

Factors affecting the movement of adult zebra mussels (*Dreissena polymorpha*)

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Abstract. Adult zebra mussels are generally thought of as sessile animals. However, when detached from their byssus, adult mussels exhibit creeping behavior similar to that of other bivalve species. Our study examined the effects of size, light, water hardness, temperature, and the presence of injured conspecifics on the movement of adult zebra mussels. Mussels were placed in aquaria and their movement was recorded after a 2-h interval. Mussels left visible trails in a thin layer of sand on the aquarium floor that allowed for accurate measurements of distance and direction of movement. The tendency to move and distance moved by the mussels was inversely proportional to size of the individual mussels. There was no significant effect of temperature on movement, though smaller mussels tended to move more at higher temperatures. Although distance traveled was not significantly different in light versus dark conditions, there was a significant effect of light on direction traveled. Zebra mussels were strongly negatively phototactic. The presence of injured conspecifics decreased movement significantly, whereas water hardness did not have a significant effect on movement. The movement of adult zebra mussels is an under-appreciated phenomenon and deserves greater consideration for understanding dispersal vectors and development of antifouling methods to be used in the future.

Key words: zebra mussel, adult movement, size, light, temperature, calcium, injured conspecifics.

The zebra mussel, *Dreissena polymorpha*, first appeared in North America in 1985 and is now found throughout a large portion of the continent (Griffiths 1993). Zebra mussels were brought to North America from their native region of eastern Europe in the ballast water of international freighters. As an exotic species, their populations in North American waters have exploded, and densities as high as 700,000 individuals/m² have been observed (Kovalak et al. 1993). The rapid spread of zebra mussels has had significant impacts on native species, food webs, and human activities (Mackie 1991, Hunter and Bailey 1992, Kovalak et al. 1993, LePage 1993, Nalepa 1994). Understanding the various

vectors of zebra mussel dispersal is important for limiting their invasive capacity.

Most zebra mussel dispersal studies have focused on the veliger stage. A great deal is known about veliger settlement rates and substrate preferences (e.g., Fraleigh et al. 1993, Kilgour and Mackie 1993, Marsden and Lansky 2000). In contrast, the motility of adult zebra mussels is an under-appreciated and little understood phenomenon. Adult zebra mussels are known to detach their byssus and move about using their foot. Juvenile mussels have been reported to crawl at a rate of 7 cm/night and adult rates of movement up to 36 cm/h have been observed (Cawein 1993, Shevchenko 1949 as cited in Ackerman et al. 1994). The stimuli for these movements are unknown. Studies of the movement and burrowing of the unionid mussel *Elliptio complanata* indicate that activity is dependent upon season; mussels burrowed into sub-

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strates in autumn and emerged to the substrate surface in summer (Balfour and Smock 1995, Amyot and Downing 1997). Amyot and Downing (1997) found that vertical movement within soft sediments was positively correlated with temperature, whereas day length was the most important cue for horizontal movements. A study of *Limnoperna fortunei* by Uryu et al. (1996) indicated that juvenile mussels could move up to 300 cm in a 24-h period; distance traveled was inversely related to the size of the individual, mussels preferentially settled in shaded areas, and they exhibited strong thigmotaxis, tending to settle in angled crevices.

The movement of adult mussels has important implications for the control of zebra mussels as a nuisance species. Adult mussels may be able to move onto substrates that can become vectors for range expansion, such as anchors and boat hulls. The movement of adults may lessen the benefits of scraping mussels from surfaces, such as intake pipes or native mussels, if the displaced zebra mussels can simply creep back onto the surface and reattach their byssus. Understanding adult mussel movement may make it possible to guide the colonization of mussels away from valuable surfaces and onto disposable ones.

