Effects of Juvenile Settling and Drift Rates on Freshwater Mussel Dispersal

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ABSTRACT.—Freshwater mussels play important roles in ecosystems and are globally imperiled. Adult mussels are sedentary and dispersal is as larvae attached to fish hosts and as juveniles in stream drift. Understanding juvenile dispersal is important for understanding the patchy distribution of adult mussels and for conservation. We propose the location in which a juvenile mussel ends up on the streambed is determined by a combination of the juvenile's settling velocity, current speed, and streambed topography. We conducted a laboratory experiment to quantify the settling velocities of juveniles of four mussel species and of polymer microparticles, later utilized as surrogates for juveniles. We performed a flume experiment where we measured drift distances of microparticles at three low flow velocities over gravel and over a simulated mussel bed (gravel combined with mussel shells). Lastly, we measured drift distances of microparticles at five sites in two small rivers under summer low flow conditions. There were no significant differences in settling velocities among the four mussel species, live juveniles sank at a significantly lower rate than dead juveniles, and there were no significant differences in settling velocities between live juveniles and microparticles. The distances microparticles drifted in the flume increased with flow velocity and were shorter over the simulated mussel bed than over gravel. In the field most microparticles were recaptured near their release locations. In this study, juvenile mussels had limited dispersal potential with most drifting < 10 m. This limited dispersal should result in many juveniles settling within mussel beds, areas where habitat conditions are favorable for survival and growth, and may contribute to the patchy spatial distribution of mussel beds in rivers.

INTRODUCTION

Dispersal, the movement of individuals from one place to another, allows organisms to colonize patches of newly created habitat and to recolonize patches in unstable or heterogeneous environments that have been affected by disturbances (Johnson and Gaines, 1990; Näslund *et al.*, 1993; Fausch *et al.*, 2002). Dispersal is frequently bimodal, with most individuals moving over either short or long distances (Wiens, 1976). Dispersal potential also greatly depends on mobility (Townsend and Hildrew, 1994). Mobile animals can conduct migrations, *i.e.*, directional, long-distance movements during specific time periods that allow them to move actively from one location to another (Gaines and McClenaghan, 1980; Johnson and Gaines, 1990; Dingle and Drake, 2007). In contrast many sedentary animals with limited mobility have evolved passive modes of dispersal such as drifting in wind or water currents (Townsend and Hildrew, 1994). The larvae of stream insects commonly drift downstream with the water currents, which enables them to escape unfavorable conditions and to colonize new habitat (Waters, 1972; Brittain and Eikeland, 1988). Dispersal via drifting has been suggested as a contributor to the typically patchy distribution of invertebrates in streams (Roughgarden *et al.*, 1977; Minshall and Petersen, 1985; McLain and Ross, 2005).

Freshwater mussels (Bivalvia, Unionidae; hereafter "mussels") are a guild of sedentary, burrowing, long-lived, filter-feeding bivalves. Mussels play important roles in rivers by transferring nutrients and energy from the water column to the benthos, and enhancing the

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production of other organisms via excreted nutrients, sediment bioturbation, and providing habitat (Vaughn *et al.*, 2008; Atkinson and Vaughn, 2015). Mussels are one of the most imperiled groups of organisms globally (Strayer, 2008). In North America 72 % of the native fauna is either federally listed as endangered or considered in need of some protection (Haag, 2009). Mussel species with greater dispersal abilities have higher local colonization rates (Vaughn, 2012) and thus may be better able to avoid extinction than more range-restricted species. Therefore, understanding mussel dispersal is key to their conservation.

In rivers mussels often occur as dense multispecies aggregations called mussel beds, where mussel abundance is 10 - 100 times greater than adjacent, nonbed areas (Strayer *et al.*, 2004; Vaughn, 2010). Mussel beds are typically patchily distributed and separated by large areas where mussels do not occur or are sparse (Strayer, 2008; Atkinson and Vaughn, 2015). Why mussel beds are patchy and where they occur is critical to conserving and managing this imperiled fauna, but is not well understood (Daraio *et al.*, 2012; Ries *et al.*, 2016). Early investigations focusing on factors such as substrate size and flow velocity could not adequately explain the patchy distribution of mussels (Holland Bartels, 1990; Strayer and Ralley, 1993; Brim Box *et al.,* 2002). Subsequent studies incorporating more complex parameters such as shear stress and substrate stability have been more successful (Layzer and Madison, 1995; Hardison and Layzer, 2001; Steuer *et al.*, 2008; Allen and Vaughn, 2010). Strayer (1999) proposed mussel beds occur where sediments remain stable during high flows, providing protection from scouring and dislodgement. Most studies exploring the patchy distribution of mussel beds have focused on adult mussels; few studies have investigated the dispersal and/or habitat requirements of juvenile mussels (Haag, 2012).

