The effects of predation and unionid burrowing on bivalve communities in a Laurentian Great Lake coastal wetland

Richard Bowers[1,2], Judy C. Sudomir[1], Mark W. Kershner[1], & Ferenc A. de Szalay[1,*]

[1]*Kent State University, Department of Biological Sciences, Kent, Ohio, 44242, USA*
[2]*Present Address: Edwards-Pitman Environmental, Inc., 1250 Winchester Parkway, Suite 200, Smyrna, Georgia, 30080, USA, E-mail: rbowers@edwards-pitman.com*
(*Author for correspondence to: E-mail: ferenc@kent.edu)

Abstract

Unionid (Mollusca: Unionidae) densities have declined dramatically throughout the Laurentian Great Lakes after the introduction of dreissenid mussels (Mollusca: Dreissenidae). Recent surveys in some Great Lake coastal wetlands have found abundant unionid populations, but the factors that reduce zebra mussels on unionids in these habitats are not well understood. In 2001–2002, we tested effects of predation and unionid burrowing on corbiculids, sphaeriids and dreissenids in a Great Lake coastal wetland in western Lake Erie. In one experiment, we reduced access by molluscivores using exclosures with two mesh sizes (1.3 cm × 1.3 cm; 5 cm × 10 cm) and sampled bivalves after 15 months. Small mesh exclosures had higher numbers of dreissenids, *Corbicula fluminea* and sphaeriids (54.9, 3.8, 22.6 individuals/m^2, respectively) than large mesh exclosures (0.0, 1.13, 0.13 individuals/m^2, respectively) or open controls (0.3, 1.0, 0.1 individuals/m^2, respectively). Numbers of dreissenids on *C. fluminea* were higher in small mesh exclosures (3.8 dreissenids/*Corbicula*) than in large mesh exclosures (0.1 dreissenids/*Corbicula*) or cageless controls (0 dreissenids/*Corbicula*). In a second experiment, we held two species of live unionids (*Leptodea fragilis*, *Quadrula quadrula*) and immobile *Pyganodon grandis* shells in exclosures (2.5 cm × 2.5 cm mesh) with either 5 cm, 10 cm, or 20 cm deep sediments and sampled bivalves after 2 months. There were fewer dreissenids on *L. fragilis* than *P. grandis* shells, but there was no difference in the number of dreissenids on *Q. quadrula* and *P. grandis* shells. Numbers of attached dreissenids were higher inside (189–494 dreissenids/unionid) than outside (8–11 dreissenids/unionid) exclosures, and densities of sphaeriid and *C. fluminea* clams were also higher inside (21.8, 4.7 individuals/m^2, respectively) than outside (0.4, 0.9 individuals/m^2, respectively) exclosures. Numbers of attached dreissenids were higher on unionids that could burrow below the sediments (20 cm depth) than unionids in shallow sediments (5 cm depth) for unexplained reasons. Our data suggest that molluscivores can play a pivotal role in limiting numbers of bivalves including dreissenids in coastal wetlands.

Introduction

The recent introduction of zebra mussels (Dreissenidae: *Dreissena polymorpha* (Pallas)) and quagga mussels (Dreissenidae: *Dreissena bugensis* Andrusov) to the Laurentian Great Lakes resulted in dramatic ecological impacts throughout North America (Schloesser & Nalepa, 1994; Ricciardi et al., 1996). Densities as high as 700 000 dreissenids/m^2 have been reported in the Great Lakes (Griffiths et al., 1991), which has caused changes in aquatic communities including rapid declines in

populations of native unionid clams (Unionidae) (Gillis & Mackie, 1994; Ricciardi et al., 1996; Schloesser et al., 1996; Schloesser & Masteller, 1999) and sphaeriid clams (Sphaeriidae) (Dermott & Kerec, 1997; Lauer & McComish, 2001). As a result, almost no offshore unionid beds remain in Lake Erie or Lake St. Clair (Ricciardi et al., 1998).

