Distribution patterns of the early invasion of zebra mussels, *Dreissena polymorpha* (Pallas, 1771), in the south basin of Lake Winnipeg

Eva C. Enders*, Colin Charles, Amanda L. Caskenette, Tyana A. Rudolfsen and Doug A. Watkinson

*Corresponding author

**Abstract**

Aquatic invasive species (AIS) pose significant threats to the biodiversity of freshwater ecosystems worldwide. Consequently, it is crucial to understand the distribution and growth rates of AIS to protect susceptible lakes and rivers from potential invasions. Zebra mussels (*Dreissena polymorpha*) originated from the Ponto-Caspian region and were first recorded in the mid-1980s in the North American Laurentian Great Lakes. In 2013, zebra mussels were first observed in four harbours on Lake Winnipeg, Manitoba, Canada. Since then, the species appears to be spreading rapidly throughout Lake Winnipeg. Here, we present the results of the distribution of zebra mussels in the south basin of Lake Winnipeg along a 7 × 7 km grid. In fall of 2016, zebra mussels were widely distributed in the south basin of Lake Winnipeg. The highest observed density of zebra mussels on artificial substrate was 16.5 individuals per cm². Mean length of zebra mussels decreased with depth and latitude. This work provides valuable information for the management of AIS prevention and monitoring programs for waterbodies with similar conditions in Central and Western Canada and the United States.

**Key words:** aquatic invasive species, distribution, growth, settlement

**Introduction**

The introduction of aquatic invasive species (AIS) into waterbodies may occur either naturally, or more frequently, accidentally or intentionally through human activities (Welcomme 1992). By displacing and outcompeting native species, invasive species can alter aquatic ecosystems (Dukes and Mooney 1999). Often, invasive species show fast population expansion in the absence of natural predators and/or competitors and thereby rapidly establish to the point where eradication of the AIS is impossible (Pagnucco and Ricciardi 2015). Considering the potential ecological and economic impacts, predicting the distribution and abundance of AIS on freshwater ecosystems is invaluable for the design and implementation of prevention and control programs. In particular, identifying factors affecting the proliferation of AIS and understanding their distribution are of key importance.
Zebra mussel, *Dreissena polymorpha* (Pallas, 1771), a freshwater mollusk that originated from the Ponto-Caspian area (Black, Caspian, and Azov seas), was introduced into various watersheds of Europe and North America likely through ballast water exchange (Ricciardi and MacIsaac 2000). In North America, zebra mussels were first observed in Lake St. Clair in the mid-1980s and spread quickly throughout the Laurentian Great Lakes and eventually the Eastern United States and Eastern Canada (Mellina and Rasmussen 1994). In mid-October 2013, zebra mussels were first observed in several harbours (Silver, Gimli, Winnipeg Beach, and Balsam Bay) in Lake Winnipeg, Manitoba, Canada (DFO 2014). In an attempt to eradicate zebra mussels at this early stage of invasion, a Potash treatment was administered in the four harbours in the south basin due to its degree of effectiveness, low environmental impact, and ability to gain regulatory approvals (Mackie and Claudi 2010; Manitoba Sustainable Development 2014; Glomski 2015). The treatment was thought to be a success based on 100% mortality of zebra mussels in bioassay cages placed at various locations throughout each harbour (Manitoba Sustainable Development 2014). However, zebra mussels re-established in all four sites, which suggests either incomplete eradication within the harbours by the Potash treatment or recolonization from the lake. Since 2013, veliger larvae have been observed in plankton surveys in the south basin and adult zebra mussels were detected in additional harbours (L. Janusz, pers. comm.). In addition, citizens have been reporting adult zebra mussels on beaches and harbours spanning the entire lake. However, no lake-wide monitoring survey for adult zebra mussels had been conducted to evaluate the distribution and abundance of the species throughout the south basin of Lake Winnipeg.

