

# A review and evaluation of the effects of hydrodynamic variables on freshwater mussel communities

Jonathan W. Lopez<sup>1,2</sup>  | Caryn C. Vaughn<sup>1,2</sup> 

<sup>1</sup>Department of Biology, University of Oklahoma, Norman, OK, U.S.A.

<sup>2</sup>Oklahoma Biological Survey, University of Oklahoma, Norman, OK, U.S.A.

## Correspondence

Jonathan W. Lopez, Oklahoma Biological Survey, Norman, OK, U.S.A.  
Email: jwlopez@ou.edu

## Abstract

1. Riverine species are governed by the physical (i.e. hydrodynamic) forces generated by flowing water. Freshwater species are also disproportionately imperilled compared to terrestrial and marine species in large part due to widespread anthropogenic alteration of the natural flow regimes to which organisms are adapted. Sedentary species such as freshwater mussels (*Bivalvia: Unionoida*) are especially vulnerable because they are unable to move quickly in response to novel flow patterns created by impoundments and water withdrawals.
2. We evaluated the effects of hydrodynamic variables on mussel communities. We reviewed the literature to synthesise the relationships between three categories of hydrodynamic variables (hydrologic, simple hydraulic, and complex hydraulic) and mussel community parameters. We evaluated which variables are most useful in predicting mussel presence, abundance, and species richness, provided recommendations to help standardise their use in characterising mussel habitat and reviewed the reciprocal influence of mussels on hydraulic forces at the sediment-water interface.
3. Hydrologic variables such as stream size and anthropogenic flow alteration were useful in predicting basin- and landscape-scale changes in mussel communities. At finer scales, complex hydraulic variables—mainly shear stress and Reynolds number—were more useful at predicting mussel community responses. Simple hydraulic variables (flow velocity, depth, discharge) had mixed success as predictors of mussel community parameters and are likely to be indirectly correlated to mussel responses because they are used to calculate more complex variables.
4. More emphasis should be placed on species- and basin-specific responses of freshwater mussels when considering the effects of the hydrologic regime on mussels, with an eye towards sustainable water management (e.g. flow restoration, environmental flows). Simple hydraulic variables should be assessed across the range of discharge at a site, in combination with channel and substrate characteristics. This allows the calculation of complex hydraulic variables that may be more directly limiting to mussel communities.
5. Mussels also alter near-bed hydraulic characteristics, resulting in feedbacks between mussel community parameters and local hydraulic variables. Researchers should consider that mussel beds have a reciprocal influence on near-bed flow

characteristics and should continue to explore the effects of such *ecological engineering* for possible interspecific facilitation benefits between mussel species.

#### KEYWORDS

bivalve, complex hydraulic, flow, hydrology, simple hydraulic

## 1 | INTRODUCTION

River and stream dwelling animals are subject to a unique set of dynamic physical limitations resulting from forces imposed by flowing water. Stream dwelling animals must be able to deal with the extreme forces created by the density and viscosity of water at high flows, as well as limitations on mobility, food delivery, and physicochemical conditions at low flows. The traditional view of fluvial systems holds that geophysical filters limit the distribution of aquatic species (Vannote et al., 1980); however, recent syntheses have called attention to the ways organisms are able to reciprocally alter their environment (Allen et al., 2014; Atkinson et al., 2018). Understanding such feedbacks between aquatic animals and their habitat is necessary for effective freshwater conservation.

Freshwater species are disproportionately imperilled compared to marine and terrestrial species due to a variety of anthropogenic factors, including hydrologic alteration from impoundments and water withdrawals (Poff et al., 1997; Strayer & Dudgeon, 2010). As such, it is critical to understand the impacts of variable flows on freshwater species (Poff et al., 1997). Among the most imperilled groups are freshwater mussels (Bivalvia: Unionoidea; Strayer & Dudgeon, 2010). Mussels are sedentary, which limits their ability to respond to changes in the physical habitat imposed by changing flows—and makes them ideal for studying interactions between organisms and the hydrodynamic forces generated by water. Freshwater mussels occur in dense aggregations (mussel beds) that produce extensive ecosystem effects (Atkinson et al., 2018; Atkinson & Vaughn, 2015; Vaughn & Hoellein, 2018), but their distributions are highly patchy (Atkinson & Vaughn, 2015; Haag, 2012). At regional to continental scales, biogeographical factors play a significant role in structuring mussel assemblages; however, the factors that limit mussel assemblage composition and abundance at local scales remain poorly understood in many instances (Haag, 2012). Thus, extensive effort has been dedicated to determining what factors limit mussel distributions at finer scales.

Early naturalists who first described the habitats of the mussel species found in Europe and North America noted that many mussels occurred in slow-flowing or sheltered areas outside of the main current, or underneath boulders, while others occurred in faster flowing habitats such as riffles (Call, 1900; Coker, 1919; Ortman, 1919). Vannote and Minshall (1982) were among the first to quantitatively evaluate whether mussels occurred in areas called flow refuges, which were sheltered from bed scour, usually by large boulders. Strayer (1999) tested and found support for this hypothesis. However, other attempts to explain the occurrence of mussel beds based on simple variables such as sediment characteristics, flow

velocity, and mesohabitat characterisation yielded mixed results (Holland-Bartels, 1990; Strayer, 1981, 1993; Strayer & Ralley, 1993). An important advancement came when ecologists began to integrate hydraulic engineering formulas to calculate complex hydraulic variables—which describe intricate flow patterns such as turbulence and the forces generated by moving fluids—to predict mussel habitat (Hardison & Layzer, 2001; Layzer & Madison, 1995).

Habitat of stream dwelling mussels cannot be adequately assessed without considering the physical limitations imposed by flowing water. Here, we review the utility of three categories of hydrodynamic variables frequently used to describe and predict mussel habitat: (1) hydrologic variables such as drought, flooding, and impoundment; (2) simple hydraulic variables—which describe the speed and volume of water flowing through a confined space—such as flow velocity, discharge, and depth; and (3) complex hydraulic variables that describe flow patterns such as turbulence and force, and are calculated using multiple simple hydraulic and geomorphic variables. We evaluated the success of 36 hydrodynamic variable types among these categories to predict mussel occurrence patterns, in an effort to standardise the ways in which mussel researchers quantify flows and increase the success rate of mussel habitat characterisation. Then, we discuss an emerging body of literature describing how mussels themselves alter flow patterns and the implications for river ecosystems. Finally, we suggest productive research directions as we move forward in understanding the mutual feedbacks between imperilled aquatic animals and the flow characteristics that govern their physical environment.