The ecology of dreissenids has been well studied in the Great Lakes since their introduction (e.g., Chase & Bailey, 1999a, b). In Lake Erie, dreissenids spawn from June to September when water temperatures are > 18 °C (Garton & Haag, 1993). Dreissenids produce up to 40 000 planktonic veligers per female during their breeding period, which are carried to new habitats by water currents (Marsden, 1992). When they settle out of the water column, veligers attach to solid substrates with proteinaceous byssal threads because they will die if they are buried in anoxic sediments (MacIsaac, 1996; Karatayev et al., 1998; Toczlowski et al., 1999). For example, dreissenids in coastal wetlands along Lake Huron were mostly attached to emergent vegetation and few were found in the benthic sediments (Brady et al., 1995). Dreissenids are often found on shells of unionids that remain above the sediment surface (Burlakova et al., 2000). High numbers of attached zebra mussels can kill unionids by outcompeting them for food or preventing them from burrowing or holding themselves upright in soft sediments (Schloesser & Nalepa, 1994, Strayer & Smith, 1996).

Marshes and swamps that are connected with the Great Lakes are termed Great Lake coastal wetlands (Maynard & Wilcox, 1997). Although dreissenids have caused widespread declines in unionids throughout the lower Great Lakes, diverse unionid populations with low numbers of attached zebra mussels were recently reported in several Lake Erie and Lake St. Clair coastal wetlands (Nichols & Amberg, 1999; Zanatta et al., 2002; Bowers & de Szalay, 2004). For example, Bowers & de Szalay (2004) surveyed Crane Creek Marsh in western Lake Erie (Ottawa Co.; Ohio, USA) and found an abundant unionid community that included 15 native species. They also found many unionids with byssal threads on their shells had no attached dreissenids, indicating that dreissenids had been removed from their shells in the past.

Factors allowing unionids to coexist with dreissenids in these wetlands are not well understood, but burial in soft benthic sediments and predation may kill attached dreissenids. For example, dreissenids are not tolerant of anoxia (Matthews & McMahon, 1999), and attached dreissenids can be smothered when unionids burrow to escape unfavorable temperatures and desiccation (Amyot & Downing, 1997; Nichols & Wilcox, 1997; Watters et al., 2001). Many studies have demonstrated that fish, waterfowl, and muskrats feed on dreissenids, sphaeriid and *Corbicula fluminea* (Müller) clams (Robinson & Wellborn, 1988; French, 1993; Hamilton et al., 1994; Tucker et al., 1996; Molloy et al., 1997; Morrison et al., 1997; Thorp et al., 1998; Petri & Knapton, 1999; Mitchell et al., 2000; Djuricich & Janssen, 2001; Magoulick & Lewis, 2002; Seitman et al., 2003). Many fish (e.g., freshwater drum, *Aplodinotus grunniens* (Rafinesque), common carp, *Cyprinus carpio* (Linnaeus), round goby, *Neogobius melanostomus* (Pallas), pumpkinseed, *Lepomis gibbosus* (Linnaeus), channel catfish, *Ictalurus punctatus* (Rafinesque)) and diving ducks (*Aythya spp.*) that feed on molluscs are common in Great Lakes coastal wetlands (Herdendorf, 1987; Bookhout et al., 1989; Johnson, 1989), but to our knowledge no studies have been done on their effects on bivalves in Great Lake coastal wetlands.

Given that diving ducks and molluscivorous fish are abundant in western Lake Erie coastal wetlands (Herdendorf, 1987; Campbell, 1995), predators probably are important in structuring bivalve assemblages, including dreissenids, in these habitats. Furthermore, effects of dreissenids on unionids in coastal wetlands may be limited by unionid burrowing behavior. Therefore, we hypothesized that: (1) molluscivores will reduce bivalve density including dreissenids; and (2) unionids that can burrow completely below the sediments will have fewer attached dreissenids than unionids that are in shallow sediments and remain above the surface. To test these hypotheses, we reduced access of potential predators to bivalve prey in exclosures with different mesh sizes. We also held unionids in exclosures with different sediment depths and tested how interactions of sediment depth and predators affected bivalve populations.

