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Zebra mussels anchor byssal threads faster and tighter than quagga mussels in flow

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SUMMARY

While the invasive zebra mussel *Dreissena polymorpha* has rapidly spread throughout the Great Lakes and inland waterways, it is being displaced by the quagga mussel *Dreissena bugensis* in shallow water habitats. However, zebra mussels remain dominant in areas with higher water velocity. We hypothesized that the persistence of zebra over quagga mussels in habitats with higher water velocity might result from greater rate and strength of byssal thread attachment. We examined whether zebra mussels relative to quagga mussels have: (1) higher byssal thread synthesis rate, (2) lower dislodgment in flow and (3) greater mechanical force required for detachment from substrate. Specifically, we examined byssal thread synthesis rate and dislodgment of both species in response to water velocities of 0, 50, 100 and 180 cm s^{-1}. Byssal thread synthesis rate was significantly higher for zebra than for quagga mussels at all velocities. Dislodgment from the substrate increased for both species with increasing velocity but was significantly lower for zebra than for quagga mussels. We also tested the mechanical force to detach mussels after short (32 h) and long (two and three months) periods of attachment on hard substrate. Detachment force was significantly higher for zebra than for quagga mussels only after short-term attachment. Higher byssal thread synthesis rate in zebra mussels was a likely factor that minimized their dislodgment in flow and increased short-term attachment strength. Differences in byssal thread synthesis rate between the two species might partly account for the ability of zebra mussels to maintain dominance over quagga mussels in habitats with high velocities.

Key words: adhesion, biological invasions, dislodgment, *Dreissena*, functional morphology, Great Lakes, hydrodynamics, niche partitioning.

INTRODUCTION

Zebra (*Dreissena polymorpha* Pallas) and quagga mussels (*Dreissena bugensis* Andrusov) are among the most costly and destructive invaders of North American freshwater ecosystems (Pimentel et al., 2005). While quagga mussels have expanded their range more slowly, they are gradually displacing existing zebra mussel populations (Jarvis et al., 2000; Mills et al., 1996; Mills et al., 1999; Stoeckmann, 2003) and are likely to pose greater ecological threats with time. Zebra and quagga mussels originated from the Black and Caspian Sea basin (Gelembiuk et al., 2006; May et al., 2006; Spidle et al., 1994) where the distribution of each species largely depended on differences in salinity tolerance (Mills et al., 1996). Thus, their recent invasions into freshwater habitats might be exposing the two species to novel evolutionary forces and challenges due to their new competitive interactions (Lee, 2002). Studies that examine functional differences between zebra and quagga mussels have not yet fully explored the dynamics of such competition between the two species and limits to their range expansions.

While quagga mussels have successfully colonized both hard and soft sediment substrates (Claxton et al., 1998; Dermott and Munawar, 1993) and are displacing and outnumbering zebra mussels in these habitats, zebra mussels generally remain dominant in habitats with high water velocity. Water velocity might be an environmental variable that affects niche partitioning between the two species. For example, zebra mussels appear to numerically dominate over quagga mussels in the Genesee and Hudson Rivers in NY, USA. Mainstream velocities vary with season and location but tend to be higher in the Genesee (~10–80 cm s^{-1}; http://nwis.waterdata.usgs.gov/nwis/measurements/?site_no=04231600&agency_cd=USGS) and Hudson Rivers (~10–130 cm s^{-1}) (Geyer and Chant, 2006) than in Lake Ontario, North America, where zebra and quagga mussels co-occur (e.g. ~8–20 cm s^{-1} in Oswego Harbor, NY, USA) (Csanady, 1974). These rivers are likely to be similarly susceptible to introductions by both zebra and quagga mussels, because they directly connect or are in close proximity to Lake Ontario where the two species have co-existed since the early 1990s (May and Marsden, 1992). However, only zebra mussels have contributed to a major part of the Hudson River biomass since 1992 (Strayer, 2006).

Byssal thread attachment might be a key functional trait that partly accounts for differences in colonization patterns between the two species in habitats with high velocities. Byssal threads are protein strands that zebra and quagga mussels synthesize in order to secure themselves to the substratum. The byssal threads are bundled together at a root within the shells but branch out like a broom from the ventral side and attach to hard surfaces with adhesive plaques (Eckroat and Steele, 1993). Factors such as byssal thread number and thickness (Bell and Gosline, 1997) and plaque adhesion (Dormon et al., 1997) can affect the attachment capacity of mussels. Differences in both byssal thread number and thickness have been found between two co-existing marine mussels, *Mytilus californianus* and *Mytilus trossulus*, and are thought to contribute to differences in their colonization of wave-exposed shores (Bell and Gosline, 1997).

Zebra and quagga mussel byssal thread attachment has been examined in the context of their removal from different materials (Ackerman et al., 1996; Dormon et al., 1997). However, studies that specifically compare attachment capacity in order to gain insights into differences in function and distribution between the two species are rare. Differences in byssal thread synthesis rate and strength of attachment could be important for colonization and

persistence of mussels in habitats that differ in hydrodynamic flow or substrate type.

The objective of the present study was to examine byssal thread attachment of zebra and quagga mussels exposed to a range of water velocities that are present in the wild (0, 50, 100 and 180 cm s^{-1}). We hypothesized that zebra mussels would have greater byssal thread synthesis rate and more secure attachment relative to quagga mussels based on the dominance of zebra mussels in habitats with high water velocity. Thus, we examined whether zebra mussels have: (1) higher byssal thread synthesis rate, (2) lower dislodgment in the face of fluid flow and (3) greater mechanical force required for detachment from hard substrate, relative to quagga mussels. We examined byssal thread synthesis and mussel dislodgment of both species in the laboratory under calm and flowing water that simulated field velocities. We also measured the mechanical detachment force of the byssal threads of both species under calm conditions.

MATERIALS AND METHODS

Population sampling

Zebra and quagga mussels were collected during the summers of 2007 and 2008 from several submerged poles made of polyvinyl chloride (PVC) at the University of Wisconsin Great Lakes WATER Institute, stationed on the shore of Lake Michigan, Milwaukee, WI, USA. We randomly sampled and removed mussels from the PVC poles by cutting their byssal threads with a sharp knife. Mussels were wrapped in damp paper towels, sealed in plastic bags and placed on ice in order to lower their metabolic rate and increase the likelihood of their survival during transport. In the laboratory they were housed in aquaria at 18–20°C and fed a commercial shellfish diet (*Isochrysis* sp., *Pavlova* sp., *Tetraselmis* sp., *Thalassiosira weissflogii*) from Reeds Mariculture (Campbell, CA, USA). A similar diet has also been used to maintain brood stocks of zebra mussels (Vanderploeg et al., 1996). Throughout this study we used water from Lake Michigan maintained at 18–20°C.

