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Responses of newly settled juvenile mussels to bed shear stress: implications for dispersal

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Abstract: The factors influencing the habitat requirements and dispersal of juvenile Unionidae (unionids) between post-larval detachment from a fish host and burrowing into the substratum are largely unknown, although bed shear stress (τ_w) has been proposed as a critical factor. We used a laboratory wall jet apparatus to manipulate τ_w experimentally to examine the suspension and burrowing of juvenile *Epioblasma triquetra*, *Villosa iris*, *Lampsilis fasciola*, and *Ligumia nasuta*. τ_w and unionid suspension were significantly related when $\tau_w > 0.26$ Pa, but this relationship also was influenced by mussel behavior. Greater τ_w was required for suspension when a mussel's foot adhered to a surface. Laboratory experiments confirmed predictions that juvenile unionids cannot become established when τ_w exceeds a critical value. Hydrodynamics and behavior strongly affect dispersal by juvenile mussels and may influence juvenile mussel habitat requirements, and thereby have implications for conservation efforts.

Key words: unionid mussel, post-settlement dispersal, adhesion, hydrodynamics, conservation, early life history

Much attention has been given to the identification and description of habitat because this knowledge is fundamental to the ecology of organisms (Elton and Miller 1954, Morrison et al. 2006). Such information can be used to direct limited resources available for conservation efforts (Franklin et al. 2011). Freshwater mussels of the family Unionidae (unionids) are important constituents of benthic environments because of their burrowing and suspension-feeding activities (Vaughn and Hakenkamp 2001, Vaughn et al. 2008). Unionids also serve as biological indicators of stream health, and a significant portion of species are considered vulnerable, threatened, or endangered in many regions in North America, primarily because of commercial exploitation, introduced species, and landuse change that has led to habitat alteration and destruction (Bogan 1993, 2008, Williams et al. 1993).

The unionid's life cycle includes a parasitic glochidial larval stage involving a vertebrate (mainly fish) host. The vertebrate host facilitates pelagic dispersal in the water column (Barnhart et al. 2008). The ecology of the glochidial and adult stages of unionids has received considerable attention (e.g., Michaelson and Neves 1995, Vaughn et al. 2008, McNichols et al. 2011). However, fewer investigators have studied the period after juveniles detach from a host fish, when they establish themselves on the stream bed and burrow into the substratum.

Planktonic larvae and juvenile forms may reach suitable habitat via passive dispersal (e.g., many marine inverte-

brates have pelagic larvae; Butman and Grassle 1992) or via active dispersal involving behavior (e.g., some juvenile bivalves thread-drift in the water column; Ackerman et al. 1994, Lundquist et al. 2004). Active and passive dispersal mechanisms are not necessarily mutually exclusive, and spatial patterns in recruitment and habitat occupancy also can arise from differential post-settlement mortality (Butman 1987, Hunt and Scheibling 1997). However, the ability of a juvenile to influence its dispersal via active means might be a mechanism by which habitats could be selected.

Neither the active/passive dispersal strategies of juvenile unionids nor their habitat requirements have been well defined (Strayer 2008), but unionids do experience post-settlement mortality. After settling on the stream bed, juveniles must resist high currents and turbulence until they can ground themselves or find refuge from high hydraulic stress. They may also face mortality in quiescent conditions because they are sensitive to low levels of O₂ (e.g., Polhill and Dimock 1996, Hardison and Layzer 2001). Juvenile mortality can also be high during unstable conditions (Strayer 1999, 2008). Morales et al. (2006) used a hydrodynamic model to demonstrate that the settlement of juveniles in high velocity areas leads to mortality. Therefore, hydrodynamic factors are important to the recruitment of unionids.

Strayer (2008) listed 8 factors that could characterize suitable unionid habitat and emphasized the importance of appropriate hydrodynamic bed shear stresses for juvenile establishment on the stream bed. Bed shear stress (τ_w) is

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the force per unit area acting parallel to the stream bed given by

$$\tau_w = \rho u_*^2 \quad (\text{Eq. 1})$$

where ρ is the density of water, and u_* is the shear velocity, which is a function of the velocity gradient (see review in Ackerman and Hoover 2001). The magnitude and fluctuations of τ_w in a stream can affect local populations of benthic macroinvertebrates by causing the suspension of organisms from the stream bed, especially when τ_w exceeds critical levels (τ_{crit} ; e.g., $\tau_{\text{crit}} \approx 0.9 \text{ kg m}^{-1} \text{ s}^{-2}$ [Pa]; Imbert and Perry 2000, Gibbins et al. 2007b). Modelers also incorporate a τ_{crit} value, which if exceeded, leads to the suspension of organisms rather than allowing them to settle on the stream bed (Morales et al. 2006, Hunt et al. 2009, Daraio et al. 2010). Areas with high τ_w generally have lower densities of adult unionids, possibly because τ_w inhibits the establishment of juveniles (Layzer and Madison 1995).