Methods

Study site

Crane Creek Marsh (CCM) is part of Ottawa National Wildlife Refuge (Ottawa and Lucas counties, Ohio), which is managed by the US Fish and Wildlife Service. A dike along Lake Erie protects the marsh from offshore waves, but a permanent 4-m opening in the dike connects the marsh to the lake (Fig. 1). Crane Creek is a third order stream, and its 144 km^2 watershed is predominantly agricultural or residential (Ohio Department of Transportation, 1987). Water levels in the 312 ha wetland are up to 2 m, but most areas are < 50 cm deep. Benthic sediments are mostly 10–50 cm deposits of soft inorganic silt-clay. Dreissenids are abundant on stone rip-rap on dikes surrounding the marsh, and reproduction is high within the wetland. For example, we found > 10 000 zebra mussels/m^2 on artificial substrates after a 2 week period in summer 2002 (R. Bowers & F. A. de Szalay, unpublished data). Fish surveys conducted at Ottawa National Wildlife Refuge found several molluscivorous species including common carp, freshwater drum, channel catfish, pumpkinseed and round goby in this wetland (Wells, 2001; Wells et al., 2002). In 2001, CCM was surveyed and 15 unionid species were collected in the marsh (Bowers & de Szalay, 2004). The most abundant species were *Quadrula quadrula* (Rafinesque), *Leptodea fragilis*
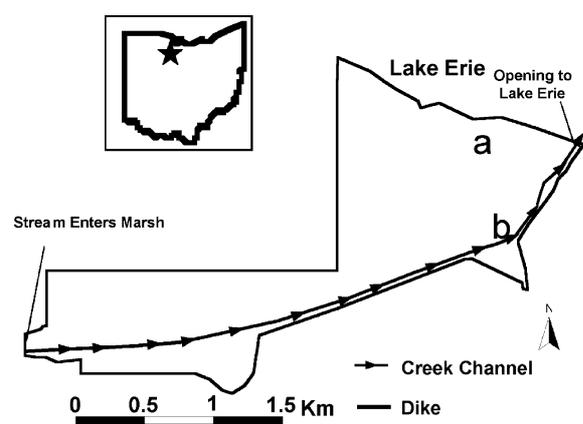

Figure 1. G.I.S. map of Crane Creek Marsh. The locations where the mesh size experiment (a) and the sediment depth experiment (b) were conducted are indicated on the map. Inset map shows the relative location of Crane Creek Marsh in Ohio.

(Rafinesque), *Amblema plicata* (Say), *Pyganodon grandis* (Say), which together comprised over 90% of all unionids collected.

Mesh size experiment

We assessed effects of predators on bivalve densities using three treatments: (1) small-mesh exclosures (L × W × H: 100 cm × 100 cm × 100 cm) constructed with metal screening with a 1.3 cm × 1.3 cm mesh size, (2) large-mesh exclosures (L × W × H: 100 cm × 100 cm × 100 cm) constructed of metal screening with a 5 cm × 10 cm mesh size and (3) open controls that were unfenced 1-m^2 areas marked off with stakes. On 11 July 2001, eight blocks of the three treatments were constructed in a 1-m deep side channel in Crane Creek Marsh, with each block containing one randomly placed replicate of each treatment type. Disturbance of the sediments during construction was minimized to avoid altering substrate integrity. After construction, the three treatments were maintained until October 2002, allowing ample time for bivalves to colonize these areas.

On 2 October 2002, we used a D-frame sweep net (500 micron mesh) to sample bivalves in the benthos of each treatment area. Sweep nets were drawn through the upper 10 cm of soft sediments throughout each 1-m^2 area, and fine silt was rinsed out of the net. The samples were placed in a white sorting tray in the field, and all live bivalves were counted and identified to the lowest possible taxonomic level. We also counted the number of dreissenids attached to other bivalves. We only counted dreissenids that were >1 mm in length because visual counts do not provide accurate counts of smaller mussels. Representatives of all bivalve taxa were preserved in ethanol for identification confirmation in the laboratory.

