



Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijgler



The distribution, density, and biomass of the zebra mussel (*Dreissena polymorpha*) on natural substrates in Lake Winnipeg 2017–2019



David C. Depew ^{a,*}, Emily Krutzelmann ^a, K. Elise Watchorn ^b, Amanda Caskenette ^c, Eva C. Enders ^c

^a Environment and Climate Change Canada, Science and Technology Branch, Burlington, ON L7S 1A1, Canada

^b Environment and Climate Change Canada, Science and Technology Branch, Winnipeg, MB, Canada

^c Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB R3L 2N6, Canada

ARTICLE INFO

Article history:

Received 3 March 2020

Accepted 4 December 2020

Available online 25 December 2020

Communicated by: Robert Brua

Keywords:

Lake Winnipeg

Zebra mussels

Invasion dynamics

Substrate limitation

ABSTRACT

The distribution, density, biomass and size-structure of the zebra mussel (*Dreissena polymorpha*) population in Lake Winnipeg were examined between 2017 and 2019. Zebra mussels have colonized most of the available hard substrate in the south basin and Narrows region, but colonization of the north basin remains low at present, even on suitable substrate. Numerical densities and shell free biomass peaked at $5530 \pm 953 \text{ m}^{-2}$ and $64.7 \pm 57.9 \text{ g shell free dry mass m}^{-2}$ respectively. The distribution appeared to be strongly limited by substrate type and availability, with further limitations on the distribution imposed by physical disturbance in shallow waters and unsuitable substrate in deeper areas of the lake. Zebra mussels <1 year old dominated the populations, and individuals >18 mm were exceedingly rare. Poor recruitment was observed at sites along the eastern side of the south basin compared to elsewhere in the lake. The proximate causes of these differences in colonization success and recruitment are not clear, but may be in part due to heterogeneous patterns of key physico-chemical environmental conditions such as calcium concentrations required for successful development of juvenile mussels and colder water temperatures in the north basin. This study provides a baseline of information on which to track further expansion of zebra mussels in Lake Winnipeg and assist efforts to develop an understanding of how zebra mussels may affect the ecology of Lake Winnipeg.

Crown Copyright © 2020 Published by Elsevier B.V. on behalf of International Association for Great Lakes Research. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

The zebra mussel (*Dreissena polymorpha*), a native of the Black and Caspian Seas region in southeastern Europe, is one of the most aggressive and successful aquatic invaders of freshwaters in the northern hemisphere (Karatayev et al., 2006). Originally introduced to the Laurentian Great Lakes region in the mid-1980s (Hebert et al., 1991), zebra mussels rapidly spread throughout the Great Lakes, Mississippi, and Hudson River basins by the mid-1990s (Nalepa and Schloesser, 2013). By 2009, zebra mussels had also invaded a number of lakes within the Red River basin in Minnesota (Mallez and McCartney, 2018); and in mid-October of 2013, adult zebra mussels were observed in several harbours around the south basin of Lake Winnipeg (DFO, 2014). Eradication efforts with potash treatments were undertaken in some harbours; however, the continued presence of veligers in plankton surveys, fouling of telemetry receivers by live mussels (Enders et al.,

2019), and accumulation of shell material on beaches indicate that zebra mussels have successfully established a naturally reproducing population in Lake Winnipeg.

Dreissenid mussels have had considerable economic and ecological impacts in both Europe and North America (Higgins and Zanden, 2010; Karatayev et al., 2015). Heavy biofouling of economically important infrastructure such as drinking or cooling water intakes, dock pilings, hydroelectric generating facilities, and boat hulls are estimated to cost approximately \$277 million USD globally on an annual basis (Nakano and Strayer 2014). The filter feeding activity of zebra mussels is considered a major factor contributing to the altered structure and function of freshwater systems where they have established large populations (Hecky et al., 2004; Vanderploeg et al., 2002). In these systems, mussels have altered the flow of energy and nutrients toward the benthic environment largely at the expense of the pelagic or pelagic/profundal environment in larger systems. Increases in water clarity (Howell et al., 1996), and re-routing of nutrients (Ozersky et al., 2009) may increase benthic primary productivity (Higgins et al., 2006; Zhu et al., 2006) while the increase benthic habitat

* Corresponding author.

E-mail address: David.Depew@canada.ca (D.C. Depew).

(Haltuch et al., 2000) and supply of organic matter may increase the density of some benthic invertebrates (Stewart et al., 1998). Fewer nutrients and phytoplankton in the pelagic environment may result in reductions in zooplankton biomass (MacIsaac et al., 1995) and subsequently impact the growth and survival of young fish, including those of significant commercial value (Hansen et al., 2020; Rennie et al., 2013).

The impacts of dreissenid mussels on lake ecosystems tend to scale with the size of their population and resultant filtration capacity. Consequently, the arrival of zebra mussels in Lake Winnipeg has prompted concern regarding potential impacts on the health of the vitally important walleye fishery (Geisler et al., 2016) and potential expansion of cyanobacterial blooms into the south basin where light limitation is thought to limit the magnitude of blooms (Binding et al., 2018). In order to assess potential impacts of zebra mussels on the structure and function of Lake Winnipeg, a first step is to document their distribution and population size within the lake. Mussel populations are highly variable through space and time, and obtaining an accurate population estimate is often difficult. Mussel occurrence and densities can vary over small scales due to differences in substrate type and stability (Mellina and Rasmussen, 1994), physical disturbance (Ozersky et al., 2011), or density dependent processes such as cannibalism (Chase and Bailey, 1999). Over larger scales, mussel occurrence and densities may be limited by variation in water chemistry (e.g., pH, calcium and nutrient concentrations; Mellina and Rasmussen, 1994; Ramcharan et al., 1992), dissolved oxygen and/or water temperature (Karatayev et al., 1998).

The purpose of this study was to assess and document the distribution, density, biomass, and population characteristics of adult zebra mussels in Lake Winnipeg during an early period of their invasion. Although zebra mussels have been found settled on telemetry receivers broadly distributed across the south basin of Lake Winnipeg (Enders et al., 2019), these may not represent populations on natural substrates or at different depths, as much of the open water area of Lake Winnipeg is dominated by unconsolidated soft substrates such as silt and clay (Brunskill et al. 1979). Colonization of such substrates by zebra mussels is generally uncommon (Karatayev et al. 1998), but shells from dead mussels may serve as a means to facilitate expansion onto less desirable substrates (Bially and MacIsaac, 2000). This study will serve to establish a baseline for tracking population trends of zebra mussels and interpretation of subsequent ecological changes associated with their establishment.

Methods

Study site

Lake Winnipeg has a surface area of nearly 24,000 km², a maximum length of 436 km, and a volume of 284 km³. Relatively shallow depths and a large surface area contribute to its status as a polymictic lake (Brunskill et al., 1979). It has two distinct basins (north and south) separated by a 2.5 km wide channel termed the Narrows. The north and south basins are unique in terms of physical and chemical conditions that characterize each basin. The south basin is smaller, shallower (mean depth of 9 m, maximum depth 14 m), and generally the warmest part of the lake with maximum summer temperatures of 18 – 24 °C. By comparison, the north basin is larger and deeper (mean depth 13 m, maximum depth 19 m) and on average is cooler than the south basin with maximum summer temperatures of 15 – 20 °C (Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020). The differences in basin size and depths also influence dissolved oxygen concentrations. Dissolved oxygen con-

centrations in the south basin ranged from 2.2 to 13.2 mg L⁻¹ and in the north basin from 1.7 to 14.4 mg L⁻¹ during the open water seasons between 1999 and 2016 (Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020).

In general, the waters of Lake Winnipeg are considered alkaline and well buffered (median pH of 8.2 and total alkalinity of 99 mg L⁻¹). Differences in the chemical constituents of inflowing waters impart some spatial differences in water quality conditions between the south and north basins. In the south basin, total phosphorus (TP) concentrations are indicative of hypereutrophic conditions (1999–2016 mean TP and total nitrogen (TN) concentrations of 0.104 mg L⁻¹ and 0.85 mg L⁻¹ respectively; Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020). In the north basin, TP concentrations are indicative of mesotrophic conditions (1999–2016 mean TP 0.039 mg L⁻¹ and mean TN 0.63 mg L⁻¹, respectively; Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020). Other notable differences in water quality include higher suspended solids concentrations in the south basin and higher specific conductance, total alkalinity, and chloride concentrations in the north basin (Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020).

The offshore sediments in the north and south basins are dominated by silty clays or clayey silts (~70%, Brunskill and Graham, 1979). Outside zones of sediment deposition (typically deeper than 8 m depth; Brunskill and Graham, 1979), sediment erosion and transport are dominant features. Bottom substrates may range from silty clays to rock/boulders and bedrock outcroppings. In the littoral zones, the western portion of the south basin generally consists of low sand and mixed sand-gravel beaches transitioning to sand-gravel mixtures toward the southern shore of the south basin (Manitoba Conservation, 2001). The southern shore consists of barrier islands and wetlands, and littoral substrates are a mixture of silt, clay, sand, and coarse woody debris. Along the eastern shore of the south basin, substrates are variable and include glacial outwash deposits of sand, clay, and silts, in addition to boulder-rich, clay and till, with an increasing presence of bedrock toward the Narrows (Brunskill et al., 1980). Beaches, shorelines, and sublittoral areas are composed of sands, pebbles, cobbles, and boulders (Manitoba Conservation, 2001).

