ZEBRA MUSSEL HABITAT SELECTION, GROWTH AND MORTALITY IN LAKES OF NORTHEASTERN WISCONSIN AND THE UPPER PENINSULA OF MICHIGAN

by

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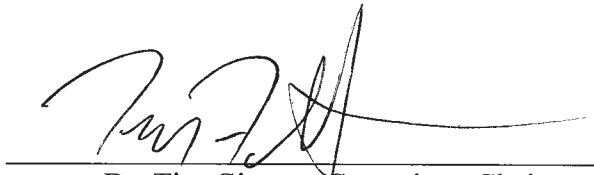

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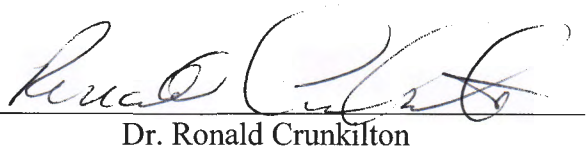

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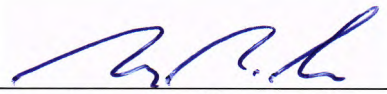

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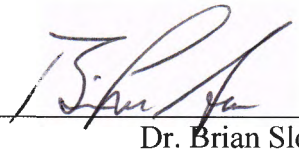

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ABSTRACT

Invasive zebra mussels (*Dreissena polymorpha*) have been anthropogenically transported to various inland locations in the midwestern United States from the Laurentian Great Lakes. In northeastern Wisconsin and the Upper Peninsula of Michigan, additional colonization is occurring along natural corridors and by inadvertent human transport. High fecundity and filtering rates of zebra mussels and the ability to attach to substrates cause tremendous ecological and economic impacts. Because management options are limited once zebra mussels become established, there is a critical need to contain their spread. Identifying characteristics of new "source" population invasions may assist early detection monitoring efforts. Suitability models based on water calcium concentrations are currently used to identify lakes in which to focus pre-invasion monitoring efforts. Understanding lake-specific habitat limitations could refine monitoring efforts by identifying locations within lakes that have the greatest establishment potential. Additionally, quantitative comparisons of zebra mussel growth and mortality among lakes across a range of colonization periods may provide information to managers and landowners on anticipated population trajectories following establishment. The objectives of this study were to: (1) determine if habitat selection by zebra mussels occurs within lakes; (2) determine if differential habitat selection occurs among lakes consistent with time since colonization and, if so, build a predictive model of potential habitat use;

(3) determine if zebra mussel mean length-at-age and mortality rates differ among sampled populations. SCUBA diving was used to sample 10 quadrats at regular intervals along 12 transects (120 total quadrats) representing a variety of habitats in eight lakes. Within quadrats, water depth was measured and substrates were visually estimated to quantify habitat availability. Zebra mussel presence / absence were recorded for available substrates in each quadrat. Selection indices were used to evaluate zebra mussel habitat selection. Zebra mussels were randomly collected from one quadrat along each transect. Length and age for each collected individual was used to evaluate zebra mussel mean length-at-age and mortality. Von Bertalanffy growth curves were estimated to determine whether zebra mussel mean length-at-age varied among lakes and catch curves were used to determine whether zebra mussel mortality rates varied among lakes. Results suggest that zebra mussels selected for hard substrates (i.e., rock, wood, and shells), avoided soft substrates (i.e., silt, particulate, and sand), and used macrophytes in proportion to availability. Zebra mussel growth varied among lakes and there was no difference in zebra mussel mortality rates among lakes. Current monitoring efforts focus on veliger tows or substrate samplers which are effective only after a population is widely established. These results can be applied to early detection monitoring protocols to detect a pioneer zebra mussel population. Few studies have evaluated zebra mussel mean length-at-age and mortality in North America and this study can be used as a template to evaluate mean length-at-age and mortality across a variety of lakes to increase our understanding of zebra mussel biology.

INTRODUCTION

Invasive species can have devastating environmental and economic impacts (Wilcove et al. 1998; Mack et al. 2000; Pimentel et al. 2005). An estimated 50 000 non-indigenous species have been introduced to the United States (Pimentel et al. 2005) and about 4 300 are considered invasive (Corn et al. 1999). Invasive species have considerable ability to rapidly adapt, allowing them to proliferate in new environments (Elton 1958) and alter community structure (Kourtev et al. 2002) and ecosystem processes (Vistousek 1990; Gordon 1998). Economic damages associated with invasive species have been reported to annually cost between $1.1 billion (OTA 1993) and $120 billion (Pimentel et al. 2005). The wide range of ecological and economic impacts of invasive species has been a concern in the United States for more than a century (Elton 1958).

The Laurentian Great Lakes have been identified as one of the most vulnerable ecosystems to species invasions (Locke et al. 1993). Transoceanic vessels annually discharge about 800 million L of ballast water into Great Lake ports (Locke et al. 1993). Ballast water may contain various microorganisms, invertebrates, and fishes and is a global vector for aquatic invasive species (Carlton 1993; Carlton and Geller 1993). Non-indigenous species dominate the Great Lakes food web and have caused significant ecological and economic impacts (Mills et al. 1993; MacIsaac 1996; Ricciardi and MacIsaac 2000). Over $2 billion in annual economic impacts are from aquatic mollusks (i.e., dreissenid mussels *Dreissena* spp., Asian clam *Corbicula fluminea*, and shipworm *Teredo navalis*), with $1 billion of damages directly related to zebra mussel (*Dreissena polymorpha*) impacts (Pimentel et al. 2005).

Zebra mussels are native to the Ponto-Caspian region of Eurasia and were brought to North America in ballast water (Hebert et al. 1989; Carlton and Geller 1993). They were first observed in North America in the Laurentian Great Lakes in the 1980s (Hebert et al. 1989; Carlton 1993), where they directly and indirectly impacted biological organisms and recreational and industrial users. Primary zebra mussel impacts are associated with their high fecundity, which may result in great population densities (Walz 1978; Sprung 1990, 1993). Zebra mussels are filter feeders and can decrease phytoplankton and zooplankton abundance disrupting trophic interactions (MacIsaac et al. 1991; reviewed in Dorgelo 1993; MacIsaac 1996). Zebra mussels attach to substrates using byssal threads, resulting in conglomerates that often clog intake pipes, attach to boats and docks (reviewed in Ludyanskiy et al. 1993; Bonner and Rockhill 1994; MacIsaac 1996), and smother native unionid mussels (Unionidae) and other crustaceans (Ricciardi et al. 1995; Burlakova et al. 2000). Following their establishment in the Laurentian Great Lakes, zebra mussels were incidentally moved by recreationists to inland lakes and streams throughout North America, primarily in the midwestern United States. Particularly in the late 1990s, zebra mussels began colonizing lakes and streams in northeastern Wisconsin and the Upper Peninsula of Michigan (hereafter referred to as upper Michigan) (Benson et al. 2012).

Since their colonization of northeastern Wisconsin and upper Michigan, zebra mussel populations have been spreading throughout the region, particularly to lakes whose calcium concentrations render them vulnerable to invasion. Vulnerable lakes have hydrologic connectivity to invaded lakes that allows zebra mussels to spread. The geology of these lakes results in adequate amounts of calcium (10 to 26 mg Ca^{+2} / L) and

pH levels between 7.1 to 8.4 to render the systems habitable to zebra mussels (Sprung 1987; Ramcharan et al. 1992; Hincks and Mackie 1997). Furthermore, proximity and connectivity to invaded waters, as well as high use by transient boaters, leaves lakes vulnerable to zebra mussel introduction (Carlton 1993; Johnson and Carlton 1996; Johnson and Padilla 1996; Bobeldyk et al. 2005). Cumulatively, these factors have resulted in a cluster of lakes in northeastern Wisconsin and upper Michigan that have been colonized by zebra mussels (Benson et al. 2012). Because most zebra mussel invasions in the Midwest have occurred in more southern lakes that are more productive and species-rich, their potential influences in less productive, north temperate lakes is largely unknown.

Managers have limited options for controlling zebra mussels and early detection of zebra mussel presence is useful to help reduce their spread (Finnoff et al. 2006). Researchers have developed tools based on biogeographic characteristics (i.e., anthropogenic movement) and water quality (i.e., calcium concentration) to provide guidance on which lakes to focus monitoring efforts (Papes et al. 2011). However, the habitat preferences and population dynamics of zebra mussels in the upper midwestern United States are poorly understood. Although calcium concentrations and pH appear to limit zebra mussel establishment (Ackerman et al. 1992, 1993; Kilgour and Mackie 1993; Mellina and Rasmussen 1994; Karatyev et al. 1998; Marsden and Lansky 2000; Jones and Ricciardi 2005), other potential habitat limitations are less known but likely exist. Understanding potential lake-specific habitat limitations could assist biologists in focusing monitoring efforts (Myers et al. 2000; Bax et al. 2001; Lodge et al. 2006). Zebra mussel population dynamics following their establishment are known to vary

among waterbodies (Ramcharan et al. 1992; Katatayev 1998), but zebra mussel demography in these north temperate lakes has not been explored. Quantitative comparisons among lakes at different phases of invasion would allow biologists to compare zebra mussel population dynamics to better predict anticipated population trajectories from early invasion to long-established colonization (Eiswerth and Johnson 2002; Brown et al. 2008; Jongejans et al. 2008).

The goal of this study was to better understand zebra mussels within north temperate lakes of northeastern Wisconsin and upper Michigan by measuring and predicting habitat preferences, growth, and mortality in lakes that vary in density. The intent of this study was to improve early detection monitoring protocols and offer guidance to biologists and landowners in understanding the range of expected growth and mortality rates of zebra mussels and ultimately, a better understanding of their dynamics within these waters. The four primary objectives were to: (1) determine if habitat selection by zebra mussels occurs within lakes; (2) determine if differential habitat selection occurs among lakes consistent with time since colonization and, if so, build a predictive model of potential habitat use; (3) determine if zebra mussel mean length-at-age vary among sampled populations; and (4) determine if zebra mussel mortality rates differ among sampled populations.

METHODS

Experimental Design

Three primary concerns were addressed in the study design: 1) which zebra mussel populations to sample; 2) how many samples were necessary from each

population to sufficiently estimate habitat use and selection; and 3) how many samples were necessary from each population to confidently estimate zebra mussel growth and mortality. Three criteria were used to select sampling locations: 1) populations had to be in lentic systems; 2) systems needed to contain only zebra mussels (i.e., no quagga mussels, *D. bugensis*) to minimize effects of competition; and 3) each site had to be proximal to the recently observed zebra mussels populations in northeastern Wisconsin and upper Michigan (Figure 1). Of 17 known zebra mussel populations in northeasternern Wisconsin and upper Michigan (11 lakes, 3 reservoirs, and 3 locations in streams; Figure 1), eight north temperate lakes were selected for this study (Figure 1). Detection dates of zebra mussels in these waterbodies ranged from 1999 to 2012. Since zebra mussel populations are not typically observed until several years after establishment, the initial colonization dates cannot be confirmed (Kraft and Johnson 2000; Karatayev et al. 2006). Therefore, the initial observation dates served as the time of reference for colonization.

Sample Collection

Surface area, maximum depth, pH, chlorophyll *a*, secchi disk depth, and dissolved oxygen profile data for study lakes were collected from various agency online data resources, grant reports, and management plans (Preul 2008; Druckery 2009; MCWC 2012; MDEQ 2012; USGS 2012; WDNR 2012; Premo 2013). Water samples were taken from each lake during 2012, placed in 200 ml Nalgene™ bottles (Nalge Nunc International Corp., Rochester NY) and sent to White Water Associates, Inc. (Amasa, MI) for analysis of calcium concentration.

Quadrats 10 000 cm^2 along transects were used to sample zebra mussels and substrates for habitat selection analysis. A total of 12 transects were sampled on each lake to evaluate relative habitat available to zebra mussels. ESRI ArcMap (2011) software was used to select 12 evenly-spaced points along the shoreline of each lake, with the first point being randomly selected. Each point was the start of a transect that extended perpendicularly into the lake center until reaching a depth of 1 m past the thermocline and not to exceed 9 m, or halfway to the opposite shore. Along each transect, 10 evenly-spaced 10 000 cm^2 quadrats were established, for a total of 120 quadrats per lake to characterize zebra mussel habitat.

Snorkeling and SCUBA diving were used to measure habitat variables and determine zebra mussel presence/absence within each 10 000 cm^2 quadrat. Since divers generally spent several hours sampling habitat per day, depths beyond about 9 m were not sampled as a precaution to avoid decompression illness and also to accommodate diver's comfort. If the habitat was homogeneous (e.g., only macrophytes), a 900 cm^2 quadrat was used because it was more efficient for the divers to carry. Water depth was measured from the center of each quadrat with a measuring tape on a reel attached to a polystyrene foam float. Visual estimates were made of the percent occurrence of bottom substrates including wood, macrophytes, and shell substrates, as well as estimates of particle sizes. Bottom mineral substrate types were classified using the Wentworth (1992) particle size scale (Table 1). Coarse woody structures used as zebra mussel attachment substrate were categorized using a modification of McHenry et al.'s (1998) and Newbrey et al.'s (2005) coarse woody structure classification (Table 1). Shell substrate (e.g., native mussels, snails) relative proportion was also classified within

quadrats (Table 1). Because this survey was conducted during the growing season and macrophytes were fully developed, macrophytes were considered a parent substrate material. Non-natural substrates (e.g., anchor, cans) were not classified because they were infrequent. Within each quadrat, presence/absence of zebra mussel and the substrate they were attached to were recorded.