Sediment depth experiment

In summer 2002, we constructed 24 exclosures (L × W × H: 75 cm × 75 cm × 100 cm) using metal screening (2.5 cm × 2.5 cm mesh). Unlike the first experiment, the bottom of these exclosures was also screened with mesh. The exclosures were set out in the marsh in eight blocks of three treatments each. We removed all unionids in the sediments below each exclosure by probing through the mud

with our hands. The mesh bottoms of the exclosures were pressed down to either 5 cm, 10 cm or 20 cm below the sediments; each block had one exclosure of each of the three sediment depth treatments. The exclosures were checked throughout the experiment to ensure that the sediment depths remained constant. On 24 June 2002, we collected two species of unionids (*Quadrula quadrula*, *Leptodea fragilis*) by searching the area outside of the exclosures. Unionid shell lengths were measured, and each was labeled with non-toxic permanent paint. Unionids had from 0 to 10 visible attached dreissenids, and all dreissenids were removed from their shells. All unionids were 6–10 cm in length and each exclosure was stocked with three *Q. quadrula* and one *L. fragilis*. We placed the unionids into the exclosure on the surface of the sediments, but unionids were observed to have burrowed into the sediments during the experiment. With this experimental design, unionids in the 10 cm and 20 cm depth treatments could burrow completely below the sediments, but unionids in the 5 cm treatment were always partially exposed above the surface.

We also placed one empty unionid shell in each exclosure to measure dreissenid colonization on immobile unionids that did not burrow below the sediments. For this, we used *Pygandon grandis* shells (10–13 cm lengths), because they were the most abundant shells collected in the wetland. Pairs of empty shells were glued together on a wooden stick. Each stick was inserted in the sediments with approximately half of the posterior portion of the shell exposed above the sediments. During the study, the shells were checked to make sure they maintained their position.

On 26 August 2002, all live *Q. quadrula* and *L. fragilis* and *P. grandis* shells were collected from each exclosure, and shell lengths of live unionids were measured. One of us (RB) searched the sediments within a 10-m perimeter around the exclosures for 1 h, and collected 10 *L. fragilis* and 12 *Q. quadrula* that were within the size range (6–10 cm) of the unionids inside the exclosures. Attached dreissenids were scraped off all unionids and counted visually. We only counted dreissenids that were > 1 mm because these had survived on the unionids for at least several weeks and because visual counts could not accurately count smaller individuals.

Densities of other bivalves inside the exclosures were compared with densities found in nearby areas outside of exclosures. Due to time constraints, we randomly selected only eight of the 24 exclosures and searched for Corbiculidae, Sphaeriidae and juvenile Unionidae clams by probing the sediments with our hands for a 10 min timed search effort to ensure an equal sampling effort. We also searched for bivalves in eight randomly placed 75 cm × 75 cm quadrats adjacent to the exclosures. Although these tactile searches probably were not as effective in finding small bivalves as the method used in the mesh size experiment, our efficiency was probably similar in areas inside and outside exclosures in this experiment.

Statistical analyses

Densities of sphaeriid and corbiculid clams and dreissenid mussels in the mesh size experiment were compared among treatments with one-way blocked ANOVAs (blocked by each set of three treatments). When sample sizes were adequate (N ≥ 4 replicates in each treatment with *C. fluminea* or sphaeriids present), numbers of dreissenids on sphaeriid or corbiculid clams were compared among treatments with a one-way blocked ANOVA. Data were log $(x + 1)$ transformed when they failed tests for normality. Significant (i.e., $p < 0.05$) ANOVA tests were followed by Tukey's multiple comparison of means tests.

In the sediment depth experiment, one-way blocked ANOVAs (blocked by exclosure set) were used to compare *Q. quadrula* and *L. fragilis* shell growth and numbers of attached dreissenids among treatments. Analyses with *Q. quadrula* data were run using the mean number of attached dreissenids and mean shell growth per exclosure, because data from the three individuals in each exclosure may not have been independent. *Pyganodon grandis* data had different sample sizes in different treatments because several samples were lost during processing. Therefore, we did not block data by exclosure sets, and instead we used a one-way ANOVA to compare numbers of attached dreissenids among sediment depths. We also used a one-way ANOVA to compare numbers of attached dreissenids on *Q. quadrula*, *L. fragilis* and *P. grandis* shells in the exclosures.

