

## ORIGINAL ARTICLE

**The effect of settling velocity on the transport of mussel larvae in a cobble-bed river: Water column and near-bed turbulence**Astrid Nadine Schwalb,<sup>1,2</sup> Todd James Morris,<sup>3</sup> and Josef Daniel Ackerman<sup>1</sup>**Abstract**

Simple transport models predict that the distance organisms drift downstream in rivers is determined by their settling velocity ( $w_s$ ), the release height ( $z_r$ ), and the stream velocity ( $U$ ). Unfortunately, empirical evidence is lacking on whether and how factors such as  $w_s$  affect mussel larvae dispersion in rivers under natural turbulent conditions. The main goal of this study was to examine how  $U$  and  $w_s$  affect the transport of freshwater unionid mussel larvae (glochidia) in a turbulent reach of the Grand River, Ontario, Canada. Glochidia of *Actinonaias ligamentina* and *Lampsilis fasciola*, which had a 2.5-fold difference in their  $w_s$  ( $0.9 \pm 0.02$  [mean  $\pm$  SE] and  $2.2 \pm 0.02$  mm s<sup>-1</sup>, respectively), were released and captured in a series of drift nets downstream. Larval dispersion in rivers appeared to be strongly affected by hydrodynamic conditions. The results indicated that glochidia are dispersed more rapidly with increased  $U$ . This is likely due to increased turbulence and lateral and vertical mixing, which were consistent with the predictions of a 3-dimensional advection–diffusion model. The decline of glochidia with distance was well described with an inverse power function, but only on days when the average  $U$  measured at 40% water depth was  $> 40$  cm s<sup>-1</sup>. In contrast to the predictions of simple transport models, the observed downstream transport did not differ significantly between glochidia with different  $w_s$ . Further studies are needed to better understand the effect of differences in  $w_s$  and  $z_r$  under different hydrodynamic conditions, which may also be important for other dispersal phenomena.

Keywords: advection–diffusion model, dispersion, glochidia, shear stress, unionid mussel

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**Introduction**

[1] The development of techniques for tracking larvae via chemical and genetic markers has led to advances in understanding the dispersal of small-bodied animals, such as the larvae of marine clams, over large distances and under natural conditions (Arnold et al. 2005; Levin 2006). Despite these advances, dispersal of larval freshwater unionid mussels (glochidia) has received little attention (Strayer 2008; Schwalb et al. 2010).

[2] In general, propagule dispersal, which is the spread of offspring from its natal site to its settlement site (Pineda et al. 2007), shows an approximately negative logarithmic decline with distance in terrestrial (e.g., terrestrial seed dispersal; Nathan and Muller-Landau 2000) and aquatic systems (e.g., marine larval dispersal; Treml et al. 2008). The dispersal of macroinvertebrates in rivers has been best described with an inverse power function (Elliott 2003).

Whereas dispersal is also affected by processes such as larval settlement and survival, larval transport depends mainly on the physical transport (Pineda et al. 2007).

[3] Hydrodynamic transport models typically include parameters such as settling velocity ( $w_s$ ; i.e., the terminal rate at which a particle settles in quiescent fluid), release height ( $z_r$ ), and velocity ( $U$ ) (Fonseca 1999; Morales et al. 2006). A simple transport model assuming uniform downstream flow without turbulence (e.g., Fonseca 1999) predicts that decreasing  $w_s$ , increasing  $U$ , or increasing  $z_r$  will increase the distance ( $x$ ) an organism is transported downstream (i.e.,  $x = Uz_r w_s^{-1}$ ). However, turbulence in rivers can also affect hydrodynamic transport, and mathematical predictions about  $U$ ,  $z_r$ , and  $w_s$  are not as simple as described in the equation above (McNair and Newbold 2001).

[4] Turbulence, which is an essential characteristic of river flows, is thought to be the driving factor of sediment transport (Bridge 2003) and a potentially important factor for the transport and settlement of larvae and propagules (Denny and Shibata 1989; Gaylord et al. 2006; Pineda et al. 2007). Large-scale turbulent flow structures have been described for gravel-bed rivers in the form of alternating regions of high and low velocity (Roy et al. 2004). Given the size and frequency of these larger structures (0.07–0.12 Hz), it is likely that they could move slowly settling larvae (i.e.,  $w_s = 1\text{--}2\text{ mm s}^{-1}$ ) upward or downward several times during downstream transport, which may affect transport distances.

[5] Simple advection–diffusion models, which incorporate turbulence as parameters, can provide a reasonable approximation of the dispersion of dissolved scalars (e.g., chemical spills) and particles for which  $w_s$  is less important compared with the impact of turbulent mixing for transport in a river (Fischer et al. 1979). These models represent solutions of differential equations using parameters derived from empirical observations (Fischer et al. 1979). Even though a number of simplifying assumptions are usually made, including the assumption that the morphology of the channel is simple, advection–diffusion models are effective in predicting the extent of longitudinal, lateral, and vertical dispersion given approximations of the appropriate turbulent diffusion coefficients.

[6] Empirical evidence is needed to determine whether differences in  $w_s$  affect transport distances under turbulent conditions in a river with large bottom roughness. The purpose of this study is, therefore, to examine whether differences in  $w_s$  affect mussel larval transport in a turbulent cobble-bed river. We also examine how differences in  $U$  affect downstream dispersion of mussel larvae and compare our field data with predictions from a 3-dimensional (3D) advection–diffusion model.

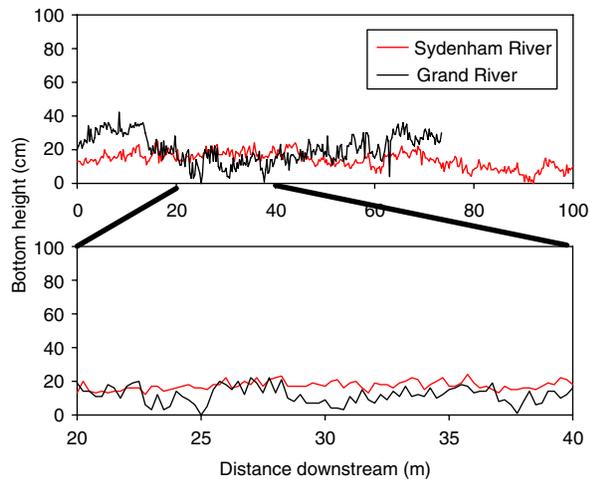
## Methods

### *Measurement of the Settling Velocities of Glochidia*

[7] The  $w_s$  of glochidia of *Actinonaias ligamentina* (Lamarck, 1819) (Mucket) have been reported previously (Schwalb et al. 2010). The methods for determining  $w_s$  of *Lampsilis fasciola* (Rafinesque, 1820) (Wavyrayed Lampmussel) follow those of Schwalb et al. (2010) and are outlined briefly here. Settling velocities were measured in a temperature-balanced settling chamber 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 = 15.8–15.9°C). Individual glochidia ( $n = 33$ ) were released in the inner cylinder, and each glochidium was used once.

### *Hydrodynamic Characteristics of the Study Reach*

[8] The field experiments took place in a seventh-order reach of the upper Grand River in southwestern Ontario, Canada (43° 24' 29" N, 80° 25' 32" W), with a width ( $W$ ) of ~50 m. The average discharge ( $Q$ ) for 2008 was  $50.1\text{ m}^3\text{ s}^{-1}$  (range = 7.0–528  $\text{m}^3\text{ s}^{-1}$ , Grand River Conservation Authority [GRCA]). During the sampling period (early July–late October 2008, and late August 2009) the water depth ( $H$ ) in the experimental reach ranged between 22 and 65 cm. Information on bottom roughness was obtained by measuring  $H$  every 25 cm along a 70-m transect parallel to the stream flow in the study reach where drift nets were placed (see below; Fig. 1) and by measuring the 3 axes of 61 haphazardly chosen roughness elements (cobble) to the nearest millimeter.