Zebra mussels have two distinct life stages: (1) a microscopic, pelagic veliger larva that allows for rapid dispersal and colonization and (2) a sessile juvenile and adult stage attached to substrate. Zebra mussels are typically attached to hard bottom surfaces, but have also been observed to directly colonize sand and silt sediments in Lake Erie by using their byssal threads to bind fine sediments into conglomerates (Berkman et al. 1998). They are filter-feeders with high filtration rates (Kryger and Riisgård 1988) resulting in increased water clarity (Fahnenstiel et al. 2010) and changes in the phyto- and zooplankton communities (Fishman et al. 2010). After invading the Great Lakes in the mid-1980s, zebra mussels rapidly achieved high population densities during the 1990s (MacIsaac et al. 1991). Several factors lead to the potential of a swift proliferation of zebra mussels in North American waters, including high growth and fecundity rates, early maturity at typically 1–2 years of age, and the absence of a native predator. Zebra mussels display a remarkable reproductive potential with females reproducing within 6–7 weeks of settlement (Borcherding 1991; Mackie 1991).
The objectives of this paper are to (1) document the distribution and densities of zebra mussels on artificial substrates and (2) describe the size spectra of zebra mussels throughout the south basin of Lake Winnipeg. This data will further serve as baseline data for long-term monitoring of zebra mussels in Lake Winnipeg and provides valuable input data to nutrient models for Lake Winnipeg.

Materials and methods

Study area

Lake Winnipeg is the largest lake in the province of Manitoba, Canada (52°7′N; 97°15′W) covering 24,514 km² (Figure 1a, b). Lake Winnipeg is a remnant of Glacial Lake Agassiz. The lake is a relatively shallow, elongated, and isothermal, with a mean water depth of 12 m and spanning 416 km from north to south (Manitoba Sustainable Development 2017). Lake Winnipeg’s watershed measures about 982,900 km² and covers much of Alberta, Saskatchewan, Manitoba, northwestern Ontario, Minnesota, and
North Dakota. The main tributaries analyzed in this study include the Red River flowing into Lake Winnipeg from the south and the Winnipeg River from the southeast (Figure 1c). The lake drains to the north into the Nelson River at an average annual rate of 2,066 m$^3\cdot$s$^{-1}$ and ultimately into the Hudson Bay. Lake Winnipeg is a eutrophic lake that receives excessive amounts of nutrient run-off from agricultural land use. Lake Winnipeg is also one of the largest hydro reservoirs in the world and supports one of the most productive commercial and recreational fisheries for walleye (*Sander vitreus*). Several aquatic invasive species are established in the lake including common carp (*Cyprinus carpio*) and spiny water flea (*Bythotrepes longimanus*) (Badiou and Goldsborough 2006; Jansen et al. 2017).

**Sample collection**

To obtain a quantitative understanding of the distribution and abundance of zebra mussels in Lake Winnipeg, we analyzed the zebra mussel colonization on a network of acoustic receiver setups that were deployed by Fisheries and Oceans Canada in the Lake Winnipeg basin including the Red River for a fish movement study. The receiver setups that were installed in the lake differed slightly from those in the river environments. In the lake, the setup consisted of a plastic receiver (VR2W, Vemco, Bedford, Nova Scotia, Canada), a foam float (Ethenyl-Viny Acetate, Lakefish Net and Twine, Winnipeg, Manitoba, Canada), an orange nylon ID tag (Ketchum Manufacturing Inc., Lake Luzerne, New York, USA), a 54 kg granite anchor block, a 4.5 kg navy anchor, and a twisted rope (3-Strand 707 Nylon, Lakefish Net and Twine, Winnipeg, Manitoba, Canada; Figure 2a), whereas in the river the receiver was mounted on a 12.7 mm threaded metal rod that was attached to the 54 kg granite anchor block, a foam float, an orange nylon ID tag, and a 27 kg metal king anchor were attached as well as (Figure 2b). Photos of the different components of the receiver setup

![Figure 2. Receiver setup used to analyze the settlement and distribution of zebra mussels in the Lake Winnipeg basin: (a) lake setup and (b) river setup.](image)
Geographic expansion of *Dreissena polymorpha* in Lake Winnipeg


**Figure 3.** Colonization of zebra mussel densities on the three different substrate types (a) float, (b) receiver, and (c) tag of the receiver setup that were installed in the south basin of Lake Winnipeg in 2016 and retrieved in 2017.

were taken at 71 stations in Lake Winnipeg, 25 stations in the Red River, and 8 stations in the Winnipeg River during the receiver downloads using a digital camera (Canon 7D DSLR with a 60 mm lens; Figure 3).

The equipment was installed between May 15–August 15, 2016 along a 7 km by 7 km grid throughout the south basin of Lake Winnipeg and in the channels of the Netley-Libeau Marsh. Along the Red and Winnipeg rivers, the receivers were deployed with varying distances between 5, 10, and 20 river km. The components of the acoustic receiver setup, while not “natural”, provided a consistent substrate of equal size and distribution that was readily colonized by zebra mussels, and consequently, represented a settling substrate that was optimal to study the distribution of zebra mussels using image analysis.