Within each lake, all zebra mussels were collected from the total surface area available for colonization of one random quadrat per transect for a total of 12 collection points per lake. These zebra mussels were aged and measured for subsequent evaluation of growth and mortality rates. Four quadrat sizes (11.1 cm^2, 100 cm^2, 900 cm^2, 10 000 cm^2) were used to collect zebra mussels. Because zebra mussels can reach densities of about 75 individuals per cm^2 (Ramcharan et al. 1992) smaller quadrats were used when mussels were very dense and larger quadrats were used when mussels were sparse. Zebra mussel shell length was measured to the nearest 0.01 mm along the ventrolateral surface using digital vernier calipers (Seed 1969). Age was determined by a single observer counting, by feel and visual observation, annual growth rings on zebra mussel shells (Chamberlain 1931). Because the lakes in this study are lentic systems that experience strong seasonal temperature variation, it was assumed that annual rings were apparent and distinct (Chamberlain 1931; Neves and Moyer 1988). Age estimates were confirmed using haphazard selection of a few quadrats to compare age estimates with estimates of experts from the University of Wisconsin-Extension and Wisconsin Department of Natural Resources.

Habitat Analysis

The techniques of Manly et al. (1993), partially based on the forage (selection) ratio (Hess and Swartz 1940; Manly et al. 1972; Hobbs and Bowden 1982), were used to evaluate zebra mussel substrate selection. Selection ratios ($\hat{w}_i$) for each substrate type were developed for each lake and for all lakes combined to determine zebra mussel substrate selection using the following equation:

$$\hat{w}_i = \frac{o_i}{\hat{\pi}_i}$$

where o_i equals $u_i \cdot u_+^{-1}$ with u_i being the sample proportion of used units in category i, and u_+being the random sample of used resource units, and $\hat{\pi}_i$ equals $m_i \cdot m_t^{-1}$ with m_i being the sample proportion of the number of available units, and m_t being the size of a sample of available resource units m_t (Manly et al. 1993). Substrates with similar parent material were condensed into categories to provide at least five resource units in each category, both in the sample of used units and in the sample of unused units, to ensure that o_i and $\hat{\pi}_i$ values were approximately normally distributed. Standard error was calculated as:

$$se(\hat{w}_i) = \hat{w}_i \sqrt{\frac{1 - o_i}{o_i u_+} + \frac{se(\hat{\pi}_i)^2}{\hat{\pi}_i{}^2}}$$

Approximate simultaneous 95% Bonferroni confidence intervals (Many et al. 1993) on the selection ratios were constructed using:

$$\hat{w}_i \pm z_{\propto/(2I)} se(\hat{w}_i)$$

where $z_{\propto/(2I)}$ is the variable of the standard normal distribution corresponding to the upper tail probability of 100α/(2I). The selection coefficient $\hat{w}_i$ is declared significantly

different from 1 if the confidence interval on $\widehat{w}_i$ does not contain the value 1. Selection for a substrate is indicated with a value >1, avoidance is indicated with a value <1, and use in proportion to availability is indicated with a value equal to 1 (Manly et al. 1993).

Forward stepwise logistic regression was used to develop resource selection functions for habitat characteristics selected by zebra mussels among study lakes (Manly et al. 1993). Resource selection functions are models that yield values proportional to the probability of use relative to a resource unit's availability. In this study, the relative probability of zebra mussel presence was determined based on habitat features used by zebra mussels relative to the availability of that feature in each lake. For the logistic regression analyses, the independent variable was binary for zebra mussel presence (present/absent). Logistic regression uses the function:

$$\pi = e^u \cdot (1 + e^u)^{-1}$$

where π is the probability of zebra mussel use and u is $k + m_1x_1 + m_2x_{2 + \ldots +} m_ix_j$, where k is constant, m_i is the regression coefficient, and x_j is the value of the independent variables. A forward stepwise logistic regression was conducted in R (R Development Core Team 2008) to determine which variables predicted zebra mussel presence.

Growth Analysis

Length-at-age data were used to model zebra mussel growth for each lake with the von Bertalanffy growth model (von Bertalanffy 1938; Ricker 1975):

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

Where L_t is the mean shell length at age (t), L_∞ is the asymptotic shell length, k is the Brody growth coefficient (the rate at which L_t approaches L_∞), and t_0 is the hypothetical

age when L_t is zero. Growth curves were fit by non-linear least squares regression routine programmed in a Microsoft Excel® 2010 spreadsheet. A likelihood ratio test was performed to compare growth curves among lakes.

Mortality Analysis

Zebra mussel mortality was calculated using catch-curve analysis (Ricker 1975). Age frequency data from zebra mussels obtained from each lake were used to estimate total instantaneous mortality of zebra mussels in each lake. To determine the age structure in each lake, zebra mussel densities for each sampled quadrat were first extrapolated to number of individuals per 10 000 cm^2 and then summed across the 12 quadrats. A catch-curve was then estimated by regressing the descending limb of $\log_e$ number of zebra mussels in each class against age, thereby enabling estimation of survival and mortality rates from a sample of a single population (Ricker 1975). The total instantaneous mortality rate (Z) was estimated as the slope of the catch curve regressions. The equation used was:

$$ln(N_t) = \ln(N_0) - Zt$$

where N_t = number present at any time, N_0 is the average recruitment, Z is the total instantaneous mortality; and t is age. The total annual survival rate, S, was estimated as $S = e^{-Z}$ and the annual mortality, A, was estimated as $A = 1 - S$. Average recruitment was estimated from the intercept of the linear regression: $N_o = e^{Log_e(N_0)}$. Analysis of covariance (ANCOVA) was used to compare slopes of catch-curve regressions among the populations using PSAW 21.0 (SPSS Inc., Chicago, IL).

RESULTS

In total, zebra mussel habitat use was sampled in 8 lakes and zebra mussel growth and mortality was estimated in 6 lakes. Historical data indicate that study lakes varied in surface area (32 - 975 hectares), maximum depth (8 - 32 m), calcium concentration (17 – 37 $mg \cdot L^{-1}$), pH (7.8 – 8.8), chlorophyll *a* (1.5 – 7 $\mu g \cdot L^{-1}$), and secchi disk depth (2.3 – 6.6 m) (Table 2). A total of 120 sample sites (quadrats) were evaluated for zebra mussel habitat selection in each lake, for a total of 960 quadrats sampled for habitat across lakes. Across lakes, zebra mussel presence in quadrats ranged from 2 (1.7%) to 119 (99.2%) out of 120 quadrats (Table 3), with a total habitat use sample size of 604 (62.9%) across the eight lakes (Table 4). Zebra mussel sample sizes for growth and mortality analysis ranged from 151 (Keyes Lake) to 1 061 (Lake Antoine) and totaled 3 776 zebra mussels across the six lakes (Table 5). Growth and mortality curves were not developed for zebra mussel populations in Emily Lake (only 3 individuals were collected) and North Lake (only 2 age classes were collected).

Habitat

Substrate compositions of the 8 study lakes varied, though some similarities are apparent. Macrophytes were predominant in Lake Antoine, Lake Noquebay, Moon Lake, Emily Lake, and North Lake (Table 3). Sand was predominant in Metonga Lake and rock was also prevalent (Table 3). Silt and macrophyes were equally abundant in Chicagon Lake and silt, sand, and rock were abundant in Keyes Lake (Table 3). Generally, organic, wood, and shell substrates were rare (<5%) within sampling sites in lakes; however, organic occurred in about 13% of quadrats in Emily Lake. Zebra mussel habitat selection was significant in few lakes (Figure 4). Where zebra mussel use of silt

and sand occurred, avoidance was observed. Organic substrate selection by zebra mussels was not significant. Zebra mussels generally selected for rock, wood, and shells where significance was found. Zebra mussels selected for macrophytes in Metonga Lake and Lake Antoine and used macrophytes in proportion to availability in other lakes (Table 4). Evaluating data from all lakes combined, zebra mussels consistently selected for hard substrates (rock, wood, and shells), avoided soft substrates (silt, organic, and sand), and used macrophytes in proportion to their availability (Table 4). Selection ratios from combined data also showed that zebra mussels had the strongest affinity for wood and shells while avoiding silt and organic material (Table 4). The forward stepwise logistic regression model showed that zebra mussel habitat selection was significantly related to depth (+), percent silt (-), percent organic (-), percent rock (+), and percent wood (+) (Table 6). The predicted relative probability of zebra mussel occurrence was greater in habitats with rock, wood, and increasing depth. Shells and macrophytes were not significant predictors of zebra mussel presence.

Growth

Zebra mussel age and mean length was estimated for all collected zebra mussels in 6 study lakes with the aforementioned Emily Lake and North Lake omitted from this analysis. Zebra mussels across all sampled lakes ranged from age-0 to age-8 and length ranged from 0.98 to 29.05 mm. As expected, younger age classes were more abundant (Table 5). The limited data for older and larger individuals in some lakes resulted in unreasonably large values for L_{∞}, so an assumed value of 35 mm was used for all lakes based on other studies (Morton 1969; Bitterman et al. 1994; Martel 1995; Cope et al.

2006). The Brody growth coefficient, *k*, for zebra mussels ranged from 0.11/year in Lake Noquebay to 0.25/year in Keyes Lake (Figure 2). The likelihood ratio test found that von Bertalanffy growth curves were significantly different among lakes ($F = 4.561$; $df = 30, 38$; $P = 0.001$). Growth rates were similar for zebra mussels in Metonga Lake and Chicagon Lake ($k = 0.19$/year), and also Lake Antoine and Moon Lake ($k = 0.16$/year).

Mortality

Total instantaneous mortality for zebra mussels ranged from -1.05 per year (65% annual mortality) in Moon Lake to -1.83 per year (84% annual mortality) in Lake Noquebay, and was not significantly different among the six lakes (ANCOVA; $F = 2.03$; $df = 5, 28$; $P = 0.126$) (Table 5). The overall instantaneous mortality rate for the six study lakes where instantaneous mortality was calculated was 1.36 per year (74% annual mortality). Because catch curves exclude age classes outside the descending limb, the age classes included in regressions varied among lakes. To reduce variation among populations being compared, an additional ANCOVA was conducted on populations with the same age classes present (age-1 through age-4) found in Lake Antoine, Lake Noquebay, Moon Lake, and Keyes Lake. No difference in instantaneous mortality was found (ANCOVA; $F = 0.638$; $df = 3, 15$; $P = 0.611$). Using this method, the overall instantaneous mortality was 1.83 (84% annual mortality). Both ANCOVA methods found no difference in zebra mussel instantaneous mortality among lakes.

DISCUSSION

The goal of this study was to predict zebra mussel habitat selection, growth, and mortality in north temperate lakes to improve early detection monitoring protocols and provide guidance to managers on expected zebra mussel mean length-at-age and mortality rates following establishment. By using habitat selection models, this study showed distinct substrate selection patterns across study lakes and offered the opportunity to build a predictive model of potential zebra mussel habitat use. Growth and mortality models developed in this study showed distinct differences in zebra mussel mean length-at-age and similar mortality rates among lakes.

Habitat

While previous studies have described zebra mussel use of artificial substrates (Ackerman et al. 1992, 1993; Kilgour and Mackie 1993; Marsden and Lansky 2000) and predicted zebra mussel abundance related to colonized substrates (Mellina and Rassmussen 1994; Karatayev et al. 1998; Jones and Ricciardi 2005), no other study has specifically examined zebra mussel habitat selection or developed empirical models of zebra mussel habitat selection. In this study, zebra mussel selection of hard substrates and hard substrates as a predictor was expected as zebra mussel shell morphology and byssal threads allow firm attachment to solid surfaces (Morton 1993). In addition to providing a solid substrate for zebra mussel attachment, rock, wood, and shells offer a textured and porous surface that provides stronger byssal adhesion (Hebert et al. 1991; Ackerman et al. 1992). Byssal threads can work their way into these pores, increasing adhesion.

Caution is urged when evaluating management priorities to prevent zebra mussel establishment as actions may be detrimental to the aquatic community. While the selection indices and predictive model identified important habitats to focus early detection zebra mussel monitoring (rock, wood, shells, and macrophytes), they could be misinterpreted as priority areas for habitat removal to reduce vulnerability to zebra mussel invasion. These are critical habitats for other aquatic biota, and removal of these habitats would be detrimental to the aquatic ecosystem; the very ecosystem that monitoring efforts are in part trying to protect. Habitat protection and restoration are consistent foundations of fisheries and lake management programs (Cook et al. 2005).

The significant positive correlation of depth with mussel occurrence is a likely indicator that oxygen and food are exerting limitations on zebra mussel distribution both of which are correlated to depth. Oxygen availability can vary within the water column and also among lakes depending on the amount of decomposing organic matter and primary production (Wetzel 2001). Zebra mussels are highly sensitive to hypoxia (Matthews and McMahon 1999) resulting in the species being predictably restricted to the oxygenated habitats among and within waterbodies (reviewed in McMahon 1996). In the current study, oxygen availability (profiles) were not measured in conjunction with sampling efforts; however separate studies in two lakes (Keyes Lake and North Lake) in the same year as the current study are consistent with oxygen availability affecting distribution. Zebra mussels in Keyes Lake and North Lake occurred in a band around the perimeter of the lake with few occurrences in shallow water (<1 m) and were absent deeper than 5 m and 4 m in Keyes Lake and North Lake, respectively. The maximum depth of zebra mussels in these two lakes is consistent with the oxygen availability

observed in the dissolved oxygen profiles reported by others (WDNR 2012; Premo 2013; Richard et al. 2013). Zebra mussels were present below the thermocline in Chicagon Lake and Moon Lake, suggesting suitable oxygen was likely present for zebra mussels despite stratification. Other lake-specific distributions are likely influenced by this potential limitation in available oxygen. Metonga Lake stratified at approximately 12 m and sampling depths were limited to about 7.5 m for diver comfort. During an exploratory dive in Metonga Lake, dense populations of 8 year old zebra mussels were observed at approximately 12 m depth. The maximum depth inhabited by zebra mussels in these lakes is unknown. Lake Antoine did not stratify. Lake Noquebay and Emily Lake were not sampled below the thermocline as few areas within the lake reached these depths.

