

Vertical Migration, Orientation, Aggregation, and Fecundity of the Freshwater Mussel *Lampsilis siliquoidea*¹

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ABSTRACT. The decline in freshwater mussels makes it imperative that more information be gathered on their population status, behavior, and habitat requirements. We examined vertical migration, aggregation, and reproductive potential of captive and field populations of *Lampsilis siliquoidea*. Both captive populations and a field population exhibited vertical migration. This movement was strongly correlated with day length, and somewhat less strongly correlated with water temperature. While captive mussels tended to orient their siphons into the current, no pattern of orientation was detected in the field population. The field population was significantly aggregated in the fall and winter. The spatial patterning of captive mussels was random in the fall and winter, but this result may have been an artifact of the small size of the artificial streams. Weather conditions prevented data collection in the spring and, therefore, no conclusions could be drawn about the relationship between aggregation and glochidia release. The average number of glochidia (parasitic larvae) produced by individuals across a limited size range was not correlated with any maternal or marsupial properties. These results are useful for implementing qualitative sampling methods under optimum conditions and for information on the reproductive potential of *Lampsilis siliquoidea*.

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INTRODUCTION

Freshwater mussels of the Families Unionidae and Margaritiferidae may represent up to 90% of the standing biomass of benthic invertebrates in streams (Økland 1963). They may remove significant amounts of particulate matter from the water through filter feeding and pedal feeding, and may have a strong impact on nutrient cycling, algal dynamics, and lake management because of their relatively unselective feeding and high filtration rates (Amyot and Downing 1991; Davis and others 1999). Due to their feeding habits, freshwater mussels are used frequently for detecting pollution and acidification (Downing and Downing 1992). Since freshwater mussels inhabit stream bottoms, they may also be good indicators of the stability of river substrates (Di Maio and Corkum 1995).

Many freshwater mussel species are now endangered due to habitat modification and the introduction of non-native mussels (Bogan 1993). By 1995, 58 species of North American freshwater mussels were federally listed as endangered, with many more presumed to be potentially endangered (Neves 1997). Some of the latter were functionally extinct, meaning individuals of a species were surviving but not reproducing (Bogan 1993). Ohio is home to 79 described taxa of freshwater mussels, with over 65% of them having some form of conservation status (Watters 1995). Recent work has estimated that the extinction rate of freshwater mussels is con-

siderably higher than that of other North American faunal groups (Ricciardi and Rasmussen 1999). The decline in freshwater mussels makes it imperative that more information be gathered on their population status, behavior, and habitat requirements.

Though mussels are generally considered to be sessile, many recent studies have documented both vertical and horizontal migration (Amyot and Downing 1991, 1997; Balfour and Smock 1995; Kat 1982; Downing and others 1993). Approximately 90% of a stream-dwelling population of *Elliptio complanata* burrowed below the substrate during the winter; these mussels began to return to the surface in February (Balfour and Smock 1995). By April, 80% of the mussels were exposed in accordance with the peak time of glochidia release. Vertical migration in lake-dwelling unionids is positively correlated with water temperature (Amyot and Downing 1997). Across the bottom of a stream, freshwater mussels are often distributed non-randomly, exhibiting a high degree of spatial heterogeneity even in homogeneous habitats (Downing and others 1993).

We investigated temporal changes in vertical migration, spatial aggregation, and orientation of *Lampsilis siliquoidea* in artificial streams (AS) and compared these findings with behavior of individuals in a field population (FP). Previous studies have evaluated vertical migration by reporting the proportion of the population exposed above the substrate at different points in time. Our study measured the vertical movement of individual mussels, which provides insight into the wintering behavior of stream-dwelling freshwater mussels. We described changes in spatial aggregation during the autumn, and also examined orientation of mussels relative to stream current. Following the conclusion of the study, we sacrificed female mussels to estimate fecundity and to relate fecundity to a variety of anatomical measurements.