Given the influence of hydrodynamics on the ecology of mussels and the proposed role of τ_w in defining their habitats (Strayer 2008), an examination of the effects of these physical factors on the early juvenile stage of unionids would be useful. We investigated the responses of juveniles to τ_w in the laboratory. We identified the response of juveniles to τ_w as passive if it was the result of suspension via hydrodynamics or active if it was a consequence of behavior.

METHODS

Study species

Juvenile *Epioblasma triquetra* (Rafinesque 1820), *Villosa iris* (Lea 1829), *Lampsilis fasciola* (Rafinesque 1820), and *Ligumia nasuta* (Say 1817) were transformed in the Hagen Aqualab at the University of Guelph on known host fish (Barnhart 2006, McNichols 2007, K. A. McNichols and JDA, unpublished data). All juveniles used in our study were 0 to 29 d old, post-excystment, and ranged in size (0.5[shell length + height]) from 158 to 458 μm (*E. triquetra*: 1–22 d old, 158–458 μm ; *V. iris*: 14–28 d old, 231–384 μm ; *L. fasciola*: 29 d old, 246–406 μm ; *L. nasuta*: 0–22 d old, 233–426 μm).

Wall jet apparatus

We used a recirculating wall jet apparatus built from polycarbonate resin thermoplastic (Lexan, SABIC, Innovative Plastics; Fig. 1A) and modeled after Ackerman et al. (1995) to generate the τ_w needed to examine the response of recently settled (0–29 d) juveniles. Water was pumped (Model 4-MD-SC; Little Giant Pump Company, Tulsa, Oklahoma) from a reservoir to a 1-m-long duct (2 cm high \times 3 cm wide, Fig. 1A), which discharged across the surface of a sediment chamber (9 cm long \times 5 cm high \times 3 cm wide) into a much larger holding chamber (Fig. 1B) before

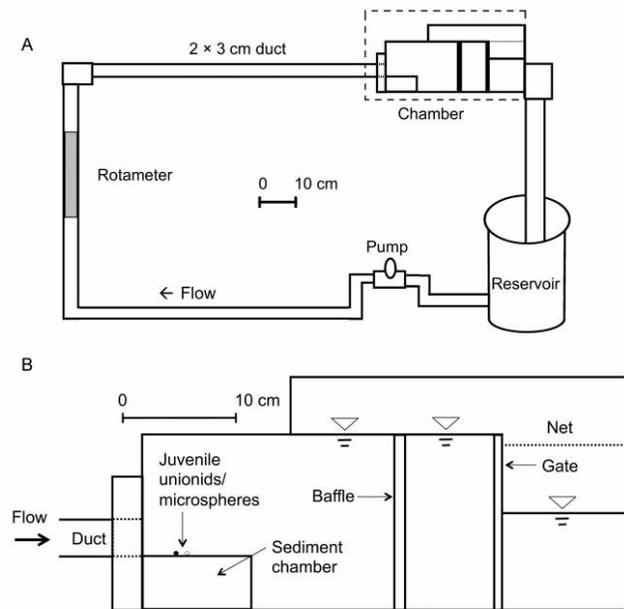


Figure 1. Schematic representation of the wall jet apparatus (A) used to examine the response of juveniles to bed shear stress in the laboratory and a close-up view of the chamber (B) (indicated by the dashed lines in panel A). The small inverted triangles and horizontal lines represent water level.

passing through a 100- μm nylon-mesh net and returning to the reservoir. The bottom of the duct was level with the top of the sediment chamber. Upstream of the duct, a ball valve controlled the flow, which was measured using a rotameter flowmeter (Model F-40750LN-16; Blue-White Industries, Ltd., Huntington Beach, California). We ran trials with juveniles placed on: 1) the smooth plastic surface of the sediment chamber, or 2) sediment (collected from Grand River, Ontario, Canada; sieved through an 850- μm -mesh sieve; and autoclaved; 1.31% organic content) in the sediment chamber. The sediment chamber was filled with sediment to a depth of 4.4 cm to give juveniles an opportunity to burrow. The smooth plastic surface and sediment surface were both positioned at a height of 5 cm above the bottom of the holding chamber during their respective trials. We filled the system with 25- μm -filtered water from the Grand River and operated it at $20.7 \pm 0.1^\circ\text{C}$ (mean \pm SE).

We used a Preston-static tube to measure τ_w across the solid surface of the sediment chamber. The Preston-static tube relates the nondimensional shear stress to the nondimensional pressure difference between the total pressure and static pressure, measured in the wall layer (i.e., the viscous sublayer of the turbulent boundary layer; Ackerman and Hoover 2001, Hoover and Ackerman 2011), with small-diameter hypodermic needles connected to a differential pressure transducer (Model PX938-01 WBDI; Omega Engineering, Inc., Stamford, Connecticut) and a laptop A/D board (version 7.0/2003, LabVIEW; National

Instruments, Austin, Texas). We recorded τ_w measurements for 5 min at each location. We compared measured values of τ_w to predicted values derived with the $1/7$ power law approximation (eq. 7.44 in White 1999; Fig. 2A) where x is the distance downstream from the duct. τ_w was contoured from 70 measurements taken over $1/2$ of the surface of the sediment chamber (i.e., at $x = 0$ – 9 cm every 0.25 cm laterally from the center line to the outer edge of the chamber) for each of 5 wall jet velocities (U) ranging from 0.11 to 0.33 m/s. We confirmed symmetry about the center line by measuring 130 points at 0.11 m/s (Fig. 2B).