Likewise, zebra mussel depth distribution would also be predictably correlated with the distribution of their planktonic food source. In lakes that stratify, a density gradient exists above the thermocline where more plankton exists above the thermocline and less below (Wetzel 2001). The presence of older zebra mussels at deeper depths in Metonga Lake may be related to a combination of oxygen availability and this planktonic gradient; these data were not collected on the lake during this study and are thus merely speculative. Future studies on within lake distribution should strongly consider measuring oxygen availability and planktonic communities.

The final sample strategy of 12 transects with 10 quadrats each may have limited the sensitivity of some habitat estimates or resulted in failure to sufficiently sample critical, rare habitats. Therefore, the identification of habitats positively or negatively selected should be considered a minimum collection of habitat types and not a fine scale

roster. Schmidt (2010) developed linear regression models based on mean depth, surface area, and maximum depth to predict the number of transects needed and surface area that can be used to predict the number of quadrats needed. Schmidt (2010) found that the minimum number of quadrats needed to properly sample littoral zone substrate is 268 and that transects are more sensitive to reductions in sampling intensity. The number of transects to describe all habitat variables ranged from 20 to 45. While fewer transects and quadrats were used in this study (10 and 120, respectively) than was recommended by Schmidt (2010), significant selection was observed of select habitats suggesting these habitats are in fact critical to zebra mussels in north temperate lakes. Future studies should attempt to incorporate the more statistically rigorous sampling objectives described by Schmidt (2010) to ensure a more robust habitat selection model for zebra mussels in these systems. The design employed in the present study was a compromise between coverage of multiple lakes representing a range of invasion histories (and thus, dates since invasion) and the depth of habitat surveys of any single system.

Aquatic macrophytes were included as a substrate because of the high variability in shape and form among macrophyte species and the high observed use of macrophytes by zebra mussels. While this allowed zebra mussel selection of macrophytes to be evaluated, the availability of silt and sand, the substrates where macrophytes typically grow, was underestimated. Even with the reduced sample of silt and sand, avoidance of these substrates by zebra mussels was observed. There may also be a relationship between zebra mussels and certain species of macrophytes. In this study, zebra mussels most frequently attached to macrophytes, but were not observed attached to *Braesenia*

scheberi, Nuphar sp., *Zizania paulustris*, among others. Future research could be conducted to determine if zebra mussels select specific macrophyte species.

A potential interaction between zebra mussels and a non-native invasive macrophyte, Eurasian water-milfoil (*Myriophyllum spicatum*), was observed in the lone lake in the study where the plant was observed. In Lake Antoine, one quadrat was encountered that contained only *M. spicatum*; the only quadrat in the entire study where *M. spicatum* was observed. Estimated zebra mussel densities in this quadrat were 3 717 mussels cm^{-2}; the highest observed density at any quadrat in this study. The next greatest density in a quadrat, also in Lake Antoine, was 262 mussels cm^{-2} and the primary substrate was rock. In a study to evaluate the interactions between the aquatic milfoil weevil (*Euhrychiopsis lecontei*) and *M. spicatum,* the *M. spicatum* was reported to have higher glycerol and uracil concentrations than the native milfoil *M. sibiricum* (Marko et al. 2005). These higher levels of glycerol and uracil were proposed as attractants of *E. lecontei* to *M. spicatum*. Since zebra mussels in Lake Antoine were observed in unusual densities on *M. spicatum,* a similar interaction may be occurring. This was only a singular observation and could represent a rare, isolated occurrence of high density and *M. spicatum* occurrence. Nevertheless, the interaction between zebra mussels and glycerol and uracil is not known and could be an important factor in understanding whether *M. spicatum* aids zebra mussel establishment. Alternatively, the overall high abundance of zebra mussels in Lake Antoine could be an important factor in the presence of such high numbers on *M. spicatum*. Future studies examining this relationship should include lakewide mussel density and *M. spicatum* as variables.

Growth

Growth rates in this study were lower than a previous estimate of growth rates in select zebra mussel populations of North America (Cope et al. 2006). Cope et al. (2006) reported growth rates of 1.43 mm/year to 2.79 mm/year in the Upper Mississippi River from 1994 to 1996 using an L_{∞} of 35 mm as in our study. The current study found lower growth rates ranging from 0.11 mm/year to 0.25 mm/year and averaging 0.17 mm/year. These lower rates were expected as zebra mussel growth rates are greater in lotic systems than in still water of lentic systems (Mackie et al. 1989; Karatayev et al. 2006). Czarnoleski et al. (2003) reported a similar low range of growth and a higher upper growth range for zebra mussels (0.11 mm/year to 1.20 mm/year; averaging 0.48 mm/year) in 19 European lakes outside their native range. These European lakes were also generally less productive lakes from similar latitude. Studies on zebra mussel growth rates in their native range were not compared to rates in this study because such studies could not be found.

Variation in growth rates among zebra mussel populations in this study could be related to various factors including time since colonization, food source and availability, and substrate. The highest zebra mussel growth rate observed in this study was in Keyes Lake, the most recently invaded lake. This high rate could be related to zebra mussels selecting for beneficial forage in this lake as has been shown by others (Ten Winkel and Davids 1982; Baker et al. 1998; Naddafi et al. 2007a; Naddafi et al. 2007b). While growth rates of pioneer zebra mussel populations have not been well-documented, mean zebra mussel body size was reported to be greater in the initial stages of colonization of

the Hudson River, New York (Strayer and Malcom 2006). This rapid zebra mussel growth corresponded with zebra mussel filtering, reduced phytoplankton biomass, and a subsequent decline in zebra mussel growth as may be observed in the younger zebra mussel age classes in Keyes Lake (Figure 2). While others reported shifts (both increasing and decreasing) in phytoplankton communities following zebra mussel colonization (Nicholls and Hopkins 1993; Baker et al. 1998; Smith et al. 1998; Idrisi et al. 2001; Barbiero et al. 2006), few have correlated these shifts with zebra mussel growth. Historical chlorophyll *a* data for lakes in this study (Table 1) suggests a negative relationship between chlorophyll *a* concentrations and zebra mussel growth rate, which potentially contradicts other reports that growth rates of zebra mussels are usually positively correlated with food availability (Waltz 1987; Bayne et al. 1989; Sprung 1995). However, the small sample of lakes and the fact that these chlorophyll *a* analyses were not taken contemporaneously suggests these finding should be considered anecdotal and ultimately, reassessed with concurrent sampling.

In addition to time since colonization and food availability, habitat might influence zebra mussel growth. Compared to zebra mussel populations in other lakes in this study and those reported by Cope et al. (2006), zebra mussel growth rates were high in Metonga Lake, and Chicagon Lake. These are large, deep lakes with a variety of substrates and greater occurrence of wood and rock (Table 1; Table 3). Macrophytes were the dominant substrate in lakes with lower zebra mussel growth rates (Lake Antoine, Lake Noquebay, and Moon Lake). Similarly, zebra mussels attached to wood or rock were often larger in length than zebra mussels attached to macrophytes. This could

be related to food and oxygen availability and should be studied further to predict zebra mussel growth following invasion.

Mortality

The lack of variation in total mortality among study lakes was surprising. Zebra mussels died at the same rate across study lakes regardless of time since invasion, available habitat, or growth rate. While they died at the same rate, zebra mussel densities varied among lakes. Given densities ranged from ~0.5 individuals per cm^2 to 360 per cm^2, this lack of variation in mussel mortality suggests mortality is not density dependent; however, there are variations in the age classes of Metonga and Chicagon Lakes that suggest otherwise as discussed later.

Zebra mussels in the current study appear to have consistent mortality rates to other zebra mussels and exotic mussel populations at similar latitudes. Conides et al. (1995) estimated a total instantaneous mortality rate of 2.15 per year (88% annual mortality) for the zebra mussel population in the Kastraki Reservoir, Greece. Smit et al. (1993) reported 75 - 85% annual mortality in the Hollandsch Diep in The Netherlands. These rates were similar to other invasive mussel species. Crooks (1996) estimated a range of annual mortality rates between 67% and 100% for an exotic Asian mussel (*Musculista senhousia*) in Mission Bay, California.

Longevity of the zebra mussel is largely determined by local conditions that affect growth rates and ultimately life span. Fast growing mussels are thought to die earlier and slow growing mussels thought to live longer (reviewed in Karatayev et al. 2006). However, this relationship was not supported in this study as there was no difference in

zebra mussel mortality despite differences in growth rates among lakes. However, the reduced numbers of younger age zebra mussels in Metonga and Chicagon Lakes may indicate that these populations exhibit density dependent constraints (Figure 3). These populations do not correspond to the earliest invasions, though they are large, deep lakes with higher zebra mussel growth rates. In contrast, Lake Antoine, Lake Noquebay, and Moon Lake are shallow lakes dominated by macrophytes and have zebra mussel populations with lower growth rates that do not appear to be exhibiting density dependence. Thus, these large, deep lakes with a variety of substrates have the fastest growing individuals and also density dependent constraints earlier than populations in other study lakes. These observations between habitat and zebra mussel density dependence and growth are speculatory and should be studied further.

Growth and mortality estimates in this study could have been hampered by incorrect aging of mussels. Most methods used to estimate zebra mussel age and longevity count annual rings on the shell. However, Karatayev et al. (2006) reported that multiple growth rings per year are possible and annual rings are difficult to distinguish from rings that are formed by factors other than annual growth. Furthermore, age validation is routinely skipped by authors (Neves and Moyer 1988) which is also a fault of this study. While age validation is essential to obtain population statistics, Neves and Moyer (1988) found that young individuals (3-6) had well-defined annuli. In addition, Neves and Moyer (1988) reported that lentic species of freshwater mussels are characterized by regular spaced, distinct annual growth rings, while lotic mussels can be difficult to distinguish. Because our study lakes were all lentic systems, annual growth

rings were likely distinct, though we support the conclusion of Neves and Moyer (1988) that validation is a necessity that this study lacks.

This study did not sample all available zebra mussel habitat which might have misrepresented population statistics. During an exploratory dive in Metonga Lake, dense populations of 8 year old zebra mussels were observed at a depth of approximately 12 m and were likely present at deeper depths. The presence of older zebra mussels at deeper depths in Metonga and Chicagon Lakes may have influenced growth and mortality curves as these curves did not include an accurate representation of all ages present. This study design could be improved with a targeted diving approach to accommodate all depths inhabited by zebra mussels.

Management Implication

The Wisconsin Council on Invasive Species explicitly aims to improve early detection of invasive species through developing protocols for detection methods that can be used by professional and citizen scientists (WISC 2013). Similarly, protocols could also be developed to examine established populations to expand knowledge of invasion dynamics. Wisconsin and Michigan's lake management programs train and coordinate volunteers to sample water clarity, chemistry, and monitor for invasive species. To aid zebra mussel detection efforts, previous research has described factors that limit lakes to zebra mussel invasion based on water chemistry (Ackerman et al. 1992, 1993; Kilgour and Mackie 1993; Mellina and Rasmussen 1994; Karatayev et al. 1998; Marsden and Lansky 2000; Jones and Ricciardi 2005; Papes et al. 2011). Current zebra mussel monitoring efforts use artificial substrate samplers and aqua scopes to search for zebra

mussels in upper Michigan or Wisconsin lakes. Once zebra mussels are detected within a waterbody, there is often a reaction of anxiety due in part to the limited knowledge of anticipated population trajectories and also to their profound ecological and economic impacts. There is a need to refine within-lake zebra mussel early detection monitoring and also to develop tools to evaluate zebra mussel growth and mortality following establishment.

This research can serve as a template for early detection monitoring programs for zebra mussels in other proximal northern lakes. These results provide the first examination of invasion and colonization characteristics for zebra mussels in northeastern Wisconsin and upper Michigan lakes. Furthermore, this study may improve zebra mussel early detection monitoring efforts by identifying lake habitats that are likely to be colonized by zebra mussels. In addition to improving monitoring efforts, this study also provides a framework to evaluate zebra mussel growth and mortality following establishment to understand population trajectories. This study suggests that wood and rock habitats within lakes could be targeted for early detection monitoring. Polyvinyl chloride (PVC) substrate samplers are currently used as early detection monitoring tools (Herman 2012). Further testing on the practicality and efficacy of using zebra mussel substrate samplers made of wood or rock versus PVC materials to assess early invasion could be examined. Oxygen profiles could dictate the appropriate depth where zebra mussels will likely occur to strategically place wood and/or artificial substrate samplers. In addition, early detection monitoring could use snorkeling and SCUBA diving focused on wood and rock in oxygenated habitats. In lakes where zebra mussels are established, the methods used in this study to age and measure zebra mussels to develop growth and

mortality curves could be applied to proximal and regional populations to increase knowledge of zebra mussel growth and mortality following establishment.

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Table 1. Substrate particle size (Wentworth 1992), coarse woody structure size (McHenry et al. 1998; Newbrey et al. 2005), macrophytes, shell, and artificial particles classification used to quanify available habitat in northeastern Wisconsin and upper Michigan study lakes in 2012.

Substrate type	Size	Code
Bottom Mineral/Organic Substrate		
Silt/fine organic matter	< 0.2 mm; fine organic discernible	1
Sand	0.2-6.3 mm	2
Gravel	6.4-76.0 mm	3
Cobble	76.1-149.9 mm	4
Rubble	150.0-303.9 mm	5
Boulder	>304.0 mm	6
Coarse organic material	Coarse particulate organic matter discernible	7
Coarse Woody Structure		
Small woody structure	0-0.5 cm in diameter, any length	8
Medium woody structure	0.6-10.0 cm in diameter, any length $\geq$ 10 cm in diameter, < 1.0 m length	9
Large woody structure	$\geq$ 10 cm in diameter, $\geq$ 1.0 m length	10
Macrophytes		
Macrophytes	All	11
Shell Substrates		
Native mussel shells	All	12
Snail shells	All	13

Table 2. Locations of zebra mussel (*Dreissena polymorpha*) populations in northeastern Wisconsin and upper Michigan lakes that were assessed in 2012 for zebra mussel habitat selection, growth, and mortality. A dash (-) indicates that the data was not found.

