

Differences in growth and survivorship of zebra and quagga mussels: size matters

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Abstract The zebra mussel (*Dreissena polymorpha*) and its congener the quagga mussel (*Dreissena rostriformis bugensis*) are both invaders in freshwater, but have very different invasion histories, with zebra mussels attaining substantially faster rates of spread at virtually all spatial scales. However, in waterbodies where they co-occur, *D. r. bugensis* can displace *D. polymorpha*. To determine if the mechanisms for this displacement are associated with different survival and growth, we kept mussels in flow-through tanks for 289 days with two temperature regimes that mimicked the natural surface water

(littoral zone) and hypolimnion conditions of Lake Erie. For the littoral zone regime, we used water directly from the surface of Lake Erie (range 4–25°C, average $11.9 \pm 0.6^\circ\text{C}$). For the profundal zone treatment, Lake Erie surface water was chilled to about 6°C (range 5–8°C, average $6.2 \pm 0.6^\circ\text{C}$) for the full duration of the experiment. For each of these temperature regimes, we used three replicate tanks with only zebra mussels present and three replicate tanks with only quagga mussels (150 ind./tank each), and three replicate tanks with both species (75 ind./tank of each species). Quagga mussels had higher survivorship and grew more than zebra mussels in all treatments. For both species, the size of the mussel entering the winter was critical for survivorship. Larger mussels had a higher survival over the winter in all treatments. For both species, there was a

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survivorship and growth tradeoff. In the warmer littoral zone treatment both species had higher growth, but lower survival than in the colder profundal zone treatment. Surprisingly, although quagga mussels outperformed zebra mussels, zebra mussel survivorship was better when they were faced with competition by quagga mussels than with just intraspecific competition. In addition, quagga mussels suffered size-specific mortality during the growing season only when facing interspecific competition with zebra mussels. Further experiments are needed to determine the possible mechanisms for these interspecific effects.

Keywords *Dreissena polymorpha* · *Dreissena rostriformis bugensis* · Growth · Survivorship · Competition · Exotic species · Great Lakes

Introduction

The zebra mussel, *Dreissena polymorpha* (Pallas, 1771), and the quagga mussel, *D. rostriformis bugensis* (Andrusov, 1897), are both important invaders in lakes, reservoirs, rivers, and canals in the northern hemisphere. Although both species were introduced into North America at the same time (Mills et al., 1996; Carlton, 2008), they have different invasion histories in terms of the timing and extent of their introduction and spread to different regions of the world (reviewed in Karatayev et al., 2007). Within a short time after their initial introduction into the Laurentian Great Lakes of North America, zebra mussels rapidly spread and dominated the shores of most of the Great Lakes. Although quagga mussels were introduced at the same time, they were restricted to the deep, soft sediment profundal zones of the lakes (Dermott & Munawar, 1993; Patterson et al., 2005). Zebra mussels spread to all of the Great Lakes within 4 years of their initial introduction (Griffiths et al., 1991), while quagga mussels were much slower to spread. Quagga mussels finally reached the last of the Great Lakes, Lake Superior, in 2005 (Grigorovich et al., 2008), over two decades after zebra mussels were first found in the Great Lakes. Recently, quagga mussels appear to be displacing the zebra mussel in certain lakes where they co-occur. These include the

shallow areas of Lake Erie, Lake Ontario (Mills et al., 1999; Watkins et al., 2007; Dermott & Dow, 2008), and Seneca Lake (D. Molloy personal communication) in North America, and several deep lakes in Europe (reviewed in Mills et al., 1996; Orlova et al., 2004, 2005). At present, the vast majority of mussels found in the littoral zone of Lake Erie are quagga mussels, while a short time ago this area was dominated by zebra mussels.

Several mechanisms have been suggested to explain the displacement of *D. polymorpha* by *D. r. bugensis* in the Great Lakes. Natural selection could be acting on *D. r. bugensis*, such that they now show genetic adaptation to new environments, allowing them to expand from deep cold-water habitats into shallow waters (Mills et al., 1996). Some have suggested that *D. r. bugensis* spawns at lower temperatures than *D. polymorpha*. If so, they would spawn earlier in the season, allowing them to outcompete zebra mussels for open space for attachment (Roe & MacIsaac, 1997; Claxton & Mackie, 1998). This could then lead to source–sink metapopulation dynamics and spatial competition, which would influence the distribution and dynamics of zebra mussel and quagga mussel populations in lakes where they co-exist (Krošek & Lewis, 2010).

