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Dispersion of freshwater mussel larvae in a lowland river

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Abstract

We examined the dispersal of larvae (glochidia) of a common unionid mussel species, *Actinonaias ligamentina*, which need to attach to a host fish in order to develop into juveniles, in a lowland river (Sydenham River, Ontario, Canada). Generally, the decline in the number of glochidia captured with distance from release was best described by an inverse power function. The highest proportion was found in the first net 4 m downstream (range 0.1–3.6%), but a small proportion of glochidia was captured 96 m downstream (0–0.03%). This indicates that infestation of host fish may occur several tens to hundreds of meters downstream of the adults' location, even at relatively low flow conditions (mean velocity, 15 cm s^{-1}). Dispersal distances increased with velocity, but the number of glochidia sampled at a given location can vary considerably due to stochastic effects of turbulence, especially at shorter distances. Individual trials could, therefore, deviate considerably from the predictions of an existing turbulent transport model (local exchange model), but overall there was a good correlation between measured data and model prediction. However, model predictions were quantitatively much higher than measured values (i.e., > 50 fold in some cases), which could be in part due to several simplifying assumptions of the model.

Larval dispersal in aquatic systems is largely mediated by hydrodynamic processes, which have received much attention in marine systems (Young 1990; Shanks 1995; Levin 2006). For example, the settlement of barnacle larvae was found to be dependent on large-scale hydrodynamic events (e.g., export from bays) and geographic features (open vs. embayed coast) (Gaines and Bertness 1992). However, local flow patterns were also found to be important for larval transport and settlement processes (Pawlik and Butman 1993; Abelson and Denny 1997). Dispersal at all scales is important since it allows organisms to (re)colonize habitat patches, and the degree of dispersal determines the connectivity among populations, which is key for metapopulation and metacommunity concepts (Hanski 1999; Leibold et al. 2004). Despite the importance of dispersal, there is a paucity of information about the role of hydrodynamics on the dispersal of freshwater invertebrate larvae, although there has been considerable interest in macroinvertebrate drift in stream ecology (Allan 1995; Hoover et al. 2007).

Whereas the effect of local hydrodynamic conditions on settlement and small-scale dispersal has been explored experimentally in flow channels (Pawlik and Butman 1993; Fonseca 1999; Jonsson et al. 2004), direct measurements of larval dispersal or transport of organisms in the field are methodologically more difficult. Consequently, larval dispersal has been examined through modeling (McLay 1970; Denny 1988; Eckman 1990), comparing model results with larval distribution in the field (Reyns et al. 2006), and by associating recruitment levels with currents and hydrodynamic events (Sponaugle et al. 2005; Ben-Tzvi et al. 2007). Denny (1988) and Denny and Shibata (1989) developed a method for predicting particle (e.g., larvae) transport times to the substratum in a turbulent boundary layer, which was refined by McNair et al. (1997). The latter found that the average particle transport time depended greatly on the settling velocity (w_s) of larvae. Gaylord et al. (2002) used that model to examine the dispersal of macroalgae spores and added turbulence components associated with waves to model the nearshore marine environment. Despite the advances in developing mathematical models for larval transport, there is a need for the empirical evaluation of transport models by using tracer particles and larvae in the field (Boudreau and Jørgensen 2001), especially since larval transport can differ from model predictions (Arnold et al. 2005).

Little is known about the extent of dispersal in freshwater unionid mussels, even though dispersal is thought to be an important limiting factor for mussel communities (Vaughn and Taylor 2000; Strayer 2008). The dispersal of unionid mussels is complicated by the interaction of physical and biological factors, including a host–parasite relationship of mussel larvae (glochidia) attaching and transforming into juveniles on host fish (Vaughn and Taylor 2000). The transport of glochidia in the water column before attachment on a host fish is mediated by fluid dynamic processes, which is also the case for the transport of juveniles after detachment from their hosts. The small size of freshwater mussel larvae and juveniles (50–400 μm, McMahon 1991) makes them difficult to track, and previous studies have focused on recruitment patterns and/or modeling (Neves and Wildlak 1987; Lee and DeAngelis 1997; Morales et al. 2006) rather than direct observation. To the best of our knowledge, there are no studies of the dispersal of freshwater mussel larvae in the field, even though lotic systems, especially smaller streams, are ideal for dispersal studies because of their unidirectional flow (Elliott 2003). In this case, dispersal can be idealized with one- or two-dimensional models, whereas the modeling of dispersal in lentic or

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marine systems is difficult because of complex currents. The objective of this study is, therefore, to examine the dispersal of glochidia of the common mussel species, *Actinonais ligamentina* (Lamarck, 1819), which broadcasts a large number of glochidia into the water column. This will also enable us to compare our field data to predictions from a turbulent transport model developed for streams (McNair and Newbold 2001). Such information will provide valuable insight into the transport of larvae and other "particles" in lotic environments, the dynamics of freshwater mussels, as well as the connectivity of benthic communities in general.

Methods

Settling velocity of glochidia—Given that empirical data on settling velocities (w_s) of freshwater mussel glochidia (larvae) are lacking (Morales et al. 2006), the w_s of glochidia of *A. ligamentina* was measured in the laboratory. Gravid females were collected from the Thames River, Ontario (Ontario Ministry of Natural Resources [OMNR], License no. 1040218) and stored at 10°C in a recirculating aquatic system, where they were fed with commercial algae (Nanno 3600, Reed Mariculture) three times a week (10^6 cells mL^{-1} $individual^{-1}$). The gills of gravid females were flushed with a syringe filled with well water to obtain glochidia. To ensure that glochidia were viable, a subsample was tested with a standard salt test (viable glochidia close in response to salt), according to ASTM (2006). For each measurement, an individual glochidium was transferred into a 1000-mL graduated glass cylinder (5.6 cm inner diameter × 40 cm high) filled with well water. This cylinder was placed within a larger glass column (14.4 cm inner diameter × 46 cm high) with water, which helped to minimize temperature fluctuations (Ackerman 2005). The apparatus was placed in a temperature-controlled room, where the water temperature in the settling cylinder remained constant during a given trial but ranged between 15.7 and 15.9°C on different days.