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MATERIALS AND METHODS

Our field population consisted of a mussel bed located in the East Fork of the Little Miami River above the Highway 68 bridge in Greene County, OH (39° 13' N, 83° 54' W). This bed was dominated by *Lampsilis siliquoidea* (72-75% of 22-28 mussels found on 3 sample dates) and also contained *L. cardium*, *Amblema plicata*, and *Fusconaia flava*. In mid-October 1996, 54 *L. siliquoidea* (18 females, 36 males) located upstream of the field population were collected for placement in artificial streams. Mussels were placed on ice in plastic bags and transported immediately to the Ecology Research Center (ERC) of Miami University. Length, width, breadth, mass, and sex were recorded for each collected mussel. A number was engraved into the shell of each mussel with a diamond tip stylus to enable identification of individuals.

Within 12 hours of their capture, the mussels were placed in 3 artificial streams that were connected to an experimental pond at the ERC. Each 1.2 m × 2.4 m stream contained approximately 20 cm of gravel sediment and 10 cm of water. These habitat parameters were similar to the headwater stream bed that contained the natural population. Water was circulated from the experimental pond by a sump pump at a current velocity of approximately 0.18 m/sec. Mussels were randomly selected and then placed in the streams 30.5 cm apart in a 6 × 3 grid arrangement. Each mussel was placed such that 2.0 cm of shell was exposed above the substrate; the umbo was protruding from the substrate at a 45° angle to the stream bottom and was parallel to the current, with the siphons facing upstream. This orientation was considered a 0° angle of deviation from the current. The captive population was fed twice per week with Microfeast Plus™ L-10 algae replacement and live algae (*Chlamydomonas* sp.).

Identical measurement procedures were followed once a month for the field population and twice a week for the captive population between October and December 1996. Data were usually collected in the early afternoon. For each individual, vertical position was determined by using a ruler to measure the maximum height of the mussel shell above the substrate, and a protractor to measure the angle at which the mussel projected out of the substrate. Vertical movement was analyzed using regressions of shell height-above-substrate versus water temperature and day length. We assessed orientation by measuring each mussel's angle of deviation from the current. A value of 0° deviation was assigned when the umbo was facing directly away from the current (that is, facing downstream). With this orientation, the siphons were pointed directly into the current. The angle of deviation was recorded but not the direction of deviation, so that all values were from 0-180°. Thus, deviations 0-45° left and 0-45° right were pooled. The same was done for deviations 46-90°, 91-135°, and 136-180°. A chi-square analysis was performed on the observed group frequencies of the field versus artificial stream populations. Both of these were compared to an even and uniform frequency distribution for the four groups of deviations. For small samples, exact

tests were conducted and a repeated measures analysis was conducted on the artificial stream populations across each sampling date (StatXact4, Cytel Software Corporation 1999). Ambient air and water temperatures and dissolved oxygen content were recorded at every stream each time orientation data were collected.

To measure aggregation, the sampling areas were considered to be x-y coordinate grids onto which individuals' positions were mapped. Aggregation was assessed using nearest neighbor spatial analysis (Crist and Wiens 1996). These analyses compared the observed aggregation with spatial patterns generated by computer simulations of a random-point process. The simulated patterns were generated by randomly placing points within a rectangle of the same size as the stream site. The number of points placed in the area was equal to the number of mussels at the stream site. The nearest neighbor distances (NND) were calculated for the observed pattern and the simulations. Of the 999 simulations, the 25th lowest and highest NND values were used to set the lower and upper 95% confidence intervals. Calculated NNDs that fell below the lower confidence limit indicated a clumped dispersion pattern; those that fell above the upper confidence limit indicated a regular dispersion pattern. Values which fell within the 95% confidence interval denoted random spacing (Crist and Wiens 1996).

