

Impact of temperature on chlorination strategies for mussel control at water treatment plants

Carlos Alonzo-Moya, Ian Lake-Thompson, Alonso Hurtado and Ron Hofmann

ABSTRACT

Drinking water treatment plants in the Great Lakes often protect their intake structures against dreissenid biofouling by prechlorinating when water temperatures exceed 12 °C. This temperature threshold is based on the reproduction characteristics of zebra mussels. However, in recent years, zebra mussels have largely given way to quagga mussels in the region. These mussels reportedly reproduce at temperatures as low as 5 °C. The objective of this study was to determine if the current 12 °C trigger point for prechlorination remains appropriate. A 3-year monitoring program using bioboxes recorded mussel veliger concentrations and settlement potential in water drawn from the intakes of three drinking water treatment plants on Lake Ontario. Water temperature was a poor predictor of veliger presence and settlement. Reproduction and settlement were observed outside of the traditional temperature thresholds. Furthermore, no relationship was found between the number of veligers in the water column and those settling, suggesting that there are complex environmental factors that influence mussel activity. Nevertheless, it was observed that settlement occurred consistently between the months of July and November in the 3 years of the study. Therefore, a calendar-based approach to trigger prechlorination, as opposed to a temperature-based approach, is suggested.

Key words | prechlorination, quagga mussels, temperature thresholds, zebra mussels

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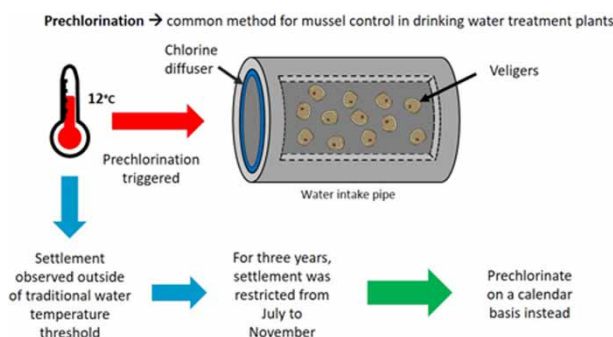
HIGHLIGHTS

- Settlement was observed at temperatures <5°C.
- Temperature is a poor predictor of mussel veliger densities and settlement rates.
- Settlement consistently occurred between the months of July and November.

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doi: 10.2166/aqua.2021.124

GRAPHICAL ABSTRACT



INTRODUCTION

Shortly after their introduction into the Great Lakes in the mid-1980s, zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) proved to be a major threat to drinking water treatment plants. The mussels' outstanding ability to attach to surfaces led to substantial decreases in the hydraulic capacity of the plants due to thick layers of mussels growing inside intake pipes. Additionally, some plants reported the obstruction of valves by large numbers of mussels, while others expressed concerns of potential damage to ultrafiltration membranes caused by the mussels' sharp shells (Hebert *et al.* 1989; Van Benschoten *et al.* 1993; AWWARF 1997). In general, the presence of mussels is a major operational and economic concern for utilities in the region (Connelly *et al.* 2007).

Utilities have adopted chemical means of mussel control because they have proved to be convenient and effective (Mackie & Claudi 2010; Claudi *et al.* 2012). Studies showed that chlorine, in particular, is effective against both adult and larval (veliger) dreissenids using doses as low as 0.3 mg/L (Van Benschoten *et al.* 1993, 1995; Rajagopal *et al.* 2002). While effective, there is a desire to keep chlorine concentrations as low as possible for economic reasons and to minimize the formation of regulated chlorination by-products in the tap water.

Research in the 1980s and 1990s suggested that zebra mussels only start to reproduce at water temperatures exceeding 12 °C (Hebert *et al.* 1989; Mackie 1991; Ram *et al.* 1996). This temperature threshold, therefore, became a de facto guideline for triggering prechlorination of the

intake lines for many drinking water treatment plants in the region. However, in more recent years, zebra mussels have been replaced by quagga mussels, which now account for as much as 99% of the mussel population in the Great Lakes (Wilson *et al.* 2006; Pennuto *et al.* 2012; Ginn *et al.* 2018). Quagga mussels have been observed to be more tolerant to lower water temperatures; the maturing of gonads and gametes, and consequently reproduction, can occur at 5–7 °C (Roe & MacIsaac 1997; Karatayev *et al.* 2015). Despite the changes in dreissenid populations, most plants have not modified their prechlorination programs, which might leave them at risk of biofouling.

Despite the extensive literature on zebra and quagga mussels in the Great Lakes and chlorine-based control methods, studies focusing on veliger presence and settlement on intake structures and on a pilot-scale are still lacking. In this study, the raw water of three drinking water utilities in northwestern Lake Ontario was monitored using bioboxes to assess the relationship of water temperature and veliger presence and settlement. The main objective of this study was to evaluate if the traditional 12 °C threshold, or another temperature-based criterion to account for quagga mussels, which are more tolerant to lower water temperatures, should be used to trigger the prechlorination of intake structures.

This study offers an overview of mussel activity in water treatment plants in terms of veliger densities, settlement rates and water temperatures. Next, the study takes a detailed focus on three particular aspects of mussel activity to shed light on whether the current temperature-based

approach for triggering chemical mussel-control methods in utilities is an efficient practice. First, the relationship between the veliger density in the influent water and the water temperature was analyzed. The second aspect was the impact of water temperature on veliger settlement. Finally, the correlation between increased incoming veliger densities and veliger settlement was tested.

MATERIALS AND METHODS

Sampling locations

Unchlorinated raw water from the sampling lines at the intake of three different water treatment utilities on Lake Ontario (named plants A, B, and C) in the Greater Toronto Area was collected from 2017 to 2019 to analyze the veliger densities in the water column and settlement rates on hard substrates. A map showing the location of the water treatment plants is included in the Supplementary Material.

Sample collection

Veliger density samples

A custom-made veliger sampler (J.J. Downs, Toronto, Ontario) was used to determine the number of veligers present in the raw water. The device consisted of a PVC cylinder with an orifice in the wall. The orifice was covered with a 61 μm stainless steel mesh to retain particles larger than the openings. When required, a 500 μm cylindrical filter was attached to the upstream end of the device to remove larger solids. After a desired volume of water was filtered, excess water was discarded through the mesh. The retentate was washed into a container with either lake water filtered through a 61 μm mesh or a preservation solution prepared with 70% (v/v) isopropanol (VWR, Mississauga, Ontario) and 0.1 g/L sodium bicarbonate (Sigma Aldrich, Oakville, Canada). If the samples were going to be analyzed the same day of their collection, filtered lake water was used for the backwash; otherwise, the samples were preserved.