Because adult mussels are largely sedentary with limited mobility, mussel dispersal occurs via their larvae or juvenile stages (Strayer, 2008; Gough *et al.*, 2012; Kappes and Haase, 2012). Mussel larvae (glochidia) are obligate ectoparasites on fish and are dispersed to new areas through fish host movement (Barnhart *et al.*, 2008). After metamorphosis on the host, juvenile mussels drop off and can be further dispersed via drift (Morales *et al.*, 2006a). Therefore, these two early life stages should be important to the spatial distribution of mussel beds. While multiple studies have examined how host fish movement (and therefore larval dispersal) affects mussel distribution (McClain and Ross, 2005; Vaughn, 2012; Irmscher and Vaughn, 2015), few studies have empirically examined the role of juvenile drift dispersal in mussel distribution.

Juvenile mussels are very small (usually < 500 μm), difficult to detect in the field, and little is known about their specific habitat requirements (Holland-Bartels, 1990; Newton *et al.*, 2008; Strayer, 2008; Daraio *et al.*, 2010a). Shear stress on the streambed may constrain successful settlement of juveniles (Layzer and Madison, 1995; French and Ackerman, 2014), and correlations between shear stress and adult mussel density may actually reflect limitations to juvenile recruitment (Hardison and Layzer, 2001; Allen and Vaughn, 2010; Daraio *et al.*, 2010a). In a recent experiment, French and Ackerman (2014) found the resuspension of newly settled juveniles was directly related to bottom shear stress. Current velocity is also important to juvenile dispersal. Schwalb *et al.* (2012) demonstrated in a field experiment that dispersal of mussel larvae was positively correlated with both current velocity and turbulence. Studies have used simulation modeling to predict juvenile mussel dispersal and to explore the importance of juvenile dispersal for the distribution of adult mussels. Lee and DeAngelis (1997) used a spatially explicit, age-structured model to simulate mussel dispersal, recolonization of previously devoid habitat areas, and the formation of new populations. Morales *et al.* (2006a, 2006b) created individual-based models to simulate effects of bottom substrate and hydrodynamic conditions on the formation of
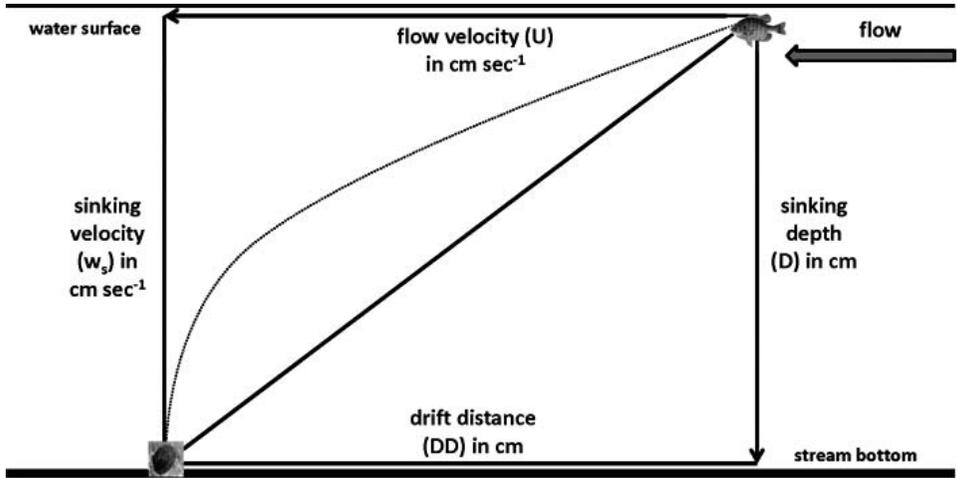
FIG. 1.—Conceptual model of juvenile unionid drift, following Fonseca (1999). The straight diagonal line shows the vector from the point of excystment to the location where the juvenile settles. The dashed, curved line is an approximation of the actual pathway of the settling juvenile in response to differing flow velocities within the water column

mussel beds. They found flow velocity was the decisive factor determining dispersal distances and colonization patterns. Finally, Daraio *et al.* (2010a, 2010b) utilized stochastic Lagrangian particle tracking in a three-dimensional flow field to integrate hydrodynamic data with the model created by Morales *et al.* (2006a, 2006b). This group found juvenile settling was mainly a function of current velocity, and hydraulic conditions had significant effects on settling of juveniles after excystment.