Substrate

Poor water clarity and zones of sediment deposition and erosion hinder the ability to classify substrate types in Lake Winnipeg on an ecosystem scale. To assess the distributional pattern of zebra mussels relative to native substrates, we used recorded observations of substrate collected during routine benthic sampling by the Lake Winnipeg Research Consortium (<http://www.lakewinnipegresearch.org>) over the period 2016–2019 to derive an aggregate indicator of the dominant substrate type observed at each site over repeated visits. Data from research cruises were tabulated according to dominant substrate type at each sampling event. Substrate types were characterized using the calculated phi (ϕ) value used by Jones and Ricciardi (2005) in their study of the St. Lawrence River (mud/clay = 9, silt = 6.5, sand = 2, gravel = -3.7, cobble = -6.19, rock = -7.72, boulder = -8.644, and bedrock as -9.45). For sites with only one substrate type recorded at each sampling event, the mean ϕ score was calculated. For sites with more than one substrate type noted at each sampling event, a weighted ϕ value was calculated prior to calculation of the site mean (Electronic Supplementary Material (ESM) Table S1).

Collection of dreissenid mussels

Samples to assess the distribution, density, shell-free dry biomass, and length-frequency distributions of dreissenid mussels were collected at locations in Lake Winnipeg (Fig. 1). At offshore and nearshore sites, samples were collected on three research cruises throughout the year (spring: late May to early June; summer: mid-July to mid-August; fall: mid-September to mid-October). Logistical challenges limited collection in 2017 and 2018 to one cruise each (fall and summer, respectively), but in 2019, samples were collected during the spring cruise as well (see ESM Table S1 for sampling details). At offshore sites, triplicate Ponar grabs (0.052 m^{-2}) of sediment were collected from the M/V Namao. At nearshore sites, sediment samples were collected from a smaller workboat using a Petite Ponar grab (0.023 m^{-2}) at the 3 m depth contour. Total sampling effort varied across the three years owing to time and logistical constraints (ESM Table S1 for additional detail).

Additional samples were collected at up to 18 shoreline sites (depths ranging from 0.2 – 1.0 m) around the lake in 2019. Depending on the type of substrate present, different sampling approaches were employed. For silt to gravel sized substrates, three to five 1 m long benthic kick-net (Canadian Aquatic Biomonitoring Network; CABIN, 400 μm mesh) drags were utilized. For cobble to rock sized substrate, three to five 0.25 m^2 quadrats were placed randomly on the lake bed and up to five individual rocks were removed. All live mussels were removed from the rocks (when present) using a paint scraper. A sheet of tinfoil (Handi-foil®; PN 51805, standard foil wrap) was placed over the surface

area of the rock and excess foil trimmed away. The foil was carefully cleaned of debris, folded and placed in a Ziploc® bag for later weighing. The weight of foil for each sampled rock was determined gravimetrically (to nearest 0.01 g) using a laboratory balance and converted to surface area using the relationship $\text{FoilArea} (\text{cm}^2) = 305.73 * \text{FoilWeight(g)} (r^2 = 0.99, df = 8)$ derived from a model-II regression of foil mass and area measurements of foil squares cut from the same roll of foil in the laboratory. For boulder to bedrock size substrates, a 0.01 m^2 wire quadrat was placed at up to five randomly selected locations and all mussels within the wire quadrat were removed. The percentage of hard substrate present at each site was determined to the nearest 10%, and the percent rock, rock surface area, and rock bottom area were used to normalize densities per m^2 of lake-bottom, following Bailey et al. (1995).

All samples were washed through an initial 2 mm sieving bucket, with a secondary 500 μm sieve. Live and dead mussels (including empty shell fragments) were transferred to WhirlPak® or Ziploc® bags, stored on ice, and frozen as soon as possible at -20°C .

For each sample collected containing mussels, all individuals were identified to species, counted, and shell lengths (SL; mm) measured as the greatest distance from the anterior tip of the umbo to the posterior edge of the shell along the ventral surface. Shell lengths of individuals 5 mm or larger were measured to the nearest 0.1 mm with electronic digital calipers, while individuals less than 5 mm in length were measured using an eyepiece micrometer at 10x magnification under a binocular dissecting microscope.

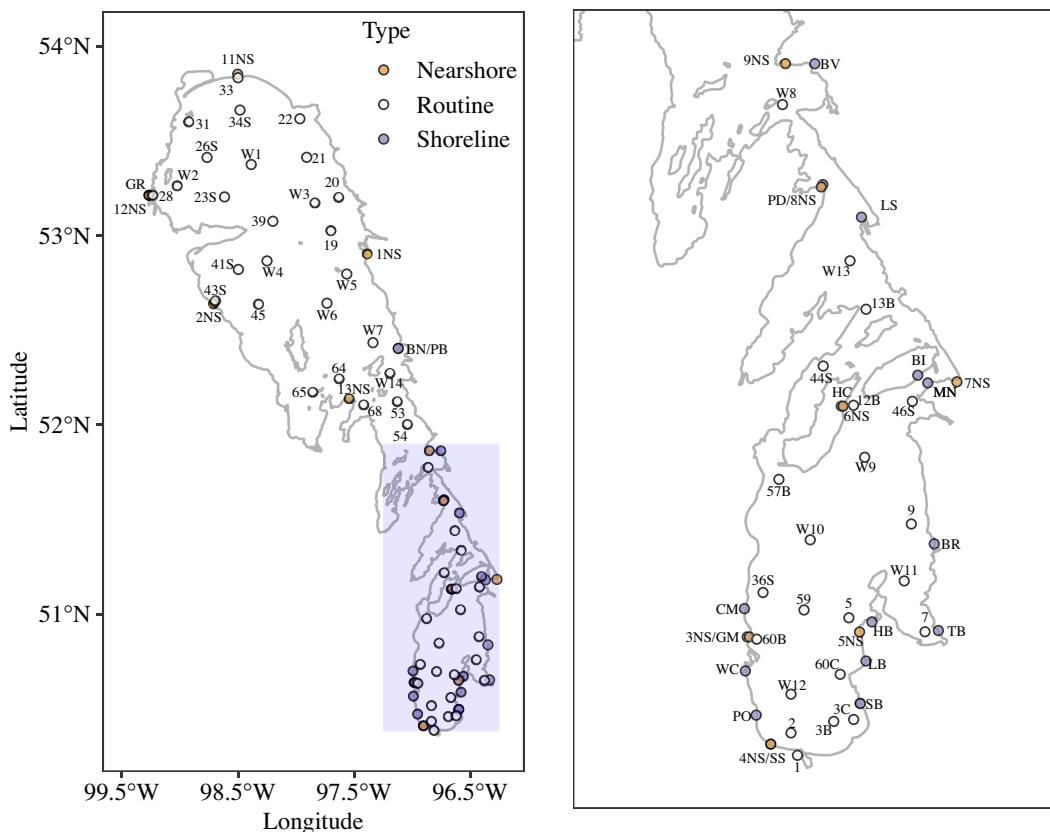


Fig. 1. Map of Lake Winnipeg (Manitoba, Canada) showing sites sampled for dreissenid mussels 2017–2019. Shaded rectangle indicates enlarged panel on the right displaying the south basin and Narrows in more detail. Shoreline site (purple circles) abbreviations as in ESM Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Shell-free dry mass and shell length relationships

To determine the relationship between soft tissue mass and shell length, mussels from samples with more than 50 mussels on at least 2 sampling dates were separated into five size categories based on relative shell length intervals (0–5, 5–10, 10–15, 15–20, 20–25 and >25 mm). Shell lengths of at least five individuals from each category were measured, as outlined above, using digital calipers. Soft tissues were removed from the shell using a scalpel and forceps, placed in individually pre-ashed, pre-weighed aluminum dishes and dried at 60 °C for 48 h. Shell-free mass per millimeter of shell length was described by the general allometric equation $SFDM = a \cdot SL^b$ where SFDM is the shell-free dry mass of the soft tissue in milligrams (mg), and SL is the shell length in millimeters (mm).

Population biomass and size structure

Zebra mussels typically lose tissue mass during spawning periods, so comparisons of SFDM vs SL relationships among seasons is often problematic. To estimate biomass, we used a pooled SFDM vs SL regression model ($\log_{e}SFDM = -5.393 + 2.943 \cdot \log_{e}SL$, $R^2 = 0.973$, $n = 103$) from three sites (W8, 57B and 3NS) sampled in September and October of 2017 and 2019 to estimate biomass at all sites/dates. An analysis of covariance (ANCOVA) for these sites during the fall season indicated that the slopes of the SFDM vs SL relationship did not differ across site or year ($F_{1,97} = 3.39$, $p = 0.1$), nor did the intercepts differ among sites ($F_{2,97} = 1.47$, $p = 0.22$) or year ($F_{1,97} = 0.18$, $p = 0.67$). To calculate total biomass, individuals were placed into 1 mm size class intervals (1–26 mm) and multiplied by the mid-shell length weight for each interval from the pooled regression model and binned increments summed. Biomass is reported as SFDM on a m^{-2} basis. We also report individual linear regressions between SFDM and SL for each sampling event to permit calculation of the weight of a standard length (15 mm) mussel. SFDM and SL were \log_{e} transformed to ensure normality and homogeneity of variance.

