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UNIONID DRIFT DISPERSAL IN SMALL RIVERS

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BIOLOGY

BY

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Les rivières sont des chemins qui marchent, et qui portent où l'on veut aller.

Blaise Pascal (1623-1662)

FOR MY FAMILY

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ABSTRACT

Freshwater mussels (Bivalvia, Unionidae) are a guild of long-lived, burrowing, sedentary, filter-feeding animals that typically occur in dense aggregations called mussel beds. Mussel beds are often patchily distributed, with densely populated areas of a river channel separated by areas where mussels are absent or only sparse. Factors that drive these patchy distribution patterns are complex and highly interactive, and include physical habitat characteristics, food, predation, fish hosts, and dispersal. Of these parameters, dispersal has received the least attention; however, it is likely to be very important for mussel distribution. Unionid mussels have a complex life cycle: while adults are sedentary, mussel larvae are obligate ectoparasites on mobile fish hosts, and the juveniles drift downstream after excystment from the fish host. To date, no one has determined the relationship between juvenile drift dispersal and the distribution of adult mussels in rivers. I developed a conceptual model that includes parameters likely to determine the extent of unionid drift dispersal in rivers. I then tested this model with a series of laboratory experiments and field studies.

In the laboratory, I measured sinking velocities of juvenile mussels of 4 species and those of polymer microparticles that I used as surrogates for juveniles in subsequent experiments. I built a re-circulating flow flume to compare distances that surrogate microparticles drifted over plain gravel versus an artificially created mussel bed. I conducted a field study where I recorded drift distance by releasing and recapturing surrogate microparticles at 5 sites in 2 small rivers in southeastern Oklahoma, USA. I found that sinking velocity values were larger, and drift distance values were smaller than previously reported for juvenile mussels, and that unionid dispersal seems to be

limited to a few centimeters to several meters. I also found that mussel shells decreased drift distances compared to plain gravel, and that rapid changes in channel bed slope created hydraulic conditions that favored juvenile settlement in certain areas.

For another field study, I hypothesized that host fish not only serve as dispersal agents for sedentary mussels, but that host movement during infestation with mussel larvae also had an upstream bias that allowed mussels to compensate for downstream displacement with the flow. To test this, I conducted a mark-and-recapture study of host fishes, and found an overall upstream movement trend of 2.25 m. I recaptured most individuals at the transect of their original capture which is in agreement with the Restricted Movement Paradigm. In combination with short drift distances of juveniles, limited host fish movement is an explanation for the patchy distribution of unionid mussels in rivers.

Finally, I examined effects of flow on juvenile dispersal and adult mussel distribution by releasing fluorescent dye into the flow at 6 well-defined mussel bed locations. This allowed me to depict potential pathways of drifting juveniles, and those of suspended particles within the channels. I recorded the spread of dye via aerial photography and geo-referenced images in GIS for further spatial analysis. In addition, I measured water depth as a basis for computing channel bed slope and aspect, and extracted dye greenness values to examine correlations with mussel density and biomass. I found that water depth was not a good predictor, while a channel's bed slope was a limiting factor to where mussels occurred. Channel bed aspect had no predictive value, whereas mussel abundance was highest for intermediate greenness values, indicating a certain range of flow velocities that selectively promote juvenile mussel

settlement and growth, as well as long-term survival of adult mussels in certain areas of a channel.

In summary, I found unionid dispersal to be limited due to restricted host fish movement and short juvenile drift distances. This is in contrast to some findings from computer simulation models, and can be regarded as an explanation for the aggregated spatial distribution that is so typical for unionid mussels. Bed morphology drives local flow patterns which in term determine where juveniles settle and grow into adults. My findings have important implications for future studies of mussel metapopulation structure and the genetic connectivity of populations of highly endangered unionid mussels. They will also support management efforts that aim for better protecting unionid mussels and their riverine habitats, especially in the context of changing flow regimes due to global climate change and the extraction of water for human usage.

CHAPTER 1

SINKING VELOCITIES AND DRIFT DISTANCE OF JUVENILE UNIONID MUSSELS IN SMALL RIVERS

Keywords:

dispersal, juvenile, unionid, freshwater mussel, reproductive cycle, drift distance, drift phase, microparticle, flow flume, field experiment

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ABSTRACT

Freshwater mussels (Bivalvia, Unionidae) are a guild of burrowing, long-lived, filter-feeding bivalves. Because adults are sedentary, they must disperse their offspring through passive modes, as larvae attached to a fish host and by drift of juveniles after excystment from the host. We developed a conceptual model to investigate the various components that determine how far juveniles are displaced downstream with the flow while sinking to the bottom of a river, and conducted experiments to empirically quantify these components. In laboratory experiments, we measured the sinking velocities of juvenile mussels of 4 species, and the sinking velocities of polymer microparticles that we utilized as surrogates for juveniles. We used a re-circulating flume to measure the distances that surrogate polymer microparticles drifted over plain gravel and an artificially created mussel bed. Lastly, we conducted a field study where we measured drift distances by releasing and capturing surrogate microparticles at 5 sites in 2 small rivers in southeastern Oklahoma, USA. We found that the sinking velocities were larger and drift distances smaller than previously reported for juvenile mussels, and that unionid drift dispersal in small rivers seems to be limited to only a few centimeters to several meters. We also found that adult mussel shells decreased drift distances in comparison to plain gravel, and that rapid changes in channel slope created hydraulic conditions that favored juvenile settlement. Our findings of restricted dispersal in small rivers and our conceptual model of juvenile drift are important for future studies of unionid dispersal and metapopulation structure.

INTRODUCTION

Dispersal, the movement of individuals from one place to another, allows organisms to colonize patches of newly created habitat, or to recolonize patches in unstable and/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, most individuals moving either short or long distances (Wiens, 1976). Dispersal potential greatly depends on mobility (Townsend and Hildrew, 1994). Mobile animals can conduct migrations, which are 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 drift of stream insect larvae and other invertebrates refers to their downstream transport with currents, which enables them to escape unfavorable conditions and re-/colonize (new) habitat (Waters, 1972; Brittain and Eikeland, 1988). Dispersal by drift also provides a reasonable model for the patchy distribution of many aquatic invertebrates that is so typical of running waters (Roughgarden, 1977; Minshall and Petersen, 1985; McLain and Ross, 2005).

Freshwater mussels (Bivalvia, Unionidae) are a guild of sedentary, burrowing, long-lived, filter-feeding bivalves that often occur as dense, multi-species aggregations called mussel beds (Strayer et al., 2004; Vaughn, 2010). Mussel beds in rivers are typically patchily distributed and separated by vast areas where mussels do not occur or are only sparse (Strayer, 2008). Although researchers have examined causes for this

patchy distribution for well over a century, questions remain about the underlying mechanisms (Daraio et al., 2012). Early investigations focusing on simple habitat parameters such as substrate size and flow velocity could not adequately explain these patchy distributions (Holland Bartels, 1990; Strayer and Ralley, 1993; Brim Box et al., 2002). Subsequent studies incorporating complex hydraulic parameters have more successfully explained spatial distributions (Layzer and Madison, 1995; Hardison and Layzer, 2001; Steuer et al., 2008; Allen and Vaughn, 2009). The flow refuge concept by Strayer (1999) assumes that mussel beds occur where sediments remain stable during high flows, providing protection from scouring and dislodgement. To date, most studies have concluded that the patchy spatial distribution of mussel beds is primarily related to the habitat requirements of adult mussels; however, only few studies have investigated the dispersal and habitat requirements of juvenile mussels (Haag, 2012).

While adult mussels are sedentary with only limited mobility, their propagules are highly mobile (Strayer, 2008; Gough et al., 2012, Kappes and Haase, 2012). Mussel larvae (glochidia) are obligate ectoparasites to fish and are dispersed to new habitats through fish movement (Barnhart et al., 2008). After metamorphosis, juveniles drop off and are further dispersed via drift (Morales et al., 2006a). Thus, these 2 early life stages are important for where mussel beds occur.

However, only few studies have empirically examined the role of juveniles in mussel distribution, likely because they are small (usually < 500 μm) and difficult to detect in the field (Holland-Bartels, 1990). While early publications hypothesized that juvenile dispersal might be important to adult distribution (Isely, 1911; Ortmann, 1919; Coker et al., 1922; Howard and Anson, 1922; Baker 1928), the specific habitat

requirements of juvenile mussels continue to be largely unknown (Newton et al., 2008; Strayer 2008; Daraio et al., 2010a). Bottom shear stress has been suggested as major parameter that determines the suitability of locations for juvenile settlement (Layzer and Madison, 1995), and strong correlations between shear stress and adult density might actually reflect juvenile recruitment (Hardison and Layzer, 2001; Allen and Vaughn, 2010; Daraio et al. 2010a).

Several researchers have used simulation modeling to predict juvenile dispersal, and to explore the importance of juveniles for the distribution of adult mussels. Lee and DeAngelis (1997) used a spatially explicit, age-structured model to simulate freshwater mussel dispersal, re-/colonization 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 freshwater mussel beds. They found that flow was the decisive factor for dispersal distances and colonization patterns. Building on the work of Morales et al., Daraio et al. (2010a; 2010b; 2012) used stochastic Lagrangian particle tracking in a three-dimensional flow field to integrate hydrodynamic data with the model created by Morales et al. They found that juvenile settling was mainly a function of flow velocity, and that hydraulic conditions had significant effects on settling of juvenile mussels after excystment. While these models provide important insights and hypotheses about juvenile dispersal, they also need to be tested empirically (Daraio et al., 2010a).

We developed a conceptual model that assumes that the distance a juvenile mussel drifts after excystment from its host is determined primarily by the combined effects of flow velocity, the juvenile's sinking distance, and its sinking velocity (Fig. 1).

We conducted laboratory experiments that quantified the sinking velocities of juveniles of 4 mussel species, as well as the mean sinking velocity of fluorescent polymer microparticles which we utilized as surrogates for juveniles in subsequent experiments. We measured drift distances of surrogate microparticles at 3 flow velocities in a flume, and under natural low flow conditions at 5 sites in 2 small rivers in southeastern Oklahoma, USA.

METHODS

Sinking velocity experiments and surrogate microparticle evaluation

We conducted a laboratory experiment to determine juvenile sinking velocity, which we define as the velocity at which a juvenile mussel sinks after excystment. We filled a glass cylinder (60x18 cm) with well water to a depth of 55 cm and placed it in a temperature-controlled room. To detect differences in temperature-induced water densities that would have affected sinking 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 expressed any temperature differences as standard deviations from the mean.

We obtained ~ 400 live juvenile mussels of 4 species (*Lampsilis cardium, Lampsilis siliquoidea, Villosa constricta, Villosa iris* – see Table 3 for mean shell diameters) from the USFWS National Fish Hatchery in White Sulphur Springs, WV, USA. The juveniles were express-shipped in a cooler overnight. Before running experiments, we determined juvenile viability by observing them under a light

microscope (Olympus CKX41, Center Valley, PA). We used only individuals that had active shell and/or foot movement. To minimize wall effects, we released all juveniles individually with a glass pipette at the surface and in the center of the glass cylinder (Vogel, 1994). Starting at a water depth of 50 cm, we recorded the time in seconds it took the juvenile to pass each interval until it reached the bottom. We conducted 30 trials per species and used a new individual for each trial.

To detect potential differences in sinking velocities between live and dead juveniles, we also measured sinking velocities of dead mussels. We froze juveniles that had not been used in previous trials, and only used individuals that had intact, closed shell valves to ensure that morphological characteristics were similar between live and dead specimens. We ran 30 trials per species, as described above.

Finally, we recorded sinking velocities of polymer microparticles, to determine whether these could be utilized as surrogates for juvenile mussels. We compiled information on juvenile shell diameter (d_m in μm) and specific gravity (ρ_m in cc^{-1}) from the literature, and also determined d_m by measuring 30 individuals per species from our samples with a light microscope (Olympus CKX41, Center Valley, PA).

In the literature, values for juvenile mussel shell diameter ranged from 150 to 500 μm, with a non-weighted mean of 250 μm (Table 1), while the values for juvenile specific gravity (ρ_m) ranged from 1 to 1.28 g cc^{-1}, with a non-weighted mean of 1.16 g cc^{-1} (Table 2). Our own measurements of juvenile shell diameter (d_m) across the 4 species ranged from 261.67 to 279.17 μm, with a mean of 270.63 μm (Table 3). Based on this information, we chose fluorescent polymer microparticles from Cospheric Inc.,

Santa Barbara, CA, with a similar diameter (d_m = 300-355 μm) and specific gravity (ρ_m = 1.28 cc^{-1}). To increase the visibility of fluorescent polymer micropsheres during trials, we placed a UV-A light source next to the glass cylinder before running 30 trials, as described above.

For live mussels, we calculated the mean sinking velocity for each species individually, as well as for all 4 species combined. In addition, we computed mean sinking velocities for dead juveniles (all species combined) and surrogate microparticles. We compared mean sinking velocities between mussel species with a One-Way ANOVA, and between live juveniles and the microparticles with an unpaired t-test. Because the data did not meet normality, we compared mean sinking velocities between live and dead juvenile mussels with a Mann-Whitney U test. We analyzed differences in drift distance over plain gravel versus mussel shells with a Two-Way ANOVA. Statistics were performed in JMP 8.0 software.

Flume drift distance experiments

To investigate the relationship between flow velocity and drift distance, we measured drift distances of fluorescent polymer microparticles (described above) in a flume under 3 different flow velocities. We utilized microparticles as surrogates because minute juveniles were not visible in the flume, whereas the fluorescent microparticles could be detected easily with UV-A light. As stated above, the size and specific gravity of microparticles was approximately the same as those of juvenile mussels, and their sinking velocities did not differ from juvenile mussels, which made

them appropriate surrogates. We built a re-circulating flow flume (following Nowell and Jumars, 1987; Vogel, 1994; Cahoon and Hoshino, 2003) 850 cm long, 60 cm wide, and 60 cm deep, with a working area length of 715 cm, above which we installed eight 61 cm UV-A light sources that illuminated fluorescent microparticles. We installed twelve 60x45 cm Lexan polycarbonate sheets in the front panel of the flume that allowed us to visually track the drifting microparticles. We covered the bottom of the flume with a layer of gravel 10 cm deep (mean particle size 18.99 mm (± 3.26 SD)) and filled it with tap water to a depth of 50 cm. Electronic speed controls allowed us to alter revolutions of 2 propellers driven by electric motors at the up- and downstream ends of the flume that created flow velocities of 0.61, 1.52, and 3.05 cm sec^{-1}. We measured the flow velocities at 66 % of the water depth with an electro-magnetic flow meter (Marsh-McBirney Flo-Mate 2000, Frederick, MD). At each flow velocity, we released 30 microparticles one at a time, and measured their drift distances, which we defined as the distance a microparticle moved until it came to rest on the bottom and stopped drifting.

Shells protruding from a mussel bed increase bottom roughness which – under low flow conditions – in turn increases the vertical extent of the bottom boundary layer (Eckman, 1990). To examine how this influenced drift distance, we modified the flume substrate by creating an artificial mussel bed constructed of mussel shells that we glued together and buried in the gravel in a natural pattern, with posterior shell edges partially exposed. 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 experiment under these modified conditions, as described above.

Field drift distance experiment

To determine how far juvenile mussels drift in small rivers, we released microparticles (diameter 300-355 μm, specific gravity 1.28 cc^{-1}, as described above) at 5 sites in 2 small rivers in southeastern Oklahoma, USA (Table 4). Sites 1 and 2 were located in the Little River, which has a basin area of 10,720 km^2 and a mean annual discharge of 183 m^3 s^{-1}. Sites 3, 4, and 5 were located in the Kiamichi River, with a basin area of 4650 km^2 and a mean discharge of 48 m^3 s^{-1} (Matthews et al., 2005). We chose these 5 sites because they have well-defined mussel beds with high mussel abundance and richness, as well as channel and flow characteristics representative of mussel bed locations in small rivers of southeastern Oklahoma (Matthews et al., 2005; Vaughn, unpublished data). We conducted these experiments in July 2012 and July 2013, under summer low flow conditions typical for the reproductive period of most unionid species in our study area.

At each site, we placed drift nets (opening 25x25 cm, 25 cm long, mesh size 300 μm) in a 10 m (spacing between transects) by 5 m (spacing between nets) grid, with the openings facing into the flow (Table 4). We measured flow velocities with an electro-magnetic flow meter (Marsh-McBirney Flo-Mate 2000, Frederick, MD) in increments of 1 m at Transect 5 at each site, before releasing 30 g of microparticles at the surface, spread out evenly across the entire width of the channel. We recovered drift nets after 24 h and placed them into large Ziploc bags. In the laboratory, we rinsed out nets and counted the number of microparticles per net with the help of UV-A lights (Table 4). We plotted the number of microparticles per drift net in relation to drift distance from the release point and water depth at each transect. We ran 1 trial per site.

RESULTS

Sinking velocity experiments and surrogate microparticle evaluation

We did not find significant differences in sinking velocity between the 4 species tested ($F_{(3)} = 1.41$, $p = 0.24$; Fig. 2a). However, there was a significant difference in the mean sinking velocities of live versus dead juveniles (pooled by species), live juveniles sinking at a significantly slower rate ($U_{(119)} = 3664$, $p < 0.001$; Fig. 2b). We detected no significant difference between mean sinking velocities of live juveniles and microparticles ($t_{(148)} = 1.039$, $p = 0.3003$; Fig. 2b). Mean water temperature during the experiment remained constant at 19.6 °C and did not vary with water depth (± 0.0826 SD).

Flow flume drift distance experiments

Drift distances in the flume over plain gravel increased exponentially with an increase in flow velocity ($R^2 = 0.98$; Fig. 3). Drift distances over the artificial mussel bed also increased exponentially with flow velocity ($R^2 = 0.98$; Fig. 3), but were consistently shorter (on average by 25 cm (± 7.93 SD) across the 3 flow velocities) than over plain gravel (Fig. 3). We ran a Two-Way ANOVA comparing drift distances over the 2 substrate types across the 3 flow velocities (0.61, 1.52, 3.05 cm sec^{-1}). We found significant differences in drift distances between the 2 substrate types ($F_{(2, 174)} = 28.33$, $p < .001$) and between flow velocities ($F_{(2, 174)} = 1332.95$, $p < .001$), but no significant interactions between the substrate types and flow velocity ($F_{(2, 174)} = 0.92$, $p = 0.39$). Water temperature remained constant at 18.4 °C for all 6 trials.

