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Influence of hyporheic exchange, substrate distribution, and other physically linked hydrogeomorphic characteristics on abundance of freshwater mussels

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ABSTRACT

Both endangered and non-endangered unionid mussels are heterogeneously distributed within the Allegheny River, Pennsylvania. Mussel populations vary from high to low density downstream of Kinzua Dam, and the direction, amount, and range of hyporheic exchange (seepage) at the sediment–water interface were suspected to influence their distribution and abundance. Nineteen hydrogeomorphic variables, including the quantification of seepage metrics, substrate size, river stage, river discharge, and shear stress, were measured at five reaches on the Allegheny River within 80 km downstream of Kinzua Dam. Analysis revealed significant ($\alpha = 0{\cdot}05$) non-linear correlations between mussel population density and directional mean seepage (positive relationship), river width (positive relationship), and median substrate size (negative relationship). Specifically, seepage findings showed that increases in upward seepage and decreases in the overall range of seepage related to increases in mussel population density. River width, directional mean seepage, and median substrate size were also found to co-vary with marginal significance ($\alpha = 0{\cdot}1$), making their individual influences on mussel population density uncertain. Absolute mean seepage, water depth, hydraulic head, temperature differences between the surface water and substrate, and other substrate metrics besides median grain size were not found to significantly correlate to mussel population density. Considering the physical processes often linking seepage to other explanatory variables, future research in seepage–mussel relationships should work to isolate the mechanistic influence of hyporheic exchange independently from its common covariation with substrate size and geomorphology. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS mussel; hyporheic; exchange; seepage; substrate; Allegheny; impoundment

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INTRODUCTION

Freshwater mussels (Bivalvia: Unionidae; hereafter unionids or mussels) are often found at or just below the sediment–water interface. They provide several ecosystem services, including energy transfer by filtering algae and other organic matter from both the water column and the sediment (Nichols *et al.*, 2005), nutrient cycling by way of nutrients transported from the water column to the sediment through biodeposition of faeces and pseudofaeces (Welker and Walz, 1998; Vaughn and Hakenkamp, 2001), and by providing a habitat on their shell for both algal and macroinvertebrate communities (Spooner and Vaughn, 2006).

River substrate, hydraulics, and morphology are widely recognized as important factors in mussel distribution (Layzer and Madison, 1995; Hardison and Layzer, 2001; Morales *et al.*, 2006). Previous studies have investigated many of these key physical factors in relation to population densities of mussels within numerous waterways around the United States and the world (Huehner 1987; Layzer and Madison, 1995; Hardison and Layzer, 2001; Morales *et al.*, 2006; Zigler *et al.*, 2008; Fulton *et al.*, 2010). Although preference of specific sediment characteristics can vary depending on mussel species, substrate size and distribution are two major factors found to influence mussel population densities across sites (Vannote and Minshall, 1982; Huehner, 1987; Layzer and Madison, 1995; Brim Box *et al.*, 2002; Steuer *et al.*, 2008; Fulton *et al.*, 2010). Additionally, heterogeneity (sorting) of the sediment plays a significant role in mussel distribution within rivers prone to large flooding events through the creation of behind-boulder eddies that shelter the smaller substrate needed by burrowing mussels (Vannote and Minshall, 1982; Layzer and Madison,

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1995; Olsen and Townsend, 2003). The surface roughness created by the presence of cobbles and boulders on the river bed also reduces shear stress at portions of the bed sheltered by these larger features. Shear stress measured locally in protected bed areas has been found to correlate negatively with mussel density (Hardison and Layzer, 2001).

Beyond these commonly assessed variables, Geist and Auerswald (2007) investigated the potential for hyporheic exchange and its influence on recruitment of juvenile mussels, *Margaritifera margaritifera*, showing a strong positive relationship between the degree of interconnectedness of surface water and hyporheic water and sites with juvenile mussels present. Hyporheic exchange, or seepage, is defined herein as the volumetric flow of water, either upward or downward, across the sediment–water interface that is a result of hydraulic gradients caused by the interaction of in-stream flow and the topography of the riverbed. Additional works investigating benthic fauna demonstrate that these relationships to hyporheic conditions are complex across and within species (Palmer *et al.*, 2000; Gayraud and Philippe, 2003; Olsen and Townsend, 2003; Olsen and Townsend, 2005; Smith, 2005; Hunt *et al.*, 2006; Schmidt *et al.*, 2007), with most indicating that more research is needed.