Byssal thread synthesis rate in calm and flowing water

We examined whether zebra and quagga mussels differ in the number of byssal threads synthesized during a 32-hour period under calm (velocity of 0 cm s^{-1}) and flowing water conditions (velocities of 50, 100 or 180 cm s^{-1}). For all treatments we enclosed mussels in rectangular channels that provided a hard surface for attachment. The channels consisted of four clear acrylic plates that could be disassembled in order to analyze the threads of each attached mussel. We used clear acrylic plates because mussels will recruit onto them in the field (Marsden and Lansky, 2000) and mussels are visible through the channel walls. Mussels for this experiment were collected on two occasions, in July and August of 2007.

For both calm and flowing water conditions, we placed 10–15 mussels, 5–10 mm in length, into rectangular channels (~5×5×30 cm) and submerged them in an aquarium with gentle aeration. An individual channel contained either all zebra or all quagga mussels. To test mussels in flow, we first allowed them to attach to the plates of the channels for 24 h in no flow. Meshed polyester fabric temporarily attached with a rubber band at each end of the channels prevented the mussels from escaping. After the initial 24-hour attachment period, we exposed the mussels to each of the four velocities for 8 h. The channels that contained mussels for the calm water treatment (0 cm s^{-1}) remained in the aquarium for this 8-hour exposure period. Channels with attached mussels for all other treatments were transferred to a recirculating flume (Fig. 1), which generated velocities of 50, 100 or 180 cm s^{-1} as measured with a Swoffer model 2100 velocity meter from Swoffer Instruments (Seattle, WA, USA). Water within the flume was pumped from a filled trough (Fig. 1A), through a pipe (Fig. 1B), into a long main channel (~5×5×100 cm) (Fig. 1C) and back into the trough. Each channel with attached mussels (Fig. 1D) was connected to the end of the main channel (Fig. 1C) where turbulence generated at the pipe-to-channel transition was minimized. We selected velocities of 50 and 100 cm s^{-1} because they are within the typical range of mainstream values in the field where zebra mussels have been found, either solely or in greater numbers than quagga mussels, whereas a velocity of 180 cm s^{-1} generally exceeds these field values [e.g. Hudson River (Geyer and Chant, 2006)].

Following the 8-hour exposure period, we disassembled the section of the channel that contained the mussels into four separate plates. We placed a drop of Methylene Blue stain on the byssal threads of the attached mussels, carefully removed the mussels from the plate with a razor blade and froze all of the mussels. We then thawed and dissected each mussel, removed the bundle of byssal threads and counted the total number produced during the entire 32-hour attachment period. Once a mussel is removed from its substrate, it naturally ejects its existing bundle of byssal threads and begins synthesizing new byssal threads. Thus, we assumed that the byssal threads that we counted for each mussel were produced during the 32-hour period of this experiment. At each velocity, we ran 4–10 replicates for each species (10–15 mussels per replicate). Different mussels were used for each treatment and each replicate. We randomized the order in which we tested the two species among the four velocity treatments. We obtained data on a total of 36–52 mussels for each species at each velocity. We were unable to use data from all mussels from each replicate, because some mussels did not reattach to the acrylic plates during the initial 24-hour attachment period.

We also determined the effect of time on byssal thread synthesis rate by examining zebra and quagga mussels during a longer 1-week period, under calm conditions (0 cm s^{-1}). We submerged individual channels (~7×7×30 cm) containing either 10–15 zebra or quagga mussels, 5–10 mm in length, in an aquarium with gentle aeration. From daily observations, we determined the total number of days each mussel was attached to the plates of the channel at the same location. After the 1-week period, we processed the mussels

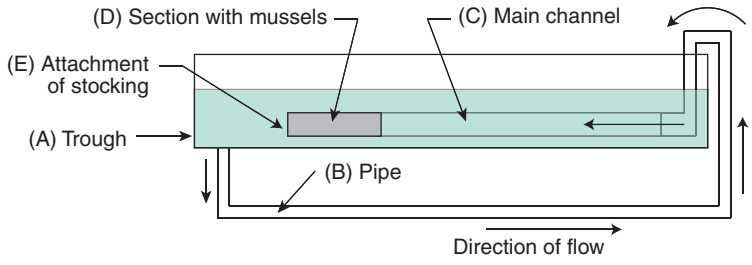

Fig. 1. Illustration of recirculating flume used to test byssal thread synthesis rate and dislodgment of mussels in flow. Water flowed from a filled trough (A), though a pipe (B), into the main channel (C), through the section of the channel that contained the attached mussels (D) and back into the trough. Any mussels dislodged in flow were collected in a nylon stocking attached to the end of the channel (E).

and byssal threads as described above. We determined the number of byssal threads synthesized per total days that a mussel was attached at a given location. There were seven replicates (10–15 mussels per replicate) for each species from which we obtained data on a total of 46 zebra and 38 quagga mussels.

Mussel dislodgment in flowing water

In the flume experiment above, we also determined whether there were differences in the percentage dislodgment of zebra *versus* quagga mussels in response to flowing water conditions. We collected mussels that dislodged in flow in a nylon stocking attached to the end of the channel (Fig. 1E), and recorded the velocity at which dislodgment of each mussel occurred. The areas of the mussel shell perpendicular (i.e. anterior–posterior, lateral views) and parallel (i.e. dorsal–ventral view) to the direction of flow are known factors that affect the magnitude of drag and lift forces, respectively. Both forces could contribute to mussel dislodgment in flow. Therefore, we used a Dragonfly IEEE-1394 digital camera from Point Grey Research (Vancouver, BC, Canada) and IMAQ software for LabVIEW (National Instruments, 2003; Austin, TX, USA) to determine the areas of the three shell views. We were able to easily determine the area parallel to flow for all mussels as the dorsal–ventral shell view, which is used to calculate lift force. However, we were unable to determine the area perpendicular to flow that is used to calculate drag force for all mussels, because their orientation in flow was often composed of different combinations of the anterior–posterior and lateral shell views.

