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Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance

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Abstract. We examined how substrate and complex hydraulic variables limit the distribution of freshwater mussels. We sampled mussels and measured substrate and hydraulic variables (at low and high flows) at 6 sites in the Little River, Oklahoma. To test which variables were most limiting to mussel species richness and abundance, we evaluated univariate and multiple 95th-, 90th-, and 85th-quantile regression models using a model selection approach. Across all 3 quantiles analyzed, hydraulic variables related to substrate stability (relative shear stress ratio [RSS] and shear stress) at high flows most limited mussel species richness and abundance. High-flow substrate stability models performed the best, but models that used substrate variables (substrate size and heterogeneity) also performed relatively well. Models that used complex hydraulic variables estimated at low flows performed poorly compared to those using the same variables estimated at high flows, a result suggesting that hydraulic conditions at low flows do not limit mussel habitat in our system. Our results demonstrate that substrate stability at high flows is an important factor governing mussel distributions. Last, our quantile regression approach successfully quantified the limiting-factor relationships of substrate and hydraulic characteristics on mussel habitat, and this approach could be used in other studies investigating habitat requirements of aquatic organisms.

Key words: Unionidae habitat, quantile regression, model selection, limiting-factor, constraint relationships.

Recent catastrophic declines in the abundance and diversity of freshwater mussel populations (Bivalvia:Unionoida) have led conservationists to recognize these animals as North America's most imperiled fauna (Strayer et al. 2004). Only ¼ of the ~300 North American species are considered to have stable populations (Williams et al. 1993). Mussel population declines have multiple causes, including invasive species, water-quality degradation, and habitat alteration by impoundments (Lydeard et al. 2004, Strayer et al. 2004). Alteration of flow regimes by impoundments, channelization, and other man-made modifications has led to biodiversity losses in many riverine faunal groups (Poff et al. 2007), but freshwater mussel communities seem particularly sensitive to changes in hydrologic conditions (Watters 2000, Strayer et al. 2004).

Freshwater mussels often occur in dense multispecies aggregations (mussel beds) that are patchily distributed within streams and rivers. Locations of these aggregations and mussel abundance at smaller scales have been predicted successfully with complex hydraulic variables (Gangloff and Feminella 2007, Steuer et al. 2008, Zigler et al. 2008). Complex hydraulic variables related to near-bed flow characteristics, such as shear stress, are thought to be important factors for mussel habitat. Excessive shear stresses (hydraulic forces parallel to the substrate surface) at high flows can initiate substrate movement, so mussel aggregations are most likely to persist in areas where shear stresses remain low during spates, i.e., where substrates are stable (Strayer 1999, 2008, Strayer et al. 2004). Excessive shear stresses can also prevent juvenile mussels from settling into streambed substrates (Layzer and Madison 1995, Hardison and Layzer 2001), and mussel abundances are low in areas of high shear stresses during high flows (Hardison and Layzer 2001, Howard and Cuffey 2003, Gangloff and Feminella 2007).

However, several issues prevent mollusk ecologists from reaching a consensus on the importance of substrate stability for freshwater mussel distributions. First, shear stress is not the only factor that influences substrate stability. Armoring and substrate size also

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are important factors determining whether substrates will become entrained during high flows (Gordon et al. 2004), so substrate characteristics also must be quantified. Studies that have used substrate characteristics and hydraulic variables have had some success predicting mussel abundance (Steuer et al. 2008). Second, very few studies have estimated hydraulic variables with data collected at both low and high flows (but see Hardison and Layzer 2001). Several authors have suggested that hydraulic variables should be more important at high than at low flows (Hardison and Layzer 2001, Howard and Cuffey 2003, Gangloff and Feminella 2007), but variables at high flows often are estimated from measurements of channel geomorphology rather than measured directly. Last, studies that have found substrate stability to be important for mussel habitat have primarily used computer simulations that have not been adequately ground-truthed. For example, the mussel dynamics model developed by Morales et al. (2006a) simulated mussel colonization using substrate stability to determine suitable habitats. However, this model has yet to be rigorously tested in the field and relies on many untested assumptions and parameter values (Morales et al. 2006b). Shear stress and substrate stability successfully predicted mussel abundance in a computer simulation by Zigler et al. (2008), but interpretation of these results was limited because of a significant time lag between the dates of collection of mussel and hydrologic data. The most rigorous support for substrate stability being an important factor for freshwater mussel habitat is from a field study in which mussels were most abundant in areas where marked stones moved the least during a spate (Strayer 1999). However, an alternative explanation for this result is that mussels themselves were stabilizing substrates, such that the marked stones moved the least in areas where mussel abundances were highest. It has been suggested that freshwater mussels might stabilize substrates (Johnson and Brown 2000, Vaughn and Spooner 2006, Strayer 2008), although the results of a recent laboratory investigation were inconclusive (Zimmerman and de Szalay 2007).

