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Role of Dreissena as ecosystem engineers : effects to native bioturbators and benthic community structure and function

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Role of *Dreissena* as ecosystem engineers: Effects to native bioturbators and benthic community

structure and function

By

Kristen M. DeVanna

Submitted as partial fulfillment of the requirements for

The Master of Science Degree in Biology (Ecology-track)

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The University of Toledo

December 2006

An Abstract of

Role of *Dreissena* as ecosystem engineers: Effects to native bioturbators and benthic community

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It is well known that invasive species, such as the dreissenid mussels in the Great Lakes, play significant roles in changing the substrate, community species composition, and habitat. This study examined the role of *Dreissena*, (zebra mussel, *D. polymorpha* and quagga mussel, *D. bugensis*) as an invasive "paver", which compacts the sediment, and its effects on two native bioturbators, *Hexagenia* (burrowing mayflies; *H. limbata* and *H. rigida*) and unionid bivalve mollusks. Resulting consequences on sediment properties, infaunal invertebrates, and microbial community composition were analyzed. I further examined the spatial relationship between *Dreissena* and *Hexagenia*. Experiments showed that *Hexagenia* density increased in the presence of *Dreissena*, nematodes decreased, and oligochaetes and microbes were unaltered. In the absence of *Dreissena*, bioturbating species altered sediment water content and increased infaunal invertebrate densities, microbial activity, and microbial functional diversity. In further

exploration of the relationship between *Dreissena* and *Hexagenia*, *Hexagenia* preferred habitat

with 50-100% spatial coverage of live *Dreissena* clusters. These experiments thus revealed

habitat facilitation by an invasive ecosystem engineer on a native ecosystem engineer,

Hexagenia, with opposite effects on invertebrates, microbes, and sediment properties.

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Chapter One

Introduction

Invasive species can significantly impact ecosystem function by competing with native species; whose consequences are most dramatic when the invasive alters physical properties of the habitat (Crooks 2002). Organisms that control the availability of resources to other organisms by physical modification of habitats are termed "ecosystem engineers" (Jones et al. 1994, 1997). The effects of an invasive ecosystem engineer on native ecosystem engineers however, have not been previously studied. I thus tested the interactions between invasive and native ecosystem engineers with opposing physical habitat modifications; mixing vs. compaction of sediment. In this study I focused on invasive *Dreissena* (zebra mussel *D. polymorpha* and quagga mussel *D. bugensis*); which alter benthic substrates by covering hard surfaces, or 'paving' the soft sediment (Silver Botts et al. 1996). Many native sediment-dwelling invertebrates dig and burrow in the sediment creating bioturbation, which is another form of ecosystem engineering. The purpose of this study was to examine the effects of an invasive "paver" on two native bioturbators and the resulting consequences on sediment properties and community composition.

Dreissena were introduced into North America in 1986 (Hebert et al. 1989), since have colonized a large range of habitats, and have the potential to continue to spread (Drake & Bossenbroek 2004). *Dreissena bugensis* are capable of inhabiting soft substrates and were initially found in deeper, cooler waters (Mills et al. 1996; Dermott & Kerec 1997; Berkman et al. 1998; Bially & MacIsaac 2000), but are currently replacing *Dreissena polymorpha* throughout the Great Lakes (Mills et al. 1999). *Dreissena bugensis* are now present in shallow, warmer waters of the western basin of Lake Erie and increased from 20% of the dreissenid population in 1998 to 80% in 2001 (Stoeckman 2003). The impact of this shift from colonies primarily on hard substrates (*D. polymorpha*) to an increase in soft substrate colonies (*D. bugensis*) is still largely unknown, as many different processes occur at the sediment water interface.

Dreissena have been found to affect the density and survival of benthic invertebrates. Studies have shown that *Dreissena* on hard substrates increase local abundance and diversity of macroinvertebrates due to increased structural complexity (Silver Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998; Gonzalez and Downing 1999), especially when the background substrate is soft (Mayer et al. 2002; Beekey et al. 2004a). Further, fish predation on benthic prey decreases in the presence of *Dreissena* clusters (Gonzalez and Downing 1999; Mayer et al 2001; Beekey et al. 2004b). Still unknown is how live *Dreissena* clusters overlying soft sediments and the build up of dead dreissenid shells affect sediment-dwelling invertebrates. Some infaunal species (eg. *Oecetis* spp., oligochaetes, and *Hexagenia*) fluctuate or decrease in abundance (Beekey et al. 2004a) and infaunal filter feeders decline after colonization by *Dreissena* (Strayer 1999; Nalepa et al. 2003; Nalepa et al. 2005). Freeman (1999) found that burrowing mayfly survival was higher in the absence of *Dreissena*. Therefore, *Dreissena* may decrease abundance

and diversity of infaunal invertebrates by direct "paving" of the sediment, which may reduce available habitat or lower dissolved oxygen, and consequently reduce numbers of bioturbators.

Bioturbators are themselves ecosystem engineers that alter conditions at the sediment water interface as a result of biogenic mixing of sediment through feeding and burrowing activity (Solan et al. 2004; De Haas et al. 2005). Each bioturbating species has been found to have a distinct effect on the surrounding fauna; as a result, the existence of a diverse bioturbating assemblage can increase both community species richness and diversity (Widdecombe et al. 2000). Bioturbation is vital to aquatic benthic communities because it can influence sediment oxygen concentration, sediment grain size, rate of organic matter decomposition, sediment water content, and microbial activity (Levinton 1995; Solan et al. 2004). The lake microbial community drives the degradation of organic material, transforming nutrients into forms available to plants and algae. As a result, changes in the microbial community can have large ecosystem level impacts. Therefore, changes in the process of bioturbation may inhibit a number of important ecosystem processes that occur at the sediment water interface, such as microbial activity and diversity, as well as affect the fundamental community structure of infaunal invertebrates.

Unionid mussels and burrowing mayflies are historically important native bioturbators in many areas of the Great Lakes region. Unionid mussels formerly were the dominant macrobenthic animal in the western basin of Lake Erie, totaling 78% of the standing crop in the 1950s (McCall et al. 1979). Unionids have been called 'biological bulldozers' because they can move and disturb large amounts of sediment (McCall et al. 1979; Thayer 1983). Unionid densities and diversity have declined throughout North America due to anthropogenic habitat loss and change, pollution, and competition with exotic species (Metcalfe-Smith et al. 1998).

Dreissena, which are also filter feeders, have contributed substantially to this decline by attaching to exposed shells and interfering with feeding, respiration, and normal burrowing activities (Williams et al. 1993; Schloesser & Nalepa 1994; Nalepa et al. 1996; Ricciardi et al. 1998). In this sense *Dreissena* may fill the ecological niche vacated by the unionids, but their effects on the sediment may be opposite: mixing by unionid vs. capping of soft sediment by *Dreissena* clusters.

Dreissena impacts on *Hexagenia* and other sediment-dwelling invertebrates are not well understood. *Hexagenia* (*H. limbata* and *H. rigida*) pump oxygenated water through their burrows, creating oxygenated layers of sediment (Wang et al. 2001). *Hexagenia* were formerly abundant in the western basin of Lake Erie, but populations declined to near extirpation in the 1950s during times of hypoxia due to their sensitivity to periods of low oxygen (Nebeker 1972; Winter et al. 1996; Gerlofsma et al. 1998). Increases in abundance and recolonization have been documented since the early 1990s (Krieger et al. 1996; Schloesser et al. 2000; Schloesser & Nalepa 2001), but populations remain unstable, with their variability linked to anthropogenic and environmental factors (Schloesser & Nalepa 2001; Bridgeman et al. 2006). Although *Dreissena* colonies on hard substrates have not yet been shown to have large impacts on the *Hexagenia* population, expansion of *Dreissena* to soft substrates (Coakley et al. 2002) has the potential to greatly alter the currently resurging, yet still variable mayfly population.

