

Long-term persistence of freshwater mussel beds in labile river channels

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Abstract

1. Freshwater mussels are among the world's most imperilled species, and much effort has been expended to understand their precipitous decline. The current paradigm is that relative river bed stability over decades is critical to maintaining mussel beds at a given river reach. Such information, however, is in stark contrast to the fundamental understanding of self-formed rivers.
2. Here, we examine the relationship between long-term occurrence of aggregated freshwater mussel communities (mussel beds) and the dynamic rivers in which they live.
3. We surveyed mussel assemblages in two streams with historical records to document their long-term persistence, and we simulated bed mobility with a two-dimensional flow and sediment transport model to estimate bedload transport during channel-forming discharges.
4. We found evidence of long-term mussel bed persistence, in time and in kind, within these two streams and that significant bed mobility within mussel beds occurs every 1–2 years, as to be expected for self-formed rivers with labile beds. Flow refugia, or bed immobility, thus cannot completely explain the persistence of these mussel beds.
5. Our results suggest that mussels have adapted to proliferate in river channels that often experience significant bed mobility, but further studies are needed to understand the biophysical mechanisms enabling the long-term persistence of mussel communities.

KEY WORDS

labile river channels, long-term persistence, river bed mobility, sediment transport, unionid mussels

1 | INTRODUCTION

Freshwater mussels (Bivalvia: Unionoida) are long-lived, sedentary, burrowing invertebrates that play important ecological roles in lakes and rivers worldwide (Vaughn & Hakenkamp, 2001). Mussels have one of the highest imperilment rates of any group of organisms and are undergoing a global decline (Lopes-Lima et al., 2014; Ricciardi & Rasmussen, 1999). Globally, 44% of the 511 mussel species are listed as near-threatened or threatened in the 2015 IUCN Red List

of Threatened Species (Lopes-Lima et al., 2017). North America has the richest fauna of mussels worldwide, but over 70% of species are considered imperilled to some degree and 37 species are presumed extinct (Lopes-Lima et al., 2017). The recognition of the decline in mussel populations has mobilised conservation efforts at local, national and international levels (FMCS, 2016; Haag & Williams, 2014; Lopes-Lima et al., 2017). Recent studies have aided in understanding the distributional range, historical records, population trends and demographic data of mussels (see Haag, 2010). Our ability to

predict mussel distribution and abundance remains inadequate (Strayer, 2008; FMCS, 2016), and temporal and spatial patterns in mussel habitat across multiple scales and life stages are poorly understood (FMCS, 2016).

In rivers, mussels often occur as dense, multispecies assemblages called mussel beds that are patchily distributed and separated by areas where mussels do not occur or are sparse (Strayer, 2008). Mussel beds have been observed to persist for many decades in the same river reach (Haag, 2012). For example, Vaughn (2000) found 19 mussel beds in nine tributaries to the Red River in Oklahoma and Texas that had persisted in the same location from as far back as 1910 (Isely, 1924; Valentine & Stansbery, 1971), and Williams and Schuster (1989) found that 64% of the mussel beds in the Ohio River surveyed in 1967 were still in existence in 1982 (as cited in Haag, 2012). As a demonstration of the widespread occurrence of this phenomenon, we compiled a list of 24 rivers in the United States where mussel beds have existed at the same river reach from 20 to more than 100 years (Table 1). The factors responsible for the patchiness and long-term persistence of mussel beds in rivers, however, are not well understood. Mussels have a unique life history in which adults are sedentary and the larvae (glochidia) are ectoparasites on fish. Thus, at a regional scale, mussel distribution is partially dependent on host fish populations and mussel aggregations likely occur in favourable habitats for fish hosts and juvenile mussels (Strayer, 2008; Vaughn & Taylor, 2000). At local scales, however, habitat variables such as water depth, water velocity and sediment composition, quantified mostly during low flow surveys, have failed to adequately explain mussel occurrence or abundance when critically examined (Brim Box, Dorazio, & Liddell, 2002; Holland-Bartels, 1990; Layzer & Madison, 1995; Strayer, 1981, 2008; Strayer & Ralley, 1993; Vaughn & Pyron, 1995). Instead, the prevailing hypothesis is that areas of the river channel where sediments are stable are a critical component to the ecological success and resiliency of mussels. Strayer (1999) further hypothesised that mussels occur in flow refugia patches where "shear stresses during floods with moderately long return periods (e.g. 3–30 years) are too low to displace unionids or the sediments in which they are bedded." This hypothesis is mainly supported by studies correlating mussel occurrence to areas of low shear stress during low flow where shear stresses are not a limiting factor to mussel distribution (Allen & Vaughn, 2010; Gangloff & Feminella, 2007; Layzer & Madison, 1995; Stone, Barndt, & Gangloff, 2004) or anecdotal evidence suggesting large boulders prevent significant scour during floods (Hastie, Boon, Young, & Way, 2001; Vannote & Minshall, 1982). Only a few studies covering a small range of rivers, flows and sediment sizes, however, have successfully correlated mussel occurrence to areas of low shear stresses during floods by directly quantifying or modelling sediment dynamics within mussel beds (Howard & Cuffey, 2003; May & Pryor, 2016; Strayer, 1999).

The suggestion, implicit or otherwise, that significant portions of a river bed in which mussels live remain immobile for decades or more is in stark contrast to the fundamental understanding of river mechanics. A central tenet in fluvial geomorphology is the concept

of channel-forming discharge, wherein a natural river channel attains bankfull flow conditions every 1–2 years. The dimensions of the channel therefore are determined by the erosive potential of this flow event and river morphology is self-formed (Williams, 1978; Wolman & Miller, 1960). River channels can further be categorised based on the frequency in which bed sediments are entrained. For example, bed sediments in labile channels are relatively easily and frequently entrained by the flow, whereas transitional channels have flow events that mobilise bed sediments less frequently (Church, 2006).