Use of mussel abundance as the sole indicator of mussel habitat quality has limited our ability to interpret the results of studies on the relationships between freshwater mussel distributions and complex hydraulic variables (but see Gangloff and Feminella 2007). A positive relationship between substrate stability and mussel abundance is expected because when substrates are more stable over time, adult mussels should be less likely to be washed out during floods and the number of colonizing juvenile mussels surviving into adulthood should increase (Strayer 1999, Hardison and Layzer 2001, Hastie et al. 2001). However, different freshwater mussel species might prefer different hydraulic conditions or different levels of substrate stability. It seems likely that if substrate stability is associated with lower adult mussel mortality and greater juvenile mussel colonization more mussel species would also be present, but studies investigating relationships between substrate stability and mussel species richness are lacking. Given that declines in mussel species richness are of as much concern as declines in mussel abundance (Lydeard et al. 2004, Strayer et al. 2004), a great need exists for studies that investigate habitat requirements for species-rich mussel beds.

Most previous studies have used predictive statistical models to analyze relationships between complex hydraulic variables and mussel habitat quality (Gangloff and Feminella 2007, Steuer et al. 2008, Zigler et al. 2008). Strayer (2008) argued that many factors in addition to hydraulic and substrate characteristics influence freshwater mussel distributions. These other factors include fish host distributions, food quality and quantity, water quality, and temperature. Therefore, even if substrate and hydraulic conditions were optimal, overall mussel habitat quality could be quite poor if these other requirements were not met (e.g., fish hosts not abundant or food quality low). Consequently, substrate and hydraulic variables should be analyzed as constraints or limiting factors rather than predictive variables because, at best, they can only partially explain mussel distributions.

We investigated how substrate stability (assessed with substrate and complex hydraulic variables) limits mussel habitat. We measured mussel species richness and abundance, substrate characteristics, and hydraulic variables in situ, and we evaluated quantile regression models to determine whether and how these factors constrained mussel distributions.

Methods

Study area and variables

We conducted our study in the Little River in southeastern Oklahoma, USA (Fig. 1). The Little River is a major tributary of the Red River that drains 10,720 km^2 in Oklahoma and Arkansas (Matthews et al. 2005). This river has high biodiversity and supports 110 fish and >36 mussel species (Matthews et al. 2005). Mussel communities in this river have been studied (Vaughn and Taylor 1999, Galbraith et al. 2008), so we selected a priori 6 sites known to have abundant, diverse, and reproducing mussel commu-

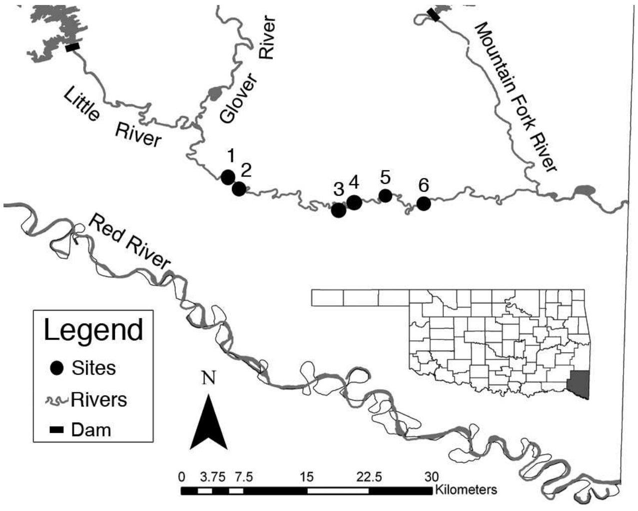

FIG. 1. Sampling sites on the Little River in southeastern Oklahoma.

nities (Fig. 1). Some mussel assemblages in the Little River are influenced by 1 mainstem and 1 tributary impoundment on the Mountain Fork River (Fig. 1; Vaughn and Taylor 1999, Matthews et al. 2005). The tributary impoundment affects mussel communities primarily through cold water releases and hydroelectric peaking, but all of our study sites were upstream of this influence. The mainstem impoundment (Pine Creek Reservoir) is used for flood control and recreation, but the influence of this reservoir is negligible downstream of the confluence with a tributary, the Glover River, which enters the Little River and modulates flows (Vaughn and Taylor 1999). Our 6 sites were all downstream of the confluence of the Glover with the Little River and were only minimally affected by Pine Creek Reservoir, as evidenced by low summer flows (mean ± SE discharge during low-flow sampling = 0.63 ± 0.08 m^3/s), warm summer temperatures (mean = 30.6°C), and diverse and abundant mussel assemblages with juvenile recruitment. Seasonal median discharges calculated from monthly averages during 1977 to 2007 at a US Geological Survey (USGS) gauging station (07338500) immediately downstream of site 4 (Fig. 1) were 63.7 m^3/s in spring (March–May), 7.9 m^3/s in summer (June–August), 11.9 m^3/s in autumn (September–November), and 60.3 m^3/s in winter (December–February).

During July 2006, a period of low flows, we established 6 equidistant transects across the river at each site. Transects were 10 to 20 m apart depending on the size of the mussel bed (mean width of our transects across the river = 21.9 ± 0.94 m) and covered both riffles and pools. We measured water depth and current velocity at the centers of 1-m cells along 1 transect at each site for discharge calculations. We placed four 0.25-m^2 quadrats, evenly spaced across the river cross-section, along each transect. This stratified-block design and distance markers along the riverbank allowed us to locate each quadrat easily by boat at higher flows (see below).

