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# Abundance and Biomass of Benthic Macroinvertebrates in Lake Michigan in 2015, with a Summary of Temporal Trends

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## 1.0 INTRODUCTION

This technical report gives results of a lake-wide benthic survey conducted in Lake Michigan in 2015. The purpose of the survey was to assess the status of the benthic macroinvertebrate community, with a primary focus on the invasive mussels *Dreissena polymorpha* and *Dreissena rostriformis bugensis*, and the native amphipod *Diporeia*. Similar lake-wide surveys were conducted to assess the status of these three taxa beginning in 1994/1995 and repeated every five years through 2010 (Nalepa et al. 2014). Based on these previous surveys, major changes in population abundances of all three taxa were observed over this 15-year period. *D. polymorpha* was first reported in Lake Michigan in 1989 (Marsden et al. 1993). Based on the surveys, densities subsequently increased to reach a peak in 2000. Thereafter, densities declined to such an extent that by 2010 it was rarely found. Over the entire period, *D. polymorpha* was mainly found at depths < 50 m. *D. r. bugensis* was first reported in the lake in 1997 (Nalepa et al. 2001), and densities have mostly continued to increase at all depths through 2010, attaining densities that exceeded those of *D. polymorpha* even at depths < 50 m. Lastly, the native amphipod *Diporeia* has been in a steady state of decline ever since *Dreissena* became established. Lower densities relative to those in pre-*Dreissena* years were first observed in the early 1990s (Nalepa et al. 1998), and declines continued at all depths from 1994/1995 through 2010. In 2010, it had mostly disappeared at depths < 50 m and had declined by 95% at depths > 50 m.

Both *Dreissena* and *Diporeia* play key roles in the ecosystem of Lake Michigan and the other Great Lakes. *Dreissena* has a great capacity to filter particulate material from the water column and excrete metabolic by-products (biodeposits, nutrients). As a result, *Dreissena* has dramatically restructured food webs and altered spatial patterns of energy and nutrient flow (Vanderploeg et al. 2002, Hecky et al. 2004). Specific impacts of *Dreissena* on the Lake Michigan ecosystem have been well-documented, including reduction of the spring phytoplankton bloom and alteration of benthic-pelagic processes (Fahnenstiel et al. 2010, Cuhel and Aguilar 2013, Vanderploeg et al. 2015). Before it declined, *Diporeia* was a keystone species in the offshore food web, accounting for over 70% of benthic biomass and serving as an energy-rich food source for many fish species. As a benthic detritivore that mainly feeds on organic material that has settled from the water column into the upper sediments, *Diporeia* was an important pathway by which energy was cycled from the benthic region to the upper food web (e. g., fish) (Nalepa et al. 2000, 2009). The decline of *Diporeia* has led to large changes in the relative health, growth, and community structure of fish communities in the lake (Pothoven et al. 2001, Hondorp et al. 2005, Bunnell et al. 2009). Because of these key ecosystem roles and noted

population shifts between 1994/95 and 2010, the statuses of *Dreissena* and *Diporeia* were of particular interest in 2015.

While the surveys in 1994/95, 2000, 2005, and 2010 focused only on *Dreissena* and *Diporeia*, the survey in 2015 was broader in scope and documented abundances and biomass of all macrobenthic taxa. Thus, the 2015 survey provides a baseline to assess future changes of the entire benthic community in Lake Michigan. Lake-wide trends in the entire benthic community have recently been examined in Lake Huron (Nalepa et al. 2007, 2018, Karatayev et al. 2020), Lake Ontario (Birkett et al. 2015), and Lake Erie (Burlakova et al. 2014).

This report provides data files that give abundances and biomasses of all macrobenthic taxa at each of the sampling sites in 2015, as well as data on *Dreissena* size structure. As such, it continues the regular practice of publishing reports that contain newly-collected data along with some perspective relative to data collected in previous surveys (Nalepa et al. 2008, 2014). Since the survey in 2015 was the fifth lake-wide survey since 1994/95, this particular report also contains summaries of long-term trends of *D. polymorpha*, *D. r. bugensis*, and *Diporeia* over this 20-year period. It also provides ancillary data collected during the 2015 survey, such as length-weight relationships and size frequencies of the *Dreissena* population. While highlights of major temporal trends are provided, more detailed analyses and discussion of trends, spatial patterns, and community composition, including comparisons to lake-wide surveys in the other Great Lakes, will be given in other publications. Raw data from the benthic macroinvertebrate lake wide surveys conducted in Lake Michigan in 2015 are provided as Excel files (see [Appendices](#)), and also archived at the NOAA National Centers for Environmental Information (NCEI Accession Number 0209222; <https://accession.nodc.noaa.gov/0209222>).

## 2.0 METHODS

Benthic samples were collected at 140 stations in Lake Michigan, July 20-29, 2015 ([Table 1](#)). Of these, 135 were located in the main basin of the lake, and 5 were located in the outer portion of Green Bay ([Table 1](#), [Fig. 1a-c](#)). The number and location of stations have generally remained consistent since 2000. For the complete list and locations of stations sampled in previous surveys, see Nalepa et al. (2014).

Field sampling procedures in 2015 were the same as in previous surveys. In brief, benthic samples were taken in triplicate at each site with a Ponar grab (area in 2015 = 0.0483 m<sup>2</sup>). Collected material was washed through an elutriation device fitted with a 0.5-mm mesh net, and retained residue was preserved in 5-10% buffered formalin containing rose bengal stain. Sample jars were labeled with the station designation, replicate number, and date. Sampling depth and a general description of the bottom substrate at each station were recorded ([Table 1](#); [Appendix A](#)).

As noted, all benthic organisms were counted and identified in 2015, whereas only *Dreissena* and *Diporeia* were counted and identified in surveys prior to 2015. While some descriptions of laboratory procedures will be presented here, more detailed accounts can be found in other publications. Procedures in 2015 followed the EPA Standard Operating Procedure (SOP) LG407 (2015). This document details procedures used by EPA in their annual benthic survey of all the lakes. As relevant to the 2015 survey in Lake Michigan, this SOP document outlines the handling, identification, and biomass determination of organisms other than *Dreissena* and

*Diporeia*. Detailed procedures to determine biomass for *Dreissena* and *Diporeia* in surveys prior to 2015 are given in Nalepa et al. (2014).

Methods to determine abundances in 2015 were straight-forward and similar to all previous surveys. All organisms were picked and counted under low magnification, with Oligochaeta and Chironomidae proportionally split when numbers were high. In 2015, biomass of *Dreissena* was determined as both ash-free dry weight (AFDW, soft tissue) and total wet weight (TWW, shell included). Surveys prior to 2015 reported dreissenid biomass only as AFDW and was calculated by first determining relationships between shell length and AFDW at select sites, and then applying these relationships to size frequencies across all sites (Nalepa et al. 2014). As given in EPA's SOP, dreissenid biomass is reported as TWW and is determined by blotting dry all dreissenids per each 5-mm size group in a sample, weighing each group, and then adding all groups together. Given these differences in determining and reporting dreissenid biomass, both methods were used to determine biomass in 2015, and values of both measures are provided.

For the 2015 survey, length-weight relationships for *Dreissena* were derived from individuals freshly-collected with a Ponar grab from 22 sites ([Table 2](#)). While priority was given to sites where individuals for length-weight relationships were collected in 2010, the ultimate criteria for site 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 so that a representative relationship could be obtained. Also, an effort was made to collect at sites located throughout the lake and at various depths. Immediately after collection of mussels at a given site, soft tissues of about 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° for at least 48 h. 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° for 1 h, and then re-weighed. AFDW was then calculated as the difference between dry weight and post-ashed weight. Corresponding shell lengths were measured to the nearest 0.5 mm. Overall, a total of 569 individuals from the 22 sites were weighed and measured. All individuals for length-weight determinations were *D. r. bugensis* since *D. polymorpha* was not found. Measured AFDWs and shell lengths (SL) were used to develop length-weight relationships according to the allometric equation:  $\log_e \text{AFDW (mg)} = b + a * \log_e \text{SL (mm)}$ . Relationships were developed for sites pooled within four different depth intervals:  $\leq 30$  m, 31-50 m, 51-90 m, and > 90 m ([Table 3](#), also see below). For size frequencies, shell lengths of all mussels in each replicate sample were measured and then binned into 1-mm size categories. Individuals < 1 mm were binned with individuals in the 1-1.99 mm size category and included in abundance and biomass estimates. The exception was at all 56 sites in the southern basin (see [Table 1](#)); at these sites individuals < 1 mm were included in abundance estimates but not biomass. Not including these small individuals would have minimal effect on biomass. In previous surveys individuals < 5 mm were not individually measured and hence binned into one category (0-5 mm).

To determine AFDW 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 of that category). All size-category weights were then summed. Broken mussels (i.e. mussels with shells broken enough to compromise the length measurement), while included in TWW biomass estimates, were incorporated into AFDW estimates by first calculating the ratio of TWW that was comprised of broken mussels and then



increasing the AFDW estimate by that ratio. In the one case where >50% of the sample consisted of broken or partial mussels (WI-3, replicate 1), TWW was directly converted to AFDW using the determined linear relationship between AFDW and TWW (see [Figure 6](#)).

For analysis of trends, sites in the main lake were divided into the same four depth intervals as in previous surveys:  $\leq 30$  m, 31-50 m, 51-90 m, and  $> 90$  m. These intervals define distinct physical habitats that result in distinguishable benthic communities (Alley and Mozley 1975, Nalepa 1989). Because physicochemical conditions in Green Bay are so different than in the main lake, results for the 5 sites located in Green Bay are given separately. All values were  $\log_e +1$  transformed before statistical tests.

Count data were converted to density (no./m<sup>2</sup>) and biomass per sample was converted to (g/m<sup>2</sup>) by multiplying the values by 20.7039. One station/replicate was compromised (MAN-2, replicate 2) and therefore all organisms in this replicate were discarded, with the exception of *Dreissena*. Further, at one station (9554) *Dreissena* in the three replicates were accidentally combined; at this station 1/3 of total abundance and biomass was assigned to each replicate. For all non-dreissena taxa, however, replicates were kept separate and therefore replicate-specific data are still available.

### 3.0 RESULTS AND DISCUSSION

The 2015 survey extended the assessment of lake-wide trends in *D. polymorpha*, *D. r. bugensis*, and *Diporeia* that were previously defined between 1994/1995 and 2010 (Nalepa et al. 2014). For *D. polymorpha*, no individuals were found in any of the samples collected in 2015 (Table 5, Fig. 2). This species peaked in 2000 at depths < 50 m and has steadily declined since. Only a few individuals were found at just one station in 2010, thus it is not surprising that no individuals were collected in 2015. The decline of *D. polymorpha* coincided with the rapid expansion of *D. r. bugensis* between 2000 and 2005 (Fig. 3). Both species are filter-feeders and compete for the same food resources. Because *D. r. bugensis* has a lower respiration rate and a higher assimilation rate than *D. polymorpha* (Baldwin et al. 2002, Stoeckmann 2003), it is more efficient in allocating resources to growth and reproduction and thus has a competitive advantage when available food resources are limited. Further, *D. r. bugensis* has a lower temperature threshold of reproduction compared to *D. polymorpha* and therefore is able to colonize to deeper depths (Karatayev et al. 2015).

For *D. r. bugensis*, some important temporal patterns emerged in 2015 that perhaps signaled a shift in population dynamics. Most notably, when compared to densities in 2010, densities in 2015 declined at all depth intervals except at the deepest (> 90 m) (Table 5, Fig. 3). In contrast, in prior surveys through 2010, densities of *D. r. bugensis* generally increased at all depth intervals. The exception was at the 31-50 m interval where densities peaked in 2005 and have declined since (Table 5). As compared to 2010, mean densities in 2015 declined by 75%, 53%, and 38% at the  $\leq 30$  m, 31-50 m, 51-90 m depth intervals, respectively. These declines were significant for each depth interval ( $P < 0.05$ , t-test). With these declines, densities of *D. r. bugensis* have seemingly peaked at depths < 90 m. The only depth interval where densities of *D. r. bugensis* were not lower in 2015 compared to 2010 was > 90 m. Mean density at this interval increased from 1,881/m<sup>2</sup> to 2,747/m<sup>2</sup>; this difference, however, was not significant ( $P > 0.05$ ).