The goal of this experiment was to analyze 1) the effects of soft sediment *Dreissena* clusters on the bioturbation process of *Hexagenia* and a unionid, and 2) the resulting consequences to the macroinvertebrate community, microbial community, and sediment properties. *Dreissena* have been a major contributor to the decline of native mussels, therefore, I hypothesized *Dreissena* would decrease the bioturbation activity of unionids. Colonization by

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Dreissena reduces the amount of soft sediment available for habitation by "paving" the sediment as well as reducing oxygen concentrations (from 1.2 to 2.6 mg mL^{-1}) underlying mussel colonies (Beekey et al. 2004a), which I hypothesized would reduce the density of *Hexagenia*. I also hypothesized that *Dreissena* would both directly and indirectly affect macroinvertebrate numbers, microbial activity and functional diversity, sediment water content, and sediment organic matter content. Therefore, I hypothesized a decrease in macroinvertebrate numbers, microbial activity and functional diversity, sediment water content, and sediment organic matter content 1) directly by *Dreissena* paving the sediment and 2) indirectly by *Dreissena* decreasing unionid and *Hexagenia* numbers, resulting in a decrease in bioturbation.

The results from the above experiment and personal observations from the western basin of Lake Erie led to a second set of experiments conducted to more closely examine the relationship between *Dreissena* and *Hexagenia*; notably whether *Hexagenia* avoid or are facilitated by soft sediment *Dreissena* clusters. Overall, these studies not only examine the effects of *Dreissena* on two important sediment-dwelling bioturbators, but also the consequences to benthic community structure and function.

Chapter Two

Methods

Bioturbation Experiments

I examined the effects of *Dreissena* on two native bioturbators, *Hexagenia* and unionids, as well as the different consequences of compacting vs. mixing the sediment on sediment properties, infaunal invertebrate densities, and microbial activity and functional diversity. I tested this question by conducting both pond and lake mesocosm experiments; the pond experiment was more controlled but the lake experiment exhibited natural conditions.

Pond mesocosm experiment: I established mesocosms in the University of Toledo's Lake Erie Center pond in Oregon, Ohio, for 8 weeks (June-August 2005). Eight treatments including all combinations of two common native bioturbators and *Dreissena* were conducted (Table 1a) with 5 replicates of each treatment (N=40).

Each experimental plastic mesocosm (41cm diameter and 43cm height) had 20 holes (~2.5cm diameter) above the sediment to increase water flow through the mesocosms, and was covered with hardware cloth (~1mm^2 mesh). Each mesocosm was filled with 20cm of nearshore western Lake Erie sediment that had been sieved through 1.0mm mesh to remove *Hexagenia* and *Dreissena*; this depth was chosen because unionids burrow as deep as 20cm (McCall et al. 1979).

The mesocosms were placed around the inside edge of the pond with the top of each mesocosm ~5cm above the water's surface, and allowed to equilibrate for one week before invertebrates were introduced. The giant floater (*Anodonta grandis)* is a common and ecologically important species of unionid and therefore was used for both bioturbation experiments. The unionids were collected from the Lake Erie Center pond in the fall of 2004 and then housed at the Freshwater Mussel Conservation and Research Center in Columbus, OH prior to my experiments. *Dreissena* and *Hexagenia* were collected from western Lake Erie at their naturally occurring ratios. *Dreissena* were collected from both hard and soft substrates, and *Hexagenia* were collected from soft substrates after spring emergence to decrease risk of emergence during the experiment.

The mesocosms had sediment surface areas of $0.138m^2$. In unionid treatments, a single unionid was added to each mesocosm ($7/m^2$), similar to densities found in Lake Erie prior to their decline (McCall et al. 1979; Dermott 1994). Since the density of *Dreissena* on soft sediments in Lake Erie can reach 3400 individuals m^{-2} (Coakley et al. 2002), I added a representative sample of 445 individuals to each *Dreissena* treatment mesocosm ($3224/m^2$). Initially, dreissenid mortality was high, so approximately 200 additional mussels were added. Based on the current proposed metric of the Ohio Lake Erie Commissions' Lake Erie Quality Index, a density of $201-300/m^2$ *Hexagenia* nymphs receives a score of "excellent" (Krieger and Hammett, 2004), therefore 38 individuals ($275/m^2$) were placed in each *Hexagenia* treatment mesocosm.

Lake experiment: Mesocosms were installed in western Lake Erie (41.8214 W, 83.1355 N) for 8 weeks (July-September 2005) at an 8m deep site that was characterized by consistently high densities of *Hexagenia* (T. Bridgeman, personal comm.). Twenty metal cylinders (41cm

diameter, 38cm height) were inserted 20cm into the sediment by SCUBA divers. Each metal cylinder had an attached lid with $1cm^2$ mesh to allow water flow, while excluding most fish.

The experiment consisted of three treatments levels (Table 1b), with five replicates placed in a random design (N=15). All species naturally occurring in the sediment where the cylinders were placed were left unaltered, except *Dreissena*. Unionids were not removed from the study site because very few, if any, unionids currently inhabit the area (Schloesser & Nalepa 1994). *Hexagenia* already inhabited the soft sediment; therefore densities of *Hexagenia* were not manipulated. Unionids and *Dreissena* were placed into the mesocosms. Collection of invertebrates, sediment surface area created by mesocosms, and experimental invertebrate densities were the same as the pond experiment.

Sampling and Data Analysis: In the pond experiment, invertebrates, sediment, and the microbial community were sampled before treatment initiation in 10 mesocosms. Invertebrates and microbes were sampled again at the conclusion of the experiment, and the microbial community was sampled in three out of five treatment replicates in the random block design. Sediment cores from each mesocosm were taken 2 weeks after initiation and at the conclusion of the experiment.

For the lake experiment, I sampled sediment properties, invertebrate community, and microbial activity and functional diversity from five baseline locations prior to mesocosm installation. Each mesocosm was sampled again at the conclusion of the experiment. As a result of low visibility, (~20-30 cm as estimated by divers) not all mesocosms were recovered. Divers were able to locate and sample 4 *Hexagenia* only treatments, 3 *Hexagenia* and unionid treatments, and 2 *Hexagenia* and *Dreissena* treatments.

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Macroinvertebrate densities, sediment properties, and microbial activity and functional diversity were measured in both experiments similarly to examine the relationship between *Dreissena* and infaunal invertebrates, as well as the resulting effect on bioturbation. Invertebrates and sediment properties were sampled to 6cm with 5.715cm diameter clear acrylic cores. The invertebrate samples were sieved though 250μm mesh, preserved in 70% ethanol, counted under a dissecting microscope, and split into ten taxonomic categories: *Hexagenia*, *Dreissena*, oligochaetes, nematodes, chironomids, fingernail clams, amphipods, ceratopogonids, snails, and odonates. All invertebrate samples were counted for the lake experiment, and in the pond experiment three replicates of the three treatments also conducted in the lake experiment (*Hexagenia* only, *Hexagenia*/*Dreissena*, and *Hexagenia*/unionid) as well as the control treatment were analyzed. Sediment water content and organic matter were determined after the cores were sliced into three equal sections: 0-2cm, 2-4cm, and 4-6 cm (Wetzel & Likens 2000).