Because sediment depths for *Q. quadrula* and *L. fragilis* collected outside the exclosures were very variable, we pooled data across all depth

treatments within exclosures and used *t*-tests to compared numbers of attached dreissenids on these species inside and outside the exclosures. *t*-tests were also used to compare numbers of sphaeriids, corbiculids and juvenile unionid clams inside and outside exclosures.

Results

Mesh size experiment

Most (84%) sphaeriids collected were *Musculium sp.*, and all corbiculids were *Corbicula fluminea*. All dreissenids that were identifiable were *Dreissena polymorpha*. We did not collect any unionids in the exclosures. Small-mesh exclosures had significantly higher densities of *C. fluminea* ($F = 4.2$; df = 2,14; $p < 0.05$), sphaeriids ($F = 7.06$; df = 2,14; $p < 0.01$) and dreissenids ($F = 11.35$; df = 2,14; $p < 0.0025$) than either large-mesh exclosures or open controls, which were not significantly different from each other for any bivalve species (Fig. 2). Block effects were not significant ($p > 0.05$) for any ANOVA analyses. Clams often had attached dreissenids, and the mean [1 SE] number of attached dreissenids on *C. fluminea* was significantly higher ($F = 4.74$; df = 2,10; $p < 0.05$) in small-mesh exclosures (3.8 [1.5]) than in large-mesh exclosures (0.1 [0.1]) or open controls (0.0 [0.0]). Too few sphaeriid clams were collected in the large-mesh exclosures

and open control for statistical analysis, but mean ([1 SE]) numbers of attached dreissenids on sphaeriids appeared to be higher in small-mesh exclosures (1.56 [0.48]) than in large-mesh exclosures (0.0 [0.0]) or open controls (0.0 [0.0]).

Sediment depth experiment

High numbers of dreissenids colonized unionids in exclosures during the 2 month experiment, and numbers of attached dreissenids were different among unionid species ($F = 6.94$; df = 2,61; $p < 0.001$). Mean [1 SE] number of attached dreissenids on *L. fragilis* (272.3 [36.9]) were lower than on *Q. quadrula* (387.9 [19.3]) and *P. grandis* shells (408.9 [43.9]), which were not different from each other. However, numbers of dreissenids on live unionids outside exclosures were low at the end of the experiment. Mean [1 SE] numbers of attached dreissenids on *Q. quadrula* (7.6 [4.4]) and *L. fragilis* (10.8 [5.6]) outside exclosures were significantly lower than numbers of attached dreissenids inside exclosures ($t = 13.30$; df = 13; $p < 0.001$, $t = 7.93$; df = 12; $p < 0.001$, respectively). Numbers of *C. fluminea* ($t = 4.27$; df = 14; $p < 0.001$) and sphaeriid ($t = 6.91$; df = 14; $p < 0.001$) clams also were much higher inside exclosures than outside exclosures. Numbers of juvenile unionids were low and were not different inside and outside exclosures ($p > 0.05$) (Fig. 3).
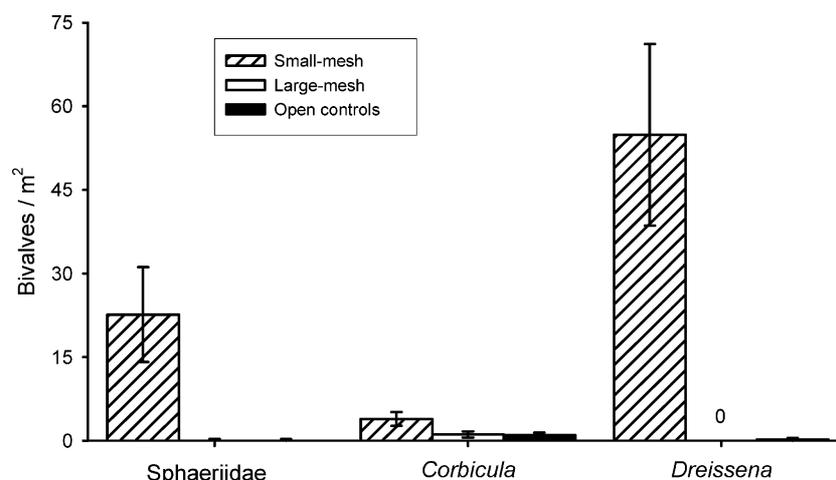

