

**ABUNDANCE AND DISTRIBUTION OF BENTHIC
MACROINVERTEBRATES IN THE LAKE HURON SYSTEM: SAGINAW
BAY, 2006-2009, AND LAKE HURON, INCLUDING GEORGIAN BAY
AND NORTH CHANNEL, 2007 AND 2012.**

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Abundance and distribution of benthic macroinvertebrates in the Lake Huron system: Saginaw Bay, 2006-2009, and Lake Huron, including Georgian Bay and North Channel, 2007 and 2012.

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1.0 INTRODUCTION

This technical report provides results of benthic macroinvertebrate surveys conducted in Saginaw Bay in 2006-2009, and in Lake Huron, including Georgian Bay and North Channel, in 2007 and 2012. The objective of these surveys was to update the status of the benthic community and thereby extend temporal assessments of previously-defined trends in these lake regions. Previous surveys were conducted in Saginaw Bay in 1991-1996, in Lake Huron in 2000 and 2003, and in Georgian Bay and North Channel in 2002. Based on these previous surveys, benthic macroinvertebrate communities in both Saginaw Bay and Lake Huron had undergone major changes since the late 1960s and early 1970s (Nalepa et al. 2003, 2007a). Factors driving community changes in Saginaw Bay were primarily attributed to phosphorus abatement and the introduction and expansion of invasive zebra mussels (*Dreissena polymorpha*) (Nalepa et al. 2003), while community changes in Lake Huron were mainly attributed to both zebra mussels and quagga mussels (*Dreissena rostriformis bugensis*) (Nalepa et al. 2007a).

While published papers summarized and interpreted results of these previous surveys, the basic, raw data were provided in two technical reports, one for Saginaw Bay (Nalepa et al. 2002), and one for Lake Huron (Nalepa et al. 2007b). These reports also included details of station locations, collection methods, and laboratory procedures. Similar to these previous technical reports, the purpose of this technical report is to provide basic data and supporting information of the most recent surveys; that is, to provide collected data in its simplest form (i.e., number of each taxon in each replicate sample), and to provide additional details of study design, station locations, sampling methods, and laboratory procedures. In addition, this report also provides summary tables and figures that link previous and recent surveys, thereby giving some perspective of current temporal trends. Further and more detailed analyses, including community shifts and interpretations of trends, will be provided in future publications.

2.0 DESCRIPTION OF LAKE HURON SYSTEM

There are several distinct regions of the Lake Huron system that are defined by broad differences in physical characteristics and benthic features. Hence, the benthic macroinvertebrate data are reported and summarized separately for each region. Saginaw Bay is a warm, shallow regional-extension of the western shoreline of the lake that can be functionally separated from the main basin by a line extending from AuSable Point to Point Aux Barques ([Figure 1](#)). The bay can be further sub-divided into inner and outer regions by a line extending along its narrowest width (21 km) from Sand Point to Point Lookout ([Figure 2](#)). Differences in physical and chemical features of the inner and outer bay are distinct. The inner bay has a mean depth of only 5.5 m, is well-mixed, and nutrient rich; it is heavily influenced by organic input from the Saginaw River, which accounts for 70% of tributary flow into the bay. The outer bay has a mean depth of 16.4 m and is more influenced by the colder, nutrient-poor waters of Lake Huron. Surface areas of the inner and outer bay are 1,625 km² and 1,255 km², respectively. Bottom substrates in the inner bay grade from mostly cobble/rock in shallow areas to silt in deeper areas. The inner bay has two shallow sand bars that extend along the southeastern and northwestern shorelines. Both sand bars have irregular areas of cobble with patches of gravel and pebbles. Water depth between the two sand bars gradually increases to a maximum of 14 m. The proportion of fine-grained material gradually increases along this depth gradient as a function of sediment deposition. At depths > 6 m, the substrate consists mostly of silt and clay. Overall, proportions of substrates by area in the inner bay are: sand/cobble = 57%, silty sand = 16%, and silt = 27% (Nalepa et al. 2003). In the outer bay, the east shore is rocky, as is the area around Charity Island. The western shore has extensive sandy areas, with rock and clay near Point Lookout. Most substrate in the outer bay consists of sand with varying amounts of overlying silt.

As a region, the main basin of Lake Huron has a mean depth of 85 m, a maximum depth of 245 m, and a surface area of 41,475 km². A till-covered, bedrock escarpment (Six-Fathom Scarp) extends from Point Clark to Alpena and divides the lake into northern and southern portions ([Figure 1](#)). In the southern portion another escarpment (Ipperwash Scarp) extends along a southeast-to-northwest line and further divides the lake into an east (Goderich Basin) and a west basin (Port Huron Basin). Maximum depths of these basins are 119 m and 88 m, respectively. The northern portion is also divided into two major basins by a sill (Thunder-Duck Sill) that extends southwest to northeast from near Alpena to the northern end of Manitoulin Island. The basin north of the sill (Mackinac Basin) has a maximum depth of 137 m and the basin south of the sill (Manitoulin Basin) has a maximum depth of 227 m. In general, these four basins serve as zones of sediment deposition. Sand and bedrock dominate the substrate in nearshore regions and on the escarpments, while fine substrates (silts and muds) dominate in the depositional basins. Overall, areas with fine substrates account for 58% of the total lake bottom (Thomas et al. 1973). Highest sedimentation rates in the lake occur in the Goderich Basin in the southeastern end of the lake between Goderich and Ipperwash (Thomas et al. 1973; Robbins 1980). Maximum sedimentation rates in this area are about 100 mg/cm²/yr (Robbins 1980).

Georgian Bay and North Channel are regions that lie north and east of the main basin, separated from the lake by land components of the Niagara Escarpment (Manitoulin Island and Bruce Peninsula) ([Figure 1](#)). Mean depth, maximum depth, and surface area are 44 m, 165 m, and 15,111 km² for Georgian Bay and 22 m, 85 m, and 3,950 km² for North Channel. Nearshore areas of both water bodies are dominated by bedrock, rock, and cobble. Beyond that, substrates in Georgian Bay are a complex pattern of glacial tills (mixture of sand, gravel, silt, and clay), lacustrine clays, and basin muds. The latter occur in offshore depositional regions that are interconnected and occur as troughs throughout the bay resembling a residual drainage system. Sedimentary muds are more prominent in the North Channel as a result of material carried by the St. Mary's River and then deposited.

3.0 STATION LOCATIONS AND FIELD PROCEDURES

In Saginaw Bay, ten stations were sampled using a Ponar grab in fall 2006, in spring, summer, and fall 2007 and 2008, and in fall 2009 (Figure 2, Table 1). These were the same ten stations sampled in 1987-1996 (Nalepa 2002). Of these stations, seven were located in the inner bay and three were in the outer bay. Some stations were not sampled in all years because of weather conditions or technical/scheduling issues; notably, most stations in the outer bay were not sampled in 2006 and 2009 (Table 1).

In the main basin of Lake Huron, samples were collected using a Ponar grab in late July/early August at 80 stations in 2007 and at 83 stations in 2012, and these stations were mostly the same stations sampled in 2000 and 2003 (Table 2). The three stations sampled in 2012 but not sampled in 2007 (GLERL18, GLERL30, GLERL45) were located along a transect near Alpena, MI and were part of a larger ecosystem study that was conducted only in that year. These three stations are not shown in Figure 1, but were in close proximity to stations near Alpena sampled in 2003 (AL20, AL30, and AL45; see Table 2, Figure 1). In Georgian Bay and North Channel, samples were collected using a Ponar grab at 17 and 13 stations, respectively, and these were the same stations sampled in 2002 (Table 3). Two stations in Georgian Bay (GB11 and GB26) were not sampled in 2012 because of poor weather conditions.

In all surveys regardless of region or year, triplicate grab samples were taken at each station. Each replicate sample was washed into an elutriation device (a funnel-shaped hopper) that was fitted with a nitex sleeve having 0.5-mm mesh openings. Grab contents were placed into the elutriation device, gently stirred, and then washed through the sleeve. Retained material (organisms and coarse substrate material) was then washed into a collection jar and immediately preserved in 5% buffered formalin containing rose bengal stain. Jars were labeled with the station, replicate number, and date.

In addition to the Ponar samples, samples for only *Dreissena* were collected at seven stations in Saginaw Bay using SCUBA divers in September 2008, 2009, and 2010 (Figure 2, Table 1). These stations were the same as those sampled by divers in fall of 1991-1996 (Nalepa et al. 2003). Four stations were located in areas with cobble that could not be effectively sampled with the Ponar grab (Stations 5, 6, 15, and 27), while three stations had sand/gravel substrates that were sampled by both divers and the Ponar grab (Stations 13, 14, and 16). At each station, divers randomly placed a 0.5 m² or 1.0 m² frame on the bottom, and hand-collected all hard material within the frame area. Frames were subdivided such that a smaller portion could be sampled if desired, but the minimum area sampled was 0.25 m². In 1991-1996, after all hard material in the sampled area within the frame was removed, divers used a suction device fitted with nitex net (0.5-mm openings) to re-sample the original area sampled (see Nalepa et al. 2003). In 2008-2010, this suction re-sampling procedure was not conducted since few if any *Dreissena* were collected by this procedure in 1991-1996. In all years, three replicate samples were collected by divers at each station except in 2009 when four replicates were collected. Divers moved directionally 2-3 m between replicates to ensure each sample was taken in an undisturbed area.

4.0 LABORATORY PROCEDURES

In the laboratory, material collected by the Ponar grab and retained in the 0.5-mm sleeve was placed into a white enamel pan or a large petri dish, and organisms were removed and counted under a 1.5x magnifier lamp, or under low-power of a binocular microscope. Organisms were sorted, counted, and placed into separate vials by major taxonomic groups: Amphipoda, Oligochaeta, Sphaeriidae, Chironomidae, *Dreissena polymorpha*, and *Dreissena rostriformis bugensis*, and “others”. Individuals in the “others” category included Gastropoda, Isopoda, Hirudinea, Ephemeroptera, and Tricoptera. Taxonomic groups observed in the samples but not counted were: turbellarians, nematodes, nemertea, and *Mysis*.

After being sorted and counted, organisms were identified to the lowest practical taxonomic level. For identification of oligochaetes, up to 75-100 individuals in a given replicate (proportionately split with a Folsom plankton splitter when numbers were higher) were mounted in CMC9 on microscope slides and their images were either projected onto a sheet of paper using a camera lucida and then traced, or captured with a microscope-mounted camera and recorded. Subsequently, individuals were identified and taxonomic designations placed alongside the respective image. Only oligochaetes with a prostomium were identified and counted; individuals without a prostomium were identified as fragments and not included in the final count. For chironomids, up to about 50 individuals were identified per replicate sample. The sample was proportionately split as described above when numbers were higher. Chironomid head capsules were removed from bodies and mounted in CMC9 on microscope slides with mentum side up. Corresponding bodies were mounted alongside respective head capsules and images recorded as described for oligochaetes.

For samples collected in 2007 from Lake Huron, Georgian Bay and North Channel, oligochaetes and chironomids were not identified beyond the group level, hence abundances were derived from the sorted counts. Since oligochaete fragments (without prostomium) were included in these counts, total abundance of oligochaetes at each station in 2007 was corrected based on the mean proportion of fragments found at the same station in 2012. For the two stations sampled in 2007 but not in 2012 (GB11 and GB26), a mean proportion of all stations in the same depth interval (see below for depth intervals) was used as the correction factor. A similar correction process was followed for oligochaete abundances in 2003 when oligochaetes were not identified (Nalepa et al. 2007a). In this case, abundances in 2003 were corrected based on the proportion of fragments found in 2000 when oligochaetes were identified.

Biomass (ash-free dry weight) of the benthic macroinvertebrate community in Saginaw Bay was determined for all years (2006-2009). Methods were the same as those used to determine biomass in Saginaw Bay in 1987-1996 (see Nalepa et al. 2002). Biomass in Lake Huron, Georgian Bay, and North Channel in 2012 was determined using the same methods as for Saginaw Bay. Biomass in previous surveys in these three water bodies in 2000, 2002, and 2003 was not determined (Nalepa et al. 2007b), nor was biomass determined in the 2007 survey.

As noted, details regarding methods to determine biomass, including length-weight relationships and direct conversion factors, are given in Nalepa et al. (2002). In brief, lengths of all traced oligochaetes and oligochaete fragments were measured using a digital map measurer or an imaging software program. For Saginaw Bay, total length was then converted to ash-free dry weight by multiplying it by a conversion factor of 0.25 mg dry weight per cm (Nalepa and Quigley 1980) and then assuming ash-free dry weight to be 90 % of dry weight (Johnson and Brinkhurst 1971). For Lake Huron, Georgian Bay, and North Channel, total oligochaete length was multiplied by 0.342 mg ash-free dry weight per cm (Nalepa and Quigley 1985). The former conversion value was determined from oligochaete communities in a shallow, nearshore region of Lake Michigan. This value would be more realistic for the community in Saginaw Bay. On the other hand, the latter conversion value was determined from oligochaete communities mostly in offshore regions of Lake Michigan, and this value would be more realistic for the community in open waters of Lake Huron. For chironomids, lengths were determined as given above and then converted to dry weights using length-weight relationships given in Nalepa et al. (2002). Ash-free dry weight was assumed to be 90% of dry weight (Johnson and Brinkhurst 1971).

For *Dreissena*, length-weight relationships used to determine biomass were derived from freshly-collected individuals. In Lake Huron, individuals for length-weight determination were collected during the 2012 survey at 13 stations: GB3, GB8, GB35, FI3, HU27, HU32, HU429, MZ44, MZ93, MZ123, SR6, PT5, and TN3. Selection of these stations was not pre-determined; that is, station selection depended on the number of mussels found at the time of sampling and by a visual estimate of the size range (shell lengths) of the population. For the latter, a broad size range of individuals was a requirement (10 mm to >

20 mm) so a representative relationship could be obtained. Also, an effort was made to collect at stations located throughout the lake and at various depths. Immediately after collection of mussels with a Ponar grab, soft tissues of about 25 individuals of various sizes were removed from shells, placed individually into pre-weighed aluminum planchets, and dried at 60°C for a minimum of 48 h. After drying, 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 for 1 h, and then re-weighed to obtain ash-free dry weights. Corresponding shell lengths were measured to the nearest 0.5 mm. Overall, 227 individuals from the 13 stations were weighed and measured. All weighed individuals from the 2012 survey were *D. r. bugensis* since *D. polymorpha* was rarely found. In Saginaw Bay, *Dreissena* were collected for determination of length-weight relationships at either Station 5 (in 2008) or at Stations 6 and 15 (in 2010) at the same time divers conducted quantitative sampling. Individuals were immediately placed in coolers, overlaid with damp towels, and kept at 4°C. Within 48 h of collection, mussels were sorted by size, and ash-free dry weights and shell lengths were determined as given above. Separate length-weights were determined for *D. polymorpha* and *D. r. bugensis* in 2008, but weights of *D. polymorpha* were not determined in 2010 due to minimal numbers and limited size ranges of individuals.