## 2 | METHODS

We searched the relevant literature using the Web of Science search engine with search terms (freshwater AND mussel\* AND (hydrolog\* OR hydraulic\*)) with no restrictions on publication year or publication type. This search returned 120 publications. We then reviewed the abstracts of all these publications, removing those that did not meet the following criteria: articles had to be primary research articles analysing the interaction between at least one *hydrodynamic variable* and at least one *mussel variable*. Hydrodynamic variables included hydrologic, simple hydraulic, and complex hydraulic (Table 1) variables. Mussel variables included presence/absence, abundance, species richness, community composition, and in a few cases mortality, recruitment, or larval settling. We then supplemented the remaining publications using citations within the initial literature search for a total of 71 publications. This resulted in 1,008 observations of mussel–hydrodynamic relationships.

**TABLE 1** Descriptions and formulas for most complex hydraulic variables used to characterise freshwater mussel habitat

Variable (symbol, unit)	Formula	Description
Froude number (Fr, dimensionless)	$\sqrt{\frac{U^2}{gd}}$	Ratio of inertial to gravitational forces
Reynolds number (Re, dimensionless)	$\frac{Ud}{\nu}$	Ratio of inertial to viscous forces (i.e. laminar vs. turbulent flow)
Boundary Reynolds number (Re., dimensionless)	$\frac{U_s k_s}{\nu}$	Turbulence of flow near the substrate
Shear velocity ( $U_*$ , cm/s)	$\frac{U}{5.75 \log_{10} \left( \frac{12d}{k_s} \right)}$	Friction velocity
Shear stress ( $\tau$ , dynes/cm <sup>2</sup> )	$\rho (U_*^2)$	Horizontal force of friction on substrate
Critical shear stress ( $\tau_c$ , dynes/cm <sup>2</sup> )	$\theta_c g D_{50} (\rho_s - \rho)$	Shear stress required to mobilise substrate for median substrate size
Relative shear stress (RSS, dimensionless)	$\frac{\tau}{\tau_c}$	Ratio of observed to critical shear stress (values >1 result in substrate movement for median substrate size)

Notes: Adapted from Allen and Vaughn (2010).  $U$  = mean current velocity (cm/s),  $g$  = acceleration of gravity (980 cm/s),  $\nu$  = kinematic viscosity of water (0.01 cm<sup>2</sup>/s),  $\rho$  = density of water (0.998 g/cm<sup>3</sup>),  $\rho_s$  = density of substrate (2.65 g/cm<sup>3</sup>),  $\theta_c$  = Shield's parameter (0.065).

To evaluate the predictive capacity of the 36 hydrodynamic variables, we recorded the number of times each type of mussel-hydrodynamic relationship was reported across the 71 publications and classified all the reported bivariate mussel-hydrodynamic relationships using the following criteria. (1) For variables that demonstrated a monotonic association with each other, we simply classified the relationship as positive or negative, whether the relationship was linear or not. (2) We classified nonmonotonic relationships by the mathematical nature of the relationship: unimodal/Ricker, multimodal, and a general polynomial category for those that showed more complex polynomial relationships. (3) We also classified the geographic location of the study (by continent).

Due to the relatively low number of studies, the diverse nature of the analyses performed and of the variables reported, and inconsistent reporting of effect sizes, we were unable to consistently use effect sizes to assist in our evaluation. While we did use effect sizes in our interpretations of each study that reported them, we do not report them in this review—we simply could not achieve a meaningful sample of effect sizes for any of the relationships we explored. As such, we frame this review not as a meta-analysis, but as a summary of a scattered existing literature body to suggest more focused and standardised research directions.

Based on the original authors' statistics and interpretations, we classified all the recorded relationships as either *significant* or *non-significant*. For Fischerian statistics,  $p$ -values were used; for model selection we used  $\Delta$ AIC values (all variables from models within  $\Delta$ AIC  $\leq 2$  of the best approximating model were interpreted as *significant*); when multivariate relationships or complex models were reported, we evaluated significance of the bivariate relationships according to the authors' interpretations and classified relationships using loadings or figures where possible, but not all multivariate and modelled relationships could be easily classified

using the above criteria. We included nonsignificant (type of relationship = null) relationships as well to evaluate the rate at which different predictor variables detected significant responses, presented as percentages. In our efforts to aggregate these data and interpret the relationships in a consistent manner, it is possible that we labelled some relationships as *significant*, when they were not highly ecologically meaningful. The potential for such misclassification is highest in multivariate relationships and model selection. Even with this caveat in mind, we provide a comprehensive review of the topic of the relationships of mussels and hydrodynamic forces and this work should be used as a guide for unifying and generating future research, not solely an interpretation of the individual studies reviewed.

### 3 | USE OF HYDRODYNAMIC VARIABLES TO CHARACTERISE MUSSEL HABITAT AND COMMUNITIES

#### 3.1 | Hydrologic variables

Hydrology fundamentally governs fluvial systems (Vannote et al., 1980). The movement of water determines all the finer scale hydraulic characteristics within aquatic systems. As sedentary organisms, mussels have limited ability to escape from extreme high and low flows. High flows pose the risk of mortality by dislodgement (Constantinescu et al., 2013; Hastie et al., 2001; Jones & Byrne, 2010) and extreme low flows can lead to overheating, drying, and stranding (Allen et al., 2013; DuBose et al., 2019; Golladay et al., 2004; Vaughn et al., 2015). Mussels are present in stream systems spanning a wide range of hydrologic conditions, but there are discernible patterns governing where they occur.

One of the most robust and easiest explained patterns in mussel distribution is that mussel presence (Table 2), abundance (Table 3), and species richness (Table 4) often increase as stream order or longitudinal distance from headwaters increase—simply put, larger rivers frequently have more mussels of more types (Atkinson et al., 2012; Baldigo et al., 2004; Daniel & Brown, 2013; Ford et al., 2016; Gangloff & Feminella, 2007; Vaughn et al., 2015). Species–area relationships such as this are common in ecology (Rosenzweig, 1995). The larger habitat area and lower risk of drying found in larger rivers should naturally result in greater numbers of organisms and species.