Due to severe cold weather in December 1996 and January 1997, the captive mussels perished after the artificial streams froze. Mussels were subsequently preserved in 70% alcohol after being fixed in 10% formalin for four weeks. The reproductive status of each individual was confirmed by examination of gill morphology. For each gravid female, each marsupium was removed and weighed. For one marsupium per female, the number of water tubes was noted and then the whole marsupium was placed in 100 mL of 15% Clorox™ bleach to dissolve the tissue and separate the glochidia. After incubating overnight, water was added to dilute the solution to 250 mL. The solution was stirred until a homogeneous mixture of glochidia was attained. Three 0.5 mL samples were taken from the mixture and the number of glochidia was counted. The average of the three samples was used to estimate the total number of glochidia housed in a marsupium and this result was multiplied by two in order to estimate total glochidia per female. Correlations between number of glochidia and measurements of body size and marsupium size were examined. The marsupium of the single non-gravid female was teased apart to look for the presence of oocytes. The log₁₀ (number of glochidia in each marsupium) was regressed against the following independent variables: mussel length, mussel width, mussel breadth, mussel weight, marsupium weight, and number of water tubes. The number of water tubes was regressed against mussel length, mussel weight, and marsupium weight.

RESULTS

Artificial Streams versus Field Population

In order to test whether behavior of mussels in the artificial streams was similar to that of mussels in the

field population, we used a one-way ANOVA to compare data collected from the field population on 26 October 1996 and from the artificial streams on 27 October. The following behaviors were examined: mean shell height-above-substrate and mean angle at which mussels projected from substrate. No significant differences were found between the 4 populations (three artificial stream populations and the field population) for these behavioral measures (ANOVA, $F = 1.52$, d.f. = 3, 66, $p = 0.22$). Mean angle of projection was also the same among these populations (ANOVA, $F = 0.33$, d.f. = 3, 66, $p = 0.80$). Thus, we concluded that behavior of the captive mussels was not significantly different from the behavior of the field population.

In order to determine whether mussel behavior differed between artificial streams, the mean length of mussel shell exposed was analyzed using 1-way ANOVA with Tukey-Kramer post-hoc tests to maintain an experimentwise error rate of 0.05. The mean height-above-substrate at each sampling date was not significantly different between AS1 and AS3 (mean \pm SE = 2.61 ± 0.29 cm and 2.60 ± 0.34 cm, respectively; $n = 11$ dates). However, the height-above-substrate was significantly lower in AS2 compared to the other artificial streams (mean height = 1.98 ± 0.23 cm, $n = 11$ dates). This disparity was probably caused by a lower water level that persisted in AS2 for several weeks due to a leak in the caulk.

Vertical Migration

Individual *Lampsilis siliquoidea* exhibited vertical migration both in field and captive populations. The shell height-above-substrate was strongly correlated with day length in all artificial streams and the field population (Fig. 1). Correlation coefficients for the regressions between day length and height-above-substrate in AS1, AS2, and AS3, and the field population were: $r = 0.918$ ($p < 0.0002$), $r = 0.864$ ($p = 0.0006$), $r = 0.966$ ($p < 0.0001$), and $r = 1.000$ ($p = 0.0039$), respectively.

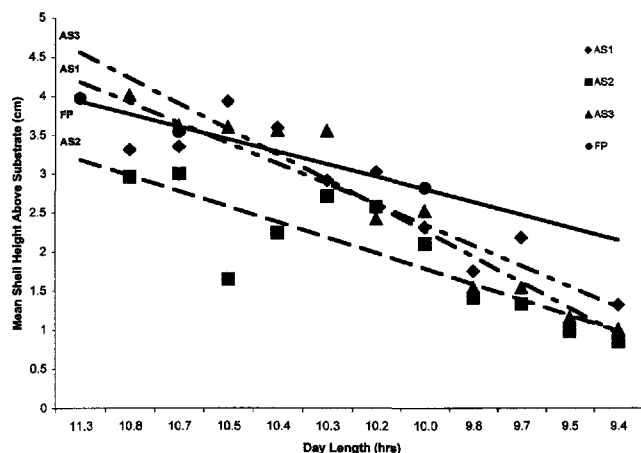


FIGURE 1. Correlation of shell height-above-substrate and day length during the fall and winter in artificial streams (AS1, AS2 and AS3) and a field population (FP) of *Lampsilis siliquoidea*. Regression equations, r , p -value and n for each treatment, respectively, are: AS1, $y = 1.840x - 15.998$, 0.918, < 0.0002 , 11; AS2, $y = 1.414x - 12.320$, 0.864, 0.0006, 10; AS3, $y = 2.277x - 20.435$, 0.966, < 0.0001 , 10; FP, $y = 0.938x - 6.568$, 1.000, 0.0039, 3.

