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LAKE HURON BENTHOS SURVEY COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2017

Technical Report

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TECHNICAL REPORT

LAKE HURON BENTHOS SURVEY

COOPERATIVE SCIENCE AND MONITORING INITIATIVE 2017

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CHAPTER 1. MAJOR FINDINGS FROM THE CSMI BENTHIC MACROINVERTEBRATE SURVEY IN LAKE HURON IN 2017 WITH AN EMPHASIS ON TEMPORAL TRENDS

INTRODUCTION

In this report we present results of a benthic survey of Lake Huron conducted as part of the United States Environmental Protection Agency (USEPA) Great Lakes National Program Office (GLNPO) Great Lakes Biology Monitoring Program (GLBMP). The benthic monitoring component of GLBMP includes sample collections from a number of long-term monitoring stations (9-16 depending on the lake) sampled every year on each of the five Great Lakes and a much more intensive lake-wide survey conducted on each lake every 5 years as part of the Cooperative Science and Monitoring Initiative (CSMI). Consistent with the sampling scheme of previous CSMI benthic surveys, in 2017, a lake-wide benthic survey was conducted at 129 stations in Lake Huron to assess the status of the benthic macroinvertebrate community. Our primary focus was on the invasive zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. rostriformis bugensis*), and to compare the current benthic community with historic data.

Lake Huron benthos is considered to be the least studied benthic community of all Great Lakes (Nalepa et al., 2007a, 2007b). Nevertheless, rather detailed basin-wide surveys were conducted in the main basin 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., 2000, 2003, 2007a). However, studies prior to the early 1970s used different sampling designs and bottom grab samplers that were less efficient than the currently used Ponar grab, hence some caution is warranted when comparing these early data to more recent findings (Nalepa et al., 2002).

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).

Although changes in the benthic community occurred in all major regions of Lake Huron, it was clearly shown that the magnitude of these changes varied between regions (Nalepa et al., 2007a) and was likely driven by different factors, requiring detailed spatial resolution to assess the current status of benthic communities. This report contains detailed descriptions of benthic communities in all major regions of Lake Huron, including the main basin, Georgian Bay, North Channel, Saginaw Bay, and Thunder Bay. This report also provides information on sampling design (station locations, sampling and laboratory procedures), taxonomy, and abundance of benthic invertebrates. Additionally, it provides summary tables and figures that link previous and recent surveys to analyze temporal trends. Primary information (number and biomass of each taxon in each replicate sample) can be requested from US EPA GLNPO. The format of the current report is similar to previous technical reports (Nalepa et al., 2002, 2007b, 2018) to provide comparable data and make analysis of long-term trends as straightforward as possible.

METHODS

Description of the Lake Huron System

Lake Huron includes several basins and embayments that differ in morphometry, bottom sediments, productivity, and have distinct benthic communities. Here we provide a brief description of major regions of Lake Huron considered in our study, including Saginaw Bay, the Main basin, Georgian Bay, and North Channel (Table 1.1, Fig. 1.1). A more detailed description of physical characteristics of Lake Huron can be found in Nalepa et al. (1995, 2003, 2018).

Table 1.1. Physical characteristics of Lake Huron regions (Chapra and Sonzogni, 1979; Nalepa et al., 1995; The Great Lakes an Environmental Atlas and Resource Book 1995; Nguyen, 2014). "NA": data not available.

Lake Regions	Surface, km^2	Volume, km^3	Maximum depth, m	Average depth, m	Retention time, year	Proportion of lake bottom (%)			
						<30m	30-50m	51-90 m	>90m
Saginaw Bay	2770	24.5	13.7	8.9	0.32	100.0	0	0	0
Main basin	43086	2 842	229	66	15.22	20.9	16.0	33.4	29.7
Georgian Bay	15111	665	165	44	30.50	41.1	19.6	30.6	8.7
North Channel	3950	86.9	85	22	NA	70.0	23.8	6.2	0

Saginaw Bay is a warm, well-mixed, productive, shallow embayment which can be sub-divided into inner (shallow, warmer, and nutrient rich) and outer (deeper, colder and more nutrient poor) regions (Nalepa et al., 2018). The proportions of bottom substrates by area in the inner bay are: sand/cobble = 57%, silty sand = 16%, and silt = 27% (Nalepa et al., 2003). Outer bay substrates are represented mostly by sand with varying amounts of overlying silt as well as a few rocky areas (Fig. 1.2.). In contrast to Saginaw Bay, the main basin, Georgian Bay, and North Channel are deep, cold, and well stratified basins with low productivity (Table 1.1). Georgian Bay and North Channel are shallower than the main basin with a much larger proportion of nearshore (<30 m) area. The eastern end of both embayments in the nearshore zone consists of bedrock (Fig. 1.2). In deeper areas of Georgian Bay bottom substrates are represented by a mixture of silt, gravel, and lacustrine clays (Nalepa et al., 2018), and sediments in the main basin are represented by hard substrates with silt, clay, and sand in the south. In the North Channel, sedimentary muds are deposited by the St. Mary's River and thus more common.

Station Locations and Field Procedures

Samples for benthic macroinvertebrates were collected in September 2017 at 129 stations located throughout the main basin, Georgian Bay, North Channel, Saginaw Bay, and Thunder Bay (Fig. 1.1, Tables 1.2-1.6). Sample locations included the historical stations sampled in 1991-1996, 2000, 2002, 2003, 2007-2010, 2012, and 2017 (Nalepa et al., 2003, 2007a, 2017). Stations were stratified based on depth zones and lake basins.

One hundred nineteen stations were sampled with a Ponar grab (all benthic organisms examined), and 10 stations in Saginaw Bay and Thunder Bay were sampled by SCUBA (for *Dreissena* and amphipods only). Of these 10 stations, three were sampled by both Ponar grab and SCUBA, and seven were sampled exclusively by SCUBA (the total list of stations with coordinates and sampler used are listed in Appendix 1). One hundred nine stations were sampled aboard the U.S. EPA R/V *Lake Guardian* using a regular Ponar grab (sampling area 0.0523 m^2, coefficient used to calculate density per m^2 = 19.12). Eleven of these stations are part of the EPA GLMBP and sampled every year. Some nearshore stations in Saginaw Bay (13 total) and Thunder Bay (4 total) were sampled on board the NOAA R/V *2601*, R/V *3011*, or R/V *Laurentian*. Of the total 10 stations in Saginaw Bay sampled with a Ponar grab, seven (SB4, SB7, SB10, SB11, SB13, SB14, and SB16) were sampled using a Ponar with a sampling area of 0.0467 m^2 (coefficient 21.42), and three stations (SB20, SB23, and SB24) were sampled with a Ponar with a sampling area of 0.0479 m^2 (coefficient 20.89). A total of six stations in Saginaw Bay were sampled by SCUBA for *Dreissena* and amphipods only using a full quadrat with sampling area 0.5256 m^2 (coefficient 1.9) (stations SB5d, SB6d, SB16d, and three more were additionally sampled by Ponar, SB13d, SB14d, and SB16d). In Thunder Bay only SCUBA samples were collected from all four stations using a quadrat with sampling area of 0.2628 m^2 (coefficient 3.8). Samples were not collected from three stations due to bad weather (TB6d in Thunder Bay) or hard substrates (GB26 in Georgian Bay, and SU09 in the main basin).

At each of the 109 stations surveyed on board the *Lake Guardian,* Ponar samples were taken in triplicate. 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 concentration of 5 – 10%. Details are described in the EPA GLNPO Standard Operating Procedure for Benthic Invertebrate Field Sampling (SOP LG406, Revision 11, June 2016). At 12 sites across the main basin and Georgian Bay (AK1, F13, GB35, HU27, HU45, HU429, MZ22, MZ23, MZ25, SR6, TN3, and TN7), live mussels were collected by additional Ponar grabs to determine length-weight relationships. Sites were selected on the basis of having a sufficient number of mussels across a broad size range (10-30 mm target shell length). Another criterion for site selection was to represent a range of depths and multiple regions across the lake. Further methods are described below under Laboratory Procedures. For the stations sampled by SCUBA, divers collected all mussels and associated substrate within one half of a 0.5256 m^2 quadrat. The quadrat was dropped haphazardly at three locations approximately 3-5 m apart at each station. The collected materials were placed in a separate 500-µm mesh bag for each replicate. Additional live quagga mussels were collected from outside of the quadrats to determine length-weight relationships at two sites in Saginaw Bay (SB5, SB15) and one site in Thunder Bay (TB3d).

Table 1.2. Stations sampled in Lake Huron by Ponar for all benthos, and additionally by SCUBA for only *Dreissena* and amphipods in 2017. Note three stations in Saginaw Bay were sampled by both Ponar and by SCUBA, therefore a total of 129 stations were sampled.

Sampling method	Sampled by Ponar for all benthos	LTM stations	CSMI stations	Sampled by SCUBA	Sampled by both SCUBA and Ponar
Main basin	79	10	69	0	0
Georgian Bay	16	0	16	0	0
North Channel	13	0	13	0	
Thunder Bay	0	0	4	4	0
Saginaw Bay	11	1	13	6	3
Total	**119**	11	115	**10**	3

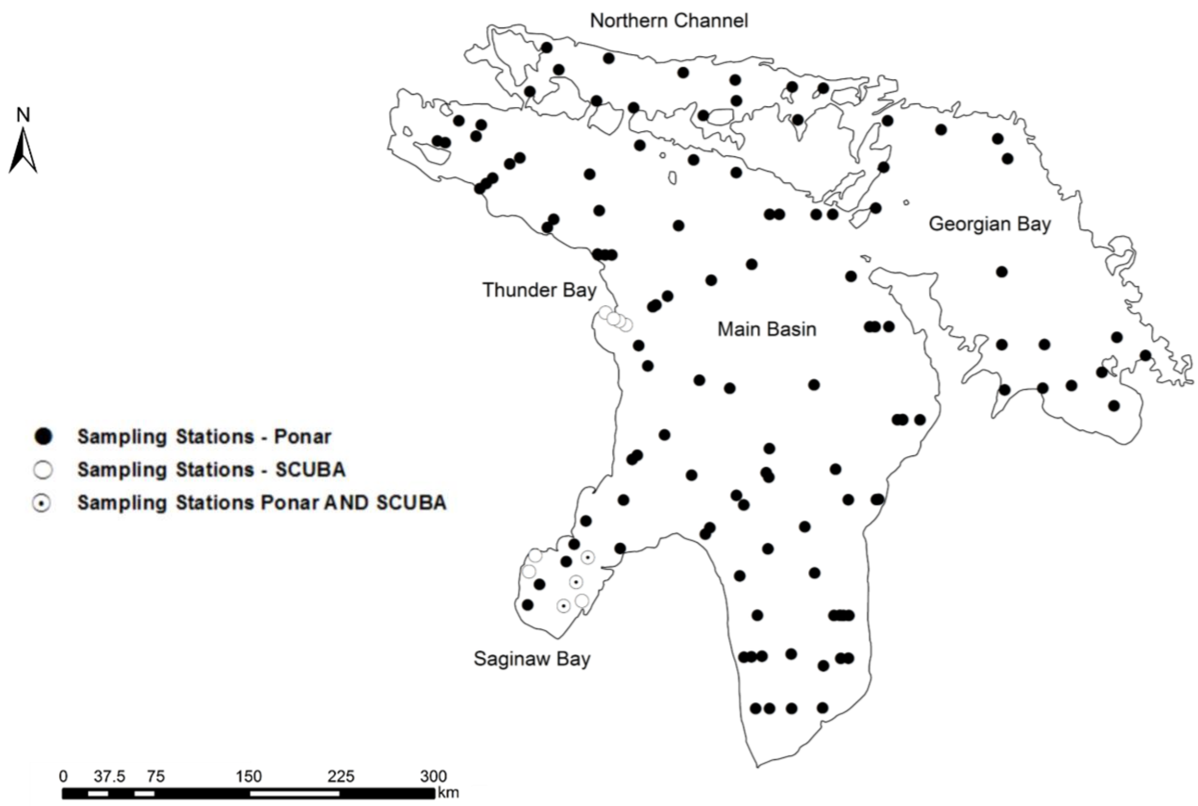


Figure 1.1. Location of Ponar (black circles), SCUBA (open circles) and both Ponar and SCUBA stations (open circle with a dot) sampled in Lake Huron in 2017.

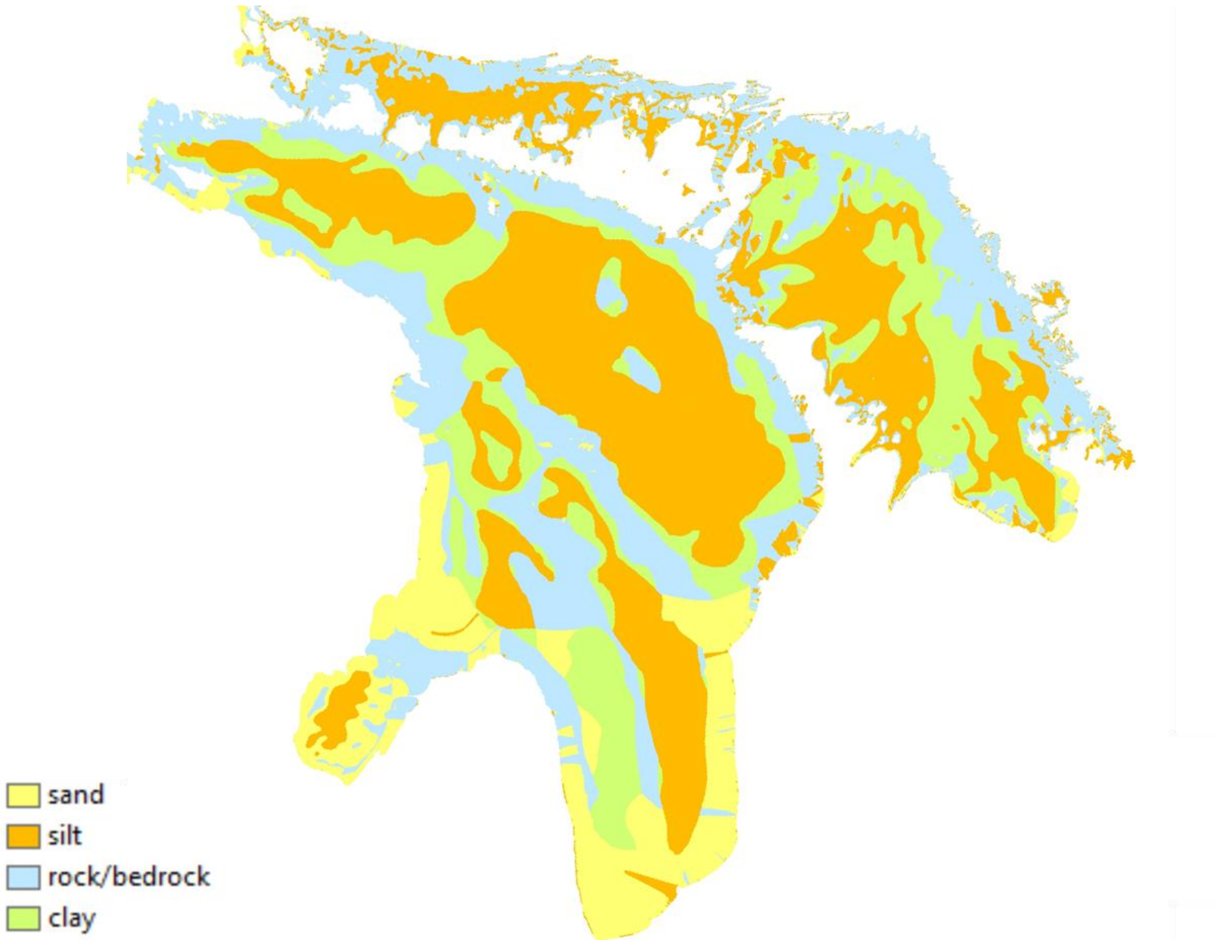


Figure 1.2. Major bottom substrates in Lake Huron (Great Lakes Aquatic Habitat Framework (GLAHF) data).

