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LAKE HURON BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2022

Technical Report

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REPORT: LAKE HURON BENTHOS SURVEY
COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2022

Lake and Year: Huron, 2022

Lead Organization: SUNY Buffalo State University

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Project Overview

In this report, we present results of a benthic survey of Lake Huron 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 surveys, a lake-wide benthic survey was conducted in 2022 in Lake Huron to assess the status of the benthic macroinvertebrate community. This study advanced the Lake Huron CSMI priority of monitoring and understanding Lake Huron'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

- 126 species and higher taxa of benthic macroinvertebrates were found in Lake Huron in 2022. The most diverse and abundant taxa throughout the lake were Oligochaeta (46 taxa, 50% of total density). The invasive mussels *Dreissena rostriformis bugensis* represented 30% and 98% of lake-wide density and biomass, respectively.

- The native Oligochaeta *Stylodrilus heringian*us was the most commonly occurring species, identified from over 71% of samples collected, followed by bivalves *D. r. bugensis* (65%) and *Pisidium* sp. (59%), Chironomidae *Heterotrissocladius subpilosus* group (53%), and Oligochaeta *Limnodrilus hoffmeisteri* (51%).

- *Diporeia*, one indicator species to assess the state of the Great Lakes, was found at 20% of all stations, with an average lake-wide density of 45 ± 14 m^{-2}, and a maximum average density at the 31-50 m depth zone (360 m-2). *Diporeia* densities remain low with little evidence of recovery. Most stations with *Diporeia* were located in the North Channel, where the lowest quagga mussel density was recorded.

- The invasive gastropod *Potamopyrgus antipodarum* was collected for the first time in Lake Huron in the North Channel at stations NC2 and NC3. The lake-wide density and biomass were 0.7 ± 0.5 ind.m^{-2} and <0.01 g m^{-2}, respectively, with a maximum density of 63.7 ind.m^{-2} (Daniel et al., 2024).

- In the main basin we found a decline in quagga mussel density basin-wide and across all depth zones except for the shallowest (<30 m) area. The increase in mussel density at the shallowest depths was caused by large quantities of small (<5 mm) recently settled mussels. In contrast to 2017, in 2022 we found a 1.6-fold decline in mussel density and a 2.2-fold decline in biomass in the deepest zone of Lake Huron's main basin. This was the first decline recorded in the deepest zone of all the Great Lakes.

Project: Major findings from the CSMI benthic macroinvertebrate survey in Lake Huron in 2022 with an emphasis on long-term trends in benthic community

Overview

A lake-wide benthic survey of Lake Huron was conducted in 2022 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 benthic surveys, benthic samples were collected at 126 stations to assess the status of the benthic macroinvertebrate community.

Detailed basin-wide surveys were conducted previously in the main basin of Lake Huron in 1971 (Schelske and Roth, 1973), in Georgian Bay and North Channel in 1973 (Loveridge and Cook, 1976), and in Saginaw Bay in late 1980s (reviewed in Nalepa et al., 2002), followed by more consistent studies starting in early 2000s as a part of CSMI (Nalepa et al., 2003, 2007a, 2007b, 2018). Earlier surveys (1950s – 1960s) in Lake Huron were analyzed in previous publications (Nalepa et al., 2003, 2007a). Previous surveys have documented major changes in the benthic community of Lake Huron since the middle of the 20th century, including a dramatic increase in density from the mid-1950s to mid-1960s and then a decline in early 1970s (Nalepa et al., 2002, 2003, 2007a). These early changes coincide with, and were likely driven by, the increase in nutrient loading in the mid-1960s. The later decline in benthic density may be a result of the nutrient abatement program implemented in the 1970s. More recent surveys have documented even more dramatic changes which were most likely driven by the introduction and spread of the zebra mussel (1989) and the quagga mussel (1996) (Nalepa et al., 2007a).

In 2017 our lake-wide benthic survey in Lake Huron recorded 125 taxa (species, genera or higher taxa) of benthic macroinvertebrates (Karatayev et al., 2020). The most abundant taxon lake-wide was Oligochaeta (52% of total benthic density), followed by *Dreissena rostriformis bugensis* (32%), Chironomidae (8%), and Sphaeriidae (3%). Following depth and productivity patterns, the highest total benthic density, as well as the highest average number of species per sample, was found in the shallowest and most productive Saginaw Bay, and the highest taxa richness in the main basin. *D. r. bugensis* dominated benthic biomass in all regions, comprising 99% of the total wet biomass in the main basin, 98% in Georgian Bay, 88% in Saginaw Bay, and 71% in the North Channel. In 2017, *Dreissena* density in the main basin in the shallowest (<30 m) depth zone declined by a factor of eight compared to 2012, remained stable at 30-90 m, and more than doubled at depths greater than 90 m. *Diporeia* and Sphaeriidae densities in 2017 continued to decline in all basins, while the abundance of oligochaetes increased since mid-2000s in almost all regions of Lake Huron, likely due to an increase in their food resources associated with quagga mussel feeding activities (Karatayev et al., 2020).

The objective of this study was to advance the 2022 Lake Huron CSMI priority of monitoring and understanding Lake Huron's lower food web and describe the status and trends in Lake Huron benthos, with a special emphasis on *Dreissena*, one of the most impactful invasive species to enter the Great Lakes, as well as *Diporeia*, which has experienced widespread declines in Lake Huron. This report contains detailed descriptions of benthic communities in Lake Huron in 2022, including information on sampling design (station locations, sampling and laboratory procedures), the taxonomy and abundance of benthic invertebrates, and changes in *Dreissena* populations.

Methods

Sampling protocol

A total of 378 benthic samples from 126 stations were analyzed for benthic macroinvertebrates in this study: 345 samples from 115 CSMI stations and 33 samples from 11 GLBMP long-term monitoring stations (Fig. 1, Table 1). The CSMI stations were sampled from July 16 through July 27, 2022, aboard the CCGS Limnos. GLBMP stations and any remaining CSMI stations were sampled September 2 through September 7, 2022, 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 16 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 (US EPA, 2021a).

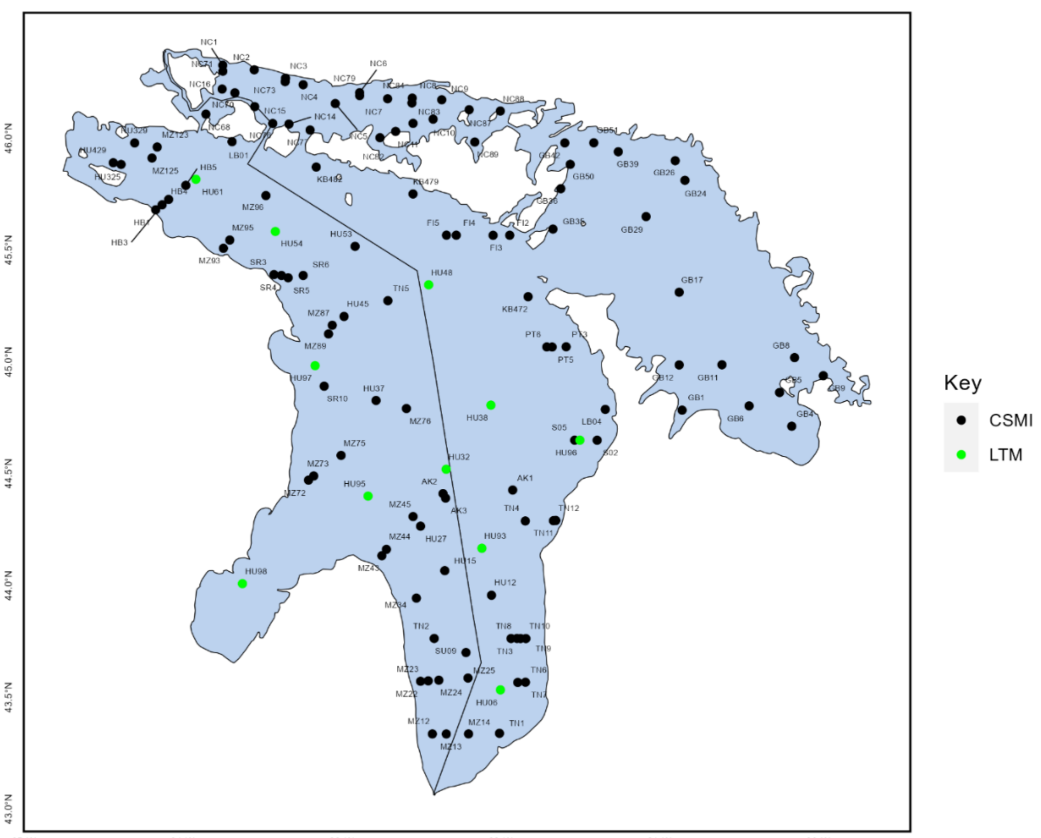

Fig 1. Location of 126 successful benthic stations surveyed in Lake Huron in 2022. The map indicates the locations of 115 CSMI benthic stations (black), and 11 GLBMP long-term monitoring (LTM) benthic stations (green).

Table 1. A list of 141 stations, including 130 CSMI stations sampled on Lake Huron in July and September 2022 and 11 GLBMP long-term monitoring benthic stations sampled in September 2022 (denoted with *), with information on basin, 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 (GB52, GB53, GB54, GB55, GB56, GB57, GB58, GB59, KB480, LB02, LB03, LB05, LB06, NC12, NC13; highlighted in grey) due to unsuccessful Ponars. In total, 378 successful benthic samples were collected from 126 stations, and 372 successful video samples from 131 stations. NA – not available.

