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The effects of dreissenid mussels on the survival and condition of burrowing mayflies (*Hexagenia* spp.) in western Lake Erie

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ABSTRACT

Burrowing mayflies (*Hexagenia limbata* and *H. rigida*) are once again prominent members of the benthic community in western Lake Erie. However, this community is now dominated by dreissenid mussels. We conducted a laboratory experiment and field sampling to investigate whether survival and condition of *Hexagenia* were affected by the presence, density, and quality of dreissenid mussels. In a laboratory experiment, *Hexagenia* survival was higher in microcosms without dreissenid mussels. We also found *Hexagenia* density to be higher at field sites with low dreissenid density, suggesting that *Hexagenia* survival is higher in these areas as well. In microcosm treatments with low dreissenid density, *Hexagenia* survival was higher in treatments with live dreissenids than in treatments containing only dreissenid shells. These findings suggest that while dreissenid shells degrade the quality of soft sediments for *Hexagenia*, some of the negative effect is offset by the presence of live dreissenids. The positive effect of live dreissenids is likely due to additional food resources made available to *Hexagenia* by the filtering activity of dreissenids. Neither dreissenid density nor shell "type" (shells alone or live dreissenids in shells) had an effect on *Hexagenia* condition. Thus, the interactions between these dominant benthic invertebrates are complex. Recovery of *Hexagenia* populations in western Lake Erie is likely affected by both changing environmental conditions due to anthropogenic activities and the introduction of exotic species into the benthic community. The results are likely to be continued instability of the benthic food web and unpredictable consequences for human utilization of this ecosystem.

Introduction

Burrowing mayflies [*Hexagenia limbata* (Serville) and *H. rigida* McDunnough] were once the most abundant macroinvertebrate species in the benthic community of western Lake Erie (Britt et al., 1973; Reynoldson and Hamilton, 1993). However, starting in the summer of 1953, the sediments and overlying water of western Lake Erie experienced an extended period of anoxia (Britt, 1955a,1955b) that resulted in a sudden decline in *Hexagenia* populations. As a result, *Hexagenia* were absent from the western basin for nearly 40 years except for a few isolated populations near the Bass Island region and around the mouths of the Detroit and Maumee Rivers (Reynoldson and Hamilton, 1993; Krieger et al., 1996).

Beginning in the summer of 1994, *Hexagenia* have experienced a dramatic recovery in western Lake Erie and have substantially increased in abundance as benthic nymphs and as nuisance swarms of adults along the Michigan, Ontario, and Ohio shorelines (Schloesser et al., 2000; Schloesser and Nalepa, 2001). However, the *Hexagenia* populations recolonizing this system are confronted with an environment that now includes a number of exotic species, notably the zebra mussel [*Dreissena polymorpha* (Pallas)] and the quagga mussel (*D. bugensis* Andrusov), as dominant benthic invertebrates. Both *Dreissena* species have spread rapidly throughout the Great Lakes and surrounding aquatic systems due to high fecundity, a passively dispersed planktonic veliger stage, and the ability of adults to attach to nearly every type of hard substrate, including boat and barge hulls, nets, and floating debris (Ram and McMahon, 1996). *Dreissena* also are able to colonize areas of soft, muddy substrate throughout western Lake Erie (Dermott and Munawar, 1993; Berkman et al., 1998). These areas comprise the historic habitat of *Hexagenia* (Shelford and Boesel, 1942; Fremling, 1967).

Dreissena filter suspended particles from the water and return some portion of these particles to the environment in the form of feces and pseudofeces (Berg et al., 1996). Suspension feeding by dense *Dreissena* populations results in density reductions of phytoplankton, diatoms, and suspended organic matter (MacIsaac et al., 1992; Holland, 1993). Further, *Dreissena* have also impacted the distribution of amphipods

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(Dermott et al., 1998) and other benthic macroinvertebrates (Thayer et al., 1997; Stewart et al., 1999a,1999b). In laboratory experiments, bioturbation by *Hexagenia* nymphs had negative effects on *Dreissena* growth, while *Hexagenia* mortality was elevated in the presence of *Dreissena* (Osterling et al., 2007). However, field patterns of distribution and abundance suggest that the recovery of the *Hexagenia* populations coincided with the increased density of *Dreissena*. The complex interactions between *Hexagenia* and *Dreissena* are likely to be important for determining the structure of the benthic community in western Lake Erie.

By altering the physical structure of the benthos, the presence *of Dreissena* mussels might affect *Hexagenia* in two ways. Dense aggregates of *Dreissena* shells can transform a previously soft substrate into a hard one. This may have detrimental effects on *Hexagenia* by impeding mayfly burrowing. Secondly, *Hexagenia* might feed on feces and pseudofeces produced by dreissenids; in this case, the presence of *Dreissena* may promote increases in *Hexagenia* populations.

We examined the effects of altered substrate quality due to *Dreissena* on survivorship and condition of *Hexagenia* through a combination of a laboratory microcosm experiment and field observations. Our objective was to determine whether modification of the aquatic substrate due to the presence of *Dreissena* is likely to have a positive, negative, or insignificant effect on *Hexagenia* populations in western Lake Erie.

Methods

Two separate data sets were collected and analyzed in this study. One data set originated from a controlled laboratory microcosm experiment conducted in 1998. A second set of data was derived from field sampling in the spring and summer of 1997 and 1998.