Shell lengths (SL) and ash-free dry weights (AFDW) were used to develop length-weight relationships according to the allometric equation: $\log_e \text{AFDW (mg)} = b + a * \log_e \text{SL (mm)}$. For Lake Huron, two relationships were developed based on weighed mussels from the 13 stations, one for mussels from stations < 50 m, and another for mussels from stations > 50 m (Table 4). To determine biomass for mussels in the diver-collected samples in Saginaw Bay in 2008, 2009, and 2010, the relationship determined for *D. polymorpha* in 2008 was also used for any *D. polymorpha* collected in 2009 and 2010, while the composite relationship for *D. r. bugensis* in 2008 and 2010 was used for *D. r. bugensis* collected in 2009 (Table 4). For mussels in the Ponar-collected samples in 2006-2009, the relationship for *D. polymorpha* in 2008 was used for *D. polymorpha* in all years, while the relationship for *D. r. bugensis* in 2008 was used for individuals of this species collected in 2006 and 2007, while the relationship used for those collected in 2009 was determined as given above.

Biomass of *Dreissena* populations was calculated using determined length-weight relationships as given above and size frequencies of the population. To determine the latter, shell lengths of mussels in each replicate sample were measured, and then binned into 1-mm size categories ranging from 5 to 33 mm. Individuals < 5 mm were binned into a single category (1-5 mm). To determine biomass, the number of individuals in each size category was multiplied by the AFDW of an individual in that category as derived from the length-weight regression (calculated from the mid-shell length within each size bin). All category weights were then summed.

To determine AFDW of the amphipod *Diporeia*, body lengths (base of rostrum to base of telson) of all individuals were measured and dry weights (DW) determined from the allometric equation: $\log_e \text{DW (mg)} = -6.889 + 3.404 * \log_e \text{SL (mm)}$ (Johnson 1980). Ash-free dry weight was assumed to be 90% of dry weight. Ash-free dry weights of Sphaeriidae, Gastropoda, Isopoda, Hirudinea, Ephemeroptera, and Amphipoda (excluding *Diporeia*) were determined by multiplying numbers of each taxa group by the mean weight per individual as determined from previous surveys in Saginaw Bay in 1987-1996 (Nalepa et al. 2002). For example, the mean weight of Sphaeriidae over all sites and dates in 1987-1996 was 0.08 mg AFDW. This mean weight was then multiplied by the number of Sphaeriidae in each sample collected in Saginaw Bay in 2006-2009 and in Lake Huron in 2012. While not as precise as direct measurements, the error introduced to overall biomass was considered minor given the relatively low abundance of these groups. Further, mean weights derived in this manner were generally similar to mean weights measured directly and reported previously (Nalepa and Quigley 1980). For instance, the mean weight of 0.08 mg per individual for Sphaeriidae was comparable to the 0.07 mg per individual measured directly (small and medium individuals). Also, the mean weight of Gastropoda was 4.72 mg per individual, which compared to 6.62 mg per individual measured directly. Other mean weights were: Amphipoda (*Gammarus* and

Hyalella)= 0.478 mg, Isopoda= 0.678 mg, Hirudinea = 0.917mg, Ephemeroptera = 8.45 mg, and Tricoptera = 0.203 mg.

5.0 DATA PRESENTATION

Benthic macroinvertebrate data collected in each survey are provided as Excel files within the following designated Appendices: [Appendix 1 Density and Biomass in Saginaw Bay, 2006-2009](#) (Ponar-collected); [Appendix 2 Density and Biomass of *Dreissena* in Saginaw Bay 2008-2010](#) (diver-collected); [Appendix 3 Density in Lake Huron, 2007 and 2012](#); and [Appendix 4 Biomass in Lake Huron, 2012](#). For all files, densities are given as the number per square meter, and biomass is given as mgAFDW per square meter. To convert from number per grab to number per square meter, values in 2012 were multiplied by 20.70, while values in all other years were multiplied by 21.42. Variables in the files include year, station, replicate number, and taxa. Season of sampling (spring=1, summer=2, fall=3) is provided as a variable only for data collected in Saginaw Bay ([Appendix 1](#)) since these data were often collected over several seasons (see [Table 1](#)). Individual taxa within the data files are identified by four letter codes, and these codes are consistent across all surveys ([Table 5](#)).

6.0 STATION GROUPINGS AND ANALYSIS

For analysis, stations within the various lake regions were grouped based on substrate type or water depth as in previous publications (Nalepa et al. 2003, 2007a). In the inner portion of Saginaw bay, station groups were: cobble (Stations 5, 6, 15), sand/gravel (Stations 13, 14, 16), silty sand (Station 11), and silt (Stations 4, 7, 10). Stations in the first two groups were in shallow regions (< 6m) that were considered to be non-depositional, while stations in the latter two groups were deeper (> 6 m) and considered to be transitional and depositional, respectively (see Nalepa et al. 2003). As noted earlier, stations in the cobble group and the sand-gravel group were specifically sampled for *Dreissena* using SCUBA divers, while stations in the sand-gravel, silty sand, and silt groups were sampled for the entire benthic community using the Ponar grab. In the outer bay, stations sampled using the Ponar grab were functionally separated by water depth: 12 m (Station 24), 16 m (Station 20), and 28 m (Station 23). These stations all had a substrate consisting of silty sand, but were not grouped because of their wide range of water depths, which contributed to great differences in community composition (Nalepa et al. 2003). In Lake Huron, Georgian Bay, and North Channel, stations were grouped based on water depth: 18-30 m, 31-50 m, 51-90 m, and > 90 m (main basin only). These depth categories are consistent with prior characterization of depth-macroinvertebrate associations in Lake Huron (Nalepa et al. 2007a).

Since the main objective of recent surveys was to define long-term trends, data from previous surveys were included in summary tables and figures. For Saginaw Bay, temporal trends in *Dreissena* and major non-*Dreissena* taxa groups are shown in figures that summarize data collected each year during the periods 1987-1996 and 2006-2010. To more closely analyze temporal changes between these time periods, yearly data in the former period were further divided into distinct periods based on prior examination of population trends in *Dreissena* and observed *Dreissena* impacts on other taxa (Nalepa et al. 2003). During the initial years after *Dreissena* became established in 1991, there were wide-scale variations (both temporal and spatial) in both dreissenid density and biomass as the population spread and colonized the bay (Nalepa et al. 2003). The population subsequently stabilized at a lower level after 1993. Hence, while the dreissenid population was surveyed every year between 1991 and 1996, the 1994-1996 period represented the most realistic (and conservative) baseline to assess if any population changes occurred in 2006-2010. For examining trends in non-dreissenid taxa, the three periods were: 1987-1990, 1994-1996, and 2006-2009, which represented the pre-*Dreissena* period, the short-term, post-*Dreissena* period, and the long-term, post-*Dreissena* period, respectively. Prior surveys in 1987-1996 showed that the major groups of non-dreissenid taxa had different responses to *Dreissena*, and these responses varied

depending on bay region (inner, outer), substrate, and time lag after *Dreissena* introduction and subsequent peak (Nalepa et al. 2003). Thus, densities of non-dreissenid taxa in 1994-1996 should be considered with this caveat in mind.

For statistical analysis of trends in Saginaw Bay, mean annual density or biomass at each station within a station group was considered a replicate for a given time period. For instance, for the category of inner bay-sand/gravel as sampled by divers, mean values of *Dreissena* at Stations 13, 14, and 16 in 1994-1996 (n=9; 3 stations x 3 years) were compared to mean values for the same stations in 2008-2010 (n=9; 3 stations x 3 years). In cases where a defined category had only one station (e. g., inner bay-silty sand), the seasonal mean was considered a replicate. Differences between periods were tested using a t-test or ANOVA after \log_e+1 transformation. Separate tests were performed for each major taxonomic group. If differences were significant ($P \leq 0.05$), Fisher's LSD was used for pairwise comparisons.

For the main basin of Lake Huron, differences in mean densities in 2000, 2003, 2007, and 2012 in each of the four depth intervals were examined by ANOVA after \log_e+1 transformation. As above, each major taxonomic group was tested separately. For Georgian Bay and North Channel, mean densities in 2002, 2007, and 2012 were compared.

7.0 TEMPORAL TRENDS IN SAGINAW BAY

7.1 *Dreissena*

As noted, trends in *Dreissena* in Saginaw Bay were derived from samples collected with both divers and the Ponar grab. Both collection methods indicated that *Dreissena* populations on hard substrates (cobble, sand/gravel) in the inner bay declined substantially between 1994-1996 and 2006-2010. For diver-collected samples, mean densities in 2008-2010 declined by 80.6% and 79.9% compared to 1994-1996 at sites with cobble and sand/gravel substrates, respectively, and biomass declined by 79.9% and 85.6% (Table 6). These declines were significant ($P \leq 0.05$) for the cobble sites, but not significant for the sand/gravel sites ($P > 0.05$). For samples collected with the Ponar grab at sites with sand/gravel, mean densities in 2006-2009 were 78.4% lower when compared to mean densities in 1994-1996 (Table 7). This decline found in the Ponar samples was thus similar to the 79.9% decline found at the same sites as sampled by divers; however, unlike the diver-collected samples, the difference between periods was not significant ($P > 0.05$). Differences between 1994-1996 and 2006-2009 at sites with silt and silty sand were also not significant ($P > 0.05$). At sites with silt, mean densities were consistently low ($< 50/m^2$ in both periods). At the site with silty sand, mean densities were 10 times greater in 2006-2009 than in 1994-1996, but year-to-year variation within periods was substantial. For instance, the range in yearly means at this site in 1994-1996 was $0/m^2$ to $50/m^2$, whereas the range in 2006-2009 was $0/m^2$ to $2,209/m^2$. Over all sites in inner Saginaw Bay, only *D. polymorpha* was collected in 1994-1996, whereas *D. r. bugensis* was the dominant dreissenid in 2008-2010, accounting for 75% of abundance and 80% of biomass of all dreissenids > 5 mm.

In the outer bay, density and biomass of *Dreissena* at the site with a cobble substrate (diver-collected; Station 27) were 94.7% and 94.8% lower in 2008-2010 than in 1994-1996, respectively, and these differences were significant ($P \leq 0.05$; Table 6). In contrast, at the three sites with silty sand substrate at 12 m, 16 m, and 28 m depths (Ponar-collected), mean densities remained the same or increased in 2006-2009 compared to 1994-1996 (Table 7). For these three sites, the extent of the temporal change appeared positively related to station depth. Mean densities at 12 m remained $< 5/m^2$ in both periods, mean densities at 16 m increased from $3/m^2$ to $77/m^2$, and mean densities at 28 m increased from $7/m^2$ to $173/m^2$. All dreissenids collected in the outer bay in 1994-1996 regardless of substrate or depth were *D. polymorpha*, whereas all dreissenids collected in 2006-2010 were *D. r. bugensis*.

7.2 Non-Dreissenid Taxa

Temporal trends in the following major, non-dreissenid taxa groups were examined: Oligochaeta, Chironomidae, Sphaeriidae, and Amphipoda. To provide an overall perspective of temporal trends of these groups in Saginaw Bay, yearly mean densities over the entire 1987-2009 period are given for each substrate type (inner bay) and depth (outer bay) ([Figure 3](#)). When densities within the three distinct temporal periods were compared (1987-1990, 1994-1996, 2006-2009) for each group, temporal changes were evident, and these changes varied by substrate and depth ([Table 7](#)).

Among the most notable temporal patterns were the large fluctuations in oligochaete densities at sites with a silt substrate in the inner bay ([Figure 3](#)). At these sites, mean densities of oligochaetes were greatest in 1987-1990 ($19,423/\text{m}^2$), decreased 8-fold between 1987-1990 and 1994-1996 (down to $2,727/\text{m}^2$), and then increased 3-fold between 1994-1996 and 2006-2009 (up to $6,055/\text{m}^2$). Mean densities in each of these three periods were significantly different from each other ($P \leq 0.05$; [Table 7](#)). These temporal changes appear to further support the hypothesis that oligochaete densities in the portion of the inner bay with a silt substrate were negatively associated with dreissenid densities in portions with a hard substrate (i.e., sand/gravel, cobble) (Nalepa et al. 2003). For example, oligochaete densities in the silt portion were greatest before *Dreissena* became established in the bay (1987-1990), greatly decreased just after *Dreissena* became widespread and abundant (1994-1996), and then increased after *Dreissena* declined from population peaks (2006-2009). Since *Dreissena* was never abundant in the silt portion of the inner bay during the entire 1991-2009 period, the hypothesis suggests that *Dreissena* populations in hard-substrate, non-depositional portions of the inner bay divert organic material from the silty, depositional portion, thereby decreasing available food for oligochaetes (Nalepa et al. 2003).

The most consistent, directional trend in the inner bay was an increase in the abundance of amphipods after *Dreissena* became established. This increase was most evident when the period just after *Dreissena* became established (1994-1996) was compared to the period before *Dreissena* (1987-1990) ([Table 7](#)). While mean densities of amphipods were lower in 2006-2009 compared to 1994-1996, densities were still greater than in 1987-1990. Amphipods in the inner bay in 1987-2009 were almost exclusively *Gammarus* (98%). This amphipod genera typically increases in abundance after *Dreissena* becomes established; it utilizes dreissenid biodeposits as a food source and inhabits dreissenid clusters which offer a refuge from fish predation (Ward and Ricciardi 2014).

Sphaeriids progressively declined at sites with sand/gravel and silty sand substrates in the inner bay, with lowest densities in the 2006-2009 period ([Table 7](#)). Differences between periods were significant for each substrate ($P \leq 0.05$). In contrast, sphaeriid densities did not decrease at sites with a silt substrate but actually increased, although differences between periods were not significant ($P > 0.05$). In general, sphaeriids are negatively impacted by *Dreissena*, likely as a result of food competition (Ward and Ricciardi 2014). Consistent temporal patterns in chironomid densities relative to *Dreissena* were not evident for any of the three substrate types in the inner bay. While densities in 2006-2009 were significantly lower ($P \leq 0.05$) than in 1987-1990 and 1994-1996 at sites with gravel/sand substrates, differences between periods were not significant for the other two substrate types ($P > 0.05$).

