<1	1
Caddisflies	Trichoptera	*Ceraclea* spp.	<1	1
Caddisflies	Trichoptera	*Triaenodes* spp.	<1	1
Snails	Gastropoda	*Valvata sincera*	<1	1
Midges	Chironomidae	*Cladopelma spp.*	<1	1
Midges	Chironomidae	*Cladotanytarsus* spp.	<1	1
Midges	Chironomidae	*Hydrobaenus* spp.	<1	1
Midges	Chironomidae	*Parakieferiella* spp.	<1	1
Midges	Chironomidae	*Potthastia* spp.	<1	1
Tubuficid worms	Tubificidae	*Limnodrilus maumeensis*	<1	1
Tubuficid worms	Tubificidae	*Tubifex tubifex*	<1	1
Naidid worms	Naididae	*Nais pseudobtusa*	<1	1
Naidid worms	Naididae	*Nais simplex*	<1	1
Naidid worms	Naididae	*Piguetilla blanci*	<1	1
Naidid worms	Naididae	*Uncinais uncinata*	<1	1

Complexity of species distribution and abundances of taxa throughout western Lake Erie emphasizes the need to analyze benthic communities in the Great Lakes based on indicator taxa, which can easily and efficiently be determined, and need for group metrics, which are specialized for groups (e.g., oligochaetes) that are common and abundant in large deep-water systems such as the Great Lakes. This is because, compared to other freshwater system types (e.g., streams, small lakes), benthic diversity in the Great Lakes is relatively low and the biological meaning of many species unique to the Great Lakes is unknown.

Length-frequency of dreissenid mussels 2014

Examination of length-frequency distributions of two of the most abundant taxa, *Dreissena bugensis* ($2,175/m^2$) and *D. polymorpha* ($784/m^2$) in 2014 indicate individuals of both taxa live for approximately

two years (Figure 2.2). Mussels are exceptionally large compared to most other taxa and, because they occur at high densities (2,175/m^2 and 784/m^2, respectively), were visually dominate components of many raw-field collected samples (Table 2.6). Often, these mussels composed > 50% of the total sample, including sediments. However, length-frequency distributions indicate the majority of mussels were young-of-the-year (ca. 1 to 10 mm long) and the less numerically abundant mussels were yearlings/1-year-olds (ca. > 10 mm) (Figure 2.2).
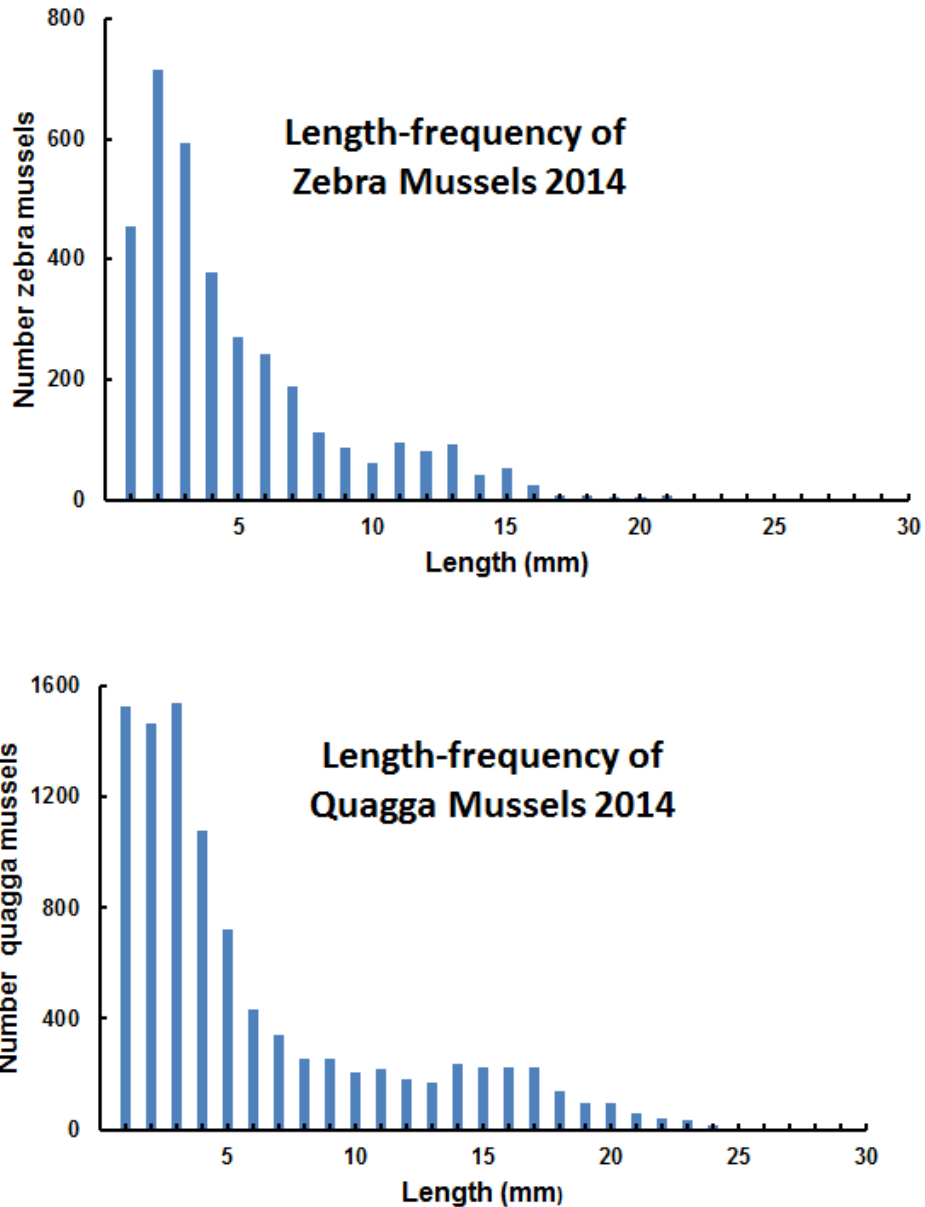

Figure 2.2. Length-frequency of zebra (*Dreissenia polymorpha)* and quagga *(D. bugensis)* mussels collected at 31 stations in western Lake Erie 2014.

A noteworthy observation of the present study is that the presence of relatively large sized and abundances of exotic mussels has created a new feature of raw-field collected samples. Mussels, both live and dead, were the most easily observed difference between samples collected before 1982 and samples collected in 1993, 2003, 2010, and 2014. Mussels often cover large proportions of hard and soft substrates in western Lake Erie. In addition, dead shells of mussels can compose a large portion of the volume of sample collections. To date, very few studies examined impacts that mussel shells may have on other ecosystem components (e.g., Botts et al., 1996). Therefore, physical impacts of exotic mussels on ecosystem processes warrants further study.

Concern about invasion of dreissenid mussels has especially been focused on impacts in western Lake Erie, partly because western Lake Erie is where mussels: first colonized North America (mid-1980s), became highly abundant and visible components of the lakes in 1989, and their impacts have been intensively studied for the past 25 years (Nalepa and Schloesser 1993, 2011). In addition, impacts of pollution-abatement programs on productivity in western Lake Erie were only just beginning to be measured in the late-1980s and there was concern mussels could delay the recovery of the western basin (Nalepa 1987; Reynoldson et al. 1989; McCall and Soster 1990; Soster and McCall 1990; Schloesser et al. 1991). After 25 years, studies that evaluate historical changes of benthos in relation to dreissenid mussels in western Lake Erie are still being conducted (Soster et al., 1990; Burlakova et al., 2014; Karatayev et al., 2014). As a whole, studies support the theory that reductions in nutrients and an improved trophic status of western Lake Erie are probably attributable to pollution abatement and dreissenid mussels, which has been observed to be a 'de-trophitizer' in European waters.

Taxonomy

A total of 95 benthic taxa were identified in western Lake Erie in 2014 (Table 2.7). Of the 95 taxa, 24 were general benthos, 19 mollusks, 19 chironomids, and 33 were oligochaetes. The 95 taxa represent about half of all identified taxa (n = 212), and it is similar to the range of taxa (88-104) identified between 2014 and 1929-30, except in 1929-30 when only 41 taxa were identified and a large proportion (63%) of these were mollusks. Numbers of identified taxa were about equal for the four arbitrary assessed groups (n = 44-63 taxa), although numbers in the four groups varied substantially between the seven studies. Examples of varied numbers of taxa in and between years include: relatively large numbers (proportions?) of mollusks occurred in 1961 and 1929-30 compared to other studies; large numbers of oligochaetes occurred 2014-1961 compared to 1929-30; and, a relatively large number of chironomids occurred 2014-1982 compared to 1961 and 1929-30.

Table 2.7. Numbers of identified taxa (Tables 2.2-2.5) in western Lake Erie 2014-1929.

	2014	2010	2003	1993	1982	1961	1930	Total 2014-1930
General benthos	24	17	14	21	21	17	11	47
Mollusks	19	16	13	15	17	37	26	63
Chironomids	19	18	19	24	15	7	1	44
Oligochaetes	33	33	36	44	36	27	3	58
Total	95	84	82	104	89	88	41	212

Historical perspective

Densities of benthic fauna, based on nine consistently-sampled stations, indicate productivity (number organisms/m^2) fluctuated 7- to 8- fold between 1930 and 2014 (Table 2.7; Figure 2.3; Appendix 2.7). Productivity was lowest in 1930 (station mean = 1,737/m^2), increased 4.0-fold in densities between 1930 and 1961 (1,737/m^2 to 7,008/m^2, respectively) and 1.9-fold between 1961 and 1982 (7,008/m^2 to 13,211/m^2). Then, productivity decreased 1.6-fold between 1982 and 1993 (13,211/m^2 to 8,451/m^2, respectively) and 3.4-fold 1993 and 2003 (8,451/m^2 to 2,470/m^2). Productivity again increased between 1993 and 2010 (2,469/m^2 to 4,656/m^2, respectively) and 2010 and 2014 (4,656/m^2 to 6,561/m^2) 1.8-fold and 1.4-fold, respectively.
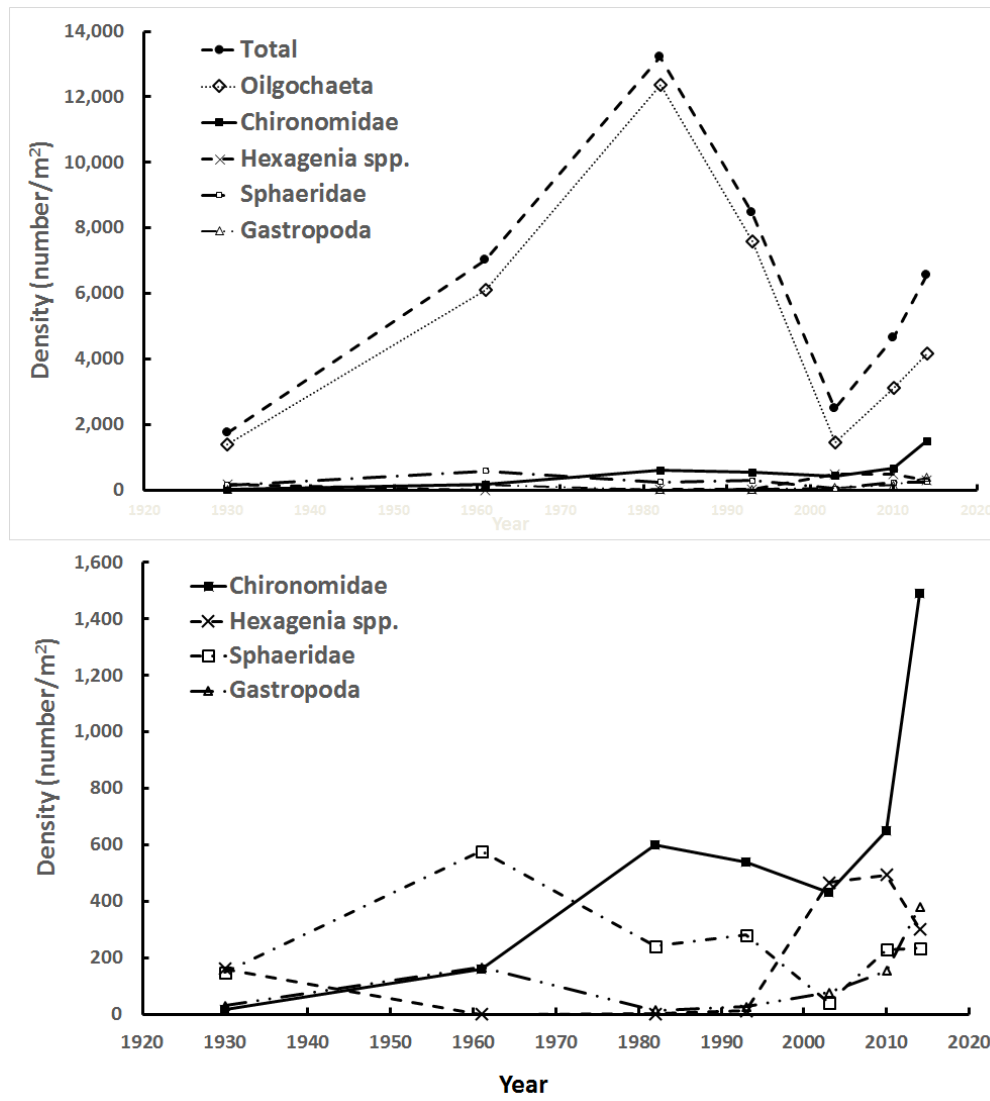

Figure 2.3. Density (number/m^2) of benthic invertebrates at nine stations (3D, 8D, 15D, 2L, 6L, 1M, 7M, 8M, and 4R) sampled for comparative benthos analysis 1930, 1961, 1982, 1993, 2003, 2010, and 2014. Top panel illustrates dominance of Oligochaeta in total benthic assemblage and bottom panel illustrates changes in important taxa groups.

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Overall, changes in productivity at the nine stations monitored between 1930 and 2014 parallel other studies that indicate the trophic status of western Lake Erie declined between the 1930s and early-1960s and early-1980s, improved between 1980s and the late-1990s, and declined again between 2000 and 2010 (Beeton 1961; Carr and Hiltunen 1965; McCall and Soster 1990; Soster and McCall 1990; Schloesser et al., 2000; Soster et al. 2011; Burlakova et al., 2014). Suggestive evidence indicates there was substantial improvement in the trophic status of western Lake Erie as early as 1982 when the densities of pollution intolerant oligochaetes increased (Schloesser et al. 1995). As the result of the dominance of oligochaete fauna in western Lake Erie (63% to 94% of total densities between 1930 and 2014), total benthic densities closely paralleled changes in oligochaetes (Figure 2.3). Numerical dominance of oligochaete fauna illustrates the need for simplified 'oligochaete metrics' that evaluate benthic health based primarily on oligochaete composition for western Lake Erie, and especially in deeper portions of the Great Lakes where other indicator taxa are absent (e.g., *Hexagenia* spp. mayflies).