The w_s of 34 glochidia was measured over five intervals of ~ 3.7 cm (700–600, 600–500, 500–400, 400–300, 300–200 mL marking on the cylinder) to ensure that the glochidia had reached terminal velocity (i.e., constant velocity, no acceleration). The shell length and height of a subsample of these glochidia (n = 15) was measured by analyzing pictures taken under the microscope using ImageJ image analysis software (NIH 2007). In this case, the glochidia were forced to close by adding a salt solution. The w_s of an additional 38 glochidia was measured six days after staining with Rose Bengal (*see* below) to determine whether staining affected w_s.

Study area and hydrodynamic characteristics—The study took place in a fourth order reach in the east branch of the Sydenham River in southwestern Ontario, Canada (42°37′35″N, 82°1′23″W), which has a relatively straight shore line for a few hundred meters (Fig. 1). The daily discharge, Q, between 1998 and 2007 ranged between 0.344 and 200 m^3 s^{-1}, with a mean of 10.8 m^3 s^{-1} (data from Environment Canada). During the sampling days (early August–early October 2007) the width (W) of the river ranged between 15 and 25 m, and the midstream water depth ranged between 24 and 49 cm.

A number of morphometric and hydrodynamic parameters were measured in the field. These included the water depth (H), which was measured every 25 cm along a 100-m transect in the middle of the reach where the drift nets were placed (Fig. 1). Additional data on bottom roughness was obtained by measuring the three axes of 17 haphazardly chosen roughness elements (flat disc or tabulate-shaped stones) to the nearest mm. The slope of the water surface (S_0) was measured over a 100-m transect in the middle of the river using a theodolite (Pentax model TH-E20C) on 29 June 2007. Measurements of U, the mean water velocity in the streamwise or longitudinal direction, were made at 0.4 H at the sampling locations using a propeller velocimeter immediately before the drift nets were deployed for each trial. A total of 21 dispersal trials were undertaken and U was measured with a Swoffer velocimeter (model 2100) for 12 trials, a Global Flow propeller velocimeter (model FP101) for five trials; technical difficulties precluded measurements for four trials. Depth and velocity measurements were measured at 2 m intervals across the stream, at the release point before the first and after the last trial on each sampling day, to determine Q, based on the product of the mean H, W, and U. In addition, hourly Q values were obtained from Environment Canada, which operates a measuring station 3.3 km upstream of the study site (42°39′02″N, 82°00′30″W).

Glochidia dispersal—The dispersal of the glochidia was examined on seven dates between early August and early October 2007 (OMNR, License no. 1040280). Two days before each trial, glochidia were obtained from gravid females, as described above, from the same river. Experimental glochidia were stained with Rose Bengal (50 mg L^{-1}) for 48 h, to distinguish them from the relatively high concentration of naturally occurring glochidia in the river. The number of glochidia released varied between 35,000 and 55,000, corresponding to the contents of one to two water tubes (compartments in gills) of a gravid female.

Drift nets (45 cm wide × 30 cm high) with a 100-μm mesh size, were deployed on the river bottom at 4, 8, 16, 32, 64, and 96 m downstream (Fig. 1). The first sampling day was the exception, when only five drift nets were deployed downstream, with the greatest distance being 48 m. The mesh size was small enough to capture all glochidia that had a length (smaller dimension than height) of 200–230 μm. The drift nets usually extended from the bottom to ~ 5 cm and on some occasions (e.g., on 23 August 2007, and at several sampling days for the net at 96 m) up to 15 cm below the water surface. The locations of the drift nets within the river were determined by tracking the drift of a water-filled 500-mL plastic bottle released at the release point. Glochidia were released in the middle of the river at 30–35 cm above the bottom (usually 5–10 cm below the water surface) using a syringe pointing downstream. A few minutes after the release (6–17 min, depending on downstream distance, x, and U), the drift nets were

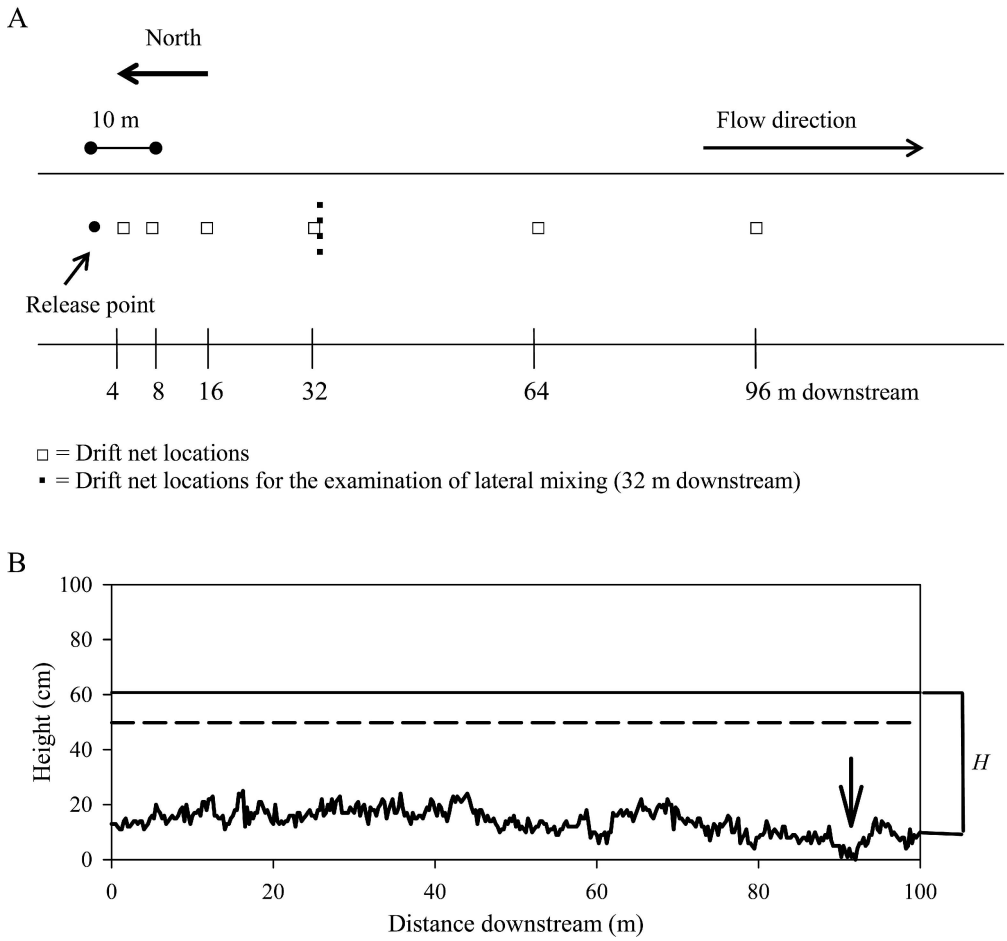

Fig. 1. (A) Schematic representation of the study reach. Drift nets were placed at 4, 8, 16, 32, 64, and 96 m downstream of the release point. Four nets were placed at 32 m downstream, 2 m apart, to examine for lateral mixing. (B) Differences in elevation (maximum depth − measured depth) measured every 25 cm along a 100-m long transect in the middle of the river reach, where the drift nets were placed. The dashed line denotes minimum water depth (H, 11 October 2007), the straight solid line maximum H (23 August 2007). The arrow indicates the deepest point.