Three samples were taken at each location for every sampling event. The volume of the sample was dependent on the setup at each plant. Some utilities had larger

sampling pumps, which allowed for filtering larger volumes of raw water. The target volumes were 100, 500, and 1,000 L at Plants A, B, and C, respectively. A flow chart describing the veliger density sampling and analysis is included in the Supplementary Material.

Settlement rate samples

The settlement rates were determined using 55.9 cm \times 38.1 cm \times 30.5 cm polypropylene bioboxes. Each biobox was equipped with plastic plates that served as a substrate for veliger adhesion. The bioboxes were supplied with raw unchlorinated water at a flow varying between 1 and 4 L/min, depending on the setup at each facility. The bioboxes held four PVC settling plates with a total area of 0.116 m² per plate. The plates were sanded to increase the roughness of the surface and to promote the attachment of veligers (Marsden & Lansky 2000).

On no occasion were there veligers in a stage of development that allowed them to be observed through the naked eye. Therefore, the sampling procedure consisted of spraying the plates with either filtered lake water or isopropanol preservation solution and then scraping off the plates' surface with a metal spatula for subsequent microscopic analysis.

The four settling plates were divided into groups of two and were sampled in an alternating manner. The samples were collected every 2 weeks until there was no more veliger attachment observed (i.e. at the onset of winter). At that point, the sampling time was adjusted to a monthly basis until settlement was observed to start again. A flow chart describing the settlement sampling and analysis is included in the supplementary material.

Sample processing

Both the veliger density and settlement rate samples were collected in 500 mL Whirl-Pak sampling bags (Nasco, Canada) and transported to the laboratory in a cooler to keep them at 4 °C to prevent degradation. To make the analysis process easier, the samples were concentrated to a smaller volume. To do so, the samples were first sieved through a 250 μm mesh to remove large debris. The retentate was rinsed with distilled water to recover any veligers that could have been retained. The retentate was then

discarded. The filtrate was recovered and sieved using a 64 μm mesh. The retentate of the 64 μm mesh was then backwashed into a 15 mL centrifuge tube using distilled water. The samples were then analyzed in the microscope following the procedure described in the next section.

After each sample was processed, the meshes were rinsed three times with hot water and then soaked in a 5% acetic acid solution to minimize the risk of contamination.

Sample analysis: microscopy

A gridded Sedgewick-Rafter cell (Wildco, Florida, USA) was filled with 1 mL of sample and analyzed under 100 \times magnification on a Nikon E600 microscope. The microscope was equipped with two polarized light camera filters, allowing for cross-polarized light microscopy (CPLM). This technique takes advantage of the birefringent properties of calcareous skeletons and shells (Johnson 1995). Under cross-polarized light, most objects block light. However, birefringent materials, such as veligers' shells, allow light to pass through. The result of seeing the samples through cross-polarized light is a dark background and illuminated veligers. CPLM has proved to be accurate for veliger detection (Frischer *et al.* 2012) while allowing sample processing speeds almost twice as fast as conventional microscopy (Johnson 1995).

For most samples, the entire slide was analyzed to enumerate the veligers present. For the veliger density samples, all the individuals found in the cell were considered, except for those that had a broken or empty shell. For the settlement samples, only individuals larger than 150 μm were counted, as smaller individuals are not ready to settle. However, this remains a conservative criterion because mussel larvae can only settle once they reach the pediveliger stage. This development stage is marked by the development of the 'foot,' an organ used to secrete the byssal threads used for attaching to surfaces. Mussel larvae reach this stage when they are 200–300 μm long (Martel *et al.* 1994; Mackie & Claudi 2010). Broken and empty shells were not considered for enumeration.

Considerations

Dreissenid larvae are free-floating organisms in the water column. Therefore, discrete sampling might offer only a

view of the instantaneous conditions of the water in terms of both veliger presence and settlement rates. These conditions might not necessarily persist for a long time as some studies have proved that both veliger concentrations and settlement rates might vary dramatically within hours (Smylie & Mackie 1992; Martel *et al.* 1994; Manuel 1996). Therefore, it might be inaccurate to assume that the veliger densities and settlement rate data points could be connected.

Factors that might affect veliger presence and settlement rates include, but might not be limited to, wind and water currents, food and nutrient availability, and weather conditions like storms (Martel *et al.* 1994; Churchill 2013). A study on blue mussels, a species of freshwater mussels, suggests that after storms or intense currents, there is more frequent contact between veligers and substrate to settle on, which could lead to increased settlement rates (Eyster & Pechenik 1987).

RESULTS AND DISCUSSION

Mussel activity in drinking water treatment utilities

Mussel veliger densities, settlement rates, and water temperature data were collected from three water treatment plants in the Greater Toronto Area from 2017 to 2019. Figure 1 shows the condensed data for Plants A, B, and C. Because of the proximity of the plants, it was expected that similar trends would be observed for these parameters; however, there were important variations. In Plants A and C, veliger densities increased in 2018 compared with 2017, but much lower settlement rates were recorded. Plant B shows the opposite trend. In 2019, both veliger densities and settlement rates decreased dramatically compared with previous years in Plant A. In Plant C, settlement rates appear similar, while the veliger density decreased. Monitoring of Plant B in 2019 was not possible because the plant was undergoing renovations that forced the experiment to stop. A rather erratic seasonal variation of dreissenids was observed during the 3 years of monitoring, but this is not an uncommon observation. A study analyzed data from 67 different studies focusing on dreissenid mussel dynamics in water bodies in Europe and North