The relative flow stability found in larger rivers might also indicate that flow variability is an important factor in determining mussel habitat. However, tests of this prediction have yielded mixed results. Mussel abundance most frequently decreased with flow variability in a range of river systems with diverse geographical and anthropogenic influences (Chiavacci et al., 2018; Davis et al., 2013; Di Maio & Corkum, 1995), but was also found to increase with flow variability in certain species and locations, for example *Amblema plicata* and *Fusconaia flava* in the upper Midwest U.S.A. and south-eastern Canada (Di Maio & Corkum, 1995); still other species may have no relationship with flow variability (Chiavacci et al., 2018). Drew et al. (2018) found that the endangered *Parvaspina steinstansana* showed a bimodal response to flow variability in North Carolina, U.S.A., with individuals occurring in either low-order (low discharge, high variability) or high-order (high discharge, low variability) streams. Such changes in species abundance in response to flow regime may lead to changes to community composition (Di Maio & Corkum, 1995), but we found no studies where flow variability was related to species richness (Table 4). Therefore, it appears that mussel abundance responses to flow conditions are species specific but that the greater species richness found in larger streams is probably a function of habitat area rather than related to flow predictability. However, it is important to note that the species–stream size pattern is limited by observation scale; it tends to manifest within biogeographical provinces to various degrees, but not necessarily at larger scales (e.g. continental; Haag, 2012).

The timing and magnitudes of extremes in high and low flows may be more limiting to sedentary organisms such as mussels than overall flow variation. In one Georgia, U.S.A. river basin, summer high flows were more strongly and positively associated with mussel survival than winter or spring high flows, although winter and spring flows were positively related to recruitment (Peterson et al., 2011). This suggests that summer flows must be high enough to keep mussel habitat submerged, while winter and spring flows in this region generally do not get low enough to be dangerous to mussels. Drew et al. (2018) found bimodal responses of *P. steinstansana* to low-flow, high-flow, and flood pulse discharges, yet Chiavacci et al. (2018) found no association across a suite of similar variables, except that the duration of extreme low-flows was negatively associated with mussel presence. However, Chiavacci et al. conducted their study in a relatively disturbed area (greater Chicago area, Illinois, U.S.A.), so it is possible that non-hydrologic anthropogenic influences were limiting to mussels in this area. Furthermore, mussels are adapted

to the natural flow regimes in their river basins—including seasonal variability—which might obfuscate the ability to detect a community-level response to flow variability in pristine ecosystems. However, few flow regimes remain unaltered by humans, and mussels are long-lived invertebrates (c. 5–200 years). Mussel generation times can be long relative to the rate at which anthropogenic change typically occurs, which limits their ability to adapt quickly in rapidly changing ecosystems.

River impoundment has been recognised as a major anthropogenic threat to freshwater mussels for over a century (Haag, 2012). The effects of impoundments on mussel communities are variable—they depend on the timing, depth, and volume of releases from the impoundment and on the physiology of the mussel species present (Allen et al., 2013; Araujo & Álvarez-Cobelas, 2016; Galbraith & Vaughn, 2011; Galbraith et al., 2010). When studies have been conducted to evaluate the effects of distance from impoundments, mussel response typically depends on the species. Some species have been found to be more abundant immediately downstream from impoundments (Davis et al., 2013; Wegscheider et al., 2019), while others are more abundant with increasing distance upstream (Chiavacci et al., 2018) or downstream from impoundments (Davis et al., 2013; Klos et al., 2015; Wegscheider et al., 2019); some species appear unaffected by impoundments (Chiavacci et al., 2018; Davis et al., 2013; Wegscheider et al., 2019). These mixed results are probably because species-specific physiological traits such as metabolic thermal tolerance levels (Spooner & Vaughn, 2008) and reproductive cues interact with reservoir management strategies to determine impoundment effects on mussels (Galbraith et al., 2010). For example, in two adjacent catchments with contrasting water management practices, a river with constant inflow-to-outflow at a 1:1 ratio had no loss in species richness or abundance over a decade-long drought period, whereas a neighbouring river that retains impounded water during droughts (thus decreasing flows below the reservoir) saw significant declines in both species richness and abundance in its mussel communities through the same period (Allen et al., 2013).

Climate change is also expected to alter flows, mainly by increasing flow variability and the frequency and severity of droughts, which is expected to have negative consequences for mussels (DuBose et al., 2019; Spooner et al., 2011). In summary, hydrologic variables can often inform landscape or regional patterns about mussel community dynamics and help managers develop sustainable flow regimes capable of conserving mussels and supporting basic ecological functioning in streams. Unfortunately, hydrology tells us little regarding more local mussel distribution patterns.

### 3.2 | Simple hydraulic variables

Mussels are widely distributed and diverse in temperate zones, where summer flows are typically low and winter and spring flows are high (Haag, 2012). It is widely accepted that mussels require habitat where flows are high enough in the summer to deliver food

**TABLE 2** Frequencies (n) of reported effects of hydrodynamic variables on mussel presence

Category	Variable type	n	Type of relationship (%)					Total significant (%)	
			Positive	Negative	Unimodal/ Ricker	Multimodal	Polynomial		Null
Hydrologic	Annual runoff	2	0.0	0.0	0.0	0.0	0.0	100.0	0.0
	Stream or catchment size	—	—	—	—	—	—	—	—
	Flow variability	22	9.1	4.5	0.0	31.8	0.0	54.5	45.5
	High-flow magnitude	4	0.0	0.0	0.0	100.0	0.0	0.0	100.0
	High-flow frequency	10	0.0	10.0	0.0	10.0	0.0	80.0	20.0
	Low-flow magnitude	4	0.0	0.0	0.0	100.0	0.0	0.0	100.0
	Low-flow frequency	11	9.1	9.1	0.0	0.0	0.0	81.8	18.2
	Elevation	—	—	—	—	—	—	—	—
	Impoundment presence	8	0.0	25.0	0.0	0.0	0.0	75.0	25.0
	Anthropogenic flow alteration	—	—	—	—	—	—	—	—
	Distance from impoundment	5	0.0	20.0	0.0	0.0	0.0	80.0	20.0
	Impoundment deposition	—	—	—	—	—	—	—	—
	Reservoir release	1	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Drought	—	—	—	—	—	—	—	—
	Groundwater exchange	—	—	—	—	—	—	—	—
Total	67	4.5	10.4	0.0	23.9	0.0	61.2	38.8	
Simple hydraulic	Flow velocity	16	18.8	12.5	12.5	0.0	0.0	50.0	50.0
	Water depth	9	0.0	22.2	11.1	0.0	0.0	55.6	44.4
	Discharge	3	0.0	0.0	33.3	0.0	0.0	66.7	33.3
	Total	28	10.7	14.3	14.3	0.0	0.0	53.6	46.4
Complex hydraulic	Flow refugia	—	—	—	—	—	—	—	—
	Shear stress	12	33.3	25.0	0.0	0.0	0.0	33.3	66.7
	High-flow shear stress	1	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	Low-flow shear stress	1	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	Shear velocity	4	25.0	25.0	0.0	0.0	0.0	50.0	50.0
	Relative shear stress (RSS)	2	0.0	50.0	0.0	0.0	50.0	0.0	100.0
	High-flow RSS	2	0.0	50.0	0.0	0.0	0.0	0.0	100.0
	Low-flow RSS	2	0.0	50.0	0.0	0.0	0.0	50.0	50.0
	Froude number	9	11.1	44.4	11.1	0.0	0.0	33.3	66.7
	High-flow Froude number	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0
	Low-flow Froude number	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0
	Reynolds number	3	33.3	33.3	0.0	0.0	0.0	33.3	66.7
	Boundary Reynolds number	4	25.0	50.0	0.0	0.0	0.0	25.0	75.0
	High-flow Reynolds number	—	—	—	—	—	—	—	—
	Low-flow Reynolds number	—	—	—	—	—	—	—	—
	Hydraulic energy	2	0.0	50.0	0.0	0.0	0.0	50.0	50.0
	Laminar layer thickness	2	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Hyporheic flow	—	—	—	—	—	—	—	—	
Total	46	17.4	32.6	2.2	0.0	2.2	36.9	63.1	