Field drift distance experiment

Across all sites, we captured most microparticles (41.73 %) at a drift distance of 10 m, with a second peak (39.58 %) at 40-50 m. Most captured microparticles (~ 93 %) traveled < 50 m (Fig. 4). Water depth decreased in a downstream direction with a sharp decrease at 10-30 m and 50-70 m (Fig. 4). At all sites, most microparticles accumulated 10-20 m upstream of those areas within the channel cross section were there was a steep gradient of the river bottom slope (as displayed in Fig. 4).

Mean flow velocities at the sites reflect summer low flow conditions typical for small rivers of southeastern Oklahoma (Table 4). The much higher mean flow velocity at Site 2 (14.75 cm sec^{-1}) relative to the other sites (0.47, 4.73, 3.86, and 0.87 cm sec^{-1}) can be explained by an increase in the local bed slope that restricts flow vertically at this site. Including Site 2, the overall mean flow velocity across all 5 sites was 4.94 cm sec^{-1} (± 5.79 SD); without it, this value dropped to 2.48 cm sec^{-1} (± 2.13 SD).

DISCUSSION

Our findings indicate that unionid mussels in small rivers have limited dispersal potential under summer low flow conditions. Our results suggest that juvenile mussels drift only relatively short distances from where they drop off their fish hosts. In relation to juvenile sinking distance and local flow conditions, some individuals will certainly drift farther distances, and secondary displacement of juvenile mussels after settling in the substrate by scouring is likely an important factor for farther downstream relocation, although most juveniles most likely disperse only little.

Sinking velocity values used in a model will have large effects on the simulated drift distances. The sinking velocities we recorded for live juvenile mussels (mean 0.27 cm sec^{-1}) were similar to, or lower than, those (mean across 4 species 0.34 cm sec^{-1}) by Schwalb and Ackerman (2011). In contrast, Morales et al. (2006a) used a value of 0.03 cm sec^{-1} in their model which is an order of magnitude lower than empirically measured values for freshwater juveniles. This value was derived from marine juvenile mussels, but the density of saltwater and, as well as the shell diameter and specific gravity of marine juvenile bivalves are different than those in freshwater. Morales et al. (2006b) concluded that, depending on flow conditions in the river, juvenile mussels can travel considerable distances (up to kilometers) before settling. This may be true in large river systems; however, the majority of rivers are small to medium in size. We suggest that underestimating juvenile sinking velocities can lead to overestimates of drift distances, which can in turn inflate estimates mussel of dispersal potential.

Juvenile unionid mussels might be able to influence their sinking through morphological and behavioral adaptations. For example, some species deploy byssal threads that are several centimeters in length, and increase buoyancy and attachment probability (Payne and Miller, 2000). Schwalb and Ackerman (2011) report of 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 may be used to produce microcurrents that enable juveniles to control their descent in the water. These observations are supported by the fact that dead individuals, on average, sank 0.1 cm sec^{-1} faster than live ones. Although these microcurrents are most likely insufficient to override strong hydraulic forces of turbulent flow (Schwalb, 2009), Daraio et al.

(2010a) point out that even small differences in sinking velocities and the vertical position after excystment can have significant effects on dispersal distance. Changes in flow (flow velocity, turbulence) might act as physical cues for settling in suitable benthic habitat, and chemical cues have been shown to promote or defer larval settlement in marine systems (Pawlik, 1992; Turner et al., 1994; Hart and Finelli, 1999). Whether juvenile unionid mussels can detect and respond to such cues remains to be verified (Schwalb and Ackerman, 2011).

Despite potential behavioral and morphological adaptations that control juvenile sinking we did not find a significant difference in sinking velocity between live juvenile mussels and the polymer microparticles we chose for our experiments. Propagating unionid mussels is complex and laborious, and because of their small size, juveniles are hard to detect and trace in the field (Neves, 2004). Our results have shown that microparticles that are relatively cheap and readily available can be utilized as surrogates for juveniles to study unionid dispersal.

Drift distances are affected by flow velocities and sinking distances. Both in our flume experiment and in the field, drift distance was positively correlated with velocity. For standardization, we released all microparticles at the water surface; however, many fish species that are hosts to unionid mussels are benthic and release juvenile mussels close to the stream bed (Barnhart et al., 2008). Thus, sinking distances in rivers may be considerably lower which also decreases drift distance. Our findings may actually over-estimate drift distance which could be restricted to a few centimeters to several meters. This is in agreement with numerous studies of the drift of stream macroinvertebrates which have shown that drift distances are usually in the range of centimeters to a few

meters (McLay, 1970; Elliot, 1971; Waters, 1972; Brittain and Eikeland, 1988; Palmer, 1992; Lancaster et al., 1996; Fonseca, 1999; Elliot, 2003), occasionally tens of meters (Waters, 1965; McLay, 1970; Palmer, Allan and Butman, 1996; Fingerut et al., 2006), and rarely up to hundreds of meters (Hemsworth and Brooker, 1979).

Based on our findings, we support the hypothesis that limited dispersal potential of juvenile unionid mussels may be an explanation for the patchy distribution of mussel beds in rivers, i.e. that most juvenile mussels settle and grow to adulthood within a short distance of where they dropped of their host. Due to the fact that juvenile mussels must settle to the bottom after excystment and because both adult and juvenile mussels live in the bottom substrate, hydraulic conditions that are most relevant for mussel distribution are those that characterize flow near the river bed (Hardison and Layzer, 2001). For the flow velocities tested in the flume, we found drift distances to be on average 25 cm shorter over a mussel bed than over plain gravel. Under low flow conditions, increases in bottom roughness also increase the vertical extent of the bottom boundary layer, the part of the water column in which velocity is less than 99 % of the free flow velocity (Statzner et al., 1988). Drifting juveniles entering this zone settle straight to the bottom, without any further displacement. We suggest that the presence of mussel beds can alter local flow conditions to an extent that promotes juvenile settlement, relative to adjacent areas without adult mussels. This leads to a self-reinforcing effect that increases the probability that juveniles settle in areas where habitat conditions are favorable for survival and growth.

Our hypothesis of restricted unionid mussel dispersal is partially based on the assumption that host fish populations overlap spatially with mussel bed locations, and that mussel host fishes have only limited movement. Although the spatial extent of fish movement certainly depends on species, numerous studies have shown that most stream fishes are stationary, have territorial behavior, and spend most time of their life within a spatially limited home range (Gerking, 1953; Funk, 1957; Miller, 1957; Gerking, 1959; Scalet, 1974; Gatz and Adams, 1994; Juanes et al., 2000; McLain and Ross, 2005; Zitek 2006). Other studies have found that the proportion of populations leaving the home range and that moves over long distances is small (e.g., Heggenes et al., 1991; Smithson and Johnston, 1999; Rodriguez, 2002). McLain and Ross (2005) speculated that the limited dispersal of darter host fishes cause patchy mussel distributions, also leading to metapopulation structure.

Our field study results were consistent with what we found in laboratory experiments. A decrease in the number of individuals found with increasing distance has been documented for other drifting invertebrate stream organisms, and it is best described as an inverse power function (McLay, 1970; Elliott, 1971; Larkin and McKone, 1985; Palmer, 1992; Fonseca, 1999; McNair and Newbold, 2001; Elliot, 2003). We consistently found many microparticles not only at 10 m, but also at 40-50 m at all sites (Fig. 4). A similar pattern was detected by Schwalb et al. (2010) in some trials where most glochidia were not captured at the first net (4 m), but in subsequent nets (8 and 16 m) downstream. Although turbulent flow conditions that can cause a re-/suspension of particles can be one potential explanation, we hypothesize that this differential settling is directly related to longitudinal channel morphology at our sites.

We captured most of the microparticles at 10 m and 40-50 m from the release transect, and consistently about 10-20 m upstream of locations with a significant decrease in water depth, where the channel bottom ascends rapidly (Fig. 4). Many mussel beds in our study rivers are situated in the downstream end of pools just before subsequent riffles. Riffles act as submerged dams that slow down the release of water from pools behind them (Yang, 1971). This "dam effect" creates locally defined areas where drifting juvenile mussels tend to settle out preferentially.

Results from our field study support the fact that settlement from drift is affected by local conditions and step gradients in the interfacial world between the water column and the river bed (Hart and Finelli, 1999). Changes in the bottom profile of a river can be quantified as differences in elevation over a defined distance, expressed in degrees as channel slope. Zigler et al. (2008) found that, besides bottom shear stress, channel slope may influence the distribution and abundance of unionid mussels in beds. Channel slope reflects overall, reach-scale hydraulic and substrate characteristics, and has potential in identifying areas of rapidly changing hydraulic conditions at the sediment-water interface that can favor the settlement of juvenile mussels (Zigler et al., 2008).

We showed that the 3 parameters of our conceptual model (Fig. 1), flow velocity, sinking distance, and sinking velocity, can be used to successfully investigate the drift distances of juvenile mussels. Our empirical experiments in a flume and 2 small rivers indicated that drift distances are small under summer low flow conditions and range from a few centimeters to meters. Juvenile mussel drift distances are highly dependent on flow conditions which, due to the turbulent nature of flow, are extremely difficult to model, especially for the wide range of spatial scales (μm to reach) at which

physical processes act on drifting juvenile mussels. Our empirical investigations in the laboratory and in the field indicate that the estimates of drift distances in large rivers from previous simulation modeling may be too high to apply to the small southern rivers where mussel biodiversity is highest (Haag, 2012). Although flow conditions in large rivers may differ from our study streams, we argue that many fish that are hosts to unionid mussels will be near the bottom when juveniles drop off, and that most of them will therefore only drift short distances. In addition, studies have shown that stream fish movement tends to be spatially restricted. Future studies that will investigate the spatial patterns of host fish populations and the movement behavior of fish during larval infestation are needed. In addition, studies examining gene flow are necessary to document dispersal within and between beds. The results from our microparticle release experiments in the flume and in the field indicate that mussel beds have a self-reinforcing effect on juvenile settlement and recruitment, and that locations just upstream of areas with rapid changes in bottom slope are preferential settling sites for juvenile mussels. Our study confirms that mussel dispersal is highly correlated with flow and changes in bottom morphology, making it sensitive to human-induced alterations of rivers and their flow regimes. The effects of water diversions for human use and of climate change are concerns that will have to be taken into account in future efforts to preserve and manage unionid mussels and their riverine habitats.

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Table 1. Publications with information on juvenile mussel shell diameters (d_m). Columns show publications that contain information on juvenile shell diameter, 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*	220x220
Daraio, Weber, and Newton, 2010a	*Lampsilis cardium*	230x250
Daraio et al., 2010b	*Amblema plicata*	220x220
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*	220x220
Wächtler et al., 2001	Anodontoides	200
	Mutela	150

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

Publication	**Species**	**ρ_m [g/cc]**
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

Table 3. Measurements of juvenile mussel shell diameter (d_m in μm) for species we used in our sinking experiment (N = 30 individuals per species).

Species	**d_m [μm]**
Lampsilis cardium	279.17 (± 24.64 SD)
Lampsilis siliquoidea	271.67 (± 33.95 SD)
Villosa constricta	261.67 (± 36.98 SD)
Villosa iris	270.00 (± 27.39 SD)
across-species mean	270.63 (± 7.18)

Table 4. Characteristics of the 5 sites located in the Little and Kiamichi Rivers. We measured channel width, water depth, and flow velocity at Transect 5 at each site. We recorded flow velocities with an electro-magnetic flow meter (Marsh-McBirney Flo-Mate 2000, Frederick, MD) in 1 m increments across the channel. The number of nets placed in the channel at each site varies with channel width. At each site, we released ~ 150,000 – 300,000 microparticles. The numbers for microparticles captured are cumulative for all the nets at each site. GPS coordinates are in UTM, NAD83, Zone N15.

	Site 1	**Site 2**	**Site 3**	**Site 4**	**Site 5**
River	Little River	Little River	Kiamichi River	Kiamichi River	Kiamichi River
GPS Coordinates	0299358/3811669	0336540/3756900	0270114/3821052	0262813/3812530	0284034/3828445
Channel Width [m]	14	17	43	18	20
Mean Water Depth [cm]	18.00 (± 4.24 SD)	7.8 (± 3.82 SD)	59.1 (± 21.87 SD)	46.83 (± 12.21 SD)	40.14 (± 16.11 SD)
Mean Flow Velocity [cm/sec]	0.47 (± 0.62 SD)	14.75 (± 6.91 SD)	0.87 (± SD 1.19)	3.86 (± SD 1.9)	4.73 (± SD 3.06)
Number of Nets	34	36	75	71	82
Number of Microparticles	168	155	334	165	237

Figure 1. Conceptual model of juvenile unionid drift. The drift distance of a juvenile mussel after excystment from its fish host depends on flow velocity, juvenile sinking distance, and its sinking velocity. 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 sinking juvenile in response to differing flow velocities within the water column. Drift distance increases with larger flow velocity and sinking distance values, and lower sinking velocities. Drift distance decreases at lower flow velocities and sinking distances, and larger sinking velocity values.

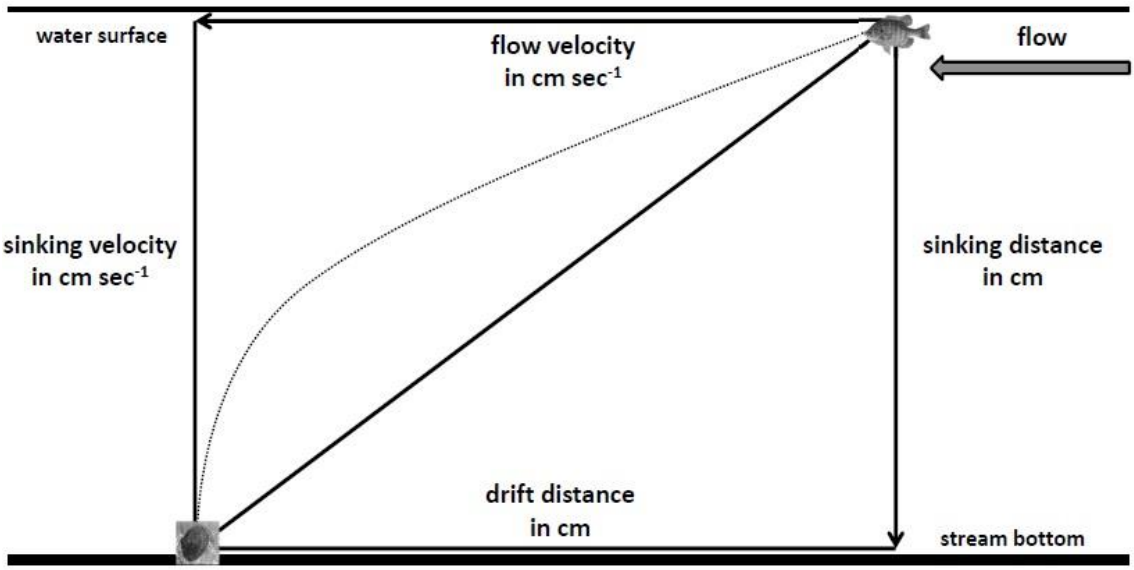
Figure 2a. Difference in sinking velocities by species. Box plots display sinking velocities for the 4 species tested (*Lampsilis cardium, Lampsilis siliquoidea, Villosa constricta*, and *Villosa iris*). Dashed lines represent means, solid lines medians. Upper box boundaries indicate 75th percentiles, bottom boundaries 25th percentiles. Error bars represent 90th and 10th, dots 95th and 5th percentiles. The mean sinking velocities are 0.26 cm sec^{-1} for *Lampsilis cardium,* 0.28 cm sec^{-1} for *Lampsilis siliquoidea*, 0.29 cm sec^{-1} for *Villosa constricta*, and 0.25 cm sec^{-1} for *Villosa iris*.