As shown in Table 1 and reported elsewhere worldwide, freshwater mussels are ubiquitous in rivers displaying a wide range of size, channel gradient and bed texture (see Bogan & Roe, 2008; Geist, 2010; Haag, 2012; Quinlan et al., 2015; Strayer, 2008; Williams, Warren, Cummings, Harris, & Neves, 1993). Self-formed rivers with labile beds are common in nature, and it is highly likely that most of the rivers listed in Table 1 would often experience channel-forming discharge events accompanied by significant sediment transport, certainly at frequencies greater than once per the lifespan of mussels (Church, 2006). As a result, river beds populated by freshwater mussels would often experience fully mobile bed conditions. Long-term sediment stability, however, is not often quantified in reaches with mussel beds, only a few studies have provided support to the flow refugia hypothesis during flood events (Howard & Cuffey, 2003; May & Pryor, 2016), and the frequency and extent to which mussels experience bed mobility have rarely been tested (but see Allen & Vaughn, 2010, 2011).

In this study, we tested the hypothesis that sediment stability is critical to the long-term persistence of mussel beds. We investigated the relationship between long-term occurrence of mussel assemblages and the dynamic river systems in which they live by: (a) documenting the long-term persistence of freshwater mussel communities at-a-station (i.e. the same reach) in a river and (b) determining the relative bed mobility within these mussel beds. We surveyed mussel assemblages in two streams with robust historical records to document their long-term persistence, and we simulated bed mobility with a two-dimensional flow and sediment transport model to estimate bedload transport during channel-forming discharges. We hypothesised that mussel assemblages would remain relatively unchanged at-a-station and that channel-forming discharges occurring every 1–2 years would be capable of mobilising large portions of the stream bed where mussels occur. Such empirical evidence would challenge the current paradigm for mussel bed persistence in rivers.

2 | METHODS

We selected two streams with historically and ecologically significant mussel communities to examine the long-term persistence of mussels and to assess the occurrence of channel-forming discharges and relative bed mobility. Tonawanda Creek originates in western New York and flows north and then west into the Niagara River (Figure 1a). A

TABLE 1 Description of select rivers with historically and ecologically significant mussel beds that have remained intact for decades or more at given river reaches. Cl = clay; St = silt; S = Sand; G = gravel; Co = cobble; Bo = boulder and R = bedrock

River (State)	Drainage area (km ²)	Bed composition	Mean gradient (m/m)	Number of extant species	Period of record	Source(s)
Fourche La Fave River (AR)	583	St, S, G, Co	0.00092	21	1992–2001	Dortch, Tillman, & Bunch, 1992; Harris, 1992; Harris et al., 2009
Kinniconick Creek (KY)	658	G	0.00169	17	1983–2012	Warren, Cicerello, Camburn, & Fallo, 1984; Evans, 2012
Elk River (TN, AL)	868	S, G, Co	0.00044	38	1924–1980	Ahlstedt, 1983; Dunn, Sietman, & Kelner, 1999
Big Darby Creek (OH)	1,442	St, S, G, Co, Bo	0.00121	35	1986–1996	Watters, 1998; State of Ohio EPA, 2004
Tonawanda Creek (NY)	1,700	St, S, G, Co	0.00183	19	1998–Present	Marangelo & Strayer, 2000; This Study
Tippecanoe River (IN)	1,890	S, G	0.00043	40	1900–1991	Cummings, Mayer, & Page, 1992
Clinton River (MI)	1,977	St, S, G, Co	0.00113	26	1870–1978	Strayer, 1980, 1981; Morowski, James, & Hunter, 2009
Bourbeuse River (MO)	2,183	G	0.00054	27	1978–1997	Hinck et al., 2012
Big River (MO)	2,473	S, G, Co, Bo	0.00118	17	1978–1997	Meneau, 1997; Hinck et al., 2012
French Creek (NY, PA)	3,200	St, S, G, Co, Bo	0.00126	25	1993–Present	Bier, 1994; Smith & Crabtree, 2010; This Study
Kiamichi River (OK)	4,740	S, G, Co	0.00151	22	1911–Present	Vaughn, Mather, Pyron, Mehlhop, & Miller, 1996; Vaughn, 1997; Atkinson, Julian, & Vaughn, 2012
Cache River (MO, AR)	5,240	Cl, St, S	0.00030	26	1914–1994	Christian, Harris, Posey, Hockmuth, & Harp, 2005
Duck River (TN)	8,100	St, G	0.00061	54	1884–2010	Ahlstedt et al., 2004; Hubbs, Chance, Colley, & Butler, 2011
Meramec River (MO)	10,255	St, S, G, Co	0.00060	34	1978–1997	Hinck et al., 2012
Little River (OK, AR)	10,889	S, G, Co	0.00196	26	1987–Present	Vaughn, 1997; Atkinson et al., 2012; Davidson, Brady, & Fotinos, 2014
Clinch River (VA, TN)	11,430	St, S, G, Co	0.00113	46	1912–2009	Ortmann, 1918; Eckert, Ferraro, Pinder, & Watson, 2008; Jones et al., 2014
Sangamon River (IL)	14,035	St, S, G	0.00026	28	1910–1989	Schanzle & Cummings, 1991
White River (IN)	14,880	S, G, Co	0.00040	59	1906–1987	Cummings et al., 1992
St. Croix River (WI, MN)	20,000	S, G, Co	0.00041	41	1945–2010	Fuller, 1980; Hornbach, 2001
Rock River (WI, IL)	27,270	St, S, G, Co	0.00026	27	1926–2009	Bales, Price, & Shasteen, 2012
Wabash River (OH, IN, IL)	39,950	Cl, St, S, G, Co	0.00027	62	1900–1988	Cummings et al., 1992
Cumberland River (KY, TN)	48,000	St, S, G, Co, Bo, R	0.00024	72	1885–1989	Wilson & Clark, 1914; Starnes & Bogan, 1988; Gordon & Layzer, 1989
Susquehanna River (NY, PA, MD)	71,225	St, S, G, Co, Bo	0.00048	11	1955–1997	Strayer & Fetterman, 1999; Pennsylvania DEP, 2014
Tennessee River (TN, AL, MS, KY)	105,000	St, S, G, Co	0.00015	126	1897–2001	Starnes & Bogan, 1988; Hubbs et al., 2011