Because none of these previous studies made direct volumetric measurements of hyporheic exchange at the sediment–water interface, there is a need to quantify the rate, direction, and range of exchange in relation to mussel population density to further clarify its direct influence. Additional research has been specifically called for to determine whether these hyporheic exchange dynamics influence the density of adult mussel populations (Fulton *et al.*, 2010). Therefore, the objective of this study is to evaluate the influences of key physical factors, primarily rate, direction, and range of hyporheic exchange, and secondary substrate characteristics and other hydrogeomorphic variables, on population distributions of adult mussels within the highly diverse community of the middle Allegheny River.

RESEARCH DESIGN

A large and diverse community of freshwater mussels still exists within the Allegheny River, particularly in the Allegheny's upper and middle reaches (Anderson, 1998; Smith *et al.*, 2001; Fulton *et al.*, 2010). The Allegheny River is ~523 km in length with a drainage basin encompassing almost 30 000 km^2 in the northern Allegheny Plateau of New York and Pennsylvania (Figure 1). Data were collected along five 200-m-long reaches over a 60 km stretch of the Allegheny River extending from 18·8 to 78·4 km below the Kinzua Dam, Pennsylvania (Figure 1). The dam moderates downstream flow by eliminating both extreme high and low flows, resulting in a stable bed, most of which remains inundated even during dry periods.

Originally, 65 sites along this section of river were randomly selected and surveyed for mussel population density as part of other unpublished work contracted by the Pennsylvania Department of Transportation (Villella and Nelson, 2003–2008). Sample reaches were selected to be of equal length (200 m) and encompass the river from bank to bank. Sampling of mussel population density was conducted in two phases. Phase one was a qualitative search for mussels at the substrate surface to separate reaches into relatively lower and higher density strata. In this primary phase, each 200-m reach was marked into four 50-m-long sections with three transects located within each 50-m section for a total of 12 transects per reach. Transect orientations were perpendicular to the reference bank. Each transect was 1 m in width, and transect length was the river width at that location. Hidden mussels were found by fanning away fine sediment and removing loose, non-embedded material (rocks, sticks, debris) at the surface. Results from this qualitative initial survey guided the quantitative secondary phase that surveyed 70% of the high-density and 20% of the low-density reaches. Methods from Smith *et al.* (2001) determined the number of quadrats to be sampled and the spacing between quadrats. All mussels detected at the substrate surface in all 0·25 m^2 quadrats were counted. Approximately 600 quadrats were surveyed in each reach and used to calculate a mean mussel density, the values of which were used for this study.

Of the 65 reaches from the original study, five were chosen for detailed physical investigation within this study,

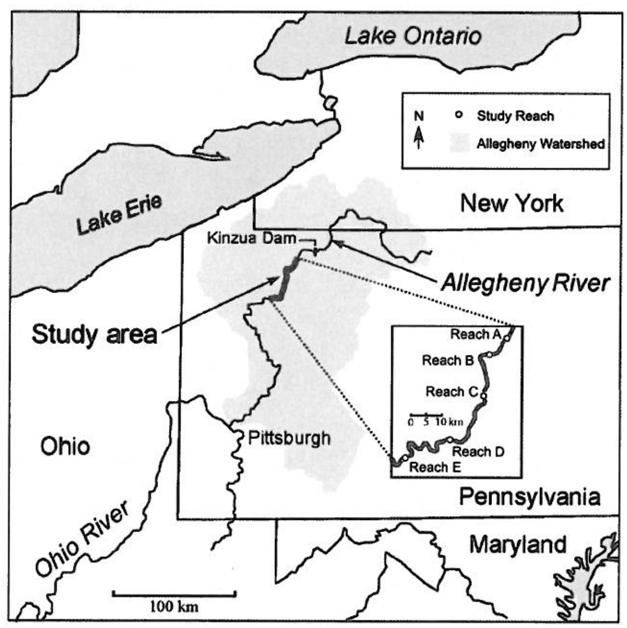

Figure 1. Area studied along the Allegheny River of western Pennsylvania from 18·8 to 78·4 km below the Kinzua Dam.