**Fig. 1** Differences in elevation (maximum depth – measured depth) measured every 25 cm along an up to 100-m long transect where the drift nets were placed in the Grand River and the Sydenham River (data from Schwalb et al. 2010). The inset provides details of the reach between 20 and 40 m illustrating the higher bottom roughness in the Grand River compared with the Sydenham River.

[9] Measurements of  $U$ , the mean water velocity in the downstream (streamwise) direction, were made at  $0.4H$  at the sampling locations for 60 s using a propeller velocimeter immediately upstream of each drift net that was deployed.  $U$  was measured with a Swoffer velocimeter (model 2100, Swoffer Instruments, USA) for most trials in 2008 and with a Global Water Flow Probe (model FP101, Global Water, USA) on 6 August 2008 and on 19 August 2009. The surface velocity ( $U_s$ ) was measured by timing the transport of a water-filled 500-ml plastic bottle from the release point to the last drift net (i.e., 64 m; only one replicate was used). In addition, hourly  $Q$  data were obtained from a GRCA measuring station  $< 3$  km downstream of the reach.

[10] The hydrodynamic characteristics of the channel were determined using the channel Reynolds number ( $Re = U H \nu^{-1}$ , where  $\nu$  is the kinematic viscosity) and the Froude number ( $Fr = U (g H)^{-0.5}$ , where  $g$  is the acceleration due to gravity). The influence of bottom roughness in the turbulent boundary layer was determined from the roughness Reynolds number ( $Re_* = u_* z_0 \nu^{-1}$ , where  $u_*$  is the friction velocity and  $z_0$  is the roughness height, which according to Soulsby (1997) is given by  $z_0 = 0.083 d_{50}$ , where  $d_{50}$  is the median width of the roughness elements).

### Water Column and Near-Bed Turbulence

[11] Velocities in the downstream ( $x$ ), cross-stream ( $y$ ), and vertical ( $z$ ) directions were measured with a SonTek (USA) acoustic Doppler velocimeter (ADV) on 2 sampling dates. On 28 August 2008, measurements were taken at 25 Hz for 2 min at  $0.4H$  at  $x = 0, 4, 8, 16, 24,$  and  $32$  m downstream, to provide information on water column turbulence. Additional measurements were taken on 22 October 2008 at 25 Hz for 1 min at  $0.1H$  and  $0.4H$  at  $x = 0, 16, 32,$  and  $48$  m downstream, to provide information on near-bed turbulence. Data were filtered using WinADV32 (version 2.027, Department of the Interior, USA). The latter measurements were taken on a different date from which the larval releases were taken.

[12] Based on the ADV measurements, we calculated the turbulence intensity as a measure of the magnitude of turbulence. The root mean square of the velocity ( $U_{\text{rms}}$ ), was normalized by the mean velocity to obtain the turbulence intensity ( $TI = U_{\text{rms}} U^{-1}$ ). The bed shear stress ( $\tau_b$ ), which provides an estimate of the near bed turbulence, was determined using a turbulent kinetic energy method (TKE) recommended for complex flow fields (Biron et al. 2004), which assumes a linear relationships between TKE and the variances given by

$$\tau_b = C_2 \rho \langle w'^2 \rangle \quad (1)$$

where  $C_2$  is 0.9 (cf. Kim et al. 2000),  $\rho$  is the water density ( $998.2 \text{ kg m}^{-3}$  at  $20^\circ\text{C}$ ), and  $\langle \rangle$  represents the temporal average. The advantage of this approach is that instrument noise errors for fluctuations in  $w$  are considerably smaller than those for  $u$  in the streamwise direction (Kim et al. 2000). The ADV measurements at  $0.1H$  were used in Eq. 1. The shear velocity  $u_*$  was determined from the relationship with  $\tau_b$ :

$$\tau_b = \rho u_*^2. \quad (2)$$

### Obtaining and Staining of Glochidia

[13] Gravid females of *A. ligamentina* were collected from the Thames River, Ontario, and *L. fasciola* from the Grand River (under the Ontario Ministry of Natural Resources [OMNR] license no. 1045920 and Species at

Risk Act [SARA]: SECT 08 SCI 004) and held at 10 °C in a recirculating water system (see Schwalb et al. 2010 for details). Glochidia were obtained from gravid females by flushing the gills with water from a syringe. The glochidia were stained with Rose Bengal (50 mg L<sup>-1</sup>) for 48 h to facilitate identification under the microscope as drift samples had a high sediment load. Glochidia were killed by the staining process, which does not have a significant effect on their  $w_s$  (Schwalb et al. 2010). In addition, glochidia of *A. ligamentina* obtained from the Thames River were placed in ethanol after staining to ensure that no foreign glochidia were introduced alive into the watershed (required by OMNR). Freshly extracted glochidia were used in the experiments, except for 6 trials in 2009, when dead glochidia stored in ethanol were used because gravid *A. ligamentina* were not available. Between 29,000 and 47,000 glochidia of *A. ligamentina*, which corresponds to the contents of 1–2 water tubes (compartments in gills) of a gravid female, were released per trial. The number of glochidia ranged between 21,000 and 34,000 per trial for *L. fasciola*.

#### Downstream Transport Experiments

[14] Downstream transport experiments were carried out on 6 dates between late July and early October 2008, and on one date in August 2009 (OMNR, license no. 1045953). Drift nets (45 cm wide × 30 cm high; 100- $\mu$ m mesh size) were deployed on the river bottom at 4, 8, 16, 32, 48, and 64 m downstream in line with the principal flow direction, which was determined using the water-filled bottle (see above). The mesh was small enough to capture all glochidia given the shell length of *A. ligamentina* (200–230  $\mu$ m) and *L. fasciola* (230–260  $\mu$ m) glochidia. The nets usually extended from the bottom to (or  $\sim$  5 cm above) the water surface for nets at 4 and 8 m, and to the water surface and up to 30 cm below the water surface farther downstream.

[15] Ideally, the drift nets would have been placed in the middle of the river; however, the unusually high water velocity and depth in 2008 (data provided by GRCA) precluded their placement. The drift nets were placed closer to the shore within 1.3–3.0 m of the shoreline ( $Q = 22.2\text{--}23.4\text{ m}^3\text{ s}^{-1}$ ) and up to 2.9–3.8 m ( $Q = 17.3\text{--}17.6\text{ m}^3\text{ s}^{-1}$ ) depending on  $Q$ . In 2009, nets were placed 4.1–5.7 m from the shore ( $Q = 12.4\text{--}$

$13.3\text{ m}^3\text{ s}^{-1}$ ). Glochidia were released at  $z_r \sim 30$  cm above the bottom (usually 2–5 cm below the water surface) using a 60-ml syringe pointing downstream, except on 29 July 2008, when glochidia were released at  $z_r \sim 20$  cm due to low water depth at the release point. A few min after the release (2–10 min, depending on  $x$  and  $U$ ), the drift nets were retrieved and rinsed to obtain all captured glochidia. This process was repeated for all trials. Drift samples were stored in a cold room (4 °C), sieved through a 500- $\mu$ m mesh within 72 h to remove large debris (e.g., leaf fragments), and stored in 70% ethanol. The number of stained glochidia in each sample was counted under a microscope.

[16] The effect of  $w_s$  on downstream transport was examined by comparing the transport of glochidia of *A. ligamentina* and *L. fasciola*, which have different  $w_s$  (see below). The releases were undertaken sequentially with *A. ligamentina* preceding *L. fasciola* to ensure that conditions were as similar as possible (i.e., within 30–60 min). This design was also used to examine the effect of  $z_r$  on transport distance in 2009, which involved a trial conducted at  $z_r \sim 30$  cm followed by one at  $z_r \sim 5$  cm (3 trials for each  $z_r$ ).