Various measures and metrics of oligochaetes have been used since 1961 (Carr and Hiltunen 1965; Hiltunen 1969; Reynoldson et al. 1989; Schloesser 1995), but they only used a fraction of the identified and enumerated taxa because there is no way to classify many oligochaete taxa relative to the trophic status of the water. At present, U.S. EPA is working on trophic classifications of individual taxa of benthic fauna in the Laurentian Great Lake, including oligichaete species, which will increase the number of 'meaningful' taxa that can be included in trophic metrics (Great Lakes Benthic Indicator Development Workshop). This improved classification, based on more individual taxa, will improve the ability to 'fine-tune' metrics used to measure trophic trends that do not change 4- to 6-fold in densities as they did between the 1930 and 1961.

Changes in densities of individual taxa groups indicate significant changes in the benthic fauna in western Lake Erie between 1930 and 2014 (Table 2.8; Figure 2.3). Densities of oligochaete taxa increased between 1930 and 1961 and 1961 and 1982, declined between 1982 and 1993 and 1993 and 2003, then remained relatively consistent (from 59% to 67% of total benthos density) between 2003 and 2014. Densities of the other four taxa groups (Chironomidae, *Hexagenia* spp., Sphaeridae, and Gastropoda) ranged between < 1 to $1,489/m^2$ and collectively composed 21% of the fauna in 1930, 12% in 1961, 8% in 1982, 10% in 1993, 42% in 2003, 33% in 2010, and 39% of the total fauna in 2014. Ranges of proportions of these four taxa groups per year include; 1% to 23% for Chironomidae, $< 1\%$ to 19% for *Hexagenia* spp. mayfies, 2% to 9% for Sphaeridae, and $< 1\%$ to 6% for Gastropoda.

Although no rigorous statistical analysis was conducted across sampling periods for the nine consistently sampled stations, preliminary F-tests indicate significant differences ($p < 0.05$) in densities of: total-benthic and oligochaete taxa between 1930 and 1982, 1982 and 2010, 2003 and 2010, and 2003 and 2014 (trend lines, Figure 2.3); *Hexagenia* spp. mayflies between 1993 and 2003; Sphaeridae between 1930 and 1961, 1961 and 1982, and 1993 and 2003; and, Gastropoda between 2003 and 2014. Relatively high variability of densities at the low number of stations (n = 9) between other comparisons negated possible significant changes even when trend analysis indicated visually distinct changes. For example, trend analysis revealed total and oligochaete fauna exhibited substantial changes between 1961 and 1982 (increased densities) and 1982 and 1993 (decreased densities). However, station variability resulted in no significant differences between these sampling periods.

Table 2.8. Mean density (number/m2) and percent composition of five comparable taxa at nine comparative stations (3D, 8D, 15D, 2L, 6L, 1M, 7M, 8M, and 4R; Schloesser et al. 2000) in western Lake Erie 1930, 1961, 1982, 1993, 2003, 2010, and 2014. Adopted (1930 and 1961) after Carr and Hiltunen 1961. For 1930, means based on unknown number of replicates (Wright 1955a, 1955b).

Taxa	1930	1961	1982	1993	2003	2010	2014
Oilgochaeta	1,379	6,102	12,354	7,593	1,452	3,129	4,153
	79%	87%	94%	90%	59%	67%	63%
Chironomidae	17	162	601	538	432	650	1,489
	1%	2%	5%	6%	18%	14%	23%
Hexagenia	162	<1	2	13	467	494	303
	9%	<1%	<1%	<1%	19%	11%	5%
Sphaeridae	149	577	241	281	41	229	234
	9%	8%	2%	3%	2%	5%	4%
Gastropoda	30	167	14	26	77	155	382
	2%	2%	<1%	<1%	3%	3%	6%
Total	1,737.0	7,008.1	13,211.4	8,451.2	2,469.7	4,656.1	6,561.1

Trend patterns of taxa densities support results of preliminary F-tests. This included all five taxonomic groups, although less abundant taxa tended to increase and decrease more than oligochaetes that occurred at relatively high densities compared to other taxa. At present, a more rigorous analysis of densities at the nine stations may add to scientific validity of productivity patterns of the total benthos, but it is unlikely to change conclusions of the present study. In addition, further scientific analysis of complete archived data, including detailed speciation and nomenclatural synonyms, for all possible sampling periods is currently being compiled. Statistical analysis that includes all possible taxonomic identifications (e.g., to species of oligochaetes and chironomids) and inclusion of more stations (1961 and 1982 = 40 stations, 1982 and 1993 = 40, 1993 and 2003 = 47, 2003 and 2010 = 31, and 2010 and 2014 = 31 stations) will undoubtedly add scientific validity.

Recent (i.e., between 1993 and 2014) increases of oligochaetes and chironomids may indicate increased nutrients and a trend toward a more eutrophic condition in western Lake Erie but there is too little data in the present study to make a confident conclusion as to the trend in trophic status of western Lake Erie. There is conflicting evidence as to the trend in trophic status of western Lake Erie over the past 25 years. In the present study, increased oligochaetes and chironomids would likely support an increased trophic trend between 1993 and 2014 (Figure 2.3). However, restoration and persistence of a key-stone indicator taxon, *Hexagenia* spp. mayflies, indicates continued mesotrophic conditions, and less eutrophic conditions than between 1930 and 1993. These mayfly populations have persisted in western Lake Erie since the early-1990s (Krieger et al., 1996; Schloesser et al., 2000). Regardless of trophic interpretation, it is certain that the benthic community changed between 1993 and when pollution-abatement programs were initiated in the 1970s and dreissenid mussels colonized substrates in the late-1980s.

Coincident with changes in the benthic fauna between 1993 and 2014 observed in the present study, there has been an invasion by dreissenid mussels that colonized and became abundant in the late-1980s. This taxa group has become a dominate key-stone species that 'engineer' many other ecosystem components in western Lake Erie since 1989 (Nalepa and Schloesser 1993, 2014). These mussels are believed to be a dominate taxa that has affected ecosystem balance in western Lake Erie for the past 25 years.

Overall, the largest changes occurred for oligochaetes and gastropods that increased between 2003 and 2014, for chironomids which increased between 2010 and 2014, and for *Hexagenia* spp. mayflies and sphaerid clams that increased between 1993 and 2003. To date, Chironomids and mayflies exhibited responses to changes in eutrophic status, and possibly to impacts of exotic dreissenid mussels (zebra and quagga mussls) of western Lake Erie between 1930 and 2014 (Figure 2.3; Table 2.8). Chironomidae, similar to Oligochaeta, increased between 1930 and 1982 and 2003 and 2014 but, unlike Oligochaeta that declined between 1982 and 2003, chironomids remained relatively stable between 1982 and 2003. Similarly, *Hexagenia* spp. mayflies responded to increase in lake trophicity between 1930 and 1961 when they disappeared, and 1993 and 2014 when they again colonized western Lake Erie.

Indicator Taxa

In the Great Lakes, use of indicator taxa and group metrics has its origins in studies of western Lake Erie conducted by Carr and Hiltunen (1961) and Hiltunen (1969). These two studies contrasted differences between benthic data collected in 1929-30 and 1961, a period marked by dramatic eutrophication and industrial pollution of western Lake Erie. Over this 30 year period, eutrophication was caused primarily by nutrient discharges from increased human population of Detroit, Michigan, and industrial pollution was caused primarily by petroleum discharges from production of war materials associated with two world-wars in the early- and mid-20th century. Hiltunen (1969) extended the work of Carr and Hiltunen (1961), and developed oligochaete-indicator taxa based on European work in which some species are 'ranked' based on tolerance to organic pollution. This resulted in long-accepted standards of taxonomic identifications and biological meaning of frequently found and abundant oligocheates, especially for western Lake Erie (Hiltunen 1969; Milbrink 1983; Reynoldson et. al., 1989; Schloesser et. al., 1995; Spencer and Hudson 2003). However, as the Great Lakes changed in response to ecosystem changes initiated by decades of pollution abatement and impacts of dreissenid mussels, there has been an increased need to evaluate and expand the knowledge of biological meaning for oligochaete taxa, such as observed in western Lake Erie (Figure 2.3).

Possible indicator taxa are assessed based on examination of specific taxa averages obtained from historical studies in 1961 (40 stations), 1982 (40 stations), 1993 (40 stations), 1993 (40 stations), 2003 (40 stations), 2010 (31 stations), and from the present study in 2014. Of the several hundred taxa identified between 1961 and 2014, only five were examined as possible indicator taxa based on changes in abundances and the presence of a trend pattern of these abundances. Although we believe these five are the most likely to show patterns in abundances (i.e., indicator taxa) examination of all taxa is recommended.

Hexagenia **spp.**

Hexagenia spp. mayflies are a relatively small component of benthic densities in western Lake Erie (Figure 2.3). However, these mayflies are large and one of the most important-indicator benthic taxa for nearshore waters in North America and Europe (Schloesser et al. 2000). In western Lake Erie, only dreissenid mussels (zebra and quagga) and unionid clams (Unionidae) are larger than *Hexagenia* spp.

After decades of documenting abundance declines and extirpation of *Hexagenia* spp. mayflies at the local and regional levels (e.g., western Lake Erie, Figure 2.4) (Britt 1955; Carr and Hiltunen 1965; Beeton 1969), use of these mayflies as an indicator taxon was suggested by Schloesser (1988). Although used outside the Great Lakes as an indicator of pollution abatement (Fremling 1964), observations of abundances of *Hexagenia* spp. over a broad geographic area of the St. Marys River by Hiltunen and Schloesser (1983)

crystalized use of this taxon to "....assess (future) pollution abatement." in the Great Lakes (Schloesser 1988). Use of *Hexagenia* spp. as a specific management goal in restoration programs specifically for western Lake Erie, and other areas of the Great Lakes, was proposed by Reynoldson et al. (1989) and later reiterated by Edsall (2001).
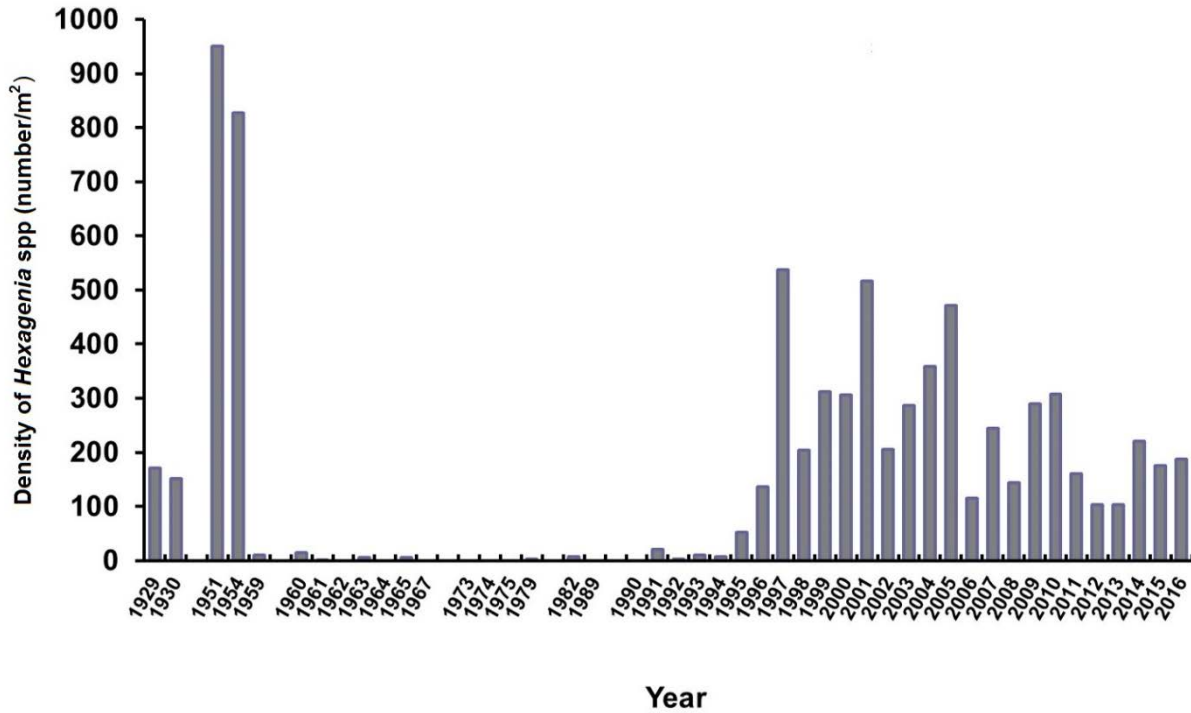

Figure 2.4. Density (number/m^2) of an indicator taxon, *Hexagenia* spp. in western Lake Erie 1929 to 2016. Historical data follows Schloesser et al. 2000) and unpublished files of the Great Lakes Science Center, Ann Arbor, Michigan.

Since the mid-1990s, the return and continued presence of *Hexagenia* spp. in western Lake Erie has been extensively documented (Figure 2.4) (Schloesser et al. 2000). This is primarily because these mayflies are easily identified and their expected return has been anticipated since initiation of pollution-abatement programs in the early-1970s (Schloesser 1988; Kolar et al. 1997). Mayflies are a measure of 'mesotrophic' conditions and their return was one of the first documented 'restoration' measures reported by management agencies around western Lake Erie (Krieger et al. 1996; Schloesser 2005; Schloesser et al. 2005; Schloesser and Krieger 2005; Schloesser and Krieger 2007; Schloesser 2008; Schloesser 2009).

Dreissena spp.

Dreissenid mussels were the most numerically abundant taxa in western Lake Erie in 2014 (Table 2.7). Collectively, zebra and quagga mussels occurred at a density of 2,959 individuals/m^2 (zebra = 784/m^2 and quagga = 2,175/m^2). However, the importance of dreissenid mussels as an indicator taxon is not known, but it is likely that because these mussels are the most abundant (density and biomass) taxa in western Lake Erie, any changes in this 'keystone' is likely to be a reflection on the productivity of the plankton on which they feed (Madenjan et al., 1998). Because these exotic mussels have changed ecosystem pathways and

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altered the physical habitat they are now believed to be a keystone species that 'engineer' other components of the ecosystem in western Lake Erie (Dobiesz and Lester 2009; Nalepa and Schloesser 2011).

