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LAKE ERIE BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2024 Technical Report



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REPORT: LAKE ERIE BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2024

Lake and Year: Erie, 2024

Lead Organization: SUNY Buffalo State University

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Project Overview

In this report, we present results of a benthic survey of Lake Erie conducted as part of the United States Environmental Protection Agency (U.S. EPA) Great Lakes National Program Office (GLNPO) Great Lakes Biology Monitoring Program (GLBMP) and Cooperative Science and Monitoring Initiative (CSMI) benthic surveys. Consistent with the sampling scheme of previous CSMI studies, a lake-wide benthic survey was conducted in 2024 in Lake Erie to assess the status of the benthic macroinvertebrate community. This study advanced the Lake Erie CSMI priority of monitoring and understanding Lake Erie's lower food web. The primary objectives of this survey were to assess the current status and long-term trends of the benthic community, as well as the distribution, abundance, and long-term dynamics of invasive *Dreissena* spp.

Study Highlights

- A lake-wide benthic survey of Lake Erie was conducted in 2024 as part of the U.S. EPA Great Lakes National Program Office's Great Lakes Biology Monitoring Program, and Cooperative Science and Monitoring Initiative survey efforts. A total of 113 species and higher taxa of benthic macroinvertebrates were collected from 95 stations, including 76 CSMI, 10 GLBMP long-term monitoring (LTM) stations, and 9 Historical Western Basin (HWB) stations. The most diverse groups were Oligochaeta (39 species and higher taxa), Chironomidae (28), and Mollusca (18). *Dreissena rostriformis bugensis* occurred at 64% of stations, and *D. polymorpha* was recorded at 30%.
- In 2024, basin-wide average benthos density was highest in the central basin, followed by the eastern and western basins. *Dreissena* spp. dominated benthic densities only in the western basin (38%), whereas oligochaetes were the dominant group in the eastern (81%) and central (59%) basins. *Dreissena* dominated wet biomass in all basins, increasing from 32% in the central basin to 77% in the western basin and 99% in the eastern basin. Excluding dreissenids, benthos density and biomass were highest in the central basin, while the eastern basin had the lowest non-dreissenid biomass.
- *Dreissena* biomass has steadily declined in all basins since 2014 and by 2024 has reached the lowest levels recorded since invasion. Dreissenid density somewhat increased only in the western basin, where the relative abundance of *D. polymorpha* increased, and its biomass exceeded that of *D. r. bugensis*.
- Over the last century, eutrophication, subsequent de-eutrophication, water-quality improvements, and dreissenid invasions were the primary drivers of benthic change in the western basin. A diverse *Hexagenia*-dominated community in the 1930s experienced species loss and became dominated by pollution-tolerant taxa in the 1960s, followed by recovery in recent decades. By 2024, the relative contribution of *Dreissena* had declined; *Hexagenia* abundance exceeded 1930s levels; oligochaete and sphaeriid densities increased, and chironomid and gastropod densities remained stable. Total benthic density at the nine historical western basin stations has increased over the last two decades, driven primarily by changes in *D. r. bugensis* and oligochaetes.
- In the central basin, bottom hypoxia remains the primary factor influencing the benthic community. Before the invasion of *Dreissena*, the benthos was dominated by hypoxia-tolerant oligochaetes, sphaeriids, and chironomids. Over the past two decades, dreissenid densities have declined and now contribute <4% of total benthic density, indicating worsening hypoxic conditions. By 2024, the community had shifted toward fewer *Dreissena* and lower overall benthic densities, driven primarily by declines in oligochaetes.
- The eastern basin historically supported deep, cold-water oligotrophic keystone species *Diporeia* and *Mysis*. Dreissenid invasion in the 1990s drove major community restructuring, including extirpation of *Diporeia*, declines in Sphaeriidae, and increases in non-*Diporeia* amphipods, gastropods, and chironomids. Over the past decade, benthic densities declined, likely due to increased predation by round goby. By 2024, *D. r. bugensis* densities continued to decline, oligochaete densities increased, amphipods, gastropods, and sphaeriids remained low, and *Diporeia* remained absent.

- Similar to the previous survey in 2019, the 2024 *Dreissena* population video assessment demonstrated strong predictive power for rapid density estimates. Compared with 2019, *Dreissena* coverage declined 2-fold in the eastern basin and 4-fold in the central basin.

Project: Major findings from the CSMI benthic macroinvertebrate survey in Lake Erie in 2024

Overview

A lake-wide benthic survey of Lake Erie was conducted in 2024 as part of the U.S. EPA Great Lakes National Program Office (GLNPO), Great Lakes Biology Monitoring Program (GLBMP), and Cooperative Science and Monitoring Initiative (CSMI) survey efforts. Consistent with the sampling scheme of previous surveys, benthic samples were collected at 95 stations to assess the status of the benthic macroinvertebrate community.

Lake Erie has the longest history of benthic studies among the Great Lakes (Wright, 1955; Carr and Hiltunen, 1965; Schloesser et al., 2017; Manny and Schloesser, 1999). Several studies analyzed the long-term dynamics of benthos in various basins (Britt et al., 1980; Schloesser et al., 2017, Karatayev et al., 2022) and lake-wide in the last decades (Dermott, 1994; Burlakova et al., 2014; Karatayev et al., 2022). In this report, we compare the results of our 2024 lake-wide survey with those of our 2019 survey and historical data to examine long-term changes in the benthic community across all three basins of Lake Erie.

The objective of this study was to advance understanding of Lake Erie's lower food web and to describe the status and long-term trends in the benthic community, with particular emphasis on *Dreissena*, one of the most impactful invasive species to enter the Great Lakes. This report contains detailed descriptions of benthic communities in Lake Erie in 2024, including information on sampling design (station locations, sampling and laboratory procedures), the taxonomy and abundance of benthic invertebrates, results of video surveys, and long-term changes in benthic community and *Dreissena* populations.

Methods

Sampling protocol

A total of 285 triplicate benthic samples from 95 stations were analyzed for benthic macroinvertebrates in this study: 27 samples from 9 Historical Western Basin (HWB) stations, 228 samples from 76 CSMI stations, and 30 samples from 10 long-term monitoring (LTM) stations (Table 1, Fig. 1, Table 2). All taxa were identified to the lowest practical taxonomic level from 76 stations (“All taxa”), and 19 additional stations were analyzed for *Dreissena* only.

All HWB stations were sampled on May 1-2, 2024, aboard SUNY Buffalo State’s R/V *John J Friedhoff* using a Petit Ponar (sampling area 0.0231 m², coefficient 43.28). 69 CSMI stations were sampled from July 15-21, 2024, and all LTM stations, along with 7 CSMI stations, were sampled from August 10-14, 2024, aboard the U.S. EPA R/V *Lake Guardian* using a standard Ponar grab (sampling area 0.0523 m²; coefficient 19.12) (US EPA, 2023). Benthic samples could not be collected at four shallow stations due to hard substrates (Table 2). Upon collection, each sample was placed separately into an elutriation device and then washed through a 500-µm mesh screen. All retained organisms and sediments were transferred into a collection jar and preserved with neutral buffered formalin containing Rose Bengal stain to a final formalin concentration of 5–10%. Detailed methods are described in the EPA GLNPO Standard Operating Procedure for Benthic Invertebrate Field Sampling SOP LG406 (US EPA, 2021a).

We collected video images using a Benthic Imaging System (BIS) equipped with two GoPro cameras (Hero11, one down-looking camera, one oblique- or side-looking camera) in deep-water housings, and two underwater lights per camera attached to a custom-built stainless-steel frame equipped with a scale bar (Burlakova et al., 2023; Karatayev et al., 2021a, 2022). At each station, the BIS was lowered from the starboard side of R/V *Lake Guardian* or from the board of SUNY Buffalo State’s R/V *John J Friedhoff* down to the lake bottom, and videos were recorded and processed according to US EPA SOP LG410 for Collection and Processing of Drop-Down Camera Images for *Dreissena* spp. and round goby (US EPA, 2025). All the 279 images successfully collected from 93 stations were rated based on image quality and categorized as high quality (mussels were well visible and could be counted with high confidence), medium (mussels were visible and could be counted with medium confidence), and low quality (images were not crisp and mussels could potentially be undercounted). For quality control purposes, at least 10% of randomly selected still images were recounted by a different analyst; images with <20% errors in *Dreissena* counts were considered acceptable, and all images with differences >20% were re-evaluated (US EPA, 2025).

Table 1. A list of 95 Lake Erie stations from which successful Ponar and video samples (in parentheses) were collected in 2024. Stations include 9 Historical Western Basin (HWB) stations sampled on Lake Erie in May 2024, 76 Cooperative Science and Monitoring Initiative (CSMI) stations sampled in July and August 2024, and 10 GLBMP long-term monitoring (LTM) benthic stations sampled in August 2024. All taxa were identified to the lowest practical taxonomic level from 76 stations (“All taxa”), and 19 additional stations were analyzed for *Dreissena* only.