Our study investigated 5 factors that may affect the movement of adult zebra mussels: individual size, water temperature, water hardness, light, and the presence of injured conspecifics. Size is a significant factor in the movement of other mollusc species; smaller individuals tend to move greater distances than larger ones (Uryu et al. 1996). Zebra mussels are poikilothermic; therefore, water temperature will regulate activity, and the distance moved should be directly related to water temperature. Concentrations of dissolved ions such as Ca play an important role in the health and growth of zebra mussels, and appear to be strongly correlated with their geographic distribution (Ramcharan et al. 1992, Hincks and Mackie 1997). In an environment with limited Ca, zebra mussels may restrict expenditure of Ca associated with muscular movement to conserve Ca for shell growth. Zebra mussels avoid bright light, and larva prefer to settle in shaded areas (Marsden and Lansky 2000). Light may serve as an indicator of exposure to predators or wave activity; therefore, it is reasonable to expect zebra mussels will move away from light. It follows that

light may also be a stimulus for increased movement. Among fishes and other species, injured conspecifics may produce alarm compounds that warn of active predation in the area (Commens and Mathis 1999). Increased movement of adult zebra mussels has been noted in the presence of injured conspecifics, indicating that zebra mussels may recognize and respond to other injured zebra mussels (JEM, unpublished observations). Thus, we predict zebra mussels will be more active and move further in the presence of injured conspecifics.

Methods

The setup for all treatments consisted of six 38-L aquaria filled with water from Lake Champlain, with a thin layer (2–5 mm deep) of fine sand covering the floor of each tank. Zebra mussels were collected from Lake Champlain within 4 h of each experiment, held in aerated lake water, and carefully removed from their byssal attachment immediately prior to initiation of each experiment. In each tank in all experiments, we placed 9 zebra mussels: 3 mussels 5 to 10 mm in length, 3 mussels 10 to 20 mm in length, and 3 mussels >20 mm. A single tank containing 9 mussels was considered to be a replicate. The mussels were randomly arranged in a square grid within each aquarium, with ~7 cm between adjacent mussels. Moving mussels left trails in the sand that allowed for an exact measure of distance and direction traveled. The position of the mussels after 2 h was photographed using an Olympus digital camera. The images were then uploaded to a computer and zebra mussel trails were measured using the Scion Image program (National Institutes of Health Image for IBM computers, available on the Internet at <http://www.scioncorp.com>). Trails were digitized to measure total distance traveled; displacement was measured as the straight-line distance from start to end point.

For all treatments, all conditions were held constant except for the factor that was being tested. Constant conditions were as follows: tanks were illuminated with overhead fluorescent lighting, temperatures were 19 to 20°C, and the water contained 67 mg CaCO₃/L. In each experiment, treatments were randomized among tanks; all treatments for a given experiment were included on each day that an experiment was conducted. Hence, for all factors ex-

TABLE 1. Summary of the experimental treatments, number of replicate tanks, and number of zebra mussels that moved in each treatment. In all experiments, 3 mussels in each of 3 size classes were used in each replicate.

Experiment	Treatment	No. of tanks	No. of mussels that moved/ total no. of mussels
Size (mm)	Large (>20)	12	3/36
	Medium (10–20)	12	17/36
	Small (5–10)	12	28/36
Temperature (°C)	15–16.5	10	47/90
	19–20	10	53/90
	24–27	10	49/90
Light	Light	9	48/81
	Dark	9	54/81
Water hardness (mg CaCO ₃ /L)	Hard water (204)	6	20/54
	Lake water (67)	6	19/54
	Soft water (9)	6	19/54
Crushed conspecifics	Crushed	9	17/81
	None	9	28/81

cept size, tanks were the experimental unit and days were blocks; blocks were treated as fixed effects in the models. In the tests for size effects, each group of 3 mussels was an experimental unit for size and each tank was a block. Treatments and sample sizes are summarized in Table 1. All mussels were used only once.

The effect of size on movement was determined by repeating the above procedure twice, so that a total of 108 mussels was examined. The distances traveled by each of the mussels were then compared among size classes.

The effect of temperature on zebra mussel movement was determined using a range of temperatures between 15 and 27°C. Cold treatments were produced by adding ice directly to the aquaria and warm treatments were produced using aquarium heaters. The treatments were randomly assigned to the tanks; the number of replicates of each temperature ranged between 1 and 3 because temperature could not be controlled exactly.