Suspension from sediments

We examined the response to τ_w of juveniles placed on river sediments (suspension trials). We placed 4 to 7 individuals of *E. triquetra*, *V. iris*, or *L. nasuta* (depending on the species, and using 1 species at a time) on top of the sediments in the sediment chamber, 2 cm downstream from the duct, and along the center line of the duct. Two minutes elapsed between the placement of the juvenile on the sediments and the start of the trial. We conducted trials at $U = 0.11, 0.17, 0.22, 0.28,$ and 0.33 m/s and at $U = 0$ m/s (control). We increased U from 0 to 0.11 m/s at a rate of 3.7×10^{-3} m/s² and made further increases at a rate of 2.7×10^{-3} m/s² to reach the desired U . We maintained U for 30 min in each trial and obtained the corresponding τ_w from the velocity-specific τ_w contours, as described above. A set of trials obtained using different juveniles in each of the 6 conditions (5 velocities and control) constituted a replicate for a given species (i.e., a total of 24–42 individuals). We randomized velocities within a replicate.

We obtained 3 replicates for *E. triquetra*, but we experienced difficulties in transforming large numbers of juvenile *L. nasuta* and in maintaining large numbers of juvenile *V. iris*, primarily because of flatworm predation. *Lampsilis fasciola* individuals were not available at this time, and hence, were not used for these trials. For *L. nasuta*, we obtained 2 replicates in which different individuals were used for each replicate. However, we reused a small number of individuals at some velocities within a replicate (at least 4 individuals for replicate 1, and at least 5 individuals for replicate 2 at $U = 0.33$ m/s). We obtained only 1 replicate for *V. iris*, and we reused at least 6 individuals at $U = 0.28$ m/s. We randomly selected reused individuals from a larger pool of individuals.

After each trial, we removed the sediment chamber and collected individuals remaining in the holding chamber with a siphon and by emptying the mesh net. We counted these individuals as the number of juveniles suspended in the trial. The sediment chamber was constructed with a moveable bottom, so that the sediment could be pushed out in 1-cm-thick layers. We examined sediment for mussels in 1-cm downstream segments with the aid of a stereomicroscope (Nikon SMZ-2T; Nikon Corp., Tokyo, Japan)

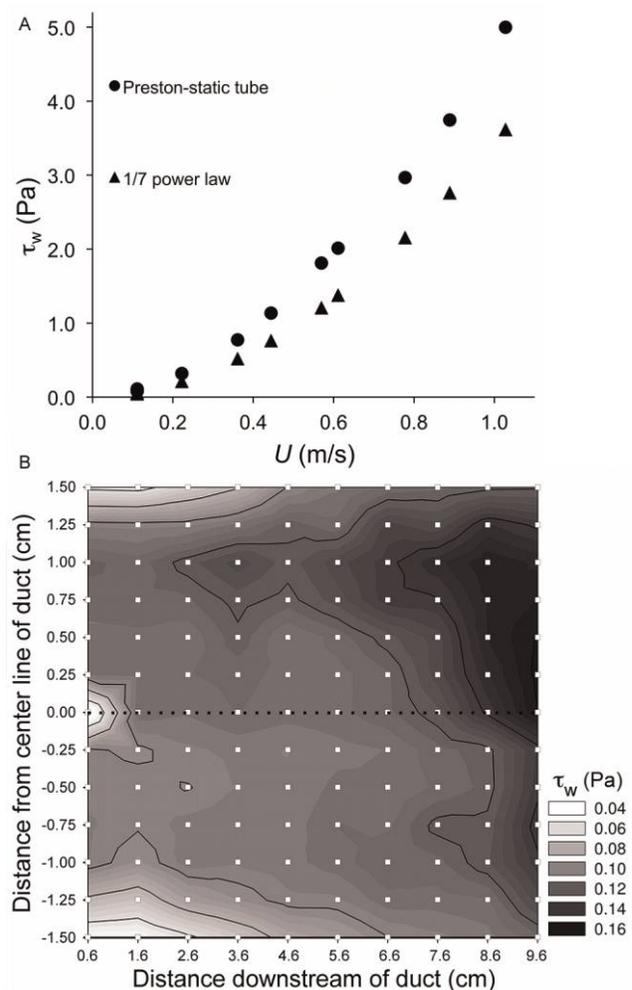


Figure 2. A.—Bed shear stress (τ_w) measured in the wall jet with a Preston-static tube at different velocities (U) and predicted by the $1/7$ power law approximation. B.—A contour plot of τ_w at $U = 0.11$ m/s from 130 measurements (white squares) taken at $x = 0$ – 9 cm every 0.25 cm laterally from the center line (dotted line) to the outer edge of the sediment chamber. The solid lines indicate intervals of 0.02 Pa.

with cross-polarizing filters. We counted the individuals found in the sediment chamber as the number of juveniles that were not suspended. If an individual could not be found in the sediment or the chamber, we excluded it from the count.