Samples/Basins	Western	Central	Eastern	Lakewide
Ponar, all taxa, total	24 (72)	34 (102)	18 (54)	76 (228)
CSMI Ponar	13 (39)	31 (93)	13 (39)	57 (171)
LTM Ponar	2 (6)	3 (9)	5 (15)	10 (30)
HWB Ponar	9 (27)	0 (0)	0 (0)	9 (27)
Ponar, <i>Dreissena</i> only (CSMI)	2 (6)	11 (33)	6 (18)	19 (57)
Benthic Video	21 (63)	44 (132)	24 (72)	89 (267)
CSMI Video	10 (30)	41 (123)	19 (57)	70 (210)
LTM Video	2 (6)	3 (9)	5 (15)	10 (30)
HWB Video	9 (27)	0 (0)	0 (0)	9 (27)

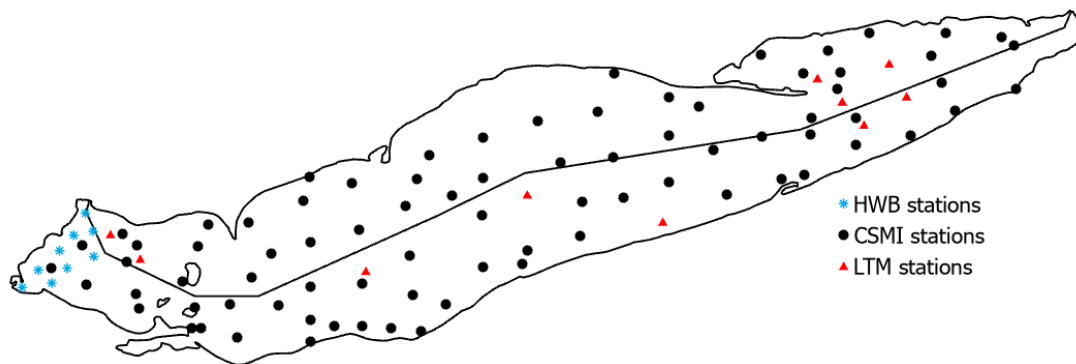


Fig. 1. Location of benthic stations surveyed in Lake Erie in 2024. The map indicates the locations of 9 Historical Western Basin (HWB) stations, 76 Cooperative Science and Monitoring Initiative (CSMI) benthic stations, and 10 GLBMP long-term monitoring (LTM) stations.

Table 2. A list of all planned 99 stations, including 9 Historical Western Basin (HWB) stations sampled on Lake Erie in May 2024, 76 Cooperative Science and Monitoring Initiative (CSMI) stations sampled in July and August 2024, 10 GLBMP long-term monitoring (LTM) benthic stations sampled in August 2024, and the 4 CSMI stations where Ponars were not collected, along with information on location (decimal degrees), water depth, main substrates, sample type and information where videos collected with Benthic Imaging System, BIS. In total, 285 successful benthic samples (228 “All taxa” and 57 *Dreissena* only samples) were collected from 95 stations, and 279 successful video from 93 stations.

Station	Depth (m)	Basin	Latitude	Longitude	Sample Type	Substrate	BIS
ECSER15D (HWB)	4	Western	42.033333	-83.152833	All Taxa	silt, gravel, sand	+
ECSER1M (HWB)	2.4	Western	41.713833	-83.425	All Taxa	-	+
ECSER2L (HWB)	7.5	Western	41.797167	-83.2305	All Taxa	silt	+
ECSER3D (HWB)	7	Western	41.938833	-83.202833	All Taxa	silt, gravel, sand	+
ECSER5/4R (HWB)	6.5	Western	41.872167	-83.263833	All Taxa	silt	+
ECSER6L (HWB)	8.5	Western	41.847167	-83.116667	All Taxa	silt	+
ECSER7M (HWB)	5	Western	41.733333	-83.297167	All Taxa	silt	+
ECSER8D (HWB)	7.3	Western	41.9555	-83.1195	All Taxa	silt, gravel, sand	+
ECSER8M (HWB)	4	Western	41.788833	-83.3555	All Taxa	silt, gravel	+
ECS932	22	Eastern	42.791667	-79.209167	All Taxa	clay, sand, silt	+
ECS934	29	Eastern	42.708667	-79.507833	All Taxa	clay, sand, silt	+
ECS935	33	Eastern	42.5925	-79.466167	All Taxa	silt	+
ECS936	15	Eastern	42.474167	-79.4075	All Taxa	shells	+
ECS937	9	Eastern	42.715	-80.245333	All Taxa	sand	+
ECS938	36	Eastern	42.63278	-80.05917	All Taxa	silt	+
ECS939	57	Eastern	42.56667	-79.91611	All Taxa	silt	+
ECS940	49	Eastern	42.44194	-79.8325	All Taxa	silt	+
ECS941	36	Eastern	42.326333	-79.833833	All Taxa	silt	+
ECS944	17	Central	42.531667	-80.640333	All Taxa	sand, clay, shells	+
ECS945	21	Central	42.367	-80.637833	All Taxa	clay, sand, shells	+
ECS946	24	Central	42.165333	-80.641667	All Taxa	clay, sand, shells, silt	+
ECS952	23	Central	42.358833	-81.440833	All Taxa	silt	+
ECS953	24	Central	42.183667	-81.4405	All Taxa	silt	+

Station	Depth (m)	Basin	Latitude	Longitude	Sample Type	Substrate	BIS
ECS954	24	Central	42.0255	-81.443667	All Taxa	silt	+
ECS955	21	Central	41.8	-81.441667	All Taxa	silt	+
ECS957	13	Central	41.683333	-81.740833	All Taxa	silt	+
ECS958	12	Central	41.525	-81.707833	All Taxa	clay, sand, silt	+
ECS959	14	Central	42.190333	-82.186667	All Taxa	sand, silt	+
ECS961	21	Central	41.907833	-82.182	All Taxa	silt	+
ECS962	20	Central	41.716667	-82.1845	All Taxa	silt	+
ECS963	16	Central	41.5745	-82.183833	All Taxa	silt, sand	+
ECS964	9.9	Central	41.483833	-82.182	All Taxa	sand, silt	+
ECS965	13	Western	41.5	-82.500333	All Taxa	silt	+
ECS966	11	Western	41.983333	-82.625	All Taxa	silt	+
ECS967	12	Western	41.891667	-82.666333	All Taxa	silt, clay, shells	+
ECS968	11	Western	41.741333	-82.733333	All Taxa	shells, sand, silt	+
ECS970	11	Western	41.826167	-82.975833	All Taxa	silt	-
ECSB07	10	Western	41.541667	-82.693333	All Taxa	silt	+
ECSB12	17	Central	41.548333	-82.08	All Taxa	silt	+
ECSB13	16	Central	41.548333	-81.96	All Taxa	silt, sand	+
ECSC05	8.8	Western	41.625	-82.921667	All Taxa	silt	-
ECSC07	14	Western	41.63	-82.681667	All Taxa	shells, silt, sand	+
ECSC10	14	Central	41.636667	-82.32	All Taxa	sand, silt, shells	+
ECSC16	17	Central	41.641667	-81.598333	All Taxa	sand, shells	+
ECSCCW20	19	Eastern	42.568213	-79.142936	<i>Dreissena</i>	clay, detritus, silt, sand, gravel	+
ECSD13	22	Central	41.73	-81.961667	All Taxa	silt	+
ECSF03	8.9	Western	41.896667	-83.165	All Taxa	silt	-
ECSF05	11	Western	41.896667	-82.928333	All Taxa	silt	-
ECSG09	14	Central	41.995	-82.45	All Taxa	sand, gravel, silt, sand	+
ECSH11	21	Central	42.086667	-82.215	All Taxa	silt	+
ECSI15	24	Central	42.181667	-81.726667	All Taxa	silt, shells	+