Mechanical detachment force

We determined the force required to mechanically detach zebra and quagga mussels from hard substrate after short-term (32-hour) and long-term (two- and three-month) attachment periods under calm water conditions. We used these different time periods in order to determine the effect of time on detachment force, which might depend on byssal thread synthesis rate. For mussels attached for a 32-hour period, we determined the detachment force (i.e. tested byssal threads) in pure tension and in shear. In general, the byssal threads are loaded in tension and shear when a mussel in flow experiences lift and drag forces, respectively. We placed zebra or quagga mussels, 10–15 each and 5–10 mm in length, in individual acrylic channels (~5×5×30 cm). These mussels were collected in June 2008. We then submerged the channels in an aerated aquarium

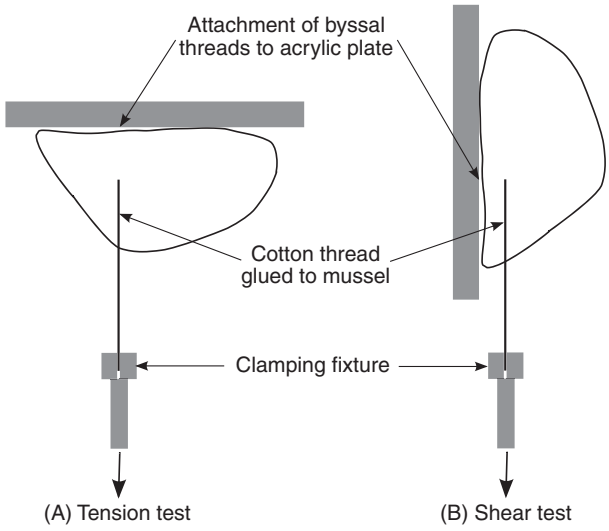

Fig. 2. Orientation of mussels for testing their mechanical detachment force in (A) tension and (B) shear. Testing was conducted using a dynamic mechanical thermal analyzer (DMTA V). Mussels were attached on their ventral side to an acrylic plate by their byssal threads. A cotton thread was glued at one end to the shell of the mussel and clamped at the other end in a fixture of the DMTA V.

for 32 h, the same time duration used in the flume experiment described above. With this short attachment period we expected the detachment forces to be very low. Therefore, we used a Rheometrics dynamic mechanical thermal analyzer (DMTA V; Piscataway, NJ, USA), specialized for low forces, to test detachment force. We used Krazy Glue (Columbus, OH, USA) to carefully attach a cotton sewing thread to one shell of each mussel. For testing detachment force in tension, the cotton thread was glued just dorsal to the location where the byssal threads exit the ventral side of the shell (Fig. 2A). We then inverted the acrylic plate with attached mussels and placed it on a stainless steel plate that was mounted to the DMTA V (Fig. 3). The inverted mussels on the acrylic plate were situated over a hole in the steel plate. The cotton thread attached to each mussel hung down through the hole and was clamped taut but without preload in a fixture of the DMTA V. Movement of the

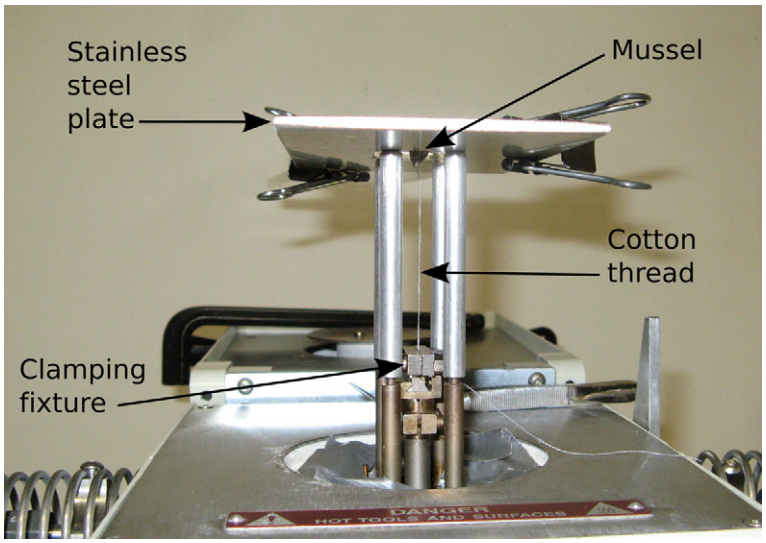

Fig. 3. Apparatus for testing the mechanical detachment force of mussels in tension and shear after short-term attachment (32 h) with a dynamic mechanical thermal analyzer (DMTA V). A mussel attached to an acrylic plate protruded through a hole in a supporting steel plate that was mounted to the DMTA V. A cotton thread was glued at one end to the mussel shell and clamped at the other end in a fixture of the DMTA V. Downward movement of the fixture placed a load on the byssal threads until detachment of the mussel occurred. The mussel shown was tested in tension but the same setup was also used to test mussels in shear.

fixture downward at a displacement rate of 0.25 mm s^{-1} placed a tensile load on the byssal threads until detachment of the mussel occurred. To examine detachment force in shear, we glued the cotton thread along one shell of each mussel, close to the hinge and clamped the acrylic plate with the attached mussel perpendicular to the stainless steel plate attached to the DMTA V (Fig. 2B). The hinge of the mussel shell was directed downward and the cotton thread was clamped in the fixture of the DMTA V. Five replicates of zebra (N=39 total) and eight replicates of quagga mussels (N=38 total) (10–15 mussels per replicate) were tested in tension, and four replicates of zebra (N=26 total) and nine replicates of quagga mussels (N=35 total) (10–15 mussels per replicate) were tested in shear.

For mussels attached for two- and three-month periods, we tested detachment force of their byssal threads in tension only. Immediately after collection, we placed 30 mussels of each species, 10–20 mm in length, in each of two 20-l aquaria that were lined with 10 PVC plates and gently aerated under calm water conditions. In one aquarium, mussels were allowed to attach for up to two months and in the other aquarium they were allowed to attach for up to three months. These mussels were collected in August 2007. Mussels were fed the commercial shellfish diet (*Isochrysis* sp., *Pavlova* sp., *Tetraselmis* sp., *Thalassiosira weissflogii*) from Reeds Mariculture (Campbell). Water within the two aquaria was changed once every two weeks. Mussel recruitment onto PVC in the field is close to, although slightly higher than, acrylic (Marsden and Lansky, 2000). We used PVC because it is the same material that we and other investigators used to collect mussels in the field, allowing us to compare our detachment forces measured in the laboratory with field data collected by others (Ackerman et al., 1996; Dormon et al., 1997). Although both Ackerman et al. and Dormon et al. examined byssal thread attachment of both zebra and quagga mussels, they did not provide a thorough comparison between the two species because it was not their study objective.

After the two- and three-month periods, we removed the PVC plates from the aquaria for mechanical testing of byssal threads and determining detachment forces of attached mussels. To test the byssal threads and obtain detachment forces, we used a stainless steel device with adjustable brackets that slid under the ventral side of the mussel shells (Fig. 4). We used slightly larger mussels for this experiment, because it was easier to position the brackets underneath the mussel without breaking any byssal threads prior to testing. The device was attached to a 22 N load cell of an Instron test machine (Norwood, MA, USA) that lifted the mussel shell up, pulling it away from the plate while applying a tensile load to the byssal threads at a displacement rate of 0.25 mm s^{-1}. Clamps bolted to the base of the test machine secured the plates, holding them stationary during each test. We acquired the force applied to the byssal threads and corresponding displacement until mussel detachment occurred. Detachment force was defined as the peak force attained prior to full detachment of the mussel from the substrate. We obtained data on a total of 19 zebra and 15 quagga mussels, and 16 zebra and 14 quagga mussels after two and three months of attachment, respectively. Not all mussels were testable, because they often packed closely together, making it difficult to slide the brackets of our test device around their shells.