Station	Basin	Latitude	Longitude	Depth (m)	Substrate	Benthic / BIS sample
AK1	Main	44.3604	-81.9231	120	clay and silt	both
AK2	Main	44.3444	-82.3614	93	silt	both
AK3	Main	44.3243	-82.3454	93	silt	both
FI2	Main	45.4998	-81.9416	32	sand and algae	both
FI3	Main	45.4996	-82.0463	45	silt and shells	both
FI4	Main	45.5	-82.2781	90	silt and clay	both
FI5	Main	45.5001	-82.3397	86	silt and clay	both
GB1	Georgian Bay	44.7175	-80.8567	91	silt	both
GB4	Georgian Bay	44.6458	-80.1667	57	silt	both
GB5	Georgian Bay	44.7967	-80.2433	59	clay	both
GB6	Georgian Bay	44.7367	-80.435	88	silt	both
GB8	Georgian Bay	44.9527	-80.1488	49	silt	both
GB9	Georgian Bay	44.8717	-79.968	28	silt	both
GB11	Georgian Bay	44.9208	-80.6058	62	silt, sand, and clay	both
GB12	Georgian Bay	44.92	-80.875	90	silt	both
GB17	Georgian Bay	45.245	-80.875	76	silt and clay	both
GB24	Georgian Bay	45.7455	-80.8388	29	silt and clay	both
GB26	Georgian Bay	45.8333	-80.9	20	clay, gravel, and shells	both
GB29	Georgian Bay	45.5833	-81.0833	43	clay and silt	both
GB35	Georgian Bay	45.5275	-81.6695	35	clay, sand, and gravel	both
GB36	Georgian Bay	45.7083	-81.62	53	clay	both
GB39	Georgian Bay	45.8733	-81.2583	26	clay and gravel	both
GB42	Georgian Bay	45.9128	-81.595	25	silt	both
GB50	Georgian Bay	45.81687	-81.56066	25	clay, sand, and gravel	both
GB51	Georgian Bay	45.91324	-81.41254	21	sand	both

Station	Basin	Latitude	Longitude	Depth (m)	Substrate	Benthic / BIS sample
GB52	Georgian Bay	45.88825	-81.05919	15	hard bottom	only BIS
GB53	Georgian Bay	45.72012	-80.71862	13	hard bottom	only BIS
GB54	Georgian Bay	45.54918	-80.6059	15	hard bottom	only BIS
GB55	Georgian Bay	45.34416	-80.40929	18	hard bottom	only BIS
GB56	Georgian Bay	45.15657	-80.21686	22	hard bottom	only BIS
GB57	Georgian Bay	44.95931	-80.03388	23	hard bottom	only BIS
GB58	Georgian Bay	44.63523	-80.37605	25	hard bottom	only BIS
GB59	Georgian Bay	45.34034	-81.65915	16	hard bottom	only BIS
HB1	Main	45.6138	-84.1698	85	sand	both
HB3	Main	45.6359	-84.1294	85	clay, silt, sand, and shells	both
HB4	Main	45.66	-84.0883	85	silt	both
HB5	Main	45.7229	-83.9803	85	clay	both
HU12	Main	43.8899	-82.0562	86	silt	both
HU15	Main	43.9999	-82.3504	66	silt	both
HU27	Main	44.1987	-82.5028	54	sand and clay	both
HU37	Main	44.761	-82.7829	71	clay and silt	both
HU45	Main	45.1367	-82.9843	97	clay, silt, and sand	both
HU53	Main	45.4502	-82.9148	89	clay and silt	both
HU325	Main	45.8166	-84.3876	57	clay, silt, and sand	both
HU329	Main	45.9127	-84.3021	36	sand	both
HU429	Main	45.8241	-84.4368	34	sand	both
KB472	Main	45.2251	-81.8259	47	silt, clay, and algae	both
KB479	Main	45.6845	-82.5503	34	sand and algae	both
KB480	Main	45.7403	-82.8198	32	hard bottom	only BIS
KB482	Main	45.8048	-83.1593	39	sand	both
LB01	Main	45.91833	-83.68914	24	sand and silt	both
LB02	Main	45.57378	-82.22149	20	hard bottom	only BIS
LB03	Main	44.93609	-81.46387	20	hard bottom	only BIS
LB04	Main	44.72098	-81.34014	18	sand	both
LB05	Main	44.15229	-81.87504	24	hard bottom	only BIS
LB06	Main	44.82306	-82.6793	25	hard bottom	only BIS
MZ12	Main	43.2697	-82.4284	20	sand	both

Station	Basin	Latitude	Longitude	Depth (m)	Substrate	Benthic / BIS sample
MZ13	Main	43.2695	-82.3407	20	silty sand	both
MZ14	Main	43.2698	-82.2007	22	sand	both
MZ22	Main	43.5051	-82.5026	18	sand	both
MZ23	Main	43.507	-82.4544	32	sand and silt	both
MZ24	Main	43.51	-82.3878	42	silty sand, gravel, and clay	both
MZ25	Main	43.5197	-82.2042	51	sand, clay, and silt	both
MZ34	Main	43.877	-82.529	46	sand	both
MZ43	Main	44.0668	-82.7463	30	sand	both
MZ44	Main	44.0951	-82.7177	39	sand	both
MZ45	Main	44.2418	-82.5499	58	silt and sand	both
MZ72	Main	44.4047	-83.2081	23	sand	both
MZ73	Main	44.4233	-83.1753	30	sand	both
MZ75	Main	44.5154	-83.0029	66	sand and clay	both
MZ76	Main	44.7248	-82.5917	77	silt, sand, and clay	both
MZ87	Main	45.0975	-83.0584	55	clay and sand	both
MZ89	Main	45.05846	-83.08203	32	sand	both
MZ93	Main	45.4415	-83.7436	32	sand	both
MZ95	Main	45.4783	-83.7035	60	silt and clay	both
MZ96	Main	45.6773	-83.4761	126	silt and sand	both
MZ123	Main	45.8944	-84.1602	51	sand and clay	both
MZ125	Main	45.8452	-84.1929	80	silt	both
NC1	North Channel	46.26018	-83.74758	13	silt and clay	both
NC2	North Channel	46.23972	-83.54961	11.3	sand and silt	both
NC3	North Channel	46.20213	-83.35259	13	sand	both
NC4	North Channel	46.1731	-83.24171	15	sand	both
NC5	North Channel	46.08886	-83.03946	14	silty sand	both
NC6	North Channel	46.1374	-82.88622	14.5	silty sand	both
NC7	North Channel	46.11028	-82.71014	20	clay and sand	both
NC8	North Channel	46.11313	-82.555	23	clay and silt	both
NC9	North Channel	46.10573	-82.36944	25	clay and gravel	both
NC10	North Channel	46.01912	-82.42369	24	clay, silt, and sand	both
NC11	North Channel	45.96418	-82.65969	23	clay and silt	both

Station	Basin	Latitude	Longitude	Depth (m)	Substrate	Benthic / BIS sample
NC12	North Channel	45.984	-82.9019	20	hard bottom	only BIS
NC13	North Channel	45.98519	-83.06287	19	hard bottom	only BIS
NC14	North Channel	45.99709	-83.33115	23	silt, clay, and sand	both
NC15	North Channel	46.07501	-83.5465	20	sand, clay, and gravel	both
NC16	North Channel	46.15354	-83.75172	17	sand and silt	both
NC68	North Channel	46.0414	-83.8536	15	silt	both
NC70	North Channel	46.1368	-83.6714	20	silt	both
NC71	North Channel	46.2336	-83.747	34	silt	both
NC73	North Channel	46.1867	-83.3551	18	sand and silt	both
NC76	North Channel	45.9997	-83.4331	58	silt	both
NC77	North Channel	45.9704	-83.1981	79	silt	both
NC79	North Channel	46.1243	-82.8859	25	silt	both
NC82	North Channel	45.9361	-82.7583	26	silt and shells	both
NC83	North Channel	46.0002	-82.55	30	clay	both
NC84	North Channel	46.0915	-82.557	35	clay	both
NC87	North Channel	46.0613	-82.1971	42	silt and sand	both
NC88	North Channel	46.0554	-82.0007	35	silt	both
NC89	North Channel	45.9167	-82.1614	38	silt	both
PT3	Main	45.001	-81.5865	46	clay and silt	both
PT5	Main	45	-81.6747	77	silt	both
PT6	Main	45.0004	-81.7083	135	silt	both
S02	Main	44.5832	-81.3913	30	sand	both
S05	Main	44.5834	-81.533	81	clay and silt	both
SR3	Main	45.3239	-83.4253	32	sand and silt	both
SR4	Main	45.32005	-83.37845	45	sand and silt	both
SR5	Main	45.30971	-83.33624	55.4	sand and clay	both
SR6	Main	45.32005	-83.24172	77	clay and sand	both
SR10	Main	44.8249	-83.1095	56	clay, silt, and sand	both
SU09	Main	43.6337	-82.2168	58	silt	both
TN1	Main	43.2724	-82.0061	20	sand and silt	both
TN2	Main	43.6966	-82.4169	51	silty clay	both
TN3	Main	43.6964	-81.9333	63	silt, sand, and shells	both

Station	Basin	Latitude	Longitude	Depth (m)	Substrate	Benthic / BIS sample
TN4	Main	44.2221	-81.8434	47	sand and shells	both
TN5	Main	45.2072	-82.7083	174	clay	both
TN6	Main	43.4999	-81.891	29	clay and silt	both
TN7	Main	43.5008	-81.8425	20	sandy silt	both
TN8	Main	43.6967	-81.8961	44	silt	both
TN9	Main	43.6963	-81.8738	30	silt	both
TN10	Main	43.6962	-81.8399	22	sand and shells	both
TN11	Main	44.2233	-81.6664	27	sand	both
TN12	Main	44.2242	-81.6517	17	sand	both
HU 06*	Main	43.466667	-82	94	silt	both
HU 32*	Main	44.453333	-82.341667	150	clay, silt	both
HU 38*	Main	44.74	-82.06	150	clay, silt	both
HU 48*	Main	45.278333	-82.451667	224	clay, silt	both
HU 54M*	Main	45.516667	-83.416667	178	clay, silt, sand	both
HU 61*	Main	45.75	-83.916667	198	clay, silt, sand	both
HU 93*	Main	44.1	-82.116667	184	silt	both
HU 95b*	Main	44.333333	-82.833333	110	silt, sand, clay	both
HU 96b*	Main	44.583333	-81.5	112	clay, silt	both
HU 97b*	Main	44.916667	-83.166667	53	cobble, sand, silt	both
HU 98b*	Saginaw Bay	43.941667	-83.623889	63	silt	Only benthic

Dreissena sampling protocol

During Lake Huron benthic surveys, two types of samples were collected to study *Dreissena*, including (1) Ponar (sampling area 0.0523 m^2) samples that were processed for mussel presence, density, size-frequency distribution, and sediment analysis; and (2) video images using BIS (Table 2).

