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Settling velocities of juvenile Lampsilini mussels (Mollusca:Unionidae): the influence of behavior

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Abstract. Juvenile unionid mussels disperse in the water column after detachment from their host fish. The settling velocity (w_s) of juvenile mussels is an important component of their dispersion in the water column but has not been measured for unionid mussels. The goal of our study was to measure the w_s of juvenile mussels in the laboratory and to examine how w_s varied within and among related species. The w_s of *Actinonaias ligamentina* and *Ptychobranchus fasciolaris* were significantly lower (2.4 ± 0.1 mm/s vs 2.5 ± 0.1 mm/s, respectively) than those of the larger-sized *Lampsilis fasciola* and *Epioblasma triquetra* (4.2 ± 0.2 mm/s vs 4.6 ± 0.2 mm/s, respectively). Overall, w_s increased with juvenile size, but considerable variation (~10×) was found within species. Observations indicated that foot movement of juvenile mussels was responsible for reductions in w_s, and this behavior may provide a potential mechanism for habitat selection at small-spatial scales. Observed w_s differed considerably from w_s predicted from Stokes' law using empirically determined shell size and density ($\rho = 1.22 \pm 0.003$ g/cm^3 for *A. ligamentina*), which indicates some of the limitations in predicting w_s from size measurements.

Key words: Stokes' law, mussel density, *Actinonaias ligamentina*, *Ptychobranchus fasciolaris*, *Lampsilis fasciola*, *Epioblasma triquetra*.

Dispersal is important for colonization of new habitats and connectivity among local assemblages and affects population dynamics and genetics as well as community structure and diversity (e.g., Hanski and Gilpin 1997, Hillebrand and Blenckner 2002). Little is known about the dispersal of freshwater unionid mussels (Strayer 2008), but adult mussels usually move only a few meters (Balfour and Smock 1995, Amyot and Downing 1997, Schwalb and Pusch 2007). Consequently, large-scale dispersal is essentially limited to their early life-history stages through transport by host fishes during the period of glochidial (larval) encystment and hydrodynamically mediated transport of glochidia and juvenile mussels (after excystment).

An essential component of all models of dispersal involves settling velocity (w_s), which is the terminal rate at which a particle settles in quiescent fluid (Fonseca 1999, McNair and Newbold 2001, Morales et al. 2006). Settling velocity for spherical type particles can be determined from Stokes' law provided by,

$$w_s = \frac{2r^2 g\,(\rho_{particle} - \rho_{fluid})}{9\mu} \quad [1]$$

where r is the radius of a sphere, g is the gravitational acceleration, $\rho_{particle}$ and ρ_{fluid} are the density of the particle and the fluid, respectively, and μ is the dynamic viscosity of the fluid. Deviations from Stokes' law occur when the Reynolds number (Re)

$$Re = \frac{l w_s}{\upsilon} \quad [2]$$

(where l is the characteristic length and υ is the kinematic viscosity) of the particle approaches unity (i.e., $Re > 0.5$) and when the shape deviates from spherical (Vogel 1994).

The w_s is considered a useful proxy for dispersal ability (Anderson 1992), and variations in w_s are predicted to affect dispersal distances considerably (McNair and Newbold 2001). However, to the best of our knowledge, w_s of juvenile unionid mussels have not been reported, and Eq. 1 has been used with shell measurements and estimates of the ρ of mussels to predict w_s (Morales et al. 2006, Daraio et al. 2010). Miklasz and Denny (2010) showed that theoretical predictions may differ considerably from empirically measured w_s. Therefore, the

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purpose of our study was to measure the w_s of juvenile mussels in the laboratory and to examine how w_s varied within and among related species.

