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LAKE ONTARIO BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2023

Technical Report



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November 2024

Suggested citation for the report:

Burlakova, L. E., A. Y. Karatayev, N. V. Barulin. S. E. Daniel, O. N. Makhutova, L. N. Denecke. 2024. Lake Ontario Benthos Survey Cooperative Science and Monitoring Initiative 2023. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State University, Buffalo, NY. Available at:

https://greatlakescenter.buffalostate.edu/sites/glc/files/documents/LakeOntarioBenthosSurve yCSMI2023FinalReport.pdf

REPORT: LAKE ONTARIO BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2023

Lake and Year: Ontario, 2023

Lead Organization: SUNY Buffalo State University

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Project Overview

In this report, we present results of a benthic survey of Lake Ontario 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 2023 in Lake Ontario to assess the status of the benthic macroinvertebrate community. This study advanced the Lake Ontario CSMI priority of monitoring and understanding Lake Ontario's lower food web. The primary focus of this survey was to assess the status of benthic community, as well as distribution, abundance, and long-term trends in invasive mussels *Dreissena* spp.

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Study Highlights

- 78 species and higher taxa of benthic macroinvertebrates were found in Lake Ontario in 2023. The
 most diverse and most widely occurred taxa throughout the lake were Oligochaeta (36 taxa),
 representing 38% of lake-wide density, followed by Chironomidae (28 taxa, 5%). The structure of
 benthic community in 2023 was not different from that in 2018, and no consistent trends were
 found in densities of oligochaetes or chironomids.
- Diporeia hoyi, an indicator species to assess the state of the Great Lakes, was absent from all sampling stations in Lake Ontario in 2023. The declines in *Diporeia* started in early 2000s, and densities were very low in 2003-2018 CSMI surveys and in 2018-2022 samples collected by the U.S. EPA's Great Lakes Biology Monitoring Program.
- The invasive gastropod *Potamopyrgus antipodarum* was collected again in Lake Ontario, where researchers first reported it in the Great Lakes region in 1991.
- Although the lake-wide density and biomass were small (2 ind. m⁻² and 0.01 g m⁻²), it contributed 79% to the total lake-wide gastropod density.
- Exotic bivalve Dreissena rostriformis bugensis was found at 96% of all stations and comprised 56% of lake-wide benthos density and 99.8% of total wet biomass. Dreissena lake-wide density in 2023 was 2710 ± 274 ind. m⁻² and biomass 1054 ± 136 g m⁻². The highest dreissenid density and biomass were found between 50 and 90 m depths. There was a slight decline in both Dreissena density and biomass in 2023 compared to 2018, but the decline was not significant. Overall, Dreissena population in Lake Ontario has likely reached its carrying capacity and appears to have stabilized.
- In 2023, over 26% of the Lake Ontario lakebed was covered by *Dreissena*, with the highest average coverage occurring in the 50 90 m depth zone and the lowest coverage found at depths greater than 90 m. The relationships between *Dreissena* coverage, density recorded by video method, as well as Ponar-estimated *Dreissena* density and biomass were strong and statistically significant. There were no significant differences between *Dreissena* coverage in 2018 and 2023.
- We found no significant differences between *Dreissena* densities estimated by Ponar and by video method across the lake (2127 ± 205 ind. m⁻²) or within each depth zone (*P* > 0.05). This suggests that underwater videography could serve as an effective tool for rapid population assessment of *Dreissena*.

Project: Major findings from the CSMI benthic macroinvertebrate survey in Lake Ontario in 2023

Overview

- A lake-wide benthic survey of Lake Ontario was conducted in 2023 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 CSMI surveys, benthic samples were collected at 69 stations to assess the status of the benthic macroinvertebrate community.
- Lake Ontario has a long history of nearly 60 years of lake-wide benthic surveys. In total, 14 lake-wide benthic surveys have been conducted in Lake Ontario (1964, 1972, 1977, 1990, 1994, 1995, 1997-1999, 2003, 2008, 2013, 2018, and 2023) (Hiltunen, 1969; Nalepa and Thomas, 1976; Golini, 1979; Lozano et al., 2001; Dermott and Geminiuc, 2003; Watkins et al., 2007; Birkett et al., 2015; Nalepa and Baldridge, 2016; Burlakova et al., 2022). Burlakova et al. (2022) describe the transformation of the benthic community over the last six decades by three major periods defined by *Dreissena* invasion. The first pre- and early *Dreissena* period (1964-1990) was characterized by high densities of *Diporeia*, Sphaeriidae, and Tubificidae. The second period (1990-2000) was defined by *D. polymorpha* dominance when *Diporeia*, Sphaeriidae, and Tubificidae remained abundant yet showed signs of decline. The third, ongoing period started in 2000 was characterized by *D. r. bugensis* (quagga mussels) dominance. The proliferation of quagga mussels resulted in the functional disappearance of *Diporeia*, and a decline in Sphaeriidae, while the densities of quagga mussels, Oligochaeta, and Chironomidae increased.
- In 2018 our lake-wide survey of benthic macroinvertebrates in Lake Ontario recorded 76 taxa (species, genera or higher taxa) of benthic macroinvertebrates (Karatayev et al., 2021b). The most diverse were Oligochaeta (33 species and higher taxa), and Insecta (Chironomidae, 28). *Dreissena r. bugensis* comprised a large percentage of lake-wide benthos densities (67%), followed by Oligochaeta (28%), and by Chironomidae (5%), while the contribution of all other groups was <1% each. Among Oligochaeta, the 8 most numerous were Tubificinae (79%) and Lumbriculidae (19%). *Dreissena r. bugensis* dominated lakewide benthos by biomass (99.8% of total wet biomass), followed by Oligochaeta (0.15%) and Chironomidae (0.02%).
- The objective of this study was to advance the understanding of Lake Ontario's lower food web and to describe the status and trends in benthic community, with a special 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 Ontario in 2023, including information on sampling design (station locations, sampling and laboratory procedures), the taxonomy and abundance of benthic invertebrates, results of video surveys, and changes in *Dreissena* populations.

Methods

Sampling protocol

A total of 206 benthic samples from 69 stations were analyzed for benthic macroinvertebrates in this study: 179 samples from 60 CSMI stations and 27 samples from 9 GLBMP long-term monitoring stations (Fig. 1, Table 1). 58 CSMI stations were sampled in September 11 - 17, 2023; GLBMP stations and 2 CSMI stations (ON 12 and ON 33M) were sampled in August 14 - 16, 2023, aboard the U.S. EPA R/V *Lake Guardian*. All samples were collected using a standard Ponar grab (sampling area 0.0523 m⁻²; coefficient 19.12) (US EPA, 2023). Benthic samples from 19 shallow planned stations were not collected due to hard substrates or survey logistical constraints. 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 placed into a collection jar and preserved with neutral buffered formalin with 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 LG407 (US EPA, 2021a).