total of 19 mussel species were recorded during a basinwide survey in 1998 (Marangelo & Strayer, 2000). French Creek also originates in western New York and flows south through Pennsylvania to its confluence with the Allegheny River (Figure 1b). French Creek is among the most biodiverse streams in the northeast (Smith & Crabtree, 2010) and contains over 80 native fish species and 29 native mussel species (Bier, 1994; Smith & Crabtree, 2010). Smith and Crabtree (2010) observed 25 mussel species during a survey in 2003–2005 and further noted that mussel density, abundance, and diversity

remained intact since a survey in 1993 (Bier, 1994). In both streams, mussel beds occur as patches in space, and they typically occur in riffle-run reaches.

Qualitative mussel surveys were conducted at select sites previously examined by Marangelo and Strayer (2000) in Tonawanda Creek and by Smith and Crabtree (2010) in French Creek. On Tonawanda Creek, surveys were conducted at sites 1, 2 and 7 during the summer of 2016 (Figure 1a). On French Creek, surveys were conducted at river kilometres (RKM) 74, 93, 109 and 125 during the

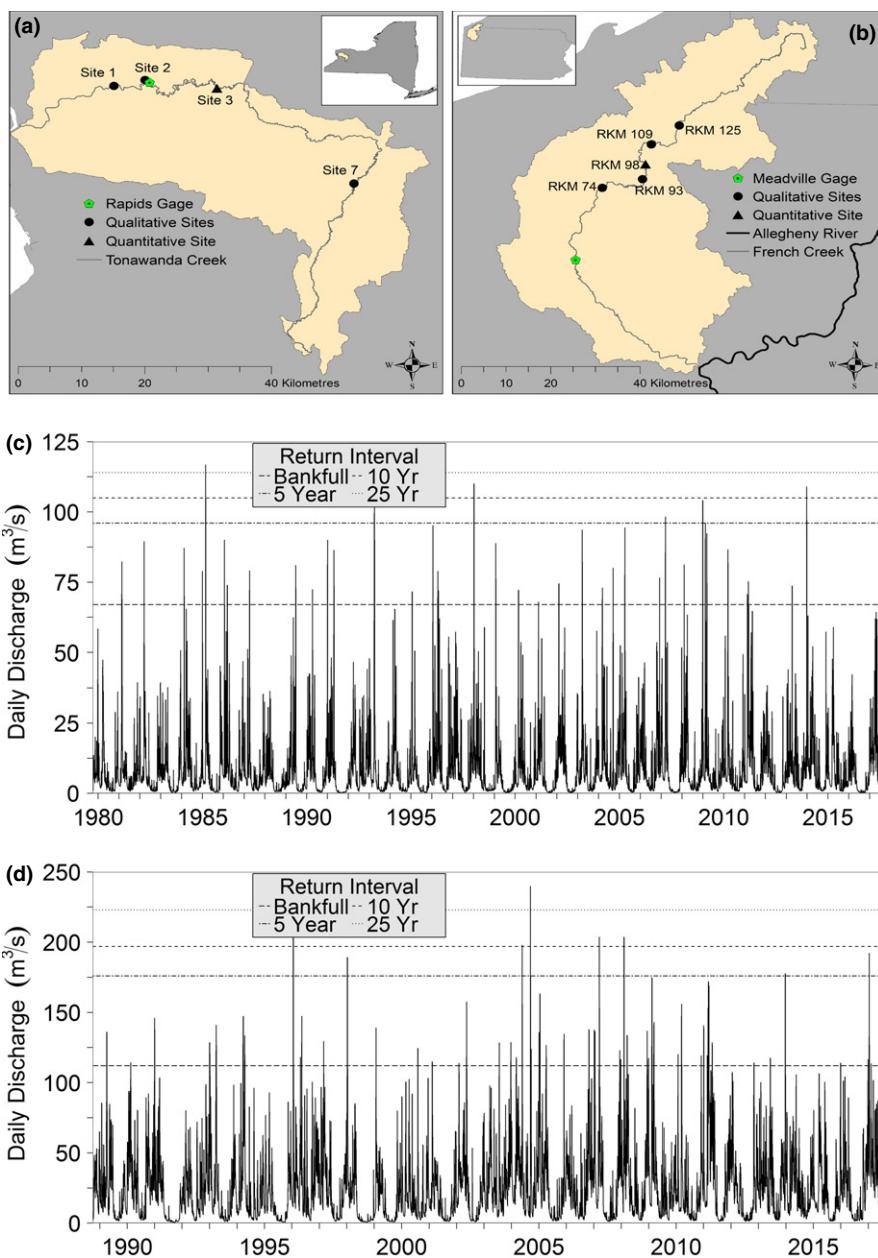


FIGURE 1 Map of the field sites in Tonawanda Creek (a) and French Creek (b). The historical daily discharge is plotted with return intervals representing the bankfull event, and a 5-, 10-, and 25-year flood to show the frequency of such events for the record of hydrologic data available at Site 3 in Tonawanda Creek (c) and RKM 98 in French Creek (d) [Colour figure can be viewed at wileyonlinelibrary.com]

summer of 2016 (Figure 1b; RKM 93 was also resurveyed during 2017). The sites, and their numbers, were selected on the basis of high species diversity and mussel abundance as previously documented in each stream (Marangelo & Strayer, 2000; Smith & Crabtree, 2010). All sites were a minimum of 2 km upstream or downstream from the next nearest mussel bed. Qualitative assessments consisted of a timed-visual mussel survey to document species richness and catch-per-unit-effort (CPUE) values (Smith, Villegas, & Lemarie, 2001). Visual surveys were conducted throughout 2016 and 2017 during low flows via mask and snorkel and followed similar protocols and effort outlined in Marangelo and Strayer (2000) and Smith and Crabtree (2010). While almost all mussels observed were visible at the surface, observers occasionally brushed away or lightly probed sediment during each search. On average, site reaches were limited to ~100 m in length with a minimum effort of one person-

hour (Table 2; Strayer, Claypool, & Sprague, 1997; Vaughn, Taylor, & Eberhard, 1997).