We used an analysis of covariance (ANCOVA; $\alpha = 0.05$) to compare the proportion of suspended juveniles and models (polyethylene microspheres; see below) to the continuous predictor variable, τ_w , and to the categorical covariate, species (*E. triquetra*, *V. iris*, *L. nasuta*, and microspheres). The ANCOVA was based on logistic regression because the suspension data were binomial (suspended or not suspended) and were converted to proportions (Craw-

ley 2007). We ran these analyses in R (version 2.15; R Project for Statistical Computing, Vienna, Austria).

Shields parameter

We examined the response of juveniles to τ_w when placed on a flat surface to determine the nondimensional critical shear stress (θ_c , Shields parameter) that caused motion of the individual (Gordon et al. 2004), given by

$$\theta_c = \frac{\tau_{\text{crit}}}{gd(\rho_s - \rho)} \quad (\text{Eq. 2})$$

where τ_{crit} is the critical shear stress causing motion, g is the acceleration caused by gravity, d is the diameter or size of the mussel (determined from photographs of shell length and height measured using ImageJ, version 1.44; Schneider et al. 2012), and ρ_s is the density of the mussels (i.e., 1200–1260 kg/m³; Schwab and Ackerman 2011). The use of θ_c facilitates the comparison of τ_{crit} among mussels of different sizes, body densities, or in water of different densities. In this case, we placed 1 juvenile on the surface at a time (at $x = 2$ cm along the center line of the duct), and increased U at 3.7×10^{-3} m/s² until we observed motion (i.e., the juvenile rolled on the surface or was suspended into the water column) with the aid of a stereomicroscope. Each mussel was examined once and, thus, constituted a replicate. We obtained data for *E. triquetra* ($n = 15$), *V. iris* ($n = 5$), *L. fasciola* ($n = 5$), and *L. nasuta* ($n = 10$).

We used multiple pairwise Mann–Whitney U tests ($\alpha = 0.05$) for nonparametric data (Shapiro–Wilk test in R) to compare θ_c between adhering and nonadhering juveniles, within and between species. We used a Kruskal–Wallis test ($\alpha = 0.05$) for nonparametric data to compare the proportions of juveniles suspended from sediment among species at a given τ_w . These nonparametric data were automatically converted by GraphPad InStat (version 3.10; GraphPad Software, San Diego, California) to an ordinal scale using rank-ordering, ranked, and corrected for ties. We compared our measured θ_c values to published results for marine mussels and sediment θ_c using a 1-sample χ^2 test ($\alpha = 0.05$).

Physical models

We used polyethylene microspheres (lot no. 090819-2; Cospheric LLC, Santa Barbara, California) as physical models to measure passive responses to hydrodynamics. The microspheres were similar in size (250–300 μm diameter) and density (1300 kg/m³) to juveniles (1200–1260 kg/m³; Schwab and Ackerman 2011). We placed 10 microspheres on the sediment surface for each of the 6 flow conditions described above, because the number of microspheres available was not constrained, and we obtained 3 replicates for the suspension experiments. We obtained 30 replicates for the θ_c experiments, in which each microsphere was

randomly selected from a pool of 15 microspheres of uniform size (i.e., $300 \pm 1 \mu\text{m}$).

RESULTS

The shear stress (τ_w) generated by the wall jet was sufficient to initiate motion in all juveniles and microspheres, but the required nondimensional critical shear stress (θ_c) varied among individuals within a species (unlike τ_w , θ_c accounts for the size and density of the mussels; Eq. 2). Juveniles that attached their foot to the flat surface of the sediment chamber required much higher θ_c to initiate motion, and they oscillated in the flow up to the moment at which they detached from the surface. The proportion of juveniles that adhered to the flat surface differed among species: 47% of *E. triquetra* individuals ($n = 7$) adhered, 80% of *V. iris* individuals ($n = 4$) adhered, none of the *L. fasciola* individuals adhered ($n = 0$), and 20% of *L. nasuta* individuals ($n = 2$) adhered. All juvenile *L. fasciola* ($n = 5$), *L. nasuta* ($n = 10$), and microspheres ($n = 30$) rolled (by saltating or creeping) over the flat surface, and some of the *L. nasuta* ($n = 2$) rolled after adhesion to the flat surface. Of those individuals that adhered to the flat surface, 40% of *E. triquetra* ($n = 6$ of 15) and 20% of *V. iris* ($n = 1$ of 5) were suspended eventually. The remaining individuals rolled, after failing to adhere to the surface or after breaking contact between their foot and the surface ($n = 8$ and 1, respectively, for *E. triquetra*; $n = 1$ and 3, respectively, for *V. iris*). The θ_c required to initiate transport differed among groups of individuals ($U_{10-45} = 1-16$, $p < 0.03$ in all cases; Fig. 3). Adhering *E. triquetra* and *V. iris* required the highest mean θ_c , followed in descending order by nonadhering *E. triquetra*, adhering *L. nasuta*, nonadhering *V. iris*, *L. fasciola*, *L. nasuta*, and microspheres.