results of which are reported here. Reaches were chosen to represent the range in variability for mussel population densities observed within this section of the Allegheny River (ranging from 0·7 to 43·3 mussel m^{-2} at the reach scale). The physical regime of each reach was characterized during the summer of 2009. Measurements were recorded at six locations within each of the five study reaches. Measurements included volumetric rate and direction of hyporheic exchange, vertical hydraulic gradient within 30 to 40 cm of the sediment–water interface, temperature difference between surface water and hyporheic water, substrate grain-size distribution, water depth, river width, river gradient, and stream velocity (Table I). The six locations for physical measurements were evenly dispersed along the length of the 200-m reach with the intent of capturing the range of variability within the reach while still allowing for a minimum water depth of 30 to 40 cm that permitted *in situ* measurement of seepage. Measurements in shallower depths (<25 cm) provided questionable data and measurements in deeper depths (>125 cm) were prohibitively difficult because of the strong current. Although this depth range is limited, it does include a high proportion of depths within each reach and thus is assumed to be representative.

Seepage metres modified for use in flowing water (Rosenberry, 2008; Rosenberry *et al.*, 2012) were used to quantify flow across the sediment–water interface (Figure 2). Seepage (q) was determined from

$$q = \Delta V / \Delta t / A \quad (1)$$

where ΔV is the change in volume of a flexible seepage bag attached to an open-ended seepage cylinder installed on the riverbed, Δt is the time the bag was attached to the cylinder, and A is the 0.25-m^2 area of the riverbed covered by the cylinder. Positive values indicate upward seepage, from the water in the substrate to the river, and negative values indicate downward seepage. A piezometer was installed directly adjacent to each seepage metre at depths ranging from 30 to 40 cm beneath the riverbed. Difference in vertical hydraulic head was determined with a suction manometer that related head at the screened interval of each piezometer to head at the riverbed (Figure 2). Vertical hydraulic gradient was determined by dividing the head difference by the distance between the riverbed and the midpoint of the 5-cm-long piezometer screen. Multiple measurements of seepage and vertical hydraulic gradient were made over an approximately 8-h period at each location. Individual seepage measurements lasted from 2 to 26 min; faster seepage rates required shorter measurement periods. At least five measurements were averaged for each of the six locations within each reach. Temperature difference was measured with thermistors installed at the piezometer screen and on the riverbed.

Near-bed and near-surface current velocities were determined at each location. Wolman (1954) pebble counts (N = 300 per reach) were used to determine the bed surface sediment grain-size distribution. Data were tabulated to derive the grain size for which 10%, 16%, 50% (median), and 84% of the samples were smaller (i.e. D_{10}, D_{16}, D_{50},

Table I. Summarized observational data from the five study reaches along the Allegheny River, Pennsylvania.

Reach identifier	Units	Reach A	Reach B	Reach C	Reach D	Reach E
Downstream distance	km	18·8	25·0	41·6	58·4	78·4
Mussel population density	mussel m^{-2}	0·7	4·8	10·0	43·4	25·6
Seepage mean (absolute)	cm day^{-1}	208·8	53·9	20·2	104·6	24·6
Seepage mean (directional)	cm day^{-1}	−70·1	11·6	20·2	104·6	24·5
Seepage range	cm day^{-1}	601·4	189·2	33·9	181·3	62·2
Seepage standard deviation	cm day^{-1}	249·8	70·3	14·2	62·9	21·3
Head difference (Δh)	mm	1·2	−4·0	0·1	0·7	−4·8
Δh range	mm	2·0	3·0	2·0	2·0	2·0
Piezometer depth (d)	m	0·3	0·4	0·4	0·3	0·3
Water depth	m	0·5	0·6	0·8	0·6	0·6
River width	m	13·5	13·5	15·0	16·5	15·5
Stream velocity	m s^{-1}	0·9	0·3	0·3	0·5	0·2
Surface–hyporheic ΔT	°C	1·2	2·2	0·2	2·4	1·0
Substrate D_{50}	mm	64·3	53·2	57·0	48·8	48·3
Substrate D_{10}	mm	6·6	4·7	11·3	9·5	7·1
Substrate D_{16}	mm	9·4	8·6	18·6	12·5	9·7
Substrate D_{84}	mm	116·2	121·5	97·0	87·9	138·6
Substrate $D_{GeometricMean}$	mm	42·4	37·8	46·8	38·1	42·1
Substrate $D_{CU\ (D60:D10)}$	ratio	9·7	14·6	6·0	6·4	10·6
Hazen $K_{(determined\ from\ D\ values)}$	cm s^{-1}	17·8	8·9	51·2	36·2	20·2
Shear stress	N m^{-2}	3·5	0·07	0·24	1·7	0·5

All data represent median values derived from the six locations within each of the five reaches (unless otherwise specified as a mean).