Manayunkia speciosa **(filter-feeding freshwater polychaetes)**

Some evidence exists that abundances of *Manayunkia* speciosa may be an indicator species sensitive to pollution (reviewed in Schloesser 2013; Schloesser et al. 2016). In short, densities of this little studied and relatively unknown genus have not been closely associated with changes in water quality. There have been vague generalizations about the habitat preferences but consensus and data are lacking to support use as an indicator taxon. However, in western Lake Erie, declines in abundances of *Manayunkia speciosa* began before the oligochaete community and *Hexagenia* spp. mayflies indicated changes in improved water quality between 1982 and 1993 (Figures 2.3, 2.4, 2.5) (Schloesser et al. 1995). Similar to improvements of oligochaetes metrics and declines in abundances between 1982 and 1993, declines of *Manayunkia speciosa* abundances indicate a rapid and consistent decline that paralleled pollution abatement of the Detroit River (Figures 2.5 and 2.6). The consistent areal decline in *Manayunkia speciosa* near the Detroit River between 1961 and 2003 makes this taxa a logical candidate as an indicator taxa. At present, further analysis of historical data bases relative to pollution changes is needed before *Manayunkia speciosa* or its close congeners can be considered a reliable indicator taxon.
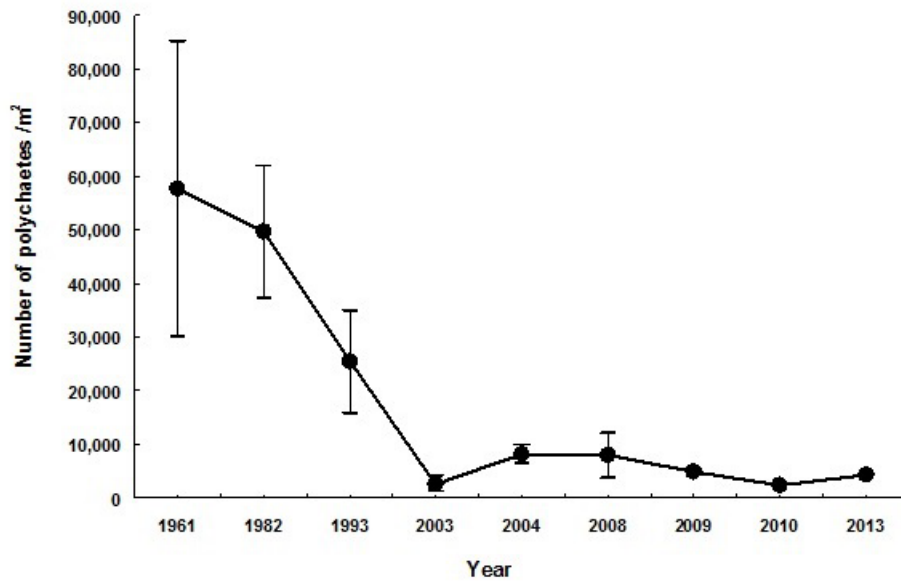

Figure 2.5. Density (number/m^2) of *Manayunkia speciosa* at one station (15D) in the lower Detroit River 1961-2013 (Schloesser et al. 2016). This taxa was not present before 1961 (Schloesser 2013). In 2014, density was similar to densities between 2009-2013 (between 4,800 and 2,355/individuals/m^2).
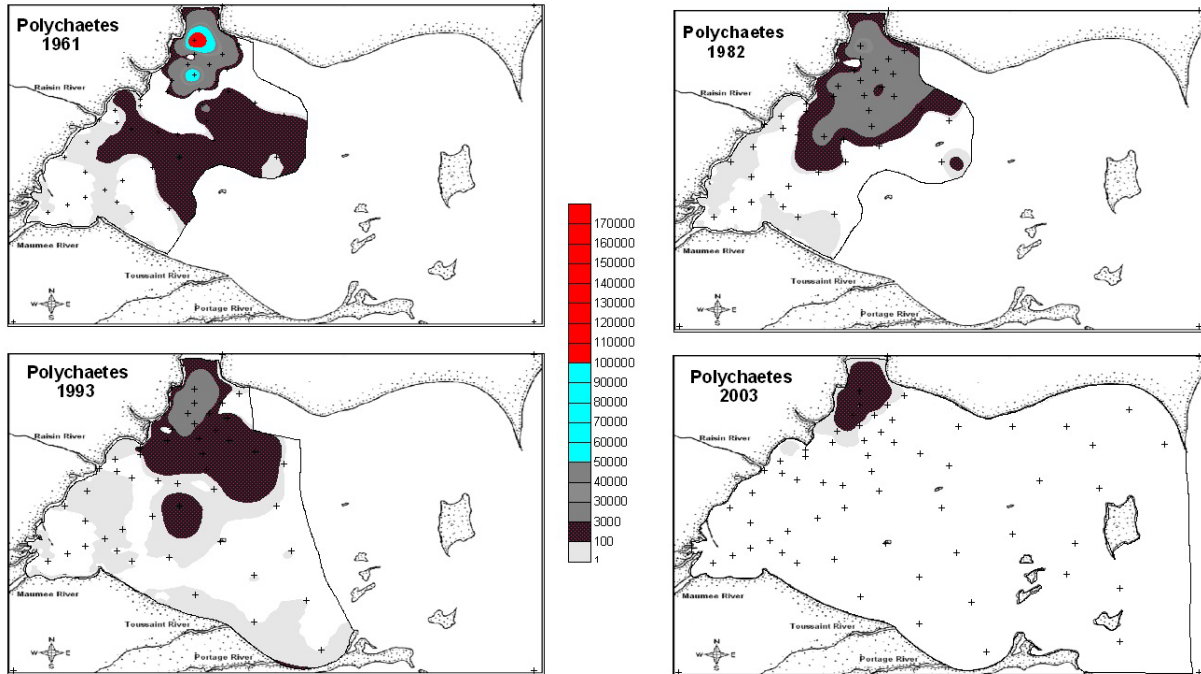
Figure 2.6. Aerial distribution and abundance of *Manayunkia speciosa* in western Lake Erie 1961, 1982, 1993, and 2003 (Schloesser 2013). This taxa was not present before 1961 (Schloesser 2013). In 2010, aerial distribution was limited to two stations (3D and 15D) near the Detroit River and one station in open waters of western Lake Erie (34C). In 2014, aerial distribution only occurred at one station (15D) near the Detroit River and one station (34C) in northeast western Lake Erie.

Oecetis spp. (predatory trichopterans)

Predatory trichopterans of the genus *Oecetis* spp. warrant special note because they increased 19-fold between 2003 ($1/m^2$) and 2010 ($19/m^2$) and 3-fold between 2010 ($19/m^2$) and 2014 ($69/m^2$) (unpublished USGS data). In addition, this taxon was found at 3 of 40 stations in 2003, 24 of 31 stations in 2010, and 31 of 31 stations in 2014. Between 1961 and 2003, densities of this taxon ranged between 1 and $8/m^2$.

In 1937, *Oecetis* spp. was one 'partner' of three benthic-community types described in western Lake Erie (Shelford and Boesel 1942). The three community types described by Shelford and Boesel (1942) were: 1) Gobiobasis-Hyropsyche, 2) Pleurocera-Lampsilis, and 3) Hexagenia-Oecetis. Of these three communities only the Hexagenia-Oecetis community was described as ..."may be regarded as permanent, stable, and probably (represents a) climax (community)..." Although we do not know accurate densities of taxa of the 1929-30 studies relative to densities of successive studies, an estimate of the Hexagenia-Oecetis ratio in 1937 was about 12/1 (LIST III, p.185 = 328 Hexagenia/27 Oecetis, Shelford and Boesel 1942). In 2014, an estimated ratio between these two taxa was 4/1 (average density = $298/m^2$ for *Hexagenia* spp. and $69/m^2$ for *Oecetis* spp.). At present, it is not known if the relative number of *Hexagenia* spp. is low or if the relative number of *Oecetis* spp. is high compared to the ratio of 1937. Further analysis is needed of 'community types' used in 1937 and how they relate to 'indicator species' used in recent decades.

Nematoda

Mention of Nematoda as a possible indicator taxon is included in the present study because of the 8- to 15-fold change in nematode densities in 2010 and 2014 from previous samplings (1961, 1982, 1993, and 2003). Between 1961 and 2003, nematode densities ranged between 133 and 400/m^2. Then in 2010 and 2014, densities increased to 1,781 and 1,656/m^2, respectively. Nematodes were widely distributed in western Lake Erie in all sampling periods between 1961 and 2014. Therefore, closer examination of geographic changes in densities and speciation nematodes relative to water-quality/restoration goals may be prudent. At present, no assessment between abundances of nematodes and lake restoration goals is possible.

SUMMARY

A total of 95 benthic taxa were identified with a total mean-station density of 9,478 individuals/m^2 at 31 stations in western Lake Erie, April 9 - May 28, 2014. This included 24 general-benthic taxa at a mean station density of 2,403/m^2, 19 mollusks at 3,336/m^2 (4 pelecypods at 3,110/m^2 and 16 gastropods at 223/m^2), 19 chironomids at 1,361/m^2, and 33 oligochaete taxa (15 tubificids at 2,209/m^2, 17 naidids at 183/m^2, and 1 enchytraeid at 1/m^2) at a mean station density of 2,393/m^2. Only 6 taxa occurred at all 31 stations including nematodes, mayflies (primarily *Hexagenia* spp.), caddisflies (primarily *Oecetis* spp.), midges (primarily *Chironomus* spp. and *Procladius* spp.), and immature tubificid worms without capilliform chaetae. Eighteen taxa were found at between 17 and 30 (55-97%) stations, 35 between 3 and 14 stations (10-45%), and 39 taxa were found at 1 or 2 stations (1-2%). Abundances of four taxa accounted for 64% (6,042/m^2) of the total mean-station density of 9,478/m^2; these taxa include the exotic quagga mussel *Dreissenia bugensis* at 2,175 individuals/m^2 (23%), nematodes at 1,656/m^2 (17%), immature tubificid oligochaetes without capilliform chaetae at 1,427/m^2 (15%), and the exotic zebra mussel *D. polymorpha* at a mean station density of 784/m^2 (8%). Twelve other taxa accounted for 26% (2,475/m^2) and the remaining 82 taxa accounted for 10% of the total mean-station density. Length-frequency distributions of dreissenid mussels, now considered to be the dominant habitat engineer in western Lake Erie, indicated the presence of two years classes of mussels (2012 and 2013 year classes).

Densities of benthic fauna, based on nine consistently-sampled stations, indicate that density fluctuated 7- to 8- fold between 1930 and 2014. Density was lowest in 1930, increased 4.0-fold between 1930 and 1961 and 1.9-fold between 1961 and 1982. Then benthos density decreased 1.6-fold between 1982 and 1993 and 3.4-fold between 1993 and 2003, then increased 1.8-fold between 2003 and 2010 and 1.4-fold between 2010 and 2014. Oligochaetes were the primary benthic fauna available for habitat evaluation. Therefore, past and future analysis of habitat quality based on benthic populations (especially oligochaetes) could greatly be improved if our understanding of indicator organisms were to improve - e.g., National Coastal Condition Assessment Great Lakes Benthic Indicator Development Workshop, 2016. Of the larger sized fauna, chironomidae and *Hexagenia* spp. were the most abundant benthic populations between 1930 and 2014.

ACKNOWLEDGEMENTS

APPENDICES

Appendix 2.1. Locations (latitude and longitude) of 31 stations sampled for benthos in western Lake Erie April 4 - May 28, 2014 (Schloesser et al. 2000).

Appendix 2.2. Individual replicate (REP 1, 2, and 3) grab counts of general benthos in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.3. Individual replicate (REP 1, 2, and 3) grab counts of mollusks in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.4. Individual replicate (REP 1, 2, and 3) grab counts of chironomids in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.5. Individual replicate (REP 1, 2, and 3) grab counts of oligochaetes in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.6. Lengths (mm) of individual zebra (Dreissena polymorpha) and quagga mussels (*Dreissena bugensis*) in individual replicate-grab samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.7. Density of five benthic taxa at nine stations in western Lake Erie 1930, 1961, 1982, 1993, 2003, 2010, and 2014. Adopted after Carr and Hiltunen (1965). For 1930, means based on unknown number of replicate samples.

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CHAPTER 3. MAJOR FINDINGS FROM THE CSMI BENTHIC MACROINVERTEBRATE SURVEY IN LAKE MICHIGAN IN 2015 WITH AN EMPHASIS ON TEMPORAL TRENDS

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INTRODUCTION

As part of the Coordinated Science and Monitoring Initiative (CSMI) in Lake Michigan in 2015, a lake-wide benthic survey was conducted to assess the status of the benthic macroinvertebrate community, with a primary focus on the invasive mussels *Dreissena rostriformis bugensis* and *Dreissena polymorpha,* and the native amphipod *Diporeia*. Similar lake wide surveys were conducted to assess the status of these three taxa beginning in 1994/1995 and repeated every five years through 2010 (Nalepa et al. 2014). Based on previous surveys, major changes in population abundances of all three taxa were observed over this 15-year period. *D. polymorpha* was first reported in Lake Michigan in 1989 (Marsden et al. 1993) and densities subsequently increased to reach a peak in 2000. Thereafter, densities declined to such an extent that by 2010 it was rarely found. Over the entire period, *D. polymorpha* was mainly found at depths < 50 m. After *D. r. bugensis* was first reported in the lake in 1997 (Nalepa et al. 2001), densities have mostly continued to increase at all depths through 2010, attaining densities that exceeded those of *D. polymorpha* even at depths < 50 m. Lastly, the amphipod *Diporeia* has been in a steady state of decline ever since *Dreissena* became established. Lower densities relative to those in pre- *Dreissena* years were first observed in the early 1990s (Nalepa et al. 1998), and declines continued at all depths from 1994/1995 through 2010. In 2010, it had mostly disappeared at depths < 50 m and had declined by 95% at > 50 m.

Both *Dreissena* and *Diporeia* play key roles in the ecosystem of Lake Michigan and the other Great Lakes. *Dreissena* has a great capacity to filter particulate material from the water column and excrete metabolic by-products (biodeposits, nutrients). As a result, *Dreissena* has dramatically restructured food webs and altered spatial patterns of energy and nutrient flow (Vanderploeg et al. 2002, Hecky et al. 2004). Specific impacts of *Dreissena* on the Lake Michigan ecosystem have been well-documented, including reduction of the spring phytoplankton bloom and alteration of benthic-pelagic processes (Fahnenstiel et al. 2010, Cuhel and Aguilar 2013, Vanderploeg et al. 2015). Before it declined, *Diporeia* was a keystone species in the offshore food web, accounting for over 70% of benthic biomass and serving as an energy-rich food source for many fish species. As a detritivore that feeds on freshly-settled material in the upper sediments, *Diporeia* was an important pathway by which energy was cycled from the benthic to the pelagic region (Nalepa 1989, Nalepa et al. 2000, 2009). The decline of *Diporeia* has led to large changes in the relative health, growth, and community structure of fish communities in the lake (Pothoven et al. 2001, Hondorp et al. 2005, Bunnell et al. 2009). Because of these key ecosystem roles and population shifts through 2010, the current status of *Dreissena* and *Diporeia* were of particular interest in 2015.

