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Yellow Perch Foraging on *Hexagenia* spp.: Effects of Hypoxia and *Dreissena*

Final Report

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Abstract

Invasive *Dreissena* spp. (zebra mussels; *D. polymorpha* and quagga mussels; *D. bugensis*) affect the distribution and abundance of benthic invertebrates and the flow of benthic energy to fish. It is not clear how the current spread of *Dreissena* onto soft sediment will affect invertebrates such as the burrowing mayfly (*Hexagenia limbata* and *H. rigida*). Preliminary experiments show that mayflies select for habitat with live *Dreissena* over bare sediment in normoxic (high oxygen) water. The goal of this study was to examine two distinct mechanisms, one biotic and one abiotic that may affect whether or not burrowing mayflies select *Dreissena*-colonized habitat. We hypothesized that 1) risk of predation by fish may promote selection of *Dreissena* habitat; whereas 2) hypoxia (low oxygen) may discourage use of *Dreissena* habitat because of already low oxygen levels. Laboratory experiments show that burrowing mayflies derive no protection from yellow perch or round goby predation due to the presence of *Dreissena*. Conversely, we found that under low oxygen conditions burrowing mayflies show equal selection for *Dreissena*-covered and bare sediment. Mayflies were also found to leave their burrows during hypoxia; however a perceived predation threat present delayed this response. Therefore, short-term periods of hypoxia may increase availability of burrowing mayflies to fish by forcing mayflies to leave their burrows to seek normoxic water.

Introduction

Hexagenia spp. (burrowing mayflies; *H. limbata* and *H. rigida*) were historically abundant in the western basin of Lake Erie, but populations declined to near extirpation in the 1950's during times of eutrophic conditions because *Hexagenia* are sensitive to low oxygen (Nebeker 1972; Gerlofsma et al. 1998). Increases in abundance and recolonization have been documented since the early 1990's (Krieger et al. 1996, Schloesser et al. 2000, Schloesser & Nalepa 2001), but populations continue to show variability linked to anthropogenic and environmental factors, such as short-term periods of hypoxia (Schloesser & Nalepa 2001, Bridgeman et al. 2006). As a result of their sensitivity to eutrophic conditions, *Hexagenia* are used as bioindicators of ecosystem health in the Lake Erie Index of Biotic Integrity. *Hexagenia* are particularly important to lake food-web function because they are a potentially large food source to many economically important fish species in Lake Erie, such as yellow perch and walleye (Hayward & Margraf 1987; Schaeffer 2000). The goal of this study was to understand how the spatial and ecological relationship of *Hexagenia* to introduced *Dreissena* spp. (zebra mussels; *D. polymorpha* and quagga mussels; *D. bugensis*) will affect the trophic role of *Hexagenia* and to investigate how *Hexagenia* - *Dreissena* interactions are modified by environmental conditions such as hypoxia.

Currently, quagga mussels, which are capable of inhabiting soft substrates, (eg., Mills et al. 1996; Berkman et al. 1998; Bially & MacIsaac 2000) are replacing zebra mussels throughout the Great Lakes (Mills et al. 1999). On hard substrates *Dreissena* increase local abundance and diversity of macroinvertebrates due to increased structural complexity (eg., Silver Botts et al. 1996; Stewart et al. 1998; Gonzalez & Downing 1999). The shift from primarily hard substrate colonies (zebra and quagga mussels) to soft substrates colonies (quagga mussels) will likely affect the infaunal invertebrate community. Previous experiments reveal the unexpected result that *Hexagenia* increased in the presence of *Dreissena* relative to other treatments, suggesting that *Dreissena* facilitate *Hexagenia* survival (DeVanna et al. in prep). Additional experiments showed that *Hexagenia* selected habitat covered with live *Dreissena* over habitats that consisted of bare Lake Erie sediment or sediment covered with artificial *Dreissena* clusters (DeVanna et al. in prep). Together, these data, observations, and previous studies suggest that *Hexagenia* utilize and benefit from *Dreissena* colonized sediments.