Temporal trends in non-dreissenid biomass (total biomass of all non-dreissenid taxa) in the inner bay were not apparent at sites with sand/gravel and silty sand substrates ([Table 8](#)). At these sites, biomass in 1987-1990, 1994-1996, and 2006-2009 was generally similar, and differences between these three periods were not significant ($P > 0.05$). In contrast, non-dreissenid biomass at sites with a silt substrate gradually declined over time. Biomass was about 2-fold lower in 2006-2009 compared to 1987-1990 ([Table 8](#)).

When mean densities between the three temporal periods at sites in the outer bay were compared, differences were apparent in some of the major non-dreissenid groups, and in some cases these differences were a function of depth. The most striking example was the depth-defined temporal pattern in oligochaete densities. Between 1987-1990 and 2006-2009, oligochaete densities declined 3.6-fold at 12 m, remained generally stable at 16 m, and increased 16.6-fold at 28 m (Table 7). The difference between time periods at 28 m was significant ($P \leq 0.05$). Reasons for the decline at the 12-m site are not clear, whereas the increase at 28-site was consistent with similar increases at sites in the 18-30 m interval in the main basin of Lake Huron in 2007 and 2012 as discussed below. Trends in amphipods in the outer bay were mostly defined by declines in *Diporeia*. At 28 m, mean densities of *Diporeia* were 819/m² in 1987-1990, 168/m² in 1994-1996, and 0/m² in 2006-2009. *Diporeia* accounted for 99.6% of all amphipods at this depth in 1987-1996. At 12 m and 16 m, mean densities of amphipods were < 20/m² in each of the three time periods and meaningful trends could not be discerned. In 1987-1996, the amphipod population at these two depths consisted of *Gammarus* (73%), *Diporeia* (22%), and *Hyaella* (5%); in 2006-2009, only *Gammarus* was collected. Sphaeriid densities declined at 12 m and 16 m ($P \leq 0.05$), but remained stable at 28 m ($P > 0.05$). On the other hand, chironomid densities declined at 28 m ($P \leq 0.05$), but did not change at 12 m and 16 m ($P > 0.05$).

In the outer bay, temporal trends in mean biomass of non-dreissenid taxa (i.e., total biomass of all non-dreissenid taxa) at 12 m and 16 m were not apparent ($P > 0.05$) (Table 8). However, at 28 m biomass in 2006-2009 was about 2.5 and 4.9 times greater than in 1987-1990 and in 1994-1996, respectively, and this difference was significant ($P \leq 0.05$). This increase in biomass occurred despite the loss of *Diporeia* and can be attributed to the great increase in density of oligochaetes at the 28-m site in 2006-2009 (Table 7).

8.0 TEMPORAL TRENDS IN LAKE HURON, GEORGIAN BAY AND NORTH CHANNEL

8.1 *Dreissena*

Between 2000 and 2012, densities of *D. r. bugensis* in the main basin increased in each of the four depth intervals (Table 9, Figure 10). When comparing more recent changes between 2007 and 2012, mean densities of *D. r. bugensis* in 2012 were 1.6, 0.7, 6.1, and 5.5 times those densities found in 2007 at the 18-30 m, 31-50 m, 51-90 m, and > 90 m intervals, respectively. Although greatest increases occurred at the two deepest intervals and an actual decline occurred at 31- 50 m, mean densities at 31-50 m were similar to or great than densities at the other intervals in both 2007 and 2012. Differences in mean densities between 2007 and 2012 were only significant at the > 90 m ($P \leq 0.05$). In contrast to *D. r. bugensis*, *D. polymorpha* was rarely found at any depth interval in 2007 and 2012 (Table 9, Figure 11). In 2012, this species was only collected at 2 of 83 stations in the main basin and accounted for only 3 of 17,960 dreissenids collected.

In Georgian Bay, densities of *D. r. bugensis* increased in each depth interval between 2002 and 2007, but in 2012 densities were lower than in 2007 at 18-30 m and 31-50 m, perhaps indicating the population may have peaked at these depths (Table 10). In contrast, at 51-90 m densities in 2012 were greater than in 2007, indicating the population continued to expand. As in the main basin, *D. polymorpha* was rarely collected in 2012, accounting for only 13 of 442 dreissenids collected. These 13 individuals were collected at just one station (GB9). *Dreissena* was not collected at any of the stations in North Channel in 2007 and 2012.

Biomass of *D. r. bugensis* in both the main basin and Georgian Bay was lowest at 18-30 m, increased to a maximum at 31-50 m, and then declined as depth increased (Table 11). Low biomass at 18-30 m could partly be explained by the dominance of small individuals in this depth interval compared to deeper intervals. For instance, in the main basin, the mean percentage of individuals < 5 mm in shell length was 94 % at 18-30 m compared to 54%, 49%, and 43% in the 31-50 m, 51-90 m, and > 90 m intervals, respectively.

8.2 Non-Dreissenid Taxa

Of the four major non-dreissenid taxa in the main basin of Lake Huron (*Diporeia*, Oligochaeta, Sphaeriidae, and Chironomidae), temporal trends in the amphipod *Diporeia* were the most consistent and pronounced (note: all amphipods in the main basin, Georgian Bay, and North Channel were *Diporeia*). Declines in *Diporeia* were first noted when densities in 2000 were compared to densities in 1972 (Nalepa et al. 2007a). Subsequently, in each of the survey years after 2000 (i.e., 2003, 2007, and 2012), mean densities of *Diporeia* progressively declined at each of the four depth intervals (Table 9, Figure 12). By 2012, *Diporeia* was not collected at any sites < 50 m and, while it was still present at sites in the 51-90 m and 90-m intervals, mean densities had declined by 96% and 85%, respectively, compared to 2000. The complete disappearance of *Diporeia* from the shallowest depth intervals in the main basin is consistent with similar findings in outer Saginaw Bay in 2006-2009 (see Table 7). The decline of *Diporeia* is temporally linked to the introduction and expansion of *Dreissena* in all the other Great Lakes except Lake Superior, however, the exact mechanism for the negative response remains unclear (Nalepa et al. 2006).

Temporal trends in the other major taxa (Oligochaeta, Sphaeriidae, and Chironomidae) in the main basin varied as a function of depth. For oligochaetes, mean densities increased 4.9-fold at 18-30 m and 2-fold at 31-50 m between 2000 and 2012, but similar increases were not evident at 51-90 m and > 90 m (Table 9). These increases at the two shallowest depth intervals, particularly apparent at the 18-30 m interval, may be a result of organic material being retained in this shallowest interval by dreissenids, a process termed the “nearshore shunt” (Heckey et al. 2004). In brief, primary producers (mainly phytoplankton) in shallow, nearshore regions are filtered by dreissenids and unassimilated organic material is subsequently deposited in the benthic zone in the form of feces and pseudofeces. These organic biodeposits serve as a food source for oligochaetes. In addition, dreissenid filtration of phytoplankton and other particulate material from the water column increases light penetration to the bottom, which, in turn, stimulates benthic macro-algae. Upon decay, this material also increases food availability for oligochaetes. While relative increases in oligochaete densities at sites in the 18-30 m depth interval were apparent throughout the main basin, most noteworthy were increases in the southeastern portion of the lake (Figure 13). Of the three stations in the 18-30 m interval in this portion of the lake that were sampled in 2003, 2007, and 2012 (TN1, TN7, TN10), mean oligochaete densities in each of these years were $5,154 \pm 539/\text{m}^2$, $21,143 \pm 7,088/\text{m}^2$, and $27,345 \pm 14,025/\text{m}^2$, respectively. Mean densities at all other sites in this interval were only $1,060 \pm 153/\text{m}^2$, $4,205 \pm 1,526/\text{m}^2$, and $4,536 \pm 1,100/\text{m}^2$ in the same three years. The southeastern portion of the lake has the highest sedimentation rates and likely the highest inputs of organic material (Thomas et al. 1973, Robbins 1980). The dominant current patterns undergo a major reversal in this portion of the lake (south to north) likely leading to high deposition (Beletsky et al. 1999).

Mean densities of sphaeriids tended to be lower at the 18-30 m, 31-50 m, and 51-90 m intervals after 2000, but a clear, distinct declining trend was not apparent between 2003 and 2012 (Table 9). Temporal trends in chironomids were not apparent at any of the depth intervals.

In Georgian Bay and North Channel, temporal trends in the major non-dreissenid taxa were generally similar to those in the main basin with some noted exceptions. Similar to the main basin, *Diporeia* densities declined in both Georgian Bay and North Channel, but the severity of the decline varied. In

Georgian Bay, the decline of *Diporeia* was consistent across all depth intervals and by 2012 was rarely found. Mean densities at the 18-30 m, 31-50 m, and 51-90 m intervals in Georgian Bay in 2002 ranged from 1,400 to 1,700/m², but in 2012 *Diporeia* densities were ranged from 0/m² to 3/m² (Table 10). In North Channel, declines in *Diporeia* were severe at 18-30 m and 51-90 m, with densities declining 83 % and 96 % respectively between 2002 and 2012, but a declining trend was not evident at 31-50 m. It is noteworthy that, overall, *Diporeia* declined in North Channel even though *Dreissena* was rare in 2002 and not collected in 2007 and 2012.

Oligochaete densities in Georgian Bay and North Channel remained relatively stable at sites in the 18-30 m interval between 2002 and 2012, which contrasts to great increases observed in this depth interval in the main basin. There were no significant differences in oligochaete densities in any of the depth intervals in both regions ($P > 0.05$). Also, distinct trends in sphaeriid and chironomid densities in Georgian Bay and North Channel were not apparent. Densities of the former taxa tended to be lower in more recent years, but distinct trends between 2002 and 2012 were not significant ($P > 0.05$).

In 2012, total mean biomass of non-dreissenid taxa in the main basin and North Channel was greatest at the 18-30 m interval, but in Georgian Bay greatest biomass occurred at 31-50 m (Table 11). Mean non-dreissenid biomass ranged from 0.18 g/m² to 1.52 g/m² across all depth intervals within regions.

9.0 SUMMARY

Benthic surveys were conducted in various regions of the Lake Huron system (Saginaw Bay, main basin, Georgian Bay, and North Channel) in 2006-2012 to assess temporal trends. Compared to earlier surveys in each of these regions, trends in the major macroinvertebrate taxa (*Dreissena*, *Diporeia*, Oligochaeta, Sphaeriidae, and Chironomidae) varied widely as a function of substrate and water depth. *Dreissena* densities declined by 80% in areas with hard substrates (cobble, gravel, coarse sand) in the inner portion of Saginaw Bay as compared to densities in the mid-1990s. In contrast, *Dreissena* densities in the main basin of Lake Huron continued to increase at all depths during the period between 2000 and 2012. Recent increases have been particularly apparent at depths >50 m. *Dreissena* densities remain low in areas with soft substrate (silt) in inner Saginaw Bay, and *Dreissena* was not found at any sampled sites in North Channel in 2007 or 2012. Over the entire lake Huron system, maximum biomass of *Dreissena* in 2012 occurred at the 31-50 m depth interval in the main basin. *D. r. bugensis* has replaced *D. polymorpha* as the dominant species in all regions of the lake, accounting for 80% of *Dreissena* in Saginaw Bay, and accounting for nearly all *Dreissena* in the main basin and Georgian Bay.

The amphipod *Diporeia* progressively declined at all depths throughout the Lake Huron system. It was not found in Saginaw Bay in 2006-2009 and in 2012 was rarely collected at depths < 50 m in the main basin and Georgian Bay, and at depths > 50 m in North Channel. Although still present at depths > 50 m in the main basin, densities declined by > 80% between 2000 and 2012.

Densities of oligochaetes fluctuated widely in depositional areas with soft substrates in inner Saginaw Bay, and this variation appeared negatively associated with densities of *Dreissena* in non-depositional areas with hard substrates in the inner bay. The hypothesis to explain this negative association posits that *Dreissena* in hard-substrate regions reduce deposition of organic material in deeper-soft substrate regions, thereby diminishing food for oligochaetes. Oligochaete densities increased in the main basin at depths < 50 m, and this increase was particularly apparent at the 18-30 m depth interval; densities in this interval increased 5-fold between 2000 and 2012. This increase was likely a result of increased deposition of organic material in the form of *Dreissena* biodeposits which served as a food source for oligochaetes. Maximum oligochaete densities in the Lake Huron system occurred at the 18-30 m interval in the southeastern portion of the lake where deposition rates of organic material are the highest. Over the Lake

Huron system, oligochaetes accounted for most non-dreissenid biomass. Densities of Sphaeriidae and Chironomidae varied widely from year-to-year, and clear temporal, long term trends were not evident in any of the lake regions.

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12.0 APPENDICES – EXCEL DATA FILES

Appendix 1. Density and Biomass in Saginaw Bay, 2006-2009

https://www.glerl.noaa.gov/pubs/tech_reports/glerl-172/tm-172-Appendix1-SaginawBay-Abundance_and_Biomass_2006-2009.xlsx

Appendix 2. Density and Biomass of Dreissena in Saginaw Bay 2008-2010

https://www.glerl.noaa.gov/pubs/tech_reports/glerl-172/tm-172-Appendix2-SaginawBay-Dreissena_Density_and_Biomass_2008-2010.xlsx

Appendix 3. Density in Lake Huron, 2007 and 2012

https://www.glerl.noaa.gov/pubs/tech_reports/glerl-172/tm-172-Appendix3-LakeHuron-Abundance_2007_2012.xlsx

Appendix 4. Biomass in Lake Huron, 2012.

https://www.glerl.noaa.gov/pubs/tech_reports/glerl-172/tm-172-Appendix4-LakeHuron-Biomass_2012.xlsx

Table 1. Location (latitude, longitude), water depth, and dominant substrate type at each of the stations sampled for benthic macroinvertebrates with a Ponar grab and with SCUBA divers in Saginaw Bay, Lake Huron in 2006-2010. Also given are the year and season of collection. For samples collected with a Ponar, the season of collection is given as: Sp = spring, S = summer, F = fall. Stations sampled for *Dreissena* by divers are designated with a "D"; all diver samples were collected in fall.