At each quadrat, we measured water depth with a meter stick and current velocity at 0.6 × depth with a Marsh–McBirney$^{\mathrm{TM}}$ Flo-Mate flowmeter (Marsh–McBirney, Frederick, Maryland). We chose a random point in each quadrat and used a trowel to collect superficial substrates until we filled a 0.72-L plastic bag ($\sim$20% of the superficial substrate in the quadrat). Larger rocks ($\sim \geq$63.5 mm) were kept in separate bags so that we had at least a 0.72 L sample to process after substrates $>$63.5 mm were excluded from the sample (to remove the bias of larger particles on substrate variables; Church et al. 1987). We sampled for mussels in each quadrat as the last step of the field protocol. We excavated each quadrat to a depth of 15 cm, removed all mussels from the quadrat, identified them, measured their shell length, and returned them to the quadrat (Vaughn and Spooner 2006, Galbraith et al. 2008). We took the substrate samples to the laboratory, dried them for 48 h at 100°C, passed the samples through a series of 12 geological sieves (63.5, 38.1, 19, 8, 3.962, 1.981, 0.991, 0.495, 0.246, 0.175, 0.088, and 0.061 mm), and weighed each fraction.

We returned to each site during periods of high flow between autumn 2006 and spring 2007 (mean discharge during high-flow sampling = 53.07 ± 7.92 m^3/s). We measured water depth and current velocity at the centers of 1-m cells along 1 transect at each site for discharge calculations, and we measured depth and current velocity at each quadrat on all 6 transects. We made all measurements from a boat secured to a cable stretched across the transect. We measured depth with a Hondex$^{\mathrm{TM}}$ digital depth sounder (Honda Electronics Co. Ltd., Toyohashi City, Japan), and we measured current velocity by suspending a Marsh–McBirney$^{\mathrm{TM}}$ Flo-Mate flowmeter fixed to a 13.6-kg Columbus-type sounding weight (Scientific Instruments, Milwaukee, Wisconsin) on a marked cable at 0.6 × depth in the center of the quadrat.

We calculated substrate and hydraulic variables from formulae in Table 1. We refer to hydraulic variables estimated at low and high flows with LF and HF, respectively. We chose 0.065 as the value for Shield's parameter (θ_c) because substrates at our sites consisted of normally packed gravel with fairly random grain arrangements (Gordon et al. 2004). We

TABLE 1. Summary of substrate variables and hydraulic variables estimated at low and high flows. D_x = substrate particle size (cm) at which x% of the sample by mass is finer, d = water depth (cm), ϕ = unit of substrate size ($\phi = -\log_2 D$ [mm]), ϕx = substrate particle size (ϕ) at which x% of the sample by mass is finer, U = mean current velocity (cm/s), g = acceleration of gravity (980 cm/s), v = kinematic viscosity of water (0.01 cm^2/s), ρ = density of water (0.998 g/cm^3), ρ_s = density of substrate (2.65 g/cm^3), θ_c = Shield's parameter (0.065) (Gordon et al. 2004).

Variable (symbol, unit)	Formula	Description	Source
Substrate variables			
D (cm)	$\frac{(D_{16}+D_{50}+D_{84})}{3}$	Mean particle size of sample	Folk 1965
Sorting index (D S.D.; ϕ converted to cm)	$\frac{(\phi 84-\phi 16)}{2}$	Substrate heterogeneity	Gordon et al. 2004
Bed roughness (k_s, cm)	$3.5\times D_{84}$	Topographical variation of stream bed	Gordon et al. 2004
Hydraulic variables			
Froude number (Fr, dimensionless)	$\sqrt{\frac{U^2}{gd}}$	Ratio of inertial to gravitational forces	Statzner et al. 1988
Reynolds number (Re, dimensionless)	$\frac{Ud}{v}$	Ratio of inertial to viscous forces	Statzner et al. 1988
Boundary Reynolds number (Re$_*$, dimensionless)	$\frac{U_* k_s}{v}$	Roughness of flow near substrate	Statzner et al. 1988
Shear velocity (U_*, cm/s)	$\frac{U}{5.75\log_{10}\left(\frac{12d}{k_s}\right)}$	Friction velocity	Statzner et al. 1988
Shear stress (τ, dynes/cm^2)	$\rho\left(U_*^2\right)$	Force of friction on substrate	Statzner et al. 1988
Critical shear stress (τ_c, dynes/cm^2)	$\theta_c g D_{50}(\rho_s-\rho)$	Shear stress required to initiate substrate motion for a typical sample substrate size (D_{50})	Gordon et al. 2004
Relative shear stress (RSS, dimensionless)	$\frac{\tau}{\tau_c}$	Ratio of observed to critical shear stress (values $>$ 1 represent substrate movement for a typical sample substrate size [D_{50}])	Morales et al. 2006a

calculated exceedance levels of our calculated discharge relative to historical data (1946–2007) from US Geological Survey (USGS) gauging station 07338500 to quantify the relative flow levels represented by our data.