The continued spread of *Dreissena* onto soft sediments and the preference of *Hexagenia* for *Dreissena* clusters may reduce fish foraging success on *Hexagenia. Dreissena* clusters provide invertebrates a refuge from predation (Gonzalez and Downing 1999; Mayer et al. 2001; Beekey et al. 2004b), as this is a potential mechanistic explanation for the observed relationship. Even though *Dreissena* may facilitate *Hexagenia* growth or survival, they may reduce *Hexagenia* connectivity to native fish, benthic-pelagic coupling, and food-web function in Lake Erie. Alternatively, the western basin of Lake Erie can undergo short periods of hypoxia and oxygen concentration beneath *Dreissena* clusters is already low (Beekey et al. 2004a), therefore hypoxic events may force *Hexagenia* into the water column where they are more vulnerable to fish predation, as fish can swim into lethally hypoxic waters when food is abundant (Rahel and Nutzman 1994). Therefore, *Hexagenia* preference for *Dreissena*-covered sediments may impede fish consumption under high oxygen conditions, but short-term hypoxia in western Lake Erie may alter *Hexagenia* behavior making them vulnerable to fish predation.

The main objective of this study was to examine the effects of hypoxia and fish predation on the spatial relationship of *Hexagenia* and *Dreissena* in Lake Erie during hypoxic and

normoxic conditions. We conducted a mesocosm experiment testing the effects of *Dreissena*-covered sediments on the foraging success of yellow perch and round gobies on *Hexagenia*. We hypothesized that:

1) *Dreissena* presence would decrease fish foraging success on *Hexagenia*
2) Yellow perch would experience a large reduction in foraging success on *Hexagenia* in the presence of *Dreissena,* whereas round goby would be relatively unaffected.

Two experiments were conducted testing the effects of hypoxia on *Hexagenia* habitat preference and how this response is altered by the presence of a predation threat. We hypothesized that:

1) under low oxygen conditions *Hexagenia* to be found more often in bare sediment or in the water column than during normoxic conditions
2) once a perceived predation threat is added under both high and low oxygen conditions, *Hexagenia* will more often be found underneath *Dreissena* clusters to decrease the threat of predation.

Methods

Fish Foraging Experiments

To assess the impacts of *Hexagenia* burrowing beneath *Dreissena*-covered sediments on the foraging success of benthivorous fishes we conducted mesocosm experiments comparing the number of *Hexagenia* consumed in bare sediment to *Dreissena*-covered sediment. All juvenile yellow perch (10 individuals; 7-12.5cm total length) and round gobies (10 individuals; 6-8cm total length) were allowed to forage in two separate treatments; 1) *Hexagenia* in bare sediment and 2) *Hexagenia* in *Dreissena*-covered sediment. Mesocosms were (circular tubs; 34cm diameter and 34cm height) filled with 6cm of western Lake Erie sediment first sieved through 0.5mm mesh to remove macroinvertebrates. 18 *Hexagenia* (200/m^2) were added to each mesocosm which was covered with a 1mm mesh lid. Each *Dreissena*-covered sediment treatment mesocosm had 1200mL of live dreissenids added prior to *Hexagenia* addition. A 1mm mesh barrier was placed above the sediment 24 hours after *Hexagenia* addition and 1 fish was placed above the barrier. The fish were allowed to acclimate to the mesocosm for 24 hours without being able to feed on *Hexagenia* or *Dreissena*, which standardized hunger levels. After the barrier was removed the fish was allowed to forage for 24 hours. After the 24 hours light measurements were taken in each mesocosm, the water was drained, the fish was removed, and all remaining *Hexagenia* in the mesocosm were counted. The number of *Hexagenia* eaten was assumed to be the difference between the number of *Hexagenia* added (18) and the number of remaining *Hexagenia*. We also conducted bare sediment (N=5) and *Dreissena*-covered sediment (N=5) treatments without fish to estimate our error in finding all *Hexagenia* initially placed in the mesocosms. As a result of each fish being tested in both treatments we could calculate the difference in consumption between the habitat types by subtracting the number of *Hexagenia* consumed in *Dreissena*-covered sediment from the number consumed in bare sediment.

