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Does Local Bed Shear Stress Predict the Occurrence of Freshwater Mussels?

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ABSTRACT

The relationship between near-bed hydrodynamics, pore-water chemistry and the presence of unionids was examined in a well-characterized multispecies mussel bed (26 species; ~24 mussels m⁻²; 70% gravel, 20% cobble and 10% sand) within a lowland river (Sydenham River) in southern Ontario, Canada. Local bed shear stress (τ_b) was determined from velocity profiles at ~1-m intervals along four laterals and three longitudinal transects in the reach providing 118, 14.3-cm diameter quadrats in which porewater was sampled and sediments were excavated for unionids. Ninety-four unionids (10–135 mm long) from 14 species were found in 56 quadrat locations that had significantly higher mass of very fine gravel (2000- μ m sieve) and lower dissolved oxygen in a comparison of individual environmental factors. Larger adult mussels (i.e., > 30 mm long; $n = 68$) were found in quadrats with $\tau_b = 0.022$ –1.34 Pa and an excavated very fine gravel mass = 616–2821 g, but smaller, juvenile mussels (< 30 mm; $n = 26$) were found in a more restricted range of τ_b and sediment content (0.075–0.77 Pa and 1151–2561 g, respectively). Using forward and backward stepwise habitat variable selection in logistic regression, models incorporating τ_b , τ_b^2 and/or very fine gravel mass provided the highest probability of locating juvenile mussels. The final model, which is based on body size, is informative at the community level rather than on a species-specific basis. These results provide insights into the relationship between near-bed hydrodynamics and these important benthic invertebrates, the location of small juvenile and larger adult unionids and their habitats in riverbeds. Conservation efforts should focus on preserving and enhancing these habitats and those of the most vulnerable early life stages of freshwater mussels.

1 | Introduction

Freshwater mussels (Unionida) are ecologically important because they provide many ecosystem services through their suspension feeding and burrowing activities (Haag 2012; Vaughn 2018). Unfortunately, ~40% of freshwater mussels are at risk (i.e., have conservation concerns) globally (217 of 535 of the assessed species of ~800 species in total; Ferreira-Rodríguez et al. 2019), and the proportion is ~75% within North America

(~300 species) (Lydeard et al. 2004; Strayer et al. 2004; Aldridge et al. 2023). Impoundments, commercial exploitation and loss of habitat through changes in land use and invasive species have all contributed to their endangerment (Shea et al. 2013; Haag and Williams 2014; Aldridge et al. 2023). For example, the spread of invasive dreissenid mussels led to the extirpation of unionids in the Laurentian Great Lakes, and now unionid populations are largely restricted to tributaries (Poos et al. 2010; Lucy et al. 2014). The complex life history of unionids also contributes

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to their endangerment because their larvae are parasitic on vertebrates (typically fish; Barnhart et al. 2008; Modesto et al. 2018) to facilitate development and dispersal (Schwalb et al. 2011), and juvenile mussels settle through the water column to the bottom following excystment from the host fish. This settlement phase is a critical period in which hydrodynamic conditions affect the recruitment of juvenile mussels through transport in which they are vulnerable to predation (Haag 2012) and through deposition in riverbed locations that differ in terms of juvenile survivability (e.g., hypoxic vs. normoxic locations). Moreover, subsequent increases in hydrodynamic forces due to high flows, for example, may scour them from the bottom and ultimately affect mussel population dynamics (Layzer and Madison 1995; Hardison and Layzer 2001; Steuer et al. 2008).

Not surprisingly, hydrodynamic factors including velocity, discharge (e.g., Di Maio and Corkum 1995) and especially complex hydraulic variables such as bed shear stress (τ_w = the force per unit area parallel to the bottom; Ackerman and Hoover 2001) are important drivers of the dynamics of unionid beds (Layzer and Madison 1995; Strayer 2008; French and Ackerman 2014; Jia et al. 2023) through analogies with sediment transport (Gordon et al. 2004). Indeed, a recent study revealed the importance of hydraulic conductivity and its relationship with mussel abundance and hyporheic habitat conditions (high dissolved oxygen concentration, diatom and chlorophyte abundance vs. low concentrations of ammonia and cyanobacteria and very fine sand; Lu et al. 2024). Moreover, bedload material including unionid mussels may experience a critical shear stress (τ_c) that leads to saltation along the bed and/or resuspension and transport downstream (Gordon et al. 2004; French and Ackerman 2014). Field studies have revealed that adult mussels are found in low shear stress areas of fast-moving rivers (Stoeckl and Geist 2016), and it has been suggested that this relationship is related to the stability of the sediment in those areas. The relationship between high shear stress and substrate stability has indicated that the former is limiting to mussel species diversity and abundance at high flows (Layzer and Madison 1995; Allen and Vaughn 2010; see review in Lopez and Vaughn 2021). Results from experimental stream channels in the lab and field demonstrate that the presence of mussels increases local bed roughness, shear velocities and erosion (Allen and Vaughn 2011; Sansom et al. 2018), which indicates that these organisms can also affect hydrodynamics (Hendriks et al. 2019).

At smaller spatial scales, hydrodynamic factors have affected mussel ecomorphology, which in the case of shell sculpturing may provide an indication of anchoring ability and thus the capacity to withstand high shear stress (Goodding et al. 2019); it has also been suggested that there is a relationship between anchoring and life history strategy associated with responses to shear stress (Randklev et al. 2019). Anchoring using byssal threads by juvenile mussels has been reported in some unionid species, but rarely in adult mussels (reviewed in Haag 2012). In terms of recently metamorphosed juvenile mussels, $\tau_c \sim 0.26$ Pa was measured for juveniles on very coarse/coarse sand (850 μ m) in the laboratory (French and Ackerman 2014), and this is consistent with reports of higher juvenile densities in lower τ_w regions in the field (Layzer and Madison 1995; Steuer et al. 2008) including depositional areas (i.e., regions downstream of bedforms and among riffles; Neves and Widlak 1987). Numerical

models of recruitment over large-spatial scales (e.g., km) predict juvenile settlement in areas protected from scouring and resuspension (i.e., in which $\tau_w < \tau_c$ and with substrate stability; Morales et al. 2006; Daraio et al. 2010; Daraio et al. 2012; i.e., flow refugia; Strayer 1999). Dispersal distance of settling juveniles is likely limited in scale < 10 m but can be influenced by local hydrodynamics described above (Irmscher and Vaughn 2018; Farrow et al. 2024); moreover, the dispersal of smaller propagules (e.g., larvae) increases disproportionately with increasing water column turbulence (Farrow et al. 2025). In contrast, adult mussels have been observed to engage in relatively large-scale (e.g., 0.1 m week⁻¹ to > 6 m year⁻¹) horizontal movements (Balfour and Smock 1995; Amyot and Downing 1997; Schwalb and Pusch 2007), suggesting that mussels can change locations post-settlement.