It is worth noting that the number of sites at  $\leq 30$  m was lower in 2015 than in 2010 ( $n = 29$  and 40, respectively; see Table 5). Many sites are located around 30 m, and in 2015 some sites were recorded as a few meters deeper than in 2010, placing them into the 31-50 m interval. Also, a few sites in the  $\leq 30$  m interval were not sampled in 2015 but were sampled in 2010. To be certain that declines in *D. r. bugensis* in 2015 at the  $\leq 30$  m and 31-50 m intervals were not a result of sites changing depth categories, means were again determined after placing these sites into the same category as in 2010. Mean densities in 2015 thus determined were  $2,713 \pm 595/\text{m}^2$  for  $\leq 30$  m ( $n=38$ ) and  $6,753 \pm 751/\text{m}^2$  for 31-50 m ( $n=37$ ). Both densities were still significantly lower than in 2010.

Trends in dreissenid AFDW biomass were similar to trends in density at  $\leq 30$  m and > 90 m. That is, mean biomass in 2015 declined at the former interval and increased at the latter interval when compared to 2010 (Fig. 4), and these year-to-year differences were significant at both depth intervals ( $P < 0.05$ ). Mean biomass at 31-50 m and 51-90 m did not decline like density (Fig. 4), and differences between 2010 and 2015 were not significant ( $P > 0.05$ ). To determine depth-weighted biomass, lake area (excluding Green Bay and Grand Traverse Bay) was first divided into 25 km<sup>2</sup> cells and then lake area in each depth interval determined. Based on this grid size, mean depth-weighted biomass for *Dreissena* in 2000, 2005, 2010, and 2015 was 0.30 g/m<sup>2</sup>, 8.9 g/m<sup>2</sup>, 13.7 g/m<sup>2</sup>, and 16.7 g/m<sup>2</sup>, respectively. Thus, total depth-weighted biomass was greater in 2015 than in 2010, which can mainly be attributed to increased biomass at > 90 m, a depth

interval that comprises 41.5% of the main-lake area. For reference, the other depth intervals comprise the following percentages of the main-lake area:  $\leq 30$  m = 12.7%, 31-50 m = 14.7%, and 51-90 m = 31.0% (Nalepa et al. 2009).

The divergence of trends in dreissenid density and AFDW biomass at the 31-50 and 51-90 m intervals between 2010 and 2015 can either be attributed to differences in length-weight, or to differences in size frequencies (or to both). With a decline in density in 2015, weight per unit shell length (AFDW/SL) must have increased, or the average size of individuals in the population must have increased. To assess differences in AFDW/SL, the AFDW of a standard 15-mm mussel was calculated and compared between the two years based on regressions given in Table 3. AFDW of a 15-mm mussel at 31-50 m was 5.46 mg and 5.17 mg in 2010 and 2015, respectively, and AFDW at 51-90 m was 6.07 mg and 5.78 mg. Thus, AFDW/SL at both intervals was lower in 2015 than in 2010, and hence cannot account for mean biomass being higher in 2015. Size frequencies in the two years were examined by placing individuals into 5-mm size categories and then determining the proportion of all mussels in each category for each depth interval. At both the 31-50 m and 51-90 m intervals, the proportion of the population  $< 10$  mm decreased, while the proportion  $> 10$  mm increased in 2015 compared to 2010 (Table 6). Individuals  $> 10$  mm increased from 29.3% to 57.0% at 31-50 m, and increased from 27.8% to 38.5% at 51-90 m. These increases in the proportion of larger-sized individuals in 2015 compared to 2010 appear to be the likely reason for biomass not declining despite significant declines in density. Since tissue weight increases exponentially with shell size, even a modest increase in the proportion of larger individuals greatly affects biomass. For the other two intervals, the proportion of individuals  $> 10$  mm was similar in 2010 and 2015 at  $\leq 30$  m (17.6% to 19.8%), but increased at  $> 90$  m (12.5% to 24.1%). Increased biomass at  $> 90$  m in 2015 relative to 2010 can thus be attributed to not only an increase in density in 2015, but also to a greater proportion of larger individuals. An increase in AFDW/SL may also have played a role (see below).

Besides using length-weight relationships to determine dreissenid biomass, these relationships are also useful to assess the relative health of the population. For *Dreissena*, the amount of tissue per unit shell length is directly related to food availability (Walz 1978, Sprung and Borchering 1991, Nalepa et al. 1995). This relationship holds true for molluscs in general (Russell-Hunter 1985). Given this, a lower AFDW/SL over time would indicate that tissue loss or tissue “degrowth” has occurred, a sign that individuals are catabolizing soft tissue while under nutritional stress. Ultimately, lower tissue weight can hinder survival (Karatayev et al. 2010) and lead to lower reproduction (Bielefeld 1991, Sprung 1995). Temporal trends in AFDW/SL can thus be a broader indicator of future population growth. As noted, the AFDW of a standard 15-mm mussel was lower in 2015 than in 2010 at 31-50 m and 51-90 m. To further explore trends at all depth intervals, AFDW of a standard 15-mm mussel was determined from regressions for *D. r. bugensis* in Lake Michigan going back to 2004 (see Table 3). Trends varied widely between the depth intervals (Fig. 5). AFDW of a 15-mm mussel was consistently greatest at the  $\leq 30$  m interval over the 11-year period, but because of great variation between years a clear temporal trend was not readily discernable. On the other hand, the most defined temporal trend occurred at 31-50 m. At this interval, the AFDW of a 15-mm mussel steadily declined between 2004 and 2015; by 2015 it was 30.8% lower than in 2004. For the two deeper intervals, 51-90 m and  $> 90$  m, regressions were only available in 2010 and 2015. At the 51-90 m interval, the AFDW of a 15-mm mussel declined by 4.8% over the 5-year period, while at the  $> 90$  m interval it increased 6.0%. Based on these trends, and the fact that relative values in 2015 were lowest at 31-50 m and

51-90 m, it appears that *D. r. bugensis* populations at these two intervals may be under nutritional stress.

Biomass estimates of *Dreissena* populations in the Great Lakes have been reported in a number of different units including AFDW, dry weight (DW), and TWW. Of these, dried mass (AFDW or DW) of mussel tissue most accurately reflects functional mass, and hence estimates of dreissenid metabolic functions such as filtering, respiration, and excretion rates are generally provided as per unit AFDW or DW (Vanderpoeg et al. 2010, Johengen et al. 2014, Tyner et al. 2015). These metabolic rates along with estimates of population biomass provided as AFDW or DW have been used to assess lake-wide ecosystem impacts (Nalepa et al. 2009, Vanderploeg et al. 2010, Rowe et al. 2015, Tyner et al. 2015). In 2015, dreissenid biomass was determined as both AFDW and TWW. To examine the relationship between AFDW and TWW, biomass estimated by both methods was plotted for each station (Fig. 6). A regression through the origin between the two values was significant ( $R^2 = 0.92$ ) and defined by:  $TWW = 50.25 * AFDW$ . Given such a strong relationship between AFDW and TWW, the equation given above may be useful in converting from one biomass estimate to the other. One caveat, however, is the wide variation between the two estimates when values of AFDW are greater than about 40 g/m<sup>2</sup> (Fig. 6). Reasons for this variation are unclear. One potential reason is that, at sites with a greater number/biomass of mussels, any differences between the TWW/SL relationship at that one site and the generalized depth-specific length-weight relationship used to calculate AFDW are compounded and therefore results in a greater discrepancy between the two methods. Also, at sites with high mussel numbers/biomass, shell weight per unit shell length may be more inconsistent, the amount of water retained in the shell cavity may be more variable, or reproductive patterns may be different leading to variable ratios of spent vs. gravid individuals. Regardless, at high numbers/biomass, AFDW is both lower and higher relative to TWW, which complicates any potential theory.

Based on the 2015 survey, the amphipod *Diporeia* continued to decline over time (Table 5, Fig. 7). In 2015, *Diporeia* was collected at only one site that was < 90 m (just one individual), and at 9 sites that were > 90 m. In comparison, in 2010 *Diporeia* was collected at 13 sites < 90 m and 11 sites > 90 m. This depth-defined pattern of decline, with densities declining first and most rapidly in nearshore, shallow regions and more slowly with increased depth, has been apparent since the decline of *Diporeia* was first reported in the lake in the early 1990s (Nalepa et al. 1998). Such a spatial pattern coincides directly with the depth-related expansion of *Dreissena*. *D. polymorpha* increased mostly in the nearshore region ( $\leq 30$  m) until 2000, and subsequently *D. r. bugensis* increased rapidly in nearshore regions and more slowly in deeper, offshore regions (> 90 m). The exact reason for the negative response of *Diporeia* to *Dreissena* has not been determined but, with the exception of Lake Superior where the *Dreissena* population is very limited, the decline of *Diporeia* has consistently occurred in all the Great Lakes within a few years after *Dreissena* became established (Nalepa et al. 2006).

Although mean density of *Diporeia* at > 90 m was not lower in 2015 than in 2010, the continued increase of *D. r. bugensis* at this depth interval would suggest that densities of *Diporeia* will most likely decrease, or the population will be completely gone, in future surveys. In 2015, not only were densities of *D. r. bugensis* greater at sites > 90 m compared to 2010, the spatial extent of the population had expanded. Of note, *D. r. bugensis* was present at 8 of 9 sites where *Diporeia* was collected in 2015. In Lake Ontario, *D. r. bugensis* expanded to deeper depths (> 90 m) sooner than in Lake Michigan, and in a lake-wide survey of Lake Ontario in 2013, only one

*Diporeia* was collected at sites > 90 m, and no individuals were collected at sites < 90 m (Nalepa and Elgin unpublished). Mean density of *D. r. bugensis* at > 90 m was 2,044/m<sup>2</sup> in Lake Ontario in 2013, which is lower than the mean density of 2,747/m<sup>2</sup> found in Lake Michigan at this depth interval in 2015. Thus, if such a density of *D. r. bugensis* nearly extirpated *Diporeia* at this depth interval in Lake Ontario, a similar outcome might be expected in Lake Michigan.

Since 2015 was the first survey year in which the entire benthic community was examined, lake-wide temporal trends in taxa other than *Dreissena* and *Diporeia* could not be assessed. However, a more limited assessment of changes in these other benthic taxa can be derived by comparing 2015 results to benthic data collected in the 1990s in just the southern basin. As part of a NOAA long-term monitoring program, benthic samples have been collected at 40 sites in the southern basin for 2 consecutive years every 5 years, beginning in 1980-1981 (Nalepa 1987, Nalepa et al. 1998). The two most recent years in which data are entirely available are in 1998-1999 (Nalepa and Elgin, unpublished). Since the same 40 Stations were sampled in 2015 (see [Table 1](#)), densities of Oligochaeta, Sphaeriidae, and Chironomidae in 2015 were compared to densities in 1992-1993 and 1998-1999 at just these 40 sites. The 1992-1993 period was just after *D. polymorpha* became established in the southern basin, and the 1998-1999 period was about when *D. polymorpha* peaked and just before *D. r. bugensis* spread into the basin (about 2001). For oligochaetes, mean densities progressively increased in each of the three sampling periods (that is, 1992-1993, 1998-1999, and 2015) at the < 30 m, 31-50 m, and 51-90 m depth intervals ([Table 7](#)). These increases, particularly apparent at the ≤ 30 m and 31-50 m intervals, may be a result of a dreissenid impact known as the “nearshore shunt” (Hecky et al. 2004). In brief, this is the process by which organic material is retained for a longer period of time in nearshore regions by the activities of *Dreissena*. *Dreissena* filters particulate material (mainly phytoplankton) from the water column and subsequently deposits this organic material in the benthic zone in the form of feces and pseudofeces. These biodeposits would then serve as an added food source for benthic detritivores. Most all oligochaetes are detritivores and thus populations would benefit from these added food inputs. Benthic inputs of organic material are more pronounced in nearshore regions since primary production is greatest in these regions, and because the water column is well-mixed giving *Dreissena* access to all phytoplankton present. Most chironomids are also detritivores but, although mean densities of chironomids were greater in 2015 than in the 1990s at the two shallowest intervals, variation was too great to state with certainty that densities increased. Oligochaetes did not increase at the deepest interval (> 90 m). Although *Dreissena* in deeper, offshore waters also deposit organic material, these biodeposits would have less of an impact on detritivores. Benthic food availability in offshore regions is greatly diminished compared to nearshore regions, not only because primary production in the upper water column is less, but also because this organic matter is fed upon by organisms (bacteria, protozoans, etc.) as it settles downward through a longer water column to ultimately reach the benthic region.