Similar strong positive correlations were found in the regressions between water temperature and height-above-substrate (Fig. 2). However, water temperature did not explain as much variation in length exposed as day length. Correlation coefficients for height-above-substrate versus water temperature for AS1, AS2, and AS3 were: $r = 0.789$ ($p = 0.004$), $r = 0.741$ ($p = 0.009$), $r = 0.853$ ($p = 0.001$), respectively. Correlation of water temperature versus shell height-above-substrate could not be calculated for the field population due to limited number of data points, although the two measurements followed the same pattern as the artificial stream measurements. Since day length and water temperature are not independent, they could not be used as multiple independent variables.

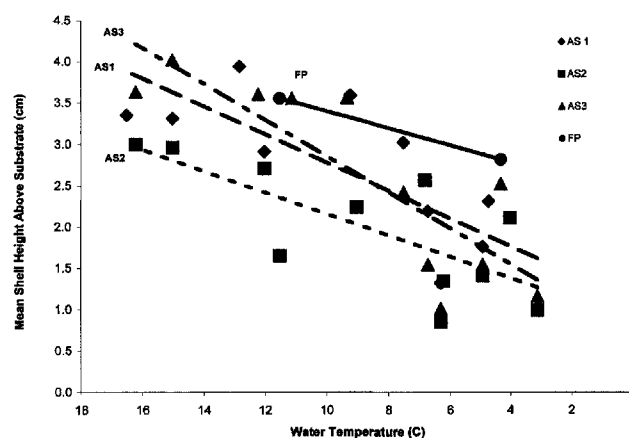


FIGURE 2. Correlation of shell height-above-substrate and water temperature during the fall and winter in artificial streams (AS1, AS2, and AS3) and a field population (FP) of *Lampsilis siliquoidea*. Regression equations, r , p -value and n for each treatment, respectively, are: AS1, $y = 0.169x - 1.092$, 0.789, 0.004, 11; AS2, $y = 0.128x - 0.832$, 0.741, 0.009, 10; AS3, $y = 0.216x - 0.660$, 0.853, 0.001, 10; FP, $y = 0.103x - 2.373$, 1.000, NV, 2. NV indicates no value reported for the regression statistics due to small sample size ($n = 2$) of field population sample dates.

Orientation

Orientation of AS mussels began at 0 degrees on Julian day 294 then steadily increased to 74.5 degrees (± 17.2 SE, $n = 44$) on Julian day 300 and then stabilized between 61 and 66 degrees for the remaining 46 days of the study (Fig. 3). Examination of the null hypothesis that mussel orientation will be evenly distributed between the 4 orientation categories indicated that freshwater mussel orientation was significantly different from uniform distribution in 10 out of 11 sampling dates (Fig. 4). More observations than expected were found in the 0–45 degree category even after a 52 day acclimation period (Fig. 4). In contrast, the field population exhibited a uniform pattern (that is, equal frequencies for each of the 4 categories) on each of the three sampling dates (Fig. 5) and average angle ($\pm 95\%$ confidence interval) was 93.5 (24.1), 104.6 (18.13), and 115.9 (27.1) for Julian days 286, 299, and 321, respectively.

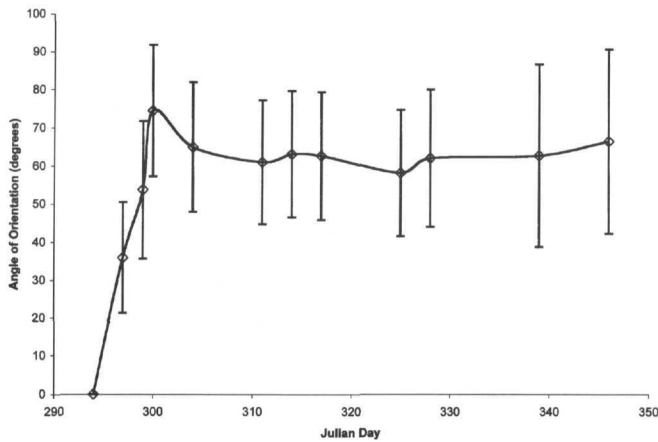


FIGURE 3. Average angle of orientation relative to current (\pm SE) of the pooled artificial stream populations over time. Zero degrees indicates the siphons pointing directly into the current.