Notes: The mathematical nature of each type of hydrodynamic effect is reported as a percentage of the total frequency at which the relationship was reported. *Positive* and *Negative* refer to monotonic relationships. The rate at which each hydrodynamic predictor was reported as statistically significant is also reported. Significant multivariate or modelling relationships may not report sign of relationship.

TABLE 3 Frequencies (n) of reported effects of hydrodynamic variables on mussel abundance

Category	Variable type	n	Type of relationship (%)						Total significant (%)
			Positive	Negative	Unimodal/ Ricker	Multimodal	Polynomial	Null	
Hydrologic	Annual runoff	1	100.0	0.0	0.0	0.0	0.0	0.0	100.0
	Stream or catchment size	10	40.0	0.0	0.0	0.0	0.0	60.0	40.0
	Flow variability	7	28.6	71.4	0.0	0.0	0.0	0.0	100.0
	High-flow magnitude	1	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	High-flow frequency	3	100.0	0.0	0.0	0.0	0.0	0.0	100.0
	Low-flow magnitude	—	—	—	—	—	—	—	—
	Low-flow frequency	—	—	—	—	—	—	—	—
	Elevation	5	0.0	60.0	0.0	0.0	0.0	40.0	60.0
	Impoundment presence	—	—	—	—	—	—	—	—
	Anthropogenic flow alteration	—	—	—	—	—	—	—	—
	Distance from impoundment	10	30.0	40.0	0.0	0.0	0.0	30.0	70.0
	Impoundment deposition	5	40.0	20.0	0.0	0.0	0.0	40.0	60.0
	Reservoir release	3	66.7	33.3	0.0	0.0	0.0	0.0	100.0
	Drought	5	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Groundwater exchange	4	50.0	0.0	0.0	0.0	0.0	50.0	50.0
Total	54	35.2	37.0	0.0	0.0	0.0	27.8	72.2	
Simple hydraulic	Flow velocity	49	24.5	16.3	32.7	0.0	0.0	26.5	73.5
	Water depth	47	27.7	21.3	2.1	2.1	0.0	46.8	53.2
	Discharge	9	22.2	11.1	0.0	0.0	0.0	66.7	33.3
	Total	105	25.7	18.1	16.2	0.9	0.0	39.0	61.0
Complex hydraulic	Flow refugia	3	100.0	0.0	0.0	0.0	0.0	0.0	100.0
	Shear stress	20	25.0	10.0	0.0	0.0	0.0	65.0	35.0
	High-flow shear stress	3	0.0	33.3	66.7	0.0	0.0	0.0	100.0
	Low-flow shear stress	4	0.0	0.0	50.0	0.0	0.0	50.0	50.0
	Shear velocity	17	76.5	5.9	0.0	0.0	0.0	17.6	82.4
	Relative shear stress (RSS)	2	50.0	0.0	0.0	0.0	0.0	50.0	50.0
	High-flow RSS	—	—	—	—	—	—	—	—
	Low-flow RSS	—	—	—	—	—	—	—	—
	Froude number	4	0.0	50.0	0.0	0.0	0.0	50.0	50.0
	High-flow Froude number	—	—	—	—	—	—	—	—
	Low-flow Froude number	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Reynolds number	21	23.8	9.5	0.0	0.0	0.0	66.7	33.3
	Boundary Reynolds number	19	68.4	5.3	10.5	0.0	0.0	15.8	84.2
	High-flow Reynolds number	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Low-flow Reynolds number	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Hydraulic energy	—	—	—	—	—	—	—	—
	Laminar layer thickness	14	0.0	85.7	0.0	0.0	0.0	14.3	85.7
Hyporheic flow	3	0.0	0.0	0.0	0.0	0.0	100.0	0.0	
Total	113	35.4	18.6	8.0	0.0	0.0	38.1	61.9	

Notes: The mathematical nature of each type of hydrodynamic effect is reported as a percentage of the total frequency at which the relationship was reported. *Positive* and *Negative* refer to monotonic relationships. The rate at which each hydrodynamic predictor was reported as statistically significant is also reported. Significant multivariate or modelling relationships may not report sign of relationship.

**TABLE 4** Frequencies (n) of reported effects of hydrodynamic variables on mussel species richness

Category	Variable type	n	Type of relationship (%)						Total significant (%)
			Positive	Negative	Unimodal	Multimodal	Polynomial	Null	
Hydrologic	Annual runoff	1	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Stream or catchment size	3	100.0	0.0	0.0	0.0	0.0	0.0	100.0
	Flow variability	–	–	–	–	–	–	–	–
	High-flow magnitude	–	–	–	–	–	–	–	–
	High-flow frequency	–	–	–	–	–	–	–	–
	Low-flow magnitude	–	–	–	–	–	–	–	–
	Low-flow frequency	–	–	–	–	–	–	–	–
	Elevation	–	–	–	–	–	–	–	–
	Impoundment presence	–	–	–	–	–	–	–	–
	Anthropogenic flow alteration	11	0.0	54.5	0.0	0.0	0.0	45.5	54.5
	Distance from impoundment	–	–	–	–	–	–	–	–
	Impoundment deposition	–	–	–	–	–	–	–	–
	Reservoir release	2	100.0	0.0	0.0	0.0	0.0	0.0	100.0
	Drought	1	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Groundwater exchange	–	–	–	–	–	–	–	–
Total	18	27.8	44.4	0.0	0.0	0.0	27.8	72.2	
Simple hydraulic	Flow velocity	1	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Water depth	1	0.0	0.0	0.0	0.0	0.0	100.0	0.0
	Discharge	13	69.2	0.0	0.0	0.0	0.0	30.8	69.2
	Total	15	60.0	6.7	0.0	0.0	0.0	33.4	66.6
Complex hydraulic	Flow refugia	–	–	–	–	–	–	–	–
	Shear stress	1	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	High-flow shear stress	2	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Low-flow shear stress	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Shear velocity	–	–	–	–	–	–	–	–
	Relative shear stress (RSS)	–	–	–	–	–	–	–	–
	High-flow RSS	3	0.0	100.0	0.0	0.0	0.0	0.0	100.0
	Low-flow RSS	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Froude number	–	–	–	–	–	–	–	–
	High-flow Froude number	–	–	–	–	–	–	–	–
	Low-flow Froude number	–	–	–	–	–	–	–	–
	Reynolds number	–	–	–	–	–	–	–	–
	Boundary Reynolds number	–	–	–	–	–	–	–	–
	High-flow Reynolds number	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Low-flow Reynolds number	1	0.0	0.0	100.0	0.0	0.0	0.0	100.0
	Hydraulic energy	–	–	–	–	–	–	–	–
	Laminar layer thickness	–	–	–	–	–	–	–	–
Hyporheic flow	–	–	–	–	–	–	–	–	
Total	10	0.0	40.0	60.0	0.0	0.0	0.0	100.0	