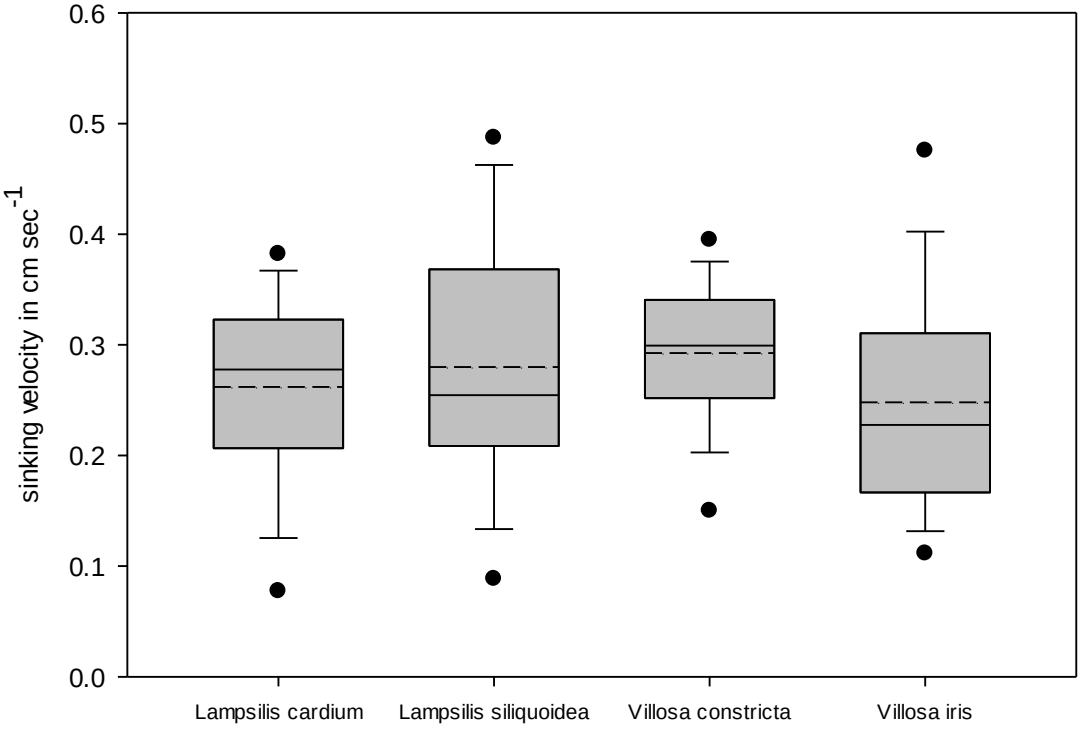
Figure 2b. Differences in sinking velocity of dead and live juveniles, as well as of live juveniles and microparticles. Box plots display sinking velocities for dead and live juveniles, and those of microparticles. Dashed lines represent means, solid lines medians. Upper box boundaries indicate 75th percentiles, bottom boundaries 25th percentiles. The error bars represent 90th and 10th, dots 95th and 5th percentiles. Mean sinking velocities are 0.37 cm sec^{-1} for dead juveniles, 0.27

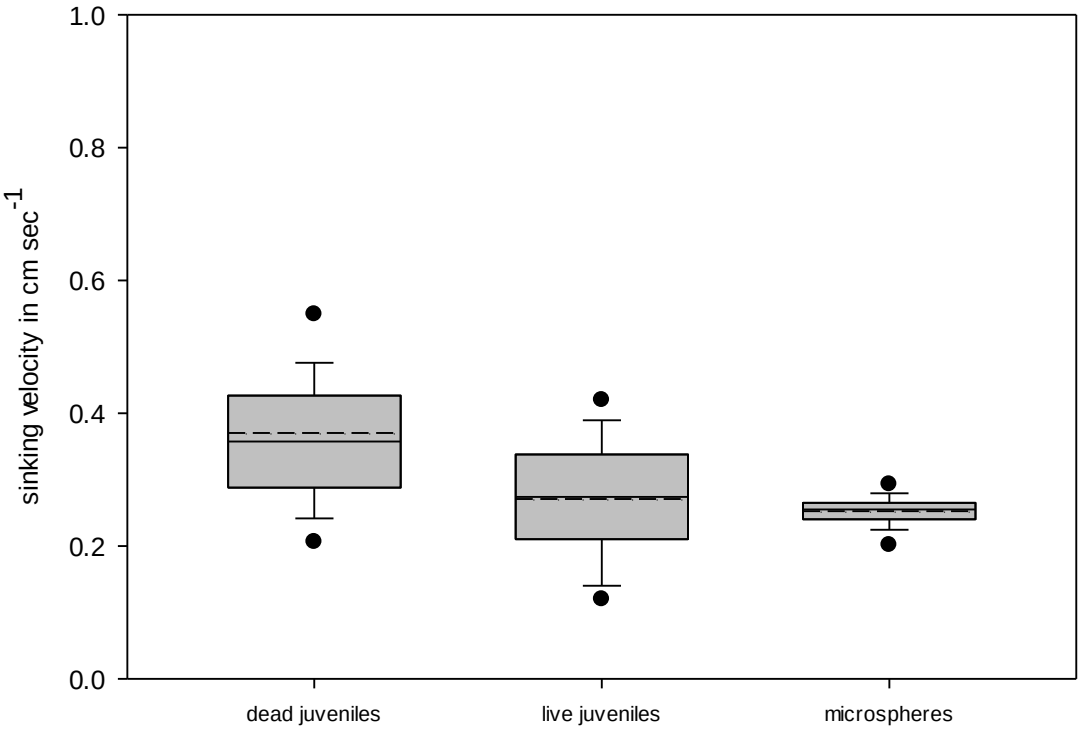
cm sec^{-1} for live juveniles, and 0.25 cm sec^{-1} for fluorescent polymer microparticles.

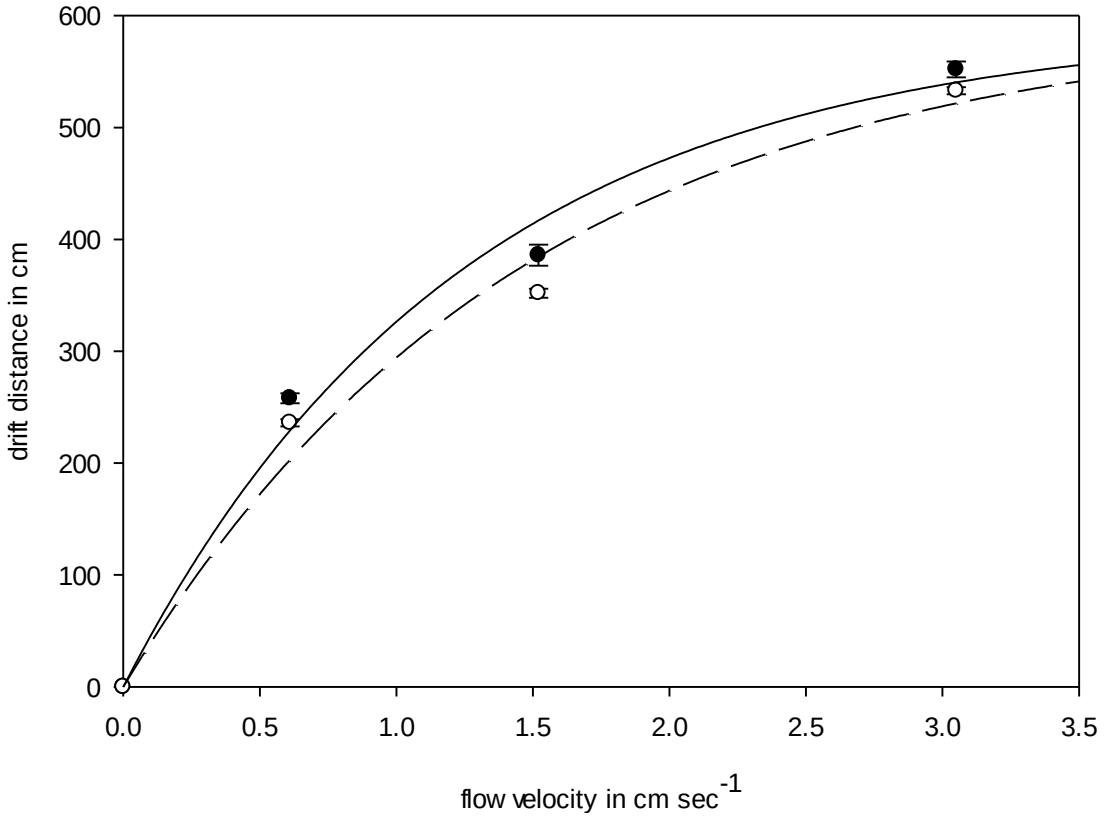
Figure 3. Drift distances in relation to flow velocities. Solid black dots represent drift distances over plain gravel of 258, 386, and 552 cm for flow velocities of 0.61, 1.52, and 3.05 cm sec^{-1}. R^2 for the non-linear regression is 0.98. White circles represent drift distances over a mussel bed of 236, 352, and 533 cm for flow velocities of 0.61, 1.52, and 3.05 cm sec^{-1}. The overall mean drift distance was 25 cm shorter over the mussel bed than over gravel. Error bars display standard errors.

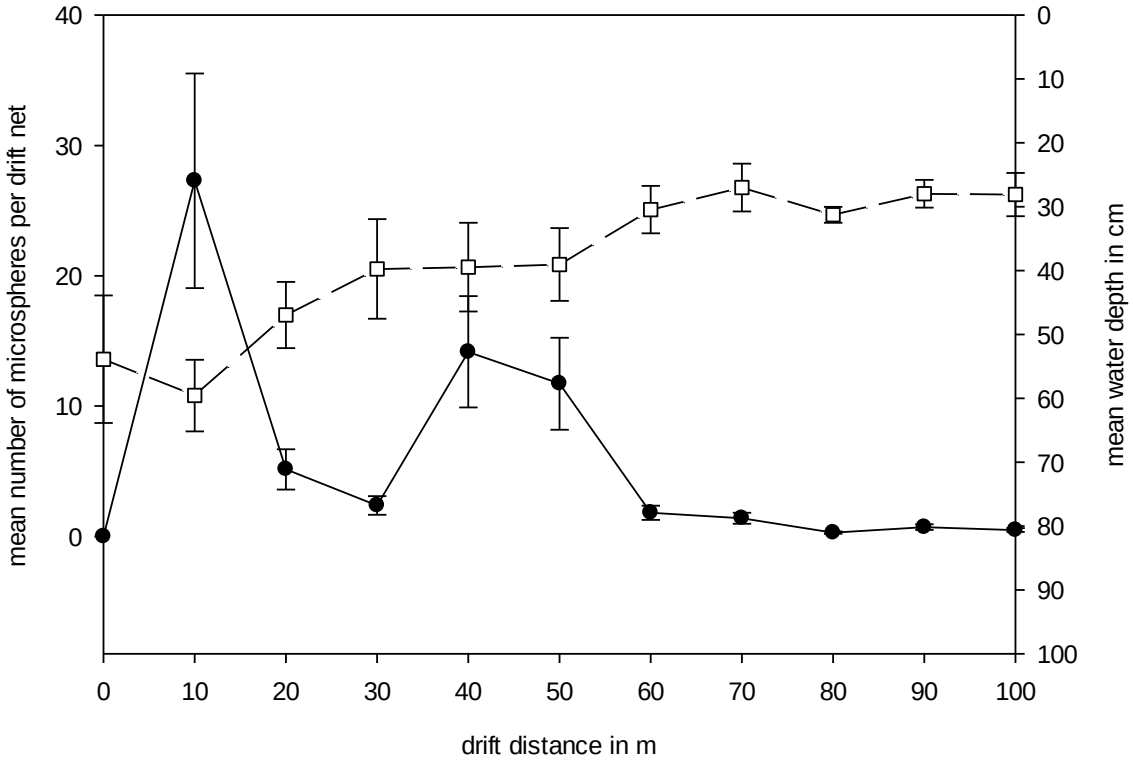
Figure 4. Mean number of microparticles per drift net and mean water depth in relation to drift distance. Solid black dots represent the mean number of microparticles per drift net in relation to drift distance. There is an initial peak at 10 m where we captured the most, and another peak at 40 to 50 m where we found the second highest number of microparticles. Beyond 50 m, values drop off markedly. White squares represent mean water depths at each drift distance; the line connecting the white squares displays the mean longitudinal bottom profile of the channels that we studied. Mean water depth consistently decreased 10 to 20 m downstream of transects where we captured most microparticles. The error bars represent standard errors.


water surface
flow velocity
in cm sec-1
flow
sinking velocity
in cm sec-1
sinking distance
in cm
drift distance
in cm
stream bottom


0.6
0.5
0.4
0.3
0.2
0.1
0.0
sinking velocity in cm sec-1
Lampsilis cardium
Lampsilis siliquoidea
Villosa constricta
Villosa iris


1.0
0.8
0.6
0.4
0.2
0.0
sinking velocity in cm sec-1
dead juveniles
live juveniles
microspheres


600
500
400
300
200
100
0
drift distance in cm
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
flow velocity in cm sec-1


mean number of microspheres per drift net
mean water depth in cm
drift distance in m
0
10
20
30
40
50
60
70
80
90
100

CHAPTER 2

LIMITED MOVEMENT OF FRESHWATER MUSSEL FISH HOSTS

Keywords:

upstream compensatory movement, downstream drift dispersal, turbulent flow, patchiness, juvenile unionid mussels, host fish species

ABSTRACT

Rivers are characterized by unidirectional, continuous flow of water that can potentially displace river organisms. Mobile river organisms can compensate for their downstream displacement by actively swimming or crawling back upstream while sedentary organisms need other means to retain their position. Freshwater mussels (Bivalvia, Unionidae) have limited movement as sedentary adults, and juvenile mussels drift downstream. Mussel larvae (glochidia) are ectoparasites on fish, and it has been assumed that fish serve as mussel dispersal agents by transporting glochidia to new areas, but this assumption has not been empirically tested. We hypothesized that fish serve as dispersal agents, and that fish movement would have an upstream bias to compensate for downstream drift displacement of mussels. We conducted a mark-and-recapture study of host fishes in four 100 m reaches of the Little River, OK, in the summer of 2011. Most recaptured fish were centrarchids, and most recaptures occurred within 20 m of original capture locations. On average, recaptured fish tended to move upstream 2.25 m. Our study took place during a drought, and recaptures decreased with decreasing discharge, likely because fish moved out of their home ranges into deeper pools. The combination of limited host fish movement with an upstream bias and the downstream displacement of juvenile mussels can help explain the patchy distribution of mussel beds in rivers.

INTRODUCTION

Flow, the continuous, unidirectional, downstream movement of water within a confined channel, is a decisive characteristic of rivers (Fausch et al., 2002; Dodds et al., 2004; Binder et al., 2011). Flowing water permanently exerts hydraulic forces on bottom features from boulders to fine particles, and continually moves dissolved and particulate matter downstream (Pringle et al., 1988). Flow velocity and bottom roughness are important parameters that determine changes in flow from laminar to turbulent (Leopold et al., 1964; Vogel, 1994; Knighton, 1998). Besides flow conditions, the size and specific density of particles determine their displacement distance which can be kilometers for dissolved and fine particulate organic matter (Cushing et al., 1993), but rapidly decreases to meters to tens-of-meters for coarse particulate organic matter (Jones and Smock, 1991).

Hydraulic forces also affect live organisms that can become entrained and displaced with the flow. This occurs primarily during high flows and associated turbulent conditions, leading to a loss of individuals from the local population (Elliott, 1971). Larger and/or more mobile animals such as fish can compensate for their downstream displacement by moving back upstream, while smaller and/or less mobile animals such as many aquatic invertebrates must use other means to compensate for their displacement. Some aquatic insects have a winged adult stage that includes pre-oviposition, upstream flight (Wilzbach and Cummins, 1989; Anholt, 1995; Koop et al., 2001). Other examples for compensatory movement include the upstream crawling of insect larvae and nymphs on the substrate or in the interstitial space of the hyporheic zone (Brittain and Eikeland, 1988), upstream swimming of amphipods (Elliott, 1971;

Townsend and Hildrew, 1976; Williams and Williams, 1993), and the directed, upstream movement of pulmonate aquatic snails (Kappes and Haase, 2012).

Freshwater mussels (Bivalvia, Unionidae; hereafter "mussels") are sedentary organisms with adult movement ranges generally limited to several meters (Schwalb and Pusch, 2007; Allen and Vaughn, 2009; Gough et al., 2012). Mussels often occur in dense, multi-species aggregates known as mussel beds that are patchily distributed in areas of rivers with stable sediments and low shear stress (Allen and Vaughn, 2009; Haag, 2012). Mussels that have been dislodged after substrate scouring during floods can be washed downstream, potentially into less suitable habitat (Strayer, 1999). Since adult mussels have only limited movement ranges, repeated dislodgement and cumulative displacement can result in mussel beds being moved downstream over extended time periods (Layzer and Madison, 1995). Mussel propagules are also subject to displacement by drift (Irmscher, unpublished data; Schwalb et al., 2010), compounding this problem. However, mussel beds are generally not displaced over ecological time scales. In fact, we have documented mussel beds that have been in the same location for over 100 years (Vaughn, 2000). We think that this is because mussels have mechanisms that allow them to compensate for downstream displacement. Mussel larvae (glochidia) are obligate ectoparasites on the fins and gills of fish (Barnhart et al., 2008; Haag, 2012). Glochidia metamorphose into juveniles that excyst from the host and sink to the bottom where they continue to grow into adults. It has been long-assumed that fish serve as dispersal agents for otherwise relatively immobile mussels and that glochidia move upstream as hitchhikers on host fish (Watters, 1992; Strayer, 2008; Haag, 2012). Genetic evidence supports this assumption (Berg et al., 1998).

However, the importance of fish as dispersal agents has not been tested experimentally. To test this hypothesis, we conducted a mark-and-recapture study of host fishes at four mussel beds during the mussels' peak reproductive time period. We predicted an overall upstream movement trend of host fishes, counteracting the downstream displacement of adult and juvenile mussels over time.

METHODS

We conducted our study in the Little River in southeastern Oklahoma, USA. This well-studied river (watershed area 10,720 km^2) harbors ~ 110 fish and ~ 38 mussel species (Vaughn and Taylor, 1999; Matthews et al., 2005; Galbraith et al., 2008). Our study sites were ~ 100 m reaches each containing a large mussel bed. All sites were located on a USFWS wildlife refuge (Fig. 1). We conducted our study in June through August 2011, which is the peak reproductive time period for many of the local mussel species. Based on the well-known mussel fauna of this river (Supplement 1) we combined information from published literature and a continuously updated fish-host database to identify host fishes for mussel species at these 4 sites (Supplement 2). The most important host fish groups in the Little River are sunfish and bass (Centrarchidae), catfish (Ictaluridae), gar (Lepisosteidae), freshwater drum (Sciaenidae), golden redhorse (Catostomidae), darters (Percidae), and shiners (Cyprinidae).

At each site we used wading and snorkeling (with SCUBA in deeper areas) to identify the up- and downstream extent of the mussel bed and established 10 transects that were spaced 10 m apart, the first being the most upstream transect (Fig. 2). We sampled the fish communities at each site weekly with a backpack electro-fisher (Smith

& Root, Model 12-A), traversing each transect twice (Büttiker, 1992; Schlosser, 1995; Smithson and Johnston, 1999). We chose electro-fishing as a collection method because it has been used both frequently and effectively (Bohlin et al., 1989; Schlosser, 1995; Lucas and Baras, 2000), and because abundant underwater obstacles prevented the use of seines. At each transect, we placed captured individuals in a plastic bucket and marked those from host fish species by dorsal fin ray clipping and/or subdermal injection of acrylic dyes (Freeman, 1995; Lucas and Baras, 2000; Catalano et al., 2001). The marks indicated the transect of initial capture for each individual. We selected these marking techniques because they are inexpensive and easy to perform (Mourning et al., 1994; Freeman, 1995; Lucas and Baras, 2000), they were suited for the length of our study (Zerrenner et al., 1997), and they do not have negative effects on fish health and performance (Hughes et al., 2000). We treated fish with API Stress Coat Fish Conditioner (API Mars Fishcare, Chalfont, PA) and released them at the initial capture transect. In subsequent weeks, newly captured and recaptured individuals were marked using the same techniques. Dorsal fin ray clipping and dye color coding allowed us to determine the distance an individual had moved in relation to its transect of initial capture. Unfortunately, small fishes (darters, shiners) showed very high sensitivity to capturing and marking, and high mortality rates forced us to omit them from our study early on.

To relate the number of fish captured to these variables, we obtained discharge data from the USGS Little River Lukfata Creek gauge near Idabel, OK. The gauge is located between Sites 1 and 2 (Fig. 1), and it is representative of our sites. In addition, we continuously recorded water depth at Site 1 with a HOBO® data logger (Onset

Computer Corporation, Cape Cod, MA). We analyzed downstream versus upstream fish movement data with a Mann-Whitney U test and used regression to examine the relation between water depth and the number of captures. Statistical analyses were performed with IBM SPSS Statistics, Version 19 (IBM Company, Armonk, NY).