Other hypotheses focus on differences in the filtering and feeding of these two species and their energetic efficiencies. Quagga mussels may have higher filtering rates, allowing them to outcompete zebra mussels if food is limiting (Diggins, 2001). If zebra mussels are adapted to high food levels, they would be more limited by low food concentrations (Baldwin et al., 2002), which could explain the success of zebra mussels in lakes with abundant food resources. Once zebra mussel populations increase and face density-dependent reduced growth due to limited food, quagga mussels may have an advantage (Mills et al., 1996, 1999; Negley et al., 2003). In addition, *D. r. bugensis* may have higher energetic efficiency than *D. polymorpha*, resulting in higher growth rates over a wide range of food concentrations (Baldwin et al., 2002; Stoeckmann, 2003). To test several of these hypotheses, we conducted an experiment that allowed us to examine the effects of water temperature and intra- and interspecific competition on the survivorship and growth of *D. polymorpha* and *D. r. bugensis*.

Materials and methods

To determine the growth rates and survivorship of *D. polymorpha* and *D. r. bugensis* under different environmental conditions, we conducted a laboratory experiment at the field station of the Great Lakes Center, Buffalo State College, for 289 days, from November 18, 2008 to September 3, 2009. To ensure that experimental mussels had been similarly acclimated and experienced the same environmental and food conditions prior to the experiment, all test animals of both species were collected in October, 2008, from a navigational buoy installed 5 months earlier in Buffalo Harbor, Lake Erie, and were kept for 1 month under flow-through conditions with Lake Erie surface water.

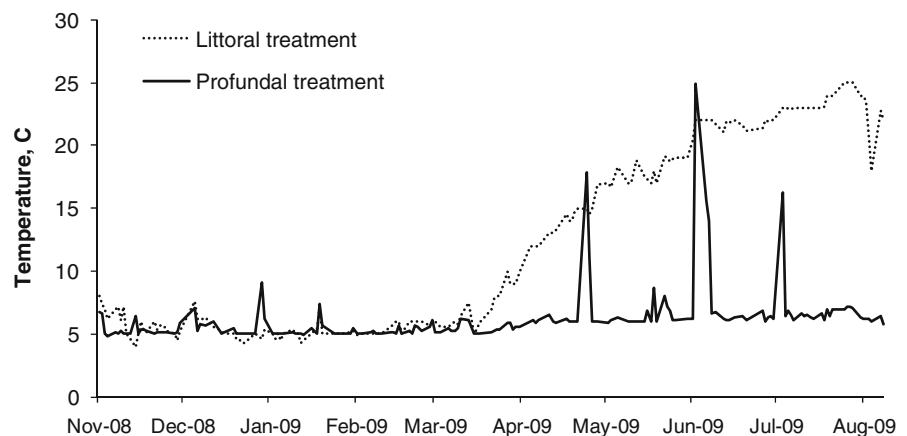
Although we tried to use zebra mussels and quagga mussels of the same size in this experiment, the average size of zebra and quagga mussels on the buoy differed. Zebra mussels were slightly smaller than quagga mussels. Zebra mussels used in the experiment ranged in size from 4.60 to 14.25 mm shell length, with an average of 7.16 ± 0.04 mm (mean \pm SE, $n = 1,350$). The quagga mussels that were used ranged in size from 3.50 to 11.52 mm, with an average of 7.66 ± 0.04 mm ($n = 1,350$). For each species, the mean size of mussels within each replicate tank across all treatments at the beginning of the experiment was not significantly different (zebra mussels: $P = 0.11$; quagga mussels: $P = 0.67$, one-way ANOVA). We used a full factorial design to test the effects of temperature regime (profundal zone vs. littoral zone) and intra- versus interspecific competition on survivorship and growth of both species. We

used three replicate tanks for each treatment. Each replicate tank of each treatment had 150 individual mussels, either all zebra mussels or all quagga mussels (intraspecific competition) or half zebra mussels and half quagga mussels (interspecific competition). Mussels were kept in flow-through tanks (exchange rate of 2.5 l/min) with 35 l of the Lake Erie water. Mussels were initially placed on a clean brick in the center of the tank, but were allowed to move.

We tested the survivorship and growth of mussels exposed to the thermal pattern in the littoral zone and the profundal zone. For the littoral zone regime, we used the natural surface temperature (range 4–25°C, average $11.9 \pm 0.6^\circ\text{C}$) of Lake Erie water. For the profundal zone treatment, Lake Erie surface water was chilled to about 6°C (range 5–8°C, average $6.2 \pm 0.6^\circ\text{C}$) in the main supply tank. Therefore, for two species, *D. polymorpha* and *D. r. bugensis*, we tested the effects of two different temperature regimes (profundal and littoral), and two types of competition (intraspecific only vs. interspecific competition), and each treatment type was replicated three times, for a total of 18 tanks.