For the first time since the lake-wide surveys were initiated in 1994/1995, the entire benthic community (i.e., all benthic taxa) was examined in 2015, which allowed an assessment of other taxa besides *Dreissena* and *Diporeia*, and provided a baseline to examine future changes of the entire benthic community in Lake

Michigan. Lake-wide trends in the entire benthic community have recently been examined in Lake Huron (Nalepa et al. 2007), Lake Ontario (Birkett et al. 2015), and Lake Erie (Burlakova et al. 2014).

This report provides a summary of recent trends of *Dreissena*, *Diporeia*, and other major taxa based on results of the 2015 survey. In addition, it also gives a synopsis of other, ancillary data collected during the survey, such as length-weight relationships and size frequencies of the dreissenid population. The primary focus is to present major findings and to place these findings into a historic perspective. More detailed analyses and discussion of trends, spatial patterns, and community composition, including comparisons to lake-wide surveys in the other Great Lakes, will be provided in other publications.

METHODS

Benthic samples were collected at 140 stations in Lake Michigan, July 20-29, 2015 (Table 3.1). Of these, 135 were located in the main basin of the lake, and 5 were located in the outer portion of Green Bay (Table 3.1, Figures 3.1a, b, c). The number and location of stations have generally remained consistent since 2000. For the complete list and locations of stations sampled in all previous surveys see Nalepa et al. (2014).

Table 3.1. Location, depth, and described substrate of sites sampling in Lake Michigan in 2015. *Stations that were originally part of NOAA's benthic monitoring program in the southern basin in the 1990s (Nalepa et al. 1998). See text for details.

Region/Station	Depth	Latitude	Longitude	Substrate
South				
A-1*	17.3	42°06.5530	086°31.9709	sand
A-2*	29.9	42°06.0153	086°36.9776	silt and clay
A-4	72.4	42°03.4904	087°06.5073	100% mud
B-2*	49.6	42°23.9931	086°27.0413	100% mud
B-3*	62.0	42°23.9757	086°35.4838	100% mud
B-4*	126.0	42°23.5103	087°00.9441	silty clay
B-5*	102.7	42°22.5024	087°20.9581	silt and clay
B-6*	82.4	42°22.5274	087°29.9469	silt
B-7*	43.7	42°21.9742	087°39.9606	silty sand
C-1*	17.7	42°49.6624	086°14.8867	sand
C-2	45.0	42°49.6581	086°18.1607	silt, clay
C-3*	77.3	42°49.1494	086°28.4125	silt
C-45	45.2	42°09.5638	087°30.1969	silty sand
C-5*	129.0	42°48.9918	086°49.9923	silty clay
C-6*	98	42°47.6759	087°26.7942	95% silt over loam, 5% sand
C-7*	58.5	42°47.5263	087°34.4815	90% sand, 10% mud
EG-12*	54.0	42°20.8597	087°36.9207	sandy silt
EG-14*	93.3	42°22.6546	086°46.4204	100% silt
EG-18*	55.3	42°17.6162	086°38.5844	100% silt
EG-22*	46.4	43°06.1985	086°21.9813	silt
F-2	44.3	42°30.0489	086°21.8592	100% mud

Region/Station	Depth	Latitude	Longitude	Substrate
F-3	71.6	42°30.1042	086°31.4951	silty mud
G-45	43.3	41°56.9564	087°13.4598	variable, mostly sand, some gravel & mud
H-8*	17.8	42°23.9597	087°46.2676	silt over loam, no *Dreissena*
H-9*	39.8	42°26.7390	087°42.3416	80% silt, some loam and sand
H-11*	69.9	42°33.2505	087°35.8191	80% silt, 20% sand
H-13*	17.9	41°55.5694	087°29.4711	90% sand, 10% shells
H-14*	34.9	42°04.3359	087°27.2110	sand
H-15*	56.2	42°09.5212	087°26.0221	silty sand
H-18*	19.8	41°58.9774	086°36.0354	silty sand
H-19*	34.8	42°00.0033	086°41.0855	silty ooze
H-20*	53.6	42°00.8410	086°45.1599	silty mud, ooze
H-21*	72.0	42°02.4175	086°53.0036	silty fine sediment, ooze like
H-22*	51.3	42°08.3490	086°39.8233	silt, soft
H-24*	19.0	42°23.2856	086°20.0614	100% sand
H-28*	22.3	42°37.7982	086°15.9440	100% sand
H-29*	37.1	42°37.8117	086°18.3111	silty sand
H-30*	73.5	42°37.8048	086°25.9938	black silt
H-31*	43.0	43°02.4984	086°19.9544	silty clay
M-25	26.0	43°12.0097	086°22.6710	sand
M-45	42.5	43°11.4208	086°25.7241	50% sand, 50% mud
N-2	37.0	41°53.5031	086°52.0062	silt
N-3	60.1	41°57.9916	086°59.0004	silt
Q-13	14.2	42°50.6140	087°47.9134	sand
Q-30	31.0	42°50.5888	087°39.2398	90% clay, 10% sand
R-20	22.4	42°45.0562	087°41.7560	100% sand
R-45	47.3	42°45.0205	087°36.3117	90% sand, rest dressenid shells
S-2*	10.3	41°45.9239	087°23.4838	100% fine sand
S-3*	26.5	41°50.9822	087°19.2111	90% fine sand, 10% siltS
S-4*	40.2	41°56.0843	087°15.1277	sand and gravel
SAU-45	43.5	42°41.1347	086°18.8971	silty ooze
T-3	71.6	42°10.0378	086°43.0227	silt, some sand
V-1*	17.5	41°41.7981	087°00.7974	variable, clay, sandy silt
V-2*	28.4	41°48.9911	087°02.9051	thick silt
X-1*	35.6	43°08.2531	086°21.6891	variable, silt/clay, some sand
X-2*	100.6	43°11.9988	086°31.0275	85% silt, 15% sand
Central				
E-1	44.9	44°37.5016	086°18.2152	85% sand, 15% mud
K-2	46.8	43°20.2260	086°30.0222	80% mud, 20% sand
KE-1	22.4	44°23.3271	087°27.6720	80% sand, 10% silt, 10% dreissenid shells
KE-2	31.7	44°23.3271	087°27.6720	Variable, mostly sand, some silt

Region/Station	Depth	Latitude	Longitude	Substrate
KE-3	48.1	44°23.3037	087°26.2201	80% sand, 20% silt
KE-5	78.5	44°23.3123	087°24.0022	50% sand, 50% silt
L-220	21.2	43°30.0506	086°30.1907	sand
L-230	33.4	43°30.0446	086°31.1570	50% mud, 50% sand
L-245	44.0	43°30.0491	086°31.8934	85% mud, 15% sand
L-260	60.4	43°30.0629	086°33.3126	100% dark mud
L-280	80.5	43°30.0621	086°36.1907	100% dark mud
LU-1	22.0	43°56.6498	086°32.1102	sand
LU-3	44.0	43°56.6455	086°36.4846	silty sand
LU-4	62.5	43°56.6250	086°37.6144	silty sand
LU-5	78.0	43°56.6410	086°39.0196	70% silt, 30% sand
MAN-1	20.9	44°24.7956	086°16.8948	100% sand
MAN-2	35.9	44°24.7813	086°17.1189	80% mud, 20% sand
MAN-3	44.8	44°24.7729	086°19.8942	silty clay, sand
MAN-4	58.6	44°24.8098	086°20.3585	silty sand, clay
MAN-5	74.0	44°24.7721	086°20.8248	sandy silt, clay
PW-2	32.0	43°26.8258	087°46.9135	80% silt, 20% fine sand
PW-3	44.9	43°26.8217	087°46.1627	80% silt, 20% fine sand
PW-4	59.5	43°26.8348	087°43.9985	silty clay, sand
PW-5	79.0	43°26.8325	087°41.8609	silty clay, sand
SY-1	22.5	43°55.0747	087°39.8279	silty sand
SY-2	31.0	43°55.0780	087°38.8513	silt
SY-4	59.0	43°55.0786	087°30.2854	sand
SY-5	77.0	43°55.1038	087°22.5379	85% sand, 15% silt
9552	83.3	43°11.1025	087°12.5799	mud over loam
9554	109.0	43°14.2628	086°53.1725	100% mud
9556	72.9	43°18.3335	087°46.3070	silty sand
9561	130.0	43°28.2513	086°47.0433	100% mud
9562	123.0	43°29.9922	087°37.0272	silt
9564	133.0	43°36.0367	087°20.4315	silty clay
9570	165.0	43°53.1746	086°54.4904	silty mud
9574	139.0	44°04.1020	087°08.8314	tin layer mud over loam
9576	164.0	44°09.0855	086°37.2796	70% silt , 30% clay
9577	78.1	44°14.6051	087°22.4592	silty sand
9582	120.0	44°24.5028	086°22.1030	silt, detritus
9587	196.0	44°37.2816	086°21.1621	100% mud
78110	33.0	43°56.6170	086°34.7150	sand, some silt
82882	58.6	44°23.3560	087°25.3558	89% fine sand, 20% silt
82902	40.0	43 55.0900	087 37.4400	silt, fine sand
82922	17.7	43°26.8127	087°47.7663	50% fine sand, 50% silt

Region/Station	Depth	Latitude	Longitude	Substrate
North				
EA-7	40.0	45°16.8126	085°26.1806	silty, clay, sand
FR-1	20.0	44°48.9956	086°08.3822	mostly *Dreissena* druses, some sand
FR-2	32.0	44°49.0038	086°09.3452	sand
FR-3	44.0	44°49.0065	086°10.1009	mostly silt, some sand
FR-4	56.4	44°48.9911	086°11.1107	60% silt, 40% sand
FR-5	78.8	44°48.9811	086°11.7992	70% mud, 30% sand
PET-2	38.5	45°26.7409	085°04.5516	silty sand
PET-3	39.0	45°26.7319	085°11.1409	silt, clay, sand
SB-2	35.0	44°51.7024	087°09.7100	sand
SB-3	47.6	44°51.4571	087°09.0359	sand, some clay
SB-4	60.0	44°51.4272	087°08.1949	70% sand, 30% silt
SB-5	79.9	44°51.4479	087°05.1681	silt, mud
SB-6	154.0	44°51.4508	086°55.3928	80% clay, 20% silt
SC-2	29.0	45°50.4724	086°06.3233	coarse sand
SC-3	43.5	45°49.0404	086°06.3392	silt, dreissenid shells
SC-4	60.0	45°47.3931	086°06.3204	silt
SC-5	83.0	45°45.3760	086°06.3413	silty ooze
WI-1	17.4	45°14.8408	086°54.2876	sand
WI-2	31.3	45°14.8303	086°52.5656	sand
WI-3	45.4	45°14.8570	086°49.8001	sand
WI-5	85.0	45°14.8361	086°38.2513	60% silt, 40% sand
9597	162.0	44°58.3213	086°22.1965	silt with clay
74880	24.0	45°54.5117	085°01.4952	90% mud, 10% fine sand
74900	54.3	45°26.7280	085°13.2994	silty sand, some clay
76442	19.3	46°00.0540	085°24.5721	dark silt
76462	64.0	45°32.0863	085°38.1520	variable, mostly silt, some and rock
76471	31.5	45°14.5004	085°33.3449	silty sand
76482	28.6	45°04.1289	085°51.4266	sand
78030	33.5	45°48.7051	085°43.0632	70% silt, 30% sand
79612	20.5	45°54.0042	086°06.3019	coarse sand
81220	37.0	45°42.6096	086°24.5279	sand
81240	56.0	45°14.8459	086°40.1503	60% sand, 40% silt
82851	80.0	45°03.0013	086°55.3601	60% clay, 40% silt
82862	13.3	44°51.4530	087°11.3734	sand
95120	134.0	44°58.3213	086°22.1965	silt
Green Bay				
BBN-1	11.8	45°41.9760	086°44.5177	rock and sand
BBN-2	25.0	45°37.2398	086°44.5132	silt
BBN-3	28.6	45°32.5008	086°44.5119	silt, alga present

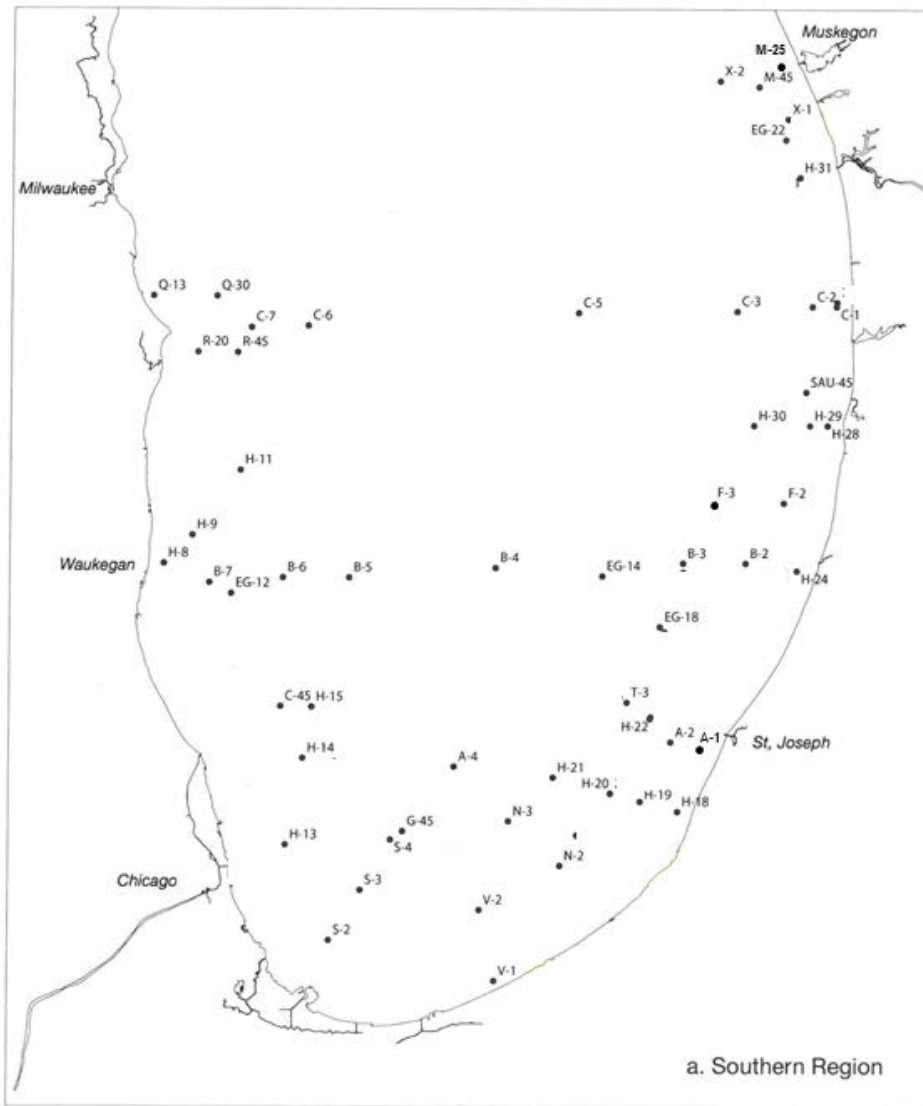| Region/Station	Depth	Latitude	Longitude	Substrate
LBDN-3	23.3	45°30.0167	087°05.7984	90% sand, 10% silt
84450	10.2	45°36.1817	087°05.7656	sand