After a juvenile drops off the fish host, the location where it comes to rest on the streambed should be determined by a combination of settling velocity of the juvenile, current velocity (Fig. 1), and streambed topography (Fonseca, 1991). Settling velocity is influenced by the specific density of the juvenile and the viscosity of the water, which is determined by temperature. Therefore, drift distance should be influenced by the juvenile's specific density, current velocity, and streambed topography. To examine these relationships, we conducted laboratory experiments to determine the settling velocities of four species of juvenile mussels, as well as of polymer microparticles used as a surrogate for juveniles. We then performed flume experiments examining the drift distances of microparticles over plain gravel and gravel with a simulated mussel bed (which increased turbulence) at three flow velocities. Finally, we measured the drift distance of microparticles at five sites in two rivers known for their high mussel biodiversity.

METHODS

SETTLING VELOCITY EXPERIMENTS

We conducted a laboratory experiment to determine quiescent settling velocities of juvenile mussels. Settling velocity was defined as the rate at which juveniles sink to the bottom. Settling velocities were measured in a glass cylinder (60 × 18 cm, wall thickness 8 mm) filled with well water to a depth of 55 cm. To detect potential differences in

temperature-induced water densities affecting settling velocities, we measured the vertical temperature profile of the water column with an infrared thermometer (Kintrex Infrared Thermometer IRT0401, Vienna, VA) at 5 cm intervals.

We obtained $\sim$ 400 live juvenile mussels of four species: *Lampsilis cardium* (mean shell diameter 279.17 $\pm$ 24.64 (SD) µm), *Lampsilis siliquoidea* (271.67 $\pm$ 33.95 µm), *Villosa constricta* (261.67 $\pm$ 36.98 µm) and *Villosa iris* (270.00 $\pm$ 27.39 µm). We used these species because we could obtain them in sufficient quantity to conduct our experiments. Juveniles were one to three days old and were express-shipped from the USFWS National Fish Hatchery in White Sulphur Springs, WV. Before running experiments, juvenile viability was determined by observing active shell and foot movement under a light microscope. Juveniles were released individually with a glass pipette at the surface and in the center of the glass cylinder to minimize wall effects (Vogel, 1994). Starting at a water depth of 50 cm, we made visual observations of the time it took the juvenile to pass 5 cm intervals until it reached the bottom at 50 cm. We conducted 30 trials per species and used a new individual for each trial.

We also examined potential differences in settling velocities between live and dead juveniles. To measure settling velocities of dead juveniles, we froze individuals not used in previous trials and that had intact, closed shell valves, to ensure that morphological characteristics were similar between live and dead specimens. Dead mussels were allowed to thaw prior to the experiment. We then ran 30 trials per species, as described above.

For live juveniles we calculated the mean settling velocity for each species individually, as well as for all four species combined. For dead juveniles we calculated the mean settling velocity of all species combined. We compared the mean settling velocities between mussel species with a one-way ANOVA. Data met the assumptions for ANOVA and were not transformed. We compared the mean settling velocities between live and dead juveniles with a nonparametric Mann-Whitney U test. All statistical analyses were performed with JMP 8.0 software.

EVALUATION OF MICROPARTICLES AS SURROGATES FOR JUVENILE MUSSELS

While we could detect juvenile mussels in the glass cylinder (above), they are difficult to observe in our flume or in the field. Thus, we wanted to determine whether we could use synthetic, fluorescent microparticles as surrogates for juveniles in our lab experiments and field observations. We compiled information on juvenile shell diameter (d_m in µm) and specific density (ρ_m in g cm^{-3}) from the literature, and also measured the diameter of 30 individuals of each species of juvenile mussel used in the settling experiment. In the literature, d_m values ranged from 150 to 500 µm, with a non-weighted mean of 250 µm (Table 1), while ρ_m values ranged from 1.00 to 1.28 g cm^{-3}, with a non-weighted mean of 1.16 g cm^{-3} (Table 2). Our own measurements of d_m across the four species ranged from 261.67 to 279.17 µm, with a mean of 270.63 µm. We used these data to select spherical, fluorescent polymer microparticles with a similar diameter (300-355 µm) and specific density (1.28 g cm^{-3}). These particles (item number UVPMS-BR-1.20 300-355um - 10g) were obtained from Cospheric Inc., Santa Barbara, CA.