retrieved and rinsed to obtain all captured glochidia. This process was repeated for the 21 trials undertaken over seven sampling days. Drift samples were sieved through a 500-μm mesh in the laboratory within 24 h to remove large debris (e.g., leaves and wood fragments) and stored in 70% ethanol. The number of stained glochidia in each sample was counted under a microscope.

Glochidia are also dispersed by lateral diffusion (K_y) due to secondary currents and turbulent diffusion. To ascertain the magnitude of this variation, three trials on three sampling days were undertaken in which four drift nets were placed perpendicular (and spaced 2 m apart) to the mean flow direction at $x = 32$ m downstream of the release point (Fig. 1).

Lateral diffusivity (K_y) can be estimated according to Fischer et al. (1979) as

$$K_y = B_y H\ u_* \tag{1}$$

where B_y is an empirical coefficient that ranges between 0.15 for straight channels and 0.6 for natural channels (Hemond and Fechner-Levy 2000) and u_* is the shear velocity, often based on the total bed shear stress derived from the slope of the surface (Ackerman and Hoover 2001). However, the slope in the study area was too small (< 1 cm) to be measured accurately, so u_* was calculated according to the "law of the wall" (e.g., Ackerman and Hoover 2001) as

$$u_* = \frac{u(z)\kappa}{\ln\left(\frac{z}{z_0}\right)} \tag{2}$$

where $u(z)$ is the velocity at height z (based on measurements of U at $0.4H$), κ is the von Kármán constant (~ 0.4), and z_0 is the roughness height, which according to Soulsby (1997) is given by

$$z_0 = \frac{d_{50}}{12} \tag{3}$$

where d_{50} is the median width of the roughness elements.

The variation (σ^2) for a Gaussian plume model (Okubo and Levin 1989) applied to these data is given by

$$\sigma_y^2 = 2\,K_y\,\frac{x}{U} \tag{4}$$

where x is the distance downstream.

Statistical analysis—The number of glochidia captured in each drift net was normalized by the number of glochidia released in each trial and expressed as a percentage. Given that propagule dispersal is best described with an inverse power function (Elliott 2003), linear regressions were undertaken using ln-transformed data (ln (% glochidia captured) vs. ln (distance downstream)). For comparison, a semi-ln plot (% glochidia captured vs. ln (distance downstream)) was used to test for a negative logarithmic decline, which is often used to describe dispersal distributions (Elliott 2003). In order to examine whether increased velocity leads to greater dispersal, the proportion of glochidia captured in a given net was correlated to the measured U using a Spearman correlation, since most of those data were not normally distributed. In addition, the slope coefficients of each of the linear regressions (% glochidia vs. ln x, and ln (% glochidia) vs. ln x) were correlated to U (measured at the first net).

To test for potential resuspension of previously released glochidia on the same day, the differences between the relative number of glochidia captured in subsequent trials were calculated (e.g., trial No. 2 − trial No. 1 at x = 48 m).

The transport model—In the simplest transport model, assuming water flowing uniformly downstream, without any turbulence, the distance, x, a particle travels downstream before it contacts the bottom depends on U, the height of an organism above the substrate z_r, and its settling velocity w_s, i.e., the rate at which a particle settles in a quiescent fluid,

$$x = \frac{U\,z_r}{w_s} \tag{5}$$

Predictions for turbulent conditions, found under natural flowing conditions, are more complicated. McNair and Newbold (2001) developed a turbulent transport model ("local exchange model") for predicting particle hitting distances by approximating the random motion of individual particles as a stochastic-diffusion process. This model has several simplifying assumptions: (1) longitudinal components of mixing are negligible; (2) the river has a flat bottom; and (3) turbulence is isotropic. In the model, a particle is assumed to move up and down with eddies (vertical mixing), so that the height in the water column at a given time $z(t)$ changes randomly. The degree of vertical particle motion depends on the height above the bed, which is determined by factors controlling the rate of viscous and turbulent mixing and by factors controlling the rate of particle sinking.

The vertical dispersion coefficient $K(z)$ is the combined viscous-turbulent diffusivity given by

$$K(z) = \frac{1}{2}\left\{\upsilon + \sqrt{\upsilon^2 + [2\,\kappa\,u_*\,z\,(1 - z/H)]^2}\right\} \tag{6}$$

where ν is the kinematic viscosity and u_* was calculated using Eq. 2.

The change in velocity with respect to height (du/dz) is given by the differential equation

$$\frac{du}{dz} = \frac{2\,u_*^2\,(1 - z/H)}{\upsilon + \sqrt{\upsilon^2 + 4\,u_*^2\,l(z)^2(1 - z/H)}} \tag{7}$$

where $l(z)$ is the Prandtl mixing length given by

$$l(z) = \kappa\,z\,\sqrt{1 - z/H} \tag{8}$$

It should be noted that Eqs. 6, 7, and 8 represent the simplest plausible fluid-mechanic assumptions that apply for smooth and flat channels (McNair and Newbold 2001); however, conditions in which significant form resistance occurs will likely require somewhat different assumptions. $G(x, z_r)$ is the function that indicates the probability that larvae will be in suspension at a distance downstream (x) from the release point and height of release z_r.

G is governed by a linear advection-diffusion partial differential equation, which for $x > 0$ and with $0 < z_r < H$ is given by

$$u(z_r)\frac{\partial G}{\partial x} - [K'(z_r) - w_s]\frac{\partial G}{\partial z_r} - K(z_r)\frac{\partial^2 G}{\partial z_r^2} = 0 \tag{9}$$

where $K'(z_r)$ is the first derivative of $K(z_r)$ (Eq. 6, McNair and Newbold 2001).