Fig. 1. Location of 69 successful Ponar benthic stations and 15 stations where only video was collected using Benthic Imaging System (BIS) surveyed in Lake Ontario in 2023. The map indicates the locations of 60 CSMI benthic stations (red), 15 CSMI BIS only stations where Ponars were unsuccessful due to hard substrate (blue), and 9 GLBMP long-term monitoring (LTM) benthic stations (green).

Table 1. A list of all planned 88 stations, including 60 CSMI stations sampled on Lake Ontario in July and August 2023, 9 GLBMP long-term monitoring benthic stations sampled in August 2023 (denoted by *), and the 19 CSMI stations where either Ponars or video or both were not collected, along with information on location (decimal degrees), water depth, main substrates, and sample type (benthic Ponar or video collected with Benthic Imaging System, BIS). Only video samples were collected at 15 stations (OCS62, OCS71b, OCS84, OCSDD2, OCSDD4, OCSDD5, OCSDD6, OCSDD7, OCSDD8, OCSDD9, OCSDD10, OCSDD13, OCSDD14, OCSDD15, and OCSDD17; highlighted in grey) due to unsuccessful Ponars. Additionally, stations OCS29, OCS42, OCS43, and OCS66 were cancelled due to an error in their coordinates. In total, 206 successful benthic samples were collected from 69 stations, and 246 successful video samples from 82 stations. NA = not available.

Station	Latitude	Longitude	Depth (m)	Substrate	Ponar	BIS
OCS6	43.4661	-79.5356	63	sand and shells	+	+
OCS8	43.6231	-79.4528	15	silt and shells	+	
OCS9	43.5867	-79.395	60	silt and shells	+	+
OCS14	43.3936	-79.4872	100	silt and shells	+	+
OCS16	43.2714	-79.36	63.2	sand, silt, and shells	+	+
OCS17	43.2247	-79.2719	12	sand, silt, and shells	+	+
OCS18	43.3036	-79.2781	86	silt	+	+
OCS19	43.3836	-79.2853	106.4	silt and shells	+	+
OCS22	43.2967	-79.0058	12	sand	+	
OCS24	43.4394	-79.1281	121.6	silt and shells	+	+
OCS26	43.6078	-79.0158	117	clay, silt, and shells	+	+
OCS27	43.69	-78.83	103.2	sand, clay, silt, and shells	+	+
OCS28	43.775	-78.855	62.5	sand and shells	+	+
OCS29	43.8183	-78.87	NA	cancelled		
OCS32	43.7831	-78.4356	75.9	sand, clay, silt, and shells	+	+
OCS34	43.4611	-78.7594	136.1	sand, clay, silt, and shells	+	+
OCS35	43.3619	-78.7294	28	silt and shells	+	+
OCS36	43.4917	-78.3867	160.7	silt and shells	+	+
OCS37	43.3917	-78.0369	26	sand, silt, and shells	+	+
OCS38	43.383	-77.99	17	sand, silt, and shells	+	+
OCS39	43.4861	-78.0003	155	silt and shells	+	+
OCS40	43.59	-78.0117	183	silt and shells	+	+
OCS42	43.8397	-78.0369	NA	cancelled		
OCS43	43.9497	-78.0497	NA	cancelled		
OCS45	43.8203	-77.7825	80	sand, clay, silt, and shells	+	+
OCS48	43.88	-77.44	36	sand, silt, and shells	+	+
OCS58	43.328	-77.438	91.5	sand, silt, and shells	+	+
OCS61	43.7861	-77.1583	54	sand and gravel	+	+

Station	Latitude	Longitude	Depth (m)	Substrate	Ponar	BIS
OCS62	43.88	-76.9994	10.3	failed, hard substrate		+
OCS64	43.5244	-76.9258	206	silt	+	+
OCS65	43.4233	-76.8833	145	silt and shells	+	+
OCS66	43.3331	-76.8392	NA	cancelled		
OCS67	43.4081	-76.7947	71	sand, clay, silt, and shells	+	+
OCS69	43.6053	-76.7147	180	silt and shells	+	+
OCS70	43.5415	-76.61767	162	silt and shells	+	+
OCS71b	43.4772	-76.5269	13.6	failed, hard substrate		+
OCS72	43.5497	-76.5253	108.6	sand, silt, and shells	+	+
OCS73	43.6314	-76.2897	39.6	sand, silt, and shells	+	+
OCS74	43.7489	-76.5194	68.7	silt and shells	+	+
OCS75	43.8433	-76.3553	28.9	sand, silt, and shells	+	+
OCS77	43.9564	-76.4081	28.6	sand and silt	+	+
OCS80	44.1422	-76.6122	22	sand, gravel, and shells	+	+
OCS81	44.0164	-76.675	36	sand, silt, and shells	+	+
OCS82	44.0661	-76.8111	27	sand, silt, and shells	+	+
OCS84	43.8867	-76.7339	36.4	failed, hard substrate		+
OCS94	43.3253	-77.2161	56.2	sand, silt, and shells	+	+
OCS101	43.638	-78.413	147.7	silt and shells	+	+
OCS102	43.734	-77.723	113	silt and shells	+	+
OCS106	43.956	-76.603	30	silt and shells	+	+
OCS715	43.6356	-76.9694	152.5	silt and shells	+	+
OCS716	43.6	-77.44	150	silt and shells	+	+
OCS717	43.2817	77.44	15.5	silt and shells	+	+
OCS93A	43.327	-78.868	18	sand, silt, and shells	+	+
OCSDD2	43.7713	-79.03382	35.7	failed, hard substrate		+
OCSDD3	43.86811	-78.60469	25	sand	+	+
OCSDD4	43.89209	-78.39791	24	failed, hard substrate		+
OCSDD5	43.92206	-78.17449	30.5	failed, hard substrate		+
OCSDD6	43.93015	-77.74838	25.1	failed, hard substrate		+
OCSDD7	43.94248	-77.67542	20.8	failed, hard substrate		+
OCSDD8	43.79096	-77.59278	22	failed, hard substrate		+
OCSDD9	43.81267	-77.33515	23	failed, hard substrate		+
OCSDD10	43.82424	-77.20467	20	failed, hard substrate		+
OCSDD11	43.83659	-77.05326	26.6	sand, silt, and shells	+	+
OCSDD12	43.9892	-76.82477	31.9	silt and shells	+	+
OCSDD13	43.85	-76.53005	36.2	failed, hard substrate		+