Suspension of juveniles and microspheres from the surface of sediments was more difficult to observe than suspension from the flat surface, but the τ_w generated by the wall jet caused motion in all cases. However, we were unable to observe mussel behavior, and the fate of the juveniles and microspheres during the trials involving suspension from sediment was difficult to discern. Therefore, at the end of the trials, we examined layers of sediment from the sediment chamber, the mesh net, and the flow chamber for juveniles or microspheres. Individuals of all species were generally found within the top 0–1 cm layer of sediment from the sediment chamber. Suspension did not occur with any individuals until $\tau_w \geq 0.26$ Pa (Fig. 4).

τ_w affected the suspension of *E. triquetra* individuals and microspheres (Deviance, $D_{1,34} = 160$, $p < 0.001$; Fig. 4). However, *E. triquetra* individuals and microspheres did not differ in their suspension rates (i.e., no change in proportion suspended per unit τ_w) across all 6 τ_w levels tested ($D_{1,33} = 0.767$, $p = 0.38$; Fig. 4). If we also consider the results from *L. nasuta* and *V. iris*, in which 19% and 16% of individuals, respectively, were used more than

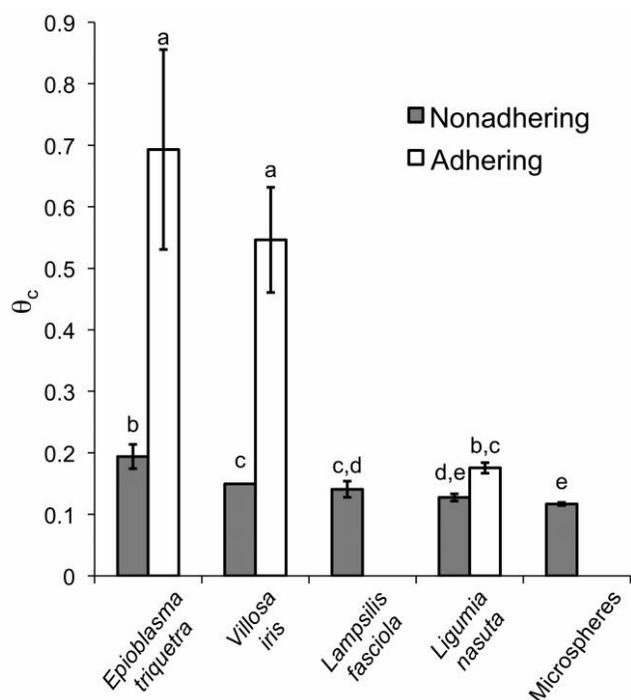


Figure 3. Mean (± 1 SE) nondimensional critical shear stress (θ_c) for juvenile unionids adhering and not adhering to a flat surface and for a physical model (polyethylene microspheres; $n = 30$). *Lampsilis fasciola* individuals did not adhere to the surface ($n = 0$ of 5), whereas 47% of *Epioblasma triquetra* individuals ($n = 7$ of 15), 80% of *V. iris* individuals ($n = 4$ of 5), and 20% of *Ligumia nasuta* individuals ($n = 2$ of 10) adhered to the flat surface. Bars with the same letter are not significantly different.

once, then this less-conservative analysis indicated that τ_w affected the suspension of juveniles and microspheres ($D_{1,52} = 207$, $p < 0.001$; Fig. 4). Differences in suspension rates were found between microspheres and juveniles ($D_{1,51} = 4.84$, $p = 0.03$; Fig. 4), but not among species ($D_{2,32} = 3.62$, $p = 0.16$; Fig. 4). No differences in the proportion of suspended juveniles were detected at any τ_w ($H_3 < 5$, $p \geq 0.18$ in all cases; Fig. 4).

The Shields curve, which is a plot of θ_c vs the roughness Reynolds number ($Re_* = u_* d / \nu$, where d is the particle diameter and ν is the kinematic viscosity), provides insight into the suspension of juveniles. Objects that lie above the curve for sediments require greater θ_c than do sediments to initiate transport, whereas those below require less. In our case, passive dispersal of nonadhering juveniles and microspheres occurred at $\theta_c \leq 0.3$ (Fig. 3), whereas juveniles with a foot adhering to the flat surface generally required much higher θ_c (i.e., up to 1.5; Fig. 5). The θ_c of microspheres did not differ from θ_c values of sediment particles of similar size ($\chi_{29}^2 = 3.42$, $p > 0.05$; Fig. 5), as was expected. θ_c values for *E. triquetra* ($\chi_{14}^2 = 127$, $p < 0.005$) and *V. iris* ($\chi_4^2 = 34.4$, $p < 0.05$; Fig. 5) were greater than the θ_c of sediments, but θ_c values for *L. fasciola* ($\chi_4^2 = 1.03$, $p = 0.90$) and *L. nasuta*

($\chi_9^2 = 2.85$, $p = 0.97$; Fig. 5) did not differ from the θ_c of sediments. This difference among species was largely a result of the proportion of juveniles of a given species that adhered. Adhering juveniles had θ_c values above the Shields curve ($\chi_{12}^2 = 159$, $p < 0.001$), whereas nonadhering juveniles did not ($\chi_{21}^2 = 6.49$, $p > 0.995$).

