# Invasive ecosystem engineers on soft sediment change the habitat preferences of native mayflies and their availability to predators

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## SUMMARY

1. Dreissenid mussels (quagga mussels, *Dreissena bugensis*, and zebra mussels, *D. polymorpha*) are invasive species that function as ecosystem engineers in the Laurentian Great Lakes. *Dreissena* are increasingly abundant on silt, sand and other soft substrates; by altering benthic habitat, these mussels can alter benthic community structure.

2. We used laboratory mesocosm experiments to examine the effects of soft-sediment *Dreissena* clusters on the habitat preference of *Hexagenia*, a native burrowing mayfly that is an important food source to fish. We conducted three experiments to test whether *Hexagenia*: (1) select for bare sediment, soft sediment covered with live *Dreissena* (added structure and food resources) or soft sediment with clusters made of empty *Dreissena* shells (added structure only), (2) prefer a specific density of live *Dreissena* on soft sediment and (3) select for or avoid sediment with an accumulation of empty *Dreissena* shells.

3. Contrary to initial expectations, we found that *Hexagenia* selected for sediment covered with live *Dreissena* clusters, followed by empty *Dreissena* shells clusters, and lastly what was previously thought to be the preferred habitat, bare sediment. Not only did *Hexagenia* prefer *Dreissena*-covered sediment, but they also preferred high densities of *Dreissena*.

4. We also experimentally tested the effects of *Dreissena*-covered soft sediment on the availability of *Hexagenia* to fish. We had three treatment levels representing three distinct habitat types: (1) bare sediment (no *Dreissena*) treatment in which water was turbid because of mayfly activity, (2) *Dreissena*-covered sediment treatment in which water was clear because of *Dreissena* filtration and (3) *Dreissena*-covered sediment with added turbidity. We found that in low light conditions, similar to many locations where both organisms are found to co-occur, both yellow perch and round goby consumption of *Hexagenia* significantly decreased when *Dreissena* covered the bottom sediment.

5. These results suggest that by choosing *Dreissena*-covered habitat, *Hexagenia* receive protection from fish predation in turbid/low light systems. However, protection from predation cannot be the only reason *Hexagenia* select *Dreissena*-covered sediments, as *Hexagenia* selected for live clusters more often than empty clusters and may be a result of additional food resources.

*Keywords*: *Dreissena*, habitat selection, *Hexagenia*, quagga mussel, zebra mussel

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# Introduction

Invasive species can significantly impact ecosystem function. Consequences may be intensified when the invader is an ecosystem engineer, meaning that it causes physical state changes in biotic or abiotic materials (Jones, Lawton & Shachak, 1994, 1997). Two invasive ecosystem engineers, zebra mussels (*Dreissena polymorpha*, Pallas 1771) and quagga mussels (*D. rostriformis bugensis*, Andrusov 1897), both alter benthic habitat in a variety of large, permanent, aquatic ecosystems (Karatayev, Burlakova & Padilla, 2002). The initial invasion by zebra mussels in North America involved clusters colonising bedrock and other hard surfaces and increasing habitat complexity on hard substrate. Subsequently, both zebra and quagga mussels have been spreading to soft substrates in many invaded lakes (Berkman *et al.*, 1998; Bially & MacIsaac, 2000). However, quagga mussels, first recorded in North America in 1989 in Lake Erie (Mills *et al.*, 1996), have become the dominant dreissenid species in the Laurentian Great Lakes and are the main coloniser of soft sediments (Roe & MacIsaac, 1997; Patterson, Ciborowski & Barton, 2005; Wilson, Howell & Jackson, 2006), increasing from 20% of the dreissenid population in the western basin of Lake Erie in 1998 to 80% in 2001 (Stoeckmann, 2003). In this article, we focus on the effects of quagga mussel-dominated clusters on soft sediment, which fundamentally change the soft bottom habitat of lakes to a more spatially complex, hard-cluster-covered substrate. The change from primarily hard substrate colonies in the Great Lakes (dominated by zebra mussels) to soft substrates colonies (dominated by quagga mussels) can be expected to affect the infaunal benthic community and higher trophic levels.