Station	Latitude	Longitude	Depth (m)	Substrate	Ponar	BIS
OCSDD14	43.80548	-76.29867	20.3	failed, hard substrate		+
OCSDD15	43.55122	-76.28621	19.1	failed, hard substrate		+
OCSDD16	43.53097	-76.40816	22.8	sand, silt, and shells	+	+
OCSDD17	43.43871	-76.62624	27.4	failed, hard substrate		+
OCSDD18	43.30406	-77.10231	22.8	sand, silt, and shells	+	+
OCSDD19	43.29803	-77.3553	22.8	silt and shells	+	+
OCSDD20	43.36436	-77.83395	19.1	silt and shells	+	+
OCSDD21	43.39212	-78.38842	22.5	sand, silt, and shells	+	+
OCSDD22	43.30676	-79.14142	18.9	sand, silt, and shells	+	+
OCSDD23	43.26584	-79.62009	23	sand, gravel, and shells	+	+
OCSDD24	44.03481	-76.42365	26	sand, gravel, and shells	+	+
OCSDD25	44.12933	-76.59826	24	silt and shells	+	+
ON 12	43.5033	-79.3531	103.2	silt	+	+
ON 33M	43.5964	-78.8144	135.3	silt, clay	+	+
ON 25*	43.51666	-79.08	142	silt	+	+
ON 41*	43.71666	-78.026667	122	silt	+	+
ON 55M*	43.44333	-77.438333	183	silt	+	+
ON 60*	43.58	-77.2	148	silt	+	+
ON 63*	43.73166	-77.016667	82	silt	+	+
ON 65b*	43.30833	-76.95	25	sand, silt	+	+
ON 67b*	43.375	-78.729444	56	silt	+	+
ON 68b*	43.58333	-79.416667	51	silt	+	+
ON 69b*	43.31833	-79.0000	15	fine sand	+	+

Dreissena sampling protocol

During the Lake Ontario benthic survey two types of samples were collected to study *Dreissena*: (1) Ponar samples that were processed for mussel presence, density, size-frequency distribution, and sediment analysis; and (2) video images using BIS (Table 2). From a total of 88 stations planned, Ponar samples were successfully collected from 69 stations (206 samples) and BIS from 82 stations (246 videos).

Table 2. Number of stations and samples (in parenthesis) planned and successfully sampled in Lake Ontario using Ponar and BIS.

Lake Regions	Ponar Planned	Ponar Sampled	BIS Planned	BIS Sampled
Lake-wide	88 (264)	69 (206)	88 (264)	82 (246)

We attempted to collect video images from every benthic station using a 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 (Lumen Subsea Light by Blue Robotics) per camera attached to a custom-built stainless-steel frame equipped with a scale bar (Burlakova and Karatayev, 2023; Karatayev et al., 2021a, 2022). At each station, the BIS was lowered from the starboard side of R/V *Lake Guardian* 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, 2021b). A total of 246 images from 82 stations were initially collected from the down-looking camera in Lake Ontario. All videos were rated based on the image quality as high (mussels were well visible and could be counted with high confidence), medium (mussels were visible and could be counted with medium confidence), and low (images were not crisp and mussels could potentially be undercounted) (Table 3). 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, 2021b).

Depth zones	High quality	Medium quality	Low quality	No mussels	Not counted*	All images
≤30 m	49	18	17	15	8	107
>30-50 m	10	7	1	0	0	18
>50-90 m	39	2	3	6	0	50
>90 m	31	22	15	0	3	71
Lake-wide	129	49	36	21	11	246

Table 3. Bottom images collected with BIS across Lake Ontario in 2023.

**Dreissena* were present but could not be counted due to high turbidity, macrophytes overgrowth, or other reasons.

Laboratory Procedures

All organisms found in each replicate sample collected at the 69 benthos stations were sorted, identified, counted, and weighed (total wet weight). Organisms were separated under low

magnification using a dissecting microscope. Oligochaetes and chironomids were mounted on slides and identified using a compound microscope; other organisms were identified using a dissecting microscope. Oligochaeta Naididae and mature Tubificidae and Lumbriculidae were identified to species; Enchytraeidae, immature Tubificidae and Lumbriculidae were identified to the lowest taxonomic level possible, usually family, and included in density and biomass estimates. Counts of oligochaete fragments were excluded from density analyses but fragment weight was considered in the determination of biomass. Chironomids were identified to the lowest practical taxonomic level, usually genus. Other invertebrates were identified to species, when possible. Details are described in the EPA GLNPO SOP LG407 for Benthic Invertebrate Laboratory Analysis (US EPA, 2023). In this study we are using the old division of Oligochaeta by Enchytraeidae, Lumbriculidae, Naididae and Tubificidae, comparable with historical data, even though former families of Naididae and Tubificidae in the order Tubificida are now combined in one family Naididae (Erseus et al., 2008).

Dreissena 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 0.0001 g after being blotted dry on absorbent paper (total wet weight of tissue and shell, TWW); details are described in the EPA GLNPO SOP for Benthic Invertebrate Laboratory Analysis (US EPA, 2023). Nearly all *Dreissena* collected during this survey were *D. r. bugensis* with only one GLBMP station (ON 65b) containing a single *D. polymorpha*.

Assessment of Dreissena population dynamics

To assess *Dreissena* spp. population dynamics we used historic data for Lake Ontario (before 2023) summarized in Karatayev et al. (2021b). This analysis is based on data from 10 lake-wide benthic surveys conducted in Lake Ontario over the course of over 30 years (1990, 1994, 1995, 1997-1999, 2003, 2008, 2013 and 2018) (Lozano et al., 2001; Dermott and Geminiuc, 2003; Watkins et al., 2007; Birkett et al., 2015; Nalepa and Baldridge, 2016).

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. To compare 2023 benthos abundance among depth zones we used one-way ANOVA on log-transformed total density and biomass followed by pairwise Tukey HSD test. We used *t*-tests to compare densities of BIS vs. Ponar densities of *Dreissena* at each depth zone by basin, checking homogeneity of variances using Levene's test, or using Kruskal-Wallis test. To compare *Dreissena* densities in different years by depth zones we used Kruskal-Wallis test. Analyses were performed using Statistica (data analysis software system), version 14 (TIBCO Software Inc. 2020, http://tibco.com). All test effects were considered significant at P < 0.05.

Results and Discussion

Status of the Lake Ontario benthic community in 2022

We found 78 species and higher taxa of benthic macroinvertebrates in Lake Ontario in 2023, in addition to unidentified Chironomidae and immature Oligochaeta (Table 4). The most diverse were Oligochaeta (36 species and higher taxa), Chironomidae (28 species and higher taxa), Mollusca (6 species and higher taxa: 2 Gastropoda and 4 Bivalvia), and Malacostraca (5 species and higher taxa: 3 Amphipoda, 1 Isopoda and 1 Mysida). Other taxa were represented by fewer than 3 species, or were not identified to species level (e.g., Hydrozoa, Nemertea, Turbellaria). Among Oligochaeta, the most diverse were Tubificidae (21 species and higher taxa), and Naididae (13).

