A Seasonal Comparison of Suspended Sediment Filtration by Quagga (Dreissena bugensis) and Zebra (D. polymorpha) Mussels

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ABSTRACT. Field evidence suggests a shift in the dreissenid population from zebra (Dreissena polymorpha) to quagga (D. bugensis) mussels is occurring within the lower Great Lakes. This laboratory study directly compared per-mussel and per-dry-weight filtration rates (volume per time) of both species, gauged by the clearance of resuspended natural sediments (1 to 12 mg/L) from gently mixed, 1-L static vessels. Mussels of 15- and 20-mm lengths were collected together from the Lake Ontario drainage basin at Oak Orchard Creek, Medina, NY, and maintained and tested in ambient Niagara River water. A 2 × 4 factorial design was employed, with species and season as independent factors. Season significantly influenced filtration rate of both size classes, and winter rates were about half those measured during the rest of the year. Species significantly influenced filtration of 20-mm mussels. Quagga mussels of this size filtered up to 37% faster than zebra mussels (data for spring: 309 vs. 226 mL/h/mussel, n = 18 and 20 individuals, respectively). Species was not a significant factor alone for 15-mm mussels, but a species x season interaction was significant. The zebra mussels employed here had 16 to 22% more ash-free dry weight (AFDW) than the quagga mussels, accentuating filtration differences when expressed per-mg-AFDW.

INDEX WORDS: Quagga mussels, zebra mussels, filtration rates.

INTRODUCTION

Dreissenid mussels morphologically distinct from typical zebra mussels (Dreissena polymorpha Pallas) were noted in the lower Great Lakes as early as 1989 (Mills et al. 1993). These were commonly named “quagga mussels” and were ultimately identified genetically as Dreissena bugensis Andrusov (May and Marsden 1992, Spidle et al. 1994). The two species do not appear to hybridize in nature (Spidle et al. 1995a).

Early indications suggested the quagga mussel was primarily occupying habitat not previously colonized by zebra mussels, particularly cold, deep zones of Lakes Erie and Ontario (Mills et al. 1993). Subsequent data have established that quagga mussels are, in fact, displacing zebra mussels from eastern Lake Erie and western Lake Ontario (Claxton and Boulding 1998, Mills et al. 1999). Within their native range, quagga mussels have likewise replaced zebra mussels in the Dnieper River drainage of the Ukraine (reviewed by Mills et al. 1996, 1999). The two dreissenids may differ in dispersal ability, as quagga mussels have been slower than zebra mussels to move beyond the lower Great Lakes (Mills et al. 1996, Wilson et al. 1999).

Investigations of temperature and salinity limits (Spidle et al. 1995b, Mitchell et al. 1996, Wright et al. 1996), and of reproductive dynamics (Roe and MacIsaac 1997, Claxton and Mackie 1998), have attempted to characterize the ecological relationship between zebra and quagga mussels. The assertion by Mills et al. (1999) that a species shift is taking place underscores the need also to establish the relative competitive abilities of these two exotics. Exploitation of phytoplankton resources is one possible mechanism by which these filter-feeders might compete.

At present, information on the filtering ability of the quagga mussel is very limited. Studies by Ackerman (1999) on the effect of current velocity on
filtering, and by Baldwin et al. (2000) on feeding and assimilation efficiencies, represent the only research to include both mussel species. In contrast, numerous studies have assessed filtration by the zebra mussel alone. However, reported zebra mussel filtration rates have ranged widely, from 2 to 287 mL/h/mussel (reviewed by Reeder et al. 1993), and may be of limited value to interspecific comparisons.

This laboratory study directly compared the filtration rates of *Dreissena bugensis* and *D. polymorpha* during each of the four seasons, under semi-natural conditions. It is hoped the comparative results presented in this paper will enhance an understanding of the dynamics of the dreissenid mussel invasion of the Great Lakes.

**METHODS**

**Study Design**

All experiments were conducted at the Buffalo State College Great Lakes Center (GLC) field station on the Black Rock Canal (BRC) of the Niagara River, in Buffalo, New York. Filtration rates of individual mussels were determined by measuring clearance from ambient BRC water of added suspended sediment particles, in gently mixed, static containers. The study employed a two-way factorial design, with species (zebra and quagga mussels) and season (fall [November 1999], winter [March 2000], spring [May 2000], and summer [July 2000]) as independent factors. Two size-classes of mussels (15 and 20-mm) were tested separately. Individual filtration rates are reported as volume/time/mussel. Mean filtration rates within species x season treatment combinations also are reported per ash-free (i.e., no shell) dry-weight (AFDW), employing mean AFDWs for the two size-classes of each species as conversion factors.