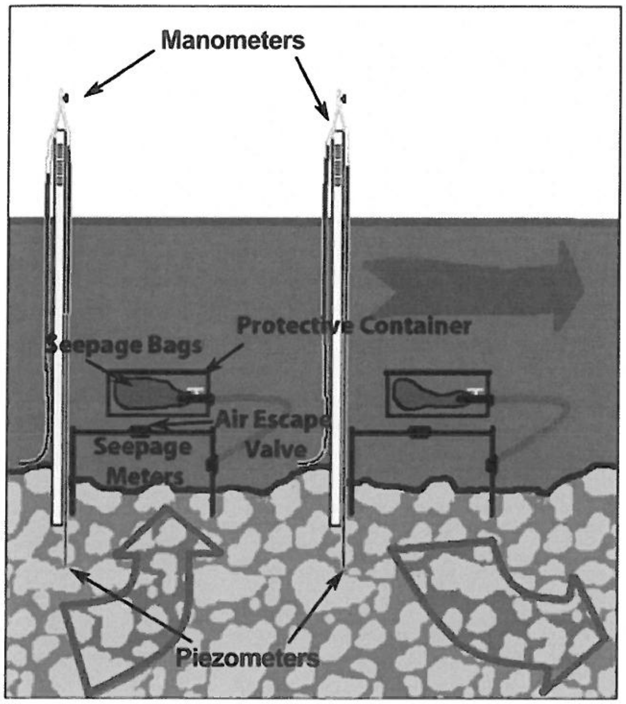

Figure 2. Experimental design for measuring flow across the sediment–water interface using half-barrel seepage metres. Vertical hydraulic gradients were measured using piezometers and manometers adjacent to the seepage metres. Upward exchange is shown on the left, and downward exchange is shown on the right. Detailed descriptions and validations of testing apparatus are outlined by Rosenberry (2008).

and D_{84}). Hydraulic conductivity (K) of the sediment was determined based on the D_{10} grain-size fraction (Okagbue, 1995). Pebble counts within this cobble-bed river were commonly determined using three Wolman surveys, one between the two sample locations that were farthest downstream, one between the two in the middle, and one between the two farthest upstream within each study reach. However, because of the complexity of Reach A, only one longer, continuous pebble count was conducted and was of equivalent resolution to the aggregated totals from the other reaches. Reach slope was measured using a theodolite, stadia rod, and measuring tape over the entire reach because most reaches were comprised geomorphically of a broad continuous run for the length of the 200-m study reach. Three slopes were determined for Reach A, however, because the reach included an upstream run, riffle, and downstream run. Shear stress (τ) was determined for all reaches from the depth–slope product relationship:

$$\tau = \rho g h s \quad (2)$$

where ρ is water density, g is acceleration of gravity, h is water depth, and s is the slope of the river water surface.

Data analysis used a Pearson's correlation coefficient matrix to identify relationships between the measured physical variables (explanatory variables) and mussel population densities (response variable) at the five study reaches where detailed physical data were collected. Within each study reach, data collected from the six individual sampling locations were aggregated, and the median was used to explore the relationship to mussel population density. Because of a sample size of $N = 6$ for the sampling locations within each reach, medians, as opposed to mean values, were deemed more appropriate for analysis, thus reducing the influence of extreme values that may not be representative of the reach as a whole. The only exception was seepage mean (Table I), where the mean value was deemed more appropriate because it was derived from 30+ individual seepage measurements from within each reach. Mussel population density was also log-transformed to improve linearity. An $\alpha = 0{\cdot}05$ threshold was used to determine significance for all statistical tests; marginally significant relationships were tested using an $\alpha = 0{\cdot}1$ threshold. Because of the exploratory nature of the study and relatively small sample size, alpha levels were not adjusted to correct for the number of comparisons. To identify possible covariance between the respective physical variables, the explanatory variables that were found to significantly correlate to mussel population density were then correlated against the strongest explanatory variable (Table II). Multiple seepage characteristics were used for correlative analysis across the study reaches to understand how mussel population density specifically relates to direction, magnitude, and variation in flow. The first is directional mean seepage, which is the reach-averaged arithmetic mean seepage velocity, including both upward and downward flows as positive and negative values, respectively. The second metric is absolute seepage, which is a reach-averaged absolute seepage velocity and ignores seepage direction, allowing for assessment of seepage magnitude independent of direction. The third is seepage range, which is the arithmetic range between the minimum (usually negative) and maximum seepage value.