The most widely occurring taxa throughout the lake was *D. r. bugensis* recorded at 66 stations (96%), followed by Oligochaeta *Stylodrilus heringianus* at 38 stations (55%) and *Potamothrix vejdovskyi* at 36 stations (52%), Chironomidae *Micropsectra* sp. (33 stations, 48%), Oligochaeta *P. moldaviensis* (33 stations, 48%) and *Limnodrilus hoffmeisteri* (29 stations, 42%). All other taxa occurred at less than 40% of the sampled stations.

Dreissena r. bugensis comprised the largest percentage (56%) of lake-wide benthos density, followed by Oligochaeta (38%) and Chironomidae (4.6%). Contribution of other groups (Gastropoda, Sphaeriidae, Malacostraca, Platyhelminthes, Nemertea, etc.) to total benthos density was less than 1% each. Among Oligochaeta, the most numerous were Tubificidae (86% of total Oligochaeta density), Lumbriculidae (10%), Naididae (2%), and Enchytraeidae (0.1%). Dreissena r. bugensis also comprised the largest share of lake-wide benthos by biomass (99.8% of total wet biomass). Contribution of other groups (Oligochaeta, Chironomidae, Sphaeriidae, Malacostraca, Platyhelminthes, Nemertea, etc.) to total benthos biomass was less than 1% each. Diporeia hoyi, one of the indicator species to assess the state of the Great Lakes, was not found in Lake Ontario in 2023.

Таха	Lake-wide (69)	≤30 m (24)	>30-50 m (4)	>50-90 m (17)	>90 m (24)
Malacostraca (ind. m ⁻²)	33.3±23	75.2±65.9	4.8±4.8	3±1.4	17.5±6.7
Malacostraca (g m ⁻²)	0.11±0.03	0.06±0.05	<0.01	0.06±0.04	0.21±0.06
Isopoda (ind. m ⁻²)	22.2±22	63.3±63.3	0	0.7±0.7	0
Isopoda (g m ⁻²)	0.01±0.01	0.04±0.04	0	<0.01	0
Amphipoda (ind. m ⁻²)	4.4±1.9	11.8±5.1	4.8±4.8	0	0
Amphipoda (g m ⁻²)	<0.01	0.02±0.01	<0.01	0	0
Diporeia sp. (ind. m ⁻²)	0	0	0	0	0
Diporeia sp. (g m ⁻²)	0	0	0	0	0

Table 4. Average (± standard error) density (ind. m⁻²) and wet biomass (g m⁻²) of major taxonomic groups of benthic invertebrates collected from 69 benthic stations in Lake Ontario in 2023 and averaged by depth zones and lake-wide (not weighted). Number of stations given in parentheses.

Таха	Lake-wide (69)	≤30 m (24)	>30-50 m (4)	>50-90 m (17)	>90 m (24)
Chironomidae (ind. m ⁻²)	221.4±54.9	386.1±65.1	911.4±805	108.7±28.4	21.5±11.1
Chironomidae (g m ⁻²)	0.19±0.04	0.37±0.07	0.54±0.47	0.08±0.02	0.03±0.02
Mollusca excluding <i>Dreissena</i> (ind. m ⁻²)	5.1±2.2	9.0±6.1	0	1.9±1.2	4.2±1.9
Mollusca excluding <i>Dreissena</i> (g m ⁻²)	0.02±0.01	0.04±0.02	0	<0.01	<0.01
Mollusca with <i>Dreissena</i> (ind. m ⁻²)	2715.0±274.4	2983.0 ±689.6	1115.3±629.7	3103.1±426.9	2438.9±191.1
Mollusca with <i>Dreissena</i> (g m ⁻²)	1054.2±135.8	1514.0±311.6	772.7±447.0	1345.9±221.2	434.6±46.1
Dreissena spp. (ind. m ⁻²)	2710.0±273.8	2974.0±687.4	1115.3±629.7	3101.2±427.2	2434.6±191.5
Dreissena spp. (g m ⁻²)	1054.15±135.79	1513.94±311.58	772.73±446.99	1345.93±221.21	434.58±46.06
Sphaeriidae (ind. m ⁻²)	2.0±0.8	0.3±0.3	0	1.9±1.2	4.2±1.9
Sphaeriidae (g m ⁻²)	<0.01	<0.01	0	<0.01	<0.01
Gastropoda (ind. m ⁻²)	3.0±2.1	8.8±5.8	0	0	0
Gastropoda (g m ⁻²)	0.01±0.01	0.03±0.02	0	0	0
Oligochaeta (ind. m ⁻²)	1832.4±414.6	3797.8±1052.6	1849.9±1043.6	1219.6±304.2	298.2±44.7
Oligochaeta (g m ⁻²)	1.46±0.25	1.73±0.54	0.81±0.4	2.26±0.53	0.72±0.18
Enchytraeidae (ind. m ⁻²)	2.2±0.7	1.5±0.7	4.8±4.8	5.6±2.2	0
Enchytraeidae (g m ⁻²)	<0.01	<0.01	<0.01	<0.01	0
Lumbriculidae (ind. m ⁻²)	179.2±36	9.4±6.8	57.4±57.4	450.3±107.5	177.4±40.1
Lumbriculidae (g m ⁻²)	0.49±0.11	0.01±0.01	0.12±0.12	1.31±0.36	0.45±0.11
Naididae (ind. m ⁻²)	40.6±26.8	104.0±76	4.8±1.6	16.5±10.6	0.3±0.3
Naididae (g m ⁻²)	<0.01	0.01±0.01	<0.01	<0.01	<0.01
Tubificidae (ind. m ⁻²)	1573.1±392.3	3628.6±971.5	1776.6±1070.4	709.7±271.5	95.3±32.2
Tubificidae (g m ⁻²)	0.55±0.15	1.23±0.4	0.5±0.32	0.28±0.09	0.06±0.02
Others (ind. m ⁻²)	18.9±7.8	36.1±21.4	14.3±9.2	16.9±8.2	4.0±1.1
Others (g m ⁻²)	0.02±0.01	0.02±0.01	0.01±0.01	0.02±0.01	<0.01
Platyhelminthes (ind. m ⁻²)	3.9±1.4	7.3±3.7	<0.01	4.5±2.4	0.8±0.6
Platyhelminthes (g m ⁻²)	<0.01	<0.01	<0.01	<0.01	<0.01
Total Benthos without <i>Dreissena</i> (ind. m ⁻²)	2115.0±434.8	4311.6±1058.6	2780.4±1813.4	1354.5±304.6	346.3±43.8
Total Benthos without Dreissena (g m ⁻²)	1.79±0.26	2.22±0.56	1.37±0.86	2.42±0.53	0.97±0.19
Total Benthos with <i>Dreissena</i> (ind. m ⁻²)	4825.0±526.1	7285.5±1254.1	3895.7±2031.5	4455.7±618.9	2780.9±214.5
Total Benthos with Dreissena (g m ⁻²)	1055.9±135.9	1516.2±311.6	774.1±447.6	1348.4±221.4	435.6±46.1

The dominant structure of benthic community of Lake Ontario in 2023 was not different from that in 2018 (Table 5). In both years *Dreissena* comprised the largest portion of total benthos density and biomass. Oligochaeta was the next most dominant group in both years by density (28% in 2017 and 38% in 2023), followed by Chironomidae. The long-term changes in *Dreissena* will be described in detail in the "*Dreissena* population assessment" section of this report. Among the major long-term trends in densities of benthic macroinvertebrates in Lake Ontario were the declines in *Diporeia* that started in the early to mid-2000s (Nalepa et al., 2018). *Diporeia* densities were very low in 2003-2018 CSMI surveys, in 2021-2022 GLBMP samples, and the species was not found in 2023. No consistent trends were found in densities of oligochaetes or chironomids (Table 5).