We repeated the settling experiment using the microparticles. A UV-A light source was placed next to the glass cylinder to illuminate the fluorescent microparticles. We ran 30 trials, as described above. We compared settling velocities between live juveniles and microparticles with a standard t-test; data met the assumptions for this test and were not transformed. Because we found no significant differences in settling velocities between juveniles and microparticles (Fig. 3), we concluded that the microparticles were appropriate

TABLE 1.—Publications with information on juvenile mussel shell diameters (d_m). Columns show publications that contain information on juvenile shell diameter (d_m), the species for which the juvenile shell diameters were assessed (if available), and actual shell diameter measurements in μm (range of values, width x length, or maximum lengths). Overall, d_m ranges from 150 to 500 μm, with a non-weighted mean of 250 μm

Publication	Species	d_m [μm]
Coker *et al.* (1922)	"muckets"	250 - 500
Daraio *et al.* (2012)	*Amblema plicata*	220 × 220
Daraio *et al.* (2010a)	*Lampsilis cardium*	230 × 250
Daraio *et al.* (2010b)	*Amblema plicata*	220 × 220
Morales *et al.* (2006a)	not defined	200
Payne and Miller (2000)	*Actinonaias ligamentina*	250
	Lampsilis fasciola	278
	Ptychobranchus fasciolaris	218
	Epioblasma triquetra	280
Stein (1973)	*Amblema plicata*	220 × 220
Wächtler *et al.* (2001)	Anodontoides	200
	Mutela	150

surrogates for estimating juvenile mussel settling and drift and used them in subsequent flume and field experiments.

DRIFT DISTANCE: FLUME EXPERIMENTS

We performed experiments to determine how current velocity influences the distance that juvenile mussels drift in the water column, and how this relationship might be affected by streambed roughness. Experiments were performed in a recirculating flume (designed following Nowell and Jumars, 1987; Vogel, 1994; and Cahoon and Hoshino, 2003), which was 850 cm long, 60 cm wide, and 60 cm deep, and had a working area length of 715 cm. A combination of eight, 61 cm UV-A light sources suspended above the flume and 12, 60 × 45 cm Lexan polycarbonate sheets in the front panel of the flume allowed visual tracking of the drifting, fluorescent microparticles. The bottom of the flume was covered with a layer of gravel 10 cm deep [mean particle size 18.99 mm (± 3.26 *SD*)] and the flume was filled with tap water to a depth of 50 cm. We used two electronically-controlled propellers to create

TABLE 2.—Publications with data on specific density (ρ_m in g cm^{-3}) of juvenile mussels. Columns show publications containing information on juvenile mussel specific density (ρ_m), the species for which specific density was assessed, and the specific density measurements in g cm^{-3} (either range of values or single values). Overall, ρ_m ranges from 1 to 1.28 g cm^{-3}, with a nonweighted mean of 1.16 g cm^{-3}