We predicted that the detachment force of mussels for the 32-hour and two- and three-month attachment periods might depend on the number of byssal threads that they synthesized. For mussels tested in tension only for all three attachment periods, we determined the number of byssal threads of each mussel from dissections as described previously in the flume study. From the byssal thread bundles extracted from the mussels, we determined whether the mode of detachment failure occurred at the root, within the byssal threads or at the adhesive plaques.

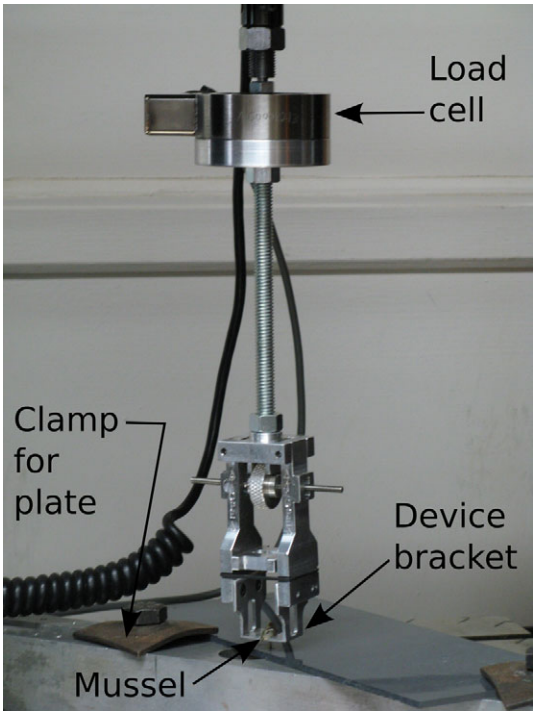

Fig. 4. Apparatus for testing the mechanical detachment force of mussels after long-term attachment (two and three months) with an Instron test machine. Mussels were attached to PVC plates that were clamped stationary to the base of the test machine. Adjustable brackets of a test device slid between an attached mussel and a PVC plate. Upward movement of the test device loaded the byssal threads in tension. Force as measured by the load cell and corresponding displacement were recorded until detachment of the mussel occurred.

Data analysis

We tested for differences in byssal thread number between zebra and quagga mussels with two separate generalized linear models, using the statistical package R (R Development Core Team, 2008). In the first model, we used data from our flume experiment to determine the effects of species, water velocity, replicate and number of days between collection and testing of mussels in the laboratory on byssal thread number. Thus, the full maximum likelihood model for the response variable, byssal thread number (τ), was:

$$\tau = e^{(\beta_0+\beta_1 x_s+\beta_2 \mathbf{x}_v+\beta_3 x_r+\beta_4 x_c)}, \quad (1)$$

with independent factors, species (x_s), velocity ($\mathbf{x}_v$), replicate (x_r) and number of days between collection and testing of mussels in the laboratory (x_c) and regression estimates of β_0–β_4. We were most interested in the effect of species and velocity on byssal thread number. In the second model, we used data on mussels that were in calm water conditions (0 cm s^{-1}) for a 1-week period to determine the effect of species, replicate, number of days between collection and testing of mussels in the laboratory on byssal thread synthesis rate and number of days that a mussel was attached at a given location. The full maximum likelihood model for the response variable, byssal thread synthesis rate as threads per day of attachment (θ), was:

$$\theta = e^{(\beta_0+\beta_1 x_s+\beta_2 x_r+\beta_3 x_c+\beta_4 x_d)}, \quad (2)$$

with independent factors, x_s, x_r, x_c and number of days that a mussel was attached at a given location (x_d). We were specifically interested in the effect of species and number of days of attachment on byssal thread synthesis rate. In these two models, we used log link functions because the data consisted of counts and quasipoisson errors to account for overdispersion. All factors were treated as fixed effects. In order to obtain the models that best fit the data, we used a model-selection approach with backward selection and an *F*-test to evaluate the significance of removing each factor (Crawley, 2008).

We used logistic regression in R to test for differences in the number of zebra *versus* quagga mussels in the flume experiment that were dislodged in response to water velocities of 0, 50, 100 and 180 cm s^{-1}. The full model for probability of dislodgment of mussels (ρ) was:

$$\rho = \frac{1}{1 + e^{-\left(\beta_0 + \beta_1 x_s + \beta_2 x_r + \beta_3 x_c + \beta_4 \mathbf{x}_v^{\,2} + \beta_5 x_{A_\parallel}\right)}}, \quad (3)$$

where factors in the model were x_s, x_r, x_c, velocity squared ($\mathbf{x}_v^2$) as a numerical quantity and mussel shell area parallel to flow ($x_{A\parallel}$). Our model used binomial errors and a logit link function because our data were binary. All factors were treated as fixed effects. The probability of dislodgment in flow might increase with increasing lift force ($\mathbf{F}_L$) imposed on a mussel according to the theoretical model:

$$\mathbf{F}_L \propto \mathbf{x}_v^2 x_{A\parallel}. \quad (4)$$

Hence, in the full logistic regression model, we included the factors $\mathbf{x}_v^2$ as a numerical quantity and $x_{A\parallel}$ even though we controlled for mussel size. We excluded shell area perpendicular to flow (i.e. anterior–posterior, lateral views), which is important for calculating drag force, because we did not know these values for all mussels. We used a model-selection approach as described previously to obtain the model that best fit the data.

To test for differences in the mechanical detachment force between zebra and quagga mussels after short (32 h) and long (two- and three-months) periods of attachment we used regression analyses in R. We tested for differences in detachment force in tension *versus* shear ($\mathbf{F}_{t/s}$) between zebra and quagga mussels after 32 h of attachment with the model:

$$\mathbf{F}_{t/s} = \beta_0 + \beta_1 x_s + \beta_2 x_r + \beta_3 x_c + \beta_4 x_t, \quad (5)$$

using factors of x_s, x_r, x_c and type of test (x_t, i.e. tension *versus* shear). We also tested for differences in detachment force in tension only ($\mathbf{F}_t$) between zebra and quagga mussels after 32 h and two and three months of attachment with the model:

$$\mathbf{F}_t = \beta_0 + \beta_1 x_s + \beta_2 x_r + \beta_3 x_b + \beta_4 x_p, \quad (6)$$

using factors of x_s, x_r (32-hour attachment only), byssal thread number (x_b) and percentage of plaque failures (x_p). All factors were treated as fixed effects. To obtain normal distributions, we used Box-Cox transformations in R using maximum likelihood to determine the optimal power transformations of detachment force for all three periods of attachment. We used a model-selection approach as described previously to obtain the models that best fit the data.