Depth zone, taxa	1998	1999	2003	2008	2013	2018	2023
≤30 m	N = 25	N = 9	N = 9	N = 13	N = 8	N = 13	N = 24
Amphipoda	138±47	n.r.	n.r.	1±1	48±41	33±16	12±5
Diporeia	1±1	202±138	0	0	0	0	0
Oligochaeta	1501±472	2100±495	n.r.	808±272	2738±1158	3681±940	3798±1053
Chironomidae	252±83	663±313	n.r.	154±61	486±261	569±116	386±65
Dreissenidae	5867±1972	1913±333	9193±3419	2366±1161	3302±1387	5037±2132	2974±687
Sphaeriidae	235±96	375±150	n.r.	0	0	0	0
Gastropoda	271±86	n.r.	n.r.	143±143	27±26	57±57	9±6
All Benthos	8382±2285	n.r.	n.r.	3471±1251	6614±1108	9401±2919	7286±1254
Benthos excluding Dreissena	2515±592	n.r.	n.r.	1106±378	3312±1108	4364±977	4312±1059
>30-50 m	N = 15	N = 6	N = 5	N = 4	N = 8	N = 3	N = 4
Amphipoda	6±2	n.r.	n.r.	9±5	10±9	0	5±1
Diporeia	67±67	9±7	1±1	0	0	0	0
Oligochaeta	651±350	1911±1380	n.r.	1025±240	1552±653	5494±4300	1850±251
Chironomidae	289±114	241±138	n.r.	278±248	125±60	74±49	911±194
Dreissenidae	1755±548	3907±1059	10949±519	4419±193	4366±127:	4587±1964	1115±152
Sphaeriidae	213±70	160±76	n.r.	0	0	0	0
Gastropoda	3±2	n.r.	n.r.	0	14±13	0	0

Table 5. Long-term dynamics of density (mean ± SE, ind. m⁻²) of major benthic taxa in Lake Ontario from 1998 to 2023 by depths zones. n.r. = not reported.

Depth zone, taxa	1998	1999	2003	2008	2013	2018	2023
All Benthos	2994±722	n.r.	n.r.	5732±1824	6067±1854	10212±6256	3896±489
Benthos excluding Dreissena	1239±412	n.r.	n.r.	1313±351	1701±649	5626±4295	2780±437
>50-90 m	N = 34	N = 24	N = 9	N = 15	N = 8	N = 16	N = 17
Amphipoda	2±1	n.r.	n.r.	1±1	0	2±1	0±0
Diporeia	1301±429	764±275	97±86	6±6	0	0	0
Oligochaeta	564±57	995±120	n.r.	631±81	1002±218	1516±263	1220±256
Chironomidae	123±33	77±16	n.r.	210±70	212±72	408±90	109±24
Dreissenidae	336±123	4487±1397	6526±2022	7149±1177	5504±700	4749±532	3101±360
Sphaeriidae	280±36	231±40	n.r.	4±2	2±2	2±2	2±1
Gastropoda	0	n.r.	n.r.	0	0	0	0
All Benthos	2630±444	n.r.	n.r.	8003±1187	6721±750	6711±665	4456±521
Benthos excluding Dreissena	2294±453	n.r.	n.r.	855±114	1216±184	1963±259	1355±256
>90 m	N = 40	N = 28	N = 13	N = 19	N = 21	N = 23	N = 24
Amphipoda	0	n.r.	n.r.	0	0	0	0
Diporeia	2343±336	2181±335	545±111	41±18	<1	0.3±0.3	0
Oligochaeta	274±49	543±109	n.r.	169±52	381±61	426±79	298±26
Chironomidae	13±3	54±17	n.r.	63±39	80±16	88±29	22±7
Dreissenidae	2±1	35±24	1099±614	655±361	2044±456	3554±501	2435±113
Sphaeriidae	108±17	104±22	n.r.	16±4	23±6	17±5	4±1
Gastropoda	0	n.r.	n.r.	0	0	0	0
All Benthos	2788±361	n.r.	n.r.	965±406	2529±496	4131±580	2781±127
Benthos excluding Dreissena	2786±360	n.r.	n.r.	310±76	485±69	577±88	346±26
Lake-wide	N = 114	N = 67	N = 36	N = 51	N = 45	N = 55	N = 69
Amphipoda	31±10	0	n.r.	1±1	12±9	7±4	4±2
Diporeia	1380±181	1238±172	281±56	21±9	<0.1±<0.1	0.1±0.1	0
Oligochaeta	647±113	1122±201	n.r.	492±71	1141±266	1921±545	1832±415

Depth zone, taxa	1998	1999	2003	2008	2013	2018	2023
Chironomidae	99±21	224±68	n.r.	135±39	197±59	249±34	221±55
Dreissenidae	1532±430	1717±296	4999±1067	2667±438	3228±420	4215±576	2710±274
Sphaeriidae	180±25	192±36	n.r.	8±2	11±3	9±2	2±1
Gastropoda	59±19	0	n.r.	31±31	7±6	12±12	3±2
All Benthos	3999±535	4513±421	n.r.	3366±453	4599±425	6455±1011	4825±526
Benthos excluding Dreissena	2467±237	2796±305	n.r.	700±101	1371±255	2239±547	2115±435

Dreissena population assessment and long-term trends

To predict the ecosystem impacts of dreissenids, it is critically important to have up-to-date information about both the population size and spatial distribution in the waterbody. However, dreissenid sampling by conventional methods (bottom grabs or diver assessments) require a long time for processing (reviewed in Karatayev et al., 2018). We used the BIS in Lake Ontario to estimate *Dreissena* populations (occurrence, coverage and density) and compared the estimated densities with densities obtained from traditional Ponar grabs collected at the same stations. In addition, we compared the most recent population density and biomass with historical data to assess long-term dreissenid dynamics in all major basins of Lake Ontario.