Effects of Hypoxia 1– Large Mesocosm Experiment

We tested whether burrowing mayflies selected for or avoided *Dreissena* clusters on sediment and how this relationship may be affected by low oxygen conditions and a perceived threat of predation. A 2x2 factorial design experiment was conducted with two levels of oxygen

(lake levels vs. hypoxic) and two levels of perceived fish predation risk (fish odor present vs. absent); resulting in four treatments replicated 5 times (N=20). Experimental mesocosms (circular tubs; 41cm diameter and 43cm height) were separated into three equal "pie-slice" shaped sections ($0.046m^2$) using metal dividers. Three different habitat types were created: 1) bare sediment, 2) live *Dreissena* clusters, 3) and artificial *Dreissena* clusters. The experiment was conducted using a density of 18 *Hexagenia* per mesocosm ($\sim 400 \cdot m^{-2}$). Live and artificial *Dreissena* treatments contained approximately 250 individuals ($5434 \cdot m^{-2}$). We created artificial *Dreissena* clusters by gluing empty, clean shells together with non-toxic glue and adding five 1g weights to each cluster. Mesocosms with a perceived predation threat present were filled with water from a large aquarium with adult Lake Erie benthivores present, all other mesocosms were filled with dechlorinated tap water. Normoxic oxygen levels were maintained by bubbling forced air to keep oxygen levels above 85% saturation. Mesocosms with hypoxic oxygen levels were kept at high oxygen for 24 hours and then the oxygen was lowered for the final 24 hours. We lowered the oxygen levels by removing the forced air and then bubbling N_2 gas until the oxygen was lowered to between 25 - 30% saturation. Once the oxygen was lowered mesocosms were covered with plastic to inhibit oxygen diffusion into the tanks from the air. After 48 hours, metal dividers were pushed into the sediment between habitat types, water was siphoned, sediment from each habitat was removed, sieved through 250μm nitex mesh, and mayflies were counted.

Effects of Hypoxia 2– Behavioral Arenas

Behavioral arenas were constructed to closely examine the burrowing behavior and location of *Hexagenia* when given a choice of bare sediment and sediment covered with dreissenid mussels. We tested two levels of perceived fish predation risk (fish odor present vs. absent); resulting in two treatments replicated 5 times (N=10). Each arena was examined under normoxic and then hypoxic oxygen levels. The arenas (25.4cm x 1.90cm x 25.4cm; Figure 1a) were constructed of acrylic sheets and filled with 6cm of Lake Erie sediment. Arenas with a perceived predation threat present were filled with water from a large aquarium with adult Lake Erie benthivores present; all other arenas were filled with dechlorinated tap water. After the water was added, we placed a layer of *Dreissena* on half of the sediment and a line was drawn to show the separation of the *Dreissena* side from the bare sediment side. A horizontal black line was drawn to represent the sediment-water interface (Figure 1b).

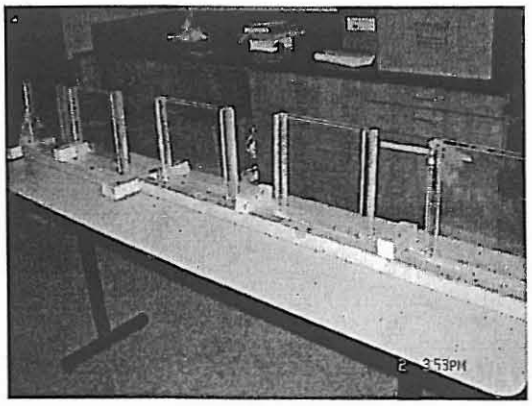

Figure 1a: A photograph of 5 behavioral arenas

After the sediment in each arena had enough time to settle, six *Hexagenia* ($1400/m^2$) were released at the center of the arena and watched carefully so that initial habitat could be recorded. The arenas were started one at a time and observed for 15 minutes. When the arenas were observed *Hexagenia* location, number of *Hexagenia* with tail only, tail and body, and full body exposures out of the sediment, the number of burrow holes, burrow length and shape, and time spent in the water column were recorded. After the initial fifteen-minute observation, each arena was video taped again for fifteen minutes to record any changes as the next arena was observed.