RESULTS

Byssal thread synthesis rate in calm and flowing water

For the flume experiment where mussels were attached for 32 h (24 h in no flow and 8 h in flow), we constructed a predictive model to test whether the number of byssal threads synthesized was affected by species, water velocity, replicate and number of days between collection and testing of mussels in the laboratory (Eqn 1). After model selection, τ for zebra and quagga mussels was best predicted by:

$$\tau_{zebra} = e^{\left(3.3 + 0.004 \cdot \mathbf{x}_v - 0.0006 \cdot x_c\right)}, \quad (7)$$

and

$$\tau_{quagga} = e^{\left(2.7 + 0.0007 \cdot \mathbf{x}_v + 0.01 \cdot x_c\right)}, \quad (8)$$

where $\mathbf{x}_v$ is the velocity and x_c is the number of days between collection and testing of mussels in the laboratory. Replicate was the only factor that did not significantly affect byssal thread number and was removed by model selection (see Materials and methods). Our results revealed that the number of byssal threads synthesized was significantly higher for zebra relative to quagga mussels (Student's *t*-test; t=6.13, P<0.00001) (Fig. 5). There was a significant interaction between species and velocity (Student's *t*-test; t=2.52, P=0.012), where zebra mussels generally synthesized a higher number of byssal threads with increasing velocity than quagga mussels. Byssal thread number decreased significantly faster for zebra relative to quagga mussels with increasing number of days between collection and testing in the laboratory (Student's *t*-test; t=–2.33, P=0.021), which was a confounding factor in this study. When we removed this confounding effect of time (i.e. x_c=0), byssal thread number was predicted to increase much more dramatically with increasing velocity for zebra (τ_{zebra}) relative to quagga (τ_{quagga}) mussels (Fig. 6).

We also constructed a predictive model to examine the effects of attachment time on byssal thread synthesis rate of mussels in calm water during an observation period of one week. Our full model included the factors of species, replicate, number of days between collection and testing of mussels in the laboratory and number of days that a mussel was attached at a given location (Eqn 2). After model selection, θ for zebra and quagga mussels was best predicted by:

$$\theta_{zebra} = e^{\left(3.46 + 0.21 \cdot x_d\right)}, \quad (9)$$

and

$$\theta_{quagga} = e^{\left(3.05 + 0.21 \cdot x_d\right)}, \quad (10)$$

where x_d is the number of days that the mussels were attached during the 1-week period. Replicate and the number of days between collection and testing of mussels in the laboratory were two factors that did not significantly affect byssal thread synthesis rate and were removed during model selection. Byssal thread synthesis rate was significantly higher for zebra relative to quagga mussels (Student's *t*-test; t=4.62, P=0.000014) and decreased significantly (relative to zero slope) with increasing days of mussel attachment for both species (Student's *t*-test; t=–8.47, P<0.00001) (Fig. 7). After roughly 14 days, values for θ_{zebra} and θ_{quagga} converged to a rate of 1–2 threads per day.

Mussel dislodgment in flowing water

In our flume experiment, our original model for the probability of dislodgment of mussels in response to flow included the factors of species, replicate, number of days between collection and testing of mussels in the laboratory, water velocity squared and mussel shell area parallel to flow (Eqn 3). Following model selection, ρ for zebra and quagga mussels was:

$$\rho_{zebra} = \frac{1}{1 + e^{-\left(-5.57 + 0.0001 \cdot \mathbf{x}_v^2\right)}}, \quad (11)$$

and

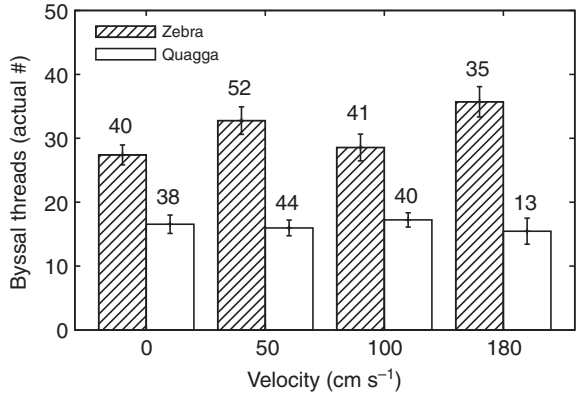

Fig. 5. Mean number of byssal threads of zebra and quagga mussels that remained attached within the flume at velocities of 0, 50, 100 and 180 cm s^{-1}. Mussels were attached for a total of 32 h (24 h in no flow followed by 8 h in flow). Error bars are standard errors of the mean. Numbers above bars are mussels that reattached to the acrylic channel of the flume during the initial 24-hour attachment period and remained attached for 8 h at each velocity.

$$\rho_{\text{quagga}} = \frac{1}{1 + e^{-\left(-2.91 + 0.0001 \cdot \mathbf{x}_v^2\right)}}, \quad (12)$$

with $\mathbf{x}_v^2$ as the velocity squared. Factors removed during model selection were replicate, number of days between collection and testing of mussels in the laboratory and shell area parallel to flow, because they did not significantly affect the percentage of mussels dislodged in flow. From our logistic regression, percentage dislodgment increased significantly (relative to zero slope) with increasing water velocity for both species (z-test; z=7.01, P<0.00001) but was significantly lower for zebra relative to quagga mussels (z-test; z=–5.11, P<0.00001) (Fig. 8). Predicted probabilities of dislodgment were 1%, 2% and 13% for zebra mussels (ρ_{zebra}) and 7%, 14% and 68% for quagga mussels (ρ_{quagga}) at velocities of 50, 100 and 180 cm s^{-1}, respectively.

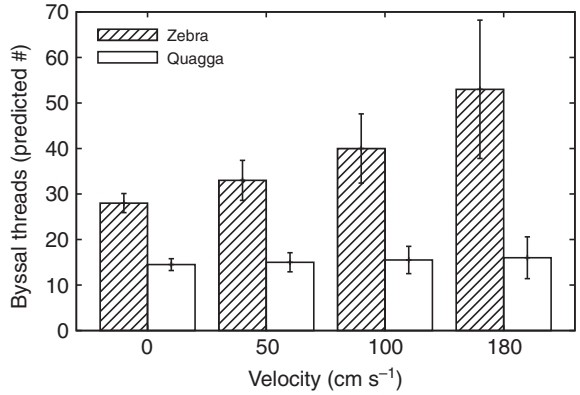

Fig. 6. Number of byssal threads of zebra and quagga mussels that remained attached within the flume at velocities of 0, 50, 100 and 180 cm s^{-1}, as predicted by the generalized linear model (Eqns 7 and 8). Mussels were attached for a total of 32 h (24 h in no flow followed by 8 h in flow). The confounding effect of number of days between collection and testing of mussels in the laboratory was removed from the model. Error bars are standard errors that were obtained from the regression estimates of the predictive models.