Temperature was usually measured daily with a digital thermometer at approximately 11:00 am in each tank throughout the experiment. From the beginning of the experiment in November to March 25 (winter), water temperature was similar in both treatments (average for profundal treatments $5.32 \pm 0.08^\circ\text{C}$, littoral treatments $5.39 \pm 0.10^\circ\text{C}$, Fig. 1). After that date, the temperature diverged for the two treatments. From March to September (growing season) the temperature in the profundal

Fig. 1 Water temperature in the profundal and littoral zone treatments in experimental tanks from November 2008 to September 2009



treatments was similar, and averaged $6.72 \pm 0.27^\circ\text{C}$. Over that same time period, in the littoral treatments the temperature gradually increased to a maximum of 25°C , and averaged $16.38 \pm 0.64^\circ\text{C}$. There were several occasions when the chiller failed, and the temperature spiked in the profundal treatments, both during the winter (November–March) and during the growing season (March–September) (Fig. 1), but in most cases the temperature returned to treatment levels within 1 day. The water temperature for the profundal zone treatment and the littoral zone treatment did not differ during the winter ($P = 0.75$, $n = 80$, $U = 3.107$, Mann–Whitney test; Fig. 1). After March 25, the temperature between these two treatments diverged, and these two treatments were significantly different ($P < 0.001$, $n = 97$, $U = 899.5$, Mann–Whitney test, Fig. 1).

Because of silt accumulation in tanks during storms, tanks were periodically cleaned and the silt was siphoned out. Initially, we were concerned that food for the mussels may have been depleted as water moved through the pipe system at the lab. Therefore, during the winter mussels were supplemented with microalgal food: 100 ml of microalgal concentrate (Reed Mariculture Shellfish Diet, 2 billion cells per ml of *Isochrysis*, *Pavlova*, *Tetraselmis*, and *Thalassiosira*) was added to each tank once per week. However, given the flushing rate of the tanks, this increased food availability was seen by the mussels for several hours that 1 day only. Therefore, we discontinued this supplemental feeding in March. For the majority of the time during both the winter and growing season animals experienced natural seston concentrations, which likely did not differ substantially from that found in the field near the intake of the water system in Lake Erie.

Before the start of the experiment, all mussels were marked with a fluorescent stain, Calcein (following Moran, 2000), which binds to the calcium in the shell, marking the initial size of each mussel. Calcein marks were observed with a fluorescence dissecting microscope, at the end of the experiment, allowing us to assess both the initial and final size of all experimental animals. When analyzing the data, we found that the initial size of each mussel in the experiment was evident from a change in the shell sculpture and shape of the mussel, with all new growth substantially different than that prior to the experiment. This mark in the shell was produced

prior to the experiment when mussels were removed from the buoy and coincided with the Calcein mark, which facilitated measurements. If there was any question about the initial size of the shell, shells were checked again with the fluorescence microscope. All mussels were measured with digital calipers to the nearest 0.01 mm while observing them through a dissecting microscope at $\times 10$ magnification. To quantify survivorship and growth, all surviving and dead mussels were counted and their initial and final size measured in all replicate tanks of all treatments on March 25 and at the end of the experiments on September 3, 2009.

Analysis of variance (ANOVA) was used to test whether the initial size of test animals differed among treatments and whether there was size-dependent mortality among treatments during the winter and during the growing season. As mussels within a replicate tank are not independent, to test for differences in growth among treatments within species we used a nested analysis of covariance (ANCOVA) with initial size as the covariate. We did not have enough degrees of freedom to test both species together, so the effects of temperature and the effects of intra- versus interspecific competition on growth were tested within species. We used ANCOVA to test for differences in growth between zebra mussels and quagga mussels at different temperatures. We used contingency table analysis (G test) to test for differences in survivorship between species and among treatments.

Results

Effects of size on survivorship

Due to a limited number of degrees of freedom, each species was tested separately for overwinter mortality as well as size-specific mortality during the growing season. During the winter, survival depended on size for both species in both profundal zone and littoral zone treatments and for both intra- and interspecific competition. The initial size of animals that survived the winter was larger than that of the animals that died over the winter (Table 1, Fig. 2).