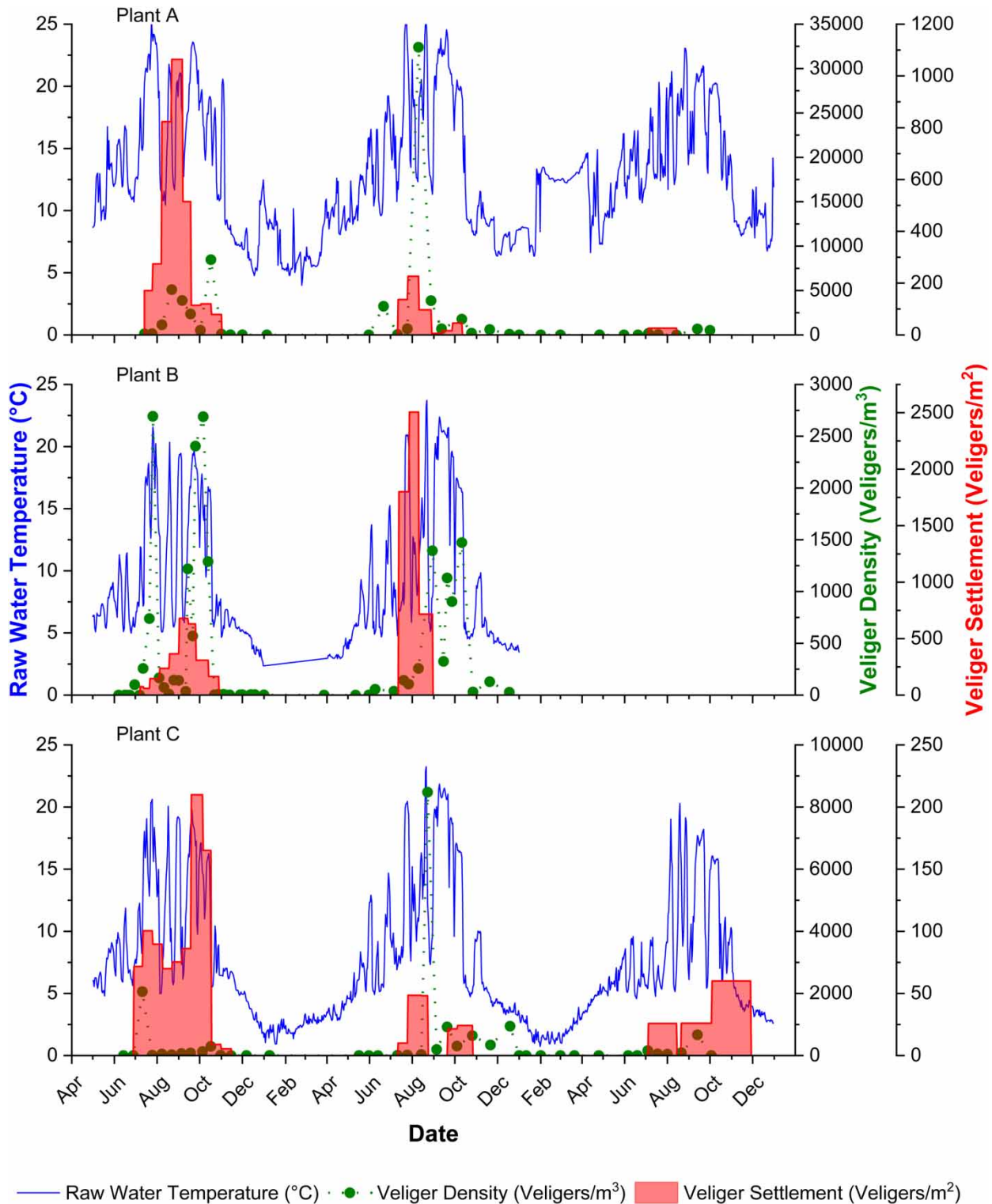


Figure 1 | Veliger densities, settlement rates, and water temperatures from July 2017 to November 2019 at three water treatment plants on Lake Ontario. Note the different scales on the vertical axes.

America and observed no clear trends in terms of mussel populations: some of them increase with time, others decrease, while others remain steady (Strayer *et al.* 2019). Even within a single water body, there are important variations in veliger density and settlement of juvenile specimens in different spatial points (Marsden *et al.* 2014; Hetherington *et al.* 2019). Several factors can impact dreissenid populations, including predation by organisms such as round gobies and waterfowl (Petrie & Knapton 1999; Barton *et al.* 2005; Carlsson *et al.* 2011), water quality (calcium concentration, dissolved oxygen, salinity, pH, and temperature) (Whittier *et al.* 2008; ERDC 2010; Garton *et al.* 2014; Karatayev *et al.* 2018), and water currents, and food availability (MacIsaac 1996; Marsden *et al.* 2014; White *et al.* 2015). This leads to the conclusion that every water body has unique ecological, physical, and chemical circumstances that impact mussel reproduction and settlement patterns in different ways (Lucy 2006; Hetherington *et al.* 2019; Strayer *et al.* 2019)

Water temperature and mussel reproduction and settlement showed no clear trends that could accurately predict

the dynamics and seasonal variations of mussel populations. Even though the highest veliger densities were registered during the summer months, there was no clear relationship between veliger presence and water temperature. For example, Figure 1 shows a period in 2018 in Plant A in mid to late September when the water temperature was above 20 °C, but the veliger counts were only ~2000 veligers/m³, while the highest density observed in previous months was up to ~30,000 veligers/m³ when the water temperature was slightly below 20 °C. The relationship between water temperature and veliger presence in the three plants is analyzed in Figure 2. The data collected from the three water treatment plants for 3 years are inconclusive in terms of the role of temperature on veliger presence. This indicates that warm water alone might not be a good predictor of mussel reproduction. A similar conclusion was reached by another study made in Lake Erie, where there was no significant relationship between water temperature and veliger presence, and veligers only appeared when the water temperature reached 18 °C (Garton & Haag 1993).

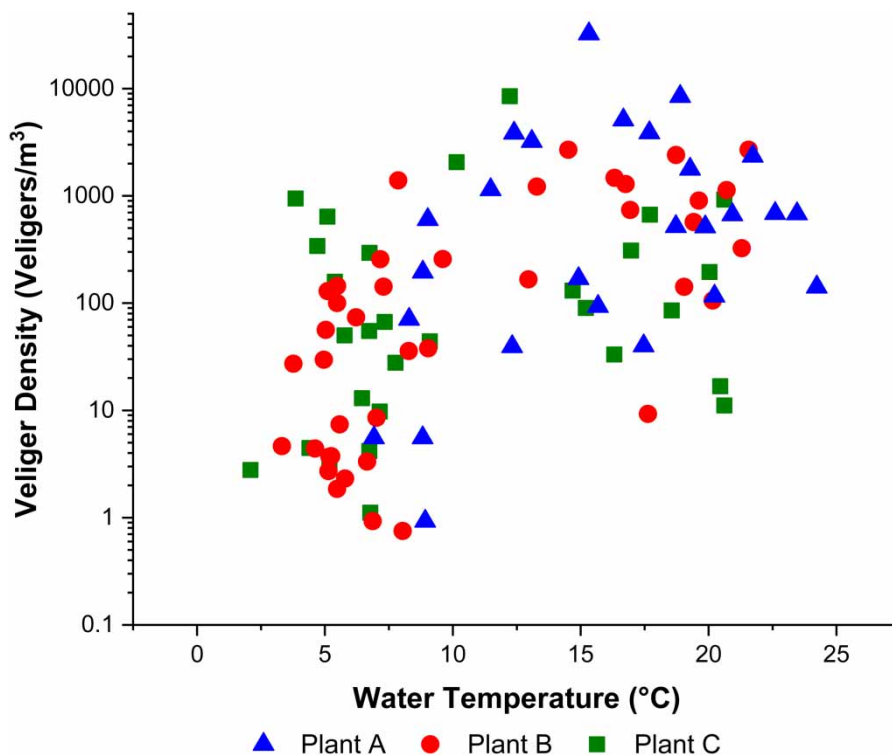


Figure 2 | Veliger densities as a function of water temperature. Note the log scale on the vertical axis.