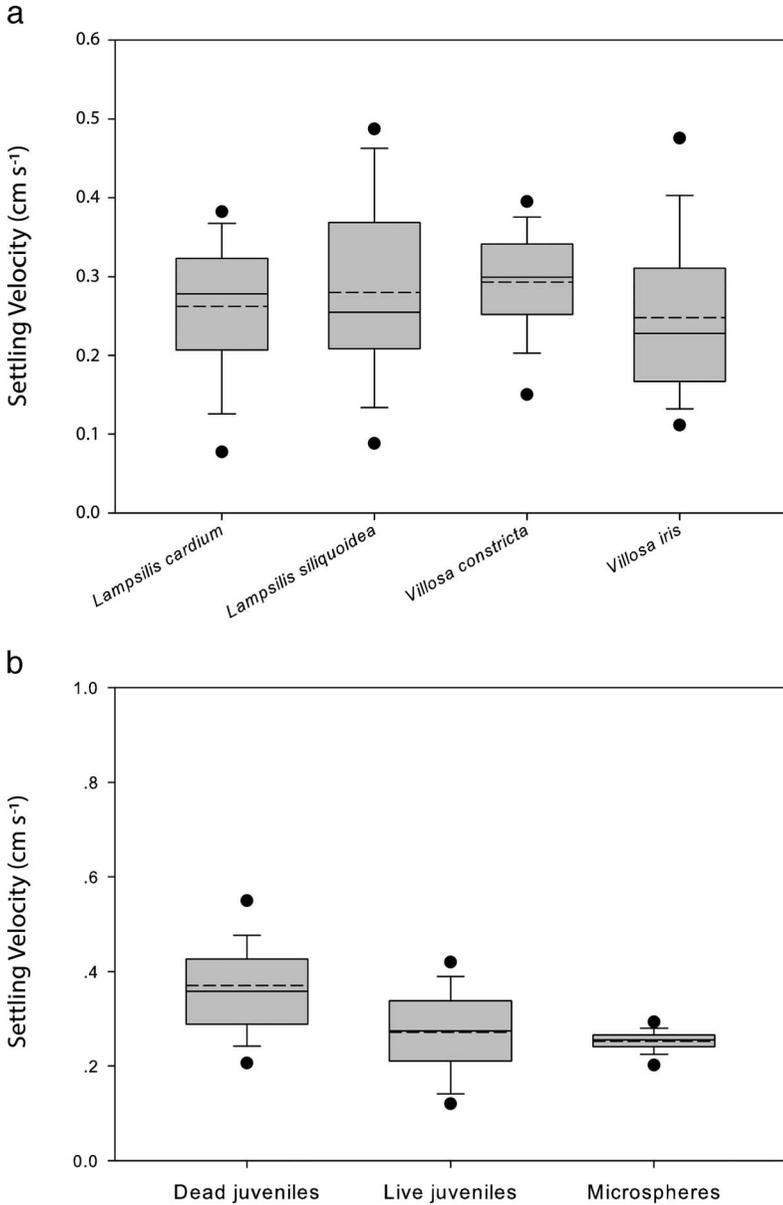| Publication	Species	ρ_m [g cm^{-3}]
Daraio *et al.* (2012)	*Actinonaias ligamentina*	1.18 - 1.22
Daraio *et al.* (2010b)	*Lampsilis cardium*	1.28
	Lampsilis higginsii	
Schwalb and Ackerman (2011)	*Actinonaias ligamentina*	1.2 - 1.26
Morales *et al.* (2006a)	marine spp.	1.01
Morales *et al.* (2006b)	marine spp.	1.0 - 1.1

a

b

FIG. 2.—(a) Difference in settling velocities by species. Box plots display settling velocities for the four species tested (*Lampsilis cardium*, *Lampsilis siliquoidea*, *Villosa constricta*, and *Villosa iris*) and (b) Settling velocities for live juveniles (pooled), dead juveniles, and microparticles. Dashed lines represent means, solid lines medians, whiskers are quartiles and the black dots the 5th and 95th percentiles
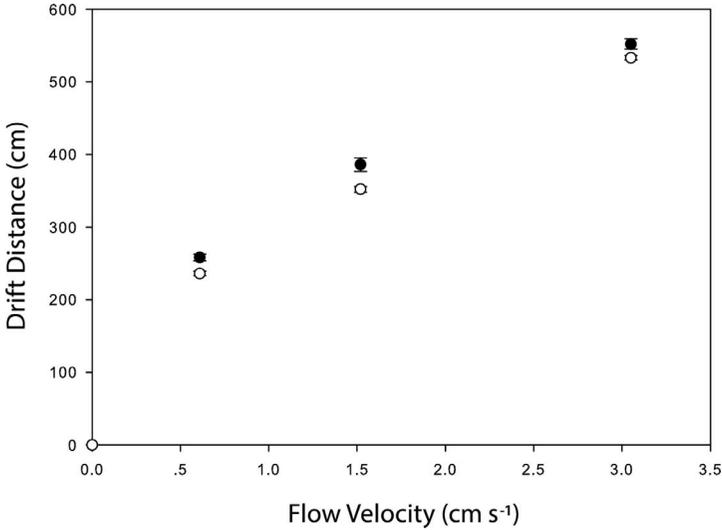
Fig. 3.—Drift distances in relation to flow velocities. Solid black dots represent drift distances over gravel and open circles represent drift distances over a simulated mussel bed. Error bars are standard errors

current velocities of 0.61, 1.52, and 3.05 cm s^{-1}, which were within the range of summer flow velocities at our field sites (Table 3). Current velocity was measured at 66% of the water depth with an electromagnetic flow meter (Marsh-McBirney Flo-Mate 2000, Frederick, MD). We released microparticles individually just below the water surface using a fine-tipped pipette and measured the drift distance of microparticles for each current velocity by tracking the distance an individual microparticle that was released just below the water surface moved until it settled on the bottom and stopped moving. We conducted 30 trials per current velocity.

