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Burrowing behavior of freshwater mussels in experimentally manipulated communities

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Abstract. We experimentally manipulated mussel community structure and observed mussel burrowing behavior in mesocosms held in a greenhouse. Vertical positions, vertical movements, and horizontal movements of *Actinonaias ligamentina, Amblema plicata, Fusconaia flava,* and *Obliquaria reflexa* were recorded during five 11-d trials. Community structure was manipulated by constructing communities with 11 different diversity treatments crossed with 3 different density treatments. Vertical positions, vertical movements, and horizontal movements of mussels differed significantly among diversity treatments, and vertical movements differed among density treatments. Differences among diversity treatments were caused by differences in species composition because the burrowing activity of mussels in multispecies communities could be predicted additively from single-species communities. The species used in our study vary in body size, but differences among species were still significant after accounting for body length. We think that differences in species burrowing behavior might be a result of niche partitioning of vertical space, might be a result of differing effects of temperature between species, or might be related to mechanisms to avoid dislodgement during high flows. The burrowing behavior of freshwater mussels has implications for mussel sampling protocols, the sensitivity of mussels to zebra mussel attachment, and how mussels influence benthic ecosystems.

Key words: burrowing, crawling, migration, Unionidae.

Freshwater mussels are one of the most imperiled faunal groups in North America (Williams et al. 1993, Lydeard et al. 2004, Strayer et al. 2004). However, management efforts are hampered by a lack of knowledge about basic mussel ecology and behavior (Vaughn and Hakenkamp 2001, Aldridge et al. 2007). Freshwater mussels are endobenthic and use their muscular foot and shell to burrow in the sediment, and their burrowing behavior could have important consequences. First, differences in species' burrowing behavior might influence sampling results of monitoring programs if mussels are not excavated from the sediment. Species that tend to be buried completely might be underrepresented in samples from catch-per-unit-effort timed sampling protocols. Second, mussel species that are able to burrow into sediments are able to avoid attachment by zebra mussels and can remove attached zebra mussels (Nichols and Wilcox 1997, Nichols and Amberg 1999). Third, burrowing by mussels physically modifies benthic habitats and influences ecosystem processes. For example, burrowing by bivalves mixes sediments, which influences physical, chemical, and microbial properties of the sediment (McCall et al. 1986), facilitates primary production via complex biogeochemical pathways (Aller 1994, Vaughn and Hakenkamp 2001, Lohrer et al. 2004), and alters abundances of co-occurring organisms (Bowers et al. 2005, Jaramillo et al. 2007). Standing crops of periphyton and macroinvertebrates are higher in than outside mussel beds, apparently because of the activities of the mussels (Spooner and Vaughn 2006, Vaughn and Spooner 2006, Vaughn et al. 2007).

Burrowing behavior of individual mussel species can vary with season and reproductive cycle (Amyot and Downing 1997, 1998, Watters et al. 2001), flow regime (Di Maio and Corkum 1997), substrate type and disturbance (Kat 1982, Lewis and Riebel 1984), and parasite abundance (Taskinen and Saarinen 2006), but also varies greatly among species. Thus, mussel activity and the ecological consequences of mussel burrowing should be influenced by mussel community

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TABLE 1. Species included in diversity treatments. Each diversity treatment was crossed with 3 density treatments (4, 8, and 16 mussels/mesocosm) for a total of 33 treatment combinations.

Single-species communities	2-species communities	4-species community
Actinonaias ligamentina	*A. ligamentina* + *A. plicata*	*A. ligamentina* + *A. plicata* + *O. reflexa* + *F. flava*
Amblema plicata	*A. ligamentina* + *O. reflexa*	
Obliquaria reflexa	*A. ligamentina* + *F. flava*	
Fusconaia flava	*A. plicata* + *O. reflexa*	
	A. plicata + *F. flava*	
	O. reflexa + *F. flava*	

composition. We present results of an experiment that examined the influence of mussel community structure on the burrowing behavior of mussel communities and individual species.

Methods

Our experiment was conducted in recirculating mesocosms ($n = 33$) held in a greenhouse. Mesocosms consisted of molded plastic liners suspended in fiberglass basins to allow water circulation below and around the liner. Liners were filled with 0.6 cm of sand (0.09–0.25 mm diameter) overlaid with 12 cm of gravel (10–25 mm diameter), which approximated substrate composition in mussel beds in the Kiamichi River in southeast Oklahoma (Vaughn and Pyron 1995). Mesocosms were 94 × 44 cm, and were filled with water from a nearby pond to a depth of 16.5 cm. Flow was maintained at a rate of ~13.7 cm/s with a 1/32 horsepower pump. Five hundred milliliters of a concentrated cultured algal assemblage was added to each mesocosm daily (mean chlorophyll *a* ± SE = 0.212 ± 0.010 mg/L) (Vaughn et al. 2004, 2008).