Laboratory Procedures

All organisms found in each replicate sample at the 119 Ponar stations were sorted, identified, counted, and weighted (total wet weight). In addition, only *Dreissena* spp. and amphipods were sorted and counted at the 10 stations sampled by SCUBA. Organisms were picked out of samples 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. Adult oligochaetes were identified to species; immature Tubificidae, Lumbriculidae, Naididae and Enchytraeidae 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. Immature Oligochaeta (in cocoons) were excluded both from density and biomass for comparison with historic data. Chironomids were identified to the lowest practical taxonomic level, usually genus. Other invertebrates were identified to species, when possible. Taxonomy followed Kathman and Brinkhurst (1998) (oligochaetes, with old division by Enchytraeidae, Lumbriculidae, Naididae and Tubificidae, comparable with historical data); Holsinger (1972) and Bousfield (1958) (amphipods); Epler (2001) and Wiederholm (1983) (chironomids); and Smith (2001), Merritt et al. (2008), and Thorp and Covitch (2001) (for other groups). *Dreissena* spp. (*D. polymorpha* and *D. r. bugensis*) from all samples were identified to species, measured to the nearest millimeter with a caliper, counted, and the whole sample was weighed to the nearest 0.001 g after being blotted dry on absorbent paper (total wet weight of tissue and shell, WW). Details are described in the EPA GLNPO Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis (SOP LG407, Revision 09, April 2015). For convenience, we will use a combined name "*Dreissena*" or dreissenids unless we refer to a particular species (*D. polymorpha*, *D. rostriformis bugensis*), and "*Diporeia*" when referring to *Diporeia hoyi*. A phylogeographic analysis of *Diporeia* across glaciated North America found no evidence to suggest the existence of two or more phylogenetic species (Uzjak, 2010).

In 2017, biomass of *Dreissena* was determined as whole mussel wet weight (WW, described above) as well as ash-free tissue dry weight (AFTDW). Surveys prior to 2017 only reported dreissenid biomass as AFTDW, which is calculated per sample based on length-weight regressions and mussel size distributions (Nalepa et al. 2018 and described below). Given differences in methods used to determine and report dreissenid biomass, both methods were used and values of both measures are provided (WW in Table 1.7; AFTDW in Table 1.8). Ultimately, conversion between WW and AFTDW can be made using the slope from the linear regression (WW = 36.36*AFTDW ($R^2 = 0.93$, $P < 0.001$), Fig. 1.3).

Length-weight relationships (in terms of AFTDW) for quagga mussels were determined from live specimens within 48 hours of collection. Soft tissues of 25 individuals between 10 mm and > 20 mm were removed from the shells, placed individually into pre-weighed aluminum planchets, and dried at 60 C^o for at least 48 hours. After drying, the planchets were placed and kept in a desiccator. Upon completion of the survey cruise and return to the laboratory, soft tissues were weighed, ashed at 550 C^o for 1 h, and then re-weighed. AFTDW was then calculated as the difference between dry weight and post-ashed weight of the mussel tissue. Corresponding shell lengths were measured to the nearest 0.1 mm. Overall, a total of 375 individuals from the 15 sites were weighed and measured. All individuals for length-weight determinations were *D. r. bugensis* since *D. polymorpha* was not found at all in the Ponar grabs and was in low abundance at the SCUBA sites. Measured AFTDWs and shell lengths (SL) were used to develop length-weight relationships according to the allometric equation: $\log_e$AFTDW (mg) = b + a*$\log_e$SL (mm). Relationships were developed for pooled sites within four different depth intervals representing the main basin and Georgian Bay: $\leq$ 30 m, 31-50 m, 51-90 m, and > 90 m; as well as for the shallow areas of Thunder Bay and Saginaw Bay (Table 1.9). The length-weight parameters for *D. r. bugensis* were applied to *D. polymorpha*.

To determine AFTDW biomass, the number of individuals in each 1 mm size category was multiplied by AFTDW as calculated from the length-weight regression for in individual with a shell length from the mid-point of that size category. Broken mussels (i.e. mussels with shells broken enough to compromise the length measurement) were incorporated into AFTDW estimates by first calculating the ratio of broken to unbroken mussel based on WW then increasing the AFTDW estimate by that ratio.

Table 1.3. Station name, main substrate, coordinates (decimal degrees), and sampling year for all Lake Huron main basin stations. An "X" indicates the station was sampled in that year, followed by the corresponding water depth (in parenthesis).

Station	Substrate	Latitude	Longitude	2000	2002	2003	2007	2012	2017
AL20	Sand	44.9523	-83.2708			X(20)			
AL30	silty sand	44.9345	-83.2468			X(30)			
AL45	silty sand	44.9180	-83.1910			X(45)			
AL60	sandy silt	44.8623	-83.1130			X(60)			
AL80	silty sand	44.8187	-83.0318			X(80)			
AP1	Sand	45.4167	-83.7122			X(23)			
AK1	fine sand	44.3604	-81.9231						X(120)
AK2	Silt	44.3444	-82.3614						X (93)
AK3	Silt	44.3243	-82.3454						X (96)
FI2	sand, clay	45.4998	-81.9416	X(30)		X(30)	X(33)	X(33)	X(32)
FI3	silty clay	45.4996	-82.0463	X(46)		X(46)	X(45)	X(44)	X(45)
FI4	silty clay	45.5000	-82.2781	X(61)		X(61)	X(69)	X(61)	X(90)
FI5	Silt	45.5001	-82.3397	X(82)		X(90)	X(86)	X(85)	X(86)
HB1	Sand	45.6138	-84.1698			X(20)	X(12)	X(12)	X(11)
HB3	silty clay	45.6359	-84.1294			X(45)	X(44)	X(42)	X(44)
HB4	Silt	45.6600	-84.0883			X(58)	X(55)	X(54)	X(56)
HB5	silty loam	45.7229	-83.9803			X(80)	X(74)	X(73)	X(78)
HU06	Silt	43.4662	-82.0003	X(51)		X(52)	X(51)	X(49)	X(50)
SU09	silt	43.6337	-82.2168	X(59)		X(60)	X(59)	X(57)	*
HU12	Silt	43.8899	-82.0562	X(90)		X(90)	X(88)	X(87)	X(88)
HU15	Silt	43.9999	-82.3504	X(66)		X(69)	X(65)	X(65)	X(67)
HU27	silty sand	44.1987	-82.5028	X(57)		X(61)	X(55)	X(53)	X(55)
HU32	Silt	44.4534	-82.3412	X(80)		X(82)	X(84)	X(78)	X(82)
HU325	sandy clay	45.8166	-84.3876	X(58)		X(60)	X(57)	X(55)	X(57)
HU329	silty sand	45.9127	-84.3021	X(37)		X(38)	X(37)	X(37)	X(36)
HU37	sandy silt	44.7610	-82.7829	X(72)		X(72)	X(74)	X(72)	X(75)
HU38	silty clay/loam	44.7399	-82.0597	X(133)		X(132)	X(138)	X(135)	X(135)
HU429	silty sand	45.8241	-84.4368	X(33)		X(33)	X(43)	X(41)	X(34)
HU429P	silty sand	45.8219	-84.4370	X(19)					
HU45	clay, sand	45.1367	-82.9843	X(91)		X(99)	X(100)	X(94)	X(97)
HU48	silty clay	45.2779	-82.4531	X(112)		X(113)	X(112)	X(107)	X(113)

Station	Substrate	Latitude	Longitude	2000	2002	2003	2007	2012	2017
HU53	silty clay	45.4502	-82.9148	X(91)		X(93)	X(92)	X(88)	X(89)
HU54M	silty clay/loam	45.5165	-83.4159	X(139)		X(93)	X(92)	X(88)	X(142)
HU61	silty loam	45.7498	-83.9163	X(116)		X(120)	X(116)	X(116)	X(119)
HU93	silt	44.0998	-82.1176	X(87)		X(90)	X(89)	X(88)	X(88)
HU95b	sandy silt	44.3332	-82.8326	X(66)		X(90)	X(89)	X(88)	X(67)
HU96	sandy silt	44.5836	-81.4999						X(47)
HU97b	silty sand	44.9159	-83.1662	X(45)		X(45)	X(44)	X(42)	X(43)
KB472	silty clay	45.2251	-81.8259				X(44)	X(44)	X(44)
KB479	silty sand	45.6845	-82.5503				X(34)	X(34)	X(32)
KB480	silty sand	45.7403	-82.8198				X(31)	X(32)	X(31)
KB482	sand, clay	45.8048	-83.1593				X(48)	X(42)	X(40)
MZ12	silty sand	43.2697	-82.4284	X(21)	X(21)	X(21)	X(20)	X(20)	X(19)
MZ13	silty sand	43.2695	-82.3407	X(31)	X(31)	X(29)	X(28)	X(20)	X(29)
MZ14	silty sand	43.2698	-82.2007	X(29)	X(28)	X(28)	X(27)	X(22)	X(22)
MZ22	silty sand	43.5051	-82.5026	X(19)	X(20)	X(21)	X(21)	X(18)	X(18)
MZ23	silty sand	43.5070	-82.4544	X(33)	X(33)	X(33)	X(34)	X(32)	X(32)
MZ24	silty clay	43.5100	-82.3878	X(43)	X(44)	X(42)	X(43)	X(42)	X(42)
MZ25	silty clay	43.5197	-82.2042	X(52)	X(53)	X(51)	X(51)	X(51)	X(51)
MZ34	silty sand	43.8770	-82.5290	X(45)	X(48)	X(45)	X(45)	X(46)	X(46)
MZ43	coarse sand	44.0668	-82.7463	X(30)	X(30)	X(30)	X(30)	X(30)	X(29)
MZ44	silty sand	44.0951	-82.7177	X(39)	X(40)	X(39)	X(39)	X(39)	X(39)
MZ45	silty sand	44.2418	-82.5499	X(58)	X(60)	X(58)	X(56)	X(58)	X(58)
MZ72	sand	44.4047	-83.2081	X(24)	X(24)	X(24)	X(24)	X(23)	X(22)
MZ73	sand	44.4233	-83.1753	X(32)	X(32)	X(31)	X(30)	X(30)	X(30)
MZ74	sand	44.4384	-83.1467	X(42)	X(42)	X(40)	X(40)		
MZ75	silty sand	44.5154	-83.0029	X(67)	X(67)	X(65)	X(63)	X(66)	X(66)
MZ76	silty loam	44.7248	-82.5917	X(79)	X(80)	X(71)	X(76)	X(77)	X(79)
MZ87	loam	45.0975	-83.0584	X(55)	X(58)	X(55)	X(50)	X(55)	X(56)
MZ88	sandy silt	45.0890	-83.0774	X(47)	X(46)	X(49)	X(47)		
MZ89	silty sand	45.0890	-83.0774	X(32)	X(32)	X(33)	X(32)	X(32)	X(31)
MZ93	silty sand	45.4415	-83.7436	X(32)	X(32)	X(33)	X(31)	X(32)	X(32)
MZ94	silty sand	45.4384	-83.7384	X(40)	X(38)	X(32)	X(38)		
MZ95	silt	45.4783	-83.7035	X(64)	X(61)	X(61)	X(62)	X(60)	X(61)
MZ96	silt	45.6773	-83.4761	X(129)	X(139)	X(125)	X(122)	X(126)	X(130)
MZ123	silty sand	45.8944	-84.1602	X(54)	X(55)	X(45)	X(45)	X(51)	X(54)
MZ125	silt	45.8452	-84.1929	X(81)	X(81)	X(80)	X(79)	X(80)	X(81)
PT2	sand	45.0008	-81.5499	X(30)					
PT3	silty clay	45.0010	-81.5865	X(45)	X(45)	X(46)	X(43)	X(46)	X(46)
PT5	silty clay	45.0000	-81.6747	X(80)	X(80)	X(77)	X(77)	X(77)	X(77)
PT6	silt	45.0004	-81.7083	X(136)	X(135)	X(137)	X(133)	X(135)	X(135)
SB23	silty sand	44.2218	-83.2627	X(28)	X(28)				
SO2	sand	44.5832	-81.3913	X(31)	X(31)	X(31)	X(30)	X(30)	X(30)
SO3	silty sand	44.5835	-81.5000	X(40)	X(48)	X(47)	X(45)		

Station	Substrate	Latitude	Longitude	2000	2002	2003	2007	2012	2017
SO4	sandy silt	44.5839	-81.4999	X(67)	X(68)	X(67)	X(65)	X(67)	X(67)
SO5	silt	44.5834	-81.5330	X(81)	X(80)	X(78)	X(78)	X(81)	X(81)
SR3	silt	45.3239	-83.4253		X(32)	X(35)	X(30)	X(33)	X(33)
SR4	sandy clay	45.3201	-83.4221		X(45)	X(45)	X(43)	X(45)	X(45)
SR5	sandy clay	45.3201	-83.3785	X(55)	X(56)	X(55)	X(58)	X(55)	X(55)
SR6	sandy clay	45.3201	-83.3361		X(77)	X(75)	X(72)	X(75)	X(75)
SR10	sandy silt	44.8249	-83.1095	X(56)	X(57)	X(56)	X(54)	X(56)	X(56)
TA20	sand	44.1526	-83.3457		X(20)				
TA45	sandy silt	44.3018	-83.1843		X(45)				
TN1	silt	43.2724	-82.0061	X(21)	X(21)	X(20)	X(21)	X(20)	X(20)
TN2	silt	43.6966	-82.4169	X(51)	X(51)	X(51)	X(51)	X(51)	X(51)
TN3	silt, clay/sand	43.6964	-81.9333	X(66)	X(65)	X(64)	X(61)	X(63)	X(64)
TN4	coarse sand	44.2221	-81.8434	X(48)	X(45)	X(47)	X(49)	X(47)	X(47)
TN5	silty clay	45.2072	-82.7083	X(170)	X(173)	X(171)	X(164)	X(174)	X(174)
TN6	silt	43.4999	-81.8910		X(31)	X(29)	X(28)	X(29)	X(28)
TN7	silt	43.5008	-81.8425		X(21)	X(21)	X(20)	X(20)	X(20)
TN8	sandy silt	43.6967	-81.8961		X(44)	X(44)	X(43)	X(44)	X(44)
TN9	silt	43.6963	-81.8738		X(32)	X(31)	X(30)	X(30)	X(30)
TN10	silt	43.6962	-81.8399		X(22)	X(22)	X(21)	X(22)	X(21)
TN11	coarse sand	44.2233	-81.6664		X(30)	X(29)	X(28)	X(27)	X(27)
TN12	sand	44.2242	-81.6517		X(20)	X(18)	X(18)	X(17)	X(17)
GLERL18	sand	44.9553	-83.2770				X(18)		
GLERL30	silty sand	44.9387	-83.2405				X(30)		
GLERL45	silty sand	44.8991	-83.1496				X(46)		

*no samples collected due to hard substrate

Table 1.4. Station name, main substrate, coordinates (decimal degrees), and sampling year for stations in North Channel (NC) and Georgian Bay (GB) of Lake Huron. An "X" indicates the station was sampled in that year, followed by the corresponding water depth (in parenthesis).