Aggregation

The results of the nearest neighbor analysis indicated that mussels in the field population were clumped; the observed spatial patterns fell below the lower confidence interval generated by the computer simulations (Fig. 6). No definitive changes over time were identified. Mussels in the artificial streams were randomly distributed; observed spatial patterns fell within the confidence intervals generated by the computer simulations (Fig. 7). There were no changes observed in the artificial streams over this interval.

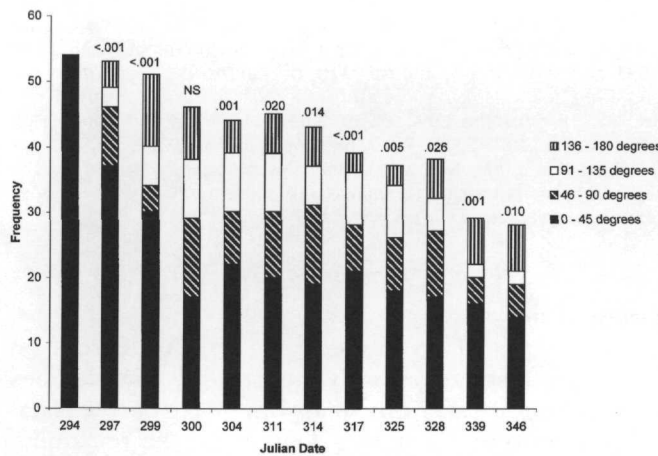


FIGURE 4. Counts for orientation of artificial stream mussels over 12 sampling dates. Each bar is made up of frequencies for four classes of orientation: 0-45 degrees, 46-90, 91-135, and 136-180. For each date, a chi-square analysis was conducted to test whether or not observed frequencies differed significantly from a uniform distribution. NS indicates no significant difference from a uniform distribution; numbers above bars indicate *p*-values of significant differences from a uniform distribution.

Fecundity

Of the females recovered from the artificial streams, nine (81.8%) were gravid, and they ranged in length from 94.3 cm to 115.2 cm. The marsupia measured contained an average of $2.66 \times 10^5 \pm 4.18 \times 10^4$ (\pm SD)

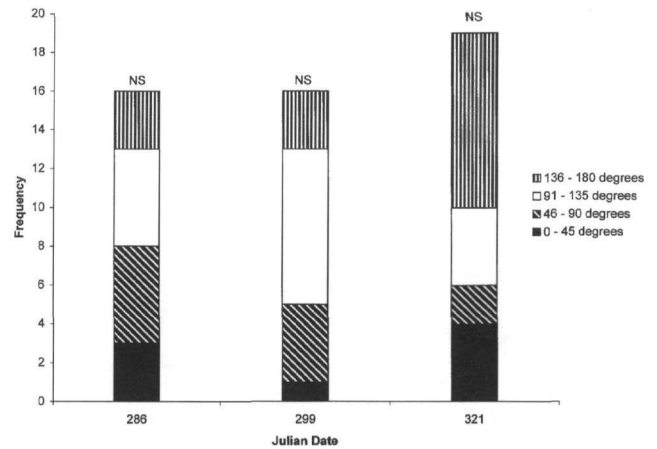


FIGURE 5. Counts for orientation of the field population over 3 sampling dates. Each bar is made up of frequencies for four classes of orientation: 0-45 degrees, 46-90, 91-135, and 136-180. For each date, a chi-square analysis was conducted to test whether or not observed frequencies differed significantly from a uniform distribution. NS indicates no significant difference from a uniform distribution; numbers above bars indicate *p*-values of significant differences from a uniform distribution.

glochidia, which yields an estimate of $5.33 \times 10^5 \pm 8.38 \times 10^4$ (\pm SD) glochidia produced per female. Marsupia were composed of a mean of 32 ± 4 (\pm SD) water tubes. There was no evidence suggesting that the glochidia were released before maternal death. The remaining non-gravid female contained no oocytes in the marsupia.