We conducted five 11-d trials of the experiment in July–September 2005. Water temperatures in the mesocosms tracked air temperature in the greenhouse and were measured at sunrise and sunset every 3rd d. Water temperatures ranged from 21.8 to 35.7°C throughout the experiment, with mean temperatures of 26.8°C for trial 1, 28.0°C for trial 2, 31.3°C for trial 3, 30.9°C for trial 4, and 30.4°C for trial 5. These temperatures are typical of water overlying mussel beds in the Kiamichi River during summer low-flow periods (Vaughn et al. 2007, 2008). Photoperiod varied naturally with light levels in the greenhouse. After each trial, mesocosms were bleached for 1 d, rinsed and soaked with well water for 1 d, and dried for 1 d before the next trial began.

Individuals belonging to 4 species of freshwater mussels, *Actinonaias ligamentina* ($n = 93$), *Amblema plicata* ($n = 87$), *Fusconaia flava* ($n = 80$), and *Obliquaria reflexa* ($n = 83$) were collected from a single site in the Kiamichi River in June 2005. These species vary in size and shell morphology. The mean lengths of mussels used in our study were: *A. ligamentina*, 105 mm; *A. plicata*, 84 mm; *F. flava*, 59 mm; and *O. reflexa*, 51 mm. Both *A. ligamentina* and *F. flava* have smooth shells, whereas *A. plicata* is ridged, and *O. reflexa* has 3 large pustules on each valve. Each mussel was individually marked with 2 Floy® shellfish tags (Floy, Seattle, Washington) attached with gel-type adhesive; 1 tag was placed on the posterior shell margin and the other on the exterior of the shell halfway along the longitudinal axis. Mussels were held in Frigid Units living streams (Frigid Units, Toledo, Ohio) for several weeks prior to the experiment to allow them to acclimate to laboratory conditions, and for 3-d periods between experimental trials.

Experimental communities were created in a factorial design with 3 different density treatments (4, 8, and 16 mussels per mesocosm, [~10, 19, and 39 mussels/m^2]) crossed with 11 diversity treatments (all possible 1-, 2-, and 4-species combinations) (Table 1). Density and diversity treatments approximated those found in natural mussel communities in the Kiamichi River (Vaughn et al. 2007). Mussels were randomly assigned to treatments and were haphazardly placed in mesocosms at the beginning of each trial. Mussels that died during the course of a trial were replaced to maintain the density of the treatment. Mean pooled observations for both individuals were used as the position and movement estimates for the replaced mussel (see below). Overall mortalities for the entire 3-mo period were: *A. ligamentina* = 18, *A. plicata* = 8, *F. flava* = 0, *O. reflexa* = 2.

Horizontal and vertical positions of mussels were recorded over the course of each trial. For all trials, the position of each mussel was recorded at the beginning and end of the experiment (days 1 and 11) in each mesocosm. In trial 1, additional observation dates were staggered, such that the position of each mussel in ⅓ of the mesocosms was recorded each day (i.e., each mesocosm was checked every 3 d, but not all on the same days). In trials 2 to 5, the position of each mussel in each mesocosm recorded was on days 3, 5, 7, and 9. We were not able to record vertical positions on

day 7 of trial 4. All observations were made in the morning.

During observations, a polyvinyl chloride (PVC) grid consisting of eight 23 × 23-cm sections was placed over each mesocosm (the grid did not touch the water). Horizontal movement (cm) was estimated using changes in grid position by a mussel between sequential observations and distances between the midpoints of cells within the grid. Total horizontal movement for each mussel in each mesocosm over the course of a trial was calculated as the sum of these horizontal movements.

The tags at the midpoints of the longitudinal axis of each mussel were used as reference points for observations of vertical position. Vertical position was recorded as the percentage of body length exposed above the sediment–water interface (i.e., 0, 25, or 75% exposed in the water column). For each observation, the length of shell exposed (mm) in the water column was estimated from body-length measurements. Vertical movement was calculated as the difference in length of shell exposed between sequential observations. Total vertical movement for each mussel in each mesocosm over the course of a trial was calculated as the sum of these vertical movements. The average vertical position of each mussel in each trial was calculated as the mean length of shell exposed during the trial.

