Freshwater Biology (2007) **52,** 1602–1610 doi:10.1111/j.1365-2427.2007.01791.x

Turbidity-mediated interactions between invasive filter-feeding mussels and native bioturbating mayflies

E. MARTIN OSTERLING*, EVA BERGMAN*, LARRY A. GREENBERG*, BRAD S. BALDWIN† AND EDWARD L. MILLS‡

*Department of Biology, Karlstad University, Karlstad, Sweden
†Biology Department, St Lawrence University, Canton, NY, U.S.A.
‡Department of Natural Resources, Cornell Biological Field Station, Bridgeport, NY, U.S.A.

SUMMARY

1. Invasive dreissenid mussels are known to cause large ecosystem changes because of their high filter-feeding capacity, while native bioturbators may interfere with the mussels filter feeding. In this experiment, we investigated indirect environmental interactions between invasive filter-feeding dreissenid mussels (zebra and quagga mussels) and native recolonizing bioturbating hexagenid mayflies (*Hexagenia*) at two mussel densities and two *Hexagenia* densities in a 2-month long laboratory experiment.

2. Mean turbidity increased with increasing density of *Hexagenia* and decreased with increasing density of mussels. Turbidity showed the fastest decline at the highest mussel density, and no decline or a lower rate of decline at the low mussel density, dependent on *Hexagenia* density.

3. Mussel growth decreased with increasing *Hexagenia* density at low but not at high mussel density. Moreover, growth of mussels decreased as a function of increased mean turbidity at low mussel density but not at high mussel density. Filtering activity at the highest mussel density increased after introduction of food at the lower two densities of *Hexagenia*, but was constantly high at the highest *Hexagenia* density.

4. There was no difference in emergence of *Hexagenia* among the treatments, but mortality of *Hexagenia* was higher in the presence of mussels than in their absence.

5. Our results indicate that interactions between dreissenids and hexagenids are mediated through the sediment, and depend on density of both dreissenids and hexagenids. As the natural densities of these animals vary considerably within lakes, their growth and survival because of indirect environmental interactions is expected to vary spatially.

Keywords: bioturbation, filter-feeding, indirect environmental interactions, mayfly, mussels

Introduction

The study of indirect interactions is fundamental when trying to understand and predict the outcomes of species interactions in complex ecosystems (Wootton, 2002). One type of indirect interaction is the indirect environmental interaction, where one species modifies the physical environment, with subsequent effects on the other species (Bronmark, Dahl & Greenberg, 1997). As these interactions involve modifications to the environment, the repercussions of these types of interactions are potentially multifaceted, not only affecting the growth and abundance of individual species, but also affecting ecosystem processes (Lohrer, Thrush & Gibbs, 2004).

One example of an indirect environmental interaction that has had profound effects on lake ecosystems involves the introduction of zebra mussels (*Dreissena polymorpha* Pallas) to the Laurentian Great Lakes region of North America in the mid-1980s (Hebert, Muncaster & Mackie, 1989). These mussels have reduced the importance of pelagic-based processes

---

Correspondence: Martin Osterling, Department of Biology, Karlstad University, S-651 88 Karlstad, Sweden.
E-mail: martin.osterling@kau.se

in favour of benthic ones, owing to the mussel's ability to rapidly filter large quantities of water and its high reproductive potential (Berg, Fisher & Landrum, 1996; Smith *et al*., 1998). Consequently, zebra mussels have increased light penetration in lakes because of their filtering activity (Idrisi *et al*., 2001; Aldridge, Elliott & Moggridge, 2004) and increased structural complexity and changed faunal composition because of their extensive coverage of lake bottoms (Botts, Patterson & Schloesser, 1996; Dermott & Kerec, 1997; Karatayev, Burlakova & Padilla, 1997; Ricciardi, Whoriskey & Rasmussen, 1997; Gonzalez & Downing, 1999; Strayer & Smith, 2001; Beekey, McCabe & Marsden, 2004). Subsequently, a second dreissenid mussel, the quagga mussel (*Dreissena bugensis* Andrusov) has invaded the Great Lakes, and the evidence to date suggests that quagga mussels can survive, grow and feed as well as zebra mussels in epilimnetic waters (Baldwin *et al*., 2002). Thus, both zebra and quagga mussels have contributed to the benthification of many lakes, favouring the proliferation of some taxa at the expense of others.