Methods

Settling velocity among species

We obtained newly metamorphosed juvenile mussels from an experimental facility at the University of Guelph (McNichols et al. 2011), in which glochidia were exposed to their known host fish. We examined 4 species of the tribe Lampsilini with different host-infection strategies (Barnhart et al. 2008): *Actinonaias ligamentina* (Lamarck) broadcasts its larvae into the water column, *Lampsilis fasciola* (Rafinesque) attracts host fish by displaying mimetic mantle flaps, *Ptychobranchus fasciolaris* (Rafinesque) releases a worm-like conglutinate (an aggregation of glochidia), and *Epioblasma triquetra* (Rafinesque) captures a host fish between its valves. Juvenile *A. ligamentina* developed on *Micropterus salmoides* (Lacépède), *L. fasciola* on *Micropterus dolomieu* (Lacépède), *P. fasciolaris* on *Etheostoma nigrum* (Rafinesque), and *E. triquetra* on *Percina caprodes* (Rafinesque). We undertook our experiments within 1 to 2 d of metamorphosis for tests among species and within 1 to 4 d for tests within species (see below).

We measured w_s of the juvenile mussels in a temperature-balanced settling chamber (Ackerman 2005) consisting of a 1000-mL graduated glass cylinder (height = 40 cm, inner diameter = 5.6 cm) placed within a larger glass cylinder (height = 46 cm, inner diameter = 14.4 cm) filled with water, which helped to minimize temperature fluctuations (range = 15.6–6.1°C; see Schwalb et al. 2010 for details). We released individual juvenile mussels in the inner cylinder, and each juvenile was examined only once (*A. ligamentina*: $n = 27$, *L. fasciola*: $n = 16$, *E. triquetra*: $n = 31$, *P. fasciolaris*: $n = 32$). We measured w_s over 6 intervals of ~3.7 cm (800–700, 700–600, 600–500, 500–400, 400–300, 300–200 mL marks on the cylinder) to ensure that the juvenile mussels had reached terminal velocity (i.e., constant velocity, no acceleration).

We measured shell length (*SL*) and height (*SH*) of each juvenile mussel by analyzing pictures taken under a stereomicroscope (SMZ 2T; Nikon, Tokyo, Japan) with ImageJ image analysis software (US National Institutes of Health, Bethesda, Maryland; http://imagej.nih.gov/ij/2007). We calculated juvenile mussel size as the average of *SL* and *SH* (size = [*SL* + *SH*]/2).

Settling velocity within species

In a separate experiment, we measured w_s of juvenile *A. ligamentina* and *L. fasciola* in a 500-mL graduated cylinder (height = 37 cm, inner diameter = 4.6 cm) without an outer water jacket to enable observations of juvenile orientation and behavior during settling with a stereomicroscope (Nikon SMZ 2T). We made observations of individual juvenile mussels with the stereomicroscope focused on a 1-cm-diameter area in the lower part of the glass column (*A. ligamentina*: $n = 33$ and *L. fasciola*: $n = 37$). Measurements had to be taken at warmer temperatures (range = 21.6–23.3°C) to accommodate this experimental set-up.

Determination of mussel density and Stokes' law

We used ½(juvenile mussel size) as an estimate for r and known values for ρ_{fluid} and μ for water at 16°C to compare observed w_s with the predictions of Stokes' law (Eq. 1). We used density gradient centrifugation with a modified silica sol (Percoll; GE Healthcare Bio-Sciences, Piscataway, New Jersey) to measure the density of the mussels ($\rho_{particle}$) (Oliver et al. 1981, Ackerman 1997). We diluted the Percoll to a density of 1.123 g/cm^3 by adding 5 mL of 1.5 M NaCl to 45 mL of Percoll and formed density gradients (1.04–1.26 g/cm^3) in 15-mL tubes under high-speed centrifugation (Sorvall AM24; Thermo Scientific, Waltham, Massachusetts) at 15,690 rpm (~25,000 *g*) for 30 min at 20°C. We layered 8 juvenile *A. ligamentina* in 0.5 mL water onto the preformed gradient in each of 3 tubes and forced them into the gradient at 1985 rpm (~400 *g*) for 10 min. Juvenile mussels were not visible in the centrifuge tubes, so we removed 3-mm layers from the tubes and examined each layer under the microscope for the presence of mussels. We determined the density of each layer by measuring its refractive index with a refractometer (Model 1 Refractometer; Carl Zeiss, Oberkochen, Germany).