Station	Depth (m)	Basin	Latitude	Longitude	Sample Type	Substrate	BIS
ECSI28	15	Central	42.181667	-80.156667	All Taxa	sand, silt, shells	+
ECSJ22	22	Central	42.271667	-80.88	All Taxa	clay, sand, shells	+
ECSK29	37	Eastern	42.371667	-80.028333	All Taxa	silt	+
ECSKM1	15	Central	41.859843	-82.35383	<i>Dreissena</i>	sand, silt	+
ECSKM11	19	Central	42.113652	-80.389981	<i>Dreissena</i>	sand, shells, silt	+
ECSKM12	18	Central	42.304009	-80.447088	<i>Dreissena</i>	shells, sand, gravel	+
ECSKM13	18	Central	42.491194	-80.51054	<i>Dreissena</i>	clay, sand, shells	-
ECSKM14	31	Eastern	42.361116	-80.237696	<i>Dreissena</i>	clay, shells sand	+
ECSKM15	14	Western	41.640933	-82.528323	<i>Dreissena</i>	silt	+
ECSKM16	14	Western	41.759906	-82.434731	<i>Dreissena</i>	sand, silt	+
ECSKM2	24	Central	41.961367	-81.973116	<i>Dreissena</i>	silt	+
ECSKM3	21	Central	42.161242	-82.004842	<i>Dreissena</i>	silt	+
ECSKM4	24	Central	41.850325	-81.754205	<i>Dreissena</i>	silt	+
ECSKM5	24	Central	42.062891	-81.773241	<i>Dreissena</i>	silt	+
ECSKM6	21	Central	41.872534	-81.24976	<i>Dreissena</i>	silt	+
ECSKM7	20	Central	41.935986	-81.021331	<i>Dreissena</i>	silt	+
ECSKM8	23	Central	42.100962	-80.834147	<i>Dreissena</i>	sand, silt, shells	+
ECSKM9	20	Central	42.468985	-80.948361	All Taxa	silt	+
ECSL29	45	Eastern	42.441667	-80.025	All Taxa	silt	+
ECSLowbanks (20m)	21	Eastern	42.80825	-79.449333	<i>Dreissena</i>	clay, sand, silt	+
ECSN22	13	Central	42.633333	-80.875	All Taxa	silt	+
ECSN30	42	Eastern	42.638333	-79.901667	All Taxa	silt	+
ECSP31	17	Eastern	42.806667	-79.776667	All Taxa	clay, silt, sand, shells	+
ECSPeacockPt (20m)	21	Eastern	42.730833	-79.954944	<i>Dreissena</i>	silt, clay	+
ECS PtAbino (20m)	21	Eastern	42.752083	-79.152667	<i>Dreissena</i>	sand, clay, silt	+
ECSW42	9.5	Western	41.945	-82.991667	All Taxa	silt	-
ECSWFD20	19	Eastern	42.366727	-79.600191	<i>Dreissena</i>	silt	+
ER30	21	Central	42.430167	-81.204003	All Taxa	silt	+
ER31	22	Central	42.253168	-81.106502	All Taxa	silt	+

Station	Depth (m)	Basin	Latitude	Longitude	Sample Type	Substrate	BIS
ER32	23	Central	42.081502	-81.011835	All Taxa	clay, silt	+
ER37	25	Central	42.109667	-81.575333	All Taxa	silt	+
ER38	22	Central	42.281668	-81.671502	All Taxa	silt	+
ER58	9.9	Western	41.685167	-82.933338	All Taxa	silt, clay	+
ER59	8	Western	41.728668	-83.149337	All Taxa	silt, clay	+
ER09 (LTM)	47	Eastern	42.538333	-79.616667	All Taxa	silt, shells	+
ER10 (LTM)	32	Eastern	42.68	-79.691667	All Taxa	silt, shells	+
ER15M (LTM)	63	Eastern	42.516667	-79.893333	All Taxa	silt	+
ER43 (LTM)	23	Central	41.788333	-81.945	All Taxa	silt	+
ER61 (LTM)	10	Western	41.946667	-83.045	All Taxa	silt	+
ER63 (LTM)	45	Eastern	42.416667	-79.8	All Taxa	silt	+
ER78M (LTM)	23	Central	42.116667	-81.25	All Taxa	silt	+
ER91M (LTM)	10.5	Western	41.840833	-82.916667	All Taxa	clay, silt	+
ER93b (LTM)	41.3	Eastern	42.616667	-80	All Taxa	silt, clay	+
ER95b (LTM)	16.3	Central	42	-80.66639	All Taxa	sand, clay, silt, gravel	+
ECS956 (failed)	12	Central	41.68867	-81.44917	All Taxa	hard substrate	+
ECS951 (failed)	21	Central	42.47583	-81.44167	All Taxa	hard substrate	+
ECSKM10 (failed)	13	Central	42.592717	-81.230724	All Taxa	hard substrate	+
ECS933 (failed)	17	Eastern	42.81667	-79.56800	All Taxa	hard substrate	+

Laboratory procedures

All organisms in samples collected from the 76 “All taxa” benthos stations were separated from sediments under low magnification using a dissecting microscope, identified, counted, and weighed (total wet weight). Oligochaetes and chironomids were mounted on slides and identified with a compound microscope; other organisms were identified using a dissecting microscope. Oligochaeta, including Naididae, mature Tubificidae, and Lumbriculidae, were identified to the species level. Enchytraeidae, immature Tubificidae, and immature Lumbriculidae were identified to the lowest taxonomic level possible, usually at the family level, and included in density and biomass estimates. Counts of oligochaete fragments were excluded from density analyses, but fragment weight was used to determine biomass. Chironomids were identified to the lowest practical taxonomic level, typically at the genus level. Other invertebrates were identified to the species level when possible. Details are described in the EPA GLNPO SOP LG407 for Benthic Invertebrate Laboratory Analysis (US EPA, 2023). In this study, we use the traditional division of Oligochaeta into Enchytraeidae, Lumbriculidae, Naididae, and Tubificidae, which aligns with historical data. Although the former families of Naididae and Tubificidae in the order Tubificida are now combined into a single family, Naididae (Erseus et al., 2008), we retain this classification for consistency. Only *Dreissena* spp. were sorted and processed from 57 samples collected at the 19 “*Dreissena* only” stations.

Assessment of long-term changes in Lake Erie benthic community

A total of 12, 8, and 9 benthic basin-wide surveys were conducted between 1930 and 2024 in the western, central, and eastern basins, respectively (Karatayev et al., 2022). Data from these surveys were used to identify long-term changes in the Lake Erie benthic community.

Data analysis

We checked the normality of data using Shapiro-Wilk's test and, when the data could not be transformed to meet the normality and homogeneity of variances assumptions, we used non-parametric tests. We used *t*-tests to compare *Dreissena* densities estimated by BIS vs. densities recorded in Ponars at each depth zone by basin, checking homogeneity of variances using Levene's test, or using the Kruskal-Wallis test. To compare *Dreissena* densities among different years by depth zones, we used the Kruskal-Wallis test. All test effects were considered significant at $P < 0.05$.

Results and Discussion

Status of the Lake Erie benthic community in 2024

A total of 104 species and higher taxa of benthic macroinvertebrates were identified from 67 stations (excluding the spring Historic Western Basin stations) collected in Lake Erie in 2024. The most diverse groups were Oligochaeta (39 species and higher taxa), Chironomidae (28), and Mollusca (18). Among Oligochaeta, Tubificidae was the most diverse with 20 species and higher taxa, followed by Naididae with 17.

Within the western basin (excluding the HWB stations), the most widespread taxa included the Chironomidae *Procladius* sp., found at every station, and *Cryptochironomus* sp., Oligochaeta *L. hoffmeisteri*, and the Hirudinea *Helobdella stagnalis* (all recorded at 93% of stations). Dreissenids *D. polymorpha* and *D. r. bugensis* were found at 87% and 67% of stations, respectively. The most

abundant species in the basin were *D. polymorpha* (28% of the total benthic density and 49% of biomass), *D. r. bugensis* (10% and 28%), and *Hexagenia* sp. (11% and 13%, respectively, Tables 3, 4). Oligochaeta represented 18% of total basin density, Mollusca (excluding *Dreissena*) - 16%, and Chironomidae - 13%. Among Oligochaeta, tubificids were the most abundant, making up 99% of the total class density. Gastropoda represented 58% of the non-dreissenid Mollusca density, and Sphaeriidae represented 42%.

The central basin had the highest benthic density and non-dreissenid biomass relative to other basins (Tables 3, 4). Here, the most widespread taxa included *Chironomus* sp., which was found at every station, as well as *L. hoffmeisteri*, the chironomid *Tanytarsus* sp., and the fingernail clam *Pisidium* sp., all recorded at 94% of stations. All the taxa are known to be tolerant of organic enrichment and low oxygen conditions. Likely due to periodic hypoxia, the central basin had the lowest occurrence of dreissenids compared to other basins: *D. r. bugensis* was recorded at 47% of stations, and *D. polymorpha* at 15%. The most abundant taxa were *S. ferox* with an average density of 1315 m⁻² (11% of the total benthic density), followed by *Pisidium* sp. (1279 m⁻², 15%) and *Chironomus* sp. (969 m⁻², 11%). *Chironomus* sp. comprised the highest biomass within the basin (11.2 g m⁻², 29% of total benthic biomass), followed by *D. polymorpha* (6.4 g m⁻², 17%), *D. r. bugensis* (5.6 g m⁻², 15%), and *S. ferox* (5.5 g m⁻², 14%). Among larger taxonomic groups, Oligochaeta comprised the highest percentage (59%) of the total central basin benthos density, followed by non-dreissenid Mollusca (16%), Chironomidae (15%), and Malacostraca (8%), while dreissenids contributed little (<1%). As in the western basin, tubificids were the most numerous, accounting for 98% of the total Oligochaeta density. Among non-dreissenid Mollusca, Sphaeriidae were the most abundant (98%).