In contrast to increased densities of oligochaetes in depth intervals < 90 m, densities of Sphaeriidae were lower at all depth intervals in 2015 compared to the 1990s ([Table 7](#)). A decline in sphaeriids at all depths was first observed soon after *Dreissena* became established in the southern basin (Nalepa et al. 1998). Reasons for the negative response of sphaeriids to *Dreissena* are not clear. Since sphaeriids are filter-feeders, it is presumed that they are being outcompeted by *Dreissena* for available food. Yet the dominant sphaeriid in the Great Lakes is *Pisidium* spp., a genus that filters bacteria in benthic interstitial waters and therefore should benefit from increased bacteria associated with dreissenid biodeposits.

Given most benthic biomass is reported as DW or AFDW, WW of non-dreissenid taxa reported here was converted to AFDW by first assuming DW was 20% of WW and then assuming AFDW was 90% of DW. Exceptions were the shelled-taxa Sphaeriidae and Gastropoda in which case AFDW was assumed to be 20% of DW. These conversion values are approximate but can be generally applied to a variety of non-shelled and shelled invertebrates (Johnson and Brinkhurst 1971, Ricciardi and Bourget 1998). Based on these conversions, total non-dreissenid biomass at the four depth intervals ranged from 0.64 g AFDW/m<sup>2</sup> at 31-50 m to 0.28 g AFDW/m<sup>2</sup> at > 90 m (Table 9). Non-dreissenid biomass comprised only a small portion of total benthic biomass (which includes *Dreissena*). Specifically, non-dreissenid biomass accounted for only 7.4%, 1.8%, 1.1%, and 3.9% of total benthic biomass at the 18-30 m, 31-50 m, 51-90 m, and > 90 m intervals, respectively.

Given the dominance of *Dreissena* in the benthic community of Lake Michigan, a general overview of population trends and patterns of *Dreissena* in Lake Michigan relative to the other Great Lakes puts our results into a broader perspective. A comparison of density trends of *Dreissena* in Lakes Michigan, Ontario, and Huron at the  $\leq 30$  m, 31-90 m, and > 90 m intervals is given in Figure 8. To make this comparison, densities at 31-50 m and 51-90 m were combined (interval becomes 31-90 m) for Lakes Michigan and Huron since these two depth intervals were not reported separately in previous studies for Lake Ontario (Watkins et al. 2007, Birkett et al. 2015). Density trends at  $\leq 30$  m are difficult to compare between lakes since high variation in physical drivers (i. e., substrate heterogeneity, wave-induced disturbance) at these shallow depths strongly influence dreissenid estimates. This is evident in the wide year-to-year variation at this depth interval in Lake Ontario (Fig. 8). Physical conditions become more stable as depth increases, and population trends at depths > 30 m are better suited for lake-to-lake comparisons. The decline of *D. r. bugensis* in Lake Michigan in 2015 at 31-90 m is similar to an ongoing decline in Lake Ontario that has been evident since 2008 (Fig. 8). If populations in both lakes have indeed peaked at this depth interval, a greater peak density was attained in Lake Michigan. Regardless, in both lakes densities increased sharply and then gradually declined. In contrast, densities at 31-90 m in Lake Huron have increased very gradually and, as of 2012, do not yet appear to have peaked. Densities at > 90 m are still increasing in all three lakes (Fig. 8). Similar comparisons of temporal trends in dreissenid biomass are not possible since biomass was not historically measured in each lake. However, most recent lake-wide surveys in each lake determined and reported biomass using the same methods, and values in the four depth intervals are given in Table 8. Considering biomass only at depths > 30 m, mean biomass in Lakes Michigan and Ontario were generally comparable at 31-50 m, 51-90 m, and > 90 m, whereas biomass in Lake Huron was about 50%, 78%, and 38% lower than in Lakes Michigan and Ontario at these three depth intervals, respectively.

## 4.0 SUMMARY

A lake-wide benthic survey was conducted in Lake Michigan in 2015 to assess the current status of the macroinvertebrate community. Similar lake-wide surveys have been conducted in the lake at 5-year intervals beginning in 1994/1995. These previous surveys only examined populations of *D. polymorpha*, *D.r. bugensis*, and *Diporeia*, whereas the 2015 survey examined the entire benthic community. Perhaps the most noteworthy finding in 2015 was the decline in densities of *D. r. bugensis* at depths < 90 m. Compared to densities in 2010, densities in 2015 declined 75%,

53%, and 38% at the  $\leq 30$  m, 31-50 m, 51-90 m depth intervals, respectively. In contrast, densities at  $> 90$  m increased 46%. Because of a greater proportion of larger individuals in the population, biomass at 31-50 m and 51-90 m remained stable or slightly increased in 2015 compared to 2010. Overall, depth-weighted biomass in the main basin increased from 13.7 g/m<sup>2</sup> in 2010 to 16.7 g/m<sup>2</sup> in 2015, largely due to increased biomass at sites  $> 90$  m. The other dreissenid species, *D. polymorpha*, was not collected at any of the sites in 2015, indicating it has essentially been entirely displaced by *D. r. bugensis* at the sites/depths historically sampled. Also, the amphipod *Diporeia* continued to disappear. It was collected at only one site  $< 90$  m and only at 9 sites  $> 90$  m. Lake-wide temporal trends in other major benthic taxa such as Oligochaeta, Sphaeriidae, and Chironomidae could not be assessed since 2015 was the first year the entire benthic community was sampled. However, based on comparisons to data collected in just the southern basin in 1992-1993 and 1998-1999, oligochaetes have progressively increased in shallower and mid-depth regions between 1992-1993 and 2015. A likely reason is an increased amount of potential food resulting from the biodeposition of organic material by *Dreissena*. In contrast, sphaeriids progressively declined all depth intervals between 1992-1993 and 2015.

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## 7.0 APPENDICES – EXCEL DATA FILES

The data in the following appendices is also available from the NOAA National Centers for Environmental Information (NCEI Accession Number 0209222; <https://accession.nodc.noaa.gov/0209222>).

### APPENDIX A. STATION INFORMATION, 2015.

Information about sampling stations in Lake Michigan in 2015, including region, depth, coordinates, and substrate type (see [Figure 1 a-c](#)).

[https://www.glerl.noaa.gov/pubs/tech\\_reports/glerl-175/tm-175-Appendix\\_A-Station\\_Information-2015.xlsx](https://www.glerl.noaa.gov/pubs/tech_reports/glerl-175/tm-175-Appendix_A-Station_Information-2015.xlsx)

### APPENDIX B. ABUNDANCE, 2015.

Density reported as no./m<sup>2</sup>. Individual taxa are identified by four letter codes (see [Table 4](#)).

[https://www.glerl.noaa.gov/pubs/tech\\_reports/glerl-175/tm-175-Appendix\\_B-Abundance-2015.xlsx](https://www.glerl.noaa.gov/pubs/tech_reports/glerl-175/tm-175-Appendix_B-Abundance-2015.xlsx)

### APPENDIX C. BIOMASS, 2015.

Biomass reported as wet weight in g/m<sup>2</sup>. Individual taxa are identified by four letter codes (See [Table 4](#)).

[https://www.glerl.noaa.gov/pubs/tech\\_reports/glerl-175/tm-175-Appendix\\_C-Biomass-2015.xlsx](https://www.glerl.noaa.gov/pubs/tech_reports/glerl-175/tm-175-Appendix_C-Biomass-2015.xlsx)

### APPENDIX D. *DREISSENA* AFDW BIOMASS, 2015.

Calculated biomass of *Dreissena r. bugensis* reported as ash-free dry weight in g/m<sup>2</sup>. Total wet weight in g/m<sup>2</sup> (from Appendix C) is also provided to facilitate comparison between the two metrics.

[https://www.glerl.noaa.gov/pubs/tech\\_reports/glerl-175/tm-175-Appendix\\_D-Dreissena\\_AFDW\\_biomass-2015.xlsx](https://www.glerl.noaa.gov/pubs/tech_reports/glerl-175/tm-175-Appendix_D-Dreissena_AFDW_biomass-2015.xlsx)

### APPENDIX E. *DREISSENA* SIZE DISTRIBUTION, 2015.

Counts per 1-mm size bin of *Dreissena r. bugensis*, based on shell length. Note: Values here have not been converted to density. Size bins are designated as “size1” for mussels 0-1.99 mm in length, “size2” for 2.00-2.99 mm mussels, etc. Broken individuals were not measured for length but were counted in the category termed “broken.”

[https://www.glerl.noaa.gov/pubs/tech\\_reports/glerl-175/tm-175-Appendix\\_E-Dreissena\\_Size\\_Distribution-2015.xlsx](https://www.glerl.noaa.gov/pubs/tech_reports/glerl-175/tm-175-Appendix_E-Dreissena_Size_Distribution-2015.xlsx)

Table 1. Location, depth, and described substrate of sites sampled in Lake Michigan in 2015.

Region/Station	Depth	Latitude (N)	Longitude (W)	Substrate
<b>South</b>				
A-1*	17.3	42°06.5530	086°31.9709	sand
A-2*	29.9	42°06.0153	086°36.9776	silt and clay
A-4	72.4	42°03.4904	087°06.5073	100% mud
B-2*	49.6	42°23.9931	086°27.0413	100% mud
B-3*	62.0	42°23.9757	086°35.4838	100% mud
B-4*	126.0	42°23.5103	087°00.9441	silty clay
B-5*	102.7	42°22.5024	087°20.9581	silt and clay
B-6*	82.4	42°22.5274	087°29.9469	silt
B-7*	43.7	42°21.9742	087°39.9606	silty sand
C-1*	17.7	42°49.6624	086°14.8867	sand
C-2	45.0	42°49.6581	086°18.1607	silt, clay
C-3*	77.3	42°49.1494	086°28.4125	silt
C-45	45.2	42°09.5638	087°30.1969	silty sand
C-5*	129.0	42°48.9918	086°49.9923	silty clay
C-6*	98.0	42°47.6759	087°26.7942	95% silt over loam, 5% sand
C-7*	58.5	42°47.5263	087°34.4815	90% sand, 10% mud
EG-12*	54.0	42°20.8597	087°36.9207	sandy silt
EG-14*	93.3	42°22.6546	086°46.4204	100% silt
EG-18*	55.3	42°17.6162	086°38.5844	100% silt
EG-22*	46.4	43°06.1985	086°21.9813	silt
F-2	44.3	42°30.0489	086°21.8592	100% mud
F-3	71.6	42°30.1042	086°31.4951	silty mud variable, mostly sand, some gravel & mud
G-45	43.3	41°56.9564	087°13.4598	
H-8*	17.8	42°23.9597	087°46.2676	silt over loam, no <i>Dreissena</i>
H-9*	39.8	42°26.7390	087°42.3416	80% silt, some loam and sand
H-11*	69.9	42°33.2505	087°35.8191	80% silt, 20% sand
H-13*	17.9	41°55.5694	087°29.4711	90% sand, 10% shells
H-14*	34.9	42°04.3359	087°27.2110	sand
H-15*	56.2	42°09.5212	087°26.0221	silty sand
H-18*	19.8	41°58.9774	086°36.0354	silty sand
H-19*	34.8	42°00.0033	086°41.0855	silty ooze
H-20*	53.6	42°00.8410	086°45.1599	silty mud, ooze
H-21*	72.0	42°02.4175	086°53.0036	silty fine sediment, ooze like
H-22*	51.3	42°08.3490	086°39.8233	silt, soft
H-24*	19.0	42°23.2856	086°20.0614	100% sand
H-28*	22.3	42°37.7982	086°15.9440	100% sand
H-29*	37.1	42°37.8117	086°18.3111	silty sand
H-30*	73.5	42°37.8048	086°25.9938	black silt
H-31*	43.0	43°02.4984	086°19.9544	silty clay

Region/Station	Depth	Latitude (N)	Longitude (W)	Substrate
M-25	26.0	43°12.0097	086°22.6710	sand
M-45	42.5	43°11.4208	086°25.7241	50% sand, 50% mud
N-2	37.0	41°53.5031	086°52.0062	silt
N-3	60.1	41°57.9916	086°59.0004	silt
Q-13	14.2	42°50.6140	087°47.9134	sand
Q-30	31.0	42°50.5888	087°39.2398	90%clay, 10% sand
R-20	22.4	42°45.0562	087°41.7560	100% sand
R-45	47.3	42°45.0205	087°36.3117	90% sand, rest dresenid shells
S-2*	10.3	41°45.9239	087°23.4838	100% fine sand
S-3*	26.5	41°50.9822	087°19.2111	90% fine sand, 10% silt
S-4*	40.2	41°56.0843	087°15.1277	sand and gravel
SAU-45	43.5	42°41.1347	086°18.8971	silty ooze
T-3	71.6	42°10.0378	086°43.0227	silt, some sand
V-1*	17.5	41°41.7981	087°00.7974	variable, clay, sandy silt
V-2*	28.4	41°48.9911	087°02.9051	thick silt
X-1*	35.6	43°08.2531	086°21.6891	variable, silt/clay, some sand
X-2*	100.6	43°11.9988	086°31.0275	85% silt, 15% sand

\* Stations that were originally part of NOAA's benthic monitoring program in the southern basin in the 1990s (Nalepa et al. 1998).