Notes: The mathematical nature of each type of hydrodynamic effect is reported as a percentage of the total frequency at which the relationship was reported. *Positive* and *Negative* refer to monotonic relationships. The rate at which each hydrodynamic predictor was reported as statistically significant is also reported. Significant multivariate or modelling relationships may not report sign of relationship.

and oxygen, but that is protected from high, scouring winter and spring flows to prevent dislodgement (Allen & Vaughn, 2010; Steuer et al., 2008). Simple hydraulic variables describe the speed and volume of flow through a confined space—in this context a fluvial ecosystem. These variables are simple to measure but vary dramatically in space and time as hydrology changes. For example, the spring flows described in Peterson et al. (2011) differed dramatically in discharge and depth from summer flows, and both types of flows were predictive of different responses by mussel communities. However, most empirical studies of mussel habitat and mussel distribution have been conducted during the low-flow summer months, when conditions are safest for researchers and it is easier to locate mussels. Here, we examine the use of velocity, depth, and discharge to determine mussel community parameters.

Observations of mean or instantaneous flow velocity show few or no discernible patterns in responses to mussel community and population parameters (Tables 2–4; Ćmiel et al., 2020; Daniel & Brown, 2013; Fulton et al., 2010; Gagnon et al., 2004; Gangloff & Feminella, 2007; Hardison & Layzer, 2001; Hastie et al., 2000, 2003; Johnson & Brown, 2000; Klos et al., 2015; Maloney et al., 2012; Moorkens & Killeen, 2014; Parasiewicz et al., 2012; Sanz-Ronda et al., 2014; Steuer et al., 2008; Stoeckl & Geist, 2016; Strayer, 1999; Wegscheider et al., 2019; Westberg, 2020). This suggests that flow velocity alone holds little predictive power for mussel communities overall. Even the few studies that reported specific velocities for both high and low flows failed to find clear relationships (Holland-Bartels, 1990; Morales et al., 2006; Zigler et al., 2008). Similarly, observations of channel depth held limited predictive power (Baldigo et al., 2004; Galbraith et al., 2010; Gangloff & Feminella, 2007; Goodding et al., 2019; Hardison & Layzer, 2001; Hastie et al., 2000; Hornbach et al., 2010; Johnson & Brown, 2000; Klos et al., 2015; Maloney et al., 2012; Negishi et al., 2012; Nishio et al., 2016; Parasiewicz et al., 2012; Sanz-Ronda et al., 2014; Steuer et al., 2008; Strayer, 1999; Wegscheider et al., 2019; Westberg, 2020; Zigler et al., 2008). However, Daraio et al. (2010) modelled the rates at which juvenile mussels settled out from suspension in the water column at high and low flows and found that high-flow water depth was positively related to settling and low-flow water depth was negatively related to settling. This relationship deserves further empirical study, as it may influence the locations of mussel beds (see Section 3.4).

Fewer studies tested relationships of instantaneous or mean discharge to mussel abundance, presence or species richness (but see Baldigo et al., 2004; Chiavacci et al., 2018; Hansen et al., 2016; Holcomb et al., 2018; Johnson et al., 2014; Spooner et al., 2011). Discharge was most often positively or non-significantly related to mussel presence (Table 2), abundance (Table 3), and species richness (Table 4). The positive discharge–mussel relationships may be partially explained by the fact that most mussel surveys are conducted in the summer when mussels require higher discharge to maintain a greater area of wetted habitat. Discharge is also a function of stream size, which is positively correlated with mussel species richness.

Overall, flow velocity was more effective than water depth and discharge at predicting mussel community parameters. This is

probably because velocity is closely related to the hydraulic forces described by more complex hydraulic variables such as shear stress. Depth and discharge are also related to these forces, but this relationship is indirect, and is linked to complex variables through the direct relationships of discharge and depth to flow velocity.

### 3.3 | Complex hydraulic variables

Complex hydraulic variables are calculated by combining simple hydraulic variables, mainly flow velocity, with substrate and geomorphic channel characteristics (Table 1). They are beneficial because they allow researchers to characterise the forces and physical environment created by flows, such as turbulence or shear stress. Freshwater organisms, especially those in fluvial benthic habitats, experience a wide range of flow conditions that cannot be adequately described by simple metrics such as velocity and depth (Statzner et al., 1988). Researchers have long recognised that mussels often inhabit areas sheltered from the high velocities of main channel flow, or flow refugia (Strayer, 1999; Vannote & Minshall, 1982).

Layzer and Madison (1995) were pioneers in quantifying the influence of complex hydraulic variables on mussel beds. Froude number (the ratio of inertial to gravitational forces) and Reynolds number (the ratio of inertial to viscous forces; i.e. turbulence) were initially found to be positively correlated to mussel densities at low flows but not at high flows; stream power and shear stress were found to be correlated to mussel density across flows (Layzer & Madison, 1995). These findings are critical for two reasons: (1) they demonstrate that different variables may limit mussel occurrence at different discharges and (2) they demonstrate that the forces mussels experience at the riverbed can be better described by using more complex calculations.