Statistical analysis

We examined potential differences in w_s and size of juvenile mussels among species with analysis of variance (ANOVA) and a post hoc Tukey test. We tested homogeneity of variances with a Bartlett test. When the assumption was not satisfied, we used a Kruskal–Wallis test and a Nemenyi test. We used a linear regression to examine the relationship between juvenile mussel size and w_s across all species.

We examined the effect of species and temperature on w_s with an analysis of covariance (ANCOVA) with shell length (*SL*) as the covariate. We examined potential differences in variances between w_s under warmer vs colder water temperature with a Levene's test. Last, we used a 2-way ANOVA to examine the effect of shell orientation (*SL* or *SH* perpendicular to vertical direction) and foot movement on w_s.

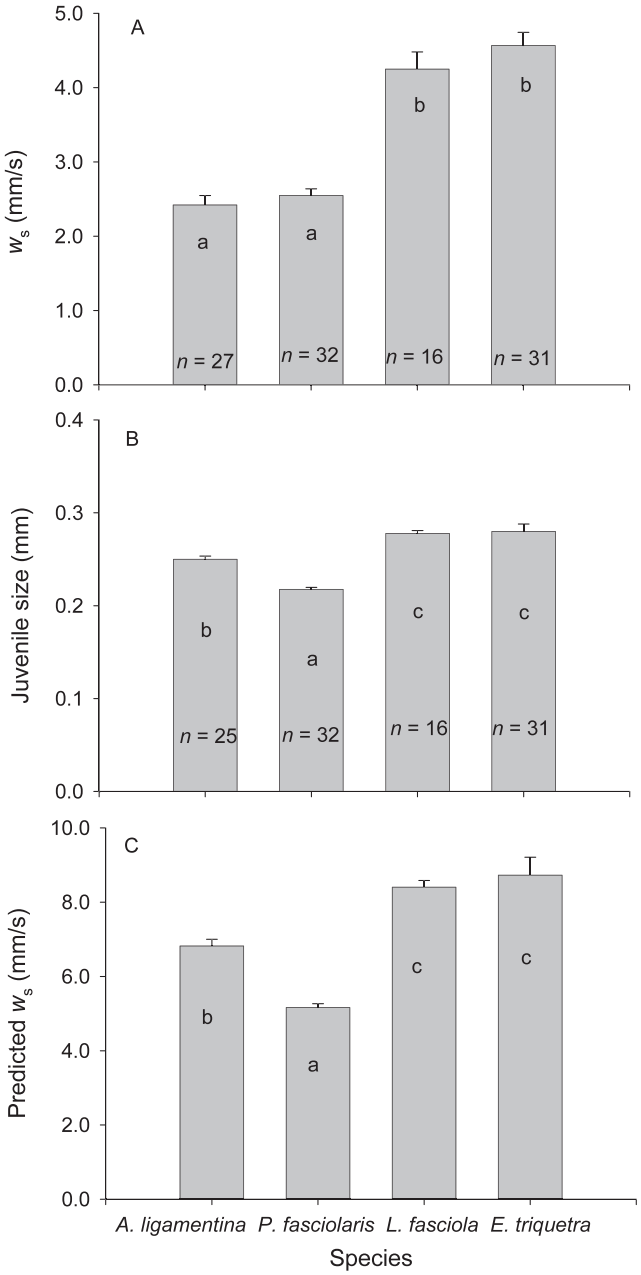

FIG. 1. Mean (±1 SE) settling velocities (w_s) (A), size ([shell length + shell height]/2) (B), and predicted w_s (C) of juvenile *Actinonaias ligamentina*, *Ptychobranchus fasciolaris*, *Lampsilis fasciola,* and *Epioblasma triquetra*. Predicted w_s was based on Stokes' law, shell measurements, and the measured density of *A. ligamentina*. Bars with the same letters are not significantly different ($p > 0.05$; panel A: Tukey test, panels B and C: Nemenyi test).