An experimental replicate consisted of a 1.1-L polypropylene cup (1 L final water volume) holding either one zebra mussel, one quagga mussel, or left empty as a control to measure particle loss through settling. Fifteen cups (five each for zebra mussels, quagga mussels, and controls, randomly arranged) were employed simultaneously during each experimental trial. Water baths kept all replicates at the same constant temperature during each trial. Three experimental trials (yielding 15 individual filtration measurements for each species) were conducted each season for 15-mm mussels. Four trials were conducted each season for 20-mm mussels (20 measurements for each species).

**Mussels**

Dreissenid mussels were collected in October 1999 from Oak Orchard Creek, Medina, New York, ~ 50 m downstream from the release point of the Glenwood hydropower station. This site is dominated by zebra mussels (~ 90%), but both species co-occur in the same clumps. About 20 kg (wet weight) of mussels were transported to the GLC, where they were rinsed largely free of trapped sediment (possibly of high oxygen demand) under BRC water. Mussels were then placed on the bottom of six 80-L glass aquaria in layers 3 to 5 cm deep for long-term holding (~ 9 months). Unfiltered BRC water at ambient temperature flowed through each of these tanks at ~ 2 L/min.

Mussels of unmistakable species-specific morphology (Pathy and Mackie 1993) were sorted from these 80-L tanks and maintained in two separate 40-L flow-through aquaria. Groups of 20 to 30 mussels of 20 and 15-mm lengths were separated by species and size-class into open-topped 500-mL polypropylene bins within their respective 40-L tanks. The 40-L tanks followed the same ambient BRC temperature cycle as the 80-L holding tanks described above. However, temperature was held constant in these 40-L tanks during the four discrete 2-week periods of experimentation.

**Sediment Particles**

Sediments were collected by 15 × 15-cm Ponar grab from the Black Rock Canal immediately in front of the GLC field station. They were wet-sieved through a 500-µm screen and stored short-term (< 2 weeks) under ambient BRC water. A vigorously aerated 30-L stock suspension (50 to 200 mg/L) was generated by a mechanical sediment resuspending system employed at the GLC. Dilutions of this suspension were typically used for three or four consecutive trials. Aeration of the suspension was discontinued at least 1 h prior to each trial, allowing larger particles to settle before use. Microscopic examination of suspended sediments in test vessels revealed that nearly all particles were < 20 µm diameter, and were not substantially aggregated.

**Procedures**

Unfiltered BRC water was added to the 1.1-L cups such that final volume after addition of stock sediment suspension and withdrawal of water for initial turbidity measurement would be 1 L. Mus-
sels were then added randomly to the cups and carefully positioned in the center. Mussels usually reopened within 5 min, but the experiment was not started for at least 30 minutes. Any mussel which failed to reopen by this time was replaced, and the new mussel was observed after 30 additional minutes. This was necessary only six times during the course of the study.

Cups were gently mixed by aeration through 4-mm diameter vinyl tubes ending in micropipette tips with ~ 0.5-mm openings. Tips were placed ~ 4 cm below the water surface, and air flow was adjusted into each vessel to ~ 3 bubbles per second. The stock sediment suspension was added to cups with a 60-mL polypropylene syringe without a needle. The amount added depended on the desired particle concentration after dilution (between 1 and 12 mg/L). This range of sediment density may realistically model baseline turbidity levels in Great Lakes waters (see Fanslow et al. 1995). Disturbance of mussels was minimized by adding this suspension slowly and aiming the stream into the air bubbles.

Five minutes after the addition of the last sediment aliquot, 30 mL were withdrawn from each cup with another syringe (in the same order as sediments were added) and transferred to pre-washed glass jars for determination of initial sediment concentrations. This marked the start of the timed filtration trial. This syringe was flushed twice with de-ionized water between withdrawals. Fall, spring, and summer experiments lasted 1 h, while winter experiments ran for 2 h, after which terminal 30-mL water samples were withdrawn.

Turbidity was measured by an HF Instruments analog turbidity meter and converted to mg/L using an empirical calibration. This calibration was generated by filtering (1.2-µm Whatman glass fiber), drying (24 h at 22°C, to constant weight), and weighing (Mettler balance) a series of BRC sediment dilutions, including pure glass-distilled water. A linear model was fitted to these turbidity and sediment concentration data ($R^2 = 0.96, p < 0.001, n = 10$). The glass cuvette for the meter was thoroughly rinsed with tap and de-ionized water between all measurements.