Figure 2. Mean (1 SE) densities of dreissenids, sphaeriids, and *Corbicula fluminea* in small-mesh exclosures, large-mesh exclosures, and open controls.
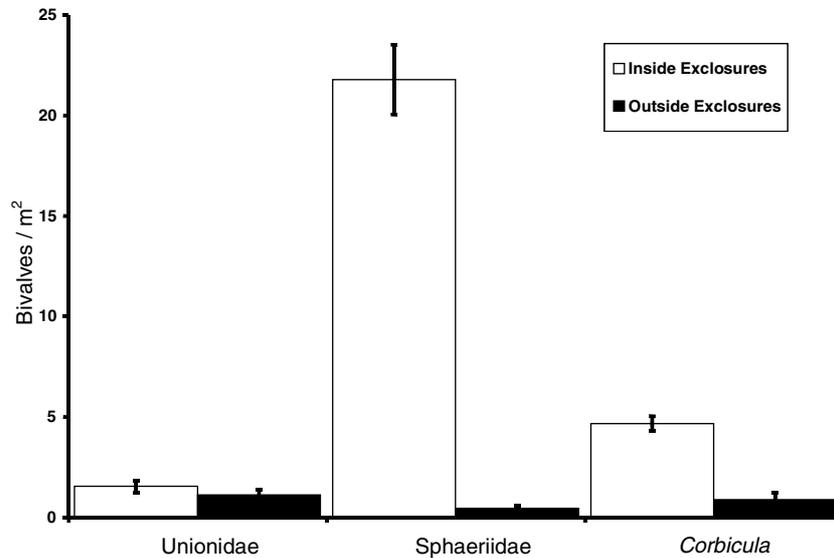
Figure 3. Mean (1 SE) densities of juvenile unionids, sphaeriids, and *Corbicula fluminea* inside and outside sediment depth exclosures.
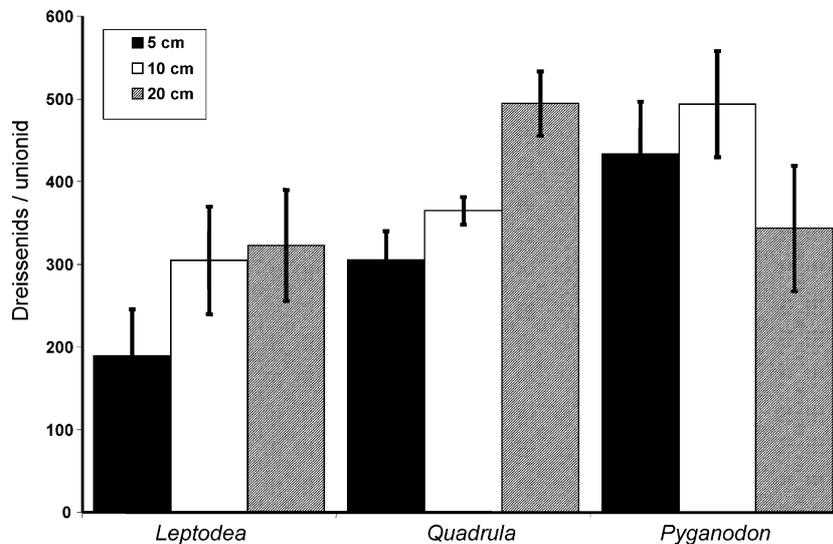

Figure 4. Mean (1 SE) number of attached dreissenids on *Leptodea fragilis*, *Quadrula quadrula* and *Pyganodon grandis* shells in exclosures with 5, 10 or 20 cm deep sediments.