Station	Depth (m)	Latitude	Longitude	Substrate	Sampling Year				
					2006	2007	2008	2009	2010
4	6.7	43 44.65	-83 52.07	silt	F	Sp, S, F	Sp, S, F	F	
5	3.0	43 53.72	-83 51.63	cobble, sand			D	D	D
6	4.0	43 53.08	-83 49.25	cobble, sand			D	D	D
7	7.0	43 50.28	-83 47.57	silt	F	Sp, S, F	Sp, S, F	F	
10	11.0	43 56.50	-83 37.43	silt	F	Sp, S, F	Sp, S, F	F	
11	9.0	44 01.23	-83 34.42	silty sand	F	Sp, S, F	Sp, S, F	F	
13	3.0	43 57.57	-83 29.32	sand, gravel	F	Sp, S, F	Sp, S, F, D	F, D	D
14	3.6	43 44.30	-83 38.45	sand, gravel	F	Sp, S, F	Sp, S, F, D	F, D	D
15	5.0	43 45.67	-83 31.58	cobble, gravel			D	D	D
16	3.0	43 50.82	-83 33.75	sand, gravel	F	Sp, S, F	Sp, S, F, D	F,D	D
20	16.0	44 07.57	-83 30.00	silty sand		Sp, S, F	Sp, S, F		
23	28.0	44 13.25	-83 15.75	sand, some silt		Sp, S, F	Sp, S, F		
24	12.5	44 00.08	-83 17.00	silty sand	F	Sp, S, F	Sp, S, F		
27	5.5	44 02.33	-83 06.66	cobble, rocks			D	D	

Table 2. Stations sampled in the main basin of Lake Huron in 2000, 2003, 2007, and 2012. Also given are the location and dominant substrate of each station. Given in parenthesis is the water depth each time the station was sampled. Blank space means not sampled.

Station	Substrate	Latitude	Longitude	Sampling Year			
				2000	2003	2007	2012
AL20	sand	44 57.140	-83 16.250		X (20)		
AL30	silty sand	44 56.070	-83 14.810		X (30)		
AL45	silty sand	44 55.080	-83 11.460		X (45)		
AL60	sandy silt	44 51.740	-83 06.780		X (60)		
AL80	silt	44 49.120	-83 01.910		X (80)		
AP1	sand	45 25.000	-83 42.730		X (23)		
FI2	sand, some clay	45 29.987	-81 56.495	X (30)	X (30)	X (33)	X (33)
FI3	silty clay	45 29.975	-82 02.776	X (46)	X (46)	X (45)	X (44)
FI4	silty clay	45 29.999	-82 16.687	X (61)	X (61)	X (69)	X (61)
FI5	silt	45 30.008	-82 20.383	X (82)	X (90)	X (86)	X (85)
GLERL18	sand	44 57.315	-83 16.620				X (18)
GLERL30	silty sand	44 56.324	-83 14.430				X (30)
GLERL45	silty sand	44 53.947	-83 08.978				X (46)
HB1	sand	45 36.830	-84 10.190		X (20)	X (12)	X (12)
HB3	silty clay	45 38.156	-84 07.764		X (45)	X (44)	X (42)
HB4	silt	45 39.600	-84 05.300		X (58)	X (55)	X (54)
HB5	silty loam	45 43.373	-83 58.820		X (80)	X (74)	X (73)
HU6	silt	43 27.970	-82 00.020	X (51)	X (52)	X (51)	X (49)
HU9	silt	43 38.020	-82 13.008	X (59)	X (60)	X (59)	X (57)
HU12	silt	43 53.393	-82 03.371	X (90)	X (90)	X (88)	X (87)
HU15	silt	43 59.991	-82 21.023	X (66)	X (69)	X (65)	X (65)
HU27	silty sand	44 11.919	-82 30.169	X (57)	X (61)	X (55)	X (53)
HU32	silt	44 27.205	-82 20.471	X (80)	X (82)	X (84)	X (78)
HU37	sandy silt	44 45.658	-82 46.974	X (72)	X (72)	X (74)	X (72)
HU38	silty clay/loam	44 44.393	-82 03.583	X (133)	X (132)	X (138)	X (135)
HU45	clay, some sand	45 08.203	82 59.059	X (91)	X (99)	X (100)	X (94)
HU48	silty clay	45 16.673	-82 27.188	X (112)	X (113)	X (112)	X (107)
HU53	silty clay	45 27.010	-82 54.885	X (91)	X (93)	X (92)	X (88)
HU54	silty clay/loam	45 30.990	-83 24.952	X (139)	X (125)	X (127)	X (140)
HU61	silty loam	45 44.989	-83 54.980	X (116)	X (120)	X (116)	X (115)
HU93	silt	44 05.988	-82 07.055	X (87)	X (90)	X (89)	X (88)
HU95	sandy silt	44 19.994	-82 49.954	X (66)	X (69)	X (67)	X (65)
HU97	silty sand	44 54.953	-83 09.973	X (45)	X (45)	X (44)	X (42)
HU325	sandy clay	45 48.996	-84 23.258	X (58)	X (60)	X (57)	X (55)
HU329	silty sand	45 54.760	-84 18.126	X (37)	X (38)	X (37)	X (37)
HU429P	silty sand	45 49.311	-84 26.219	X (19)			

Station	Substrate	Latitude	Longitude	Sampling Year			
				2000	2003	2007	2012
HU429	silty sand	45 49.447	-84 26.208	X (33)	X (33)	X (43)	X (41)
KB472	silty clay	45 13.503	-81 49.555			X (44)	X (44)
KB479	silty sand	45 41.070	-82 33.020			X (34)	X (34)
KB480	silty sand	45 44.420	-82 49.190			X (31)	X (32)
KB482	sand, some clay	45 48.290	-83 09.560			X (48)	X (42)
MZ12	silty sand	43 16.181	-82 25.705	X (21)	X (21)	X (21)	X (20)
MZ13	silty sand	43 16.170	-82 20.439	X (31)	X (31)	X (29)	X (28)
MZ14	silty sand	43 16.188	-82 12.044	X (29)	X (28)	X (28)	X (27)
MZ22	silty sand	43 30.303	-82 30.155	X (19)	X (20)	X (21)	X (21)
MZ23	silty sand	43 30.419	-82 27.265	X (33)	X (33)	X (33)	X (34)
MZ24	silty clay	43 30.601	-82 23.268	X (43)	X (44)	X (42)	X (43)
MZ25	silty clay	43 31.180	-82 12.250	X (52)	X (53)	X (51)	X (51)
MZ34	silty sand	43 52.617	-82 31.737	X (45)	X (48)	X (45)	X (45)
MZ43	coarse sand	44 04.009	-82 44.775	X (30)	X (30)	X (30)	X (30)
MZ44	silty sand	44 05.705	-82 43.063	X (39)	X (40)	X (39)	X (39)
MZ45	silty sand	44 14.505	-82 32.993	X (58)	X (60)	X (58)	X (56)
MZ72	sand	44 24.279	-83 12.484	X (24)	X (24)	X (24)	X (23)
MZ73	sand	44 25.397	-83 10.515	X (32)	X (32)	X (31)	X (30)
MZ74	sand	44 26.304	-83 08.802	X (42)	X (42)	X (40)	X (40)
MZ75	silty sand	44 30.924	-83 00.174	X (67)	X (67)	X (65)	X (63)
MZ76	silty loam	44 43.487	-82 35.500	X (79)	X (80)	X (71)	X (76)
MZ87	loam	45 05.854	-83 03.497	X (55)	X (58)	X (55)	X (50)
MZ88	sandy silt	45 05.341	-83 04.643	X (47)	X (46)	X (49)	X (47)
MZ89	silty sand	45 04.771	-83 05.781	X (32)	X (32)	X (33)	X (32)
MZ93	silty sand	45 26.469	-83 44.591	X (32)	X (32)	X (32)	X (31)
MZ94	silty sand	45 26.304	-83 44.304	X (40)	X (38)	X (32)	X (38)
MZ95	silt	45 28.688	-83 42 208	X (64)	X (61)	X (61)	X (62)
MZ96	silt	45 40.641	-83 28.575	X (129)	X (139)	X (125)	X (122)
MZ123	silty sand	45 53.661	-84 09.611	X (54)	X (55)	X (45)	X (45)
MZ125	Silt	45 50.712	-84 11.575	X (81)	X (81)	X (80)	X (78)
PT2	sand	45 00.049	-81 32.991	X (30)			
PT3	silty clay	45 00.057	-81 35.192	X (45)	X (45)	X (46)	X (43)
PT5	silty clay	44 59.998	-81 40.479	X (80)	X (80)	X (77)	X (77)
PT6	silt	45 00.023	-81 42.495	X (136)	X (135)	X (137)	X (133)
SB23	silty sand	44 13.306	-83 15.761	X (28)	X (28)		
SO2	sand	44 34.992	-81 23.478	X (31)	X (31)	X (31)	X (30)
SO3	silty sand	44 35.036	-81 29.993	X (40)	X (48)	X (47)	X (45)
SO4	sandy silt	44 35.002	-81 31.978	X (67)	X (68)	X (67)	X (65)
SO5	silt	44 35.007	-81 34.983	X (81)	X (80)	X (78)	X (78)

Station	Substrate	Latitude	Longitude	Sampling Year			
				2000	2003	2007	2012
SR3	silt	45 19.203	-83 25.323		X (32)	X (35)	X (30)
SR4	sandy clay	45 19.203	-83 22.707		X (45)	X (45)	X (43)
SR5	sandy clay	45 19.203	-83 20.165	X (55)	X (56)	X (55)	X (58)
SR6	sandy clay	45 19.203	-83 14.503		X (77)	X (75)	X (72)
SR10	sandy silt	44 49.482	-83 06.555	X (56)	X (57)	X (56)	X (54)
TA20	sand	44 09.154	-83 20.739		X (20)		
TA45	sandy silt	44 18.107	-83 11.055		X (45)		
TN1	silt	43 16.343	-82 00.361	X (21)	X (21)	X (20)	X (21)
TN2	silt	43 41.800	-82 25.000	X (51)	X (51)	X (51)	X (51)
TN3	silt, clay/sand	43 41.782	-81 55.995	X (66)	X (65)	X (64)	X (61)
TN4	coarse sand	44 13.344	-81 50.480	X (48)	X (45)	X (47)	X (49)
TN5	silty clay	45 12.447	-82 42.492	X (170)	X (173)	X (171)	X (164)
TN6	silt	43 30.002	-81 53.489		X (31)	X (29)	X (28)
TN7	silt	43 30.037	-81 50.558		X (21)	X (21)	X (20)
TN8	sandy silt	43 41.800	-81 53.734		X (44)	X (44)	X (43)
TN9	silt	43 41.800	-81 52.421		X (32)	X (31)	X (30)
TN10	silt	43 41.800	-81 50.366		X (22)	X (22)	X (21)
TN11	coarse sand	44 13.406	-81 39.987		X (30)	X (29)	X (28)
TN12	sand	44 13.458	-81 39.121		X (20)	X (18)	X (18)

Table 3. Stations sampled in Georgian Bay and North Channel in 2002, 2007, and 2012.. Also given are the location, water depth, and dominant substrate of each station. Blank space means not sampled.

Station	Substrate	Depth (m)	Latitude	Longitude	Sampling Year		
					2002	2007	2012
<i>Georg.Bay</i>							
GB1	silt	89.0	44 43.05	-80 51.40	X (89)	X (88)	X (89)
GB3	silty coarse sand	32.0	44 43.50	-80 37.00	X (32)	X (31)	X (35)
GB4	sandy silt	57.0	44 38.75	-80 10.00	X (57)	X (57)	X (57)
GB5	sandy clay	57.6	44 47.80	-80 14.60	X (58)	X (58)	X (58)
GB6	sandy silt	86.0	44 44.20	-80 26.10	X (86)	X (87)	X (87)
GB8	silty clay	51.0	44 57.16	-80 08.93	X 51)	X (51)	X (51)
GB9	sandy clay	32.0	44 52.30	-79 58.08	X 32)	X (27)	(31)
GB11	sandy clay	61.0	44 55.25	-80 36.35	X (61)	X (62)	
GB12	silty clay	87.0	44 55.20	-80 52.50	X (87)	X (87)	X (87)
GB17	silt/clay/loam	77.5	45 14.70	-80 52.50	X (78)	X (78)	X (76)
GB24	silty sand, clay	39.0	45 44.73	-80 50.33	X 39)	X (40)	X (31)
GB26	sand, some clay	26.0	45 50.00	-80 54.00	X (26)	X (21)	
GB29	silty clay loam	42.0	45 35.00	-81 05.00	X (42)	X (43)	X (42)
GB35	silty sand,some clay	33.4	45 31.65	-81 40.17	X (33)	X (36)	X (37)
GB36	loam, coarse sand	52.0	45 42.50	-81 37.20	X (52)	X (53)	X (56)
GB39	silty sand	28.0	45 52.40	-81 15.50	X (28)	X (28)	X (28)
GB42	silty clay	26.0	45 54.77	-81 35.70	X (26)	X (26)	X (26)
<i>N. Channel</i>							
NC68	sandy silt	16.7	46 02.50	-83 51.20	X (17)	X (17)	X (16)
NC70	silt	21.5	46 08.20	-83 40.30	X (22)	X (22)	X (22)
NC71	silt	35.0	46 14.00	-83 44.80	X 35)	X (35)	X (35)
NC73	course sand	18.7	46 11.20	-83 21.30	X (19)	X (17)	X (20)
NC76	silt	58.0	46 00.00	-83 26.00	X 58)	X (58)	X (57)
NC77	silt	77.8	45 58.20	-83 11.90	X (78)	X (78)	X (76)
NC79	silt	25.4	46 07.40	-82 53.15	X 25)	X (25)	X (27)
NC82	silt	27.2	45 56.20	-82 45.50	X (27)	X (29)	X (28)
NC83	silt	30.4	46 00.00	-82 33.00	X (31)	X (30)	X (32)
NC84	silty clay	35.3	46 05.50	-82 33.40	X (35)	X (36)	X (36)
NC87	silty clay	32.0	46 03.67	-82 11.83	X 32)	X (37)	X (44)
NC88	silt	33.9	46 03.33	-82 00.00	X (34)	X (34)	X (36)
NC89	silt	38.8	45 55.00	-82 09.67	X 39)	X (38)	X (38)

Table 4. Relationships between shell length (SL, mm) and tissue ash-free dry weight (AFDW, mg) for *Dreissena polymorpha* and *Dreissena rostriformis bugensis* at sites in Lake Huron and Saginaw Bay. The AFDW/SL relationship is defined as $\log_e \text{AFDW} = b + a \cdot \log_e \text{SL}$. Also given are the number of individuals used to define the relationship (n) and their median shell length (range in parentheses). Included is the AFDW of a standard 15-mm individual as derived from the determined relationship. #Weights in 2009 were not measured directly; regression values were derived by combining data collected in 2008 and 2010.