Fall and spring experiments were conducted at 14°C, and summer tests at 22°C. These temperatures were within 2°C of ambient BRC temperature at the time of the experiments. Winter experiments were conducted at 8°C, which was 4 to 5°C warmer than ambient. Mussel activity declines dramatically below 4°C (personal observation, see also Reeder and bij de Vaate 1990) so this higher temperature was a necessary compromise to yield measurable filtration rates. Conditions during the “winter” trials were probably more representative of those experienced by mussels at or near spring mixis.

Filtration rates were calculated using the logarithmic equation of Coughlan (1969):

$$FR = \frac{V}{nt} \cdot [\ln(C_0 - C_t) - (\ln(C'_0 - C'_t))]$$  \hspace{1cm} (1)

where: $FR =$ filtration rate (mL/h), $V =$ vessel volume (mL), $n =$ number of mussels per vessel, $t =$ duration of test (h), $C_0$ and $C_t =$ beginning and ending particle concentrations (mg/L) in a vessel holding a mussel, $C'_0$ and $C'_t =$ beginning and ending particle concentrations (mg/L) in a mussel-free control.

Particle settling can be averaged among control replicates, yielding a single dimensionless term $\alpha$. Equation 1 can then be rewritten as:

$$FR = \frac{V}{nt} \cdot [\ln(C_0 - C_t) - \alpha]$$  \hspace{1cm} (2)

A new $\alpha$ term was calculated for each experiment. During this study $\alpha$ averaged (± SE) 0.096 ± 0.010 ($n = 28$). Alpha exceeded 0.150 during only two trials.

**Non-filtering Mussels**

Because the objective of this study was to compare filtration rates of active zebra and quagga mussels, recognizing and excluding specimens which remained inactive during trials avoided underestimating filtering abilities. This study was not designed to quantify the activity level of individual mussels (Morton 1969, Sprung and Rose 1988, Horgan and Mills 1997) or to evaluate factors controlling it. Mussels were carefully observed from ~ 2 m away several times during each trial. Specimens with closed valves and retracted siphons were presumed not filtering, and were excluded from the trial. Particle “clearance” by the eight mussels excluded by this criterion was indistinguishable from controls (settling).

Additionally, some individuals apparently had not filtered during the experiments, even though their valves seemed to be open. A mussel also was excluded from consideration if turbidity reduction
in its vessel fell within the control range for that trial. The 19 such individuals excluded produced virtually no pseudofeces during experiments, while actively filtering mussels always produced noticeable amounts. Of the 27 out of 280 mussels (9.6%) excluded as inactive by these two criteria, 15 were quagga mussels and 12 were zebra mussels. With the exception of 15-mm quagga mussels in fall 1999 (of which four did not filter), inactive mussels were relatively evenly distributed temporally.

Ash-free Dry Weight (AFDW) Measurements

After fall filtration experiments, mussels were returned to their holding tanks, from which specimens were selected for retesting during winter (provided they had not grown out of the size class). Mussels were then weighed. Starting with spring experiments, mussels were sacrificed for weighing after each trial. Whole mussels (with shell) were first preserved frozen. They were later placed on pre-weighed foil trays and air-dried in a fume hood at 22°C for 14 d, to constant weight. Total dry weight was measured on a Mettler balance. Specimens were then ashed for 1 h at 500°C in a muffle furnace and weighed again to determine loss on ignition, which represents AFDW. The great majority of shell is left as ash. Mean AFDW of all weighed mussels was determined for both size classes of each species. These mean AFDWs were employed to convert average per-mussel filtration rates to per-weight rates.

Statistics

Influences of season, species, and season x species interaction on per-mussel filtration rate were explored by two-way ANOVA (SPSS, Version 10, SPSS Inc., Chicago IL). The 15 and 20-mm size classes were evaluated independently. Per-mussel filtration data were log10 transformed to yield homogeneous variances (verified by Levene’s test). Where season was a significant factor, a posteriori Tukey’s honestly significant difference (HSD) tests compared filtration rates between seasons. Because there were only two species, a posteriori comparisons were not conducted for species. Where season x species interaction was significant, Tukey’s tests compared filtration rates between all pairings of treatment combinations.

Associations between total mussel dry weight and AFDW, and between AFDW and filtration rate (where such data were available for individual mussels) were determined by linear regression. Significant regression lines were compared between species by calculation of the t statistic following Zar (1996).

RESULTS

Per-mussel Filtration Rates

Seasonal per-mussel filtration rates of some 20-mm individuals of both species exceeded 300 mL/h/mussel during this study (Fig. 1), and a number of quagga mussels exceeded 400 mL/h. The highest individual filtration rates for 15-mm mussels approached 300 mL/h/mussel (Fig. 2).