Figure 1 shows the average settlement recorded over 2-week periods rather than instantaneous measurements. Settlement started in early to mid-July every year during the experiment and did not appear to have a strong correlation with water temperature. In 2018, all the plants showed periods of no settlement even when temperatures were well above 15 °C. The highest settlement rate observed from 2017 to 2019 was ~2,500 veligers/m² and was recorded in Plant B in 2018 when the temperature was slightly above 5 °C. Settlement observed in this study was considerably lower than the recruitment densities observed on Lake Ontario's bed, which are recorded to be up to approximately 10,000 specimens/m² (Pennuto *et al.* 2012). However, *Dreissena* populations in Lake Ontario have declined through time (Wilson *et al.* 2006; Pennuto *et al.* 2012). Dramatic decreases in *Dreissena* densities of up to 43% have been reported in a 5-year period from 2003 to 2008 (Birkett *et al.* 2015). Additionally, some studies have found that the number of veligers observed in the low-level service pumps of a water treatment plant in Lake Erie was only a fraction of the total of those counted at the lake near the intake (Fraleigh *et al.* 1993), which could partially explain the lower settlement rates observed in the present study.

Figure 3 presents the dates and range of temperatures in which settlement started and stopped for the duration of the experiment. There was no strong indication that 12 °C is an accurate water temperature threshold for mussel settlement. Water temperature at which settlement was first observed varied greatly from plant to plant and from year to year. The onset of settlement occurred through a wide range of water temperatures, with the lowest one being 5 °C for Plant B in 2017. Similarly, the end of the settling period varied considerably throughout the monitoring period. The lowest temperature that marked the end of a mussel reproduction season happened in 2019 in Plant C, where settlement occurred until late November when the temperature was approximately 3 °C. These data suggest that dreissenid mussel seasonal variations appear to be independent of water temperature.

Figure 4 compares the settlement rates and water temperature observed in Plants A, B, and C to determine if there is a correlation between these two parameters. The linear regression analysis for each plant shows that temperature

did not adequately predict veliger settlement (95% CI), and temperature accounted for less than 10% of the explained variability in veliger settlement ($R^2 < 0.1$). For example, there are data showing that at temperatures <7.5 °C, there are settlement rates >2,000 veligers/m², and at temperatures of approximately 25 °C, there are settlement rates <10 veligers/m². The temperature-based criterion for starting prechlorination when water reaches 12 °C is based on zebra mussel spawning (Hebert *et al.* 1989; Mackie 1991; Ram *et al.* 1996), but as seen in Figures 3 and 4, high temperatures were not necessarily indicative of either the beginning or end of the mussel settlement season or increased veliger settlement. Therefore, it can be hypothesized that mussel reproduction and attachment to surfaces are bound to a complex process that depends not only on water temperature but also on other environmental, physical, and chemical factors (Strayer *et al.* 2019). Some of these factors could include food and nutrient availability (Hecky *et al.* 2004), water currents that may disperse gametes or prevent veligers from settling (MacIsaac 1996), and chemical conditions that may impact the mussels, like low pH levels (Garton *et al.* 2014) or low calcium levels (Whittier *et al.* 2008). However, the role that each of these factors plays are not yet fully understood. Thus, lowering the temperature threshold to accommodate for the lower temperatures at which settlement was recorded might not be an appropriate option for utilities located along Lake Ontario.

Additionally, as seen in Figure 1, there are significant and sudden variations in water temperature in Lake Ontario, especially between the months of June and November, when the water temperature can fall from approximately 25 °C to less than 5 °C within days, and then quickly climb up to more than 20 °C. These sudden temperature variations are due to downwelling and upwelling events, which involve the movement of water from the bottom of the lake to the surface due to wind currents. These phenomena have been documented previously in Lake Ontario (Csanady 1977) and have been linked to decreased *Dreissena* densities (Wilson *et al.* 2006; Pennuto *et al.* 2012). The role of upwelling in changes in dreissenid populations is not fully understood, but some mechanisms that might impact mussels include the displacement of larvae with the currents, sudden changes in food and