To examine how mussel beds might influence the distance a juvenile drifts, we conducted a second flume experiment where we added mussel shells to the gravel to mimic a mussel bed. In mussel beds shells protruding from the sediment increase bottom roughness, which increases vertical mixing and creates interstitial spaces that could trap mussels on the bottom, preventing their further drift. We created sham mussels by gluing mussel shells together, and buried them in the gravel with the posterior shell edges partially exposed, as in a natural mussel bed. This increased mean bed substrate particle size from 18.99 mm (± 3.26 SD) to 56.06 (±45.41 SD) mm (U $_{(149)}$ = 6296.5, P < 0.001). We repeated the above experiment under these modified conditions. We examined differences in drift distances over gravel alone versus gravel and mussel shells combined with a two-way ANOVA.

DRIFT DISTANCE: FIELD EXPERIMENT

To determine how far juveniles drift in natural streams, we conducted a field experiment in two perennial rivers in southeastern Oklahoma, the Kiamichi River, and Little River (Table 3). These adjacent rivers are tributaries to the Red River and are known for their diverse and abundant freshwater mussel populations (Matthews *et al.*, 2005). The Kiamichi River is a 5th order stream with a 4650 km^2 basin area. The Little River is a 6th order stream

TABLE 3.—Characteristics of the five sites in the Little and Kiamichi rivers. Based on the grid design (10 m between transects, 5 m between locations), the number of nets placed in the channel at each site varied with channel width. At each site, we released 30 g of microparticles. The reported numbers of captured microparticles are cumulative for all nets per site. GPS coordinates are in UTM, NAD83, Zone N15

River	LR-1 Little River	LR-2 Little River	KR-1 Kiamichi River	KR-2 Kiamichi River	KR-3 Kiamichi River
GPS Coordinates	0299358/3811669	0336540/3756900	0270114/3821052	0263813/3812530	0284034/38284445
Channel width [m]	14	17	43	18	20
Mean water depth [cm]	18.0 (± 4.24 SD)	7.8 (± 3.82)	59.1 (± 21.87)	46.8 (± 12.21)	40.1 (± 16.11)
Mean flow velocity [cm/s]	0.47 (± 0.62 SD)	14.75 (± 6.91)	0.87 (± 1.19)	3.86 (± 1.9)	4.73 (± 3.06)
Froude number	0.0035	0.1687	0.0036	0.0180	0.0239
Reynolds number	6500.08	88502.39	39550.14	138960.62	6520.76
Number of nets	34	36	75	71	82
Number of recaptured microparticles	168	155	334	165	237

with a basin area of 10,720 km^2. We selected five sites (KR-1, KR-2, and KR-3 in the Kiamichi River and LR-1 and LR-2 in the Little River) with well-described mussel beds that have been used in multiple studies of mussel ecology by our laboratory (Spooner and Vaughn, 2006; Allen and Vaughn, 2010; Galbraith and Vaughn, 2011; Atkinson *et al.*, 2012; Atkinson and Vaughn, 2015).

The Kiamichi and Little rivers typically have variable hydrographs, with moderate flows for much of the year, spring flooding, and often very low flows during mid to late summer (Vaughn *et al.,* 2015). Mean annual discharge in the Little River is 183 m^3 s^{-1} (Matthews *et al.*, 2005), but mean July discharge was only 23 m^3 s^{-1} for 2000 - 2013 (USGS gage 07338500). Mean annual discharge in the Kiamichi River is 48 m^3 s^{-1} (Matthews *et al.,* 2005), but mean July discharge was only 12 m^3 s^{-1} for 2000 - 2013 (USGS gage 7335790). Our experiments were performed in July 2012 and 2013 under these low flow conditions (Table 3). To further characterize flow conditions at the sites, we calculated Froude and Reynolds numbers for each site following Gordon *et al.* (1992), based on data from Table 3. The Froude number describes the general tranquility or rapidity of flow and the Reynolds number turbulence. All of our sites had turbulent flow (as do all natural streams, laminar flow only occurs in pipes) but had Froude numbers less than one, indicating slow, tranquil flow conditions (Gordon *et al.*, 1992).

At each site we placed drift nets (opening 25 × 25 cm, 25 cm long, mesh size < 300 μm) in a 10 m (spacing between transects) by 5 m (spacing between nets) grid, with the net openings facing into the flow (Table 3). We measured current velocity with an electromagnetic flow meter (Marsh-McBirney Flo-Mate 2000, Frederick, MD) in 1 m increments at Transect 5 at each site, before releasing 30 g of microparticles (∼ 150,000 - 300,000 microparticles) at the water surface, spread out evenly across the width of the channel. We recovered drift nets after 24 h and placed them in large Ziploc bags. We ran one trial per site. In the laboratory we rinsed nets into a white pan and counted the number of microparticles per net with the help of an UV-A light (Table 3). We plotted the number of microparticles per drift net in relation to drift distance from the release point.