Statistical analyses

We used general linear model and mixed effects model frameworks to assess spatial and temporal variation of zebra mussels, mussel densities, SFDM biomass and empty shell mass. Potential differences in the degree of colonization of different substrate types (hard, mixed, soft) among basins (south, Narrows, north), were modelled as presence (1) or absence (0) using a binomial error distribution with basin and substrate type as predictor variables. We used a mixed effects model framework to fit models for mean density, mean SFDM biomass and mean empty shell mass using year, basin, depth and site-specific weighted ϕ value as fixed effects (basin as a factor, year, depth and site ϕ value as continuous predictor variables). Site ID (station number) and season were treated as partially crossed random effects as not all sites were sampled in the same season. Mean density was modeled with Poisson distributed errors (log-link function), while mean SFDM and empty shell mass were modeled with a gamma error structure with log-link function as they are non-negative continuous variables (Zuur et al. 2013). We added a small constant (0.00001) to all SFDM and empty shell measures (Zuur et al. 2013). Models were fit using maximum likelihood methods and the significance of fixed effects was assessed using likelihood-ratio tests (LRT) compared with the full model. We used the *glmmTMB* package (Brooks et al., 2017) to fit the models. Post-hoc contrasts to assess differences among basins of mean density, SFDM and empty shell mass were conducted using the *glht* function of the *multcomp* pack-

age and alpha values were Bonferroni corrected when multiple contrasts were employed (Hothorn et al., 2008).

Size-frequency distributions at sites where >50 mussels were collected were examined for normality, skewness and kurtosis using standard tests. If a size-frequency distribution was not normally distributed, we tested for the presence of multi-modality using Hartigan's dip test (null hypothesis is uni-modality) using the *dip* package (Maecher and Ringach, 2004). Differences in the proportion of newly recruited mussels (<5 mm SL) among sites was tested using beta regression via the *betareg* package (Cribari-Neto and Zeileis, 2010) with depth, substrate (ϕ value), latitude and longitude as predictor variables. Beta regression shares properties with conventional linear models, but is more suitable for modelling non-normal proportional data restricted between 0 and 1. Because the proportion of mussels <5 mm SL included the lower extreme 0 at some sites, proportions were transformed following $y^* = (y(n-1) + 0.5)/n$, where n is the sample size (Smithson and Verkuilen, 2006). All statistical analyses were conducted using the statistical software R (R Core Team, 2016).

Results

Mussel distribution and density

All mussels collected over the three years of study were *Dreissena polymorpha* (hereafter zebra mussels); no quagga mussels (*Dreissena bugensis*) were observed in any samples. Live individuals were collected at 2 of 26 sites in 2017 (8%), 6 of 32 sites in 2018 (18.7%), and 25 of 78 sites in 2019 (32%). No mussels were collected at north basin sites in 2017 or 2018, but were present at three sites in 2019. Over the three years, the north basin had the lowest proportion of sites colonized (9%) compared to the Narrows (56%; Tukey HSD, $Z - \Delta = -2.79$, $p < 0.005$) and south basin (53%; Tukey HSD, $Z - \Delta = -2.86$, $p < 0.001$). These differences were more apparent when comparing across basins within dominant sub-

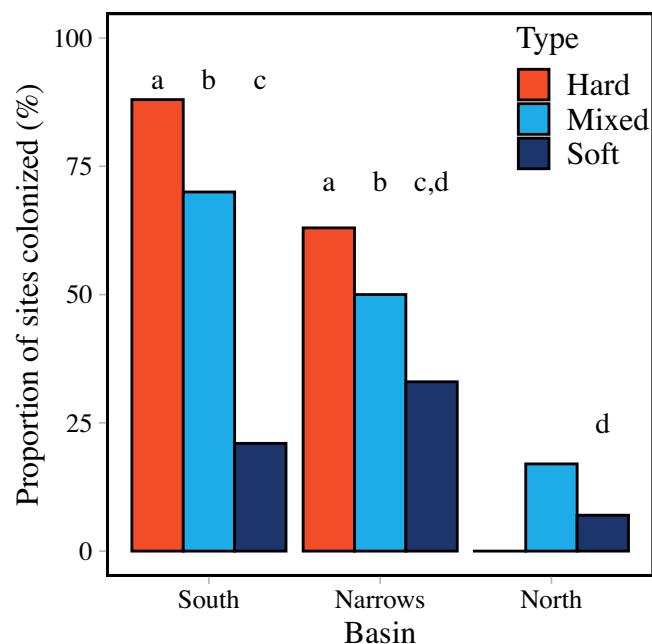


Fig. 2. Barplot showing the proportion of sites colonized by zebra mussels (expressed as a percentage) in Lake Winnipeg (Manitoba, Canada) in the south basin, Narrows and north basin stratified by substrate type according to site ϕ values. Letters above bars indicate no statistical differences at a Bonferroni adjusted p -level of 0.016.

strate types (Fig. 2). For sites dominated by hard substrates ($\phi = -10\text{--}0$), no sites in the north basin had been colonized by the end of the study compared to 63% of sites in the Narrows and 88% of sites in the south basin (Fig. 2). For sites dominated by mixed substrates ($\phi = 0\text{--}6.5$), a similar pattern was evident, with 17% of sites colonized in the north basin compared to 50% and 70% in the Narrows and south basin respectively (Fig. 2). Differences in the proportion of sites dominated by soft substrates ($\phi > 6.5$) were less apparent, ranging from 7 – 33% (Fig. 2).

Mean densities ranged from a low of $1 \pm 2.1 \text{ m}^{-2}$ to a maximum of $5530 \pm 953 \text{ m}^{-2}$ but overall, lake-wide mean densities were low due to the preponderance of sites with no mussels present (Fig. 3). Lake wide densities (mean \pm SE) increased over time from $83 \pm 62 \text{ m}^{-2}$ in 2017 to $166 \pm 85 \text{ m}^{-2}$ in 2019 (Fig. 3, Table 1). Densities increased with depth and substrate size/stability (Table 1), with greater densities of mussels on larger more consolidated substrate such as boulders and rocks (Fig. 4). Mean densities were lowest in the north basin compared to the Narrows (Tukey HSD, $Z - \Delta = -2.95$, $p < 0.01$) and south basin (Tukey HSD, $Z - \Delta = -3.29$, $p < 0.005$) although densities in the south basin and Narrows were similar (Tukey HSD, $Z - \Delta = 0.52$, $p = 0.86$).

$\Delta = -2.95$, $p < 0.01$) and south basin (Tukey HSD, $Z - \Delta = -3.29$, $p < 0.005$) although densities in the south basin and Narrows were similar (Tukey HSD, $Z - \Delta = 0.52$, $p = 0.86$).

Shell free dry mass biomass

Shell-free dry mass (SFDM) biomass ranged from $0.01 \pm 0.01 \text{ g SFDM m}^{-2}$ to a maximum of $64.7 \pm 57.9 \text{ g SFDM m}^{-2}$ (Fig. 3). As with mean densities, the overall lake-wide SFDM biomass was low due to the preponderance of sites with no mussels, ranging from $0.47 \pm 0.35 \text{ g SFDM m}^{-2}$ to $2.17 \pm 0.26 \text{ g SFDM m}^{-2}$ across 2017–2019 with no clear trend over the three years (Table 1). Mean SFDM increased with depth and substrate size/stability (Table 1), and mean SFDM was lowest in the north basin compared to the Narrows (Tukey HSD, $Z - \Delta = -3.99$, $p < 0.001$) and south basin (Tukey HSD, $Z - \Delta = -5.11$, $p < 0.001$). Mean SFDM did not differ between the south basin and Narrows (Tukey HSD, $Z - \Delta = 0.83$, $p = 0.67$).