More detailed quantitative surveys were also conducted at one site in each stream (Site 3 in Tonawanda Creek; RKM 98 in French Creek; Figure 1). Similar to the selection of the qualitative sites, the quantitative sites had high species diversity and mussel abundance reported in the previous surveys, and provided an accurate representation of the typical mussel-covered reaches within each stream. Quantitative assessments included a timed-visual mussel survey as well as (a) an excavated quadrat analysis (30, 0.25 m² quadrats excavated up to 0.15 m deep) to determine mussel density, (b) channel cross sections to generate bathymetry maps, (c) stream gaging using a hand-held FlowTracker ADV (SonTek, San Diego, CA, USA) and (d) a Wolman's pebble count (Wolman, 1954) to determine the surface texture of the channel bed. All quadrats

TABLE 2 Channel dimensions and grain size distribution for the sites surveyed in Tonawanda Creek, NY, and French Creek, PA

	Tonawanda Creek				French Creek				
	Site 1	Site 2	Site 3 ^a	Site 7	RKM 74	RKM 93	RKM 98 ^a	RKM 109	RKM 125
Length (m)	90	100	90	115	90	90	100	90	100
Mean Width (m)	15	12	13	9	27	24	22	20	18
D ₁₆ (mm)	3.4	1.7	0.4	0.6	7.7	3.6	3.0	1.0	0.9
D ₃₅ (mm)	6.5	6.6	1.5	1.2	20.1	7.8	7.6	6.5	3.1
D ₅₀ (mm)	10.5	11.3	3.8	1.9	28.5	10.7	11.7	10.0	7.5
D ₈₄ (mm)	56.9	39.8	28.9	12.0	61.1	30.7	49.8	43.1	28.5
D ₉₅ (mm)	97.2	79.6	81.3	28.9	90.0	52.6	84.8	64.0	81.3

Note. ^aSite 3 in Tonawanda Creek and RKM 98 in French Creek are the quantitative sites used for the modelling efforts and are displayed in Figures 2 and 3.

were georeferenced with a hand-held GPS (Garmin eTrex 20; Garmin, Olathe, KS, USA). The pebble count began at the downstream end of the study site and proceeded upstream in a zigzag pattern until reaching the upstream end. A minimum of 100 pebbles were measured at each site. The quantitative surveys were conducted throughout 2016 and 2017, also during low flow conditions. Species richness (live and total), abundance and CPUE data were grouped by site within each stream, and differences between survey years were compared using a Wilcoxon signed-rank test (V statistic) to test the null hypothesis that mussel communities (i.e. mussel richness, abundance, CPUE) were not significantly different between survey years (using $p < 0.05$).

At each quantitative site, a flow frequency analysis was conducted using the maximum daily flow rate from the closest downstream USGS gage station. For Tonawanda Creek, 38 years (1979–2017) of data were obtained at Rapids, NY (USGS gage 04218000). For French Creek, 29 years (1988–2017) of data were obtained at Meadville, PA (USGS gage 03023100). To account for hydrologic differences between the quantitative sites and downstream gaging stations, the flow frequency analysis was empirically corrected for upstream drainage area by determining the proportion of catchment area at the respective gaging station.

Flow and sediment transport were simulated at the quantitative sites using the International River Interface Cooperative (iRIC) Nays2DH solver, a two-dimensional depth-averaged numerical model (Nelson et al., 2016). Nays2DH solves the depth-averaged momentum equations, and model inputs include discharge, topography, Manning's roughness coefficient and downstream water surface elevation.

Hydrodynamic models without sediment transport were first calibrated by adjusting Manning's roughness coefficient n to match measured flow depth and flow velocity from one stream-gaging activity (Tonawanda Creek discharge of 1.1 m³/s; French Creek discharge of 3.5 m³/s). Initial selection of Manning's n was estimated as $n = 0.062d_{50}^{1/6}$ (Chow, 1959; d_{50} is the median grain size of the bed) and subsequently adjusted as needed. Calibrated models were

obtained by adjusting Manning's n to 0.04 for Tonawanda Creek and 0.055 for French Creek to minimise the mean absolute error of linear regressions between observed and predicted depth and velocity measurements (Figure 2b, c, respectively; Supporting Information Table SI-1). Similarly, models were subsequently validated for separate flow events (Tonawanda Creek discharge of 2.3 m³/s; French Creek discharge of 3.0 m³/s) that were also measured with the stream-gaging activities (Figure 2a, d, respectively; Supporting Information Table SI-1). Once validated, sediment transport was simulated for two constant discharges at each site: base-flow and bankfull conditions. The former was simulated to aid in further validating the model by comparing the predicted hydrodynamic variables with sediment transport to our stream-gaging measurements. When sediment transport was activated for the base-flow conditions, the predicted hydrodynamic results were unchanged and bedload transport was minimal, as expected. Bankfull condition was simulated to estimate bedload transport rates at the channel-forming discharge.