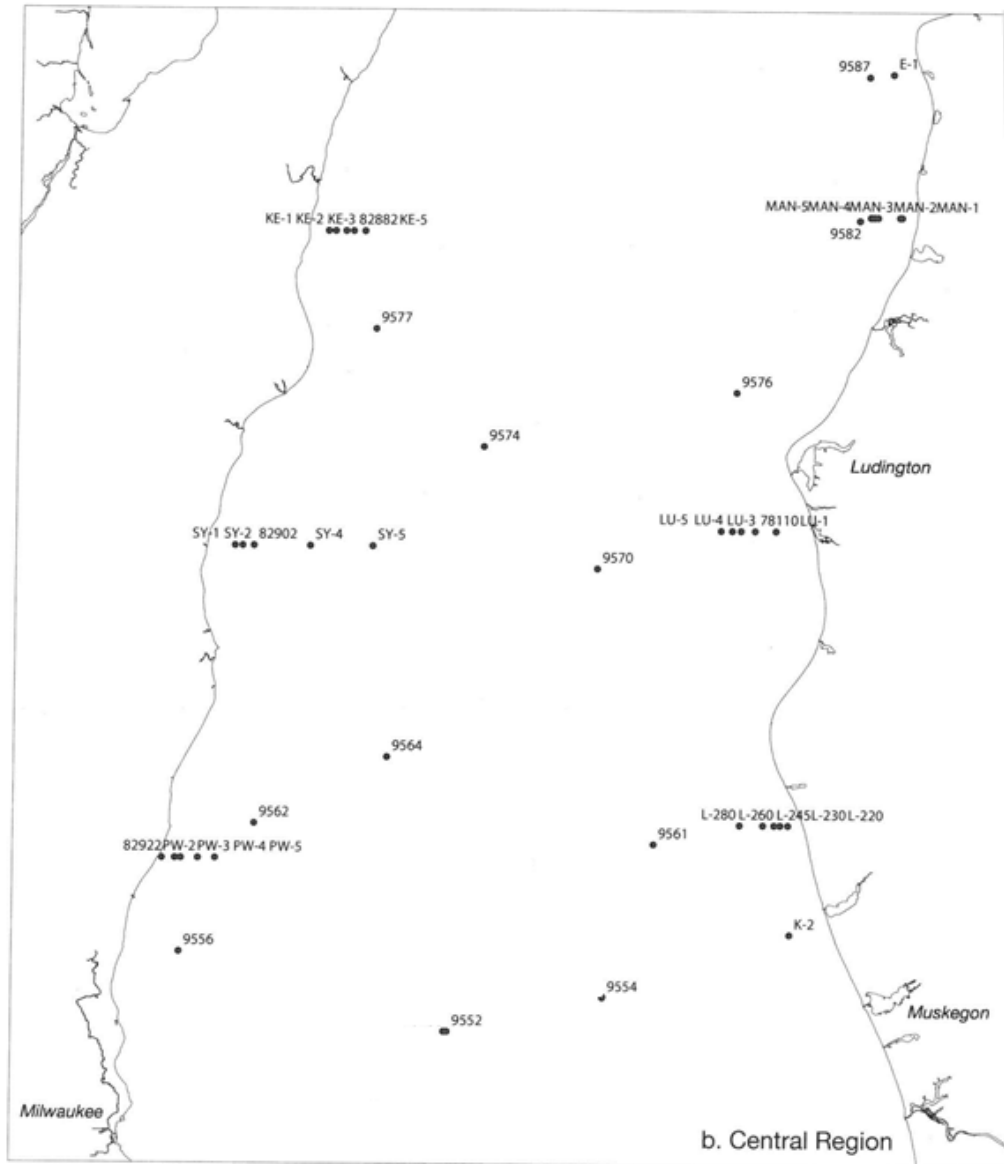**Figure 3.1a.** Location of sampling sites in the southern region of Lake Michigan in 2015.

Figure 3.1b. Location of sampling sites in the central region of Lake Michigan in 2015.
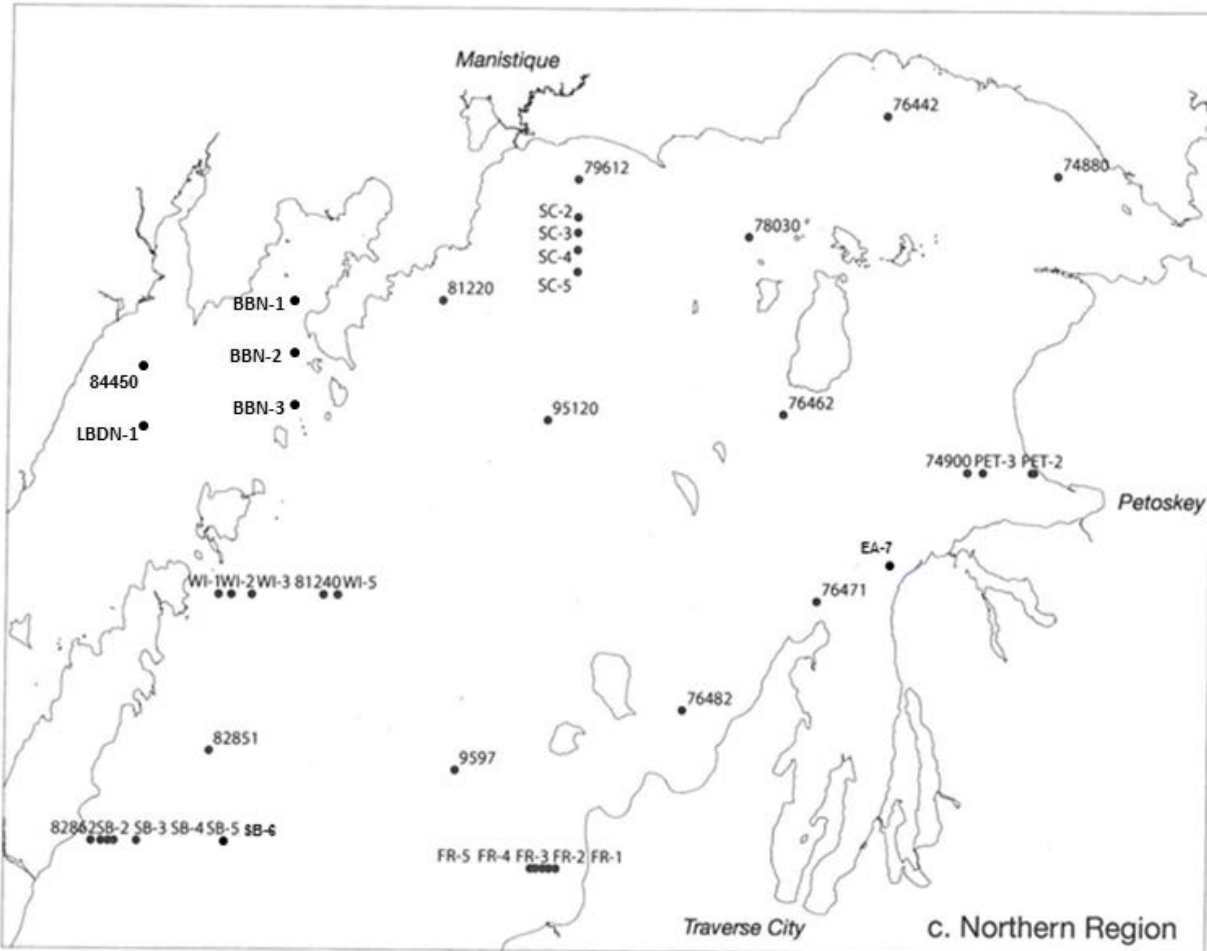
Figure 3.1c. Location of sampling sites in the northern region of Lake Michigan in 2015.

Sampling procedures in 2015 were the same as in previous surveys. In brief, benthic samples were taken in triplicate at each site with a Ponar grab (area in 2015 = 0.048 m^2). Collected material was washed through an elutriation device fitted with a 0.5-mm mesh net, and retained residue was preserved in 5-10% buffered formalin containing rose bengal stain. Sample jars were labeled with the station designation, replicate number, and date. Sampling depth and a general description of the sediments at each station were recorded (Table 3.1).

As noted, only *Dreissena* and *Diporeia* were counted and identified in surveys prior to 2015, whereas all organisms were counted and identified in 2015. Details of laboratory procedures and protocols will not be provided here. Procedures prior to 2015 are given in Nalepa et al. (2014). Procedures in 2015 followed those in the EPA Standard Operating Procedure (SOP) LG407 "Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis" (Revision 09, April 2015) as given in: https://www.epa.gov/sites/production/files/2017-01/documents/sop-for-benthic-invertebrate-lab-analysis-201504-13pp.pdf

Methods to determine densities were straight-forward and similar across all survey years. All organisms were picked and counted under low magnification, with dreissenids proportionally split when numbers were

high. In 2015, biomass of *Dreissena* was determined as both ash-free dry weight (AFDW, soft tissue) and total wet weight (TWW, shell included). Surveys prior to 2015 reported dreissenid biomass as AFDW, which was calculated by first determining relationships between AFDW and shell length, and then applying these relationships to size frequencies (Nalepa et al. 2014). As given in EPA's SOP, dreissenid biomass is determined as TWW, which is determined directly by blotting dry all dreissenids in a sample and then weighing. For consistency, dreissenid biomass was determined by both methods in 2015.

Length-weight relationships were derived from individuals freshly-collected with a Ponar grab from 22 sites during the 2015 survey (Table 3.2). While priority was given to sites where individuals for length-weight relationships were collected in 2010, the ultimate criteria for site selection depended on the number of mussels found at the time of sampling, and by a visual estimate of the size range (shell lengths) of the population. For the latter, a broad size range of individuals was a requirement (10 mm to > 20 mm) so that a representative relationship could be obtained. Also, an effort was made to collect at sites located throughout the lake and at various depths. Immediately after collection of mussels, soft tissues of about 25 individuals between 10 mm and > 20 mm were removed from the shells, placed individually into pre-weighed aluminum planchets, and dried at 60 C° for at least 48 h. After drying, the planchets were placed and kept in a dessicator. Upon completion of the survey cruise and return to the laboratory, soft tissues were weighed, ashed at 550 C° for 1 h, and then re-weighed. AFDW was then calculated as the difference between dry weight and post-ashed weight. Corresponding shell lengths were measured to the nearest 0.5 mm. Overall, a total of 569 individuals from the 22 sites were weighed and measured (Table 3.3). All individuals for length-weight determinations were *D. r. bugensis* since *D. polymorpha* was not found. Measured AFDWs and shell lengths (SL) were used to develop length-weight relationships according to the allometric equation: $\log_e$AFDW (mg) = b + a*$\log_e$SL (mm). Relationships were developed for pooled sites within four different depth intervals: $\leq$ 30 m, 31-50 m, 51-90 m, and > 90 m (Table 3.3, also see below). For size frequencies, shell lengths of all mussels in each replicate sample were measured and then binned into 1-mm size categories. In prior surveys, individuals < 5 mm were not individually measured and were therefore binned into one category (0-5 mm). In 2015, these small individuals were measured and binned into 1-mm size categories. Further, mussels < 1 mm were not included in biomass calculations.

Table 3.2. Sites where additional *Dreissena* was collected for determination of length-weight relationships in 2010 and 2015.

Depth Interval	Year	Stations
$\leq$ 30 m	2010	H-18, MAN-2, PW-2, SB-2, SC-2
	2015	FR-1, H-28, M-25
31-50 m	2010	B-7, H-19, MAN-3, PW-3, SB-3, SC-3
	2015	82902, B-2, B-7, FR-3, LU-3, M-45,SB-3, SC-3
51-90 m	2010	EG-12, H-20, H-21, MAN-4, MAN-5, PW-4, PW-5, SB-4, SB-5, SC-4, SC-5, 82851
	2015	FR-5, H-21, LU-5, SB-5, SC-5, SY-5
> 90 m	2010	9582
	2015	9561, 9582, B-5, EG-14, X-2

Table 3.3. Relationship between shell length (SL in mm) and tissue ash-free dry weight (AFDW in mg) for *D. polymorpha* and *D. r. bugensis* at various depth intervals in Lake Michigan in 2004, 2008, 2010, and 2015. Regression constants (a, b) derived from the linear regression: $Log_e AFDW = a + b*Log_e SL$; n = total number of mussels used to derive the relationship. Also given is the AFDW of a standard 15-mm individual as derived from the given regression. Regressions in 2004 and 2008 were from Nalepa et al. (2010), and regressions in 2010 were from Nalepa et al. (2014). [#]AFDWs in 2010 were likely underestimated by 15 % (Nalepa et al. 2014).

Year/Depth Interval (m)	No. of Stations	Species	a	b	n	R^2	15 mm
2004							
≤ 30	2	*D. polymorpha*	-5.256	2.672	242	0.76	7.24
31-50	2	*D. polymorpha*	-5.255	2.652	242	0.80	6.87
≤ 30	2	*D. r. bugensis*	-6.095	2.968	244	0.85	6.98
31-50	2	*D. r. bugensis*	-6.969	3.316	247	0.90	7.47
2008							
≤ 30	1	*D. r. bugensis*	-6.299	3.193	199	0.92	10.46
31-50	1	*D. r. bugensis*	-5.469	2.659	193	0.93	5.65
2010[#]							
≤ 30	5	*D. r. bugensis*	-5.857	2.814	122	0.63	5.83 (6.70)
31-50	6	*D. r. bugensis*	-5.528	2.617	172	0.85	4.75 (5.46)
51-90	12	*D. r. bugensis*	-5.601	2.683	269	0.87	5.28 (6.07)
> 90	1	*D. r. bugensis*	-5.993	2.854	24	0.98	5.67 (6.52)
2015							
≤ 30	3	*D. r. bugensis*	-5.608	2.879	77	0.92	8.92
31-50	8	*D. r. bugensis*	-5.793	2.746	211	0.88	5.17
51-90	6	*D. r. bugensis*	-5.392	2.639	153	0.91	5.78
> 90	5	*D. r. bugensis*	-5.259	2.656	128	0.85	6.91

To determine AFDW biomass, the number of individuals in each size category was multiplied by the AFDW of an individual in that category as derived from the length-weight regression (calculated from the mid-shell length of that category). All size-category weights were then summed.