Region (year)	a	b	n	R²	Median SL	15 mm
<i>Lake Huron (2012)</i>						
<50 m	2.589	-5.060	140	0.759	19.4 (9.6-36.3)	7.0
>50 m	2.899	-5.915	87	0.916	19.1 (9.8-26.9)	6.9
<i>Saginaw Bay</i>						
<i>D. polymorpha</i> (2008)	2.027	-3.948	25	0.795	15.0 (10.0-22.0)	4.7
<i>D. r. bugensis</i> (2008)	2.775	-5.836	27	0.903	16.0 (11.0-22.0)	5.4
<i>D. r. bugensis</i> (2009) [#]	2.316	-4.697	76	0.793	---	4.8
<i>D. r. bugensis</i> (2010)	2.094	-4.144	49	0.774	16.9 (9.9-23.6)	4.6

Table 5. List of taxa collected in Saginaw Bay, 2006-2009, and in Lake Huron, 2012. The four-letter code identifies taxa in Excel files given in the appendices.

Taxa	Code	Taxa	Code
Amphipoda	AMPH	Oligochaeta (continued)	
Pontoporeiidae		Naidinae	
<i>Diporeia spp.</i>	DIPO	<i>Arcteonais lomondi</i>	ALOM
Gammaridae		<i>Chaetogaster sp.</i>	CHAE
<i>Gammarus sp.</i>	GAMM	<i>Dero sp.</i>	DERO
Hyalellidae		<i>Dero nivea</i>	DNIV
<i>Hyalella sp.</i>	HYAL	<i>Nais sp.</i>	NAIS
Isopoda	ISOP	<i>Nais bretscheri</i>	NBRE
Hirudinea	HIRU	<i>Nais communis</i>	NCOM
Glossiphoniidae		<i>Nais eliguis</i>	NELI
<i>Helobdella stagnalis</i>	HSTA	<i>Nais pardalis</i>	NPAR
Piscicolidae		<i>Nais pseudobtusa</i>	NPSE
<i>Piscicola sp.</i>	PISC	<i>Nais simplex</i>	NSIM
unidentified Hirudinea	HIRU	<i>Nais variabilis</i>	NVAR
Oligochaeta	OLIG	<i>Opistonais serpentina</i>	OSER
Enchytraeidae	ENCH	<i>Piguetiella blanchi</i>	PBLA
Lumbriculidae		<i>Piguetiella michiganensis</i>	PMIC
<i>Stylodrilus heringianus</i>	SHER	<i>Pristina sp.</i>	PRIS
Naididae		<i>Slavina appendicula</i>	SAPP
Tubificinae		<i>Specaria josinae</i>	SJOS
<i>Aulodrilus americanus</i>	AMME	<i>Stylaria fossularis</i>	SFOS
<i>Aulodrilus limnobius</i>	ALIM	<i>Stylaria lacustris</i>	SLAC
<i>Aulodrilus pigueti</i>	APIG	<i>Uncinaiis uncinata</i>	UUNI
<i>Aulodrilus plurisetia</i>	APLU	<i>Vejdovskyella intermedia</i>	VINT
<i>Branchiura sowerbyi</i>	BSOW	Diptera	
<i>Ilyodrilus templetoni</i>	ITEM	Chironomidae	TCHI
<i>Isochaetides freyi</i>	IFRE	Chironomini	
<i>Limnodrilus cervix</i>	LCER	<i>Chironomus spp.</i>	CHIR
<i>Limnodrilus claparedianus</i>	LCLA	<i>Cladopelma sp.</i>	CLAD
<i>Limnodrilus hoffmeisteri</i>	LHOF	<i>Cryptochironomus sp.</i>	CRYP
<i>Limnodrilus profundicola</i>	LPRO	<i>Demicryptochironomus sp.</i>	DEMI
<i>Limnodrilus maumeensis</i>	LMAU	<i>Dicrotendipes sp.</i>	DICR
<i>Limnodrilus spiralis</i>	LSPI	<i>Dicrotendipes neomodestus</i>	DNEO
<i>Limnodrilus udekemianus</i>	LUDE	<i>Harnischia sp.</i>	HARN
<i>Potamothrix bavaricus</i>	PBAV	<i>Hydrobaenus sp.</i>	HYDR
<i>Potamothrix moldaviensis</i>	PMOL	<i>Microtendipes sp.</i>	MPED
<i>Potamothrix vejdoivskyii</i>	PVEJ	<i>Paracladopelma nereis</i>	PNER
<i>Rhyacodrilus coccineus</i>	RCOC	<i>Paracladopelma undine</i>	PUDI

Taxa	Code	Taxa	Code
<i>Spirosperma ferox</i>	SFER	<i>Paracladopelma winnelli</i>	PWIN
<i>Spirosperma nikolskyi</i>	SNIK	<i>Paralauterborniella nigrohalteralis</i>	PNIG
<i>Tasserkidrilus superiorenensis</i>	TSUP	<i>Paratendipes albimanus</i>	PALB
<i>Tubifex tubifex</i>	TTUB	<i>Polypedilum sp.</i>	POLY
<i>Varichaetadrilus angustipenis</i>	VANG	<i>Polypedilum halterale</i> grp.	PHAL
Immatures		<i>Polypedilum scalaenum</i>	PSCA
without hair setae	IMWO	<i>Polypedilum tuberculum</i>	PTUB
with hair setae	IMWH	<i>Pseudochironomus sp.</i>	PSEU
Diptera (continued)		Pelecypoda	
<i>Sticochironomus sp.</i>	STIC	Sphaeriidae	SPHA
<i>Tribelos sp.</i>	TRIB	Dreissenidae	
Tanytarsinii		<i>Dreissena polymorpha</i>	DPOL
<i>Cladotanytarsus sp.</i>	CTAN	<i>Dreissena rostriformis bugensis</i>	DBUG
<i>Micropsectra sp.</i>	MICR	Gastropoda	GAST
<i>Paratanytarsus sp.</i>	PARA	Hydrobiidae	
<i>Tanytarsus sp.</i>	TANY	<i>Amnicola limnosa</i>	ALMO
Orthoclaadiinae		<i>Bythinia tentaculata</i>	BTEN
<i>Heterotrissocladius changi</i>	HCHA	Valvatidae	
<i>Heterotrissocladius oliveri</i>	HOLI	<i>Valvata sincera</i>	VSIN
<i>Othocladius sp.</i>	ORTH	Ephemeroptera	EPHE
<i>Psectrocladius simulans</i>	PSMI	Ephemeridae	
<i>Parakiefferiella sp.</i>	PKIE	<i>Hexagenia sp.</i>	HEXA
Tanypodinae	TAYP	Tricoptera	
<i>Ablabesmyia spp.</i>	ABLA	Leptoceridae	
<i>Coelotanypus sp.</i>	COEL	<i>Ocetis sp.</i>	OECE
<i>Procladius sp.</i>	PROC	Zygoptera	ZYGO
<i>Thienemannimyia grp.</i>	THIE	Other (biomass only)	OTHE
Diamesinae			
<i>Monodiamesia sp.</i>	MONO		
<i>Monodiamesia tuberculata</i>	MTUB		
<i>Potthastia longimanus</i>	PLOG		
<i>Protanypus sp.</i>	PROT		
Unidentified Chironomidae	UNDE		

Table 6. Mean (\pm SE) density (no./m²) and biomass (gAFDW/m²) of *Dreissena* at sites with different substrates in inner and outer Saginaw Bay in 1991-1996 and in 2008-2010. Samples collected by SCUBA divers in the fall of each year. Inner bay- cobble = Stations 5, 6 and 15; Inner bay-sand/gravel = Stations 13, 14, and 16; Outer bay-cobble = Station 27. Station 13 was not sampled in 1991, Station 16 was not sampled in 2008 and 2009, and Station 27 was not sampled in 2010.

Year	Inner Bay-Cobble		Inner Bay-Sand/Gravel		Outer Bay- Cobble	
	Density	Biomass	Density	Biomass	Density	Biomass
1991	25,271 \pm 11,260	16.34 \pm 9.07	18 \pm 91	0.05 \pm 0.04	3,408	0.73
1992	28,157 \pm 23, 576	41.45 \pm 32.71	35,519 \pm 16,040	82.29 \pm 34.50	4,695	19.49
1993	3,712 \pm 2,052	3.43 \pm 1.89	4,238 \pm 2,080	5.56 \pm 3.18	5,813	15.29
1994	7,803 \pm 2,439	11.59 \pm 3.12	2,160 \pm 905	5.07 \pm 1.92	9,925	32.55
1995	3,345 \pm 1,731	5.90 \pm 2.12	945 \pm 811	2.28 \pm 1.89	3,824	27.10
1996	6,909 \pm 5,415	13.59 \pm 10.27	4,186 \pm 2,067	13.59 \pm 6.79	6,981	57.54
2008	695 \pm 205	2.27 \pm 0.45	239 \pm 116	1.22 \pm 0.30	356	2.11
2009	516 \pm 130	2.17 \pm 0.64	494 \pm 2	0.47 \pm 0.23	366	1.97
2010	2,289 \pm 1,929	1.79 \pm 0.60	1,514 \pm 998	1.26 \pm 0.44		

Table 7. Mean (\pm SE) density (no./m²) of major taxonomic groups at sites with different substrates and depths in inner and outer Saginaw Bay during three periods: 1987-1990, 1994-1996, and 2006-2009. All samples collected with a Ponar grab. Sources of variation are yearly (multiple stations) or seasonal means (single station). Differences between periods were tested with ANOVA (p-value given). If the P-value was ≤ 0.05 , Fisher's LSD was used for pairwise comparisons. Results of such comparisons are provided by subscripts; values with the same subscript were not significantly different ($P > 0.05$). 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.

Region/Taxa	Period			P-Value
	1987-1990	1994-1996	2006-2009	
<i>Inner Bay-Sand/Gravel</i>				
Amphipoda	66 \pm 17 ^a	296 \pm 86 ^b	126 \pm 42 ^{ab}	0.04
Oligochaeta	653 \pm 113	716 \pm 89	679 \pm 127	0.73
Chironomidae	106 \pm 24 ^a	148 \pm 73 ^a	38 \pm 10 ^b	0.02
Sphaeriidae	27 \pm 9 ^a	7 \pm 3 ^b	1 \pm < 1 ^c	<0.01
<i>Dreissena</i>	0 \pm 0 ^a	2,247 \pm 1,038 ^b	480 \pm 185 ^b	<0.01
<i>Inner Bay-Silty Sand</i>				
Amphipoda	6 \pm 4	51 \pm 4	26 \pm 18	0.21
Oligochaeta	6,799 \pm 2,379	3,268 \pm 710	5,281 \pm 1,107	0.36
Chironomidae	6,942 \pm 4,256	2,145 \pm 576	2,072 \pm 963	0.33
Sphaeriidae	535 \pm 66 ^a	116 \pm 55 ^{ab}	37 \pm 13 ^b	0.04
<i>Dreissena</i>	0 \pm 0	54 \pm 31	630 \pm 528	0.07
<i>Inner Bay-Silt</i>				
Amphipoda	1 \pm <1 ^a	12 \pm 2 ^b	10 \pm 6 ^b	<0.01
Oligochaeta	19,423 \pm 1,466 ^a	2,727 \pm 775 ^b	6,055 \pm 966 ^c	< 0.01
Chironomidae	1,507 \pm 170	1,901 \pm 487	1,654 \pm 312	0.96
Sphaeriidae	93 \pm 22	151 \pm 57	284 \pm 69	0.09
<i>Dreissena</i>	0 \pm 0 ^a	10 \pm 6 ^{ab}	46 \pm 25 ^b	0.03
<i>Outer Bay-12 m</i>				
Amphipoda	9 \pm 2	19 \pm 13	2 \pm 2	0.27
Oligochaeta	3,089 \pm 1,305	2,246 \pm 1,077	823 \pm 225	0.18
Chironomidae	965 \pm 299	1,645 \pm 1,094	344 \pm 174	0.23
Sphaeriidae	42 \pm 17 ^a	6 \pm 5 ^b	2 \pm 2 ^b	0.03
<i>Dreissena</i>	0 \pm 0	3 \pm 1	2 \pm 2	0.32
<i>Outer Bay-16 m</i>				
Amphipoda	3 \pm 2 ^{ab}	10 \pm 2 ^a	0 \pm 0 ^b	0.03
Oligochaeta	1,894 \pm 548	2,582 \pm 814	1,241 \pm 213	0.48
Chironomidae	1,382 \pm 116	1,797 \pm 661	637 \pm 451	0.32
Sphaeriidae	373 \pm 162 ^a	86 \pm 13 ^a	1 \pm 1 ^b	<0.01
<i>Dreissena</i>	0 \pm 0	3 \pm 2	77 \pm 73	0.07
<i>Outer Bay-28 m</i>				
Amphipoda	819 \pm 189 ^a	168 \pm 102 ^b	0 \pm 0 ^c	<0.01
Oligochaeta	387 \pm 88 ^a	727 \pm 155 ^a	6,421 \pm 143 ^b	< 0.01

Region/Taxa	Period			P-Value
	1987-1990	1994-1996	2006-2009	
Chironomidae	218 ± 49 ^{ab}	515 ± 144 ^a	62 ± 43 ^b	0.04
Sphaeriidae	228 ± 68	202 ± 70	216 ± 43	0.93
<i>Dreissena</i>	0 ± 0 ^a	7 ± 7 ^a	163 ± 4 ^b	<0.01

Table 8. Mean (\pm SE) biomass (gAFDW/m²) of *Dreissena* and non-dreissenid taxa at sites in inner and outer Saginaw Bay with different substrate types and depths. Relevance of the three periods is given in the text. Samples collected with a Ponar grab. Differences between periods were tested with ANOVA (P-value given). If the P-value was ≤ 0.05 , Fisher's LSD was used for pairwise comparisons. Results of such comparisons are provided by subscripts; values with the same subscript were not significantly different ($P > 0.05$). 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.

Region/Taxa	Period			P-Value
	1987-1990	1994-1996	2006-2009	
<i>Inner Bay-Sand/Gravel</i>				
<i>Dreissena</i>			1.87 \pm 0.67	
Non- <i>Dreissena</i>	0.10 \pm 0.01	0.47 \pm 0.24	0.21 \pm 0.05	0.13
<i>Inner Bay-Silty Sand</i>				
<i>Dreissena</i>			2.40 \pm 1.88	
Non- <i>Dreissena</i>	2.15 \pm 0.43	1.60 \pm 0.63	1.35 \pm 0.32	0.47
<i>Inn Bay-Silt</i>				
<i>Dreissena</i>			0.01 \pm <0.01	
Non- <i>Dreissena</i>	5.50 \pm 0.79 ^a	2.97 \pm 0.72 ^b	2.58 \pm 0.31 ^b	<0.01
<i>Outer Bay-12 m</i>				
<i>Dreissena</i>			<0.01 \pm <0.01	
Non- <i>Dreissena</i>	0.50 \pm 0.18	0.55 \pm 0.34	0.24 \pm 0.06	0.60
<i>Outer Bay-16 m</i>				
<i>Dreissena</i>			0.01 \pm 0.01	
Non- <i>Dreissena</i>	0.48 \pm 0.03	0.74 \pm 0.24	0.36 \pm 0.10	0.39
<i>Outer Bay-28 m</i>				
<i>Dreissena</i>			0.05 \pm 0.01	
Non- <i>Dreissena</i>	0.38 \pm 0.06 ^{ab}	0.19 \pm 0.03 ^a	0.92 \pm 0.42 ^b	0.05

Table 9. Mean (\pm SE) density (no./m²) of major taxa at sites in the 18-30 m, 31-50 m, 51-90 m, and > 90 m intervals in the main basin of Lake Huron in 2000, 2003, 2007, and 2012. See Table 2 for the number of sites per year per interval. Differences between years were tested with ANOVA (P-value given). If the P-value was ≤ 0.05 , Fisher's LSD was used for pairwise comparisons. Results of such comparisons are provided by subscripts; values with the same subscript were not significantly different ($P > 0.05$).