Bedload transport was modelled in Nays2DH using the Ashida–Michiue formula for each grain size with a heterogeneous bed (Ashida & Michiue, 1972). A computational mesh maintained a 2:1 (streamwise:cross-stream) aspect ratio with grid discretisation approximately 1.0:0.5 m. A k - ϵ turbulence model was selected for turbulence closure. The downstream boundary flow condition used a constant water surface elevation derived from the stage–discharge relationship and the upstream boundary condition assumed uniform and steady flow calculated from the bathymetry data. Sediment transport was initiated after the hydrodynamics reached steady state (around 200 s). The time step of calculation was 0.01 s, and the maximum number of iterations for water surface computation was 20. All simulations were run until hydrodynamics and sediment transport reached steady state (c. 1,000 s). The spatial distribution of mussels within each quantitative site was statistically compared to the simulated bedload transport during the bankfull flow event using a linear regression analysis. Simulated transport rates within a one metre diameter around the excavated quadrats were averaged and regressed on mussel density within the respective quadrat to

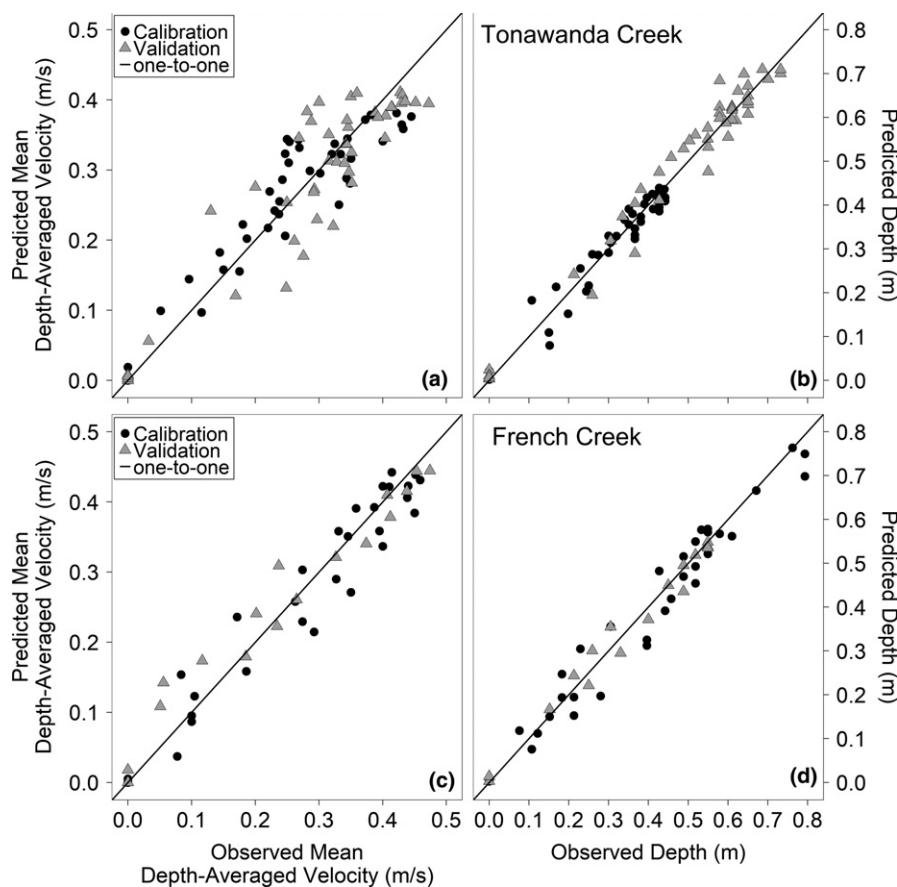


FIGURE 2 Model calibration and validation for mean depth-averaged velocity (m/s) and water depth (m) in Tonawanda Creek (a and b, respectively) and French Creek (c and d, respectively). The solid line on each panel represents the one-to-one expected performance. All regression analyses between the observed and predicted values were significant and had $r^2 > 0.97$ (Supporting Information Table SI-1). Mean error associated with the observed velocity and observed depth measurements were 0.05 m/s and 0.02 m in both Tonawanda Creek and French Creek, respectively

determine whether mussels exhibited a spatial preference in regard to transport rate.

3 | RESULTS

In Tonawanda Creek, a total of 958 mussels from 21 species (17 live species) were observed in the qualitative surveys (Table 3). CPUE ranged from 104 to 391 mussels/p-hr (median = 243 mussels/p-hr). At the quantitative site in Tonawanda Creek, 165 mussels from 13 species were observed in the quadrat analysis. Mussel density ranged from 0 to 56 mussels/m² (median = 12 mussels/m²; Figure 3a). In French Creek, a total of 1,445 mussels from 21 species (18 live species) were observed in the qualitative mussel surveys (Table 3). CPUE ranged from 58 to 191 mussels/p-hr (median = 160 mussels/p-hr). At the quantitative site in French Creek, 203 mussels from 17 species were observed in the quadrat analysis. Mussel density ranged from 0 to 108 mussels/m² (median = 26 mussels/m²; Figure 3b).

Despite a span of nearly 20 years between the mussel surveys, mussel diversity and abundance at specific locations in Tonawanda Creek and French Creek have remained relatively unchanged in time (Table 3). Mean abundance, mean species richness and CPUE were statistically similar for the two surveys in both streams (Tonawanda Creek—species richness, live: $V = 0$, $p = 0.10$; species richness, total: $V = 4.5$, $p = 0.59$; abundance: $V = 0$, $p = 0.13$; CPUE: $V = 0$,

$p = 0.13$; French Creek—species richness, live: $V = 15$, $p = 0.06$; species richness, total: $V = 10$, $p = 0.10$; abundance: $V = 15$, $p = 0.06$; CPUE: $V = 0$, $p = 0.06$).