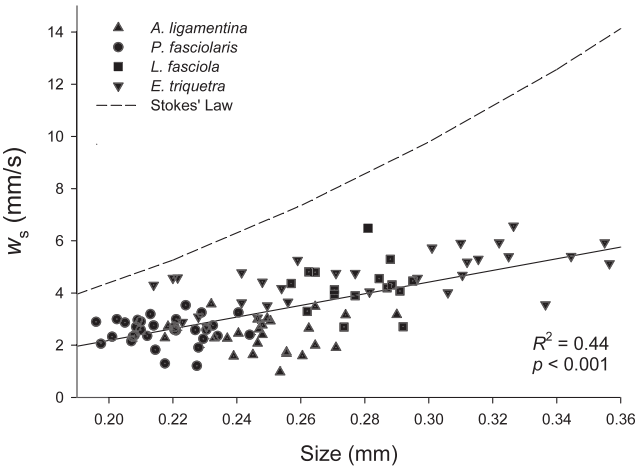

FIG. 2. Observed and predicted settling velocities (w_s) of juvenile *Actinonaias ligamentina*, *Ptychobranchus fasciolaris*, *Lampsilis fasciola,* and *Epioblasma triquetra* in relation to their size ([shell length + shell height]/2) in a low-temperature (15.6–16.1°C) experiment. Predicted w_s (dashed line: $w_s = 108.7\text{size}^2$) was based on Stokes' law, shell measurements, and the measured density of *A. ligamentina*. The linear regression line (solid line) was based on all observed values: $w_s = (22.4 \pm 2.5)\text{size} + (2.3 \pm 0.6)$.

Results

Settling velocity among species

Terminal velocity (i.e., w_s) was achieved within the first 10.1 cm of settling (1000–700-mL mark). The average w_s of juvenile *A. ligamentina* was similar to *P. fasciolaris* (2.4 ± 0.1 [mean ± SE] and 2.5 ± 0.1 mm/s, respectively) but significantly lower than *L. fasciola* and *E. triquetra* (4.2 ± 0.2 and 4.6 ± 0.2 mm/s, respectively; ANOVA: $F_{3,102} = 48.8$, $p < 0.001$; Fig. 1A), which were similar to each other. Juvenile mussel size corresponded somewhat to the observations of w_s, and significant differences were detected among species (Kruskal–Wallis $H_3 = 61.0$, $p < 0.001$; Fig. 1B). *Ptychobranchus fasciolaris* was significantly smaller (0.218 ± 0.003 mm) than all other species, followed in size by *A. ligamentina* (0.250 ± 0.003 mm), which also differed from the other species. *Lampsilis fasciola* and *E. triquetra* were larger but similar in size (0.278 ± 0.003 and 0.280 ± 0.004 mm, respectively).

The differences in the average w_s were larger (maximum difference = 1.9×) than the differences in the average juvenile mussel size (maximum difference = 1.3×). Overall, w_s increased significantly with juvenile size, and juvenile size explained 44% of the variation in w_s ($R^2 = 0.44$, $p < 0.001$, $n = 104$), but variation in w_s for juvenile mussels with similar size was considerable (Fig. 2). The *Re* determined from the w_s and size of these juvenile mussels (i.e., Eq. 2) ranged between 0.2 and 2.1 (for the smallest and largest juvenile mussels, respectively).

Influence of water temperature on w_s

The w_s of *A. ligamentina* and *L. fasciola* examined at 21.6 to 23.3°C were 1.9 ± 0.2 mm/s and 3.3 ± 0.2