The highest total benthic biomass in the lake was recorded in the eastern basin (Table 3), where *D. r. bugensis* created the highest density, as well as the highest biomass that accounted for the highest proportion of total benthic biomass, by far, of every other basin (99%). The most widespread taxon in the basin was tubificid *Potamotheix vejdovskyi*, which was found at every station, followed by *D. r. bugensis* and Oligochaeta *P. moldaviensis*, both occurring at 94% of stations. Oligochaeta made up the largest percentage (81%) of the total benthic density, followed by *D. r. bugensis* (14%) and Chironomidae (5%). As in other basins, tubificids accounted for the majority (97%) of the Oligochaeta total density. *Dreissena polymorpha* was very rare in the eastern basin, accounting for only 0.04% of the total density.

Table 3. Average ($\pm$ standard error) density (ind. m⁻²) of major taxonomic groups and common species of benthic invertebrates collected at 67 benthic stations in Lake Erie in 2024 (excluding Historic Western Basin stations) and averaged by basin. *Dreissena* spp. average density was calculated separately for “All-taxa” stations as well as for all stations combined (“All taxa” + “*Dreissena*-only” stations, in parentheses).

Taxa	Western	Central	Eastern
<i>Number of Stations</i>	15 (2)	34 (11)	18 (6)
Malacostraca (total)	40.8 $\pm$ 13.8	652.1 $\pm$ 257.2	1.1 $\pm$ 0.8
-Isopoda	0	645.4 $\pm$ 257.7	0.4 $\pm$ 0.4
- <i>Mysis diluviana</i>	0	0	0.7 $\pm$ 0.5
-Amphipoda	40.8 $\pm$ 13.8	6.8 $\pm$ 4.4	0
Chironomidae	388.3 $\pm$ 63.5	1287.4 $\pm$ 141.2	234.0 $\pm$ 109.2
Mollusca with <i>Dreissena</i> (total)	1645.6 $\pm$ 589.3	1472.8 $\pm$ 193.7	664.6 $\pm$ 207.3

Taxa	Western	Central	Eastern
-Sphaeriidae	200.1±72.7	1349.3±201.0	0
-Gastropoda	281.3±59.1	21.0±4.7	0.7±0.7
- <i>Dreissena polymorpha</i>	857.0±518.2 (757.3±460.4)	66.2±42.4 (55.1±32.2)	1.8±1.2 (10.9±7.1)
- <i>Dreissena rostriformis bugensis</i>	307.2±122.5 (272.9±110.2)	36.4±16.4 (70.1±31.8)	662.1±207.2 (755.2±259.5)
Oligochaeta (total)	546.0±132.3	5104.9±381.5	3852.0±432.7
-Enchytraeidae	2.1±2.1	1.1±0.6	0
-Lumbriculidae	0	5.1±2.6	72.6±45.7
-Naididae	3.8±1.2	96.0±24.5	45.3±19.4
-Tubificidae	535.4±132.1	4981.7±374.4	3687.0±431.3
<i>Hexagenia</i> spp.	339.9±122.7	0	0
Hirudinea	76.9±11.5	97.9±36.7	3.2±2.2
Platyhelminthes	7.7±4.2	24.7±7.0	3.9±1.6
Others	1.3±0.9	1.7±0.9	17.0±7.1
Total Benthos without <i>Dreissena</i>	1882.3±242.9	8538.9±612.5	4111.9±421.5
Total Benthos with <i>Dreissena</i>	3046.4±591.1	8641.0±610.8	4775.8±469.1

Table 4. Average ($\pm$ standard error) wet biomass (g m^{-2}) of major taxonomic groups and common species of benthic invertebrates collected in Lake Erie in 2024 (excluding Historic Western Basin stations) and averaged by basin. *Dreissena* spp. average biomass was calculated separately for “All-taxa” stations as well as for all stations combined (“All taxa” + “*Dreissena*-only” stations, in parentheses).

Taxa	Western	Central	Eastern
<i>Number of Stations</i>	15 (2)	34 (22)	18 (6)
Malacostraca (total)	0.06±0.02	0.63±0.23	<0.01
-Isopoda	0	0.62±0.22	<0.001
-Mysis	0	0	<0.01
-Amphipoda	0.06±0.02	<0.01	0
Chironomidae	1.05±0.28	11.38±1.71	0.20±0.07
Mollusca with <i>Dreissena</i> (total)	43.20±22.37	17.48±6.97	605.46±174.77
-Sphaeriidae	0.81±0.56	5.30±0.81	0
-Gastropoda	1.91±0.42	0.14±0.02	<0.001
- <i>Dreissena polymorpha</i>	25.90±16.45 (22.85±14.60)	6.40±3.77 (5.28±2.86)	1.35±0.94 (1.25±0.73)
- <i>Dreissena rostriformis bugensis</i>	14.58±6.54 (12.88±6.54)	5.63±3.58 (34.34±29.93)	604.11±174.58 (618.80±195.21)
Oligochaeta (total)	1.49±0.49	8.31±1.02	3.25±0.43
-Enchytraeidae	<0.0001	<0.001	0

Taxa	Western	Central	Eastern
-Lumbriculidae	0	0.02±0.01	0.16±0.10
-Naididae	<0.001	0.02±0.01	<0.01
-Tubificidae	1.41±0.49	7.79±1.02	1.93±0.29
Hexagenia	6.63±2.43	0	0
Hirudinea	0.20±0.04	0.15±0.06	<0.01
Platyhelminthes	0.01±0.01	0.03±0.01	<0.01
Others	<0.01	<0.001	0.02±0.01
Total Benthos without <i>Dreissena</i>	12.20±2.55	25.96±2.94	3.49±0.40
Total Benthos with <i>Dreissena</i>	52.68±22.10	38.00±6.70	608.95±174.90

Long-term changes in Lake Erie benthic community

Western Basin

Historically, the benthic community of the western basin was dominated by larvae of the mayfly *Hexagenia* spp. (Wright and Tidd, 1933; Shelford and Boesel, 1942; Britt, 1955; Wright, 1955; Manny, 1991, Table 5). During the first basin-wide study conducted in 1929-1930, eutrophication and the accumulation of organic matter in sediments were still localized, oligochaete density was very low, and coincided with high abundance of *Hexagenia*. Drastic degradation of water and sediment quality in the following decades led to increased densities of pollution-tolerant tubificids, chironomids, and sphaeriids, while pollution-sensitive species (e.g., mayflies, caddisflies, amphipods) declined (Carr and Hiltunen, 1965; Beeton, 1961, 1969). By 1961, when the second basin-wide survey was conducted, the average density of *Hexagenia* had fallen from 155 m⁻² to 1 m⁻², while the basin-wide density of oligochaetes increased sevenfold along with their relative abundance in the benthic community. The densities of chironomids, gastropods, and sphaeriids doubled in 1961, but their relative proportions in the benthos declined. In the 1970s, benthic invertebrate densities declined significantly, mainly due to a roughly twofold decrease in oligochaete density compared to 1961, while the densities of other taxa remained fairly stable. By 1982, benthic density had increased again, by a factor of 7 compared to 1979, reaching the highest levels recorded in the basin. As before, this increase was solely driven by a substantial rise in oligochaete density. In the next decade, following the invasion of zebra and quagga mussels, dreissenids became important members of the community. From 1982 to 2003, the density and relative abundance of oligochaetes decreased by a factor of 15, returning to levels seen before eutrophication in the 1930s. In 2024, Oligochaeta contributed the most to the increase in non-dreissenid benthos: their mean density reached 1600 m⁻², about double the 2014 and 2019 levels. *Hexagenia* showed early signs of recovery in 1982, with a basin-wide average density of 7 ± 4 m⁻², and by 2010, it reached 307 ± 41 m⁻², which was higher than the levels reported in 1930 (reviewed in Karatayev et al., 2022). Similar high density was recorded in 2024 (254 ± 80 m⁻²) (Table 5). Sphaeriidae also showed a substantial two-fold increase in densities, while Chironomidae, Gastropoda, and Hirudinea remain roughly stable. Over the past decade, the relative contribution of *Dreissena* to total benthic density declined from approximately 73% in 2014 to about 39% in 2019-2024, indicating a shift from a *Dreissena*-dominated state to a more balanced community structure.