Dreissena population assessment using BIS vs. Ponar

In Lake Ontario, of all 214 usable collected images with mussels present in 2023, 60% were evaluated as high quality, 23% as medium, and 17% images as low quality. The quality of images did not decline significantly with increasing depth (Table 3). Considering the ongoing shift of the bulk of *Dreissena* populations in the Great Lakes into deeper areas, we suggest that BIS may be even more efficient in dreissenid assessment in the future.

BIS and Ponar density data for all stations sampled in all depth zones of Lake Ontario in 2023 produced similar results (Table 6). We found no significant differences between *Dreissena* densities estimated by BIS and Ponar (P > 0.05) (Table 6, Fig. 3).

Table 6. *Dreissena* population density (ind. m⁻², average ± standard error) for all stations sampled using Ponar grab and BIS in the main basin of Lake Ontario, in 2023, and for matching stations only. Number of successful samples in parenthesis. Depth zone- and lake-wide *Dreissena* densities were not significantly different (Kruskal-Wallis test).

Lake Ontario, depth zone	Ponar, All stations	BIS, All stations	Ponar to BIS ratio, All stations	Ponar, matching stations	BIS, matching stations	Ponar to BIS ratio, matching stations
≤30 m	2974±687 (24)	1508±265 (35)	1.97	2985±729 (22)	903±216 (22)	3.30
>30-50 m	1115±630 (4)	2344±954 (6)	0.47	1115±630 (4)	1753±796 (4)	0.63
>50-90 m	3101±427 (17)	3301±617 (17)	0.94	3101±427 (17)	3301±617 (17)	0.94
>90 m	2435±192 (24)	2145±223 (24)	1.13	2435±192 (24)	2145±223 (24)	1.13
Lake-wide	2710±274 (69)	2127±205 (82)	1.27	2706±276 (67)	2007±221 (67)	1.34



Fig. 2. Density (ind. m⁻²*) of Dreissena in Lake Ontario based on Ponar grab in 2018 and 2023 and BIS survey in 2023.*

Dreissena spatial and temporal trends

Among the deep Great Lakes (all lakes except Lake Erie), Lake Ontario has the longest history of dreissenid invasion (since 1989 for zebra mussels, Griffiths et al., 1991, and since 1990 for quagga mussels, Mills et al., 1993); therefore, trends observed in Lake Ontario may provide insight into the potential long-term dynamics of *Dreissena* populations in other deep lakes of North America and Europe. To document long-term trends in *Dreissena* population dynamics in Lake Ontario, we compiled a dataset of *Dreissena* spp. densities by station and depth for 1990, 1995, 1997, 1998, 1999, 2003, 2008, 2013 and 2018 (Dermott and Geminiuc, 2003; Lozano et al.,

2001; Watkins et al., 2007; Birkett et al., 2015; Nalepa and Baldridge, 2016; Karatayev et al., 2021b) to complement the data from 2023 presented here. To increase the spatial resolution of the 2003, 2008, 2013 and 2018 surveys, we added data from the U.S. EPA Great Lakes National Program Office (GLNPO) long-term monitoring stations (9 to 10 stations per survey, Burlakova et al., 2018).

A sharp increase in *Dreissena* density from 1990 onwards was found across all depth ranges (Fig. 4). The highest densities were recorded in the early 2000s, particularly at depths of <50 m, with peak values observed in 2003. Following this peak, *Dreissena* density gradually declined, although the population remains significantly higher than in the 1990s. In deeper areas (>50-90 m and >90 m) the expansion of dreissenids continued after 2003, with maximum densities occurring in 2008 and 2018. There was a slight decline in both *Dreissena* density and biomass in 2023 compared to 2018, but the decline was not significant (Table 7, Fig. 2, 3). Overall *Dreissena* population in Lake Ontario likely reached its carrying capacity and maybe stabilized. This highlights the ongoing adaptation of *Dreissena* to new habitats within the lake, emphasizing the need for continued monitoring across all depth ranges.

Table 7. *Dreissena* spp. density (ind. m⁻², average ± standard error) and wet biomass with shells (g m⁻²) in Lake Ontario in 2018-2023. Lake-wide densities were calculated as weighted averages from four depth zones. Number of successful samples in parenthesis. Depth zone- and lake-wide *Dreissena* densities were not significantly different (Kruskal-Wallis test).

Depth zone	Density, 2018	Density, 2023	Biomass, 2018	Biomass, 2023
≤30 m	5037±2133 (13)	2974±687 (24)	1432±455 (13)	1514±312 (24)
>30-50 m	4587±1965 (3)	1115±630 (4)	1007±228 (3)	773±447 (4)
>50-90 m	4749±532 (16)	3101±427 (17)	1931±236 (16)	1346±221 (17)
>90 m	3554±501 (23)	2435±192 (24)	539±112 (23)	435±46 (24)
Lake-wide	4308±566 (55)	2710±274 (69)	1181±156 (55)	1054± 136 (69)



Fig. 3. Biomass (ind. m^2) of Dreissena spp. in Lake Ontario based on Ponar grab in 2018 and 2023.

Dreissena vs. Diporeia

Historically, since the last glaciation, the benthos of Great Lakes was dominated by amphipod *Diporeia hoyi* (Beeton, 1965, 1969; Cook and Johnson, 1974). Like other Great Lakes, the decline in *Diporeia* in Lake Ontario had likely started after the arrival of zebra mussels but was exacerbated by the proliferation of quagga mussels (Nalepa et al., 2007a, 2007b; Barbiero et al., 2011, 2018; Burlakova et al., 2018) (Fig. 4). From the 1960s until the late 1990s, *Diporeia* was the dominant species, reaching densities of 1,763 ind. m⁻² at depths of \leq 30 m in 1977 and 8,784 ind. m⁻² at depths of >50-90 m in 1994. Since the early 2000s, there has been a sharp decline in *Diporeia* numbers. In 2023 we did not find a single *Diporeia* across all samples, indicating significant changes in the ecosystem.



Fig. 4. Long-term dynamics of average density (ind. $m^{-2} \pm standard error$) of Dreissena and Diporeia hoyi density in Lake Ontario. Historical (before 2023) data summarized in Karatayev et al. (2021b).

Dreissena coverage

Dreissena coverage was determined as a percentage of each screenshot area covered with mussels. According to US EPA SOP LG410 (US EPA, 2021b) for quality control purposes, 24 (10%) still images were randomly selected to recount *Dreissena* coverage by a different analyst. Percent errors in *Dreissena* coverage less than 20% was considered acceptable, and all images with differences >20% were re-evaluated (US EPA, 2021b). The overall difference in *Dreissena* coverage calculated by different analysts was 13.3%. However, higher percentage of error was found in images with low area of coverage (<10%), or where mussels were covered with algae or mud (samples OCS48 FD2, OCS82 FD2, OCSDD17 RFS, OCSDD21 FD1, OCS35 RFS, and LTM60 FD1). Across all images where the area of coverage was >10% (17 samples), the average difference in *Dreissena* coverage was 9.2%.