Stations	Substrate	Latitude	Longitude	2002	2007	2012	2017
NC68	sandy silt	46.0414	-83.8536	X(17)	X(17)	X(16)	X(15)
NC70	silt	46.1368	-83.6714	X(22)	X(22)	X(22)	X(20)
NC71	silt	46.2336	-83.7470	X(35)	X(35)	X(35)	X(34)
NC73	coarse sand	46.1867	-83.3551	X(19)	X(17)	X(20)	X(18)
NC76	silt	45.9997	-83.4331	X(58)	X(58)	X(57)	X(58)
NC77	silt	45.9704	-83.1981	X(78)	X(78)	X(76)	X(79)
NC79	silt	46.1243	-82.8859	X(25)	X(25)	X(27)	X(24)
NC82	silt	45.9361	-82.7583	X(27)	X(29)	X(28)	X(26)
NC83	silt	46.0002	-82.5500	X(31)	X(30)	X(32)	X(30)
NC84	silty clay	46.0915	-82.5570	X(35)	X(36)	X(36)	X(35)
NC87	silty clay	46.0613	-82.1971	X(32)	X(37)	X(44)	X(42)

Stations	Substrate	Latitude	Longitude	2002	2007	2012	2017
NC88	silt	46.0554	-82.0007	X(34)	X(34)	X(36)	X(35)
NC89	silt	45.9167	-82.1614	X(39)	X(38)	X(38)	X(38)
GB1	silt	44.7175	-80.8567	X(89)	X(88)	X(89)	X(91*)
GB3	silty coarse sand	44.7250	-80.6167	X(32)	X(31)	X(35)	X(33)
GB4	sandy silt	44.6458	-80.1667	X(57)	X(57)	X(57)	X(57)
GB5	sandy clay	44.7967	-80.2433	X(58)	X(58)	X(58)	X(59)
GB6	sandy silt	44.7367	-80.4350	X(86)	X(87)	X(87)	X(88)
GB8	silty clay	44.9527	-80.1488	X(51)	X(51)	X(51)	X(49)
GB9	sandy clay	44.8717	-79.9680	X(32)	X(27)	X(31)	X(28)
GB11	sandy clay	44.9208	-80.6058	X(61)	X(62)		X(62)
GB12	silty clay	44.9200	-80.8750	X(87)	X(87)	X(87)	X(90)
GB17	silt/clay/loam	45.2450	-80.8750	X(78)	X(78)	X(76)	X(79)
GB24	silty sand, clay	45.7455	-80.8388	X(39)	X(40)	X(31)	X(29)
GB26	sand, some clay	45.8333	-80.9000	X(26)	X(21)		**
GB29	silty clay loam	45.5833	-81.0833	X(32)	X(31)	X(35)	X(43)
GB35	silty sand, clay	45.5275	-81.6695	X(33)	X(36)	X(37)	X(35)
GB36	loam, coarse sand	45.7083	-81.6200	X(52)	X(53)	X(56)	X(53)
GB39	silty sand	45.8733	-81.2583	X(28)	X(28)	X(28)	X(26)
GB42	silty clay	45.9128	-81.5950	X(26)	X(26)	X(26)	X(25)

* although the station was approx. 91m in depth, for consistency with historic data in data analysis we kept it grouped in the 51-90m depth range

**no samples collected due to hard substrate

Table 1.5. List of stations, main substrate, depth, coordinates (decimal degrees), and sampling years for Saginaw Bay of Lake Huron. Stations sampled with a Ponar and by SCUBA are designated with a ‘P’ and a ‘S’, respectively.

Station	Substrate	Depth (m)	Latitude	Longitude	2006	2007	2008	2009	2010	2017
SB4	silty sand	6.5	43.7442	-83.8678	P	P	P	P		P
SB5	gravel, sand	3	43.8953	-83.8605			S	S	S	S
SB6	sand	4	43.9680	-83.8208			S	S	S	S
SB7	silt	6.7	43.8380	-83.7928	P	P	P	P		P
SB10	silt	12.1	43.9417	-83.6238	P	P	P	P		P
SB11	silt, fine sand	10.7	44.0205	-83.5737	P	P	P	P		P
SB13	coarse sand	3.7	43.9595	-83.4887	P	P	P, S	P, S	S	P, S
SB14	sand	3.8	43.7383	-83.6408	P	P	P, S	P, S	S	P, S
SB15	gravel, rocks	5	43.7612	-83.5263			S	S	S	S
SB16	sand	3.0	43.8470	-83.5625	P	P	P, S	P, S	S	P, S

Station	Substrate	Depth (m)	Latitude	Longitude	2006	2007	2008	2009	2010	2017
SB20	silty sand	16	44.1262	-83.5000		P	P			P
SB23	sand, silt	28	44.2208	-83.2625		P	P			P
SB24	silty sand	12.5	44.0013	-83.2833	P	P	P			P
SB27	cobble, rocks	5.5	44.0388	-83.1110			S	S		

Table 1.6. List of stations, main substrate, depth, and coordinates (decimal degrees) sampled in Thunder Bay of Lake Huron by SCUBA divers in 2017.

Station	Substrate	Depth (m)	Latitude	Longitude
TB1d	rocks	6.09	45.0622	-83.3778
TB3d	cobble, sand	6.31	45.0069	-83.2497
TB4d	cobble, sand	7.19	45.0245	-83.2913
TB5d	sand, cobble	6.55	45.0346	-83.3266
TB6d*				

*no sample collected due to bad weather

RESULTS AND DISCUSSION

Benthic Taxonomy, Density and Biomass

We found 125 taxa (species, genera or higher taxa) of benthic macroinvertebrates in Lake Huron (Appendix 2). Annelida were the most diverse phylum (56 species and higher taxa), followed by Arthropoda (49) and Mollusca (16). Class Oligochaeta and family Chironomidae had the highest diversity, with 49 and 39 taxa, respectively. Among Mollusca, 11 taxa of Gastropoda and 5 species of Bivalvia were identified.

The most abundant taxon lake-wide were Oligochaeta (average density 1,923 ± 292 m^{-2}, mean ± standard error here and elsewhere; 52% of total benthic density), represented by Tubificidae (67% of Oligochaeta density, 35% of total benthos density) and Lumbriculidae (26%, 13% respectively). *Dreissena r. bugensis* comprised 32% of total lake-wide benthic density, Chironomidae – 8%, Sphaeriidae – 3%, *Diporeia* (1%), and Gastropoda – 0.7%. *Dreissena r. bugensis* dominated in terms of biomass, comprising 98% of total wet biomass of the whole benthos.

The highest total benthic density in 2017 was found in Saginaw Bay (8,198 ± 1,971 m^{-2}) (Table 1.7) dominated by oligochaetes (46% of total density), *D. r. bugensis* (25%), Sphaeriidae (8%) and Chironomidae (7%). Total benthic density in the main basin was lower (3,989 ± 459 m^{-2}) (Table 1.7) and was represented by oligochaetes (53% of total density), *D. r. bugensis* (38%) and Chironomidae (7%). The highest dominance of oligochaetes was found in Georgian Bay (71% of the total benthic density 1,448 ± 444 m^{-2}), and each *D. r. bugensis* and Chironomidae comprised only 13% from total density. North Channel had the lowest total density of benthic invertebrates relative to the other regions (1,006 ± 129 m^{-2}) and was dominated by Oligochaeta (38%), Chironomidae (21%), Sphaeriidae (20%) and *Diporeia* (17% of total benthic density). Only five *D. r. bugensis* and one *D. polymorpha* were found in this region in 39 samples collected from 13 stations in 2017.

Dreissena 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 North Channel. In North Channel we also found the lowest average biomass (11.8 ± 8.3 g m^{-2}), and non-dreissenid benthos was dominated by *Diporeia* (33%), Oligochaeta (31%) and Chironomidae (21%). In the main basin and Georgian Bay Oligochaeta were responsible for the majority of non-dreissenid biomass (85 and 90%). In contrast, in Saginaw Bay, Chironomidae (mostly *Chironomus* spp.) contributed a larger percentage of total benthic biomass than Oligochaeta (42 vs. 35%)

Table 1.7. Average density (N, ind. m^{-2}) and wet biomass (B, g wet weight per m^{-2}) of benthic invertebrates collected in different basins of Lake Huron by Ponar (P) and SCUBA divers (S) in 2017.

Species	Main		Georgian Bay		North Channel		Saginaw Bay		Thunder Bay	
	N	B	N	B	N	B	N	B	N	B
Amphipoda (w/o *Diporeia*)	0.3	<0.001	0.4	<0.001	0.5	0.003	197.8	0.389	64.9	0.164
Diporeia hoyi	24.7	0.038	2.4	<0.001	174.5	0.597	1.3	0.001	0	0
Sphaeriidae	36.1	0.036	18.7	0.010	200.0	0.177	669.4	0.724		
Dreissena total (P)	1497.7	336.075	178.1	157.166	7.9	9.999	2386.1	170.611		
D. polymorpha	0	0	0	0	0.5	1.660	372.9	12.083		
D. r. bugensis	1497.7	336.075	178.1	157.166	7.4	8.339	2013.1	158.528		
Dreissena total (S)							3184.3	77.155	918.6	880.609
D. polymorpha							1723.2	17.446	149.9	125.182
D. r. bugensis							1461.1	59.709	768.7	755.427
Gastropoda	2.2	0.035	4.8	0.015	18.1	0.026	138.8	0.101		
Chironomidae	282.3	0.259	190.4	0.157	207.4	0.367	568.8	4.001		
Hirudinea	0	0	0	0	0.5	0.010	37.0	0.125		
Isopoda	5.8	0.013	4.4	0.003	0	0	220.4	0.253		
Oligochaeta total	2096.7	2.906	1031.3	2.206	387.3	0.560	3864.4	3.308		
Enchytraeidae	39.9	0.011	42.2	0.013	0.5	<0.001	16.8	0.004		
Lumbriculidae	593.1	1.285	693.5	1.633	50.5	0.071	57.0	0.067		
Naididae	117.7	0.015	59.8	0.013	2.9	0.001	76.6	0.016		
Tubificidae	1345.9	1.008	235.8	0.162	327.0	0.366	3635.9	2.870		
Platyhelminthes	11.7	0.003	4.0	0.002	1.5	0.001	151.9	0.215		
Total benthos	**3988.7**	**339.491**	**1447.5**	**159.619**	**1006.0**	**11.781**	**8198.2**	**180.069**		

Total benthos without *Dreissena*	2491.0	3.415	1269.5	2.454	998.2	1.782	5812.1	9.458
Average # species per sample (without *Dreissena*)	11.7		10.7		12.5		22.4	

Table 1.8. Average biomass (ash free tissue dry weight, AFTDW; mean + standard error, g m^{-2}) of *Dreissena* spp. collected in different basins of Lake Huron by Ponar and SCUBA divers in 2017.

Species	Main	Georgian Bay	North Channel	Saginaw Bay	Thunder Bay
			Ponar samples		
Sample size	79	16	13	11	0
Dreissena total	9.10±1.48	3.99±2.26	0.19±0.17	4.45±2.84	
D. polymorpha	0	0	0.02±0.02	0.24±0.15	
D. r. bugensis	9.10±1.48	3.99±2.26	0.17±0.17	4.20±2.80	
			SCUBA samples		
Sample size	0	0	0	6	4
Dreissena total				1.49±0.62	16.02±6.70
D. polymorpha				0.41±0.17	2.22±1.07
D. r. bugensis				1.09±0.48	13.79±6.97

Table 1.9. Relationship between shell length (SL in mm) and ash-free tissue dry weight (AFTDW in mg) for *D. r. bugensis* from various depth intervals (representing main basin and Georgian Bay), plus Saginaw Bay and Thunder Bay in Lake Huron in 2017. Regression constants (m, b) derived from the linear regression: $\log_e$AFTDW = m*$\log_e$SL + b; n = total number of mussels used to derive the relationship. Also given is the AFTDW of a standard 15 mm individual as calculated from the corresponding regression.

Region/Depth Zone	M	b	N	15-mm mussel AFTDW
Saginaw Bay	2.786058	-5.653217	50	6.63
Thunder Bay	2.649812	-5.043217	25	8.44
< 30 m	2.680369	-5.081301	50	8.82
31-50 m	2.765265	-5.646714	100	6.31
51-90 m	2.644391	-5.454659	100	5.51
>90 m	2.72751	-5.47447	50	6.77