In Lake Huron, from a total of 140 stations planned in the main basin, Georgian Bay and North Channel (excluding Saginaw Bay), Ponar samples were successfully collected from 125 stations (375 samples) and BIS from 131 stations (372 videos) in July 2022 aboard Canadian Coast Guard Coastal Research and Survey Vessel CCGS Limnos and in September aboard R/V Lake Guardian. During both surveys, three replicate Ponar samples were collected using the protocol described in Standard Operating Procedure for Benthic Invertebrate Field Sampling (US EPA, 2021a) and in previous publications (Burlakova et al., 2022; Karatayev et al., 2021b, 2022a).

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

Lake Regions	Ponar Planned	Ponar Sampled	BIS Planned	BIS Sampled
Main basin	85 (255)	80 (240)	85 (255)	80 (224)
Georgian Bay	26 (78)	18 (54)	26 (78)	22 (62)
North Channel	29 (87)	27 (81)	29 (87)	29 (86)
Lake Huron lake-wide	140 (420)	125 (375)*	140 (420)	131 (372)

* HU 98b station (Saginaw Bay) was not included

We attempted to collect video images from every benthic station using a BIS equipped with two GoPro cameras (Hero5, 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 & Karatayev, 2023; Karatayev et al., 2021b, 2022a). At each station, the BIS was lowered from the starboard side of CCGS *Limnos* down to the lake bottom and videos were recorded and processed according to US EPA Standard Operating Procedure for Collection and Processing of Drop-Down Camera Images for *Dreissena* spp. and round goby (US EPA, 2021b). A total of 420 images from 140 stations were initially collected from the down-looking camera in Lake Huron. 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) quality (Fig. 2, 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).

Table 3. The quality of bottom images collected with BIS across Lake Huron.

Depth zones	High quality	Medium quality	Low quality	No mussels	Not counted	All images
Main basin, ≤30	11	5	0	35	9	60
Main basin, >30-50	21	13	14	2	16	66
Main basin, >50-90	64	1	0	17	11	93
Main basin, >90	23	0	0	9	4	36
Main basin, basin-wide	119	19	14	63	40	255

Depth zones	High quality	Medium quality	Low quality	No mussels	Not counted	All images
Georgian Bay, ≤30	0	14	10	6	12	42
Georgian Bay, >30-50	2	1	0	6	3	12
Georgian Bay, >50-90	8	0	0	12	1	21
Georgian Bay, >90	0	0	0	3	0	3
Georgian Bay, basin-wide	10	15	10	27	16	78
North Channel, ≤30	12	3	3	47	1	66
North Channel, >30-50	1	0	0	14	0	15
North Channel, >50-90	1	0	0	5	0	6
North Channel, basin-wide	14	3	3	66	1	87
Huron lake-wide, ≤30	23	22	13	88	22	168
Huron lake-wide, >30-50	24	14	14	22	19	93
Huron lake-wide, >50-90	73	1	0	34	12	120
Huron lake-wide, >90	23	0	0	12	4	39
Huron lake-wide, lake-wide	143	37	27	156	57	420

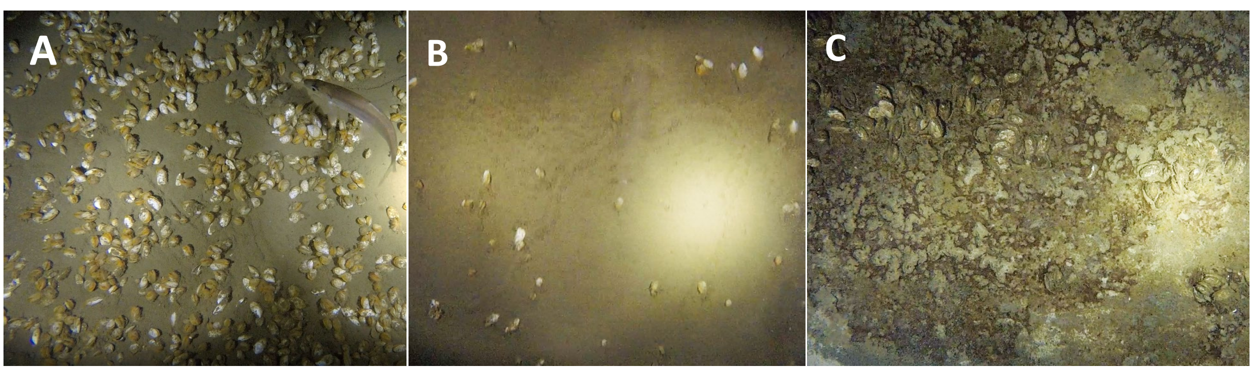

Fig. 2. Examples of images with the high (A), medium (B) and low (C) confidence of Dreissena estimation in Lake Huron.

Laboratory Procedures

All organisms found in each replicate sample collected at the 126 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. 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 Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis (US EPA, 2023).

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 Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis (US EPA, 2023). All Dreissena collected during this survey were quagga mussels (*D. r. bugensis*).

Assessment of Dreissena population dynamics

To assess *Dreissena* spp. population dynamics we used historic data for Lake Huron main basin (before 2022) summarized in Karatayev et al. (2021a) (Fig. 5). For *Dreissena* density in Georgian Bay and North Channel as well as for *Diporeia hoyi* density in all Lake Huron basins for 2000, 2002, 2003, 2007, and 2012 we used data from Nalepa et al. (2007a, 2007b, 2018), and for 2017 from Karatayev et al. (2020). While *Dreissena* and *Diporeia* densities were available for all surveys used in this study, mussel weight was not always measured directly. *Dreissena* biomass was not recorded in the main basin, Georgian Bay and North Channel of Lake Huron in 2000 – 2007 (Nalepa et al. 2007b, 2018), and was estimated using an average of 5.19 mg ash-free tissue dry weight (AFTDW) per mussel, as calculated from 2012 samples (Karatayev et al., 2021a). Although these data may not account for potential differences in relative mussel weights over time, and in some cases at different depths, we followed Karatayev et al. (2021a) estimations to reconstruct the population dynamics of dreissenid biomass for Georgian Bay (Fig. 6). We did not provide mussels biomass for the North Channel as only a few dreissenids were occasionally found in this basin. In 2017, the biomass of *Dreissena* in Lake Huron was determined as whole mussel wet weight with shell (WW, described above) as well as ash-free tissue dry weight (Karatayev et al., 2020). It was shown that the conversion between WW and AFTDW can be made using the slope from the linear regression (WW = 36.36*AFTDW (R^2 = 0.93, P < 0.001). We used this ratio to convert our 2022 WW estimation into the AFTDW.

Table 4. *Dreissena r. bugensis* population density (m^{-2}, average ± standard error) for all stations sampled using Ponar grab and BIS in the main basin of Lake Huron, Georgian Bay and North Channel in 2022, and for matching stations only. Number of successful samples in parenthesis.

Lake Huron basins	Ponar, All stations	BIS, All stations	Ponar to BIS ratio, All stations	Ponar, Matching stations	BIS, Matching stations	Ponar to BIS ratio, Matching stations
Main basin	1120 ± 221 (240)	1198 ± 121 (224)	0.93	1040 ± 168 (215)	1167 ± 124 (215)	0.89
Georgian Bay	149 ± 81 (54)	255 ± 48 (62)	0.58	138 ± 63 (43)	191 ± 60 (43)	0.72
North Channel	17 ± 16 (81)	61 ± 21 (86)	0.28	17 ± 16 (80)	12 ± 5 (80)	1.42

Table 5. *Dreissena r. bugensis* density (m^{-2}, average ± standard errors) and wet biomass with shells (g m^{-2}) in different basins of Lake Huron. Lake-wide densities were calculated as weighted averages from four depth zones. Number of successful samples in parenthesis.

Depth zone	Density 2017	Density 2022	Biomass 2017	Biomass 2022
Main basin, ≤30 m	163 ± 70 (16)	1242 ± 817 (17)	7 ± 4 (16)	35 ± 27 (17)
Main basin, >30-50 m	1429 ± 406 (23)	1032 ± 299 (21)	486 ± 116 (23)	412 ± 101 (21)
Main basin, >50-90 m	2202 ± 471 (29)	1124 ± 273 (30)	405 ± 78 (29)	236 ± 41 (30)
Main basin, >90 m	1721 ± 738 (11)	1091 ± 436 (12)	321 ± 146 (11)	145 ± 57 (12)
Main basin, basin-wide	1510 ± 278 (79)	1124 ± 238 (80)	310 ± 54 (79)	195 ± 28 (80)
Georgian Bay, ≤30 m	107 ± 96 (4)	277 ± 199 (7)	160 ± 154 (4)	278 ± 192 (7)
Georgian Bay, >30-50 m	510 ± 334 (4)	127 ± 127 (3)	399 ± 267 (4)	102 ± 102 (3)
Georgian Bay, >50-90 m	48 ± 25 (8)	45 ± 26 (8)	35 ± 20 (8)	42 ± 25 (8)
Georgian Bay, basin-wide	163 ± 77 (16)	156 ± 86 (18)	158 ± 82 (16)	151 ± 82 (18)
North Channel, ≤30 m	15 ± 7 (6)	23 ± 21 (20)	18 ± 18 (6)	79 ± 76 (20)
North Channel, >30-50 m	0 (5)	0 (5)	0 (5)	0 (5)
North Channel, >50-90 m	0 (2)	0 (2)	0 (2)	0 (2)
North Channel, basin-wide	11 ± 5 (13)	16 ± 15 (27)	13 ± 13 (13)	55 ± 53 (27)

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 2022 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. To compare *Dreissena* densities in different years by depth zones we used Kruskal-Wallis test. Two-way ANOVA with following post-hoc Tukey test on log-transformed *Diporeia* densities was used to compare temporal changes in *Diporeia* between 2017 and 2022 by depth zone. 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 Huron benthic community in 2022

We found 126 species and higher taxa of benthic macroinvertebrates in Lake Huron in 2022, in addition to unidentified immature Oligochaeta, Chironomidae, Gastropoda, and Hirudinea. The most diverse were Oligochaeta (46 species and higher taxa), Chironomidae (43 species and higher taxa), Mollusca (15 species and higher taxa: 12 Gastropoda and 3 Bivalvia), Malacostraca (9 species and higher taxa: 6 Amphipoda, 2 Isopoda and 1 Mysida), and Trichoptera (3 species and higher taxa). Other taxa were represented by fewer than 3 species, or were not identified to species level (e.g., Trichoptera, Hydrozoa, Nemertea). Among Oligochaeta, the most diverse were Tubificidae (23 species and higher taxa), and Naididae (21).