Bankfull discharges of 67 and 113 m³/s, corresponding to a return interval of 1.8 and 1.4 years for Tonawanda Creek and French Creek, respectively, were calculated from the Log-Pearson Type III flow frequency analysis and used as the discharge boundary conditions. In Tonawanda Creek, the mean bedload transport for this flow was 116.9 cm³/s (0–3,621 cm³/s) and 90% of the bed area was mobile for the bankfull flow condition (Figure 3a). While 10% of the bed remained immobile, no mussels were found in these locations during the visual survey or quadrat analysis. In French Creek, the mean bedload transport for this flow was 223.6 cm³/s (0–1,139.6 cm³/s) and 92% of the bed area was mobile for the bankfull flow condition (Figure 3b). Likewise, no mussels were found within the 8% of the bed that remained immobile. The spatial patterns of mussel density showed no statistical relation to variation in relative bedload transport rate (Tonawanda Creek: $df = 34$, $F = 0.48$, $p = 0.49$, Figure 3a; French Creek: $df = 25$, $F = 3.15$, $p = 0.09$, Figure 3b). Based on a probability density function, mussels were not generally found within the portions of the stream with the highest bedload transport, but nearly all of the excavated quadrats in Tonawanda Creek and French Creek were located in areas of the stream bed that were mobile during bankfull conditions and would remain within the active channel during base-flow conditions.

TABLE 3 Mussel abundance and species richness from the qualitative surveys conducted in Tonawanda Creek from 1998 (Marangelo & Strayer, 2000) and French Creek from 2003 (Smith & Crabtree, 2010) compared to the current study (2016–2017). D = recent spent shell; d = old spent shell

Tonawanda Creek species abundance	French Creek species abundance										RKM 93		RKM 98		RKM 109		RKM 125		
	Site 1		Site 2		Site 3		Site 7		RKM 74		RKM 93		RKM 98		RKM 109		RKM 125		
	1998	2016	1998	2016	1998	2016	2003	2016	2003	2017	2003	2016	2003	2016	2003	2016	2003	2016	
<i>Actinonaias ligamentina</i>																			
<i>Alasmidonta marginata</i>	0	2	0	3	1	3	d	0	35	2	8	d	21	3	24	2	11	0	
<i>Alasmidonta viridis</i>					d	0													
<i>Ambloia plicata</i>	13	69	26	36	>133	210					2	2	2	3	1	3			
<i>Anodontoides fenusacianus</i>							10	7	3	0			2	0	1	D			
<i>Elliptio dilatata</i>	1	2	2	150	d	0			68	16	15	3	31	12	1	4	55	31	
<i>Epioblasma torulosa rangiana</i>									184	97	D	D	D	0					
<i>Epioblasma triquetra</i>	d	0			d	0			6	2	3	d	D	2	1	2	20	1	
<i>Fusconaia flava</i>	d	2	4	9	6	7													
<i>Fusconaia subrotunda</i>									1	2	6	4	14	5	2	0	0	1	
<i>Lampsilis fasciata</i>					0	D			0	4					21	4	1	0	
<i>Lampsilis ovata^a</i>	2	3	4	15	>57	82			26	4	15	2	14	5	15	15	3	9	
<i>Lampsilis siliquoidea</i>	2	8	41	17	6	11	20	166	3	3	2	0	2	0	4	3	79	27	
<i>Lasmigona compressa</i>	D	1	3	1	1	0	1	5	1	1	1	0	1	0	1	1	1	1	
<i>Lasmigona costata</i>	11	2	18	9	7	3			27	8	1	1	1	1	27	8	29	22	
<i>Leptodea fragilis</i>	2	0	6	0	2	0													
<i>Ligumia recta</i>	d	9	4	23	22	32			3	0		1	1	0	4	5	8	0	
<i>Pleurobema clava</i>															0	3	D		
<i>Pleurobema sintoxia</i>					0	1			1	3	5	0	5	4	4	2	12	6	
<i>Potamilus alatus</i>					0	1	0	1											
<i>Ptychobranchus fasciolaris</i>	1	10	d	9	2	15			36	20	35	26	35	64	70	60	202	88	
<i>Pyganodon grandis</i>	1	D	2	5	1	4	0	3			6	1	2	2	4	2	7	1	0
<i>Quadrula cylindrica</i>											37	3	4	0	4	0	2	0	
<i>Strophitus undulatus</i>	D	1	1	9	1	1	0	7											
<i>Truncilla truncata</i>					3	1													
<i>Villosa fabalis</i>	D	1	2	0	D	1					30	1	17	D	17	2	7	D	0
<i>Villosa iris</i>																			
Unidentified/Juvenile	1	1							0	4						1	0		
Live Species Richness	8	12	13	14	12	13	3	5	17	16	9	16	13	18	13	12	11		
Total Species Richness	14	13	14	14	16	14	4	5	17	16	17	13	18	18	18	16	12	12	
CPUE (mussels/p-hr)	15	104	37	298	47	391	23	188	189	191	57	58	119	169	57	126	103	160	

Note. ^aSmith and Crabtree (2010) also reported abundance data for *L. cardium*, a mussel similar in morphology to *L. ovata*. Due to the convoluted taxonomy between *L. cardium* and *L. ovata* (Parmalee & Bogan, 1998), only *L. ovata* was used in this study. For the purpose of this comparison, *L. cardium* abundance data reported in Smith and Crabtree (2010) were grouped with *L. ovata* and species richness was adjusted accordingly.