Data analysis

Multicollinearity among estimated hydraulic variables has been observed in other studies (Hardison and Layzer 2001). We wanted to reduce redundancy and multicollinearity bias ($r > 0.8$) in our statistical models because it can interfere with interpretation of results even though it would not violate the assumptions of our model selection approach described below (Burnham and Anderson 2002). We calculated Pearson correlation coefficients between all substrate and estimated hydraulic variables. Shear velocity (U_*) and shear stress (τ) were strongly correlated at low and high flows (r = 0.87 and 0.97, respectively), Froude number (Fr) and τ were strongly correlated at low and high flows (0.81 and 0.92), and HF boundary Reynolds number (Re$_*$) was strongly correlated with mean substrate particle size (D) (r = 0.83). Therefore, we dropped U_*, Fr, and Re$_*$ from all subsequent analyses. We chose to keep τ and drop Fr and U_* because previous studies have shown relationships between τ and mussel distributions (Hardison and Layzer 2001, Howard and Cuffey 2003, Gangloff and Feminella 2007) and because τ is important for substrate stability (Gordon et al. 2004). We chose to retain D instead of Re$_*$ because substrate stability should be inversely related to substrate size given equal shear stresses (Gordon et al. 2004), and because Steuer et al. (2008) found that substrate size was a predictor of mussel abundance.

Quantile regression models have been used in ecological studies to estimate functions along or near the upper boundary of the response distribution to measure limiting factors (Cade and Noon 2003). Quantile regression is based on least absolute deviation regression, which models the conditional median (50th quantile), but the approach can be extended to any quantile (Cade et al. 1999, Cade and Noon 2003, Koenker 2005). Quantile regression estimates are semiparametric; no parametric distributional form is assumed for random errors but is assumed for the deterministic portion of the model (Cade and Noon 2003). Therefore, unlike traditional least-squares regression, quantile regression relaxes the assumptions of normally distributed data and homoscedacity (Hao and Naiman 2007). In ecological studies, 95th-quantile regressions have been used to estimate limiting-factor relationships; i.e. ~95% of the observations are below the fitted line (Schooley and Wiens 2005).

One limitation of focusing on the 95th quantile is that a large sample size is required for the analysis to be robust because a small fraction of the data (in this case, ~5%) is heavily weighted when parameter estimates are generated for regression functions and model fit is calculated. Our sample size was relatively small ($n = 144$), so we modeled 3 extreme quantiles (95th, 90th, 85th) for a more robust analysis. We $\sqrt{x+1}$-transformed mussel abundance data before analysis (Zar 1999). We fit linear, quadratic, or Ricker curves to the data (with and without y-intercepts), and chose the best-fitting model based on Akaike information criterion (AIC) provided it had non-0 parameter estimates for model coefficients. We used the same functions to fit multivariate quantile regression models. We conducted quantile regression analyses using the quantreg package (version 4.24 developed by R. Koenker) for R software (version 2.8.1; R Foundation for Statistical Computing, Vienna, Austria).

We evaluated quantile regression models with AIC. We followed Schooley and Wiens (2005) and calculated AIC for quantile regression models as $\mathrm{AIC}=n(\log\hat{\sigma}^2)+2K$ (Hurvich and Tsai 1990), where K is the number of estimated variables + 2 (intercept and residual variance) and substituted the weighted absolute deviations (the absolute deviation of values predicted by the model from observed values, weighted by p for the p^{th} quantile if the predicted value > observed value and [1 – p] if the predicted value < observed value; Hao and Naiman 2007) for $\hat{\sigma}$. We converted AIC to small-sample AIC ($\mathrm{AIC_c}$; Burnham and Anderson 2002), and calculated the coefficient of determination (R) as 1 – (sum of the weighted absolute deviations of the model of interest divided by sum of the weighted absolute deviations of the intercept-only model) (Schooley and Wiens 2005, Hao and Naiman 2007). We report a pseudo-R^2 for quantile regression models as $1 - (1 - R)^2$ to provide a unit of measure comparable to R^2 (McKean and Sievers 1987, Schooley and Wiens 2005).

We generated 15 models (7 multivariate models and 8 univariate models) a priori to avoid data-dredging and to ease interpretation of results (Johnson and Omland 2004). We chose the 7 multivariate models to represent different hypotheses that might explain mussel distributions: 1) substrate model (D + substrate heterogeneity [D S.D.]), 2 and 3) LF and HF hydraulics models (LF or HF Re + τ + RSS), 4 and 5) LF and HF hydraulics and substrate models (LF or HF Re + τ + RSS + D + D S.D.), 6) HF substrate stability model (HF τ + RSS), and 7) a global model (all substrate and flow variables, an overparameterized model used for comparison). For each quantile, we report $\mathrm{AIC_c}$ differences (Δ_i) and Akaike weights (w_i, the relative likelihood of a model given a data set and set of models) for the 5 best models and the pseudo-R^2 of an averaged model based on predicted values from the best-performing models ($\Delta_i < 2$) weighted by w_i (Burnham and Anderson 2002). Last, we determined the 5 best models across the 95th, 90th, and 85th quantiles by averaging w_i for each model from all 3 quantile model selection analyses.