The boundary conditions are defined by

$$G(x,0) = 0[\partial G/\partial z_r]_{z_r = H} = 0 \tag{10}$$

and the initial condition is

$$G(0,z_r) = \begin{cases} 1 & \text{if} \quad 0 < z_r \le H, \\ 0 & \text{if} \quad z_r = 0. \end{cases} \tag{11}$$

The partial differential equation was approximated using a fully implicit finite difference scheme (Thomas 1995). A backward difference approximation was used for the derivative of the downstream distance, and a centered difference approximation was used for the depth derivatives. The resulting (sparse) tridiagonal linear system was solved using Matlab's (Matlab 7.0.4) Backslash command (direct solver equivalent to Gaussian elimination).

To test whether our model results correspond to those of McNair and Newbold (2001), we parameterized our model with their data and found that our results provided the same values as in fig. 8 in McNair and Newbold (2001).

Comparison of model and field data—The model assumes that water depth (H) and the velocity profile (du/dz) remain constant in the downstream direction. The measured H at the release point was used to compare each trial with

predictions from the model, and those data were used to determine u_* as a parameter for the model. H for the first sampling day was not measured at the release point and so H measured at the location of the first drift net (4 m downstream) was used. The modeled velocity profile (Eq. 7) was multiplied by a constant (2.2–2.4) to match U (at $0.4H$) measured in the field at the first net. The constant was based on the ratio of modeled and measured U. Given that velocity data were not available for four trials from the first three sampling dates, the value from subsequent trials on the same sampling day was used instead.

Several assumptions were made in order to compare predicted and measured glochidia capture rates. First, the model predicts the probability that glochidia are still suspended before encountering the bed and does not account for resuspension. We assumed that an insignificant proportion of glochidia were resuspended while the nets were deployed (10–15 min). Second, we assumed that each net would only remove a small fraction of the total number of glochidia released and would not have a significant effect on the subsequent capture in drift nets downstream. Third, we assumed that glochidia would disperse laterally while drifting downstream in accordance with Eqs. 1 and 4. Therefore, we normalized the predictions of the model (i.e., the proportion of glochidia in suspension) by the area calculated as the product of the lateral spatial variation (2 × standard deviation [SD]) at a given downstream distance (Eq. 4) and the average water depth (mean H), assuming a homogenous distribution within that area for simplification. The measured glochidia capture rates were normalized by the area of the net opening. This provided comparable quantities (i.e., glochidia m^{-2}), which could be used to determine the flux of glochidia (glochidia m^{-2} s^{-1}) by dividing by the time for the passage of the larval cloud. This was based on the difference in time between the arrival of the leading and trailing edges of the larvae cloud, which was estimated as follows. Similar to the lateral diffusion (Eq. 4), the spatial variance in the longitudinal direction, σ_x^2, is given by

$$\sigma_x^2 = 2\,K_x \frac{x}{U} \tag{12}$$

where the longitudinal dispersion coefficient (K_x) was estimated as 5 m^2 s^{-1}, which is an average value found in rivers with similar Q (Rutherford 1994). The time (T) the larval cloud would pass through a net was determined by dividing the spatial SD σ_x by the mean velocity

$$T = \frac{\sqrt{\sigma_x^2}}{U} \tag{13}$$

Results

Settling velocity of glochidia—The settling velocity (w_s) of glochidia ranged between 0.65 and 1.10 mm s^{-1} with a mean of 0.87 ± 0.02 mm s^{-1} (mean ± standard error [SE], n = 34) for glochidia that were 0.214 ± 0.002 mm long and 0.240 ± 0.002 mm high (n = 15). Whereas all live glochidia were observed to settle with their valves open slightly, most stained glochidia (same size as live glochidia) were closed when they settled, since they were killed by the staining process. The average w_s of the stained glochidia was only slightly higher at 0.93 ± 0.03 mm s^{-1} (n = 38, range, 0.58–1.16 mm s^{-1}), but this difference was significant (t = 2.2, p = 0.03, n = 72).

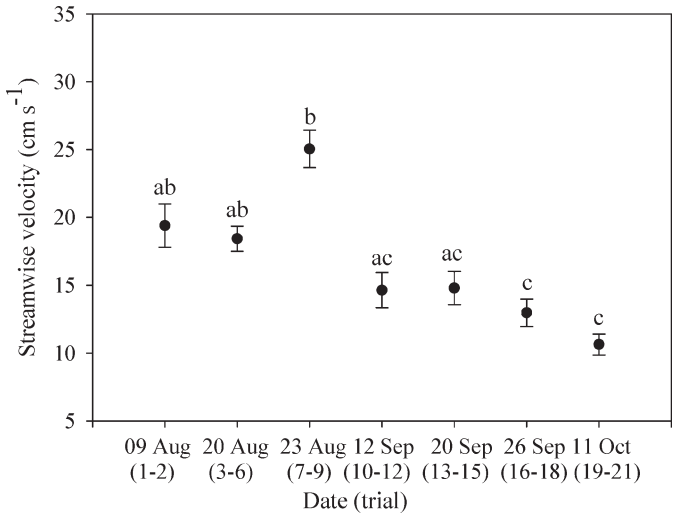

Fig. 2. Streamwise velocity measured at 0.4-m water depth for each sampling date, based on daily averages for each net location (n = 6, except for 09 August 2007, where n = 5). Error bars represent SE. Different letters represent a significant difference (Tukey test, $p < 0.05$). The numbers in parentheses under the dates correspond to the trial number.

Field measurements—The bottom profile varied little along the 100-m transect with a mean difference in elevation (maximum depth − measured depth) of 14 ± 5 cm (mean ± SD, Fig. 1), where the deepest point on the profile (H_{max}) at 92 m downstream was taken as z = 0. Because of variation in Q (*see* below), the average water depth H varied among sampling dates (overall average, 38 ± 4 cm, n = 7). On a given date, H was relatively constant for the first 64 m downstream, and increased slightly by an average of 5 cm between the net at 64 m and 96 m (Fig. 1). Roughness elements, which were flat disc- or tabulate-shaped stones (13.2 ± 1 [mean ± SE] cm × 9.5 ± 1 cm × 1.9 ± 0.2 cm, n = 17), protruded only a few centimeters into the flow.