Community analysis: Is community burrowing behavior a function of community structure?

Two-way multivariate analysis of variance (MANOVA) with density and diversity treatments as main effects was used to test whether mean mussel burrowing behaviors (shell exposed, horizontal movement, vertical movement) varied with community structure. Dependent variables were mesocosm-level mean values for shell exposed (mm), horizontal movement (cm), and vertical movement (cm). Mesocosm-level means were calculated across all individuals in a mesocosm, regardless of species. For example, if a mesocosm contained a 2-species community of *A. ligamentina* and *A. plicata*, we averaged all *A. ligamentina* and *A. plicata* movements over the course of the trial to generate 1 datum for each dependent variable for the mesocosm. If the MANOVA model was statistically significant, each dependent variable was analyzed with a separate 2-way analysis of variance (ANOVA) to determine which of the dependent variables differed significantly among treatments (Zar 1999). If the diversity treatment effect was statistically significant, 2 sets of multiple comparison procedures were used to test 2 different hypotheses. First, all possible contrasts between single-species communities were used to test for significant behavioral differences among single-species communities. Second, contrasts between multispecies treatments and single-species communities were used to test whether species behaved differently in multispecies communities than in single-species communities. All contrasts used Cicchetti's method to control for type I errors (Toothaker 1993).

Species analyses: Is species burrowing behavior a function of body size?

Mussels were reused in each trial. Therefore, repeated-measures MANOVA, with species and trial as factors, was used to test whether differences in burrowing behavior between species were related to differences in body size. Dependent variables were proportion of shell exposed, and horizontal movement and vertical movement standardized by body length of individual mussels. Proportion of shell exposed was arcsine($\sqrt{[x]}$)-transformed, and standardized vertical and horizontal movements were $\log(x + 1)$-transformed to meet assumptions for normality and homogeneity of variances (Zar 1999). This analysis was restricted to individuals that were used in all 5 trials, and individuals were randomly deleted from the data set until $n = 68$ for each species. If the repeated-measures MANOVA model was statistically significant, each dependent variable was analyzed with a separate repeated-measures ANOVA to determine which of the dependent variables differed significantly among treatments. Linear trend analyses and all possible contrasts among species within a trial were used to help interpret the results of significant trial × species interaction. Contrasts were made with Cicchetti's method to control for type I errors (Toothaker 1993).

Results

Community analyses

Diversity (Roy's root = 0.953, $F_{10,132} = 12.578$, $p < 0.001$) and density (Roy's root = 0.076, $F_{3,131} = 3.329$, $p = 0.022$) affected mussel community burrowing behaviors. The density × diversity interaction term was not statistically significant (Roy's root = 0.188, $F_{20,132} = 1.239$, $p = 0.233$). Diversity significantly influenced shell exposed (Fig. 1A), vertical movement (Fig. 1B), and horizontal movement (Fig. 1C), and density significantly affected vertical movement (Table 2). Mussels in the low-density treatment moved less vertically (1.75 ± 0.21 cm; mean ±1 SE) than did mussels in the medium-density (2.25 ± 0.16 cm) and