RESULTS

We captured 765 and recaptured 89 (11.63 %) fish, most of them at the transect of initial capture (Fig. 3). Recaptures decreased with increasing distance from original capture transects in either direction with a slightly positive (upstream) leptokurtic distribution (Fig. 3). On average, recaptured individuals moved 2.25 (± 14.04 SD) m upstream. This trend of little to no movement was observed for all fish groups investigated and most recaptures occurred within 20 m upstream or downstream of the initial capture transect (Fig. 3). Stationary and upstream movements were significantly great than downstream movements (Mann-Whitney U = 126, $p < 0.0001$).

Centrarchids comprised the largest proportion of all recaptures (Fig. 3). Although sunfish movements ranged from 30 m downstream to 50 m upstream, most individuals remained in their initial capture transect. Mean movement was 3.38 (± 13.37 SD) m upstream (Fig. 4). Bass had a slightly larger movement range of 50 m down- to 20 m upstream, while recaptures for other fish groups were low (catfish, freshwater drum, golden redhorse) or did not occur at all (gar). When individuals were recaptured, this occurred in the transect of original capture (Fig. 3).

The mean number of fish captured decreased with a decrease in mean discharge over the course of our study period (Fig. 5). Coincidently, an increase in discharge in

the end of the study period was associated with a concurrent increase in mean fish captures. In addition, the number of fish captured at all sites was positively correlated with changes in water depth ($R^2 = 0.74$, $p = 0.027$) (Fig. 6).

DISCUSSION

In our study, fishes that are hosts to unionid mussels showed a greater tendency to move upstream than downstream. Based on previous studies investigating the sinking and drift rates of juvenile mussels (Irmscher unpublished data; Schwalb et al., 2010; Schwalb and Ackerman, 2011) we estimated juveniles to drift approximately 50 to 250 cm during summer low flow conditions, which is within the same range of upstream movement of host fishes in the Little River. Kopp et al. (2001) introduced the term Exact Compensation to describe net upstream movements that *exactly* compensate for the drift of propagules settling in the vicinity of the parents. The idea that upstream migration by immature stages of stream animals compensates for downstream drift was previously considered (e.g. Bishop and Hynes, 1969; Elliott, 1971; Bird and Hynes, 1981; Williams and Moore, 1982; Wilzbach and Cummins, 1989), but has not been applied to unionid mussels. Studies of mussel-host relationships have frequently investigated luring strategies and aspects of glochidia-host interactions (e.g. Siteman et al., 2012), however upstream dispersal is an obvious advantage that mussels gain from the relationship with their host (Mansur and da Silva, 1999; Barnhart et al., 2008; Horký et al., 2014).

Our study of host fishes at 4 sites in one season is obviously only a snapshot in time and space. However, many stream fishes have been shown to a have tendency to move upstream in the summer (Gatz and Adams, 1994). Centrarchids are common and frequently used hosts of unionid mussels (Haag and Warren, 1997; Khym and Lazer, 2000) and have a greater tendency to move up- than downstream (Freeman, 1995). The same is true for white crappie (*Pomoxis annularis*), smallmouth bass (*Micropterus dolomieu*), and yellow bullhead (*Ameiurus natalis*) (Funk, 1957). Upstream movements in mottled sculpins (*Cottus bairdii*) were 23.4 % greater than downstream (McCleave, 1964), and both the common carp (*Cyprinus carpio*) and gizzard shad (*Dorosoma cepedianum*) move upstream in large numbers (Winston et al., 1991). A study by Gerking (1950) showed that stream fish moved upstream an average of 33.5 m farther than downstream during high flows. This makes sense since not only adult fish but also propagules are subject to currents that move eggs and fry downstream (Larimore et al., 1959; Platania and Altenbach, 1998; Zitek, 2006). Upstream movement by fishes is often tied to reproduction and necessary to provide agents for gene dispersal and to maintain local populations (Hall, 1972).

Although we found an overall upstream movement trend, most fish in our study moved about very little and were recaptured at the same transect of their initial capture. Many stream fish can be considered sedentary, spending their entire lives within just one pool or a reach, their home range (e.g. Bailey, 1953; Gerking, 1959; McCleave, 1964; Reed, 1968; Berra and Gunning, 1972; Scalet, 1973; Brown and Downhower, 1982; Fish and Savitz, 1983; Hill and Grossman, 1987; Gatz and Adams, 1994; Freeman, 1995; Petty and Grossman, 2004). For example, sunfishes tend to have

restricted movements (Paukert et al., 2004; Smithson and Johnston, 1999). Gerking (1953) showed that sunfishes occupied the same home range for 2 to possibly 3 years. Freeman (1995) found that 93 % of juvenile centrarchids and 88 % of darters were recaptured within 33 m of the original capture location. Limited fish movement can be particularly prevalent during reproductive times when many stream fish occupy territories which they defend aggressively against intrusion of competitors or predators (Gerking, 1953; Scalet, 1973; Bridcut and Giller, 1993). The reproductive behavior of sunfishes that includes the building of breeding nests and aggressive defense against intrusion of predators and competitors is a prime example for this (Gatz and Adams, 1994).

Most home ranges of stream fishes are < 100 m (Rodriguez, 2002), which is within the spatial extent of the mussel beds we studied. In combination with the low juvenile mussel drift distances we documented in the Little River under summer low flow conditions (Irmscher, unpublished data), the restricted movement of host fishes during periods of peak glochidial infestation can be seen as one explanation for the aggregated, patchy spatial distribution of unionid mussels in the form of mussel beds (Brittain and Eikeland, 1988; Watters, 1992; McLain and Ross, 2005). A recent study showed that infestation of European chub (*Squalius cephalus*) with duck mussel (*Anodonta anatina*) glochidia resulted in a reduction of the host's activity and movement, restricting mussel dispersal (Horký et al., 2014). Similar to our study, Terui et al. (2014) found an upstream bias in movements of Masu Salmon (*Oncorhynchus masou masou*), the host of the Japanese freshwater pearl mussel (*Margaritifera laevis*), recapturing ~ 70 % of hosts near their original capture location. Schwalb et al. (2011)

recaptured 82 % of logperch (*Percina caprodes*) within 30 m of the original capture locations, and McLain and Ross (2005) recaptured 94 % of all marked tessellated darter (*Etheostoma olmstedi*) in locations where they were originally marked. These studies support our findings of limited movement of many fishes that are hosts to unionid mussels.

It is important to keep in mind that there is variation in movement of stream fish within and between species (Funk, 1957). While most individuals undertake short movements, few move over intermediate and some over long distances (Wiens, 1976; Smithson and Johnston, 1999; Fausch et al., 2002). Longer-distance movements tend to occur in juvenile fish and/or less competitive individuals (Fish and Savitz, 1983; Freeman, 1995) and are necessary for recolonization of previously defaunated stream sections (Gatz and Adams, 1994). Life histories may also require longer-distance movements since spawning habitat and feeding habitats of adults and juveniles may differ (Schlosser, 1991). Although many unionid host fishes are sedentary, some host fish migrate long distances. For example, channel catfish (*Ictalurus punctatus*) in the Wisconsin River occupied small home ranges in the summer, but migrated downstream into the Mississippi River in autumn, and back up the Wisconsin River in the spring to spawn at the same summer home sites (Pellett et al., 1998). Gars and drums also typically swim over longer distances (Vaughn, 2012).

While most stream fishes move little, the small proportion that move longer distances are of great importance to mussel dispersal potential (Horký et al., 2014). Mussel beds represent local subpopulations that are linked into a larger metapopulation through infrequent dispersal (Vaughn, 1993; Newton et al., 2008; Vaughn, 2012).

Mussels are long lived (15-40 years on average, but up to 200 years) (Strayer, 2008; Haag and Rypel, 2011; Haag, 2012). The genetic similarity of mussel subpopulations may be the result of spatially limited, yet temporally prolonged dispersal of relatively few individuals over long time periods (Nagel, 2000; Elderkin et al., 2007). Dispersal and gene flow among mussel populations is a function of fish movement, which in turn determines mussel distribution (Lee et al., 1998; Vaughn, 2012; Vaughn and Taylor, 2000; Zanatta and Murphy, 2006; Vaughn, 2012). For example, mussels that have darters as hosts frequently form genetically isolated subpopulations (Berg et al., 2007), while those with migrating hosts tend to form more homogenous populations (Berg et al., 1998). Although our findings indicate that mussel dispersal via fish movement in the Little River is limited, subpopulations have been shown to be genetically connected (Reagan, 2008). Cureton and Vaughn (unpublished data) found that genetic connectivity between subpopulations of the threeridge mussel (*Amblema plicata*) in the Kiamichi River could be maintained by the movement of only 3.5 propagules per generation. Genetic connectivity of mussel populations likely depends on many factors such as mussel habitat suitability and spatial configuration and host fish identity, abundance and behavior (Newton et al., 2008; Roe et al., 2001; Kelly, 2005; Berg et al., 2007).

The relative immobility, long lifespan and reproductive characteristics of freshwater mussels make them particularly vulnerable to habitat disturbance, especially habitat fragmentation (Strayer, 2008). Southeastern Oklahoma experienced severe drought conditions in the summer of 2011, which was reflected by low discharge and a continuing reduction of water depths in the Little River over the course of our study (Atkinson et al., 2014). These decreasing water levels may have increased the limited

movement of fish hosts, decreasing connectivity between mussel subpopulations. Low water levels can force host fish to seek refugia in deep pools (Sedell et al., 1990; Schlosser, 1991; Schaefer et al., 2003) where the chances for glochidia attachment and survival of juveniles are greatly reduced (Neves and Widlak, 1987). Drought in this region and the southern US is predicted to become more frequent and more severe with climate change (Seager and Vecchi, 2010), all while the human population is growing and using more water (Sabo et al., 2010). This will likely negatively impact both fish and mussel dispersal.

In summary, we found that fishes that are hosts to uniond mussel in the Little River move little during the summer. In combination with low drift distances of juvenile mussels, this limited movement helps explain the patchy distribution of mussels in mussel beds. On average, when fish moved, they moved farther up- than downstream, allowing mussels to compensate for downstream displacement. Changes in flow conditions in the context of global climate change and water diversion for human consumption will likely negatively affect mussels and their hosts, including mussel dispersal potential and metapopulation structure. Future studies will need to further investigate the complex interactions between mussels and fish, including the co-evolution of the life histories of these two animal groups and their effects on mussel dispersal, spatial distribution patterns, and the genetic connectivity of mussel metapopulations in rivers.

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FIGURE CAPTIONS

Figure 1. Location of the Little River and sample sites in McCurtain County, OK. The USGS Lukfata Creek gauge (discharge data) is located between Sample Sites 1 and 2, the HOBO ® logger (water depth data) was placed at Site 1. All sample sites are located on the USFWS Little River National Wildlife Refuge near Broken Bow, OK (http://www.fws.gov/refuge/little_river/).

Figure 2. Schematic of transect sampling in river reaches. The diagram shows the alignment of transects in 10 m increments over mussel beds with the first transect being the most upstream.

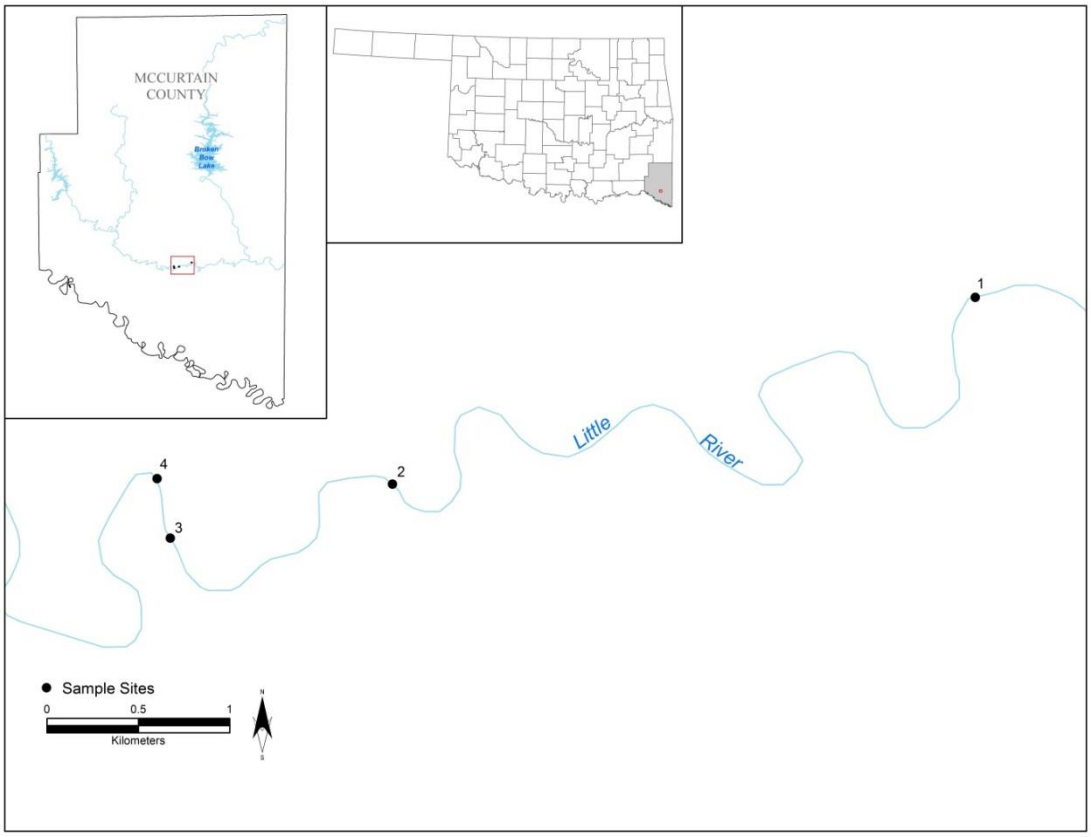
Figure 3. Number of fish recaptured per movement distance. Bar graph subsections represent the number of fish for each fish group at the respective distances from the original capture transect. Negative numbers represent distances moved downstream of the initial capture transect, positive numbers movement distances upstream.

Figure 4. Mean number of centrarchids recaptured in relation to movement distance. Error bars represent standard deviations.

Figure 5. Mean number of captures in relation to discharge over time. Mean discharge in the Little River (white boxes) and mean number of fish individuals captured (black circles) over the duration of the study (capture periods). Error bars represent standard errors.

Figure 6. Number of captures in relation to water depth.