All data were analyzed using SAS 9.1 using an alpha level of 0.05. Macroinvertebrate densities and sediment properties in the bioturbation experiments were analyzed using Analysis of Variance (ANOVA), followed by a Tukey's multiple comparison test when the overall ANOVA model was significant. Sediment property data were analyzed by treatment, as well as grouped, and analyzed according to invertebrate presence (*Dreissena*, *Hexagenia*, or unionid). Percent water content and percent organic matter were arcsin square root transformed to normalize percentage data (Zar 1999). Sediment water content and organic matter for the pond experiment were graphed as percent change from the control mesocosms, thus eliminating any tank effect. This analysis could not be replicated for the lake experiment due to the lack of a control treatment (i.e., no *Hexagenia*), and the data were thus graphed as percent change from the initial sampling.

The microbial community was sampled by collecting surface sediment ~3cm deep in a 50mL sterile tube. Community-level physiological profiling (CLPP) of the microbial community was conducted using Biolog EcoPlate microtiter plates to estimate microbial activity and functional diversity. Although CLPP analysis is selective and focuses only on the culturable portion of the heterotrophic bacterial community, the analysis provides a community level index of the metabolic potential of the microbial community (Haack et al. 1995; Lohner et al. in press) and is currently the only quick and easy gross method for sampling the microbial community. These plates contained 31 wells, each with a tetrazolium dye, and a single carbon (C) source. A control well containing no carbon source was present. This array of 31 wells was replicated three times on each plate. Plates were inoculated following the procedure of Lohner et al. (in press).

The microbial community data were analyzed using two parameters describing the metabolic activity of the communities. The utilization of any C-source resulted in the respiration-dependent reduction of the dye, producing a purple coloration in the well containing the utilized carbon source, and an absorbance value was measured daily. After subtracting of the absorbance value of the control well from each of the remaining 30 wells; the average well color development (AWCD), which is an index of microbial activity (Garland 1996) and community metabolic diversity (S) (Zak et al. 1994), were analyzed. The three replicates of each plate were averaged to estimate AWCD and S for each treatment. The AWCD estimated the overall respiration of the heterotrophic community (Bitton and Koopman 1986) and was calculated for each sample as the average absorbance of all 93 wells (31 carbon source-containing wells x 3 replicates) at each time point. S estimates the overall metabolic or functional diversity of the microbial community, and was calculated by summing the number of wells at each time point

that exhibited an absorbance exceeding 0.25 (Garland 1996). Both AWCD and S were measured throughout, and only the readings when AWCD and S leveled off were statistically analyzed (pond=72 hours, lake=127 hours). ANOVA was conducted for both experiments to analyze AWCD and S by treatment. For the pond experiment, a T-test was conducted that compared the mean AWCD and S in treatments at the conclusion of the experiment with and without bioturbators.

Habitat Preference Experiments

Based on findings from the pond and lake experiments, mesocosm experiments were conducted during the summer of 2006 to more closely examine the spatial relationship between *Hexagenia* and *Dreissena*. *Dreissena* and *Hexagenia* were collected as in the pond experiment. All mesocosms in these experiments were filled with 6cm of either nearshore or offshore sediment that was first sieved through 1.0mm mesh. Before experiments began, trials for the habitat type selection were run at different time intervals between 24 and 72 hours and no differences were seen between trials. Therefore, as a result of sampling logistics, each experiment ran for a different length of time, but all trials within an experiment ran for the same length of time.

Habitat type selection: I tested whether *Hexagenia* selected for or avoided *Dreissena* clusters on sediment. Experimental mesocosms (41cm diameter and 43cm height) were separated using metal dividers into three equal "pie-slice" shaped sections, each having an area of $0.046m^2$ and filled with nearshore sediment. Three different habitat types were created: 1) bare sediment, 2) live *Dreissena* clusters, 3) and artificial *Dreissena* clusters. Live and artificial *Dreissena* treatments contained approximately 250 individuals ($5434/m^2$). I created artificial

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Dreissena clusters by gluing empty, clean shells together with non-toxic glue and adding five 1g weights to each cluster.

The experiment was conducted using 5 densities of *Hexagenia* that fell within the range seen in western Lake Erie (0 to 2000/m2; Krieger 1999): 5 individuals ($\sim 100/m^2$), 9 ($\sim 200/m^2$), 18 ($\sim 400/m^2$), 36 ($\sim 800/m^2$), and 54 ($\sim 1200/m^2$). Each mayfly density was replicated three times (N=15). *Hexagenia* were added at the water's surface after the habitat-types were established. Treatments were run in random order, and due to a limited supply of *Hexagenia* and *Dreissena* replicates were run sequentially in blocks.

After 48 hours, metal dividers were again pushed into the sediment between habitat types, to prevent *Hexagenia* from moving. Water was siphoned and sediment from each habitat was removed, sieved through 250μm nitex mesh, and *Hexagenia* were counted in each habitat section. Dead *Hexagenia* in a habitat were counted as a part of that habitat type, but those that were in the water column or were severed by the metal dividers were not counted.

The habitat selection experiment was repeated with sediment collected from an offshore site in western Lake Erie (41.7976 W, 83.3136 N), where *Hexagenia* were very abundant. Experiments were run as described above using nearshore sediment, except that three densities of *Hexagenia* were used, 9 individuals ($\sim 200/m^2$), 18 ($\sim 400/m^2$), and 36 ($\sim 800/m^2$), and were replicated three times (N=9).

Dreissena density selection: I manipulated the density of *Dreissena* to create four habitats based on percent coverage of live shells to better understand if *Hexagenia* prefer a specific density of *Dreissena*. Each rectangular mesocosm (80cm x 30cm) was split into four equal sections (20cm x 30cm) and a mixture of offshore and nearshore western Lake Erie sediment was added. The four levels of *Dreissena* coverage were: 0%, 25%, 50% and 100%.

Numbers of *Dreissena* needed for each coverage level were estimated using a template of the appropriate area. An intermediate density of *Hexagenia*, ~ 400 mayflies/m^2, was used in this experiment. Four replicates were conducted (N=4) and the order of habitats within the mesocosms was randomly selected for each replicate. After 68 hours, metal dividers were placed into the sediment between habitat types. *Hexagenia* were removed and counted as described above.

 Effect of dead shells: The final habitat selection experiment examined the effect of accumulated *Dreissena* shell fragments on mayfly habitat preference. Experimental mesocosms (41cm diameter and 43cm height) were divided into two sections, each 0.069m^2. Both sections were filled with nearshore Lake Erie sediment, and one section had 515g of dead *Dreissena* shells mixed in. *Hexagenia* were added at an intermediate density of ~ 400 mayflies/m^2. Five replicates were run for 60 hours (N=5), trials were run sequentially, and *Hexagenia* were removed and counted as above.