Results

Mussel communities were diverse and abundant at all 6 sites. Mean mussel species richness at our sites was 18.33 ± 0.76 (SE), and mean mussel abundance (no./m^2) was 44.95 ± 4.80. Juvenile mussels (individuals < 30 mm in length) were recorded at all sites. For more detailed descriptions of the mussel communities in the Little River, see Vaughn and Taylor (1999) and Galbraith et al. (2008). Low and high flow levels corresponded to exceedances of 95.15 ± 0.99 and 27.02 ± 2.06, respectively. Safety concerns prevented us from recording depth and flow measurements at peak flow levels (311.49 m^3/s was the highest recorded discharge at the USGS gauging station near our sites between 2006–2007).

Substrate and hydraulic variables estimated at low and high flows showed limiting-factor relationships with mussel species richness and abundance (Figs 2A–H, 3A–H). The limiting-factor relationships between D and mussel species richness and abundance were unimodal and best described by the Ricker function for all extreme quantiles (Figs 2A, 3A). In contrast, the shape of the limiting-factor relationships between D S.D. and species richness and abundance differed depending on the quantile (Figs 2B, 3B). The limiting-factor relationships between Re and τ and species richness and abundance were unimodal and described by Ricker and quadratic functions at both low and high flows (Figs 2C–F, 3C–F). However, the shape of the limiting-factor relationships between RSS and species richness and abundance depended on flow level. The limiting-factor relationships between LF RSS and species richness and abundance were unimodal and described by the Ricker function (Figs 2G, 3G), whereas the limiting-factor relation-

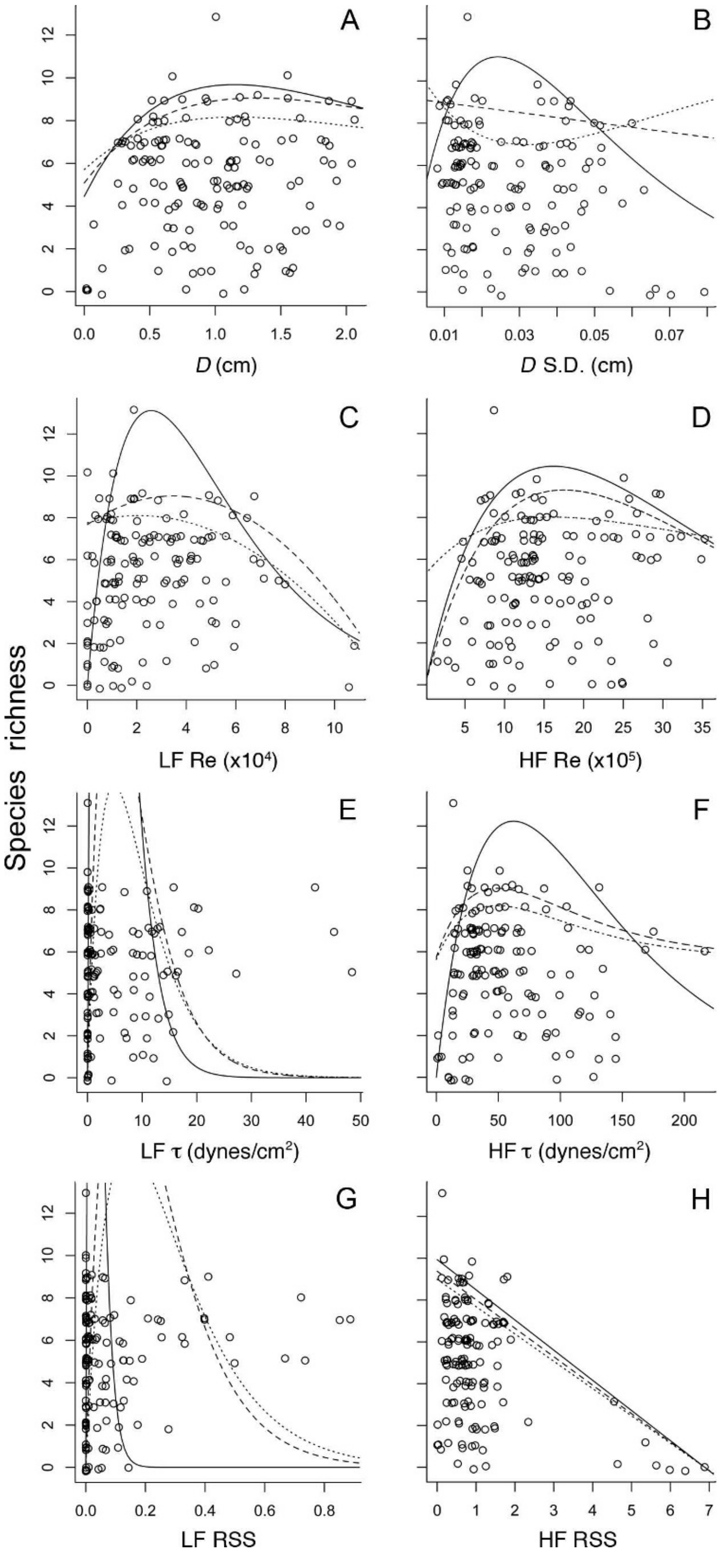

FIG. 2. Quantile regression models for mussel species richness/0.25-m^2 quadrat for substrate (A, B) and hydraulic (C–H) variables. Solid, dashed, and dotted lines represent 95th, 90th, and 85th quantile regression lines, respectively. LF and HF designate that the variable was estimated at low or high flows. Abbreviations for variables are given in Table 1.