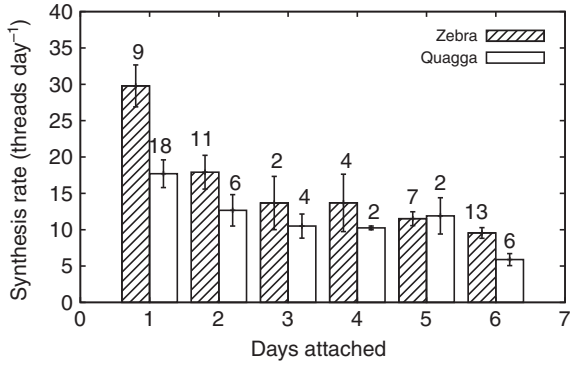

Fig. 7. Mean number of byssal threads synthesized per day by zebra and quagga mussels attached to acrylic channels in calm water over a 1-week period. Number of days that mussels were attached during the 1-week period ranged from 1 to 6 days. Error bars are standard errors of the mean. Numbers above bars are different individual mussels that were attached for the number of days indicated.

Mechanical detachment force

We tested whether mechanical force required for detachment differed between zebra and quagga mussels attached for 32 h in calm water. Specifically, we tested whether detachment force depended on species, replicate, number of days between collection and testing of mussels in the laboratory and type of test (i.e. tension *versus* shear) (Eqn 5). Of the factors tested, replicate and number of days between collection and testing of mussels in the laboratory did not significantly affect detachment force and were removed by model selection. Detachment force in both tension and shear was significantly higher for zebra relative to quagga mussels (Student's t-test; t=8.73, P<0.00001). Tensile force was marginally lower than shear force (Student's t-test; t=–2.00, P=0.048). The mean detachment force in tension was 0.31 N (s.e.m.=0.031 N, N=39) for zebra and 0.12 N (s.e.m.=0.019 N, N=38) for quagga mussels. The mean detachment force in shear was 0.40 N (s.e.m.=0.033 N, N=26) for zebra and 0.14 N (s.e.m.=0.018 N, N=35) for quagga mussels. In addition, we tested whether detachment force in tension only of zebra and quagga mussels attached for 32 h depended on species, replicate, byssal thread number and percentage of plaque failures (Eqn 6). The factors of replicate and percentage of plaque failures did not significantly affect detachment force and were removed by

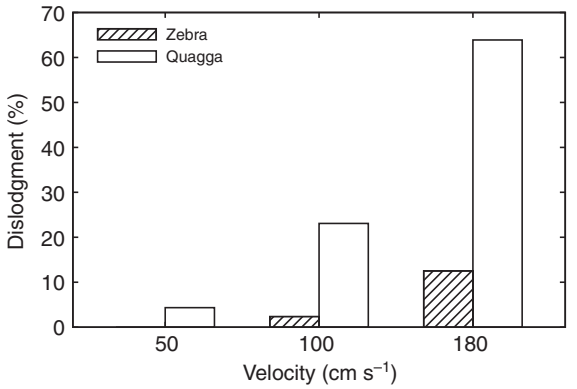

Fig. 8. Percentage of zebra and quagga mussels that dislodged from the acrylic channel of the flume at velocities of 50, 100 and 180 cm s^{-1}. Mussels were first attached for at least 24 h in no flow. Dislodgment of mussels occurred at some point during 8 h of exposure to a given velocity.

model selection. Detachment force increased significantly (relative to zero slope) with increasing byssal thread number for both species (Student's *t*-test; t=6.08, P<0.00001) and was significantly higher for zebra relative to quagga mussels (Student's *t*-test; t=8.84, P<0.00001) (Fig. 9). Mean byssal thread numbers for zebra and quagga mussels were 23 (s.e.m.=2, N=38) and 13 (s.e.m.=1, N=37), respectively.

We also tested whether detachment force in tension of zebra and quagga mussels attached in calm water for two and three months depended on species, byssal thread number and percentage of plaque failures (Eqn 6). Detachment force did not depend significantly on species or percentage of plaque failures for either attachment period and were removed by model selection. For two months of attachment, detachment force increased significantly (relative to zero slope) with increasing byssal thread number for zebra (Student's *t*-test; t=2.75, P=0.011) but not for quagga mussels (Student's *t*-test; t=–1.2, P=0.23). For three months of attachment, detachment force did not depend significantly on byssal thread number for either species (Student's *t*-test; t=1.3, P=0.19). After two and three months of attachment, respectively, detachment forces were 1.13 N (s.e.m.=0.46 N, N=16) and 1.56 N (s.e.m.=0.17 N, N=16) for zebra, and 0.97 N (s.e.m.=0.09 N, N=15) and 1.69 N (s.e.m.=0.23 N, N=12) for quagga mussels. Mean byssal thread numbers were 75 (s.e.m.=12, N=18) and 126 (s.e.m.=18, N=13) for zebra, and 103 (s.e.m.=9, N=14) and 118 (s.e.m.=15, N=13) for quagga mussels after two and three months of attachment, respectively.

The shape of the mechanical force–displacement curve of byssal threads tested in tension, while variable within and between zebra and quagga mussels, had some similarities between the two species attached for three months (Fig. 10). The curves had an initial steep slope that became more shallow before reaching peak force as either damage accumulated in the byssal threads and plaques or their viscoelasticity changed. The force gradually dropped after the peak as byssal threads broke or plaques detached from the substrate. Detachment failure from the substrate for both species occurred mostly at the plaques combined with byssal thread breakage. For mussels attached for two and three months (pooled) the mean percentage of byssal threads that failed at the plaques was 85% (s.e.m.=4.0%, N=31) for zebra and 95% (s.e.m.=1.1%, N=27) for quagga mussels. Only two zebra mussels detached due to failure at the byssal thread root within the shells. For zebra and quagga mussels attached for 32 h, the mean percentage of byssal threads that failed at the plaques was 51% (s.e.m.=5%, N=36) and 83% (s.e.m.=4%, N=37), respectively.

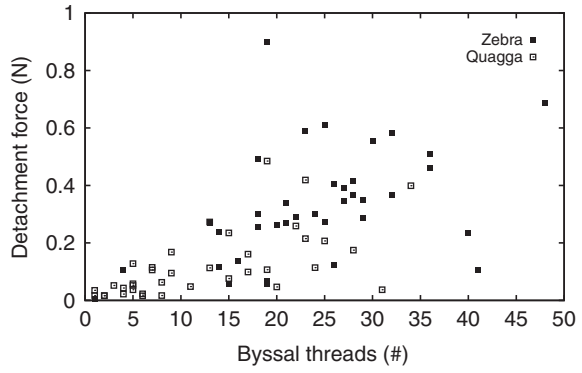

Fig. 9. Relationship between mechanical detachment force of zebra and quagga mussels and the number of byssal threads that they synthesized during 32 h of attachment to acrylic channels. Mussels were tested in tension with a dynamic mechanical thermal analyzer (see Figs 2 and 3).