The most widely occurring taxa throughout the lake was *Stylodrilus heringianus*, which was found at 89 stations (71% of stations), followed by *D. r. bugensis* recorded at 82 stations (65%), *Pisidium* sp. at 74 stations (59%), the Chironomidae *Heterotrissocladius subpilosus* group at 67 stations (53%). Among Oligochaeta, the most widespread were Tubificinae found at 84% of stations (and immatures), Lumbriculidae (81%), Enchytraeidae (51%), and Naidinae (51%).

Oligochaeta comprised the largest percentage (50%) of lake-wide benthos density, followed by *D. r. bugensis* (30%), Chironomidae (11%), Sphaeriidae (4.7%), and Malacostraca (2.8%) (Table 6). Contribution of other groups (Hirudinea, Trichoptera, Platyhelminthes, Nemertea, etc.) to total benthos density was less than 1% each. Among Oligochaeta, the most numerous were Tubificinae (62% of total Oligochaeta density), Lumbriculidae (30%), Naidinae (5.2%), and Enchytraeidae (1.8%). *D. r. bugensis* also comprised the largest share of lake-wide benthos by biomass (98% of total wet biomass). The remaining benthic biomass was represented by Oligochaeta (1.2%). Contribution of other groups (Chironomidae, Sphaeriidae, Malacostraca, Hirudinea, Trichoptera, Platyhelminthes, Nemertea, etc.) to total benthos biomass was less than 1% each.

Table 6. Average (± standard error) density (ind. m^{-2}) and wet biomass (g m^{-2}) of major taxonomic groups of benthic invertebrates collected from 125 benthic stations in Lake Huron in 2022 and averaged by basin. Number of stations given in parentheses.

Taxa	Main (80)	Georgian Bay (18)	North Channel (27)
Total Malacostraca (ind. m^{-2})	22.1 ± 7.8	12.4 ± 5.4	164.3 ± 54.5
Total Malacostraca (g m^{-2})	0.07 ± 0.02	0.08 ± 0.03	0.39 ± 0.12
Isopoda (ind. m^{-2})	0.7 ± 0.6	6.4 ± 4.4	6.4 ± 4
Isopoda (g m^{-2})	0 ± 0	0.03 ± 0.02	0.02 ± 0.02
Total Amphipoda (ind. m^{-2})	17.7 ± 7.7	1.4 ± 0.8	154.8 ± 54.3
Total Amphipoda (g m^{-2})	0.03 ± 0.01	0 ± 0	0.36 ± 0.12
-*Diporeia* sp. (ind. m^{-2})	17 ± 7.7	0.4 ± 0.4	154.6 ± 54.3
-*Diporeia* sp. (g m^{-2})	0.03 ± 0.01	0 ± 0	0.36 ± 0.12
Chironomidae (ind. m^{-2})	153.3 ± 21.5	131.7 ± 37.1	538.4 ± 125.5

Taxa	Main (80)	Georgian Bay (18)	North Channel (27)
Chironomidae (g m^{-2})	0.17 ± 0.02	0.14 ± 0.04	0.46 ± 0.1
Total Mollusca without *Dreissena* (ind. m^{-2})	43.1 ± 11.7	53.8 ± 16.8	357.6 ± 73.1
Total Mollusca without *Dreissena* (g m^{-2})	0.05 ± 0.01	0.04 ± 0.01	0.5 ± 0.15
Total Mollusca with *Dreissena* (ind. m^{-2})	1163.1 ± 220.8	202.5 ± 77.2	374.4 ± 71.9
Mollusca with *Dreissena* (gm^{-2})	225.7 ± 35.2	144 ± 78.02	59.07 ± 56.28
-*Dreissena* spp. (ind. m^{-2})	1120 ± 221.3	148.7 ± 81	16.8 ± 15.6
-*Dreissena* spp. (g m^{-2})	225.65 ± 35.2	143.96 ± 78.02	58.58 ± 56.3
Sphaeriidae (ind. m^{-2})	40.3 ± 11.5	53.5 ± 16.8	298.4 ± 57.8
Sphaeriidae (g m^{-2})	0.04 ± 0.01	0.03 ± 0.01	0.3 ± 0.08
Gastropoda (ind. m^{-2})	2.8 ± 1.5	0.4 ± 0.4	59.2 ± 23.3
Gastropoda (g m^{-2})	0.02 ± 0.01	0 ± 0	0.2 ± 0.08
Oligochaeta (ind. m^{-2})	1401.1 ± 175.2	770.5 ± 190.5	833 ± 302.6
Oligochaeta (g m^{-2})	2.51 ± 0.31	1.54 ± 0.43	1.18 ± 0.49
-Enchytraeidae (ind. m^{-2})	29.4 ± 7.8	19.1 ± 9.9	4.2 ± 1.9
-Enchytraeidae (g m^{-2})	0.01 ± 0	0.01 ± 0	0 ± 0
-Lumbriculidae (ind. m^{-2})	423.5 ± 47	425.2 ± 104.8	192.1 ± 82.1
-Lumbriculidae (g m^{-2})	1.09 ± 0.15	0.98 ± 0.28	0.32 ± 0.13
-Naididae (ind. m^{-2})	45.5 ± 13.3	48.5 ± 28.3	127 ± 52.4
-Naididae (g m^{-2})	0 ± 0	0.01 ± 0	0.03 ± 0.01
-Tubificida (ind. m^{-2})	890.8 ± 176.4	276.9 ± 110.3	506.8 ± 272.7
-Tubificida (g m^{-2})	0.89 ± 0.22	0.3 ± 0.15	0.62 ± 0.32
Hirudinida (ind. m^{-2})	0 ± 0	0 ± 0	0.2 ± 0.2
Hirudinida (g m^{-2})	0 ± 0	0 ± 0	0.02 ± 0.02
Ephemeroptera (ind. m^{-2})	0.1 ± 0.1	0 ± 0	1.2 ± 0.7
Ephemeroptera (g m^{-2})	0 ± 0	0 ± 0	0 ± 0
Trichoptera (ind. m^{-2})	0 ± 0	0 ± 0	1.2 ± 0.7
Trichoptera (g m^{-2})	0 ± 0	0 ± 0	0.02 ± 0.01
Others (ind. m^{-2})	14 ± 4.1	5.7 ± 3.9	10.9 ± 3.9
Others (g m^{-2})	0.02 ± 0.01	0.01 ± 0	0.01 ± 0
Platyhelminthes (ind. $m^{-2)}$	14.1 ± 3.2	2.8 ± 1.5	18.9 ± 6.7
Platyhelminthes (g m^{-2})	0.01 ± 0	0 ± 0	0.01 ± 0
Total Benthos without *Dreissena* (ind. m^{-2})	1647.8 ± 188.8	976.9 ± 210.1	1927.6 ± 460.9
Total Benthos without *Dreissena* (g m^{-2})	2.82 ± 0.32	1.8 ± 0.46	2.56 ± 0.65
Total Benthos with *Dreissena* (ind. m^{-2})	2767.9 ± 341.4	1125.6 ± 233.2	1944.3 ± 459.5
Total Benthos with *Dreissena* (g m^{-2})	228.47 ± 35.27	145.76 ± 78.08	61.14 ± 56.22

In 2022 *Diporeia*, one of indicator species to assess the state of the Great Lakes, was found at 20% of all stations, with an average lake-wide density of 45 ± 14 m^{-2}, and a maximum average density at the 31-50 m depth zone (360.1 m^{-2}). *Diporeia* densities remain low with little evidence of recovery. The majority of stations with *Diporeia* were located in the North Channel (Fig. 3).

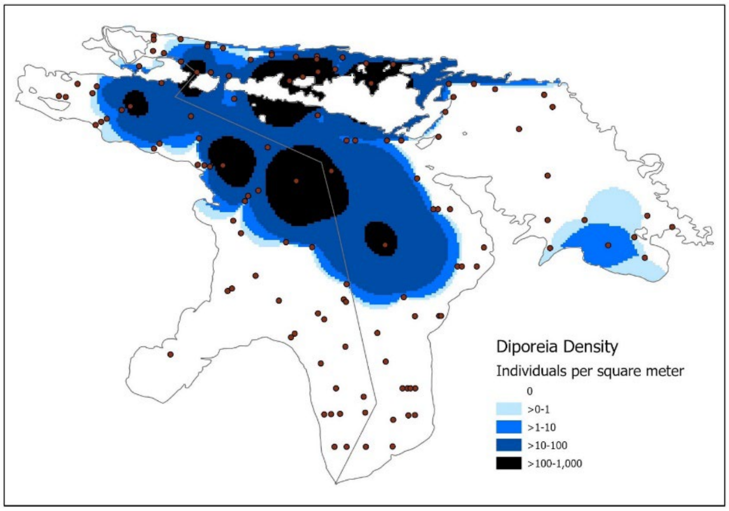

Fig. 3. Densities of Diporeya hoyi found in Lake Huron in 2022.

Therefore, the structure of benthic community of Lake Huron in 2022 was not different from 2017. In both years *Dreissena* comprised a third of community by density and >98% by biomass. Oligochaeta was the dominant group in both years by density (50%), followed by Chironomidae, and Sphaeriidae. The long-term changes in *Dreissena* and *Diporeia* 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 Huron were the declines in Sphaeriidae that started in early to mid-2000s and was consistent across all depth zones (Nalepa et al., 2018), however no large changes in this group were found in the last five years. No consistent trends were found in densities of oligochaetes or chironomids.

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). In this current study, we used the Benthic Imaging System (BIS) in Lake Huron to estimate *Dreissena* populations (presence/absence, and density). These preliminary data were later compared with dreissenid densities obtained from traditional Ponar grabs collected at the same stations. In addition, we compared the most recent population density and biomass with historic data to assess long-term dreissenid dynamics in all major basins of Lake Huron. For Lake Huron's Georgian Bay and North Channel, where mussel densities were extremely low in 2017, we expected that BIS application on bottom areas with hard (rocks, bedrock) substrates would reveal higher dreissenid densities than were previously reported based on Ponar sampling limited by soft substrates (Karatayev et al., 2020).