*Dreissena* on hard substrates have been shown to increase local abundance and diversity of macroinvertebrates because of: (1) habitat complexity, (2) increased food resources from *Dreissena* faeces and pseudofaeces (e.g. Silver Botts, Patterson & Schloesser, 1996; Ricciardi, Whoriskey & Rasmussen, 1997; Stewart, Miner & Lowe, 1998) and (3) decreased fish predation (González & Downing, 1999; Mayer *et al.*, 2001; Beekey, McCabe & Marsden, 2004a). Quagga mussel colonies on soft sediment fundamentally shift habitat type (bare sediment to hard substrate), and infaunal invertebrates are likely to respond to added

structure differently than hard substrate dwelling invertebrates. Few infaunal species have been shown to increase in the presence of soft sediment *Dreissena* clusters (Bially & MacIsaac, 2000; Beekey, McCabe & Marsden, 2004b), while others have declined (Beekey *et al.*, 2004b) including the dramatic decrease of infaunal filter feeders (Strayer *et al.*, 1999; Nalepa *et al.*, 2003; Nalepa, Fanslow & Messick, 2005). We focussed on native *Hexagenia* spp. (*H. limbata*, Serville 1829 and *H. rigida*, McDunnough 1924), burrowing mayflies important to fish and to ecosystem function, whose preferred habitat type has always been perceived as bare sediment (Freeman, 1999; Schloesser & Nalepa, 2001; Wang, Tessier & Hare, 2001).

*Hexagenia* became rare in the Great Lakes during the 1950s during eutrophic conditions (Britt, 1955; Nebeker, 1972; Gerlofsma & Ciborowski, 1998), but their recent recolonisation of Lake Erie provides an additional food source to many economically important fish species, such as yellow perch (*Perca flavescens*, Mitchill 1814) (Hayward & Margraf, 1987; Schaeffer, Diana & Haas, 2000). *Dreissena* clusters on soft sediments may reduce the consumption rate of fish feeding on benthic prey that are protected in the interstitial spaces of mussel clusters (González & Downing, 1999; Mayer *et al.*, 2001; Beekey *et al.*, 2004a); however, the density of mayflies inhabiting mussel clusters may be higher than on bare soft sediments, which could compensate for the reduced rate of consumption. Further, a reduction in consumption rate may differ between fish species with different feeding strategies, and we examined the effects of *Dreissena* clusters on consumption of *Hexagenia* by two fish types, a visual feeder, the yellow perch, and a primarily benthic feeder adapted to low light, the round goby (*Neogobius melanostomus*, Pallas 1814). Fish such as yellow perch that feed visually (Diehl, 1988) may have greatly reduced consumption because *Dreissena* clusters add structure (González & Downing, 1999; Mayer *et al.*, 2001). Alternately, *Hexagenia* are bioturbators, meaning they mix the sediment through feeding, respiration and burrowing activities (Bartsch, Cope & Rada, 1999), resulting in high turbidity at the sediment-water interface (Bachteram, Mazurek & Ciborowski, 2005), and *Dreissena* filtering is likely to reduce turbidity. In contrast, fish such as the invasive round goby may be more able to find *Hexagenia* despite the presence of *Dreissena* because they are primarily benthic

feeders, feed in low light (Dubs & Corkum, 1996) and also consume dreissenid clusters (Ray & Corkum, 1997; Carman, Janssen & Berg, 2006). While multiple factors (e.g. prey density, abiotic conditions) will ultimately determine the quantity of benthic prey transferred to higher trophic levels, the addition of structure to previously soft sediment and increased water clarity are both substantial habitat alterations that are likely to affect the amount of biomass consumed by fish.

The direction and strength of interactions between *Dreissena* and *Hexagenia* are important, as they may change ecosystem processes at the sediment-water interface in addition to affecting the flow of benthic energy to fish. In this study, we tested experimentally the ecological interactions between invasive *Dreissena* and native *Hexagenia* on soft sediment, examining both habitat preference and availability of *Hexagenia* to fish. Specifically, we hypothesised that, unlike many invertebrates on hard substrates that congregate in *Dreissena* clusters, *Hexagenia* will avoid this habitat. Our first objective was therefore to examine burrowing mayfly habitat preference with respect to *Dreissena* presence on soft sediments. To assess this, we conducted three separate habitat preference experiments: (1) *Habitat type selection* – tested whether burrowing mayflies select for bare sediment (no structure), empty *Dreissena* clusters (structure only) or live *Dreissena*-colonised habitat (structure and increased food resources) for two types of western Lake Erie sediment, (2) *Dreissena density selection* – examined how *Hexagenia* respond across a gradient of increasing *Dreissena* densities and (3) *Effect of accumulated shells* – tested whether burrowing mayflies would avoid sediment with a build-up of empty *Dreissena* shells, a phenomenon that has been observed in many *Dreissena*-colonised lakes. Our second objective was to assess the effects of *Dreissena*-colonised sediment on the availability of *Hexagenia* to fish, and we hypothesised that, like other hard substrates, the presence of *Dreissena* will reduce fish consumption of *Hexagenia*. We conducted an experiment to test the effects of *Dreissena*-covered sediments, examining both added structure and changes in water clarity, on fish consumption of *Hexagenia* by two different fish species, yellow perch and round gobies, which vary in feeding strategy. Our expectation was that *Dreissena* will act strongly as ecosystem engineers on soft substrate where they

cause a switch in habitat type. The direction of these effects may differ from what has been observed previously for zebra mussels on hard substrate habitats.