Central Basin

In Lake Erie's central basin, bottom hypoxia remains the primary factor influencing benthic community structure (reviewed in Karatayev et al., 2022; Table 6). Historically, the central basin has consistently experienced seasonal hypoxia (Beeton, 1961, 1963; Delorme, 1982), but the extent of the hypoxic zone greatly increased in the 1950s and 1960s during cultural eutrophication and subsequently decreased after phosphorus reduction measures were implemented (Makarewicz and Bertram, 1991; Beeton, 1963; Bertram, 1993; Burlakova et al., 2017). Three main groups of invertebrates, oligochaetes, sphaeriids, and chironomids, typically contributed over 90% of the total benthic density in the central basin before the introduction of *Dreissena* spp. (Fig. 4). The lowest overall benthic invertebrate densities were observed in 1973. By the following survey in 1978, benthic density increased by about 50%, and by 1979, it more than doubled the densities seen in 1973.

Over the following four decades (1979-2019), the density of major taxa in the central basin remained relatively stable, except for the 1990s, likely due to improvements in the oxygen regime, dreissenid density briefly exceeded 20% of all benthos (Karatayev et al., 2022). Since the beginning of the 2000s, however, dreissenid densities in the basin have been declining, and in the last two surveys (2019 and 2024), they comprised <4% of the total benthic density, indicating worsening hypoxic conditions. The relative contribution of *Dreissena* to total benthic density has declined from 5.2% in 2014 to 1.2% in 2024. Analysis of benthic densities over the past decade indicated a decline in benthos from $11611 \pm 1343 \text{ m}^{-2}$ (2014) to $7967 \pm 487 \text{ m}^{-2}$ (2024) (Table 6). Overall, these data indicate that from 2014 to 2024, the central basin shifted toward a community with fewer *Dreissena* and lower overall densities, primarily due to declines in Oligochaeta, whereas the densities of Chironomidae, Sphaeriidae, and Hirudinea increased slightly. Other groups (Amphipoda, Gastropoda) remained consistently low.

Eastern Basin

The eastern basin is the deepest and most oligotrophic basin of Lake Erie and has a historically well-oxygenated hypolimnion (Kemp et al., 1977; Mortimer, 1987; Karatayev et al., 2018). In the 1960s and 1970s, the eastern basin supported deep, cold-water oligotrophic benthic crustaceans *Diporeia* and *Mysis diluviana*, as well as the oligotrophic lumbriculid *Stylodrilus heringianus* (Beeton, 1965, 1969; Cook and Johnson, 1974; Flint and Merckel, 1978, Table 6). Oligochaetes were the dominant group by density from 1973 to 1979, comprising 63-85% of the entire benthic density, followed by sphaeriids (8-21%), and chironomids (5-10%). Other taxa made up less than 1% of the benthic density. Most major taxa in the eastern basin, except Chironomidae, showed significant interannual variation, including *D. polymorpha*, *D. r. bugensis*, oligochaetes, and sphaeriids (Karatayev et al., 2022).

Dreissenids became the second most abundant component of eastern basin benthos in the 1990s (Burlakova et al., 2014). In 1992, *D. polymorpha* had already reached its maximum density ($4544 \pm 2120 \text{ m}^{-2}$), causing significant changes in the entire community. *Diporeia* density declined, and the species was not reported after 1992 (Dahl et al., 1995; Dermott and Kerec, 1997; Dermott and Dow, 2008). Other changes associated with the introduction of dreissenids included a decline in sphaeriids and an increase in non-*Diporeia* amphipods, gastropods, and chironomids (Dermott and Kerec, 1997). Initially, *D. polymorpha* dominated until 1998, when it was nearly completely outcompeted by *D. r. bugensis*, which peaked in 2002 (Patterson et al., 2005; Karatayev et al., 2014, 2021a, 2021b).

The decline in non-dreissenid benthos during the 2010s was unexpected and was primarily driven by reduced densities of oligochaetes, amphipods, gastropods, sphaeriids, and leeches. This decline may be due to increased consumption of benthic invertebrates by round gobies, whose densities

dramatically increased in the basin between 1999 and 2002 (Barton et al., 2005; Johnson et al., 2005; Karatayev et al., 2022). Although non-dreissenid benthos has partially recovered after 2019, key sensitive groups such as Amphipoda, Gastropoda, and Sphaeriidae remain low, and *Diporeia* continues to be absent. A partial recovery of Oligochaeta primarily drives the recent slight increase in non-dreissenid benthos, while Chironomidae keep declining. The eastern basin also experienced declines in dreissenid benthic densities from 2014 to 2024, mainly due to a 3-fold decline in *D. r. bugensis*. Overall, these patterns suggest an ongoing structural shift in the eastern basin community toward a less *Dreissena*-dominated state, but with key deep-water taxa not fully recovered.

Long-term changes in benthos at Historical Western Basin stations

In 2024, the average benthic density at the HWB was the highest since 2003 ($7949 \pm 3304 \text{ m}^{-2}$). Dreissenids made up about 39% of the total benthos and were observed at the highest density ($3111 \pm 1614 \text{ m}^{-2}$) in the western basin across all years (Table 8). Ninety-four percent of all dreissenids were *D. r. bugensis*, in contrast to the results of a larger survey conducted in the summer of 2024, where *D. polymorpha* were dominant. This could be due to sampling season, depth, or location. The HWB stations were sampled in May, are shallower (5.8 m vs. 10.6 m), and located in the westernmost part of the lake. Overall, the dominance of *Dreissena* species has varied in the last two decades (Table 8).

In 2024, we identified 63 species and higher taxa of benthic macroinvertebrates from the historic western basin stations in Lake Erie. The most diverse groups were Oligochaeta (23 species and higher taxa), Chironomidae (15 species and higher taxa), Mollusca (14 species and higher taxa), and Hirudinea (4 species and higher taxa). Among Oligochaeta, Tubificidae was the most diverse with 13 species and higher taxa, followed by Naididae (10). The most widespread taxa found at the HWB stations were the chironomids *Coelotanytus* sp. and *Procladius* sp., recorded at 89% of stations. *D. r. bugensis* attained the highest density (Table 8) and biomass (115 g m^{-2} , 75% of total benthos biomass), followed by *D. polymorpha* (21 g m^{-2} , 14%). Oligochaetes were the most prevalent taxonomic group, accounting for 42% and 75% of the total benthos with and without *Dreissena*, respectively.

Table 5. Average density (ind. m⁻²) of major taxa and common species of benthic invertebrates (mean $\pm$ standard error) in the western basin of Lake Erie (including Historical Western Basin stations). For the data sources, see Karatayev et al., 2022. Average *Dreissena* density in 2002 from Patterson et al. (2005). *Dreissena* spp. average density was calculated for all stations combined (“All taxa” + “*Dreissena*-only” stations, total number of stations in parentheses).

Taxa	1930	1961	1970	1973	1979	1982	1992	1993
<i>Stations sampled</i>	<i>N</i> = 67	<i>N</i> = 40	<i>N</i> = 12	<i>N</i> = 13	<i>N</i> = 52	<i>N</i> = 40	<i>N</i> = 10	<i>N</i> = 11
Amphipoda	NA	12 $\pm$ 4	55 $\pm$ 28	5 $\pm$ 5	6 $\pm$ 3	5 $\pm$ 3	.	46 $\pm$ 9
Chironomidae	137 $\pm$ 32	355 $\pm$ 46	341 $\pm$ 108	544 $\pm$ 107	419 $\pm$ 42	538 $\pm$ 59	.	416 $\pm$ 47
<i>D. polymorpha</i>	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	839 $\pm$ 620	1201 $\pm$ 615
<i>D. r. bugensis</i>	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	2 $\pm$ 2	8 $\pm$ 8
Gastropoda	66 $\pm$ 12	159 $\pm$ 45	104 $\pm$ 79	51 $\pm$ 33	4 $\pm$ 2	22 $\pm$ 8	.	.
<i>Hexagenia</i>	155 $\pm$ 24	1	0 $\pm$ 0	.	1 $\pm$ 1	7 $\pm$ 4	.	10 $\pm$ 2
Hirudinea	64 $\pm$ 16	31 $\pm$ 7	51 $\pm$ 27	22 $\pm$ 5	23 $\pm$ 6	13 $\pm$ 4	.	11 $\pm$ 2
Oligochaeta	1163 $\pm$ 520	5990 $\pm$ 1292	2699 $\pm$ 724	2893 $\pm$ 349	1614 $\pm$ 259	12410 $\pm$ 2336	.	5801 $\pm$ 2521
Sphaeriidae	307 $\pm$ 83	600 $\pm$ 117	403 $\pm$ 213	231 $\pm$ 86	347 $\pm$ 114	227 $\pm$ 31	.	.
All Benthos	1891	7159 $\pm$ 1308	3653 $\pm$ 937	3748 $\pm$ 423	2414 $\pm$ 274	17068 $\pm$ 3160	.	9437
Benthos w/o <i>Dreissena</i>	1891	7159 $\pm$ 1308	3653 $\pm$ 937	3748 $\pm$ 423	2414 $\pm$ 274	17068 $\pm$ 3160	.	8228 $\pm$ 3257