On average, $26.7 \pm 2.0\%$ of Lake Ontario bottom in 2023 was covered with *Dreissena* (Table 8). The highest coverage was found at the >50-90 m depth zone, and the lowest at >90 m depths (Table 8, Fig. 5). The differences between these depth zones were statistically significant, while coverage among other depth zones did not differ.

Table 8. *Dreissena* population coverage (percent, average \pm standard error) in four depth zones and lakewide averages weighted by depth zone estimated using BIS in 2023. Densities that were not significantly different are identified with the same letters (Kruskal-Wallis test, P < 0.05).

Depth zone	n	% of area ± SE
≤30 m	35	28.6±4.5 ^{AB}
>30-50 m	8	33.5±11.1 ^{AB}
>50-90 m	14	38.2±6.5 ^A
>90 m	25	15.5±2.1 ^B
Lake-wide	82	26.7±2.0



Fig. 5. Representative screen shots of Dreissena coverage at \leq 30 m (a, OCS35, 27 m), >50-90 m (b, OCS9, 56.6 m), and >90 m (c, OCS40, 181 m) depth zones.

All stations with the highest coverage (>85%) were shallow with a maximum depth of 34.5 m (Fig. 6). The highest absolute coverage (99.1%) was found on a rocky substrate at station OCSDD23 (22.3 m depth). *Dreissena* coverage at most sampled stations did not exceed 30%.



Fig. 6. Coverage (%) of Lake Ontario bottom with Dreissena based on BIS survey in 2023.

The largest number of stations with both the highest (>85%) *Dreissena* coverage and where *Dreissena* was absent were found at depths <40 m (Fig. 7). This could be explained by the type of substrate at these shallow depths: While the rocky substrates were completely covered by *Dreissena*, on sandy substrates *Dreissena* were absent (Fig. 8). The deepest zone (>90 m) had neither high nor zero coverage and the average percent of bottom covered by *Dreissena* did not exceed 45%.



Fig. 7. Dreissena percent coverage along depth gradient in Lake Ontario in 2023 (Pearson's r = -0.298, P < 0.007).



Fig. 8. Representative screen shots of Dreissena coverage at \leq 30 m zone. Stations: left: OCSDD8 (29.4 m), right: OCS93A (17.4 m).

The correlation between *Dreissena* BIS density and coverage was significant and high (Pearson's r = 0.763, P < 0.001, Fig. 9). However, we obtained some contradicting results: *Dreissena* density at \leq 30 m depth zone was lower than at >90 m depth zone while its coverage at \leq 30 m depths was almost twice as high. The difference in *Dreissena* density between \leq 30 m depth zone and >90 m depth zone, however, was not significant due to large variability among samples.



Fig. 9. The relationship between Dreissena density recorded by BIS and coverage (Pearson's r = 0.763, P < 0.001) in Lake Ontario in 2023.

The relationships between *Dreissena* coverage and density recorded in Ponars (Fig. 10), as well as between *Dreissena* coverage and Ponar biomass (Fig. 11) were significant, but weaker (Pearson's r = 0.539 and 0.550, respectively, P < 0.001).



Fig. 10. Relationship between Dreissena coverage (%) and Ponar density (ind. m^{-2}) in Lake Ontario in 2023 (Pearson's r = 0.539, P < 0.001).



Fig. 11. Relationship between Dreissena coverage (%) and Ponar biomass (g m^{-2}) in Lake Ontario in 2023 (Pearson's r = 0.550, P < 0.001).

In 2018, *Dreissena* coverage was assessed using a GoPro camera mounted on a benthic sled towed behind R/V *Lake Guardian* for about 500 m (Karatayev et al., 2020) at a notably smaller number of stations. There were no significant differences between *Dreissena* coverage in 2018 and 2023 (Table 9).

Table 9. Average *Dreissena* population percent coverage (% of area ± standard error) across depth zones (m) in 2018 (using benthic sled) and 2022 (using BIS), Lake Ontario. n represents the number of stations per depth zone. Depth zone-wide *Dreissena* coverage were not significantly different (Kruskal-Wallis test).

Depth zone	n	2018	n	2023
≤30 m	7	25.3±3.2	35	28.6±4.8
>30-100 m	12	58±8.4	24	35.8±5.3
>100 m	14	16.1±5.1	23	14.5±1.9

In summary, the use of BIS for assessing *Dreissena* populations in Lake Ontario significantly enhanced both the quality and quantity of video images available for estimating *Dreissena* coverage compared to the benthic sled and for assessing mussel densities. This approach maybe the only one available in shallow and rocky substrate where Ponars are not efficient. Moreover, analyzing video images requires less time and facilitates the rapid assessment of mussel populations. Overall, our study demonstrated that underwater imagery serves as a useful tool for quantifying mussel bed structure and aggregation patterns, which are crucial for assessing the ecological impact of *Dreissena* across various depth zones and valuable addition to conventional (Ponar) method.

Acknowledgements

This study was funded by the U.S. EPA through the Great Lakes Restoration Initiative via a Cooperative Agreement with Cornell University, Department of Natural Resources under Award GL00E03089 "Great Lakes Biology Monitoring Program: Zooplankton, Mysis, Benthos 2022-2027" (PI J. Watkins) and Subaward # 82839-10916 to SUNY Buffalo State. We appreciate the assistance of the captain and crew of the U.S. EPA R/V *Lake Guardian*, Y. Monakhov Stockton (University of Hawaii), P. Glyshaw and R. Orzechowski (NOAA) in sample collection. We thank Great Lakes Center technicians K. Hastings, B. Tulumello, L. Denecke, S. Geary, A. Tulumello, N. Mikulska, and student technicians K. Albayed, K. Kudlowitz, and Y. Mikulska for help with sample processing. We are grateful to A. Scofield and E. K. Hinchey (U.S. EPA GLNPO) for reviewing this report, and Great Lakes Center Administrative Assistant S. Dickinson for report proofreading. Any views expressed in this report are those of the authors and do not necessarily represent the views or policies of the U.S. EPA. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. EPA.