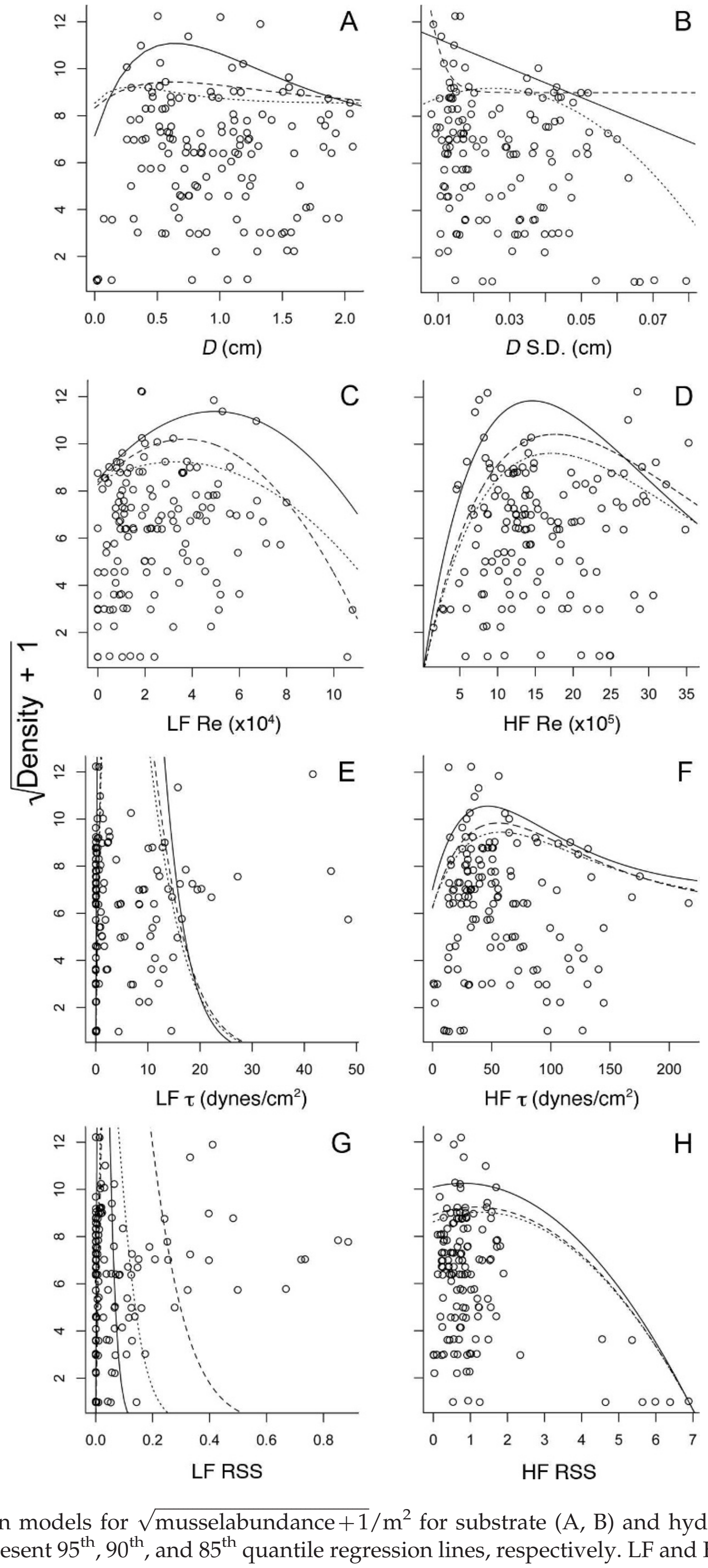

FIG. 3. Quantile regression models for $\sqrt{\text{musselabundance}+1}/\text{m}^2$ for substrate (A, B) and hydraulic variables (C–H). Solid, dashed, and dotted lines represent 95th, 90th, and 85th quantile regression lines, respectively. LF and HF designate that the variable was estimated at low or high flows. Abbreviations for variables are given in Table 1.

TABLE 2. Summary of small-sample Akaike information criterion (AIC_c) selection of univariate and multiple 95th, 90th, and 85th quantile regression models for mussel species richness. LF and HF designate that the model used hydraulic variables estimated at low or high flows. K = number of parameters in model + 2, Δ_i = AIC_c of model relative to lowest AIC_c, w_i = Akaike weight, R^2 = pseudo-R^2 of an averaged model using the best-performing models ($\Delta_i < 2$). Only the 5 best-performing models are shown. Abbreviations for variables are given in Table 1.