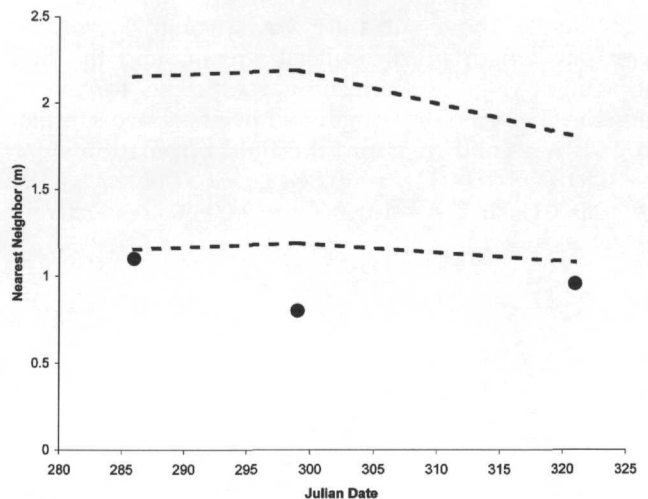


FIGURE 6. Mean nearest neighbor distances for the field population across three dates (●) and 95% confidence interval (---) for random dispersion of individuals. Since the observed nearest neighbor distances fell below the lower 95% confidence interval, the mussels are considered to be clumped.

The coefficients of variation for the means of the 3 samples taken from the homogenate of each marsupium were small, ranging from 0.00287 to 0.140. Therefore, the sampling procedure used to estimate number of glochidia was precise. Several regressions were performed to determine if relationships existed between number of glochidia and measurements of female and

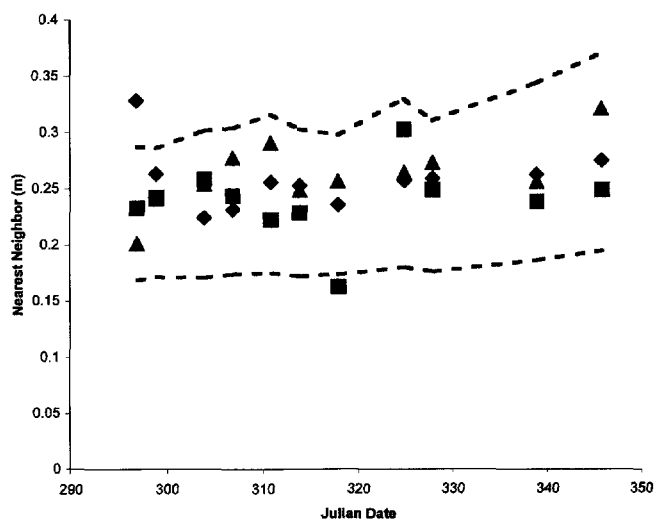


FIGURE 7. Mean nearest neighbor distances for the artificial stream populations across 12 dates (AS1 = \blacklozenge , AS2 = \blacksquare , AS3 = \blacktriangle) and 95% confidence interval (---) for random dispersion of individuals. Since the observed nearest neighbor distances fell within the 95% confidence interval, the mussels are considered to be randomly dispersed.

marsupial size. None of the regressions were significant and r values did not exceed 0.283.

DISCUSSION

Vertical migration behavior was similar among mussels in the field population and those populations in the artificial streams. However, both orientation and aggregation differed among these populations.