The mean velocities (U) measured at each drift net location varied between ~ 7 cm s^{-1} (26 September 2007 at 32 m, 11 October 2007 at 96 m) and ~ 30 cm s^{-1} (23 August 2007 at 16 m and 32 m). U did not differ significantly among net locations when the means for each sampling date were compared ($F_{5,35}$ = 0.9, p = 0.49), but U varied significantly among sampling dates (Fig. 2). The overall average U was 15 ± 5 cm s^{-1} (n = 7). Q measured at the field site varied between 0.66 m^3 s^{-1} and 1.8 m^3 s^{-1} and correlated well with the hourly discharge data obtained from the Environment Canada measuring station 3.3 km upstream (Pearson r = 0.99, $p < 0.01$, n = 6), which varied between 0.7 m^3 s^{-1} (11 October 2007) and 1.47 m^3 s^{-1} (23 August 2007).

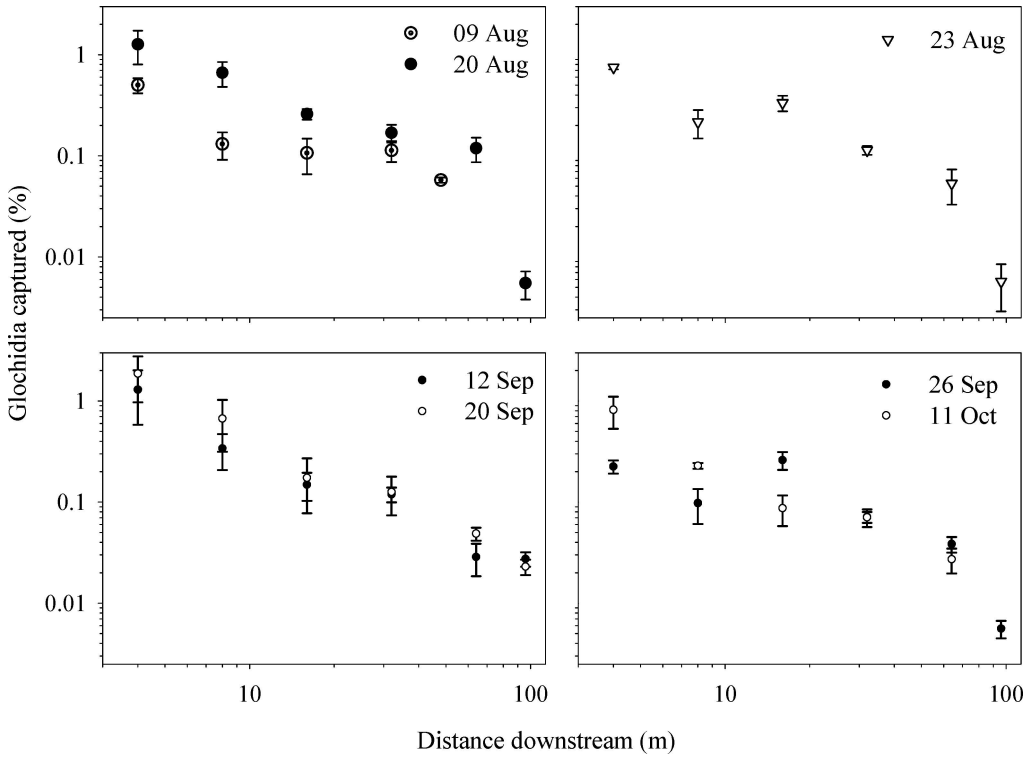

Fig. 3. Proportion of glochidia (number of glochidia captured per number of glochidia released × 100%) captured at different distances downstream for seven sampling dates (mean ± SE). Sampling dates with similar U (Fig. 2) were grouped together.

Glochidia dispersal—Only a small proportion of the released glochidia were captured in the drift nets, on average 1.7% (range 0.6–5.6%). The largest proportion 0.036 or 3.6% (1365 of 38,400 released) was found in the first net at 4 m downstream. In general, the largest proportion of glochidia (0.1–3.6%) was captured at this location, with the exception of one trial where the largest number was found at 8 m. Glochidia capture usually decreased continuously from the first net (4 m) to the net located farthest downstream (96 m), where few glochidia were captured (i.e., 0–15; 0–0.03%, Fig. 3). However, in some trials, more glochidia were found in the drift net at 16 m than at 8 m.

There was no clear indication that resuspension led to increases in the capture rate of subsequent trials on the same sampling day, since the frequency of increases between consecutive trials was similar to that of decreases (Table 1). Whereas the frequencies were of similar magnitude for the nets between 32 and 96 m downstream, the magnitude of the increases were considerably higher for the nets at 4 and 8 m downstream. However, the capture rates did not differ significantly among trials for these distances ($F_{17,2}$ = 1.9 and 2.7, p = 0.2 and 0.1 for 4 m and 8 m, respectively).

The glochidia capture rate was positively correlated with U for the nets at 16, 32, and 64 (48) m (Spearman r = 0.69, 0.71, and 0.78, respectively, $p < 0.01$, n = 17). However, significant correlations were not found at the other distances (4, 8, and 96 m, $r < 0.5$ and $p > 0.05$). Hourly discharges (from Environment Canada) were also positively correlated to the glochidia capture rate at 32 m (r = 0.51, p = 0.02, n = 21) and somewhat at 64 (48) m (r = 0.41, p = 0.06, n = 21).

Most of the trials showed an approximately negative logarithmic decrease in glochidia capture with distance but were best described with an inverse power function (Fig. 3;

Table 1. Potential for glochidia resuspension in subsequent dispersal trials on the same day. Note that the number of comparisons for 96 m downstream is lower, since glochidia were not sampled at that distance on 09 August 2007, and on 11 October 2007 no glochidia were captured 96 m downstream.

Location of net (m)	n	Decreases	Relative decrease (%)	Increases	Relative increase (%)
4	14	6	64±31	8	117±29
8	14	6	22±7	8	93±28
16	14	6	71±20	8	48±12
32	14	6	40±8	8	43±16
64 (or 48)	14	6	56±23	8	59±26
96	11	7	50±16	4	51±29

Table 2. Strength of the decline in glochidia capture with distance, the corresponding significance levels and number of trials, for the negative logarithmic and the inverse power model.