Interval/ Year	Taxa					
	<i>Diporeia</i>	<i>Oligochaeta</i>	<i>Sphaeriidae</i>	<i>Chironomidae</i>	<i>D. polymor</i>	<i>D. r. bugensis</i>
<u>18-30 m</u>						
2000	244 \pm 237 ^a	1,648 \pm 410 ^a	457 \pm 196	883 \pm 451	386 \pm 342	3 \pm 2 ^a
2003	97 \pm 92 ^{ab}	1,783 \pm 417 ^a	47 \pm 21	238 \pm 55	297 \pm 209	297 \pm 180 ^a
2007	1 \pm 1 ^b	8,114 \pm 2,742 ^b	183 \pm 64	754 \pm 210	0 \pm 0	850 \pm 283 ^b
2012	0 \pm 0 ^b	8,138 \pm 2,854 ^b	66 \pm 25	228 \pm 57	19 \pm 19	1,332 \pm 780 ^b
P-value	<0.01	0.01	0.30	0.28	0.08	<0.01
<u>31-50 m</u>						
2000	876 \pm 287	1,196 \pm 314 ^a	237 \pm 37 ^a	379 \pm 140 ^a	6 \pm 2 ^a	2 \pm 1 ^a
2003	248 \pm 103 ^a	1,460 \pm 368 ^a	67 \pm 13 ^b	62 \pm 14 ^b	7 \pm 4 ^{ab}	1,469 \pm 757 ^b
2007	17 \pm 10 ^b	3,076 \pm 824 ^b	113 \pm 25 ^b	256 \pm 52 ^a	1 \pm 1 ^{bc}	2,217 \pm 664 ^b
2012	0 \pm 0 ^b	2,403 \pm 412 ^b	137 \pm 31 ^b	472 \pm 164 ^a	0 \pm 0 ^c	1,619 \pm 513 ^b
P-value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
<u>51-90 m</u>						
2000	1,908 \pm 183 ^a	805 \pm 89 ^a	335 \pm 44 ^a	71 \pm 11 ^a	0 \pm 0	0 \pm 0 ^a
2003	914 \pm 133 ^b	383 \pm 42 ^b	109 \pm 17 ^{bc}	28 \pm 5 ^b	18 \pm 18	72 \pm 45 ^{ab}
2007	170 \pm 57 ^c	489 \pm 60 ^{bc}	128 \pm 14 ^b	27 \pm 6 ^b	0 \pm 0	276 \pm 172 ^b
2012	67 \pm 30 ^c	693 \pm 88 ^{ac}	93 \pm 16 ^{bc}	49 \pm 13 ^b	0 \pm 0	1,690 \pm 678 ^c
P-value	<0.01	<0.01	<0.01	<0.01	0.24	<0.01
<u>> 90 m</u>						
2000	1,707 \pm 232 ^a	627 \pm 69	94 \pm 32	58 \pm 12	0 \pm 0	0 \pm 0
2003	924 \pm 83 ^{ab}	404 \pm 76	71 \pm 38	17 \pm 4	0 \pm 0	2 \pm 1
2007	427 \pm 82 ^{bc}	559 \pm 138	109 \pm 50	21 \pm 5	0 \pm 0	135 \pm 135
2012	252 \pm 69 ^c	489 \pm 154	92 \pm 25	49 \pm 15	0 \pm 0	748 \pm 612
P-value	0.05	0.30	0.24	0.15	-	0.22

Table 10. Mean (\pm SE) density (no./m²) of major taxa at sites in the 18-30 m, 31-50 m, and 51-90 m intervals in Georgian Bay and North Channel in 2002, 2007, and 2012. See Table 2 for the number of stations in each interval in each of the three sampling years. Differences between years were tested with ANOVA (P-value given). If the P-value was ≤ 0.05 , Fisher's LSD was used for pairwise comparisons. Results of such comparisons are provided by subscripts; values with the same subscript were not significantly different ($P > 0.05$ ND = not determined).

Interval/ Year	Taxa					
	<i>Diporeia</i>	<i>Oligochaeta</i>	<i>Sphaeriidae</i>	<i>Chironomidae</i>	<i>D. polymor</i>	<i>D. r. bugens</i>
Georg. Bay						
<u>18-30 m</u>						
2002	1,687 \pm 830	707 \pm 344	1,814 \pm 525 ^a	162 \pm 34	19 \pm 10	0 \pm 0
2007	55 \pm 55	1,388 \pm 1,043	61 \pm 21 ^b	555 \pm 302	21 \pm 21	278 \pm 278
2012	3 \pm 3	573 \pm 145	0 \pm 0 ^c	148 \pm 121	0 \pm 0	3 \pm 3
P-value	0.07	0.99	<0.01	0.61	0.48	0.68
<u>31-50 m</u>						
2002	1,457 \pm 596 ^a	767 \pm 293	853 \pm 214	94 \pm 26	24 \pm 23	36 \pm 34
2007	50 \pm 48 ^{ab}	728 \pm 332	195 \pm 114	195 \pm 155	5 \pm 5	1,335 \pm 1,330
2012	0 \pm 0 ^b	2,499 \pm 576	195 \pm 81	63 \pm 58	18 \pm 18	382 \pm 221
P-value	0.02	0.18	0.14	0.18	0.89	0.59
<u>51-90 m</u>						
2002	1,684 \pm 306 ^a	413 \pm 144	291 \pm 110 ^a	44 \pm 11	2 \pm 2	0 \pm 0 ^a
2007	99 \pm 56 ^b	150 \pm 60	84 \pm 14 ^{ab}	56 \pm 13	2 \pm 2	1 \pm 1 ^a
2012	0 \pm 0 ^c	391 \pm 107	55 \pm 16 ^b	21 \pm 8	0 \pm 0	144 \pm 130 ^b
P-value	< 0.01	0.11	0.05	0.07	0.65	0.05
N. Channel						
<u>18-30 m</u>						
2002	2,046 \pm 705	653 \pm 269	875 \pm 280	99 \pm 22	1 \pm 1	0 \pm 0
2007	1,022 \pm 423	478 \pm 230	232 \pm 41	676 \pm 384	0 \pm 0	0 \pm 0
2012	357 \pm 171	1,245 \pm 549	914 \pm 319	275 \pm 72	0 \pm 0	0 \pm 0
P-value	0.25	0.32	0.11	0.42	ND	ND
<u>31-50 m</u>						
2002	896 \pm 401	322 \pm 163	357 \pm 163	198 \pm 57	0 \pm 0	0 \pm 0
2007	660 \pm 432	257 \pm 119	338 \pm 137	470 \pm 243	0 \pm 0	0 \pm 0
2012	751 \pm 320	239 \pm 158	346 \pm 146	170 \pm 75	0 \pm 0	0 \pm 0
P-value	0.64	0.72	0.59	0.89	ND	ND
<u>51-90</u>						
2002	3,349 \pm 43	,174 \pm 232	635 \pm 200	54 \pm 25	0 \pm 0	0 \pm 0
2007	253 \pm 253	307 \pm 244	79 \pm 21	29 \pm 21	0 \pm 0	0 \pm 0
2012	121 \pm 107	483 \pm 311	224 \pm 100	490 \pm 345	0 \pm 0	0 \pm 0
P-value	ND	ND	ND	ND	ND	ND

Table 11. Mean (\pm SE) biomass (gAFDW/m²) of major taxa at sites in the 18-30 m, 31-50 m, and 51-90 m intervals in the main basin, Georgian Bay and North Channel in 2012 See Table 2 for the number of stations in each interval in each of the three sampling years.

Region/ Interval	Taxa					
	<i>Diporeia</i>	Oligochaeta	Sphaeriidae	Chironomidae	<i>D. polymo</i>	<i>D. r. bugen</i>
Main basin						
18-30 m	0 \pm 0	1.48 \pm 0.37	<0.01 \pm <0.01	0.03 \pm 0.01	0.02 \pm 0.02	2.64 \pm 1.76
31-50 m	0 \pm 0	0.63 \pm 0.09	0.01 \pm <0.01	0.03 \pm 0.01	0 \pm 0	14.39 \pm 4.56
51-90 m	0.01 \pm <0.01	0.32 \pm 0.05	0.01 \pm <0.01	0.01 \pm <0.01	0 \pm 0	5.23 \pm 2.36
>90 m	0.04 \pm 0.01	0.23 \pm 0.07	0.01 \pm <0.01	0.01 \pm <0.01	0 \pm 0	4.32 \pm 3.97
Georg. Bay						
18-30 m	0 \pm 0	0.45 \pm 0.29	0.01 \pm 0.01	0.03 \pm 0.03	0 \pm 0	0.13 \pm 0.13
31-50 m	0 \pm 0	0.94 \pm 0.39	0.01 \pm <0.01	0.04 \pm 0.04	0.77 \pm 0.77	11.30 \pm 4.95
51-90 m	0 \pm 0	0.17 \pm 0.06	0.01 \pm <0.01	<0.01 \pm <0.01	0 \pm 0	2.97 \pm 2.93
N. Channel						
18-30 m	0.17 \pm 0.07	0.38 \pm 0.16	0.07 \pm 0.02	0.08 \pm 0.05	0 \pm 0	0 \pm 0
31-50 m	0.12 \pm 0.05	0.15 \pm 0.07	0.02 \pm 0.01	0.10 \pm 0.08	0 \pm 0	0 \pm 0
51-90 m	<0.01	0.08	0.01	0.14	0 \pm 0	0 \pm 0

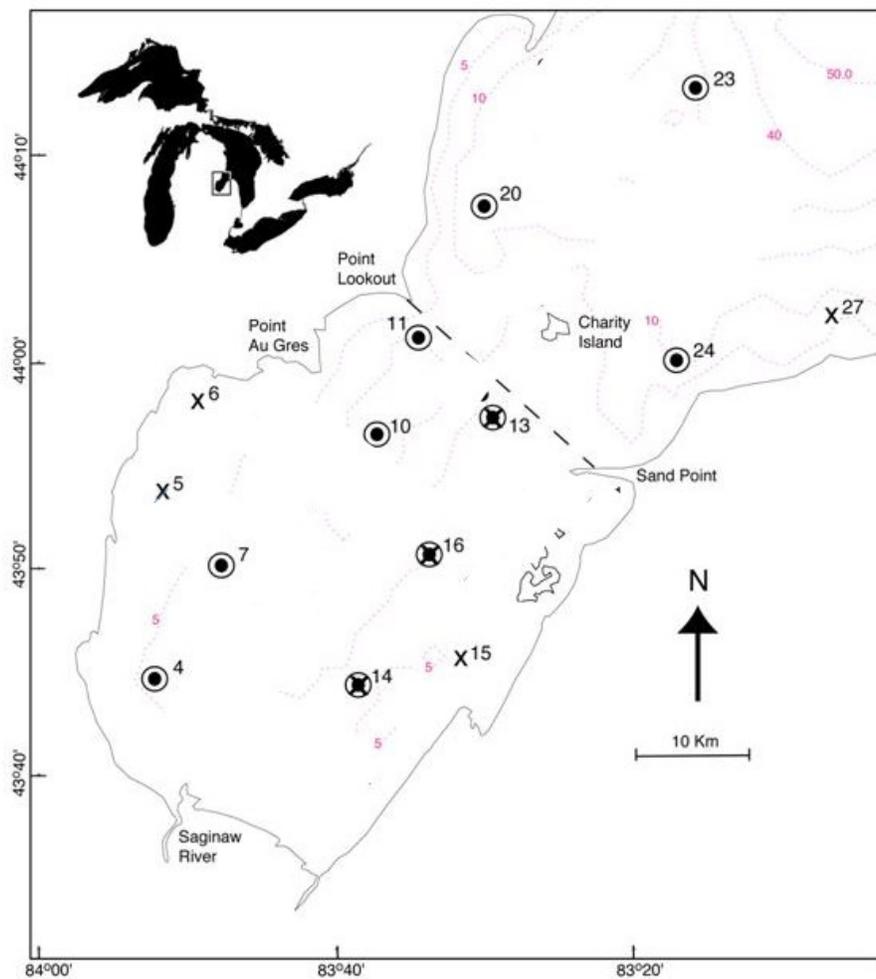


Figure 2. Location of sampling sites in Saginaw Bay in 2006-2010. These were the same sites sampled in 1987-1996. Dashed line separates the inner bay from the outer bay. Depth contours given in meters. An “x” indicates sites sampled with SCUBA divers and a circled black dot indicates sites sampled with a Ponar grab.