It is hypothesized that bed shear stress will be a determinant of unionid mussels at the local subreach scale. We predict that the presence of small juvenile mussels will be related to τ_w because it determines the settlement, resuspension and saltation of small sediment particles (i.e., newly excysted juvenile mussels) on riverbeds (Boano et al. 2014; Franca and Brocchini 2015). We predict that larger adult mussels will inhabit a wider range of conditions because they are less vulnerable to small changes in τ_w due to their larger size and their burrowing and anchoring abilities. These predictions were examined in a study of the relationship between near-bed hydrodynamics determined at large and small local scales (e.g., τ_w vs. τ_b), pore-water chemistry and unionid mussels at fine-spatial resolution in a multispecies mussel bed.

2 | Materials and Methods

2.1 | Study Reach

The study was conducted in the Sydenham River in southwestern Ontario, which is a hotspot of biodiversity historically containing 35 species of unionids (nomenclature per MolluscaBase eds. 2025), in which 14 of the current 34 species have conservation concerns (Special Concern, Threatened or Endangered; Staton et al. 2003; McNichols-O'Rourke et al. 2012; Canada 2025). The river consists of two main branches, the North Sydenham ~70 km in length and East Sydenham ~100 km in length that drain ~1450 and ~275 km², respectively, of Carolinian Life Zone into Lake St. Clair (Staton et al. 2003). Land cover is mostly agricultural (75%) followed by forests (12%) and urban centres distributed in towns (2%; Staton et al. 2003). The study site near Florence, Ontario, Canada (N 42.651389; E -82.009722) in the East Sydenham River (12.3 m³ s⁻¹ mean monthly discharge 1984–2024; <https://wateroffice.ec.gc.ca>) was selected because it is a Fisheries and Oceans Canada (DFO) Unionid Monitoring and Biodiversity Observation (UMBO) mussel reference site that contains one of the highest known densities of unionid mussels (23.6 mussels m⁻²) and species richness (26 species) with evidence of juvenile recruitment in central Canada (Gibson et al. 2024). The river at the site is 18–19 m wide with a bankfull width of 30 m, is approximately 0.45 m deep and consists of 70% gravel, 20% cobble and 10% sand (MacLennan-Nobrega et al. 2024). The study reach has been surveyed systematically

at ~10-year intervals beginning in 2003 by excavating 75 randomly selected 1-m² quadrats to a depth of 10–15 cm distributed over the ~400 m² of the mussel bed (Gibson et al. 2024). Mussel surveys conducted in 2003, 2015 and 2024 revealed that mussel density increased considerably from 2003 to 2015 but remained similar between 2015 and 2024 (McNichols-O'Rourke and Morris 2024).

The study reach is 20 m long with a slight curve as it transitions from a riffle section into a run flowing downstream (North to South) before pooling; it was assessed close to baseflow conditions in 2018 and 2019 (Figure 1). The study concentrated on the transition of a riffle into a run to include the known location of the mussel bed, as well as a range of environmental conditions associated with the transition (Figure 2). The channel banks are gently sloped on the western side and abruptly sloped with slightly undercut banks on the eastern side. The substrate varies with mostly cobble and boulder elements dominating the thalweg and eastern banks, and gravel, sand and silt dominating the western bank.

2.2 | Sampling Transects

A high-spatial resolution bed survey was conducted in 2018 using a SXBlue Platinum Global Navigation Satellite System (GNSS; SXBlue, Montreal, Canada) receiver utilizing Real Time Kinetic (RTK) satellite corrections accurate to 1 cm, to measure bed elevation and spatial position (i.e., GPS: Geographic Position System). A handheld acoustic Doppler velocimeter (ADV; Flow Tracker II, SonTek, San Diego, USA) was used to measure water speed in three dimensions (u = downstream, v = cross stream and w = vertical velocity components; mean speed ($\sqrt{u^2 + v^2 + w^2}$); samples at 40-Hz burst frequency and stores averages at 2 Hz; sample period of 15–30 s) at each of the survey points. A fixed grid system consisting of a 20-m long streamwise tagline, which served as the anchor for cross-stream oriented, 16-m long transects, was used to ensure consistent mapping methodology. The river substrate was physically inspected and the dominant

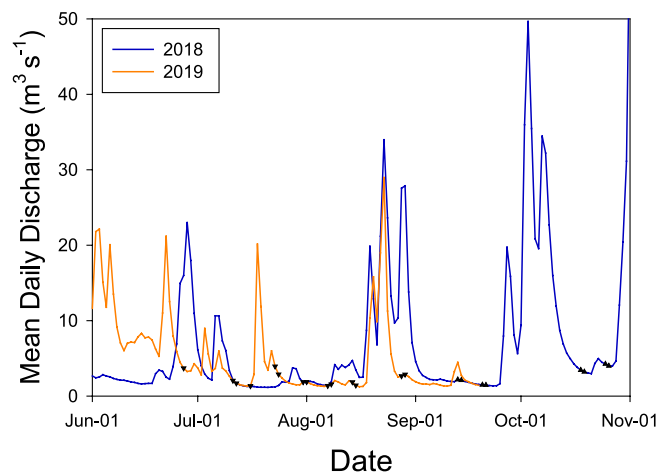


FIGURE 1 | Mean daily discharge measured at a hydrometric gauging station located upstream of the sampling site. Sampling occurred from early June to late October during the 2018 (black triangles) and 2019 (downward pointing black triangles) field seasons. Data retrieved from wateroffice.ec.gc.ca.

(≥40%–50%) substrate type (i.e., boulder, cobble, pebble, gravel, sand and silt; Wentworth scale, Wentworth 1922) was estimated at each point along the survey. This characterization provided information on bed elevation (1-cm vertical resolution), water speed and dominant substrate type at a 50 cm × 50 cm throughout the reach.

Large reach-scale determinations of the shear stress are given by the depth-slope product, $\tau_w = \rho ghS$, where ρ is the density of the water (kg m^{-3}), g is the acceleration due to gravity (9.81 m s^{-2}), h is the depth of the river (m) and S is the slope of the water surface throughout the reach (unitless) (Ackerman and Hoover 2001). This measurement was applied at a large-spatial scale (10 m) and includes both local shear stress (τ_b) and pressure associated with drag over the large-scale roughness elements in the river (e.g., boulders and woody debris; Kostaschuk et al. 2004).