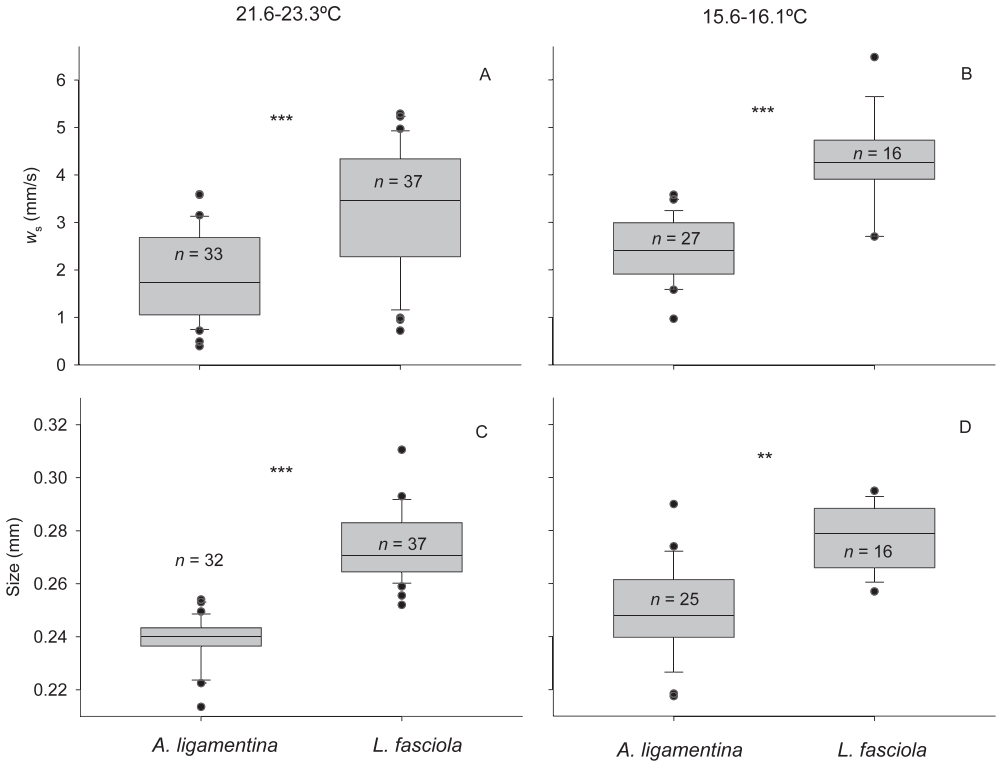

FIG. 3. Settling velocity (w_s) (A, B) and shell length (C, D) of juvenile *Actinonaias ligamentina* and *Lampsilis fasciola* at 21.6 to 23.3°C (A, C) and 15.6 to 16.1°C (B, D). The ends of the boxes are quartiles, the whiskers are 10th and 90th percentiles, points indicate outliers, and the line in the box marks the median. ** = $p < 0.01$, *** = $p < 0.001$.

mm/s, respectively (Fig. 3A). These values were somewhat lower than at 15.6 to 16.1°C (1.3×; Fig. 3B), but also involved juvenile mussels of slightly smaller size (0.238 ± 0.002 mm and 0.275 ± 0.003 mm, respectively, Fig. 3C, D). The difference in juvenile mussel size between lower and higher water temperature was significant for *A. ligamentina* (Welch $t_{36} = 3.0$, $p < 0.01$), but not for *L. fasciola* ($t_{51} = 0.5$, $p = 0.63$). ANCOVA revealed that both species ($F_{1,102} = 51.4$, $p < 0.001$) and temperature ($F_{1,102} = 11.1$, $p = 0.001$) significantly affected w_s, but the covariate, juvenile mussel size, did not ($F_{1,102} = 0.4$, $p = 0.51$).

Water temperature also appeared to influence the variation in w_s observed within species. The coefficient of variation (CV) of w_s was lower at cooler than at warmer water temperatures (0.23 vs 0.40 for *A. ligamentina*, and 0.22 vs 0.49 for *L. fasciola*; Fig. 3A, B). This difference was significant for *A. ligamentina* (Levene's test $F_{1,58} = 4.3$, $p = 0.04$) and marginally significant for *L. fasciola* (Levene's test $F_{1,51} = 3.9$, $p = 0.05$).

The influence of behavior on w_s

Observation with the stereomicroscope revealed that a significant portion of the juvenile mussels displayed active behavior during settling (Fig. 4A, B). We observed a sweeping-like pattern of the foot in which the foot extended (sometimes to a great extent) and contracted. Juvenile mussels waved their foot, sometimes slightly, sometimes extensively, from posterior to anterior and vice versa. The degree to which the valves gaped open varied from rather narrow to wide. Sometimes mussels changed their orientation while moving the foot, and sometimes valve movement (opening and closing of the valve) could be observed. This type of behavior was observed in 33% (11 of 33) of the *A. ligamentina* trials and 54% (20 of 37) of the *L. fasciola* trials (Fig. 4A, B). Most of the observations involving foot movement were associated with w_s values that were below the median w_s (10 of 11 in *A. ligamentina* and 13 of 20 in *L. fasciola*; Fig. 4A, B).