During the growing season, we found no evidence of size-selective mortality for *D. polymorpha* in any treatment, even though the profundal zone treatment

Table 1 Results of ANOVA to test for differences in the initial size of *D. polymorpha* and *D. r. bugensis* that survived the winter (those alive in March) versus those that suffered over winter mortality (had died by March 25)

Factor	SS	DF	MS	F	P
<i>D. polymorpha</i> , intraspecific competition					
Intercept	682.973	1	682.973	6552.351	≪0.001
Temperature	0.407	1	0.407	3.905	0.084
Dead or live	4.380	1	4.380	42.023	<0.001
Temperature × dead or live	0.175	1	0.175	1.681	0.231
Error	0.834	8	0.104		
<i>D. polymorpha</i> , interspecific competition					
Intercept	668.864	1	668.864	15972.87	≪0.001
Temperature	0.0200	1	0.0200	0.48	0.509
Dead or live	4.7251	1	4.7251	112.84	<0.001
Temperature × dead or live	0.0102	1	0.0102	0.24	0.635
Error	0.3350	8	0.0419		
<i>D. r. bugensis</i> , intraspecific competition					
Intercept	742.6133	1	742.613	85768.62	≪0.001
Temperature	0.0040	1	0.0040	0.47	0.514
Dead or live	4.0136	1	4.0136	463.56	<0.001
Temperature × dead or live	0.0341	1	0.0341	3.94	0.082
Error	0.0693	8	0.0087		
<i>D. r. bugensis</i> , interspecific competition					
Intercept	728.2092	1	728.209	11594.15	≪0.001
Temperature	0.0027	1	0.0027	0.04	0.841
Dead or live	3.7185	1	3.7185	59.20	<0.001
Temperature × dead or live	0.0147	1	0.0147	0.23	0.642
Error	0.5025	8	0.0628		

Mussels were grown with conspecifics (intraspecific competition) or with an equal number of heterospecifics (interspecific competition). For both types of competition for both species, mussels were grown under two different temperature regimes, one simulating the profundal zone and the other the littoral zone (Fig. 1). Bold values are significant at $P < 0.001$

remained at the same temperature as during the winter (Table 2, Fig. 2). For *D. r. bugensis*, the initial size of mussels that survived throughout the growing season was larger than that of those that died during the growing season in both temperature regimes, but only for those that faced interspecific competition with zebra mussels. Quagga mussels grown only with conspecifics showed no similar size-specific mortality during the growing season in either temperature treatment (Table 2, Fig. 2).

Effects of temperature regime and competition on survivorship

In the profundal zone treatment, quagga mussels had higher survivorship than zebra mussels during the winter ($G = 261.6$, $df = 1$, $P \ll 0.001$) and during the growing season ($G = 226.6$, $df = 1$, $P \ll 0.001$) (Fig. 3). Similarly, in the littoral zone treatment quagga mussels had higher survivorship than zebra mussels over the winter ($G = 13.6$, $df = 1$, $P < 0.01$)

and during the growing season ($G = 118.0$, $df = 1$, $P \ll 0.001$).

For zebra mussels during winter survivorship differed between temperature regime treatments and between inter- versus intraspecific competition treatments (Fig. 3). Zebra mussels had higher survivorship in the profundal zone treatment than in the littoral zone treatment ($G = 17.62$, $df = 1$, $P < 0.005$). In just the profundal zone treatment zebra mussel survivorship was greater when they were competing against quagga mussels than an equal number of conspecifics in both the winter and during the growing season (Fig. 2; $G = 4.5$, $df = 1$, $P < 0.05$). For quagga mussels, during the winter there was no significant difference in survivorship between the two temperature regime treatments ($G = 1.8$, $df = 1$, $P > 0.05$). For quagga mussels, survivorship was not affected by inter- versus intraspecific competition ($G = 2.3$, $df = 1$, $P > 0.05$).

During the growing season, the survivorship of zebra mussels differed between the two temperature