Two-way ANOVA revealed significant influences of both season and species on filtration rate of 20-mm mussels (Table 1). Filtration rate of quagga mussels was up to 37% higher than that of zebra mussels (Fig. 3A). A season x species interaction was not significant.

For 15-mm mussels, season was significant but species was not (Table 2). Season x species interaction, however, was significant. Apparent interspecific differences in filtration rate among 15-mm mussels (Fig. 4A), therefore, are not attributed solely to species, but contribute to this interaction term.

Tukey’s tests indicated that per-mussel filtration rates of both size classes were significantly lower in winter than during spring, summer, and fall; generally less than half those measured during the rest of the year (note Figs. 3A and 4A).

Mussel Weights

Mean (±SE) total dry weight of 20-mm quagga mussels was 328.2±25.8 mg (n = 20), and that of 20-mm zebra mussels was 429.8 ± 18.6 mg (n = 22). Mean AFDWs were 26.4 ± 3.0 mg and 32.4 ± 1.4 mg, respectively. Mean total dry weight of 15-mm quagga mussels was 152.8 ± 6.2 mg (n = 32), and that of 15-mm zebra mussels was 185.1 ± 5.8 mg (n = 34). Mean AFDWs were 13.7 ± 0.9 mg and 15.9 ± 0.7 mg, respectively. AFDW was significantly linearly related to total dry weight in both quagga mussels (R² = 0.58) and zebra mussels (R² = 0.85). The two regressions did not differ statistically (p > 0.05), in terms of slope or intercept.

Per-AFDW Filtration Rates

Incorporating the greater AFDW of the zebra mussels appeared to accentuate the filtration advan-
tage of quagga mussels (Figs. 3 and 4). However, this trend was not evaluated statistically, due to the use of simple conversion factors for mussel weight. Per-AFDW filtration rates of 15-mm mussels of both species were higher than for 20-mm mussels during spring and summer (compare Figs. 3B and 4B).

Among specimens for which both AFDW and filtration rate were determined individually (32 quagga mussels and 31 zebra mussels from spring and summer experiments), filtration rate was not linearly related to AFDW for either species ($R^2 < 0.21$, $p > 0.05$).

**DISCUSSION**

Per-mussel filtration rates presented here for both dreissenids are at the high end of the range of published values for zebra mussels (Reeders et al. 1993, Horgan and Mills 1997), and are exceeded only by rates reported for 30+ mm size classes (Kryger and Riisgard 1988, Ackerman 1999). Per-AFDW filtration rates also fall toward the top of the range reported by Kryger and Riisgard (1988) for zebra mussels of similar weight. A number of factors may have contributed to high filtration rates during the present study. Minimizing disturbance and the need for acclimation (Reeders et al. 1989, Reeders and bij de Vaate 1990) may have allowed mussels to filter near optimum rates during the test periods. The modest densities of natural sediment employed were well below those shown to limit zebra mussel filtration (Reeders and bij de Vaate 1990, Lei et al. 1996). The aeration that kept the sediment suspensions homogeneous, meeting one of Coughlan’s (1969) assumptions, may also have

**FIG. 1. Filtration rate per 20-mm mussel (mL/h) vs. initial suspended sediment concentration (mg/L). Data points are measurements for individual mussels.**
produced moderate currents near the mussels, shown by Ackerman (1999) to enhance filtration rate. Also, the exclusion of obviously inactive mussels assured that data were considered only for specimens actively filtering particles from the water. However, even if rates were recalculated by assuming filtration of 0 mL/h/mussel for each inactive individual excluded (*data not shown*), resulting values would still exceed most reported data for zebra mussels of similar size.

The ongoing shift from zebra to quagga mussels in the lower Great Lakes (Mills *et al.* 1999) represents a replacement of up to 90% of benthic secondary production (Johannsson *et al.* 2000). Neither the mechanisms nor the implications of this interaction are fully understood. The present study re-

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**TABLE 1. ANOVA table for filtration rate of 20-mm dreissenid mussels.**

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>3.38</td>
<td>3</td>
<td>1.13</td>
<td>23.02</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Species</td>
<td>0.50</td>
<td>1</td>
<td>0.50</td>
<td>10.29</td>
<td>0.002</td>
</tr>
<tr>
<td>Season x Species</td>
<td>0.05</td>
<td>3</td>
<td>0.02</td>
<td>0.36</td>
<td>0.783</td>
</tr>
<tr>
<td>Error</td>
<td>6.79</td>
<td>139</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**TABLE 2. ANOVA table for filtration rate of 15-mm dreissenid mussels.**

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>5.44</td>
<td>3</td>
<td>1.81</td>
<td>37.601</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Species</td>
<td>0.07</td>
<td>1</td>
<td>0.07</td>
<td>1.42</td>
<td>0.237</td>
</tr>
<tr>
<td>Season x Species</td>
<td>0.43</td>
<td>3</td>
<td>0.15</td>
<td>3.00</td>
<td>0.034</td>
</tr>
<tr>
<td>Error</td>
<td>4.68</td>
<td>97</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
revealed that interspecific filtration differences were most notable within the warmer seasons, and favored the quagga mussel. Quagga mussels thus could hold some advantage during times of high activity, growth, and reproductive allocation. However, this may not necessarily imply that exploitation competition for food resources has solely driven the observed species displacement.