 Data Analysis: The percentage of *Hexagenia* in each habitat type was arcsin square root transformed to normalize data (Zar 1999). All habitat type selection data were analyzed using a 2 way ANOVA model, followed by a Tukey multiple comparison test when appropriate (SAS 9.1, alpha=0.05) with habitat type and density as main effects and the interaction of the main effects. The *Dreissena* density gradient experiment was examined using a one-way ANOVA model comparing the percentage of *Hexagenia* in each *Dreissena* habitat. The effect of dead shells was analyzed using a two-sample t-test.

Chapter Three

Results

Bioturbation Experiments

    Hexagenia in the pond experiment showed a trend towards increased density in both the *Hexagenia*-only and *Hexagenia*/*Dreissena* treatments (ANOVA; $F_{3,8}$=3.21, p=0.083; Figure 1a). Nematode densities were significantly greater in the *Hexagenia*/unionid treatment than the *Hexagenia*/*Dreissena* treatment, and the control and *Hexagenia* only treatments were not different from any other treatments based on Tukey test results (ANOVA; $F_{3,8}$=5.24, p=0.027; Figure 1a). Oligochaetes showed a trend towards increased density in *Hexagenia* only and *Hexagenia*/unionid treatments, however samples were highly variable within treatments and no significant differences were observed (ANOVA; $F_{3,8}$=1.11, p=0.401; Figure 1a). The type of invertebrate, 'pavers' vs. bioturbators, placed in each mesocosm altered sediment properties, such as water content and organic matter. On the final day of the experiment at 0-2cm depth, treatments with *Dreissena* showed a trend towards decreased sediment water content (ANOVA; $F_{7,32}$=3.61, p=0.067; Figure 1b). Also, at the conclusion of the experiment at 2-4cm depth, treatments with *Hexagenia* showed a trend towards increased sediment water content and organic matter (*sediment water content*: ANOVA; $F_{7,32}$=3.42, p=0.074, Figure 1b; *sediment organic*

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matter: ANOVA; $F_{7,32}=3.04$, p=0.091). No significant differences in sediment properties or the microbial community were seen between treatments. Unlike sediment properties, the microbial community was unchanged by the "type" of bioturbation, but what was important was simply whether bioturbators were present or absent. Treatments with bioturbators had significantly higher microbial activity, AWCD, and microbial functional diversity (S), than treatments without bioturbators (*AWCD*: T-test; $t_{0.05,22}=2.22$, p=0.037, Figure 2a; *S*: T-test; $t_{0.05,22}=2.54$, p=0.019, Figure 2b).

In contrast, I did not find differences in nematode or oligochaete densities between treatments in the lake experiment (*Nematodes*: ANOVA; $F_{3,8}=0.48$, p=0.706; *Oligochaete*: ANOVA; $F_{3,8}=0.23$, p=0.871). *Hexagenia* density, although not significant, was lowest in treatment with only *Hexagenia*. *Hexagenia* density thus increased in both treatments with *Dreissena* and a unionid, although the latter treatment was highly variable (ANOVA; $F_{3,8}=3.01$, p=0.095; Figure 3a). No differences were seen in macroinvertebrates between the initial densities and the *Hexagenia*-only treatment at the conclusion of the experiment, suggesting no mesocosm effect. Again, the type of invertebrate, i.e., 'pavers' vs. bioturbators, placed in each mesocosm showed altered sediment properties such as sediment water content. On the final day of the experiment at 0-2cm depth, the *Hexagenia*-only treatment had significantly lower sediment water content than did the *Hexagenia*/unionid treatment (ANOVA; $F_{2,6}=5.22$, p=0.049; Figure 3b). The *Hexagenia*/*Dreissena* treatment was intermediate, and unlike the pond experiment, showed a trend towards greater sediment water content than found in treatments with *Hexagenia*-only (Figure 3b). No differences were found in sediment organic matter or sediment water content at depths greater than 2cm for the lake experiment. No differences were seen in the microbial community.

Habitat Selection Experiments

In both nearshore and offshore sediment habitat selection experiments, *Hexagenia* were most often collected in the live *Dreissena* habitat (Figure 4 a,b,c) underneath the clusters suggesting no edge effect. In the experiment using nearshore western Lake Erie sediment all three habitat types, live *Dreissena* spp, artificial *Dreissena*, and bare sediment were found to significantly differ from one another (ANOVA; $F_{2,42} = 86.41$, p<0.0001). The live *Dreissena* habitat had the highest percentage of *Hexagenia*, followed by artificial *Dreissena*. The bare sediment habitat had the lowest percentage of *Hexagenia* at the conclusion of the experiment (Figure 4a).

A similar result was found when using the offshore western Lake Erie sediment, notably, there were significantly more *Hexagenia* in the live *Dreissena* habitat (ANOVA; $F_{2,24} = 11.45$, p = 0.0003; Figure 4b). Unlike nearshore sediment, no difference occurred between the artificial *Dreissena* and bare sediment habitats (Figure 4b). No difference was found in the percentage of *Hexagenia* in each habitat type across the gradient of *Hexagenia* densities in both nearshore and offshore sediment experiments (ANOVA; *nearshore habitat*density*: $F_{5,39} = 2.79$, p = 0.074; *offshore habitat*density*: $F_{5,21} = 0.38$, p = 0.690; Figures 4a and 4b respectively).

Hexagenia habitat preference differed with percent *Dreissena* coverage (ANOVA; $F_{3,12} = 14.54$, p = 0.0003; Figure 5). A Tukey multiple comparison test showed a difference between the low-density habitats (0% and 25% *Dreissena* coverage) and the high-density habitats (50% and 100% *Dreissena* coverage). Notably, approximately 75% of *Hexagenia* inhabited the high-density habitats at the conclusion of the experiments. *Hexagenia* did not show a preference between bare sediment and sediment with *Dreissena* shells (T-test; $t_{0.05,8} = 1.71$, p = 0.127; Figure 6).

Chapter Four

Discussion

Dreissena have had major system-wide impacts consistent with their role as ecosystem engineers, as they modify the physical structure of habitats (Vanderploeg et al. 2002). Many studies have shown that *Dreissena* on hard substrates increase the density of other invertebrates (eg. Silver Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998; Gonzalez and Downing 1999). However, the goal of this study was to examine the direct and indirect effects of *Dreissena* clusters on soft sediment, where they "pave" and compact substrate that was once available to native infaunal bioturbators. By affecting organisms that are themselves ecosystem engineers (i.e., bioturbators), *Dreissena* may initiate an "engineering cascade" in which their habitat modification is intensified. In this study, I found that while *Dreissena* positively affected one bioturbator, *Hexagenia*, *Dreissena* had opposite effects from other ecosystem engineers in general on the surrounding infaunal invertebrate and microbial communities, as well as on sediment properties in the pond experiment.

Paving of soft sediments by *Dreissena* impacted population density of native bioturbators as well as sediment water content, but did not impact microbial activity and functional diversity. Contrary to our hypothesis and studies examining the relationship between *Dreissena* and

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Hexagenia (Freeman 1999; Beekey et al. 2004a), I found that *Hexagenia* densities were higher in the presence of *Dreissena* (Figures 1a, 3a, and 4a, b). This is despite the fact that *Dreissena* clusters can decrease water quality and oxygen concentration beneath them (Burks et al. 2002; Beekey et al. 2004a). *Hexagenia* consistently and strongly preferred sediments covered by live *Dreissena* clusters. Bare sediment, usually thought to be the choice habitat of burrowing mayflies, was always the least selected habitat type (Figure 4a, b, and 5). This is similar to the positive effects of *Dreissena* on epifaunal invertebrates (Silver Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998; Mayer et al. 2002; Beekey et al. 2004a), as an apparent result of increased habitat complexity and decreased predation (Gonzalez and Downing 1999, Mayer et al 2001; Beekey et al. 2004b).