Lake name	Location (County, State, Latitude/Longitude)	Year First Detected	Area (hectares)	Maximum depth (m)	Calcium (mg/L)	pH	Chlorophyll *a* (µg/L)	Secchi disk depth (m)
Metonga Lake	Forest, WI, 45.5409, -88.9041	1999	806	24.0	17	7.8	2.4	6.6
Lake Antoine	Dickinson, MI, 45.8374, -88.0360	2001	303	8.0	19	8.8	3.9	-
Lake Noquebay	Marinette, WI, 45.2566, -87.9083	2006	975	15.5	37	8.2	3.5	2.5
Chicagon Lake	Iron, MI 45.0591, -88.5030	2007	445	32.0	28	8.0	-	-
Moon Lake	Dickinson, MI 45.8516, -88.0572	2007	38	16.0	32	-	-	-
Keyes Lake	Florence, WI 45.8990, -88.3061	2010	85	23.0	18	8.1	2.2	6.0
Lake Emily	Iron, MI 45.1144, -88.5013	2011	130	9.8	29	8.4	7.0	2.3
North Lake	Florence, WI 45.9040, -88.1384	2012	32	13.0	25	8.5	1.5	4.5

Table 3. Relative availability and use (parentheses) of substrates by zebra mussels (*Dreissena polymorpha*) in upper Michigan and northeastern Wisconsin lakes in 2012. Values represent the percent of all sampled sites that were characterized as a given substrate with values in parentheses being the proportion of sites of each substrate type occupied by zebra mussels. A dash indicates the substrate was not observed in samples. Lakes are listed from the oldest known zebra mussel population (Metonga Lake) to the most recently observed population (North Lake) and followed by all lakes combined.

Lake	Silt	Organic	Sand	Rock	Wood	Shells	Macrophytes	N
Metonga Lake	0.10 (-)	-	0.51 (0.29)	0.26 (0.65)	<0.01 (<0.01)	<0.01 (0.01)	0.13 (0.05)	120 (70)
Lake Antoine	0.24 (<0.01)	-	0.04 (<0.01)	0.07 (0.10)	<0.01 (0.03)	-	0.65 (0.85)	120 (119)
Lake Noquebay	0.10 (-)	<0.01 (<0.01)	0.17 (<0.01)	0.03 (0.05)	<0.01 (0.04)	0.02 (0.21)	0.67 (0.68)	120 (86)
Chicagon Lake	0.31 (0.01)	<0.01 (0.05)	0.10 (0.86)	0.23 (0.32)	0.05 (0.21)	-	0.31 (0.32)	120 (102)
Moon Lake	0.05 (-)	<0.01 (-)	0.08 (0.01)	0.05 (0.04)	<0.01 (0.05)	<0.01 (<0.01)	0.82 (0.89)	120 (107)
Keyes Lake	0.29 (0.01)	0.07 (0.05)	0.24 (0.20)	0.20 (0.31)	0.04 (0.23)	<0.01 (0.24)	0.15 (0.14)	120 (65)
Emily Lake	0.06 (-)	0.13 (-)	0.04 (-)	0.06 (1.00)	0.01 (-)	0.02 (-)	0.67 (-)	120 (2)
North Lake	0.25 (-)	<0.01 (-)	0.09 (-)	0.06 (0.23)	<0.01 (0.10)	<0.01 (0.10)	0.59 (0.57)	120 (53)
All lakes	0.17 (<0.01)	0.03 (0.02)	0.16 (0.06)	0.12 (0.24)	0.02 (0.10)	0.01 (0.08)	0.50 (0.51)	960 (604)

Table 4. Habitat selection ratios with upper and lower Bonferroni confidence intervals (in parentheses) for zebra mussel (*Dreissena polymorpha*) populations in upper Michigan and northeastern Wisconsin lakes in 2012. Selection is indicated with a value > 1 or < 1, and use is in proportional to availability with a value of 1. A dash indicates that either the substrate or zebra mussels were not observed in samples. Lakes are listed from the oldest known population (Metonga Lake) to the most recently observed population (North Lake), followed by all lakes combined.

Lake	Silt	Organic	Sand	Rock	Wood	Shells	Macrophytes
Metonga Lake	0.00 -	-	0.57 (0.33, 0.80)	2.60 (2.00, 3.10)	0.00 (-)	67.00 (-94.00, <0.01)	0.35 (-0.17, 0.86)
Lake Antoine	0.04 (-0.09, 0.16)	-	0.24 (-0.71, 1.20)	0.38 (0.26, 2.48)	22.00 (-4.70, 49.00)	-	1.30 (1.18, 1.43)
Lake Noquebay	0.00 (-)	2.70 (-6.30, 12.00)	0.06 (-0.15, 0.26)	1.40 (-0.47, 3.30)	14.00 (-3.40, 32.00)	11.00 (5.60, 16.00)	1.00 (0.84, 1.20)
Chicagon Lake	0.02 (-0.06, 0.11)	6.50 (0.53, 12.00)	0.86 (0.20, 1.50)	1.40 (0.97, 1.90)	4.50 (2.60, 6.50)	-	1.00 (0.70, 1.40)
Moon Lake	0.00 (-)	0.00 (-)	0.12 (-0.40, 0.62)	0.97 (-0.30, 2.30)	8.50 (-1.20, 18.00)	34.00 (-53.00, <0.01)	1.10 (1.00, 1.20)
Keyes Lake	0.034 (-0.08, 0.15)	0.75 (-0.30, 1.80)	0.08 (-0.10, 0.27)	1.60 (0.95, 2.20)	5.30 (2.70, 8.00)	29.00 (17.00, 42.00)	0.91 (0.29, 1.50)
Lake Emily	0.00 (-)	0.00 (-)	0.00 (-)	18.00 (-13.00, 48.00)	0.00 (-)	0.00 (-)	0.00 (-)
North Lake	0.00 (-)	0.00 (-)	0.00 (-)	3.80 (-1.60, 9.20)	10.00 (-23.00, 44.00)	24.00 (-53.00, 101.00)	1.00 (0.52, 1.50)
All lakes	0.02 (-0.02, 0.07)	0.65 (0.20, 1.10)	0.37 (0.22, 0.51)	1.98 (1.65, 2.32)	6.20 (4.45, 7.92)	10.76 (7.37, 14.15)	1.03 (0.93, 1.13)

Table 5. Total number of zebra mussels (*Dreissena polymorpha*) sampled in upper Michigan and northeastern Wisconsin study lakes in 2012. Total cm^2 coverage is the total area that zebra mussels were sampled from for age, growth, and mortality analysis. For each age class (x) the mean length (mm) with standard deviation (±) of sampled zebra mussels is given. The sample size (N) for each age category is listed below the average length, followed by the extrapolated N per m^2 (in parentheses) that was used for mortality analysis. A dash (-) indicates that the age class was not observed in samples. Lakes are listed from the oldest known zebra mussel population (Metonga Lake) to the most recently observed population (North Lake).

Lake name	N	Total cm^2 coverage	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8
Metonga Lake	423	2 600	5.14±1.02 25 (68)	7.41±1.55 119 (177)	9.99±2.08 78 (80)	16.09±3.52 34 (187)	19.58±2.20 94 (569)	22.12 ±2.56 57 (408)	25.29±2.58 15 (118)	29.06 1 (8)	-
Lake Antoine	1 031	1 911	3.68±1.04 333 (16 219)	6.53±1.63 535 (16 873)	10.35±1.92 113 (2 349)	12.3±2.89 35 (425)	18.54±2.35 11 (92)	21.67±2.92 4 (33)	-	-	-
Lake Noquebay	784	9 100	4.65±1.10 104 (119)	7.18±1.68 452 (500)	10.54±2.20 198 (287)	13.00±2.35 27 (62)	13.85±1.61 2 (2)	18.92 1 (23)	-	-	-
Chicagon Lake	465	31 700	3.81±2.10 21 (68)	7.84±1.80 57 (338)	12.80±2.41 67 (322)	17.10±2.01 117 (369)	19.83±2.28 120 (267)	22.12±3.08 55 (47)	25.95±2.36 20 (3)	28.80±1.54 7 (1)	24.88 1 (8)
Moon Lake	892	1 000	4.6±1.06 280 (2 333)	7.54±1.70 503 (4 192)	10.92±2.07 84 (700)	15.10±2.95 14 (117)	17.45±1.26 10 (83)	-	24.59± 1 (8)	-	-
Keyes Lake	151	5 400	5.29±1.11 26 (24)	8.41±1.90 90 (83)	11.50±2.26 26 (24)	22.80±3.59 8 (7)	25.46 1 (1)	-	-	-	-

Table 6. Stepwise logistic regression coefficients for predicting zebra mussel (*Dreissena polymorpha*) substrate use in upper Michigan and northeastern Wisconsin study lakes in 2012.

Variables	Coefficient	SE	Wald	P
Depth	<0.01	<0.01	13.30	<0.001
Silt	-0.01	<0.01	23.60	<0.001
Organic	-0.03	<0.01	20.60	<0.001
Rock	<0.01	<0.01	9.82	<0.001
Wood	0.05	0.02	7.67	<0.001
Constant	0.32	0.13	6.19	0.010

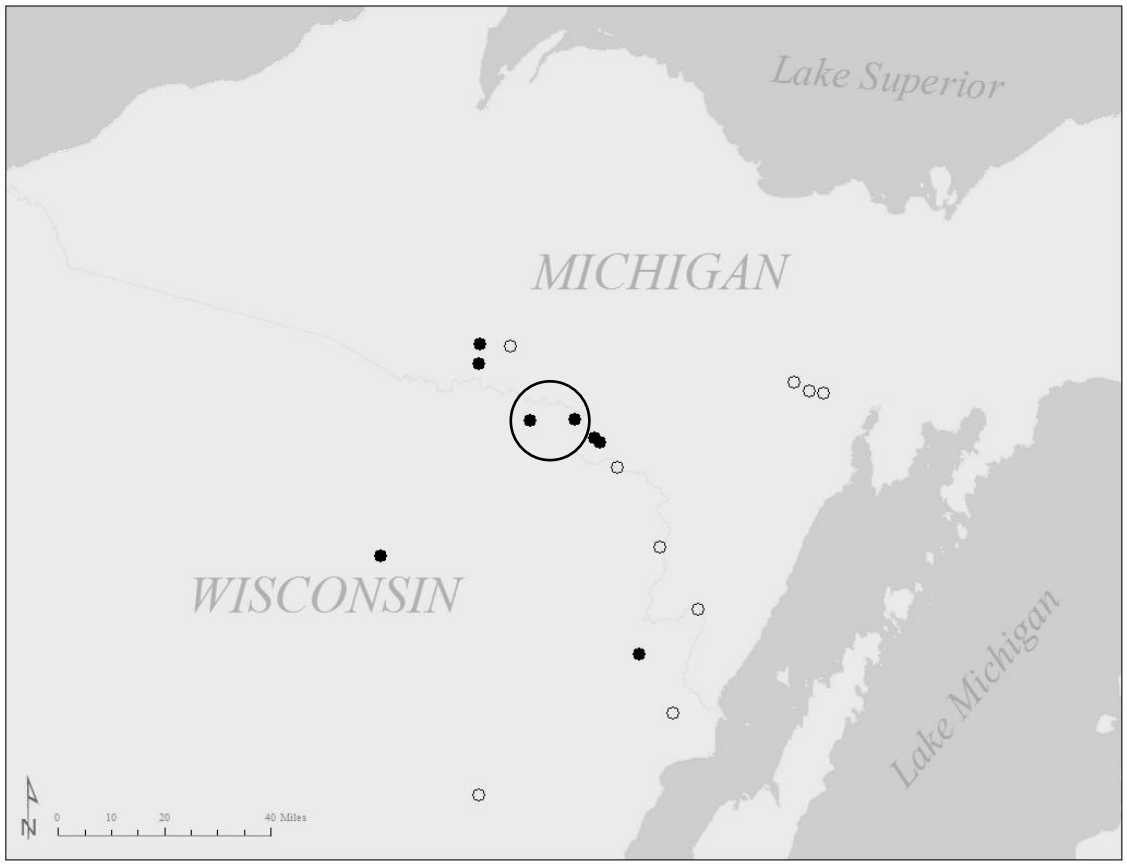

Figure 1. Geographic distribution of zebra mussel (*Dreissena polymorpha*) populations in upper Michigan and northeastern Wisconsin in 2012. The circle identifies recently observed zebra mussel population. Black dots represent study lake locations and open circles represent other known zebra mussel locations. There were 17 known water bodies with zebra mussel populations, 8 of which were included in this study.