FIGURES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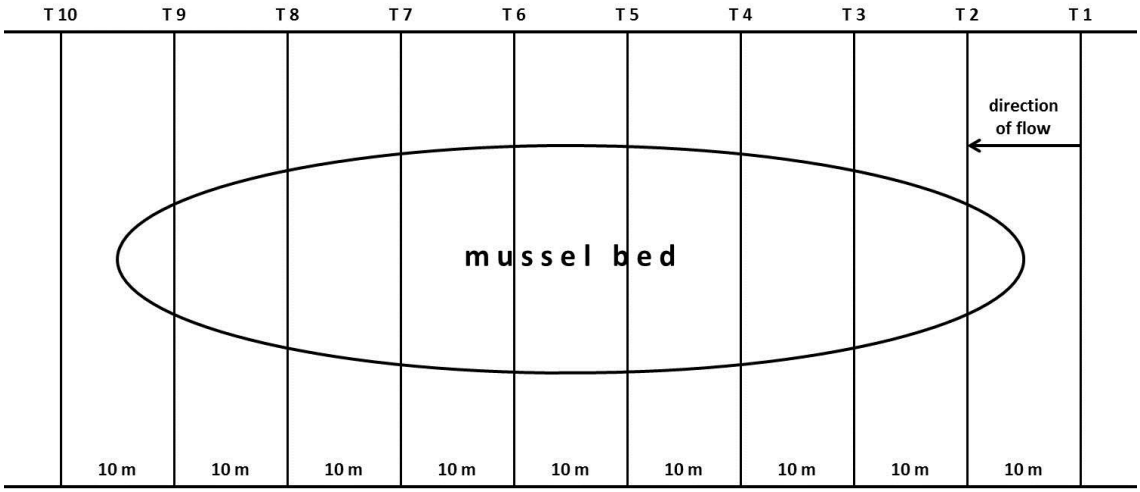
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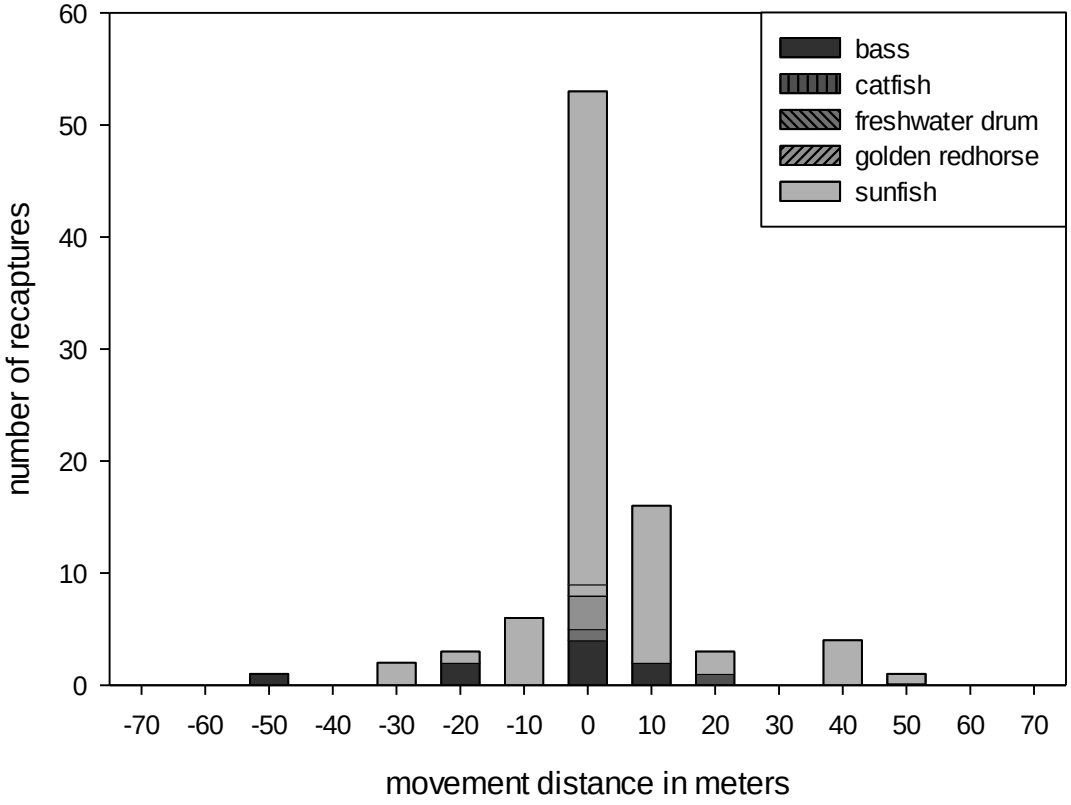
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catfish
freshwater drum
golden redhorse
sunfish
number of recaptures
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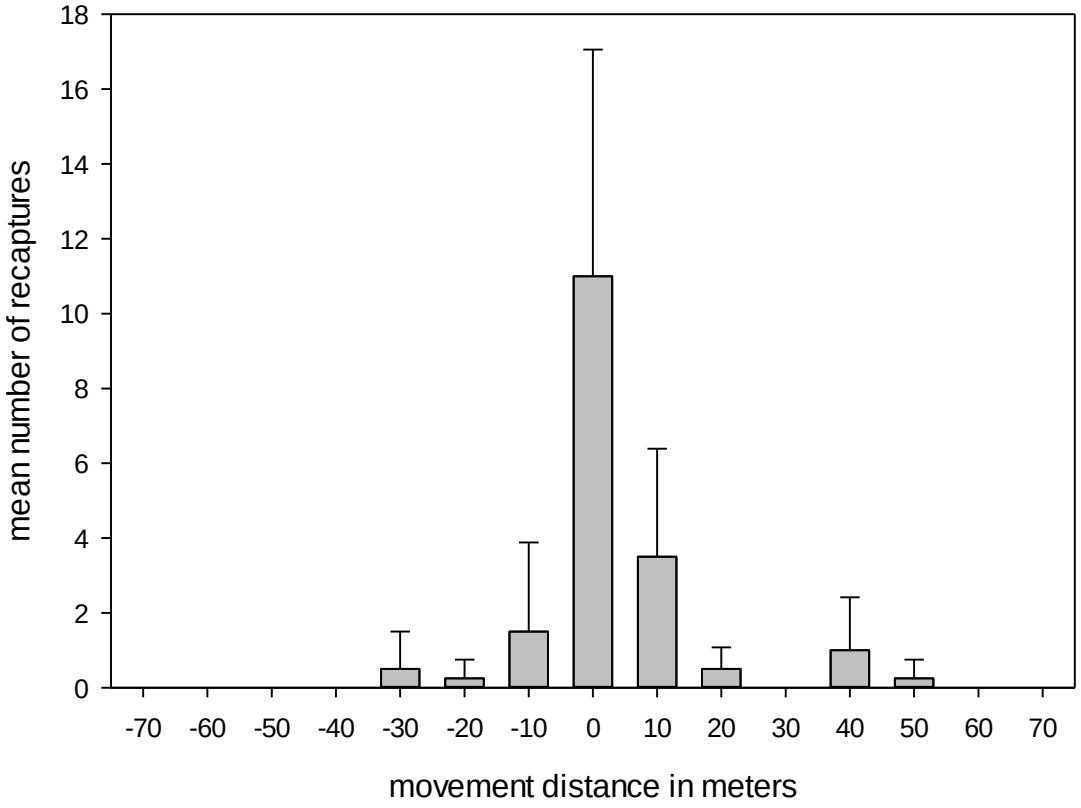
movement distance in meters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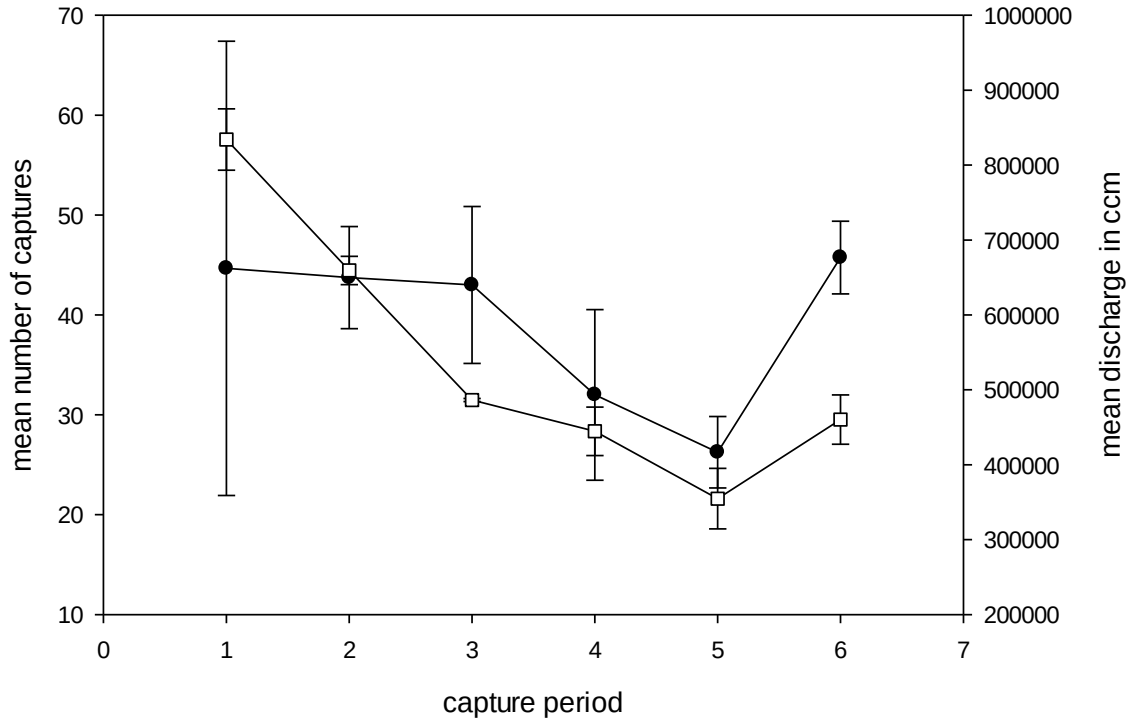
movement distance in meters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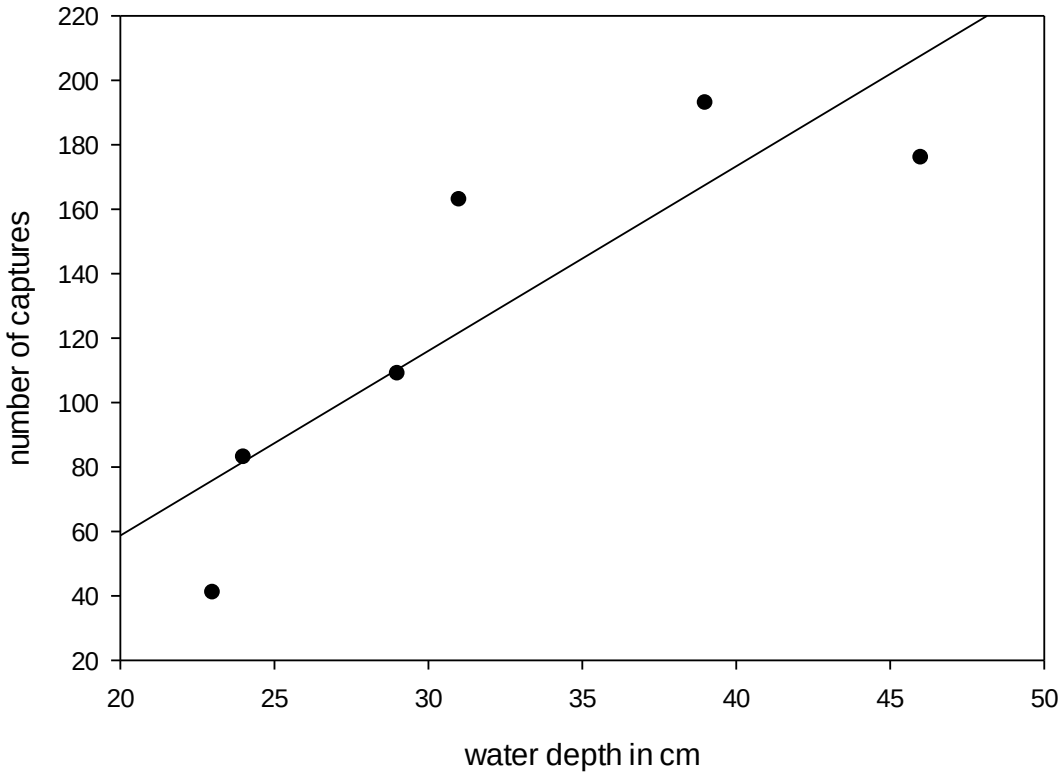
mean number of captures
mean discharge in ccm
capture period


220
200
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number of captures
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water depth in cm

Supplement 1: Little River unionid mussel species. Based on long term studies by Dr. Vaughn and her students.

Mussel Species Common Name	**Mussel Species Scientific Name**
Bankclimber	*Plectomerus dombeyanus*
Bleufer	*Potamilus purpuratus*
Butterfly	*Ellipsaria lineolata*
Creeper	*Strophitus undulatus*
Deertoe	*Truncilla truncata*
Fatmucket	*Lampsilis siliquoidea*
Fawnsfoot	*Truncilla donaciformis*
Fluted Shell	*Lasmigona costata*
Fragile Papershell	*Leptodea fragilis*
Giant Floater	*Pyganodon grandis*
Lilliput	*Toxoplasma parvus*
Little Spectaclecase	*Villosa lienosa*
Mapleleaf	*Quadrula quadrula*
Mucket	*Actinonaias ligamentina*
Ouachita Creekshell	*Villosa arkansasensis*
Ouachita Kidneyshell	*Ptychobranchus occidentalis*
Ouachita Rock Pocketbook	*Arkansia wheeleri*
Paper Pondshell	*Utterbackia imbecillis*
Pimpleback	*Quadrula pustulosa*
Pistolgrip	*Quadrula verrucosa*
Plain Pocketbook	*Lampsilis cardium*
Pondmussel	*Ligumia subrostrata*
Pyramid Pigtoe	*Pleurobema rubrum*
Rabbitsfoot	*Quadrula cylindrica*
Rainbow	*Villosa iris*
Round Pigtoe	*Pleurobema sintoxia*
Sand Pocketbook	*Lampsilis satura*
Southern Mapleleaf	*Quadrula apiculata*
Spike	*Elliptio dilatata*
Texas Lilliput	*Toxolasma texasensis*
Threehorn Wartyback	*Obliquaria reflexa*
Threeridge	*Amblema plicata*
Wabash Pigtoe	*Fusconaia flava*

Wartyback	*Quadrula nodulata*
Washboard	*Megalonaias nervosa*
White Heelsplitter	*Lasmigona complanata*
Winged Mapleleaf	*Quadrula fragosa*
Yellow Sandshell	*Lampsilis teres*

Supplement 2: Potential host fish species in the Little River, OK. Mussel–host relations are based on information from the literature and the Mussel/Host Database of the Museum of Biological Diversity, Division of Molluscs, at Ohio State University (http://140.254.118.11/MusselHost/). Known host fish species that occur in the Little River, OK are shown in bold.

Host Fish Species Common Name	Host Fish Species Scientific Name
Alligator Gar	***Atractosteus spatula***
American Eel	***Anguilla rostrata***
Banded Darter	*Etheostoma zonale*
Banded Killifish	*Fundulus diaphanous*
Banded Sculpin	*Cottus carolinae*
Bigeye Chub	*Hybopsis amblops*
Black Bullhead	*Ameiurus melas*
Black Crappie	***Pomoxis nigromaculatus***
Blotched Chub	*Erimystax insignis*
Bluebreast Darter	*Etheostoma camurum*
Blue Catfish	***Ictalurus furcatus***
Blue Danio	*Brachydanio kerri*
Bluegill	***Lepomis macrochirus***
Bluntnose Minnow	***Pimephales notatus***
Bowfin	***Amia calva***
Brook Stickleback	*Culaea inconstans*
Brown Bullhead	***Ameiurus nebulsus***
Central Stoneroller	***Campostoma anomalum***
Channel Catfish	***Ictalurus punctatus***
Chinese Algae-Eater	*Gyrinocheilus aymonieri*
Common Carp	***Cyprinus carpio***
Common Shiner	*Luxilus chrysocephalus*
Creek Chub	***Semotilus atromaculatus***
Eastern Blacknose Dace	*Rhinichthys atratulus*
Emerald Shiner	***Notropis atherinoides***
Fantail Darter	*Etheostoma flabellare*

Fathead Minnow	***Pimephales promelas***
Flame Gourami	*Colisa lalia*
Flathead Catfish	***Pylodictis olivaris***
Florida Gar	*Lepisosteus platyrhincus*
Freshwater Drum	***Aplodinotus grunnies***
Giant Danio	*Danio malabaricus*
Gizzard Shad	***Dorosoma cepedianum***
Glass Knifefish	*Eigenmannia virescens*
Glowing Tetra	*Hyphessobrycon erythrozonus*
Greenside Darter	*Etheostoma blennioides*
Greenthroat Darter	*Etheostoma lepidum*
Golden Barb	*Barbus semifasciolatus*
Goldfish	***Carrasius auratus***
Golden Redhorse	***Moxostoma erythrurum***
Golden Shiner	***Notemigonus crysoleucas***
Golden Topminnow	*Fundulus chrysotus*
Green Sunfish	***Lepomis cyanellus***
Greenside Darter	*Etheostoma blennioides*
Guppy	*Lebistes reticulata*
Iowa Darter	*Etheostoma exile*
Johnny Darter	***Etheostoma nigrum***
Largemouth Bass	***Micropteris salmoides***
Lavender Gourami	*Trichogaster trichopterus*
***Lepomis* hybrids**	***Lepomis* spp.**
Logperch	***Percina caprodes***
Longear Sunfish	***Lepomis megalotis***
Longnose Dace	*Rhinichthys cataractae*
Longnose Gar	***Lepisosteus osseus***
Marble Chiclid	*Haplochromis venustus*
Mooneye	***Hiodon tergisus***
Mosquitofish	***Gambusia affinis***
Mottled Sculpin	*Cottus bairdi*
Northern Hogsucker	*Hypentelium nigricans*
Northern Pike	*Esox lucius*
Northern Redbelly Dace	*Phoxinus eos*
Northern Studfish	*Fundulus catenatus*
Orangespotted Sunfish	***Lepomis humilis***

Orange Throat Darter	***Etheostoma spectabile***
Orange Belly Darter	***Etheostoma radiosum***
Panchax killifish	*Aplocheilus lineatus*
Peacock cichlid	*Aulanacara stuartgranti*
Pumpkinseed	*Lepomis gibbosus*
Rainbow Darter	*Etheostoma caeruleum.*
Rio Grande Cichlid	*Cichlasoma cyanoguttatum*
River Carpsucker	***Carpiodes carpio***
River Chub	*Nocomis micropogon*
River Redhorse	***Moxostoma carinatum***
Rock Bass	*Ambloplites rupestris*
Sand Shiner	***Notropis lundibundus***
Sauger	*Sander canadensis*
Scarlet Shiner	*Lythurus fasciolaris*
Shortnose Gar	***Lepisosteus platostomus***
Shovelnose Sturgeon	***Scaphirhynchus platorynchus***
Siamese Fighting Fish	*Beta splendens*
Silver Shiner	*Notropis photogenis*
Silverjaw Minnow	*Ericymba buccata*
Silver Tip Tetra	*Hemigrammus nanus*
Skipjack Herring	***Alosa chrysochloris***
Smallmouth Bass	***Micropteris dolomieu***
Southern Redbelly Dace	*Phoxinus erythrogaster*
Speckled Madtom	*Noturus leptacanthis*
Spotfin Shiner	*Cyprinella spiloptera*
Spotted Bass	***Micropterus punctulatus***
Spotted Gar	***Lepisosteus oculatus***
Steelcolor shiner	***Cyprinella whipplei***
Streamline Chub	*Erimystax dissimilis*
Striped Shiner	***Luxilus chrysocephalus***
Suwanee Bass	*Micropterus notius*
Tippecanoe Darter	*Etheostoma tippecanoe*
Von Rio Tetra	*Hyphessobrycon flammeus*
Walleye	***Sander vitreus***
Warmouth	***Lepomis gulosus***
White Crappie	***Pomoxis annularis***
White Sucker	***Catostomus commersoni***

Whitetail Shiner	*Cyprinella galactura*
Yellow Bullhead	***Ameiurus natalis***
Yellow Perch	*Perca flavescens*
Yoke Darter	*Etheostoma juliae*

CHAPTER 3

FACTORS INFLUENCING FRESHWATER MUSSEL DISTRIBUTION IN RIVER REACHES

Keywords:

unionid, freshwater mussel, adult distribution, juvenile dispersal, stream flow, channel bed morphology, fluorescent dye, aerial photography, GIS

ABSTRACT

The distribution of freshwater mussels (Bivalvia, Unionidae) is usually clumped, both in rivers and within river reaches. The factors that underlie this patchy distribution are poorly understood, but likely include complex hydraulic parameters that affect adult mussels, as well as the drifting and settling of juveniles. Besides other parameters, discharge and channel bed morphology determine spatial patterns of flow. We investigated the predictive values of 3 parameters that describe channel bed morphology (water depth, channel bed slope and aspect), and that of turbulent flow for determining spatial distribution of unionid mussels at 6 sites in 2 rivers in southeastern Oklahoma, USA. Since turbulent flow in a natural river channel is difficult to assess, we released fluorescent dye in reaches to depict potential pathways of drifting juvenile mussels as well as areas with high concentrations of suspended food particles that are important for filter-feeding mussels. We recorded spatial patterns of dispersing dye with aerial photography and analyzed them in GIS. Fluorescent dye dispersion indicated that areas of intermediate flow were the preferred areas for juvenile settlement and the delivery of suspended food to adult mussels. Channel bed slope limited where mussels occurred. Neither water depth nor channel bed aspect was predictive of mussel distributions. Our approach combined tracking dye plumes with assessments of channel bed morphology, and allowed us to determine factors that underlie mussel patchiness, and to successfully predict mussel occurrence. We have added to the knowledge of mussel habitat requirements that will be useful for identifying areas of river systems that are valuable for the protection of existing mussel populations, or to determine river reaches for translocations of threatened mussel beds.