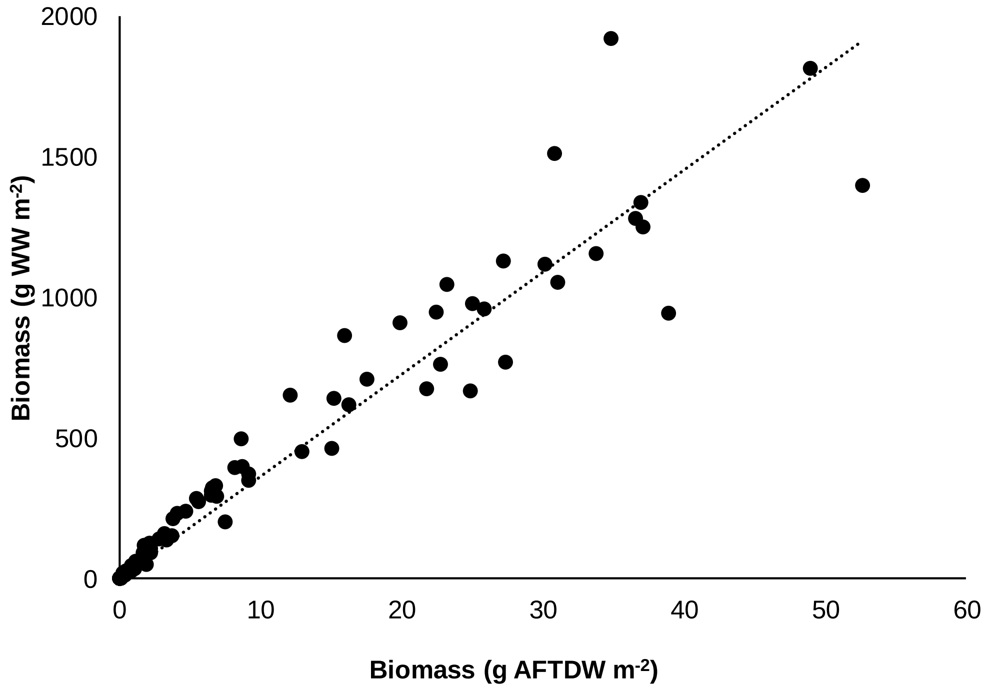


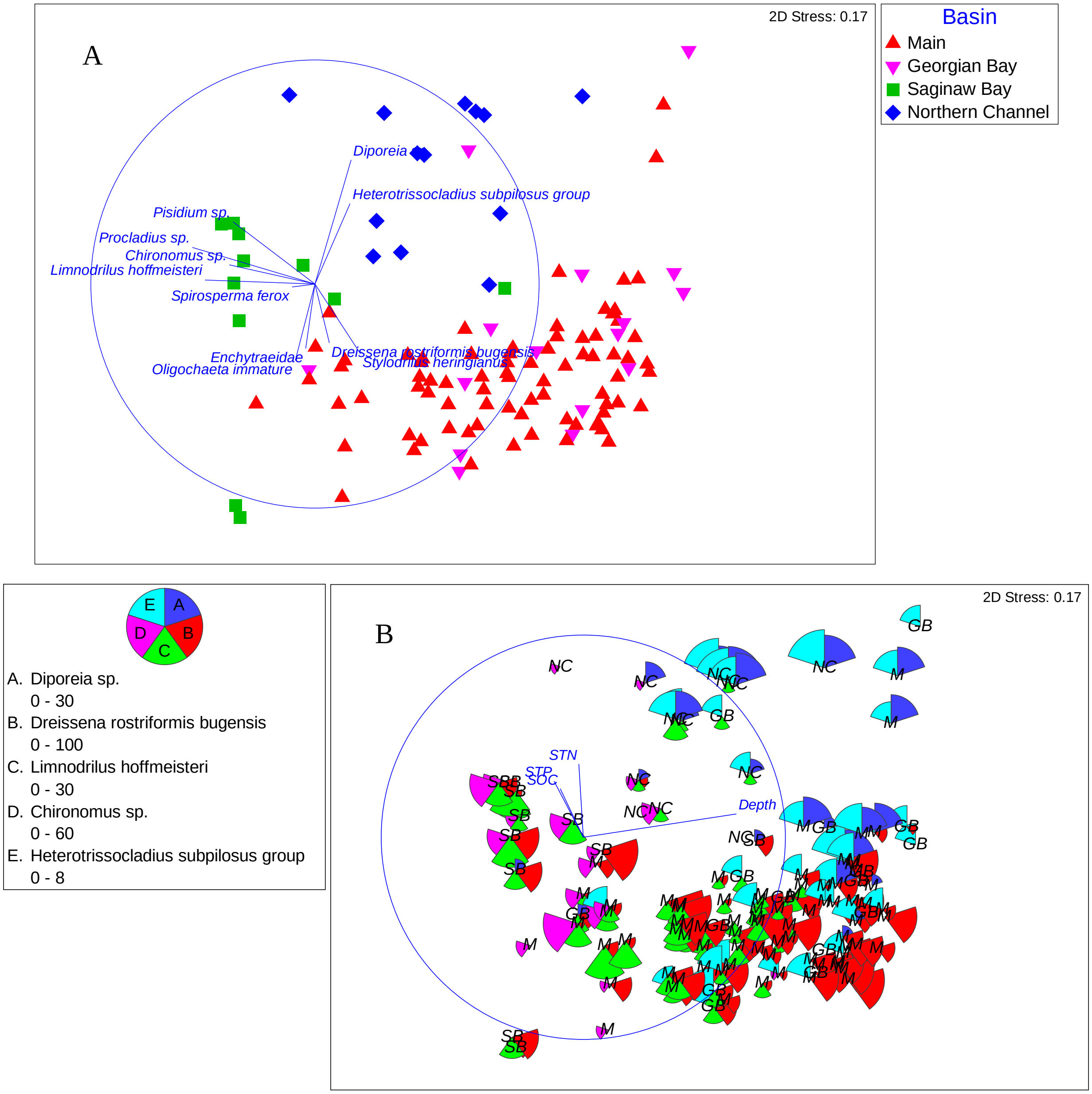
Figure 1.3. Relationship between biomass measured as ash free tissue dry weight (g AFTDW m^{-2}) and biomass measured as total wet weight (g WW m^{-2}, whole mussel, tissue and shell) of *Dreissena* spp. for each Lake Huron 2017 station. The regression through the origin is defined as: Biomass (g WW m^{-2}) = 36.36*Biomass (g AFTDW m^{-2}) ($R^2 = 0.93$, $P < 0.001$).

Community Analysis

Following depth and productivity patterns, the greatest average number of species and the most taxa per sample were found in the shallowest and most productive Saginaw Bay (22 species) (Table 1.7). Basin-wise highest taxa richness was found in the largest main basin (90 species and higher taxa, Margalef index d = 25.5), followed by Saginaw Bay (75 species, d = 17.7), and Georgian Bay (54 species, d =16.4). The lowest taxonomic richness (50 species, d = 14.6) was found in North Channel.

The largest difference in benthic communities was found among regions (basins) (R = 0.498, P = 0.001, one-way ANOSIM, Fig. 1.4). Main basin and Georgian Bay were the most similar (R = 0.147, P = 0.023), while the main basin and Saginaw Bay were most dissimilar in their community composition (R = 0.725, P = 0.001). Species characteristic of communities in different regions (shown as NMDS vectors that have the highest correlation with NMDS 1 and/or NMDS 2 in Fig. 1.4A) were *Diporeia* and the chironomid *Heterotrissocladius* common in the North Channel, and *D. r. bugensis* and *Stylodrilus heringianus* and Enchytraeidae (oligochaetes intolerant to organic pollution) abundant in the main basin and in Georgian

Bay. Species tolerant to organic pollution and hypoxia (oligochaetes *Limnodrilus hoffmeisteri* and *Spirosperma ferox*, *Chironomus* sp., and fingernail clams *Pisidium* spp.) were the most common in Saginaw Bay (Fig. 1.4A, B).



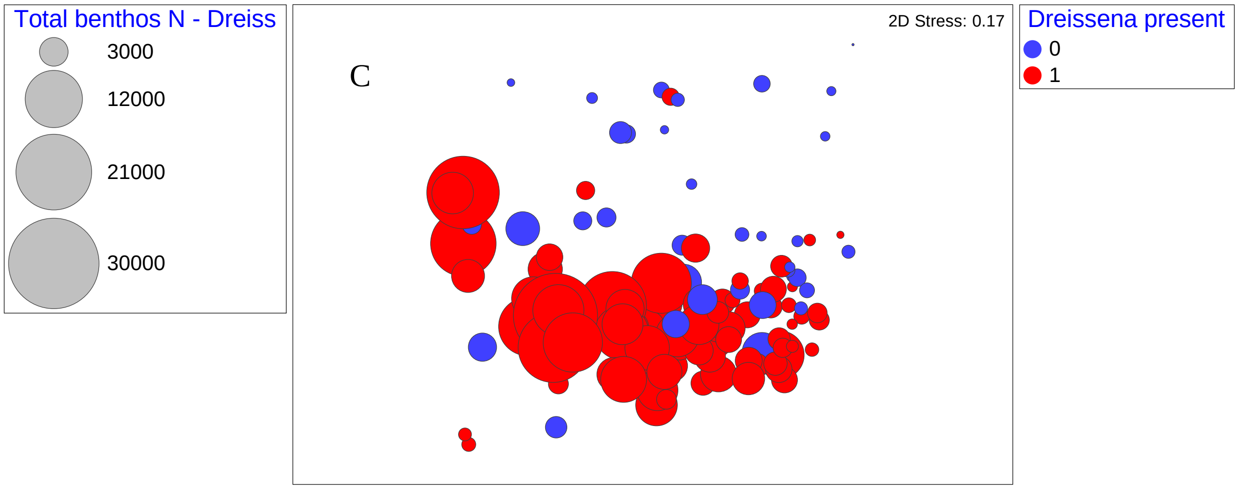


Figure 1.4. NMDS plots of Huron Lake benthic community structure for samples collected in 2017. Stress = 0.17. Density (ind./m^2) of benthic taxa collected with Ponar were fourth-root transformed and converted to similarity matrix using Bray-Curtis similarity index. A: Grouping of communities by region (red triangles – Main basin, magenta inverse triangles – Georgian Bay, green squares – Saginaw Bay, blue diamonds – North Channel. NMDS vectors (density of taxa) that have the highest correlation with NMDS 1 and/or NMDS 2 are indicated. B: Bubble NMDS plot of Lake Huron benthic communities with major taxonomic groups or indicator species highlighted. Densities of each group are indicated by bubble size. C: NMDS plot with total densities of non-dreissenid benthos indicated by bubble size indicating that higher benthic densities were found in *Dreissena* aggregations.

Dreissena r. bugensis together with oligochaetes *S. heringianus* and Enchytraeidae contributed 47% to the similarity within the main-basin benthic community. The same taxa were most common in Georgian Bay, but this region had lower *Dreissena* density. The benthic community of North Channel, where very few *Dreissena* were found, was characterized by collector-filterers *Pisidium* spp., Chironomidae *Micropsectra* sp., and *Diporeia* (together 42% of community similarity). The benthic community of Saginaw bay was represented by *Dreissena* spp. and species tolerant to organic pollution and low oxygen (*Pisidium* sp., oligochaeta *L. hoffmeisteri*, chironomids *Chironomus* sp. and *Procladius* sp.) contributing 87% to community similarity.

Depth also significantly affected benthic community structure (0-30 m, 31-50 m, 51-90 m, and >90 m, R = 0.384, P = 0.001, two-way ANOSIM), and communities were significantly different depending on the presence of *Dreissena* (R = 0.363, P = 0.001). Communities with and without *Dreissena* were different in the densities of immature unidentified Oligochaeta, Lumbriculidae and Tubificidae that were respectively three, two, and four times more abundant in *Dreissena* aggregations. Combined, these taxa explained 40%

of dissimilarity between communities with and without *Dreissena*. Communities without *Dreissena* were characterized by higher densities of *Pisidium* and *Diporeia*.

The effect of *Dreissena* on the total non-dreissenid benthos density was significant in both nearshore and offshore zones (less and greater than 70 m depth, P=0.008, 2-way ANOVA). At depths < 70 m *Dreissena* increased average densities three-fold (from 1,802 ± 797 to 5,128 ± 494 m^{-2}), and four-fold at > 70 m (512 ± 1201 vs. 2,041 ± 938 m^{-2}). Most of the increase was due to significantly higher density of Oligochaeta in *Dreissena* aggregations (< 70 m: 1,261±741 m^{-2} vs. 4,389 ± 459 m^{-2}; > 70 m: 335 ± 1,117 vs. 1,949 ± 873 m^{-2}, P = 0.005, 2-way ANOVA). All Oligochaeta groups increased in the presence of *Dreissena* lake-wide, but the gain in Lumbriculidae was significant at both depth zones (P = 0.002, 2-way ANOVA).

Long-Term Trends in Benthos

In this section we briefly describe long-term trends of all major groups of benthic invertebrates with the exception of *Dreissena*, whose trends will be described in detail in the "*Dreissena* Spatial and Temporal Trends" section of this report.

Among the major long-term trends in densities of benthic macroinvertebrates in the main basin, Georgian Bay, and North Channel the most important trends were the declines in *Diporeia* and Sphaeriidae that started in early to mid-2000s and were consistent across all depth zones (Tables 1.10-1.13). In Georgian Bay and the main basin, these declines coincided with the increase in densities of *D. r. bugensis*. Note, however, that the decline in Sphaeriidae and *Diporeia* (although not as strong as in the main basin and Georgian Bay) was also found in North Channel, where very few *Dreissena* were found. Similar trends in *Diporeia* densities were observed in lakes Michigan (Nalepa et al., 2018) and Ontario (Nalepa and Elgin, 2016). In Lake Ontario, which was colonized with *Dreissena* about 7 years earlier than lakes Michigan and Huron (Mills et al. 1993), the decline of *Diporeia* started earlier and was even more pronounced. Only one individual of *Diporeia* was found during the 2013 lake-wide benthic survey (Nalepa and Elgin, 2016). In contrast, Oligochaeta abundance increased since mid-2000s in almost all regions of Lake Huron likely due to an increase in food resources associated with quagga mussel feeding and filtering activities. No consistent patterns were found in long-term trends of chironomids.

There were no consistent trends in Amphipoda (mainly *Gammarus* and *Hyalella*) dynamics in the shallow Saginaw Bay over the last 30 years. At all Inner Bay stations amphipod densities substantially increased from 2006–2009 to 2017 (Table 1.13), while in the Outer Bay their densities strongly declined at some stations but did not change or even increase at others. Further, no consistent trends were found in densities of oligochaetes or chironomids. Sphaeriidae declined at almost all stations with exception of silty stations of the Inner Bay (Stations SB4, SB7 and SB10).

Table 1.10. Long-term dynamics of density (mean ± SE, ind. m^{-2}) of major benthic taxa in the main basin of Lake Huron by depths zones. The 1971 data are from Nalepa et al. (2007), data for 2000, 2003, 2007, and 2012 from Nalepa et al. (2018).

Taxa	1971 (52)	2000 (65)	2003 (85)	2007 (80)	2012 (83)	2017 (79)
0 - 30 m						
Diporeia	223 ± 100	244 ± 237	97 ± 92	1 ± 1	0 ± 0	0 ± 0
Oligochaeta	491 ± 171	1,648 ± 410	1,783 ± 417	8,114 ± 2,742	8,138 ± 2,854	4,999 ± 1,498
Sphaeriidae	451 ± 219	457 ± 196	47 ± 21	183 ± 64	66 ± 25	58 ± 28
Chironomidae	53 ± 14	883 ± 451	238 ± 55	754 ± 210	228 ± 57	419 ± 130
D. polymorpha	0 ± 0	386 ± 342	297 ± 209	0 ± 0	19 ± 19	0 ± 0
D. r. bugensis	0 ± 0	3 ± 2	297 ± 180	850 ± 283	1,332 ± 780	163 ± 70
31 - 50 m						
Diporeia	492 ± 208	876 ± 287	248 ± 103	17 ± 10	0 ± 0	0 ± 0
Oligochaeta	509 ± 166	1,196 ±314	1,460 ± 368	3,076 ± 824	2,403 ± 412	2,362 ± 442
Sphaeriidae	164 ± 52	237 ± 37	67 ± 13	113 ± 25	137 ± 31	29 ± 7
Chironomidae	29 ± 12	379 ± 140	62 ± 14	256 ± 52	472 ± 164	489 ± 172
D. polymorpha	0 ± 0	6 ± 2	7 ± 4	1 ± 1	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	2 ± 1	1,469 ± 757	2,217 ± 664	1,619 ± 671	1,431 ± 405
51 - 90 m						
Diporeia	539 ± 87	1,908 ± 183	914 ± 133	170 ± 57	67 ± 30	6 ± 5
Oligochaeta	314 ± 54	805 ± 89	383 ± 42	489 ± 60	693 ± 88	882 ± 118
Sphaeriidae	340 ± 251	335 ± 44	109 ± 17	128 ± 14	93 ± 16	33 ± 12
Chironomidae	29 ± 8	71 ± 11	28 ± 5	27 ± 6	49 ± 13	142 ± 66
D. polymorpha	0 ± 0	0 ± 0	18 ± 18	0 ± 0	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	72 ± 45	276 ± 172	1,690 ± 672	2,202 ± 471
>90 m						
Diporeia	480 ± 82	1,707 ± 232	924 ± 83	427 ± 82	252 ± 69	161 ± 48
Oligochaeta	212 ± 64	627 ± 69	404 ± 76	559 ± 138	489 ± 154	523 ± 161
Sphaeriidae	33 ± 16	94 ± 32	71 ± 38	109 ± 50	92 ± 25	27 ± 8
Chironomidae	11 ± 4	58 ± 12	17 ± 4	21 ± 5	49 ± 15	21 ± 5
D. polymorpha	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	2 ± 1	135 ± 135	748 ± 612	1,721 ± 738

Table 1.11. Long-term dynamics of density (mean ± SE, ind. m^{-2}) of major benthic taxa in Georgian Bay of Lake Huron by depths zones. Data for 1973 from Nalepa et al. (2007), data for 2002, 2007, and 2012 from Nalepa et al. (2018).