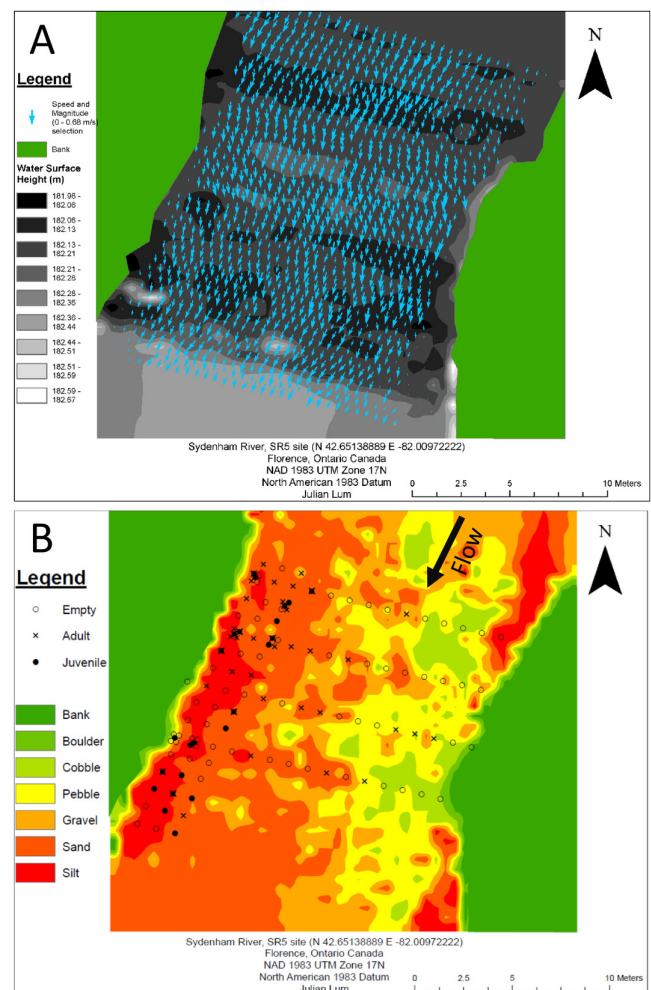


FIGURE 2 | Characteristics of the study reach at Florence site (Sydenham River): (A) Water speed indicated by arrows indicating flow direction and magnitude with contours of water surface elevation interpolated using IDW tool in ArcGIS; (B) substrate composition with points displaying the locations of quadrat excavation and unionid mussels along each transect. Note the four (two low shear stress [7 and 13 m downstream] and two high shear stress [4 and 10 m downstream]) cross-stream transects and the three streamwise transects 1, 2 and 3 m from the western bank.

Seven sampling transects were established in the reach including low ($n=2$) and high ($n=2$) shear stress cross-stream transects (~14 m long) based on the depth-slope product, as well as streamwise transects ($n=3$; ~15 m long) located in finer sediments on the western side of the reach (see Figure 2B). The placement of the streamwise transects was based on reports of juvenile mussels in areas with fine sediments (Isely 1911). The quadrat sampling procedures (τ_b measurements, porewater samples and excavations; see Section 2.2.1) were completed at each location along a transect before moving to the next transect. Transect sampling was conducted as follows: low τ_w transect at 7-m downstream and high τ_w transect at 4 m in 2018; low τ_w transect at 13 m, high τ_w transect at 10 m and streamwise transects at 3, 1 and 2 m from the western bank in 2019 (see triangular symbols in Figure 1 for dates of field work).

2.2.1 | Quadrat Sampling Procedures

Small-scale, local bed shear stress (τ_b) was determined at 1-m intervals along the transects from near-bed velocity profiles (15–30-s periods in 2-cm height increments from 3 to 4 cm above the bottom to below the water surface) fit to the Law of the Wall given by

$$U = \frac{U_*}{\kappa} \ln\left(\frac{z}{z_0}\right) \quad (1)$$

where U is the velocity (m s^{-1}), U_* is the shear velocity (m s^{-1}), κ is the von Karman constant, z is the height above the bottom (m) and z_0 is the roughness height (m) (Ackerman and Hoover 2001). The local shear stress was then determined using,

$$\tau_b = \rho U_*^2 \quad (2)$$

assuming (1) that shear stress is constant throughout the vertical profile, (2) that shear stress in the viscous sublayer can be predicted by the τ in the log layer and (3) that ≥ 5 velocity measurements in the log layer of the velocity profile were used for the regression analysis.

At each τ_b measurement location, a pushpoint piezometer (MHE Products, East Tawas, Michigan, USA) was inserted ~8 cm into the riverbed and pore water was withdrawn at ~60 mL min⁻¹ using a syringe (60 mL; BD Syringe). The first aliquot (~60 mL) was discarded due to high turbidity and the remaining fluid was discharged along the wall of a plastic beaker to minimize mixing with air. Water samples were immediately examined using a YSI multiparameter probe (YSI ProDSS; Yellow Springs Instruments, Yellow Springs, OH, USA) to measure water temperature, oxygen, pH, conductivity and turbidity. A steel quadrat (14.3-cm diameter) was then pushed to a depth of 8 cm (the depth to which juvenile unionids have been observed burrowing in the laboratory; Yeager et al. 1994; Box et al. 2002), and the contents were excavated by hand in the case of larger mussels and larger bed material (i.e., > 4-mm diameter [fine gravel]) and using an airlift system that transferred the finer sediments into a 20-L high-density polyethylene (HDPE) bucket. The material (~2.29 kg based on the nominal volume [1285 cm³] excavated and the density of gravel

[1780 kg m⁻³]) was processed through a series of stainless-steel sieves (2000 μm [i.e., very fine gravel or granules], 850 μm [i.e., very coarse and coarse sand], 500 μm [i.e., coarse sand], 250 μm [i.e., medium sand] and 180 μm [i.e., fine sand] sieve size), which were weighed using an electronic scale (Model# 93016, Starfrit, Quebec, Canada; > 4-mm fine gravel and 2000 μm very fine gravels were weighed together).

The three largest sieve sizes were examined visually for the presence of small bivalves, which when found were counted, photographed and returned with the excavated sediment to the riverbed along with the larger bivalves before the quadrat frame was removed. When small mussels were located, four additional quadrats located diagonally (~45°) 20 cm from the original grid point were examined and excavated.

2.3 | Juvenile Mussels

Juvenile mussels are, by definition, not sexually mature and range in size from newly excysted juveniles (e.g., 10 s –100 s of μm) to much larger individuals that may be up to 11-years old depending on the species (Haag 2012). The sexual maturity of mussels was not determined; rather, it was inferred from the following shell-length relationships. The length at maturity (l_m) of all the species found at the Sydenham River Florence site was determined via the von Bertalanffy growth model.

$$l_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \quad (3)$$

where l_t is the length at a given time, K is the growth rate and L_∞ is the asymptotic length at which growth is zero (Brown and Rothery 1993). The age of maturity and L_∞ were taken from appendix A in Haag (2012), K was estimated from figure 6.6 in Haag (2012) and l_m was determined using Equation (3). Data for 21 of the species observed were determined from values in Haag (2012), 10 of these were based on average values for a genus for species not listed in Haag (2012) and the determination was repeated using L_∞ provided in Clarke (1981) for the species at the study site (Florence, Ontario). The mean length at maturity (l_m) was 53.84 ± 20.3 (mean $\pm$ SD) mm using L_∞ from Haag (2012) and 59.53 ± 22.11 using L_∞ from Clarke (1981). Given these results, we set a conservative measurement of 30 mm, which is one standard deviation smaller than the mean l_m , as the size threshold for referring to small mussels as juvenile mussels in this study. We recognize that this model may overestimate the number of juvenile mussels for species with low L_∞ (e.g., *Paetulunio fabalis*), but it is a conservative limit for many of the species at the Florence Site. It is relevant to note that length criteria of similar scale for juveniles have been used in past studies (i.e., 25 mm for 17 species, Haag and Warren 2007; < 30.3 mm for four species, Neves and Widlak 1987; < 30 mm for > 18 species, Allen and Vaughn 2010), and this is analogous to the use of the lowest 5% of the size range for each species (Hornbach et al. 2018).