However, unlike other invertebrates (Gonzalez and Downing 1999; Silver Botts et al. 1996), *Hexagenia* selected for artificial *Dreissena* clusters significantly less than live *Dreissena* clusters, suggesting that habitat complexity is not the sole mechanism. Further, *Hexagenia* selected equally for habitat with 50 and 100% coverage of live *Dreissena* (Figure 5), unlike epifaunal invertebrates that show a linearly increasing response to *Dreissena* density (Mayer et al 2002). *Hexagenia* may be responding to the food resource of feces and pseudofeces (Stewart et al. 1998; Roditi et al. 1997) that are present in the clusters. Alternatively, *Dreissena* are very efficient filter feeders (Kryger and Riisgard 1988) that may increase the flow of well-oxygenated water above the clusters. Although the water within and below *Dreissena* clusters has lower dissolved oxygen and water quality (Burks et al. 2002; Beekey et al. 2004a), the water just above the cluster may still be well oxygenated and available for *Hexagenia*. The increasing spread of *Dreissena* to soft sediments and the preference of *Hexagenia* for live *Dreissena* clusters, has

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potentially had large impacts to the benthos and higher trophic levels, and thus may lead to significant changes in *Hexagenia* population densities.

Not all infaunal invertebrates responded to *Dreissena* habitat modification similarly to *Hexagenia*. For example, oligochaete density was unaffected, a result similar to previous studies (Silver Botts et al. 1996; Beekey et al. 2004a). Oligochaetes can tolerate prolonged periods of low dissolved oxygen concentration (Smith 2001), and may not be impacted by degraded water quality and low oxygen beneath the *Dreissena* clusters (Burks at al. 2002; Beekey et al. 2004a). However, the present study showed that nematode density decreased in the pond experiment (Figure 1a). Although nematodes can also withstand poor water quality, they can only survive low oxygen conditions for one to three weeks (Smith 2001). Therefore habitat underneath *Dreissena* clusters with consistently low oxygen concentration may have led to the observed decrease in numbers. Nematodes are also a very important bioturbator, and although *Hexagenia* densities increased, bioturbation actually may be inhibited or altered as a result of soft sediment *Dreissena* clusters.

Dreissena presence affected sediment water content, although cascading effects on *Hexagenia* may have also led to observed changes in sediment properties. As hypothesized, sediment water content in treatments with *Dreissena* decreased in the top 0-2 cm of sediment in the pond experiment (Figure 1b). This effect is likely to be a result of direct physical habitat modification, i.e., the weight of *Dreissena* shells compressing the sediment. Further, bioturbation may have been suppressed as a result of decreased number of nematodes that are also an important bioturbator (Smith 2001). Lastly, although *Hexagenia* density did not decline, their bioturbation activity may decrease in the presence of *Dreissena*; personal observations of *Hexagenia* in the presence of *Dreissena* have suggested that some *Hexagenia* live in empty

Dreissena shells or just below a live dreissenid and do not actually burrow in the sediment (Figure 7). The effect of *Dreissena* clusters on soft sediment may not only alter infaunal invertebrate community density and diversity, but more surprising, may change the behavior of native ecosystem engineers, resulting in a decrease in bioturbation.

Interestingly, the microbial community in our experiments was not altered by the presence of *Dreissena*, suggesting no effect of "paving" or *Dreissena* themselves.   *Dreissena* may indirectly affect microbes by increasing the numbers of epifaunal invertebrates and *Hexagenia*, which then consume microbes attached to particulate material and result in lower microbial densities (Graca et al. 2001). *Dreissena* also lowered sediment water content in the pond experiment (Figure 1b), suggesting a decrease in sediment mixing, which may have led to lower microbial activity (Levinton 1995). However, Lohner et al. (in press) found that *Dreissena* clusters themselves have high microbial activity and functional diversity as a result of the accumulation of carbon-rich compounds. The data suggest that this effect is localized to the clusters and may not extend to nearby sediment. Moreover, increases in benthic invertebrates and decreases in bioturbation may have hindered this effect. Microbial activity, structural complexity, and functional diversity are very important to overall lake ecosystem functioning, and a decrease in the microbial community by *Dreissena* directly or indirectly may disrupt many system-wide processes.

Bioturbation strongly affected the invertebrate community, microbial activity and functional diversity, and sediment water content in a manner opposite to that of *Dreissena*, which compact the sediment. Large bioturbators, *Hexagenia* and unionids, increased the density of oligochaetes and nematodes in the pond experiment, with densities highest in the treatment having the most diverse bioturbating assemblage (*Hexagenia* and unionid) (Figure 1a). In the

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lake experiment, *Hexagenia* densities were higher in the treatment with a unionid, another

bioturbator (Figure 3a). These results support the hypothesis that a diverse bioturbating

assemblage in turn increases the diversity and richness of the surrounding infaunal invertebrate

community by increasing sediment water content, sediment organic matter, and microbial

activity (Widdecombe et al. 2000; Solan et al. 2004).

Sediment water content and microbial activity and functional diversity were increased in

the presence of bioturbators, as hypothesized. Treatments with unionids, but without *Dreissena*,

revealed higher sediment water content at the sediment water interface (Figure 1b), although

unionids are known to mix sediment as deep as 10cm (McCall et al. 1979). When *Dreissena*

were present with unionids, the sediment water content was lower, suggesting that *Dreissena* led

to a decrease in bioturbation activity by the unionids or the unionids bioturbation may have been

masked by the overall effect of *Dreissena* paving the sediment. *Hexagenia* treatments increased

the sediment water content at 2-4 cm depth (Figure 1b), consistent with the fact that *Hexagenia*

burrows are 2.5-3cm deep (Wang et al. 2001). The *Hexagenia*-only treatment in the lake

experiment showed lower sediment water content than in the treatment with *Dreissena*, and also

had a lower final density of *Hexagenia*. (Figure 3a, b). Therefore sediment water content was

not only affected by the number of bioturbating species, but also by the respective density of

each species.

Microbial activity and functional diversity were both increased in the presence of

bioturbators (Figure 2a, b), as hypothesized based on previous research that suggests bioturbation

is essential to benthic communities since it stimulates microbial activity by mixing the sediment,

adding organic matter, and increasing the sediment particle surface area and the area of the

sediment water interface (Levinton 1995; Solan et al. 2004). This reaffirms that bioturbators are

essential to soft sediment communities. Thus, negative effects on bioturbation will lead to ecosystem level consequences.