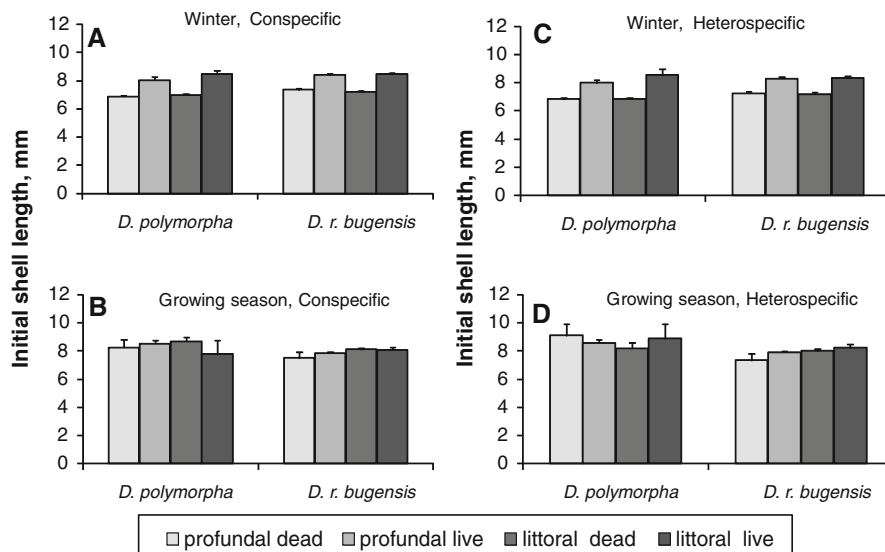


Fig. 2 Average initial length of *Dreissena polymorpha* and *Dreissena rostriformis bugensis* that died or survived in the winter, and those that survived until the end of the experiment, versus those that survived the winter, but died during the growing season. Data are mean initial shell length (mm) \pm standard error. **A** Mean initial shell length of mussels

during winter kept with conspecifics only. **B** Mean initial shell length during growing season with conspecific competition. **C** Mean initial shell length during winter with heterospecific competition. **D** Mean initial shell length during growing season with heterospecific competition

regime treatments; survival was greater in the profundal zone treatment than in the littoral zone treatment ($G = 129.8$, $df = 1$, $P \ll 0.001$) (Fig. 3). As during the winter, during the growing season zebra mussels had higher survivorship when competing with quagga mussels than when competing with an equal number of conspecifics ($G = 9.05$, $df = 1$, $P < 0.05$). During the growing season, quagga mussels had greater survivorship in the profundal zone treatment than the littoral zone treatment ($G = 370.0$, $df = 1$, $P \ll 0.001$). As during the winter, survivorship of quagga mussels during the summer was not affected by interspecific competition as compared to intraspecific competition ($G = 1.79$, $df = 1$, $P > 0.05$).

Effects of temperature regime and competition on growth

Neither species grew during the winter in any treatment. In contrast, during the growing season in the littoral zone treatments zebra mussels grew an average of 46% and quagga mussels grew an average of 106%. During the growing season in the profundal zone treatments zebra mussels grew an average of

27%, and quagga mussels grew an average of 77%. During the growing season quagga mussel growth was both size- and temperature dependent. Overall quagga mussels grew more in the warmer littoral treatment than in the profundal treatment (Fig. 4, Table 3). For quagga mussels there was no effect of interspecific competition on growth (Table 3). Zebra mussels also grew faster in the littoral zone treatment than in the profundal zone treatment. The significant three-way interaction between size and temperature and type of competition on growth (Table 3) indicates that the effects of these three factors are complex and not consistent among treatments. Although mean shell growth in the profundal zone treatment was the same between the two competition treatments, the mean growth of zebra mussels in the littoral zone treatment was lower for those exposed to interspecific competition than those for intraspecific competition. The low survivorship of zebra mussels in this treatment and high variance among replicates greatly reduced our statistical power, making it difficult to draw conclusions from our statistical tests. Further experimentation is needed to disentangle the relationships among these three variables on zebra mussel growth.

Table 2 Results of ANOVA to test for differences in the initial size of *Dreissena polymorpha* and *D. r. bugensis* that survived during the growing season, versus those that died during the growing season (were alive in March, but had died by September)

Factor	SS	DF	MS	F	P
<i>D. polymorpha</i> , intraspecific competition					
Intercept	757.2765	1	757.2765	526.6806	≪0.001
Temperature	0.5849	1	0.5849	0.4068	0.544
Dead or live	0.0641	1	0.0641	0.0446	0.839
Temperature × dead or live	0.3618	1	0.3618	0.2516	0.631
Error	10.0648	7	1.4378		
<i>D. polymorpha</i> , interspecific competition					
Intercept	740.6809	1	740.681	545.8503	≪0.001
Temperature	0.0322	1	0.0322	0.0237	0.883
Dead or live	0.4455	1	0.4455	0.3283	0.588
Temperature × dead or live	2.1546	1	2.1546	1.5879	0.254
Error	8.1416	6	1.3569		
<i>D. r. bugensis</i> , intraspecific competition					
Intercept	775.5384	1	775.538	3396.643	≪0.001
Temperature	0.4921	1	0.4921	2.155	0.180
Dead or live	0.0752	1	0.0752	0.329	0.582
Temperature × dead or live	0.6960	1	0.6960	3.048	0.119
Error	1.8266	8	0.2283		
<i>D. r. bugensis</i> , interspecific competition					
Intercept	666.3388	1	666.339	5900.907	≪0.001
Temperature	0.6381	1	0.6381	5.651	0.049
Dead or live	0.3634	1	0.3634	3.218	0.116
Temperature × dead or live	0.2387	1	0.2387	2.114	0.189
Error	0.7904	7	0.1129		