**Central**

E-1	44.9	44°37.5016	086°18.2152	85% sand, 15% mud
K-2	46.8	43°20.2260	086°30.0222	80% mud, 20% sand
KE-1	22.4	44°23.3300	087°28.5020	80% sand, 10% silt, 10% dreissenid shells
KE-2	31.7	44°23.3271	087°27.6720	Variable, mostly sand, some silt
KE-3	48.1	44°23.3037	087°26.2201	80% sand, 20% silt
KE-5	78.5	44°23.3123	087°24.0022	50% sand, 50% silt
L-220	21.2	43°30.0506	086°30.1907	sand
L-230	33.4	43°30.0446	086°31.1570	50% mud, 50% sand
L-245	44.0	43°30.0491	086°31.8934	85% mud, 15% sand
L-260	60.4	43°30.0629	086°33.3126	100% dark mud
L-280	80.5	43°30.0621	086°36.1907	100% dark mud
LU-1	22.0	43°56.6498	086°32.1102	sand
LU-3	44.0	43°56.6455	086°36.4846	silty sand
LU-4	62.5	43°56.6250	086°37.6144	silty sand
LU-5	78.0	43°56.6410	086°39.0196	70% silt, 30% sand
MAN-1	20.9	44°24.7956	086°16.8948	100% sand
MAN-2	35.9	44°24.7813	086°17.1189	80% mud, 20% sand
MAN-3	44.8	44°24.7729	086°19.8942	silty clay, sand
MAN-4	58.6	44°24.8098	086°20.3585	silty sand, clay
MAN-5	74.0	44°24.7721	086°20.8248	sandy silt, clay
PW-2	32.0	43°26.8258	087°46.9135	80% silt, 20% fine sand

<b>Region/Station</b>	<b>Depth</b>	<b>Latitude (N)</b>	<b>Longitude (W)</b>	<b>Substrate</b>
PW-3	44.9	43°26.8217	087°46.1627	80% silt, 20% fine sand
PW-4	59.5	43°26.8348	087°43.9985	silty clay, sand
PW-5	79.0	43°26.8325	087°41.8609	silty clay, sand
SY-1	22.5	43°55.0747	087°39.8279	silty sand
SY-2	31.0	43°55.0780	087°38.8513	silt
SY-4	59.0	43°55.0786	087°30.2854	sand
SY-5	77.0	43°55.1038	087°22.5379	85% sand, 15% silt
9552	83.3	43°11.1025	087°12.5799	mud over loam
9554	109.0	43°14.2628	086°53.1725	100% mud
9556	72.9	43°18.3335	087°46.3070	silty sand
9561	130.0	43°28.2513	086°47.0433	100% mud
9562	123.0	43°29.9922	087°37.0272	silt
9564	133.0	43°36.0367	087°20.4315	silty clay
9570	165.0	43°53.1746	086°54.4904	silty mud
9574	139.0	44°04.1020	087°08.8314	tin layer mud over loam
9576	164.0	44°09.0855	086°37.2796	70% silt , 30% clay
9577	78.1	44°14.6051	087°22.4592	silty sand
9582	120.0	44°24.5028	086°22.1030	silt, detritus
9587	196.0	44°37.2816	086°21.1621	100% mud
78110	33.0	43°56.6170	086°34.7150	sand, some silt
82882	58.6	44°23.3560	087°25.3558	89% fine sand, 20% silt
82902	40.0	43 55.0850	087 37.4460	silt, fine sand
82922	17.7	43°26.8127	087°47.7663	50% fine sand, 50% silt
<b>North</b>				
EA-7	40.0	45°16.8126	085°26.1806	silty, clay, sand
FR-1	20.0	44°48.9956	086°08.3822	mostly <i>Dreissena</i> druses, some sand
FR-2	32.0	44°49.0038	086°09.3452	sand
FR-3	44.0	44°49.0065	086°10.1009	mostly silt, some sand
FR-4	56.4	44°48.9911	086°11.1107	60% silt, 40% sand
FR-5	78.8	44°48.9811	086°11.7992	70% mud, 30% sand
PET-2	38.5	45°26.7409	085°04.5516	silty sand
PET-3	39.0	45°26.7319	085°11.1409	silt, clay, sand
SB-2	35.0	44°51.7024	087°09.7100	sand
SB-3	47.6	44°51.4571	087°09.0359	sand, some clay
SB-4	60.0	44°51.4272	087°08.1949	70% sand, 30% silt
SB-5	79.9	44°51.4479	087°05.1681	silt, mud
SB-6	154.0	44°51.4508	086°55.3928	80% clay, 20% silt
SC-2	29.0	45°50.4724	086°06.3233	coarse sand
SC-3	43.5	45°49.0404	086°06.3392	silt, dreissenid shells
SC-4	60.0	45°47.3931	086°06.3204	silt
SC-5	83.0	45°45.3760	086°06.3413	silty ooze
WI-1	17.4	45°14.8408	086°54.2876	sand

<b>Region/Station</b>	<b>Depth</b>	<b>Latitude (N)</b>	<b>Longitude (W)</b>	<b>Substrate</b>
WI-2	31.3	45°14.8303	086°52.5656	sand
WI-3	45.4	45°14.8570	086°49.8001	sand
WI-5	85.0	45°14.8361	086°38.2513	60% silt, 40% sand
9597	162.0	44°58.3213	086°22.1965	silt with clay
74880	24.0	45°54.5117	085°01.4952	90% mud, 10% fine sand
74900	54.3	45°26.7280	085°13.2994	silty sand, some clay
76442	19.3	46°00.0540	085°24.5721	dark silt
76462	64.0	45°32.0863	085°38.1520	variable, mostly silt, some and rock
76471	31.5	45°14.5004	085°33.3449	silty sand
76482	28.6	45°04.1289	085°51.4266	sand
78030	33.5	45°48.7051	085°43.0632	70% silt, 30% sand
79612	20.5	45°54.0042	086°06.3019	coarse sand
81220	37.0	45°42.6096	086°24.5279	sand
81240	56.0	45°14.8459	086°40.1503	60% sand, 40% silt
82851	80.0	45°03.0013	086°55.3601	60% clay, 40% silt
82862	13.3	44°51.4530	087°11.3734	sand
95120	134.0	45°31.4113	086°10.1710	silt
<b><i>Green Bay</i></b>				
BBDN-1	11.8	45°41.9760	086°44.5177	rock and sand
BBDN-2	25.0	45°37.2398	086°44.5132	silt
BBDN-3	28.6	45°32.5008	086°44.5119	silt, alga present
LBDN-3	23.3	45°30.0167	087°05.7984	90% sand, 10% silt
84450	10.2	45°36.1817	087°05.7656	sand

Table 2. Sites where additional *Dreissena* was collected for determination of length-weight relationships in 2010 and 2015.

<b>Depth Interval</b>	<b>Year</b>	<b>Stations</b>
≤ 30 m	2010	H-18, MAN-2, PW-2, SB-2, SC-2
	2015	FR-1, H-28, M-25
31-50 m	2010	B-7, H-19, MAN-3, PW-3, SB-3, SC-3
	2015	82902, B-2, B-7, FR-3, LU-3, M-45, SB-3, SC-3
51-90 m	2010	EG-12, H-20, H-21, MAN-4, MAN-5, PW-4, PW-5, SB-4, SB-5, SC-4, SC-5, 82851
	2015	FR-5, H-21, LU-5, SB-5, SC-5, SY-5
> 90 m	2010	9582
	2015	9561, 9582, B-5, EG-14, X-2



Table 3. Relationship between shell length (SL in mm) and tissue ash-free dry weight (AFDW in mg) for *D. polymorpha* and *D. r. bugensis* at various depth intervals in Lake Michigan in 2004, 2008, 2010, and 2015. Regression constants (a, b) derived from the linear regression:  $\text{Log}_e\text{AFDW} = a + b * \text{Log}_e\text{SL}$ ; n = total number of mussels used to derive the relationship. Also given is the AFDW of a standard 15-mm individual as derived from the given regression. Regressions in 2004 and 2008 were from Nalepa et al. (2010), and regressions in 2010 were from Nalepa et al. (2014).

Year/Depth Interval (m)	No. of Stations	Species	a	b	n	R <sup>2</sup>	15 mm
<b>2004</b>							
≤ 30	2	<i>D. polymorpha</i>	-5.256	2.672	242	0.76	7.24
31-50	2	<i>D. polymorpha</i>	-5.255	2.652	242	0.80	6.87
≤ 30	2	<i>D. r. bugensis</i>	-6.095	2.968	244	0.85	6.98
31-50	2	<i>D. r. bugensis</i>	-6.969	3.316	247	0.90	7.47
<b>2008</b>							
≤ 30	1	<i>D. r. bugensis</i>	-6.299	3.193	199	0.92	10.46
31-50	1	<i>D. r. bugensis</i>	-5.469	2.659	193	0.93	5.65
<b>2010*</b>							
≤ 30	5	<i>D. r. bugensis</i>	-5.857	2.814	122	0.63	5.83 (6.70)
31-50	6	<i>D. r. bugensis</i>	-5.528	2.617	172	0.85	4.75 (5.46)
51-90	12	<i>D. r. bugensis</i>	-5.601	2.683	269	0.87	5.28 (6.07)
> 90	1	<i>D. r. bugensis</i>	-5.993	2.854	24	0.98	5.67 (6.52)
<b>2015</b>							
≤ 30	3	<i>D. r. bugensis</i>	-5.608	2.879	77	0.92	8.92
31-50	8	<i>D. r. bugensis</i>	-5.793	2.746	211	0.88	5.17
51-90	6	<i>D. r. bugensis</i>	-5.392	2.639	153	0.91	5.78
> 90	5	<i>D. r. bugensis</i>	-5.259	2.656	128	0.85	6.91

\* AFDWs in 2010 were likely underestimated by 15 % (Nalepa et al. 2014).

Table 4. List of taxa collected in Lake Michigan, 2015. The four-letter code identifies each taxa in excel files given in the [appendices](#).

<b>Taxa</b>	<b>Code</b>	<b>Taxa</b>	<b>Code</b>
Amphipoda	AMPH	Oligochaeta (continued)	
Pontoporeiidae		<i>Tasserkidrilus superiorenensis</i>	TSUP
<i>Diporeia</i> spp.	DIPO	<i>Tubifex tubifex</i>	TTUB
Gammaridae	GAMM	Immatures	
<i>Echinogammarus</i> sp.	EISC	with hair setae	IMWH
<i>Echinogammarus ischnus</i>	ECHI	without hair setae	IMWO
<i>Gammarus fasciatus</i>	GFAS	oligochaete immature	OIMM
Hyallorellidae		Naidinae	
<i>Hyallorella</i> sp.	HYAL	<i>Arcteonais lomondi</i>	ALOM
Isopoda	ISOP	<i>Chaetogaster diaphanus</i>	CDIA
Asellidae		<i>Chaetogaster diastrophus</i>	CDIS
<i>Caecidotea</i> sp.	CAEC	<i>Nais bretscheri</i>	NBRE
<i>Lirceus</i> spp.	LIRC	<i>Nais simplex</i>	NSIM
Hirudinea		<i>Nais variabilis/communis</i>	NVAR
Erpobdellidae	ERPO	<i>Opistonais serpentina</i>	OSER
Piscicolidae		<i>Piguetiella michiganensis</i>	PMIC
<i>Piscicola milneri</i>	PISC	<i>Pristina</i> sp.	PRIS
Oligochaeta		<i>Pristina osborni</i>	POSB
Enchytraeidae	ENCH	<i>Slavina appendicula</i>	SAPP
<i>Enchytraeus</i> sp.	ENCY	<i>Specaria josinae</i>	SJOS
<i>Mesenchytraeus</i> sp.	MESE	<i>Stephensoniana trivandrana</i>	STRI
Lumbriculidae		<i>Stylaria lacustris</i>	SLAC
<i>Stylodrilus heringianus</i>	SHER	<i>Uncinaiis uncinata</i>	UUNI
Naididae		<i>Vejdovskyella intermedia</i>	VINT
Tubificinae		Diptera	
<i>Aulodrilus americanus</i>	AMME	Chironomidae	
<i>Aulodrilus limnobius</i>	ALIM	Chironomini	
<i>Aulodrilus pigueti</i>	APIG	<i>Chironomus</i> spp.	CHIR
<i>Aulodrilus plurisetia</i>	APLU	<i>Cryptochironomus</i> sp.	CRYP
<i>Ilyodrilus templetoni</i>	ITEM	<i>Dicrotendipes</i> sp.	DICR
<i>Isochaetides freyi</i>	IFRE	<i>Dicrotendipes fumidus</i>	DFUM
<i>Limnodrilus cervix</i>	LCER	<i>Endochironomus</i> sp.	ENDO
<i>Limnodrilus claparedianus</i>	LCLA	<i>Glyptotendipes</i> sp.	GLYP
<i>Limnodrilus hoffmeisteri</i>	LHOF	<i>Harnischia</i> sp.	HARN
<i>Limnodrilus profundicola</i>	LPRO	<i>Hydrobaenus</i> sp.	HYDR
<i>Limnodrilus udekemianus</i>	LUDE	<i>Microchironomus</i> sp.	MICH
<i>Paranais frici</i>	PFRI	<i>Microtendipes</i> sp.	MICO
<i>Potamothenrix bavaricus</i>	PBAV	<i>Microtendipes pedullus</i>	MPED
<i>Potamothenrix moldaviensis</i>	PMOL	<i>Parachironomus</i> sp.	PCHI
<i>Potamothenrix vejdoskyii</i>	PVEJ	<i>Paracladopelma</i> sp.	PCLA
<i>Psammoryctides californianus</i>	PCAL	<i>Paracladopelma undine</i>	PUDI
<i>Quistadrilus multisetosus</i>	QMUL	<i>Paracladopelma winnelli</i>	PWIN
<i>Spirosperma ferox</i>	SFER	<i>Paralauterborniella</i> sp.	PLAU
<i>Spirosperma nikolskyi</i>	SNIK	<i>Paratendipes</i> sp.	PART
<i>Tasserkidrilus americanus</i>	TAME	<i>Paratendipes albimanus</i>	PALB