For asymmetrical exploitation competition to occur the exploited resource must be limiting, and the superior competitor must reduce resource acquisition by the inferior competitor (Tilman 1977). Dreissenids have likely contributed substantially to decreases in Great Lakes phytoplankton (Holland 1993, Nicholls and Hopkins 1993, Fahnenstiel et al. 1995, Madenjian 1995), and locally dense populations can be limited by food quantity or quality (MacIsaac et al. 1992; Nalepa et al. 1995, 1996). However, it is not clear if dreissenid mussels regularly draw down phytoplankton to the point where they become limiting at a wide geographic scale. Mills et al. (1999) noted that from 1992 to 1995 Lake Erie and Ontario quagga mussels grew faster than zebra mussels as they increased in numerical

FIG. 3. Mean seasonal filtration rates ± SE (mL/h) of 20-mm quagga and zebra mussels. Sample size given above bars in A. Error bars are not presented in B because per-AFDW data were generated using a simple conversion factor for each species.

FIG. 4. Mean seasonal filtration rates ± SE (mL/h) of 15-mm quagga and zebra mussels. Sample size given above bars in A. Error bars are not presented in B because per-AFDW data were generated using a simple conversion factor for each species.
dominance. While this suggests an asymmetrical competition, both species had increased in absolute abundance and biomass despite low phytoplankton standing crop, casting doubt on food limitation. Experimental studies (replacement series) where food availability can be manipulated might reveal whether quagga mussels can actually outcompete zebra mussels, or if quagga mussels simply outperform zebra mussels without inhibiting their uptake of food.

Filtration differences experimentally demonstrated within a 20-mm size class (chosen for reliability of individual mussel measurements) might not reflect the relative abilities of smaller size classes that now dominate the Great Lakes benthos (Mills et al. 1999). In the present study, species alone was not a significant independent factor among 15-mm mussels, and Ackerman (1999) also found no significant interspecific filtration difference within an 11-mm size class. Even among larger mussels, interspecific differences may not be universal. Baldwin et al. (2000) reported no filtration differences in the 20-mm size range, and an apparent quagga mussel advantage seen by Ackerman (1999) in a 31-mm size class was not significant. Comparative data are still too limited to fully understand the influences of geographic origin of mussels, and of experimental conditions, on the relative filtering abilities of the two dreissenids.

Reports of a higher quagga mussel growth rate (Mills et al. 1998, 1999, Baldwin et al. 2000, but see MacIsaac 1994), however, suggest the possibility of an additional competitive dynamic previously overlooked. At any given time, faster growing quagga mussels would tend to be larger than members of the corresponding zebra mussel cohort, and could exert more pressure on phytoplankton resources. Comparing filtration rates based on age rather than size (as in the present study) might accentuate any advantage of the quagga mussel.

Mussels may also compete for space, which can itself be a limiting resource (Connell 1961). The observation that Lake Erie and Ontario quagga mussels have grown faster than zebra mussels in both size and abundance (Mills et al. 1999) also provides circumstantial evidence for interference competition mediated by differential growth rates. A faster-growing species should be better at exploiting space. Larger mussels may additionally be expected to produce more gametes than smaller individuals (Sprung 1991, 1995), and any filtration and growth advantages of quagga mussels could translate into greater reproductive output (Mills et al. 1999). Interspecific differences in reproduction might produce dramatic community-level effects among such productive (Karateyev et al. 1997, Chase and Bailey 1999b, Johannsson et al. 2000), fecund (Sprung 1991), and relatively short-lived species (Chase and Bailey 1999a) as the dreissenid mussels.

It is becoming increasingly apparent that a better understanding of the interaction between zebra and quagga mussels will require thorough interspecific performance comparisons, including studies of filtration rates, growth rates, and reproductive output. It should not be assumed these two species are equivalent. Given the wide variability in filtration rate generated by previous studies of the zebra mussel alone, further comparative studies should be conducted at a range of geographic sites, and under a variety of experimental conditions.

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