The effect of water hardness on movement was determined using 3 treatments: soft water, lake water, and hard water. Soft water with 9 mg CaCO₃/L was produced using US Environmental Protection Agency standards for reconstituted water (Weber et al. 1989). Hard water was produced using the same method as for soft water and contained 204 mg CaCO₃/L. Both hard- and soft-water treatments were constituted with distilled water. Lake water was taken directly from Lake Champlain and con-

tained 67 mg CaCO₃/L. The treatments were randomly assigned to tanks and each treatment was replicated 6 times.

Two treatments, light and dark, were used to determine the effect of light on movement. The dark treatment was produced by covering the entire aquarium in aluminum foil. The light treatment consisted of an aquarium that was completely enclosed in foil except at one end, where a 32-W fluorescent household light was placed. Each treatment was replicated 9 times. The displacement and angle from start to end point were measured in addition to the total distance traveled by each mussel. The angle of movement was measured by drawing a line from the mussel's start point directly towards the light source and considering this line to be 0°; the angle from this line to the mussel's final position was determined.

The presence of injured conspecifics was simulated by crushing 150 mL of randomly sampled zebra mussels in 350 mL of lake water and then adding 50 mL of this liquid to each aquarium after the experimental mussels were placed in the tank. A control with no treatment added was run at the same time; adding a further 150 mL of lake water as a control was not deemed necessary. The treatment and control were each replicated 9 times.

Data analysis

The response variable in all but the light experiment was total distance traveled in 2 h. We

used a 2-way factorial ANOVA to evaluate the main effects and interactions of size (in all cases) and treatment (temperature, calcium concentration, crushed conspecifics, and light). Post-hoc comparisons among treatment groups were made using Sheffe's test. In general, we did not report results of nonsignificant comparisons. All comparisons except the size experiment were re-analyzed using only the smallest size class of mussels in the analysis; the size experiment indicated that the smallest mussels moved most, so the largest effect would be expected in this size class. The temperature experiment was analyzed using a regression, followed by a Bonferroni adjustment for multiple comparisons made simultaneously. Differences among the numbers of mussels moving in each treatment were compared using a χ^2 test. The expected values were the total number of moving individuals divided equally among the treatments.

For the water hardness experiment, we compared the soft and hard water treatment, and then compared these 2 treatments with the lake water treatment. Variation in the angle of travel of mussels in the light and dark treatments was quantified by partitioning direction into six 60° segments. We compared the observed number of individuals traveling in each segment to an equal distribution among all segments using a χ^2 test. In the light and dark treatments, the displacement of each mussel from start to end point at 2 h was compared using an ANOVA.

Results

The distance traveled by adult zebra mussels in a 2-h period varied significantly with the size of the individual ($p < 0.001$, Fig. 1). Small individuals traveled a mean distance of 22.1 ± 3.6 cm, medium individuals moved a mean distance of 5.4 ± 1.9 cm, and large individuals moved a mean distance of 0.4 ± 0.2 cm. These and all other reported mean distances included individuals that did not move during the 2-h period; excluding mussels that did not move yielded distances of 28.4 ± 3.4 , 11.5 ± 2.3 , and 4.7 ± 0.4 cm for small, medium, and large mussels, respectively. The maximum distance moved by any mussel in any treatment in 2 h was 96.2 cm, by a small mussel in the warm-water treatment. The post-hoc comparison revealed significant differences between small and medium mussels, and between small and

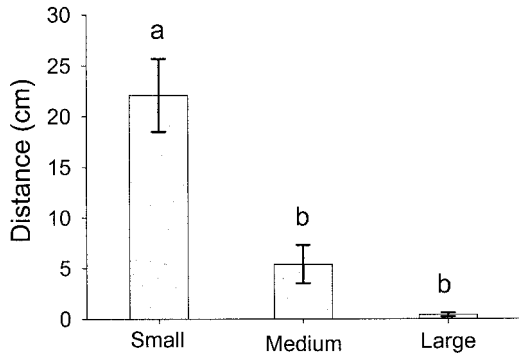


FIG. 1. Mean (\pm SE) distance traveled by adult zebra mussels after 2 h for 3 size classes of mussels: small (5–10 mm), medium (10–20 mm), and large (>20 mm). Letters above the bars denote treatments that were significantly different in post-hoc comparisons ($p < 0.001$).

large mussels ($p < 0.0001$). The same size relationship was observed in all the other experiments except the light–dark experiment, in which all paired comparisons among size classes were significant.