DISCUSSION

We examined byssal thread attachment as a functional trait that might limit the expansion of quagga mussels relative to zebra mussels into habitats with rapid water velocity. As predicted, our results revealed that compared with quagga mussels, zebra mussels exhibited significantly higher byssal thread synthesis rate, lower dislodgment in flow and greater force required for mechanical detachment from the substrate after short-term (32-hour) attachment. Of the traits that we measured, the number of byssal threads synthesized per unit time period was the factor most likely to affect mussel dislodgment in flow and mechanical detachment from hard substrate. Higher byssal thread synthesis rate in zebra mussels might partly account for their persistence in habitats with rapid flow relative to quagga mussels, and is likely to have important implications for differences in range expansions between the two species.

Zebra mussels anchor faster and tighter than quagga mussels

Our results strongly supported our hypothesis that zebra mussels have a higher rate of byssal thread synthesis than quagga mussels, particularly within a short-term attachment period of 32 h. In our laboratory flume experiment, zebra mussels synthesized byssal threads about two times faster than quagga mussels at all water velocities (Fig. 5). We found that the number of byssal threads synthesized declined more rapidly in zebra than in quagga mussels as the time between collection and testing of mussels in the laboratory increased. Most interestingly, when we accounted for this confounding effect of time period on byssal thread synthesis rate, our predictive model revealed a much greater increase in byssal thread synthesis rate in zebra relative to quagga mussels with increasing velocity (Fig. 6). Thus, this predictive model suggests that zebra mussels exhibit greater phenotypic plasticity in byssal thread synthesis rate in response to flow than do quagga mussels. This prediction was consistent with results of Clarke and McMahon (Clarke and McMahon, 1996a), which showed that the rate of byssal thread synthesis in zebra mussels generally increased in response to increasing velocity (10–20 cm s^{-1}) over a 3-week period. The low velocities in their study were more typical of habitats where zebra and quagga mussels co-occur in the field (e.g. Oswego Harbor, Lake Ontario). Our present findings further indicated that zebra mussels have much greater capacity than quagga mussels to increase byssal thread synthesis rate in response to higher velocities and over a relatively short time period of 8 h in flow.

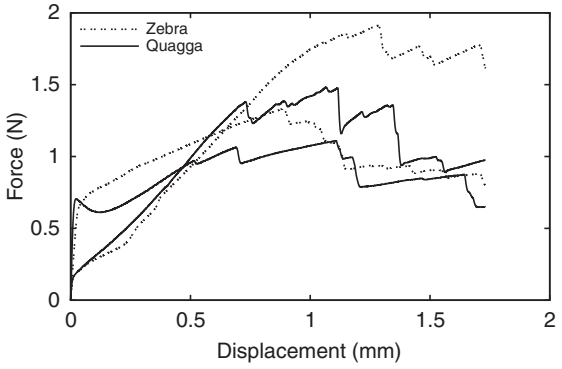

Fig. 10. Mechanical force–displacement curve of zebra and quagga mussel byssal threads tested in tension. Byssal threads were tested in tension with an Instron test machine (see Fig. 4). The load–displacement curves shown are for two arbitrary zebra and two arbitrary quagga mussels that were attached to PVC plates for three months.

We also hypothesized that zebra mussels would require greater force for mechanical detachment from the substrate than quagga mussels. This hypothesis was supported for mussels that were attached for a short time period of 32 h in calm water (Fig. 9). The greater detachment force of zebra relative to quagga mussels was most likely due to a higher number of byssal threads synthesized by zebra mussels during this time period (Fig. 9). Differences between zebra and quagga mussels in the amino acid composition of byssal thread proteins (Anderson and Waite, 1998; Anderson and Waite, 2000; Anderson and Waite, 2002) might also contribute to differences in mechanical properties, such as detachment force, between the two species. However, functional consequences of such differences in byssal thread composition have not been examined.

Our hypothesis, that zebra mussels have higher mechanical detachment force than quagga mussels, was not supported for mussels that were attached for longer periods of time in calm water (two months: zebra=1.13 N, quagga=0.97 N; three months: zebra=1.56 N, quagga=1.69 N). Over a 1-week period in calm water, the mean number of byssal threads synthesized per day decreased and converged for the two species as the number of days that the mussels were attached increased (Fig. 7). Such convergence in byssal thread synthesis rate might partly explain why we found no differences in detachment force between zebra and quagga mussels attached for two and three months in calm water. Rates of byssal thread synthesis might have converged between the two species over time in calm water, because of a plastic response by zebra mussels to reduce byssal thread synthesis rate under conditions of no flow. After 14 days, the predicted rate of byssal thread synthesis for both species was ~1–2 threads per day. Based on this prediction, mean byssal thread numbers would range from ~70–140 after two months, and ~95–190 after three months of attachment. Actual mean byssal thread numbers were within these predicted ranges for both species (two months: zebra=75, quagga=103; three months: zebra=126, quagga=118).

The detachment forces that we measured in the laboratory after two and three months of attachment were similar in magnitude to the results of Ackerman et al. (Ackerman et al., 1996) for pooled samples of zebra and quagga mussels that recruited onto PVC and attached for a shorter time period of one month in the field. Also, consistent with results from Dormon et al. (Dormon et al., 1997), who examined zebra and quagga mussels that recruited onto PVC in the field, we observed a combination of plaque and byssal thread failures for both species. While we did not find detachment force between the two species to depend on the percentage of plaque failures, Dormon et al. (Dormon et al., 1997) found that the detachment force of pooled zebra and quagga mussels depended on the material of settlement and generally decreased as the percentage of plaque failures increased. The high percentage of plaque failures and physical interactions among plaques might contribute to the lack of difference in detachment force between zebra and quagga mussels and the lack of correlation between detachment force and byssal thread number for the attachment periods of two (for quagga mussels) and three months (for zebra and quagga mussels). While each individual byssal thread was attached to the substrate by a unique plaque, the plaques of all byssal threads from a single mussel were often in physical contact with one another. At times we observed that the failure of one plaque led to the failure of adjacent plaques prior to breakage within the byssal threads themselves.