<center>RESULTS</center>

There were no significant differences in settling velocities between the four mussel species [$F_{(3,116)}$ = 1.41, P = 0.24; Fig. 2a]. However, there was a significant difference in mean settling velocities of live and dead juveniles (pooled by species), with live juveniles settling at a significantly slower rate [$U_{(119)}$ = 3664, P < 0.001; Fig. 2b]. We detected no significant difference between mean settling velocities of live juveniles and microparticles [$t_{(148)}$ = 1.039, P = 0.3003; Fig. 2b]. The mean water temperature during the experiment remained constant at 19.6 C and did not vary with water depth (± 0.0826 *SD*), and therefore our results were not influenced by temperature.

Drift distances in the flume over gravel and the simulated mussel bed increased with an increase in flow velocity (Fig. 3). However, drift distances over the mussel bed were consistently shorter than over plain gravel, by ∼25 cm on average (Fig. 3). There was a significant difference in drift distance between substrate type (gravel versus mussel shells) [$F_{(2, 174)}$ = 28.33, P < 0.001], and between flow velocities [$F_{(2, 174)}$ = 1332.95, P < 0.001], but no significant interaction between substrate type and flow velocity [$F_{(2, 174)}$ = 0.92, P = 0.39]. Water temperature remained constant at 18.4 C for all six trials.

In the field study, recapture rates for polymer microparticles in drift nets were low (Table 3). For particles that were recaptured, ∼ 42% were detected at a distance of 10 m from their release location (Fig. 4). Particle drift decreased rapidly across all sites except for site LR-1,
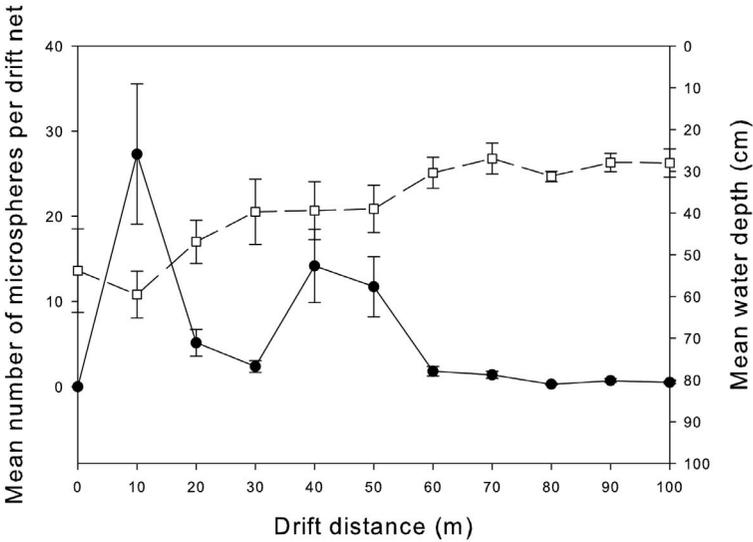
Fig. 4.—Mean number of microparticles per drift net for the five sites. Solid black dots and the solid line represents mean number of microparticles per drift net, white boxes and the dashed line represent water depth. Error bars are standard errors

where there was a second recapture peak at 40 to 50 m from the initial release location (Fig. 4).

Discussion

In our study juvenile mussels had limited dispersal potential after falling off the fish host, with most drifting < 10 m. The drift distances of an array of stream invertebrates are also typically restricted to a range of a few meters to tens of meters (Lancaster *et al.*, 1996; Palmer *et al.*, 1996; Fonseca, 1999; Elliot, 2003; Fingerut *et al.*, 2006), and this limited dispersal contributes to the typical patchy distribution of many stream invertebrates (Townsend, 1989; Tompson and Townsend, 2006). If juvenile mussels settle and grow to adulthood within a short distance of where they dropped off the fish host, then this limited dispersal ability could contribute to the patchy spatial distribution of mussel beds. Indeed, a recent study of mussel distribution in the Upper Mississippi River found high overlap between the distribution of adult and juvenile mussels at a fine spatial scale (Ries *et al.*, 2016).