Bioturbating species may be involved in an indirect environmental interaction with dreissenid mussels as they affect water turbidity. One example of a bioturbator, which is known to achieve high abundances, is the hexagenid mayfly larvae *Hexagenia* sp., which was responsible for most (98%) of the bioturbation caused by burrowing insect larvae in Lake St Joseph (Quebec, Canada) (Charbonneau & Hare, 1998). Prior to the 1950s, hexagenids were among the most abundant benthic macro invertebrates in the Laurentian Great Lakes region. The abundance of hexagenids (*Hexagenia limbata* Serville and *H. rigida* McDunnough) decreased dramatically during the 1950s, presumably as a result of frequent periods of anoxia in bottom waters in association with eutrophication (Krieger *et al*., 1996). Recently, however, the abundances of hexagenids have increased in a number of lakes, including Lake Erie, reaching average densities as high as 392 individuals m^{-2} (Schloesser *et al*., 2000). In other lakes, such as Oneida Lake (New York, U.S.A.) no recovery of hexagenids has occurred. The recent introduction and rapid colonization of filter feeding dreissenid mussels in lakes such as Lake Erie and Oneida Lake in combination with the current recolonization of bioturbating hexagenid mayfly larvae in the Great Lakes (Krieger *et al*., 1996; Schloesser *et al*., 2000) raise questions about indirect environmental interactions among these species, given that the mussels increase and the mayflies decrease water clarity.

In this study, we test indirect environmental interactions between dreissenid mussels and hexagenid mayfly larvae. Two dreissenid mussel species, quagga and zebra mussels, were used as both have been shown to have large influences on lake ecosystems (Mills *et al*., 1996, 1999; Baldwin *et al*., 2002). We hypothesize that turbidity is dependent on the densities of both hexagenid mayfly larvae and mussels. Specifically, we predict that increasing the density of hexagenids will increase turbidity and consequently decrease mussel growth, whereas increasing the density of mussels will reduce turbidity, with negative effects on the emergence rate and survival of hexagenids as the mussels' filter feeding should reduce food availability for hexagenids, as they are collector-gatherers.

Methods

We experimentally examined interactions between dreissenid mussels and *Hexagenia* (*H. limbata* and *H. rigida*), using a 3 × 3 orthogonally crossed design, with mussel density as one factor and *Hexagenia* density as the other. The response variables measured were growth, feeding activity and mortality of the mussels, emergence and mortality of *Hexagenia* and water turbidity. The mussel densities used were 0, 100 (four zebra and four quagga mussels per aquarium) and 1000 (38 zebra and 38 quagga mussels per aquarium) mussels m^{-2}, and the *Hexagenia* densities were 0, 50 (four per aquarium) and 300 (23 per aquarium) mayflies m^{-2}. These densities correspond to natural densities (Schloesser *et al*., 2000). The experiment was conducted using a sediment created by mixing clay and potting soil in the ratio of 1.0–2.3 by mass as described by Corkum & Hanes (1992). The organic content was 6.05 ± 2.3 (mean ± 1 SE) % of total ash free dry weight.

Seventeen-litre plastic tanks (outer dimensions of 41 × 28 × 25 cm) were used as aquaria. Lids were placed over each aquarium to hinder emerging mayflies from escaping. Sediment was added to the aquaria to a depth of 6.5 cm. Ten litres of tap water were added to each aquarium, and each aquarium was aerated throughout the experiment. Temperature in the experimental room was held at 15 °C during the experiment, and a 10 : 14 h light : dark cycle was used to simulate conditions in the natural environment.

Nymphs of *Hexagenia* were collected in western Lake Erie outside of Port Clinton, Ohio (Ohio State University, Stone laboratory) on 12–13 May 2003. *Hexagenia*, which were carefully pat dried and weighed, had a mean mass of 0.087 ± 0.0045 (mean ± 1 SE) g at the start of the experiment. Zebra and quagga mussels, 6–9 mm in shell length, were collected in Oneida Lake and in the St Lawrence River, respectively, in late May. This size was selected to ensure that the growth rates of dreissenid mussels would be high and more importantly, measurable, for the conditions of this experiment (in terms of duration, temperature and food). All animals were held in aerated tanks at Cornell Biological Field Station at Oneida Lake prior to commencement of the experiment.

The different treatments were randomly assigned to the aquaria, with three replicates of each treatment. *Hexagenia* were placed into the aquaria on 21 May. The experiment started on 7 June when mussels were added and was terminated 11 August (65 days).

All eight mussels in the 100 mussels m^{-2} treatment and 20 mussels of each species in the 1000 mussels m^{-2} treatment were individually marked to obtain individual changes in wet mass. Wet mass was measured after carefully drying the mussels with a paper towel. Mussel mortalities during the experiment ranged from 0 to 2 mussels $aquaria^{-1}$ at the low mussel density and from 7 to 8 mussels $aquaria^{-1}$ at the high mussel density, and was not significantly different between *Hexagenia* densities (one-way ANOVAS, $P > 0.05$). Emerging individuals of *Hexagenia* were counted and replaced as larvae to maintain constant densities over the experimental period.