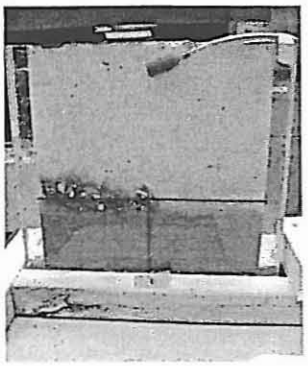

Figure 1b: Behavioral arena showing bare sediment and *Dreissena* habitats.

After 24 hours the arenas were again observed for 15 minutes before lowering the oxygen levels. We lowered the oxygen levels by removing the forced air and then bubbling in N_2 gas until the oxygen was lowered to between 15 - 20% saturation. Once the oxygen was lowered the arenas were covered with plastic to inhibit oxygen diffusion into the water from the air. Each arena was again observed visually for 15 minutes after hypoxia was introduced and then video taped for the next 15 minutes to note any changes in preference or behavior due to decreased oxygen. We then let each arena set after introducing hypoxia and 3 hours post-hypoxia we observed them one last time for 15 minutes and then video taped for the next 15 minutes.

Results

Fish foraging on *Hexagenia* was not impacted by the presence of *Dreissena*-covered sediments. Yet, light levels at the surface differed between to the two treatments (*Dreissena*-covered sediment: 0.798mE/m^2/s, bare sediment: 0.290mE/m^2/s). Yellow perch consumed about 4 mayflies in a 24-hour period regardless of the presence of *Dreissena* (Figure 2a). Round gobies behaved similarly, consuming about 6 mayflies in a 24-hour period and there was no difference between the bare sediment and *Dreissena*-covered sediments (Figure 2b). However, round gobies in the *Dreissena*-covered sediment treatments actually consumed more food than when in bare sediment treatments as they also were found to eat small dreissenids in the mesocosms.

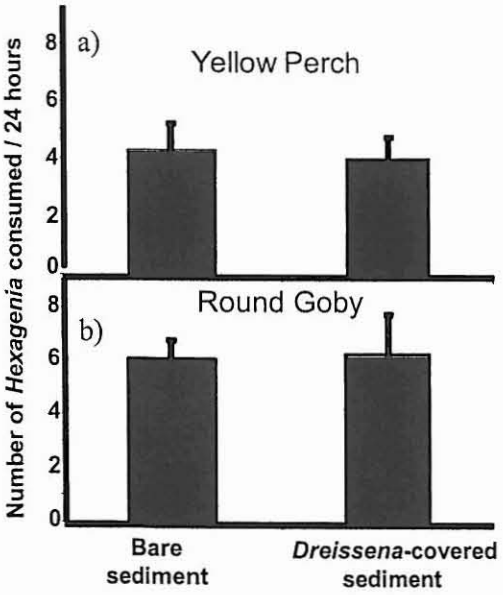

Figure 2: The number of *Hexagenia* consumed in 24 hours by a) Yellow perch and b) Round gobies

Although direct effects of *Dreissena* on fish foraging were not found, hypoxia impacted *Hexagenia* behavior, which may in turn affect fish foraging success. The results from the large hypoxia mesocosm experiment did not show effects of hypoxia on *Hexagenia* habitat preference. We did observe that in tanks with lowered oxygen *Hexagenia* were found in the water column while others were lying on top of the sediment, this result was not found in treatments with normoxic conditions. We also did not find an effect of a perceived threat of predation on *Hexagenia* habitat

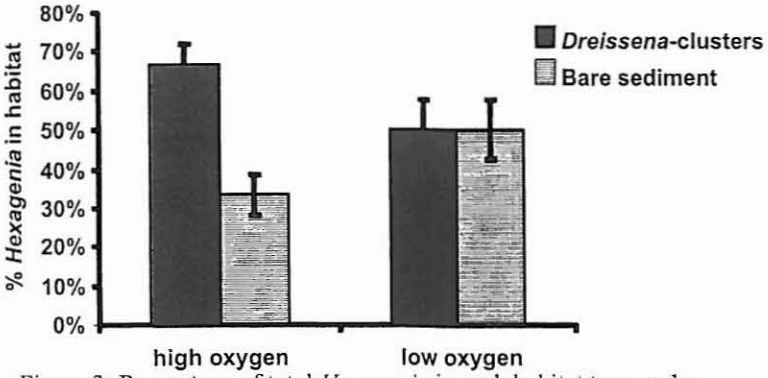

Figure 3: Percentage of total *Hexagenia* in each habitat type under high and low oxygen concentrations.