INTRODUCTION

Organisms frequently exhibit patchy distribution, often in response to patchily distributed resources (Pickett and White, 1985). Understanding the factors that affect patchiness is important because they have effects on the maintenance of populations and on other ecosystem compartments (Strayer et al., 2004; Vaughn and Spooner, 2006). Despite the unidirectional flow of water within channels (Hershey et al., 1993; Williams and Williams, 1993; Anholt, 1995), river invertebrates are notorious for their patchy distributions (Pringle et al., 1988; Downes et al., 1993; Allan and Castillo, 2007). Patches can be defined as relatively homogenous areas that differ in nature and appearance from their surroundings (Turner et al., 2001). A patch is also a spatial unit that is defined by the organism(s) studied and the questions investigated (Pringle, 1988). Patchiness in rivers results from flow patterns that depend on multiple factors and vary over space and time, such as current velocity, water volume, substrate size and type, as well as the structure and morphology of river beds (Knighton, 1998).

Flow can be measured and quantified by a number of simple (e.g. flow velocity and discharge) and complex (e.g. shear stress, Froude number) hydraulic parameters that can be used to describe hydraulic conditions in an open channel. For example, shear stress is the dragging force of flowing water that acts upon any particle or organism in the water column, and that can potentially entrain or move it downstream. Shear stress and complex other hydraulic parameters change in relation to a number of parameters (e.g. flow velocity, water depth) that are interdependent and can vary greatly across spatial and temporal scales (Knighton, 1998). In combination, they determine flow or hydraulic conditions in a river reach.

Riverine systems can be classified into hierarchically organized, physical environments that incorporate microhabitat, habitat, the reach, subbasins, and drainage basins (Schlosser and Angermeier, 1995). Reaches are distinguished by the type and degree of constraints imposed by geomorphic features such as bedrock, landslide deposits, and alluvial fans (Gregory et al., 1991). Each reach has its own geomorphic context and associated history (Montgomery, 1999). Similarly, a pool/riffle system is a subsystem of a river reach with characteristic topography, slope, depth, and velocity patterns. In turn, microhabitats are defined by locally restricted patches within the pool/riffle system with relatively homogenous substrate type, water depth, and velocity pattern distributions (Frissell et al., 1986).

Freshwater mussels (Bivalvia, Unionidae) are a guild of long-lived, burrowing, sedentary, filter-feeding animals (Vaughn et al., 2007) and are patchily distributed at multiple spatial scales, in rivers but also within river reaches (Vaughn and Spooner, 2006). In rivers, they typically occur as dense aggregations known as mussel beds that are separated by large stretches where mussels do not occur or are sparse (Strayer et al., 2004; Spooner and Vaughn, 2009). Within reaches that contain mussel beds, mussels are also patchily distributed and occur in clumps surrounded by areas with few or no mussels (Downing et al., 1993; Strayer, 2008). At both spatial scales, mussel distribution is likely controlled by a suite of interacting ecological factors, such as dispersal, habitat, hosts, food, enemies and predation (Strayer, 2008).

Unionid mussels have a complex reproductive cycle that includes an obligate ectoparasitic stage during which mussel larvae need to attach to a fish host of suitable species (Barnhart et al., 2008). After metamorphosis, juveniles drop off the fish host

and sink to the bottom (Haag, 2012). In rivers, this sinking process is accompanied by downstream displacement with the flow, and spatially distinctive hydraulic conditions likely determine where juveniles settle and grow into adults (Morales et al., 2006). Thus, juvenile dispersal is important to adult distribution. Few studies have examined the effects of flow on juvenile dispersal and how it contributes to the distribution and persistence of mussel populations (Newton et al., 2008; Strayer, 2008). Holland-Bartels (1990) suggested that high flows displaced settling juveniles before they could burrow in the substrate, and that adult mussel distributions reflected juvenile mussel's tolerance to flow. Neves and Widlak (1987) showed that juveniles tended to clump in areas of low flow velocities behind boulders. Bed morphology can be a significant factor for mussel distribution, and upstream hydraulics and juvenile sources affect interactions of bed morphology and juvenile settling (Brainwood et al., 2008). Multiple researchers have hypothesized that juvenile mussels need areas of low shear stress to become established (Layzer and Madison, 1995; Strayer, 2008; Dario et al., 2010).

In this paper, we examine relationships between the patchiness of mussels, and flow patterns and bed morphology within river reaches. We used aerial photography and GIS to document and analyze the spatial distributions of mussel beds at 6 sites in 2 small rivers, and their correlation with local flow patterns and 3 variables that describe channel morphology. Flow in natural river channels is always turbulent, which makes it difficult to measure, predict, and model flow patterns (McLay, 1970; Vogel, 1994; McNair et al., 1997). Flow measurements are usually made at a limited number of points, which often does not capture the spatial complexity of flow sufficiently. Thus, we documented dispersion of fluorescent dye through river reaches with well-defined

mussel beds as proxy for the flow conditions affecting mussel distributions (Aldous and Smart, 1988; Jobson, 1997; Fox et al., 2011). We assumed that differential dispersion of dye with the flow would be an indicator of areas in reaches where the likelihood of juvenile settlement and the availability of suspended food particles were high. We hypothesized that (as has been established in the past; see e.g. Strayer et al., 1994; Strayer, 1999; Strayer, 2008; Haag, 2012), water depth would not be a good predictor of mussel abundance. We predicted that mussel abundance was lower in areas of steep channel slopes because juveniles would not be able to settle, and adults would not be able to persist in these areas. We predicted that channel bed morphology (expressed by channel bed aspect oriented perpendicular to the flow), would create a dam effect that supports settlement of drifting juveniles, relative to bed structures more or less parallel to the flow where juveniles continue to drift downstream. Lastly, we hypothesized that large greenness values, derived from fluorescent dye dispersion, indicated those areas within river reaches where both mussel densities and biomass values would be high as well.

METHODS

Study Area

We conducted our study at 6 sites in 2 rivers in southeastern Oklahoma, USA. The Kiamichi River has a basin area of 4680 km^2, mean discharge of 48 $m^3\ s^{-1}$, and a mean water temperature of 16.7 °C. The Little River has a basin area of 10,720 km^2, a mean discharge of 183 $cm^3\ s^{-1}$, and a mean water temperature of 16.5 °C (Matthews et al., 2005). Maximum channel widths for study sites in these 2 rivers were in the range

of ~ 30 to 50 m. The mussel fauna in these 2 rivers is speciose (up to 26 species per bed; Vaughn, 1997) and highly abundant (up to 84 animals per m^2; Vaughn and Spooner, 2006). We conducted our study in the summer (June-August) of 2010, under summer low flow conditions that are typical for the reproductive time period of the mussel fauna in these 2 rivers.

Grid Sampling System

At each site, we determined the spatial extent of the bed by wading, snorkeling, and scuba diving, using visual and tactile detection methods. We marked the up- and downstream boundary of each bed with flagging tape. Starting at the upstream boundary we established a sampling grid consisting of 10 transects across the river 10 m apart and sampling locations every 5 m along these transects (Fig. 1). We marked each sampling location with a 1 m long rebar rod and recorded its position with a GPS (Garmin 60 Cx, Garmin International, Inc., Olathe, KS). Depending on cloud and leaf cover, the spatial accuracy of GPS measurements was 3 m or higher. We also took GPS readings of up to 10 reference locations (30 cm diameter orange bucket lids mounted on rebar rods) that we placed in a random pattern at each site. The lids were later visible in aerial photos and served as reference points for geo-referencing images in GIS.

Dye Release and Aerial Photography

We used non-toxic, liquid yellow-green fluorescent dye from Bright Dyes (item #106001, Miamisburg, OH). This version of Xanthene is certified by NSF International to ANSI/NSF Standard 60 for the use in drinking water and is biodegradable in 7 days.

It is visual above 100 ppb and 50 ml of dye fluid color ~ 475000 l of water lightly, and ~ 47500 l of water strongly (Bright Dyes FLT Yellow/Green Technical Data Bulletin). After contact with water, the brown-colored dye fluid turns bright-fluorescent green. At each site, we poured the contents of one 4 l jug in a band across the channel as evenly as possible, one channel width upstream of the upstream boundary of the bed (Fig. 2). Due to extremely low flow velocities, dye plumes at sites 4 and 5 did not disperse far enough to spatially overlap with the extent of the mussel beds and we excluded these 2 sites from further analysis of greenness value – mussel abundance correlations. In addition, if the dye plume had only dispersed partially over the mussel bed (Site 3), we limited the interpolation model in GIS and the data used from this model to the most downstream point of the dye plume (see images in Fig. 4). We assumed that the greenness of the dye recorded in aerial photos was in relation to its dilution (concentration) in the water, thus serving as a proxy for otherwise non-visible flow patterns in river reaches over mussel bed sites.

We followed the recommendations for aerial photography in Aber et al. (2010), to assess spatial dimensions of dye plume dispersion in reaches. We used a heavy-duty polyurethane balloon (2 m diameter, 4 m^3 volume) filled with helium, and a maximum lifting capacity of 4 kg. The balloon was tethered to a manually, crank-operated plastic winch (drum size 15 cm) via a 9 kg fishing line. We attached a camera rig constructed of light-weight wooden rods 100 cm below the balloon (Fig. 3) to which we mounted a Canon PowerShot G5 camera with a resolution of 5 megapixels, 35 mm lens, weighing 410 g. This digital camera features continuous TTL autofocus and an interval-shooting mode that allows for automatically taking pictures every minute (Canon USA, Inc.,

Melville, NY). After setting up the balloon and starting the interval shooting mode, we released the balloon to an altitude of ~ 100 m. At each site, we took aerial photos at 1 minute intervals for up to 4 hours, documenting the dispersion of dye plumes with the flow.

Hydraulic and Mussel Data

After documenting dye dispersion with aerial photography, we measured water depth as well as flow velocity (Marsh-McBirney Flo-Mate 2000, Frederick, MD) at each location of the sampling grid system (Fig. 1). Flow velocities were too low to be detected at most locations, and we had to omit this parameter from further analysis. Then, we excavated all mussels at each sampling location within a 0.25 m^2 PVC frame to a depth of 15 cm (Vaughn et al., 1997). We identified all mussels to species and measured their maximum shell lengths. For the 2 most common species at each of the sites (*Amblema plicata* and *Actinonaias ligamentina* at all sites except for Site 3, where the second most common species was *Quadrula pustulosa*) we used established shell length – dry weight regression models to estimate shell-free biomass (Vaughn et al., 2007; Atkinson and Vaughn, in press.).

Spatial Analysis and Computation of Channel Bed Slope and Aspect in GIS

We geo-referenced aerial photos, and created layers for subsequent modeling in ArcGIS (ArcMap Version 10.1, Esri Inc., Redlands, CA). Following Zigler et al. (2008), we transformed water depth data into channel bed slope (0-90 degrees) and channel bed aspect (0-360 degrees) data, using the slope and aspect tools provided in

ArcMap 10.1 (Esri Inc., Redlands, CA). Slope identifies the steepest downhill slope for a location on the surface; the ArcMap slope tool calculates the maximum rate of change in value from a DEM cell to its surrounding neighbors (3x3 cell neighborhood). The maximum change in elevation over the distance between the cell and its 8 neighbors identifies the steepest downhill descent from that cell (Burrough and McDowell, 1998). Aspect identifies the downslope direction of the maximum rate of change in value from each cell to its neighbors and indicates the compass direction that the surface faces at that location, i.e. aspect can be thought of as the slope direction (Burrough and McDowell, 1998). As a next step, we converted the local data from grid sampling locations into raster models via spatial interpolation (method: IDW) at a resolution of 10 cm for the following variables: water depth (cm), channel bed slope (degrees), channel bed aspect (degrees), mussel density (individuals per m^2), mussel biomass as shell-free dry weight (g per m^2) (Fig. 4A-F). Then, we extracted interpolated values for these variables by converting raster data into point data for each of the sampling locations (Fig. 1). We also extracted greenness values of dispersing fluorescent dye plumes from the green (Band 2) channel of the tricolor aerial images (Fig. 4A) for sites 1, 2, 3, and 6. We did not use aerial photos for Sites 4 and 5 because low flow conditions did not move dye plumes downstream far enough to achieve sufficient spatial overlap with the extent of the mussel beds. For each of the remaining sites, we chose that aerial photo which had that had the highest spatial overlap of the plume in relation to the extent of the mussel bed. These extracted point data from the sampling locations of the grid system then served as input for subsequent analyses.

Statistical Analysis

Because mussels could not live there, we excluded sampling locations from the data set that were located on the water–shore interface (i.e. points on the outer edge of the layers created in GIS; Figs. 1, 5-8). We used logistic regression (cut value 0.5) to determine whether water depth, channel bed slope, channel bed aspect, and/or greenness could predict mussel presence or absence. We examined these relationships between mussel density and/or biomass with standard linear and quadratic regressions, and with linear regression models at the 95th, 90th, and 85th quantiles. We chose to add quantile regression to the analysis due to the large number of dependent variable data points with values of "0" and frequent low goodness-of-fit of standard regression models. Quantile regression estimates do not require normal distributions and homoscedasticity (Cade and Noon, 2003; Hao and Naiman, 2007). They have been used in ecological studies to estimate functions near the upper boundary of response distributions, and to measure limiting factors (Cade and Noon, 2003; Schooley and Wiens, 2005). We conducted logistic regressions in SPSS (Version 19, IBM SPSS Statistics), standard linear and quadratic analyses in the Sigma Plot (Version 12.5) statistics tool, and quantile regression analyses in the quantreg package (Version 5.05 developed by R. Koenker) for R software (Version 3.1.1, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Mean mussel densities at the 6 sites ranged from 1.38 to 5.45 individuals per m^2, with an absolute range of 0 to 52 animals per m^2. Mean mussel biomass was 17.43 (SD 45.77) g per m^2. The mean water depth was 54.76 (SD 41.31) cm, the mean channel bed slope 26.72 (SD 23.09) degrees, ranging from a horizontal (0.11 degrees) to an almost vertical (87.84 degrees) bed. Channel bed aspect was highly variable (mean 184.29, SD 108.15 degrees), and the mean fluorescent dye greenness was 161.62 (SD 41.4).

We investigated probabilities of predictive values of the 4 independent variables (water depth, channel slope, channel aspect, and greenness) with logistic regression. The total number of cases was 522, the overall percentage of the null model excluding the effects of predictors was 72 %. Estimated changes in model fit were $5.47_{(1)}$ for water depth ($p = 0.019$), $1.242_{(1)}$ for channel bed slope ($p = 0.265$), $0.059_{(1)}$ for channel bed aspect ($p = 0.807$), and $2.577_{(1)}$ for greenness ($p = 0.108$). The score for the overall model was $9.197_{(4)}$ with a marginally significant value of $p = 0.056$. The omnibus test of model coefficients was non-significant ($p = 0.52$; $Chi^2 = 9.389$), indicating that the model with predictor variables was not an improvement over the null model. This was also reflected by a low Nagelkerke R^2 (0.055) and the fact that the overall percentage remained at 72 (same as null model). Only water depth (B = -0.011; SE = 0.005; Wald $5.511_{(1)}$; Exp(B) 0.989) yielded a significant probability ($p = 0.019$); the probabilities for all other variables included in the model were not significant. Results for logistic regression variables in the equation of the model are presented in Table 2.

We examined relationships between the 4 independent variables (water depth, channel slope, channel aspect, and greenness) and mussel density with linear regression,

quadratic regression, and linear regression models for the 95th, 90th, and 85th quantiles. We also used these regression models to examine relationships between greenness and mussel biomass. While quadratic regression produced a significant relationship between mussel density and water depth ($p < 0.0001$, $R^2 = 0.0378$), this relationship explained very little variation (Table 3; Fig. 5). Channel bed slope and mussel density showed a classic constraining pattern (Fig. 6) where the range of mussel densities was larger for flatter channel bed slopes, but small for steeper channel bed slopes. We found a strong negative relationship between channel bed slope and mussel density at the 95th quantile ($p < 0.001$, $t = 8.93$), showing that channel bed slope was a limiting factor for mussel distributions (Table 3). The relationship between channel bed aspect and mussel density were explained by the 85th quantile ($p < 0.001$, $t = 6.24$), although with limited value for predicting mussel abundance (Fig. 7; Table 3). The 95th quantiles most successfully described relationships between greenness and mussel density (Fig 8; $t = 0.02$, $p < 0.001$), and between greenness and mussel biomass (Fig. 9; $t = 3.85$, $p < 0.001$). Distributions showed that mussel density and biomass values were highest for intermediate greenness values that most likely corresponded with areas of intermediate flow conditions.

DISCUSSION

Our approach allowed us to examine flow patterns that are complex and hard to measure by tracking the dispersion of fluorescent dye within river reaches. Along with variables describing bed morphology, this approach revealed that mussel densities were highest in areas of intermediate flow. This is in contrast to our initial hypothesis where

we predicted mussel densities to be highest at high dye concentrations, and also to other studies predicting mussel densities to be high in areas of low flow, with associated low flow velocities and low shear stresses. Layzer and Madison (1995) found that 50 % of the sites with high mussel densities had no measurable flow, and 37 % of the mussels were located at zero velocity. Daraio et al. (2010) stated that juveniles fall out of the water column in high concentrations where flow velocities are reduced, and that the settling of low density particles primarily occurs when vertical velocities near the river bed are low. Standard methods for measuring flow velocities are often unsuccessful at very low flows, but the differential dispersion of dye plumes in our study showed that variation of flow does exists even under low flow conditions, and that it most likely contributes to the patchy distribution of mussels.