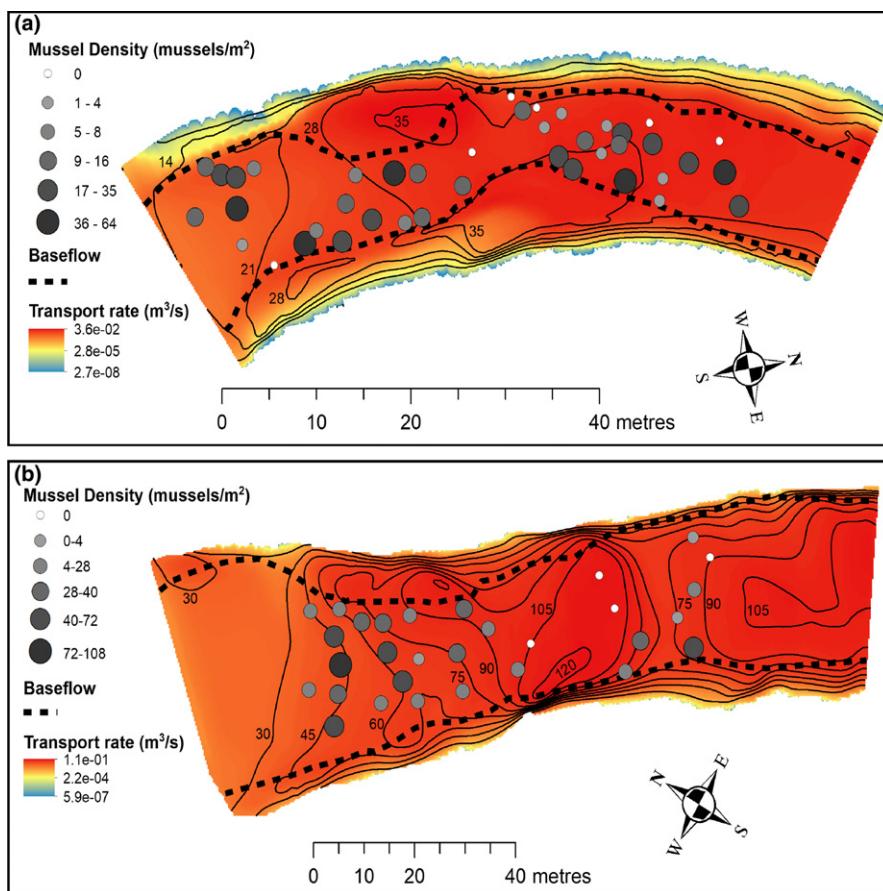


FIGURE 3 Bedload transport (m^3/s ; heat map) and bed shear stress (Pa; contour lines) at bankfull conditions in Tonawanda Creek (a) and French Creek (b). Mussel densities determined from the quadrat surveys during 2016 were limited to the extent of the base-flow condition, indicated by the dashed line, and are represented with graduated symbols for each stream [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

We found that aggregations of mussels, or mussel beds, remained in the same stream locations and had similar mussel abundance and community composition over a 20-year time span. In other words, mussel beds persisted in space, in time and in kind. Moreover, typical environmental drivers of change, such as hydrologic variability, land use/land cover and other anthropogenic activities, while not quantified here, appear to have had little effect on these mussel communities over the past two decades. Other studies have also documented mussel bed persistence over long periods of time from both small streams and rivers (Vaughn, 2000) to large rivers such as the Mississippi (Ries, De Jager, Zigler, & Newton, 2016).

We also effectively demonstrate that the bed sediments in which mussels live in these two streams are mobilised during bankfull flow events with recurrence intervals of <2 years. The frequency of sediment mobility predicted by the model is consistent with the concept of channel-forming discharge events in labile river channels (Church, 2006). Further, the results of the flow frequency analysis demonstrate that bankfull flow events in each stream are numerous and recurred frequently for the historical record of flow (Figure 1c, d). As a result, mussels in Tonawanda Creek and French Creek have often experienced significantly large flow events that mobilised almost the entirety of the stream bed. Moreover, mussel density in Tonawanda Creek showed no variation to local bedload transport rates at

bankfull flow events, while only a weak and negative, but not significant, correlation was observed in French Creek. This suggests additional forces other than long-term sediment stability are important to mussel bed persistence in these two streams.

The mussel beds we sampled have persisted for more than two decades at the same river reach in Tonawanda Creek and French Creek. Despite low statistical power to compare mussel richness, abundance and effort for the Wilcoxon tests (min = 0.09, mean = 0.47, max = 0.98), a high percentage of species were observed in both temporal surveys in each stream. Additionally, because mussels are long-lived and relatively sedentary, it is probable that many individuals we sampled have also persisted within the same river reach despite experiencing multiple flow events capable of mobilising much of the stream bed. Verifying this would require mark-recapture of tagged individual mussels. While we do not have such data for this system, Vaughn (unpublished data) has consistently recaptured tagged individual mussels within metres of their release point in the Kiamichi and Little rivers in Oklahoma, some over more than 20 years. Further, it is unlikely that adult mussels moved from one mussel bed to another in this system. The sites sampled in Tonawanda Creek and French Creek were a minimum of 2 km from the next nearest mussel bed, and mussel mortality may be considerable if mussels become dislodged during high flow events and fail to re-establish in suitable habitat (Fraley & Simmons, 2006; Haag, 2012; Hastie et al., 2001). While dislodged mussels have been shown to

successfully re-establish and create new mussel beds if suitable habitat is present (Hastie et al., 2001), no new mussel beds have been observed in Tonawanda Creek since 2014 (Sansom, personal observation) despite multiple bankfull flow events. Any emigration or immigration from one mussel bed to another would most likely occur by larvae attached to fish hosts or by drifting juveniles (Vaughn, 2012). These events are relatively rare (Vaughn, 2000) and cannot explain the persistence of mussel beds that we observed.

The primary issue here is defining the mechanism by which adult mussels can repeatedly withstand flow events capable of mobilising the sediments in which they live, thus allowing the persistence of mussel beds for decades or more. Although mussels may move horizontally across or vertically into the substrate, such movement is limited in time and space (cm/hr vertically and cm/day horizontally; Schwalb & Pusch, 2007; Allen & Vaughn, 2009; Kappes & Haase, 2012). While mussels can burrow as deep as 0.3 m, most mussels are found at modest depths ranging from 0.05 to 0.1 m (Schwalb & Pusch, 2007). The active layer thickness, or the effective thickness of the moving bed layer during a sediment transport event, depends on transport stage. The active layer thickness can be estimated as a function of grain size (Parker, 2008; van Niekerk, Vogel, Slingerland, & Bridge, 1992) or bedform height or flow depth (Armanini & Di Silvio, 1988; Langendoen, 2000; Rahuel, Holly, Chollet, Belleudy, & Yang, 1989). In Tonawanda Creek and French Creek, for example, the mean (maximum) thickness of the active layer as a function of grain size is 5.3 (15.9) and 13.1 (35.1) cm, respectively (van Niekerk et al., 1992). Similarly, as a function of flow depth, the mean (maximum) thickness of the active layer in Tonawanda Creek and French Creek is 14.1 (26.1) and 14.1 (27.5) cm, respectively (Langendoen, 2000). As such, the bed-mobilising hydrologic events are likely to have shorter timescales and larger length-scales than those for mussel reaction, movement and burrowing depth. Moreover, it also seems likely that many of the river reaches with long-term records of mussel assemblages, summarised in Table 1, are labile river channels, experiencing relatively frequent hydrologic events with significant sediment transport and bed mobility.