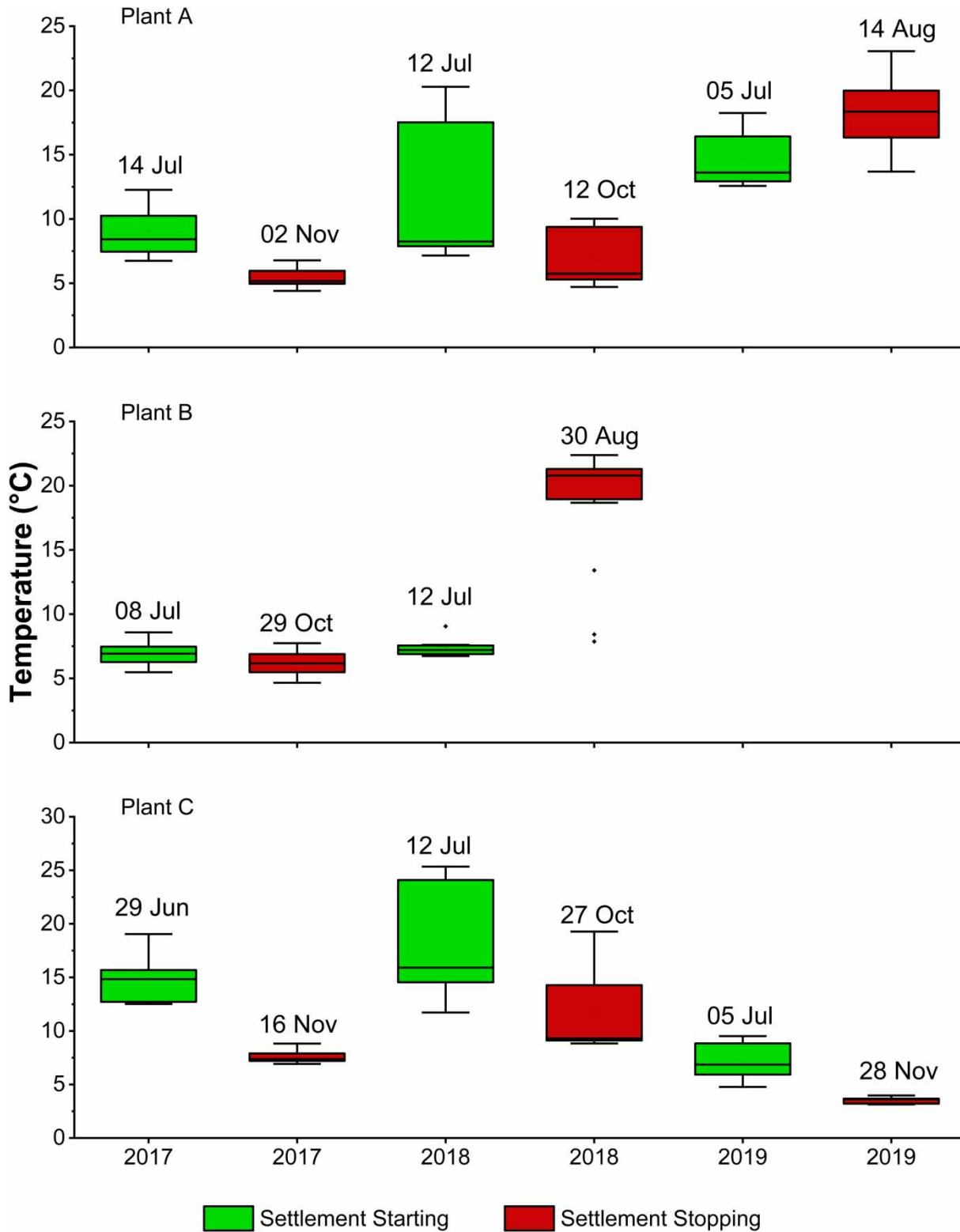


Figure 3 | Initial and final settlement temperatures for Plants A, B, and C from 2017 to 2019. The date when settlement was first and last observed are written on top of each box plot.

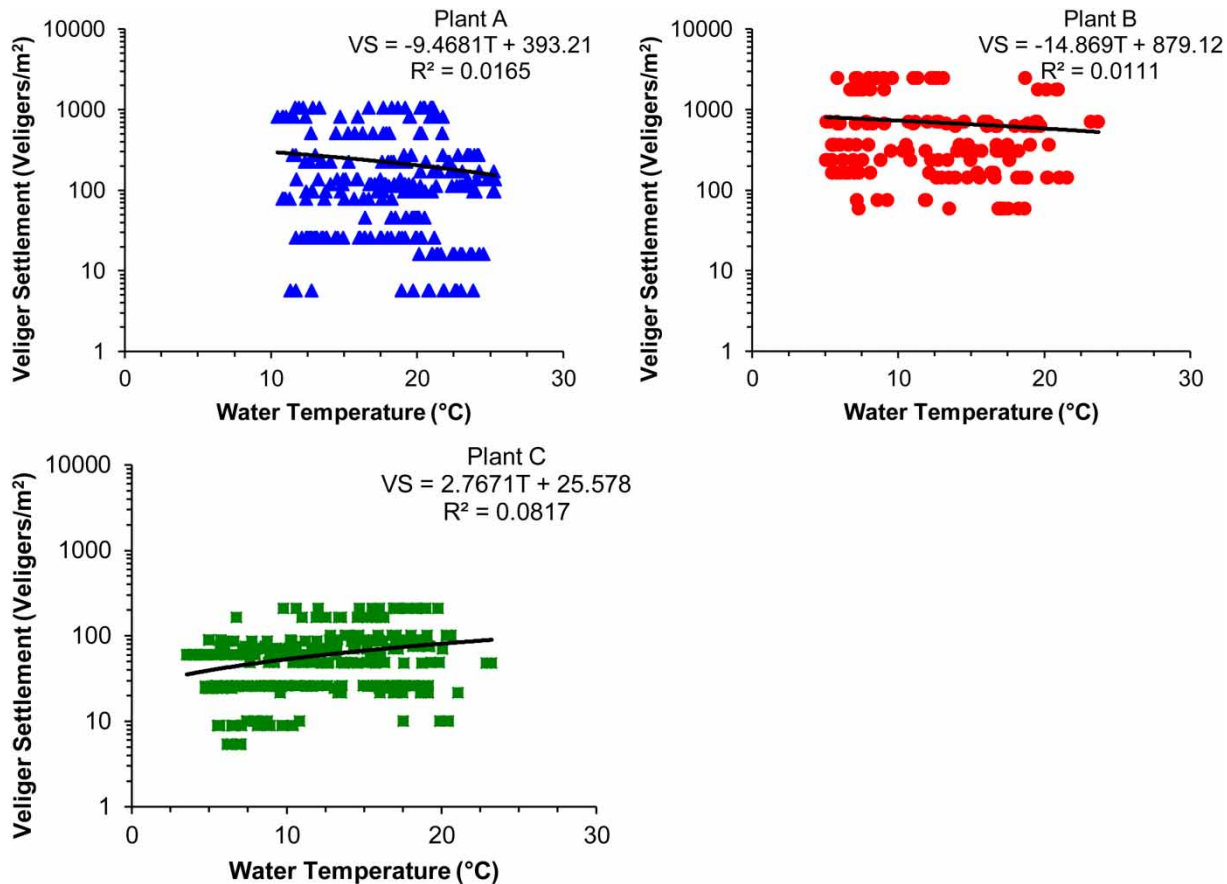


Figure 4 | Relationship between settlement rates and water temperatures.

nutrient availability, and shear stress exerted on the established individuals. Thus, water treatment plants along northwestern Lake Ontario should reconsider relying on water temperature as a sole parameter for starting prechlorination of the intake structures.