Visual observation also revealed that the orientation of the shells differed during the settling trials. *SL* (the smaller dimension) was perpendicular to the vertical direction in 55% of the *A. ligamentina* trials and 84% of the *L. fasciola* trials. The trials in which *SH* was perpendicular to the vertical direction occurred mostly at w_s values below the median w_s (12 of 15 in *A. ligamentina* and 5 of 6 in *L. fasciola*).

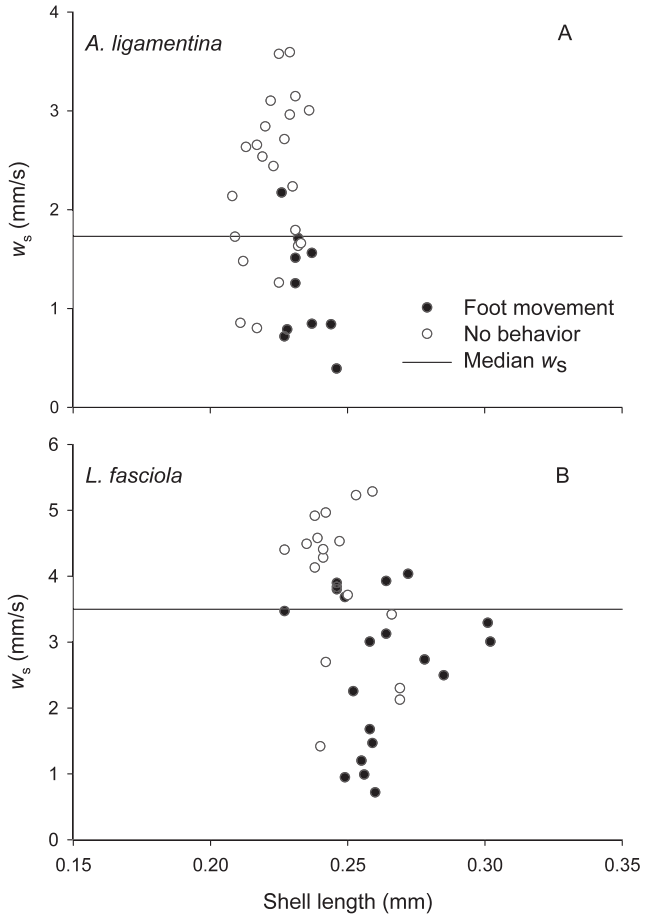

FIG. 4. Settling velocity (w_s) in relation to shell length and juvenile mussel behavior for *Actinonaias ligamentina* (A) and *Lampsilis fasciola* (B).

A 2-way ANOVA with the binary variables, foot movement (yes/no) and orientation (*SH*/*SL* perpendicular to vertical direction), as factors revealed that foot movement significantly affected w_s of both species (*A. ligamentina*: $F_{1,29} = 18.6$, $p < 0.001$, *L. fasciola*: $F_{1,33} = 16.4$, $p < 0.001$), whereas shell orientation during settling significantly affected w_s of only *L. fasciola* ($F_{1,33} = 18.9$, $p < 0.001$, *A. ligamentina*: $F_{1,29} = 0.7$, $p = 0.39$). The interaction term was not significant.

Mussel density and Stokes' law

Juvenile *A. ligamentina* were found in layers of the Percoll corresponding to densities between 1.20 and 1.26 g/cm^3 (Fig. 5). Most juvenile mussels (19 of 24) were found in a layer with a density of 1.21 to 1.22 g/cm^3, providing an average density ($\rho_{particle}$) of 1.22 $\pm$ 0.003 g/cm^3 for an average mussel size = 0.249 $\pm$ 0.003 mm (n = 19; 3 juveniles were crushed when layers were removed from the gradient and *SL* measurements were not obtained for 2 others).