Numbers of attached dreissenids on *Q. quadrula* were different among treatments ($F = 7.10$; df = 2,14; $p < 0.001$), but numbers were only higher in the 20 cm sediment depth than in the 5 cm sediment depth (Fig. 4). Number of dreissenids on *L. fragilis* and *P. grandis* shells did not differ among sediment depths ($p > 0.05$). Most unionids grew in exclosures during the experiment, and mean shell growth (1 SE) for *L. fragilis* was 11.1 (1.9) mm and the mean growth for *Q. quadrula* was 1.9 (0.2) mm. However, growth rates for *Q. quadrula* and *L. fragilis* were not affected by the sediment depth treatment ($p > 0.05$). Block effects were not significant ($p > 0.05$) for any ANOVA analyses.

Discussion

Our results indicate that dreissenids are able to colonize and survive in CCM, and bivalves in this coastal wetland are exposed to high rates of colonization by their veligers and juveniles. In a laboratory experiment, attached dreissenids were dislodged or smothered when unionids burrowed into soft benthic sediments (Nichols & Wilcox, 1997). Our results suggest that this also occurs at CCM because numbers of dreissenids were lower on live *L. fragilis* than on immobile *P. grandis* shells. Live *Q. quadrula* also had somewhat fewer attached dreissenids than the *P. grandis* shells, but these differences were not significant. We found more dreissenids on *Q. quadrula* than on *L. fragilis*, which was also reported in a previous field survey at CCM (Bowers & de Szalay, 2004). This may indicate that there are species-specific factors that determine which species are colonized by dreissenids. We did not observe the behavior of *Q. quadrula* or *L. fragilis* in exclosures, but differences in their burrowing may have affected colonization by dreissenids. *Leptodea fragilis* are very mobile and will burrow through the sediments (Watters, 1995). In contrast, *Q. quadrula* usually remain exposed above the surface of the sediments throughout the summer (Watters et al., 2001). If these patterns occurred in Crane Creek Marsh, *Q. quadrula* may have been exposed to higher numbers of settling dreissenid larvae than *L. fragilis*. Other species-specific factors (e.g., shell texture or morphology) probably also affect dreissenid survival on unionids, and further experiments are necessary to determine the underlying causes for the differences between species.

Although Nichols & Wilcox (1997) showed that unionids held in laboratory aquaria reduce numbers of attached dreissenids by burrowing into the sediments, no studies have tested how unionids or dreissenids are affected by sediment depths in coastal wetlands. In the exclosure experiment, burrowing should have been prevented in the 5 cm treatment, and we expected the highest dreissenid infestation in this treatment. Instead, dreissenid numbers on *Q. quadrula* in 5 cm sediment treatment were lower than in 20 cm treatment. Therefore, the pattern of dreissenid numbers was opposite of what we expected. *Leptodea fragilis* also showed a trend of increasing dreissenid numbers in deeper sediments, although this was not statistically significant. Therefore, sediment depth probably affected dreissenids or unionids in some unexpected way. An alternate explanation is that the differences were due to some uncontrolled effects of the exclosure. For example, unionids in exclosures with shallow sediments may have dislodged some dreissenids from their shell by scraping against the bottom mesh when they burrowed. Further experiments are necessary to provide a better explanation of the causes.