Taxa	Code	Taxa	Code
Diptera (continued)		Pelecypoda	
<i>Phaenopsectra obediens</i> gr.	POBE	Sphaeriidae	
<i>Polypedilum</i> sp.	POLY	<i>Pisidium</i> sp.	PISI
<i>Polypedilum scalaenum</i> gr.	PSCA	<i>Sphaerium</i> sp.	SPHA
<i>Polypedilum tuberculum</i>	PTUB	Dreissenidae	
<i>Pseudochironomus</i> sp.	PSEU	<i>Dreissena rostriformis bugensis</i>	DBUG
<i>Stictochironomus</i> sp.	STIC	Gastropoda	
<i>Tribelos</i> sp.	TRIB	Hydrobiidae	
Unidentified Chironomidae	UNCH	<i>Amnicola limnosa</i>	ALMO
Diamesinae		Planorbidae	
<i>Potthastia</i> sp.	POTT	<i>Gyraulus parvus</i>	GYRA
<i>Protanypus</i> sp.	PROT	Physidae	
Orthocladiinae		<i>Physella</i> sp.	PHYS
<i>Cricotopus</i> sp.	CRIC	Valvatidae	
<i>Heterotrissocladius</i> sp.	HETE	<i>Valvata sincera</i>	VSIN
<i>Heterotrissocladius changi</i>	HCHA	<i>Valvata sincera/perdepressa</i>	VPER
<i>Heterotrissocladius marcidus</i> gr.	HMAR	Platyhelminthes	
<i>Heterotrissocladius subpilosus</i> -gr.	HSUB	Turbellaria	TURB
<i>Othocladius</i> sp.	ORTH	<i>Girardia tigrina</i>	GIRA
<i>Paracricotopus</i> sp.	PCRI	Neorophora	
<i>Parakiefferiella</i> sp.	PKIE	<i>Hydrolimax grisea</i>	HGRI
<i>Paratrichocladius</i> spp.	PTRI	Rhabdozoa	
<i>Psectrocladius</i> sp.	PSEC	<i>Mesostoma</i> sp.	MESO
<i>Psectrocladius psilopterus</i>	PPSI	Nemertea	
Unidentified Orthocladinae	UNOR	<i>Prostoma</i> sp.	PROS
Tanypodinae		Coelenterata	
<i>Ablabesmyia</i> sp.	ABAL	<i>Hydra</i> sp.	HDRA
<i>Ablabesmyia mallochi</i>	AMAL	Arachnida	
<i>Procladius</i> sp.	PROC	<i>Hydrachnidia</i> spp.	HACH
<i>Procladius tuberculum</i>	PRTU	Coleoptera	
<i>Thienemannimyia</i> gr.	THIE	<i>Stenelmis</i> sp.	STEN
Unidentified Tanypodinae	UNTA	Mysidacea	
Tanytarsini		<i>Mysis relicta</i>	MYSI
<i>Cladotanytarsus</i> sp.	CTAN	Unknown	UNKN
<i>Micropsectra</i> sp.	MICR	Oligochaeta fragment	OFRA
<i>Paratanytarsus</i> sp.	PARA		
<i>Stempellinella</i> sp.	STEM		
<i>Tanytarsus</i> sp.	TANY		

Table 5. Mean ( $\pm$  SE) density (no./ m<sup>2</sup>) of *Diporeia*, *Dreissena polymorpha*, and *Dreissena r. bugensis* at four depth intervals (< 30 m, 31-50 m, 51-90 m, and > 90 m) in each survey year. n = number of stations sampled. T-tests were used to determine differences between 2010 and 2015: \* significant at P < 0.05, \*\* significant at P < 0.01. Note: Values for 2010 are slightly different than values given in Table 5 of Nalepa et al. (2014) as some stations in Table 5 of Nalepa et al. (2014) were placed into the wrong depth interval.

Depth Interval/Taxa	Year				
	1994-95	2000	2005	2010	2015
$\leq 30$ m	n = 16	n = 38	n = 41	n = 40	n = 29 <sup>1</sup>
<i>Diporeia</i>	3,907 $\pm$ 1,005	853 $\pm$ 315	104 $\pm$ 88	1 $\pm$ 1	0 $\pm$ 0
<i>D. polymorpha</i>	730 $\pm$ 509	2,113 $\pm$ 539	258 $\pm$ 86	0 $\pm$ 0	0 $\pm$ 0
<i>D. r. bugensis</i>	0 $\pm$ 0	51 $\pm$ 26	7,547 $\pm$ 1,566	9,443 $\pm$ 1,593	2,405 $\pm$ 710**
31-50 m	n = 11	n = 36	n = 36	n = 39	n = 46 <sup>2</sup>
<i>Diporeia</i>	6,111 $\pm$ 1,377	2,116 $\pm$ 563	24 $\pm$ 16	<1 $\pm$ <1	0 $\pm$ 0
<i>D. polymorpha</i>	252 $\pm$ 239	1,021 $\pm$ 511	427 $\pm$ 109	1 $\pm$ 1	0 $\pm$ 0
<i>D. r. bugensis</i>	0 $\pm$ 0	11 $\pm$ 9	15,838 $\pm$ 2,860	12,595 $\pm$ 1,166	5,880 $\pm$ 642**
51-90 m	n = 32	n = 41	n = 41	n = 41	n = 42 <sup>3</sup>
<i>Diporeia</i>	6,521 $\pm$ 562	3,469 $\pm$ 464	548 $\pm$ 131	98 $\pm$ 49	1 $\pm$ <1
<i>D. polymorpha</i>	< 1 $\pm$ <1	16 $\pm$ 8	38 $\pm$ 29	0 $\pm$ 0	0 $\pm$ 0
<i>D. r. bugensis</i>	0 $\pm$ 0	0 $\pm$ 0	6,472 $\pm$ 1,704	14,811 $\pm$ 1,310	9,223 $\pm$ 793*
>90 m	n = 25	n = 13	n = 13	n = 18	n = 18
<i>Diporeia</i>	4,547 $\pm$ 385	2,804 $\pm$ 453	1,244 $\pm$ 217	429 $\pm$ 122	528 $\pm$ 186
<i>D. polymorpha</i>	0 $\pm$ 0	0 $\pm$ 0	<1 $\pm$ <1	0 $\pm$ 0	0 $\pm$ 0
<i>D. r. bugensis</i>	0 $\pm$ 0	0 $\pm$ 0	12 $\pm$ 7	1,881 $\pm$ 907	2,747 $\pm$ 858
Green Bay ( $\leq 30$ m)				n = 6	n = 5
<i>Diporeia</i>		26 $\pm$ 25	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
<i>D. polymorpha</i>		820 $\pm$ 444	80 $\pm$ 53	0 $\pm$ 0	0 $\pm$ 0
<i>D. r. bugensis</i>		1 $\pm$ 1	6,640 $\pm$ 3,637	5,990 $\pm$ 2,140	3,797 $\pm$ 1,270

<sup>1</sup>n=26 for *Diporeia*

<sup>2</sup>n=38 for *Diporeia*

<sup>3</sup>n=37 for *Diporeia*

Table 6. Percentage of measured *D. r. bugensis* within various size categories at four depth intervals ( $\leq 30$  m, 31-50 m, 51-90 m, and  $> 90$  m) in 2010 and 2015. Categories based on shell length (mm). All collected mussels were measured in 2015. In 2010, mussels were measured from representative sites (details for 2010 are given in Nalepa et al. 2014). Data excludes mussels collected in Green Bay.

Interval/Year	Shell Length (mm)						
	< 5	5-10	10-15	15-20	20-25	25-30	> 30
$\leq 30$ m							
2010	62.0	19.4	12.4	5.1	1.0	<0.1	0.0
2015	74.5	5.8	5.4	8.8	4.8	0.7	<0.1
31-50 m							
2010	41.1	29.6	16.8	8.9	3.3	0.3	<0.1
2015	22.2	20.8	24.5	21.0	9.6	1.7	0.2
51-90 m							
2010	55.1	17.0	17.2	8.5	1.9	0.2	<0.1
2015	40.5	21.1	18.1	15.0	4.7	0.7	<0.1
$> 90$ m							
2010	73.5	13.9	7.7	4.5	0.3	<0.1	0.0
2015	55.3	20.6	12.0	7.7	3.7	0.7	<0.1

Table 7. Mean ( $\pm$  SE) density (no./ m<sup>2</sup>) of major macroinvertebrate taxa at four depth intervals ( $\leq$  30 m, 31-50 m, 51-90 m, and  $>$  90 m) at 40 sites in the southern basin of Lake Michigan. n= 12, 10, 12, and 6 for the four intervals, respectively.

Depth Interval/Taxa	Year		
	1992-1993	1998-1999	2015
$\leq$ 30 m			
<i>Diporeia</i>	2,624 $\pm$ 568	183 $\pm$ 125	0 $\pm$ 0
<i>Dreissena</i>	1,159 $\pm$ 855	1,521 $\pm$ 524	1,227 $\pm$ 555
Oligochaeta	1,684 $\pm$ 430	1,965 $\pm$ 355	4,087 $\pm$ 1,265
Chironomidae	187 $\pm$ 29	297 $\pm$ 46	531 $\pm$ 437
Sphaeriidae	900 $\pm$ 287	330 $\pm$ 139	87 $\pm$ 45
31-50 m			
<i>Diporeia</i>	7,857 $\pm$ 852	1,425 $\pm$ 450	0 $\pm$ 0
<i>Dreissena</i>	16 $\pm$ 6	955 $\pm$ 333	7323 $\pm$ 1,637
Oligochaeta	3,050 $\pm$ 315	4,077 $\pm$ 762	6,626 $\pm$ 1,430
Chironomidae	100 $\pm$ 18	52 $\pm$ 12	202 $\pm$ 156
Sphaeriidae	1,677 $\pm$ 304	1,069 $\pm$ 181	7 $\pm$ 7
51-90 m			
<i>Diporeia</i>	5,911 $\pm$ 385	3,487 $\pm$ 616	0 $\pm$ 0
<i>Dreissena</i>	1 $\pm$ $<$ 1	3 $\pm$ 1	9,541 $\pm$ 1,757
Oligochaeta	1,693 $\pm$ 125	2,019 $\pm$ 244	2,924 $\pm$ 650
Chironomidae	66 $\pm$ 12	28 $\pm$ 7	6 $\pm$ 3
Sphaeriidae	597 $\pm$ 139	620 $\pm$ 68	12 $\pm$ 8
$>$ 90 m			
<i>Diporeia</i>	3,201 $\pm$ 477	3,314 $\pm$ 597	207 $\pm$ 207
<i>Dreissena</i>	0 $\pm$ 0	2 $\pm$ 2	5,819 $\pm$ 1,792
Oligochaeta	1,124 $\pm$ 141	996 $\pm$ 131	887 $\pm$ 196
Chironomidae	45 $\pm$ 10	26 $\pm$ 7	7 $\pm$ 6
Sphaeriidae	106 $\pm$ 36	175 $\pm$ 62	15 $\pm$ 8

Table 8. Mean ( $\pm$  SE) biomass (gAFDW/m<sup>2</sup>) of *Dreissena* at  $\leq 30$  m, 31-50 m, 51-90 m, and  $> 90$  m depth intervals based on the latest lake-wide surveys in Lake Michigan, Lake Ontario, and Lake Huron. Given in parenthesis is the number of stations sampled.