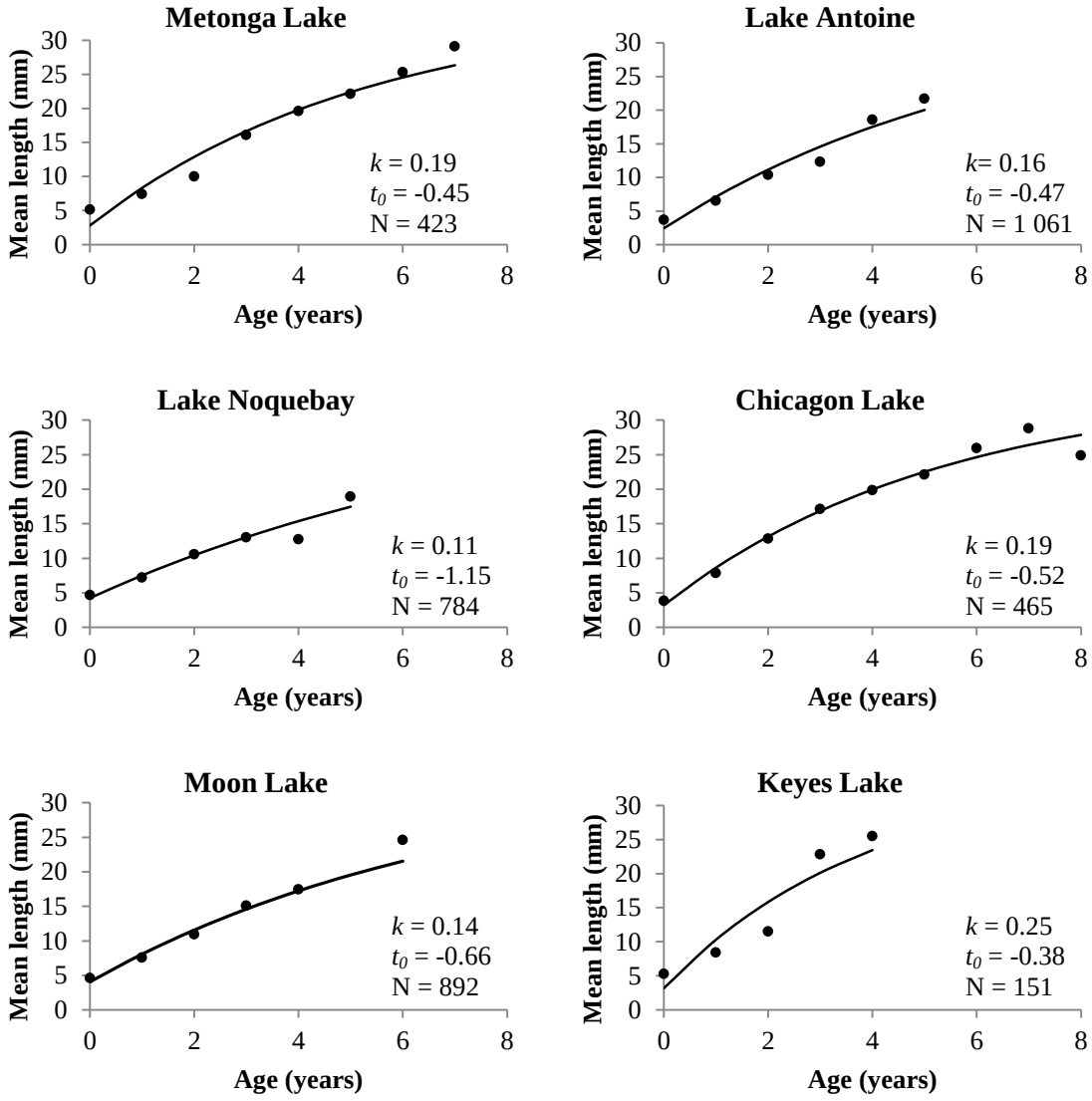

Figure 2. von Bertalanffy growth curves for zebra mussel (*Dreissena polymorpha*) populations in upper Michigan and northeastern Wisconsin study lakes in 2012. The equation is $\boldsymbol{L_{mean} = L_{\infty}1 - e^{-k(t-t_0)}}$. Lakes are ordered from the oldest known population (Metonga Lake) to the most recently observed population (Keyes Lake).

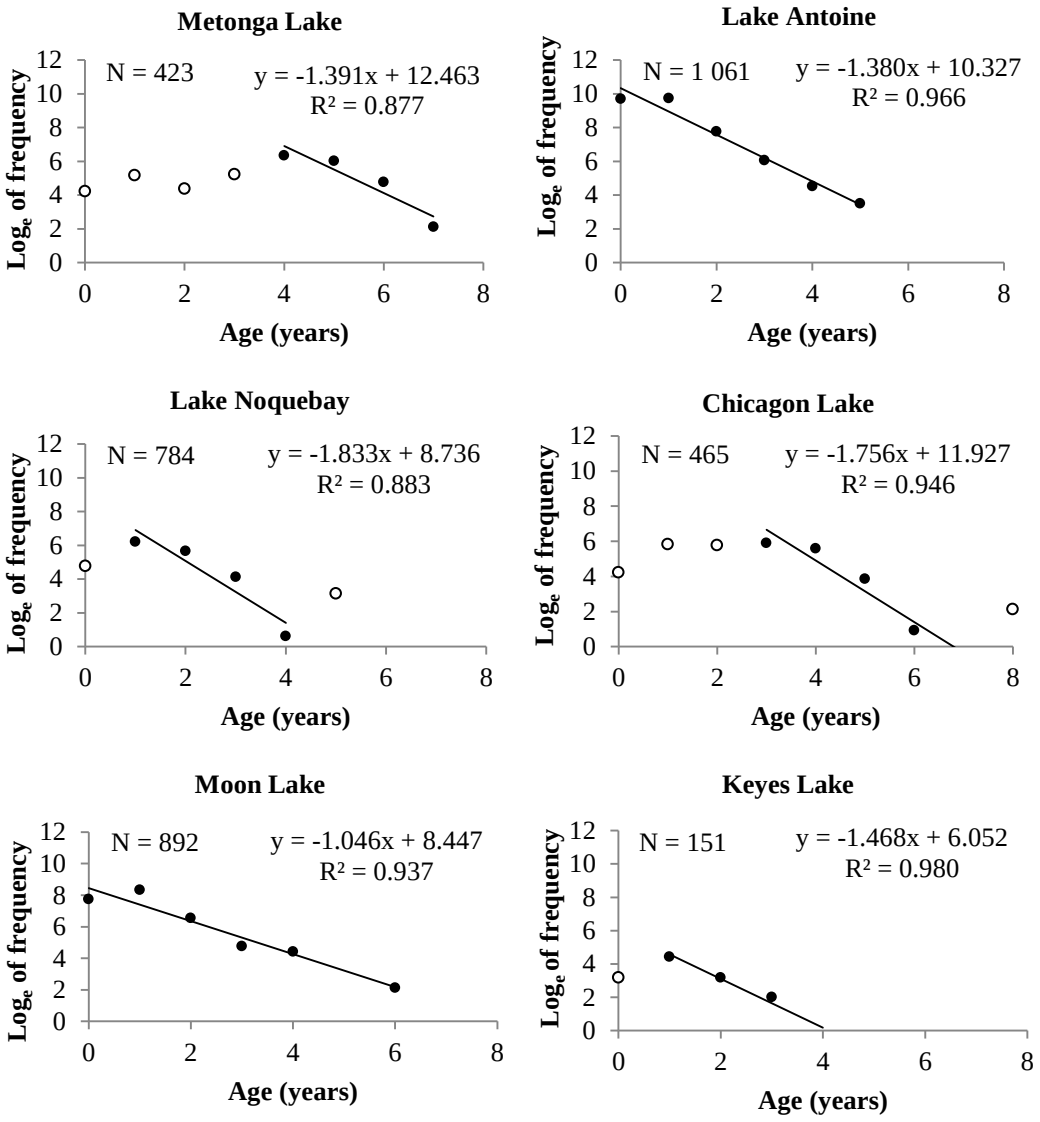

Figure 3. Catch curves for zebra mussel (*Dreissena polymorpha*) populations in upper Michigan and northeastern Wisconsin study lakes in 2012. The equation is $\boldsymbol{ln(N_t) = ln(N_0) - Zt}$. Open circles represent age classes not part of the descending limb and excluded from the model. Lakes are listed from oldest zebra mussel population (Metonga Lake) to the most recently observed population (Keyes Lake).

CHAPTER 2: ZEBRA MUSSEL LITERATURE REVIEW

OVERVIEW

Zebra mussels are native to the Ponto-Caspian region of Eurasia and were brought to North America in ballast water (Hebert et al. 1989; Carlton and Geller 1993). They were first observed in North America in the Laurentian Great Lakes in the 1980s (Hebert et al. 1989; Carlton 1993), where they directly and indirectly impacted biological organisms and recreational and industrial users. Primary zebra mussel impacts are associated with their high fecundity, which may result in great population densities (Walz 1978; Sprung 1990, 1993). Zebra mussels are also filter feeders and can decrease phytoplankton and zooplankton abundance potentially disrupting trophic interactions (MacIsaac et al. 1991; reviewed in Dorgelo 1993; MacIsaac 1996). Zebra mussels attach to substrates, which allows them to clog intake pipes, attach to boats and docks (reviewed in Ludyanskiy et al. 1993; Bonner and Rockhill 1994; MacIsaac 1996), and smother native unionids and other crustaceans (Ricciardi et al. 1998; Burlakova et al. 2000). Research has largely focused on two key areas, firstly on the ecology and the role of dreissenids as ecosystem engineers (Karatayev et al. 2006) and secondly on the infrastructural impacts of biofouling and the development of appropriate control methods (Mackie and Claudi 2010).

TAXONOMY

The Russian naturalist Peter Pallas was the first to describe zebra mussels after discovering them in the River Volga and the Black Sea in 1754 (reviewed in Ludyanskiy et al. 1993). Zebra mussels are classified in the Dreissenidae family, which superficially resembles the Corbiculidae (i.e. Asiatic clams) and Sphaeriidaae family (ie. Fingernail,

pea, or pill clams) (Van Beneden 1835; Gray 1840; Young and Campbell 1968; Korniushin 2007). *Dreissena* is the only genera from the Dreissenidae family in the United States and contains two species: *D. polymopha* and *D. bugensis*. *D. bugensis*, or quagga mussel, also has negative interactions with native communities and is expected to have greater ecological impacts than the zebra mussel (Mills et al. 1996; Korniushin 2007).

NATIVE ORIGIN AND SPREAD

Zebra mussels are native to the Ponto-Caspian region which includes the Caspian and Aral Seas, low salinity portions of the Azov and Black Seas and some waterbodies in the Balkan Peninsula (reviewed in Ludyanski et al. 1993). The first appearance of zebra mussels outside their native range was in Western Europe in the mid-1800s (Table 1). The construction of canal systems throughout Europe is suspected to have been the primary vector for the initial introductions. Timbers imported from Russia as well as the retreat of Napoleon's army to Europe are other suggested routes of initial European dispersal. Between 1800 and 1900, the zebra mussel range nearly doubled and is attributed to human mediated dispersal (reviewed in Ludyanskiy et al. 1993).

In North America, zebra mussels were first discovered near the Belle River in Lake St. Claire which is connected to the Laurentian Great Lakes (Herbet et al. 1989). The generally accepted date of discovery is 1988 (Hebert et al. 1989), though there is some evidence that it may have been in 1985 or 1986 (reviewed in Ludyanskiy et al. 1993). Zebra mussels were likely introduced to the Great Lakes during ballast water exchange of shipping vessels from the north shore of the Black Sea, where they originated from (Hebert et al. 1989; reviewed in Mackie et al. 1989; McMahon 1996).

The high genetic variability of zebra mussels in the United States suggests multiple source populations from north-western and north central Europe (Stephen et al 2002). Within two years of establishment, zebra mussels were observed throughout the Great Lakes, likely due to natural dispersal via surface water corridors and also additional ballast water discharge (Benson et al. 2012). Once established in the Great Lakes, zebra mussels were transferred to inland lakes, initially aided by stream connectivity and later via human activity (Griffiths et al. 1991). Currently, zebra mussels have been reported in 31 states (Table 2).

LIFE HISTORY

The zebra mussel life cycle includes the following stages: fertilization; development of the egg into the pediveliger; metamorphosis following primary settlement of the pediveliger to the plantigrade stage; post-metamorphic behavior including secondary settlement, and translocation (Ackerman et al. 1994).

Fertilization

In mature zebra mussels, gametogenesis begins in the fall and continues through winter where females produce oocytes and males produce spermatozoa (Pathy 1994). By spring oocytes and spermatozoa begin to grow when mussel shells reach 8-9 mm (Pathy 1994). Gametes are expelled directly into the water, where fertilization and development occur. Spawning temperatures in Europe are typically 10-17°C, and in North America spawning begins at 12°C and is maximized above 17-18°C (Pathy 1994). A female can release more than one million eggs (20 000 – 1 610 000) in a single spawning event (Walz 1978; Mackie et al. 1989; Sprung 1990, 1993), and spawn two to five times annually (Walz 1973). Oocytes are fertilized by sperm in the water column (Mackie

1991). Eggs are fertilized 2.50 to 4.75 hours after release within a temperature range of 12-24°C (Sprung 1993).

Larval stage

Following fertilization, the embryo undergoes cleavage, blastulation, and gastulation to form a 57-121 µm trochophore larva (reviewed in Ackermann et al. 1994). Within 6-96 hours of fertilization, the free swimming trochophore develops a velum, a cilliated organ for feeding and locomotion, at which point it becomes a veliger (reviewed in Ackermann et al. 1994; reviewed in McMahon 1996). The developing veliger secretes a D-shaped shell from the shell glands to form a 70-160 µm straight-hinged veliger within 2-9 days of fertilization, (reviewed in Ackermann et al. 1994). A second larval shell is secreted by the mantle tissue 7-9 days after fertilization to form a pronounced umbonal region near the hinges that is round or clam-like in profile (Ackermann et al. 1994). This is the 120-280 µm veliconcha, the last veliger stage that is free-swimming (reviewed in Ackermann et al. 1994). About ten days following fertilization, the veliconcha develops several organs, including a foot and becomes a pediveliger that is 167-300 µm in size (reviewed in Ackerman et al. 1994; Ackerman and Claudi 1991). The foot allows the pediveliger to swim near the bottom and crawl on surfaces in search of suitable substrate (Ackerman and Claudi 1991). Using byssal retractor mussels, zebra mussels secrete a byssum through the foot which allows the mussel to attach to firm substrates (Eckroat et al. 1993; reviewed in Ludyanskiy et al. 1993). The byssum produces temporary and permanent attachment threads, differentiated by length, thickness, number, arrangement, and plaque morphology (Eckroat et al. 1993). The majority of this byssal mass is comprised of permanent attachment threads, which are

formed in clumps or rows and provide stable attachment to substrates (Eckroat et al. 1993). Temporary threads appear to function as searching threads for zebra mussels to look for new substrate to attach to; permanent threads offer a more secure attachment. About one month after veligers were first found and at the same time of the second veliger peak. Veliger settling stages are the most sensitive and have mortality rates of 90-99% (reviewed in Mackie et al. 1989). The veliger stage typically lasts for about two weeks (reviewed in Mackie et al. 1989; Rittschof et al. 1998). Veliger densities, as well as the length of the spawning season, depend on the parent population size, and maturity of parent population (Lucy 2006). In early June in Lake Erie, Fraleigh et al. (1993) observed a peak in veligers followed by a second peak in late July.