DISCUSSION

Effect of behavior on the suspension of juveniles

τ_w significantly affected the suspension of juvenile unionids and microspheres used as physical models of juveniles, but the behavior of juveniles was also important. Adhesion via the foot allowed juveniles to withstand greater τ_w and θ_c before rolling or becoming suspended. These results suggest that juveniles might be able to avoid suspension after settling onto the stream bed in areas of high shear stress (Hunt 2004) and would support the prediction by Strayer (2008) that shear stresses must allow for the establishment of juveniles on sediment. We identified this threshold as $\tau_w = 0.26$ Pa on sediment with particle diameter = 850 μm from the Grand River. Above this threshold, the suspension of juveniles probably was influenced by whether they remained on the surface of the sediments or fell through interstitial pores. This threshold is consistent with the peak adult unionid density at $\tau_w \approx 0.1$ Pa reported by Steuer

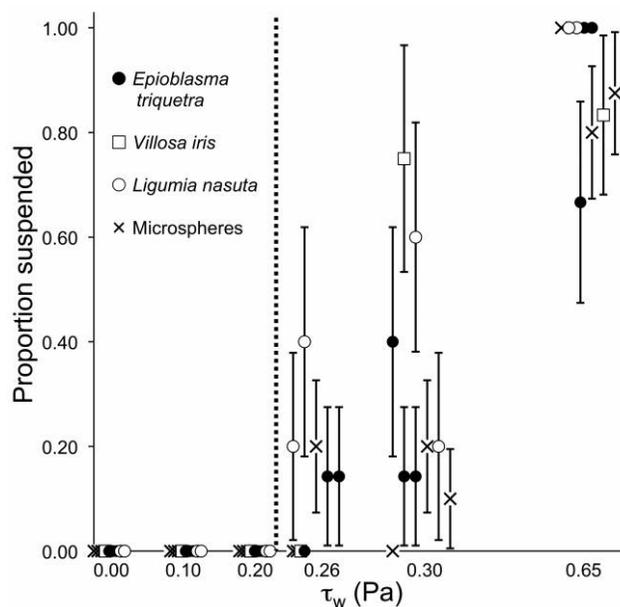


Figure 4. Mean (± 1 SE) proportion of suspended juvenile unionids and polyethylene microspheres at 6 values of bed shear stress ($\tau_w = 0, 0.1, 0.2, 0.26, 0.3$, and 0.65 Pa) in a wall jet. Each point represents a replicate (4–7 juvenile mussels or 8–10 microspheres) of which 3 were obtained for *Epioblasma triquetra*, 2 for *Ligumia nasuta*, 1 for *Villosa iris*, and 3 for microspheres. Suspension occurred at $\tau_w \geq 0.26$ Pa (indicated by a vertical dotted line). Overlapping points have been offset for clarity.

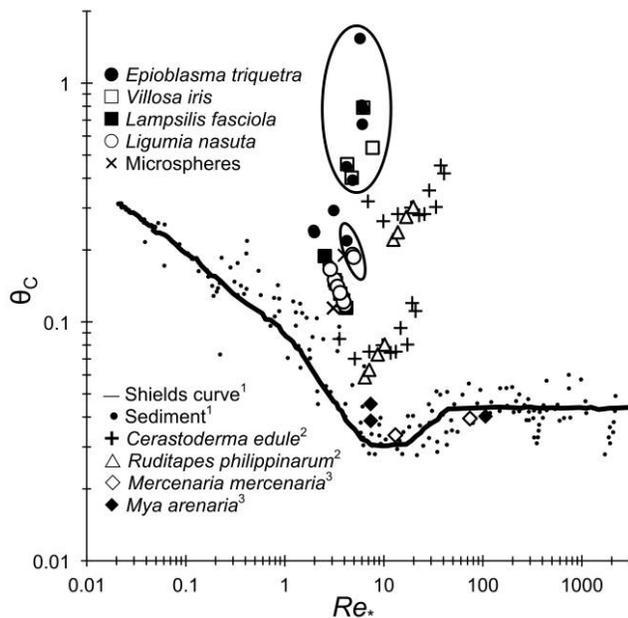


Figure 5. Nondimensional critical shear stress (θ_c) vs roughness Reynolds number ($Re_* = du_* / \nu$ where d = diameter, u_* friction velocity, ν = kinematic viscosity) for 4 species of juvenile unionids (*Epioblasma triquetra*, $n = 15$; *Ligumia nasuta*, $n = 10$; *Villosa iris*, $n = 5$; *Lampsilis fasciola*, $n = 5$) and polyethylene microspheres ($n = 30$) examined in this study, compared to sediment, and juvenile marine clams and cockles. The black ellipses identify unionids that adhered to the surface with their foot. ¹Gordon et al. (2004), ²de Montaudouin (1997), ³Paphitis et al. (2002), ⁴Hunt (2004).