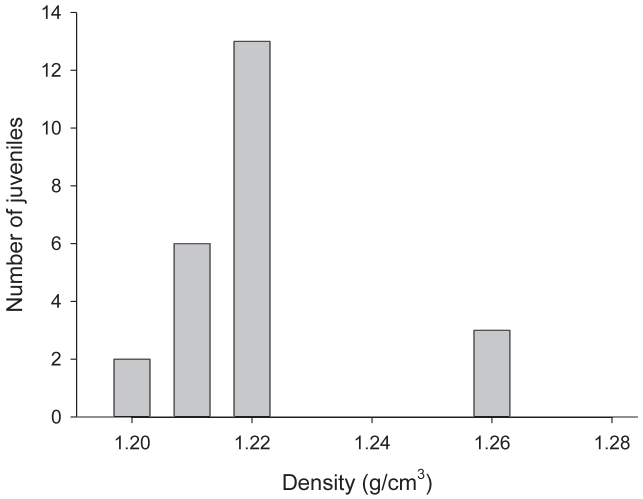

FIG. 5. Frequency distribution of the density determined for juvenile *Actinonaias ligamentina* mussels using density-gradient centrifugation with a modified silica sol (Percoll).

The shell measurements and the measured density of *A. ligamentina* were used to predict w_s based on Stokes' law (Eq. 1). Neither the pattern nor the magnitude of the w_s predicted by Stokes' law was consistent with the observed w_s (Fig. 2). Specifically, *A. ligamentina* was predicted incorrectly to have significantly higher w_s than *P. fasciolaris* (Fig. 1C). Moreover, the predicted w_s was on average 2 to 3$\times$ higher than the observed w_s. The magnitude of the differences among species also differed between predicted and observed w_s. We observed a 1.9$\times$ difference between the lowest and highest observed w_s (*A. ligamentina* and *E. triquetra*, respectively) compared to a 1.3$\times$ difference in predicted values.

Size and size^2 explained the same relative amount of variation in the observed w_s (in both cases $R^2 = 0.44$, $p < 0.001$; Fig. 2) and the w_s predicted by Stokes' law (size: $R^2 = 0.99$, $p < 0.001$, size^2: $R^2 = 1$; Fig. 2). The slope of the linear regression of w_s vs size was ~2 to 3$\times$ higher for the predicted than the observed w_s (predicted: w_s = [58.1 $\pm$ 0.5]size $-$ [7.6 $\pm$ 0.1], observed: w_s = [22.4 $\pm$ 2.5]size + [2.3 $\pm$ 0.6]), which indicates that the predicted w_s increased faster with size than the observed w_s (Fig. 2).

Discussion

The w_s of juvenile unionid mussels varies somewhat with mussel size, as was evident for the differences detected among species (Fig. 1A). However, variation in the size of juvenile mussels explained <½ of the variation in w_s (Fig. 2), and behavior may be an important factor for this variation (see below). This result is in contrast to those from studies of other

macrozoobenthic larvae in which body size was closely linked to w_s (Beukema and de Vlas 1989, Fonseca 1999).

The prediction of w_s based on Stokes' law (Eq. 1) did not correctly capture the observed magnitude in differences among species (Fig. 1C), despite the fact that empirical measurements of mussel size and mussel density were used. Measured mussel densities were higher than what is usually assumed for marine larvae (Morales et al. 2006) but were within the range of dinoflagellate cysts (Anderson et al. 1985). Stokes' law (Eq. 1) used to predict w_s has 2 main assumptions: 1) particles are settling without acceleration within a fluid dynamic regime where viscosity dominates (i.e., $Re < 0.5$), and 2) the particles are spherical in shape. In our study, Re ranged between 0.2 and 2.1, which clearly violated the 1st assumption. In the situation where $0.5 < Re < 100$, w_s increases less rapidly with size than predicted by Stokes' law because w_s is proportional to size and not the square of the size as in Eq. 1 (Vogel 1994; Fig. 2). Our results indicate that the predicted w_s increased more rapidly with size than the observed w_s, but the range in sizes was too narrow to evaluate whether size or size^2 had a stronger relationship with w_s.