Dreissena population assessment using BIS vs. Ponar

In Lake Huron, of all 207 usable collected images with mussels present in 2022, 69% were evaluated as high quality, 18% as medium, and 13% images as low quality. The quality of images in the main basin generally increased with depth from low in shallow zones (where only 69% of all usable images with mussels present were of the high quality at <30 m and 44% at >30-50 m) to 98% at >50-90 m and 100% at >90 m zone (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.

In 2022, *Dreissena* on BIS images were found at 65% of all 131 stations sampled lake-wide, identical to the occurrence at stations sampled by Ponar (65% of all 125 stations). In the main basin, the occurrence recorded by BIS was lower than found in Ponar samples (75% vs. 86% of 80 stations each). In contrast, higher occurrence was recorded by BIS in Georgian Bay (BIS: 64% of 22 stations; Ponar: 50% at 18 stations) and much higher in the North Channel (BIS: 35% of 29 stations; Ponar: 11% of 27 stations).

BIS and Ponar density data for all stations sampled in the main basin of Lake Huron in 2022 produced similar results: 1198 ± 121 ind.m^{-2} (BIS) vs. 1120 ± 221 ind.m^{-2} (Ponar) (difference 7%, P = 0.70, *t*-test) (Table 4). In contrast to the main basin, in Georgian Bay and especially in the North Channel we found a substantial, although nonsignificant, difference between the average population density estimated with BIS and Ponar at all sampled stations (Georgian Bay: P = 0.13, North Channel: P = 0.10, *t*-test). Ponar underestimated *Dreissena* density because of its inefficiency in sampling hard substrates that occupy over 30% of the bottom in Georgian Bay and over 50% in the North Channel. Therefore, more stations were successfully sampled with BIS than with Ponar. Much smaller differences were found between the two methods when matching stations only were compared, suggesting that BIS could be a good addition to conventional (bottom grabs) sampling, especially on hard substrates (Table 4).

Dreissena spatial and temporal trends

In 2022, the highest *Dreissena* density in the main basin of Lake Huron was at ≤30 m, exceeding 2017 density by 7.6-fold (Fig. 5; Table 5). This large increase in mussel density in the shallowest depth zone was caused by a large proportion of small (<5 mm) recently settled mussels comprising 45% of all dreissenids in this zone. This increase, however, was not significant (P = 0.89, Kruskal-Wallis test). As overwinter survival of small mussels is low, further observations are needed to evaluate whether this massive settlement will end up in larger long-term mussel densities at this shallowest zone. In other depth zones and basin-wide, *Dreissena* density in 2022 declined 30 – 100 % compared to 2017, but these declines were not significant (P > 0.33).

An increase in quagga mussel density was found in 2022 at the shallowest zone of Georgian Bay, however, this increase was much smaller than in the main basin. At >30-50 m depth zone, mussels density declined by a factor of 4, but the basin-wide densities in 2017 and in 2022 were almost identical (Fig. 6; Table 5). In the North Channel, quagga mussel density was very low in both 2017 and 2022, but to some extent the lower density in 2017 was due to the sampling bias as Ponar was not successful in sampling hard substrates (Table 4). Even though higher densities were recorded with BIS in 2022, basin-wide *Dreissena* density in the North Channel was at least by the order of magnitude lower than in the main basin.

Changes in quagga mussel biomass in the main basin in 2022, compared to 2017, were similar to that in density. It was unexpected to find a 5-fold increase in biomass in the shallowest zone (P = 0.80, Kruskal-Wallis test) and 2.2-fold decline in the deepest zone (P = 0.97). Although the change was not significant, this was the first time a decline in dreissenid biomass was recorded in the deepest zone of the Great Lakes, contradicting with the general pattern of the ongoing shift of the bulk of *Dreissena* population into the deeper areas.

Dreissena vs. Diporeia

Historically, since the last glaciation, the benthos of Great Lakes was dominated by amphipod *D. hoyi* (Beeton, 1965, 1969; Cook & Johnson, 1974). However, starting from 1990s – early 2000s, there was a sharp decline in *Diporeia* density associated with, and likely driven by, *Dreissena* invasion in the Great Lakes (Nalepa et al., 2007a, 2009a, 2009b, 2014; Burlakova et al., 2018, 2022; Barbiero et al., 2018; Karatayev & Burlakova, 2022b). Similar to other Great Lakes, the decline in *Diporeia* in Lake Huron 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) (Figs. 4, 5, 6).

We found that, despite quagga mussels populations in the Great Lakes differing by three orders of magnitude, from the highest in lakes Michigan (4,347 m^{-2}, average for 2000 – 2015) and Ontario (2,196 m^{-2}, average for 1995 – 2018) to only 177 m^{-2} in Georgian Bay and 2.7 m^{-2} in North Channel (both averaged for 2002 – 2017), the scale of the decline in *Diporeia* was not proportional to *Dreissena* population densities (Karatayev & Burlakova, 2022b). The second largest (547-fold) decline in *Diporeia* densities was recorded in Georgian Bay with very low mussel abundance, compared to 31-fold decline in Lake Michigan (during 1994 – 2021) with one of the highest *Dreissena* abundance. Because nearly all Ponar samples in both Georgian Bay and North Channel were collected from soft substrates at 17-89 m depth range, we feel that quagga mussel populations in these basins could potentially be underestimated if the majority of mussels was located in the nearshore zone with bedrock substrates (Karatayev et al., 2020).

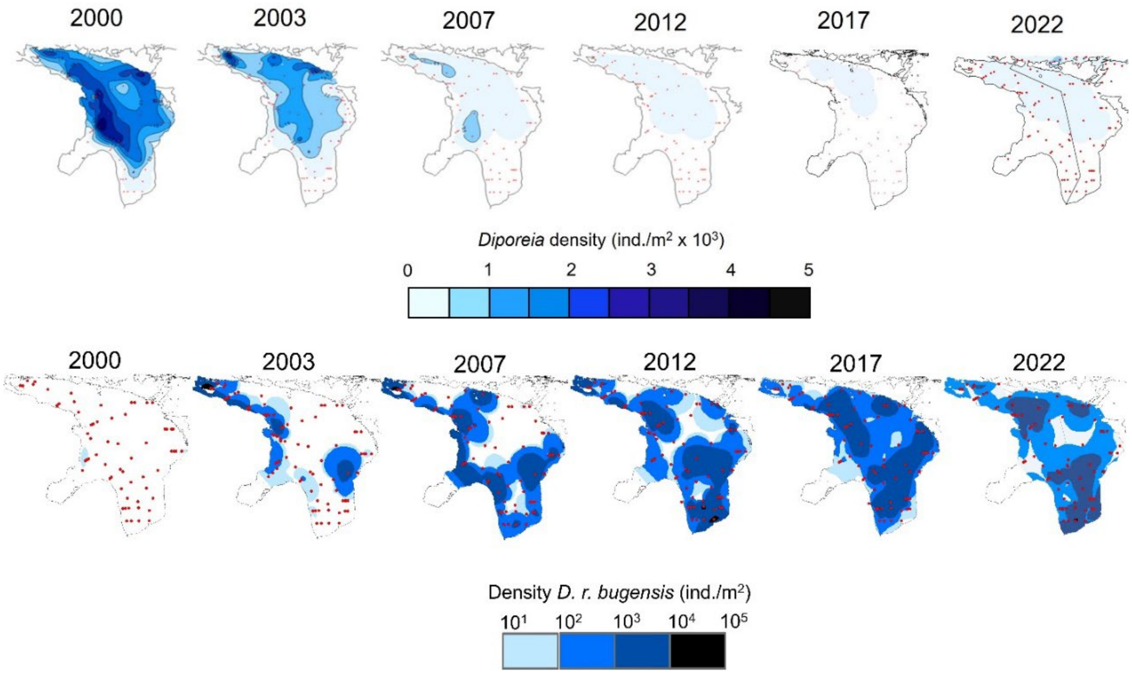

Fig. 4. Densities of D. hoyi and D. r. bugensis in the main basin of Lake Huron from 2000 to 2022.

To address this concern, in 2022 we largely targeted shallow areas with hard substrates using BIS that were never sampled before. We found that, although Ponar grabs did underestimate *Dreissena,* the average mussel density was still very low in Georgian Bay and especially in North Channel, even with additional data collected from hard substrates using BIS (Table 4). It is not entirely clear how such low quagga mussel density can cause such a strong decline in *Diporeia* abundance (Fig. 6). Perhaps food resources in these basins are so low that even very small *Dreissena* population may outcompete *Diporeia*, or some other mechanisms beside food competition may be causing *Diporeia* declines. In agreement with our prediction, in 2022 we found a further decline in *Diporeia* density in the main basin and in Georgian Bay of Lake Huron, while in the North Channel *Diporeia* density in both 2017 and 2022 were almost identical (164 ± 79 m^{-2}, in 2017 vs. 174 ± 56 m^{-2} in 2022). Therefore, the highest *Diporeia* density in the North Channel among all basins in four lower Great Lakes colonized with dreissenids coincides with the lowest *Dreissena* density in the channel (basin-wide 16 ± 14 m^{-2} in 2022).