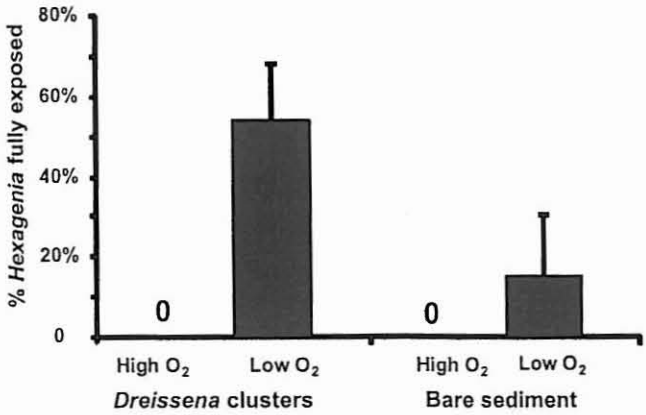

Figure 4: Percentage of *Hexagenia* in each habitat fully exposed under high and low oxygen conditions when a perceived threat of fish predation was present.

selection in the large mesocosm experiment. Many of the results from this experiment were inconclusive because we found that most of the changes in *Hexagenia* due to hypoxia were behavioral and hard to measure in a large mesocosm. Therefore we conducted experiments in behavioral arenas, which allowed us to more closely observe *Hexagenia* behavior. *Hexagenia* in behavioral arenas at high oxygen concentration selected for *Dreissena*-covered sediments both with and without a perceived threat of predation (Figure 3) as hypothesized from previous experiments. Once the oxygen in the mesocosms was lowered, *Hexagenia* no longer selected for *Dreissena*-colonized habitat and were evenly spaced between the habitat types in both treatments (Figure 3).

Hexagenia behavior changed after oxygen levels were lowered in the arenas. After 24 hours all *Hexagenia* in both habitat types with predation threat present were burrowed and no *Hexagenia* were fully exposed (Figure 4). Three hours after hypoxia in the *Dreissena*-covered sediment over 50% of the mayflies in that habitat section were fully exposed, and on the bare sediment over 10% were exposed (Figure 4). *Hexagenia* in behavioral arenas without a perceived predation threat began to leave their burrows and fully expose their bodies immediately after the oxygen was lowered (Figure 5). This response was delayed when the perceived predation threat was present (Figure 5).

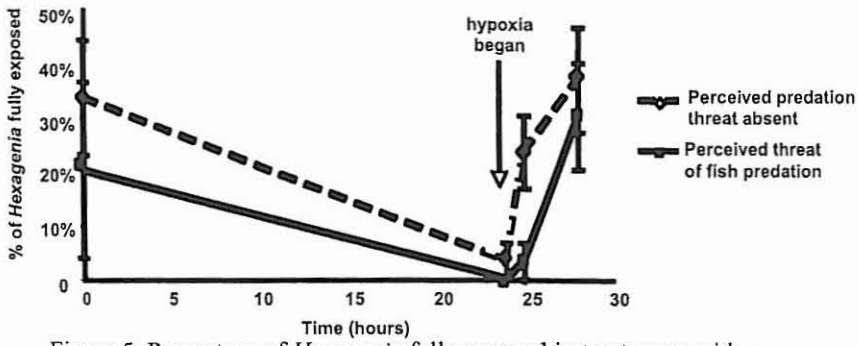

Figure 5: Percentage of *Hexagenia* fully exposed in treatments with a perceived threat of predation and without.