RESULTS

Directional mean seepage ranged from downward at $-70\,\text{cm day}^{-1}$ at Reach A to upward at $104{\cdot}6\,\text{cm day}^{-1}$ at Reach D (Table I, Figure 3). Absolute seepage (not accounting for seepage direction) varied by an order of magnitude, from approximately 20 to $200\,\text{cm day}^{-1}$. Seepage range was greatest along Reach A with a variation of approximately $600\,\text{cm day}^{-1}$ across sites, whereas Reach C displayed the minimum observed range in seepage of approximately $30\,\text{cm day}^{-1}$ (Table I).

Several physical variables were significantly related with mussel population density (Table II). Strongest correlations

Table II. Pearson correlation coefficient values between measured variables presented in Table I.

Correlation comparison	Log_{10} population density	Seepage mean (directional)
Downstream distance	0·85*	0·63
Seepage mean (absolute)	−0·67	−0·49
Seepage mean (directional)	0·93**	—
Seepage range	−0·82*	−0·68
Head difference (Δh)	−0·28	−0·07
Δh range	−0·19	−0·06
Water depth	0·40	0·34
River width	0·90**	0·85*
Stream velocity	−0·70	−0·52
Surface–hyporheic ΔT	0·18	0·42
Substrate D_{50}	−0·92**	−0·84*
Substrate D_{10}	0·44	0·43
Substrate D_{16}	0·29	0·29
Substrate D_{84}	−0·22	−0·48
Substrate $D_{GeometricMean}$	−0·17	−0·37
Substrate $D_{CU\ (D60:D10)}$	−0·35	−0·37
Hazen $K_{(\text{determined from D values})}$	0·41	0·42
Shear stress	−0·56	−0·45

Column 2 compares mussel population density (response variable) to all physical variables (explanatory variables). Column 3 identifies covariation between directional mean seepage (the strongest explanatory variable of mussel density) and all other measured physical variables.
*Significant within $\alpha = 0{\cdot}1$.
**Significant within $\alpha = 0{\cdot}05$.

were with directional mean seepage ($r = 0{\cdot}93$, $p = 0{\cdot}02$) and seepage range ($r = -0{\cdot}82$, $p = 0{\cdot}09$). A significant negative relationship with D_{50} substrate size and a significant positive relationship with river width also existed. Downstream distance was marginally significantly related with mussel population density (positive relationship). Directional mean seepage, the strongest explanatory variable of mussel density, was directly correlated with river width and inversely correlated with substrate D_{50}, although with marginal significance. Reaches with a smaller range in seepage, and with larger upward mean seepage, contained higher mussel population densities (Figure 3).

DISCUSSION

Influence of seepage

The finding that mussel population density increases with increased upward seepage and decreased seepage variability (Figure 3) supports the speculation of Geist and Auerswald (2007), who suggested that juvenile mussel recruitment would improve with increased hyporheic exchange. Biologically, there may be several mechanisms that are possibly controlling these observed relationships. Low dissolved oxygen levels have been shown to have a negative influence on mussel survival (Sparks and Strayer, 1998). Increased hyporheic exchange increases circulation of interstitial waters surrounding mussels, resulting in higher concentrations of dissolved oxygen. Furthermore, riverbed areas where upward seepage occurs may include inputs from regional-scale groundwater discharge that contributes to and mixes with hyporheic water. Mixing hyporheic water with groundwater discharge can create a different water chemistry or temperature regime that is beneficial to mussel communities. Increased groundwater input can increase levels of beneficial nutrients, such as calcium, or dilute levels of toxic chemicals found in in-stream waters, such as ammonia, which has been shown to have a negative influence on mussel populations given sufficiently large concentrations (Newton, 2003). Briggs *et al.* (2013) demonstrated that another endangered unionid species (*Alasmidonta heterodon*) was found in areas of the upper Delaware River where the bed was substantially colder because of prodigious rates of groundwater discharge, potentially offering refuge from thermal stress during summer low-flow events or mediating the effects of warmer summer temperatures under a changing climate.