[17] The relative importance of  $w_s$  compared to turbulent mixing for dispersion of the glochidia was determined using the dimensionless Rouse number ( $R = w_s [u_* \kappa]^{-1}$ , where  $\kappa$  is the von Kármán constant,  $\sim 0.4$ ). As velocity could not be controlled, the effect of velocity on downstream transport was examined a posteriori using correlation analysis. We examined whether (1)  $U$  at the release point ( $U_{0m}$ ), (2)  $U$  at the drift net locations (4–64 m), (3) the average  $U$  for all drift net locations (0–64 m), and (4) the surface velocity ( $U_s$ , determined from a water filled bottle) were related to the slope of the regression of  $\ln(\text{glochidia captured})$  versus  $\ln(\text{distance downstream})$ .

[18] Particulates transported downstream are also dispersed by lateral diffusion, leading to lateral variation in the downstream drifting “cloud” (Hemond and Fechner-Levy 2000). The magnitude of the lateral variation in the study reach was examined in 4 trials on 28 August 2008 in which 5 drift nets were placed perpendicular to the principal flow direction at  $x = 32$  m downstream. The central net was placed in the assumed main flow path, 2 nets were placed 1 and 3 m toward midstream,

and 2 nets were placed 1 and 2 m toward the shore.  $H$  ranged from 25 cm for the net closest to the shore to 66 cm for the net closest to midstream. For this analysis, the percentage of captured glochidia in each drift net was normalized by the fraction of  $H$  sampled by the drift net (height of net  $H^{-1}$ , with  $\max = 1$ ) to account for potential differences in  $H$ .

[19] Lateral ( $K_y$ ) and vertical diffusivity ( $K_z$ ) were estimated (Fischer et al. 1979) as

$$K_y = B_y H u_* \quad (3a)$$

and

$$K_z = \frac{\kappa}{6} H u_* \quad (3b)$$

where  $B_y$  is an empirical coefficient = 0.6 for natural channels (Hemond and Fechner-Levy 2000). Based on  $K_z$ , the distance over which particles released from a point source at mid-depth become well mixed (i.e., 98%) in the vertical direction can be estimated as

$$x = 0.134 \frac{U H^2}{K_z}, \quad (4)$$

whereas the distance is 4 times larger when the point source is at the bottom or the surface (i.e.,  $x = 0.536 U H^2 K_z^{-1}$ ; Rutherford 1994). Estimates of the characteristic length scales for the cloud of particles in the lateral direction is given by the standard deviation ( $\sigma_y$ ):

$$\sigma_y = \sqrt{2K_y \frac{x}{U}}. \quad (5)$$

[20] Observed glochidia capture was also compared with values predicted by a 3D advection–diffusion model (Fischer et al. 1979), which models the distribution of concentration  $C$  downstream of an instantaneous release at time  $t$ :

$$C(x, y, z, t) = \frac{M}{(4\pi t)^{3/2} (K_x K_y K_z)^{1/2}} \times \exp \left[ \left( \frac{x^2}{4K_x t} \right) - \left( \frac{y^2}{4K_y t} \right) - \left( \frac{z^2}{4K_z t} \right) \right] \quad (6)$$

where  $M$  is the mass released (average of 30,000 glochidia released),  $K_y$  and  $K_z$  were determined from Eqs. 3a and 3b, and  $K_x$  is the longitudinal diffusivity, which can

be determined using Elter's analysis of a logarithmic velocity profile and an approximate procedure for real streams (Fischer et al. 1979), given respectively by

$$K_x = 5.93 H u_* \quad (7a)$$

and

$$K_x = 0.011 U^2 W^2 / H u_* \quad (7b)$$

In this case, the average values for  $H$  (= 40 cm) and  $U$  (= 40 cm s<sup>-1</sup>) were used, and  $W$  (channel width) was 50 m. In order to predict glochidia capture based on Eq. 6, we focused on  $y = 0$  (for the center of the plume) and calculated  $C$  for each downstream net location (4, 8, 16, 32, 48, and 64 m) from  $z = 0.05$  to 0.3 m (net height; in increments of 5 cm) for  $t = 600$  s (the period the nets were in the water; in increments of 1 s). The predicted number of glochidia in each net was based on the product of the integration of  $C(z, t)$  and the volume of water sampled (area of net opening  $\times U$ ).

#### Statistical Analysis

[21] The number of glochidia captured in each drift net was expressed as a percentage of the number of glochidia released per trial. To examine how well larval transport can be described with a power function (Elliott 2003), linear regressions were undertaken using ln-transformed data; i.e., the distance of each drift net downstream of the release point was transformed with  $\ln(x)$ , as was the proportion of glochidia captured.

[22] Differences in glochidia capture rates under different  $w_s$  and  $z_r$  were assessed with a paired  $t$ -test by comparing (1) the slope coefficients determined from a linear regression ( $\ln[\text{glochidia captured}]$  vs.  $\ln[x]$ ) between sequential trials (i.e., trial with *A. ligamentina* followed by trial with *L. fasciola*), and (2) glochidia capture between sequential trials with  $z_r = 30$  versus 5 cm. The slope coefficients were also used to examine the relationship between glochidia capture and mean velocity.

## Results

### Settling Velocity of Glochidia

[23] The settling velocity ( $w_s$ ) of *L. fasciola* glochidia was 2.5 times higher than that of *A. ligamentina* ( $w_s = 2.2 \pm 0.02$  [mean  $\pm$  SE] mm s<sup>-1</sup>,  $n = 33$  vs.

$0.87 \pm 0.02 \text{ mm s}^{-1}$ ,  $n = 34$ ; Welch  $t_{51} = 36.7$ ,  $p < 0.001$ ; data for *A. ligamentina* from Schwalb et al. 2010).

#### Hydrodynamic Characteristics of the Study Reach

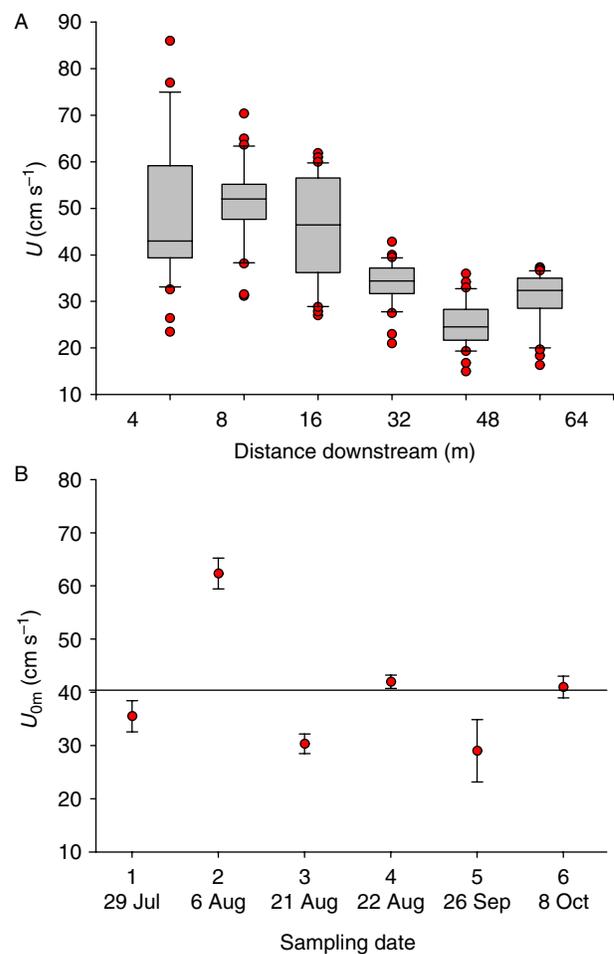
[24] Experiments were undertaken in a riffle area with subcritical, turbulent flow conditions based on a channel  $Re = 1.6 \times 10^5$  and an  $Fr = 0.2$  based on an average  $U = 40 \pm 1 \text{ cm s}^{-1}$  and an average  $H = 40 \pm 2 \text{ cm}$ . The bottom profile showed relatively large bottom roughness and varied considerably along the 70-m transect with a mean difference in elevation (maximum depth – measured depth) of  $23 \pm 8 \text{ cm}$  (mean  $\pm$  SD; Fig. 1), where the deepest point on the profile ( $H_{\text{max}}$ ) at 25 m downstream was taken as  $z = 0$ . Roughness elements were primarily angular cobbles ( $14.2 \pm 0.5$  [mean  $\pm$  SE]  $\text{cm} \times 10.7 \pm 0.4 \text{ cm} \times 7.0 \pm 0.3 \text{ cm}$ ,  $n = 61$ ) and protruded several centimeters above the bottom into the flow. The median particle diameter ( $d_{50}$ ) was 10.8 cm, and the relative roughness of the reach ( $d_{50} H^{-1}$ ) was 0.27. The flow conditions were hydraulically rough based on the roughness Reynolds number ( $Re_* = 430$ ), indicating that the roughness elements affected the flow outside the roughness sublayer (Stoesser et al. 2004).