95th quantile ($R^2 = 0.14$)					90th quantile ($R^2 = 0.20$)					85th quantile ($R^2 = 0.18$)				
Rank	Model	K	Δ_i	w_i	Rank	Model	K	Δ_i	w_i	Rank	Model	K	Δ_i	w_i
1	D + D S.D.	6	0.000	0.472	1	HF τ + RSS	5	0.000	0.336	1	HF RSS	3	0.000	0.371
2	HF RSS	3	1.142	0.267	2	HF Re + τ + RSS	7	0.304	0.289	2	HF τ + RSS	5	0.220	0.333
3	HF Re + τ + RSS	7	2.427	0.140	3	HF RSS	3	0.517	0.259	3	HF Re + τ + RSS	7	0.802	0.258
4	D	4	3.705	0.074	4	D + D S.D.	5	4.050	0.044	4	D + D S.D. + HF Re + τ + RSS	11	7.750	0.011
5	HF τ + RSS	5	4.944	0.040	5	HF Re + τ + RSS + D + D S.D.	10	4.496	0.035	5	HF τ	4	7.897	0.007

ships between HF RSS and species richness and abundance were decreasing functions. For species richness, the negative constraint was described by a linear function (Fig. 2H), whereas for abundance, it was described by the decreasing portion of a concave quadratic function (Fig. 3H).

Models with substrate variables performed best for the 95th quantile, whereas models with hydraulic variables related to substrate stability performed best for the 90th and 85th quantiles (AIC_c selection; Tables 2, 3). When Akaike weights (w_i) were averaged from our 3 quantile model selection analyses, models using hydraulic variables estimated at high flows performed better than models using substrate variables (Table 4). Summed average w_i for models with HF hydraulic variables were 0.79 and 0.61 for species richness and abundance, respectively, whereas summed average w_i for models with substrate variables for were 0.23 and 0.33 for species richness and abundance, respectively. HF RSS appeared to be the most important HF hydraulic variable because it was included in all of the best-performing models with HF variables for both species richness and abundance. HF τ was important only in models that also included HF RSS for both species richness and abundance. HF Re was important only in models that included both HF RSS and HF τ, and only for species richness. Among models with substrate variables, summed average w_i for models with D were 0.23 and 0.17 for species richness and abundance, whereas summed average w_i for models with D S.D. were 0.18 and 0.31 for species richness and abundance, respectively. Models with LF hydraulic variables performed poorly (summed average w_i = 0.002 and 0.09 for species richness and abundance, respectively).

Discussion

The most important result of our study was that across all 3 extreme quantiles analyzed, hydraulic variables related to substrate stability at high flows were most limiting for mussel species richness and abundance. Substrate models also performed well in our AIC_c selection analysis, but only at more extreme quantiles (95th for species richness and abundance, and 90th for abundance). Second, models with hydraulic variables estimated at high flows performed much better than models with the same variables estimated at low flows. Last, quantile regression is a useful analytical tool for investigating the ability of any single group of habitat factors to explain mussel distributions.

Hydraulic variables describing substrate stability at high flows were most limiting to freshwater mussel

TABLE 3. Summary of small-sample Akaike information criterion (AIC_c) selection of univariate and multiple 95th, 90th, and 85th quantile regression models for mussel abundance. LF and HF designate that the model used hydraulic variables estimated at low or high flows. K = number of parameters in model + 2, Δ_i = AIC_c of model relative to lowest AIC_c, w_i = Akaike weight, R^2 = pseudo-R^2 of an averaged model using the best-performing models ($\Delta_i < 2$). Only the 5 best-performing models are shown. Abbreviations for variables are given in Table 1.

95th quantile (R^2 = 0.22)					90th quantile (R^2 = 0.14)					85th quantile (R^2 = 0.17)				
Rank	Model	K	Δ_i	w_i	Rank	Model	K	Δ_i	w_i	Rank	Model	K	Δ_i	w_i
1	D + D S.D.	4	0.000	0.415	1	HF τ + RSS	6	0.000	0.356	1	HF τ + RSS	6	0.000	0.351
2	D S.D.	3	0.926	0.261	2	HF RSS	4	0.188	0.324	2	HF RSS	4	0.691	0.249
3	HF τ + RSS	6	1.860	0.164	3	D S.D.	4	1.563	0.163	3	HF Re + τ + RSS	8	1.024	0.211
4	LF Re	4	2.590	0.114	4	LF Re	4	3.551	0.060	4	HF τ	4	3.879	0.051
5	HF τ	4	5.797	0.023	5	HF τ	4	4.010	0.048	5	LF Re	4	4.184	0.043

TABLE 4. Akaike weights (w_i) averaged from small-sample Akaike information criterion (AIC_c) selection of univariate and multiple 95th, 90th, and 85th quantile regression models for mussel species richness and abundance. LF and HF designate that the model used hydraulic variables estimated at low or high flows. Models with 5 highest average Akaike weights (w_i) are shown, abbreviations for variables are given in Table 1.

Species richness		Abundance	
Model	Average w_i	Model	Average w_i
HF RSS	0.299	HF τ + RSS	0.290
HF τ + RSS	0.236	HF RSS	0.195
HF Re + τ + RSS	0.229	D S.D.	0.151
D + D S.D.	0.174	D + D S.D.	0.146
D	0.034	HF Re + τ + RSS	0.078

abundance and species richness. HF RSS alone or in conjunction with HF τ performed very well for both species richness and abundance. HF Re appeared to be less important, and only performed well in conjunction with HF RSS and HF τ. These results support those of other studies suggesting that substrate stability during high flows restricts mussel abundance (Strayer 1999, Morales et al. 2006a, Gangloff and Feminella 2007). Moreover, our analysis is the first to show that substrate stability during high flows also restricts mussel species richness. Therefore, substrate stability during spates is likely to limit the distribution of dense and speciose mussel beds. Our analysis also suggests that τ might not always be a useful surrogate measure for substrate stability, even when estimated at high flows. By itself, HF τ performed poorly in our analysis, and HF τ performed well only in the presence of HF RSS. This result shows the importance of quantifying both substrate characteristics and hydraulic variables to estimate substrate movement when assessing suitability of mussel habitat.