Juvenile/adult stage

Ackermann et al. (1994) reviewed the development of the juvenile to adult stage. The "settled" pediveliger undergoes metamorphosis to become a post veliger or plantigrade mussel, beginning the juvenile stage. The plantigrade ranges from <158 to 500 µm in size. The morphological changes associated with the plantigrade mussel involve losing the velum, developing the gills and mouth, and secreting the adult shell to form the juvenile. The gills take over the filter feeding function of the velum upon development of siphons. Upon completion of these changes, the plantigrade becomes a 500-5000 µm juvenile. With further growth and the onset of maturity, the juvenile becomes an adult. Adults are distinct in that they have a bivalve shell with flattened ventral margins and an acute ventrolateral shoulder with a distinct carina (reviewed in Ludyanskiy et al. 1993). A female zebra mussel begins to reproduce within 6-7 weeks of settling (Borcherding 1991). Zebra mussels in Europe reach sexual maturity in their

second year (reviewed in Mackie et al. 1989), while in North America maturity can be reached in the first year (8 to 10 mm) (reviewed in Mackie and Schloesser 1996). Although only two to five percent of zebra mussels reach adulthood, one adult female may produce between 30 000 and 1.6 million eggs per year (reviewed in Mackie et al. 1989). In North America, the lifespan of zebra mussels is typically 3-5 years (rarely exceeding 7 years) and thus an individual female may produce up to 5 000 000 eggs in a lifetime (Walz 1973; Sprung 1990; reviewed in Ludyanski et al. 1993).

DISPERSAL

Although dispersal of individuals across life stages of zebra mussels is similar in that it occurs in water, the mechanisms of dispersal may differ. Veligers are microscopic and may be carried long distances in translocated water (e.g. water current, live wells, ballast water), and on floating plant material or other objects (reviewed in Ackerman et al. 1994; Johnson and Padilla 1996). Juvenile mussels spread to new locations when crawling in search of substrates (Ackerman and Claudi 1991). Adults can attach to substrates using byssal threads, which enable them to reach and colonize new locations within a waterbody or to a different waterbody (reviewed in Claudi and Mackie 1994). Vectors for adult zebra mussels include recreational equipment (e.g. boat hulls, live wells, wet suits, and trailers) (Johnson and Padilla 1996), floating macrophyte fragments (Horvath and Lamberti 1997), and water current (reviewed in Mackie et al. 1989).

HABITAT PREFERENCE

Water quality

Zebra mussel survival, reproduction, growth, and density are strongly linked to pH (Hincks and Mackie 1997, Ramcharan et al. 1992, Sprung 1987). Hincks and Mackie

(1997) observed 100% mortality in water with a pH < 7.1; growth was positively correlated with pH > 7.1 and calcium levels above 8.5 mg L^{-1}. Zebra mussel density is positively related to pH levels greater than 7.3 (Ramcharan et al. 1992). In addition, Sprung (1987) observed minimal deformities in veligers at pH levels of 8.4 and maximal growth for adults at levels 7.4 to 8.0.

Calcium concentration is believed to be the primary factor determining adult zebra mussel presence/absence as it directly affects zebra mussel development, growth, and shell carapace development (Sprung 1987; Ramcharan et al. 1992; Mellina and Rasmussen 1994; Hinks and Mackie 1997; Jones and Ricciardi 2005). In laboratory experiments, Sprung (1987) found that veliger survival was limited below 12 mg Ca^{2+} L^{-1} and that deformities occurred above 34 mg Ca^{2+} L^{-1}. Contrarily, Sprung (1987) also found that fertilization success and survivorship of embryos were enhanced by calcium concentrations above 47 mg Ca^{2+} L^{-1} and pH values of about 8.5. Mellina and Rasmussen (1994) found an average calcium threshold of 15 mg Ca^{2+} L^{-1} for zebra mussel populations studied in the St. Lawrence River, Hudson River, and Oneida Lake. In North American zebra mussel populations, minimum calcium concentrations of 10-11 mg Ca^{2+} L^{-1} are needed for initial shell growth and 25-26 mg Ca^{2+} L^{-1} for maintenance of moderate shell growth (Claudi and Mackie 1994) and in Europe, zebra mussels were absent in lakes with pH < 7.3 and Ca^{2+} concentrations < 28.3 mg Ca^{2+} L^{-1} (Ramcharan et al. 1992). In the St. Lawrence River, Jones and Ricciardi (2005) found that biomass increased with calcium concentrations > 25 mg Ca^{2+} L^{-1}.

Globally, zebra mussels have different salinity tolerances in different localities suggesting founder effects from similar populations (Karatayev et al. 1998). The

subspecies found in North America does not tolerate salinities above 4% (reviewed in Ludyanskiy et al. 1993). Zebra mussel tolerance to salinity is influenced by temperature, life stage, and acclimation (Kilgour et al. 1994). Zebra mussels are more successful in brackish water that is 10-12°C and their ability to produce gametes is impaired near 20°C. Based on life stage, the lethal salinity is near 4.5% for veliger larvae, near 2% for postveligers, and 2-4% for larger adults (5-15 mm) (Kilgour et al. 1994). Their tolerance to salinity improves with acclimation (Kilgour et al. 1994). While zebra mussels may acclimate to brackish waters, fertilization does not occur above 0.7% salinity (Fong et al. 1995).

Zebra mussels are the least hypoxia tolerant bivalve (Matthews and McMahon 1999) and are restricted to oxygenated habitats among and within waterbodies (reviewed in McMahon 1996). Mackie et al. (1989) summarized an experimental observation that zebra mussels require oxygen saturation greater than 26%. This metabolic limitation may account for their poor colonization success in eutrophic lakes and preclude them from inhabiting hypolimnetic waters (reviewed in Mackie et al. 1989). Likewise, during thermal stratification in Lake Erie, Fraleigh et al. (1993) did not observe veligers in the hypolimnion which had little oxygen. Mackie et al. (1989) reviewed that mortality of mussels in oxygen deficient conditions increased as water temperatures increased. Matthews and McMahon (1999) found that zebra mussels are able to survive hypoxic conditions significantly longer in warmer (25°C) temperatures versus colder (5°C) temperatures. In addition, acclimation to declining temperatures significantly increased hypoxia tolerance time. Larger individuals (20-24.9 mm) are more tolerant to hypoxia

than smaller (1-4.9 mm) individuals; therefore, small mussels die first in anaerobic conditions (reviewed in Mackie et al. 1989; Matthews and McMahon 1999).

Physical Factors

In water bodies with suitable water quality, substrate is the dominant factor affecting local abundance (Mellina and Rasmussen 1994; reviewed in McMahon 1996). Zebra mussel larvae selectively choose habitats to settle on (reviewed in Ackerman et al. 1993, Kilgour and Mackie 1993). In a review of European and Russian literature, Ackerman et al. (1994) summarized preferential selection of filamentous substrates such as macrophytes (e.g. *Chara spp.*) and the underside of artificial substrates by pediveligers. Once they settle and further develop, the postveligers and adults will later move to other locations with suitable substrates. Since adhesive strength of byssal threads is dependent on the composition of materials to which they are attached, they will be more abundant on certain surfaces (reviewed in Ackerman et al. 1992). Postveligers attach in greater numbers on textured substrates, such as macrophytes and unionids (Hebert et al. 1991; reviewed in Ackerman et al. 1994), versus smooth substrates (Marsden and Lansky 2000). Adult zebra mussels prefer natural substrates such as gravel, wood, macrophytes, and mollusks (Kilgour and Mackie 1993; Mellina and Rasmussen 1994; Karatayev et al. 1998), and will also attach to artificial substrates such as stainless steel and pressure-treated wood (Kilgour and Mackie 1993). Zebra mussel density, biomass, and population stability are correlated to substrate size and type. Using Wentworth (1992) substrate classification in studies along the St. Lawrence River, Mellina and Rasmussen (1994) found that substrate size explained 38-91% of the variability in zebra mussel density. Jones and Ricciardi (2005) found that substrate size

accounted for 20% of the variability in biomass. Biomass and density of zebra mussels decline with decreasing substrate size (Mellina and Rasmussen 1994; Jones and Ricciardi 2005). Karatayev et al. (2006) found that populations are less stable in lakes if submerged macrophytes are the dominant attachment substrate, compared to lakes with a variety of substrates; larger ones in particular. Lakes with a variety of substrates tend to have more balanced age distributions and less variation in annual recruitment (Karatayev et al. 1998; reviewed in Karatayev et al. 2006). In the absence of suitable substrates, zebra mussels form dense colonies with over 100 000 mussels per square meter and up to 0.3 m thick (Griffiths et al. 1991).

Zebra mussel distribution is affected by light. The variation in vertical distribution of veligers can be attributed to light, which decreases with depth (reviewed in Mackie et al. 1989). There appears to be a diurnal movement of veligers, with maximum densities occurring near the surface during early morning when light intensity is low, and at 5-7 m during the day (reviewed in Mackie et al. 1989). Settlement of post-veliger mussels on experimental plates indicated that mussels attach in greater numbers on shaded versus sunlit surfaces (Marsden and Lansky 2000). In determining factors that affect movement of zebra mussels, Toomey et al. (2002) reported that zebra mussels demonstrated strong negative phototaxic behavior as they moved away from light. Mellina and Rasmussen (1994) found a negative correlation between adult zebra mussel abundance and secchi depth readings in the St. Lawrence River, which may relate to their preference for dark areas. While they appear to prefer darker, lower light areas like crevices and undersides (Morton 1969a), this behavior could also be linked to predators, turbulence, current, or ice scour (Yankovich and Haffner 1993).

Water depth clearly affects the distribution of zebra mussel veligers and adults. Maximum veliger abundance typically occurs along the 3 to 7 m depth contour (with 11-12 m being common) of a waterbody (reviewed in Mackie et al. 1989). If the water column is mixed vertically by wind, veligers may be found higher in the water column than they are when it is not mixed vertically (Fraleigh et al. 1993). Few veligers occur below the thermocline (reviewed in Mackie et al. 1989), though Fraleigh et al. (1993) did observe veligers throughout 5 m and the bottom in Lake Erie when thermal gradients were weak. Zebra mussels are typically found in the littoral and sublittoral zones and rarely on profundal sediments (reviewed in Strayer 1991). Mills et al. (1999) observed the greatest zebra mussel abundance at depths of 15 to 25 m in Lake Erie. Adult zebra mussel biomass decreases with depth (Jones and Ricciardi 2005). Using cages to study the effect of depth on zebra mussels in Hargus Lake, Ohio, Yu and Culver (1999) found that zebra mussel growth is greatest at pelagic sites (2.5-4 m depth) and in the littoral zone (2.5 m), while zebra mussels held below the thermocline died. Relationships between depth and abundance also depend upon light, oxygen availability, pressure, temperature, and food availability (Domm et al. 1993).

Thermal thresholds dictate zebra mussel spawning, distribution, development, and growth. McMahon (1996) indicated that in Lake Ontario, spawning may be initiated at ~12°C and on average is maximized at 17-18°C with upper thermal limits of 30-31°C (McMahon et al. 1994). Nichols (1996) stated that the time it takes for a fertilized egg to develop into a juvenile varies inversely with water temperature. The peak spawning threshold of 17-18°C corresponds to the optimum temperature for larval development (Sprung 1987). Temperature also influences veliger distribution in the water column as

Fraleigh et al. (1993) observed that in Lake Erie, veligers were absent from warmer surface water and at greatest densities at deeper depths in July. In addition, few veligers occur below the thermocline, though this is more related to oxygen (reviewed in Mackie et al. 1989, Fraleigh et al. 1993) and food availability (McMahon 1996; Petrie and Knapton 1999) rather than temperature. In addition to spawning and larval development, peak pediveliger settlement is also optimal at 17-18°C (reviewed in Mackie et al. 1989). Metamorphosis from the pediveliger to the D-shaped veliger requires 90 hours at 12°C, or 31 hours at 34°C (Sprung 1987). Morton (1969b) indicated that shell growth initiates between 11-12°C; however, discrepancies remain regarding temperature effects on growth rate and thermal tolerance limits (McMahon 1996).

Habitat Changes

Habitat changes that influence zebra mussels include aerial exposure (i.e., desiccation) and hydrological alterations. Zebra mussels are able to survive aerial exposure (i.e. desiccation) in cool, moist environments for 5-10 continuous days, though survival declines above 20°C (Ricciardi et al. 1995b, Paukstis et al. 1999). Bowers and De Szalay (2004) observed less zebra mussel colonization in areas that are periodically dewatered due to water level fluctuations. In Lake Erie, Fraleigh et al. (1993) observed that wind driven currents also affect vertical distribution of veligers as they are found deeper in the water column when not mixed vertically by wind. Continued exposure to turbulence may cause larval mortality and affect survival of newly settled larvae (Horvath and Lamberti 1999).