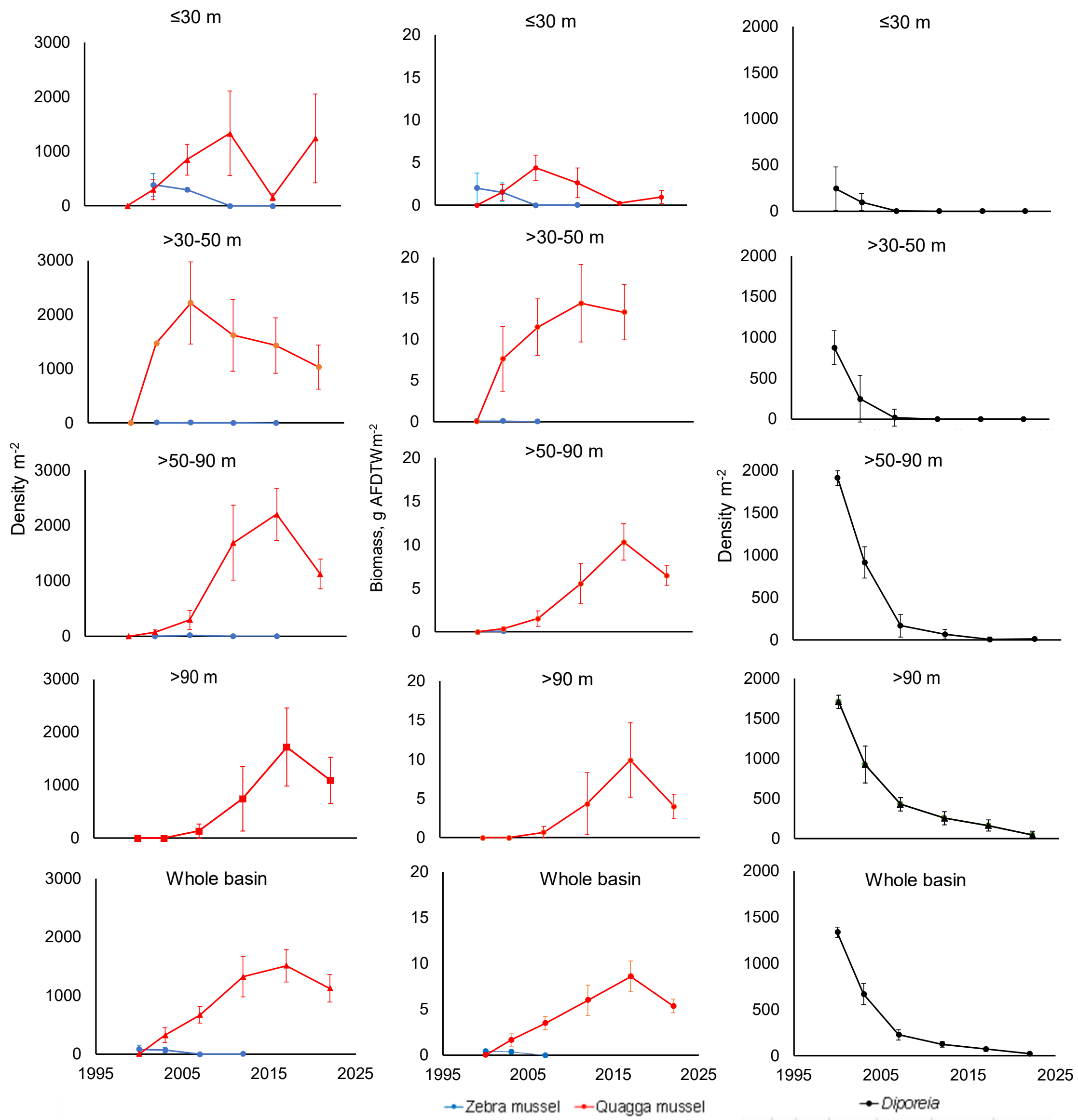

Fig. 5. Long-term dynamics of average (± standard error) density of zebra mussels, quagga mussels and D. hoyi density in the main basin of Lake Huron. Historic (before 2022) Dreissena data summarized in Karatayev et al. (2021a). Historic D. hoyi density for 2000, 2003, 2007, and 2012 are from Nalepa et al. (2007a, 2007b, 2018), and for 2017 are from Karatayev et al. (2020).

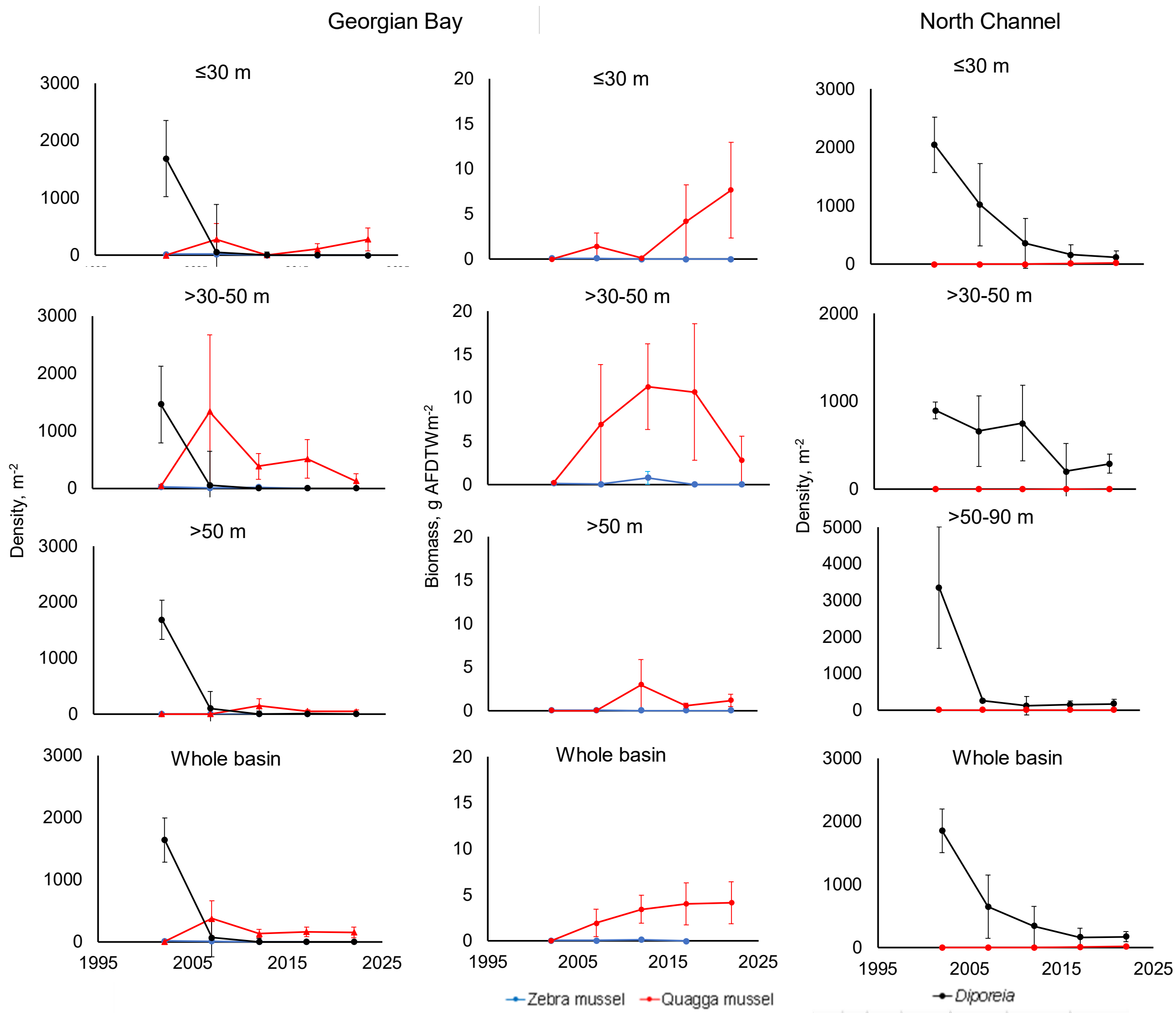

Fig. 6. Long-term dynamics of average (± standard error) density and biomass of zebra mussels, quagga mussels and D. hoyi density in Georgian Bay and North Channel of Lake Huron. Historic (before 2022) Dreissena data summarized in Karatayev et al. (2021a). Historic D. hoyi density for 2002, 2007, and 2012 are from Nalepa et al. (2007a, 2007b, 2018), and for 2017 are from Karatayev et al. (2020). No Dreissena was found at >50-90 m depth zone in the North Channel. No Dreissena biomass are given for the North Channel due to the extremely low mussel population.

Dreissena coverage

The 2022 Benthic Imaging System (BIS) survey data were collected from 136 stations in all Lake Huron basins. In the main basin, approximately 17% of the lake's bottom area was covered by *Dreissena* (Table 7). The highest coverage was observed in the depth zone of >30-50 meters, while the lowest coverage occurred in the ≤ 30 meters depth zone (Table 7; Fig. 7).

Table 7. Average *Dreissena* population percent coverage (% of area ± standard error) across depth zones (m) and basin-wide averages weighted by depth zone estimated using BIS in 2022, Huron. n represents the number of stations per depth zone.

Depth zone (m)	n	Main basin	n	Georgian Bay	n	North Channel
≤30	19	9.4 ± 6.4	13	19.6 ± 5.7	22	3.8 ± 2.4
>30-50	22	22.8 ± 5.9	4	6.0 ± 5.3	5	0.3 ± 0.3
>50-90	29	18.5 ± 3.9	8	1.9 ± 1.2	2	0.04
>90	12	16.7 ± 6.1	-	-	-	-
Basin-wide	82	16.8 ± 2.8	-	-	-	-

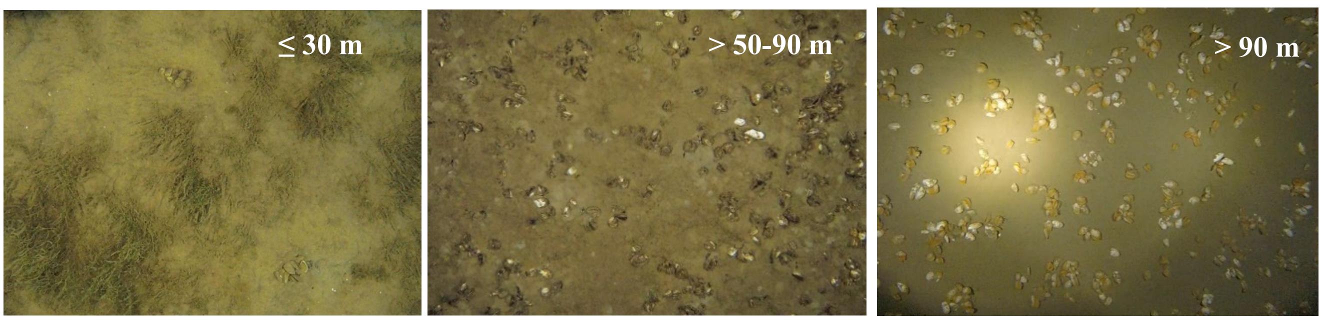

Fig 7. Dreissena representative screen shots for ≤30 m, >50-90 m, and >90 m depth zones in the main basin. Stations: MZ12 (20 m), HB3 (85 m), PT6 (135 m).