[25] Hourly discharge ( $Q$ ) data obtained from the GRCA varied between  $13.1$  and  $25 \text{ m}^3 \text{ s}^{-1}$  during the 2008 trials;  $Q$  was  $12.4 \text{ m}^3 \text{ s}^{-1}$  during the trials in 2009, but there was a poor relationship with measurements of  $U$  (e.g.,  $r = 0.17$ ,  $p = 0.75$ , for daily averages of  $U_{0\text{m}}$  vs.  $Q$ ). Mean velocities ( $U$ ) varied among net locations and decreased with  $x$  ( $U = [51.1 \pm 1.2] - [0.41 \pm 0.03] x$ ,  $R^2 = 0.42$ ,  $p < 0.001$ ,  $n = 186$ ; Fig. 2A).  $U$  also varied among days, and  $U_{0\text{m}}$  was lower than the average  $U_{0\text{m}}$  (i.e.,  $< 40.5 \text{ cm s}^{-1}$ ) on sampling days 1, 3, and 5 and higher than the average on sampling days 2, 4, and 6 (Fig. 2B).

#### Turbulence Measurements

[26] Measurements of water-column and near-bed turbulence were obtained under similar discharge of  $Q \sim 13 \text{ m}^3 \text{ s}^{-1}$  ( $Q = 13.2 \text{ m}^3 \text{ s}^{-1}$  on 28 August 2008 and  $Q = 13.6 \text{ m}^3 \text{ s}^{-1}$  on 22 October 2008, respectively), which represent the lower end of the range measured during the 2008 and 2009 experiments. Consequently, these estimates of turbulence may be relatively conser-

vative. The velocity measured at  $0.4H$  at  $x = 0, 4, 8, 16, 24,$  and  $32 \text{ m}$  downstream varied considerably in all directions ( $u$ ,  $v$ , and  $w$  in the downstream, lateral, and vertical directions, respectively), and the average  $U$  was  $54 \pm 6 \text{ cm s}^{-1}$  (Table 1A). The turbulence intensity ( $TI = U_{\text{rms}} U^{-1}$ ) was on average  $0.17 \pm 0.02$  ( $n = 6$ ; Table 1A). The variation in velocity was similar for measurements obtained at  $0.1H$  (Table 1B), but the magnitude was lower, where the average  $U$  was  $20 \pm 3 \text{ cm s}^{-1}$ . Based on estimates of TKE and  $\langle w'^2 \rangle = 2.9 \pm 0.9 \times 10^{-3} \text{ m}^2 \text{ s}^{-2}$  ( $n = 4$ ) at  $0.1H$ , the bed shear stress ( $\tau_b$ )



**Fig. 2** A — Downstream velocity ( $U$ ) at different distances downstream ( $x$ ) measured on 6 sampling days involving 31 dispersal trials. The boundaries of the box plot indicate the 25th and 75th percentiles, and the whiskers the 10th and 90th percentiles; points indicate outliers; and the line in the box marks the median. B —  $U$  at the release point ( $U_{0\text{m}}$ ) on different sampling dates; the line represents the average  $U$  at this distance.

**Table 1** Velocity and hydrodynamic parameters measured in downstream ( $u$ ), lateral ( $v$ ), and vertical ( $w$ ) direction in the Grand River, Ontario. Velocity was measured using an acoustic Doppler velocimeter at 25 Hz. A — Results from 28 August 2008 involving 2-min samples ( $n = 6$ ); measurements were taken at 0.4 water depth ( $H$ ) at downstream distances of  $x = 0, 4, 8, 16, 24,$  and  $32$  m. B — Results from 22 October 2008 involving 1-min samples; measurements were taken at  $0.1H$ .

A		Velocity magnitude $\pm$ RMS ( $\text{cm s}^{-1}$ )		Turbulence intensity ( $U_{\text{rms}}U^{-1}$ )	
Velocity component	Velocity mean $\pm$ SE ( $\text{cm s}^{-1}$ )	Min	Max		
$U$	$54 \pm 6$	$36 \pm 6$	$78 \pm 11$	$0.17 \pm 0.02$	
$V$	$3 \pm 3$	$-4 \pm 10$	$15 \pm 8$	—	
$W$	$-3 \pm 1$	$-0.04 \pm 3.4$	$-5 \pm 7$	—	
B					
Distance (m)	$u \pm u_{\text{RMS}}$ ( $\text{cm s}^{-1}$ )	$v \pm v_{\text{RMS}}$ ( $\text{cm s}^{-1}$ )	$w \pm w_{\text{RMS}}$ ( $\text{cm s}^{-1}$ )	Bed shear stress $\pm$ 95% CI (Pa)	Shear velocity ( $\text{cm s}^{-1}$ )
0	$20 \pm 9$	$4 \pm 9$	$0.4 \pm 6.1$	$3.34 \pm 0.25$	5.8
16	$24 \pm 11$	$17 \pm 14$	$-1.3 \pm 7.0$	$4.42 \pm 0.31$	6.7
32	$22 \pm 8$	$38 \pm 8$	$3 \pm 5$	$2.08 \pm 0.16$	4.6
48	$12 \pm 4$	$2 \pm 5$	$0.3 \pm 2.4$	$0.5 \pm 0.04$	2.2
Mean $\pm$ SE	$20 \pm 3$	$6 \pm 4$	$1 \pm 1$	$2.6 \pm 0.8$	$4.8 \pm 1.0$

was  $2.6 \pm 0.8$  Pa ( $n = 4$ ), which corresponded to a shear velocity ( $u_*$ ) of  $5 \pm 1$   $\text{cm s}^{-1}$  ( $n = 4$ ; Table 1B).

#### Downstream Capture of Glochidia

[27] The number of glochidia that were captured in the nets declined downstream, although the shape of this relationship differed with river velocity ( $U$ ) on the day of sampling (Fig. 3A–D). Specifically, on days 2, 4, and 6 (Fig. 3B,D) the downstream decline in glochidia capture was well described with an inverse power function ( $R^2 = 0.84$ – $0.92$ ; Fig. 3B,D). The average river velocity at the release position ( $U_{0\text{m}}$ ) on these days ( $U_{0\text{m}} = 48 \pm 7$   $\text{cm s}^{-1}$ ) was higher than the overall average  $U_{0\text{m}}$  for all sampling days ( $40.5 \pm 2.4$   $\text{cm s}^{-1}$ ). On days 1, 3, and 5, when the average  $U_{0\text{m}}$  was much lower ( $U_{0\text{m}} = 32 \pm 2$   $\text{cm s}^{-1}$ ), the relationship was much weaker ( $R^2 = 0.60$ – $0.70$ ; Fig. 3A,C). Importantly, differences in  $U_{0\text{m}}$  among dates did not affect the overall average water depth ( $H$ ) for all drift nets, which was reasonably similar on all days ( $40 \pm 2$  cm; range, 35–45 cm on day 6 vs. day 2).