		Number of trials	
R^2	p	Inverse power model	Negative logarithmic model
0.67–0.99	<0.05	18	11
0.52–0.71	0.05–0.1	2	7
0.37–0.59	0.13–0.2	1	3

Table 2). However, the percentages of glochidia captured at 96 m were often lower than expected with an inverse power function relative to the trend observed from the shorter distances (Fig. 3). Moreover, the slope coefficients determined from the linear regressions of the percentage of glochidia captured vs. the ln x (negative logarithmic decline model) were negatively correlated with U (Spearman $r = -0.46$, $p = 0.06$, $n = 17$). This indicates that the lower U, the steeper the slope and, therefore, the more rapid the decline of glochidia capture (i.e., glochidia travel shorter distances). However the slope coefficients derived from the ln (% glochidia captured) vs. ln x plot (inverse power model) did not correlate with U ($r = 0.06$ and $p = 0.81$, $n = 17$).

Lateral mixing—The majority (80–90%) of the glochidia at $x = 32$ m were captured in the net that was -1 m away (i.e., east, Fig. 1) of the assumed flow path in two of the three lateral mixing trials (Fig. 4A). In the third trial, an almost equal proportion of glochidia ($\sim$ 50%) were captured within $\pm$ 1 m of the assumed flow path. Only a small proportion of glochidia were found in the nets that were $\pm$ 3 m away from the assumed flow path (Fig. 4A).

Lateral diffusivity (K_y) ranged between 1.1×10^{-3} m^2 s^{-1} (for $B_y = 0.15$, straight channels) and 4.3×10^{-3} m^2 s^{-1} (for $B_y = 0.6$, natural channels), assuming an H of 0.38 m. Given a $U \sim 0.15$ m s^{-1}, the spatial variation (σ^2) was 0.5 and 1.8 m^2 for straight and natural channels, respectively (i.e., the standard deviation [σ or SD] was 0.7 and 1.4 m). Accordingly, and assuming a normal distribution, 68% ($\pm$ 1 SD) of all glochidia should be found within 0.7 and 1.4 m, and 95% ($\pm$ 2 SD) should be found within 1.4 and 2.7 m of the main flow path 32 m downstream (Fig. 4B). At that downstream distance in the field, 92% $\pm$ 5% of glochidia were captured in the two nets within $\pm$ 1 m from the assumed flow path, and the remaining 8% $\pm$ 5% were captured up to $\pm$ 3 m away (Fig. 4A).

Comparison of model and field data—The simplest transport model (Eq. 5) predicted that glochidia should settle 50 m downstream ($U = 0.15$ m s^{-1}, $z_r = 0.3$ m). Conversely, settling in the field was distributed longitudinally in the study reach with most (i.e., 96%) of glochidia being captured between 4 and 32 m downstream, and a small proportion captured 96 m downstream (*see* above, Fig. 3). The local exchange model predicted a similar trend, but only $\sim$ 80% of the glochidia were predicted to have settled by 50 m downstream.

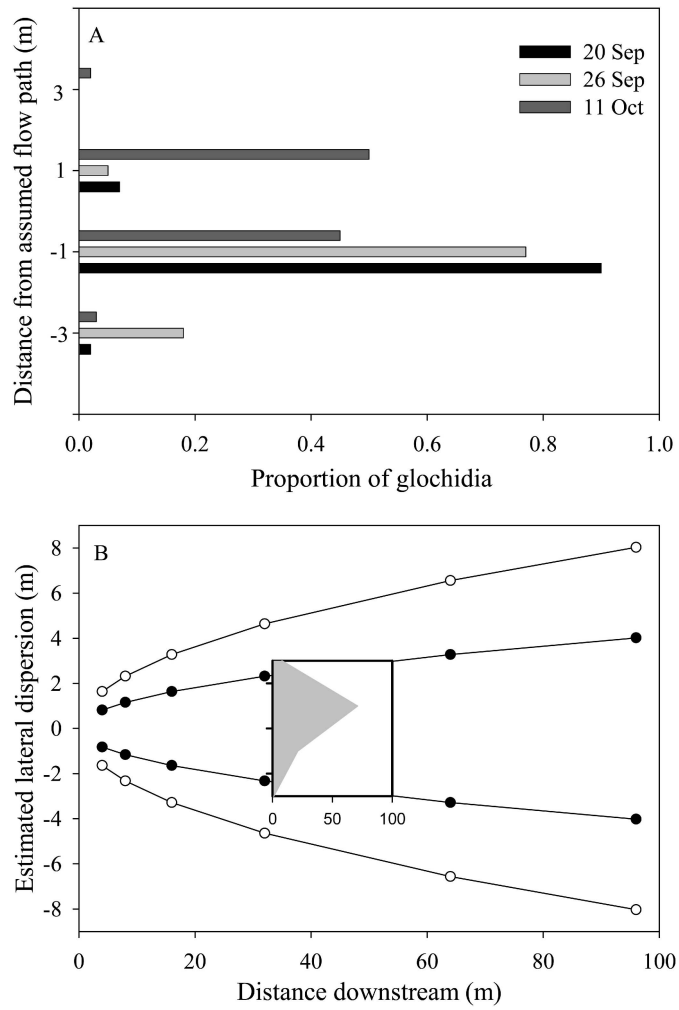

Fig. 4. (A) Lateral distribution of glochidia captured in four nets 32 m downstream of the release point. The proportion of glochidia is based on the quotient of glochidia captured in one net and the total number of glochidia captured at that distance and date. (B) Estimates for lateral distances, in which 95% ($\pm$ 2 SD) of glochidia should be found. Dots represent the location of the nets. Solid dots represent estimates for a straight channel, and hollow dots are for a natural channel. The inset in the middle shows the mean proportion of glochidia captured at 32 m.

There was a significant association between the averaged values of the modeled and observed glochidia fluxes (glochidia m^{-2} s^{-1}; $r = 0.98$, $p = 0.01$, Fig. 5A), as well as between the modeled and observed areal glochidia capture rate (glochidia m^{-2}; $r = 0.96$, $p = 0.01$; data not provided). However, modeled values were $\sim$ 50 times higher than the observations, and the differences were greatest for 8 and 16 m downstream (e.g., on average $>$ 60 times) and lowest (e.g., on average $\leq$ 40 times) for 4, 64, and 96 m downstream (Fig. 5C). The observations for 4 and 8 m did differ significantly from the model, likely because of the variability between trials.