## Methods

### Habitat preference experiments

To examine the possible association between burrowing mayflies and *Dreissena*, laboratory mesocosm experiments were conducted at the University of Toledo's Lake Erie Center. All experiments were run indoors at room temperature along a set of large windows to allow for natural light cycles. *Dreissena* and mayflies were collected from western Lake Erie. *Dreissena* were collected from soft substrates, and age-one burrowing mayfly nymphs (>10 mm) were collected to decrease risk of emergence during the experiment, and *H. limbata* and *H. rigida* were collected at their natural occurring proportions. Quagga mussels dominated *Dreissena* clusters collected; however, zebra mussels were present in small numbers. Three separate experiments were conducted: (1) habitat type selection, including differences in habitat selection between coarse nearshore sediment and very fine offshore sediment, (2) *Dreissena* density selection and (3) effect of accumulated *Dreissena* shells. All mesocosms in these experiments were filled with 6 cm of either nearshore (41.6885 W, 83.4250 N) or offshore (41.7976 W, 83.3136 N) Lake Erie sediment that was first sieved through 1.0 mm mesh. The three experiments (habitat type selection, *Dreissena* density selection and effects of accumulated shells) ran for different lengths of time, but all trials within an experiment ran for the same length of time, and no statistical comparisons were made between the three experiments.

*Experiment 1 – Habitat type selection.* We tested whether burrowing mayflies selected for or avoided *Dreissena* clusters on soft sediment. Experimental mesocosms (circular plastic tubs; 41 cm diameter and 43 cm height) filled with 6 cm of nearshore sediment were separated into three equal 'pie-slice' shaped sections (0.046 m²) using metal dividers, and three different habitat types were created: (1) bare sediment, (2) live *Dreissena* clusters and (3) empty *Dreissena* clusters. Live and empty *Dreissena* cluster

treatments contained approximately 250 individuals (5434 $m^{-2}$; Patterson *et al.*, 2005). We created empty *Dreissena* clusters by gluing clean shells together with non-toxic glue and adding five 1 g lead weights to each cluster. To ensure the weights did not influence results of the experiment, lead weights were added to all treatments. Metal dividers were removed after habitat types were in place.

The experiment was conducted using five densities of burrowing mayflies that fell within the range seen in western Lake Erie (0–2000 $m^{-2}$; Krieger, 1999): five individuals (~100 $m^{-2}$), 9 (~200 $m^{-2}$), 18 (~400 $m^{-2}$), 36 (~800 $m^{-2}$) and 54 (~1200 $m^{-2}$). Each mayfly density treatment was replicated three times ($N = 15$). Mayflies were added to the centre of the mesocosm at the water surface and allowed to select between the habitat types. One replicate of each density was run at the same time, and mesocosms were placed in a straight line in random order. After 48 h, metal dividers were again pushed into the sediment between habitat types, water was siphoned, sediment from each habitat was removed and sieved through 250-$\mu$m nitex mesh, and mayflies in each habitat type were counted.

The habitat selection experiment was repeated with offshore Lake Erie sediment from a site where burrowing mayflies were very abundant (41.7976 W, 83.3136 N) to test whether sediment type had an effect. Experiments were run as described above with three densities of burrowing mayflies: nine individuals (~200 $m^{-2}$), 18 (~400 $m^{-2}$) and 36 (~800 $m^{-2}$). Each density was replicated three times ($N = 9$).

*Experiment 2 – Dreissena density selection.* The design for experiment 2 and selection of treatment conditions was based, in part, on results from experiment 1. We manipulated the density of *Dreissena* to better understand whether burrowing mayflies prefer a specific percent coverage of live *Dreissena* clusters. Each rectangular mesocosm ($80 \times 30$ cm) was split into four equal sections containing a mixture of offshore and nearshore western Lake Erie sediment covered with 0, 25, 50 or 100% live *Dreissena* clusters. Coverage was estimated by covering a template of the appropriate area with shells. An intermediate density of mayflies, ~400 $m^{-2}$, was used in this experiment. Four replicates were conducted ($N = 4$); each replicate consisted of all four *Dreissena*-coverage habitat types,

and the arrangement of habitats within the mesocosms was randomly determined for each replicate. Metal dividers were placed into the sediment between habitat types after 64 h. Mayflies were removed and counted as described in the mayfly habitat selection experiment above.