2.4 | Statistical Analysis

The survey data, including bed elevation, water speed and substrate type (0.5 $\times$ 0.5-m grid resolution), were mapped in ArcGIS (Version 10.6) using inverse distance weighting to interpolate

various surfaces. This assumes that the information contained within points that are close together is more alike than points that are farther apart.

A two-tailed *t*-test was used to determine whether the means of potential habitat variables (i.e., hydraulic, physical and pore-water chemistry) differed between quadrats with and without mussels, following a two-sample *F*-test for homogeneity of variances and the Shapiro–Wilk test for normality. Nonparametric Mann–Whitney tests were used when normality could not be met.

The relationship among these potential habitat variables (*physical conditions* including the mass of the 2000- μm sieve; *hydraulic conditions* including τ_b ; and *pore-water chemistry*, i.e., DO, temperature, pH, turbidity (FNU) and conductivity) made at the quadrat level was examined using principal component analysis (PCA). These potential habitat variables were standardized by conversion to z-scores (i.e., mean = 0 and variance = 1; Bowley 2015). Components were considered significant when their associated eigenvalue was ≥ 1 (Bowley 2015). Patterns of adult and juvenile clustering were ascertained using the associated loadings and eigenvalues of the respective habitat variables presented in Section 3.

The prediction of the probability of occurrence of juvenile mussels (< 30 mm; a binary response) was examined using a logistic regression model via the generalized linear model (GLM) function because there were a number of potential continuous predictor variables other than τ_b , as indicated above. Forward and backward stepwise variable selection of models was run using all potential habitat variables (hydraulic, physical and pore-water chemistry), but only the hydraulic and physical variables (i.e., τ_b , mass of material in the 2000-, 850-, 500-, 250- and 180- μm sieves) remained after an assessment using Akaike's Information Criterion (AIC) and residual deviance. A final polynomial model was selected based on the AIC rank (lowest value), lowest residual deviance, appropriate number of independent variables (i.e., parsimony of 10 observations per independent variable; Peduzzi et al. 1996; Stoltzfus 2011) and fit to the observed distribution of juveniles. The following assumptions of logistic regression were verified, namely: (1) The relationship between response and predictor variables can be described by the model used in the regression when logit-transformed; (2) there is independence of errors, i.e., for any given value of a predictor variable, the response variable values are independent; (3) no redundancy or collinearity between independent variables; and (4) there are few to no outliers whose observed response strongly differs from the predicted outcome (Stoltzfus 2011; Bowley 2015).

A sensitivity analysis of the prediction of the probability of occurrence of mussels of different sizes was examined through a series of logistic regressions using τ_b as the predictor. In this case, separate logistic models were applied to all mussels, mussels in large-size categories (< 30 mm vs. > 30 mm, < 40 mm vs. > 40 mm), as well as mussels in 10-mm size classes (10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90, 90–100 and > 100 mm).

All statistical analyses (`glm()`, `stepAIC()` and `princomp()`) were performed on RStudio Version 1.2.1335 (R Core Team 2017).

3 | Results

3.1 | Hydrodynamics of the Study Reach

There was a pattern in water speed, which averaged 0.352 ± 0.005 m/s (mean $\pm$ SE) in the reach; areas of slower speed were evident along the western bank and further downstream beyond the site, whereas areas of high speed were observed through the thalweg towards the eastern bank (Figure 2A). This pattern in water velocity was associated with patterns in the sediment composition, with mostly cobble and boulder elements dominating the thalweg and eastern bank, likely due to erosion (Figure 2B). The western bank was shielded from high velocity, allowing vegetation to grow into the channel in a depositional area of gravel, sands and silts (Figure 2B).

Local shear stress, τ_b , was determined using the velocity profiles measured at 118 locations in the field using Equations (1) and (2). A mean $\tau_b = 0.71 \pm 0.03$ Pa (mean $\pm$ SE; range: 0.0031–1.44 Pa) was determined at these locations with a mean square error (MSE) of 0.0033 ± 0.0003 (range: 0.000087–0.016). Most of the velocity profiles fit the law of the wall reasonably well, as reflected in the MSE; however, some fits were poorer as a result of upstream bedforms or roughness elements that likely disturbed the flow.

3.2 | Mussels and Characteristics of Their Habitats

Approximately half of the excavated quadrats (i.e., 56/118) contained unionid mussels ($n = 94$) as well as many other types of bivalves (sphaeriid clams; $n = 1561$). Whereas the larger mussels

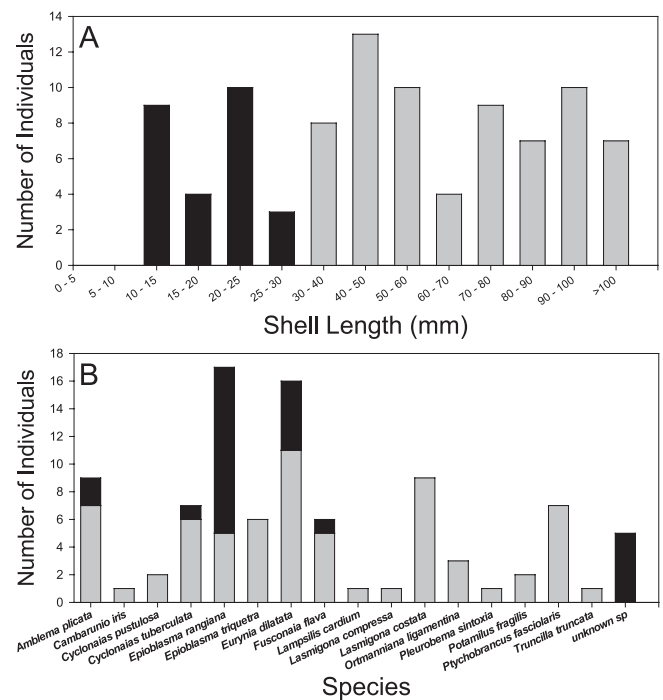


FIGURE 3 | Frequency of unionids found in the Florence site (Sydenham River) arranged by (A) species and (B) shell length. The dark colour indicates juvenile mussels < 30-mm shell length. Nomenclature follows MolluscaBase eds. (2025).

(68/94 > 30 cm SL) were scattered in different locations in the reach, the smaller individuals (26/94 < 30 mm) were largely located near the west bank (Figures 2B and 3A), which contained finer substrate (i.e., gravel and sand). All mussels were identified to one of the 16 species encountered, with the exception of five small individuals (~10 mm; Figure 3B). The most abundant mussel species were *Epioblasma rangiana* (Northern Riffleshell, $n=17$) and *Eurynia dilatata* (Spike, $n=16$) (Figure 3B). The mussel density calculated from the distribution of mussels in quadrats and quadrat area ($1.61 \times 10^{-2} \text{ m}^{-2}$) was 20.7 ± 2.8 mussels m^{-2} for all mussels, 29.5 ± 5.1 mussels m^{-2} ($n=118$) for adult mussels and 13.7 ± 2.7 mussels m^{-2} for small, juvenile mussels.