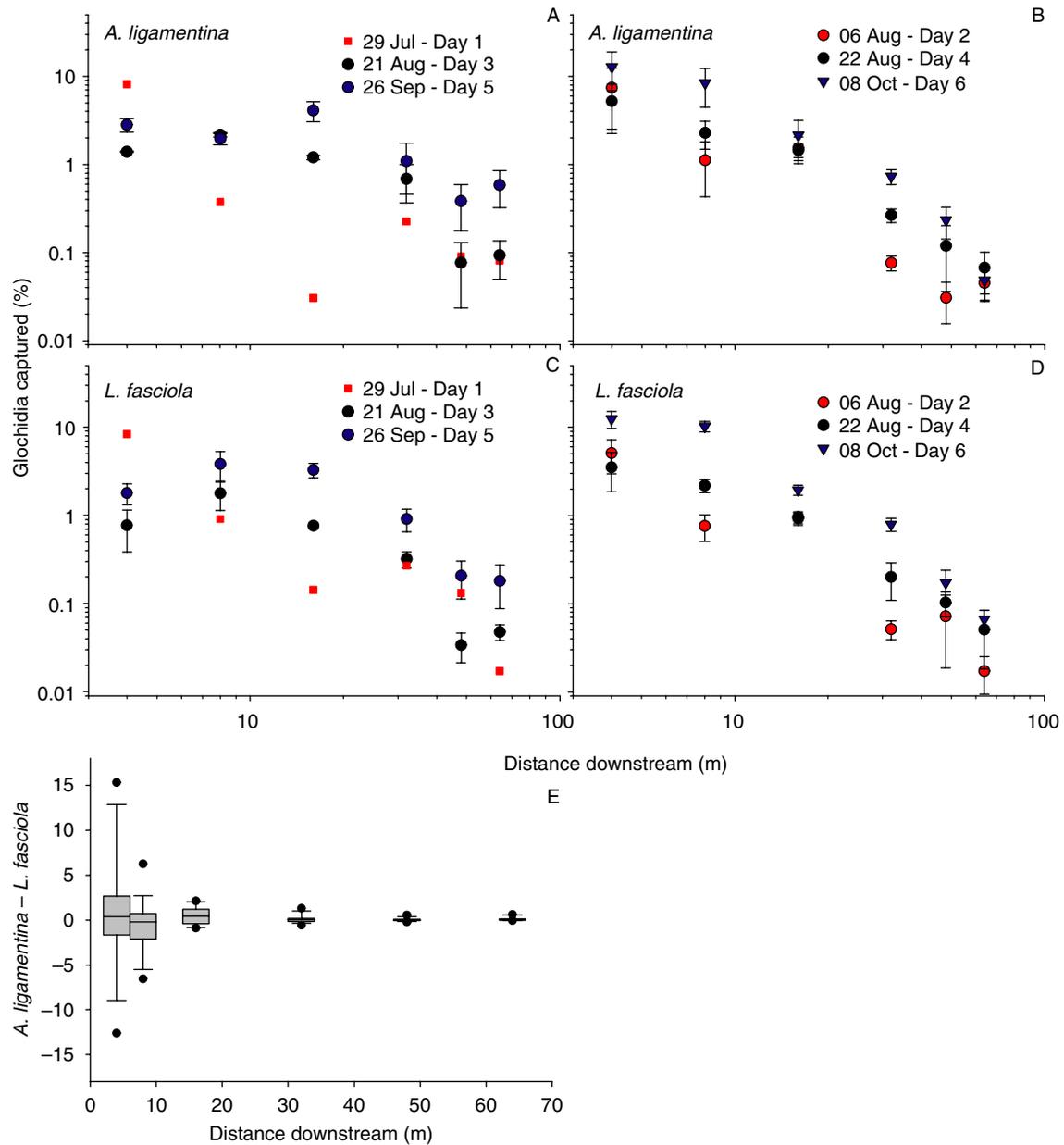
[28] As indicated above (Fig. 3A–D), the percentage of glochidia captured declined logarithmically with downstream distance, and  $\ln(x)$  explained  $>50\%$  of the variation in  $\ln(\text{glochidia capture})$  for both *A.*

*ligamentina* and *L. fasciola* ( $R^2 = 0.51$ ,  $p < 0.001$ ,  $n = 90$  and  $R^2 = 0.58$ ,  $p < 0.001$ ,  $n = 96$ , respectively). A relationship between glochidia capture and  $U$  was revealed in the negative correlation between the slope coefficients from the linear regression of  $\ln(\text{captured glochidia})$  versus  $\ln(x)$  and  $U_{0\text{m}}$  ( $r = -0.61$ ,  $p < 0.001$ ,  $n = 31$ ; Fig. 4) as well as  $U_s$  ( $r = -0.60$ ,  $p = 0.02$ ,  $n = 15$ ; no significant correlation was found with the other measures of  $U$ ). This indicates that the higher the  $U$ , the steeper the slope and the stronger the decline in glochidia capture with  $x$ .

[29] Significant differences were not detected between the slope coefficients obtained from linear regression of  $\ln(\text{captured glochidia})$  versus  $\ln(x)$  of sequential trials of *A. ligamentina* and *L. fasciola* (paired  $t$ -test,  $t_{16} = 0.02$ ,  $p = 0.99$ ). The median differences in percentage of glochidia captured were small and ranged from  $-0.2\%$  and  $-7.8 \times 10^{-3}\%$  at  $x = 8$  and 48 m, respectively, to  $0.02\%$ – $0.42\%$  at  $x = 4, 16, 32,$  and 64 m (Fig. 3E).

#### Lateral and Vertical Dispersion of Glochidia

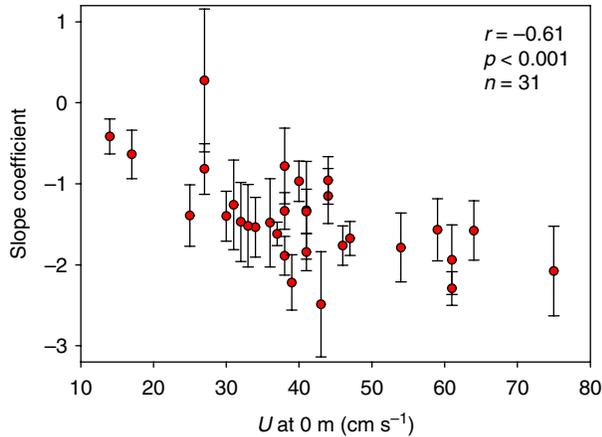
[30] The Rouse number ( $R$ ) based on the  $w_s$  of glochidia and measured friction velocity ( $u_*$ ) was less than unity ( $R = 0.04$  for *A. ligamentina*;  $R = 0.11$  for *L. fasciola*),



**Fig. 3** Percentage of glochidia captured (number of glochidia captured per number of glochidia released  $\times$  100) at different distances downstream for *Actinonaias ligamentina* (A, B) and *Lampsilis fasciola* (C, D) on 6 sampling dates (mean  $\pm$  SE). The sample size of  $n = 2$  was too low to calculate SE for day 1 (29 July 2008). Sampling dates where the velocity at the release point ( $U_{0m}$ ) was less than the average  $U$  ( $40.5 \text{ cm s}^{-1}$ ; days 1, 3, 5) were plotted separately (left panels) from sampling dates with  $U_{0m} > 40.5 \text{ cm s}^{-1}$  (days 2, 4, 6; right panels). E — Differences between subsequent trials of *A. ligamentina* and *L. fasciola* ( $n = 17$ ). Box plots represent the difference of glochidia captured at the same distance between subsequent trials (e.g., [trial for *A. ligamentina* at 4 m] - [trial for *L. fasciola* at 4 m]).

which indicated the importance of turbulence in the transport of glochidia. The lateral diffusivity ( $K_y$ ) of the reach was  $1.2 \times 10^{-2} \text{ m}^2 \text{ s}^{-1}$  given  $H = 0.40 \text{ m}$  (Eq. 3a), which provided an estimate of  $\sigma_y = 1.4 \text{ m}$  at  $x = 32 \text{ m}$  given  $U \sim 0.40 \text{ m s}^{-1}$  (Eq. 5). Of the captured glochidia, 80%–94% were found within  $\pm 1 \text{ m}$  from