There was a significant positive relationship between distance traveled and temperature for the smallest size class (p -value for the slope < 0.039 , $r = 0.39$), but not for the other 2 size classes (medium mussels $p < 0.92$, $r = 0.019$; large mussels $p < 0.77$, $r = 0.056$); however, this small-size-class relationship with temperature was not significant when using a Bonferroni adjustment for multiple comparisons. The mean distance traveled by mussels of all size classes in cold water (15.0–16.5°C) was 9.4 ± 1.4 cm, in room-temperature water (19.0–20.0°C) was 12.8 ± 1.8 cm, and in warm water (24.0–26.0°C) was 13.2 ± 2.1 cm.

The manipulation of water hardness did not result in a significant difference in the distance traveled in 2 h ($p < 0.166$). The mean distance traveled by all size classes of mussels in soft water was 6.3 ± 1.5 cm, in lake water was 8.0 ± 1.9 cm, and in hard water was 9.2 ± 2.1 cm. Re-analysis using only the smallest size class did not change the outcome of the tests.

There was no significant difference in distance traveled by mussels in light and dark treatments ($p < 0.746$, Fig. 2). Mussels traveled a mean distance of 14.4 ± 1.9 cm in the light and a mean distance of 15.8 ± 2.3 cm in the dark during the 2-h period. The displacement of

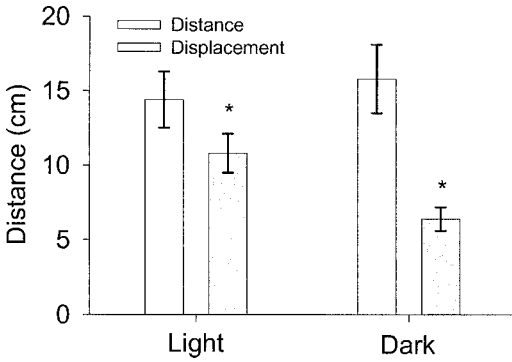


FIG. 2. Mean (\pm SE) distance traveled and total displacement of all size classes of adult zebra mussels at 2 h when held in light or dark conditions. Displacement is the linear distance traveled between the starting point and position after 2 h. * = significant difference in light and dark displacement ($p < 0.0001$).

mussels in the light was significantly greater than the displacement of mussels in the dark ($p < 0.0001$, Fig. 2). The mean displacement of mussels from start to end point in the light was 10.8 ± 1.3 cm, and in the dark was 6.4 ± 0.8 cm. There was a significant interaction between size and light, with smallest mussels having the greatest difference in displacement between light and dark treatments ($p < 0.001$). There was a significant difference between the direction choices of mussels in light and a random distribution ($p < 0.01$, Fig. 3), but no significant difference between direction choices in dark and a random distribution. All mussels in the light moved at angles between 120° and 240° from the light source at 0° . The directional choice of mussels in the dark did not differ significantly from an equal distribution throughout the 60° segments of the circle ($p < 0.96$).

Mussels in the injured conspecific treatment (mean distance traveled = 5.4 ± 0.96 cm) trav-