A number of physical and chemical properties differed between quadrats that contained juvenile unionids and those that did not (Figure 4). Juveniles were present in quadrats with significantly lower shear stress (τ_b ; $t_{49}=3.89$, $p=0.0003$), pore-water temperature (T ; $t_{116}=2.13$, $p=0.035$) and pore-water dissolved oxygen saturation (DO%; $W_{23,95}=1435.5$; $p=0.02$). Conversely,

juveniles were found in quadrats with a higher mass of sediment regardless of the size class obtained from the excavation (significant for 2000 μm : $t_{51}=-3.23$, $p=0.0022$; 850 μm : $W_{23,95}=754.5$, $p=0.022$; 500 μm : $t_{46}=-2.99$, $p=0.0043$; and 250 μm : $W_{23,95}=801$, $p=0.048$; but not significant for 180 μm : $t_{116}=-1.55$, $p=0.12$). The relative proportion of the total mass excavated was similar for the various sediment size fractions between quadrat types (e.g., 70.9%, 13%, 9.9%, 4.7% and 1.5%, respectively) except for the 180- μm size, where juveniles were present in quadrats with a lower proportion of the size fraction (i.e., present in $1.2\% \pm 0.1\%$ vs. $1.4\% \pm 0.1\%$, where they were absent). No differences, however, were detected for pore-water pH ($t_{116}=0.80$, $p=0.4$), turbidity (FNU; $W_{23,95}=1190.5$; $p=0.508$; note the high variation indicated by the error bar) and specific conductivity (SPC $\mu\text{S}/\text{cm}$; $W_{23,95}=948.5$; $p=0.33$).

There was an association among the habitat factors in the case of τ_b and fine gravel/sandy substrates, which was noted during the transect sampling and in the plot of τ_b vs. 2000- μm size fraction

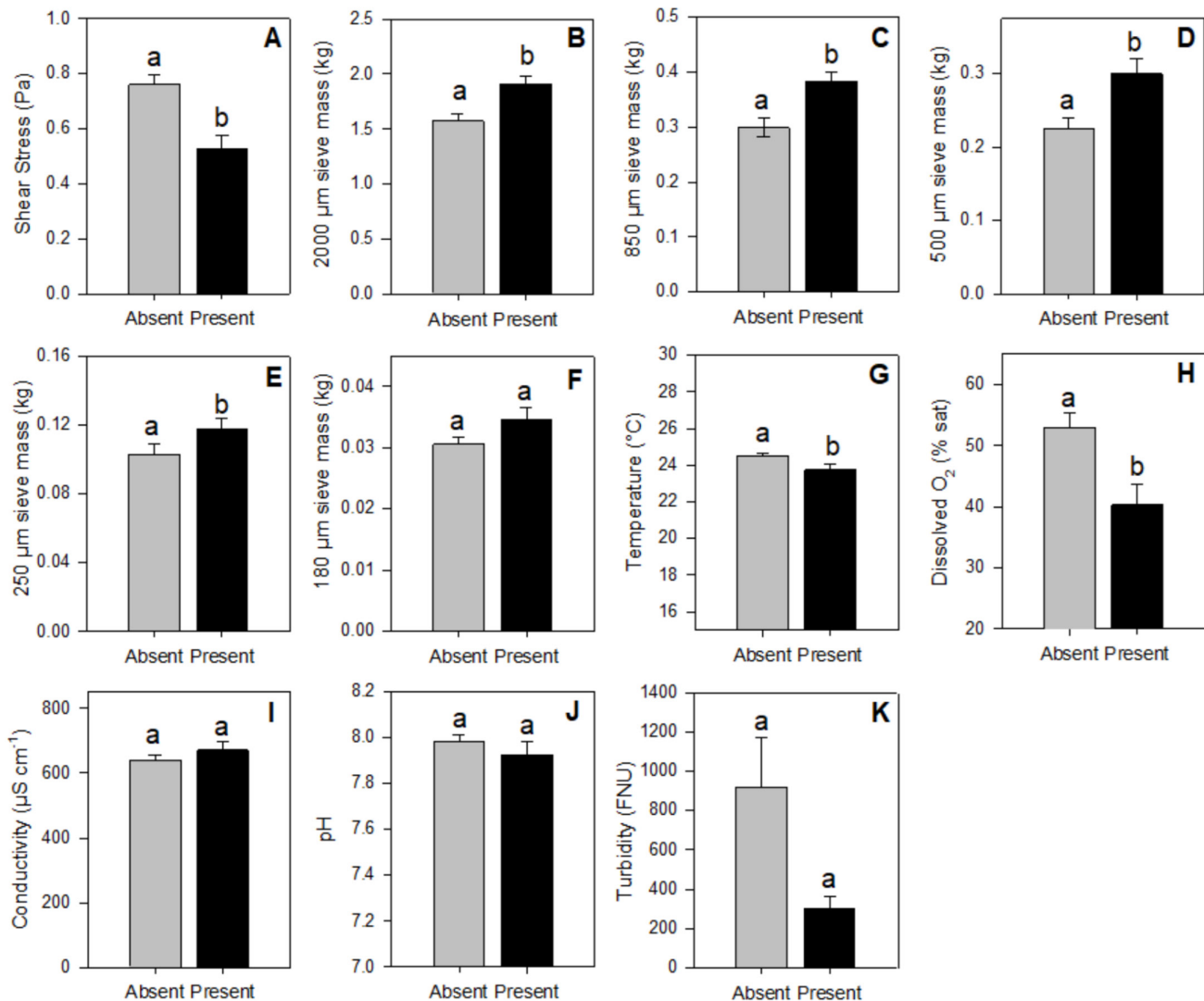


FIGURE 4 | Comparison of the presence vs. absence of juvenile unionids in quadrats ($n=118$) with different physical conditions—(A) shear stress (τ_b) measured above bottom and the mass of excavated sediments in (B) 2000-, (C) 850-, (D) 500-, (E) 250- and (F) 180- μm sieves; and pore-water chemistry—(G) temperature, (H) dissolved oxygen, (I) conductivity, (J) pH and (K) turbidity. Bars represent mean $\pm$ SE; different letters indicate significant differences ($p < 0.05$).