Three different sampling collections were conducted. Firstly, from September 15–November 10, 2016, photos were taken from all the different equipment parts of each of the acoustic receiver setup (receiver, float, ID tag, and anchor). Secondly, from July 13–August 15, 2017, zebra mussels were scraped from the receivers on the same 7 km by 7 km grid throughout the south basin of Lake Winnipeg. Thirdly, in the same time period in 2017, Ponar® grab substrate samples (229 × 229 mm surface sample area, 23 kg empty weight) were taken at 51 of the receiver stations located in the south basin of Lake Winnipeg.

**Image and sample analyses**

Using ImageJ (https://imagej.nih.gov/ij/), all images were scrutinized for the presence or absence of zebra mussels. For images in which zebra mussels were observed, the number of individuals were counted. The density of zebra mussels was estimated for each component of the receiver setup (i.e., receiver, float, and ID tag, respectively). Receivers were set at water depths of 3.3–11.5 m (mean depth: 8.3 m, S.D.: 1.4 m) in the lacustrine environments and 2.2–11.0 m (mean depth: 6.2 m, S.D.: 1.8 m) in the riverine environments. The zebra mussels scraped from the receivers
and collected in substrate samples were also counted and measured to determine length (mm) and weight (mg). Sediment samples were sieved for zebra mussels.

Data and statistical analyses

Using the zebra mussel counts obtained from the floats, counting all individuals, we spatially interpolated the density and size of zebra mussels in the south basin of Lake Winnipeg using ordinary kriging. Covariance estimates were calculated using a variogram and a spherical correlation function where values were interpolated over a 200 × 200 m grid created over the south basin of Lake Winnipeg. We limited the range of interpolation to the waterbody, removing all points outside the boundaries of the lake.

In order to understand better zebra mussel attachment rates to different artificial substrates, differences between the attachment objects (i.e., material) were compared using the mean and the 95% confidence intervals that were calculated as:

$$95\% \ CI = \mu \pm 1.96 \times \left( \frac{\sigma}{\sqrt{n}} \right)$$

where $\mu$ represents the mean, $\sigma$ the standard deviation, and $n$ is the sample size. Tukey’s tests were used to compare the means of the different substrate types (receiver, float, and ID tag).

We used generalized linear models (GLM) to create relationships between the water depth and latitude with density and mean length of zebra mussels attached to the receivers, respectively. For the latitude and mean length relationship, we tested three different link functions within the Gaussian family; (1) identity, (2) inverse, and (3) log. Akaike’s Information Criterion (AIC) was used to determine which GLM best represent the relationship between latitude and mean length of zebra mussels in the south basin of Lake Winnipeg.

Assuming that only zebra mussel veliger larvae attached to the receiver equipment (i.e., no movement of later life stages) and that they attached shortly after installation, we used the largest individual on the receiver to calculated a potential annual zebra mussel growth rate in Lake Winnipeg for the approximate one year time period between the installation of the equipment and the date the zebra mussels were scraped.

All data and statistical analyses were conducted using the R statistical programming language (R Core Team 2017).

Results

Zebra mussel distribution and densities

In fall of 2016, zebra mussels were found on 68 of 71 receiver stations installed in south basin of Lake Winnipeg. Higher numbers of zebra mussels...
settled on the floats and receivers (Tukey’s test, $t = -1.95$, $p = 0.13$) in comparison to the ID tags ($t = -4.77$, $p < 0.005$ and $t = -3.11$, $p = 0.001$, respectively) (Figure 4). The highest density of zebra mussels was attached to a float located close to Gimli Harbour with 16.5 individuals per cm$^2$ (165,000 individuals per m$^2$), followed by 14.8 individuals per cm$^2$ near Sliver Harbour (Figure 5a). Zebra mussels were observed on three receivers installed in channels of the Netley-Libau Marsh. But in contrary to the lake environment, zebra mussels were not observed on the receiver stations that were installed in the thalweg of the Red River or the Winnipeg River. Observed zebra mussel densities correlated only very weakly with water depth at which the receivers were set whereas latitude had no significant effect on zebra mussel density (GLM, $R^2 = 0.08$, $p = 0.03$ value for depth, $p = 0.09$ for latitude).