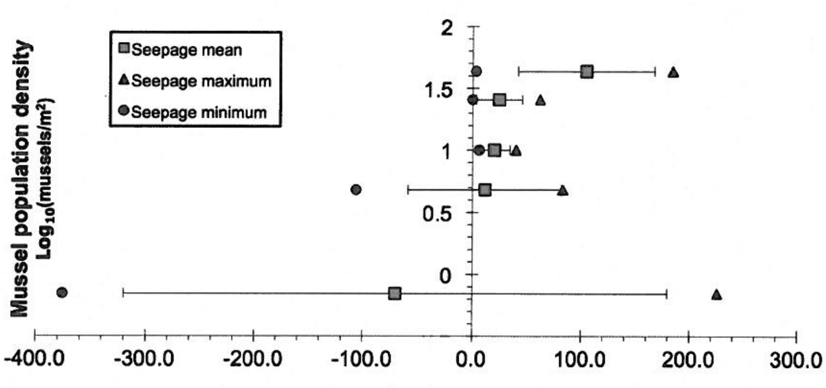

Figure 3. Relationships between log-transformed mussel population density and multiple seepage characteristics within the five reaches under study. Seepage metrics include seepage mean, seepage maximum, seepage minimum, and seepage range. Bars are two standard deviations in length.

Additional work is needed to determine the proportion of hyporheic water derived from groundwater discharge in relationship to the proportion of hyporheic water derived from in-stream water that enters the hyporheic zone somewhere upstream. Future work in differentiating the sources of upwelling hyporheic waters can further clarify the mechanism(s) and variable sources of water influencing this apparent control on mussel population density.

The inverse correlation between range of seepage and mussel density may be related to mussel habitat stability. Riverbed areas with a smaller range of seepage suggest greater habitat stability that may be advantageous to mussel populations. Rapid movement of adult mussels is limited; therefore, rapid changes in seepage, particularly changes between upward and downward flow across the sediment–water interface, could make feeding more difficult for unionid species dependent on a stable and dependable seepage regime from which to filter food sources. Additional work is needed to evaluate the concentration and distribution of suspended organic material in relation to direction, magnitude, and stability of hyporheic exchange and how these linkages may influence mussel population density.

Influence of substrate-size distribution

The negative correlation between median (D_{50}) grain size and mussel population density indicates that the unionids of the middle Allegheny River occurred at higher densities with increasingly finer-grained substrates (Table I). These values are based on surface Wolman (1954) pebble counts because the sediment was too coarse or the currents were too fast to effectively sample the sub-surficial sediment in many locations. However, at a location where a good sub-surface sample (i.e. no loss of fines during sample collection) could be collected (Reach A), bulk sediment beneath the armour layer remained coarse and in the medium gravel range, with a D_{50} value of 22 mm. Previous lab and field tests found that unionid mussels exist within a wide range of substrate types, with the dominant grain size ranging from silt to sand to gravel among species and locations (Vannote and Minshall, 1982; Huehner, 1987; Layzer and Madison, 1995; Brim Box *et al.*, 2002; Hunt and Stanley, 2003; Geist and Auerswald, 2007; Steuer *et al.*, 2008; Fulton *et al.*, 2010). The grain sizes present at the reaches downstream from Kinzua Dam (median diameter of ~50 mm for the surficial armour layer and median diameter of ~20 mm for the sediment below the surficial layer) were much larger than those reported in other literature on mussel grain-size preference. Previous works have mainly reported sediments approximately an order of magnitude smaller in diameter than what was found in the Allegheny River (Brim Box *et al.*, 2002, maximum diameter ~12 mm; Steuer *et al.* 2008, mean diameter ~2·4 mm). The negative correlation between population density and grain size observed within our studied sites may indicate that mussel population densities increase until grain sizes approach the smaller grain sizes reported in previous studies, suggesting an upper limit of these unionids' preferred range in substrate size.