It is apparent from these experiments that burrowing alone will not prevent dreissenid infestation because the unionids, sphaeriids and corbiculids that could burrow below the sediments in exclosures still had high numbers of attached dreissenids. Although the unionids in the exclosures did grow, others have reported that 10–50 attached dreissenids can increase unionid mortality after several years (Ricciardi et al., 1995; Hart et al., 2001). Mean numbers of attached dreissenids on *L. fragilis* and *Q. quadrula* in exclosures in the sediment depth experiment ranged from 189 to 494 dreissenids per unionid, and these densities are probably enough to kill these unionids. Mean numbers of attached dreissenids on sphaeriids and corbiculids in small mesh exclosures were only < 4 dreissenids per bivalve, but less is known about what dreissenid densities are lethal to these species. However, given the small size of sphaeriids and corbiculids, dreissenids may have reduced the survival of these species in the exclosures. In contrast, all bivalves collected outside the exclosures had low numbers of attached dreissenids, and densities on unionids are similar to those reported in other coastal wetlands (Nichols & Amberg, 1999; Zanatta et al., 2002) and in CCM in 2001 (Bowers & de Szalay, 2004). Therefore, additional factors, such as molluscivory, probably reduced numbers of dreissenids outside of the exclosures.

Predator access to bivalves was reduced by the exclosures, which probably caused the dramatic differences in dreissenids, sphaeriids and *C. fluminea* numbers inside and outside the exclosures in our experiments. Exclosure experiments in lakes and rivers have demonstrated that fish (Thorp et al., 1998; Magoulick & Lewis, 2002) and diving ducks (Hamilton et al., 1994; Mitchell et al., 2000) reduce densities of dreissenids on artificial substrates. Although effects of molluscivores in coastal

wetlands have not been examined, it is likely that fish are important predators of bivalves in CCM. We did not test which species of predators are the most important in CCM, but we frequently observed common carp near our exclosures and occasionally saw freshwater drum carcasses in the marsh. Fish surveys at CCM show that these and other molluscivores (e.g., pumpkinseed, channel catfish) are common in this wetland (Wells, 2001). Diving ducks (e.g., ruddy duck, *Oxyura jamaicensis*; common goldeneye, *Bucephala clangula*; bufflehead, *B. albeola*) that feed on mollusks are abundant at Ottawa National Wildlife Refuge during the autumn migration (Herdendorf, 1987). However, waterfowl were probably not important predators when we conducted our experiments because few diving ducks remain in Lake Erie during the summer (Prince et al., 1992). Furthermore, large mesh (5 cm × 10 cm) did not eliminate predation, suggesting that molluscivores that were able to get through this size opening may have been medium-bodied fish (e.g., round goby, pumpkinseed) or juveniles of larger species (e.g., channel catfish, carp, freshwater drum).

An alternate explanation for the treatment effects is that water currents carrying planktonic dreissenid veligers may have been reduced within the exclosures, potentially increasing the number of settling veligers. This could have had a similar effect on small *C. fluminea* that are sometimes carried by water currents (Prezant & Chalermwat, 1984). We did not measure water flow inside or outside of the exclosures, and therefore cannot conclusively rule out this potential factor. Based on several pieces of evidence however, we feel this factor is unlikely to play a major role in our experiments. First, other experiments have used mesh exclosures that were comparable to our exclosures, and they concluded that cages did not significantly affect the number of colonizing dreissenids in their treatments (Hamilton et al., 1994; Thorp et al., 1998). Second, if changes in flow affected numbers of dreissenids, this probably would also elevate numbers of dreissenids in the nearby vicinity outside the exclosures. However, we did not observe high numbers of dreissenids on unionids within 0.5 m of the exclosures (R. Bowers, pers. observ.). Finally, sphaeriid numbers were also higher inside exclosures, but these lack a free-swimming life-cyle

stage and colonize new habitats by burrowing (Thorp & Covich, 1991) or by attaching temporarily to other animals (e.g., fish; Carbine, 1942). Therefore, it is unlikely that their densities were affected by changes in water flow.

In summary, our results demonstrate that unionid burrowing is not the only factor affecting dreissenid infestation of bivalves in coastal wetlands, and fish predation probably plays an important role in controlling numbers of dreissenids and also other bivalves in CCM. Additional research is needed to determine which molluscivore species are the most important in CCM and if predators play a pivotal role in reducing mortality of unionids caused by dreissenid infestation in other habitats. Moreover, it is not understood how the impacts of predation and unionid burrowing on attached dreissenids changes in response to seasonal differences in predator numbers and unionid behavior.

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