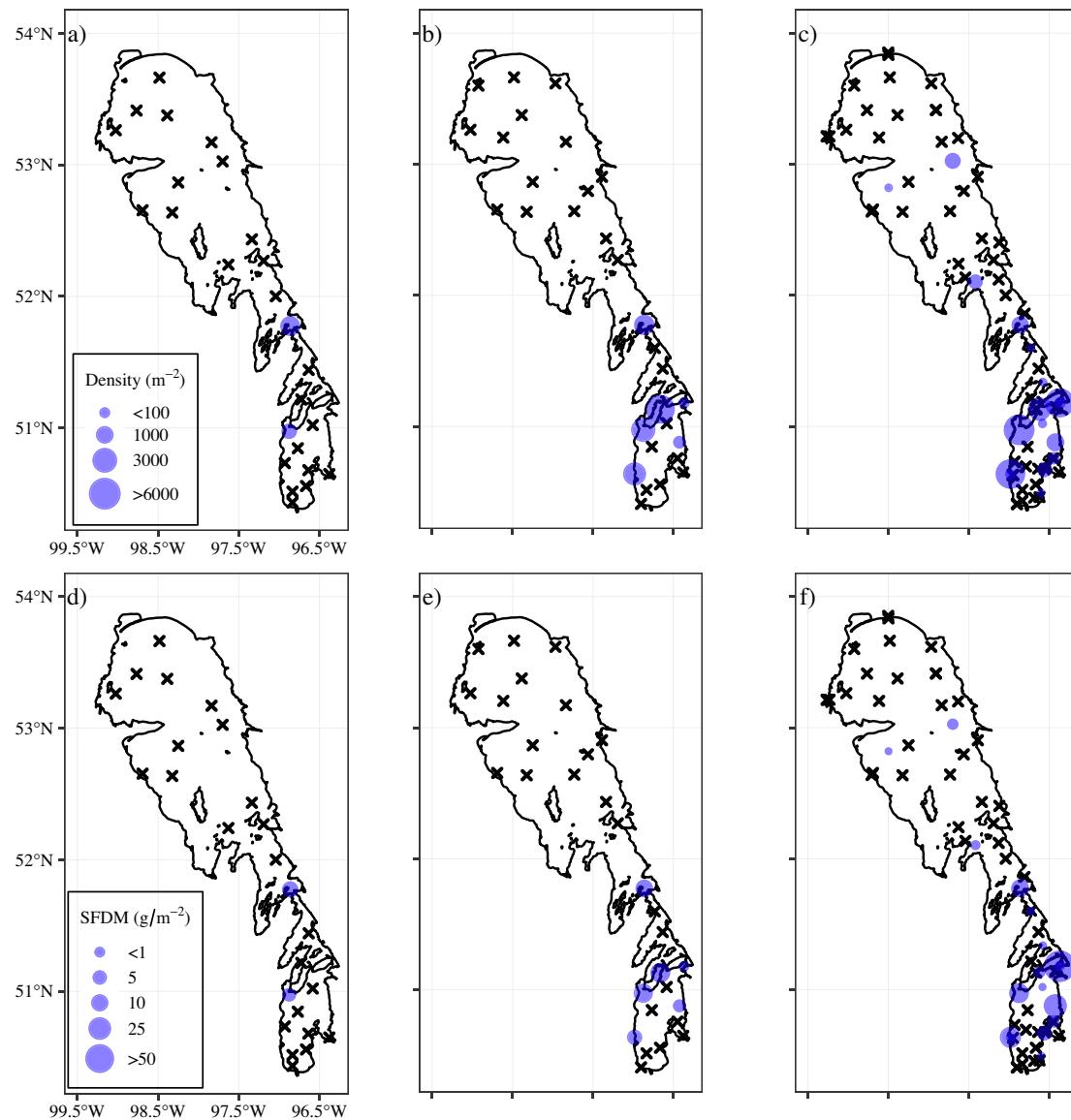


Fig. 3. Maps showing the distribution of the mean density ($\# \text{ m}^{-2}$) in a) fall 2017, b) summer 2018, c) fall 2019 and mean SFDM (g m^{-2}) in d) fall 2017, e) summer 2018, f) fall 2019 of zebra mussels in Lake Winnipeg (Manitoba, Canada). Sites denoted by an “x” indicate no mussels present.

Table 1

Fixed effects from generalized linear mixed models for the effects of year, basin, depth and substrate size/stability (ϕ value) on mean dreissenid density, shell free dry mass biomass and empty shell mass. Estimates, standard error, Z-value, χ^2 value, degrees of freedom and p-values are given for each response variable as derived from LRT against the full model. Boldface text indicates coefficients that are significantly different from zero (continuous) or from reference level (categorical). All models contain partially crossed random intercept terms for site and season as not all sites were sampled in all seasons or years.

Name	Dreissenid Density				SFDW Biomass				Empty Shell Mass			
	Estimate (SE)	Z-value	χ^2 (df)	P	Estimate (SE)	Z-value	χ^2 (df)	P	Estimate (SE)	Z-value	χ^2 (df)	P
Year	0.11 (0.07)	14.47	213.75 (1)	<0.001	0.28 (0.21)	1.35	1.76 (1)	0.18	0.01 (0.16)	0.05	0.03 (1)	0.96
Basin(N)	-7.76 (2.62)	-2.95	15.5 (2)	<0.001	-6.22 (1.56)	-3.99	24.9 (2)	<0.001	-6.43 (1.53)	-4.21	22.8 (2)	<0.001
Basin(S)	1.17 (2.25)	0.52			1.31 (1.56)	0.83			0.62 (1.64)	0.38		
Depth	0.54 (0.26)	2.06	4.74 (1)	<0.05	0.39 (0.16)	2.41	5.64 (1)	<0.05	0.31 (0.17)	1.89	3.51 (1)	0.06
Phi	-0.78 (0.21)	-3.63	12.56 (1)	<0.001	-0.63 (0.15)	-4.16	15.8 (1)	<0.001	-0.76 (0.15)	-4.93	20.5 (1)	<0.001

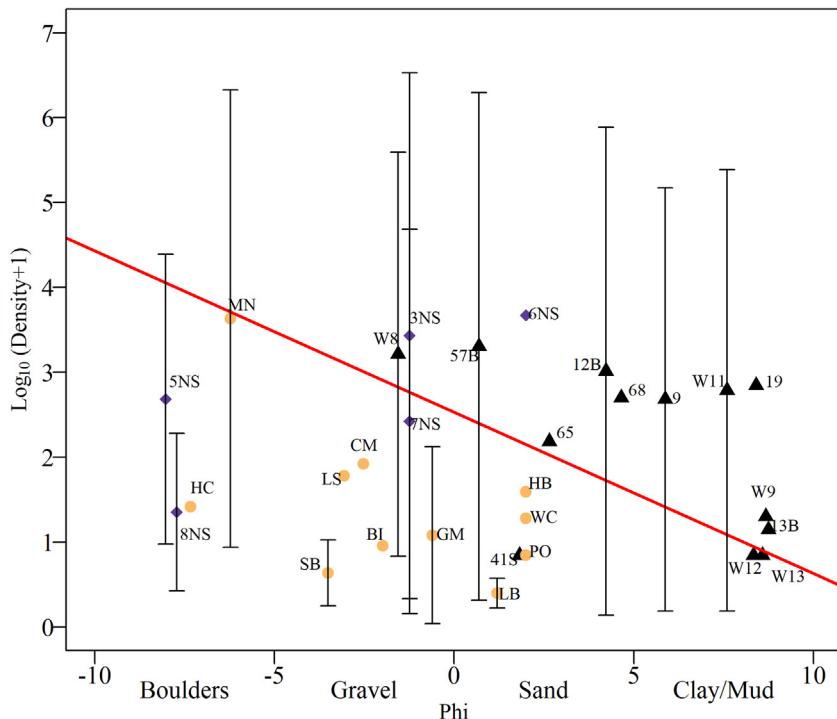


Fig. 4. Relationship between zebra mussel density (\pm SE) and substrate size (the mean weighted ϕ value for each site 2017–2019) for sites in Lake Winnipeg. Offshore sites indicated by black triangles, nearshore sites by purple diamonds and shoreline sites by yellow circles. The red solid line is the general model developed by Mellina and Rasmussen (1994) relating mussel density to substrate size. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Empty shell mass

Empty shells of deceased zebra mussels were observed in most samples that contained live mussels, ranging from 0 to 66.2 g DW m^{-2} . Over the three years of study, empty shell mass was similar, ranging from 8.85 ± 2.01 g DW m^{-2} to 11.86 ± 4.90 g DW m^{-2} (Table 1). Empty shell mass increased with substrate size/stability but not with site depth (Table 1). Empty shell mass in the north basin was lower than that in the Narrows (Tukey HSD, $Z - \Delta = -4.21$, $p < 0.0001$) and south basin (Tukey HSD, $Z - \Delta = 4.64$, $p < 0.0001$), but no differences existed between the south basin and the Narrows (Tukey HSD, $Z - \Delta = 0.38$, $p = 0.93$).

Size-frequency distributions

Across all sites, median shell length (SL) ranged from 3.9 to 18.4 mm, in part due to seasonality of sampling. Mussels with SL > 18 mm were rare and the maximum shell length was 26.8 mm (Table 2). Size-frequency distributions for all but four sites deviated from normality, with most size-frequency distributions characterized by positive skewness (Table 2). Skewness was negatively correlated to median shell length (Pearson $r = -0.59$,

$p < 0.01$) indicating that larger mussels were relatively rare. Identification of cohorts in the size-frequency distributions that might represent different year classes was challenging, as most distributions did not yield statistical evidence of multi-modality (Table 2). Of those that did, multiple modes were present during the summer surveys (July – August) only, with modes at 5 mm and 13 mm (station 57B in 2018; ESM Fig. S1) and 3 mm and 9 mm (station 12B in 2019; Fig. S1). Despite the lack of strong cohort structures in the size – frequency distributions, we observed evidence of recent recruitment (presence of mussels < 5 mm SL) at 7 of 10 sites where sufficient numbers of mussels were present (3NS, 57B, 12B, W8, 19, 68, 6NS). The proportion of mussels < 5 mm SL varied considerably (0 – 75%) depending on location and timing of sampling (Fig. 5). The proportion of mussels < 5 mm SL was un-related to latitude, depth, substrate size/stability or year, but was negatively related to longitude with poor recruitment success at sites along the east shore of the south basin (Fig. 5).

Length-weight relationships

Site-specific regressions for the relationship between SFDM and SL for three sites in the south basin are provided in Table 3. The

Table 2

Values of various statistical tests on the length-frequency distributions of zebra mussel populations in Lake Winnipeg. Sites correspond to locations in Fig. 1 and ESM Table S1, sample size (n), median shell length (SL_{MED} ; mm), Shapiro-Wilk test statistic for normality and associated p-value, D'Agostino test for skewness and associated p-value, Anscombe-Glynn test for kurtosis and associated p-value and Hartigan's Dip test statistic (D_H) for unimodality and associated p-value are also indicated.