Mussels were fed three times a week with mixed cultures of the algal species *Chlamydomonas* sp. and *Selenastrum* sp., both of which were cultured close to fluorescent lights. Density of algae was measured with a Coulter Counter (model ZM). The amount of algae added to the aquaria was the same for all treatments and averaged 6.3×10^3 cells mL^{-1}. *Hexagenia* were fed with a suspension of yeast (Hanes & Ciborowski, 1992). A stock suspension of 20 g of Tetramin fish-food flakes, 15 g of alfalfa powder, 14 g of baker's powder yeast and 500 mL of distilled water was created. This suspension was allowed to ferment for 10 days at room temperature. Five ml of the stock suspension and 10 mL of sugar were added to 500 mL distilled water to create the feeding suspension. This suspension was kept at room temperature and 6.9 mg of the suspension was added to each aquarium three times a week.

Turbidity was measured every third day using a Hach 2100P turbidimeter (Oakton Instruments, Vernon Hills, Illinois, U.S.A.). Seston was sampled by passing water samples through a 18 μm nitex screen. The seston was then dried on a GF/F filter at 60 °C for 24 h. There was a linear relationship between turbidity (NTU) and dry mass concentration of seston (g L^{-1}) ($y = 0.0007x - 0.02$, $r^2 = 0.99$, $P < 0.0001$).

Growth of mussels was measured as the instantaneous rate of mass change, and calculated by the formula, $G = 100(\log W_2 - \log W_1)/T$, where G is the instantaneous rate of mass change (day^{-1}), W_1 is the wet mass before the mussels were put into the aquariums, W_2 is the wet mass when the experiment was terminated and T is time in days (Baldwin *et al.*, 2002).

Filtering activity was defined as the difference in the proportions of mussels that were observed feeding before and after food was added to the aquaria. Statistical analyses were only performed for the 1000 mussels m^{-2} treatment due to the few number of individuals present and our inability to observe individual mussels at the lower density. Mussels with open valves and extended siphons were classified as feeding individuals. The mussels could not be accurately identified to species because of high turbidity.

Results

The day before the mussels were added, the mean turbidity levels were 11 ± 3, 672 ± 25 and 2709 ± 380 (mean ± 1 SE) NTU in the treatments with 0, 50 and 300 *Hexagenia* m^{-2}, respectively (Fig. 1). In the two treatments with only mussels (no *Hexagenia*), turbidity never exceeded 30 NTU, and was lower than in the aquaria lacking both mussels and *Hexagenia*. The strongest declines in turbidity after mussels were added were observed in the two treatments with 1000 mussels m^{-2} and *Hexagenia* (Fig. 1).

Mean turbidity increased significantly with increasing *Hexagenia* densities at all mussel densities. The slopes of the regressions for the treatments with 0 and

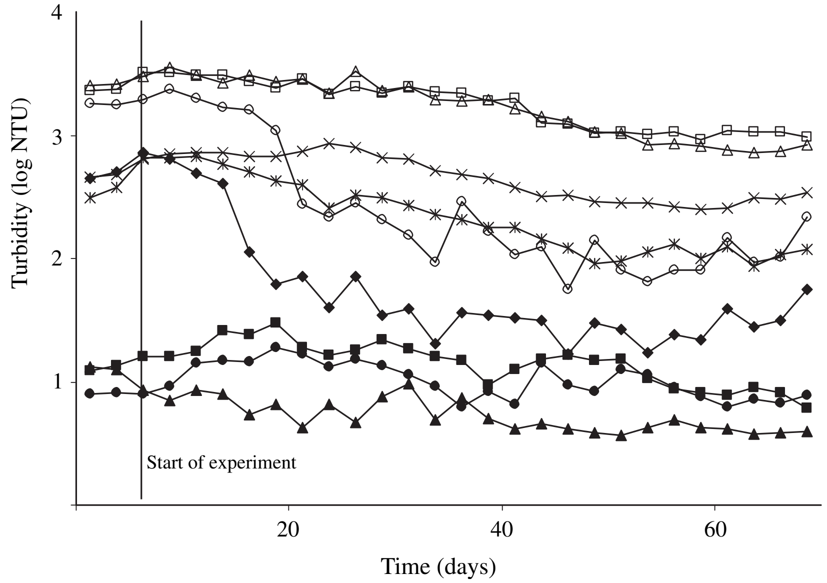

Fig. 1 Turbidity (log NTU) in relation to different combinations of *Hexagenia* and mussel densities (*Hexagenia* m^{-2} – mussels m^{-2}) over the experimental period: 0 *Hexagenia* – 0 mussels (■); 0 *Hexagenia* – 100 mussels (▲); 0 *Hexagenia* – 1000 mussels (●); 50 *Hexagenia* – 0 mussels (×); 50 *Hexagenia* – 100 mussels (⋇); 50 *Hexagenia* – 1000 mussels (◆); 300 *Hexagenia* – 0 mussels (□); 300 *Hexagenia* – 100 mussels (△); 300 *Hexagenia* – 1000 mussels (○). Turbidities are log-transformed.