Mussels were grown with conspecifics (intraspecific competition) or with an equal number of heterospecifics (interspecific competition). For both types of competition for both species, mussels were grown under two different temperature regimes, one simulating the profundal zone and the other the littoral zone. Bold value is significant at $P < 0.05$

Discussion

By most measures, quagga mussels outperformed zebra mussels under all conditions in our experiments. Quagga mussels had higher survivorship and grew more than zebra mussels under environmental conditions that mimicked the thermal environment of the profundal zone, where they were expected to perform well. Surprisingly, they also outperformed zebra mussels in terms of survivorship and growth in the thermal environment reflecting the littoral zone of Lake Erie. This result supports the notion that quagga mussels have a greater energetic efficiency than zebra mussels (Stoeckmann, 2003), and this advantage is not temperature dependent.

For both species, we found that the size of the mussel entering the winter season was critical for survivorship (Fig. 2, Tables 1, 2). Larger mussels had a higher probability of surviving the winter across all

treatments. The same size-selective survivorship was not seen for the growing season for zebra mussels in either competition treatment or for quagga mussels grown only with conspecifics. However, when quagga mussels were grown with zebra mussels rather than an equal number of conspecifics, smaller quagga mussels died disproportionately, even though the quagga mussels on the whole were larger than the zebra mussels.

Although quagga mussels outperformed zebra mussels in general, zebra mussel survivorship was greater at low temperatures when they were grown with quagga mussels rather than an equal number of conspecifics (Fig. 3). It was in these same treatments that smaller quagga mussels were at a disadvantage relative to those grown only with conspecifics. These intriguing results suggest that there may be some local interactions between zebra mussels and quagga mussels that affect their performance. Due to the very

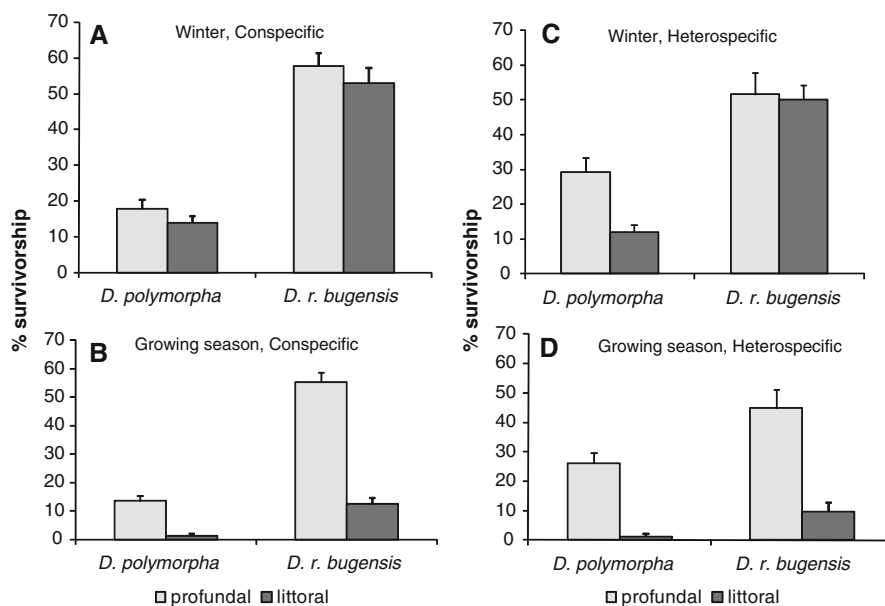


Fig. 3 The survival of *Dreissena polymorpha* and *Dreissena rostriformis bugensis* under different water temperature treatments conspecific or heterospecific competition. Data are mean percentage (\pm standard error) of individuals that survived per replicate tank. All replicate tanks started with 150 individuals of one species in the conspecific competition treatments, and 75 of each species in the heterospecific competition treatments.

Temperature treatments: profundal zone (mean $6.2 \pm 0.1^\circ\text{C}$) and littoral zone (mean $11.9 \pm 0.6^\circ\text{C}$). **A** Survivorship during winter with conspecifics only. **B** Survivorship during growing season with conspecifics only. **C** Survivorship during winter with heterospecific competition. **D** Survivorship during growing season with heterospecific competition