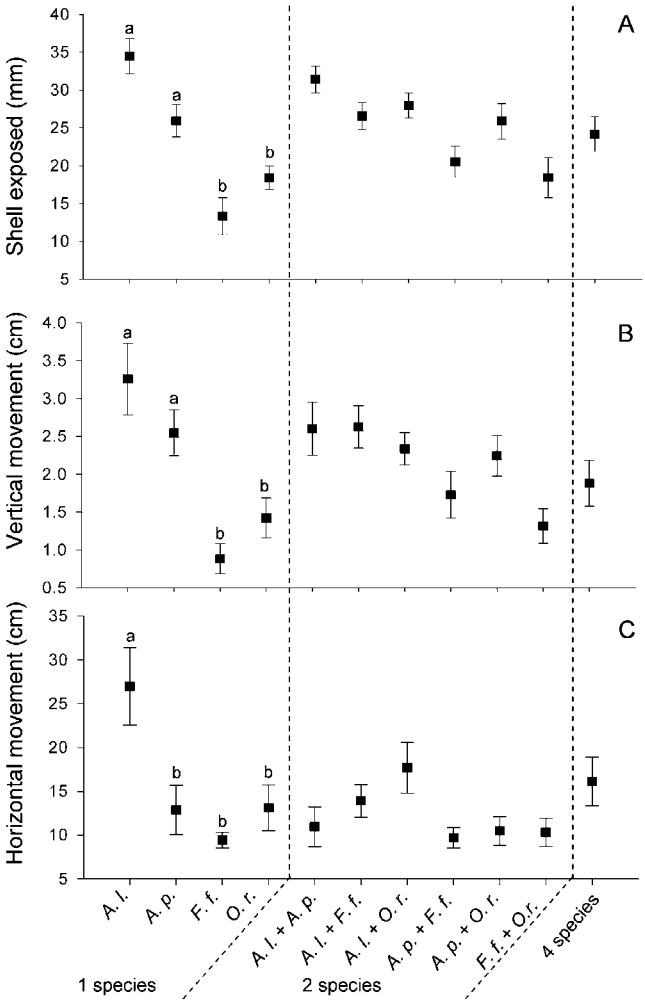

FIG. 1. (A) Mean (±1 SE) shell length exposed above the sediment, (B) vertical movement, and (C) horizontal movement of mussels in each diversity treatment. Vertical dashed lines separate 1-, 2-, and 4-species communities. Single-species communities that do not share a letter are significantly ($p < 0.05$) different. *A.l. = Actinonais ligamentina, A.p. = Amblema plicata, F.f. = Fusconaia flava, O.r. = Obliquaria reflexa.*

high-density (2.23 ± 0.17 cm) treatments. In single-species communities, *A. ligamentina* had the highest and *F. flava* had the lowest values for mean shell exposed (Fig. 1A), vertical movement (Fig. 1B), and horizontal movement (Fig. 1C). *Amblema plicata* and *O. reflexa* had intermediate values for shell exposed and vertical movements but had values of horizontal movement that did not differ from those of *F. flava*. Burrowing behaviors did not differ between multispecies treatments and respective single-species communities (Fig. 1A–C).

Species analyses

Species (Roy's root = 0.148, $F_{3,268} = 13.262$, $p < 0.001$), trial (Roy's root = 0.867, $F_{12,257} = 18.574$, $p = 0.019$), and the species × trial interaction (Roy's root = 0.160, $F_{12,259} = 3.448$, $p < 0.001$) significantly affected mussel burrowing behaviors that were standardized by body length. Proportion of shell length exposed (Fig. 2A), vertical movement (Fig. 2B), and horizontal movement (Fig. 2C) differed significantly among species and among trials (Table 3), and proportion of shell length exposed was significantly affected by an interaction between species and trial (Table 3). Species effects on proportion of shell exposed changed across the 5-trial course of the experiment (Fig. 2A). The proportion of shell exposed increased significantly over the course of the experiment for all species (post hoc linear trend analyses, *A. ligamentina*, $p = 0.011$; *A. plicata* $p < 0.001$; *F. flava*, $p < 0.001$; *O. reflexa*, $p < 0.001$). However, these increases appeared linear for *F. flava* and *A. plicata* and nonlinear for *A. ligamentina* and *O. reflexa* (Fig. 2A). Vertical movement of *F. flava* was significantly less than vertical movement of the other 3 species (Fig. 2B), and horizontal movement of *A. ligamentina* and *O. reflexa* was significantly greater than that of *A. plicata* (Fig. 2C).

Discussion

The burrowing behavior of a mussel community depends on the diversity (species composition) of the community. Burrowing behaviors differ among species, but the burrowing behavior of individual species does not depend on community structure. Thus, the differences in community-level shell exposure and vertical and horizontal movements among diversity treatments resulted from behavioral differences among

TABLE 2. Results of 2-way analyses of variance with mussel density and diversity as main effects and length of shell exposed (mm), horizontal movement (cm), and vertical movement (cm) as dependent variables.

	Diversity			Density			Diversity × density		
Dependent variable	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Shell exposed	10, 131	7.932	<0.001	2, 131	0.139	0.870	20, 131	0.556	0.936
Vertical movement	10, 131	5.384	<0.001	2, 131	3.186	0.045	20, 131	0.676	0.844
Horizontal movement	10, 131	4.291	<0.001	2, 131	0.034	0.966	20, 131	0.997	0.471