The current range expansion of *Dreissena* onto soft sediments and the resulting shift in the type of ecosystem engineer present, bioturbator vs. paver, will likely have large consequences to the already changing benthos of temperate lakes. Further, the spread of *Dreissena* from hard substrates to soft will affect native ecosystem engineer diversity, density, and behavior. This can have large impacts not only to the benthos, but cascading effects to higher trophic levels and overall ecosystem functioning. For example, I found a preference of *Hexagenia* for live *Dreissena* clusters. Although protection from predation was not found to be a primary mechanism for the observed relationship, it may have impacts to higher trophic levels, such as predatory fish. *Hexagenia* are an important food source of many economically important fish species such as yellow perch (*Perca flavescens*) (Hayward & Margraf 1987; Schaeffer 2000; Tyson & Knight 2001), and may be less available to fish beneath *Dreissena* clusters. Although *Dreissena* on hard substrates have been found to positively affect epifaunal invertebrates (Silver Botts et al. 1996; Ricciardi et al. 1997; Stewart et al. 1998; Gonzalez and Downing 1999; Mayer et al. 2002; Beekey et al. 2004a), the observed relationships between infaunal invertebrates and invasive *Dreissena* may have negative consequences on the benthos and higher trophic levels. Furthermore, these effects will be magnified and possibly more severe as many impacted infaunal invertebrates are bioturbators and are essential to overall benthic and lake wide ecosystem functioning.

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VI. Table

Table 1: Treatment levels conducted in a) pond and b) lake mesocosm bioturbation experiments.

Manipulated invertebrates: H=*Hexagenia*, D=*Dreissena*, U=unionid

a)

Treatment	1	2	3	4	5	6	7	8
Invertebrate(s)	None	D	H	U	D/H	D/U	H/U	D/H/U

b)

Treatment	1	2	3
Invertebrate(s)	H	H/D	H/U
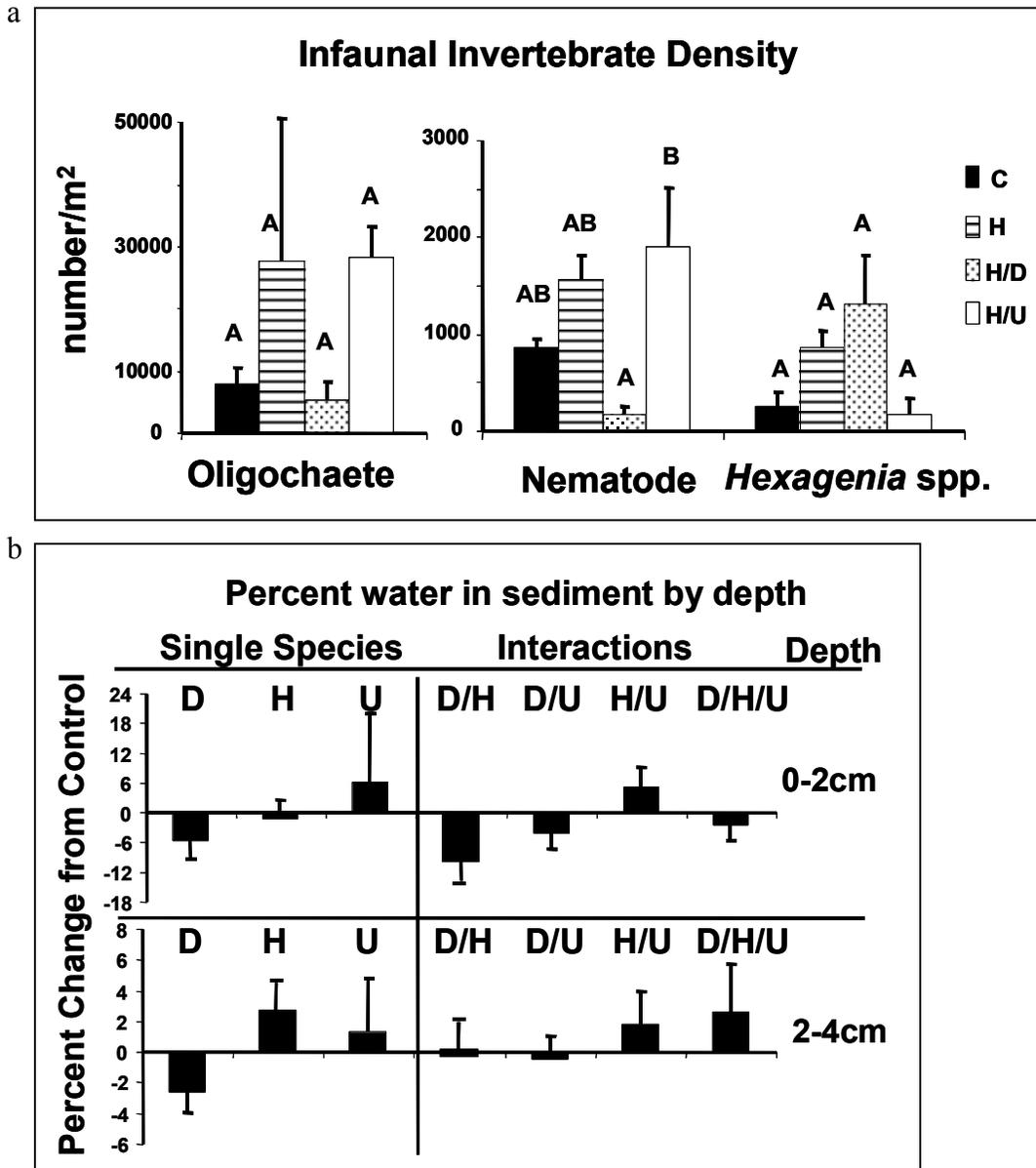
Figure 1: a) Invertebrate density in the pond experiment graphed for each invertebrate by treatment b) Percent water content in sediment at two different depths graphed as percent change from the control treatment. Error bars represent ± 1 standard error and different letters represent statistically different treatments based on the Tukey multiple comparison test (α=0.05). Treatments: C=control, H=*Hexagenia*, D= *Dreissena*, and U=unionid.