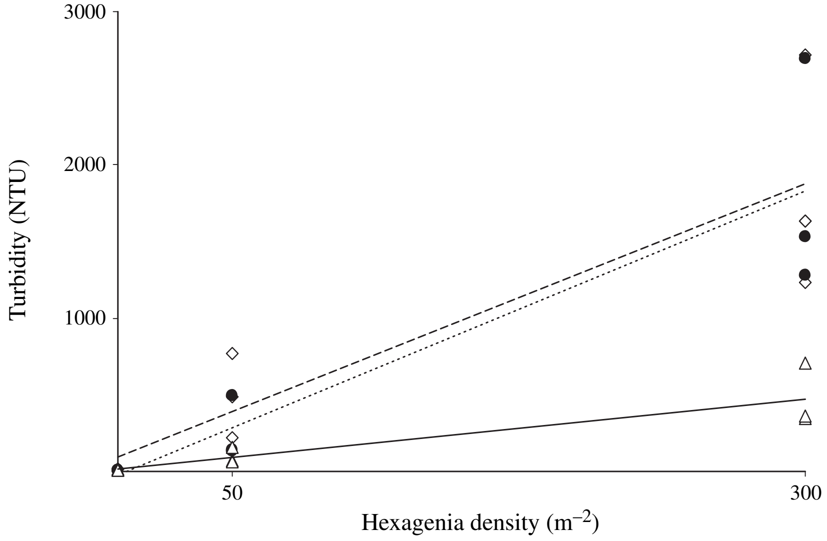

Fig. 2 Regressions between mean turbidity (NTU) and density of *Hexagenia* (0, 50 and 300 *Hexagenia* m^{-2}) for the three mussel densities (0 mussels m^{-2} (broken line): $y = 5.4x + 96.5$, $r^2 = 0.80$, $P = 0.001$; 100 mussels m^{-2} (dotted line): $y = 6.2x - 20.8$, $r^2 = 0.83$, $P = 0.0007$; 1000 mussels m^{-2} (solid line): $y = 1.5x + 15.2$, $r^2 = 0.83$, $P = 0.001$). The squares, circles and triangles depict 0, 100 and 1000 mussels m^{-2}, respectively.

100 mussels m^{-2} were approximately four times greater than for the relationship for 1000 mussels m^{-2} (Fig. 2).

A two-way ANOVA for mussel growth rates showed a significant effect of mussel density (MD) but not of *Hexagenia* density (HD) (Table 1). However, there was a significant interaction between MD and HD, which was due to an effect of *Hexagenia* density at the low mussel density but not at the high mussel density (SNK-test, Table 1). Growth rate at low mussel density was lower at the highest *Hexagenia* density than at the other *Hexagenia* densities, but growth rates at high mussel density were quite low and did not differ between *Hexagenia* densities (Fig. 3).

Table 1 Two-way ANOVA testing the effects of mussel density (MD) and *Hexagenia* density (HD) on the instantaneous growth rate of mussels (mass change day^{-1})

Source	d.f.	*F*-value	*P*-value
Mussel density, MD	1	47.3	<0.0001
Hexagenia density, HD	2	0.032	0.095
MD × HD	2	4.02	0.046
Aq (MD, HD)	12	4.4	<0.0001

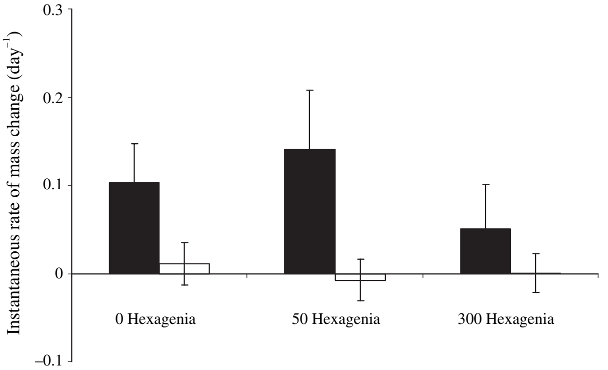

Fig. 3 Instantaneous rate of mass change (day^{-1}) (wwt ± SE) of mussels at low mussel density (100 mussels m^{-2}, solid columns) and at high mussel density (1000 mussels m^{-2} open columns).