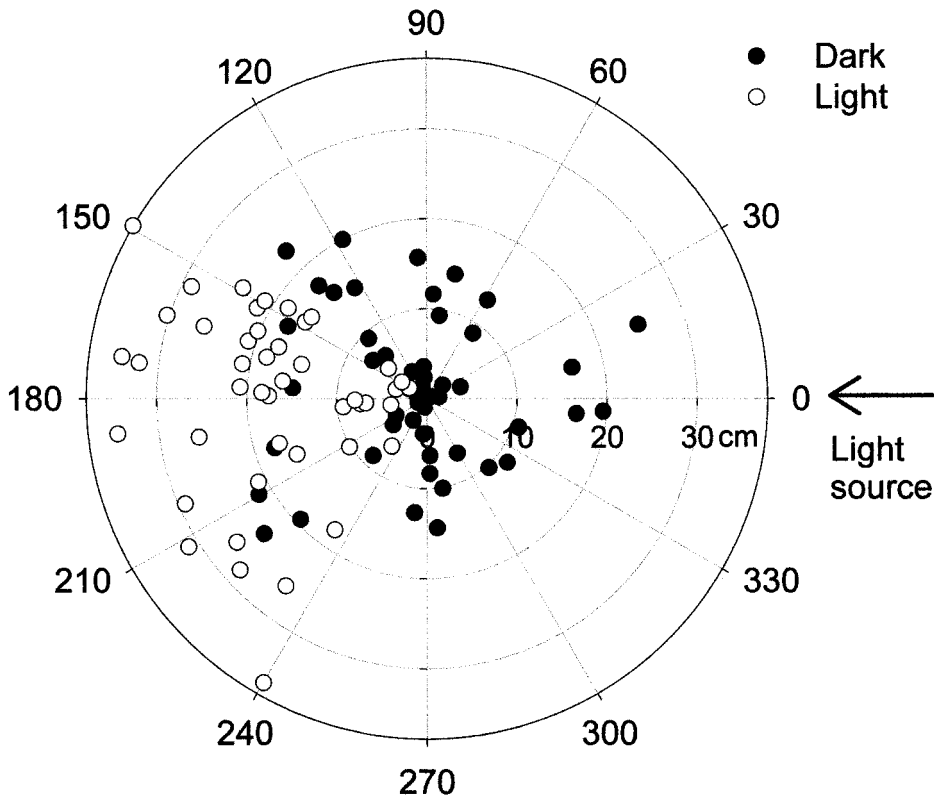


FIG. 3. Angle and displacement from start to end point of zebra mussel movement in 2 h. Angle of movement is relative to light source in the light treatment, and a fixed point that was identical in all replicates of the dark treatment.

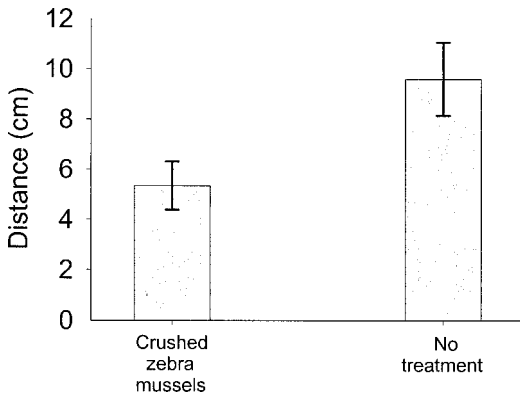


FIG. 4. Mean (\pm SE) distance traveled by adult zebra mussels after 2 h when exposed to odor from injured conspecifics relative to a control without the odor.

eled significantly shorter distances than mussels in the untreated tanks (9.6 ± 1.5 ; $p < 0.014$; Fig. 4). There was a significant effect as a result of date (blocking factor; $p < 0.04$), and there was a significant interaction between size and treatment ($p < 0.003$), with the smallest size class showing the greatest reduction in distance traveled.

The proportion of mussels that moved was similar among treatments in all experiments, with the exception of the size experiment, in which differences among treatments were significant ($p < 0.01$). In the 2-h period, 28 (78%) of the small mussels, 17 (47%) of the medium-sized mussels, and 3 (8%) of the large mussels moved.

Discussion

Our results demonstrated quantitatively that detached zebra mussels will move readily, at rates of up to 48 cm/h. These data compare with a mean of 12.1 ± 6.7 cm/h and a maximum of 36.4 cm/h observed in similar experiments (Cawein 1993); however, Cawein measured total displacement rather than actual distance traversed by each mussel. The experimental design used in our experiments provided a complete record of the distance, rate, and path used by adult mussels in response to various stimuli.

Smaller mussels had a significantly greater tendency to move than larger mussels, and there was an inverse relationship between individual

size and distance moved. Smaller zebra mussels (8–12 mm in length) produce fewer permanent byssal threads than larger mussels (21–26 mm in length; Eckroat et al. 1993). Therefore, smaller mussels are more likely to become detached and re-settle, requiring greater mobility. There was no effect of temperature on movement in our experiments, though small mussels tended to move more at higher temperatures. Although zebra mussels moved the same distance in light and darkness, there was significantly greater displacement under light conditions. This result, coupled with the significant effect of light on direction of travel, indicated that zebra mussels moved along a straighter trajectory in light than in darkness.