Interestingly, it was found that, counterintuitively, there was not a strong relationship between veliger presence and settlement. A clear example can be observed in Figure 1 for Plant B in 2018, where, from September to August, despite the relatively high veliger concentrations, there was no settlement registered. These two parameters were compared in Figure 5. It can be observed that there is no clear trend that correlates veliger density with new recruitment. The current temperature-based criterion for prechlorination relies on the spawning of mussels, following the idea that an increased number of veligers will correspond to high settlement rates. However, the initial spawning of veligers would not necessarily translate into immediate high

settlement rates due to various reasons, such as the high mortality rates experienced by veligers before developing into adults (99% mortality) (Keough & Downes 1982; Hunt & Scheibling 1997; Mackie & Claudi 2010), the length of time (18–30 days) it takes for veligers to develop from free-swimming larvae to when the foot is developed (Mackie & Claudi 2010), and the potential for veligers to be transported to other areas via water currents. Some short-term studies have found positive correlations between veliger abundance and settlement (Fraleigh *et al.* 1993; Martel *et al.* 1994). However, a study conducted in Lake Erie showed that this relationship varied between 2 years. In 1989, a very close relationship between veliger presence and settlement rates was observed, while in 1990, the correlation was not significant (Garton & Haag 1993). On the other hand, long-term studies (>20 years long) have concluded that veliger density is a poor predictor of specimens that can attach to a substrate and mature (Hetherington *et al.* 2019; Strayer *et al.*

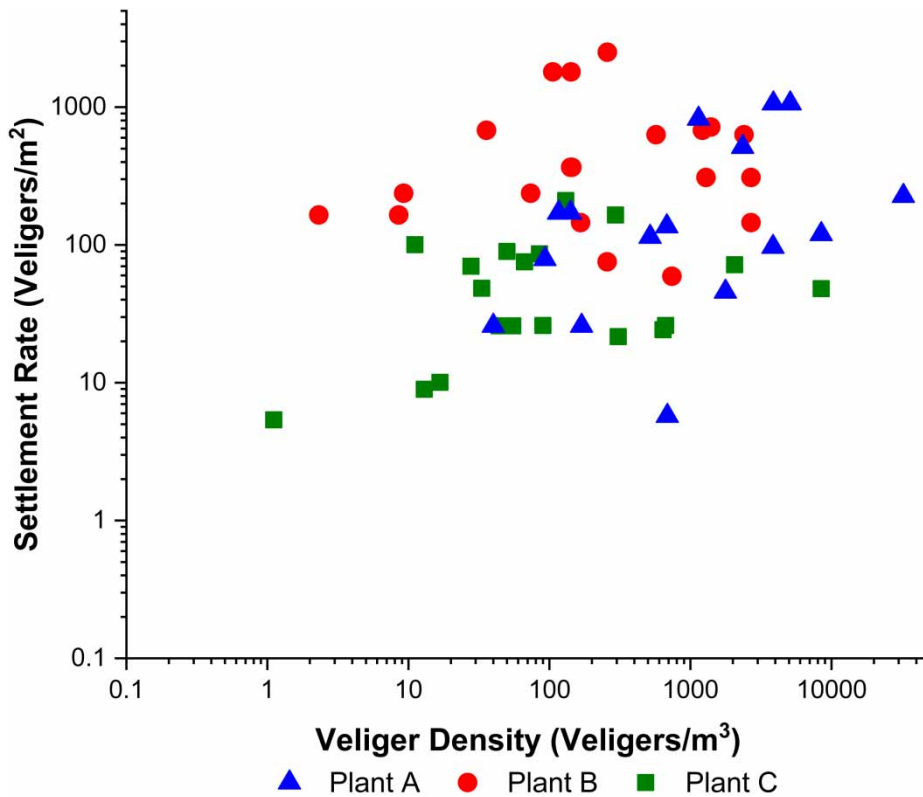


Figure 5 | Settlement rates compared with veliger density. Note the log scale on the vertical and horizontal axes.

2019). Therefore, even if many veligers are present in the water column, they may not be ready to settle and cause damage to water treatment plant infrastructure. It must be noted that the size of veligers in the water column was not considered in this study, and, as only pediveligers can settle, it is possible that a portion of the incoming veligers was not ready to do so. Additionally, many of the samples were preserved, meaning that it was impossible to discern if all the individuals were viable.

While there were no clear correlations between water temperature, veliger density, and settlement potential, it was observed that during the 3 years of monitoring, mussel settlement was restricted to the months of July to November. The exact reasons that restrict mussel settlement to these periods remain unknown. Further studies should be conducted to elucidate the roles of different environmental, physical, and chemical factors that could contribute to this phenomenon.

This period is, therefore, when the water treatment plants are likely to be most vulnerable to mussel fouling. This

suggests that prechlorination of intake structures could be applied during these months only, instead of starting prechlorination, as soon as the water temperature reaches 12 °C. If any settlement were to occur outside of that window, considering that mussels grow at a rate of approximately 1–2 mm/month (Claudi & Mackie 1994), the settled individuals would not grow to a considerable size and could be treated when prechlorination is restarted in the following summer. In addition, the effectiveness of chlorine treatments is temperature-dependent. Adult mussel mortality rates induced by chlorine have been shown to increase by approximately three times when the temperature rises from 10 to 20 °C. Therefore, the warmer months are likely the best time to perchlorinate (Van Benschoten *et al.* 1995).

SUMMARY AND CONCLUSIONS

Raw unchlorinated water from three water treatment plants was monitored for 3 years in terms of mussel larvae

presence and new settlement and compared with water temperature. No strong relationship between water temperature and veliger presence or settlement was found, leading to the conclusion that water temperature is a poor indicator of mussel activity. Additionally, it was found that water temperature in Lake Ontario varies dramatically within days due to downwelling and upwelling events. Therefore, for this location, water temperature is not a reliable parameter to predict periods in which utilities are vulnerable to mussel fouling or to predict mussel population dynamics. Instead, it was observed that for three consecutive years, settlement was restricted to the months of July to November despite the predominant presence of quagga mussels, which are known to be able to reproduce at temperatures as low as 5 °C. Therefore, a calendar-based approach for triggering the prechlorination of intake structures may be a rational solution for utilities in this part of Lake Ontario. Adopting this approach could result in economic benefits for utilities because sometimes the water temperature reaches 12 °C early in the year; however, the mussels would not start settling until July. Utilities would minimize the use of chlorine and would not have to use energy to pump the chlorine to the inlet of the intake pipes.

This study also demonstrated the value of the bioboxes for near-real-time monitoring of settlement. Water treatment plants, power plants, or any facility that uses zebra and quagga mussel-infested water in their systems can benefit from installing bioboxes onsite to track the onset and ending of mussel settlement and adjust their prechlorination programs accordingly.

ACKNOWLEDGEMENTS

The authors are grateful for the support provided by Renata Claudi of RNT Consulting Inc., Revathy Vattukkalathil from Toronto Water, Teodor Kochmar from Water and Wastewater from the Region of Peel, and Barry Ward and Nick Halliwushka from the Works Department from the Durham Region. This work was funded by the Natural Sciences and Engineering Research Council of Canada Industrial Research Chair in Drinking Water Research at the University of Toronto, project IRCPJ428979-16. Carlos

Alonzo-Moya acknowledges the financial support from MITACS for graduate studies.

DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

REFERENCES

- AWWARF 1997 *Controlling Zebra Mussels at Water Treatment Plant Intakes*. AWWA Research Foundation and American Water Works Association, Denver, Colorado, p. 86.
- Barton, D. R., Johnson, R. A., Campbell, L., Petruniak, J. & Patterson, M. 2005 *Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in Eastern Lake Erie, 2002–2004*. *J. Great Lakes Res.* **31**, 252–261. [https://doi.org/10.1016/S0380-1330\(05\)70318-X](https://doi.org/10.1016/S0380-1330(05)70318-X).
- Birkett, K., Lozano, S. J. & Rudstam, L. G. 2015 *Long-term trends in Lake Ontario's Benthic Macroinvertebrate Community from 1994–2008*. *Aquat. Ecosyst. Heal. Manag.* **18**, 76–88. <https://doi.org/10.1080/14634988.2014.965122>.
- Carlsson, N. O. L., Bustamante, H., Strayer, D. L. & Pace, M. L. 2011 *Biotic resistance on the increase: native predators structure invasive zebra mussel populations*. *Freshw. Biol.* **56**, 1630–1637. <https://doi.org/10.1111/j.1365-2427.2011.02602.x>.
- Churchill, C. J. 2013 *Spatio-temporal spawning and larval dynamics of a zebra mussel (*Dreissena polymorpha*) population in a North Texas Reservoir: implications for invasions in the Southern United States*. *Aquat. Invasions* **8**, 389–406. <https://doi.org/10.3391/ai.2013.8.4.03>.
- Claudi, R. & Mackie, G. L. 1994 *Zebra Mussel Monitoring and Control*. Lewis Publishers, Inc., Boca Raton, FL.
- Claudi, R., Graves, A., Taraborelli, A. C., Prescott, R. J. & Mastitsky, S. E. 2012 *Impact of pH on survival and settlement of dreissenid mussels*. *Aquat. Invasions* **7**, 21–28. <https://doi.org/10.3391/ai.2012.7.1.003>.
- Connelly, N. A., O'Neill, C. R., Knuth, B. A. & Brown, T. L. 2007 *Economic impacts of zebra mussels on drinking water treatment and electric power generation facilities*. *Environ. Manage.* **40**, 105–112. <https://doi.org/10.1007/s00267-006-0296-5>.
- Csanady, G. T. 1977 *Intermittent 'full' upwelling in Lake Ontario*. *J. Geophys. Res.* **82**, 397–419. <https://doi.org/10.1007/BF00380003>.
- ERDC 2010 In: *Environmental Habitat Conditions Associated with Freshwater Dreissenids* (M. D. Farr & B. S. Payne, eds). Report for the Aquatic Nuisance Species Research Program. U.S. Army Corps of Engineers, Vicksburg, MS, p. 24.
- Eyster, L. S. & Pechenik, J. A. 1987 *Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water*

- agitation. *J. Exp. Mar. Biol. Ecol.* **114**, 99–110. [https://doi.org/10.1016/0022-0981\(88\)90131-1](https://doi.org/10.1016/0022-0981(88)90131-1).
- Fraleigh, P. C., Klerks, P. L., Gubanich, G., Matissof, G. & Stevenson, R. C. 1993 Abundance and settling of zebra mussel (*Dreissena polymorpha*) veligers in Western and Central Lake Erie. In: *Zebra Mussels: Biology, Impacts, and Control* (T. F. Nalepa & D. Schloesser, eds). Lewis Publishers, Boca Raton, FL, pp. 129–142.
- Frischer, M. E., Kelly, K. L. & Nierzwicki-Bauer, S. A. 2012 Accuracy and reliability of *Dreissena* spp. larvae detection by cross-polarized light microscopy, imaging flow cytometry, and polymerase chain reaction assays. *Lake Reserv. Manag.* **28**, 265–276. <https://doi.org/10.1080/07438141.2012.731027>.
- Garton, D. W. & Haag, W. R. 1993 Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in Western Lake Erie. In: *Zebra Mussels: Biology, Impacts, and Control* (T. F. Nalepa & D. Schloesser, eds). Lewis Publishers, Boca Raton, FL, pp. 111–128.
- Garton, D. W., McMahon, R. & Stoeckmann, A. M. 2014 Limiting environmental factors and competitive interactions between zebra and quagga mussels in North America. In: *Quagga and Zebra Mussels. Biology, Impacts and Control* (T. F. Nalepa & D. Schloesser, eds). CRC Press, Boca Raton, FL, pp. 383–402.
- Ginn, B. K., Bolton, R., Coulombe, D., Fleischaker, T. & Yerex, G. 2018 Quantifying a shift in benthic dominance from zebra (*Dreissena polymorpha*) to quagga (*Dreissena rostriformis bugensis*) mussels in a Large, Inland Lake. *J. Great Lakes Res.* **44**, 271–282. <https://doi.org/10.1016/j.jglr.2017.12.003>.
- Hebert, P. D. N., Muncaster, B. W. & Mackie, G. L. 1989 Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **46**, 1587–1591. <https://doi.org/10.1139/f89-202>.
- Hecky, R. E., Smith, R. E. H., Barton, D. R., Guildford, S. J., Taylor, W. D., Charlton, M. N. & Howell, T. 2004 The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* **61**, 1285–1293. <https://doi.org/10.1139/f04-065>.
- Hetherington, A. L., Rudstam, L. G., Schneider, R. L., Holeck, K. T., Hotaling, C. W., Cooper, J. E. & Jackson, J. R. 2019 Invader invaded: population dynamics of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) in Polymictic Oneida Lake, NY, USA (1992–2013). *Biol. Invasions* **21**, 1529–1544. <https://doi.org/10.1007/s10530-019-01914-0>.
- Hunt, H. L. & Scheibling, R. E. 1997 Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* **155**, 269–301. <https://doi.org/10.3354/meps155269>.
- Johnson, L. E. 1995 Enhanced early detection and enumeration of zebra mussel (*Dreissena* spp.) veligers using cross-polarized light microscopy. *Hydrobiologia* **312**, 139–146. <https://doi.org/10.1007/BF00020769>.
- Karatayev, A. Y., Burlakova, L. E. & Padilla, D. K. 2015 Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia* **746**, 97–112. <https://doi.org/10.1007/s10750-014-1901-x>.
- Karatayev, A. Y., Burlakova, L. E., Mehler, K., Bocaniov, S. A., Collingsworth, P. D., Warren, G., Kraus, R. T. & Hinchey, E. K. 2018 Biomonitoring using invasive species in a large lake: *Dreissena* distribution maps hypoxic zones. *J. Great Lakes Res.* **44**, 639–649. <https://doi.org/10.1016/j.jglr.2017.08.001>.
- Keough, M. J. & Downes, B. J. 1982 Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* **54**, 348–352. <https://doi.org/https://doi.org/10.1007/BF00380003>.
- Lucy, F. 2006 Early life stages of *Dreissena polymorpha* (zebra mussel): the importance of long-term datasets in invasion ecology. *Aquat. Invasions* **1**, 171–182. <https://doi.org/10.3391/ai.2006.1.3.12>.
- MacIsaac, H. J. 1996 Population structure of an introduced species (*Dreissena polymorpha*) along a wave-swept disturbance gradient. *Oecologia* **105**, 484–492. <https://doi.org/10.1007/BF00330011>.
- Mackie, G. L. 1991 Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia* **219**, 251–268. <https://doi.org/https://doi.org/10.1007/BF00024759>.
- Mackie, G. L. & Claudi, R. 2010 *Monitoring and Control of Macrofouling Mollusks in Fresh Water Systems*, 2nd ed. CRC Press, Boca Raton, p. 508.
- Manuel, J. L. 1996 *Population and Temporal Variations in the Vertical Migrations of Scallop (Placopecten Magellanicus) Veligers*. Doctoral Thesis, Dalhousie University.
- Marsden, J. E. & Lansky, D. M. 2000 Substrate selection by settling zebra mussels, *Dreissena polymorpha*, relative to material, texture, orientation, and sunlight. *Can. J. Zool.* **78**, 787–793. <https://doi.org/10.1139/z00-004>.
- Marsden, J. E., Stangel, P. & Shambaugh, A. 2014 Influence of environmental factors on zebra mussel population expansion in Lake Champlain, 1994–2010. In: *Quagga and Zebra Mussels. Biology, Impacts and Control* (T. F. Nalepa & D. Schloesser, eds). CRC Press, Boca Raton, FL, pp. 33–53.
- Martel, A., Mathieu, A. F., Findlay, C. S., Nepszy, S. J. & Leach, J. H. 1994 Daily settlement rates of the zebra mussel, *Dreissena polymorpha*, on an artificial substrate correlate with veliger abundance. *Can. J. Fish. Aquat. Sci.* **51**, 856–861. <https://doi.org/10.1139/f94-084>.
- Pennuto, C. M., Howell, E. T., Lewis, T. W. & Makarewicz, J. C. 2012 *Dreissena* population status in nearshore Lake Ontario. *J. Great Lakes Res.* **38**, 161–170. <https://doi.org/10.1016/j.jglr.2012.04.002>.
- Petrie, S. A. & Knapton, R. W. 1999 Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie: possible influence of waterfowl predation. *J. Great Lakes Res.* **25**, 772–782. [https://doi.org/https://doi.org/10.1016/S0380-1330\(99\)70776-8](https://doi.org/https://doi.org/10.1016/S0380-1330(99)70776-8).