Taxa	2002	2003	2004	2010	2014	2019	2024
<i>Stations sampled</i>	<i>N = 49</i>	<i>N = 60</i>	<i>N = 87</i>	<i>N = 31</i>	<i>N = 52</i>	<i>N = 26 (29)</i>	<i>N = 24 (26)</i>
Amphipoda	.	60±27	.	27±12	221±78	33±7	68±23
Chironomidae	.	353±35	.	628±69	263±58	556±107	443±62
<i>D. polymorpha</i>	270±127	NA	357±88	42±16	369±122	843±270	557±306
<i>D. r. bugensis</i>	258±123	NA	1105±177	1349±608	2475±1317	393±118	1193±591
Gastropoda	.	14±5	.	141±24	248±120	242±77	239±50
<i>Hexagenia</i>	.	295±56	.	307±41	234±35	121±29	254±80
Hirudinea	.	14±3	.	63±11	87±24	88±21	88±20
Oligochaeta	.	1158±133	.	1924±443	751±210	770±169	1600±676
Sphaeriidae	.	91±23	.	148±58	91±20	104±33	245±97
All Benthos	.	NA	.	4743±903	3917	3199±501	4833±1329
Benthos w/o <i>Dreissena</i>	.	2082±187	.	3351±579	2231±503	1962±251	2939±824

Table 6. Average density (ind. m⁻²) of major taxa and common species of benthic invertebrates (mean ± standard error) in the central basin of Lake Erie. For the data sources see Karatayev et al., 2022. Average *Dreissena* density in 2002 from Patterson et al. (2005). *Dreissena* spp. average density was calculated for all stations combined (“All taxa” + “*Dreissena*-only” stations, total number of stations in parentheses).

Taxa	1973	1978	1979	1992	1993	2002	2004	2014	2019	2024
<i>Stations sampled</i>	<i>N</i> = 36	<i>N</i> = 52	<i>N</i> = 17	<i>N</i> = 22	<i>N</i> = 20 (24)	<i>N</i> = 41	<i>N</i> = 121	<i>N</i> = 42	<i>N</i> = 32 (49)	<i>N</i> = 34 (45)
Amphipoda*	1±0	4±3	0±0	10±6	169±52	.	.	29±26	29±23	7±4
Chironomidae	335±68	343±75	436±85	1315±314	983±269	.	.	1073±244	1151±198	1287±141
<i>Diporeia</i>	2±2	3±1	0±0	NA	2±2	.	.	0±0	0±0	0±0
<i>D. polymorpha</i>	0±0	0±0	0±0	997±604	767±226	25±10	5±2	15±7	27±16	55±32
<i>D. r. bugensis</i>	0±0	0±0	0±0	134±83	1980±668	540±200	350±88	593±223	357±196	70±32
Gastropoda	8±3	29±22	7±5	12±5	30±15	.	.	25±8	25±6	21±5
Hirudinea	3±2	10±4	2±2	6±4	4±4	.	.	24±8	83±28	98±37
Oligochaeta	2531±275	3460±453	7183±1861	4993±892	6935±1341	.	.	7856±1284	5978±709	5105±381
Sphaeriidae	554±78	1098±131	702±205	930±215	579±236	.	.	1114±245	1229±204	1349±201
All Benthos	3519±331	5227±539	8414±1972	8704	11521	.	.	11611±1343	9440±1241	7967±487
Benthos excluding <i>Dreissena</i>	3519±331	5227±539	8414±1972	7573±1107	8774±1508	.	.	11002±1485	9056±1063	7867±486

*excluding *Diporeia*

Table 7. Average density (ind. m⁻²) of major taxa and common species of benthic invertebrates (mean ± standard error) in the eastern basin of Lake Erie. For the data sources, see Karatayev et al., 2022. Average *Dreissena* density in 2002 as reported by Patterson et al. (2005). *Dreissena* spp. average density was calculated for all stations combined (“All taxa” + “*Dreissena*-only” stations, total number of stations in parentheses).

Taxa	1974	1976	1978	1992	1993	1998	2002	2004	2014	2019	2024
<i>Stations sampled</i>	<i>N</i> = 26	<i>N</i> = 25	<i>N</i> = 37	<i>N</i> = 15	<i>N</i> = 10 (10)	<i>N</i> = 13 (15)	<i>N</i> = 17	<i>N</i> = 76	<i>N</i> = 28 (43)	<i>N</i> = 19 (24)	<i>N</i> = 18 (24)
Amphipoda*	232±60	76±34	21±13	237±138	2±1	561±328	.	.	86±47	2±1	0±0
Chironomidae	255±34	430±115	373±100	1319±1088	293±182	1353±606	.	.	633±207	293±182	234±109
<i>Diporeia</i>	1313±339	1754±556	787±196	90±77	0±0	0±0	.	.	0 ± 0	0±0	0±0
<i>D. polymorpha</i>	0±0	0±0	0±0	4544±2120	1203	502±390	0±0	0±0	4±3	2±2	11±7
<i>D. r. bugensis</i>	0±0	0±0	0±0	1463±484	3615	5284±2071	9481±2710	1622±290	2283±468	1011±181	755±260
Gastropoda	NA	130±45	27±11	237±147	1±1	1016±678	.	.	3±2	1±1	1±1
Hirudinea	NA	67±29	48±14	32±22	0±0	204±155	.	.	1±1	0±0	3±2
Oligochaeta	4658±1006	9567±3936	3901±609	16926±3912	2972±519	18121±6958	.	.	5552±795	2972±519	3852±433
Sphaeriidae	1104±207	1074±179	425±66	517±257	0±0	182±97	.	.	20±19	0±0	0±0
All Benthos	7905±1167	14015±3988	6131±723	25776	4354	57757	.	.	8842	4314±620	4754±466
Benthos excluding <i>Dreissena</i>	7905±1167	14015±3988	6131±723	19769±3723	3301±530	51971±12936	.	.	6555±887	3301±530	4090±419

*excluding *Diporeia*

Over the period from 1930 to 2024, the average benthic density excluding *Dreissena* at historical stations fluctuated by 7-8-fold (Table 9). The lowest benthic density was recorded in 1930 (1737 m⁻²), but it increased in the following decades to 7008 m⁻² by 1961 and to 13211 m⁻² by 1982, which was the highest basin-wide benthic density recorded before the introduction of *Dreissena* spp. Between 1982 and 2003, non-dreissenid benthos decreased by 5.3-fold and has fluctuated since. The density of Oligochaeta was the primary contributor to overall non-dreissenid benthic abundance, peaking in 1982. Densities of all other major groups (Chironomidae, Gastropoda, *Hexagenia*) fluctuated during this period but, overall, remain higher than in the 1930s (Table 9). The 1930 survey reported robust *Hexagenia* densities (on average 162 m⁻²); however, by 1961, they were nearly extirpated and remained low until 1993 (reviewed in Karatayev et al., 2022). In the early 2000s, *Hexagenia* densities increased, peaked in 2010, and have since declined (Table 9). Again, this is in contrast to the results of a larger survey conducted in the summer of 2024, which reported the 3rd highest *Hexagenia* densities during the whole period of observation (Table 5).

Table 8. Average density (ind. m⁻²) of major taxa and common species of benthic invertebrates (mean ± standard error) recorded at the nine consistently sampled historical stations in the western basin of Lake Erie (1930–2024). Historical data from Kennedy et al. 2023, Schloesser et al. 2017, and Karatayev et al., 2022.