Site	Season	Year	n	SL_{MED}	Shapiro-Wilk	Skewness	Kurtosis	D_H
W8	Fall	2017	477	10.0	0.993 ($p < 0.05$)	0.21 ($z = 1.87$, $p = 0.06$)	2.94 ($z = -0.10$, $p = 0.91$)	0.011, $p = 0.97$
57B	Fall	2017	99	10.7	0.952 ($p < 0.001$)	-0.11 ($z = -0.45$, $p = 0.6$)	1.88 ($z = -4.75$, $p < 0.01$)	0.044, $p = 0.15$
3NS	Summer	2018	166	6.9	0.973 ($p < 0.005$)	0.38 ($z = 2.05$, $p < 0.05$)	2.82 ($z = -0.27$, $p = 0.78$)	0.029, $p = 0.44$
6NS	Summer	2018	326	6.9	0.790 ($p < 0.001$)	3.58 ($z = 13.6$, $p < 0.001$)	33.7 ($z = 10.7$, $p < 0.05$)	0.019, $p = 0.76$
57B	Summer	2018	442	8.5	0.946 ($p < 0.001$)	0.26 ($z = 2.27$, $p < 0.05$)	1.87 ($z = -13.1$, $p < 0.01$)	0.036, $p < 0.001$
W8	Summer	2018	256	11.0	0.982 ($p < 0.001$)	0.48 ($z = 3.07$, $p < 0.005$)	4.29 ($z = 3.04$, $p < 0.005$)	0.019, $p = 0.76$
W8	Spring	2019	129	11.4	0.993 ($p = 0.79$)	0.08 ($z = 0.43$, $p = 0.66$)	2.96 ($z = 0.21$, $p = 0.83$)	0.023, $p = 0.93$
12B	Summer	2019	71	8.0	0.888 ($p < 0.001$)	0.46 ($z = 1.66$, $p = 0.09$)	1.97 ($z = -3.18$, $p < 0.001$)	0.087, $p < 0.001$
57B	Summer	2019	110	7.8	0.913 ($p < 0.001$)	0.66 ($z = 2.77$, $p < 0.01$)	2.24 ($z = -2.32$, $p < 0.05$)	0.031, $p = 0.61$
W11	Summer	2019	159	8.6	0.845 ($p < 0.001$)	2.08 ($z = 7.52$, $p < 0.001$)	10.7 ($z = 5.85$, $p < 0.001$)	0.023, $p = 0.80$
MN	Summer	2019	228	12.8	0.992 ($p = 0.29$)	0.19 ($z = 1.24$, $p = 0.21$)	3.21 ($z = 0.86$, $p = 0.34$)	0.014, $p = 0.99$
W8	Summer	2019	248	13.4	0.955 ($p < 0.001$)	-0.72 ($z = -4.34$, $p < 0.001$)	4.01 ($z = 2.56$, $p < 0.05$)	0.016, $p = 0.93$
12B	Fall	2019	392	6.5	0.887 ($p < 0.001$)	0.68 ($z = 5.13$, $p < 0.001$)	2.13 ($z = -6.73$, $p < 0.001$)	0.026, $p = 0.06$
19	Fall	2019	110	7.3	0.981 ($p = 0.14$)	0.02 ($z = 0.07$, $p = 0.94$)	2.47 ($z = -1.27$, $p = 0.22$)	0.024, $p = 0.93$
3NS	Fall	2019	347	8.3	0.976 ($p < 0.001$)	0.33 ($z = 2.51$, $p < 0.05$)	2.33 ($z = -3.69$, $p < 0.001$)	0.015, $p = 0.92$
57B	Fall	2019	870	6.8	0.852 ($p < 0.001$)	1.56 ($z = 14.0$, $p < 0.001$)	5.42 ($z = 7.33$, $p < 0.001$)	0.008, $p = 0.99$
68	Fall	2019	79	3.9	0.617 ($p < 0.001$)	3.78 ($z = 7.68$, $p < 0.001$)	20.8 ($z = 5.95$, $p < 0.001$)	0.025, $p = 0.98$
9	Fall	2019	168	18.4	0.985 ($p < 0.001$)	-0.20 ($z = -1.09$, $p = 0.27$)	2.77 ($z = -0.42$, $p = 0.68$)	0.020, $p = 0.95$
MN	Fall	2019	185	14.9	0.991 ($p = 0.29$)	0.32 ($z = 1.82$, $p = 0.07$)	3.49 ($z = 1.44$, $p = 0.15$)	0.016, $p = 0.99$
W8	Fall	2019	153	13.5	0.974 ($p < 0.005$)	0.63 ($z = 3.11$, $p < 0.01$)	3.41 ($z = 1.19$, $p = 0.23$)	0.015, $p = 0.97$

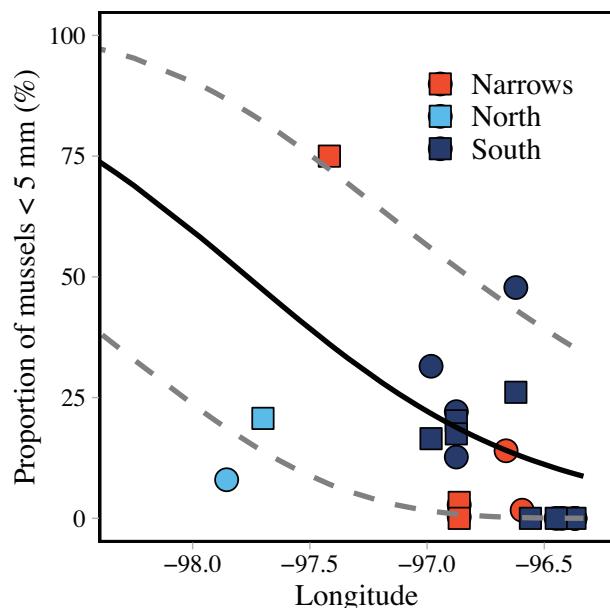


Fig. 5. Beta regression model (solid line) and 5th and 95th percentiles (dashed lines) for the proportion of zebra mussels < 5 mm (expressed as a percentage) as a function of longitude. Symbols represent season of collection for summer (circles) and fall (squares).

weight of a standard size 15 mm zebra mussel ranged from 6.19 to 17.41 mg, with lower weights occurring in the summer months, although this was not consistent across all sites (Table 3). For example, at site 57B, the mean weight of a 15 mm mussel declined ~ 58% between spring and summer 2019. In contrast, mean weight of a 15 mm mussel at W8 increased 23% between spring and summer 2019.

Discussion

We observed zebra mussels more frequently and at higher densities on hard, consolidated substrates such as boulders, rocks and gravel compared to unconsolidated clays, silts and muds. Such patterns are consistent with known substrate preferences of zebra

mussels (Karatayev et al., 1998; Mellina and Rasmussen, 1994) and indicate that the distribution and density of mussels in the south basin and Narrows of Lake Winnipeg is predominantly limited by substrate availability. Mussel densities were low at shallow shoreline sites, likely due to a higher degree of physical exposure to wave action and ice scour (Ozersky et al., 2011). The maximum density recorded in our study was 5530 m^{-2} , which is lower than densities reported during the initial invasive phase in the Laurentian Great Lakes (up to $350,000 \text{ m}^{-2}$ Leach, 1993). However, it is important to consider that our study began ~4 years after zebra mussels were detected in Lake Winnipeg (DFO, 2014) so extremely high densities typical of the first or second year of invasion would have been missed. In addition, very few of our study sites had substrate types conducive to supporting very high densities of mussels, such as bedrock outcroppings and large boulders (Mellina and Rasmussen, 1994; Wilson et al., 2006). Gear inefficiencies due to the use of Ponar grabs probably underestimate densities at the few sites that did have large boulders (i.e. sites 5NS and 8NS); however, despite these shortcomings, the densities measured in this study are comparable to other systems with similar substrate types.

Zebra mussel populations typically have rapid growth rates, high densities and good recruitment (Karatayev et al., 2015), although a number of factors such as water temperatures, trophic status, depth, turbidity, predation pressure, substrate availability and stability, and water turbulence may influence different aspects of population growth and development (Karatayev et al., 2006). Size-frequency distributions in this study were positively skewed and often uni-modal, with median SL averaging 9.8 mm. A similar size-frequency distribution was observed from mussels collected from buoys and telemetry receivers deployed across the south basin of Lake Winnipeg from mid 2016 to mid 2017 where >90% of mussels had SL < 10 mm (mean 5.9 mm, range 0.2 – 23.4 mm; Enders et al., 2019). This suggests that zebra mussel populations in Lake Winnipeg are dominated by mussels < 1 year old (Baldwin et al., 2002). The presence of small numbers of larger mussels (>18 mm) in our samples is likely a result of high adult mortality, while the presence of larger mussels (>18 mm) on telemetry receivers probably reflects detachment and transport of live individuals during wind/storm events (Martel, 1993) followed by subsequent relocation to preferred substrates (Ackerman et al., 1994).

Table 3

Relationship between shell length (SL, mm) and shell free tissue dry mass (SFDM, mg) for *Dreissena polymorpha* at selected sites in Lake Winnipeg. The SFDM/SL relationship is presented as $\log_e \text{SFDW} = b + a \log_e \text{SL}$. Also provided are estimates of SFDM for a 15-mm individual as derived from the individual linear regression models.