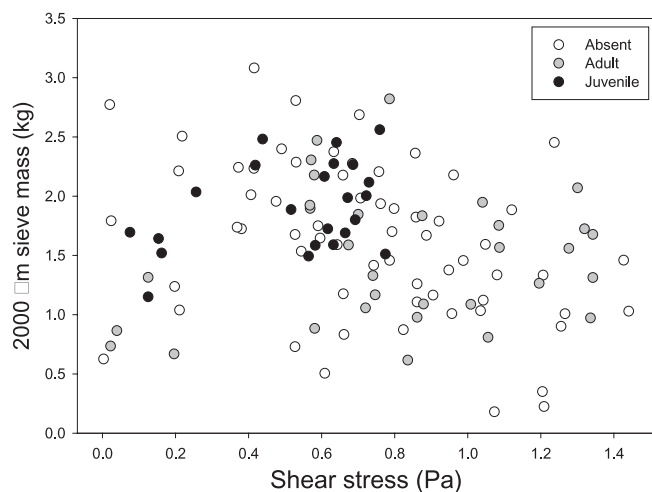


FIGURE 5 | Distribution of quadrats with juvenile ($n=23$) and adult ($n=43$) unionids and quadrats without mussels ordinated by bed shear stress (τ_b) vs. the mass of the 2000- μm sieve.

(Figure 5). In contrast to adult mussels that were found between 0.022 and 1.34 Pa and 616 to 2821 g of 2000- μm sediment (i.e., 27% to >123% of the total nominal mass excavated; latter includes larger clasts), juveniles were found in a more restricted range of τ_b (i.e., 0.075 to 0.77 Pa) and mass of 2000- μm sediment (i.e., 1151 to 2561 g in the 2000- μm sieve or 50% to >112% of the total nominal mass excavated).

Bed shear stress (τ_b) was a meaningful variable in a PCA used to examine the relationship among the hydraulic, physical and pore-water chemistry observations and juvenile and unionids. Specifically, τ_b had moderate loading on PCA#1 (~40% variance explained) in both juvenile and adult models, which also included dissolved oxygen, pH, temperature and specific conductivity; the latter was negative (Table S1). Very fine gravel ($\times 2000$) was moderately loaded on PCA#3 (~15% variance explained) for juvenile mussels and moderately loaded but negative on PCA#2 (~18% variance explained) for adult mussels. There was some ordination of species on PCA plots, as in the case of juvenile *Epioblasma rangiana* ($n=12$; negatively on PCA #1 and positively on PCA #2) and juvenile *E. dilatata* ($n=5$; positively with both PCA #1 and PCA #2) (Figure S1). Conversely, the distribution of adult mussels was more scattered without discernible patterns among species (Figure S2).

3.3 | Prediction of the Occurrence of Unionids of Juvenile Mussels by Bed Shear Stress

The numerical density of juvenile mussels exhibited a unimodal response to τ_b (mean $\tau_b = 0.53 \pm 0.05$ Pa) as well as the mass of the 2000- μm sediment (mean mass = 1.91 ± 0.08 kg) (bars in Figure 6), which indicated the need to include polynomial terms in a logistic regression. Eight logistic models were identified that incorporated the hydraulic and physical variables using step-wise selection (other variables were not significant); AIC values ranged from 98.7 to 114.3 with residual deviance from 88.7 to 107.7, indicating reasonably similar fits to the data (Table 1). After ranking by AIC and their associated residual deviance, the predictive curve of each of the ranked models was plotted to

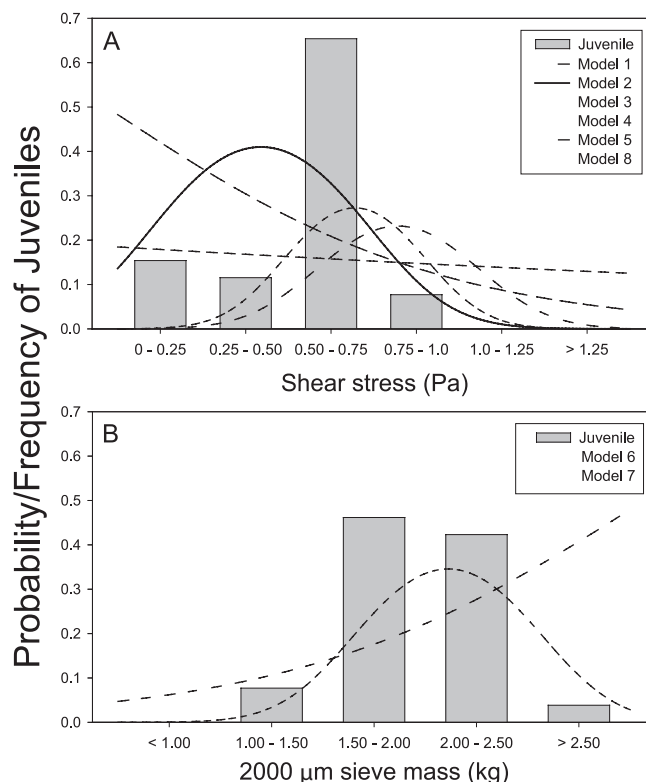


FIGURE 6 | Frequency distribution of juvenile unionids (bars) and logistic regression models (lines) predicting the probability of their presence for (A) bed shear stress (τ_b) and (B) mass of excavated sediment retained in the 2000- μm sieve. Results of the logistic regressions are presented in Table 1.

assess how well the model predicted the observed distribution of juvenile mussels (Figure 6).

Three models predicted monotonically increasing or decreasing numbers of juveniles, whereas five of the models provided predictions that were unimodal. Of the latter, Model #2 was selected because its peak and dispersion best matched the observed distribution of juveniles (Figure 6A). Moreover, this model best fits the criterion of the number of parameters for model selection (i.e., 10 events per independent variable, i.e., 2 independent variables for $n=26$ observations, AIC and residual deviance). Model #2 ($Y = [7.41 \pm 3.8] \tau_b - [9.13 \pm 3.88] \tau_b^2 - [1.87 \pm 0.92]$) indicated that τ_b and τ_b^2 had marginally significant and significant effects, respectively, on the probability of the presence of juveniles (τ_b : $z=1.928$, $p=0.054$; τ_b^2 : $z=-2.366$, $p=0.018$; intercept: $z=-2.04$, $p=0.041$). The model gave the highest probability (logit(Y) = -0.364 , Probability = 0.4099) of the presence of juvenile mussels at 0.4 Pa, which is 0.13 Pa lower than the observed mean τ_b (0.53 ± 0.046 Pa) observed for juvenile mussels (Figure 6A). Importantly, the probability declines asymptotically both to ~13% as τ_b approaches 0 Pa and to 0% beyond the maximum τ_b observed ($\tau_b = 0.77$ Pa).

The results of the sensitivity analysis of the logistic regression of local bed shear stress (τ_b) on the prediction of the occurrence of mussels in the size range of the mussels examined revealed differences for mussels >40-mm SL. The pseudo- R^2

TABLE 1 | Logistic regression models, using stepwise selection, for the presence of juvenile mussels ordered by AIC. Bold text indicates the model used in the study.