<b>Depth Interval</b>	<b><i>Dreissena</i> Biomass (gAFDW/m<sup>2</sup>)</b>		
	<b>Lake Michigan in 2015</b>	<b>Lake Ontario in 2013</b>	<b>Lake Huron in 2012</b>
$\leq 30$ m	8.02 $\pm$ 3.33 (29)	21.53 $\pm$ 7.92 (8)	2.65 $\pm$ 1.77 (19)
31-50 m	26.75 $\pm$ 3.07 (46)	28.79 $\pm$ 9.63 (8)	13.91 $\pm$ 4.43 (30)
51-90 m	28.59 $\pm$ 1.99 (42)	20.86 $\pm$ 1.82 (8)	5.43 $\pm$ 2.45 (26)
$> 90$ m	6.90 $\pm$ 2.26 (18)	7.08 $\pm$ 2.16 (21)	4.32 $\pm$ 3.97 (8)

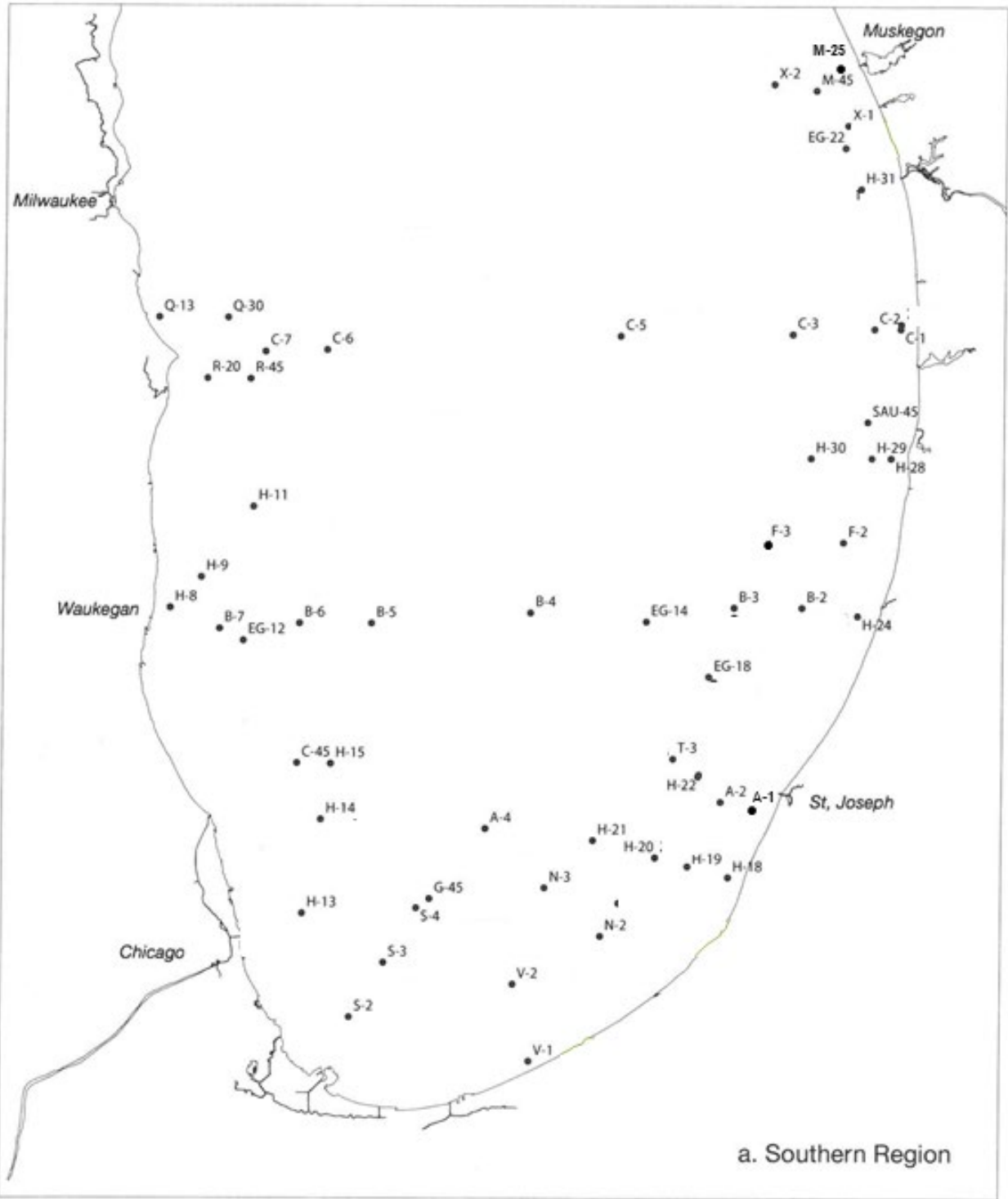
Table 9. Mean ( $\pm$ SE) biomass (gAFDW/m<sup>2</sup>) of non-dreissenid taxa at sites in the 18-30 m, 31-50 m, 51-90 m, and >90 m depth intervals in Lake Michigan in 2015. Values were determined from wet weight (g WW/ m<sup>2</sup>; [Appendix C](#)) using conversion factors given in the text.

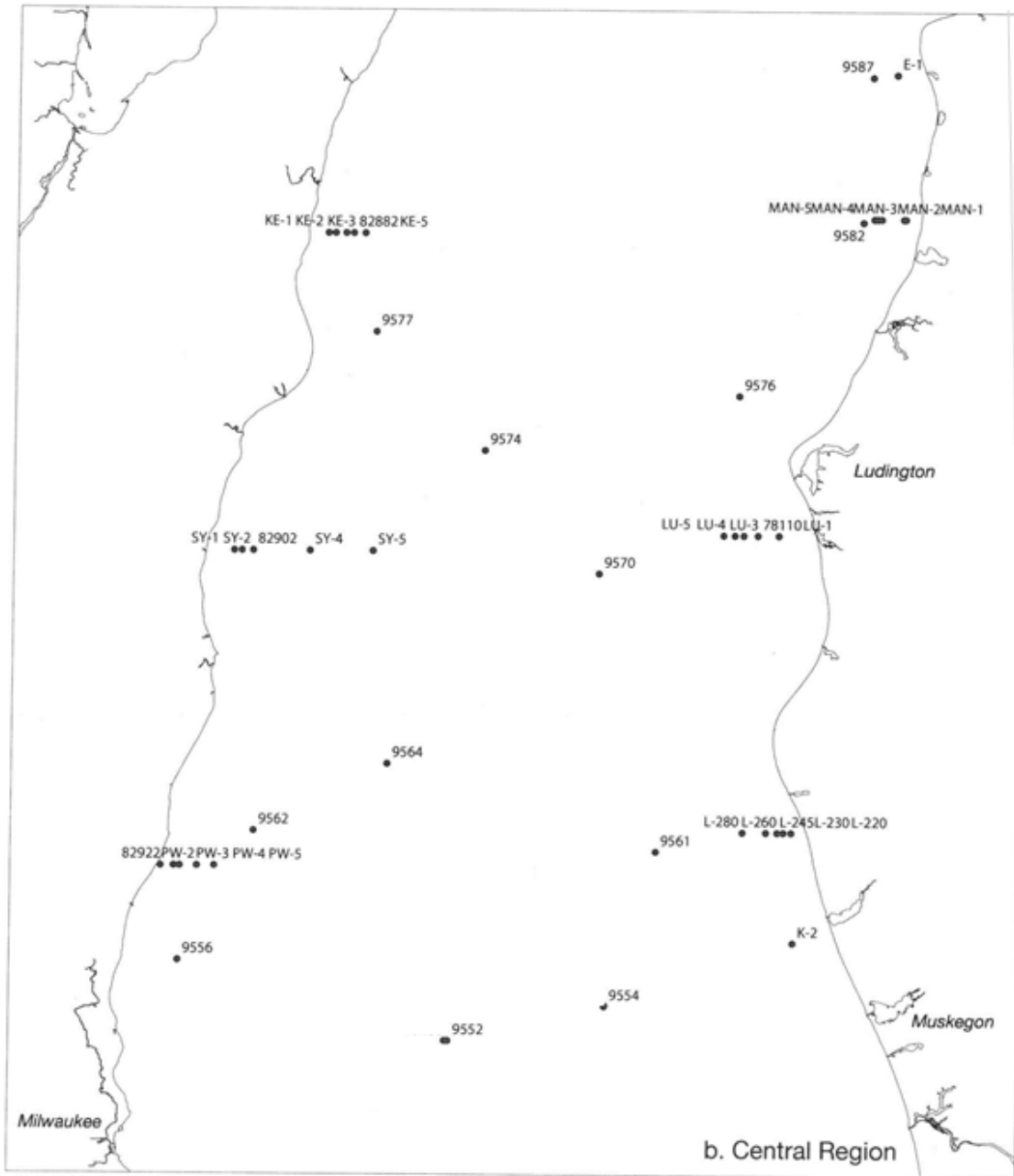
Depth Interval	Taxa				
	<i>Diporeia</i>	Oligochaeta	Chironomidae	Sphaeriidae	Other <sup>*</sup>
18-30 m	0 $\pm$ 0	0.39 $\pm$ 0.10	0.07 $\pm$ 0.04	<0.01 $\pm$ < 0.01	0.16 $\pm$ 0.07
31-50 m	0 $\pm$ 0	0.59 $\pm$ 0.09	0.02 $\pm$ <0.01	0 $\pm$ 0	0.03 $\pm$ 0.02
51-90 m	0 $\pm$ 0	0.32 $\pm$ 0.05	0.01 $\pm$ <0.01	0 $\pm$ 0	<0.01 $\pm$ <0.01
>90 m	0.17 $\pm$ 0.06	0.10 $\pm$ 0.02	<0.01 $\pm$ <0.01	<0.01 $\pm$ <0.01	<0.01 $\pm$ <0.01