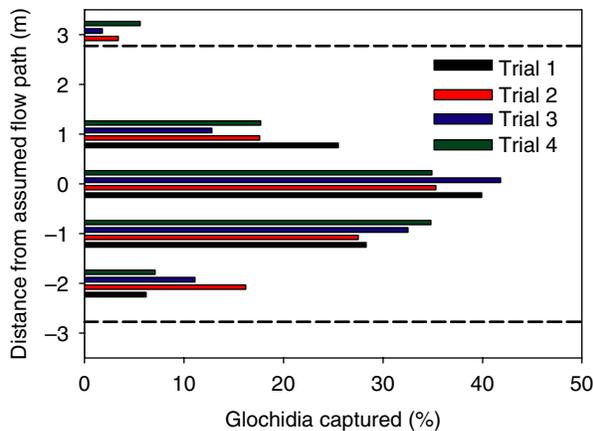
the assumed flow path indicated by the water-filled bottle, with a small percentage captured 2 and 3 m away, which was within a 95% limit defined statistically by  $\pm 2\sigma_y$  (Fig. 5). The highest percentage of glochidia (35%–42%) was captured in the central net, and 13%–35% was captured at  $\pm 1 \text{ m}$  (Fig. 5). About twice



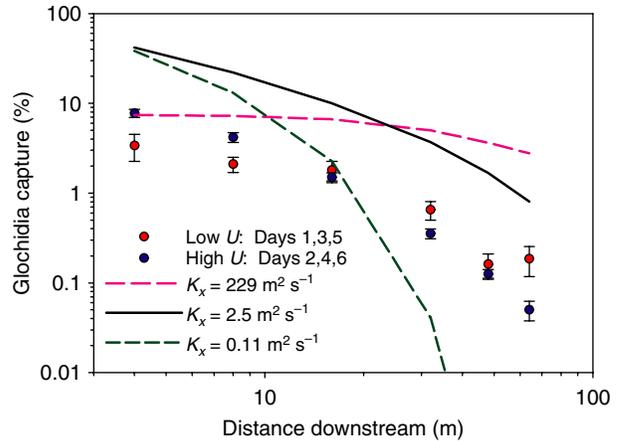
**Fig. 4** Relationship between velocity at the release point ( $U_{0m}$ ) and the slope coefficients ( $\pm$  SE) from a regression of  $\ln(\text{captured glochidia})$  versus  $\ln(x)$ .

as many glochidia were captured in the net 1 m closer to the shore relative to the net 1 m closer to midstream.

[31] The pattern of glochidia capture with distance downstream ( $x$ ) predicted by the 3D advection–diffusion equation (Eq. 6) depended on the choice of the longitudinal diffusivity ( $K_x$ ). A  $K_x = 0.11 \text{ m}^2 \text{ s}^{-1}$  (Eq. 7a) overestimated the decline in glochidia capture downstream, indicated by a larger exponent in an exponential fit to the data (glochidia capture =  $260 e^{-0.31x}$ ,  $R^2 = 0.94$ ,  $p < 0.01$ ), which was smaller using the data from days 1, 3, and 5 or days 2, 4, and 6 (glochidia capture (%) =  $3.6 e^{-0.05x}$ ,

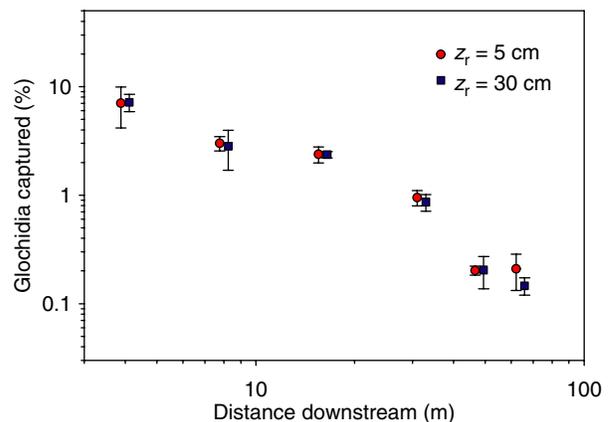


**Fig. 5** Capture of glochidia in 5 nets oriented lateral to the flow direction at  $x = 32 \text{ m}$  downstream of the release point. The proportion of glochidia is based on the quotient of glochidia captured in one net and the total number of glochidia captured at that distance and date. Negative distances are closer to the shore than positive distances. Dashed lines indicate  $\pm 2\sigma_y$ , the theoretical value for the region where 95% of glochidia should be found in a natural channel.



**Fig. 6** Measured (symbols; mean  $\pm$  SE) and predicted (lines) glochidia capture based on a 3-dimensional advection diffusion model for different values of  $K_x$ . The predicted values for glochidia capture for  $K_x = 0.11 \text{ m}^2 \text{ s}^{-1}$  (Eq. 7a) were  $< 0.01$  for  $x > 32 \text{ m}$ .

$R^2 = 0.93$ ,  $p < 0.01$  and glochidia capture =  $7.4 e^{-0.08x}$ ,  $R^2 = 0.98$ ,  $p < 0.01$ , respectively; Fig. 6). Conversely,  $K_x = 229 \text{ m}^2 \text{ s}^{-1}$  (Eq. 7b) underestimated the decline in glochidia capture indicated by a smaller exponent in the exponential fit (glochidia capture =  $8.3 e^{-0.02x}$ ,  $R^2 = 0.94$ ,  $p < 0.01$ ; Fig. 6). The best linear relationship between predicted and observed glochidia capture was found using  $K_x = 2.5 \text{ m}^2 \text{ s}^{-1}$  ( $R^2 > 0.99$ ,  $p < 0.001$  for days 2, 4, 6 and  $R^2 = 0.92$ ,  $p < 0.01$  for days 1, 3, and 5), which predicted  $\sim 10$ -fold higher capture overall ( $4\text{--}12\times$  for days 1, 3, and 5, and  $5\text{--}16\times$  for days 2, 4, and 6; Fig. 6). The predicted glochidia capture per-



**Fig. 7** Proportion of glochidia (number of glochidia captured per number of glochidia released  $\times 100$ ) captured at different distances downstream for release heights of  $z_r = 5 \text{ cm}$  ( $n = 3$ ) and  $z_r = 30 \text{ cm}$  ( $n = 3$ ). Data points at the same distance were separated for better visibility.

centage decreased  $\sim 3$ -fold if either the lateral ( $K_y$ ) or vertical diffusivity ( $K_z$ ) was increased 10-fold. Clearly, turbulence has a large effect on the predicted dispersion and capture of glochidia.

[32] Based on  $K_z = 1.3 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}$  given  $H = 0.40 \text{ m}$  (Eq. 3b), the particles should become well mixed vertically at  $x = 7 \text{ m}$  and at  $x = 27 \text{ m}$  if they were released at the bottom or the surface (Eq. 4). The observed number of glochidia captured was similar for both release heights ( $z_r = 30$  and  $5 \text{ cm}$ ) at all distances (Fig. 7). No significant difference in glochidia capture was detected between subsequent trials of  $z_r = 30 \text{ cm}$  and  $z_r = 5 \text{ cm}$  (paired  $t$ -test,  $t_2 = -1.2$  to  $0.07$ ,  $p = 0.34\text{--}0.98$ ).