For analysis of trends, sites in the main lake were divided into the same four depth intervals as in previous surveys: ≤ 30 m, 31-50 m, 51-90 m, and > 90 m. These intervals define distinct physical habitats that result in distinguishable benthic communities (Alley and Mozley 1975, Nalepa 1989). Because physicochemical conditions in Green Bay are so different than in the main lake, results for the 5 sites located in the bay are given separately. All values were log_e +1 transformed before any statistical tests.

RESULTS AND DISCUSSION

The 2015 survey extended the assessment of lake-wide trends in *D. polymorpha*, *D. r. bugensis*, and *Diporeia* that were previously defined between 1994/1995 and 2010 (Nalepa et al. 2014). For *D.*

polymorpha, no individuals were found in any of the samples collected in 2015 (Table 3.4, Figure 3.2). This species peaked in 2000 at depths < 50 m and has steadily declined since. Only a few individuals were found at just one station in 2010, thus it is not surprising that no individuals were collected in 2015. The decline of *D. polymorpha* coincided with the rapid expansion of *D. r. bugensis* between 2000 and 2005 (Figure 3.3). Both species are filter-feeders and compete for the same food resources. Because *D. r. bugensis* has a lower respiration rate and a higher assimilation rate than *D. polymorpha* (Baldwin et al. 2002, Stoeckmann 2003), it is more efficient in allocating resources to growth and reproduction and thus has a competitive advantage when available food resources are limited. Further, *D. r. bugensis* has a lower temperature threshold of reproduction compared to *D. polymorpha* and therefore is able to colonize to deeper depths (Karatayev et al. 2015).

Table 3.4. Mean (± SE) density (no./ m^2) of *Diporeia, Dreissena polymorpha*, and *Dreissena r. bugensis* at four depth intervals ($\leq$ 30 m, 31-50 m, 51-90 m, and > 90 m) in each survey year. n = number of stations sampled. t-tests were used to determine differences between 2010 and 2015: * significant at P < 0.05, ** significant at P < 0.01. Note: Values for 2010 are slightly different than values given in Table 5 of Nalepa et al. (2014) as some stations in Table 5 were placed into the wrong depth interval.

Depth Interval/Taxa	Year				
	1994-95	2000	2005	2010	2015
$\leq$ 30 m	n = 16	n = 38	n = 41	n = 38	n = 29[1]
Diporeia	3,907 ± 1,005	853 ± 315	104 ± 88	1 ± 1	0 ± 0
D. polymorpha	730 ± 509	2,113 ± 539	258 ± 86	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	51 ± 26	7,547 ± 1,566	9,254 ± 1,689	2,052 ± 697**
31-50 m	n = 11	n = 36	n = 36	n = 41	n = 46[2]
Diporeia	6,111 ± 1,377	2,116 ± 563	24 ± 16	<1 ± <1	0 ± 0
D. polymorpha	252 ± 239	1,021 ± 511	427 ± 109	1 ± 1	0 ± 0
D. r. bugensis	0 ± 0	11 ± 9	15,838 ± 2,860	13,133 ± 1,086	5,800 ± 640**
51-90 m	n = 32	n = 41	n = 41	n = 39	n = 42[3]
Diporeia	6,521 ± 562	3,469 ± 464	548 ± 131	103 ± 51	1 ± <1
D. polymorpha	< 1 ± <1	16 ± 8	38 ± 29	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	6,472 ± 1,704	14,846 ± 1,335	8,955 ± 762*
>90 m	n = 25	n = 13	n = 13	n = 19	n = 18
Diporeia	4,547 ± 385	2,804 ± 453	1,244 ± 217	406 ± 117	528 ± 186
D. polymorpha	0 ± 0	0 ± 0	<1 ± <1	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	12 ± 7	2,037 ± 872	2,797 ± 824

Depth Interval/Taxa	Year				
	1994-95	2000	2005	2010	2015
Green Bay ($\leq$ 30 m)				n = 6	n = 5
Diporeia		26 ± 25	0 ± 0	0 ± 0	0 ± 0
D. polymorpha		820 ± 444	80 ± 53	0 ± 0	0 ± 0
D. r. bugensis		1 ± 1	$6,640 \pm 3,637$	$5,990 \pm 2,140$	$3,797 \pm 1,270$

[1]n=26 for *Diporeia*
[2]n=38 for *Diporeia*
[3]n=37 for *Diporeia*
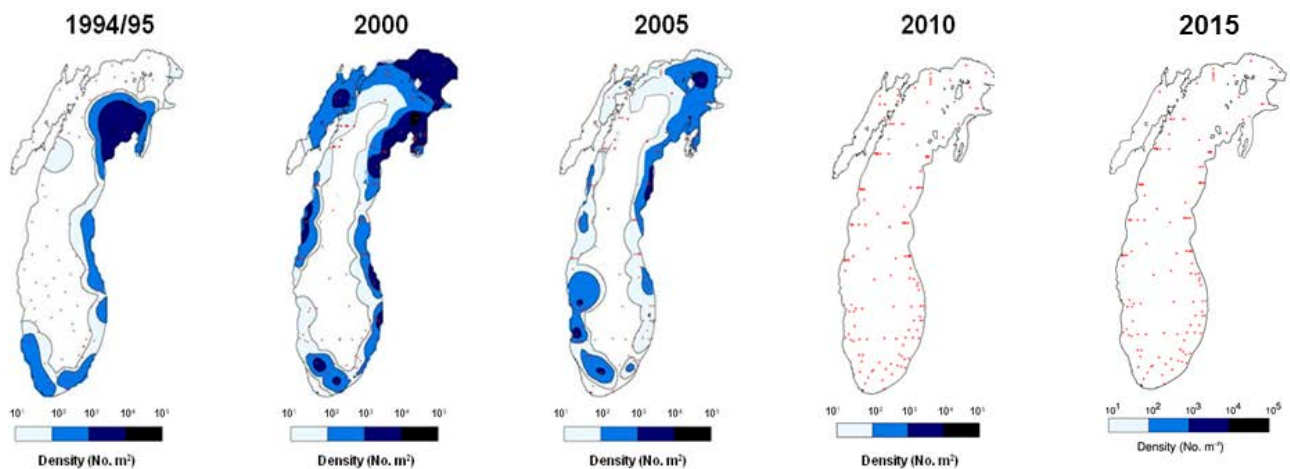
Figure 3.2. Density (no. per m^2) of *Dreissena polymorpha* in Lake Michigan based on lake-wide surveys in 1994/1995, 2000, 2005, 2010, and 2015. Small red dots indicate location of sampling sites.

For *D. r. bugensis,* some important temporal patterns emerged in 2015 that perhaps signaled a shift in population dynamics. Most notably, when compared to densities in 2010, densities in 2015 declined at all depth intervals except at the deepest (> 90 m) (Table 3.4, Fig. 3.3). In prior surveys through 2010, densities of *D. r. bugensis* have generally increased at all depth intervals. The exception was at the 31-50 m interval where densities peaked in 2005 and have declined since (Table 3.4). In 2015, mean densities declined by 79%, 56%, and 40% at the $\leq$ 30 m, 31-50 m, 51-90 m depth intervals, respectively. These declines were significant for each interval (P < 0.05, t-test). With these declines, densities of *D. r. bugensis* have seemingly peaked at depths < 90 m. The only depth interval where densities of *D. r. bugensis* were not lower in 2015 compared to 2010 was > 90 m. Mean density at this interval increased from 2,037/m^2 to 2,797/m^2; this difference, however, was not significant (P > 0.05).
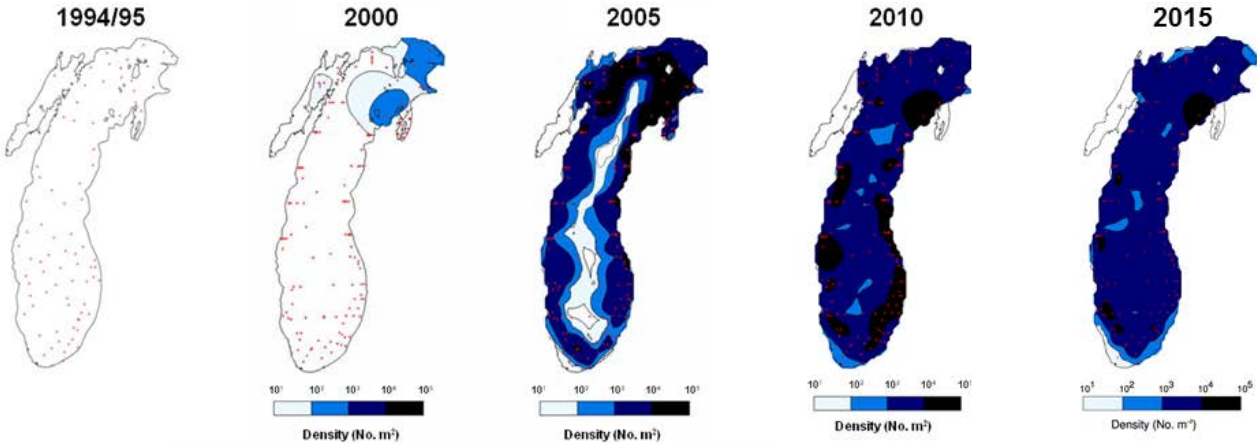
Figure 3.3. Density (no. per m²) of *Dreissena r. bugensis* in Lake Michigan based on lake-wide surveys in 1994/1995, 2000, 2005, 2010, and 2015. Small red dots indicate location of sampling sites.

It is worth noting that the number of sites at $\leq$ 30 m was far lower in 2015 than in 2010 (n = 29 and 38, respectively; see Table 3.4). Many sites are located around 30 m, and in 2015 some sites were recorded as a few meters deeper than in 2010, placing them into the 31-50 m interval. Also, two sites in the $\leq$ 30 m interval were not sampled in 2015 but were sampled in 2010. To be certain that declines in *D. r. bugensis* in 2015 at the < 30 m and 31-50 m intervals were not a result of sites changing depth categories, means were again determined after placing these sites into the same category as in 2010. Mean densities in 2015 thus determined were 2,780 ± 661/m² for $\leq$ 30 m (n=36) and 5,817 ± 707/m² for 31-50 m (n=41). Both densities were still significantly lower than in 2010.

Trends in dreissenid AFDW biomass were similar to trends in density at $\leq$ 30 m and > 90 m. That is, mean biomass in 2015 declined at the former interval and increased at the latter interval when compared to 2010 (Figure 3.4), and these year-to year differences were significant at both depth intervals (P < 0.05). Mean biomass at 31-50 m and 51-90 m did not decline like density (Figure 3.4), and differences between 2010 and 2015 were not significant (P > 0.05). Considering biomass on a lake-wide basis, the mean, depth-weighted biomass for *Dreissena* in 2000, 2005, 2010, and 2015 was 0.30 g/m², 8.9 g/m², 13.7 g/m², and 16.5 g/m², respectively. Thus, total depth-weighted biomass was greater in 2015 than in 2010, which can mainly be attributed to increased biomass at > 90 m, a depth interval that comprises 41.5% of the main-lake area.
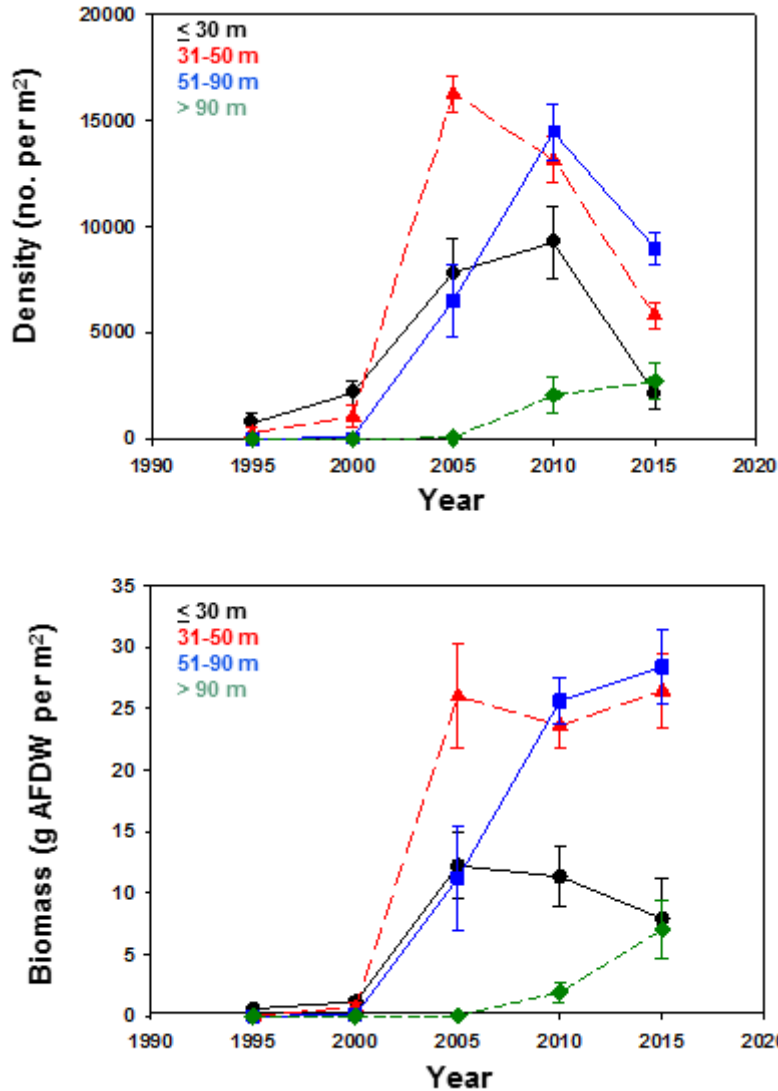
Figure 3.4. Long-term trends of total *Dreissena* in Lake Michigan in 1994/1995, 2000, 2005, 2010, and 2015. Values given are lake-wide means (± SE) at four depth intervals: ≤ 30 m (black, circles), 31-50 m (red, triangles), 51-90 m (blue, squares), and > 90 m (green, diamonds). Upper panel = density; lower panel = biomass.