Model#	Independent variables	df	p value	AIC	Ranked by AIC	Residual deviance
4	$\tau_b +$	113	0.3107	98.7	1	88.7
	$\tau_b^2 +$		0.111			
	Mass 2000 +		0.0252			
	Mass 2000 ²		0.0278			
5	$\tau_b +$	114	0.00472	100.34	2	92.3
	Mass 2000 +		0.01			
	Mass 2000 ²		0.01328			
2	$\tau_b +$	115	0.0539	104.23	3	98.2
	τ_b^2		0.018			
3	$\tau_b +$	114	0.1199	105.1	4	97.1
	$\tau_b^2 +$		0.045			
	Mass 2000		0.2941			
7	Mass 2000 +	115	0.0166	107.84	5	101.8
	Mass 2000 ²		0.02499			
8	$\tau_b +$	115	0.011	109.28	6	103.2
	Mass 2000		0.0437			
1	τ_b	116	0.00512	111.66	7	107.7
6	Mass 2000	116	0.0187	114.33	8	110.3

value, which is a ratio indicating how close the model fit is to being perfect, was used as an indication of whether τ_b is a predictor statistically. In this case, a significant pseudo- R^2 indicated that τ_b was predictive of the occurrence of smaller mussels rather than larger ones or categories of larger mussels, including mussels of all sizes (Figure S3). Specifically, τ_b predicted the occurrence of mussels that were <40 mm (Deviance $p=0.0003$), <30 mm ($p=0.004$) and 10–20 mm ($p=0.02$) in length and was marginally predictive for mussels that were 30–40 mm ($p=0.08$).

4 | Discussion

Bed shear stress (τ_w) has long been known as a driving factor for benthic organisms affecting their often-patchy distribution, displacement downstream and mortality in extreme events (e.g., Hoover and Ackerman 2011; review in Schwendel et al. 2010). It has also been shown to be an important factor pertaining to unionid habitat in general, and for juvenile settlement in particular, because mussels are vulnerable to shear forces during and post-settlement in the riverbed (Layzer and Madison 1995; Strayer 2008; Lopez and Vaughn 2021). The results of the present study demonstrate that local bed shear stress (τ_b) predicts the location of juvenile mussels in the field. This is likely because the association between τ_b and juvenile unionids was made at fine-spatial scales (i.e., <15 cm) that are ecologically relevant to the hydraulic forces acting on mussels (e.g., Schwendel et al. 2010; French and Ackerman 2014; Ackerman 2014). Indeed, logistic

regression identified a significant polynomial model (τ_b^2 and τ_b) for the probability of detecting the occurrence of juveniles using the lowest AIC rank and residual deviance, the appropriate number of events per independent variable (Peduzzi et al. 1996; Stoltzfus 2011), and matched to the observations. The ability to determine where to locate the juvenile life history stage of any organism not only provides insight into their habitats but also into how to protect and enhance those habitats; this is especially true for unionid mussels given conservation concerns (Ferreira-Rodríguez et al. 2019).

A previous study concluded that the greatest number of juveniles was found in depositional areas downstream of boulders and in riffles at high water speeds ($>0.32\text{ m s}^{-1}$ Neves and Widlak 1987). In contrast, juvenile mussels in the present study were observed on the western bank in a depositional area, and along a transition between riffle and run, with similar velocities ($\sim 0.24\text{ m s}^{-1}$ within 1 m of the riverbank). Higher settlement in the channel margins and areas with steep gradients in bed elevation is expected given the high variability in predicted juvenile dispersal distances in these types of areas (Daraio et al. 2012) and the slower velocities observed. These differing results speak to the variety of hydrodynamic conditions that characterize mussel habitats and the need to use more complex hydraulic criteria such as shear stress, rather than water depth or velocity alone, to characterize mussel habitats (Layzer and Madison 1995; Hardison and Layzer 2001; Allen and Vaughn 2010; Jia et al. 2023). For example, shear stress based on the depth-slope product and Equations (1) and (2) was negatively

associated with the density of adult mussels due to the inclusion of locations in areas of high τ_w ; consequently, it was also proposed that high τ_w limited the settlement of juvenile mussels (Layzer and Madison 1995). It is important to note that the present study focused on an existing and diverse mussel bed within a region of low to moderate τ_w . To the best of our knowledge, this is the first study in which a quantifiable parameter, such as τ_b , has been used to identify the habitats of juvenile unionid mussels empirically.

There has been remarkable consistency in inferring the critical shear for the settlement and retention of juvenile mussels used in large-spatial scale computational models (Morales et al. 2006; Daraio et al. 2010), correlations in the field (Layzer and Madison 1995; Hardison and Layzer 2001) and from direct measurement of τ_c in the laboratory (French and Ackerman 2014). For example: (1) models proposed a settlement threshold or critical shear stress (τ_c) of 0.05 and 0.1 Pa (Morales et al. (2006) and Daraio et al. (2010), respectively); (2) juveniles in the field were found where $\tau_w < 0.77$ Pa (Figure 5); and (3) a τ_c of 0.26 Pa was determined for small juvenile mussels ($< 426 \mu\text{m}$) using a wall jet (French and Ackerman 2014). The τ_c determined in the present study, which is based on the maximum τ_b at which juvenile mussels were found, is consistent with those models and observations. It should be noted that this τ_c is $\sim 3\times$ larger than the values from French and Ackerman (2014), likely due to the larger-sized juveniles in the present study, the physical conditions in the river that differed from idealized conditions in the laboratory and the observation that mussel behaviour, including burrowing and adhering to sediments, can affect τ_c (French and Ackerman 2014). It is important to note that the results of the present study were obtained under baseflow, which is not representative of periods of higher discharge. We are confident that our interpretations are correct; however, because we obtained similar results in the same reach over two field seasons, including locating the same individuals in different years. A separate mapping of bed elevation of the central 40% of the width of the reach in 2022 indicated a difference of 1.3 ± 6.3 cm (SD) with Figure 2A using 507 measurements interpolated in ArcGIS (Dr. C. Farrow, University of Guelph, pers. comm.). Moreover, the population density of the mussels at the site has remained similar between 2015 and 2024 based on Fisheries and Oceans Canada surveys (McNichols-O'Rourke and Morris 2024). The effects of extreme high-flow events on the unionids at this site have not been examined.