*Experiment 3 – Effect of accumulated shells.* The final habitat selection experiment examined the effect of accumulated *Dreissena* shell fragments on mayfly habitat preference. *Dreissena* shells and shell fragments accumulate in colonised lakes and may also affect the habitat preference of burrowing animals. Experimental mesocosms (circular plastic tubs; 41 cm diameter and 43 cm height) were divided into two sections, each 0.069 $m^2$. Both sections were filled with nearshore Lake Erie sediment, and one section had 515 g of empty *Dreissena* shells mixed in. The shells used in each trial were from a single ponar collected in western Lake Erie and therefore represented the natural density and size distribution of shell fragments. Mayflies were added at an intermediate density of ~400 $m^{-2}$. Five replicates were run for 60 h ($N = 5$); trials were run sequentially, and mayflies were removed and counted as above.

*Data analysis.* The percentage of total number of burrowing mayflies in each habitat type was arcsin square root transformed to help achieve a normal distribution (Zar, 1999) for all three experiments. For experiment 1, all habitat type selection data (nearshore and offshore sediment experiments) were analysed using a split-plot ANOVA model (SAS 9.1, $\alpha = 0.05$) followed by a Tukey multiple comparison test when appropriate, with initial mayfly density as a main plot factor, habitat type as a subplot factor and their interaction (Potvin, 2001). A split-plot model was used because each experimental mesocosm was split into three different habitat types, and treatments were applied to different scales; habitat type was applied to one-third of the mesocosm (subplot) while mayfly density was applied to the full mesocosm (main plot). Experiment 2, the *Dreissena* density selection experiment, was analysed using a one-way ANOVA, followed by a Tukey multiple comparison test. Lastly experiment 3, the effect of accumulated empty shells, was analysed using a two-sample, two-tailed, *t*-test (SAS 9.1, $\alpha = 0.05$).

*Fish foraging experiments*

To assess the effects of *Hexagenia* habitat choice on their availability to fish as a food resource, we conducted mesocosm experiments measuring number of *Hexagenia* consumed by fish in different habitats. We had three treatment levels representing three distinct habitat types: (1) bare sediment (no *Dreissena*) treatment in which water was turbid because of mayfly bioturbation, (2) *Dreissena*-covered sediment treatment in which water was clear because of *Dreissena* filtration and (3) *Dreissena*-covered sediment with added turbidity (*Dreissena* + turbidity). The *Dreissena* + turbidity treatment was included to assess the effects of *Dreissena* and water clarity separately. *Hexagenia* bioturbation in the bare sediment treatments without *Dreissena* increased turbidity levels (200–400 NTU) and reduced light levels (average 0.308 $\mu$E m$^{-2}$ s$^{-1}$), while *Dreissena* filtering in the *Dreissena*-covered sediment treatment resulted in decreased turbidity and increased light levels (average 0.873 $\mu$E m$^{-2}$ s$^{-1}$). We attempted to create a clear water treatment with no *Dreissena*, but could not achieve this condition.

To establish the *Dreissena* + turbidity treatment, two large tanks were filled with dechlorinated water and nearshore lake sediment (same sediment as used on bottom of experimental tanks) until turbidity levels reached 400 NTU. The highly turbid water from each tub was pumped into two experimental mesocosms to keep bottom light levels similar to the bare sediment treatment ($\sim$0.300 $\mu$E m$^{-2}$ s$^{-1}$). The flow of water pumped into experimental mesocosms was slow to minimise disturbance, and a small tube was inserted to the top of the mesocosm to allow overflow water to return to the turbid water tanks. Light readings were taken at the start of the experiment, end of day 1, beginning of day 2 and at the conclusion of the experiment (beginning of day 3). Light levels were not statistically different in the bare (mean and standard deviation; 0.31 ± 0.32 $\mu$E m$^{-2}$ s$^{-1}$) and *Dreissena* + turbidity (0.13 ± 0.08 $\mu$E m$^{-2}$ s$^{-1}$) treatments at the end of experimentation, while light levels in both treatments were significantly lower than that in the *Dreissena*-covered sediment treatment (0.87 ± 0.35 $\mu$E m$^{-2}$ s$^{-1}$) (ANOVA $F_{2,40}$ = 29.87, $P < 0.0001$, Tukey $P < 0.05$). All other aspects of the *Dreissena* + turbidity treatment were kept the same as the bare and *Dreissena*-covered sediment treatments described below.