a
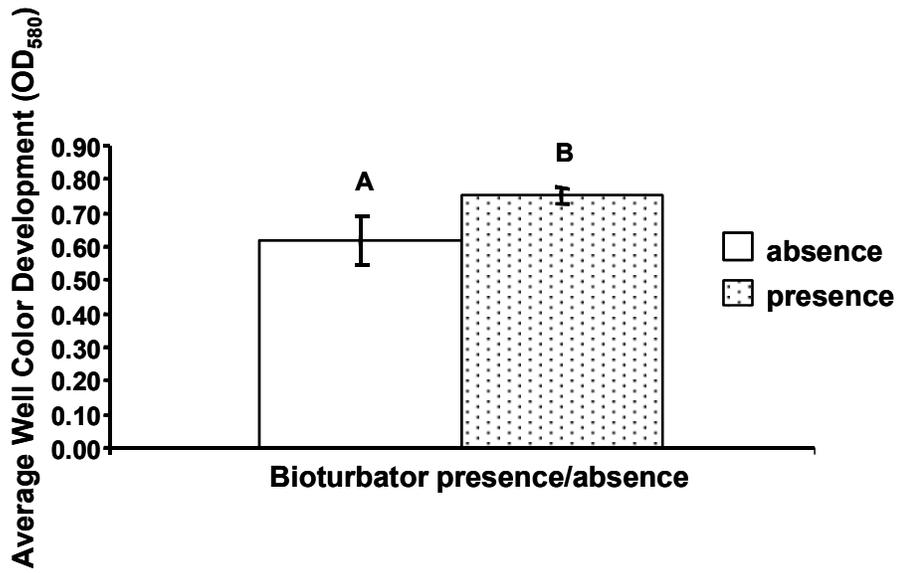
b
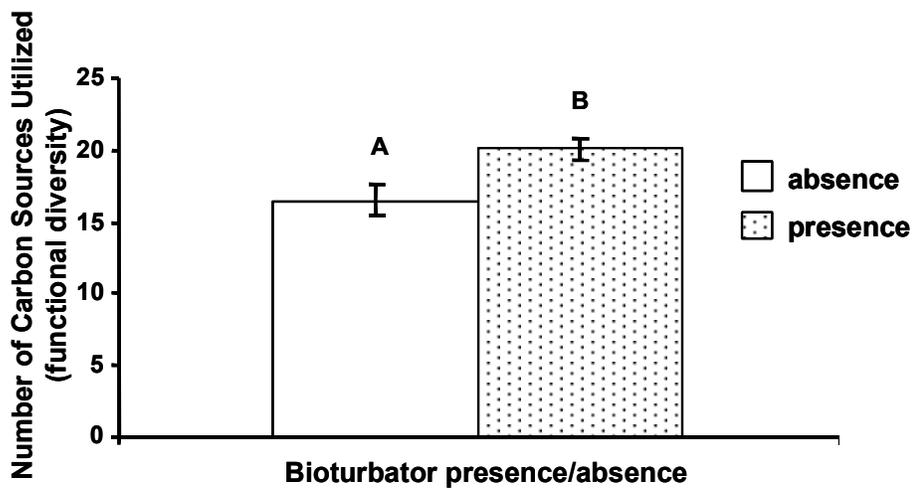
Figure 2: Average well color development (a) and community functional diversity (b) for the pond experiment analyzed as treatments with bioturbators (presence = all treatments with *Hexagenia* and unionid), and treatments without bioturbators (absence = *Dreissena* only and control). Error bars represent ± 1 standard error and different letters represent statistically significant treatments based on the Tukey multiple comparison test (α=0.05).
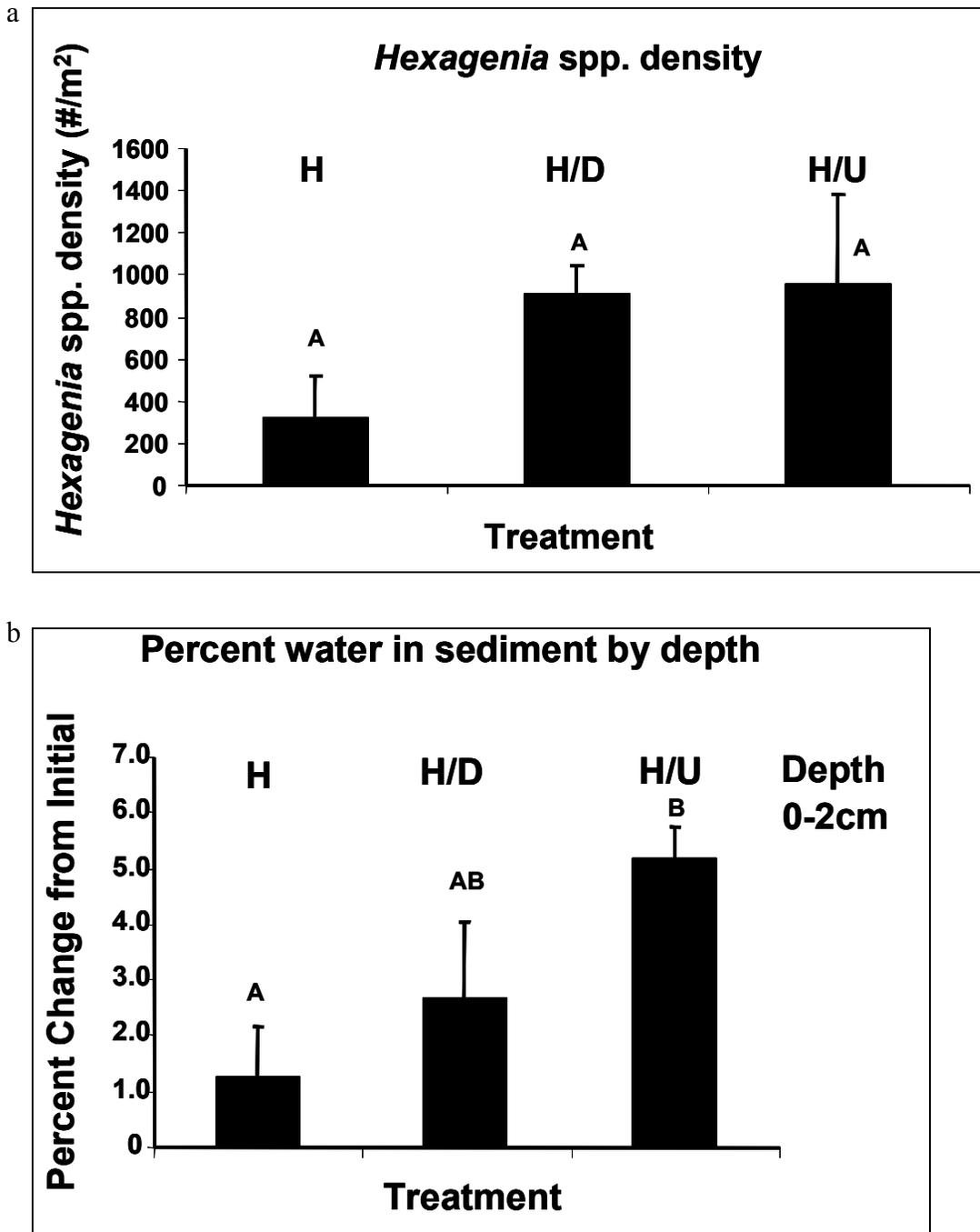
Figure 3: a) *Hexagenia* density in the lake experiment graphed by treatment. b) Percent

water in sediment at 0-2cm depth graphed as percent change from initial. Error bars

represent ± 1 standard error and different letters represent statistically significant treatments