Site	Year/Season	Size range (mm)	n	b	a	r^2	15-mm
57B	Fall 2017	3.3 – 18.6	20	-5.082	2.775	0.96	11.41
	Summer 2018	3.9 – 18.8	20	-5.432	2.829	0.94	9.29
	Spring 2019	3.3 – 14.9	12	-5.085	2.881	0.98	15.21
	Summer 2019	3.4 – 18.0	20	-4.899	2.520	0.98	6.85
	Fall 2019	3.4 – 20.6	22	-5.194	2.866	0.97	13.03
W8	Fall 2017	4.3 – 21.4	21	-6.110	3.311	0.99	17.41
	Summer 2018	7.8 – 22.3	17	-5.115	2.589	0.95	6.67
	Spring 2019	3.9 – 20.1	19	-4.243	2.371	0.88	8.81
	Summer 2019	3.7 – 18.8	20	-5.103	2.765	0.98	10.86
	Fall 2019	8.1 – 24.2	20	-4.689	2.673	0.94	12.81
3NS	Summer 2018	3.7 – 18.2	18	-5.308	2.633	0.95	6.19
	Spring 2019	3.8 – 13.5	15	-4.782	2.442	0.92	6.23
	Fall 2019	3.3 – 17.6	20	-5.469	2.939	0.99	12.08

The lack of multi-modality in the size-frequency distributions makes assessment of longevity difficult (Karatayev et al., 2006). Our data suggest zebra mussels have a short life span in Lake Winnipeg, but it is difficult to say if it is abnormally shorter than other North American lakes (Karatayev et al., 2006). Zebra mussels are thought to employ flexible energy allocation strategies that maintain reproductive efforts at the expense of longevity (Stoeckmann and Garton, 2001). The high percentage of inorganic clays and silt in the sediments of Lake Winnipeg, particularly in the south basin, and their tendency to be frequently re-suspended (Brunskill and Graham, 1979) may be one factor that contributes to higher adult mortality by reducing the quantity and quality of food available (Pires et al., 2004). The weight of a standard size 15 mm mussel is often used as an index of food limitation (Nalepa et al., 1995). Maximum soft tissue weight of zebra mussels generally occurs in the spring when mussels are laden with gametes. As temperatures increase and spawning is initiated, weight loss occurs throughout the summer months, although weight loss due to energy imbalances may also occur at this time (Nalepa et al., 1995). In our study, the weight of a 15 mm standard mussel was both above and below the 8 mg threshold suggested to indicate food limitation in spring, always below this threshold in summer, and always above this threshold in fall (Table 3). While not conclusive, our data support a synchronous convergence of mass loss due to spawning, increasing temperatures and a more dilute food supply (due to resuspension of sediments) could play a role in reducing the longevity of zebra mussels in Lake Winnipeg.

Lagging colonization of the north basin

In contrast to other large lakes in North America, our data suggest that zebra mussels have not colonized the north basin to the extent that might be expected based on invasion events observed elsewhere (Karatayev et al. 2011). This could indicate that spread of zebra mussels in Lake Winnipeg is in a prolonged initial invasive phase, or that conditions in the north basin are less favorable for recruitment and survival than in the south basin or Narrows. In most lakes and rivers across Europe and North America, the invasive phase lasts on average $\sim 2.5 \pm 0.2$ years from initial detection to maximum population size (Karatayev et al., 2011). For example, zebra mussels were thought to have arrived in Lake St. Clair sometime in 1986 or 1987 but reached eastern Lake Erie in late 1989, a time frame on par with the residence time of lake Erie (~ 2.7 years; Griffiths et al., 1991). In Lake Winnipeg, zebra mussels were first detected in the south basin in the fall of 2013 (DFO, 2014). Based on reported residence times (3–5 years; Brunskill et al., 1980) and a predominantly northeastward flow of water in the

lake (Zhao et al., 2012), colonization of the north basin might have been expected as early as 2016. It is possible that our failure to detect mussels in the north basin in 2017 and 2018 was due to our irregular sampling frequency or patchiness of mussels that might be missed using standard sampling methods, particularly in large lakes (Karatayev et al., 2018). In addition, we were unable to sample shallow areas along the northeastern shores of the north basin as this part of the lake is not accessible due to navigational hazards and lack of road access. On the other hand, we observed zebra mussels consistently at station W8, approximately midway between the south and north basins in the Narrows, yet did not detect settled mussels at any sites in the north basin until summer of 2019. Veligers have been detected in plankton hauls from the southern end of the north basin since 2014, yet their presence in the north basin does not appear to be widespread (Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020), implying that colonization of the north basin is indeed lagging relative to the rest of the lake.

Cooler water temperatures characteristic of the north basin may also explain the lag in colonization. Growth and reproduction of zebra mussels is constrained at temperatures $< 10^\circ\text{C}$, and spawning is restricted until temperatures reach $\sim 12^\circ\text{C}$ (Karatayev et al., 2006; 1998). The south basin tends to warm quickly and generally remains isothermal through much of the open water season, while the north basin warms much more slowly and may develop a deep thermocline for parts of the summer (Zhao et al., 2012). Although surface water temperatures between the north and south basins may differ by up to 6°C in the spring, they tend to converge to similar temperatures in the summer (Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020). In contrast, temperature near the lake bottom shows that suitable temperatures for growth, development and recruitment may not occur until mid-July (Fig. 6). Given that the bathymetry of the north basin is relatively flat, this indicates that a large area of the north basin may be sub-optimal for mussel growth and reproduction for much of the open water season. By the time the north basin becomes isothermal in mid-to late July, cyanobacterial blooms are typically well developed and continue to expand in size and intensity until October (Binding et al., 2018). Cyanobacteria are deficient in polyunsaturated fatty acids (PUFA) which are important for reproductive investment by adult dreissenids and the success of juveniles post-metamorphosis (Wacker and von Elert, 2002, 2003). Cyanobacteria may also produce toxins which are lethal to zebra mussel larvae (Boegholt et al., 2019). Although speculative, the possibility that a mismatch in seasonal phenology of optimal water temperatures for growth and reproduction and increasing degradation of food quality (e.g.

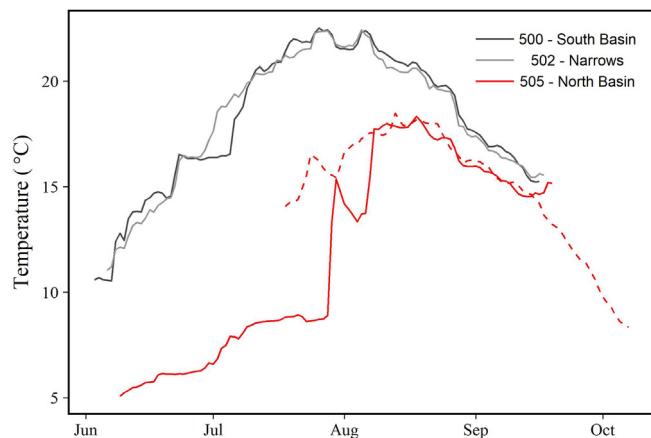


Fig. 6. Time series plots of daily mean water temperature from temperature sensors mounted ~0.25 m above the lake bottom at moorings in the centre of the south basin, Narrows and north basin in 2019 (solid lines) and 2018 (dashed line). Red color indicates sensors from the north basin showing delayed warming. Note sensors from south basin and Narrows in 2018 were lost.

cyanobacterial blooms) explains the poor colonization of the north basin merits further study.

Variation in dreissenid recruitment in the south basin

Our data also suggest consistently poor recruitment of zebra mussels at sites along the east shore of the south basin (9, W11 and MN) throughout the study period. Due to a variety of factors, inter-annual variation in recruitment can be appreciable (Chase and Bailey, 1999; Martel et al., 1994), yet recruitment at these sites was consistently poor. Despite similar densities at sites elsewhere in the south basin, the proportion of mussels <5 mm at these sites was always <5%. This is somewhat counter to our expectation as zebra mussels are thought to preferentially settle on conspecifics, particularly if available substrate is in low supply (Chase and Bailey, 1999; Mackie, 1991). Density dependent effects such as cannibalism or localized food depletion (MacIsaac et al., 1991) seem unlikely explanations for the poor recruitment observed at these sites. Poor recruitment at these sites could be due to less suitable substrate or a greater degree of exposure to wind and waves compared to sites on the western side of the south basin. However, Enders et al. (2019) observed a similar pattern of few to no mussels present on telemetry receivers in the same area as these sites, suggesting factors other than substrate might be responsible for poor recruitment.

Other obvious factors that may affect recruitment and the size structure of dreissenid populations include predation, both on veligers and settled juveniles/adults. Young fish and some copepods will consume veligers (Nack et al., 2015), but we do not have any quantitative estimates of larval predation rates so cannot evaluate this. The common carp (*Cyprinus carpio*), freshwater drum (*Aplodinotus grunniens*) and lake whitefish (*Coregonus clupeaformis*) are present in Lake Winnipeg and are known to consume larger mussels (French and Bur 1996, Madenjian et al. 2010), however a recent study suggests zebra mussels are a minor component of the diet of freshwater drum (Wong et al., 2021). Predation by diving ducks also seems unlikely given the high turbidity in Lake Winnipeg and the abundant wetland habitat surrounding Lake Winnipeg (Watchorn et al., 2012) which may be preferred by waterfowl.

Another potential explanation for the poor recruitment at these sites is low calcium concentrations. Production of veligers is severely curtailed at concentrations of less than 12–15 mg L⁻¹,

and those that are produced may be deformed and unable to survive (Hincks and Mackie, 1997; Sprung, 1987). Approximately half of the hydraulic load to Lake Winnipeg is derived from rivers draining Precambrian shield watersheds on the east side of the lake, and these waters are typically low in calcium (Brunskill et al., 1979). While calcium concentrations in most of Lake Winnipeg are generally well above limiting levels, calcium concentrations within Traverse Bay and other locations along the eastern margin of Lake Winnipeg can at times be as low as 10 mg L⁻¹ (Environment and Climate Change Canada and Manitoba Agriculture and Resource Development, 2020) and could explain persistently poor recruitment here. A sustained presence of larger zebra mussels (>10 mm) at these sites could arise from translocation or immigration during wind and/or storm events (Martel et al. 1994, Miller and Payne 1997). Such mussels would be capable of mobilizing calcium from their shell in order to survive periods of low calcium (Vinogradov et al., 1993).