Taxa	2003*	2010*	2014**	2019***	2024***
Amphipoda	74.9±59.5	73.3±43.0	77.7±23.8	30.5±15.3	113.8±54.7
Chironomidae	435.6±78.1	687.5±183.5	605.3±145.6	573.1±66.6	533.8±127.7
Mollusca with <i>Dreissena</i>	132.6±69.9	2325.7±1801.7	3660.5±1930.7	2672.1±1151.5	3601.9±1812.2
Sphaeriidae	86.1±58.8	257.4±191.2	220.0±143.6	59.3±42.2	320.6±236.7
Gastropoda	46.5±30.8	168.4±65.9	478.1±205.9	371.9±204.3	169.9±88.1
<i>Dreissena</i> spp.	0	1899.9±1776.1	2962.4±1777.4	2240.9±974.2	3111.4±1614.3
<i>Dreissena polymorpha</i>	0	61.1±33.0	794.7±463.8	1572.5±758.7	179.5±128.1
<i>Dreissena rostriformis bugensis</i>	0	1838.8±1750.7	2167.8±1317.0	668.4±322.2	2931.8±1588.7
Oligochaeta	1266.3±446.0	3383.6±1472.6	1894.7±865.4	1018.0±371.8	3358.2±1685.1
Lumbriculidae	0	0	0	4.81±4.81	0
Naididae	28.4±28.4	182.6±180.1	159.5±158.1	2.6±2.2	176.3±171.0
Tubificida	1237.9±427.6	3201.0±1313.6	1735.2±788.2	1010.7±372.6	3148.2±1584.9
Hexagenia	253.1±118.8	501.0±94.5	299.6±98.4	152.3±75.8	110.6±31.2
Hirudinea	22.4±11.9	64.6±23.4	37.5±15.9	42.5±15.6	107.4±52.3
Platyhelminthes	15.5±9.9	52.6±38.3	77.4±50.5	16.0±4.5	85.0±34.0
Others	5.2±4.3	0.9±0.9	0	6.4±6.4	8.0±4.9
Total Benthos without <i>Dreissena</i>	2205.5±567.4	5189.3±1747.1	3690.2±1111.8	2270.0±331.2	4837.7±2117.3
Total Benthos with <i>Dreissena</i>	2205.5±567.4	7089.1±2801.7	6652.6±2209.2	4510.9±1115.01	7949.1±3304.1

* - Kennedy et al. 2023, ** - Schloesser et al. 2017, *** - our data

Table 9. Average density of major taxa and common species of benthic invertebrates (excluding *Dreissena*) recorded at the nine consistently sampled historical stations in the western basin of Lake Erie (1930–2024). Historical data from Schloesser et al 2017 and Karatayev et al., 2022.

Taxa	1930	1961	1982	1993	2003	2010	2014	2019	2024
Oligochaeta	1379	6102	12354	7593	1266	3384	1895	1018	3358
Chironomidae	17	162	601	538	436	688	605	573	534
Hexagenia	162	<1	2	13	253	501	300	152	111
Sphaeriidae	149	577	241	281	86	257	220	59	321
Gastropoda	30	167	14	26	47	168	478	372	170
Total	1737	7008	13211	8451	2088	4998	3498	2175	4493

Dreissena long-term population dynamics

D. 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 1992, their combined densities across all basins were already high ($842 \pm 620 \text{ m}^{-2}$ in the western, $1131 \pm 679 \text{ m}^{-2}$ in the central, and $6003 \pm 2093 \text{ m}^{-2}$ in the eastern basins, Karatayev and Burlakova, 2017). Since these initial peaks in the late 1990s - early 2000s, the combined density and wet biomass of dreissenids continued to decline in all basins except in the western basin, where density fluctuates (Fig. 2).

In the western basin, *Dreissena* biomass has been steadily declining since 2004; however, the density has not followed that same pattern. This could indicate larger mussel die-offs and a shift toward smaller, newly settled mussels due to occasional episodes of severe oxygen depletion following temporary thermal stratification typical of the western basin (Ackerman et al., 2001; Bridgeman et al., 2006; Karatayev et al., 2018). This trend continued in 2024, with the lowest *Dreissena* biomass ever recorded in the basin since invasion ($34 \pm 30 \text{ g m}^{-2}$, Table 4, Fig. 2). After an initial peak in 1993, *D. polymorpha* density declined, and *D. r. bugensis* became dominant in the early 2000s. In 2019, however, *D. polymorpha* again attained a higher density than *D. r. bugensis* (Karatayev et al., 2021a). In 2024, the relative abundance of *D. polymorpha* further increased; moreover, their biomass also exceeded that of the quagga mussel. The shift from quagga to zebra mussel dominance is rare and may signal large-scale environmental changes that require further monitoring (Figs. 2 and 3).

In the central basin, the combined density and biomass of *Dreissena* were highest in the late 1990s, declined in the early 2000s, and have not changed substantially since (Fig. 2; Karatayev et al., 2018, 2021a). *D. polymorpha* density had steadily declined since the first lake-wide study in 1992, and by 1998, it had almost disappeared from the basin. Conversely, *D. r. bugensis* density increased throughout the 1990s, peaking in 1998 ($2958 \pm 1111 \text{ m}^{-2}$), but then declined nearly fivefold by 2002 and remained low (Fig. 3), indicating worsening hypoxia in the basin. The dreissenid density in this basin reached its lowest in 2024 since 1992, and the current *D. r. bugensis* abundance (density $70 \pm 32 \text{ m}^{-2}$ and biomass $34 \pm 30 \text{ g m}^{-2}$) was at its lowest over the entire monitoring period (Table 2, 3).

In the eastern basin during the first survey in 1992, dreissenids were already extremely abundant (over $6,000 \text{ m}^{-2}$) and dominated by *D. polymorpha*. By 1993, *D. r. bugensis* outcompeted *D. polymorpha*, which continued to decline, while *D. r. bugensis* peaked in 2002 (Fig. 3). This high

abundance may have been partly due to an overrepresentation of bedrock habitats heavily colonized by mussels in the 2002 survey (Patterson et al., 2005), while following surveys have largely excluded these habitats (Karatayev et al., 2014, 2022). Surveys in 2004 showed a sharp decline of *D. r. bugensis* in the basin, and densities have remained stable since (Fig. 3). In 2024, *D. r. bugensis* density and biomass ($755 \pm 260 \text{ m}^{-2}$ and $619 \pm 195 \text{ g m}^{-2}$) reached the lowest values since the species was first recorded in 1992. The declines in dreissenid abundance in the eastern and central basins could be driven by predation pressure from round gobies, first reported in 1994 (Johnson et al., 2005) and peaking in 2000-2010 (Sinclair et al., 2021; NYSDEC, 2021).

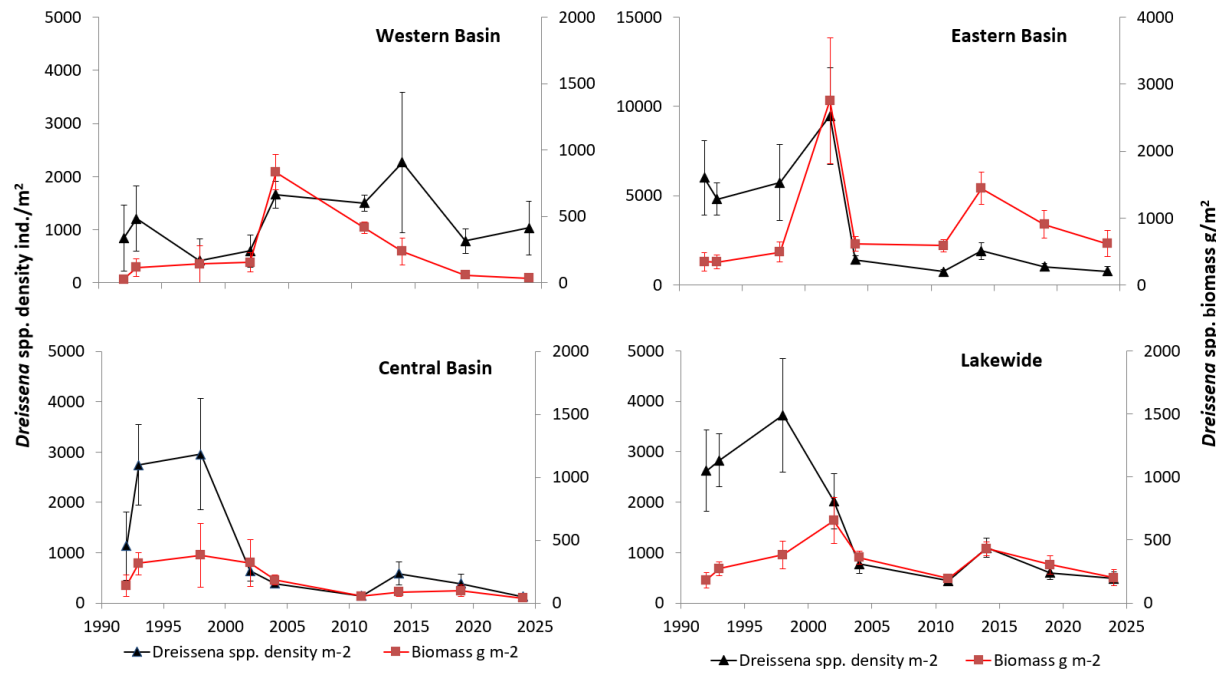


Fig. 2. Long-term dynamics of combined *Dreissena* spp. density (in black) and total wet biomass (in red) in Lake Erie (averages for all survey stations with standard errors). Data represent a variety of sampling stations and differing sampling methods over the years (1992-1998: Jarvis et al., 2000; 2002: Patterson et al., 2005, 2004: Karatayev et al., 2014, 2009-2011: average for 2009, 2011, 2012, Karatayev et al., 2014, 2014 – 2024: all taxa and *Dreissena* only stations from CSMI and LTM surveys, excluding HWB stations, Karatayev et al., 2022, and this report).