Similarly in the 2017 sampling, zebra mussels were detected on all of 67 sampled receiver stations in Lake Winnipeg but not in the Red River or the Winnipeg River. Only one of the 51 sediment samples taken in 2017 contained zebra mussels. This station (50°56’50.9″N; 96°55’48.8″W) was situated close Balaton Beach near Hnausa, Manitoba. Sediment particle size at the site did not differ substantially from that of the other sites, and consisted of colloid ($< 0.001$ mm), clay ($0.001–0.004$ mm), and silt ($0.004–0.063$ mm).
Geographic expansion of *Dreissena polymorpha* in Lake Winnipeg


**Figure 5.** (a) Zebra mussel densities (in individuals per cm²) as counted on the floats of the acoustic receiver setup that were installed in the south basin of Lake Winnipeg in 2016. (b) Zebra mussel mean shell length (in mm) from individuals scraped of the receivers in fall of 2017. Circles with crosses indicate the four harbours (Silver, Gimli, Winnipeg Beach, and Balsam Bay) in the south basin of Lake Winnipeg where zebra mussels were first detected in 2013.

**Figure 6.** Frequency distribution of the zebra mussel length (in mm) observed on acoustic receiver equipment in Lake Winnipeg, Canada, in 2017.

**Analysis of zebra mussel shell length**

From the 2017 sampling, a total of 13,426 zebra mussels were counted and their shell length was measured (Figure 5b). Mean length was 5.9 mm (± S.D. 2.8 mm, ranging 0.2 to 23.4 mm; Figure 6). Larger individuals were observed in the southern part of the south basin at shallower water depth (GLM, R² = 0.66) and mean length decreased with water depth (p < 0.001; Figure 7a) and latitude (p < 0.0001; Figure 7b). Using the Akaike’s Information Criterion, we determined that the GLM with the inverse link
best represented the relationship between latitude and mean length of zebra mussels in the south basin of Lake Winnipeg (Table 1, Figure 7b).

Under the assumption that later life stages are immobile and only veliger larvae attach and that larvae attached shortly after installation to the equipment, we estimated the growth rate of zebra mussels in Lake Winnipeg. Using the largest settled individual and the installation period of the receivers of approximately a year, the observed maximum growth rate of zebra mussels was 23.4 mm per year.

In the one sediment sample taken Lake Winnipeg in 2017 that contained zebra mussels, a total of 124 zebra mussels were observed. In comparison to the individuals found on the equipment, the mean length of zebra mussels detected in the sediment sample was substantially higher with 11.8 mm (± S.D. 2.2 mm; range 5.1 to 16.8 mm); but the maximum length was smaller (i.e., 16.8 mm vs 23.4 mm on the receivers).
Discussion

Distribution and densities of zebra mussels on artificial substrate and local sediment

Zebra mussels were first observed in Lake Winnipeg in October 2013 at very low densities of ~3 individuals per m² on available substrate in four harbours. Initial data collected in the fall of 2013 indicated that zebra mussels were in the early stage of colonization (DFO 2014). An environmental DNA (eDNA) study conducted in 2014 determined the presence of zebra mussels in Lake Winnipeg and the Red River (Gingera et al. 2017). At the time of our sampling in 2016, zebra mussels were already observed in almost all acoustic stations installed in the south basin of Lake Winnipeg, with the exception of the three receivers in Traverse Bay, which is the inflow basin of the Winnipeg River. The Winnipeg River drains from the Canadian Shield with very low calcium concentrations that are not likely to support zebra mussel populations (Therriault et al. 2012). As with other bivalves, a significant quantity of calcium is required for shell development and establishment of zebra mussels, where concentrations of >12 mg·l⁻¹ are required for survival and reproduction of adult zebra mussels (Mackie and Claudi 2010). Consequently, the low calcium concentration (<15 mg·l⁻¹) from the Canadian Shield (i.e., Winnipeg River) likely lead to limited zebra mussel distribution (Mellina and Rasmussen 1994). Zebra mussels were first detected the Red River in eDNA samples from 2014 (Gingera et al. 2017), however, zebra mussels were not observed until June 2015, when individuals were found in Selkirk Harbour. Prior to these observations, zebra mussels were not thought to be present in the Manitoban portion of the Red River (Therriault et al. 2012). Likely, zebra mussel veliger larvae did not settle on the receivers in the Red River due to the strong current in the thalweg. Highest densities were observed on two receiver stations that were close to harbours where zebra mussels were first observed in Lake Winnipeg (Gimli and Silver harbours).