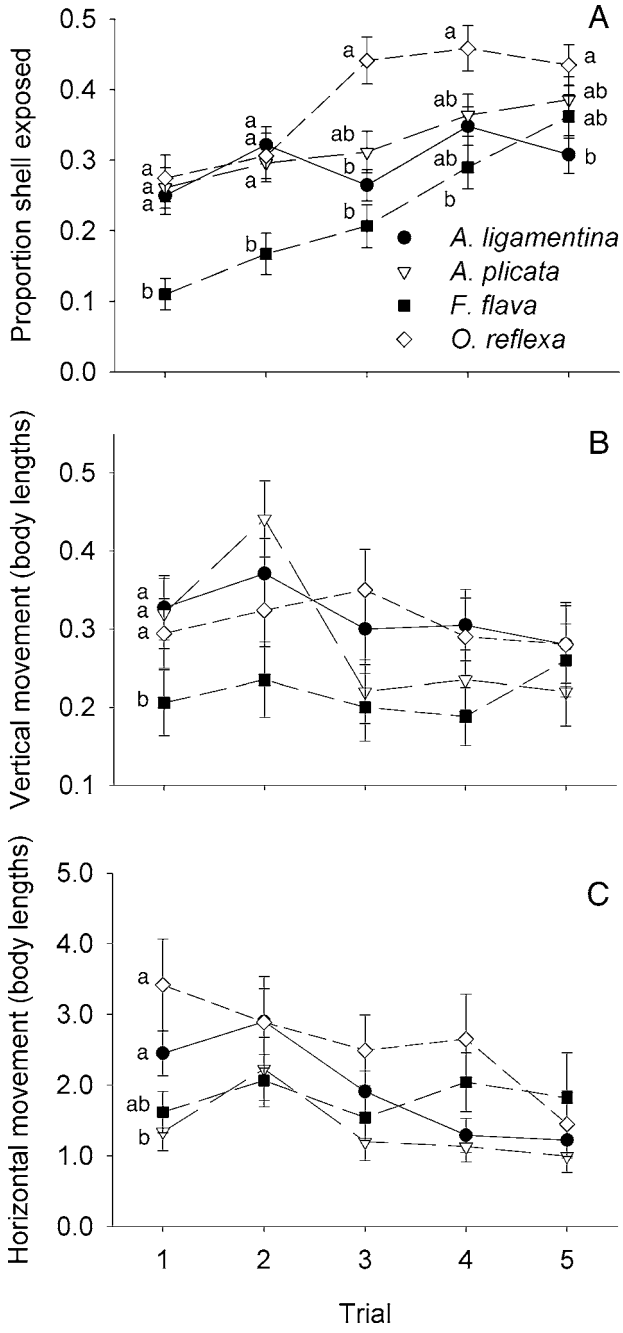

FIG. 2. (A) Mean (±1 SE) proportion of shell length exposed above the sediment, and body-length standardized (B) vertical and (C) horizontal movement of mussels in each species across 5 experimental trials. In panel A, data points within each trial that do not share a letter are significantly different; in panels B and C, species that do not share a letter are significantly different over all trials.

species, rather than from changes in species' behaviors in response to other species. These results have implications for mussel sampling strategies, mussel conservation and management, and our understanding of how mussels influence ecosystem processes.

Interspecific differences in burrowing behavior

Mussel species in our study differed in their use of the vertical substrate profile, and mussel density affected vertical movements of individuals within the substrate. Mussels moved less in vertical directions in low- than in medium- and high-density treatments. Thus, mussels appear to adjust their vertical position within the substrate as density increases. Mussels occur in densities as high as $300/m^2$ in rivers in southeast Oklahoma (DCA and CCV, unpublished data). When densities are this high, mussels are stacked on top of each other in the substrate, and space could be limiting. Mussel species might have evolved preferences for different strata within the sediment, which might affect their access to fish hosts or food (suspended or buried).

Several mechanisms, including differences in size, morphology, and the influence of temperature, might underlie differences in burrowing behavior among mussel species. Larger mussels did move greater distances than smaller mussels, so body size did influence how much a species could burrow. However, differences in burrowing behavior remained apparent after standardizing for body length, so other factors than size must have contributed to the observed differences in burrowing behavior.

Movement through the sediment might be easier for species with smooth shells than for species with textured shells. The ridges of *A. plicata* and pustules of *O. reflexa* help anchor them in the substrate and prevent them from being dislodged during high flow (Watters 1994). Watters (1994) hypothesized that smooth-shelled species should have mechanisms other than shell texture that facilitate anchoring and reduce the potential for dislodgement during floods. One of these alternate mechanisms is burrowing behavior. The 2 smooth-shelled species in our study, *A. ligamentina* and *F. flava,* differed markedly in their burrowing behavior, but both behavioral traits could reduce dislodgement during floods. *Fusconaia flava* burrowed deeper and was more sedentary than other species, so it might be able to reduce the risk of dislodgement by avoiding exposure to strong scouring forces. *Actinonaias ligamentina* burrowed very actively, and might be able to avoid dislodgement by burrowing quickly into the sediment if it detects rising flow. Studies of vertical positions of mussels in the field before and after high-flow events might clarify how burrowing behavior could prevent dislodgement during floods.