Mussel beds change hydraulic conditions on the streambed, which may in turn constrain the drift of juvenile mussels. In our flume experiment, drift distances were an average of ~ 25 cm shorter over a mussel bed than over gravel. This is likely because the increased bottom roughness created by the shells of adult mussels increases turbulent eddies, which increases the vertical exchange of water with the streambed and accelerates the descent of particles to the streambed (Hart and Finelli, 1999; Schwalb *et al.*, 2012). In addition, once on the streambed, the heterogenous topography of protruding shells in mussel beds likely traps drifting juveniles within the mussel beds and prevents their resuspension or further drift. In combination these factors may increase the probability that juveniles settle in areas where habitat conditions are favorable for survival and growth, since mussel beds are limited to

stream areas with that display appropriate hydrodynamic conditions under both high and low flow conditions (Strayer, 1999; Allen and Vaughn, 2010; Ries *et al.*, 2016).

Juveniles might be able to influence their settling velocity through morphological and behavioral adaptations. Schwalb and Ackerman (2011) reported active foot waving and shell opening, and we observed strong, rapid movement of cilia located on juvenile feet. In addition to pedal feeding, these cilia might be used to produce microcurrents that enable juvenile mussels to affect their descent in the water column. Although these microcurrents are most likely insufficient to over-ride strong hydraulic forces of turbulent flow conditions (Schwalb, 2009), Daraio *et al.* (2010a) suggest that even small differences in settling velocities and vertical position after excystment can have significant effects on dispersal distance. Chemical cues have been shown to promote and/or defer larval settlement in marine systems (Pawlik, 1992; Turner *et al.*, 1994; Hart and Finelli, 1999), and changes in flow conditions (flow velocity, turbulence) might act as physical cues for settling in suitable areas in lotic systems. Whether juveniles can detect and respond to such cues remains to be verified and merits further research (Schwalb and Ackerman, 2011).

Our hypothesis of restricted juvenile mussel dispersal influencing the spatial distribution of mussel beds assumes host fish populations overlap spatially with mussel bed locations, and most host fishes have limited dispersal. Indeed, many stream fish spend their life within a spatially restricted home range of < 100 m (Gerking, 1959; Gatz and Adams, 1994; Juanes *et al.*, 2000). McLain and Ross (2005) speculated limited dispersal of darter host fishes led to patchy distributions of mussels. In summer 2011 we conducted a mark-recapture study of host fish at four sites in one of our study rivers (the Little River) and found most fish moved < 20 m (Irmscher and Vaughn, 2015). Of course some fish species and individuals in mostly stationary populations do move longer distances, which is likely of great importance for long term mussel dispersal, and to maintain genetic connectivity (Horký *et al.*, 2014). For example mussels that have darters as their hosts frequently form genetically isolated subpopulations (Berg *et al.*, 2007), while those with more mobile hosts tend to form more homogenous populations (Berg *et al.*, 1998).

While juvenile dispersal was restricted in our study, migration must sometimes occur over longer distances or mussel populations would become genetically isolated. This dispersal over longer distances could be infrequent, yet still maintain genetic mixing among mussel subpopulations. For example Olson (2017) used microsatellites to examine genetic relatedness among multiple subpopulations of a common mussel species, *Amblema plicata*, in one of our study rivers, the Little River. He found significant isolation by distance, indicating that mussels that were spatially closer to one another were more closely related. However, he also found some close relatives were located over 100 km apart, indicating some propagules can move long distances. Dispersal over longer distances could occur if juveniles are carried downstream by higher flows than we had in our study (Daraio *et al.*, 2010a), or as larval mussels attached to their fish hosts. Studies of juvenile dispersal in larger, more turbulent systems than ours have found generally longer dispersal distances (Schwalb *et al.*, 2012). Ultimately, temporal differences in hydraulic conditions among rivers, as well as seasonally within rivers, should lead to differences in the dispersal potential of juvenile mussels, and thus affect the spatial distribution of adult mussels.

Mussel populations have become increasingly fragmented from dams and other anthropogenic factors, which has contributed to their overall decline (Haag, 2012). A rigorous understanding of mussel dispersal, including juvenile dispersal, is essential for establishing workable conservation strategies (FMCS, 2016). This and other recent studies (Daraio *et al.*, 2010a, 2010b; Schwalb and Ackerman, 2011; Schwalb *et al.*, 2012) have shown

that dispersal of juvenile mussels can be successfully predicted if settling velocities and hydraulic conditions are known. Settling velocities can be measured in the laboratory using actual juveniles, and we have shown that microparticles can be reasonably utilized as surrogates if juvenile mussels are not available, or cannot be used. However, large gaps in our understanding of the dispersal of juveniles and distribution of adult mussels remain. Additional experimental studies conducted across a broad range of riverine systems and flow conditions, combined with modeling efforts, should help alleviate this issue.

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