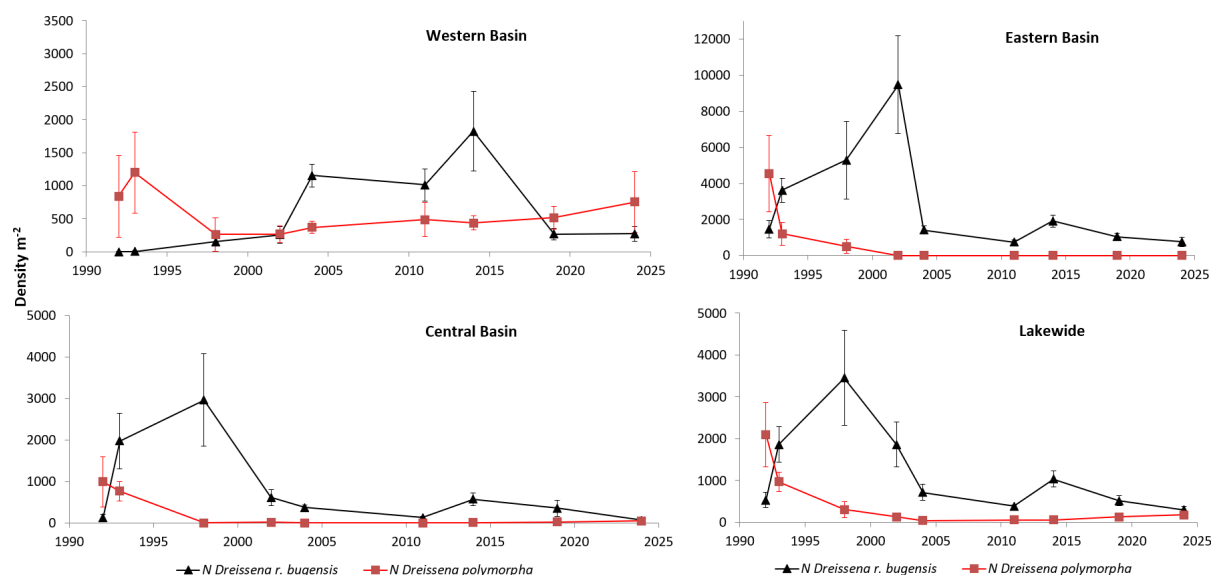


Fig. 3. Long-term dynamics of *Dreissena polymorpha* (in red) and *D. r. bugensis* (in black) density in Lake Erie (basin averages with standard errors). Data represent a variety of sampling stations and differing sampling methods over the years (1992-1998: Jarvis et al., 2000; 2002: Patterson et al., 2005; 2004: Karatayev et al., 2014; 2009-2011: average for 2009, 2011, 2012, Karatayev et al., 2014; 2014-2024: combined all taxa stations and *Dreissena* only stations from CSMI and LTM surveys (excluding HWB stations), Karatayev et al., 2022, and this report).

Dreissena population assessment using BIS

Similar to 2019, the 2024 *Dreissena* population assessment using the BIS showed strong predictive power for rapid density estimates. According to the BIS rapid assessment, *Dreissena* density in 2024 compared to 2019 declined by 5.7-fold in the central basin and by 1.7-fold in the eastern basin, whereas it increased by 9.2-fold in the western basin. In comparison, Ponar-based estimates between 2024 and 2019 indicated a 3-fold decrease in the central basin, a 1.3-fold decrease in the eastern basin, and a 1.4-fold increase in the western basin (Table 10).

Table 10. *Dreissena* population density (ind. m⁻², average ± standard error) in depth zones and basin-wide averages estimated using Ponar grab in 2014 and 2019, and BIS in 2019 and 2024.

Depth zone, m	2019 Ponar	2019 BIS	2019 Ponar to BIS ratio	2024 Ponar	2024 BIS	2024 Ponar to BIS ratio
≤20 Eastern	612.9±213.2	666.6±320.9	0.92	360.7±263.3	621.4±376.1	0.58
>20-40 Eastern	1206.0±358.9	554.4±212.1	2.2	866.8±489.2	420.0±226.7	2.06
>40 Eastern	1130.0±239.4	1760.7±458.9	0.6	881.1±385.8	750.8±226.2	1.17
Basin-wide Eastern	1032±179	977.9±221.5	1.05	766.0±259.2	570.1±145.6	1.34
≤20 Central	290.0±87.7	563.2±265.1	0.5	242.8±105.6	100.0±61.4	2.4
>20-40 Central	466.0±364.0	7.9±5.3	59.0	22.3±12.9	0.2±0.2	111.5
Basin-wide Central	383±196	261.4±126.4	1.5	125.0±51.8	45.8±31.3	2.7
Basin-wide Western*	1236.0±352.2	18.1±9.8	68.3	1750.6±661.5	166.6±150.5	10.5

* - including HWB stations

The discrepancies between BIS and Ponar data in the western and central basin were most likely due to high turbidity and a large proportion of juvenile mussels (< 10 mm) that were very hard to detect on video images (Karatayev et al., 2021a).

Dreissena coverage was estimated using the BIS in both 2019 and 2024. In 2024, the highest coverage was observed in the eastern basin, exceeding that in the central and western basins by 10.5- and 6.2-fold, respectively. In the eastern basin, the highest *Dreissena* coverage was observed at depths >40 m (Table 11, Fig. 3). Current *Dreissena* coverage in the eastern and central basins declined by 2- and 4-fold, respectively, compared to 2019, but, due to large variation, the differences were not statistically significant.

Table 11. Average *Dreissena* coverage (percent of frame area occupied by mussels, $\pm$ standard error) by depth zones and basin-wide estimated using BIS in 2019 and 2024. Basin-wide *Dreissena* coverages that were not significantly different between 2019 and 2024 are identified with identical letters (A, Kruskal-Wallis test, $P < 0.05$).

Depth zone, m	2019	2024
≤ 20 Eastern basin	18.4 $\pm$ 10.6	11.4 $\pm$ 6.2
>20-40 Eastern basin	15.2 $\pm$ 6.7	7.9 $\pm$ 3.5
>40 Eastern basin	40.5 $\pm$ 7.7	19.9 $\pm$ 6.1
Basin-wide Eastern basin	24.3 $\pm$ 5.1 ^A	12.6 $\pm$ 3 ^A
≤ 20 Central basin	9.9 $\pm$ 4.8	2.5 $\pm$ 1.7
>20-40 Central basin	0.04 $\pm$ 0.02	0.01 $\pm$ 0.01
Basin-wide Central basin	4.5 $\pm$ 2.3 ^A	1.2 $\pm$ 0.8 ^A
Basin-wide Western basin	0.3 $\pm$ 0.23 ^A	2.02 $\pm$ 1.54 ^A

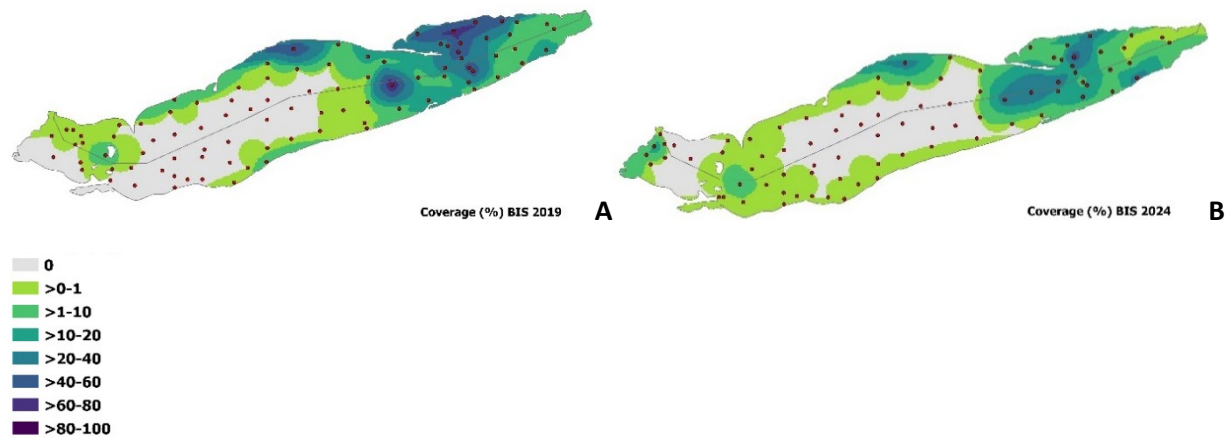


Fig. 3. Coverage (%) of Lake Erie bottom with *Dreissena* based on BIS survey in 2019 (A) and 2024 (B)

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