Taxa	1973 (17)	2002 (17)	2007 (17)	2012 (15)	2017 (16)
0 - 30 m					
Diporeia	2,117 ± 661	1,687 ± 830	55 ± 55	3 ± 3	5 ± 5
Oligochaeta	781 ± 628	707 ± 344	1,388 ± 1,043	573 ± 145	997 ± 486
Sphaeriidae	302 ± 189	1,814 ± 525	61 ± 21	0 ± 0	33 ± 23
Chironomidae	57 ± 19	162 ± 34	555 ± 302	148 ± 121	234 ± 116
D. polymorpha	0 ± 0	19 ± 10	21 ± 21	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	278 ± 278	3 ± 3	107 ± 96
31 - 50 m					
Diporeia	1,603 ± 665	1,457 ± 596	50 ± 48	0 ± 0	0 ± 0
Oligochaeta	522 ± 307	767 ± 293	728 ± 332	2,499 ± 576	2,272 ± 750
Sphaeriidae	806 ± 383	853 ± 214	195 ± 114	195 ± 81	8 ± 6
Chironomidae	200 ± 141	94 ± 26	195 ± 155	63 ± 58	462 ± 381
D. polymorpha	0 ± 0	24 ± 23	5 ± 5	18 ± 18	0 ± 0
D. r. bugensis	0 ± 0	36 ± 34	1,335 ± 1,330	382 ± 221	510 ± 334
51 - 90 m					
Diporeia	1,507 ± 354	1,684 ± 306	99 ± 56	0 ± 0	2 ± 2
Oligochaeta	270 ± 239	413 ± 144	150 ± 60	391 ± 107	428 ± 116
Sphaeriidae	389 ± 203	291 ± 110	84 ± 14	55 ± 16	17 ± 6
Chironomidae	35 ± 10	44 ± 11	56 ± 13	21 ± 8	33 ± 10
D. polymorpha	0 ± 0	2 ± 2	2 ± 2	0 ± 0	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	1 ± 1	144 ± 130	48 ± 25

Table 1.12. Long-term dynamics of density (mean ± SE, ind. m^{-2}) of major benthic taxa in North Channel of Lake Huron by depths zones. Data for 2002, 2007, and 2012 from Nalepa et al. (2018).

Taxa	1973 (13)	2002 (13)	2007 (12)	2012 (13)	2017 (13)
0 - 30 m					
Diporeia	1,369 ± 471	2,046 ± 705	1,022 ± 423	357 ± 171	163 ± 106
Oligochaeta	952 ± 592	653 ± 269	478 ± 230	1,245 ± 549	456 ± 163
Sphaeriidae	983 ± 384	875 ± 280	232 ± 41	914 ± 319	296 ± 44
Chironomidae	231 ± 57	99 ± 22	676 ± 384	275 ± 72	227 ± 79
D. polymorpha	0	1 ± 1	0	0	1 ± 1
D. r. bugensis	0	0	0	0	15 ± 7
31 - 50 m					
Diporeia	1,520 ± 96	896 ± 401	660 ± 432	751 ± 320	200 ± 107
Oligochaeta	205 ± 51	322 ± 163	257 ± 119	239 ± 158	181 ± 125
Sphaeriidae	780 ± 236	357 ± 163	338 ± 137	346 ± 146	130 ± 73
Chironomidae	126 ± 53	198 ± 57	470 ± 243	170 ± 75	206 ± 48
D. polymorpha	0	0	0	0	0
D. r. bugensis	0	0	0	0	1 ± 1
51 - 90 m					
Diporeia	3,441 ± 1,663	3,349 ± 43	253 ± 253	121 ± 107	147 ± 127
Oligochaeta	29 ± 10	174 ± 232	307 ± 244	483 ± 311	698 ± 481
Sphaeriidae	898 ± 236	635 ± 200	79 ± 21	224 ± 100	86 ± 48
Chironomidae	104 ± 85	54 ± 25	29 ± 21	490 ± 345	150 ± 41
D. polymorpha	0	0	0	0	0
D. r. bugensis	0	0	0	0	0

Table 1.13. Density (mean ± SE, ind. m^{-2}) of major benthic taxa found in Ponar samples in Saginaw Bay of Lake Huron. Data for 1987–1990, 1994–1996, and 2006–2009 from Nalepa et al. (2018). Inner bay-sand/gravel = Stations 13, 14, and 16; Inner bay-silty sand (Station 11); Inner bay silt = Stations 4, 7 and 10; Outer bay- 12 m = Station 24; Outer bay- 16 m = Station 20; Outer bay-28 m = Station 23. For 2017 densities of *Diporeia* are shown separately in parenthesis in Amphipoda. In 2006-2009 *Dreissena* were not identified to species and reported as *Dreissena* spp.

Taxa	1987-1990	1994-1996	2006-2009	2017
Inner Bay-Sand/Gravel, Stations SB13, SB14, SB16				
Amphipoda	66 ± 17	296 ± 86	126 ± 42	381 ± 292 (2 ± 2)
Oligochaeta	653 ± 113	716 ± 89	679 ± 127	707 ± 204
Chironomidae	106 ± 24	148 ± 73	38 ± 10	79 ± 38
Sphaeriidae	27 ± 9	7 ± 3	1 ± < 1	12 ± 12
D. polymorpha	0 ± 0	2,247 ± 1,038	n.d.	1,247 ± 825
D. r. bugensis	0 ± 0	0 ± 0	n.d.	2,721 ± 1,352
Dreissena spp.			480 ± 185	
Inner Bay-Silty Sand, Station SB11				
Amphipoda	6 ± 4	51 ± 4	26 ± 18	486 ± 400 (0)
Oligochaeta	6,799 ± 2,379	3,268 ± 710	5,281 ± 1,107	11,431 ± 1,963
Chironomidae	6,942 ± 4,256	2,145 ± 576	2,072 ± 963	678 ± 157
Sphaeriidae	535 ± 66	116 ± 55	37 ± 13	378 ± 94
D. polymorpha	0 ± 0	54 ± 31	n.d.	278 ± 278
D. r. bugensis	0 ± 0	0 ± 0	n.d.	3,313 ± 3,015
Dreissena spp.			630 ± 528	
Inner Bay-Silt, Stations SB4, SB7 and SB10				
Amphipoda	1 ± <1	12 ± 2	10 ± 6	31 ± 16 (0)
Oligochaeta	19,423 ± 1,466	2,727 ± 775	6,055 ± 966	7,390 ± 3,759
Chironomidae	1,507 ± 170	1,901 ± 487	1,654 ± 312	1,123 ± 276
Sphaeriidae	93 ±22	151 ± 57	284 ± 69	2,011 ± 744
D. polymorpha	0 ± 0	10 ± 6	n.d.	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	n.d.	302 ± 277
Dreissena spp.			46 ± 25	

Taxa	1987-1990	1994-1996	2006-2009	2017
		Outer Bay-12 m, Station SB24		
Amphipoda	9 ± 2	19 ± 13	2 ± 2	0
Oligochaeta	3,089 ± 1,305	2,246 ± 1,077	823 ± 225	968 ± 351
Chironomidae	965 ± 299	1,645 ± 1,094	344 ± 174	355 ± 91
Sphaeriidae	42 ± 17	6 ± 5	2 ± 2	7 ± 7 (0)
D. polymorpha	0 ± 0	3 ± 1	n.d.	0
D. r. bugensis	0 ± 0	0 ± 0	n.d.	0
Dreissena spp.			2 ± 2	
		Outer Bay-16 m, Station SB20		
Amphipoda	3 ± 2	10 ± 2	0 ± 0	418 ± 418 (0)
Oligochaeta	1,894 ± 548	2,582 ± 814	1,241 ± 213	822 ± 171
Chironomidae	1,382 ± 116	1,797 ± 661	637 ± 451	808 ± 91
Sphaeriidae	373 ± 162	86 ± 13	1 ± 1	49 ± 7
D. polymorpha	0 ± 0	3 ± 2	n.d.	84 ± 84
D. r. bugensis	0 ± 0	0 ± 0	n.d.	9,101 ± 8,715
Dreissena spp.			0 ± 0	
		Outer Bay-28 m, Station SB23		
Amphipoda	819 ± 189	168 ± 102	0 ± 0	7 ± 7 (7 ± 7)
Oligochaeta	387 ± 88	727 ± 155	6,421 ± 143	2,576 ± 477
Chironomidae	218 ± 49	515 ± 144	62 ± 43	160 ± 108
Sphaeriidae	228 ± 68	202 ± 70	216 ± 43	153 ± 66
D. polymorpha	0 ± 0	7 ± 7	n.d.	0
D. r. bugensis	0 ± 0	0 ± 0	n.d.	662 ± 151
Dreissena spp.			163 ± 4	

"n.d." – not determined (*Dreissena* was not identified to species level).

Dreissena **Spatial and Temporal Trends**

For all *Dreissena* biomass comparisons across time, we used ash free tissue dry weight (AFTDW) as the measure. When stations were sampled by both Ponar and SCUBA (stations SB13, SB14, and SB16), we used only SCUBA data. Therefore, the number of stations in Ponar calculations are lower than what was actually sampled by Ponars. In 2009 and 2010, *Dreissena* spp. collected at SCUBA stations in Saginaw Bay were not separated by species. To reconstruct density and biomass by species we used ratios between zebra and quagga mussels based on data from stations SB13 and SB14 sampled by both Ponar and SCUBA where *Dreissena* was identified by species in Ponar samples (the ratio of zebra to quagga mussels density: 20% to 80%, and the ratio of zebra to quagga mussels biomass: 33% to 67%).

Saginaw Bay

No *Dreissena* was found in the bay during the 1990 survey, but by 1991 the average zebra mussel density was already very high across all substrates (average for the bay 5,853±3,489 m^{-2}), while biomass was still low due to the presence of a large number of juvenile mussels (Nalepa et al., 2002, Fig. 1.5). By 1992, zebra mussels reached maximum population density (17,692±7,102 m^{-2}) and biomass (31.9±12.3 gm^{-2}) and declined thereafter. These high average values were due to extremely high densities found on hard substrates sampled by SCUBA divers (33,170±10,760 m^{-2}). On soft substrates (sampled by Ponar grab) zebra mussels were always rare ranging between 1 and 20 m^{-2} in 1991–1996. When Saginaw Bay was colonized by quagga mussels (app. 1997), zebra mussel population declined dramatically, causing a significant reduction in the average basin-wide combined dreissenid density and biomass. Due to a large gap in sampling (no surveys were conducted between 1997 and 2005) we do not know exactly when quagga mussels became dominant. In 2006, nine years after coexistence, dreissenids were already dominated by the quagga mussel. In 2008, quagga mussels comprised 79% density and 75% biomass of all dreissenids. The combined density and biomass of both species, however, was much lower compared to early 1990s, when the lake was colonized by zebra mussels alone. In 2017, the combined density of dreissenids across all substrates was 7 times lower, and biomass - 8 times lower than in 1992. The difference was drastic and due to the extremely high density previously comprised by zebra mussels on hard substrates in 1992 (33,171 ± 10,761 m^{-2}) which was 22 times higher than the maximum quagga mussel density recorded on the same substrates in 2017 (1461 ± 480 m^{-2}). Due to higher byssal production rates, attachment strength, and flattened ventral edge, *D. polymorpha* is more resistant to dislodgment than *D. r. bugensis* (Mackie, 1991; Dermott and Munawar, 1993; Claxton and Mackie, 1998; Peyer et al. ,2009, 2010), creating higher density than quagga mussels on hard substrates in areas exposed to wave activity. In contrast, on soft substrates in 2017, quagga mussels formed much higher densities than zebra mussels had at the same stations during their density peak in 1993 (1,997 ± 1,263 m^{-2} vs. 20 ± 19 m^{-2}). Zebra mussels in 2017 were still common in Saginaw Bay after 20 years of coexistence with quagga mussels, comprising about 15% of density and 7% of biomass of all dreissenids.

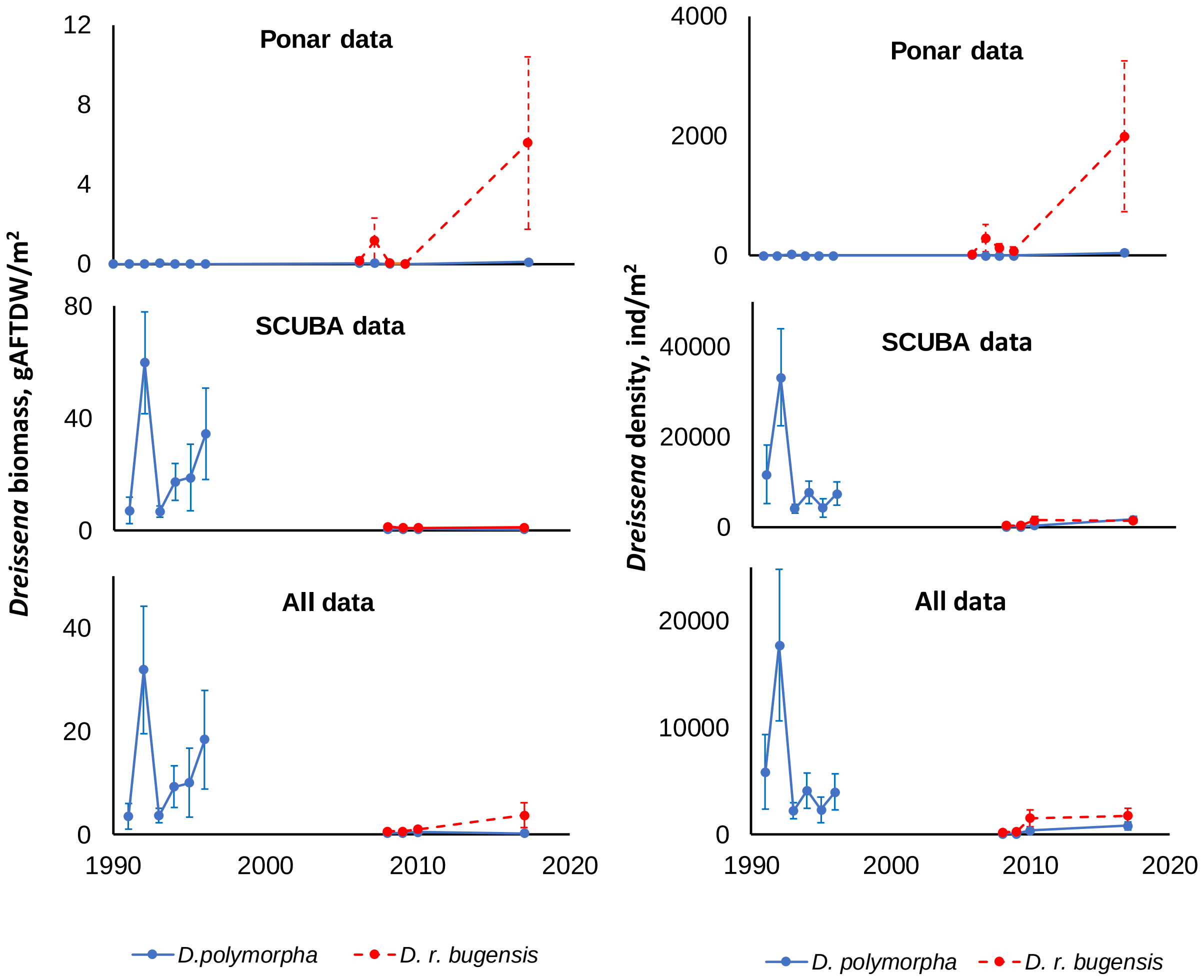


Figure 1.5. Long-term dynamics of zebra (blue line) and quagga (red dashed line) mussels density (ind. m^{-2}) and biomass (g m^{-2} AFTDW) in Saginaw Bay of Lake Huron on hard substrates sampled by SCUBA (stations SB5d, SB6d, SB13d, SB14d, SB15d, SB16d, SB27d), soft substrates sampled by Ponar (Stations SB4, SB7, SB10, SB11, SB20, SB23, SB24), and all stations combined.