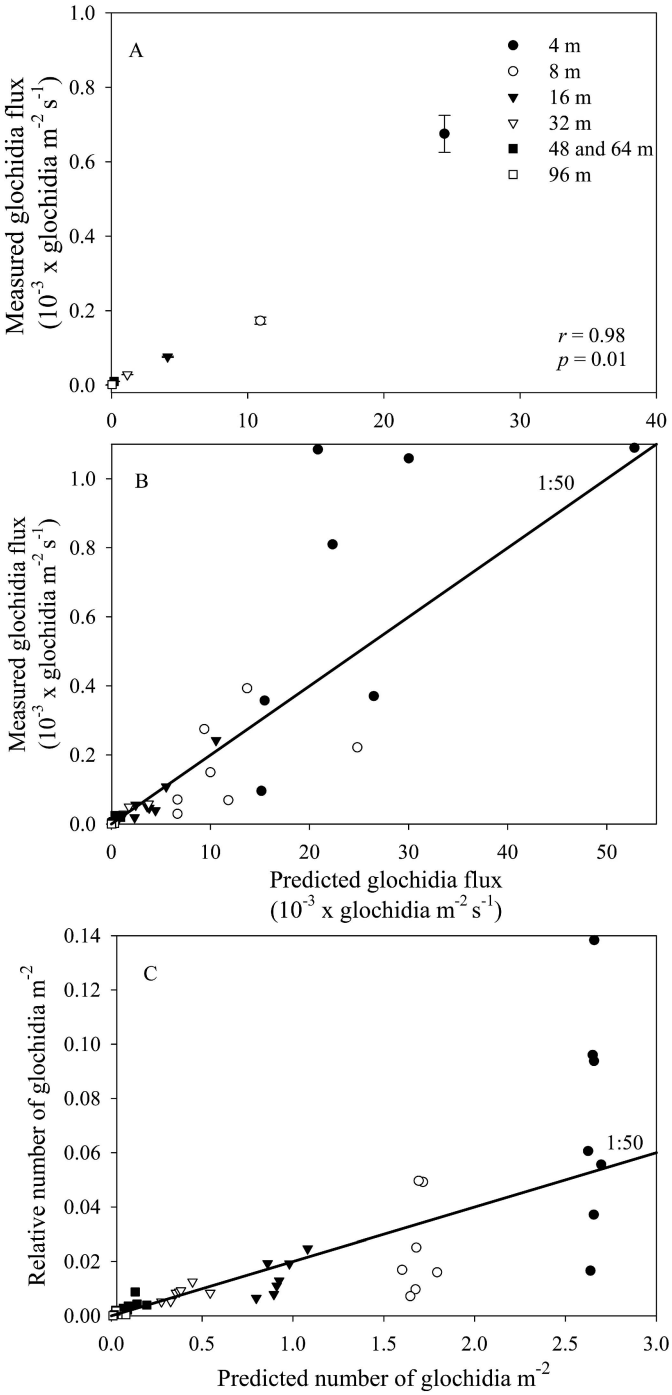

Fig. 5. Comparison of (A) the overall mean flux of glochidia (± SE, $n = 21$, and $n = 19$ for nets at 64 and 96 m), (B) the mean daily flux at different distances downstream ($n = 3$, $n = 2$ for 20 August 2007, and $n = 4$ for 09 August 2007), and (C) observed mean daily areal capture rate vs. the corresponding model predictions at different distances downstream.

Discussion

Dispersal of glochidia—Glochidia were found to disperse over scales of 10 to 100 m. Ecologically, this would indicate that glochidia may infest host fish up to 100 m downstream, even in streams with relatively low velocities and shallow water depths provided that they are released high enough into the water column. This is likely for larger mussels like *A. ligamentina* (≤ 15 cm shell length, Clarke 1981), which was found to eject its glochidia up to the surface of a 30-cm deep aquarium (Schwalb unpubl. data). The decline of captured glochidia with distance was best described with an inverse power function, which was also found to have a better fit than exponential decline models for 10 species of stream invertebrates (Elliott 2003). Inverse power functions predict longer travel distances than exponential models, and the good fit with this model suggests that glochidia could still be suspended even much farther than 100 m. In any case, transport distances would likely be larger under higher discharges (higher H and U) that occur in spring when *A. ligamentina* and other species that are reproductive over the winter likely release their glochidia (Clarke 1981).

Propagule dispersal scales range over five orders of magnitude in marine and terrestrial environments, with sessile suspension feeders varying between tens of meters to several hundred kilometers (Kinlan and Gaines 2003). In freshwater ecosystems, stream macroinvertebrates drift in the range of centimeters to meters before settling and have larger dispersal distances under increased velocity (Lancaster et al. 1996; Fonseca 1999; Elliott 2003). Passive transport of juvenile freshwater mussels has been estimated to range from a few meters to several kilometers for a large river as the Upper Mississippi River (average annual $Q \sim 2000\ m^3\ s^{-1}$) based on a numerical model (Morales et al. 2006). It is not surprising that the dispersal distances estimated for the Sydenham River (average annual $Q = 11.2\ m^3\ s^{-1}$) are much smaller, especially under low water conditions in summer, when most of the mussels are thought to be reproductive. These dispersal distances may decrease if low discharges become more common with climate change (Mortsch and Quinn 1996).

The maximal distance at which a host fish could be infested by glochidia will depend on the combined probability of glochidia being in suspension (L), glochidia encountering a host fish (F), and the success rate of the infestation (α). The probability of successful infestation (P_x) at a distance downstream (x) would be

$$P_x = L\,F\,\alpha \tag{14}$$

For the conditions measured at our field site, L was on average equal to 0.002 at 96 m. Assuming F at this distance is bounded by 1% and 0.01% (i.e., 10^{-2}–10^{-4}) and that α is on average 10% (based on host fish experiments in the lab, Schwalb unpubl. data), we estimate that between 5×10^5 and 5×10^7 glochidia would be needed to successfully infest a fish ~ 100 m downstream of its release. Given that gravid females of *A. ligamentina* contain $> 10^6$ glochidia, it is likely that some glochidia may infest a host fish at these distances.

There are several other parameters and processes that may also affect the dispersal distances of glochidia, including resuspension, the survival period, and the stability of mucous webs (floating aggregates of glochidia in some species; Haag and Warren 2003). Glochidia of many common mussel species such as *A. ligamentina* are

able to survive for more than a week (Farris and van Hassel 2007), which means that the period during which glochidia can be resuspended and travel downstream is relatively long. Black fly larvae drift with silk threads (Fonseca 1999; Fingerut et al. 2006) and mucous webs may similarly facilitate greater dispersion in glochidia. However, resuspension and the behaviour of mucous webs in the water column need further research to understand their potential effects on glochidia dispersion.