Each experimental mesocosm (circular plastic tubs of diameter 34.3 cm and height 43 cm) included 6 cm of sieved (1 mm mesh) nearshore western Lake Erie sediment, 18 *Hexagenia* ($\sim$200 *Hexagenia* m$^{-2}$, a common density in Lake Erie; Krieger, 1999) and one fish. Each treatment was replicated 10 times ($N = 10$), totalling 10 individual yellow perch (total length 7.0–13.0 cm) and 10 round gobies (total length 6.0–9.8 cm). Treatments with *Dreissena* had 15 000 individuals m$^{-2}$, a density observed on soft sediments (Patterson *et al.*, 2005). As above, *Dreissena* and mayflies were collected from western Lake Erie. Prior to the experiment, sediment, *Hexagenia* and *Dreissena* (if applicable) were added to establish the correct habitat type, and a mesh screen was placed above the sediment surface to restrict fish access to *Hexagenia* or *Dreissena*. Four mesocosms for the same fish species were run simultaneously, and treatments were randomly assigned to mesocosms. Individual fish were placed in the experimental mesocosms above the mesh 24 h prior to experimentation to allow for acclimation to surroundings and standardisation of hunger levels. The mesh was then removed, and fish were allowed to feed for 24 h. After 24 h, light levels were recorded, fish were removed, and the number of prey consumed was determined by sieving the mesocosm sediment through 250-$\mu$m nitex mesh and counting the remaining *Hexagenia*. When only a head or tail end of a *Hexagenia* was left, we counted that as 0.5 eaten in our total numbers consumed. To assess our error in recovering *Hexagenia*, trials (three per treatment) with no fish present were run at the same time as the fish foraging experiment to measure the number of *Hexagenia* recovered at the end of the experiment without loss to predation.

The effect of *Dreissena*-covered sediment and turbidity on consumption of *Hexagenia* was tested separately for yellow perch and round gobies by comparing the number of *Hexagenia* consumed across the three habitat types using a one-way nonparametric Kruskal–Wallis test (SAS 9.1, $\alpha$ = 0.05). The Kruskal–Wallis test was followed by a Nemenyi test, a nonparametric multiple comparisons test, which is an analogue to a Tukey's test (Zar, 1999). We used nonparametric statistics because the response variable (number eaten) is a count variable, and there were many low values resulting in a non-normal distribution.

## Results

### Habitat selection experiments

In experiment 1, habitat type selection, burrowing mayflies were most often located in the live *Dreissena* habitat for both sediment types (Fig. 1). In nearshore sediment, mayfly density differed among all three habitat types (split-plot ANOVA: $F_{24,20} = 95.17$, $P < 0.0001$, Tukey: $P < 0.05$). The live *Dreissena* habitat had the highest percentage of mayflies, followed by empty *Dreissena*, then bare sediment. There was a significant interaction in percentage of mayflies in each habitat type based on mayfly density (split-plot ANOVA: *nearshore habitat\*density*: $F_{24,20} = 4.86$, $P < 0.0001$), showing that the percentage of mayflies selecting each habitat type changes with mayfly density. In offshore sediment, there were also significantly more burrowing mayflies in the live *Dreissena* habitat (split-plot ANOVA: $F_{14,12} = 6.85$, $P = 0.0104$, Tukey $P < 0.05$), but no difference occurred between the empty *Dreissena* and bare sediment habitats. There was no significant interaction in percentage of mayflies in each habitat type based on mayfly density (split-plot ANOVA: *offshore habitat\*density*: $F_{14,12} = 0.52$, $P = 0.7213$).
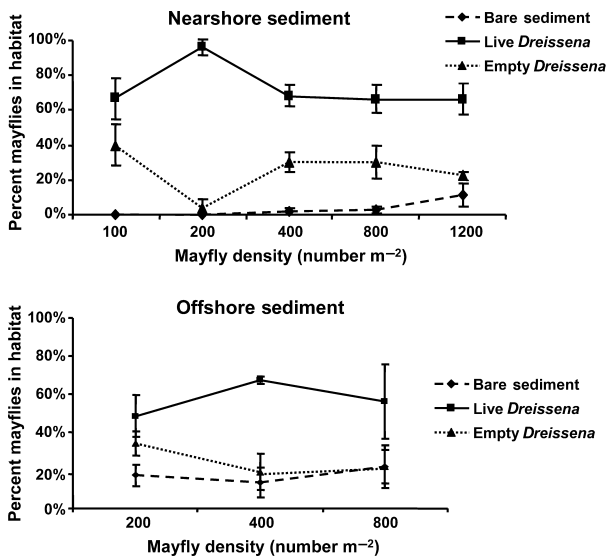


**Fig. 1** Mean (±1 standard error) percent of total number of burrowing mayflies found in each habitat type (bare sediment, live mussel clusters and empty mussel clusters) in laboratory habitat preference experiments. Experiments were conducted on two different sediment types, nearshore (coarse) and offshore (fine), across a range of burrowing mayfly densities.
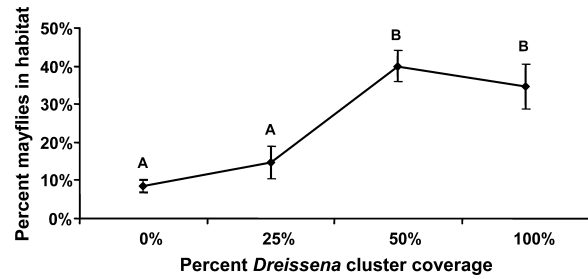


**Fig. 2** Mean (±1 standard error) percent of total number of burrowing mayflies found in each habitat, each with varying percentages of *Dreissena* spatial coverage, in laboratory habitat preference experiments. Letters represent statistically significant differences based on the Tukey multiple comparison test ($\alpha = 0.05$).