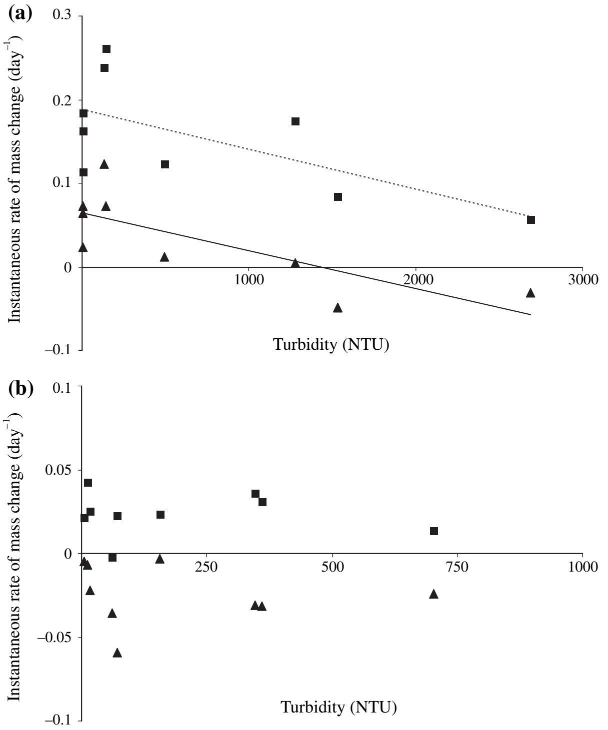

Fig. 4 Regressions between instantaneous rate of mass change (day^{-1}) and mean turbidity for zebra (dotted line) and quagga (solid line) mussels at the low mussel density (zebra: $y = -0.0005x + 0.9$, $r^2 = 0.44$, $P = 0.051$; quagga: $y = -0.0005x + 0.064$, $r^2 = 0.60$, $P = 0.014$) (a) and at the high mussel density (zebra: $F_{1,7} = 0.03$, $P = 0.87$; quagga: $F_{1,7} = 0.12$, $P = 0.74$) (b). The squares depict zebra mussels and the triangles depict quagga mussels. Note that the different scales on the x- and y-axes.

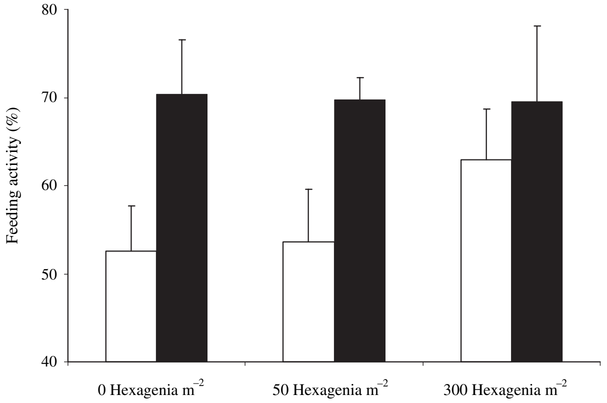

Fig. 5 Feeding activity of mussels at 1000 mussels m^{-2} ± SD at three *Hexagenia* densities (0, 50 and 300 m^{-2}) before (white bars) and after (black bars) food was added to the aquaria.

We also examined mussel growth as a function of turbidity. The growth of both quagga ($P = 0.014$) and zebra mussels ($P = 0.051$) decreased with increasing mean turbidity (Fig. 4a) at 100 mussels m^{-2}, but there was no significant relationship between growth and turbidity at 1000 mussels m^{-2} (Fig. 4b). Moreover, the zebra mussels grew faster than the quagga mussels for any given turbidity level.

The mussel filtering activity increased by 17.8% and 16.0% after food was added in the 0 and 50 *Hexagenia* m^{-2} densities, respectively. These increases in filtering activity were significantly higher than at the 300 *Hexagenia* m^{-2} density, where filtering activity increased by 7.4% (Fig. 5) (one-way nested ANOVA, F_2,9 = 4.74, SNK-test, $P = 0.039$).

The percentage of emerged *Hexagenia* at 50 *Hexagenia* m^{-2} and 300 *Hexagenia* m^{-2} was between 8.3 ± 8.3 and 20.3 ± 3.8 (mean ± 1 SE) %, and did not differ significantly between mussel densities (Table 2). There were no differences in the percentage of dead *Hexagenia* between mussel densities at the low density of *Hexagenia* (Table 2, Fig. 6). At the high *Hexagenia* density, mortality was affected by mussel density, with mortality being higher in the treatments with 100 and 1000 mussels m^{-2} than in the treatment with 0 mussels m^{-2} (Table 2, Fig. 6).