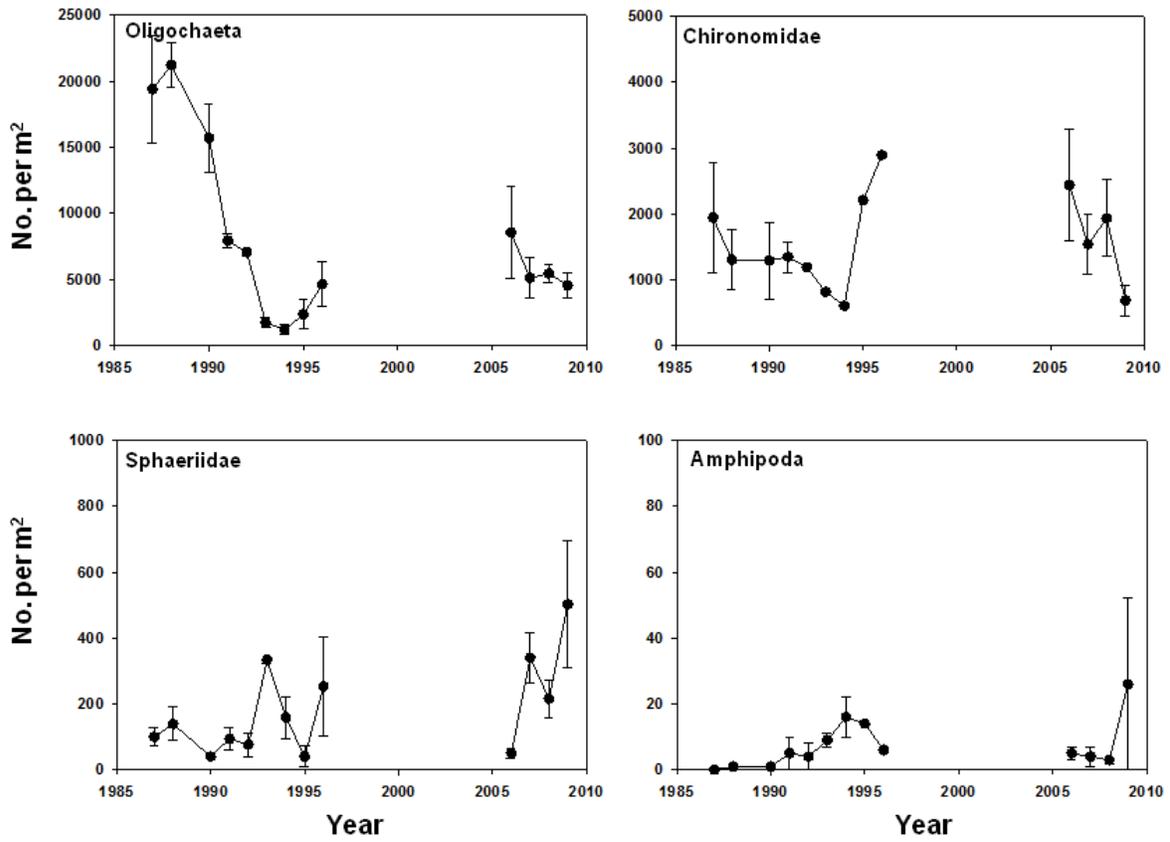


Figure 3. Mean (\pm SE) density (no./m²) of major macroinvertebrate groups at stations in inner Saginaw Bay with water depths of > 6 m and with a substrate of silt (Stations 4, 7, and 10). Densities in 1987-1996 were taken from previous surveys (Nalepa et al. 2002). Note different scales of the Y-axis.

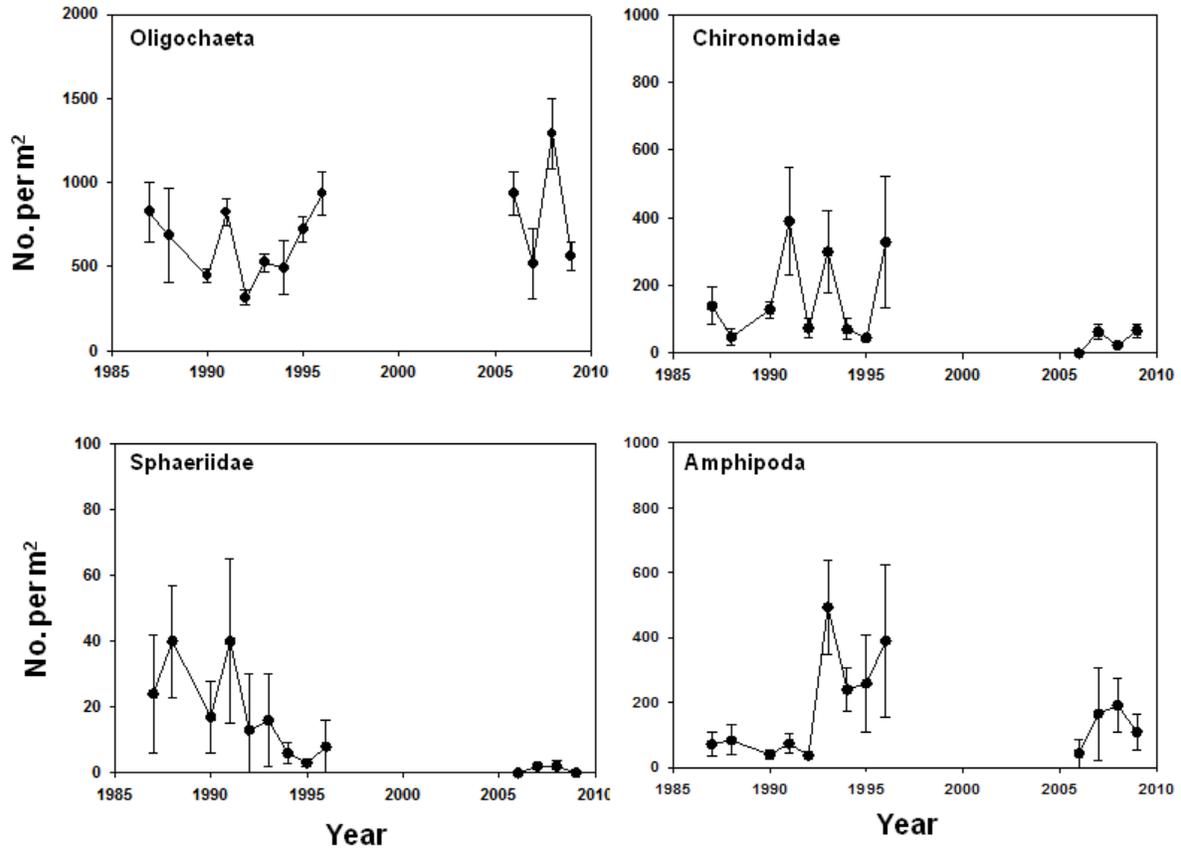


Figure 4. Mean (\pm SE) density (no./m²) of major macroinvertebrate groups at stations in inner Saginaw Bay with water depths of < 6 m and with a substrate of sand/gravel (Stations 13, 14, and 16). Densities in 1987-1996 were taken from previous surveys (Nalepa et al. 2002). Note different scales of the Y-axis.

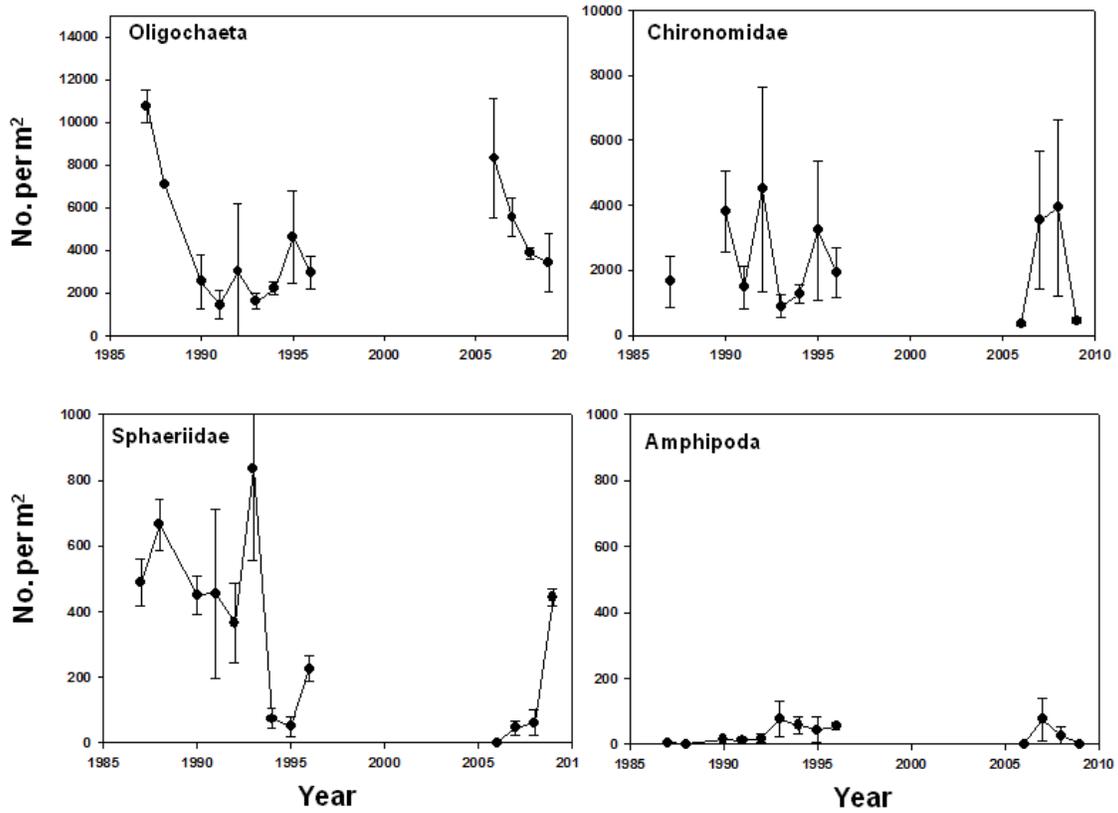


Figure 5. Mean (\pm SE) density (no./m²) of major macroinvertebrate groups at a station in inner Saginaw Bay with a substrate of silty sand (Station 11). Densities in 1987-1996 were taken from previous surveys (Nalepa et al. 2002). Note different scales of the Y-axis.

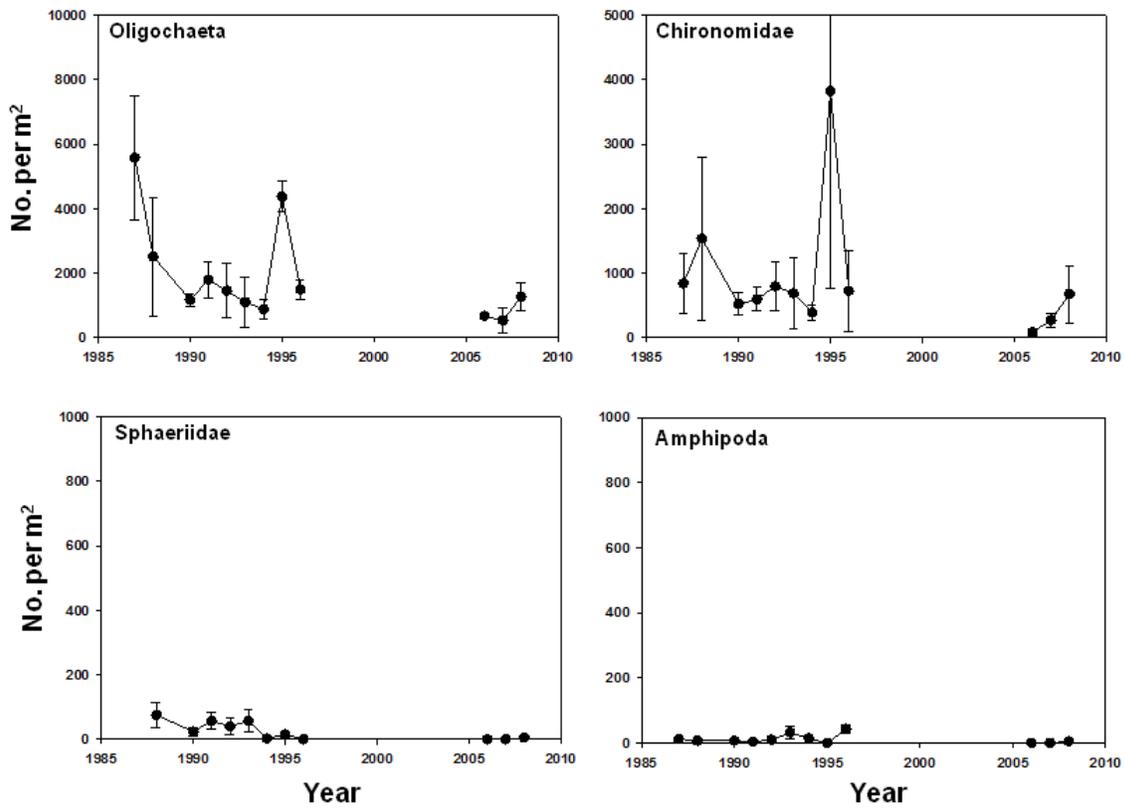


Figure 6. Mean (\pm SE) density (no./m²) of major macroinvertebrate groups at a station in outer Saginaw Bay with water depth of 12 m (Station 24). Densities in 1987-1996 were taken from previous surveys (Nalepa et al. 2002). Note different scales of the Y-axis.

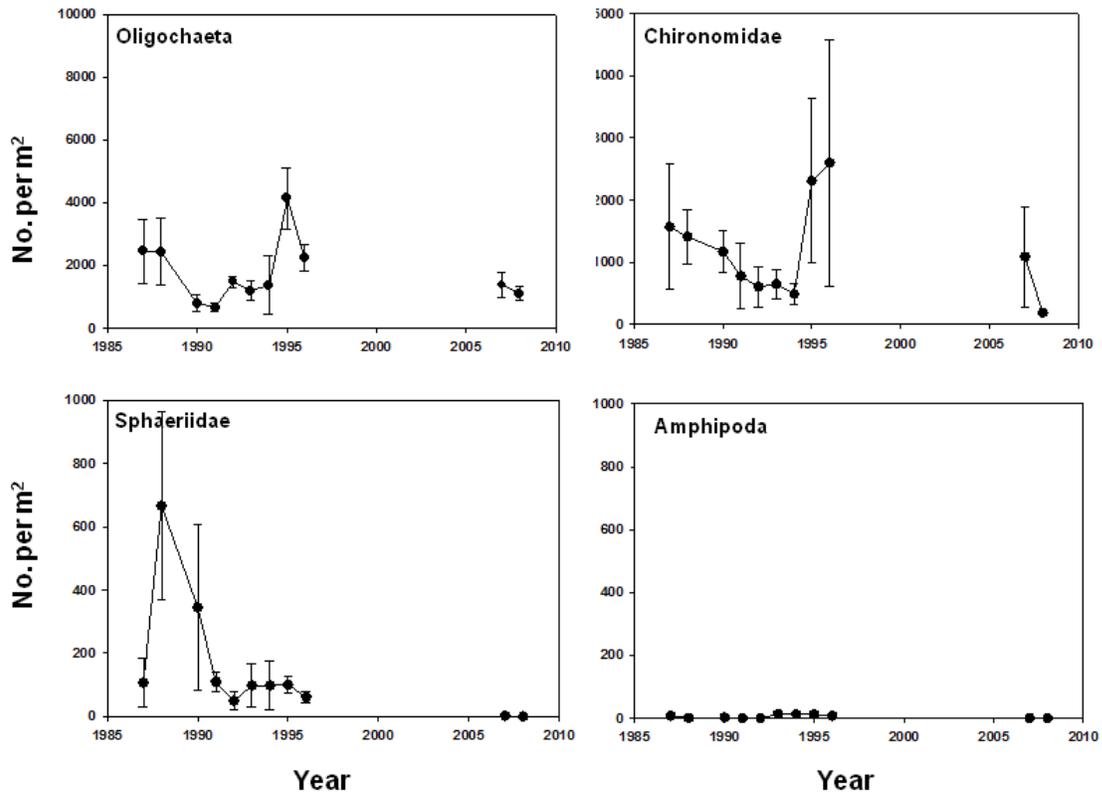


Figure 7. Mean (\pm SE) density (no./m²) of major macroinvertebrate groups at a station in outer Saginaw Bay with water depth of 16 m (Station 20). Densities in 1987-1996 were taken from previous surveys (Nalepa et al. 2002). Note different scales of the Y-axis.