### Discussion

[33] The dispersion of mussel larvae in rivers appears to be strongly affected by hydrodynamic conditions. The effect of hydrodynamics was indicated by a sharper decline in glochidia capture with distance at higher velocities ( $U$ ) in the Grand River (Figs. 3, 4). This is in contrast to previous findings in the Sydenham River (Ontario) that indicated that larval transport distances increased with  $U$  (Schwalb et al. 2010) and where the slope from the regression of  $\ln(\text{captured glochidia})$  versus  $\ln(x)$  ( $-1.1 \pm 0.1$ ; Schwalb et al. 2010) was significantly smaller compared to the Grand River ( $-1.5 \pm 0.1$ ,  $t_{35} = 2.7$ ,  $p < 0.01$ ). This difference may have been due to greater dispersion of the drifting glochidia cloud caused by greater turbulence in the Grand River (Table 1;  $K_y = 1.2 \times 10^{-2} \text{ m}^2 \text{ s}^{-1}$ ,  $K_z = 1.3 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}$ , channel  $Re \sim 1.6 \times 10^5$ , and average  $U \sim 40 \text{ cm s}^{-1}$  vs. Sydenham River  $K_y = 4.3 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}$ ,  $K_z = 4.8 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ , channel  $Re \sim 6 \times 10^4$  and average  $U \sim 15 \text{ cm s}^{-1}$ ; Schwalb et al. 2010). This statement is supported in part by the predictions of an advection–diffusion model (Eq. 6), which demonstrated that the pattern of relative glochidia capture could be predicted with reasonably high levels of turbulence. In this case, the pattern was less sensitive to changes in  $K_y$  and  $K_z$  and more sensitive to changes in  $K_x$ , as would be expected (Fischer et al. 1979). Interestingly, the  $K_x$  level that provided the best fit to the data was closer to the estimate based on Eq. 7a than the model presented for real streams.

[34] The decline of glochidia with distance fit an inverse power function on days when the average  $U_{0m}$  was  $> 40 \text{ cm s}^{-1}$ . This is in contrast to glochidia dispersal in the Sydenham River mentioned above and the dispersal of macroinvertebrates, which showed a near-perfect fit with an inverse power function with  $U = 4\text{--}35 \text{ cm s}^{-1}$  (Elliott 2003).

[35] Differences in  $w_s$  of glochidia *A. ligamentina* and *L. fasciola* did not result in detectable differences in downstream transport (Fig. 3), which is in contrast to predictions from the simple model ( $x = U z_r w_s^{-1}$ ) that glochidia of *A. ligamentina* would encounter the bottom 2.5 times farther downstream than those of *L. fasciola*. Although the  $w_s$  of *A. ligamentina* glochidia were 2.5 times slower than those of *L. fasciola*, the size of its glochidia was only 0.8 times smaller. This is not surprising because  $w_s$  increases with the square of the particle radius and the excess density according to Stokes's law (Vogel 1994). It is possible that larger differences in the size of glochidia than the ones examined in this study could lead to detectable differences in the downstream transport of glochidia. For example, a recent genetic study indicated that interpopulation genetic distances of *Quadrula pustulosa* increased with geographic distance but not for *Quadrula quadrula* (Levine et al. 2009), which have glochidia that are  $\sim 3$  times smaller (Barnhart et al. 2008). Both species should have similar dispersal abilities via their host based on reported host fishes (Schwalb et al. 2011). Thus, it is possible that the higher  $w_s$  of *Q. pustulosa* could lead to lower transport distance and may have contributed to lower connectivity and the higher genetic differentiation reported by Levine et al. (2009).

[36] Both water column and near-bed turbulence may have mitigated the differences in downstream transport due to  $w_s$ , as indicated by Rouse numbers  $\leq 0.1$ . The velocities and water depths examined here were comparable to those examined by Roy et al. (2004), who found large-scale turbulent flow structures in a gravel-bed river, although the conditions in the present study may have had higher near-bed turbulence due to the 2-fold larger  $d_{50}$ . It is likely that the bed roughness was partly responsible for the turbulent pattern as the roughness elements (cobble) in the Grand River had an angular shape that extended several centi-

meters into the flow ( $Re_* = 430$ ; Fig. 1). In contrast, the Sydenham River had roughness elements that consisted of flat disk-shaped or tabulate stones protruding only a few centimeters into the flow (Fig. 1; Schwalb et al. 2010) and had a lower  $Re_* = 150$  (A. N. Schwalb, unpublished data). The magnitude of the turbulence in the Grand River indicated by the turbulence intensity ( $TI$ ; Table 1A) supports this assertion as it was similar to what has been reported for other cobble-bed rivers with similar bed roughness ( $d_{50} = 8.5\text{--}11.8$  cm; Stone and Hotchkiss 2007) but was higher than a gravel-bed channel with lower bed roughness ( $d_{50} = 2$  cm; Carollo et al. 2005).

[37] The rough bottom also led to high near-bed turbulence indicated by the bed shear stress ( $\tau_b$ ). Such  $\tau_b$  could lead to resuspension of glochidia after their initial contact with the river bottom and in so doing transport them farther downstream (Daraio et al. 2010a). Whereas we do not have empirical values of critical  $\tau_b$  needed to resuspend glochidia (i.e., Shields parameter), the  $\tau_b$  measured here were up to 50 times higher than the theoretical critical  $\tau_b$  needed to resuspend particles of the size and density of juvenile mussels (Daraio et al. 2010a). Importantly, resuspension is most likely to occur when near-bed flow conditions are highly turbulent and eddies formed behind one roughness element interact with an eddy formed in front of the next one, and it is less likely when roughness elements are so close together that flow skims over the roughness elements (Vogel 1994). Both scenarios are possible in a cobble-bed river (Davis and Barmuta 1989). However, resuspension would more likely play a role for longer-term downstream transport and may be less applicable here, since drift nets were only deployed for 2–10 min (i.e., the time needed to travel to the nets).

[38] We did not detect differences in glochidia capture from different release heights ( $z_r$ ), even though the simple transport model predicted a 6-fold difference in downstream transport. However, based on  $K_z$ , any potential differences due to a 25-cm difference in  $z_r$  would diminish relatively quickly downstream, and given our low sample size ( $n = 3$  comparisons) it is difficult to draw definitive conclusions. Nonetheless, a hydrodynamic model of juvenile mussel dispersal in the

Mississippi River suggested that a difference in  $z_r$  can have a major effect on transport distance depending on local hydrodynamic conditions ( $H \sim 2$  m; mean annual  $Q \sim 2000$  m<sup>3</sup> s<sup>-1</sup>; Daraio et al. 2010b).

[39] Clearly, turbulence has an important effect on glochidia dispersion, which makes it difficult to predict transport distances (McNair and Newbold 2001). In the situation examined here, the effect of bottom turbulence ( $u_*\kappa$ ) was larger than the settling of the glochidia ( $w_s$ ; i.e., Rouse numbers,  $R \leq 0.1$ ), which has also been observed for larval settlement in laboratory flow chambers (Hendriks et al. 2006). This result likely applies to other small organisms and particles with low excess density and  $w_s$  in turbulent waters with  $R \ll 1$ , such as river plankton, fine particulate organic matter, and juvenile unionid mussels after they detach from their host fish (Cushing et al. 1993; Daraio et al. 2010a, 2010b). However, turbulence appears to have less of an effect on the dispersion of larger macroinvertebrates, such as blackfly larvae, with higher excess density and  $w_s$  whose  $R > 1$  in similarly turbulent flows (i.e.,  $u_* = 0.05$  m s<sup>-1</sup>; Fonseca 1999). It is evident that further empirical study of the effects of turbulence on the dispersion of unionid mussel larvae and other organisms is needed.

#### *Significance to Aquatic Environments*

[40] The biology of many stream organisms involves a dispersal stage, which in the case of freshwater unionid mussels is a glochidia larva that is a parasite of fish. Prior to attachment to their host fish, many glochidia are dispersed in the downstream flow. One of the central problems in dispersal ecology is predicting how hydrodynamics will affect glochidia transport, and related to this issue is the question of how far they will be transported. We examined how the settling velocity of 2 species of unionid mussels affected their transport in the Grand River, Ontario.