Many field studies and modelling exercises have suggested that mussels are found in stream areas where sediments are stable, and in particular where shear stresses are relatively low during high flow events (Allen & Vaughn, 2010; Gangloff & Feminella, 2007; Howard & Cuffey, 2003; May & Pryor, 2016; Morales, Weber, Mynett, & Newton, 2006; Steuer, Newton, & Zigler, 2008; Vannote & Minshall, 1982; Zigler, Newton, Steuer, Bartsch, & Sauer, 2008). While it is likely that mussels occupy stream areas that are relatively more stable (i.e. riffles and runs composed of gravel-sized substrate; Bey & Sullivan, 2015; Clifford & Richards, 1992; Macwilliams, Wheaton, Pasternack, Street, & Kitanidis, 2006; Parmalee & Bogan, 1998), our results indicate that even these areas do not remain immobile for decades at a time and that the flow refugia hypothesis (Strayer et al., 2004) alone cannot explain the long-term persistence of mussel beds at-a-station. It is clear that mussels have adapted to live in such dynamic environment, but the mechanisms enabling such persistence are not known.

Strayer et al. (2004) synthesised possible mechanisms that could affect the local occurrence of mussel communities and recognised that shear stress and sediment stability may only provide a partial explanation. Additional mechanisms include complex interactions between host fish distribution, food quality and quantity, well-oxygenated sediments for juvenile establishment, refuge from predators, negative mechanisms (e.g. downstream washout, burial, starvation) and positive mechanisms (e.g. high fecundity in favourable habitats or habitat selection by juveniles (Strayer et al., 2004). These mechanisms, however, do not adequately explain the ability of mussels to persist in chronically unstable environments.

Rather than long-term immobility of channel substrates, an alternative hypothesis is that mussels may actively engineer their habitat to enhance anchoring abilities and to increase local bed stability through biologically mediated activity. For example, Di Maio and Corkum (1997) found that mussels in a hydrologically variable river were oriented more parallel to the flow than mussels in a hydrologically stable river. Burrowing activity can increase sediment compaction and local stability (Zimmerman & De Szalay, 2007), and dense assemblages of adult mussels may stabilise sediments (Strayer et al., 2004; Vaughn & Spooner, 2006). Mussels with thin, slender shells can burrow more rapidly and to greater depths (Stanley, 1981; Watters, 1994), whereas shells with ridges and other ornaments can increase or decrease mussel-anchoring potential (Levine, Hansen, & Gerald, 2014; Watters, 1994) or reduce scour around exposed shell material (Stanley, 1981). Vannote and Minshall (1982) found that in the Salmon River, Idaho, *Margaritifera falcata* was restricted to areas behind boulders, whereas *Gonidea angulata*, with well-formed distal inhalant and exhalant siphons and a strong angular and wedge-shaped shell, appears adapted for aggrading areas. Dense, multi-species assemblages of mussels with different shell morphology also can provide vertical niche partitioning that might help avoid dislodgment during high flows (Allen & Vaughn, 2009). This brief summary suggests that the complex interactions between shell size, shape and sculpture, burrow behaviour, anchor potential and bed composition need further examination.

While there is ample evidence for long-term persistence of mussel assemblages throughout the United States, the implications of mussel persistence in labile channels in this study are limited to the recent past. There are only 38 and 29 years of hydrologic data and 20 and 15 years of mussel assemblage data in Tonawanda Creek and French Creek, respectively. It is well known that anthropogenic activities such as agriculture, urbanisation and reservoir impoundments have significantly altered the magnitude of sediment transport in rivers, the form of river channels and the delivery of this sediment to the oceans, and these altered hydrologic and geomorphic processes would greatly impact aquatic ecology (Knox, 2006; Merritts et al., 2011; Poff, Bledsoe, & Cuhacian, 2006; Syvitski, Vorusmarty, Kettner, & Green, 2005; Wilkinson & McElroy, 2007; Wolman & Schick, 1967). Such long-term trends, as well any short-term perturbations, are not captured in our data set. Therefore, the results of our model, and future modelling efforts, are limited to the context of modern sediment regimes. Events responsible for excessive sediment

yields (e.g. dam removal, urbanisation and other land cover/land use changes) should be considered on a case-by-case situation. Modelling efforts similar to ours, however, are important to understand the occurrence, frequency and magnitude of sediment transport events in rivers where mussels live, and to enhance the understanding of mussel distribution throughout stream ecosystems.

A physically robust explanation for the persistence of mussel location and biodiversity with time remains unresolved. We contend that mussels have adapted to proliferate in labile river channels with hydrologic events known to fully mobilise bed sediments. That is, self-formed rivers with labile beds are common in nature (Church, 2006), and the long-term success and proliferation of mussels should not depend upon exceptions to this rule, as evidenced by their widespread occurrence and persistence (Table 1). Studies investigating the interaction between biologically mediated activity and morphological adaptations are necessary to provide a better understanding of the biophysical mechanisms enabling the persistence of long-term mussel biodiversity, which will measurably enhance conservation and management efforts.

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SUPPORTING INFORMATION

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