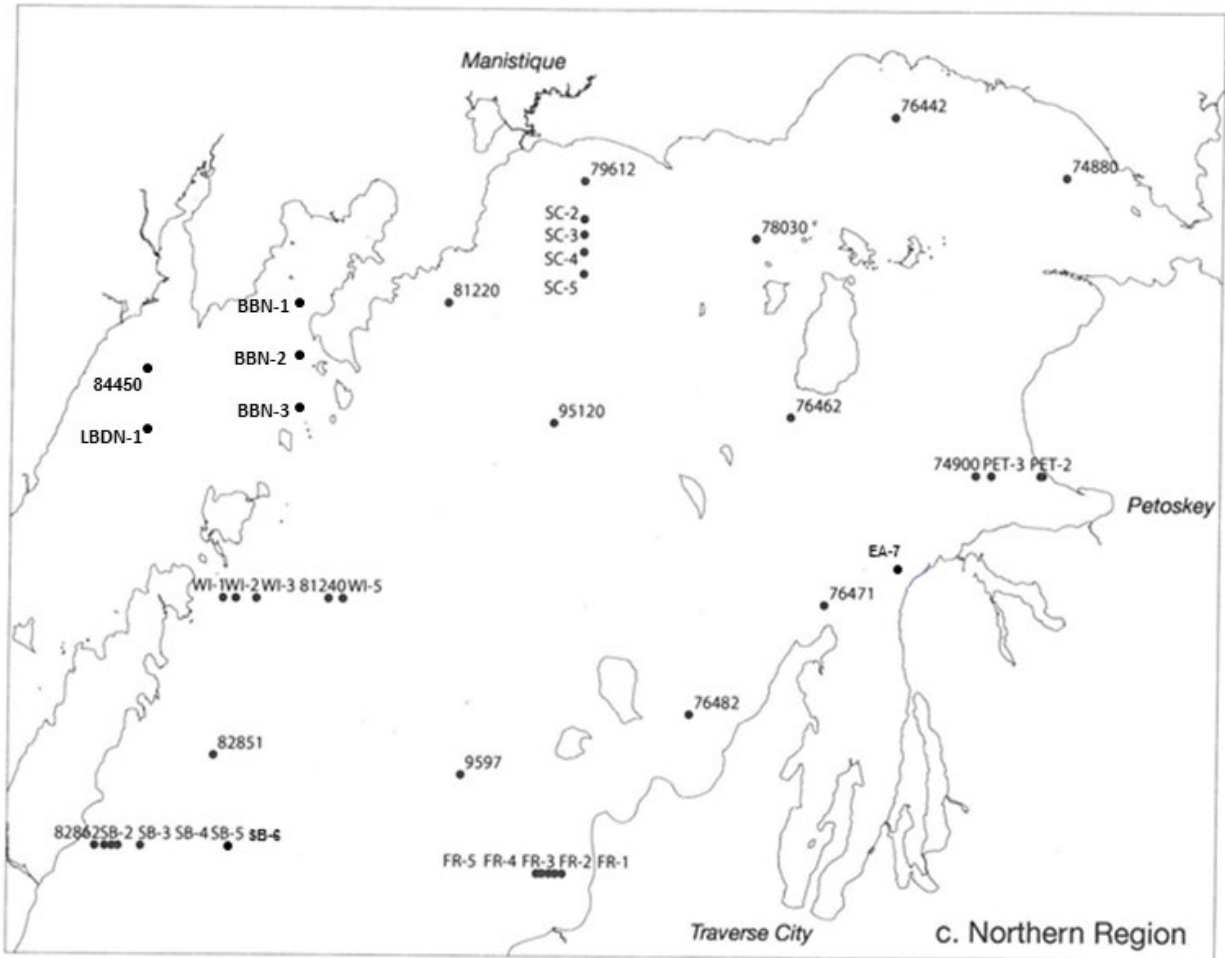
<sup>\*</sup>Does not include *Mysis relicta*.



Figures 1a-c. Location of sampling sites in Lake Michigan in 2015 (see Table 1; [Appendix A](#)).







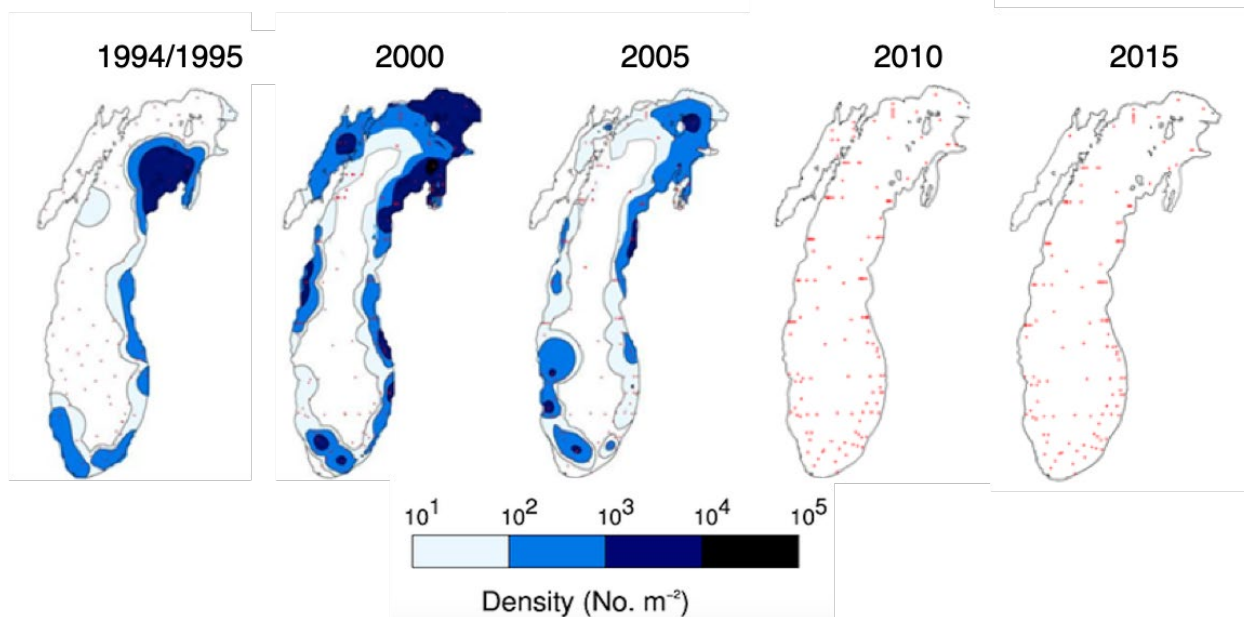


Figure 2. Density (no. per m<sup>2</sup>) of *Dreissena polymorpha* in Lake Michigan based on lake-wide surveys in 1994/1995, 2000, 2005, 2010, and 2015. *Dreissena polymorpha* was not found in the 2015 survey. Small red dots indicate location of sampling sites.

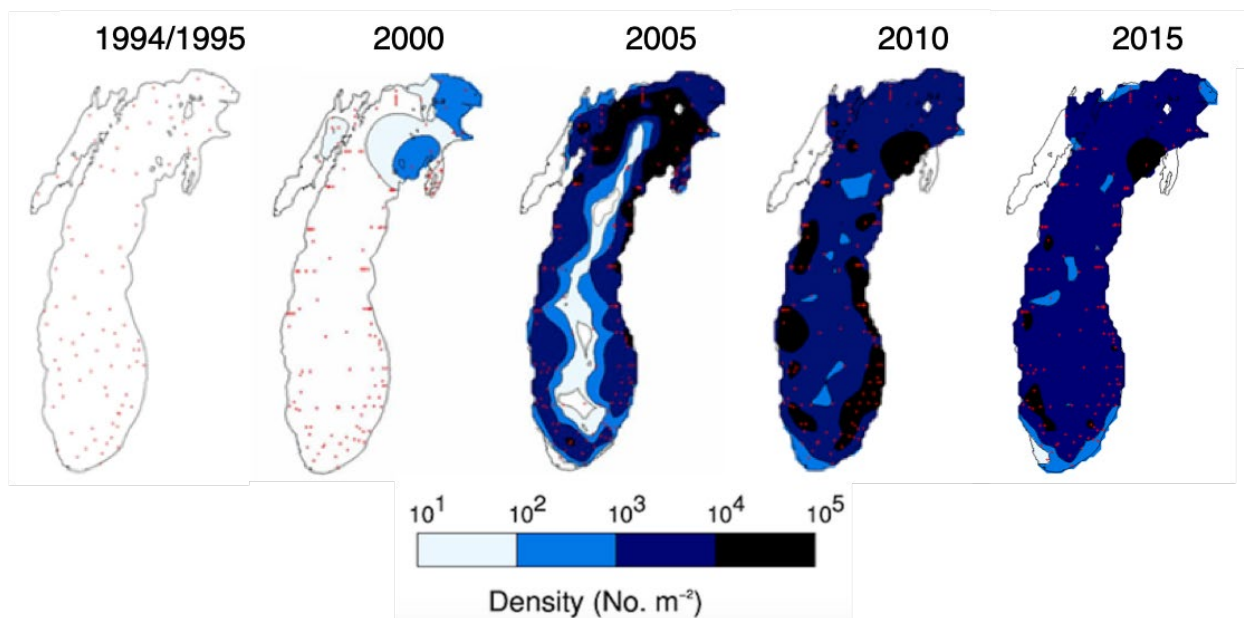


Figure 3. Density (no. per m<sup>2</sup>) of *Dreissena r. bugensis* in Lake Michigan based on lake-wide surveys in 1994/1995, 2000, 2005, 2010, and 2015. Small red dots indicate location of sampling sites.

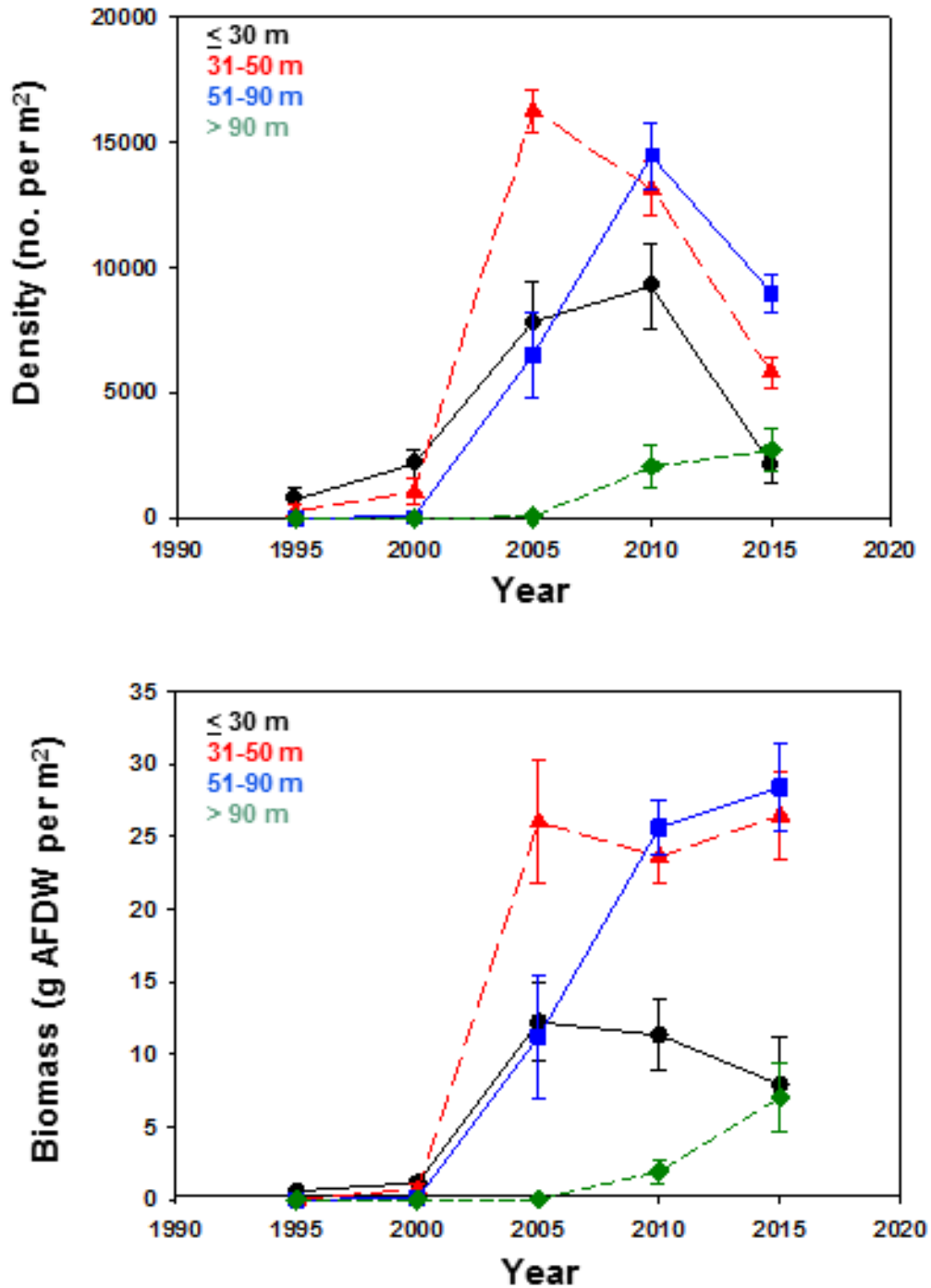


Figure 4. Long-term trends of total *Dreissena* in Lake Michigan in 1994/1995, 2000, 2005, 2010, and 2015. Values given are lake-wide means ( $\pm$  SE) at four depth intervals:  $\leq 30$  m (black, circles), 31-50 m (red, triangles), 51-90 m (blue, squares), and  $> 90$  m (green, diamonds). Upper panel = density; lower panel = biomass.