For experiment 2, *Dreissena* density selection, mayfly habitat preference differed significantly with percent *Dreissena* coverage (Fig. 2; ANOVA: $F_{3,12} = 14.54$, $P = 0.0003$). Densities in the 0 and 25% *Dreissena*-coverage habitats were significantly lower than in the 50 and 100% *Dreissena*-coverage habitats (Tukey: $P < 0.05$). Our third experiment, the effect of shell accumulations, showed that mayflies did not show a preference between unaltered sediment and sediment mixed with accumulated empty *Dreissena* shells (mean = 43 and 57% of mayflies added, respectively) (*t*-test: $t_{0.05,8} = 1.71$, $P = 0.127$).

### Fish foraging experiments

The control tanks used to estimate error in retrieving *Hexagenia* in the absence of predation showed that the average error was very low and not significantly different between treatments (Kruskal–Wallis: $\chi_2^2 = 2.67$, $P = 0.2636$; mean number of *Hexagenia* not counted: bare = 0.0, *Dreissena* = 0.33, *Dreissena* + turbidity = 0.60) and therefore was not included in the subsequent analyses. The presence of different bottom habitat types (*Dreissena*-covered sediment and bare sediment) did affect the consumption of *Hexagenia* by both yellow perch and round gobies (Fig. 3; Kruskal–Wallis: yellow perch $\chi_2^2 = 12.44$, $P = 0.0020$; round gobies $\chi_2^2 = 10.27$, $P = 0.0059$). Overall, the presence of *Dreissena* only reduced yellow perch and round goby consumption of *Hexagenia* when water was turbid (200–400 NTU) and light levels were low ($\sim 0.300\ \mu E\ m^{-2}\ s^{-1}$) (Fig. 3). Yellow perch did not consume fewer *Hexagenia* when *Dreissena* were present without added turbidity (Nemenyi: $q_{0.05,\ \infty,\ 3} = 0.23$,
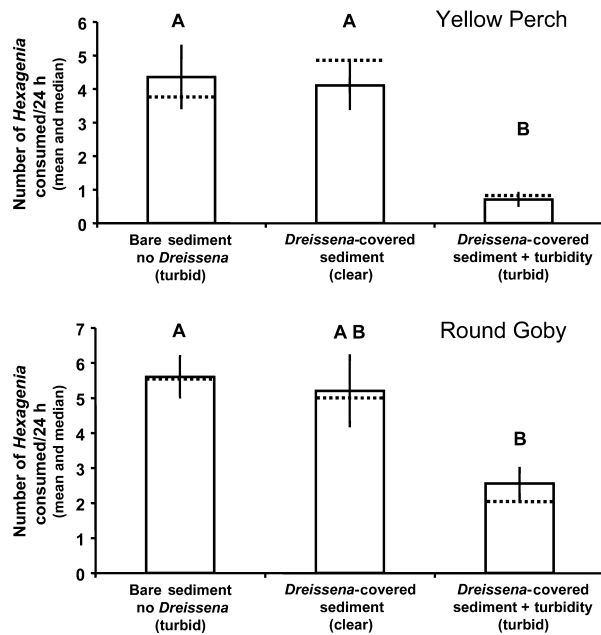
Fig. 3 Number of *Hexagenia* consumed by yellow perch and round gobies in a 24-h period for three different habitat treatments. Vertical lines represent ±1 standard error, and dashed lines represent median values. Letters represent statistically significant differences based on the Nemenyi's nonparametric multiple comparison test ($\alpha = 0.05$).

$P > 0.50$), but consumed fewer *Hexagenia* in the *Dreissena* + turbidity treatment than in the bare (Nemenyi: $q_{0.05, \infty, 3} = 4.40$, $0.01 > P > 0.005$) and *Dreissena* only treatments (Nemenyi: $q_{0.05, \infty, 3} = 4.17$, $0.01 > P > 0.005$; Fig. 3). Similarly, round gobies were not affected by the presence of *Dreissena*-covered sediment in clear water, as predation of *Hexagenia* was relatively high (Nemenyi: $q_{0.05, \infty, 3} = 1.13$ $P > 0.50$). However, the presence of *Dreissena* reduced consumption when light levels were kept low because of high turbidity. Round gobies in the bare sediment treatment consumed more *Hexagenia* than in the *Dreissena*-covered sediment with added turbidity treatment (Nemenyi: $q_{0.05, \infty, 3} = 4.31$ $0.01 > P > 0.005$; Fig. 3). Both species of fish therefore consumed fewer *Hexagenia* only when *Dreissena*-covered sediment and low light ($\sim 0.300 \, \mu E \, m^{-2} \, s^{-1}$) were present together, and the magnitude of effects between fish species was also similar.