POPULATION DYNAMICS

Recruitment

Recruitment of zebra mussels occurs in two phases: 1) settlement of pediveligers and subsequent metamorphosis and 2) translocation of mussels (plantigrades, juveniles, and adults) to new locations (reviewed in Ackerman et al. 1994). Ackerman et al. (1994) summarized that pediveligers recruit preferentially to aquatic plants and later migrate to other substrates such as adult mussel colonies, while Hebert et al. (1991) observed the greatest recruitment at the periphery of mussel beds. Claudi and Ackerman (1992) observed post-settlement movement throughout the year in Lake Erie. Post settlement and metamorphosis, juvenile mussels can crawl over substrates at a rate of 7 cm/night (reviewed in Ackerman et al. 1994). Plantigrades and small juveniles that had overwintered under rocks and in crevices, as well as adult mussels, translocate onto freshly deployed substrates in the spring. Spring translocation is temperature dependent, as juveniles may first be observed when water temperatures were above 8°C (reviewed in Ackermann et al. 1994). Juveniles (~1 mm) and post metamorphic mussels are also observed in plankton tows, indicating the ability to be re-suspended in the water column, enabling translocation (Claudi and Ackerman 1992; Martel 1993). Re-suspension occurs through a variety of mechanisms: rafting on macrophytes (Martel 1993; reviewed in Ackerman et al. 1994) and crawling on the air-water interface (reviewed in Ackerman et al. 1994). Zebra mussels have been observed to use threads from the siphon or foot to contact the surface (reviewed in Ackermann et al. 1994). These threads are also used for drifting through the water column, which explains the presence of post-metamorphic mussels and juveniles in plankton tows (Ackerman and Claudi 1991; Claudi and Ackerman 1992; Martel 1993).

Abundance

Zebra mussel population densities vary among and within lakes where they occur. Kovalak et al. (1993) reported mussel densities up to 750 000 m^{-2} at the Monroe Power Plant in western Lake Erie, while in an adjacent lakebed densities were <5,000 m^{-2}. Likewise, in a study of 278 European lakes with zebra mussels, Ramcharan et al. (1992) found that zebra mussel density varied considerably among lakes (22.00 to 7 541.01 m^{-2}). Zebra mussel populations exhibit wide fluctuations in density among years (about three orders of magnitude); therefore, a single year density estimate may not provide a long term mean population density (reviewed in Strayer et al. 1991; Ackerman et al. 1994). For example, the zebra mussel mean density in Long Point Bay, Lake Erie declined each year from 2 050 m^{-2} in 1991 to 606 m^{-2} in 1995 (Petrie and Knapton 1999).

The range of zebra mussel population trajectories is influenced by environmental conditions. Population densities range from boom-and-bust cycles (reviewed in McMahon 1996; Petrie and Knapton 1999; Strayer and Malcom 2006) to stable (Ramcharan et al. 1992), while some populations experience irregular fluctuations (reviewed in McMahon 1996; Strayer and Malcom 2006). Because zebra mussels have short life-spans, mature early, have small gametes, high fecundity, and rapid growth rates, life history characteristics are adapted to unstable habitats where unpredictable environmental disturbance can result in periodic massive population reductions (McMahon 1996). These characteristics allow zebra mussels to reach high densities rapidly after introduction to a favorable habitat, or to rapidly recolonize an unstable habitat from which they were extirpated by environmental disturbance (McMahon 1996). Petrie and Knapton (1999) found that following colonization of Inner Bay, Lake Erie, the zebra mussel density rapidly increased and then consistently declined in numbers and

density. Established populations that are stable initially experienced a peak in densities (Casagrandi et al. 2007). Populations can also be constant in lakes with larger surface areas, lower levels of calcium, and higher levels of phosphates where environmental conditions are relatively more stable (Ramcharan et al. 1992). Conversely, Strayer and Malcom (2006) indicate that space-limited populations, which likely occur in small lakes, may be relatively stable. In addition, Burklakova et al. (2006) reported that populations are more stable if submerged macrophytes are the dominant substrate versus lakes with a variety of substrates. While many zebra mussel populations become stable following initial boom-and-bust recruitment, some population densities fluctuate greatly from year to year showing large, irregular fluctuations and no long term trends in population density (Ramcharan et al. 1992). Populations may persistently cycle if suitable substrate is abundant, but larval development is limited by food (Strayer and Malcom 2006). For example, Strayer and Malcom (2006) noted that the zebra mussel population in the Hudson River estuary fluctuated 11-fold over a 13 year period, following a cycle with a 2-4 year period. This was caused by low recruitment during years of high adult population size, rapid growth of settled mussels, and adult survivorship of 50% per year. In addition, maximum abundance of adults varies among lakes and seasons due to mortality and translocation.

Growth

In North America and Europe, most adult zebra mussels grow 1.43-2.9 cm $year^{-1}$ with a maximum size of 2.5-3.0 cm (Mackie et al. 1989; Mackie et al. 1991; Cope et al. 2006). Growth rates are determined by physical and water quality factors (reviewed in Mackie 1991). Physical factors affecting growth rate include temperature, depth, and

water motion; however, it is difficult to study effects of a single factor (reviewed in Karatayev et al. 2006). Larval growth rates are directly related to temperature (Sprung 1989) though there is an upper thermal threshold. Shell growth for all sizes is positive throughout the summer and stops from fall to early spring (Waltz 1978; bij de Vaate 1991; Smit et al. 1992; Allen et al. 1999). Allen et al (1999) observed asymptotic growth throughout the year due to temperature fluctuation in the Lower Mississippi River. Shell growth rates were highest during spring and fall when temperatures ranged from 16-28°C; however, growth ceased when temperatures increased to 29-31°C. Researchers have found that zebra mussels grow faster in the water column above the bottom (e.g. on buoys, floating objects) compared to on the bottom (bij de Vaate 1991, Dorgelo 1993). This may be caused by lower temperature and/or reduced food (reviewed in Mackie et al. 1989, Garton and Johnson 2000). Yu and Culver (1999) tested the effect of cage location and found the highest growth at their pelagic site (2.5-4 m depth) and in the littoral zone at 2.5 m depth. Wave action inhibits zebra mussel young-of-the-year growth (reviewed in Mackie et al. 1989) while zebra mussel adults grow faster in a constant current than in still water; however, strong currents inhibit growth (reviewed in Karatayev 2006). Moderate currents facilitate zebra mussel feeding and respiration which allow them to reach greater lengths than mussels out of currents (reviewed in Mackie et al. 1989). Water quality factors that affect food for zebra mussels include food condition, trophic state, and food availability / accessibility. Shell growth is positively correlated to food conditions and quality (Sprung 1995; Schneider et al. 1998). Dorgelo (1993) reported that multispecies diets have more nutritional value than algal monocultures. Zebra mussel growth rates are greater in eutrophic lakes (mean increase in shell length of 0.54-

0.59 mm/week) than in meso-oligotrophic lakes (0.35 mm/week) (Dorgelo 1993) as more food is available in eutrophic lakes than oligotrophic lakes. However, high concentrations of suspended matter inhibit filtration, ingestion, assimilation, and growth potential (Reeders et al. 1989, Alexander et al. 1994, Mardon et al. 1998, Schneider et al. 1998) as growth rates are positively correlated to respiration rates (Mardon et al. 1998). Growth rates can vary within years (Morton 1969b, bij de Vaate 1991; reviewed in McMahon 1996) and among years (Dorgelo 1993, Chase and Bailey 1999) due to the variations in food availability. Growth occurs primarily during summer and is reduced during winter (Morton 1969b; bij de Vaate 1991; reviewed in McMahon 1996). Based on a bioenergetics model of zebra mussel growth in the Laurentian Great Lakes, Schneider (1992) predicted positive growth in spring and fall when high phytoplankton biomass associated with spring and fall turnover coincides with temperatures near the optimum for growth. Annual variation in the composition of algae is a key factor determining growth rate (Dorgelo 1993). However, Strayer and Malcom (2006) found that growth and body condition were weakly correlated with phytoplankton biomass in the Hudson River.

Mortality

Longevity of the zebra mussel is largely determined by local conditions, which affect growth rates and ultimately longevity. Fast growing mussels die earlier and slow growing mussels live longer (reviewed in Karatayev et al. 2006). Zebra mussel populations in North America have an average longevity of 1.5-2 years (Mackie 1991), whereas European populations live from 3-9, or up to 12 years (reviewed in Mackie et al. 1989).

Zebra mussel mortality is influenced by a variety of environmental factors including pH, calcium, salinity, oxygen, and temperature, among others. Hincks and Mackie (1997) found 100% mortality in water with pH < 7.1. Calcium concentrations below 12 mg L^{-1} limit zebra mussel veliger survival (Sprung 1987) and concentrations below 10 mg L^{-1} and above 25 mg L^{-1} influence shell growth (Claudi and Mackie 1994). Kilgour et al. (1994) reported that lethal salinity values for postveligers were 2% and for adult zebra mussels is 2-4%. Zebra mussels are relatively intolerant of hypoxia or anoxia (McMahon 1996). Acute adult mortality is observed in late spring when dissolved oxygen levels are low and water temperatures are above 29°C (Mihuc et al. 1999). Likewise, Morton (1971) reported that two-thirds of mussels die at temperatures exceeding 30°C. Allen et al. (1999) found that periodic summer mortality depends primarily on temperature along with population size structure, and spring tissue condition. Zebra mussels are less susceptible to predation in lower light areas, which indirectly connects light and mortality (Yankovich and Haffner 1993). Relationships between depth and survival depend upon light, oxygen availability, and temperature (Domm et al. 1993). Zebra mussels are intolerant to desiccation and freezing (McMahon 1996). High veliger mortality occurs during downstream transport (Horvath and Lamberti 1999).

Although zebra mussels are starvation tolerant, it may have an effect on tissue and cause some mortality (McMahon 1996). For example, zebra mussel filtering activity on Long Point Bay, Lake Erie increased water clarity and reduced availability of their planktonic food sources, contributing to the decline of the zebra mussel population (Petrie and Knapton 1999). MacIsaac (1996) reported that zebra mussels in Lake Erie

exposed to 10-25 g L^{-1} of cyanobacteria (*Mycrocystis aeruginosa*) stopped feeding and experienced 30-100% mortality.

Life expectancy in zebra mussel populations is significantly affected by predation (Molloy et al. 1997, Eggleton et al. 2004). Fish, waterfowl, and unionids are active predators of settled mussels. An increase in predation by scaup (*Aythya affinis* and *A. marila*) and bufflehead (*Bucephala albeola*) populations is a contributing factor in the decline of zebra mussels in Long Point Bay, Lake Erie (Petrie and Knapton 1999). Some authors documented that fish prefer small mussels (French and Bur 1993; Hamilton et al. 1994), while other authors have reported that they prefer large individuals (Prejs et al. 1990) or that there is little (Bartsch et al. 2005) of no size selectivity (Perry et al. 1997). Similarly, waterfowl prefer either small (Werner et al. 2005) or large mussels (MacIsaac 1996; Petrie and Knapton 1999). Smit et al. (1993) reported an annual estimate that diving ducks consumed 14–63% of a zebra mussel population in Lake Ijsselmeer in the Netherlands. Unionid mussels, as well as zebra mussels, predate upon zebra mussel veligers (Welker and Waltz 1998). Although it is suspected that increased levels of predation could reduce zebra mussel populations, it may result in higher abundances due to density-dependent effects on recruitment (Casagrandi et al. 2007).

ECOLOGICAL INTERACTIONS

Feeding

Zebra mussels use cilia on the mantle (gills, labial, and foot) and stomach (Morton 1969a, Sprung and Rose 1988, reviewed in Mackie et al. 1989) to filter about one L of water per day (MacIssac 1996). They select suspended phytoplankton, zooplankton, and organic and inorganic particles of 15-40 μm and can also filter out

particles as small as 0.7-1.0 μm in diameter from the water column for food (Jorgensen et al. 1984; Sprung and Rose 1988). Populations of small zooplankton, particularly rotifers and Dreissenid veligers, are also inhaled by zebra mussels during filtering (MacIssac et al. 1991). Zebra mussel filtering is discontinuous and is decreased in either low or high turbidity or low or high temperatures, and increased by certain algal cells (reviewed in Dorgelo 1993). Zebra mussels have difficulty processing high levels of suspended inorganic particles (Mardon et al. 1998) and also reject some particles, such as diatoms and cattail detritus (Baker et al. 1998), which are enveloped by mucus and expelled as negatively buoyant pseudofecal pellets through the inhalant siphon rather than as real feces through the exhalant siphon (Reeders and bij de Vaate 1992; MacIssac 1996). This deposition, in addition to ingesting suspended particles, increases water clarity (MacIssac 1996).

Habitat alterations

Zebra mussels have been shown to increase water clarity substantially by filtering chlorophyll *a*, particles, phytoplankton, and zooplankton from the water column and altering habitat for the benthic community and fish (Zhu et al. 2006). Phytoplankton biomass, as estimated by chlorophyll *a* concentrations, decreased about 60% in the western and southwestern basins of Lake Erie between 1988 and 1991, and 50% in Saginaw Bay following the establishment of zebra mussels (Leach 1993; Fahnenstiel et al. 1995). Qualls et al. (2007) found that the decrease in chlorophyll *a* concentrations in portions of Green Bay, Wisconsin was likely caused by zebra mussel filter feeding abilities. In Lake St. Clair, Michigan, secchi disk depth readings were 0.5-1.5 m in 1972 and 1980 (pre-zebra mussel period) (Leach 1972, 1980) and 1.8-2.8 m in 1990 (post-

zebra mussel period) (Griffiths 1993). Likewise, in the southern portion of the west basin of Lake Erie, mean number of total planktonic diatoms was 86% lower in the post-zebra mussel period (1961-1965) and 92% lower in the pre-zebra mussel period (1984-1986), causing water transparency to be higher (Holland 1993). The removal of phytoplankton and small zooplankton also causes an increase in light penetration as reported in the Hudson River (Strayer et al. 1999). Increased light penetration also affected the diversity and frequency of submerged macrophytes in a large eutrophic/mesotrophic lake (Zhu et al. 2006). In Oneida Lake, New York, Zhu et al. (2006) found that macrophyte species richness increased, the frequency of occurrence of most species increased, and the community changed from low-light species to a range of species with different light tolerances. Removal of seston caused a shift in habitat from turbid water with homogenous silty sand to clear water with patches of silty sand, macrophytes, and mussel colonies which provide habitat for benthic invertebrates. Also, zebra mussel shells create habitat for benthic macroinvertebrates (Stewart et al. 1998). For example, Griffiths (1993) reported that the abundance of some benthic species such as amphipods, flatworms, snails, and worms increased from 0-2.5% (median 1.2%) in 1983 prior to zebra mussel colonization to 10-29% (median 27%) of the fauna following zebra mussel establishment in southeastern Lake St. Clair in 1990. In addition, the deposition of psuedofeces created habitat for worms (Griffiths 1993) as the fecal and psuedofecal settling rates exceed normal sedimentation processes (Dean 1994). The deposition of feces and psuedofeces increases benthic resources and subsequently increases macroinvertebrate diversity around zebra mussel beds (Stewart and Haynes 1994; Strayer et al. 1999). The increased water transparency has also altered walleye habitat and

distribution in Lake St. Clair as walleye are now found primarily in the deepest and most turbid portions of Lake St. Clair (MacIssac 1996). The changes in benthic community structure and an increase in water clarity following zebra mussel colonization indicate that zebra mussels can cause oligotrophication (Griffiths 1993).