Implications

The distribution of suitable substrate for attachment clearly limits the distribution of zebra mussels in the south basin and Narrows of Lake Winnipeg at present. Most of the suitable substrates in the south basin and Narrows are colonized, but reasons for the relative scarcity of zebra mussels on similar substrates in the north basin remains unknown. Such a delayed colonization is anomalous relative to invasion histories in other large lakes of North America (Karataev et al., 2015). It is difficult to predict whether the population has peaked and is now at some equilibrium level, or whether colonization is much slower compared to other systems.

The ecological effects of zebra mussels are linked to the size of the population and their filtration capacity. Given the relatively limited spread of zebra mussels throughout Lake Winnipeg at present, the potential for dramatic ecological impacts may be somewhat less than in other systems unless their colonization of unconsolidated offshore sediments increases. The presence of empty shell material within mussel colonies provides one mechanism by which zebra mussels could further expand their range onto soft substrates, but the effectiveness of such a mechanism will likely be reduced due to frequent, vigorous wind driven mixing which can redistribute empty shell material or bury newly deposited shells with sediment. Episodes of hypoxia can also reduce survival and longevity of zebra mussels (Karataev et al., 2018). Although hypoxia does not appear to be a frequent occurrence in Lake Winnipeg, it can occur under quiescent conditions (Wassenaar, 2012) and may limit the ability of zebra mussels to colonize deeper parts of the lake.

On the other hand, the arrival of zebra mussels frequently precedes the arrival of quagga mussels (Karataev et al., 2015, 2011). Quagga mussels are more capable of colonizing soft substrates such as silts and muds and can tolerate lower temperatures and oxygen concentrations than zebra mussels (Karataev et al., 1998). In shallow lakes without large profundal zones, quagga and zebra mussels can co-exist, with zebra mussels largely restricted to the littoral zone and quaggas occupying the littoral and profundal zones (Karataev et al., 2015). By having different spatial distributions in a waterbody, the ecological impacts are likely to differ if quagga mussels successfully colonize the larger area of soft substrates in Lake Winnipeg, particularly in the north basin where temperatures are cooler. Continued monitoring of adult populations and veliger abundance should provide useful data to better predict the trajectory of the zebra mussel population in Lake Winnipeg and provide a means to detect any potential invasion by quagga mussels.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was funded by Environment and Climate Change Canada's Lake Winnipeg Basin Program. The authors would like to thank the captain and crew of the M.V. Namao and the Lake Winnipeg Research Consortium Inc. for logistics, organizational support, ship time, and safe sampling on Lake Winnipeg. The authors would also like to thank Todd Breedon, Derek Rainey, Kim Rattan, Megan Lee, Victoria Vasey, Ross Li, Allison Waedt, Janine Hunt, Spencer Hruden, Sarah Hnytka, Sarah Glowka, Emilie Barker and Ryann Teillet for tireless assistance in the field and laboratory. The comments of two anonymous reviewers improved the original manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2020.12.005>.

References

- Ackerman, J.D., Sim, B., Nichols, S.J., Claudi, R., 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparisons with marine bivalves. *Can. J. Zool.* 72, 1169–1179. <https://doi.org/10.1139/z94-157>.
- Bailey, R.C., Chase, M., Bechtold, J.-P., 1995. An improved technique for estimating the density of benthic macroinvertebrates on cobble. *J. Freshwat. Ecol.* 10, 189–192. <https://doi.org/10.1080/02705060.1995.9663434>.
- Baldwin, B.S., Mayer, M.S., Dayton, J., Pau, N., Mendilla, J., Sullivan, M., Moore, A., Ma, A., Mills, E.L., 2002. Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. *Can. J. Fish. Aquat. Sci.* 59, 680–694. <https://doi.org/10.1139/f02-043>.
- Bially, A., MacIsaac, H.J., 2000. Fouling mussels (*Dreissena spp.*) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwat. Biol.* 43, 85–97.
- Binding, C.E., Greenberg, T.A., McCullough, G., Watson, S.B., Page, E., 2018. An analysis of satellite-derived chlorophyll and algal bloom indices on Lake Winnipeg. *J. Great Lakes Res.* 44, 436–446. <https://doi.org/10.1016/j.jglr.2018.04.001>.
- Boegehold, A.G., Johnson, N.S., Kashian, D.R., 2019. Dreissenid (quagga and zebra mussel) veligers are adversely affected by bloom forming cyanobacteria. *Ecotox. Environ. Safety* 182. <https://doi.org/10.1016/j.ecoenv.2019.109426> 109426.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9, 378–400.
- Brunskill, G.J., Campbell, P., Elliott, S.E.M., 1979. Temperature, oxygen, conductance and dissolved major elements in Lake Winnipeg (No. 1526), Fisheries and Marine Service Manuscript Report. Department of Fisheries and Environment. <https://science-catalogue.canada.ca/record=3940360-S6>.
- Brunskill, G.J., Elliott, S.E.M., Campbell, P., 1980. Morphometry, hydrology, and watershed data pertinent to the limnology of Lake Winnipeg (Technical Report). Department of Fisheries and Oceans. <https://science-catalogue.canada.ca/record=3877167-S6>.
- Brunskill, G.J., Graham, B.W., 1979. The offshore sediments of Lake Winnipeg (Technical Report). Fisheries and Marine Service. <https://science-catalogue.canada.ca/record=3924815-S6>.
- Chase, M.E., Bailey, R.C., 1999. The ecology of the zebra mussel (*Dreissena polymorpha*) in the lower Great Lakes of North America: I. Population dynamics and growth. *J. Great Lakes Res.* 25, 107–121. [https://doi.org/10.1016/S0380-1330\(99\)70720-3](https://doi.org/10.1016/S0380-1330(99)70720-3).
- Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. *J. Stat. Soft.* 34, 1–24. <https://doi.org/10.18637/jss.v034.i02>.
- DFO, 2014. Lake Winnipeg Zebra Mussel treatment. Canadian Science Advisory Secretariat. Department of Fisheries and Oceans.
- Enders, E., Charles, C., Caskenette, A., Rudolfsen, T.A., Watkinson, D.A., 2019. Distribution patterns of the early invasion of zebra mussels, *Dreissena polymorpha* (Pallas, 1771), in the south basin of Lake Winnipeg. *Biolnv. Rec.* 8, 329–342. <https://doi.org/10.3391/bir.2019.8.2.15>.
- Environment and Climate Change Canada, Manitoba Agriculture and Resource Development, 2020. State of Lake Winnipeg (2nd Ed). https://gov.mb.ca/water/pubs/water/lakes-beaches-rivers/state_lake_wpg_report_tech.pdf.
- French, J.R.P., Bur, M.T., 1996. The effect of zebra mussel consumption on growth of freshwater drum in Lake Erie. *J. Fresh. Ecol.* 11, 283–289.
- Geisler, M.E., Rennie, M.D., Gillis, D.M., Higgins, S.N., 2016. A predictive model for water clarity following dreissenid invasion. *Biol. Invasions* 18, 1989–2006. <https://doi.org/10.1007/s10530-016-1146-x>.
- Griffiths, R.W., Schloesser, D.W., Leach, J.H., Kovalak, W.P., 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48, 1381–1388. <https://doi.org/10.1139/f91-165>.
- Haltuch, M.A., Berkman, P.A., Garton, D.W., 2000. Geographic information system (GIS) analysis of ecosystem invasion: Exotic mussels in Lake Erie. *Limnol. Oceanogr.* 45, 1778–1787. <https://doi.org/10.4319/lo.2000.45.8.1778>.
- Hansen, G.J.A., Ahrenstorff, T.D., Bethke, B.J., Dumke, J.D., Hirsch, J., Kovalenko, K.E., LeDuc, J.F., Maki, R.P., Rantala, H.M., Wagner, T., 2020. Walleye growth declines following zebra mussel and *Bythotrephes* invasion. *Biol. Invasions* 22, 1481–1495. <https://doi.org/10.1007/s10530-020-02198-5>.
- Hebert, P.D.N., Wilson, C.C., Murdoch, M.H., Lazar, R., 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Can. J. Zool.* 69, 405–409. <https://doi.org/10.1139/z91-063>.
- Hecky, R.E., Smith, R.E., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., Howell, T., 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61, 1285–1293. <https://doi.org/10.1139/f04-065>.
- Higgins, S.N., Hecky, R.E., Guildford, S.J., 2006. Environmental controls of *Cladophora* growth dynamics in eastern Lake Erie: Application of the *Cladophora* Growth Model (CGM). *J. Great Lakes Res.* 32, 629–644. [https://doi.org/10.3394/0380-1330\(2006\)32](https://doi.org/10.3394/0380-1330(2006)32).
- Higgins, S.N., Zanden, M.J.V., 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecol. Monogr.* 80, 179–196. <https://doi.org/10.1890/09-1249.1>.
- Hincks, S.S., Mackie, G.L., 1997. Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth, and reproductive success of zebra mussel (*Dreissena polymorpha*) in Ontario lakes. *Can. J. Fish. Aquat. Sci.* 54, 2049–2057. <https://doi.org/10.1139/f97-114>.
- Hothorn, T., Bretz, F., Westfall, R., 2008. Simultaneous inference in general parametric models. *Biometr. J.* 50, 346–363.
- Jones, L.A., Ricciardi, A., 2005. Influence of physicochemical factors on the distribution and biomass of invasive mussels (*Dreissena polymorpha* and *Dreissena bugensis*) in the St. Lawrence River. *Can. J. Fish. Aquat. Sci.* 62, 1953–1962. <https://doi.org/10.1139/f05-096>.
- Karatayev, A.Y., Burlakova, L.E., Mastitsky, S.E., Padilla, D.K., Mills, E.L., 2011. Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena rostriformis bugensis*, at different spatial scales. *J. Shellfish Res.* 30, 923–931. <https://doi.org/10.2983/035.030.034>.
- Karatayev, A.Y., Burlakova, L.E., Mehler, K., Bocaniov, S.A., Collingsworth, P.D., Warren, G., Kraus, R.T., Hinche, E.K., 2018. Biomonitoring using invasive species in a large Lake: *Dreissena* distribution maps hypoxic zones. *J. Great Lakes Res.* 44, 639–649. <https://doi.org/10.1016/j.jglr.2017.08.001>.
- Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. *Hydrobiol.* 746, 97–112. <https://doi.org/10.1007/s10750-014-1901-x>.
- Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2006. Growth rate and longevity of *Dreissena polymorpha* (Pallas): a review and recommendations for future study. *J. Shellfish Res.* 25, 23–32. [https://doi.org/10.2983/0730-8000\(2006\)25](https://doi.org/10.2983/0730-8000(2006)25).
- Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 1998. Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). *J. Shellfish Res.* 17, 1219–1235.
- Leach, J.H., 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie, In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Zebra Mussels: Biology, Impacts, and Control*. Lewis Publishers, pp. 381–399.
- MacIsaac, H.J., Lonnee, C.J., Leach, J.H., 1995. Suppression of microzooplankton by zebra mussels: importance of mussel size. *Freshwat. Biol.* 34, 379–387. <https://doi.org/10.1111/j.1365-2427.1995.tb00896.x>.
- Mackie, G.L., 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiol.* 219, 251–268. <https://doi.org/10.1007/BF00024759>.
- MacIsaac, H.J., Sprules, W.G., Leach, J.H., 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics?. *Can. J. Fish. Aquat. Sci.* 48, 2051–2060. <https://doi.org/10.1139/f91-244>.
- Madenjian, C.P., Pothoven, S.A., Schneeberger, P.J., Ebener, M.P., Mohr, L.C., Nalepa, T.F., Bence, J.R., 2010. Dreissenid mussels are not a "dead end" in Great Lakes food webs. *J. Great Lakes Res.* 36, 73–77.
- Maecher, M., Ringach, D., 2004. The Diptest package. R program documentation.
- Mallez, S., McCartney, M., 2018. Dispersal mechanisms for zebra mussels: population genetics supports clustered invasions over spread from hub lakes in Minnesota. *Biol. Invasions* 20, 2461–2484. <https://doi.org/10.1007/s10530-018-1714-3>.
- Manitoba Conservation, 2001. Lake Winnipeg Shoreline Management Handbook.
- Martel, A., 1993. Dispersal and recruitment of zebra mussel (*Dreissena polymorpha*) in a nearshore area in west-central Lake Erie: the significance of postmetamorphic drifting. *Can. J. Fish. Aquat. Sci.* 50, 3–12. <https://doi.org/10.1139/f93-001>.