## Discussion

### Habitat selection experiments

We hypothesised that burrowing mayflies would avoid the structure created by *Dreissena* clusters, as

has been suggested previously (Freeman, 1999; Beekey *et al.*, 2004b; Osterling *et al.*, 2007). However, our habitat choice experiments showed that burrowing mayflies consistently and strongly preferred sediments covered by live *Dreissena* clusters over empty clusters and bare sediment, regardless of the type of sediment used (coarse nearshore vs. fine offshore) (Figs 1 and 2). We were often able to observe where the entrances to burrows were positioned; they were frequently directly beneath clusters, suggesting that the mayflies were burrowing directly under clusters, not seeking cluster margins. This occurred despite the fact that *Dreissena* clusters can decrease water quality and oxygen concentration beneath them (Burks *et al.*, 2002; Beekey *et al.*, 2004b). Bare sediment, typically thought to be the habitat of burrowing mayflies (Freeman, 1999; Schloesser & Nalepa, 2001; Wang *et al.*, 2001), was the least selected habitat type (Figs 1 and 2). Selecting *Dreissena*-covered habitat may not be beneficial over long time spans as *Hexagenia* survival has been found to be lowest in mesocosms with *Dreissena* (Freeman, 1999; Osterling *et al.*, 2007), but this may be an effect of the mesocosm, as mayfly larvae residing in clusters are densely aggregated and may compete for food. As a result, the strength of habitat preference in natural situations is also likely to depend on food availability and needs to be evaluated in a natural lake system. Our results suggest that burrowing mayflies can alter their behaviour to take advantage of increased habitat complexity created by the mussels. The observed preference of burrowing mayflies for *Dreissena* clusters could impact the spatial distribution of burrowing mayflies if they select for 'low-quality' sediment covered with *Dreissena* over 'high-quality' bare sediment.

Epifaunal invertebrates living in interstital spaces of hard substrate mussel clusters have been shown to occur both in equal densities in live and empty *Dreissena* cluster habitats (Silver Botts *et al.*, 1996; González & Downing, 1999), and similarly to our experiment, prefer live mussel clusters over empty ones (Ricciardi *et al.*, 1997; Stewart *et al.*, 1998). Further, burrowing mayflies in our study selected equally for high levels of live *Dreissena* spatial coverage (Fig. 2) and are unlike epifaunal invertebrates that show a linearly increasing response to *Dreissena* density (Mayer *et al.*, 2002). The build-up of empty *Dreissena* shells did not affect *Hexagenia* habitat choice as expected, suggesting that this material does not

create difficulties in burrowing and, although not significant, we did find more *Hexagenia* in the accumulated *Dreissena* shell habitat.

The provision of structure is evidently not the only mechanism affecting mayfly selection for *Dreissena* habitat because burrowing mayflies preferred live *Dreissena* to empty clusters (Fig. 1). Burrowing mayflies may be responding to the food resource represented by mussel faeces and pseudofaeces, similarly to other invertebrates (Roditi, Strayer & Findlay, 1997; Stewart *et al.*, 1998). Alternatively, *Dreissena* are very efficient filter feeders (Kryger & Riisgard, 1988) and may increase the flow of well-oxygenated water above the clusters. Therefore, although water within and below *Dreissena* clusters has been shown to have lower dissolved oxygen and water quality (Burks *et al.*, 2002; Beekey *et al.*, 2004b), water just above the cluster may still be well oxygenated, and *Dreissena* may direct highly oxygenated microcurrents into their burrows.

While removing mayflies from the habitat choice experiments, we observed that some mayflies occupied empty *Dreissena* shells or space just below a live *Dreissena* and were not actually burrowing into the sediment. Furthermore, mayflies maintained in the laboratory sought shelter near *Dreissena* shells and dug very shallow burrows. Bioturbation is vital to benthic community structure because it influences sediment properties (Levinton, 1995; Solan *et al.*, 2004), nutrient and contaminant fluxes at the sediment-water interface (Matisoff & Wang, 1998; Bartsch *et al.*, 1999; Chaffin & Kane, 2010) and may influence species richness and diversity (Widdicombe *et al.*, 2000). Therefore, the effect of *Dreissena* clusters on soft sediment may not only alter infaunal invertebrate community density and diversity, but more surprisingly, may change the behaviour of native ecosystem engineers, resulting in changes in bioturbation activity and in the ability of fish to detect *Hexagenia* as prey.