In the main basin, *Dreissena* coverage in the shallow zone was significantly lower than in the mid-depth zones (Kruskal-Wallis test, $P < 0.05$). In contrast, in Georgian Bay and North Channel, *Dreissena* coverage in the shallow zone were the highest (Table 7). *Dreissena* coverage in the shallow zone in Georgian Bay was significantly higher compared to that in the main basin and North Channel (Kruskal-Wallis test, $P < 0.05$). *Dreissena* coverage in the >30-50 meters depth zone in the main basin and Georgian Bay were significantly higher compared to that in North Channel (Kruskal-Wallis test, $P < 0.05$). *Dreissena* coverage in the >50-90 meters depth zone in the main basin were significantly higher compared to that in Georgian Bay (Kruskal-Wallis test, $P < 0.05$, Table 7).

All stations exhibiting the highest *Dreissena* coverage (>75%) were located in shallow and mid-depth zones, with a maximum depth of 47 meters (Fig. 8, 9). Notably, the station TN4 (FD1), situated at a depth of 47 meters on a rocky substrate, recorded the highest absolute coverage of 99.6%. In the main basin, *Dreissena* was entirely absent at 21 stations, accounting for 26% of the total number of stations (Fig. 9). The largest number of stations without *Dreissena* (13 stations) were located in the shallow zone (≤30 meters) representing 68% of the total number of shallow stations. The percentage of stations without *Dreissena* was lower at deeper depths; thus, 17% of stations in the mid-depth zone (>50-90 meters, 5 stations) and 25% (3 stations) in the deep zone (>90 meters) (Fig. 9). In the >30-50-meter mid-depth zone, *Dreissena* was present in all stations.

In Georgian Bay, *Dreissena* was entirely absent at 10 stations, accounting for 40% of the total number of stations. The majority of stations without *Dreissena* (5 stations) were located in the >50-90 meters zone representing 63% of the total number of these mid-depth stations. The percentage of stations without *Dreissena* was lower at shallower depths (23% of stations at ≤30 m zone vs 50% of stations in the >30-50 meters zone, Fig. 9). In the North Channel, *Dreissena* was entirely absent at 19 stations, accounting for 66% of the total number of stations (≤30 meters: 64% -14 stations; >30-50 meters: 80% - 4 stations; >50-90 meters: 50% - 1 station).

Consequently, the *Dreissena* population in the shallow zone of the main basin exhibited a high degree of heterogeneity. This may be attributed to differences in substrate type and physical disturbances, such as wave action and currents, prevalent at these shallow depths. Notably, rocky substrates were entirely covered by *Dreissena*, whereas sandy substrates lacked *Dreissena* (Fig. 10). *Dreissena* populations exhibited the greatest expansion in the mid-depth zone (>30-50 meters) where food resources remain available and physical disturbances are relatively limited.

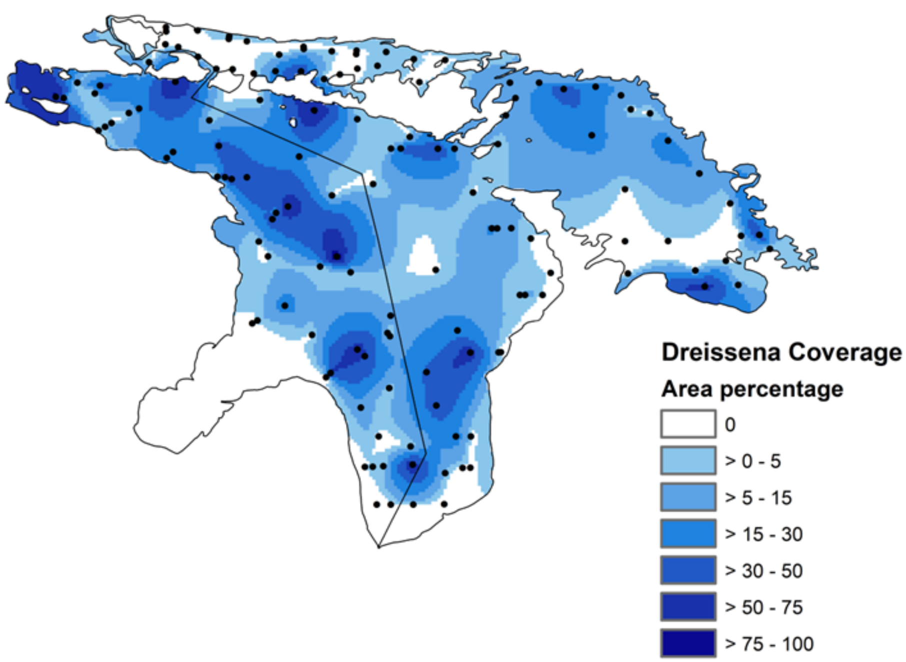

Fig. 8. Coverage (% of area) of Lake Huron bottom with Dreissena based on video survey in 2022.

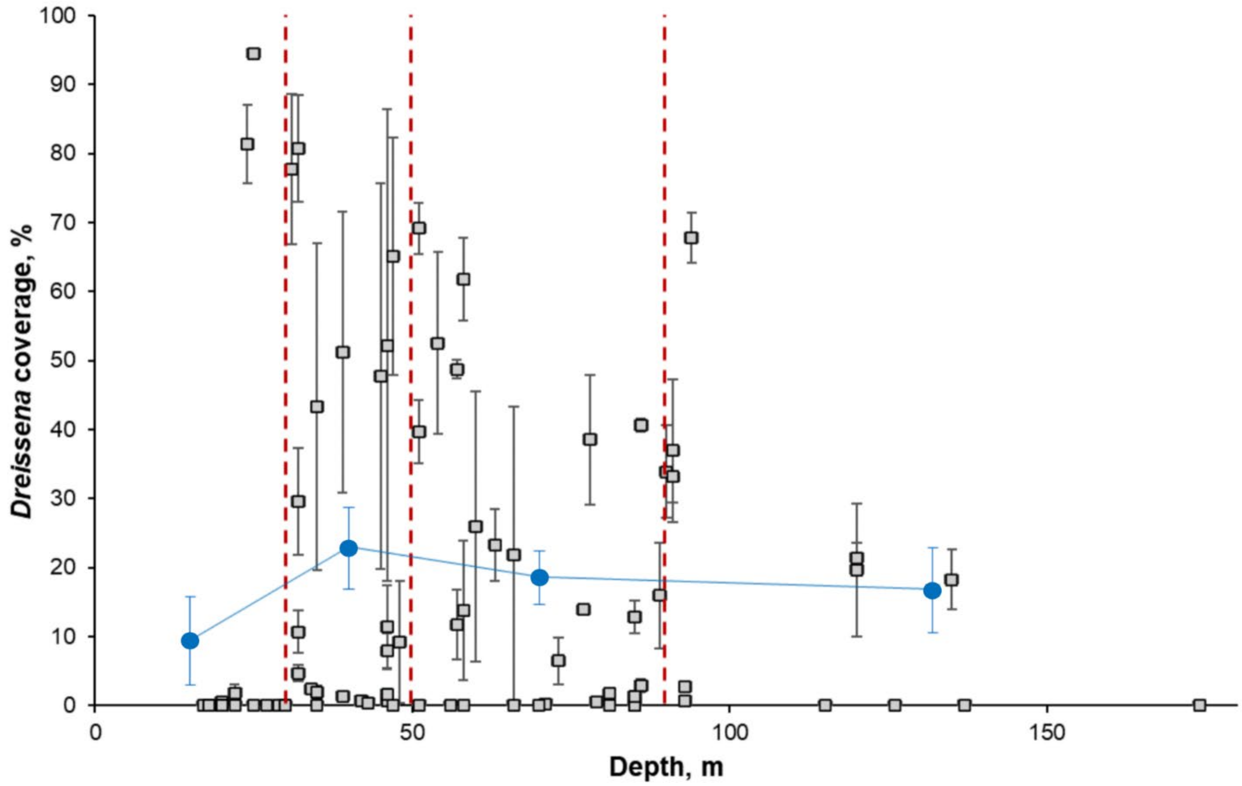

Fig. 9. Average Dreissena percent coverage by station ± standard error (gray square) and by depth zone ± standard error (blue circle) along depth gradient in the main basin of Lake Huron in 2022. Dashed red lines denote 30 m, 50 m, and 90 m depth ranges.

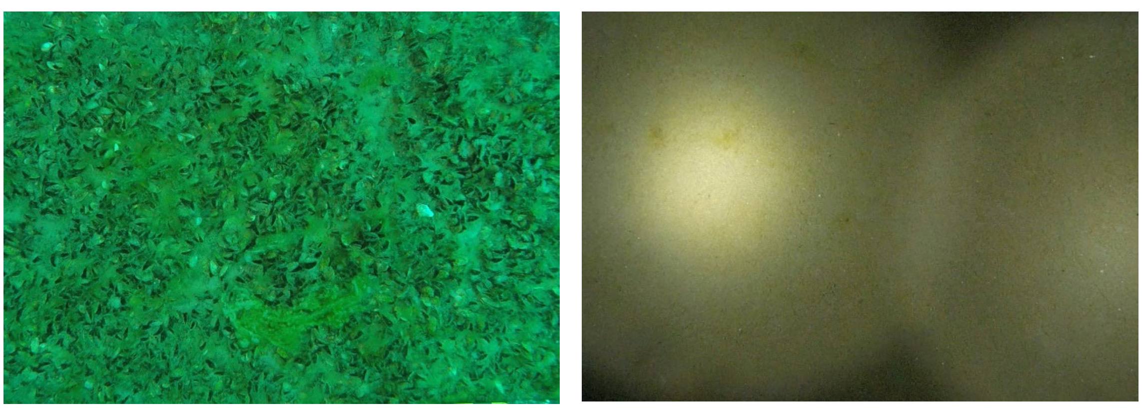

Fig. 10. Dreissena representative screen shots for ≤30 m zone in the main basin of Lake Huron in 2022. Stations: LB06 (25 m), TN11 (27 m). Rocky substrates were entirely covered by Dreissena, whereas sandy substrates lacked Dreissena.