et al. (2008). The thresholds observed for juveniles on a smooth surface during our θ_c trials were strongly influenced by the behavior of juveniles. Juveniles that adhered to the surface were able to withstand greater θ_c ($\theta_c = 0.57$ or $\tau_w \approx 0.45$ Pa) than juveniles that did not adhere to a surface ($\theta_c = 0.16$ or $\tau_w \approx 0.10$ Pa). These results indicate that the probability of suspension is influenced by behaviors, such as adhesion, and that the interstitial pores of sediment may provide a refuge to avoid suspension because suspension occurred at $\tau_w \geq 0.26$ Pa on sediment, but at $\tau_w \geq 0.10$ Pa on the smooth plastic surface. The differences in suspension between sediment and smooth, hard surfaces may be the result of differential responses by juveniles to τ_w because of substrate differences, a phenomenon that has been observed in zebra mussels (Ackerman et al. 1995), because of microscale roughness, and because of sediment–bed dynamics. The suspension and transport of juvenile marine bivalves are also affected by τ_w . For example, higher τ_w led to significantly more transport of juvenile mussels and clams (de Montaudouin 1997, Hunt 2004, Lundquist et al. 2004).

θ_c values for other unionids are not available, but θ_c values for juvenile marine bivalves might provide insight. For example, θ_c for juvenile *Cerastoderma edule* and *Rudi-*

tapes philippinarum (de Montaudouin 1997) were above the Shields curve at high τ_w (0.101 Pa; $\chi_{13}^2 = 51.5$, $p < 0.001$; Fig. 5), probably because of observed adhesion behavior, but not at low $\tau_w = 0.027$ Pa ($\chi_{13}^2 = 1.17$, $p > 0.05$; Fig. 5), which is below the τ_w examined in our study. Conversely, θ_c for juvenile *Mya arenaria* and *Mercenaria mercenaria* (Hunt 2004) did not differ from sediment values ($\chi_4^2 = 0.0107$, $p > 0.05$; Fig. 5), nor was an adhesion response reported. Thus, these results are consistent with our conclusion regarding the importance of adhesion behavior. θ_c for shell fragments of juvenile *C. edule* and *Mytilus edulis* (Paphitis et al. 2002) were also similar to sediment values ($\chi_{11}^2 = 0.0272$, $p > 0.05$; data not shown), as expected, because a behavioral response was not possible.

The differences in θ_c values within and among certain unionid species, depending on their adhesion behavior during the θ_c trials, indicate that a single threshold τ_w value for suspension may not be appropriate for use in modeling (e.g., Daraio et al. 2010). θ_c values of adhering juveniles (up to $\theta_c = 1.5$ or $\tau_w = 0.72$ Pa) are greater than the range of τ_w (i.e., 0.05–0.1 Pa) Daraio et al. (2010) used to model the distribution of juveniles with densities of 1100–2400 kg/m³ and shell diameters of 200–500 μm . Moreover, such models do not incorporate other unionid behavior, such as foot movement during settling (Schwalb and Ackerman 2011), adhesion to sediment (observed in our study and in the larvae of the marine gastropod *Phostilla sibogae*; Koehl and Hadfield 2004), or burrowing behavior, any of which could influence dispersal on a microhabitat scale (Daraio et al. 2010). For example, the ability of a juvenile unionid to adhere to a surface may improve its establishment on a stream bed at a microhabitat scale, even though τ_w affects both large-scale dispersal (e.g., several kilometers) and small-scale establishment of juveniles (Morales et al. 2006, Hunt et al. 2009). Therefore, adhesion may provide a mechanism for selection of higher- vs lower-flow microhabitats by juvenile unionids, probably in combination with passive dispersal caused by hydrodynamics (i.e., τ_w). This interaction between passive and active dispersal has been noted in the larvae of marine bivalves (e.g., *C. edule*) and a number of polychaete species that exhibit intermittent swimming behavior while undergoing passive saltation along a sediment bottom, especially under high velocities, which may help larvae select an optimal sediment type on which to settle (Jonsson et al. 1991, Pawlik et al. 1991, Butman and Grassle 1992).

The adhesion abilities of juveniles in our study were much lower than those reported for other juvenile or small freshwater and marine taxa, largely because those taxa used byssal thread adhesion, whereas the use of byssal threads was not observed in our study (cf. Smith 2000). *Mytilus* spp., *Dreissena bugensis*, and *Limnoperna fortunei*, which use byssal threads, have much greater adhesive strengths (Crisp et al. 1985, Ackerman et al. 1995, Hunt and Scheibling 2001, Matsui et al. 2001) than the juvenile unionids in our

Table 1. The stress and force needed to detach juvenile unionids and other benthic invertebrates, acting parallel and normal to attachment surfaces. Detachment stress and nominal adhesive force were calculated from their respective formulae when necessary (detachment stress = nominal adhesive force/shell length², nominal adhesive force = shell length² × detachment stress). Values are mean ± 1 SE.