Discussion

Several studies have shown that filter-feeders and bioturbators may be involved in complex indirect interactions that affect ecological processes in aquatic communities. Not only do filter-feeders and bioturbators affect water clarity, albeit in opposite ways, but they also alter benthic nutrient dynamics via feeding and excretion (MacIsaac, 1996; Jack & Thorp, 2000;

Table 2 One-way ANOVAs for 50 and 300 *Hexagenia* m^{-2}, with per cent emerged and dead *Hexagenia* as independent variables, and mussel density as the dependent variable (0, 100 and 1000 mussels m^{-2})

Hexagenia density	Independent variable	d.f.	*F*-value	*P*-value
50 *Hexagenia* m^{-2}	Emerged	2	0.33	0.73
300 *Hexagenia* m^{-2}	Emerged	2	1.32	0.34
50 *Hexagenia* m^{-2}	Dead	2	0.14	0.87
300 *Hexagenia* m^{-2}	Dead	2	8.56	0.02

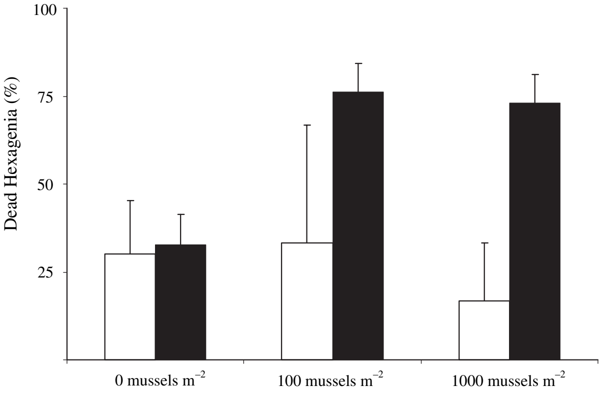

Fig. 6 Percentage of dead *Hexagenia* ± SE at different mussel densities (0, 100 and 1000 mussels m^{-2}) and *Hexagenia* densities. The white histobars show the results for 50 *Hexagenia* m^{-2} and the black histobars show the results for 300 *Hexagenia* m^{-2}.

Stahl-Delbanco & Hansson, 2002; Inglis & Gust, 2003; Lohrer *et al.*, 2004; Ranvestel *et al.*, 2004). The results of our experiment indicate that the potential interactions between these two feeding guilds are complex, with effects on growth and survival that depend on both intraspecific and interspecific interactions.

Turbidity levels were highly variable in our experiment, ranging up to over 3000 NTUs. However, variation in the field is also high, and our values lie within the total range of this natural variation (Alexander, Thorp & Fell, 1994; MacIsaac & Rocha, 1995; Summers *et al.*, 1996; Johnson & Hines, 1999). Even if variation in turbidity was high in our experiment, it was nonetheless related to the densities of *Hexagenia* and mussels. Increased *Hexagenia* density resulted in increased turbidity. However, when mussels were introduced, the high mussel density reduced turbidity at every *Hexagenia* density. On the other hand, the low mussel density did not influence turbidity at the highest *Hexagenia* density, and turbidity stayed high over the entire experimental period in this treatment.

The relationships between densities of mussels and mayflies and their effects on turbidity levels seemed to have repercussions for mussel growth. There was a negative effect on mussel growth with increasing *Hexagenia* density at the low mussel density. This was presumably an effect of turbidity as there was a negative relationship between mussel growth and turbidity. Clearance rates have been shown to decrease with increasing inorganic : organic ratios (Baldwin *et al.*, 2002). Moreover, high inorganic turbidity has been shown to decrease oxygen consumption of dreissenids, resulting in low growth (Alexander *et al.*, 1994). Thus, the low growth of mussels at high *Hexagenia* density seems to be a result of an indirect environmental interaction, where *Hexagenia* transferred sediments with a high clay content (30.3%) from the bottom to the water column.

We had expected an effect of turbidity on mussel growth at the highest mussel density, but no effect was found. We attribute this finding to the possibility that intraspecific competition was so intense at high mussel densities that any effect of turbidity was secondary. Nevertheless, the behavioural differences in feeding indicate that the high turbidity levels at high *Hexagenia* densities were stressing the mussels. Mussels at the two lowest densities of *Hexagenia* opened their siphons to a higher degree than the mussels at the highest density of *Hexagenia* when food was added. The changes in filtering activity at the two lowest densities of *Hexagenia* is in accordance with other studies, as filtering activity of dreissenid mussels may decrease when disturbed by turbidity and increase at increased food concentration (MacIsaac & Rocha, 1995; Horgan & Mills, 1997). On the other hand, the stress of turbidity on the mussels at the highest density of *Hexagenia* may have been so high (Alexander *et al.*, 1994) that the mussels had to forage intensely all of the time at this treatment.