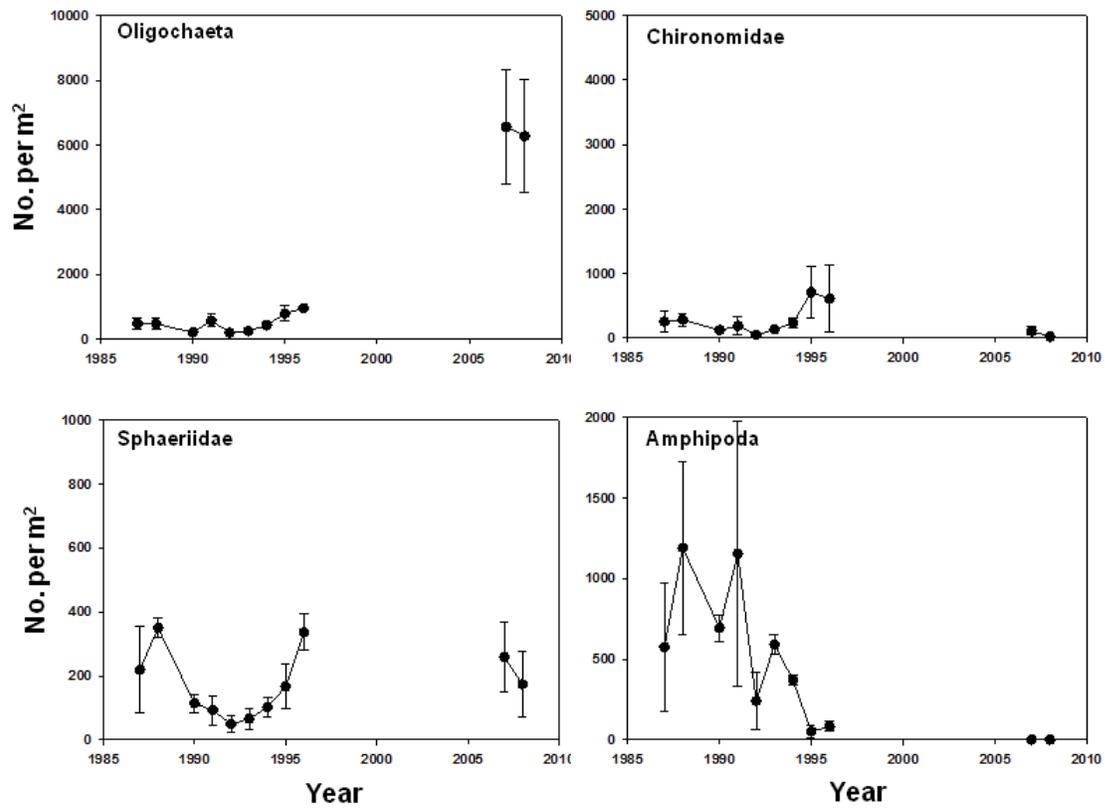


Figure 8. Mean (\pm SE) density (no./m²) of major macroinvertebrate groups at a station in outer Saginaw Bay with water depth of 28 m (Station 23). Densities in 1987-1996 were taken from previous surveys (Nalepa et al. 2002). Note different scales of the Y-axis.

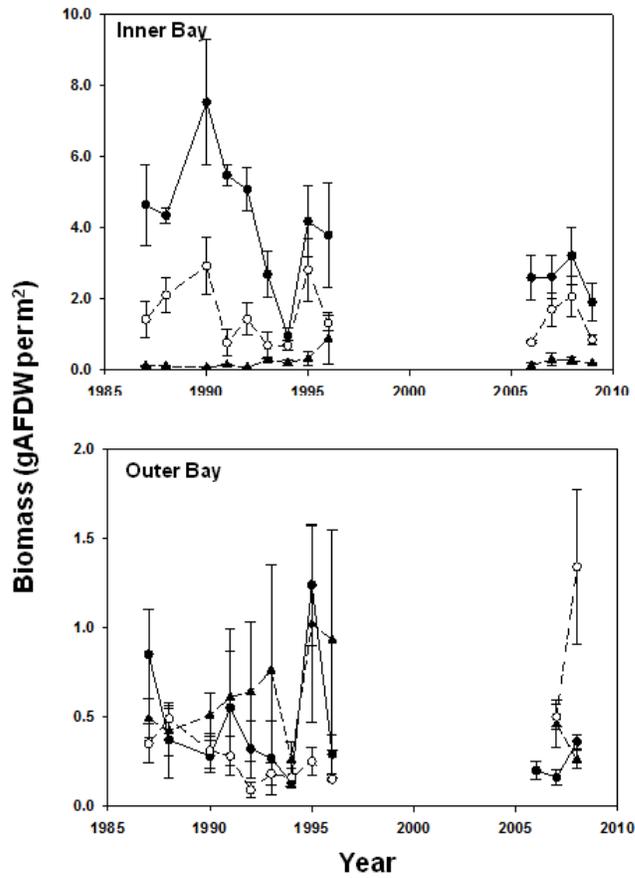


Figure 9. Yearly mean (\pm SE) biomass (g AFDW/m²) of non-dreissenid taxa for the various stations and station groups in the inner (upper panel) and outer (lower panel) portions of Saginaw Bay during the periods 1987-1996 and 2001-2009. Inner Bay: silt = solid line, solid point; silty sand = dashed line, open point; sand/gravel = dashed line, solid point. Outer Bay: 12 m = solid line, solid point; 16 m = dashed line, solid point; 28 m = dashed line, open point.

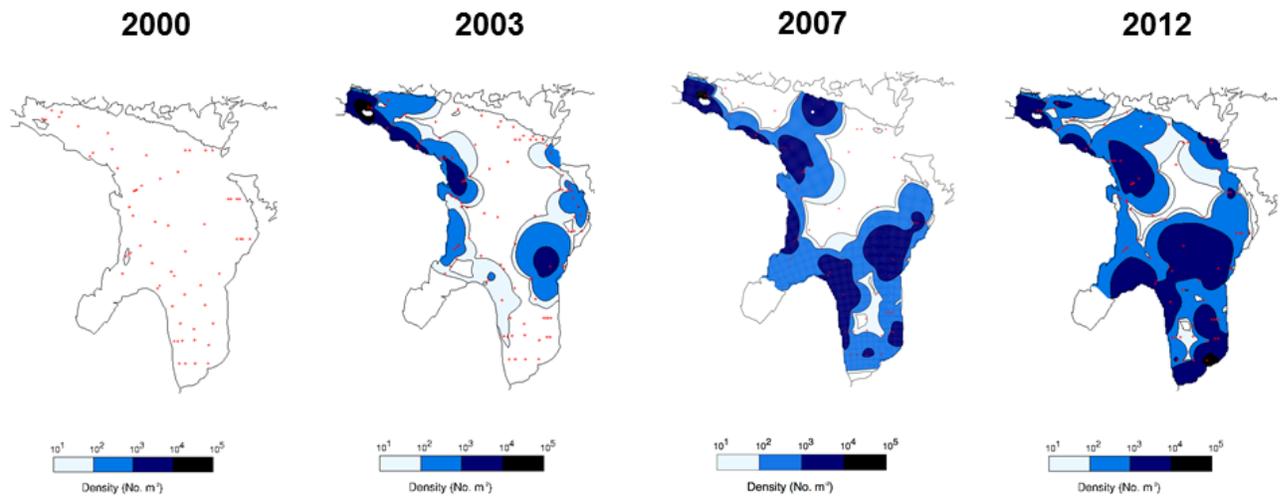


Figure 10. Mean density (no./m²) of *D. r. bugensis* in the main basin of Lake Huron in 2000, 2003, 2007, and 2012.

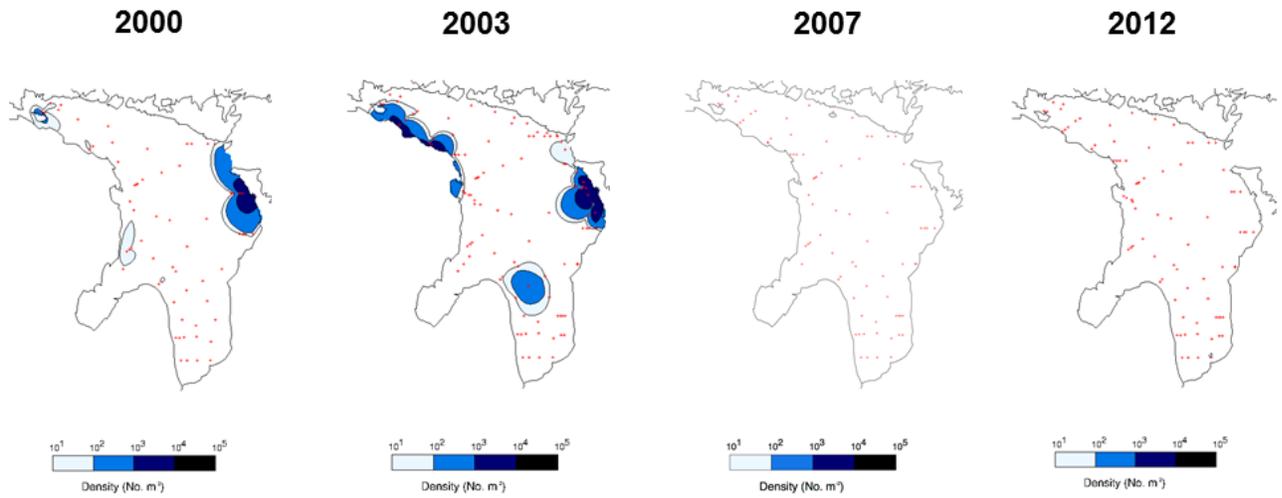


Figure 11. Mean density (no./m²) of *D. polymorpha* in the main basin of Lake Huron in 2000, 2003, 2007, and 2012.

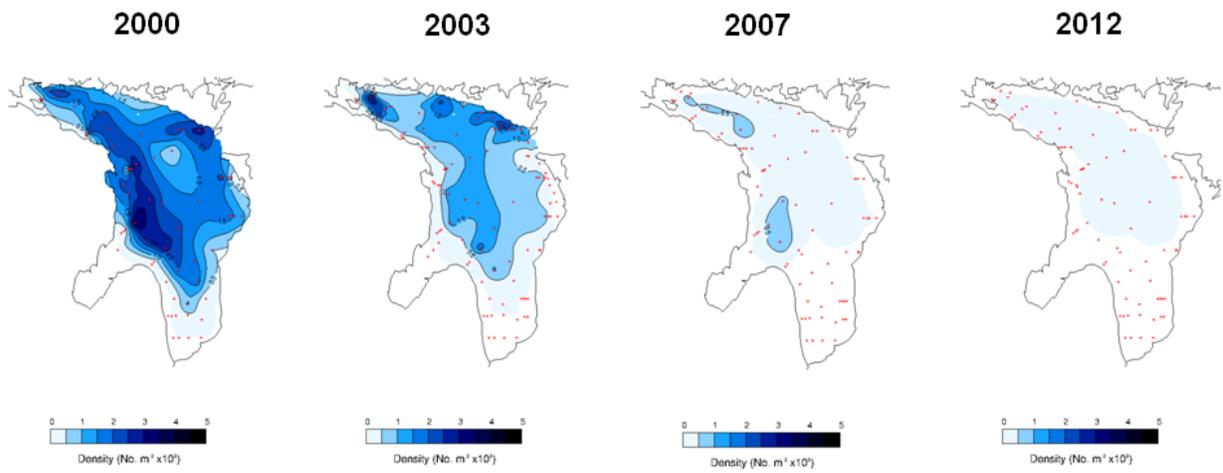


Figure 12. Mean density (no./m^2) of *Diporeia* in the main basin of Lake Huron in 2000, 2003, 2007, and 2012.

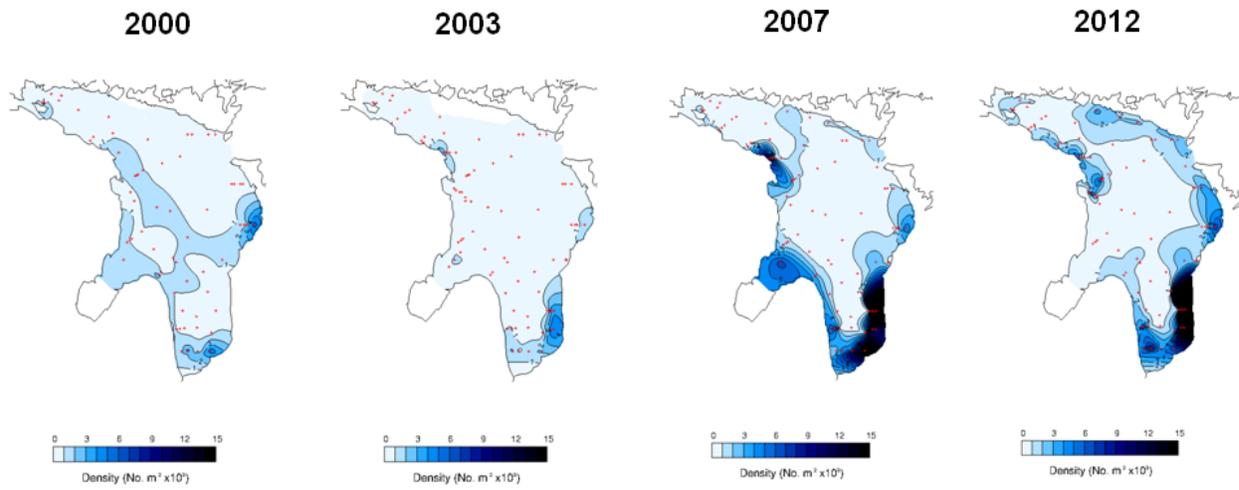


Figure 13. Mean density (no./m³) of Oligochaeta in the main basin of Lake Huron in 2000, 2003, 2007, and 2012.