Microcosm experiments

We performed a laboratory microcosm experiment at F. T. Stone Laboratory on South Bass Island in the western basin of Lake Erie during a 10-week period in the summer of 1998. A 3×3×3 experimental design was implemented with zero, low, and high densities of *Hexagenia* (0, 300, and 600 m^{-2}, respectively), zero, low, and high densities of *Dreissena* shells (0, 3000, and 6000 m^{-2}, respectively), and varying “quality” of *Dreissena* shells (live dreissenids, shells-only, and a combination of 50% live/50% shells). Because one-third of the microcosms had zero *Hexagenia* added, these acted as “controls” for *Hexagenia* that were too small to be removed by sieving at the start of the experiment or were unintentionally introduced via the flow-through system over the course of the experiment. Because one-third of the microcosms contained zero *Dreissena*, there was a confounding of *Dreissena* density with *Dreissena* type (i.e., there was no way to have live, shells-only, and “combination” treatments in the zero *Dreissena* microcosms). Thus, we analyzed the experiment as a 2 *Hexagenia* densities (high, low)×2 *Dreissena* densities (high, low)×3 *Dreissena* types (live, shell-only, combination) design. The densities of *Hexagenia* and *Dreissena* used in the experiment were consistent with densities encountered in the western basin of Lake Erie in 1996 (Schloesser et al., 2000 for *Hexagenia*, KAK unpublished data for *Dreissena*). A treatment group along with a corresponding microcosm number was generated via a double randomization process.

We obtained dried *Dreissena* shells by allowing live dreissenids to dry in the sun for a period of 5 weeks in early summer, which was sufficient time for decomposition of most mussel tissue. The dried *Dreissena* shells were placed into beakers where a common volume was established for addition to each respective microcosm (500 mL≈low density of 3000 m^{-2}, 1000 mL≈high density of 6000 m^{-2}). For the live *Dreissena* treatment group, divers collected live *Dreissena* off Gibraltar Island, and we then counted and placed them into beakers where a common volume was established for addition to each respective microcosm (500 mL≈low density of 3000 m^{-2}, 1000 mL≈high density of 6000 m^{-2}). A 1:1 mixture of live *Dreissena* and *Dreissena* shells served as the combination treatment. *Dreissena* were placed into beakers where a common volume was established for addition to each respective microcosm (250 mL shell+250 mL live≈low density of 3000 m^{-2}, 500 mL shell+500 mL live≈high density of 6000 m^{-2}).

Hexagenia were allowed to hatch from eggs supplied by L. Corkum (Univ. of Windsor) and were added randomly to each microcosm immediately after hatching relative to each respective density (23 nymphs=low density of 300 m^{-2}, 46 nymphs=high density of 600 m^{-2}). Nymphs were given 1 week to construct burrows, during which there was no flow of water through the microcosms. During this period of time, dissolved oxygen levels ranged from 5.0 to 5.6 mg L^{-1}, suggesting sufficient dissolved oxygen was present for survival of both *Hexagenia* nymphs and dreissenids. During the experiment, a constant supply of flowing lake water was provided to each microcosm. Oxygen concentrations throughout the experiment ranged from 4.5 to 6.2 mg L^{-1} in all treatment combinations, again suggesting that oxygen was not a limiting factor in the experiment.

For microcosms, we used 81 plastic containers (three per treatment combination), each measuring 0.08 m^2 in area and 11.35 L in volume. Each container was filled to a depth of 4.0 cm with sieved Lake Erie sediment (600 μm sieve) collected by a diver from an area between Gibraltar and Middle Bass islands. This area was shown to have relatively high densities of *Hexagenia* in the summers of 1997 and 1998, suggesting that the sediment was suitable for *Hexagenia* colonization. We sieved the collected sediment in order to remove any *Hexagenia* nymphs, and then immediately transferred it into each microcosm and covered it with lake water pumped continuously into the laboratory. Water flowed equally into each microcosm via a manifold and aquarium tubing to approximately 2.5 cm above the sediment–water interface, assuring that all microcosms received the same quality of water and that the sediment was sufficiently oxygenated, but not disturbed. An outflow tube approximately 5 cm below the rim of each microcosm allowed water to flow out the opposite end from which it entered.

At the conclusion of the experiment, we sieved the sediment from each microcosm with a 600 μm sieve. Surviving *Hexagenia* were counted, flash-frozen in liquid nitrogen, and stored at −20 °C. We determined size of individual nymphs at the conclusion of the experiment by measuring wet mass (in grams) and head capsule width (in millimeters). Because these values were highly correlated in field samples ($r=0.976$, $p<0.0001$, $n=972$), we report only wet mass analyses. To determine *Hexagenia* condition, we planned to conduct biochemical analyses that measure glycogen levels (short-term energy storage) and lipid levels (long-term energy storage). In our microcosm experiments, only glycogen analyses (Naimo et al., 1998) were conducted to determine condition of surviving *Hexagenia*. Due to the paucity of surviving *Hexagenia*, lipid analyses were not performed.

We used logistic regression to determine if *Dreissena* type, *Dreissena* density, *Hexagenia* density, and interactions of these factors had effects on the proportion of *Hexagenia* that survived the microcosm experiment. Pairwise contrasts were used to detect differences between individual treatments. The effects of *Dreissena* type, *Dreissena* density, and *Hexagenia* density on mean wet mass and mean mass-specific glycogen were analyzed via an incomplete (because not all factor combinations had surviving *Hexagenia*), three-factor ANOVA following log transformation of dependent variables.

Field collection of Hexagenia

To determine if the presence of *Dreissena* was correlated with the condition of *Hexagenia* throughout the western basin of Lake Erie, we made field collections in June 1997 (spring), late September-early October 1997 (autumn), June 1998 (spring), and October 1998 (autumn). We identified three sites in the western basin as low *Dreissena* and three sites as high *Dreissena* (Fig. 1) prior to or on the first sampling date in June 1997, based on previous experiences (KAK, pers. obs). Sample sites were