Literature Cited

- Barbiero, R. P., K. Schmude, B. M. Lesht, C. M. Riseng, G. J. Warren & M. L. Tuchman, 2011. Trends in Diporeia populations across the Laurentian Great Lakes, 1997–2009. J. Great Lakes Res. 37: 9–17.
- Barbiero, R. P., B. M. Lesht, G. J. Warren, L. G. Rudstam, J. M. Watkins, E. D. Reavie, K. E. Kovalenko & A. Y. Karatayev, 2018. A comparative examination of recent changes in nutrients and lower food web structure in Lake Michigan and Lake Huron. J. Great Lakes Res. 44: 573–589.
- Beeton, A. M., 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.
- Beeton, A. M., 1969. Changes in the environment and biota of the Great Lakes, in: Eutrophication: Causes, Consequences, Correctives. The National Academies Press, Washington, D.C.: 157–187.
- Birkett, K., S. J. Lozano, L. G. Rudstam, 2015. Long-term trends in Lake Ontario's benthic macroinvertebrate community from 1994-2008. Aquat. Ecosystem Health Manag. 18: 78–88.
- Burlakova, L. E. & A. Y. Karatayev, 2023. Lake Michigan Benthos Survey Cooperative Science and Monitoring Initiative 2021. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State University, Buffalo, NY. Available at: http://greatlakescenter.buffalostate.edu/sites/greatlakescenter.buffalostate.edu/files/uploads/Docu ments/Publications/LakeMichiganBenthosSurveyCSMI2021FinalReport.pdf.
- Burlakova, L. E., R. P. Barbiero, A. Y. Karatayev, S. E. Daniel, E. K. Hinchey & G. J. Warren, 2018. The benthic community of the Laurentian Great Lakes: analysis of spatial gradients and temporal trends from 1998–2014. J. Great Lakes Res. 44: 600–617.
- Burlakova, L. E., A. Y. Karatayev, A. R. Hrycik, S. E. Daniel, K. Mehler, L. G. Rudstam, J. M. Watkins, R. Dermott, J. Scharold, A. K. Elgin & T. F. Nalepa, 2022. Six decades of Lake Ontario ecological history according to benthos. J. Great Lakes Res. 48: 274–288.
- Cook, D.C. & M. C. Johnson, 1974. Benthic macroinvertebrates of St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763–782.

- Dermott, R. & M. Geminiuc, 2003. Changes in the benthic fauna of Lake Ontario 1990–1995, with local trends after 1981. In State of Lake Ontario (SOLO)—Past, Present, and Future, M. Munawar, ed., pp. 323-345. Leiden, The Netherlands: Ecovision World Monograph Series, Backhuys Publishers.
- Erseus, C., M. J. Wetzel & L. Gustavsson, 2008. ICZN rules—a farewell to Tubificidae (Annelida, Clitellata). Zootaxa 1744(1): 66–68.
- Golini, V. I., 1979. Benthic macro-and meioinvertebrates of Lake Ontario 1977: distribution and relative abundance. Fish. Environ. Can., Fish. Mar. Serv. MS Rep 1519.
- Griffiths, R. W., D. W. Schloesser, J. H. Leach & W. P. Kovalak, 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48: 1381–1388.
- Hiltunen, J. K., 1969. The benthic macrofauna of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 14, 39– 50.
- Karatayev, A. Y., K. Mehler, L. E. Burlakova, E. K. Hinchey & G. J. Warren, 2018. Benthic video image analysis facilitates monitoring of *Dreissena* populations across spatial scales. J. Great Lakes Res. 44: 629–638.
- Karatayev, A. Y., L. E. Burlakova, K. Mehler, S. E. Daniel, A. K. Elgin & T. F. Nalepa, 2020. Lake Huron Benthos Survey Cooperative Science and Monitoring Initiative 2017. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State, Buffalo, New York, USA: 59. Available at: http://greatlakescenter.buffalostate.edu/sites/greatlakescenter.buffalostate.edu/files/upl oads/Documents/Publications/LakeHuronBenthosSurveyCSMI2017FinalReport.pdf.
- Karatayev, A. Y., L. E. Burlakova, K. Mehler, E. K. Hinchey, M. Wick, M. Bakowska & N. Mrozinska, 2021a. Rapid assessment of *Dreissena* population in Lake Erie using underwater videography. Hydrobiologia 848: 2421–2436.
- Karatayev, A. Y., L. E. Burlakova, K. Mehler, S. E. Daniel & A. R. Hrycik, 2021b. Lake Ontario Benthos Survey Cooperative Science and Monitoring Initiative 2018. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State, Buffalo, NY.
- Karatayev, A. Y., L. E. Burlakova, K. Mehler, A. K. Elgin, L. G. Rudstam, J. M. Watkins & M. Wick, 2022. *Dreissena* in Lake Ontario 30 years post-invasion. J. Great Lakes Res. 48: 264–273.
- Lozano, S. J., J. V. Scharold & T. F. Nalepa, 2001. Recent declines in benthic macroinvertebrate densities in Lake Ontario. Can. J. Fish. Aquat. Sci. 58: 518–529.
- Mills, E. L., R. M. Dermott, E. F. Roseman, D. Dustin, E. Mellina, D. B. Corm & A. P. Spidle, 1993.
 Colonization, ecology, and population structure of the "quagga" mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. 50: 2305–2314.
- Nalepa, T. F., D. L. Fanslow, S. A. Pothoven, A. J. Foley III & G. A. Lang, 2007a. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. J. Great Lakes Res. 33: 421– 436.
- Nalepa, T. F., D. L. Fanslow, S. A. Pothoven, A. J. Foley III, G. A. Lang, S. C. Mozley & M. W. Winnell, 2007b. Abundance and distribution of benthic macroinvertebrate populations in Lake Huron in 1972 and 2000-2003. NOAA Technical Memorandum GLERL-140. Great Lakes Environmental Research Laboratory, Ann Arbor, MI.
- Nalepa, T. F., C. M. Riseng, A. K. Elgin & G. A. Lang, 2018. Abundance and distribution of benthic macroinvertebrates in the Lake Huron system: Saginaw Bay, 2006–2009, and Lake Huron, including Georgian Bay and North Channel, 2007 and 2012. NOAA Technical Memorandum GLERL-172. Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.

- Nalepa, T. F. & N. A. Thomas, 1976. Distribution of microbenthic species in Lake Ontario in relation to sources of pollution and sediment parameters. J. Great Lakes Res. 2: 150–163.
- Nalepa, T. F. & A. K. Baldridge, 2016. Benthos. Lake Ontario Cooperative Science and Monitoring Initiative (CSMI) 2013. Summary Report.
- US EPA, 2021a. SOP LG406, Standard Operating Procedure for Benthic Invertebrate Field Sampling, Revision 14, January 2021. Great Lakes National Program Office. U.S, Environmental Protection Agency, Chicago, IL.
- US EPA, 2021b. SOP LG410, Standard Operating Procedure for Collection and Processing of Drop-Down Camera Images for *Dreissena* spp. and round goby (*Neogobius melanostomus*) monitoring. Version 1, February 2021. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.
- US EPA, 2023. SOP LG407, Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis, Revision 10, May 2023, Effective July 2022. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.
- Watkins, J. M., R. Dermott, S. J. Lozano, E. L. Mills, L. G. Rudstam & J. V. Scharold, 2007. Evidence for remote effects of dreissenids mussels on the amphipod *Diporea*: analysis of Lake Ontario benthic surveys, 1997-2003. J. Great Lakes Res. 33: 642–657.