Analyses revealed no correlation between mussel density and the smallest sediment grain-size fraction, D_{10}. Because hydraulic conductivity (K) is controlled primarily by the finest fraction of grain-size distributions (Okagbue, 1995), K may have little influence on the population density of unionid mussels within the upper reaches of the Allegheny River. D_{10} grain-size values at all study reach locations were relatively large compared with other studies of mussel habitat (e.g. Brim Box *et al.*, 2002; Steuer *et al.*, 2008), with the smallest D_{10} grain-size from this study (1·5 mm) still indicating sediments in the medium sand range. Large values for K (Hazen K, Table I), as well as large seepage rates in both directions (Figure 3), indicate that the water flows relatively easily through the near-surface hyporheic sediment. Rosenberry *et al.* (2012) highlighted the lack of 'bed clogging' from fine-grained sediment within this section of the Allegheny River downstream from Kinzua Dam. Despite a lack of flood-level flows (compared with unregulated rivers where the bed is regularly mobilized), the supply of fine-grained sediment from tributaries that discharge to this reach of the Allegheny did not greatly limit seepage and the ability for hyporheic exchange (Rosenberry *et al.*, 2012). Because the potential for water to flow to, from, and within hyporheic sediments did not appear to be related directly to mussel population densities, the control instead may be the range, direction, and magnitude of actual volumetric flow at the sediment–water interface. Results also represented conditions during relatively constant, moderately low river discharge. Additional research could determine the extent to which changes of river discharge would influence mussel population density through alterations in substrate distribution or through fluctuations in the rate and direction of exchange at the sediment–water interface.

Influence of river width and downstream distance

Mussel population density is related to both river width and distance downstream. Because river width often increases with increased downstream distance, the assumed relationship between increased mussel density and increased river width (which varies little in the study area, from only 13·5 to 16·5 m) may be misleading and instead could actually be a reflection of the influence of increased downstream distance alone. Correlations between downstream distance and mussel population density have been shown in other areas (Vaughn and Taylor, 1999; Galbraith and Vaughn, 2009; Galbraith and Vaughn, 2011; Atkinson *et al.*, 2012).

In Oklahoma, Vaughn and Taylor (1999) also found a linear increase in mussel abundance with increasing downstream distance from impoundments. Multiple explanations for this relationship were suggested, including increases in bed instability created by a more extreme flow regime closer to the dams, artificial reductions in summer water temperature caused by bottom releases from the upstream reservoir and/or reduction of suspended organic material within water released from the dam. Reduced suspended organic material would reduce the supply of food for feeding mussels. Others have speculated that unnaturally cool water temperatures downstream of dams may hinder mussel population density and success of mussel gametes; Galbraith and Vaughn (2009 and 2011) highlight evidence showing lower abundance and reproductive success under cooler-than-normal temperatures. Atkinson *et al.* (2012) further expanded on this influence of downstream distance by showing that the downstream distance from the headwaters, and not just impoundments, can also influence mussel community composition.

Scale and sampling influences

Although shear stress measured on a stream-reach scale did not correlate with mussel population density, localized measurements of shear stress may relate to mussel habitat as was found by Hardison and Layzer (2001). Because this study is limited in its statistical power with only five study reaches, an increased possibility exists of an error occurring because of chance. As well, this study may have shown some explanatory factors as being non-significant when they may actually be found significant under a larger sampling framework. Additional work would be needed to evaluate the temporal and spatial scale at which many of these explanatory variables become significant controls on mussel population densities in different river settings and discharge rates. Discharge also influences rates of hyporheic exchange, and thus changes in discharge may have resulting impacts on mussel species, which are long-lived sessile organisms that exist under a range of flow regimes during their lifespan. Large discharge events, such as floods, can also disturb bedforms and change the substrate composition. Because large events are usually infrequent, the ability to observe the influence of these events on mussel distributions becomes difficult and therefore offers avenues for future research.

CONCLUSIONS

Previous studies that related physical properties to mussel density either did not consider or were unable to quantify hyporheic exchange as an explanatory factor. This study quantified several of these relationships and found increased upward seepage to be positively correlated, and increased range in seepage negatively correlated, to increased mussel population density. Measured seepage direction and rate may therefore either directly or indirectly affect the population density of these unionid mussels and should be considered as potentially important parameters in future research. Directional mean seepage, river width, and D_{50} substrate size were found to cross-correlate with marginal significance as well, so the individual influence of each on mussel population density is uncertain. It is possible that all of the physical factors found to significantly (or marginally) correlate to increased mussel population density were acting through independent biological mechanisms. Alternatively, one factor, such as upward seepage, may have been primary but covariant with others, making its influence indeterminable in this field-based study. Considering this, laboratory studies in conjunction with field studies may more effectively isolate the relative influence of individual seepage variables on mussels, thus further expanding these and other mechanistic findings.

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