The role of shear stress in structuring mussel beds has now been demonstrated repeatedly (Addy et al., 2012; Allen & Vaughn, 2010; Bartsch et al., 2010; Gangloff & Feminella, 2007; Goodding et al., 2019; Hardison & Layzer, 2001; Hornbach et al., 2010; Morales et al., 2006; Randklev et al., 2019; Steuer et al., 2008; Stoeckl & Geist, 2016; Stone et al., 2004; Zigler et al., 2008). These studies often calculate and report a number of other variables related to shear stress such as Froude number, stream power and shear velocity—but these variables are typically less consistent in predicting mussel community parameters (Tables 2–4). Shear stress is a concern for mussels because greater shear stress increases the likelihood of dislodgement and entrainment, which can result in downstream transport to an unfavourable habitat. The most informative studies calculated shear stresses at multiple discharge levels, and included *relative shear stress* (RSS)—the ratio of observed shear stress to the critical shear stress value required to mobilise the riverbed substrate (Allen & Vaughn, 2010; Morales et al., 2006; Randklev et al., 2019; Zigler et al., 2008). Randklev et al. (2019) took this a step further and analysed the influence of complex hydraulic variables on individual mussel species occurrence in addition to the mussel community as a whole, finding species-specific responses to RSS, depending on life-history and shell morphology.



In addition to the limitations placed on mussels by shear stress at high flows, Reynolds number is also important. Most studies have used simple linear analyses to relate Reynolds number to responses in mussel community parameters, and have found mixed results (Goodding et al., 2019; Hardison & Layzer, 2001; Layzer & Madison, 1995; Steuer et al., 2008). However, studies that used limiting factor analyses, such as quantile regression, found that Reynolds number tended to be positively related to mussel abundance and species richness at low flows, but less limiting as flows increased (Allen & Vaughn, 2010; Randklev et al., 2019). Studies that evaluated Reynolds number at the boundary layer, where flow is slowest and least turbulent, detected the strongest relationships (Goodding et al., 2019; Hardison & Layzer, 2001; Hornbach et al., 2010; Parasiewicz et al., 2012; Steuer et al., 2008). This is probably a result of increased exchange of materials created by higher levels of turbulence—indicated by higher Reynolds number—between the overlying water and the boundary layer where mussels exist. Turbulence increases diffusion and exchange of food and waste particles—food can enter from the overlying flow with the boundary layer and waste can exit (Vogel, 1981). Both of these conditions are vital to sedentary organisms in the benthic zone.

Although a great deal of overlap seems to occur in the microhabitat preferences of individual mussel species at the mussel bed scale (Haag, 2012; Strayer, 1981), species-specific hydraulic preferences may be important in explaining changes in assemblage structure at the landscape or regional scales (e.g. Randklev et al., 2019).

### 3.4 | Juvenile and larval settling

Mussel larvae (glochidia) are obligate ectoparasites of fish and rely on them for development and dispersal. Once a glochidium has completed development from larva to juvenile mussel, it drops off the host fish and settles passively to the bottom. Several studies we reviewed reported the effects of hydraulic parameters on larval or juvenile settling. Modelling exercises demonstrate that juvenile settling should occur just downstream of locations where bed shear stress decreases below the critical shear stress threshold required to mobilise the substrate ( $RSS < 1$ ). These areas tended to correspond to areas with lower velocities and more complex flow patterns, such as the upstream ends of islands, bends, and side channels (Daraio et al., 2010; Zigler et al., 2008). Existing mussel beds also tend to promote settling by decreasing the distance juveniles and larvae drift in the current, probably by increasing riverbed roughness (Irrmscher & Vaughn, 2018) and decreasing RSS (Morales et al., 2006). Juvenile and larval settling must be heavily influenced by hydrodynamics, but the ability to study settling dynamics in the field is extremely limited, which makes it difficult to verify modelling results (Daraio et al., 2010; Morales et al., 2006).

Once settled, juveniles undergo a post-parasitic phase where they live burrowed below the sediment—this phase can last several years in longer-lived species (Geist & Auerswald, 2007). Ćmiel et al. (2020) found higher juvenile abundances in areas with higher

flow velocities. This counterintuitive pattern can be explained by the fact that, at low flows, mussels need enough turbulence (represented by Reynolds number) to exchange materials from the boundary layer. Ćmiel et al. (2020) conducted the aforementioned study in an extremely low-flow environment—a slow-flowing Polish lake. Indeed, Ćmiel et al. (2020) found a positive relationship between Reynolds number and juvenile occurrence. Furthermore, juvenile mussel recruitment has been found to rely on higher flow velocities that increase oxygen supply to the substrate and interstitial water quality (Geist & Auerswald, 2007). This indicates that it is not the higher velocity driving the positive relationship to juvenile occurrence, but rather the correlation is a by-product of either the fact that Reynolds number is positively related to flow velocity or the need of juveniles for interstitial oxygen and water quality, or perhaps both. Despite the challenges presented in this section, a deeper understanding of factors regulating juvenile mussel settling and development is vital because a mussel bed cannot form in a location where larvae or juveniles do not settle.

## 4 | RESULTS OF QUANTITATIVE COMPARISON OF FLOW VARIABLES

Of all the reported relationships between hydrodynamic-associated variables and mussel population or community parameters ( $n = 1,008$ ), the most commonly reported mussel response variable was abundance ( $n = 272$ ; Table 3), followed by presence/absence ( $n = 141$ ; Table 2), and species richness ( $n = 43$ ; Table 4). Fewer relationships were reported with juvenile or larval settling as a response ( $n = 11$ ). Other less frequently reported mussel community response variables included community composition ( $n = 4$ ), annual survival ( $n = 12$ ), recruitment ( $n = 16$ ), or mortality ( $n = 4$ ) as responses (Table 5). There were 29 relationships reported where mussels were demonstrated to reciprocally influence hydrodynamic variables (Section 5). Of the six continents that host freshwater mussel species—every continent but Antarctica—the vast majority of the 1,008 observations we recorded were from North America (87.00%). Europe was the next best represented (8.53%), with Asia making up the only other substantial share of the data (4.07%). Australia and Oceania (0.30%) and South America (0.10%) comprised the remaining fraction of the observations, with none from Africa (0%).

To evaluate patterns in the rates at which certain variables were reported as significant predictors of mussel community parameters, we report below the number of relationships between a given hydrodynamic variable and a given mussel variable that were reported ( $n$ ) across all studies we reviewed and the percentage of those relationships which were reported as significant (%). It is important to interpret these rates of significance in the context of the  $n$  value and to consider that they may be inflated due to publication bias towards statistically significant results.