Trophic Cascade

In addition to altering habitat directly, zebra mussels affect resources available for other organisms. Selective predation on phytoplankton and small zooplankton by zebra mussel filtering may reduce food availability to consumers, such as planktivorous fish that depend on these particles (MacIssac 1996; Strayer et al. 1999). Strayer and Smith (1996) believe that unionid clams are suffering from inadequate phytoplankton caused by zebra mussel filtering as they found that body condition of large unionid clams declined 40% and recruitment fell by 90% in the Hudson River; two of the three formerly abundant species will likely experience local extinction. At deep water sites, oligochetes and amphipods also declined (Strayer et al. 1998). Increases in macroinvertebrates could channel energy from zebra mussels to higher trophic levels as macroinvertebrates are important prey for benthivorous fishes and crayfish (Stewart et al. 1998).

Bioaccumulation

Zebra mussels are exposed to contaminants during water filtration and ingesting contaminated algae and particles, which may aid in the transfer of contaminants to higher trophic levels (Bruner et al. 1994). Stumpf et al. (2010) found that zebra mussels that were exposed to avian influenza for 48 hours contained the virus after 14 days in freshwater, demonstrating that zebra mussels are capable of accumulating the virus and it remains in the mussel for an extended period. Since waterfowl are natural predators of

zebra mussels, transmission of the virus to birds is possible even several weeks after contamination of the water (Stumpf et al. 2010). In addition, the deposition of pseudofeces and feces increases the transfer of contaminants to the benthic food chain (Bruner et al. 1994). Because zebra mussels ingest and retain particles, such as contaminants or algae, they have been intentionally stocked in lakes in the Netherlands as "biomanipulation" tools to remedy poor water quality (Reeders and bij de Vaate 1992). However, Knoll et al. (2008) found strong evidence that selective feeding by zebra mussels may increase concentrations of microsystin, which are toxic to aquatic and terrestrial organisms. Zooplankton feeding may be deterred by the presence of microcystin, affecting herbivore control of harmful algae and the efficiency of the planktonic food web (Fulton and Pearl 1987).

Biofouling

Zebra mussels are one of the most notorious "biofoulers" in the world (reviewed in Ludyanskiy et al. 1993). The zebra mussel byssal threads enable their attachment to a variety of substrates, including water intake pipes, recreational structures, and unionid mussels (Bonner and Rockhill 1994). Fouling of water intake structures and docks may be the most costly impact of zebra mussels (reviewed in Ludyanskiy et al. 1993). Fouling can impair water delivery to hydroelectric, municipal, and industrial users (MacIssac 1996) and even temporary structures like buoys (MacIssac 1996). Zebra mussels are also able to overgrow and smother other mollusks which may lead to the reduction, and perhaps loss, of many unionid populations (Ricciardi et al. 1998).

MITIGATION

A variety of measures have been explored to mitigate zebra mussel impacts including manual removal, habitat alterations, electricity, biological control, and chemical control. Wimbush et al. (2009) used manual removal to eradicate an early establishment of zebra mussels in Lake George, New York, which has suboptimal habitat. While the zebra mussels were thought to have been successfully eradicated, re-introduction enabled them to recolonize. Alterations of the physical environment include use of heat, desiccation, flushing in high flow rates, applying surface coatings, and exposure to an electronic field; however, these methods are suitable for confined areas, such as power plant intake pipes, and not as feasible for lake-wide control efforts (Jenner and Janssen-Mommen 1993). Electricity (reviewed in Mackie et al. 1989) and sonic vibrations (Kowalewski et al. 1993) have been explored to kill adult mussels and larvae.

Biocontrol

Several organisms have been identified as potential biological control agents for zebra mussels. In laboratory experiments, Perry et al. (1997) found that several crayfish species (*Orconectes rusticus, O. propinquus,* and *O. virilis*) reduced densities of zebra mussels by 31% in enclosures over a 28 day period and that the size of zebra mussel consumed was related to crayfish size. Although crayfish feed on zebra mussels between 1-15 mm long, they are not practical biocontrol agents as their feeding is affected by water temperatures and biological traits (reviewed in Mackie et al. 1989). In addition, rusty crayfish are also invasive in many places including Wisconsin and Upper Michigan (Olden et al. 2006) Zebra mussels are important prey for several fish species. Freshwater drum (*Aplodinotus grunniens*) (French and Bur 1993; Magoulick and Lewis

2002) and redear sunfish (*Lepomis microlophus*) (French and Morgan 1995; Magoulick and Lewis 2002) use pharyngeal teeth for crushing and consuming zebra mussels. Blue catfish (*Ictalurus furcatus*) heavily prey upon zebra mussels (Magoulick and Lewis 2002). Predation by waterfowl may be superimposed on depletion of food resources by zebra mussel feeding, as well as abundance and ease of exploitation (Petrie and Knapton 1999). Petrie and Knapton (1999) found that Lesser Scaup (*Aythya affinis*), Greater Scaup (*A. marila*), and Buffleheads (*Bucephala albeola*) consistently consumed zebra mussels in Lake Erie. Although diving duck (e.g., the tufter duck, *Athya fuligula*) *predation* decrease biomass, they have no significant effect on densities (Hamilton et al. 1994). The effect of freshwater sponge epibiont growth on zebra mussels has shown to be lethal (Ricciardi et al. 1995a; Early and Glonek 1998; Lauer and Spacie 2002). Conn and Conn (1993) reported that zebra mussels in a tributary of the St. Lawrence River were smothered and killed by the bryozoan *Pectinatella magnigica.* In the Rhine River, the amphipod *Corophium curvispinum*, which originate from the Ponto-Caspian area, are filter feeders and use hard substrata for settlement, utilizing similar resources as zebra mussels (Van der Velde et al. 1994). *C. curvispinum* was found to smother adult zebra mussels to death and the bare solid substrates needed for zebra mussel settlement, rendering hard substrata unsuitable for settling zebra mussel larva (Van der Velde et al. 1994). Freshwater sponge (either *Ezmapius fragrlis* or *Ephydaria muelleri*) biofouling may cause starvation and reduced energy stores, reductions in gas exchange, water excretion, and increased metabolic demands (Lauer and Spacie 2000). The potential length of time freshwater sponges may biofoul zebra mussels is from May to October (Lauer and Spacie 2000). Although crayfish, fish, waterfowl, and freshwater sponge

have been explored as biological control agents, none have demonstrated effective reduction of zebra mussel populations. Zebra mussel clumping has an anti-predation value that is physically and chemically induced (Wainman et al. 1996; Czarnoleski et al. 2006). In addition, studies by Czarnoleski et al. (2006) suggested that predator pressure, as well as water chemistry, influence shell resistance to crushing and growth rates. Recent research at the New York State Education Department identified *Pseudomonas fluorescens*, bacteria found in soil, as a biological control for zebra mussels as it produces > 90% adult zebra/quagga mussel and 100% larval mortality (Molloy 2002; Molloy 2004). In addition, no bacteria induced mortality was recorded among tested non-target organisms including fish, ciliates, daphnids, and bivalves (Molloy and Mayer 2008).

Chemical

Chlorination of intake pipes has long been used to control zebra mussel biofouling (Clarke 1952; Jenner 1984) as it has proven efficient, is economically feasible, and works in a variety of industrial settings (Whitehouse et al. 1985). At the Perry Nuclear Power Plant in Lake Erie, Barton (1993) found that continuous chlorination was needed for adult zebra mussel control and intermittent chlorination is sufficient for veliger control. However, chlorine can react with dissolved organic matter to produce organo-halogen compounds (Whitehouse et al. 1985), which are persistent, bioaccumulate, and have negative effects on ecological and human health (reviewed in Mariussen and Fonnum 2006). In 2006, the Virginia Department of Game and Inland Fisheries effectively eradicated zebra mussels from Millbrook Quarry using elevated concentrations of potassium chloride with no known impacts to native biota (Virginia Department of Game and Inland Fisheries 2008). Aldridge et al. (2006) developed microencapsulated

BioBullets to bypass detection of potassium chloride and the subsequent valve closure by zebra mussels. Waller et al. (1993) tested the toxicity of various molliscides to zebra mussels and found potassium chloride and a polyquarternary ammonium compound were two to three times more toxic to zebra mussels than non-target species.

Summary

The rapid global dispersal of zebra mussels has prompted broad research to understand the biology and ecology of invasive zebra mussels. The life history and dispersal mechanisms are well understood and research currently aims to identify how habitat influences zebra mussel life history and population dynamics in order to find strategies that can abate their impacts.

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Table 1. Chronology of living *Dreissena* discoveries in Russia and Europe (reviewed in Ludyanskiy et al. 1993).

Location	**Year**
Russian, Europe	1769
Ural River	1771
Volga River	1771
Caspian Sea	1794
Hungary	1800
Dnieper River	1824
England	1826
The Netherlands	1830
Germany	1840
Denmark	1840s
France	1845
Dvina River	1845
Daugava River	1847
Moscow River	1855
Don River	1875
Kama River	1940s
Scandinavia	1960s
Switzerland, Yugoslavia, Italy, and Spain	1970s

Table 7. Chronology of living zebra mussels (*Dreissena polymorpha*) discoveries in the United States (Benson et al. 2012).

Year	Location
1986	Lake St. Claire
1990	All Great Lakes
1991	Indiana, Illinois, Iowa, Ohio, Kentucky, Michigan, Minnesota, Missouri, New York, and Wisconsin.
1992	Alabama, Arkansas, Louisiana, Mississippi, and Tennessee, West Virginia
1993	Oklahoma, Vermont
1994	Pennsylvania
1998	Connecticut
1999	Nebraska
2001	Kansas
2002	Virginia
2003	South Dakota
2007	Arizona, California, and Nevada
2008	Utah and Colorado
2009	Texas, Massachusetts
2010	North Dakota

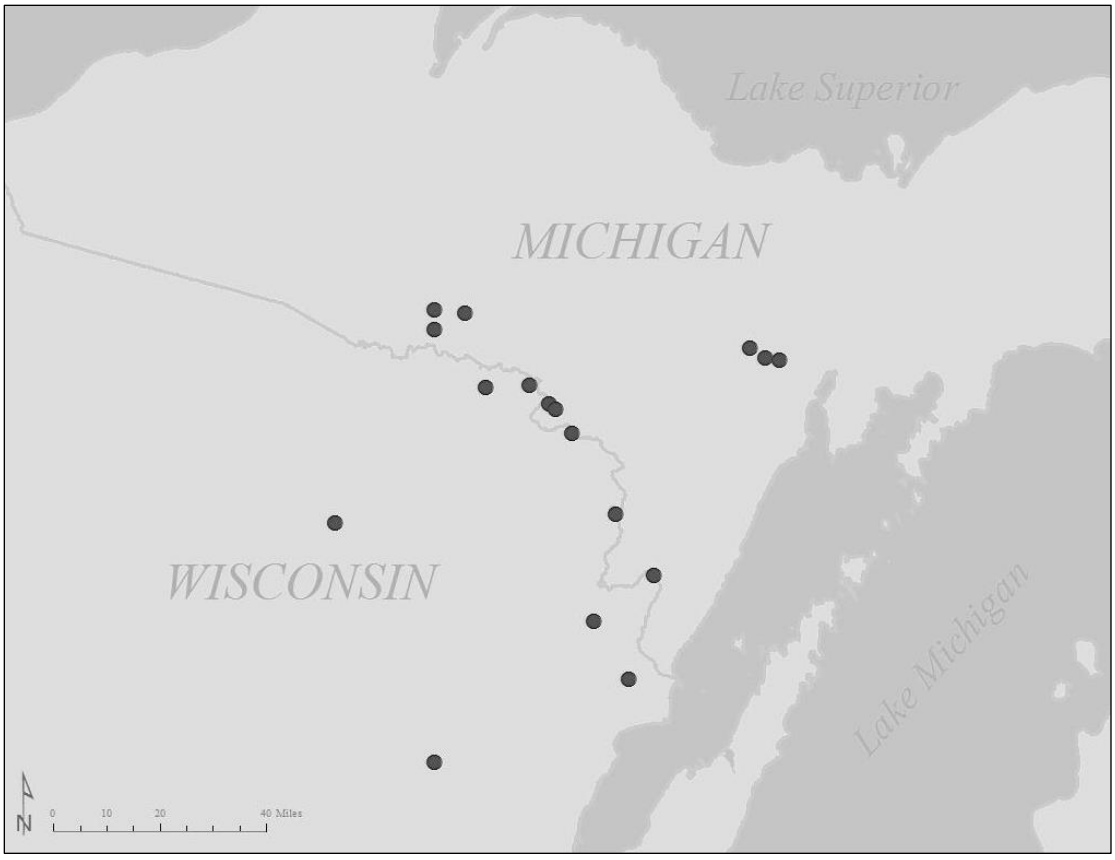

Figure 5. Zebra mussel (*Dreissena polymorpha*) distribution in northeastern Wisconsin and upper Michigan lakes in 2012.