4.1 | Mussel Habitat

Small juvenile unionids have been assumed to occupy similar habitat as adults; however, results from a number of studies suggest that juveniles occupy a narrower niche of habitat (Layzer and Madison 1995; Hastie et al. 2000; Hardison and Layzer 2001). Indeed, juvenile mussels in the present study were found within a small range of τ_b (i.e., 0.075 to 0.77 Pa) in contrast to adult mussels, which were found over almost twice as large a range of τ_b (i.e., 0.022 to 1.34 Pa). Whereas the final logistic regression model chosen only included τ_b , the PCA indicated strong associations of dissolved oxygen, pH and water temperature with juvenile mussels and moderate associations with conductivity, turbidity, τ_b and the mass of sediment in

the 2000- μm sieve. Moreover, comparisons of single factors indicated significant differences in DO and water temperature and large, but not significant differences in turbidity between quadrats with and without juvenile mussels (Figure 4). This is consistent with observations of the importance of pore-water chemistry to juvenile mussels in the field (Lu et al. 2024). For example, high turbidity can reduce feeding in juvenile mussels (Tuttle-Raycraft et al. 2017), whereas coarse sediment grain size (i.e., $\geq 2000\text{-}\mu\text{m}$ sieve) may indicate more bed stability (Hassan and Church 2000) and support higher interstitial flow and algal flux and thus higher feeding rates in juvenile mussels (Mistry and Ackerman 2017; Fung and Ackerman 2020). We found juvenile mussels in quadrats with a higher mass of very fine gravel, which tended to have lower turbidity, and a low mass of fine sand, which tends to reduce hydraulic conductivity (e.g., Lu et al. 2024). The association of juvenile mussels with lower temperature and dissolved oxygen concentrations is likely a consequence of their occupancy of low τ_b regions relative to the higher velocity and coarser substrates found in the thalweg and eastern bank of the reach, which likely had higher values of temperature and DO due to higher rates of exchange of surface water. Whereas the focus on single factors provided valuable information, it may not be as informative as more complex factors (e.g., bed shear stress), which may underlie the biophysico-chemical processes that affect unionid mussels. These results support Strayer's (2008) concept of functional mussel habitat, which involves factors that facilitate mussel settlement and persistence through the provisioning of resources and protection.

Two post-settlement mechanisms—post-settlement mortality and post-settlement movement—could explain the differences in spatial patterns between small and large mussels found in this and other studies (Nishizaki and Ackerman 2019). In an exclusively post-settlement mortality model, the settlement of juvenile mussels occurs over the range of mussel habitats, and due to spatial differences in mortality either continuously or episodically (i.e., during high-flow events), only a few individuals survive to adulthood in the 'adult areas'. Whereas this mechanism would lead to spatial differences in occupancy between juveniles and adults, it would not explain the absence of juvenile mussels in adult areas unless one invokes periodicity in either recruitment success and/or changes in channel/bottom morphometry. Alternatively, juvenile mussels as small 'particles' in suspension are more likely to settle in depositional areas (i.e., lower shear stress leading to finer bed material; Daraio et al. 2010; Sumaiya et al. 2025) where they experience post-settlement mortality. Over time, some of the surviving individuals might undertake post-settlement movements of 4–5 m per year based on an average of 0.11 ± 0.15 m per week (Schwalb and Pusch 2007). Ultimately, this would provide a mechanism to explain how larger adult mussels occupy a wider range of habitats compared to juvenile mussels. At present, there is no evidence to discount either model, nor is there reason to assume that the two mechanisms are mutually exclusive. It is more likely that they act at very different temporal and/or spatial scales.

4.2 | Implications for Conservation

It is very difficult to find juveniles in the field and, in so doing, measure aspects of their habitat. The results obtained in this

study, while limited numerically, provide some insight into the habitats of small juvenile mussels. Foremost of which, juvenile mussels are likely vulnerable to processes that affect the characteristics of riverbed, especially the local shear stress and sedimentology, which can reduce hydraulic conductivity (Lu et al. 2024). For example, extreme rainfall events (Tucker and Bras 2000) or prolonged periods of high flow due to flow management (Clausen et al. 2004) would result in elevated τ_b , which could scour juveniles from the riverbed (e.g., Layzer and Madison 1995). In such cases, juvenile mussels would be resuspended along with other riverbed sediment and transported downstream, where they would be vulnerable to mortality from predation as well as deposition in unsuitable habitat (French and Ackerman 2014). This would be especially problematic if the increase in flow occurred following juvenile excystment from fish hosts. The examination of extreme high-flow events on mussel habitats warrants further study, especially if the effects can be related to river discharge, which would inform natural resource management.

In contrast to the effects of hydrodynamics, changes in land use or riparian buffers that lead to increased erosion could result in the infilling of riverbeds by fine sediments, which would affect stream morphology and pore-water flow and chemistry (Williams et al. 1993; Box and Mossa 1999; Lu et al. 2024). The former could change τ_b , leading to changes in the availability of suitable habitat for the settlement and recruitment of juvenile mussels, especially if they were buried under sediments due to prolonged scour–deposition events (Peterson 1999; Gibbins et al. 2007). The latter would reduce the pore-water flow (Lu et al. 2024), which would affect pore-water chemistry by reducing dissolved oxygen concentration (Polhill and Dimock 1996), fostering the production of toxic un-ionized ammonia (Newton et al. 2003), and altering the composition of suitable algal resources (Fung and Ackerman 2020). An appreciation of these factors would support the application of natural flow regimes to lotic systems containing unionid mussels (Vaughn and Taylor 1999).

Knowledge of where to locate juvenile mussels in the field will provide an opportunity to assess their habitats as well as the best management practices that have been implemented to protect and recover their habitats. For example, Lu et al. (2024) evaluated the efficacy of riparian buffers in sustaining the hyporheic habitats of mussels, which were strongly affected by hyporheic conductivity. This type of approach could aid in the enhancement of habitats for existing populations by facilitating more recruitment of juvenile mussels to increase population sizes. In addition, this information will provide insight into where, spatially, juvenile mussels should be placed during population augmentation or reintroduction using juvenile mussels propagated in the laboratory. Given the limitations of the present study, specifically the small number of juvenile mussels observed at one study reach, further research involving great sampling effort is, therefore, warranted.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Results of the principal components analysis of habitat variable for (A) juvenile and (B) adult unionids. Top table indicates eigenvalues, and percent variance and cumulative variance explained by each component (bold indicates significant components). Bottom table indicates variable loadings on each component (bold indicates strong variable loadings, i.e., > 0.800). **Figure S1:** Principal component analysis for juvenile unionids ($n = 26$). Shapes used represent species (filled circle = *Amblema plicata*, filled square = *Epioblasma rangiana*, filled diamond = *Cyclonaias tuberculata*, upside down triangle = *Fusconaia flava*, upright triangle = *Eurynia dilatata* and crossed circle = unknown) and colour represents the associated length of the juvenile (see legend). **Figure S2:** Principal component

analysis for adult unionid individuals ($n=68$). Shapes used represent species observed (filled circle=*A. plicata*, filled square=*E. rangiana*, filled diamond=*C. tuberculata*, upside down triangle=*F. flava*, open square=*Epioblasma triquetra*, open circle=*Ptychobranthus fasciolaris*, crossed diamond=*Truncilla truncata*, square framed triangle=*Potamilus fragilis*, crossed square=*Cyclonaias pustulosa*, crossed circle=*Lampsilis cardium*, open triangle=*Lasmigona costata*, asterisk=*Lasmigona compressa*, crossed square=*Pleurobema sintoxia*, x mark=*Ortmanniana ligamentina* and cross=*Cambarunio iris*), and the relative size and colour of each point represents the associated length of the adult (see legend). **Figure S3:** Results of the logistic regression analysis of local shear stress (τ_b) on the occurrence of mussels of different sizes identified in the study. Psuedo R^2 are provided for comparative purposes; significant values (Deviance $p < 0.05$) are indicated by *, and marginal significant are underlined. Mussel sizes provided in Figure 3.