The divergence of trends in dreissenid density and AFDW biomass at the 31-50 and 51-90 m intervals between 2010 and 2015 can either be attributed to differences in length-weight, or to differences in size frequencies (or to both). With a decline in density in 2015, weight per unit shell length (AFDW/SL) must have increased, or the average size of individuals in the population must have increased. To assess differences in AFDW/SL, the AFDW of a standard 15-mm mussel was calculated and compared between the two years based on regressions given in Table 3.3. AFDW of a 15-mm mussel at 31-50 m was 5.46 mg and 5.17 mg in 2010 and 2015, respectively, and AFDW at 51-90 m was 6.07 mg and 5.78 mg. Thus, AFDW/SL at both intervals was lower in 2015 than in 2010, and hence cannot account for mean biomass being higher in 2015. Size frequencies in the two years were examined by placing individuals into 5-mm size categories and then determining the proportion of all mussels in each category for each depth interval. At both the 31-50 m and 51-90 m intervals, the proportion of the population < 10 mm decreased, while the

proportion > 10 mm increased in 2015 compared to 2010 (Table 3.5). Individuals > 10 mm increased from 30.4% to 58.4% at 31-50 m, and increased from 27.9% to 40.3% at 51-90 m. These increases in the proportion of larger-sized individuals in 2015 compared to 2010 appear to be the likely reason for biomass not declining despite significant declines in density. Since tissue weight increases exponentially with shell size, even a modest increase in the proportion of larger individuals greatly affects biomass. For the other two intervals, the proportion of individuals > 10 mm declined at ≤ 30 m (37.1% to 30.2%), but increased at > 90 m (26.5% to 45.6%). Increased biomass at > 90 m in 2015 relative to 2010 can thus be attributed to not only an increase in density in 2015, but also to a greater proportion of larger individuals. An increase in AFDW/SL may also have played a role (see below).

Table 3.5. Percentage of measured *D. r. bugensis* within various size categories at four depth intervals (≤ 30 m, 31-50 m, 51-90 m, and > 90 m) in 2010 and 2015. Categories based on shell length (mm). All collected mussels were measured in 2015. In 2010, mussels were measured from representative sites (details for 2010 are given in Nalepa et al. 2014).

Interval/Year	Shell Length (mm)						
	< 5	5-10	10-15	15-20	20-25	25-30	> 30
≤ 30 m							
2010	62.0	19.4	12.4	5.1	1.0	<0.1	0.0
2015	69.7	6.7	6.3	10.2	5.6	0.8	<0.1
31-50 m							
2010	41.1	29.6	16.8	8.9	3.3	0.3	<0.1
2015	21.1	21.1	24.8	21.3	9.8	1.7	0.2
51-90 m							
2010	55.1	17.0	17.2	8.5	1.9	0.2	<0.1
2015	38.6	21.6	18.7	15.5	4.9	0.7	<0.1
> 90 m							
2010	73.5	13.9	7.7	4.5	0.3	<0.1	0.0
2015	54.4	21.1	12.2	7.9	3.8	0.7	<0.1

Besides using length-weight relationships to determine dreissenid biomass, these relationships are also useful to assess the relative health of the population. For *Dreissena*, the amount of tissue per unit shell length is directly related to food availability (Walz 1978, Sprung and Borchering 1991, Nalepa et al. 1995). This relationship holds true for molluscs in general (Russell-Hunter 1985). Given this, a lower AFDW/SL over time would indicate that tissue loss or tissue "degrowth" has occurred, a sign that individuals are catabolizing soft tissue while under nutritional stress. Ultimately, lower tissue weight can hinder survival (Karatayev et al. 2010) and lead to lower reproduction (Bielefeld 1991, Sprung 1995). Temporal trends in AFDW/SL can thus be a broader indicator of future population growth. As noted, the AFDW of a standard 15-mm mussel was lower in 2015 than in 2010 at 31-50 m and 51-90 m. To further explore trends at all depth intervals, AFDW of a standard 15-mm mussel was determined from regressions for *D. r. bugensis* in Lake Michigan going back to 2004 (see Table 3.3). Trends varied widely between the depth intervals (Figure 3.5). AFDW of a 15-mm mussel was consistently greatest at the ≤ 30 m interval over the 11-year

period, but because of great variation between years a clear temporal trend was not readily discernable. On the other hand, the most defined temporal trend occurred at 31-50 m. At this interval, the AFDW of a 15-mm mussel steadily declined between 2004 and 2015; by 2015 it was 30.8% lower than in 2004. For the two deeper intervals, 51-90 m and > 90 m, regressions were only available in 2010 and 2015. At the 51-90 m interval, the AFDW of a 15-mm mussel declined by 4.8% over the 5-year period, while at the > 90 m interval it increased 6.0%. Based on these trends, and the fact that relative values in 2015 were lowest at 31-50 m and 51-90 m, it appears that *D. r. bugensis* populations at these two intervals may be under nutritional stress.
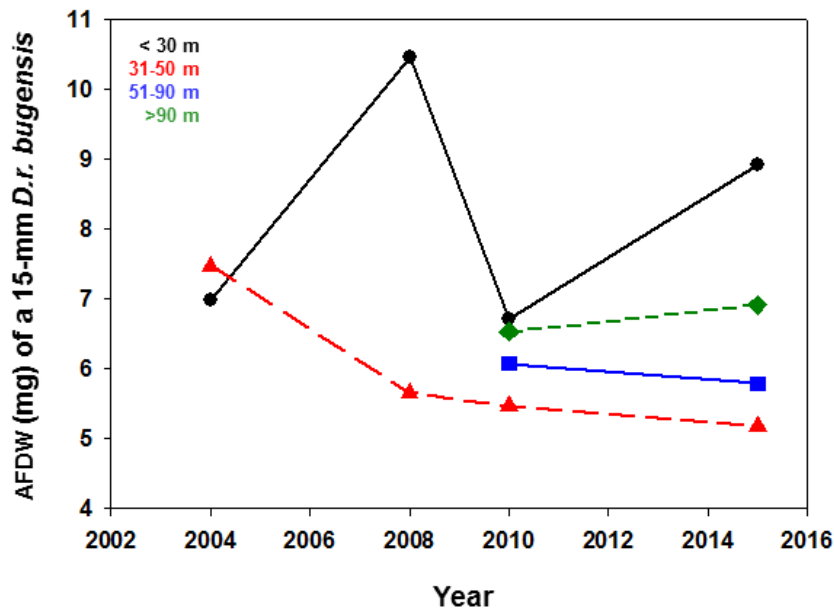

Figure 3.5. Ash free dry weight (AFDW, mg) of a standard 15-mm *D. r. bugensis* at four depth intervals intervals in Lake Michigan between 2004 and 2015. Values derived from regressions given in Table 3.4. Depth intervals: $\leq$ 30 m (black, circles), 31-50 m (red, triangles), 51-90 m (blue, squares), and > 90 m (green, diamonds).

Biomass estimates of *Dreissena* populations in the Great Lakes have been reported in a number of different units including AFDW, dry weight (DW), and TWW. Of these, dried mass (AFDW or DW) of mussel tissue most accurately reflects functional mass, and hence estimates of dreissenid metabolic functions such as filtering, respiration, and excretion rates are generally provided as per unit AFDW or DW (Vanderpoeg et al. 2010, Johengen et al. 2014, Tyner et al. 2015). These metabolic rates, along with population biomass provided as AFDW or DW, have been used to estimate lake-wide ecosystem impacts (Nalepa et al. 2009, Vanderploeg et al. 2010, Rowe et al. 2015, Tyner et al. 2015). In 2015, dreissenid biomass was determined as both AFDW and TWW. To examine the relationship between AFDW and TWW, biomass estimated by both methods was plotted for each station (Figure 3.6). A regression through the origin between the two values was significant (R^2 = 0.92) and defined by: TWW = 50.09*AFDW. Given this strong relationship between AFDW and TWW, the equation given above may be useful in converting from one biomass estimate to the other. One caveat, however, is the wide variation between the two estimates when values of AFDW are greater than about 40 g/m^2 (Figure 3.6). Reasons for this variation are unclear. One potential reason is that at sites with a greater number/biomass of mussels, any differences between the TWW/SL relationship at that one site and the generalized depth-specific length-weight relationship used to calculate

AFDW are compounded and therefore results in a greater discrepancy between the two methods. Also, at high mussel numbers/biomass, shell weight per unit shell length may be more inconsistent, the amount of water retained in the shell cavity may be more variable, or more debris might be found on shells. Regardless, at high numbers/biomass AFDW is both lower and higher relative to TWW which complicates any potential theory.
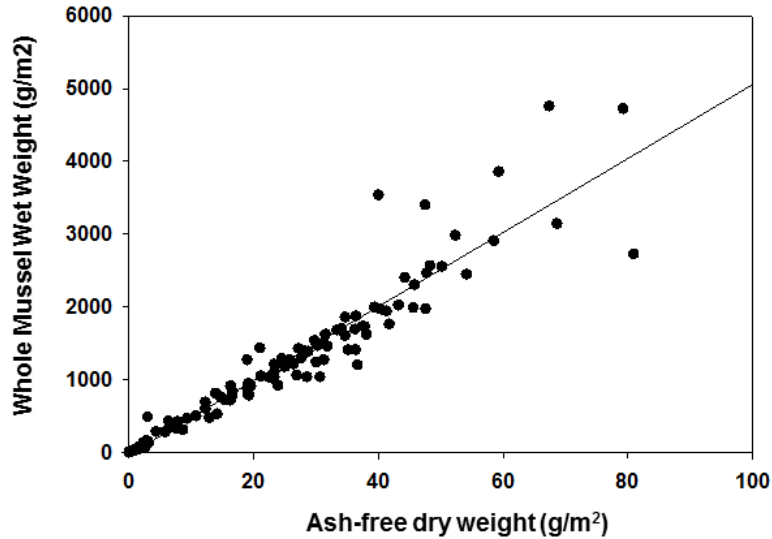

Figure 3.6. Relationship between ash free dry weight (AFDW) and total wet weight (TWW, whole mussel, tissue and shell) of *D. r. bugenisis* at each sampling site in the main basin of Lake Michigan in 2015 (n = 135). The regression through the origin was defined as: TWW = 50.09*AFDW (R^2 = 0.92)

Based on the 2015 survey, the amphipod *Diporeia* continued to decline (Table 3.4, Figure 3.7). In 2015, *Diporeia* was collected at only one site that was < 90 m, and at 9 sites that were > 90 m. In comparison, in 2010 *Diporeia* was collected at 13 sites < 90 m and 11 sites > 90 m. This depth-defined pattern of decline, with densities declining first and most rapidly in nearshore, shallow regions and more slowly with increased depth, has been apparent since the decline of *Diporeia* was first reported in the lake in the early 1990s (Nalepa et al. 1998). Such a spatial pattern coincides directly with the depth-related expansion of *Dreissena*. *D. polymorpha* increased mostly in the nearshore region (≤ 30 m) until 2000, and subsequently *D. r. bugensis* increased rapidly in nearshore regions and more slowly in deeper, offshore regions (> 90 m). The exact reason for the negative response of *Diporeia* to *Dreissena* has not been determined but, with the exception of Lake Superior where the *Dreissena* population is very limited, the decline of *Diporeia* has consistently occurred in all the Great Lakes within a few years after *Dreissena* became established (Nalepa et al. 2006).
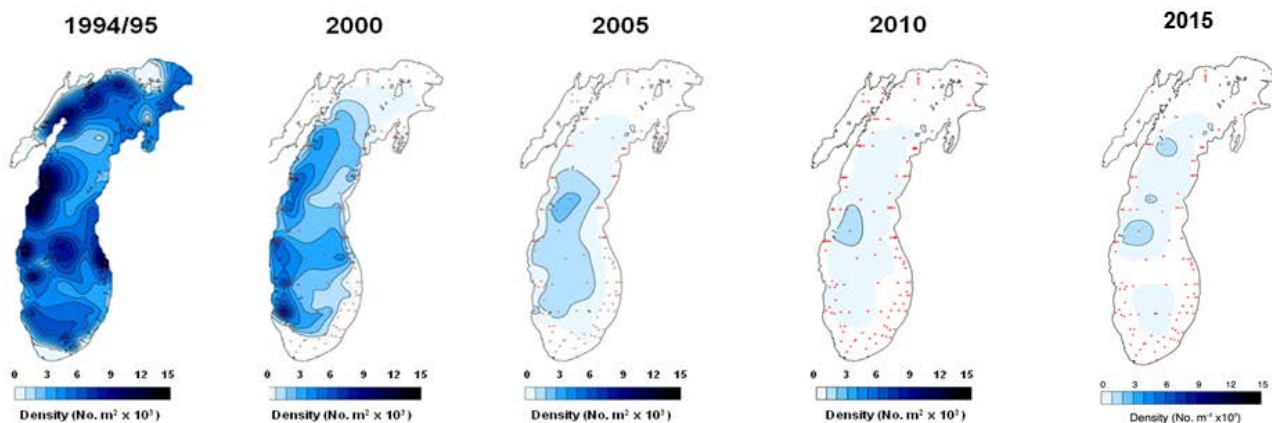
Figure 3.7. Density (no. per m^2) of *Diporeia spp.*in Lake Michigan based on lake-wide surveys in 1994/1995, 2000, 2005, 2010, and 2015. Small red dots indicate location of sampling sites.

Although mean density of *Diporeia* at > 90 m was not lower in 2015 than in 2010, the continued increase of *D. r. bugensis* at this depth interval would suggest that densities of *Diporeia* will most likely decrease, or the population will be completely gone, in future surveys. In 2015, not only were densities of *D. r. bugensis* greater at sites > 90 m compared to 2010, the spatial extent of the population had expanded. *D. r. bugensis* was present at 8 of 9 sites where *Diporeia* was collected in 2015. In Lake Ontario, *D. r. bugensis* expanded to deeper depths (> 90 m) sooner than in Lake Michigan, and in a lake-wide survey of Lake Ontario in 2013, only one *Diporeia* was collected at sites > 90 m, and no individuals were collected at sites < 90 m (Nalepa and Elgin unpublished). Mean density of *D. r. bugensis* at > 90 m was 2,044/m^2 in Lake Ontario in 2013, which is comparable to the mean density of 2,797/m^2 found in Lake Michigan at this depth interval in 2015. Thus, if such a density of *D. r. bugensis* nearly extirpated *Diporeia* at this depth interval in Lake Ontario, a similar outcome might be expected in Lake Michigan.