Although we did not test for differences between zebra and quagga mussels in this experiment we found that both mussel species were affected similarly by both Hexagenia density and turbidity. Nevertheless, the growth rates of zebra mussels were consistently higher than those of quagga mussels. Without further study, it is difficult to identify the cause of this difference, but it may be related to the relatively high temperature and food levels used in this experiment (Baldwin *et al*., 2002).

Mussels negatively influenced mortality of *Hexagenia* at the high *Hexagenia* density. When mussels were present, the mussels must have removed most of the food in suspension, thereby increasing the presumably already intense intraspecific competition that the *Hexagenia* larvae must have experienced at this high *Hexagenia* density. Both survival and growth of *Hexagenia* have been shown to be positively affected by high food levels (Giberson & Rosenberg, 1992; Hanes & Ciborowski, 1992). However, mussels are also known to add material through deposition of faeces and pseudofaeces, which is known to increase when high levels of inorganic material such as clay are in suspension (MacIsaac & Rocha, 1995). Pseudofaeces should represent an additional food resource for the mayflies (MacIsaac & Rocha, 1995), but despite this potential food subsidy, the high mortality of Hexagenia indicates that there may be interspecific competition for food between dreissenid mussels and *Hexagenia*.

Hexagenia in western Lake Erie have been found at densities exceeding 300 m^{-2} (Schloesser *et al*., 2000), and dreissenid mussel density in North American lakes has varied from 0 to over 100 000 m^{-2} (Dermott & Kerec, 1997; Idrisi *et al*., 2001; Beekey *et al*., 2004). This study shows that the presence of these filter feeders and bioturbators may result in complex interactions that affect growth and survival of both species, depending on their densities. Our experiment indicated that the outcome of these interactions acts through the physical environment, namely the sediment. As the organic and inorganic fractions of the sediment vary spatially, the nature and intensity of the interactions between dreissenid mussels and *Hexagenia* may vary geographically. Thus, it is likely that indirect interactions between dreissenid mussels and *Hexagenia* may vary considerably depending on not only densities of mussels and mayflies but also on sediment composition, making general predictions about future population trends for these exotic mussels and native mayflies difficult to make.

Acknowledgments

We thank Greg Oshier, Travis Spier and Josh Tryninewski at the Cornell Biological Field Station for diligently working in the laboratory and in the field. Bill Thelen and Brian Young are kindly acknowledged for practical help at Cornell Biological Field Station. We thank John Hageman and Matt Thomas at Ohio State University's Stone Laboratory for assistance with collection of mayfly nymphs in Lake Erie. Two anonymous reviewers are kindly acknowledged for valuable comments on the manuscript. A special thanks goes to the Ohio Sea Grant for funding the field collections and both the U.S. Fish and Wildlife Service and the New York Department of Environmental Conservation for funding the research. This is contribution number 247 of the Cornell Biological Field Station.

References

Aldridge D.C., Elliott P. & Moggridge G.D. (2004) The recent and rapid spread of the zebra mussel (*Dreissena polymorpha*) in Great Britain. *Biological Conservation*, **119**, 253–261.

Alexander J.E., Thorp J.H. & Fell R.D. (1994) Turbidity and temperature effects on oxygen consumption in the zebra mussel (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 179–184.

Baldwin B.S., Mayer M.S., Dayton J., Pau N., Mendilla J., Sullivan M., Moore A., Ma A. & Mills E.L. (2002) Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 680–694.

Beekey M.A., McCabe D.J. & Marsden J.E. (2004) Zebra mussel colonisation of soft sediments facilitates invertebrate communities. *Freshwater Biology*, **49**, 535–545.

Berg D.J., Fisher S.W. & Landrum P.F. (1996) Clearance and processing of algal particles by zebra mussels (*Dreissena polymorpha*). *Journal of Great Lakes Research*, **22**, 779–788.

Botts P.S., Patterson B.A. & Schloesser D.W. (1996) Zebra mussel effects on benthic invertebrates: physical or biotic? *Journal of the North American Benthological Society*, **15**, 179–184.

Bronmark C., Dahl J. & Greenberg L.A. (1997) Complex trophic interactions in freshwater benthic food chains. In: *Evolutionary Ecology of Freshwater Animals* (Eds: B. Streit T. Städler & C.M. Lively), pp. 55–88. Birkhauser Verlag.

Charbonneau P. & Hare L. (1998) Burrowing behavior and biogenic structures of mud-dwelling insects. *Journal of the North American Benthological Society*, **17**, 239–249.