Our results are supported by other studies showing that mussels are limited by complex and interacting factors (Strayer, 2008; Atkinson et al. 2012). Intermediate greenness values that we found to be predictive of mussel distribution most likely indicate areas of intermediate flow in river reaches, and represent the combined effects of a number of physical and biological variables that affect mussel distributions over long time spans. Water depth, flow velocity, and thus substrate type and turbidity depend on discharge (Leopold et al., 1964), and important habitat descriptors are also directly linked to discharge (Horwitz, 1978). High discharge leads to hydraulic conditions that can scour bed substrate and dislodge mussels. In many ecological communities, space is the primary limiting resource (Paine and Levin, 1981). Low discharge can decrease water levels to a degree that can limit the extent of mussel beds within river reaches. Intermediate greenness values are likely to indicate those areas

with intermediate flow velocities that are favorable for juvenile settlement, and that at the same time maximize delivery of suspended particles for feeding. The juvenile stage is the most sensitive and vulnerable of the unionid life cycle (Neves and Widlak, 1987; Hardison and Layzer, 2001), and mussel beds may be the product of differential mortality in which juveniles settle evenly on the river bottom, but perish in unsuitable habitats (Strayer, 1999). Intermediate flows in river reaches we studied may represent areas where shear stresses are low enough for drifting juveniles to settle and establish, but high enough to prevent accumulation of fine particles. Hydrodynamic conditions required for the erosion of fine particles can be considerably higher than those required for deposition (Jowett, 2003). Juveniles are small particles and are unlikely to settle in areas where particles are actively moved with the flow (Morales et al., 2006). Sedimentation leads to the clogging of interstitial space that juveniles require after settling, and decaying organic matter reduces oxygen concentrations and creates unfavorable habitat conditions. Adult mussels filter suspended particles, and optimal food delivery requires sufficient flow for particles to stay suspended, but at the same time flow low enough for particles not to be transported downstream too quickly (Vaughn et al., 2008).

Although water depth was the only variable that significantly predicted mussel presence or absence within the 6 sites (likely because mussels cannot survive where they are not submerged) overall it was not a good predictor of mussel abundance within these sites. Across the 6 study sites, mussels occurred between 20 and 120 cm, and the linear regression models found no relationship between water depth and mussel density. We conducted our study during a drought period with extraordinarily low water levels

(Atkinson et al., 2014). Thus, our data reflect the bottom range of water depth values that occur throughout the year, which is also shown by the relatively small variation in water depths across sites and within reaches. Unionid mussels have limited mobility and do not survive prolonged exposure to the atmosphere. Low water levels during summers can lead to water temperatures lethal to mussels (Galbraith et al., 2010; Gough et al., 2012). Although the hyporheic zone can serve as a refuge from periodic droughts or unfavorable temperatures (Sedell et al., 1990), burrowing into the substrate also limits food supply, oxygen uptake, and reproduction. At the same time, conditions for mussel survival are also poor in deep areas (pools) where food and oxygen supply are limited (McMahon and Bogan, 2001). Natural rivers are very dynamic systems, and water depth can vary greatly in relation to discharge. The most common natural disturbances associated with rivers are related to increases in discharge accompanied by high flow velocities and bed movement (Minshall, 1988). Populations in rivers are particularly likely to be subject to random perturbation and catastrophes due to variation in flow (Anholt, 1995). Extreme flow events at the upper (floods) and lower (droughts) end of the spectrum constitute important disturbances that determine the spatial distribution of mussel beds by either exposure and lethal temperatures, or by scouring of bed substrate and dislodgment of individuals (Zigler et al., 2008).

Our results indicated that channel bed slope was a limiting factor for mussel distribution. We found a wide range of mussel densities in flat (< 20 degrees) areas of the reaches, but mussels were not abundant in areas where bed slopes were steep (> 50 degrees) (Fig. 6). Atkinson et al. (2012) also found channel bed slope to be significantly correlated at the site scale in similar rivers of southeastern Oklahoma. Steep bed slopes

may prevent drifting juvenile mussels from settling successfully in the substrate due to direct effects of steep slopes on substrate types and composition, and/or indirect effects of channel bed forms creating hydraulic conditions that are unfavorable for juvenile settling. In a previous field study, we had released microparticles of similar size and density as juvenile mussels in river reaches with mussel beds. We captured the most particles with drift nets in areas with flat channel bed slopes and just upstream of areas with rapidly ascending channel morphology (Irmscher and Vaughn, unpublished data). This might indicate a dam effect that decreases flow velocities locally in relation to the rest of the channel, and that causes drifting juveniles to settle in these areas of low flow velocity and shear stress. Steep channel bed slopes are often associated with unstable substrates (Gangloff and Feminella, 2007), and mussels have been shown to persist in areas where shear stresses and scouring during high flow are low (Strayer, 1999; Steuer et al., 2008; Allen and Vaughn, 2010). In addition, steep channel bed slopes can cause hydraulic conditions that limit the availability of suspended food particles (Brim Box and Mossa, 1999). CART analysis conducted by Zigler et al. (2008) revealed that shear stress and channel bed slope were the two most important factors for the distribution of mussels in the Upper Mississippi River. Most of the terminal nodes were the result of interactions between shear stress and channel bed slope, and all splits on channel bed slope indicated positive relations between bed slope and the presence of mussels (Zigler et al., 2008).

We had assumed that channel bed aspect affected mussel distributions similarly to channel bed slope, but this hypothesis was not supported. We had predicted that areas of river reaches with bed morphology oriented perpendicular to the main flow direction

would create flow conditions that are favorable for juvenile settlement and adult mussel survival; however, we found mussels occurring in varying densities at almost all channel bed aspects (0 to 358 degrees), and that the orientation of areas in relation to the main flow direction was not important for mussel distribution. This could be because mussels did not have a preference regarding their orientation in relation to the flow, or it could be an artifact of our sampling design. The spatial resolution of our grid sampling system with distances of 10 m between the transects and 5 m between locations may have been too coarse to detect the spatial patterns of highly variable channel bed morphology affecting unionid mussels.

Strayer et al. (2004) proposed two broad classes of processes that are likely to affect the distribution of unionid mussels: negative censoring mechanisms and positive censoring mechanisms. Positive censoring mechanisms such as habitat selection and high fecundity in favorable habitats are directly or indirectly affected by hydraulics conditions. However, hydraulic processes themselves are mostly negative censoring mechanisms (Daraio et al., 2010). In either case, understanding flow patterns and hydraulic conditions at the reach scale is fundamental to understanding mussel patchiness. These are very difficult to quantify, in particular during low flow when measurements of flow velocity are not successful. Our approach to combine the release of fluorescent dye with an assessment of channel morphology allowed us to determine factors that govern mussel patchiness, and to predict the presence of mussel beds in river reaches.

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Table 1. Means and standard deviations (in parentheses) for measured and computed variables.

	Mean Water Depth [cm]	**Mean Channel Bed Slope [degrees]**	**Mean Channel Bed Aspect [degrees]**	**Mean Greenness [unit less]**	**Mean Mussel Density [ind/m^2]**	**Mean Mussel Biomass [g/m^2]**
Site 1	46.04 (29.52)	22.57 (23.17)	174.18 (109.85)	169.73 (28.85)	2.81 (4.9)	8.51 (17.29)
Site 2	74.49 (40.99)	26.52 (21.51)	189.06 (113.8)	157.22 (40.33)	1.38 (4.44)	8.14 (26.15)
Site 3	47.71 (39.37)	19.62 (21.9)	165.03 (108.03)	171.99 (52.76)	1.81 (4.59)	3.95 (10.3)
Site 4	38.12 (30.65)	27.14 (22.6)	193.66 (103.43)	n/a	6.45 (10.36)	38.53 (69.88)
Site 5	76.98 (51.37)	27.84 (24.85)	193.06 (102.48)	n/a	4.00 (9.36)	23.55 (61.16)
Site 6	35.98 (29.58)	43.67 (18.5)	181.06 (110.01)	150.53 (27.43)	4.27 (7.49)	25.54 (51.34)
All Sites Comb.	54.76 (41.31)	26.72 (23.09)	184.29 (108.14)	161.62 (41.4)	3.30 (7.26)	17.43 (45.77)

Table 2. Results of logistic regression analysis of the model examining probabilities between the 4 independent, continuous variables water depth, channel bed slope, channel bed aspect, and greenness, and the dependent, categorical variable mussel presence ("0" = no mussels present, "1" = mussels present)

	B	**S.E.**	**Wald**	**df**	***p***	**Exp(B)**	**Lower 95% CI**	**Upper 95% CI**
Water Depth	-0.011	0.005	5.511	1	0.019	0.989	0.981	0.998
Channel Bed Slope	-0.009	0.008	1.271	1	0.260	0.991	0.975	1.007
Channel Bed Aspect	0.000	0.001	0.022	1	0.882	1.000	0.998	1.003
Greenness	0.005	0.004	2.212	1	0.137	1.005	0.998	1.012
Constant	-0.885	0.755	1.373	1	0.241	0.413		

Table 3. Results of regression analyses. Slope, R^2 value (linear/quadratic regressions) or t value (quantile regressions), and p value

	Water Depth [cm] vs. Mussel Density [ind/m^2]		**Channel Bed Slope [degrees] vs. Mussel Density [ind/m^2]**		**Channel Bed Aspect [degrees] vs. Mussel Density [ind/m^2]**		**Greenness [unit less] vs. Mussel Density [ind/m^2]**		**Greenness vs. Mussel Biomass [g per m^2]**	
Linear	- 0.0205	0.0093	- 0.0348	0.0074	0.0038	0.003	0.002	0.0002	- 0.0605	0.0077
		0.0275		0.0714		0.2519		0.8193		0.1747
Quadratic	- 0.0008	0.0378	- 0.0007	0.0087	- 6E-05	0.0095	0.0002	0.0065	0.0001	0.0077
		<0.0001		0.148		0.1245		0.4587		0.3958
95th quantile	0.00000	3.37215	- 0.20686	8.92859	0.02544	4.46429	0.00000	2.32195	- 0.43207	3.84942
		0.00079		0.00000		0.00001		0.02096		0.00015
90th quantile	0.00000	3.89225	- 0.18683	7.92689	0.02149	2.55862	0.00000	1.15301	- 0.17395	1.58402
		0.00011		0.00000		0.01079		0.24990		0.11433
85th quantile	0.0000	3.85431	- 0.14020	6.86371	0.00000	6.24098	0.03846	- 0.31062	0.12960	-0.19134
		0.00013		0.00000		0.00000		0.75633		0.84840

Figure 1. Grid sampling point system. The sampling grid point system consisted of 10 transects 10 m apart with T1 located at the upstream boundary of the mussel bed. Along each transect, we established sampling locations every 5 m (actual number of points depending on channel width) at which we measured and recorded flow velocity, water depth, mussel density, mussel species, and mussel shell length. Based on the last 2 parameters, we calculated mussel biomass for the 2 dominant species at each site. For each location of the grid sampling point system, we also extracted point data for the calculated channel bed slope and aspect values from interpolated GIS raster layers.

Figure 2. Aerial photos of a spreading dye plume. This sequence of 16 aerial photos shows the dispersion of a dye plume with the flow at Site 2. The photos are not geo-referenced based on the orange plastic lids that can be seen in the images. Only one aerial photo with the maximum spatial overlap of the dye plume with the mussel bed was used for spatial analysis at each site. The time span covered in this sequence is ~ 2h, reflecting low flow conditions with very small (mostly undetectable) flow velocities that are typical for small rivers in southeastern Oklahoma in summer.

Figure 3. Helium balloon and camera rig. The 3 photos display the reusable helium balloon, fully inflated and attached via tethered lines to a plastic drum, which is in turn tied to a kayak. The smaller images show the camera and camera rig below the balloon, respectively, and their attachment to the balloon via a set of lines.

Figure 4. GIS layers. The 6 images show the geo-referenced aerial photo (A) and the raster layers created in GIS for the variables mussel density (B), mussel biomass (C), water depth (D), channel bed slope (E), and channel bed aspect (F) at Site 3. The major flow direction within the channel at this site is more or less from North (0 degrees) to South (180 degrees). There is good spatial overlap of the dye plume (A) with areas where mussels occur in high densities (B). There is no obvious correlation between the spatial extent of the mussel bed (B and C) and water depth (D). Due to the graphical output of these two layers, potential correlations between channel bed slope (E) and aspect (F) and mussel density (B) cannot easily be detected visually.

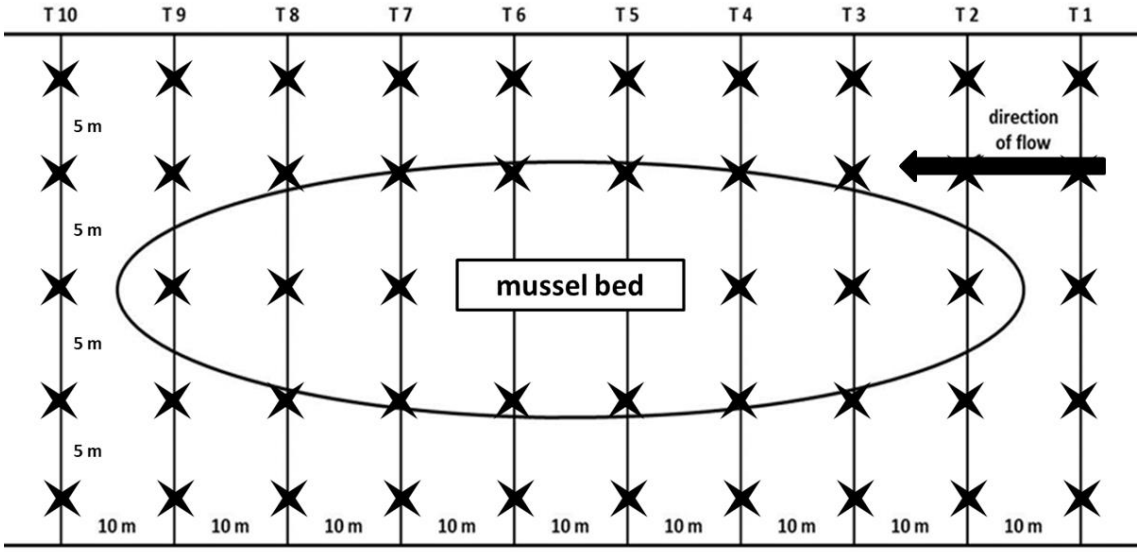
Figure 5. Relationship between water depth and mussel density. Mussels occurred at water depths from 10-120 cm, with the highest densities at 30-90 cm at the 6 sites. All four regression model lines have a slope of or near 0. The quadratic and 90th quantile model have the highest significance, but low R^2 values and regression line slopes indicate that water depth was not a good predictor for mussel density.

Figure 6. Relationship between channel slope and mussel density. Highest mussel densities occurred at channel bed slopes from 0 to 20 degrees. The standard linear and quadratic models are strongly influenced by the large number of "0s" of the dependent variable whereas the quantile regression lines have negative slopes that identify channel bed slope as a limiting factor. This is reflected by highly significant p-values for all 3 quantiles, 95 having the highest t-value.

Figure 7. Relationship between channel aspect and mussel density. The plot for channel bed aspect does not reveal a clear pattern and data points indicate that this parameter was not a useful predictor for mussel density at the sites. Overall, there is a slightly positive trend for the 95th and 90th quantiles yet the distribution did not support our hypothesis that orientation of the channel bed in relation to the main direction of flow had an effect on where mussels occur in rivers channels.

Figure 8. Relationship between greeness and mussel density. The data points for greenness values derived from fluorescent dye cluster around a mid-range of 120-240, and have a defined peak at 130-150. Once again, regression lines are strongly influenced by the large number of "0s" of the dependent variable. Overall, the distribution of data points indicates that most mussel occur at an intermediate range of greenness values.

Figure 9. Relationship between greeness and mussel biomass. Data for greenness values in relation to mussel biomass show a similar pattern as for mussel density, although the peak for highest mussel biomass values is shifted to lower greenness values of 110-160. All regression line slopes are negative for all regression models except for the 85th quantile.


T10
T9
T8
T7
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5 m
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direction
of flow
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10 m
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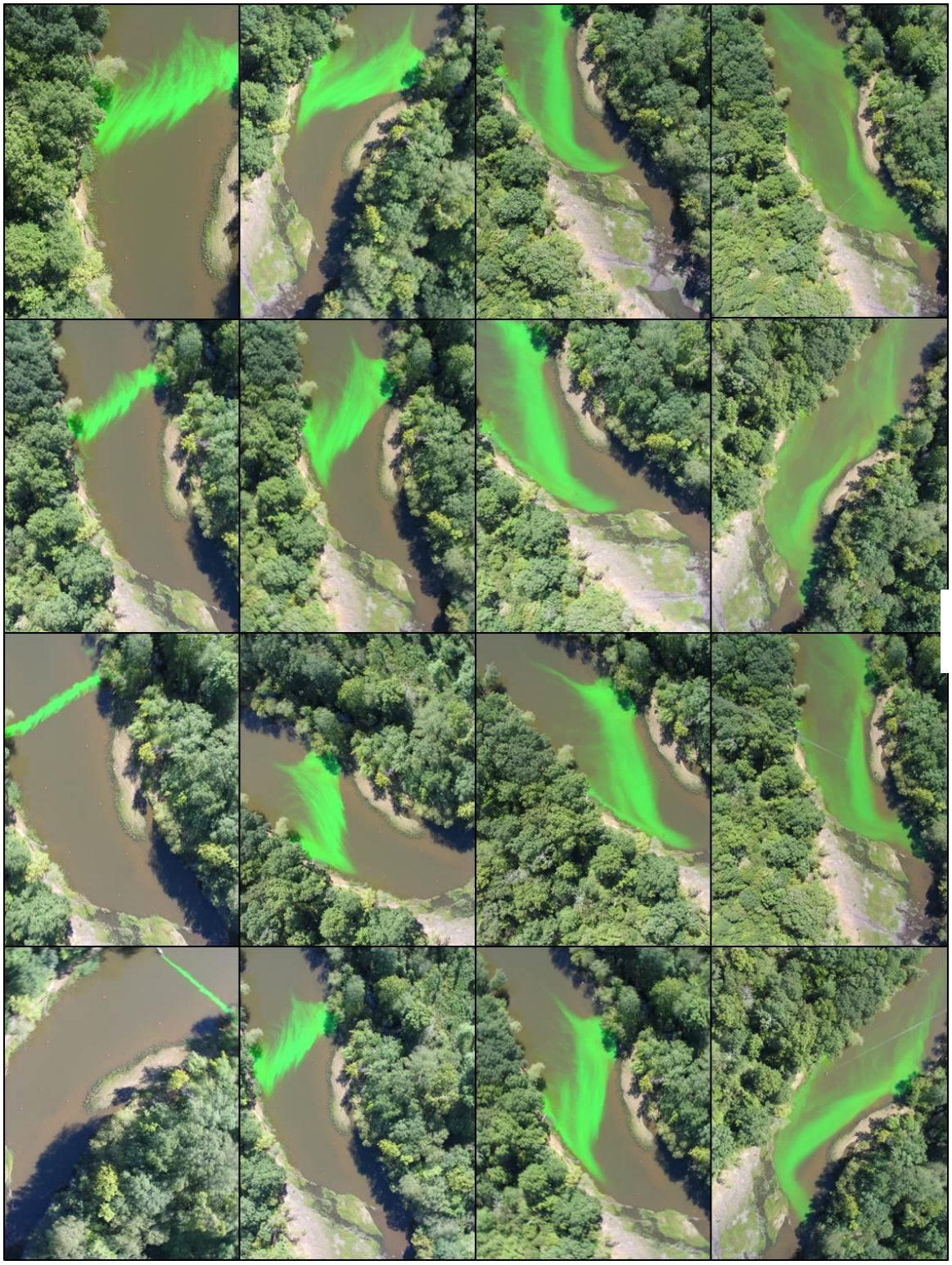