Main basin

Both *Dreissena* species were reported in the main basin of Lake Huron at the same time as in Lake Michigan, however densities of both species have always been lower in Lake Huron (Fig. 1.6). In the first lake-wide study of *Dreissena* spp. in 2000, which was 11 years after zebra mussels were first recorded in the lake, *Dreissena* densities in the main basin were still generally low (83 m^{-2}). Mussels were largely limited to 18–30 m depth zone where over 98% of the basin-wide population density was located at the time. It should be mentioned, however, that shallow areas with high zebra mussel density might have been overlooked as depths < 18 m were not sampled in 2000. In 2000, basin-wide average quagga mussel density (0.8 m^{-2}) was even lower than zebra mussel average density (Fig. 1.6). By 2003, quagga mussel density had increased at the < 30 m depth zone by two orders of magnitude, and by three orders of magnitude at 31–50 depth zone. Quagga mussels became dominant (comprising 82% of all dreissenid density and biomass) in the main basin in 2003, six years after coexistence, and zebra mussels were not recorded in surveys since 2007 (Fig. 1.6). As of 2017, quagga mussel lake-wide density was over 18 and biomass 20 times higher than that of zebra mussels in 2000. The bulk of quagga mussel population in the main basin of Lake Huron shifted deeper with time (Fig. 1.6). At < 30 m depth zone, after achieving a population maximum (1,332 ± 780 m^{-2}) in 2012, quagga mussel average density has declined over eight times by 2017 (163 ± 70 m^{-2}) (Fig. 1.6). The decline was less evident at 31–50 m, and densities were still growing at depths greater than 50 m, resulting in a slight increase in the lake-wide population density between 2012 and 2017 (14%, 1,324 vs. 1,510 m^{-2}). In contrast to density, the decline in biomass was found at the shallow (0–30 m) zone only. At 31–50 m the biomass likely stabilized between 2012 and 2017, but it is still growing substantially at deeper zones, as well as lake-wide (43% increase in lake-wide biomass in 2017, compared to 2012).

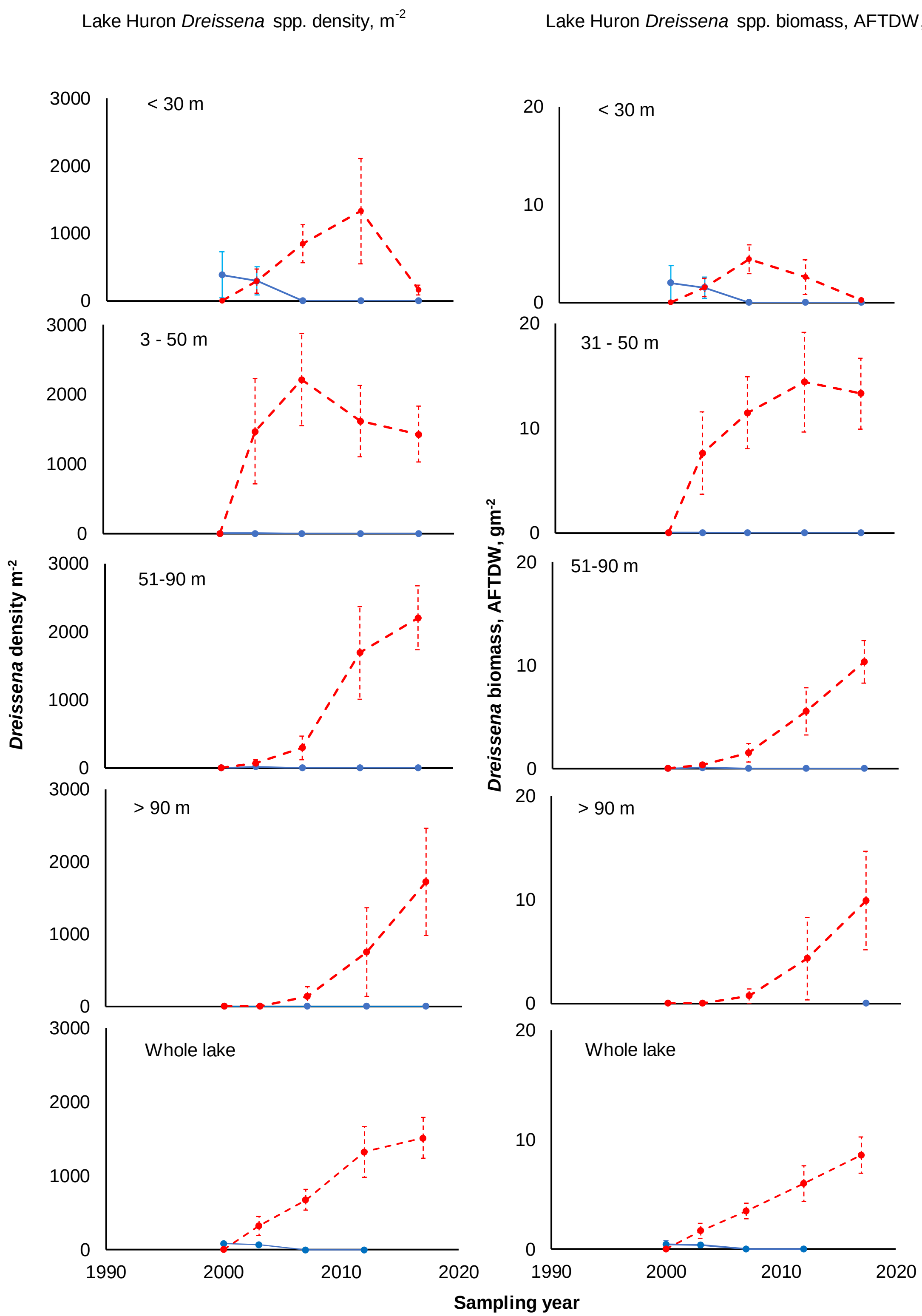


Figure 1.6. Long-term dynamics of zebra (blue line) and quagga (red dashed line) mussel density (ind. m^{-2}) and biomass (g m^{-2} AFTDW) in main basin of Lake Huron.

Georgian Bay

Comparison of *Dreissena* spp. and *Diporeia* population dynamics at three depth zones in the Georgian Bay indicates that the decline in *Diporeia* may have coincided with dreissenid populations increase in the bay (Fig. 1.7).

In Georgian Bay, nearly all stations were located on soft substrate in 26–89 m depth range and the quagga mussel population could potentially be underestimated if the majority of quagga mussels was located in the nearshore zone with bedrock substrates which cannot be sampled with a Ponar. To address this concern, we analyzed 26 bottom images taken by a video camera (described in Angradi 2018; view surface area 0.16 m^{-2}), mostly from hard substrates at the 6–29 m depth zone (images provided by Ted Angradi, U.S. EPA Duluth). We found that neither *Dreissena* occurrence (59 vs. 52%) nor average density (258 ± 93 vs. 285 ± 70 m^{-2}) was different between Ponar grabs and video camera estimations confirming low quagga mussel density in Georgian Bay.

North Channel

Both *Dreissena* species were always extremely rare in North Channel. Only 15 individual quagga mussels (10 of them smaller than 1 mm) and one large zebra mussel were found in all 39 samples collected in 2017. Similar to Georgian Bay, all stations in the North Channel were located on soft substrate in rather deep areas (17–78 m) and the quagga mussel population could potentially be underestimated. We compared our *Dreissena* density estimations from Ponar grab with 19 bottom images taken by video camera from a variety of substrates (from cobble to mud) at the 7–49 m depth zone. Although both occurrence (8 vs. 17%) and densities (0.5 vs. 16 m^{-2}) of quagga mussels were somewhat higher in video images, both estimations were very low. Historically, dreissenids were even more rare, as only one individual zebra mussel was found during all previous surveys. Extremely low population density prevents analysis of spatial distribution and temporal dynamics of dreissenids in the North Channel. The density of *Diporeia,* however, continued to decrease in the North Channel in spite of the absence of *Dreissena* (Fig. 1.8), indicating that some other mechanisms beside food competition may be causing negative population trends.

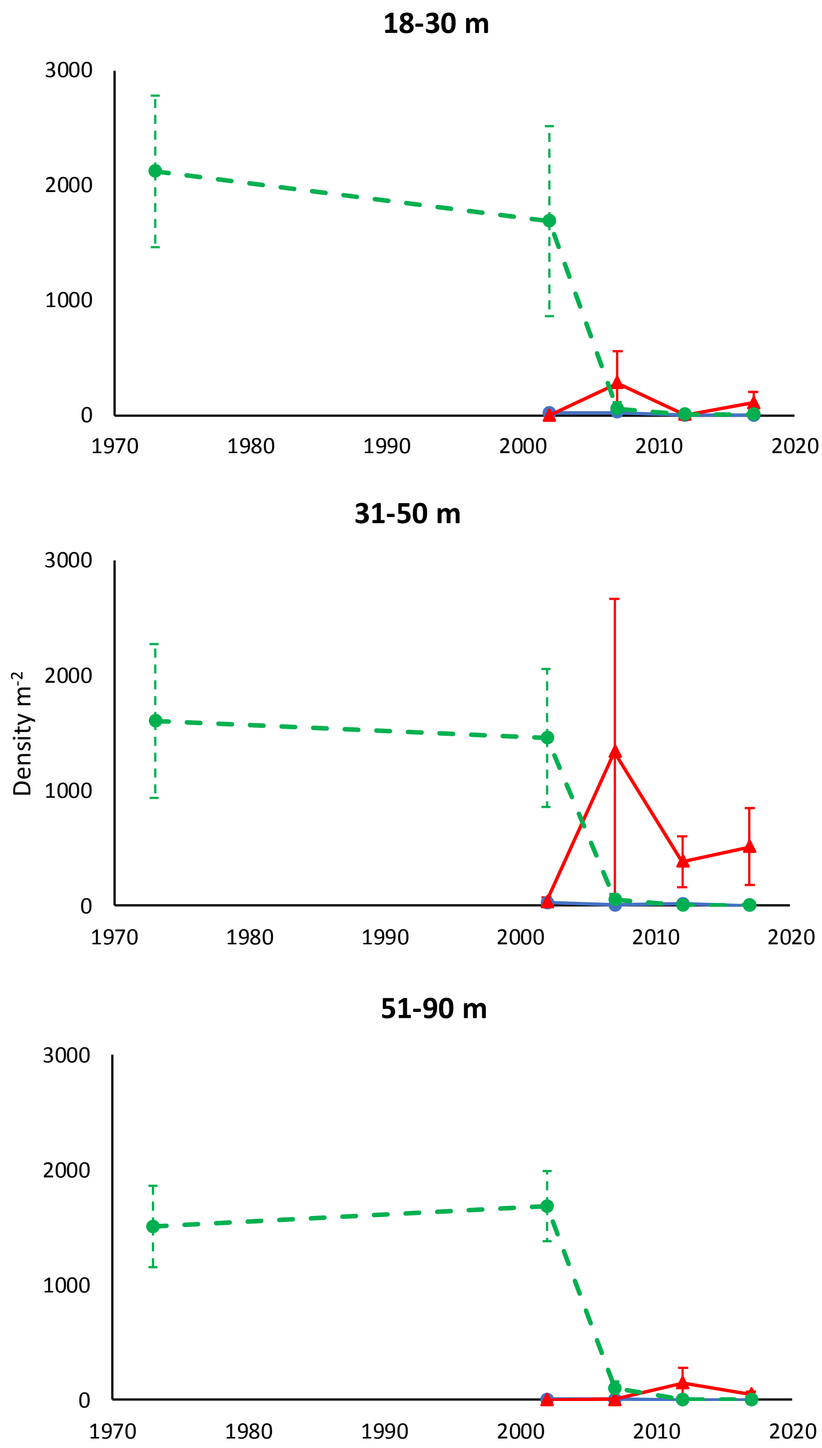


Figure 1.7. Long-term dynamics of zebra (blue line, circles), quagga (red line, triangles) mussel and *Diporeia* (green dashed line, circles) density (ind. m^{-2}) (mean ± standard error) in Georgian Bay of Lake Huron. Note that the zebra values (in blue) lie close to the x-axis.

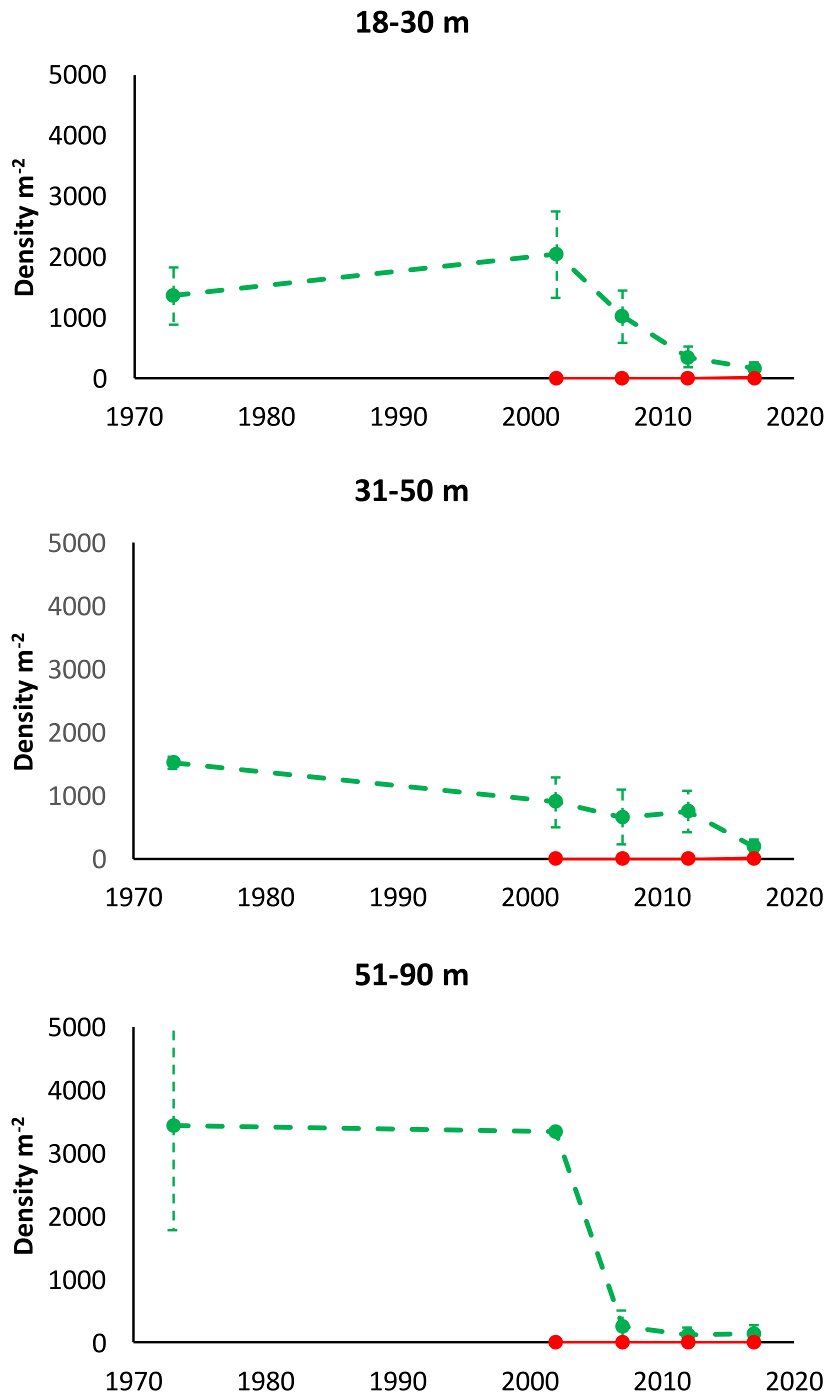


Figure 1.8. Densities of *Diporeia* (green dash line) and combined *Dreissena* (red line) in the North Channel of Lake Huron from 1973 to 2017.