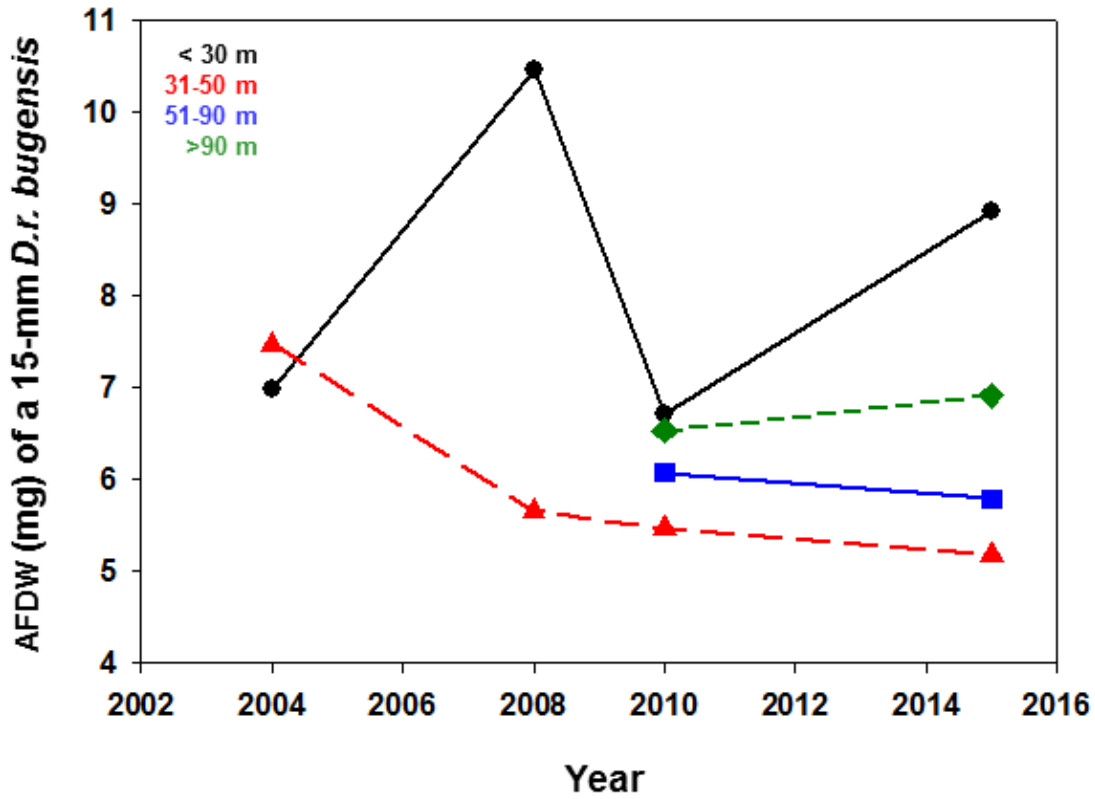


Figure 5. Ash free dry weight (AFDW, mg) of a standard 15-mm *D. r. bugensis* at four depth intervals in Lake Michigan between 2004 and 2015. Values derived from regressions given in Table 4. Depth intervals:  $\leq 30$  m (black, circles), 31-50 m (red, triangles), 51-90 m (blue, squares), and  $> 90$  m (green, diamonds).

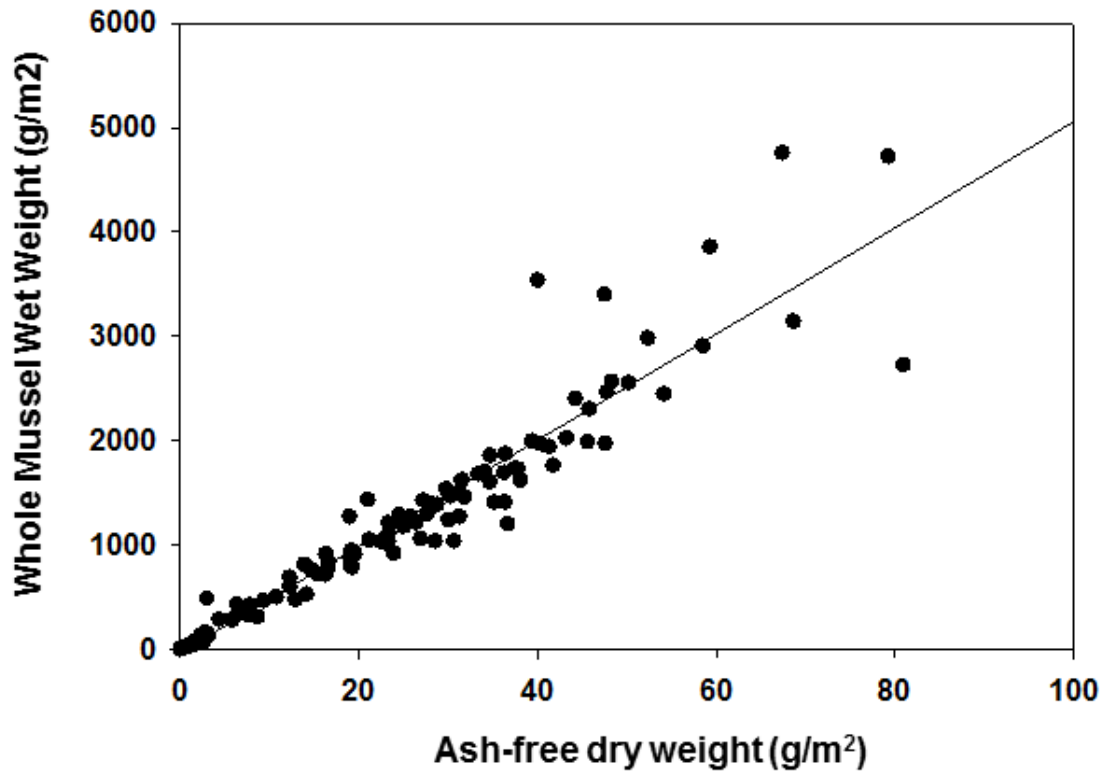


Figure 6. Relationship between ash free dry weight (AFDW) and total wet weight (TWW, whole mussel, tissue and shell) of *D. r. bugenisis* at each sampling site in the main basin of Lake Michigan in 2015 (n=135). The regression through the origin was defined as:  $TWW = 50.25 * AFDW$  ( $R^2 = 0.92$ )



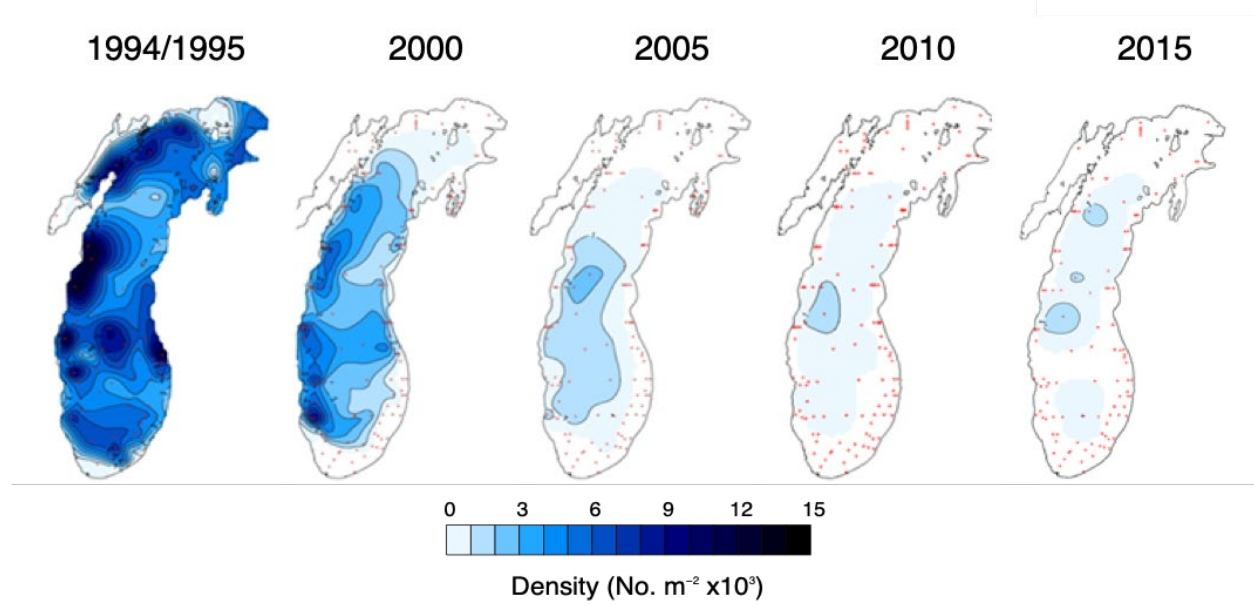


Figure 7. Density (no. per m<sup>2</sup>) of *Diporeia* spp. in Lake Michigan based on lake-wide surveys in 1994/1995, 2000, 2005, 2010, and 2015. Small red dots indicate location of sampling sites.

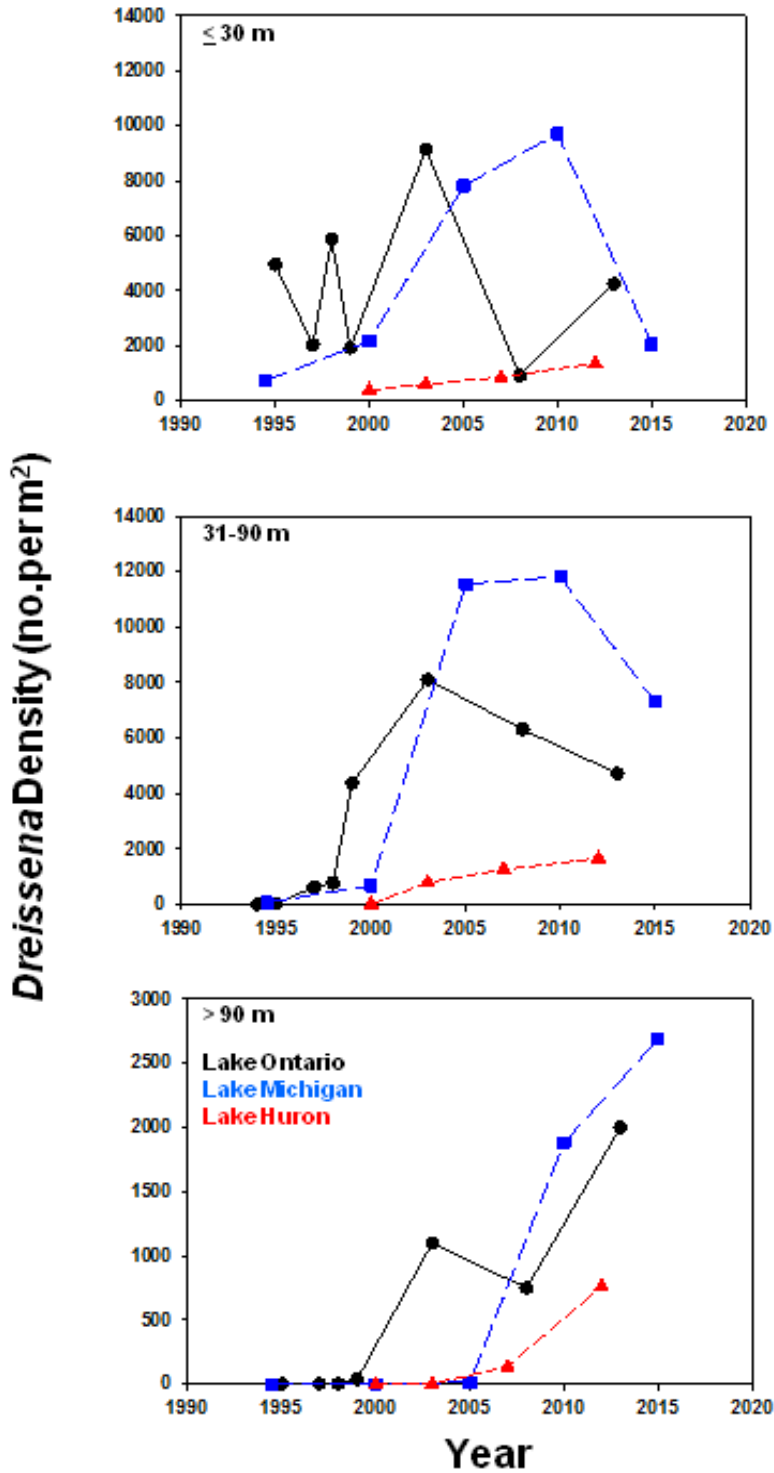


Figure 8. Density (no. per m<sup>2</sup>) of total *Dreissena* at < 30 m (upper panel), 31-90 m (middle panel), and > 90 m (lower panel) in Lake Ontario (black, circle), Lake Michigan (blue, square), and Lake Huron (red, triangle). Values taken from the following sources: Lake Ontario (Birkett et al. 2015, Nalepa and Elgin unpublished), Lake Michigan (Nalepa et al. 2014, this study); Lake Huron (Nalepa et al. 2007, Nalepa et al. 2018). Note the different scale for the > 90 m interval.