All mussel populations exhibited vertical migration as the season progressed. Individuals did not return to the surface once they were completely buried in the substrate. Proposed functions of vertical migration are protection from predation, from displacement by water currents, from extreme cold temperatures, and from other adverse conditions (Amyot and Downing 1997). The regression analyses of height-above-substrate versus day length and versus water temperature imply that vertical migration may be controlled more by day length than by water temperature. Water temperature may have produced a weaker regression because it is much more variable from day-to-day than day length. Other studies have found that vertical migration was more closely correlated with water temperature than with day length (Amyot and Downing 1997), or that it was not possible to separate the effects of these two parameters (Watters and others 2001). Regardless of the proximal mechanism, it seems clear that mussels do exhibit vertical migration in the substrate and that failure to take such behavior into account when planning visual field surveys may result in underestimates of mussel density and biomass.

Our orientation results in the artificial streams are similar to those of another study in which the greatest percentage of individual mussels were orientated with their umbo facing downstream, thereby having the siphons facing upstream (Di Maio and Corkum 1997). This orientation, parallel to flow, might reduce the chance of mussels becoming dislodged and also in aiding fil-

tering by having the inhalant siphon most upstream and exhalant most downstream (Di Maio and Corkum 1997). In contrast, several studies have reported that when *Lampsilis siliquoidea* are found near shore, their orientation is perpendicular to flow (Tevesz and others 1985; Di Maio and Corkum 1997). This orientation might be a function of movement toward or away from the bank in shallow low-flow habitats (Tevesz and others 1985; Di Maio and Corkum 1997). Thus, differences among our study and these others may be a function of water velocity.

When comparing the orientation of the field population with the artificial stream population in our study, it is obvious that the field population is not behaving in a manner similar to the artificial stream populations. One explanation for this observed difference in behavior is that the field population was made up of several species of mussels, while the artificial streams contained only *Lampsilis siliquoidea*. Species-specific differences in orientation behavior may have influenced the overall distribution in the field population samples. Furthermore, the artificial stream population may not have had enough time to equilibrate to a natural orientation distribution before mussels changed their behavior for the winter months (that is, burrowing below the sediment surface). Additionally, flow and habitat were homogenous in the artificial streams, thereby possibly influencing orientation preference in the artificial streams compared to the more heterogeneous field habitat.

Based on the clumped aggregation of the field population and other studies showing aggregated spatial distributions in unionids (Downing and Downing 1992; Amyot and Downing 1998), the random distribution of mussels in the artificial streams may have been an artifact of the small stream size. The density of mussels in the artificial streams (6.04 mussels/ m^2) was much greater than the density of mussels in our field population (0.11 mussels/ m^2). Although the density found in the artificial stream may not be unusual for some unionids such as *Elliptio complanata* (Fisher and Tevesz 1974), the density of our field population suggests that our artificial stream densities were unrealistic when compared with their source population. Aggregation of our field population may have been due to the heterogeneity of the substrate. For example, a portion of the stream bottom at the field site was bordered by bedrock, restricting mussels to a narrow strip of sand and gravel substrate. Therefore, the mussels likely clumped in the portion of the stream that contained suitable substrate. Because the artificial streams contained uniformly suitable habitat, mussels were not forced to aggregate. Aggregation of mussel populations can affect food intake (Holloway 1990), predation (Okamura 1986), levels of parasitism (Krause 1994), and fertilization success (Downing and others 1993; Amyot and Downing 1998).

The insignificant relationship between the number of glochidia and maternal and marsupial properties likely resulted from small sample size ($n = 9$ female mussels) and the limited size range of maternal shell length (maximum difference of 20.9 cm or 22% of the

total length of the shortest mussel). However, our estimated fecundity of *Lampsilis siliquoidea* is within the range reported in an earlier study (Coker and others 1922). Fecundity is size-dependent in other unionids (Hanson and others 1989; Jansen and Hanson 1991). Thus, it is likely that a larger number of *L. siliquoidea*, encompassing a great difference in maternal lengths, would also show size-dependent fecundity.

Our results provide further evidence that freshwater mussels do move within their local habitats. These movements are both horizontal and vertical, with many of them seemingly designed to control exposure in the substrate, orientation to currents, and distances among individuals. Such movements must be taken into account when surveys and field manipulations are conducted.

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