SUMMARY

In 2017 we conducted a lake-wide survey of benthic macroinvertebrates in Lake Huron and compared the current status of the community with historic data. We found 125 taxa (species, genera or higher taxa) of benthic macroinvertebrates, including Annelida (56 taxa), Arthropoda (49), and Mollusca (16). The most abundant taxon lake-wide was Oligochaeta (52% of total benthic density), followed by *D. r. 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 dominated by oligochaetes (46% of total density), *D. r. bugensis* (25%), Sphaeriidae (8%) and Chironomidae (7%). Basin-wise, highest taxa richness was found in the main basin (90 species and higher taxa), followed by Saginaw Bay (75), Georgian Bay (54), and the North Channel (50). Benthic communities were the most similar in the main basin and Georgian Bay, and the largest differences were found between communities of the main basin and Saginaw Bay. *Dreissena 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 the North Channel we also found the lowest average biomass among all basins, and non-dreissenid benthos was dominated by *Diporeia* (33%), Oligochaeta (31%) and Chironomidae (21%). In the main basin and Georgian Bay, Oligochaeta were responsible for the majority of non-dreissenid biomass (85 and 90% of total benthic wet biomass). In contrast, in Saginaw Bay Chironomidae (mostly *Chironomus* spp.) contributed a larger percentage of total benthic biomass than Oligochaeta (42 vs. 35%). Quagga mussels were most abundant in the main basin, less common in Georgian Bay, and almost absent in North Channel. Comparing the 2017 findings to 2012 data, *Dreissena* density in the main basin in the shallowest (< 30 m) depth zone declined by a factor of eight, remained stable at 30-90 m, and more than doubled at depths greater than 90 m. As a result, the bulk of the population is now found deeper than 50 m. *Diporeia* and Sphaeriidae densities continued to decline in all basins including the North Channel, where very few quagga mussels were found. In contrast, 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. No consistent patterns were found in long-term trends of chironomids.

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CHAPTER 2. UNDERWATER VIDEO IMAGE ANALYSIS OF *DREISSENA* DISTRIBUTION IN LAKE HURON IN 2017

INTRODUCTION

Significant progress made during the last few decades in studies of distribution pattern and patch structure of large bodied benthic sessile organisms in marine systems (e.g. seagrasses, mussel beds, etc.) was largely due to the implementation of various underwater remote sensing methods, including acoustic and video surveys (reviewed in van Rein et al., 2009; Zajac, 2008). In spite of a growing number of attempts to use these methods in freshwaters (reviewed in Zajac, 2008; Lietz et al., 2015; Mehler et al., 2018; Karatayev et al., 2018), their application for freshwater benthic invertebrates, until recently, was limited by the lack of large sessile organisms that form spatial aggregations that could be detected by remote sensing. Colonization of the Great Lakes by dreissenids in 1990s has dramatically changed the situation. Zebra and later quagga mussels quickly colonized all Great Lakes where they form large aggregations (except in Lake Superior) that can be recorded using remote sensing (e.g. underwater image analysis). Incorporation of underwater image analysis into designs of benthic surveys allows the assessment of much larger bottom areas than assessments based on traditional bottom grabs or SCUBA. Such analysis provides valuable information about the distribution patterns and structure of *Dreissena* beds at various spatial scales and may significantly increase the precision of population size estimates (Karatayev et al., 2018).

Underwater video methods have been previously used in the Great Lakes, however these studies were largely limited to the nearshore zone and analyzed relatively few video images per station (Custer and Custer, 1997; Ozersky et al., 2009, 2011; Lietz et al., 2015; Mehler et al., 2018). In 2015 we conducted the first *Dreissena* lake-wide video study in Lake Michigan and collected continuous video footage from 500 m-long transects at 47 locations along the lakebed. In 2017 we estimated *Dreissena* coverage, density, and biomass in the main basin of Lake Huron by coupling underwater image analysis with traditional bottom grab sampling and using procedures previously developed for Lake Michigan (Karatayev et al., 2018).

METHODS

To study *Dreissena* spatial distributions and aggregation patterns along depth gradients, we analyzed bottom video images taken during the 2017 CSMI study in Lake Huron. Video images were obtained from a GoPro Hero 4 Black camera mounted on the Ponar grab, and from a GoPro camera mounted on a benthic sled towed behind R/V *Lake Guardian* for about 500 m (Fig. 2.1., 2.2). Details of video methods and analysis used are provided in Karatayev et al. (2018).

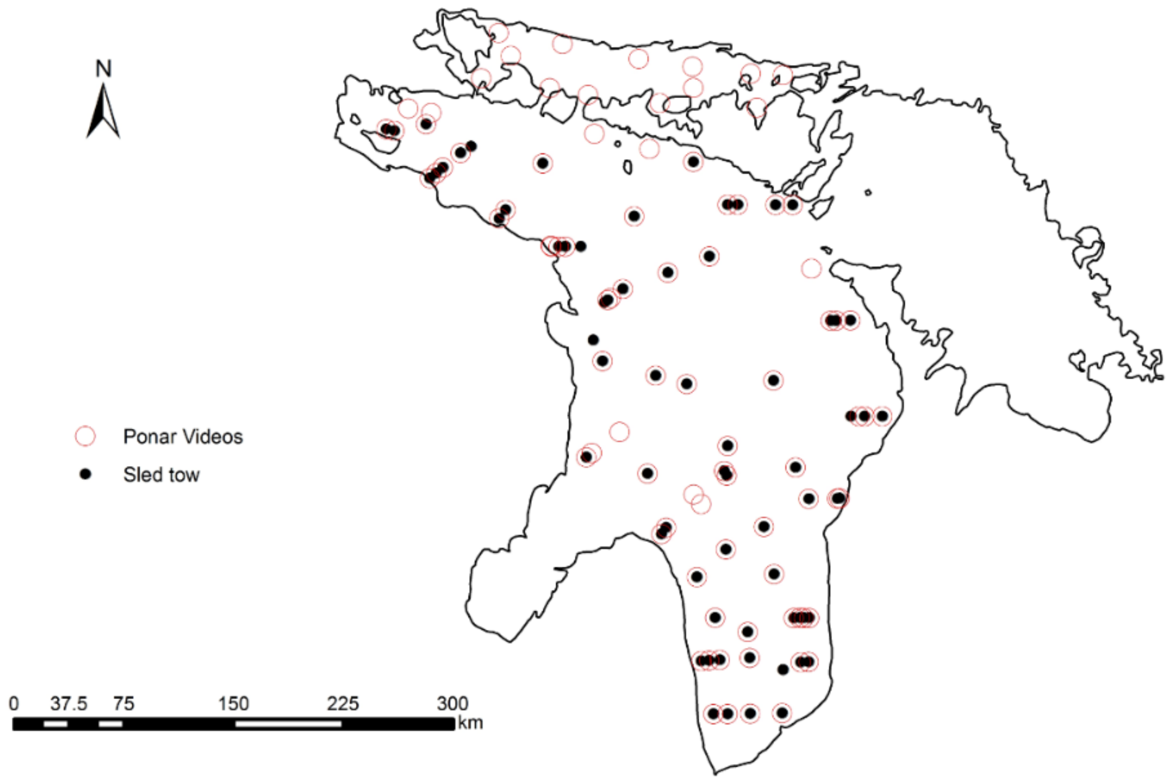


Figure 2.1. Location of stations in Lake Huron sampled in 2017 with Ponar videos (open red circles) and benthic sled videos (filled circles).

Figure 2.2. R/V *Lake Guardian* marine technician Maxwell Morgan attaching GoPro camera to the benthic sled during the Lake Huron CSMI benthic survey in 2017.

Before the beginning of analysis, the quality of both Ponar and sled videos were classified as acceptable or unacceptable to assess *Dreissena* density and aggregations. A video was considered acceptable for analysis if *Dreissena* presence/absence could be determined and, if *Dreissena* were present, the percent mussel coverage could be estimated (as the ratio between the area within an image covered by mussels and the area of the entire image, Karatayev et al. 2018). Unacceptable videos were further classified as controllable (camera not in focus, insufficient light) or uncontrollable (high water turbidity, benthic macrophyte coverage). Only Ponar and sled tow videos of acceptable quality were used in further analysis. More than 90% of the Ponar videos and 70% of the sled videos had acceptable quality (Table 2.1). Half of the videos categorized as unacceptable had controllable issues (camera not in focus, insufficient light, etc., sled not on bottom, etc.) while the other half had uncontrollable reasons such as algae cover or *Dreissena* buried in sediment.

Table 2.1. Number of acceptable (percent of total in parenthesis) and unacceptable bottom images collected in Lake Huron in 2017 using GoPro cameras attached to Ponar grab and benthic sled. Unacceptable images were classified as controllable (if due to factors such as equipment malfunction or human error) or uncontrollable (if due to high turbidity, macrophyte coverage, etc.).

Parameters	Ponar videos	Sled videos
Number of stations sampled	90	68
Number of acceptable images	82 (91%)	47 (71%)
Number of unacceptable images	8 (9%)	21 (29%)
Controllable	7	10
Uncontrollable	1	11

Sled tow videos from each transect were clipped into individual non-overlapping screen shots (a total of ca. 850 - 920 screen shots per transect) in Photoshop CS6. *Dreissena* percent coverage was analyzed from a subset of 100 screen shots randomly selected from each transect following methods described in Karatayev et al. (2018). Image area (0.300 m^{-2}) was estimated based on the distance between the sled skids (82.5 cm). Videos from each Ponar replicate were clipped to the part where the Ponar hit the lake bottom. *Dreissena* druses in each screen shot from sled tow video as well as from the Ponar videos were digitized in Photoshop CS6. In each screen shot, *Dreissena* coverage was determined in both cm^2 and bottom percentage, and the number of druses was counted.

To convert *Dreissena* percent coverage obtained from video images into density and biomass, we compared the density and biomass of *Dreissena* in three replicate Ponar samples with the mussel coverage estimated from the Ponar video images obtained from the exact spot of Ponar impact. Each Ponar was taken sequentially and paired with the Ponar videos, leading to three paired values for each station. We then estimated the relationship between these parameters using multiple regression in General Regression Models.

RESULTS AND DISCUSSION

Dreissena Coverage

Dreissena coverage varied between 0 and 79% (mean: 9.4% ± 2.5 SE) with the maximum coverage found at 97 m depth at station HU45. The predominance of rocky substrate at that station likely contributed to the unusually high coverage at that depth. The lowest coverage (0.6%) was found in the nearshore zone (< 30 m), increased to 13.6% in the mid depth zone (31–100 m), and then declined to 8.1% at depths >100 m (Table 2.2). A similar bell-shaped distribution pattern of *Dreissena* was found in Lake Michigan in 2015, however, coverage in the nearshore and mid-depth intervals, as well as lake-wide coverage in Lake Huron was much lower than in Lake Michigan,

In the shallow, warm, and well mixed nearshore environment there is an abundant food supply for *Dreissena*, but physical disturbances (wave and currents) limit *Dreissena* to areas with suitable substrate for attachment (e.g. gravel, rocks, bedrock). Therefore, the *Dreissena* population in such areas is very heterogeneous, with higher densities on stable rocky substrates compared with areas with less stable substrates (Fig. 2.3).

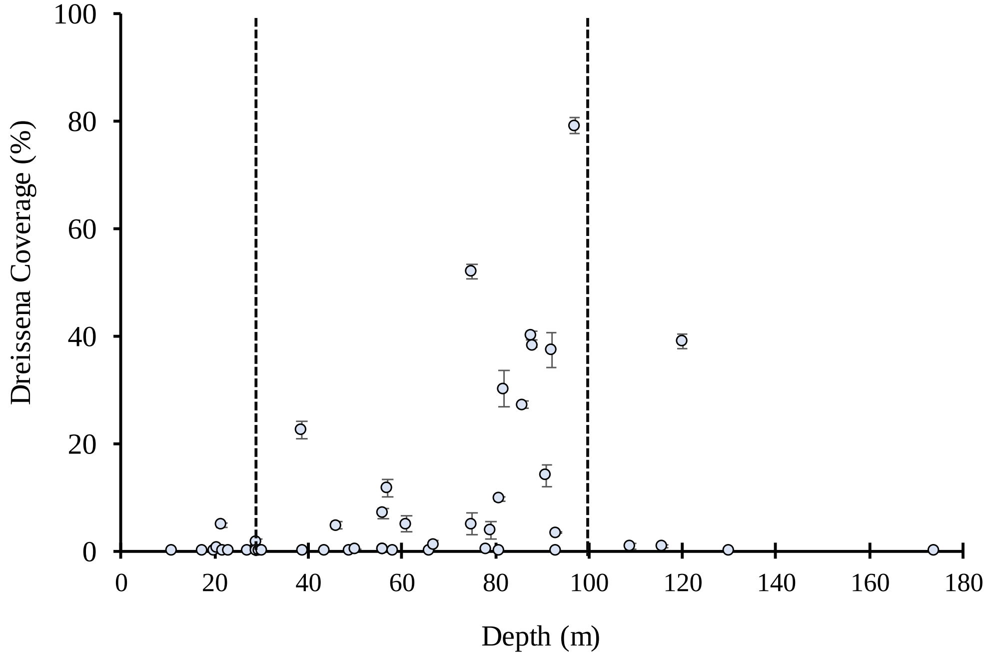
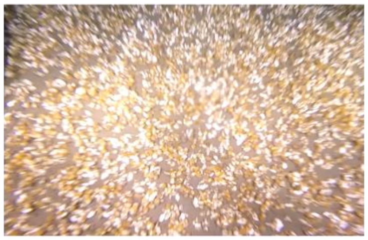


Figure 2.3. *Dreissena rostriformis bugensis* percent coverage along depth gradient in main basin of Lake Huron in 2017. Error bars represent ±1 standard error. Dashed lines denote 30 m and 100 m depth ranges.