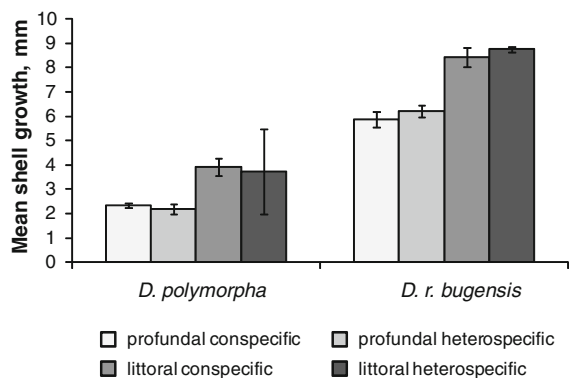


Fig. 4 Growth of *Dreissena polymorpha* and *D. r. bugensis* in different treatments. Data are mean (\pm standard error) of growth (difference between initial and final shell length) of mussels from different temperature regimes for 289 days, with either con- or heterospecific competition

low survivorship of zebra mussels in warm temperatures, these experiments need replication to verify the strength of these interactions. Further experimentation is clearly needed to determine the nature of both intra- and interspecific interactions.

For both species, in both intra- and interspecific competition treatments, there was a survivorship/growth tradeoff (Stearns, 1992) in the littoral zone treatment. Many studies have found an increased growth rate in zebra mussels with warmer temperatures (reviewed in Karatayev et al., 2006). We found that both zebra mussels and quagga mussels had higher growth in the warmer water, but lower survival. For quagga mussels, overall survivorship was much higher than that of zebra mussels, and this difference was consistent among treatments (Table 1, Fig. 3). This difference in survivorship was especially pronounced during the winter, when both the littoral zone treatment and the profundal zone treatment maintained cold temperatures.

For zebra mussels, survivorship in our experiments was far lower than has been seen for mussels followed in the field in lakes colonized by zebra mussels only. Karatayev (1983, 1984) found that *D. polymorpha* of a similar size as the mussels in our experiments and kept in cages in Lake Lukomskoe had an 8% annual mortality rate. Unfortunately, there are no data on the survivorship of quagga mussel in

Table 3 Results of ANCOVA to test for differences in growth of *Dreissena rostriformis bugensis* and *Dreissena polymorpha* among treatments during the growing season

Treatment	DF	F value	P value
<i>D. r. bugensis</i>			
Temperature	8	64.6442	<0.0001
Competition	8	1.256	0.2949
Size	394	4.7717	0.0295
Temperature × competition	8	0.0058	0.9414
Temperature × size	394	5.0588	0.0251
Competition × size	394	0.0012	0.9724
Temperature × competition × size	394	0.8972	0.3441
<i>D. polymorpha</i>			
Temperature	7	33.7419	0.0007
Competition	7	0.1661	0.6958
Size	108	0.9527	0.3312
Temperature × competition	7	0.5047	0.5004
Temperature × size	108	7.4489	0.0074
Competition × size	108	0.4404	0.5084
Temperature × competition × size	108	5.99	0.016

Treatments included two temperature regimes, littoral or profundal zone, and whether the mussels were grown only with conspecifics (intraspecific competition) or with an equal number of heterospecifics (interspecific competition). Initial size of mussels was used as the covariate

Bold values are significant at $P < 0.05$

the field that can be used to compare with our data. Our data are consistent with survivorship data from another laboratory study that examined the effects of low seston concentration on both zebra mussels and quagga mussels (Baldwin et al., 2002). Baldwin et al. (2002) found a 5–10% mortality rate for zebra mussels and a 0–10% mortality rate for quagga mussels over 38–43 day laboratory experiments using water from Lake Onondaga. Their observed mortality rates increased to 35% when animals were provided with low food concentrations. They also found a much higher mortality rate for mussels fed Oneida Lake seston (47% for quagga mussels and 79% for zebra mussels, over 52 days) (Baldwin et al., 2002). Thus, the mortality rates found by Baldwin et al. (2002) in short-term experiments were similar to or higher than those seen in our experiments. Low seston concentrations in the Lake Erie water used in our experiment could be responsible for the higher rates of mortality in zebra mussels than quagga mussels. Such differences could reflect differences in energetic efficiency of

these two species (Baldwin et al., 2002), and may contribute to the decline of zebra mussels and expansion of quagga mussels currently seen in Lake Erie.

Our results caution against the use of short-term experiments for assessing survivorship and growth. Also, because different treatments produced different results depending on the season, we would have drawn different conclusions if experiments were conducted in the winter versus the summer. None of the experimental animals of either species grew from November to March. Animals only grew from March through the end of the experiment in September.

Contrary to predictions, zebra mussels grew in the profundal zone temperature regime during the growing season. Previous work on *D. polymorpha* has concluded that shell growth does not occur at temperatures below 10°C (Morton, 1969a, b; Alimov, 1974; Karatayev, 1983; Mackie, 1991; Jantz & Neumann, 1992). However, these conclusions were based on field observations during the winter, when low temperatures are coincident with low phytoplankton abundance due to both the cold temperatures and light limitation. Our data support the hypothesis that it is the lack of food rather than low temperatures per se that limits the growth of both dreissenid species during winter.