based on Tukey multiple comparison test (α=0.05). Treatments: C=control, H=*Hexagenia*,
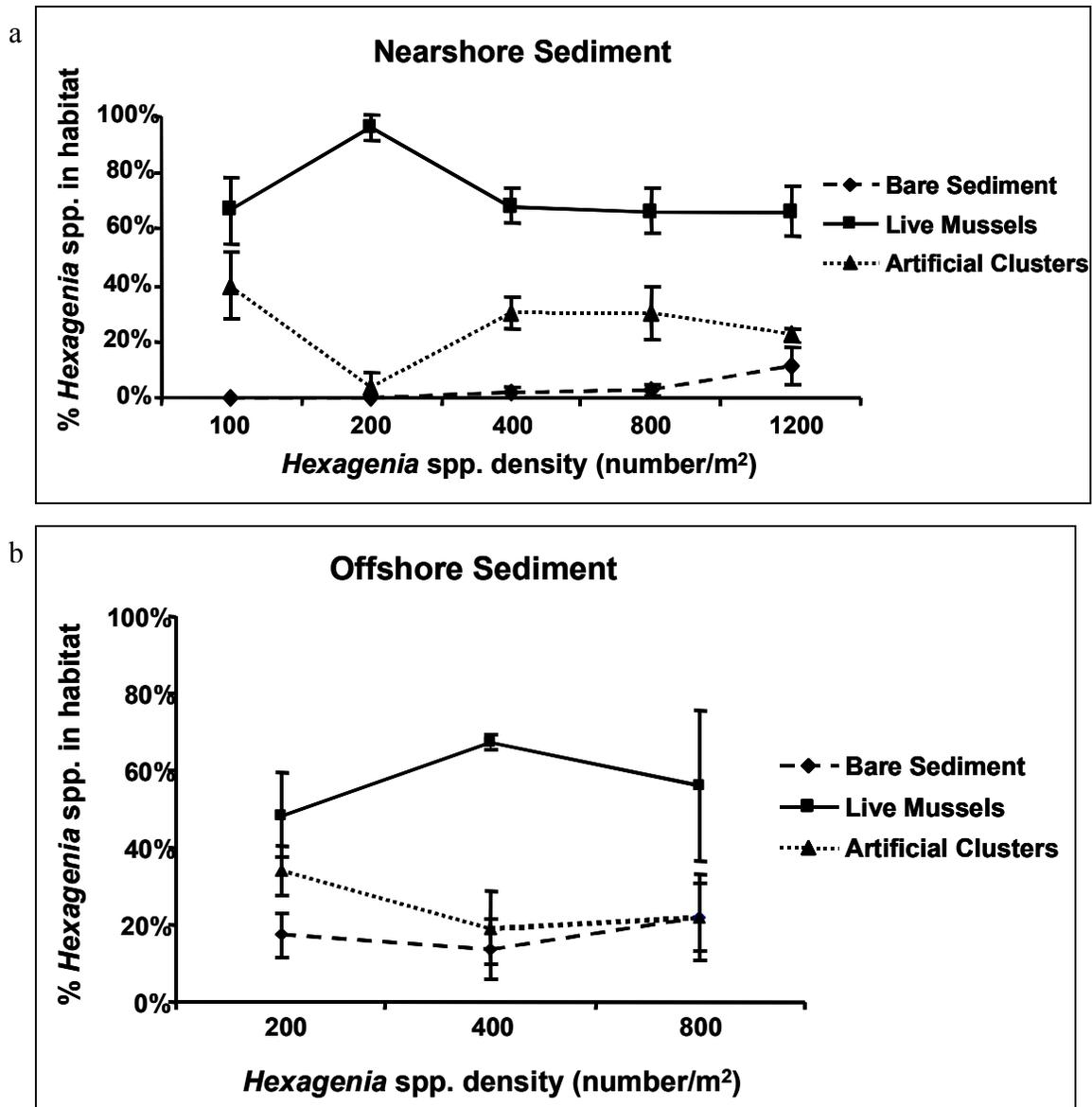
D=*Dreissena*, and U=unionid.

Figure 4: Percentage of *Hexagenia* found in each habitat type, bare sediment, live mussel clusters, and artificial mussel clusters. Two different sediments were tested, a) nearshore and b) offshore across a range of *Hexagenia* densities. Error bars represent ± 1 standard error.
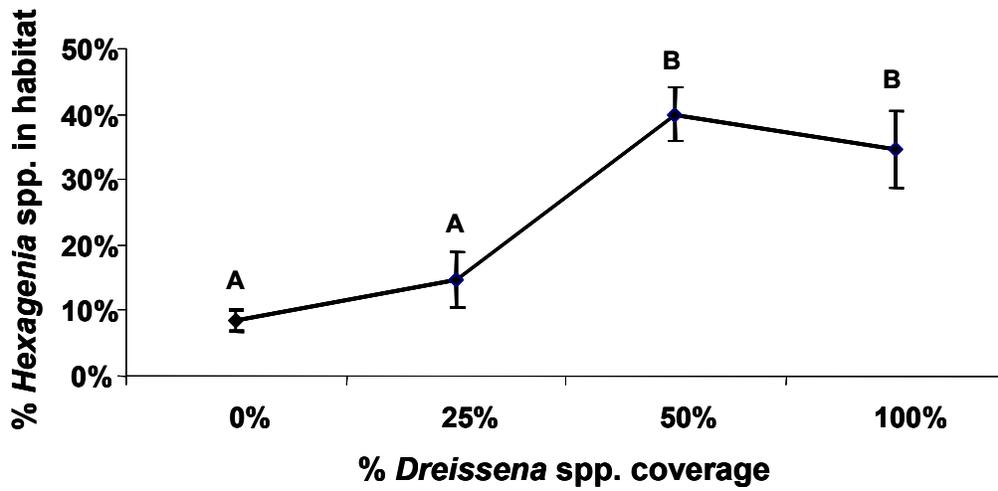
Figure 5: Percentage of *Hexagenia* found in each habitat, each with varying percentages of *Dreissena* spatial coverage. Error bars represent ± 1 standard error and different letters represent statistically significant habitats based on the Tukey multiple comparison test (α=0.05).

% *Hexagenia* spp. in Habitat
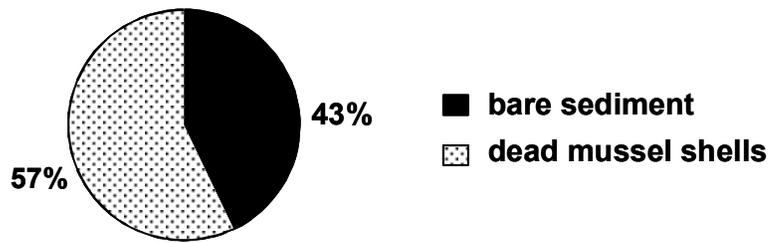

43%

57%

■ bare sediment

▨ dead mussel shells

Figure 6: Percentage of *Hexagenia* found in each habitat in bare sediments vs. habitat with sediment and dead mussel shells.
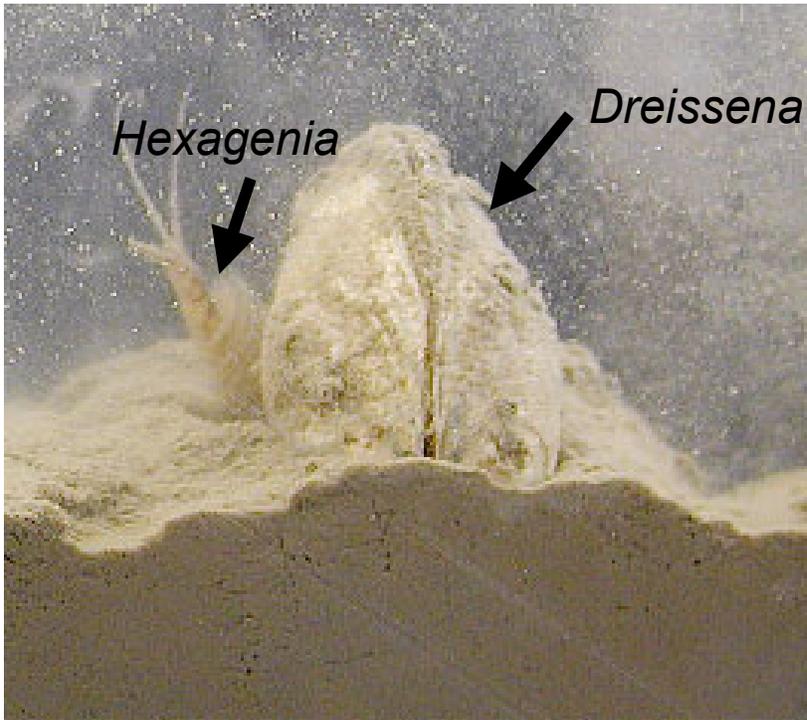
Figure 7: Photograph of *Hexagenia* burrowing beneath an individual live *Dreissena*.