[41] The results demonstrated that glochidia transport was affected by the river's velocity, especially under high velocities where the decline in glochidia capture matched closely with the dispersal of stream macroinvertebrates (Elliott 2003). We were unable, however, to detect differences in larval transport related to the 2.5-fold difference in settling velocity of the 2

species. We assert that this latter result was related to the high water column and near-bed turbulence, which redirected the larvae to the riverbed. Turbulence has been shown to affect the transport of particles such as macroalgal spores (McNair and Newbold 2001; Gaylord et al. 2002). For example, under strong turbulence caused by rapid currents and large waves, the dispersal distances of macroalgal spores depended primarily on current velocities, whereas under less turbulent conditions, differences in settling velocity had a stronger effect on dispersal distances (Gaylord et al. 2002). It is likely that the characteristics of the biological particle (e.g., settling velocity, difference in density between the particle and the water) will determine in part how strongly it is affected by turbulence. Dense and fast-settling particles are likely to be less affected than less-dense and slow-settling particles such as glochidia larvae. The modulating effect of turbulence on biological parameters should be considered when studying transport and dispersal of organisms/propagules in aquatic systems.

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## References

- Arnold, W. S., G. L. Hitchcock, M. E. Frischer, R. Wanninkhof, and Y. P. Sheng. 2005. Dispersal of an introduced larval cohort in a coastal lagoon. *Limnol. Oceanogr.* **50**: 587–597, doi:10.4319/lo.2005.50.2.0587.
- Barnhart, M. C., W. R. Haag, and W. N. Roston. 2008. Adaptations to host infection and larval parasitism in Unionoida. *J. N. Am. Benthol. Soc.* **27**: 370–394, doi:10.1899/07-093.1.
- Biron, P. M., C. Robson, M. F. Lapointe, and S. J. Gaskin. 2004. Comparing different methods of bed shear stress estimates in simple and complex flow fields. *Earth Surf. Process. Landf.* **29**: 1403–1415, doi:10.1002/esp.1111.
- Bridge, J. S. 2003. *Rivers and Floodplains: Forms, Processes, and Sedimentary Record*. Blackwell Science.
- Carollo, F. G., V. Ferro, and D. Termini. 2005. Analyzing turbulence intensity in gravel bed channels. *J. Hydraul. Eng.* **131**: 1050–1061, doi:10.1061/(ASCE)0733-9429(2005)131:12(1050).
- Cushing, C. E., G. W. Minshall, and J. D. Newbold. 1993. Transport dynamics of fine particulate organic matter in two Idaho streams. *Limnol. Oceanogr.* **38**: 1101–1115, doi:10.4319/lo.1993.38.6.1101.
- Daraio, J. A., L. J. Weber, and T. J. Newton. 2010a. Hydrodynamic modeling of juvenile mussel dispersal in a large river: The potential effects of bed shear stress and other parameters. *J. N. Am. Benthol. Soc.* **29**: 838–851, doi:10.1899/09-118.1.
- Daraio, J. A., L. J. Weber, S. J. Zigler, T. J. Newton, and J. M. Nestler. 2010b. Simulated effects of host fish distribution on juvenile unionid mussel dispersal in a large river. *River Res. Appl.*, doi:10.1002/rra.1469.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshw. Biol.* **21**: 271–282, doi:10.1111/j.1365-2427.1989.tb01365.x.
- Denny, M. W., and M. F. Shibata. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.* **134**: 859–889, doi:10.1086/285018.
- Elliott, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. *Freshw. Biol.* **48**: 1652–1668, doi:10.1046/j.1365-2427.2003.01117.x.
- Fischer, H. B., J. E. List, R. C. Y. Koh, J. Imberger, and N. H. Brooks. 1979. *Mixing in Inland and Coastal Waters*. Academic Press.
- Fonseca, D. M. 1999. Fluid-mediated dispersal in streams: Models of settlement from the drift. *Oecologia*. **121**: 212–223, doi:10.1007/s004420050923.
- Gaylord, B., D. C. Reed, P. T. Raimondi, and L. Washborn. 2006. Macroalgal insights revealed by theory and experiment. *Ecol. Monogr.* **76**: 481–502, doi:10.1890/0012-9615(2006)076[0481:MSDICE]2.0.CO;2.
- Gaylord, B., D. C. Reed, P. T. Raimondi, L. Washborn, and S. R. McLean. 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology*. **83**: 1239–1251, doi:10.1890/0012-9658(2002)083[1239:APBMOM]2.0.CO;2.
- Hemond, H. F., and E. J. Fechner-Levy. 2000. *Chemical Fate and Transport in the Environment*. 2nd ed. Academic Press.
- Hendriks, I. E., L. A. van Duren, and M. J. Herman. 2006. Turbulence levels in a flume compared to the field: Implications for larval settlement studies. *J. Sea Res.* **55**: 15–29, doi:10.1016/j.seares.2005.09.005.
- Kim, S.-C., C. T. Friedrichs, J. P.-Y. Maa, and L. D. Wright. 2000. Estimating bottom shear stress in tidal boundary layer from acoustic velocimeter data. *J. Hydraul. Eng.* **126**: 399–406, doi:10.1061/(ASCE)0733-9429(2000)126:6(399).

- Levin, L. A. 2006. Recent progress in understanding larval dispersal: New directions and digressions. *Integr. Comp. Biol.* **46**: 282–297, doi:10.1093/icb/icj024.
- Levine, T. D., J. P. Carney, A. D. Christian, J. L. Metcalfe-Smith, N. Benight, and D. J. Berg. 2009. Range-wide phylogeography of two *Quadrula* species: Common features and contrasts. Meeting of the North American Benthological Society 2008, Grand Rapids, Michigan, <http://nabs.confex.com/nabs/2009/webprogram/Paper4373.html> (accessed 9 September 2009).
- McNair, J. N., and J. D. Newbold. 2001. Turbulent transport of suspended particles and dispersing benthic organisms: The hitting-distance problem for the local exchange model. *J. Theor. Biol.* **209**: 351–369, doi:10.1006/jtbi.2001.2273.
- Morales, Y., L. J. Weber, A. E. Mynett, and T. J. Newton. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. *J. N. Am. Benthol. Soc.* **25**: 664–676, doi:10.1899/0887-3593(2006)25[664:EOSAHC]2.0.CO;2.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* **15**: 278–285, doi:10.1016/S0169-5347(00)01874-7.
- Pineda, J., J. A. Hare, and S. Sponaugle. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* **20**: 22–39, doi:10.5670/oceanog.2007.27.
- Roy, A. G., T. Buffin-Bélanger, H. Lamarre, and A. D. Kirkbride. 2004. Size, shape and dynamics of large-scale turbulent flow structures in a gravel-bed river. *J. Fluid Mech.* **500**: 1–27, doi:10.1017/S0022112003006396.
- Rutherford, J. C. 1994. *River Mixing*. John Wiley & Sons.
- Schwalb, A. N., M. Garvie, and J. D. Ackerman. 2010. Dispersion of freshwater mussel larvae in a lowland river. *Limnol. Oceanogr.* **55**: 628–638, doi:10.4319/lo.2009.55.2.0628.
- Schwalb, A. N., M. S. Poos, K. Cottenie, and J. D. Ackerman. 2011. Dispersal limitation of unionid mussels and implications for their recovery. *Freshw. Biol.* **56**: 1509–1518, doi:10.1111/j.1365-2427.2011.02587.x.
- Soulsby, R. 1997. *The Dynamics of Marine Sands*. Thomas Telford Publications.
- Stoesser, T., W. Rodi, and G. H. Jirka. 2004. Large eddy simulation of flow over rough channel beds. Pp. 265–270. *In* M. Greco, A. Carravetta, and R. Della Morte [eds.], *River Flow*. Taylor & Francis.
- Stone, M. C., and R. H. Hotchkiss. 2007. Turbulence descriptions in two cobble-bed river reaches. *J. Hydraul. Eng.* **133**: 1367–1378, doi:10.1061/(ASCE)0733-9429(2007)133:12(1367).
- Strayer, D. L. 2008. *Freshwater Mussel Ecology. A Multifactor Approach to Distribution and Abundance*. University of California Press.
- Treml, E. A., P. N. Halpin, D. L. Urban, and L. F. Pratson. 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecol.* **23**: 19–36, doi:10.1007/s10980-007-9138-y.
- Vogel, S. 1994. *Life in Moving Fluids: The Physical Biology of Flow*. 2nd ed. Princeton University Press.

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