A higher rate of byssal thread synthesis was the most likely factor that we examined that minimized dislodgment of zebra mussels from hard substrate at high water velocities relative to quagga mussels. While percentage dislodgment increased with increasing velocity for both species, as we hypothesized, zebra mussel dislodgment was lower at all three velocities (Fig. 8). Our mechanical tests on mussels attached for 32 h also revealed that detachment force tended to increase with increasing byssal thread number for both species (Fig. 9). Thus, a higher initial byssal thread synthesis rate (i.e. ~1–2 days) and a possible greater response in byssal thread synthesis rate to different water velocities might be key traits that confer zebra mussels with greater ability than quagga mussels to persist under field conditions with variable velocities. Our mechanical tests on mussels attached for 32 h also indicated similar, although slightly higher detachment forces in shear (zebra=0.40 N, quagga=0.14 N) than in tension (zebra=0.31 N, quagga=0.12 N). Therefore, with respect to their strength of attachment in flow, mussels were no more likely to be dislodged from drag (i.e. shear) than from lift forces (i.e. tension). However, shell shape and the orientation of mussels in flow, which affects the shell area perpendicular to flow, are two other factors that we did not measure and that might also contribute to dislodgment due to lift and drag forces.

Byssal thread synthesis and strength have been shown to depend on other environmental factors, such as temperature (Clarke and McMahon, 1996b) and season (Moeser and Carrington, 2006). In some studies, zebra mussels have generally been found to be more tolerant of higher temperatures than quagga mussels (Domm et al., 1993; Spidle et al., 1995). However, opposite findings (Thorp et al., 2002) and recent invasions of quagga mussels into warm southern waterways (e.g. Lake Mead, NV, USA) suggest that there is variation in thermal tolerance among populations or that our understanding of the effects of temperature on the two species is still somewhat limited. Any possible differences in thermal tolerance between the two species could affect other physiological processes, such as byssal thread synthesis, in different ways and to different degrees. We chose temperatures (18–20°C) within the range (15–30°C) for high byssal thread synthesis in zebra mussels (Clarke and McMahon, 1996b) and that support growth of both species (Baldwin et al., 2002), such that contrasts in byssal thread synthesis rate between the two species were unlikely to be due to the confounding factor of temperature tolerance. Season has been found to affect byssal thread strength and extensibility in the blue mussel, *Mytilus edulis*, in which both mechanical properties were significantly higher in the spring than in all other seasons (Moeser and Carrington, 2006). Condition and gonad indices, which also were shown to vary throughout the year, were thought to be involved in the variation in these mechanical properties. In particular, mechanical properties of byssal threads of *M. edulis* tended to be highest when their condition index (i.e. total dry tissue mass/shell volume) was also relatively high in the spring. Similar to *M. edulis*, zebra and quagga mussels are likely to experience fluctuations in condition and gonad indices in the field, which in turn, might affect byssal thread attachment throughout the year. However, seasonal effects were unlikely to contribute to any differences in the mechanical detachment force between zebra and quagga mussels in our present study, because all mussels were collected for a given mechanical test on the same date.

Costs of byssal threads and implications for habitat expansions

Costs associated with byssal thread synthesis have been found in different mussel species. In the blue mussel, *M. edulis*, a significant portion of the carbon and nitrogen budget was allocated to byssal thread production (Hawkins and Bayne, 1985). Other mussels, such as *Perna viridis* and *Brachidontes variabilis*, synthesized more numerous, thicker and longer byssal threads when exposed to the

crab predator, *Thalamita danae* (Cheung et al., 2006). Such a plastic response by these mussels was thought to reduce their risk of being pulled from the substrate by predators. More secure byssal thread attachment in zebra mussels has also been found to deter their fish predators, the common bream (*Abramis brama*), the white bream (*Blicca bjoerkna*) and the roach (*Rutilus rutilus*). These predators were found to spend no more than 2 s attempting to detach individual zebra mussels from stone (Nagelkerke and Sibbing, 1996).

Results from our present study suggest that such costs of byssal thread synthesis might be higher for zebra mussels, with higher byssal thread synthesis rate, than for quagga mussels. Tradeoffs between byssal thread synthesis rate *versus* growth and reproduction might contribute to niche partitioning between zebra and quagga mussels. While we found quagga mussels to have lower byssal thread synthesis rate, suggesting lower allocation to byssal threads, they have shown higher growth rate (Baldwin et al., 2002; Stoeckmann, 2003) and larger body size (Mills et al., 1999) than zebra mussels. Such higher growth rate and larger body size might enable quagga mussels to reproduce earlier or at a greater rate. Lower byssal thread synthesis rate in favor of growth and reproduction by quagga mussels might contribute to their inability to displace zebra mussels in habitats with rapid water velocity, while overtaking zebra mussels in calmer habitats. Similar tradeoffs between byssal threads *versus* growth and reproduction were thought to occur in two marine mussel species in which the invasive *Mytilus galloprovincialis* was outcompeting the native *Perna perna* (Zardi et al., 2006). *M. galloprovincialis*, with its low attachment strength, fast growth and high reproductive output, was predicted to displace *P. perna* most easily in habitats with less extreme hydrodynamics.

While our results indicated that quagga mussels are more limited in distribution by higher water velocity than zebra mussels, our results also suggest the potential for quagga mussels to adapt to such conditions. Even at the highest water velocity, roughly 36% of quagga mussels remained attached to the substrate. If the ability of these quagga mussels to sustain high velocities involves heritable traits, then selection of flow-tolerant mussels might occur in the field (e.g. Lee et al., 2007). The ability of quagga mussels to evolve in order to exploit habitats with high velocity has not been well studied but might have important implications for their gradual habitat expansion and ecological threat.

Within the Great Lakes, quagga mussels are currently outnumbering zebra mussels but throughout North America the distribution of zebra mussels became established at a faster rate and remains more widespread. A suite of physical environmental factors has been thought to influence zebra and quagga mussel expansions (Karatayev et al., 1998; Ramcharan et al., 1992). Some of these factors are also likely to affect their physiology at various developmental stages. While a number of factors might affect zebra and quagga mussel colonization of new habitats, our results suggest that byssal thread attachment is likely to play a key role in the expansion of both species into habitats of different hydrodynamic flow.

LIST OF ABBREVIATIONS

$\mathbf{F}_L$	force due to lift
$\mathbf{F}_t$	detachment force in tension
$\mathbf{F}_{t/s}$	detachment force in tension *vs* shear
$x_{A\parallel}$	mussel shell area parallel to flow
x_b	byssal thread number
x_c	number of days between collection and testing of mussels in the laboratory
x_d	number of days that a mussel was attached at a given location
x_p	percentage of plaque failures
x_r	replicate
x_s	species
x_t	type of mechanical detachment force test
$\mathbf{x}_v$	velocity
$\mathbf{x}_v^2$	velocity squared
θ	byssal thread synthesis rate
ρ	probability of dislodgment of mussels
ρ_{quagga}	predicted probabilities of dislodgment for quagga mussels
ρ_{zebra}	predicted probabilities of dislodgment for zebra mussels
τ	byssal thread number
τ_{quagga}	byssal thread number for quagga mussels
τ_{zebra}	byssal thread number for zebra mussels

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