Of the three coarse categories of hydrodynamic predictor variables, complex hydraulic variables were reported as significantly related to mussel presence/absence data at the highest rate ( $n = 46$ ,

**TABLE 5** Frequencies (*n*) of reported effects of hydrodynamic variables on mussel responses other than abundance, presence/absence, or species richness with the associated citation

Category	Predictor	Response	Relationship	<i>n</i>	Citation(s)
Hydrologic	Flooding	Mortality	Positive	1	Hastie et al. (2001)
Simple hydraulic	Water depth	Mortality	Negative	1	Galbraith et al. (2010)
Simple hydraulic	Flow velocity	Mortality	Negative	1	Gagnon et al. (2004)
Simple hydraulic	Water depth	Mortality	Unimodal	1	Gagnon et al. (2004)
Complex hydraulic	Reynolds number residual	Recruitment	Positive	3	Ćmiel et al. (2020)
Hydrologic	Spring high-flow discharge	Recruitment	Null	1	Peterson et al. (2011)
Hydrologic	Spring median discharge	Recruitment	Null	1	Peterson et al. (2011)
Hydrologic	Spring low-flow discharge	Recruitment	Positive	1	Peterson et al. (2011)
Hydrologic	Summer high-flow discharge	Recruitment	Positive	1	Peterson et al. (2011)
Hydrologic	Summer median discharge	Recruitment	Positive	1	Peterson et al. (2011)
Hydrologic	Summer low-flow discharge	Recruitment	Positive	1	Peterson et al. (2011)
Hydrologic	Winter high-flow discharge	Recruitment	Null	1	Peterson et al. (2011)
Hydrologic	Winter median discharge	Recruitment	Null	1	Peterson et al. (2011)
Hydrologic	Winter low-flow discharge	Recruitment	Null	1	Peterson et al. (2011)
Simple hydraulic	Discharge	Recruitment	Positive	1	Johnson et al. (2014)
Simple hydraulic	Flow velocity	Recruitment	Positive	3	Gagnon et al. (2004)
Complex hydraulic	Duration of hydrodynamic spin	Survival	Negative	1	Gagnon et al. (2004)
Complex hydraulic	Hydrodynamic spin rate (RPM)	Survival	Negative	1	Horvath and Crane (2010)
Hydrologic	Minimum monthly discharge	Survival	Positive	1	Horvath and Crane (2010)
Hydrologic	Spring high-flow discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Spring median discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Spring low-flow discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Summer high-flow discharge	Survival	Negative	1	Peterson et al. (2011)
Hydrologic	Summer median discharge	Survival	Negative	1	Peterson et al. (2011)
Hydrologic	Summer low-flow discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Winter high-flow discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Winter median discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Winter low-flow discharge	Survival	Null	1	Peterson et al. (2011)
Hydrologic	Stream or catchment size	Community composition	Ordination	2	Atkinson et al. (2012) and Ford et al. (2016)
Hydrologic	Drought	Community composition	Ordination	1	Galbraith et al. (2010)
Hydrologic	Longitudinal distance	Community composition	Ordination	1	Atkinson et al. (2012)

63.1%). Shear stress variables were often important, although studies exhibited a wide range in the type of shear stress variable reported (Table 2), including instantaneous shear stress ( $n = 12$ , 66.7%), high-flow shear stress ( $n = 1$ , 100%), low-flow shear stress ( $n = 1$ , 100%), instantaneous RSS ( $n = 2$ , 100%), high-flow RSS ( $n = 2$ , 100%), and low-flow RSS ( $n = 2$ , 50%). Reynolds number was reported less often, but both instantaneous Reynolds number ( $n = 3$ , 66.7%) and boundary layer Reynolds number ( $n = 4$ , 75%) appeared to be fairly predictive of mussel presence/absence data. This dataset also included several observations of the effects of RSS—whether shear stress is high enough in magnitude to mobilise riverbed sediments. Hydrologic factors were reported as significant predictors at a much

lower rate ( $n = 67$ , 38.8%). Simple hydraulic variables were similarly low ( $n = 28$ , 46.4%).

The coarse category reported as significantly related to mussel abundance at the highest rate (Table 3) was hydrologic variables ( $n = 54$ , 72.2%). Simple hydrodynamic ( $n = 105$ , 61.0%) and complex hydrodynamic ( $n = 113$ , 61.9%) variables were reported as significant at lower rates. However, a few complex hydraulic variables stand out, albeit with variable sample sizes: high-flow shear stress ( $n = 3$ , 100%); shear velocity ( $n = 17$ , 82.4%); boundary layer Reynolds number ( $n = 10$ , 84.2%); and laminar layer (i.e. boundary layer) thickness ( $n = 14$ , 85.7%). High-flow shear stress and laminar layer thickness tended to be negatively associated with mussel

abundance; boundary Reynolds number and shear velocity tended to have positive associations (Table 3).

The smallest dataset we compiled consisted of hydrodynamic-species richness relationships (Table 4). Here, the numbers of studies were mostly too small to assess finer variable types for patterns in the rates at which they were reported as significant. However, all three hydrodynamic variable categories were fairly effective at detecting significant relationships. Although the sample size for complex hydraulic variables was small ( $n = 10$ ), 100% of the reported relationships were significant. Hydrologic ( $n = 18$ , 72.2%) and simple hydraulic ( $n = 15$ , 66.6%) variables, especially discharge ( $n = 13$ , 69.2%), were also moderately effective.

## 5 | ECOLOGICAL ENGINEERS: FLOW AND HABITAT MODIFICATION BY MUSSELS

Within the past decade, a greater emphasis has been placed on not just how stream-dwelling organisms are influenced by their physical conditions, but how they modify their surroundings through biological activity, producing ecogeomorphic feedbacks (Allen et al., 2014; Atkinson, Allen, et al., 2018). As the most abundant source of benthic biomass in many fluvial ecosystems, mussels are likely to have significant geomorphic effects. Recent evidence suggests that mussel species modify the stream bed's physicochemical and microbial characteristics more strongly than other invertebrates (Boeker et al., 2016). This is especially important to consider in light of Section 4, where we described the most effective hydraulic variables for predicting mussel community parameters. Mussel presence or movement is likely to affect the values of hydraulic variables by altering the physical characteristics of the near-bed environment. However, mussel behaviour varies; some species burrow deeper or are less mobile (Allen & Vaughn, 2009; Zieritz et al., 2014), potentially leading to over- or underestimation of their relationship to flow characteristics. This suggests that species identity and diversity or community composition are important factors in considering the geomorphological impacts of freshwater mussels.

The use of flume studies and technology typical of engineering research has begun to reveal how mussels alter their own hydraulic environment. Mussel presence decreases shear velocity, near-bed flow velocity (Brunke et al., 2001; Kumar et al., 2019; Sansom et al., 2018, 2020), and bedload transport and increases median sediment size (Koerner, 2018). Mussel diversity also influences gravel erosion from stream beds (Allen & Vaughn, 2011). Mussel shells create small, irregular vortices immediately downstream of their protruding shells; this suggests mussel aggregations may trap particles such as food, sperm, or settling juvenile mussels from the current (Constantinescu et al., 2013; Irmscher & Vaughn, 2018; Kumar et al., 2019). However, there is also evidence that mussels displace the boundary layer to a greater distance above the riverbed (Sansom et al., 2020). This should reduce shear stress, decreasing the odds of dislodgement, but could also interfere with the exchange of materials between the boundary layer and the overlying water column.