The 2nd assumption of Stokes' law also was violated in that juvenile mussels have a clam-like shape rather than a spherical one, and the shape of juvenile mussels can differ within and among species. Such variation could be accounted for by a shape factor (i.e., $\varphi = ⅓$ or ½ in Fig. 2) in Eq. 1, but φ probably will be species specific. Moreover, our predictions of w_s were based on density measurements from *A. ligamentina*. Differences in density were observed within species and certainly can occur among species and, thus, contribute to the observed difference related to the predictions of Stokes' law.

Variation in w_s of juvenile mussels within a species can be greater than differences between species. Behavior appears to be the important cause of this variation, in that foot movement of juvenile mussels appears to reduce w_s. Settling velocities were significantly lower and the variation was more pronounced at higher water temperature (21.6–23.3°C; Fig. 3A) because juvenile mussels probably were more active than at the lower temperature (15.6–16.1°C). Juvenile mussels were also more active in Petri dishes when shell measurements were taken at a higher water temperature. The observed foot movement is remarkably similar to pedal feeding in which juvenile mussels sweep their foot by extending and contracting it posteriorly to anteriorly and vice versa to draw in food particles (see Yeager et al. 1994). Temperature fluctuations leading to convection of the fluid could have potentially contributed to the variation at the higher temperature because the outer water-filled glass column was not used to allow visual observations. However, an increase in the variation in w_s of *A. ligamentina* glochidia, which do not possess a foot, did not occur under the same conditions ($CV = 0.08$, $n = 28$, *A. ligamentina*, ANS unpublished data).

Implications for juvenile mussel dispersal

Juvenile mussels prolong suspension in turbulent water with long drifting threads in marine (Lane et al. 1985, Beukema and de Vlas 1989) and freshwater habitats (review in Ackerman et al. 1994). Foot and valve movements in juvenile mussels could have a similar effect and could potentially prolong their suspension in the water column. This ability would be important for downstream dispersal and may be a potential mechanism for habitat selection at small spatial scales. Habitat selection by juvenile unionid mussels remains to be studied (Strayer 1999), but such behavior is important for recruitment in marine invertebrates (Butman 1987). Habitat selection would require that juvenile mussels react to chemical or physical cues associated with suitable habitats or the presence of adult mussels. A potential mechanism would be an active behavioral change, such as a change in foot movement or closing the valves, in response to a suitable cue. Whether juvenile unionid mussels react to such cues remains to be determined.

The observed variation in w_s could potentially lead to considerable difference in transport distances experienced by newly detached juvenile mussels (i.e., post excystment). For example, the results of a simplistic model used to predict downstream transport distances (x; $x = Uz_r/w_s$, where U is the velocity and z_r is the height of release) provides $x = 33$ and 300 m for *A. ligamentina* juvenile mussels under conditions typical in the Grand River in southwestern Ontario, Canada (Schwalb 2009). These values are based on: 1) w_s between 0.4 and 3.6 mm/s as was observed at warmer water temperatures that occur in the river, 2) a river velocity $U = 40$ cm/s, and 3) the location of the fish in the water column $z_r = 30$ cm. However, turbulence in rivers can affect downstream transport considerably, so more hydrodynamically realistic models have been developed. Among these, the local exchange model (McNair and Newbold 2001), which includes vertical mixing from turbulence, predicts average hitting distances (x) between 39 and 46 m for *A. ligamentina* juvenile mussels in the Grand River (see application to *A. ligamentina* glochidia dispersal in Schwalb et al. 2010). However, the effect of different w_s in the field remains to be examined empirically.

Most theoretical models assume that organisms are passive particles that can vary in size, shape, or density. Predictions, such as those provided by Stokes' law for w_s appear to be of limited value for unionid mussels even with measurements of particle density. Moreover, we have shown that behavioral responses also can be important, and these responses are not included in such models. Further study of the early life history of unionid mussels is needed.

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