Corkum L.D. & Hanes E.C. (1992) Effects of temperature and photoperiod on larval size and survivorship of a burrowing mayfly (Ephemeroptera, Ephemeridae). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **70**, 256–263.

Dermott R. & Kerec D. (1997) Changes to the deepwater benthos of eastern Lake Erie since the invasion of Dreissena: 1979–1993. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 922.

Giberson D.J. & Rosenberg D.M. (1992) Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a northern population of *Hexagenia* (Ephemeroptera, Ephemeridae). *Journal of the North American Benthological Society*, **11**, 181–193.

Gonzalez M.J. & Downing A. (1999) Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish-amphipod interactions. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 679–685.

Hanes E.C. & Ciborowski J.J.H. (1992) Effects of density and food limitation on size variation and mortality of larval *Hexagenia rigida* (Ephemeroptera, Ephemeridae). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **70**, 1824–1832.

Hebert P.D.N., Muncaster B.W. & Mackie G.L. (1989) Ecological and genetic studies on *Dreissena polymorpha*, Pallas, a new mollusc in the Great Lakes. *Canadian Journal of Fish and Aquatic Sciences*, **54**, 249–255.

Horgan M.J. & Mills E.L. (1997) Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 249–255.

Idrisi N., Mills E.L., Rudstam L.G. & Stewart D.J. (2001) Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1430–1441.

Inglis G.J. & Gust N. (2003) Potential indirect effects of shellfish culture on the reproductive success of benthic predators. *Journal of Applied Ecology*, **40**, 1077–1089.

Jack J.D. & Thorp J.H. (2000) Effects of the benthic suspension feeder *Dreissena polymorpha* on zooplankton in a large river. *Freshwater Biology*, **44**, 569–579.

Johnson J.E. & Hines R.T. (1999) Effect of suspended sediment on vulnerability of young razorback suckers to predation. *Transactions of the American Fisheries Society*, **128**, 648–655.

Karatayev A.Y., Burlakova L.E. & Padilla D.K. (1997) The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. *Journal of Shellfish Research*, **16**, 187–203.

Krieger K.A., Schloesser D.W., Manny B.A., Trisler C.E., Heady S.E., Ciborowski J.J.H. & Muth K.M. (1996) Recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: Hexagenia) in western Lake Erie. *Journal of Great Lakes Research*, **22**, 254–263.

Lohrer A.M., Thrush S.F. & Gibbs M.M. (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, **431**, 1092–1095.

MacIsaac H.J. (1996) Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist*, **36**, 287–299.

MacIsaac H.J. & Rocha R. (1995) Effects of suspended clay on zebra mussel (*Dreissena polymorpha*) feces and pseudofaeces production. *Archiv fur Hydrobiologie*, **135**, 53–64.

Mills E.L., Rosenberg G., Spidle A.P., Ludyanskiy M., Pligin Y. & May B. (1996) A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. *American Zoologist*, **36**, 271–286.

Mills E.L., Chrisman J.R., Baldwin B., Owens R.W., O'Gorman R., Howell T., Roseman E.F. & Raths M.K. (1999) Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *Journal of Great Lakes Research*, **25**, 187–197.

Ranvestel A.W., Lips K.R., Pringle C.M., Whiles M.R. & Bixby R.J. (2004) Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. *Freshwater Biology*, **49**, 274.

Ricciardi A., Whoriskey F.G. & Rasmussen J.B. (1997) The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2596–2608.

Schloesser D.W., Krieger K.A., Ciborowski J.J.H. & Corkum L.D. (2000) Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: Hexagenia) in Lake Erie of the Laurentian Great Lakes. *Journal of Aquatic Ecosystem Stress and Recovery*, **8**, 125–141.

Smith T.E., Stevenson R.J., Caraco N.F. & Cole J.J. (1998) Changes in phytoplankton community structure during the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson River (New York). *Journal of Plankton Research*, **20**, 1567–1579.

Stahl-Delbanco A. & Hansson L.-A. (2002) Effects of bioturbation on recruitment of algal cells from the ''seed bank'' of lake sediments. *Limnology and Oceanography*, **47**, 1836–1842.

Strayer D.L. & Smith L.C. (2001) The zoobenthos of the freshwater tidal Hudson River and its response to the zebra mussel (*Dreissena polymorpha*) invasion. *Archiv fur Hydrobiologie Supplement, Monogr. Stud.*, **139**, 1–52.

Summers R.B., Thorp J.H., Alexander J.E. & Fell R.D. (1996) Respiratory adjustment of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) in response to chronic turbidity. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1626–1631.

Wootton J.T. (2002) Indirect effects in complex ecosystems: recent progress and future challenges. *Journal of Sea Research*, **48**, 157–172.

(Manuscript accepted 4 April 2007)