Zebra mussels have been described to preferentially settle at water depths of 4–6 m, however, colonization is possible at both shallower and deeper water depths (Bially and MacIsaac 2000). In our study, zebra mussels were observed to settle over wide range of water depths (2.2–11.5 m) in Lake Winnipeg. The sediment samples containing zebra mussels showed that even fine sediments (<0.063 mm) can serve as suitable settling substrates for zebra mussels, as it has been observed in other lakes in North America (Berkman et al. 1998). The highest observed zebra mussel density on the artificial substrates was 165,000 individuals per m², which is relatively low and likely to increase in future years as zebra mussels can reach very high densities (exceeding a 1,000,000 individuals per m²) where environmental conditions are favorable (MacIsaac et al. 1991; Effler et al. 1996).
Size spectra of zebra mussels throughout the south basin of Lake Winnipeg

Zebra mussel growth rate is temperature dependent (similar to other bivalves) with higher water temperatures promoting increased growth rates (Ram et al. 1996; Lucy 2006) with their principal growing season extending from May to September (Hecky et al. 2004). The shell growth occurs at water temperatures of 6–8 °C. We observed a maximum growth rate of 23.4 mm per year. Similarly, Allen et al. (1999) described annual growth rate of 20–22 mm with most of the shell growth occurring during the spring. Comparable growth rates (22–24 mm) were observed for quagga mussels (Dreissena rostriformis bugensis) in Lake Mead, Nevada-Arizona, USA (Wong et al. 2012). The authors also observed that growth rates decreased with an increase in mussel size.

In the present study, the longest shell lengths were observed in the southern part of the south basin. Higher growth rates are likely a result of higher water temperatures and higher organic carbon concentrations at the confluence of the Red River (McCullough 2001) in comparison to the northern part of the south basin. Temperature profiles illustrate the earlier onset of warmer water from the Red River flowing into southern part of Lake Winnipeg from the south in comparison to a sampling site in the northern part of the south basin of Lake Winnipeg near to Hecla Island (Figure 8). In addition, the water from the Red River reaches higher temperatures over the summer in comparison to the northern part of the south basin of Lake Winnipeg. Similar patterns can be observed in Travers Bay at the confluence of the Winnipeg River with an earlier onset of warmer water and slightly higher summer water temperatures than the south basin (Figure 8).
Ecological impacts of zebra mussel invasion

Zebra mussels can have significant effects on the invaded ecosystem with respect to environmental impacts (i.e., water quality) and biological impacts (i.e., flora and fauna) (Nalepa and Schloesser 2013). While considerable variation exists in the effects of zebra mussel invasions on water quality and biota of lake and river ecosystems, consistent patterns in the direction and magnitude of impacts are evident. For example, zebra mussel invasions often result in persistent changes to water quality (e.g., Secchi depth, total phosphorus concentration) (Higgins et al. 2011). Also, impacts of zebra mussels on multiple trophic levels, from bacteria to top predators such as piscivorous fishes, seem a common result of zebra mussel invasions (Higgins and Vander Zanden 2010). The magnitude of impact on the food web is related to the filtration capacity of the mussel population, which is a function of population density, the size of the ecosystem, and a variety of factors that affect individual filtration rates (e.g., temperature, water velocity, turbidity) and access to the water-column (e.g., depth, vertical and horizontal mixing). Dreissenid densities may vary by several orders of magnitude over space (within and among lakes or rivers) and time (e.g., years), and whole-ecosystem densities are often unknown. The impacts of zebra mussel invasions on fish community structure and fish population status appear related to the energy pathway from which fish obtain their food. A collapse of planktivore and predator communities has been observed in Lake Huron where the fish species were unable to effectively exploit the littoral resources after pelagic resources declined (Rennie et al. 2009).

An increase in water clarity has been observed in lakes after the invasion of zebra mussels as the filter feeding activity of zebra mussels removes phytoplankton and other suspended particulate matter from the water column (Therriault et al. 2012). This increased water clarity may lead to deeper penetration of solar energy into the lake, which can affect the heat budget of lake and algal and submergent plant growth and lead to changes in fisheries yields (Geisler et al. 2016). Data collected here regarding zebra mussel growth, distribution, and abundance on artificial substrate and local sediment provides valuable baseline conditions to be used for long-term monitoring of zebra mussels and as input data for nutrient models in Lake Winnipeg that will inform future management decisions for the Lake Winnipeg watershed.

Acknowledgements

We thank Colin Kovachik and Doug Leroux for providing assistance with the field sampling efforts, Lindsey Divers for the image analysis, Sarah Hnytka and Laura Murray for the sample processing, and Charlene Stacey for the sediment particle size analysis. Sample collection, sample processing, image and data analysis were funded by Fisheries and Oceans Canada. We would like to thank David Wong and two anonymous reviewers for the constructive review of an earlier version of the manuscript.
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