Mean temperatures increased over the course of our 5 trials. Mussels are ectotherms, and their metabolic rates increase with temperature. Thus, they might have

TABLE 3. Results of repeated-measures analysis of variance with mussel species as the main effect, trial as the repeated factor, and proportion of shell length exposed, vertical and horizontal movement (standardized by body length) as dependent variables.

	Species			Trial			Species × trial		
Dependent variable	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Proportion shell length exposed	3, 267	27.162	<0.001	4, 1072	38.503	<0.001	12, 1072	4.345	<0.001
Vertical movement	3, 267	3.649	0.013	4, 1072	2.930	0.020	12, 1072	1.265	0.234
Horizontal movement	3, 267	3.102	0.027	4, 1072	7.243	<0.001	12, 1072	1.158	0.309

had more energy for burrowing at the higher temperatures at the end of the experiment. However, high temperatures can cause significant physiological stress (Spooner and Vaughn 2008), which also would influence activity. For example, *A. ligamentina* moved more than other species in our study. This species is more sensitive to warm temperatures than are the other species used in our study (Spooner and Vaughn 2008). In addition, *A. ligamentina* moves to deeper water under summer drought conditions in local streams (DCA and CCV, personal observation). The high level of burrowing activity by *A. ligamentina* might have been a response to seek deeper water and cooler temperatures.

Actinonaias ligamentina activity decreased over the course of the experiment, and this change also could have been related to temperature. *Actinonaias ligamentina* is intolerant of higher water temperatures and becomes stressed and catabolyzes its own tissues at temperatures >33°C (Spooner and Vaughn 2008). Individuals were reused across trials in our experiment. Thus, repeated exposure to warm temperatures might have caused this species to deplete energy reserves during early trials, leaving them with less energy to burrow in later trials. Among species in our experiment, we observed the most deaths in *A. ligamentina*, an indication of the stress that the experimental conditions placed on this species.

Implications for management, conservation, and ecosystem processes

Several other authors have suggested that mussel sampling that does not include excavation will underestimate abundances of species that tend to burrow deep in the substrate (Strayer and Smith 2003, Smith 2006). However, excavation is time consuming, and knowledge of the burrowing traits of a species would be useful when constructing appropriate sampling designs. If the target species tends to burrow deeply, then excavation would be necessary, but if the target species burrows shallowly and is usually exposed, then visual searches might suffice.

The burrowing traits of a mussel species also might influence resistance to infestation by zebra mussels. Zebra mussels attach directly to exposed unionid mussels and stress unionid populations by competing with them for food (Baker and Hornbach 2000). These processes lead to declines of unionid communities (Strayer and Smith 1996). However, mussel species differ in their responses to zebra mussel infestation (Hallac and Marsden 2000), and some of these differences might be explained by differences in burrowing behavior. Mussels that are completely buried in the sediment probably will resist zebra mussel attachment. Furthermore, if mussels with attached zebra mussels can burrow completely within the sediment, they can kill attached zebra mussels, which cannot tolerate the lower O_2 levels of interstitial water (Nichols and Wilcox 1997). Thus, burrowing traits of mussel species might allow some coexistence of some unionid species and zebra mussels (Nichols and Amberg 1999).

Unionid mussel communities influence ecosystem processes in different ways (Spooner and Vaughn 2006, Vaughn et al. 2007, 2008). Our results indicate that differences in burrowing behavior among mussel species might underlie these differences. Burrowing activity of benthic organisms causes bioturbation of sediments (Lohrer et al. 2004), which redistributes nutrients within sediments and enhances primary production via complex biogeochemical pathways (Lohrer et al. 2004). Burrowing behavior is directly related to bioturbation, so mussel species probably differ in their ability to stimulate primary production via bioturbation. Freshwater mussel communities, especially those dominated by *A. ligamentina* (the most active burrower in our experiment), are associated with higher standing crops of benthic algae (Vaughn et al. 2007). Thus, enhanced bioturbation caused by burrowing might be an important pathway for facilitation of primary production by mussels.

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