In any case, it is clear that mussels are both influenced by hydraulic forces and exert their own reciprocal influence on the environment. Further exploration into this ecogeomorphic *engineering* is a burgeoning and fruitful research avenue.

## 6 | CONCLUSIONS AND FUTURE DIRECTIONS

### 6.1 | Conclusions and recommendations for predicting mussel occurrence using hydrodynamics

The limits placed on life in fluvial ecosystems by hydrodynamic variables are widely studied, yet significant knowledge gaps exist in our understanding of how such variables, especially complex hydraulics, affect freshwater mussels. Thus, we sought to narrow the suite of variables used to describe the hydrodynamic habitat of freshwater mussels—a taxonomic group of great conservation and ecological concern (Strayer & Dudgeon, 2010; Vaughn & Hoellein, 2018). We make the following recommendations regarding efficient and consistent use of hydrodynamic variables in mussel ecology.

#### 6.1.1 | Hydrologic variables

The influence of hydrologic variation on mussel communities is well-established. Researchers investigating freshwater mussel habitat should continue to explore how anthropogenic flow alteration and climate change may negatively affect freshwater mussels. However, there is an established base of knowledge on broader influences of hydrology on mussels, so we encourage the collection and use of species-specific and system-specific data that can be directly useful to water managers and conservation agencies. These data would be especially useful in the implementation of *environmental flows* designed to maintain baseline ecological functioning in managed rivers (e.g. Gates et al., 2015).

#### 6.1.2 | Simple hydraulic variables

Flow velocity, discharge, and water depth are and always will be critical to understanding the habitat needs of any stream dwelling species. As discussed previously, different hydrodynamic variables may limit mussels at different discharge levels (Allen & Vaughn, 2010; Randklev et al., 2019). Thus, it is important that researchers collect flow velocity data over a range of flow conditions to adequately evaluate mussel habitat. This presents substantial logistical and safety problems. While we do not have all the solutions to these challenges, we can suggest that ecologists collaborate with hydrologists or engineers to conduct fieldwork under high-flow conditions. Researchers in these fields are necessarily prepared to work under high-flow conditions and may help ecologists work safely in unfamiliar conditions.

### 6.1.3 | Complex hydraulic variables

We recommend that RSS and near-bed Reynolds number be calculated whenever assessing mussels' hydraulic habitat needs. We also encourage more studies with full community composition sampling to explore mussel community composition and species richness as response variables to complex hydraulic predictors. The small number of papers reporting such relationships in our review show promise for better understanding mussel habitat needs by exploring these patterns. For example, Randklev et al. (2019) found species-specific responses to shear stress variables. Complex hydraulic variables may reveal important ecological filters that had previously gone unrecognised.

## 6.2 | Future research directions

As research continues to expand on the world's imperilled freshwater mussels, there are a few key areas of future research that should be highlighted beyond the recommendations from the preceding section. One looming question is to what degree hydrodynamic forces influence mussel distributions as larvae and juveniles, which is quite difficult to assess in the field. Modelling exercises are useful, but empirical verification is challenging (Daraio et al., 2010; Morales et al., 2006). Flumes can be used to manipulate flow characteristics, while lasers or fluorescence can be used to trace particles (Irmscher & Vaughn, 2018), but this approach might not accurately capture the complex hydrodynamics of field conditions. Novel approaches are needed to study the relationship larval and juvenile distributions and hydrodynamic forces under natural conditions.

One major challenge we faced in conducting this literature review was the failure of many studies to report metrics such as effect sizes and precision. Thus, while we could categorise and interpret relationships, our ability to make quantitative inferences was limited. We could make recommendations about which hydrodynamic variables appeared most closely related to mussel communities, but not about how strongly they were related. When possible, we encourage the reporting of parameter estimates as well as their standard error values and confidence intervals. Of course, there are limitations to the amount of data that can be included in any single study; so, even when it is logical to report mainly *p*-values and test statistics, we encourage researchers to either include more detailed statistical descriptions in the supplementary material or make such data available in a repository.

Efforts to understand how mussels themselves influence the flow and sediment characteristics of the river bottom should also be expanded. Recent findings show that mussels substantially alter near-bed flow and sediment (Constantinescu et al., 2013; Kumar et al., 2019; Sansom et al., 2018, 2020). This has important implications for mussel habitat restoration projects and for sediment transport in fluvial systems where mussels are abundant. These studies resulted from collaborations featuring engineers with access to technology not typically found in ecological laboratories (lasers,

particle tracing). To fully appreciate the role mussels play as ecological engineers, it is vital to continue such collaborative efforts between ecologists and engineers.

Finally, the literature regarding freshwater mussels is extraordinarily geographically biased. North America's diverse fauna has been studied most extensively, and the less diverse mussel fauna of Europe is a distant second. However, there is tremendous mussel diversity in southeast Asia that requires further exploration, and we know very little about the mussels of South America and Africa—there was only one observation in the entire dataset between these two continents (Jara et al., 2019). Australia was similarly neglected with only three observations (Jones & Byrne, 2010), although species diversity is considerably lower in Australia (Haag, 2012). The ecosystems in these understudied locales deserve further study.

Many of the study locations we reviewed also face increasing conflict over the use and exchange of water as a commodity, especially as existing water scarcity issues are compounded by the progression of global climate change (Jackson et al., 2001; Reid et al., 2019). Research into the physical habitat needs of aquatic organisms such as mussels allows managers and regulators to establish guidelines for sustainable water management such as environmental flows (e.g. Gates et al., 2015; Spooner et al., 2011). Ideally, a balance can be reached between human needs and mitigation of the damage done to the ecosystem by anthropogenic flow alteration, water withdrawal and climate change. The human population is expanding at a rate faster than the rate at which new freshwater sources can be appropriated (Jackson et al., 2001), and those regions which have further freshwater resources to tap are going to be forced to use those resources. Global climate change will compound these issues, threatening the biological health and sustainability of freshwater habitats. Lack of biological integrity in freshwaters leads to declines in water quality and greater expense to local communities through increased water treatment costs and loss of recreational and aesthetic value. Thus, we must continue to value the hydrodynamic needs of the organisms inhabiting freshwaters even when humans are presented with water scarcity.

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### DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

### ORCID

Jonathan W. Lopez  <https://orcid.org/0000-0001-8560-4919>

Caryn C. Vaughn  <https://orcid.org/0000-0003-3749-836X>

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