Dreissena Coverage: Ponar vs. Video Images

The correlation between *Dreissena* coverage (BIS) and density (as counted in BIS images) exhibited a significant and strong relationship (Spearman ρ = 0.96, $P < 0.001$, n=123). The relationships between *Dreissena* coverage (BIS) and density recorded in Ponars, and between *Dreissena* coverage (BIS) and Ponar biomass were also significant, but considerably weaker (Spearman ρ = 0.73 and 0.78, respectively, $P < 0.001$, n=123).

The biomass measured in Ponar samples exhibited a weak but statistically significant relationship with *Dreissena* percent coverage obtained from BIS images (Biomass = 81.925 + 7.192 × Coverage, multiple R^2 = 0.25, $P < 0.001$, n=123, Fig. 11). When we excluded shallow stations from the analysis, the relationship between *Dreissena* percent coverage and biomass became stronger (Biomass = 71.946 + 8.289 × Coverage, R^2 = 0.46, $P < 0.001$, n=82). The weaker relationship of *Dreissena* coverage with biomass was mostly found at (1) stations where most mussels were covered by sediment (e.g., stations GB26 and NC10, Fig. 11), and (2) at rocky substrates where the coverage was extensive, but the Ponar grab was unable to sample effectively, resulting in lower biomass estimates (e.g., stations LB01 and GB39, Fig. 11).

While conventional grabs like the Ponar are effective in collecting *Dreissena* on soft substrates, their efficacy is limited at shallow zone due to the prevalence of hard substrates, making them inadequate for understanding of mussel aggregation patterns. Using underwater video surveys, we were able to assess the *Dreissena* distribution more accurately in shallow zone (Karatayev & Burlakova, 2024). Furthermore, the regression model established to elucidate the relationship between *Dreissena* coverage in sled tows and *Dreissena* biomass, developed in 2017 in Lake Huron, demonstrated enhanced accuracy in predicting biomass based on coverage.

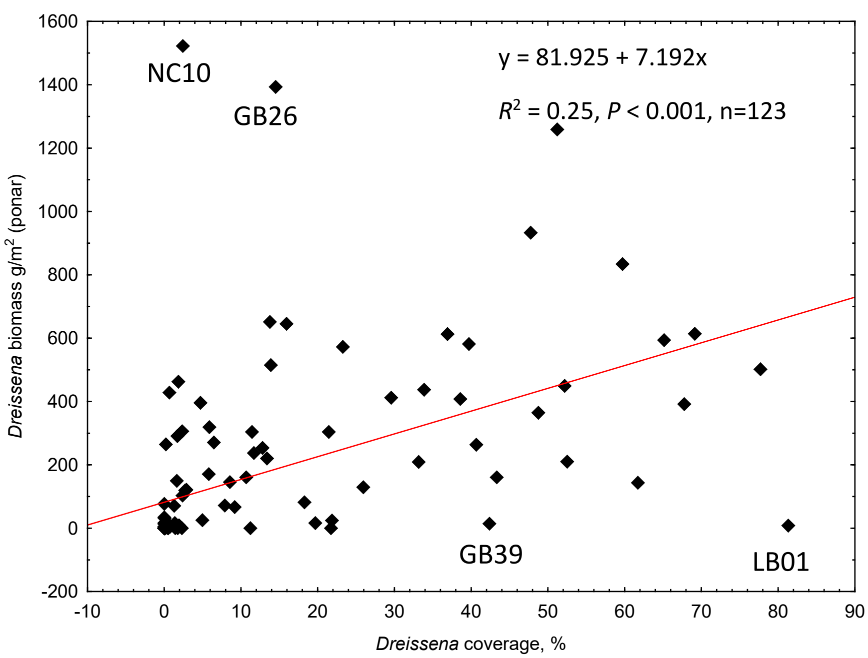

Fig. 11. Relationship between Dreissena coverage (%) and biomass (Ponar data, g/m²) in Lake Huron in 2022.

The density measured using BIS images had a strong and statistically significant relationship with *Dreissena* percent coverage obtained from BIS images (Density = 90.406 + 57.950 × Coverage, multiple R^2 = 0.71, P < 0.001, Fig. 12).

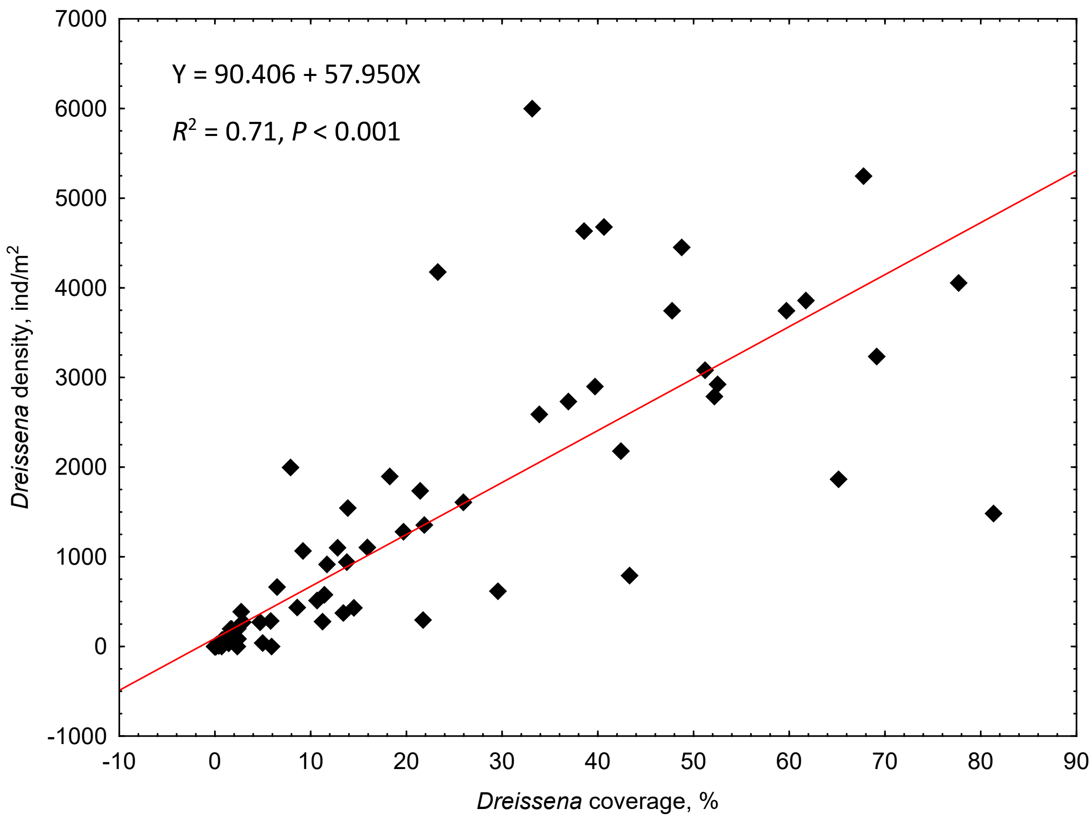

Fig. 12. Relationship between Dreissena coverage (%) and density (BIS data, ind./m²) in Lake Huron in 2022.

In 2017, *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, limited to the main basin exclusively. As a result, the coverage observed in 2017 in the shallow zone was 14-fold lower compared to that in 2022 (Table 8). However, *Dreissena* coverage at the same stations previously sampled in 2017, did not differ significantly between 2017 and 2022 in any depth zone (≤30 meters: *t*-test = 1.09, P = 0.288; >30-100 meters: *t*-test = 0.26, P = 0.799; >100 meters: *t*-test = 0.52, P = 0.616, Table 8). Therefore, no significant changes were found in *Dreissena* distribution in Lake Huron estimated by coverage over the past 5 years.

Expanding the scope of surveyed stations enabled a more precise assessment of *Dreissena* coverage across the lake bottom, particularly in the shallow zone. Prior research has demonstrated that increasing the number of replicates can significantly enhance survey sensitivity by improving accuracy and bolstering the statistical power of testing (Karatayev et al., 2018).

Table 8. Average *Dreissena* population percent coverage (% of area ± standard error) across depth zones (m) in 2017 (using benthic sled) and 2022 (using BIS), Lake Huron. n represents the number of stations per depth zone.

Depth zone (m)	n	2017	n	2022	n	2022*
≤30	11	0.7 ± 0.4	11	0.2 ± 0.2	19	9.4 ± 6.4
>30-100	25	13.3 ± 3.9	25	11.9 ± 3.7	55	20.8 ± 3.3
>100	5	13.2 ± 8.2	5	8.2 ± 5.0	8	12.0 ± 5.0

* - all stations of 2022 in the main basin

To summarize, the use of BIS for assessing *Dreissena* population in Lake Huron allowed us to enhance significantly both the quality and quantity of video images available for estimating *Dreissena* coverage and for counting mussels within a known surface area of the bottom. This approach improves the accuracy of *Dreissena* density estimates compared to Ponar grabs, particularly in shallow, rocky bottom regions where Ponars are not efficient. Moreover, the process of analyzing video images requires less time and facilitates the rapid assessment of mussel populations. We also found that the combined assessment of *Dreissena* coverage and density based on video images offers additional valuable insights into the size structure and condition of mussel populations in the Great Lakes. While it's important to note that the *Dreissena* coverage may presently be underestimated, these data are very important for assessing the distribution and coverage of bottom algae (periphyton) and other organisms on mussel shells (Daniel et al., 2024). Our study demonstrated that underwater imagery serves as a valuable tool for quantifying mussel bed structure and aggregation patterns, both of which are crucial factors requiring assessment when evaluating the ecological impact of *Dreissena* across various depth zones.

Resources and Products

A manuscript describing video vs. Ponar estimations of *Dreissena* populations and long-term dreissenid trends in Lake Huron based on this survey has been published (Karatayev & Burlakova, 2024). Another manuscript is being prepared for a peer-reviewed publication on long-term trends in Lake Huron benthic community. Long-term monitoring data are available from the EPA's Great Lakes Environmental Database (US EPA, 2023). Additional data are available by request.

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