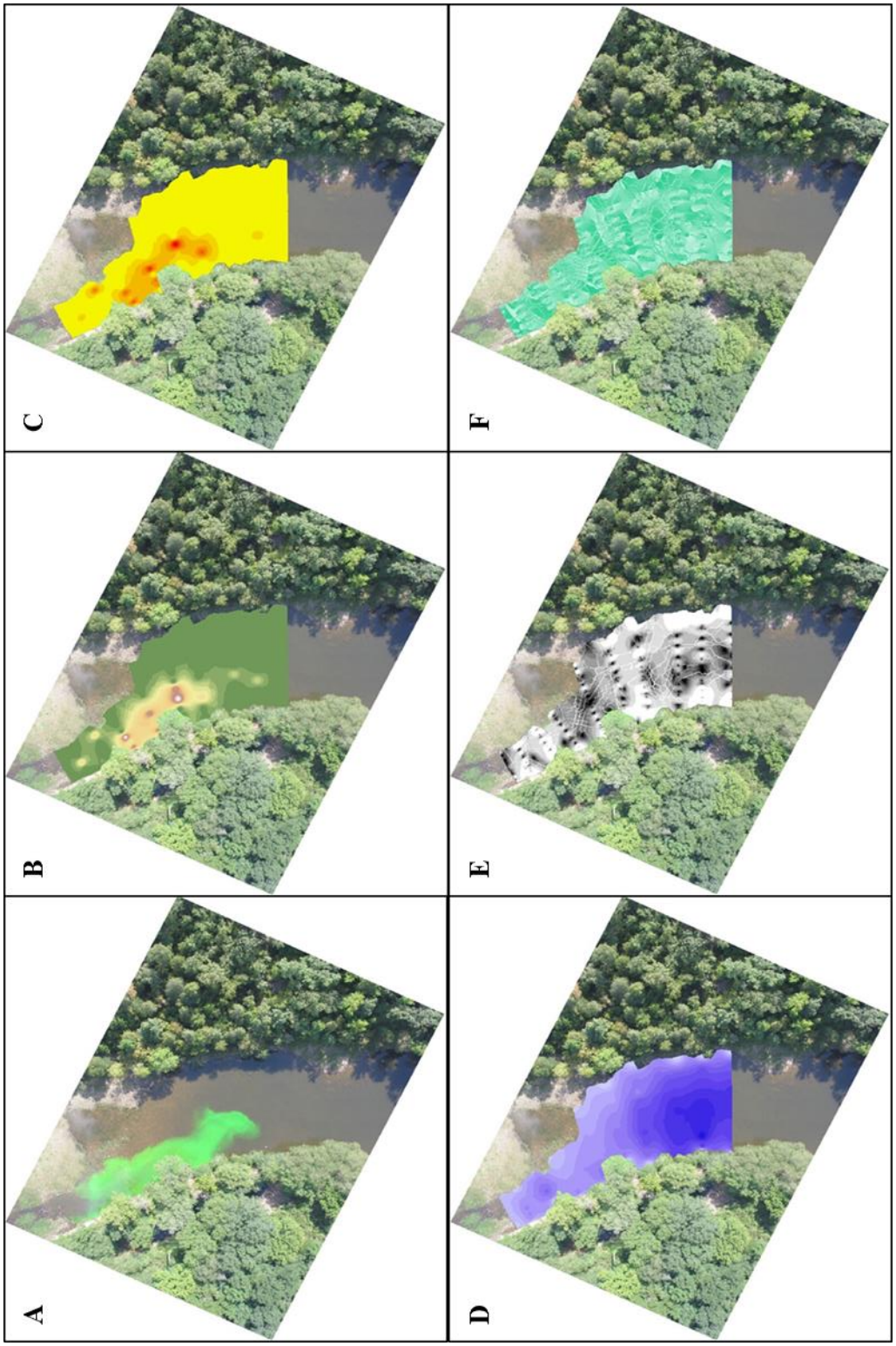
C
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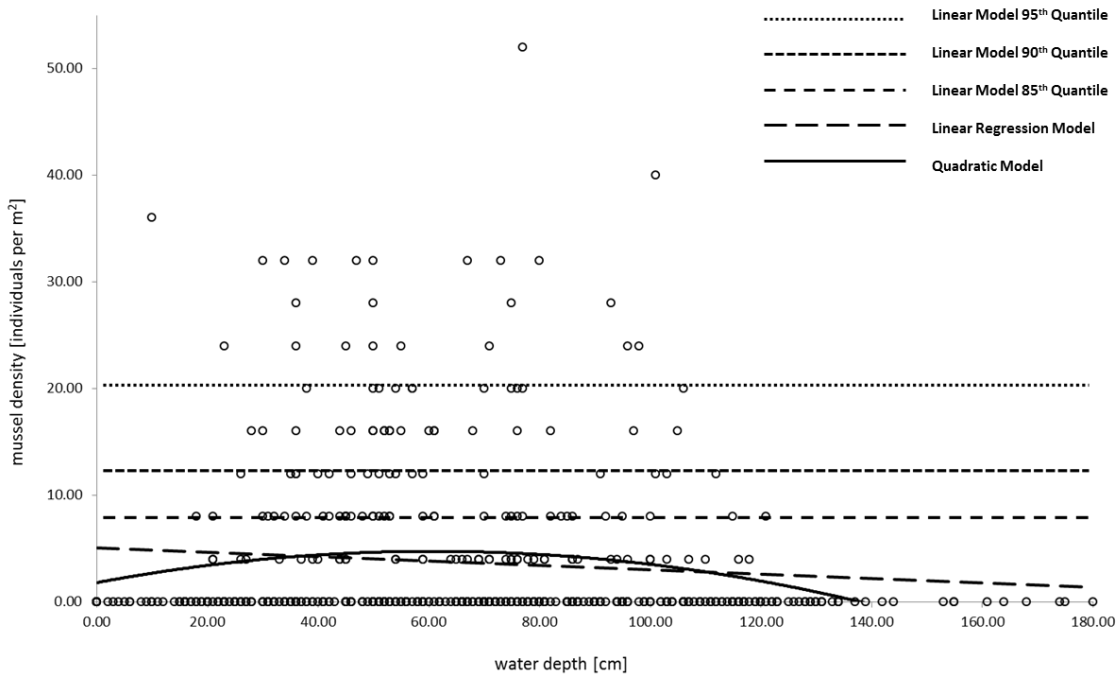
Linear Model 95th Quantile
Linear Model 90th Quantile
Linear Model 85th Quantile
Linear Regression Model
Quadratic Model
mussel density [individuals per m2]
water depth [cm]
0.00
10.00
20.00
30.00
40.00
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0.00
20.00
40.00
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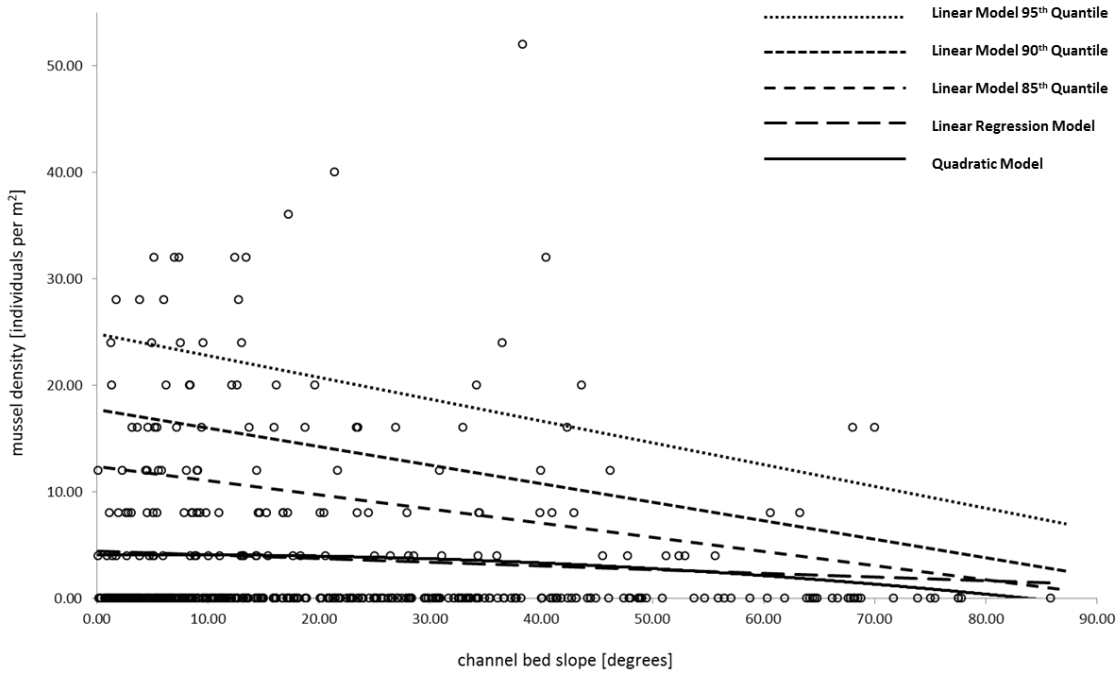
80.00
100.00
120.00
140.00
160.00
180.00


Linear Model 95th Quantile
Linear Model 90th Quantile
Linear Model 85th Quantile
Linear Regression Model
Quadratic Model
mussel density [individuals per m2]
channel bed slope [degrees]
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10.00
20.00
30.00
40.00
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10.00
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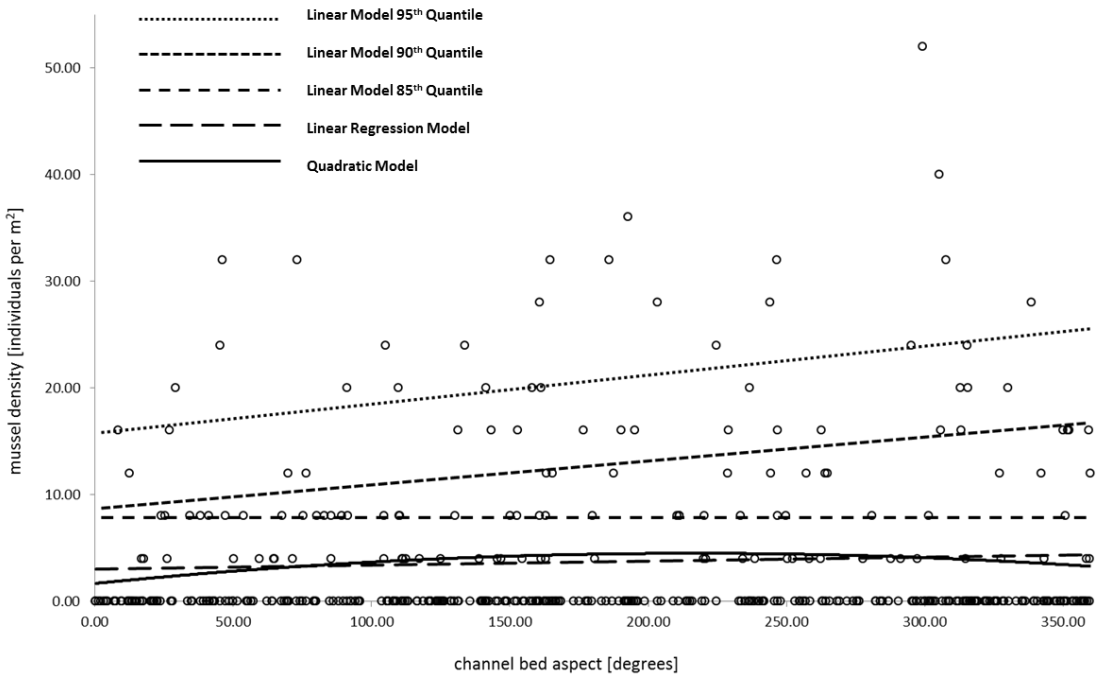
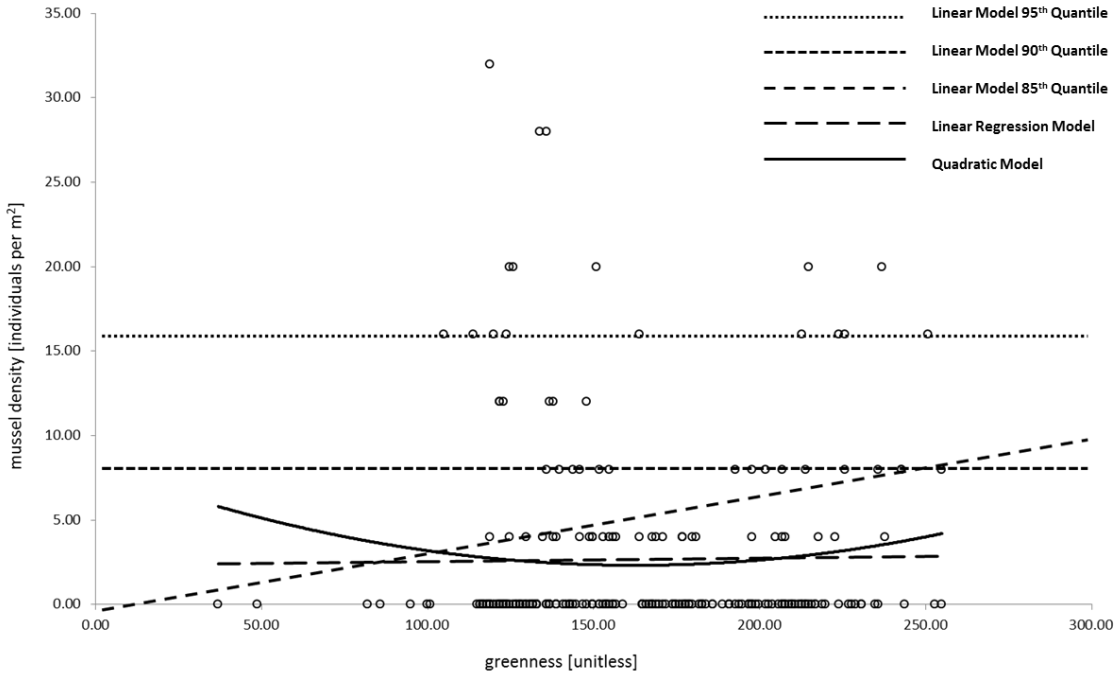
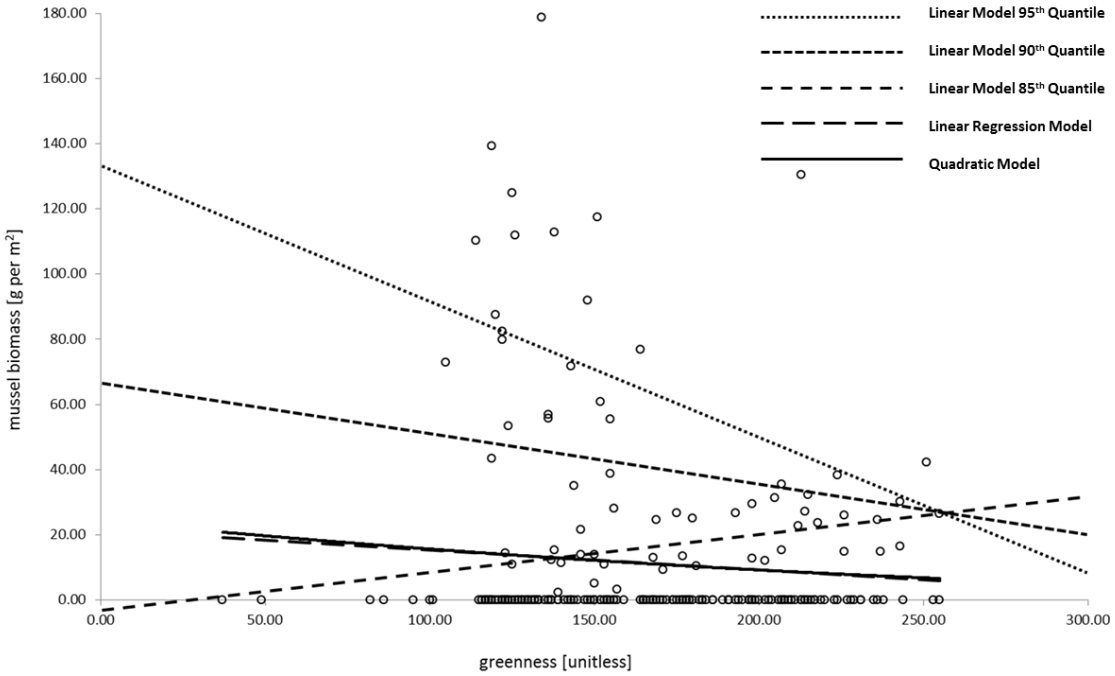
70.00
80.00
90.00


Linear Model 95th Quantile
Linear Model 90th Quantile
Linear Model 85th Quantile
Linear Regression Model
Quadratic Model
mussel density [individuals per m2]
0.00
10.00
20.00
30.00
40.00
50.00
0.00
50.00
100.00
150.00
200.00
250.00
300.00
350.00
channel bed aspect [degrees]


Linear Model 95th Quantile
Linear Model 90th Quantile
Linear Model 85th Quantile
Linear Regression Model
Quadratic Model
mussel density [individuals per m2]
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
0.00
50.00
100.00
150.00
200.00
250.00
300.00
greenness [unitless]


Linear Model 95th Quantile
Linear Model 90th Quantile
Linear Model 85th Quantile
Linear Regression Model
Quadratic Model
mussel biomass [g per m2]
greenness [unitless]
180.00
160.00
140.00
120.00
100.00
80.00
60.00
40.00
20.00
0.00
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100.00
150.00
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