Discussion and Conclusions

The presence of *Dreissena*-covered sediments did not affect the foraging success of yellow perch and round gobies in this experiment (Figures 2 and 3) as we had originally hypothesized. Our results therefore suggest that the effect of *Dreissena* on fish consumption of *Hexagenia* is very different than that of hard substrate *Dreissena* clusters, which decrease fish foraging on epifaunal invertebrates such as amphipods (Gonzalez and Downing 1999; Mayer et al. 2001; Beekey et al. 2004b). Overall, round gobies may actually benefit from the presence of *Hexagenia* beneath *Dreissena* clusters because they can feed on both food sources. We suggest that differences in light were responsible for the lack of *Dreissena* treatment effect on fish

foraging. *Dreissena* are very good filter feeders and can increase water clarity (Vanderploeg et al. 2002), and light levels were higher in treatments with *Dreissena*. Even though *Dreissena* clusters may provide structural refuge from predation, fish feeding near clusters are in a higher light, lower turbidity environment than fish feeding over bare sediment. As part of her dissertation research K. DeVanna will conduct a similar study this summer, holding light levels constant by adding turbidity to the *Dreissena*-covered sediment treatments. This additional study will allow us to understand the exact mechanisms by which soft-sediment dwelling *Dreissena* affect the foraging of fish. Nonetheless, the conditions mimicked by the current study most closely reflect conditions observed in lakes; fish attempting to feed on *Hexagenia* in bare sediment experience high turbidity, whereas fish feeding near *Dreissena* experience low turbidity, but a more complex benthic habitat.

These findings support previous *Hexagenia* habitat selection experiments, which found that *Hexagenia* preferred live *Dreissena* cluster sediment over artificial clusters and bare sediment (DeVanna et al. in prep). This result suggests that *Hexagenia* are not selecting for *Dreissena*-covered sediments as protection from predation, but rather some added benefit from live dreissenids. Burrowing mayflies may be responding to the food resource of feces and pseudofeces, similarly to other invertebrates (Stewart et al. 1998; Roditi et al. 1997). Alternatively, *Dreissena* are very efficient filter feeders (Kryger & Riisgard 1988) and may increase the flow of well-oxygenated water above the clusters, although water within and below *Dreissena* clusters has lower dissolved oxygen and water quality (Burks et al. 2002; Beekey et al. 2004*a*). Water just above the cluster may still be well oxygenated and available to mayflies, and *Dreissena* may direct strong currents into their burrows. However during short periods of hypoxia in the western basin of Lake Erie *Hexagenia* may be negatively impacted by their selection of *Dreissena*-covered sediment.

Hexagenia habitat selection was impacted by the presence of hypoxia. Initially *Hexagenia* selected for *Dreissena*-covered sediment, but shortly after hypoxia was achieved *Hexagenia* were evenly spread out in the behavioral arenas (Figure 3). Even more interesting was that *Hexagenia* exited their burrows under low oxygen conditions, and this response was most often observed when *Hexagenia* were burrowed beneath *Dreissena* clusters (Figure 4). *Hexagenia* do receive protection from predation by burrowing in the sediment, and leaving the burrow significantly increases a mayfly's risk of being preyed upon. Even under hypoxic conditions fish will swim into the low oxygenated benthos to feed and then return to well oxygenated pelagic water (Rahel and Nutzman 1994). This leads to a trade-off between low oxygen conditions and refuge from predation vs. well-oxygenated water and increase the risk of predation. When we added the perceived threat of fish predation into the behavioral arenas, we found that the *Hexagenia* stayed in their burrows longer after hypoxia, but still came out of the burrows and fully exposed themselves three hours after hypoxia (Figure 5). Therefore, although we did not see an affect of *Dreissena*-covered sediments on the foraging success of yellow perch or round gobies, many important fish species may actually be positively affected by this relationship during periods of hypoxia when they can swim into hypoxic waters and feed on *Hexagenia* emerged from their burrows.

Information Dissemination

Portions of this research have been presented as oral presentations at the University of Toledo – Department of Environmental Sciences colloquium series and the University of Toledo Sigma Xi conference. Results from this project will also be presented orally at the 2008 International Association for Great Lakes Research Conference and as a poster presentation at the 2008 Lake Erie Millennium Network Conference in Windsor, Ontario.

A portion of this research was conducted during the summer of 2007 by a NSF funded Research Experience for Undergraduates (REU) and therefore supported NSF's goal of training undergraduates in research. This undergraduate student shared results through a research paper and presentation. This research will also be included as a chapter in K. DeVanna's Ph.D. dissertation and a manuscript will be submitted to a scientific journal within one year of this final report.

Acknowledgements

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