*Fish foraging experiments*

Increased habitat complexity may not have been the only reason *Hexagenia* chose *Dreissena* clusters, but in high turbidity habitats, *Dreissena* on soft sediment do afford *Hexagenia* some protection from predators. In treatments with *Dreissena* present, decreased water clarity affected yellow perch and round goby consumption of *Hexagenia* equally when at a density of 200 m$^{-2}$. Light conditions, turbidity and structural complexity can have large impacts on the foraging of visually oriented fish (e.g. Diehl, 1988; Miner & Stein, 1993; Utne-Palm, 2002). There are other potential effects of increased turbidity, such as clogging gills and interfering with respiration, but the visual affects of turbidity have been shown to be most important (Wellington *et al.*, 2010). Turbid conditions are common in lakes where *Hexagenia* and *Dreissena* co-occur. One example is the western basin of Lake Erie, where bottom light measurements vary widely based on season and weather, but are frequently near zero, resulting in the photic zone not reaching maximum depth, even in very shallow areas (T. Bridgeman, unpubl. data). Moreover, *Hexagenia* can create turbid plumes at the sediment-water interface through their bioturbating activity. A common density of 400 *Hexagenia* m$^{-2}$ has been found to resuspend sediment at a rate of 12 g m$^{-2}$ per hour (Bachteram *et al.*, 2005), which is more than can be filtered out by dense clusters of *Dreissena* (Bachteram *et al.*, 2005). Therefore, fish may not only be experiencing low light, but spikes of turbidity near the sediment-water interface, making finding prey more difficult.

Contrary to our original hypothesis, yellow perch and round gobies showed similar reduction in consumption of *Hexagenia* when water clarity was low. Round gobies have a good lateral line system and feed efficiently in low or no light (Dubs & Corkum, 1996). However, the lateral line may not be effective when benthic prey are found in structurally complex habitat. As a result, round gobies may rely more on visual foraging when *Dreissena* are present and may explain why like yellow perch, they consumed lower numbers of *Hexagenia* with low water clarity and *Dreissena*-covered sediment. Therefore, even if fish are able to feed in very low light conditions, the added structure and filter-feeding activities of *Dreissena* may impede these abilities.

We found that *Dreissena* presence did not reduce fish prey consumption when the mussel's filtration was allowed to increase water clarity. Similarly, several species of fish (Beekey *et al.*, 2004a) and yellow perch (Cobb & Watzin, 2002) did not show reduced consumption of non-burrowing benthic prey with patchy coverage of zebra mussels on sandy substrate where water clarity was likely high. Zebra mussel clusters on hard substrates have been shown to decrease fish consumption of benthic prey even

with high water clarity (González & Downing, 1999; Mayer *et al.*, 2001; Dieterich, Mörtl & Eckmann, 2004). However, in the complex lake habitat, increased water clarity partially compensates for the negative effect of increased structure on yellow perch prey consumption (Mayer *et al.*, 2001). *Hexagenia* burrowing activity and sediment resuspension prevented the creation of high water clarity + bare sediment treatment, but this situation is unlikely to occur in lakes where *Dreissena* are absent because of *Hexagenia* sediment preference. The net effect of *Dreissena* on trophic transfer of mayflies to fish will also depend on changes in mayfly density in mussel colonised and other habitats. In many instances, increased prey density results in increased consumption, but yellow perch show no such increasing relationship for benthic prey in laboratory experiments or long-term data from Oneida Lake (Mayer *et al.*, 2001). Consequently, the possible reduction of mayfly-derived energy available to fish associated with *Dreissena* will likely depend on the level of water clearing near the sediment-water interface. In locations where sediment resuspension or thick algal blooms are prominent, the effect is likely to be more severe.

In conclusion, the current range expansion of dreissenid mussels onto soft sediments and consequent ecosystem engineering effects resulting in changes to available habitat can be expected to alter the already vulnerable benthos of temperate lakes. The observed habitat selection by burrowing mayflies for *Dreissena* clusters may impact their spatial distribution and possibly also that of other benthos with potential cascading effects to higher trophic levels and overall ecosystem functioning. We have shown that *Dreissena* clusters on soft sediment have similar effects on *Hexagenia* susceptibility to predation by yellow perch and round goby; *Dreissena* presence only decreased consumption in high turbidity/low light conditions. Given the water clarity of areas such as the western basin of Lake Erie, *Hexagenia* may not be as readily exploited by fish as a food source. Also, *Hexagenia* densities under *Dreissena* clusters may increase because of their habitat preference, thereby making them more available to fish. However, in western Lake Erie, *Dreissena* and *Hexagenia* densities are not positively correlated (D. Schloesser, unpubl. data). Research should continue to look at the relationship between *Hexagenia* and *Dreissena* in lake systems, to see whether selection for *Dreissena* habitat

is affecting the distribution and abundance of this dominant benthic organism.

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