In the mid-depth zone where food is still available and physical disturbance is limited, *Dreissena* forms the largest population. In the deepest zone where limited food resources support smaller densities, *Dreissena* were almost evenly distributed on the surface of bottom sediments, a distribution pattern likely to reduce food competition (Fig 2.4). *Dreissena* forms sizable density in this area only on ridges, trenches, or rocks emerging above the sediment surface.

MZ44 – 20.7 m



HU45 – 97 m

HU61– 115.9 m

Figure 2.4. *Dreissena rostriformis bugensis* representative screen shots for <30 m, 31 - 100 m, and >100 m depth intervals. Stations numbers and depth are provided for each screen shot.

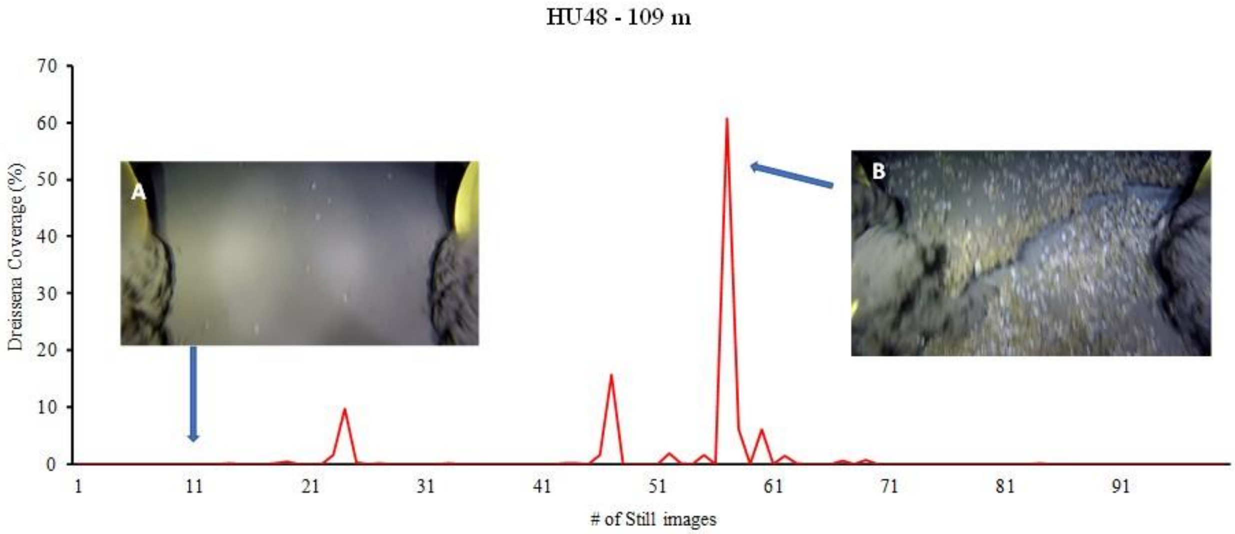


Figure 2.5. *Dreissena rostriformis bugensis* percent coverage analyzed from 100 randomly selected screen shots recorded at 109 m depth and corresponding representative screen shot for a flat part of the bottom (A) and a trench (B).

These irregularities in the bottom floor create turbulence that could deposit additional food and thus support more mussels compared to the flat bottom areas (Fig. 2.5). This phenomenon was revealed by video surveys. *Dreissena* spp. are known to be efficient ecosystem engineers, profoundly modifying benthic habitats and creating 3D reef-like structures (Karatayev et al., 1997, 2002; Burlakova et al., 2012). However, this effect largely depends on the size and structure of *Dreissena* aggregations as well as their distribution. Conventional grabs such as the Ponar are efficient for studies of *Dreissena* density, but due to limited sampling areas they are ineffective tools for understanding mussel bed structure and aggregation patterns. Using underwater video surveys, we were able to show that these parameters change drastically in the deep Great Lakes along the depth gradient.

Dreissena Density: Ponar *vs*. Video Images

The mussel density and biomass measured in Ponar grab samples had a strong relationship with *Dreissena* percent coverage obtained from Ponar video images. The relationships were: Density = 129 × coverage, multiple $R^2 = 0.85$, $p = 0.001$ (Fig. 2.6A); Biomass = 24.9 × coverage, multiple $R^2 = 0.84$, $p = 0.001$ (Fig. 2.6B). These coefficients (Fig. 2.6) were used to convert *Dreissena* coverage in sled tows into density and biomass.

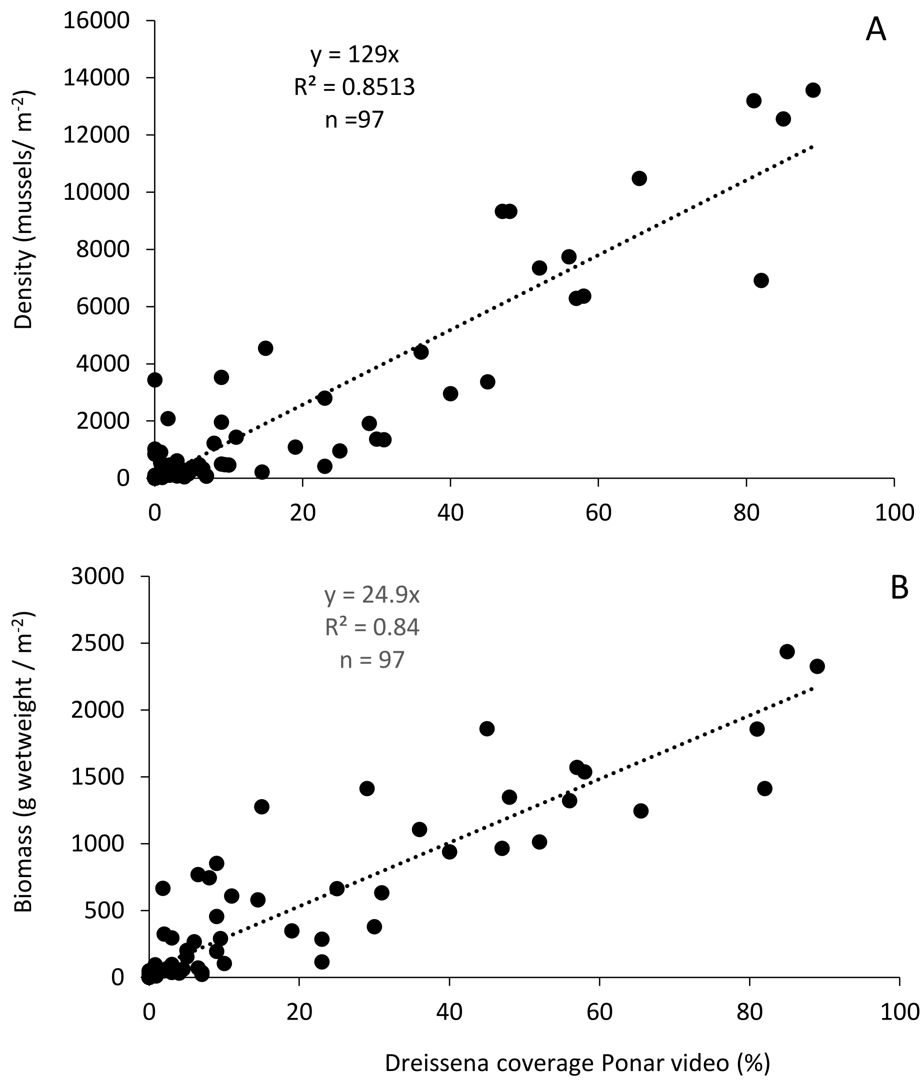


Figure 2.6. Relationship between *Dreissena* coverage in Ponar video, and density (ind. m^{-2}) and biomass ($g\ m^{-2}$) obtained from the same Ponar grabs in Lake Huron in 2017.

We compared density and biomass estimated from video transects with Ponar samples for 47 stations where we had data from both bottom grabs and video. The mean density and biomass estimated from video transects did not differ from Ponar grabs within any of the three depth intervals (Table 2.2) when averaged by stations for each depth zone. Similar to our previous study of Lake Michigan (Karatayev et al., 2018), we found that in Lake Huron, both video transects and Ponar samples exhibited higher average density and biomass of *Dreissena* within the 30–100 m depth zone compared to both the shallow and deep zone. However, in contrast to Lake Michigan, where in the shallowest zone *Dreissena* density and biomass were more than twice as high than in the deepest zone, in Lake Huron the deepest zone in 2017 exhibited mussel density an order of magnitude higher than in the shallowest zone (Table 2.2).

In the main basin of Lake Huron, the combined sampling area for all 47 video transects (1,410 m^2) was more than 200 times greater than the combined Ponar sampling area (6.6 m^2), and the total number of replicates for transects (4,700) was 33 times higher than for Ponar samples collected at the same stations (141). The increase in the number of replicates allowed us to greatly improve survey sensitivity via increases in precision and the statistical power of testing (Karatayev et al., 2018).

Table 2.2. Average *Dreissena rostriformis bugensis* percent coverage (% ± standard error), average density (m^{-2}) and average total wet biomass (g m^{-2}, shell plus tissue) across depth zones (m) sampled in lakes Huron in 2017 and Michigan in 2015. N represents the number of stations per depth zone. Data for Lake Michigan from Karatayev et al. (2018).

Depth zone (m)	n	Coverage (%)	Transect video density (m^{-2})	Ponar density (m^{-2})	Transect video biomass (g m^{-2})	Ponar biomass (g m^{-2})
			Lake Huron			
<30	12	0.6 ± 0.4	82 ± 52	65 ± 32	16 ± 10	17 ± 12
31 - 100	28	13.6 ± 3.7	1814 ± 484	1567 ± 645	350 ± 143	291 ± 111
>100	7	8.1 ± 7.7	1049 ± 996	1150 ± 724	202 ± 124	207 ± 124
			Lake Michigan			
<30	9	11.7 ± 8.6	1930 ± 1418	2034 ± 931	336 ± 247	543 ± 281
31 - 100	23	53.8 ± 5.1	8867 ± 849	7201 ± 1105	1544 ± 148	1232 ± 140
>100	10	6.3 ± 3.0	1045 ± 500	1544 ± 1091	182 ± 87	90 ± 46

Due to larger sample sizes, the standard error of the station mean in video transects in the main basin of Lake Huron was on average 6.7 times lower than in Ponar samples, resulting in significant increases in precision of the average estimation of density at the local (station) scale (Fig. 2.7). However, like in our previous study (Karatayev et al., 2018), we found that at a larger spatial scale (by depth zone, or lake-wide), the average *Dreissena* density and biomass were not significantly different between Ponar and video transects (Table 2.2.). There was also no difference in the size of standard errors calculated for the different depth zones from video transects or Ponar grabs, despite the large difference in precision of the station average estimations between video transects and Ponar grabs. The lack of significant differences between averages obtained by traditional Ponar sampling and video transects have at least two very important implications: (1) Ponar grabs provide reliable estimates of *Dreissena* density; (2) the gain in precision by using video transects will be at the station scale, the scale used as a target in GLNPO Biology Monitoring Program to monitor changes in benthic species densities.

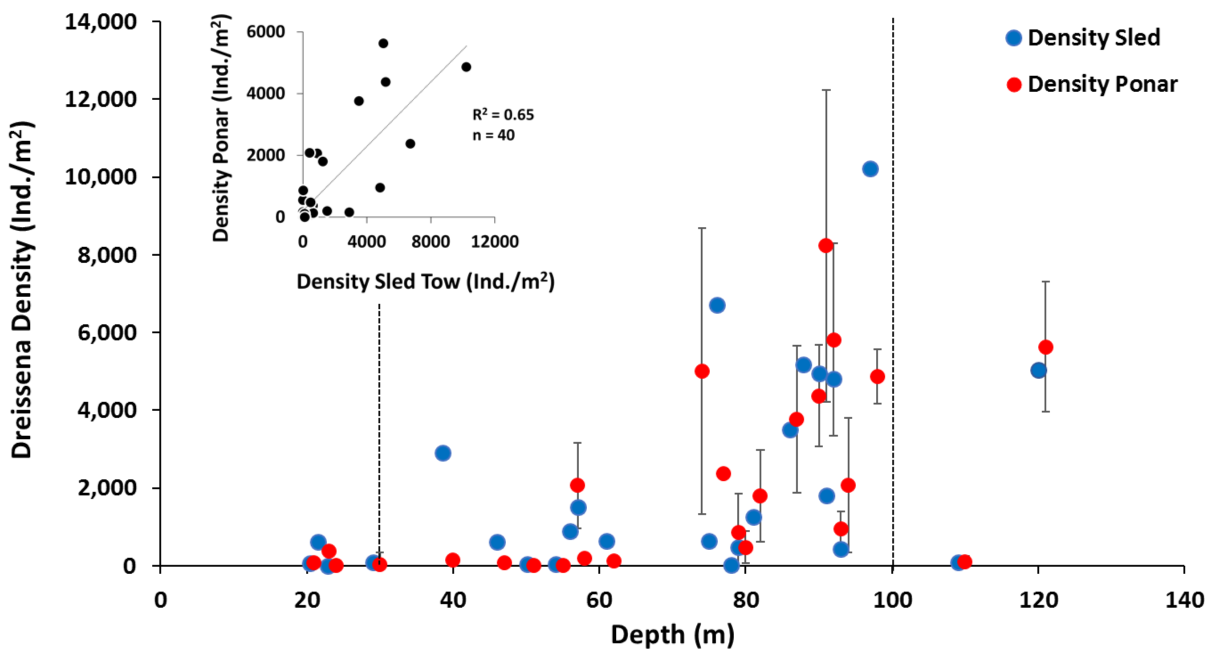


Figure 2.7. Mean *Dreissena rostriformis bugensis* density (individuals m^{-2}) estimated from video transects (100 screen shots analyzed per station, blue circles) and Ponar grab (3 grabs processed per station, red circles). Error bars represent ± 1 standard error. Dashed lines denote 30 m and 100 m depth ranges. Figure inset: Regression between *Dreissena* densities in Ponar versus calculated densities from sled tows. Only stations were *Dreissena* were found in both Ponar grabs and video transects are included.

SUMMARY

The use of video image analysis for *Dreissena* population assessment in Lake Huron not only substantially increased the number of video replicates that enumerate mussels in a known surface area of the bottom, but also increased the precision of station-average estimates compared to Ponar grabs. The lack of significant differences of *Dreissena* densities calculated from sled images and Ponar samples at larger scales underscores the importance of incorporating underwater video imagery into *Dreissena* monitoring, especially in areas were Ponar sampling would not be applicable (rocky bottom). The lower average *Dreissena* coverage in Lake Huron compared to Lake Michigan indicates that physico-chemical factors affecting the spatial distribution of *Dreissena* populations may be much more important than previously thought. Our results also show that the utility of underwater imagery for measurement of mussel bed structure and aggregation patterns, both of which are important factors to quantify when assessing the ecological impact of *Dreissena* at different depth zones.

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