Since 2015 was the first survey year in which the entire benthic community was examined, lake-wide temporal trends in taxa other than *Dreissena* and *Diporeia* could not be assessed. However, a more limited assessment of changes in these other benthic taxa can be derived by comparing 2015 results to benthic data collected in the 1990s in just the southern basin. As part of a NOAA monitoring program, benthic samples have been collected at 40 sites in the southern basin for 2 consecutive years every 5 years beginning in 1980-1981 (Nalepa 1987, Nalepa et al. 1998). The two most recent years in which data are entirely available are in 1998-1999 (Nalepa and Elgin, unpublished). Since the same 40 sites were sampled in 2015 (see Table 3.1), densities of Oligochaeta, Sphaeriidae, and Chironomidae in 2015 were compared to densities in 1992-1993 and 1998-1999 at just these 40 sites. The 1992-1993 period was just after *D. polymorpha* became established in the southern basin, and the 1998-1999 period was about when *D. polymorpha* peaked and just before *D. r. bugensis* spread into the basin (about 2001). For oligochaetes, mean densities progressively increased in each of the three sampling periods (that is, 1992-1993, 1998-1999, and 2015) at the three depth intervals < 90 m (Table 3.6). These increases, particularly apparent at the ≤ 30 m and 31-50 m intervals, may be a result of a dreissenid impact known as the "nearshore shunt" (Hecky et al. 2004). In brief, this is the process by which organic material is retained for a longer period of time in nearshore regions by the activities of *Dreissena*. *Dreissena* filters particulate material (mainly phytoplankton) from the water column and subsequently deposits this organic material in the benthic zone in the form of feces and pseudofeces. These biodeposits would then serve as an added food source for benthic detritivores. Most all oligochaetes are detritivores and thus populations would benefit from these added food inputs. Benthic inputs of organic material are more pronounced in nearshore regions since primary production is greatest in this region, and because the water column is well-mixed giving *Dreissena* access to all phytoplankton present. Most

chironomids are also detritivores but, although mean densities of chironomids were greater in 2015 than in the 1990s at the two shallowest intervals, variation was too great to state with certainty that densities increased. Oligochaetes did not increase at the deepest interval (> 90 m). Although *Dreissena* in deeper, offshore waters also deposit organic material, these biodeposits would have less of an impact on detritivores. Benthic food availability in offshore regions is greatly diminished compared to nearshore regions not only because primary production in the upper water column is less, but also because this organic matter is fed upon by organisms (bacteria, protozoans, etc.) as it settles downward through a longer water column to ultimately reach the benthic region.

Table 3.6. Mean (± SE) density (no./ m^2) of major macroinvertebrate taxa at four depth intervals ($\leq$ 30 m, 31-50 m, 51-90 m, and > 90 m) at 40 sites in the southern basin of Lake Michigan. n = 12, 10, 12, and 6 for the four intervals, respectively.

Depth Interval/Taxa	Year		
	1992-1993	1998-1999	2015
$\leq$ 30 m			
Diporeia	2,624 ± 568	183 ± 125	0 ± 0
Dreissena	1,159 ± 855	1,521 ± 524	627 ± 284
Oligochaeta	1,684 ± 430	1,965 ± 355	4,087 ± 1,265
Chironomidae	187 ± 29	297 ± 46	531 ± 431
Sphaeriidae	900 ± 287	330 ± 139	87 ± 45
31-50 m			
Diporeia	7,857 ± 852	1,425 ± 450	0 ± 0
Dreissena	16 ± 6	955 ± 333	7,076 ± 1,639
Oligochaeta	3,050 ± 315	4,077 ± 762	6,031 ± 1,248
Chironomidae	100 ± 18	52 ± 12	202 ± 156
Sphaeriidae	1,677 ± 304	1,069 ± 181	7 ± 7
51-90 m			
Diporeia	5,911 ± 385	3,487 ± 616	0 ± 0
Dreissena	1 ± <1	3 ± 1	8,753 ± 1,591
Oligochaeta	1,693 ± 125	2,019 ± 244	2,924 ± 650
Chironomidae	66 ± 12	28 ± 7	6 ± 3
Sphaeriidae	597 ± 139	620 ± 68	12 ± 8
>90 m			
Diporeia	3,201 ± 477	3,314 ± 597	207 ± 207
Dreissena	0 ± 0	2 ± 2	5,644 ± 1,712
Oligochaeta	1,124 ± 141	996 ± 131	887 ± 196

Chironomidae	45 ± 10	26 ± 7	7 ± 6
Sphaeriidae	106 ± 36	175 ± 62	15 ± 8

In contrast to increased densities of oligochaetes in the shallower depth intervals, densities of sphaeriids were lower at all depth intervals in 2015 compared to the 1990s (Table 3.6). A decline in sphaeriids at all depths was first observed soon after *Dreissena* became established in the southern basin (Nalepa et al. 1998). Reasons for the negative response of sphaeriids to *Dreissena* are not clear. Since sphaeriids are filter-feeders, it is presumed that they are being outcompeted by *Dreissena* for available food. Yet the dominant sphaeriid in the Great Lakes is *Pisidium* spp., a genus that filters bacteria in benthic interstitial waters and therefore should benefit from increased bacteria associated with dreissenid biodeposits.

The dominance of *Dreissena* in the benthic community of Lake Michigan and the other Great Lakes has clear implications for other benthic taxa. While detailed comparisons of benthic community trends between lakes will not be provided here, a general overview of between-lake trends in *Dreissena* puts Lake Michigan results into a broader perspective. A comparison of density trends of *Dreissena* in Lakes Michigan, Ontario, and Huron at the $\leq$ 30 m, 31-90 m, and > 90 m intervals is given in Figure 3.8. To make this comparison, densities at 31-50 m and 51-90 m were combined (interval becomes 31-90 m) for Lakes Michigan and Huron since these two depth intervals were not reported separately for Lake Ontario in previous studies (Watkins et al. 2007, Birkett et al. 2015). Density trends at $\leq$ 30 m are difficult to compare between lakes since high variation in physical drivers (i.e., substrate heterogeneity, wave-induced disturbance) strongly influence dreissenid estimates. This is evident in the wide year-to-year variation at this depth interval in Lake Ontario (Figure 3.8). Physical conditions become more stable as depth increases, and population trends at depths > 30 m are better suited for lake-to-lake comparisons. The decline of *D. r. bugensis* in Lake Michigan in 2015 at 31-90 m is similar to an ongoing decline in Lake Ontario that has been evident since 2008 (Figure 3.8). If populations in both lakes have indeed peaked at this depth, a greater peak density was attained in Lake Michigan. In both lakes, densities increased sharply and then gradually declined. In contrast, densities at 31-90 m in Lake Huron have increased gradually and, as of 2012, do not yet appear to have peaked. Densities at > 90 m are still increasing in all three lakes (Figure 3.8). Similar comparisons of temporal trends in dreissenid biomass are not possible since biomass was not historically measured in each lake. However, the most recent lake-wide survey in each lake determined and reported biomass using the same methods, and values in the four depth intervals are given in Table 3.7. Again, considering biomass only at depths > 30 m, mean biomass in Lakes Michigan and Ontario were generally comparable at 31-50 m, 51-90 m, and > 90 m, whereas biomass in Lake Huron was about 50%, 78%, and 38% lower than in Lakes Michigan and Ontario at these three depth intervals, respectively.
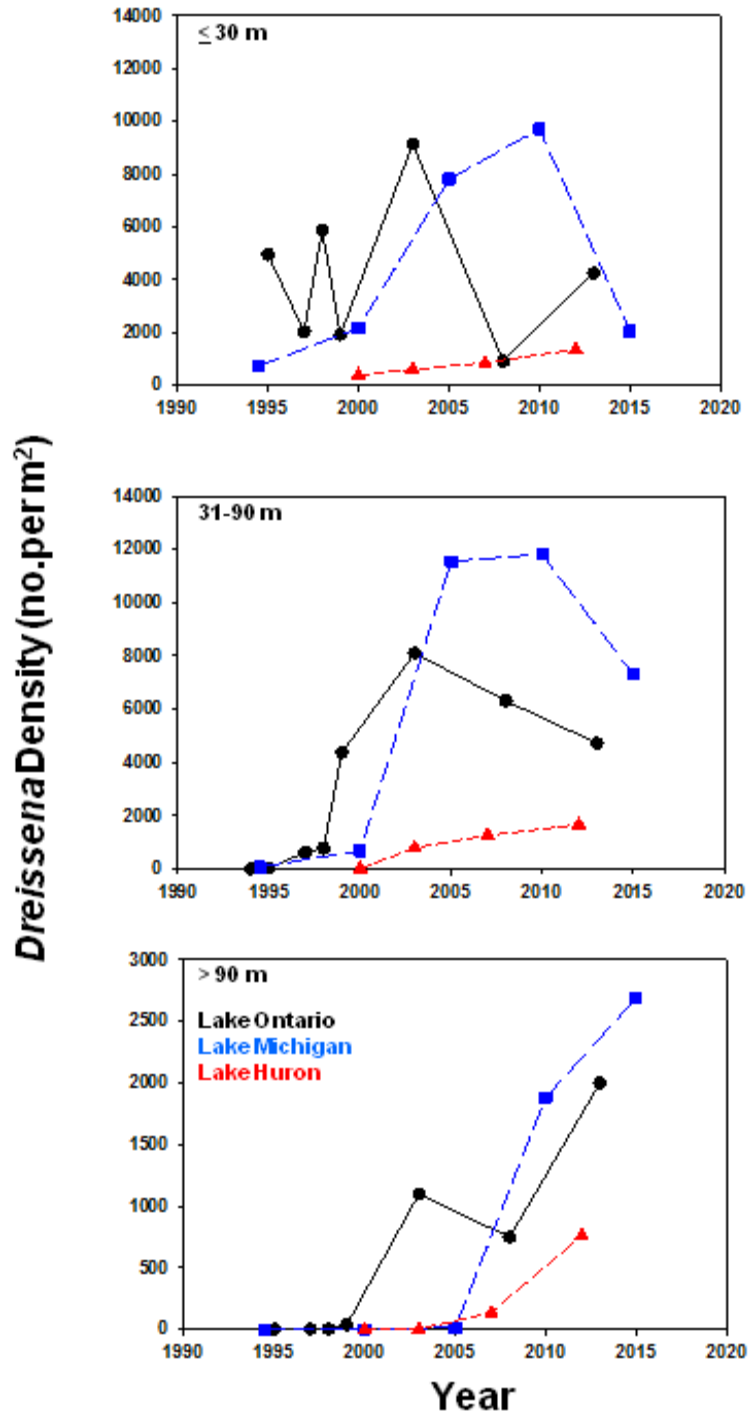
Figure 3.8. Density (no. per m²) of total *Dreissena* at ≤ 30 m (upper panel), 31-90 m (middle panel), and > 90 m (lower panel) in Lake Ontario (black, circle), Lake Michigan (blue, square), and Lake Huron (red, triangle). Values taken from the following sources: Lake Ontario (Birkett et al. 2015, Nalepa and Elgin unpublished), Lake Michigan (Nalepa et al. 2014, this study); Lake Huron (Nalepa et al. 2007, Nalepa unpublished). Note the different scale for the > 90 m interval.

Table 3.7. Mean (± SE) biomass (gAFDW/m^2) of *Dreissena* at ≤ 30 m, 31-50 m, 51-90 m, and > 90 m depth intervals based on the latest lake-wide surveys in Lake Michigan, Lake Ontario, and Lake Huron. Given in parenthesis is the number of stations sampled.

Depth Interval	*Dreissena* Biomass (gAFDW/m^2)		
	Lake Michigan in 2015	Lake Ontario in 2013	Lake Huron in 2012
≤ 30 m	7.93 ± 3.30 (29)	21.53 ± 7.92 (8)	2.65 ± 1.77 (19)
31-50 m	26.44 ± 3.05 (46)	28.79 ± 9.63 (8)	13.91 ± 4.43 (30)
51-90 m	28.39 ± 1.98 (42)	20.86 ± 1.82 (8)	5.43 ± 2.45 (26)
> 90 m	6.81 ± 2.23 (18)	7.08 ± 2.16 (21)	4.32 ± 3.97 (8)

SUMMARY

A lake-wide benthic survey was conducted in Lake Michigan in 2015 to assess the current status of the macroinvertebrate community. Similar lake-wide surveys have been conducted in the lake at 5-year intervals beginning in 1994/1995. These previous surveys only examined populations of *Dreissena polymorpha*, *Dreissena r. bugensis*, and *Diporeia*, whereas the 2015 survey examined the entire benthic community. Perhaps the most significant finding in 2015 was the decline in densities of *D. r. bugensis* at depths < 90 m. Compared to densities in 2010, densities in 2015 declined 79%, 56%, and 40% at the ≤ 30 m, 31-50 m, 51-90 m intervals, respectively. In contrast, densities at > 90 m increased 37%. Because of a greater proportion of larger individuals in the population, biomass at 31-50 m and 51-90 m remained stable or slightly increased in 2015 compared to 2010. Overall, depth-weighted biomass increased from 13.7 g/m^2 in 2010 to 16.5 g/m^2 in 2015, largely due to increased biomass at sites > 90 m. The other dreissenid species, *D. polymorpha*, was not collected at any of the sites in 2015, indicating it has essentially been displaced by *D. r. bugensis*. Also, the amphipod *Diporeia* continued to disappear. It was not collected at any sites < 90 m and only at 9 sites > 9 0 m. Lake-wide temporal trends in other major benthic taxa such as Oligochaeta, Sphaeriidae, and Chironomidae could not be assessed since 2015 was the first year the entire benthic community was sampled. However, based on comparisons to data collected in just the southern basin in 1992-1993 and 1998-1999, oligochaetes have progressively increased in shallower and mid-depth regions between 1992-1993 and 2015. A likely reason is an increased amount of potential food resulting from the biodeposition of organic material by *Dreissena*. In contrast, sphaeriids progressively declined all depth intervals between 1992-1993 and 2015.

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APPENDICES

Appendix 1.1. Karatayev, A. Y., L. E. Burlakova, K. Mehler, S. A. Bocaniov, P. D. Collingsworth, G. Warren, Kraus, R. T., and E. K. Hinchey. Biomonitoring using invasive species in a large lake: *Dreissena* distribution maps hypoxic zones. Journal of the Great Lakes Research. Published on-line DOI 10.1016/j.jglr.2017.08.001.

Appendix 1.2. Taxa recorded from 80 benthic stations sampled in Lake Erie in 2014. The information is provided for the lowest identified taxa, in most cases species or genus. In cases where taxa was identified only to a family or higher taxonomic level, it was listed at the level it was identified. Species occurrence (P, in percent of all 80 stations samples, for *Dreissena*: from 107 stations), average density (N, ind./m^2), average wet biomass (B, g/m^2).

Appendix 2.1. Locations (latitude and longitude) of 31 stations sampled for benthos in western Lake Erie April 4 - May 28, 2014 (Schloesser et al. 2000).

Appendix 2.2. Individual replicate (REP 1, 2, and 3) grab counts of general benthos in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.3. Individual replicate (REP 1, 2, and 3) grab counts of mollusks in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.4. Individual replicate (REP 1, 2, and 3) grab counts of chironomids in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.5. Individual replicate (REP 1, 2, and 3) grab counts of oligochaetes in samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.6. Lengths (mm) of individual zebra (Dreissena polymorpha) and quagga mussels (*Dreissena bugensis*) in individual replicate-grab samples collected at 31 stations in western Lake Erie 2014. Excel file, available by request.

Appendix 2.7. Density of five benthic taxa at nine stations in western Lake Erie 1930, 1961, 1982, 1993, 2003, 2010, and 2014. Adopted after Carr and Hiltunen (1965). For 1930, means based on unknown number of replicate samples.