Sources of variation—Significant associations between glochidia capture and velocity were found at 16, 32, and 64 m downstream, indicating that dispersal distances increase with velocity. The number of glochidia was probably too low to detect significant associations with velocity at 96 m, and velocities were likely high enough to keep most glochidia in suspension at shorter distances. Importantly, we did not find a clear indication for resuspension, so we therefore assume that the number of suspended glochidia was too low to affect the results, given that drift nets were deployed within 10–15 min, and there was ~ 1 h between trials.

The lateral diffusivity determined assuming a natural channel ($K_y = 4.3 \times 10^{-3}$ m^2 s^{-1} vs. 4.7×10^{-3} m^2 s^{-1} for $Q = 0.7$ to 1.5 m^3 s^{-1}) was similar to the empirical values reported for a straight channel at a similar discharge (1.5 m^3 s^{-1}; Hemond and Fechner-Levy 2000). K_y results at 32 m confirmed this, since most glochidia were found within 1 m of the assumed flow path (compare Fig. 4A,B). The measured data were more consistent with the predictions for a natural channel, which could be an indication that secondary currents affected the lateral diffusivity in our study (Rutherford 1994). Secondary currents would make it difficult to identify the main flow path; hence, nets located outside the main glochidia cloud may have contributed to the observed variation. This effect would likely be more pronounced at shorter distances (*see* Figs. 3, 5), where lateral diffusion had not had sufficient time to disperse the larvae far across the stream (Fig. 4B). A net outside of the main glochidia cloud would capture considerably less glochidia, whereas farther downstream glochidia should be distributed more homogenously in the lateral direction, and misalignment of the net location would have less of an effect on capture rates.

It is reasonable to argue that turbulence is likely the main source of variation in glochidia capture observed in the study. This was also the case for the near-source distribution of kelp spores in the coastal zone (Gaylord et al. 2006). Specifically, turbulence did not mix the suspended particles effectively at short distances, which resulted in a noisy distribution. However, at larger distances the suspended particles had a smoother distribution with less variation (Gaylord et al. 2006). In a coastal environment, orbital wave motions affect spore dispersal, whereas turbulence in rivers is driven by turbulent events, such as low-speed fluid being pushed away from the bed (i.e., ejections), followed by the downward movement of high-speed fluid (i.e., sweeps). Both of these processes can nevertheless affect the transport of particles considerably (Cellino and Lemmin 2004) and may have contributed to the differences in variation observed between glochidia capture at shorter vs. longer distances.

Comparison with model—Without turbulence all glochidia should settle to the bottom ~ 50 m downstream of release. However, the vertical mixing in the river led to a wider distribution of transport distances. This is consistent with theoretical findings that turbulence may decrease dispersal distances for small particles and organisms, but also that an organism's dispersal distance can be much greater than expected on average (McNair et al. 1997; McNair and Newbold 2001).

In general, the model predictions correlated significantly with the measured values. This confirms the utility of approximating turbulent particle transport as a stochastic-diffusion process with the diffusivity varying parabolically with water depth (McNair et al. 1997). However, it is important to note that the model predictions were 1–2 orders of magnitude higher than the observed values and that they showed the largest variation for the shortest distances, although these differences diminished slightly with downstream distances. It is possible that some glochidia were diverted from drift net openings by secondary currents and by pressure created by the water movement through the fine mesh of the nets, leading to lower than expected values. On the other hand, several simplifying assumptions of the model may have contributed as well, in that the model assumes a homogenous distribution of particles across water depth as an initial condition. In the case of the field experiments, larvae were released from a point source. It is relevant, therefore, to determine the distance over which particles from a point source become well mixed, in the vertical direction. This can be estimated (i.e., 98% complete mixing) according to Rutherford (1994) by

$$x = 0.536 \frac{UH^2}{K_z} \tag{15}$$

where

$$K_z = \frac{\kappa}{6} H u_* \tag{16}$$

K_z calculated as an average based on Eq. 6 used for the model provides the same estimate as Eq. 16. According to Eq. 15, particles should become well mixed in z by $x = 24$ m. Consequently, as drift nets were often submerged 5–15 cm below the water surface (i.e., 0.14 to 0.33H), it is likely that a lower proportion of glochidia were captured at locations < 24 m downstream than would be expected for a homogenous distribution of glochidia in z.

The model also assumes a flat bottom and no effect of bottom roughness. Roughness features, however, can affect larval settlement significantly depending on their density and height (Eckman 1990). For example, when the wake of one roughness element interferes with the wake of the next one, turbulence and high local velocities are produced (Young 1992). The bottom at our study site was relatively smooth for a cobble-bed river with roughness elements protruding only a few centimeters into the flow. The near-bed turbulence in this case would be higher relative to a flat bottom and result

in a lower proportion of suspended glochidia given that increased turbulence decreases the hitting distances of particles (McNair and Newbold 2001). The local exchange model also assumes that turbulence is isotropic, but Cellino and Lemmin (2004) found that ejections (low-speed fluid pushed away from bed) dominate away from the bed (> 0.2 relative depth) in a flume. Hence, propagules in the upper water column may be kept in suspension by ejections and travel longer distances than predicted for isotropic turbulence. This and the incomplete vertical mixing near the release point may have contributed to the smaller difference between modeled and observed values at the larger downstream distances (e.g., Fig. 5C).

Establishing transport distances is a necessary first step to understand the effect of dispersal on connectivity and dynamics of populations, their spatial and temporal patterns, and their colonization potential. It is often assumed that dispersal distances and connectivity between mussel populations depend only on host fish (Vaughn and Taylor 2000; Woolnough 2006), but the transport of larvae and juveniles in the water column may also have a significant effect on the dispersal of freshwater mussels (Morales et al. 2006). Some inferences about the connectivity can be drawn from genetic studies (Levin 2006), which indicate that freshwater mussel populations can have low to high levels of genetic differentiation both within and among watersheds (Berg et al. 1998; Kelly and Rhymer 2005; Zanatta and Murphy 2007). One explanation for this variation is a wide variation in dispersal abilities of different freshwater mussel species, which may be related, among other things, to the diversity in host attraction strategies (Barnhart et al. 2008). The effects of these factors on the dispersal mechanisms, host fish transport, and fluid-mediated dispersal warrant further investigation.

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