- Rajagopal, S., Van Der Velde, G. & Jenner, H. A. 2002 Effects of low-level chlorination on zebra mussel, *Dreissena polymorpha*. *Water Res.* **36**, 3029–3034. [https://doi.org/10.1016/S0043-1354\(01\)00516-4](https://doi.org/10.1016/S0043-1354(01)00516-4).
- Ram, J. L., Fong, P. P. & Garton, D. W. 1996 Physiological aspects of zebra mussel reproduction: maturation, spawning, and fertilization. *Integr. Comp. Biol.* **36**, 326–338. <https://doi.org/10.1093/icb/36.3.326>.
- Roe, S. L. & MacIsaac, H. J. 1997 Deepwater population structure and reproductive state of quagga mussels (*Dreissena bugensis*) in Lake Erie. *Can. J. Fish. Aquat. Sci.* **54**, 2428–2433. <https://doi.org/10.1139/f97-151>.
- Smylie, P. & Mackie, G. L. 1992 Growth and Abundance of Veliger Larvae of *Dreissena polymorpha* in Relation to Environmental Factors in the Lower Great Lakes. Report Submitted to the Great Lakes University Research Fund. <https://doi.org/10.13140/RG.2.1.1218.0564>.
- Strayer, D. L., Adamovich, B. V., Adrian, R., Aldridge, D. C., Balogh, C., Burlakova, L. E., Fried-Petersen, H. B., G-Tóth, L., Hetherington, A. L., Jones, T. S., Karatayev, A. Y., Madill, J. B., Makarevich, O. A., Marsden, J. E., Martel, A. L., Minchin, D., Nalepa, T. F., Noordhuis, R., Robinson, T. J., Rudstam, L. G., Schwalb, A. N., Smith, D. R., Steinman, A. D. & Jeschke, J. M. 2019 Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis. *Ecosphere* **10**. <https://doi.org/10.1002/ecs2.2701>
- Van Benschoten, J. E., Jensen, J. N., Brady, T. J., Lewis, D. P., Sferrazza, J. & Neuhauser, E. F. 1993 Response of zebra mussel veligers to chemical oxidants. *Water Res.* **27**, 575–582. [https://doi.org/10.1016/0043-1354\(93\)90166-F](https://doi.org/10.1016/0043-1354(93)90166-F).
- Van Benschoten, J. E., Jensen, J. N., Harrington, D. & DeGirolamo, D. J. 1995 Zebra mussel mortality with chlorine. *J. Am. Water Works Assoc.* **87**, 101–108. <https://doi.org/10.1002/j.1551-8833.1995.tb06368.x>.
- White, J. D., Hamilton, S. K. & Sarnelle, O. 2015 Heat-induced mass mortality of invasive zebra mussels (*Dreissena polymorpha*) at sublethal water temperatures. *Can. J. Fish. Aquat. Sci.* **72**, 1221–1229. <https://doi.org/10.1139/cjfas-2015-0064>.
- Whittier, T. R., Ringold, P. L., Herlihy, A. T. & Pierson, S. M. 2008 A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp). *Front. Ecol. Environ.* **6**, 180–184. <https://doi.org/10.1890/070073>.
- Wilson, K. A., Howell, E. T. & Jackson, D. A. 2006 Replacement of zebra mussels by quagga mussels in the Canadian Nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. *J. Great Lakes Res.* **32**, 11–28. [https://doi.org/10.3394/0380-1330\(2006\)32](https://doi.org/10.3394/0380-1330(2006)32).

First received 15 October 2020; accepted in revised form 5 March 2021. Available online 22 March 2021