In laboratory experiments on zebra mussels, Korgina (1982) also indicated that movement was inversely related to mussel size, and that mussels moved away from light. Korgina (1982) noted that more mussels moved at night and mussels moved more rapidly during the night than in the day, suggesting that light is a negative stimulus for movement. Korgina (1982) noted a mean speed of only 2.1 cm/h, though speed appeared to be averaged over a 12-h period, and the time of day when movement occurred was not reported. Curiously, movement was slowest on glass, faster on silt, and fastest on sand substrate, though mussels were more likely to move on glass than sand or silt.

The mean distance moved by adult zebra mussels was significantly lower in the presence of injured conspecifics than in their absence. Many aquatic species respond to the odor of injured conspecifics by either increasing or decreasing movement (Pfeiffer 1977, Commens and Mathis 1999). For a byssally attached mussel, remaining attached or setting down byssal threads is clearly advantageous in the presence of a predator or water movement because attached mussels are difficult to dislodge, whereas escape by movement is unlikely. Increasing water hardness tended to increase movement; however, the difference among treatments in our experiment was not statistically significant.

Our experiments tested only the response of artificially detached mussels to stimuli or environmental variables. Factors that actually stimulate detachment and subsequent movement may be quite different. Zebra mussels move extensively as newly settled juveniles prior to establishing their first byssal attachment (Marsden

and Lansky 2000). They can also detach their byssal connection at will and move about as adults. One of us (JEM), while observing colonies of zebra mussels in the wild, has noted on several occasions zebra mussels that were extending their foot and moving over the surface of the colony. Mussels collected in the field will readily detach from hard objects and move up the sides of a collecting bucket or aquarium (Cawein 1993, JEM, personal observation). Although this behavior is commonly observed in mussels collected from Lake Michigan, it is rare in mussels from Lake Champlain (JEM, unpublished data). Water from Burlington Bay, Lake Champlain (the source for our experiments) is relatively soft (17.6 mg Ca/L; Eliopoulos and Stangel 1998). The lower limit for zebra mussel shell growth is 10 to 11 mg Ca/L (McMahon 1996), and Ca is required for muscular movement, so we hypothesized that mussels may conserve Ca in soft-water environments by reducing movement. We observed a trend of increasing distance traveled in high Ca concentrations, but there was no significant difference among treatments.

What is the adaptive advantage of zebra mussel movement? Like many sessile colonial animals, zebra mussels need adjacent conspecifics for reproduction and predator protection, but compete with them for food and other resources. Burks et al. (2002) demonstrated that water quality at the base of a thick zebra mussel colony is severely degraded; in artificial colonies composed of detached mussels, smaller mussels moved rapidly from the base of the colony to the surface, presumably to find higher water quality. In an established colony, such movement may be hampered by a network of byssal connections among neighbors. However, Lauer (1997) observed that an artificially cleared patch in the center of a zebra mussel colony will rapidly become recolonized by migrants moving in from the surrounding colony. These movements are apparently motivated by competition for space, which is related to competition for food and, possibly, oxygen. Random detachment and migration by individual mussels may trigger predation, but may also result in discovery of a better environment and improved growth. Because shaded areas (under rock overhangs, in crevices) offer protection from predators and water movement, negative phototaxis is advantageous. The relationship between size and

movement may be a result of a slow loss of the juvenile capability for movement, or a consequence of the higher effort needed to move a larger body.

Understanding factors that motivate or depress movement of adult zebra mussels is useful for programs that aim to reduce their spread. Movement of adult mussels is often overlooked or underestimated, yet mussels readily become attached to anchors and other immersed objects overnight and can be carried to other bodies of water. Transportation of adults into uncolonized bodies of water may be more serious than transport of veligers because the adults may have a higher probability of survival during transport, and may be ready to reproduce.

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