- Martel, A., Mathieu, A.F., Findlay, C.S., Nepszy, S.J., Leach, J.H., 1994. Daily settlement rates of the zebra mussel, *Dreissena polymorpha*, on an artificial substrate correlate with veliger abundance. Can. J. Fish. Aquat. Sci. 51, 856–861. <https://doi.org/10.1139/f94-084>.
- Mellina, E., Rasmussen, J.B., 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. Can. J. Fish. Aquat. Sci. 51, 1024–1036. <https://doi.org/10.1139/f94-102>.
- Nack, C.C., Limburg, K.E., Schmidt, R.E., 2015. Diet composition and feeding behavior of larval American shad, *Alosa sapidissima* (Wilson), after the introduction of the invasive zebra mussel, *Dreissena polymorpha* (Pallas), in the Hudson River estuary, NY. Northeast. Nat. 22, 437–450. doi: 10.1656/045.022.0216.
- Nakano, D., Strayer, D.L., 2014. Biofouling animals in fresh water: biology, impacts, and ecosystem engineering. Front. Ecol. Environ. 12, 167–175. <https://doi.org/10.1890/130071>.
- Nalepa, T.F., Schloesser, D.W., 2013. Quagga and Zebra Mussels: Biology, Impacts, and Control. CRC Press.
- Nalepa, T.F., Wojcik, J.A., Fanslow, D.L., Lang, G.A., 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: Population recruitment, density, and size structure. J. Great Lakes Res. 21, 417–434. [https://doi.org/10.1016/S0380-1330\(95\)71056-5](https://doi.org/10.1016/S0380-1330(95)71056-5).
- Ozersky, T., Barton, D.R., Depew, D.C., Hecky, R.E., Guildford, S.J., 2011. Effects of water movement on the distribution of invasive dreissenid mussels in Lake Simcoe, Ontario. J. Great Lakes Res. 37, 46–54. <https://doi.org/10.1016/j.jglr.2010.07.006>.
- Ozersky, T., Malkin, S.Y., Barton, D.R., Hecky, R.E., 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of Lake Ontario shoreline. J. Great Lakes Res. 35, 321–328. <https://doi.org/10.1016/j.jglr.2009.05.001>.
- Pires, L.M.D., Jonker, R.R., Donk, E.V., Laanbroek, H.J., 2004. Selective grazing by adults and larvae of the zebra mussel (*Dreissena polymorpha*): application of flow cytometry to natural seston. Freshwat. Biol. 49, 116–126. <https://doi.org/10.1046/j.1365-2426.2003.01173.x>.
- Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ramcharan, C.W., Padilla, D.K., Dodson, S.I., 1992. Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 49, 2611–2620. <https://doi.org/10.1139/f92-289>.
- Rennie, M.D., Evans, D.O., Young, J.D., 2013. Increased dependence on nearshore benthic resources in the Lake Simcoe ecosystem after dreissenid invasion. Inland Waters 3, 297–310. <https://doi.org/10.5268/IW-3.2.540>.
- Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol. Methods 11, 54–71. <https://doi.org/10.1037/1082-989X.11.1.54>.
- Sprung, M., 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. Archiv für Hydrobiol. 79, 69–86.
- Stewart, T.W., Miner, J.G., Lowe, R.L., 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. J. North Am. Benth. Soc. 17, 81–94. <https://doi.org/10.2307/1468053>.
- Stoeckmann, A.M., Garton, D.W., 2001. Flexible energy allocation in zebra mussels (*Dreissena polymorpha*) in response to different environmental conditions. J. North Am. Benth. Soc. 20, 486–500. <https://doi.org/10.2307/1468043>.
- Howell, E.T., Marvin, C.H., Bilyea, R.W., Kauss, P.B., Somers, K., 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. J. Great Lakes Res. 22, 744–756. [https://doi.org/10.1016/S0380-1330\(96\)70993-0](https://doi.org/10.1016/S0380-1330(96)70993-0).
- Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59, 1209–1228. <https://doi.org/10.1139/f02-087>.
- Vinogradov, G.A., Smirnova, N.A., Sokolov, V.A., Brunnitsky, A.A., 1993. Influence of chemical composition of the water on the mollusk *Dreissena polymorpha*. In: Nalepa, T.F., Schloesser, D.W. (Eds.), Zebra Mussels: Biology, Impacts, and Control. Lewis Publishers, Boca Raton FL, pp. 283–293.
- Wacker, A., von Elert, E., 2002. Strong influences of larval diet history on subsequent post-settlement growth in the freshwater mollusc *Dreissena polymorpha*. Proc. Royal Soc. B: Biol. Sci. 269, 2113–2119. <https://doi.org/10.1098/rspb.2002.2139>.
- Wacker, A., von Elert, E., 2003. Food quality controls reproduction of the zebra mussel (*Dreissena polymorpha*). Oecologia 135, 332–338.
- Wassenaar, L.I., 2012. Dissolved oxygen status of Lake Winnipeg: Spatio-temporal and isotopic ($\delta^{18}\text{O}$ – $\delta^2\text{O}$) patterns. J. Great Lakes Res. 38, 123–134. <https://doi.org/10.1016/j.jglr.2010.12.011>.
- Watchorn, K. Elise, Goldsborough, L. Gordon, Wrubleski, Dale.A, Mooney, Brian.G, 2012. A hydrogeomorphic inventory of coastal wetlands of the Manitoba Great Lakes: Lakes Winnipeg, Manitoba, and Winnipegosis. Journal of Great Lakes Research 38 (3), 115–122. <https://doi.org/10.1016/j.jglr.2011.05.008>.
- Wilson, K.A., Howell, E.T., Jackson, D.A., 2006. Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. J. Great Lakes Res. 32, 11–28. [https://doi.org/10.3394/0380-1330\(2006\)32](https://doi.org/10.3394/0380-1330(2006)32).
- Wong, C.H.S., Enders, E.C., Hasler, C.T., 2021. Limited evidence of zebra mussel (*Dreissena polymorpha*) consumption by freshwater drum (*Aplodinotus grunniens*) in Lake Winnipeg. J. Great Lakes Res. 47, 592–602.
- Zhao, J., Rao, Y.R., Wassenaar, L.I., 2012. Numerical modeling of hydrodynamics and tracer dispersion during ice-free period in Lake Winnipeg. J. Great Lakes Res. 38, 147–157. <https://doi.org/10.1016/j.jglr.2011.02.005>.
- Zhu, B., Fitzgerald, D.G., Mayer, C.M., Rudstam, L.G., Mills, E.L., 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. Ecosystems 9, 1017–1028. <https://doi.org/10.1007/s10021-005-0049-y>.
- Zuur, A.F., Hilbe, J.M., Ieno, E.N. 2013. A Beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists. Highland Statistics Ltd. 256 pp.