Our estimates of substrate stability at high flows suggest that mussels might be able to tolerate some substrate movement. Mussel abundance and mussel species richness were high when HF RSS was >1, but dropped sharply when HF RSS was >2 (RSS > 1 indicates substrate movement; Figs 2H, 3H). However, our estimates of RSS used a typical sized particle (D_{50}) to estimate substrate movement. Therefore, RSS > 1 does not necessarily mean that the entire stream bed is in motion because D_{50} could represent just a small fraction of the larger materials sampled from the bed surface (Gordon et al. 2004). Thus, mussels might be able to tolerate movement of smaller substrate particles during high flows, but not movement of larger particles or the entire stream bed.

Furthermore, we omitted substrate particles $>$ 63.5 mm from our substrate analysis to reduce the bias larger particles can have on substrate variables (Church et al. 1987). Omitting the largest substrate particles reduces D_{50} values and could have caused overestimation of substrate movement. Alternatively, if mussels themselves stabilize substrates as other authors have suggested (Johnson and Brown 2000, Vaughn and Spooner 2006, Strayer 2008), all substrates might have remained stable at RSS $>$ 1. Mussels increase sediment compaction and cohesion (Zimmerman and de Szalay 2007), which should decrease the ability of substrate particles to become entrained (Gordon et al. 2004). Estimates of substrate stability based on RSS use substrate and hydraulic variables, so biological influences on substrate stability are not taken into account. We think in-depth study of the influence of mussels on substrate stability is warranted.

Models with the substrate variables D and D S.D. performed the best in 95th quantile regressions for both mussel species richness and abundance, but did not perform as well for any other quantile. This result might indicate that model performance was strongly influenced by data points at the boundary of the response distribution. Further evidence of this possibility is given by the differences among the best-fitting functions of the quantile regressions for D S.D. across the 95th, 90th, and 85th quantiles. For both species richness and abundance, the best-fitting quantile regressions for D S.D. did not have consistent mathematical functions. Instead the functions were linear, concave, or convex depending on the quantile (Figs 2B, 3B). However, substrate variables were not entirely absent from models that performed well for quantiles other than the 95th because the D S.D. model had w_i = 0.163 for the 90th quantile of mussel abundance. Therefore, substrate model performance might be somewhat spurious for the 95th quantile, but we think that substrate variables probably have a small limiting effect that is overwhelmed by HF hydraulic variables related to substrate stability in our system. This disparity in the size of the effects might explain why substrate variables were important factors for mussel habitat in some studies (Steuer et al. 2008) but not in others (Strayer 1999).

Hydraulic variables estimated at high flows outperformed the same variables estimated at low flows. This result supports our hypothesis that hydraulic characteristics are more important to mussel habitat at high than at low flows, a conclusion that has been suggested by other authors (Hardison and Layzer 2001, Howard and Cuffey 2003, Gangloff and Feminella 2007). However, our results contrast with those of Steuer et al. (2008), who found that hydraulic variables estimated at low flows were better predictors of mussel abundance in the Upper Mississippi River than hydraulic variables estimated at high flows. Steuer et al. (2008) suggested that minimum Re$*$ and Fr might be required during low flows to deliver food or transport waste products. Thus, hydraulic variables estimated at low flows might not limit mussel distributions in smaller rivers, such as our system, but might be important in larger rivers, such as the Upper Mississippi River.

Quantile regression was a useful tool for studying the limiting effect of substrate and complex hydraulic variables on mussel species richness and abundance. The prevailing view in freshwater mussel ecology is that many factors in addition to hydraulic and substrate variables influence freshwater mussel distributions, including fish host distributions, food quantity and quality, and water quality (Strayer 2008). Thus, we should not expect any single group of variables to predict mussel habitat quality adequately. Rather, these variables should have limiting-factor relationships that constrain mussel distributions. For example, in our study the highest mussel abundances and species richness occurred in quadrats with low HF RSS, but mussel abundance and species richness in other quadrats were low when HF RSS values were low (Figs 2H, 3H). Presumably, some unmeasured factor was limiting in quadrats we estimated to be stable at high flows but with low mussel abundances or species richness.

We were able to quantify limiting-factor relationships with quantile regression models, in cases where predictive models would have had very low power. For example, the predictive power of substrate size, water depth, and water velocity on mussel abundance was very low ($r^2 < 0.05$) in a study by Strayer (1999), but a reanalysis with quantile regression of the data shown in fig. 4 in Strayer (1999) would be interesting and might show unimodal limiting-factor relationships. Quantile regression has the additional benefit that it relaxes the assumptions of normally distributed and homoscedastic data (Hao and Naiman 2007), and therefore, is very useful for analysis of ecological data (Cade and Noon 2003). Future studies investigating any single group of factors on mussel distributions should also use analyses that focus on quantifying limiting-factor relationships.

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