Our data also contrast with a study by MacIsaac (1994). MacIsaac (1994) found that the growth and survival rates of quagga and zebra mussels grown in the field in Lake Erie for 56 days were very similar. In his laboratory experiments which lasted 34 days, *D. polymorpha* grew faster than *D. r. bugensis*, and small zebra mussels survived longer than quagga mussels. Additional experimental studies are needed to resolve the differences in findings between our study and that of MacIsaac. We especially need additional long-term studies that control for both food quality and quantity as well as temperature.

Although in our experiments, the growth of *D. polymorpha* was substantially less than that reported for field growth rates in other studies, the growth rate of quagga mussels was similar to those reported for zebra mussels in other field studies (Table 4). The low growth rates of *D. polymorpha* in our study could be due to low seston concentration or low food quality in the Lake Erie water used in this experiment, as it is well known that both food quantity and quality are crucial factors affecting

Table 4 Shell growth of *Dreissena polymorpha* and *D. r. bugensis* over their second growing season (1-year-old mussels) in different water bodies

Waterbodies	Initial length (mm)	Final length (mm)	Growth (mm)	Mean temperature (°C)	Reference
<i>Dreissena polymorpha</i>					
Uchinskoe Reservoir, Russia					
1967	8	21.2 ± 0.29	13.2	17.0	Lvova (1980)
1968	8	19.5 ± 0.27	11.5	16.4	Lvova (1980)
1969	8	16.8 ± 0.18	8.8	n.r.	Lvova (1980)
Lukomskoe Lake, Belarus	8.9 ± 0.1	12.4 ± 0.1	3.5	16.0	Karatayev (1983)
Mikolajskie Lake, Poland	8	16.2	8.2	n.r.	Stanczykowska & Lewandowski (1995)
Naroch Lake, Belarus	8.30 ± 1.60	12.35 ± 1.35	4.05	19.0	Burlakova (1998)
Myastro Lake, Belarus	7.42 ± 1.15	12.92 ± 1.15	5.5	19.8	Burlakova (1998)
Svisloch River, Belarus: caged	7.90 ± 1.09	15.07 ± 1.09	7.17	18.7	Burlakova (1998)
Uncaged	7.65 ± 1.51	18.30 ± 1.95	10.65	18.7	Burlakova (1998)
Lake Constance, Germany	8	15	7	14.3	Walz (1978)
Lake Wawasee, USA	8.6 ± 0.2	14.1 ± 0.5	5.5	n.r.	Garton & Johnson (2000)
Average			7.73		
Lake Erie, USA					
Profundal zone treatment	8.55 ± 0.17	10.80 ± 0.19	2.25 ± 0.07	6.7 ± 0.3	Current study
Littoral zone treatment	8.19 ± 0.73	12.30 ± 0.65	4.11 ± 0.54	16.4 ± 0.6	Current study
<i>Dreissena r. bugensis</i>					
Lake Erie, USA					
Profundal zone treatment	7.89 ± 0.06	13.90 ± 0.09	6.00 ± 1.41	6.7 ± 0.3	Current study
Littoral zone treatment	8.134 ± 0.13	16.57 ± 0.24	8.44 ± 0.23	16.4 ± 0.6	Current study

Except for data from the current study and uncaged mussels kept on rocks in the Svisloch River, Belarus, growth was followed for mussels kept in cages in waterbodies under natural conditions

n. r. not reported

zebra mussel growth rates (reviewed in Karatayev et al., 2006). The very low survivorship for zebra mussels in our experiments was also unexpected. Further experiments are needed to determine if the experimental conditions per se favored quagga mussels over zebra mussels, especially the accumulation of fine sediment in the tanks.

An intriguing result of our experiment was the performance of zebra mussels and quagga mussels when grown together. Zebra mussels survived better in the presence of quagga mussels at low temperatures than when with an equal number of conspecifics, suggesting that intraspecific competition among zebra mussels is important. Although there was no growth effect on quagga mussels due to competition with zebra mussels, there was an increase in size-selective mortality. These effects of competition were

surprising given that the mussels were kept at very low densities, far lower than they are found in the field. The direct interactions between these two species need to be tested. Differences in growth and survivorship can both have large impacts on the demographics of each species. The coexistence of zebra mussels and quagga mussels or the displacement of one species by the other may result from environmentally driven differences in performance, and how those features affect the population dynamics of each species in these heterogeneous environments.

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