Species	Shell length (mm)	Adhesion mechanism	Detachment stress (Pa)	Nominal adhesive force (N)	Parameter measured	Reference
Parallel to attachment surface						
<i>Epioblasma triquetra</i>	0.27 ± 0.01	Foot	0.4 ± 0.1	17 ± 3 × 10 ⁻⁹	τ _{crit} ^a	This study
<i>Villosa iris</i>	0.30 ± 0.02	Foot	0.5 ± 0.1	29 ± 8 × 10 ⁻⁹	τ _{crit} ^a	This study
<i>Lampsilis fasciola</i>	0.34 ± 0.03	Foot	0.14 ± 0.01	12 ± 2 × 10 ⁻⁹	τ _{crit} ^a	This study
<i>Ligumia nasuta</i>	0.36 ± 0.01	Foot	0.146 ± 0.009	15 ± 2 × 10 ⁻⁹	τ _{crit} ^a	This study
<i>Dreissena bugensis</i>	0.5 ± 0.1	Byssal thread	58 ± 4	2 ± 1 × 10 ⁻⁵	τ _w ^{a,b}	Ackerman et al. 1995
<i>Phestilla sibogae</i>	0.2	Foot, mucus	4 ± 1 (SD)	1.70 × 10 ⁻⁷	τ _w ^a	Koehl and Hadfield 2004
Normal to attachment surface						
<i>Limnoperna fortunei</i>	20–30	Byssal thread	300–675	0.27 ± 0.06	Detachment force ^b	Matsui et al. 2001
<i>Mytilus edulis</i>	50.7	Byssal thread	7.5	0.019	Breaking load ^a	Crisp et al. 1985
<i>Mytilus</i> spp.	10	Byssal thread	3000–21000	0.3–2.1	Dislodgement force ^b	Hunt and Scheibling 2001

^a Detachment stress used

^b Nominal adhesive force used

study, which used foot adhesion (Table 1). The adhesive strength of the larval nudibranch *P. sibogae* is more similar to that of juvenile unionids because they also use a foot adhesion mechanism (Koehl and Hadfield 2004). Although the adhesive strength of the juveniles used in our study is not as strong as that of these other taxa, adhesion may enable those individuals or species more adept at adhering to better withstand τ_w on the stream bed, giving them an opportunity to burrow. The adhesion capabilities of juveniles, including differences among species and mechanisms (i.e., foot adhesion vs byssal thread adhesion), are subjects that warrant further investigation.

A field component was undertaken to determine whether juvenile unionids would be found in higher densities downstream vs upstream of boulders in low vs high shear stress regions, respectively. Unfortunately, only a single *Strophitus undulatus* (1.4 cm shell length) was found at a downstream location in the study, although marginally more *Pisidium casertanum* (Sphaeriidae) were found in downstream vs upstream locations. Whereas those results are consistent with the hypothesis presented, they remain inconclusive for juvenile unionids.

Implications for conservation

Our results indicate that settlement and recruitment of postmetamorphic juveniles could be affected by any process that changes stream characteristics, specifically τ_w . For example, the erosion of stream banks can cause the infilling of regions with fine sediments, resulting in unstable stream beds, decreasing habitat quality, and affecting habitat composition and structure (Williams et al. 1993, Box and Mossa 1999). Juveniles will not develop if sediment cannot physically support them, and they could be suspended into the water column with other entrained sediment particles, or crushed by or buried under infilled sediments (Peterson 1999, Gibbins et al. 2007a). Stream flow modification could also lead to the destruction of mussel habitat (Bogan 1993). Under controlled flow regimes, stream beds must be flushed occasionally to mobilize fine sediments (Clausen et al. 2004), which could restrict the settling of juveniles (Strayer 2008). Flow managers should consider the hydrodynamic requirements of newly settled juveniles when setting the timing of flushing flows. However, gaps exist in our knowledge of the gravidity periods of unionid mussels and juvenile release from their host fish. The frequency and intensity of flushing flows should be dynamic to accommodate different sites, species and their respective life-history stages, and nonbiological considerations (Clausen et al. 2004).

The habitat requirements of juveniles have not been thoroughly defined, but generally are assumed to be similar to the requirements of adult unionids for conservation initiatives (e.g., Department of Fisheries and Oceans 2010). Conservation measures for juveniles should reflect differ-

ent habitat requirements across species (Strayer 2008), life histories (Neves and Widlak 1987), and body sizes (Brainwood et al. 2008). Future studies should focus on habitat requirements across taxa. Both τ_w and behavior affect the establishment of juveniles on sediments, and hence their distribution and abundance. However, an investigation of the relationship between the ability of juvenile unionids to use behavior to withstand greater θ_c in the laboratory and their defined hydraulic habitats in the field is needed.

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