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MICROHABITAT USE BY FRESHWATER MUSSELS AND RECOMMENDATIONS FOR DETERMINING THEIR INSTREAM FLOW NEEDS

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ABSTRACT

A conventional application of the instream flow incremental methodology (IFIM) assumes that target organisms have specific microhabitat preferences and the ability to move to areas of suitable hydraulic conditions in response to changes in stream discharge. We investigated the use of the IFIM for determining the instream flow needs of a diverse mussel assemblage in Horse Lick Creek, a fourth-order stream in the upper Cumberland River drainage in Kentucky. We determined habitat availability by measuring water depth, velocity and substrate at 60 cm intervals along 23 transects during low, medium and high flows. The distribution of mussels within the study site was highly contagious. Although habitat suitability curves developed from data collected on 2004 mussels indicated a clear preference for particular hydraulic conditions, the limited mobility of mussels in the coarse substrate of Horse Lick Creek implies that these curves are flow-conditional—that is, mussels appear to prefer different hydraulic conditions at different stream discharges. Consequently, these curves are of limited value for determining conservation flows for mussels. Nonetheless, water depth and velocity were important factors limiting the distribution of mussels during base flow periods. Similarly, substrate characteristics were of limited value in defining mussel distributions; unfractured bedrock excluded mussels from portions of the study site, but mussels did not utilize all areas with preferred substrate. Because the larvae (glochidia) of mussels in Horse Lick Creek are obligate parasites on fish, data were also collected on habitat preferences of the host fishes. These data were incorporated in the physical habitat simulation system (PHABSIM) to determine the relationship between the availability of host fish habitat and stream discharge during periods of glochidia release and juvenile settlement.

Unlike simple hydraulic variables, complex hydraulic characteristics such as shear stress were significantly correlated with mussel abundance for flows ranging from 0·03 to 2·18 m³ s⁻¹. This range encompasses most flows during the period of juvenile settlement. We suggest that the high shear stress in some portions of the study site is a major factor limiting mussel recruitment. The lack of a significant correlation between mussel abundance and shear stress at high flow (9·35 m³ s⁻¹) resulted from a variable relationship between shear stress and discharge among transects due to channel morphology. The higher shear stresses at most transects over mussel beds during a discharge of 9·35 m³ s⁻¹ suggests that spates occurring during or shortly after juvenile settlement may result in a loss of juveniles.

The unique life history and limited mobility of mussels necessitates a more complicated procedure than generally used for fish and other macroinvertebrates for determining conservation flows. Specifically, we recommend an approach that incorporates concepts of hydraulic stream ecology with the more common practice of modelling only simple hydraulic variables in habitat simulations. Estimating the complex hydraulic key characteristics can be performed with minimal effort through the selection of appropriate subroutines with PHABSIM. This approach may also be suitable for simulating habitat of other sessile organisms.

KEY WORDS: mussels; habitat; IFIM; hydraulic stream ecology; instream flows; mussel hosts

INTRODUCTION

Water development projects in the south-eastern USA have severely impacted freshwater mussel populations. For instance, construction and operation of the Center Hill Dam were directly responsible for the extirpation of at least 25 of the 60 species known from the Caney Fork River drainage (Layzer *et al.*, 1993). Dams affect mussels by inundating riverine habitat, eliminating host fish populations, changing water quality (including temperature regimes) and altering the daily and seasonal hydrographs. Despite the historically abundant and diverse mussel fauna in the USA little is known about the physical habitat necessary to maintain mussel populations. Nonetheless, habitat degradation is the most commonly cited

cause of the extirpation and extinction of mussels (Havlik, 1981; Layzer *et al.*, 1993). Consequently, identifying the habitat requirements of endangered mussels is a top priority of most recovery plans developed for endangered species (e.g. US Fish and Wildlife Service, 1989). Moreover, because of the construction of new dams and water diversions, there is an urgent need for determining how altered flow regimes affect mussel habitats.

The instream flow incremental methodology (IFIM) has been widely used to evaluate flow-related changes in fish habitat, but it has not been applied for assessing such changes in mussel habitat. Detailed information on the use of microhabitats is requisite to applying the physical habitat simulation (PHABSIM) component of IFIM. Numerous accounts of the habitat preferences of mussels appear in published work (e.g. Ortmann, 1919; Baker, 1928; Sickle, 1980); however, most of these preferences are based on qualitative observations. Furthermore, the preferences of many species seem to be site-specific and within-site preferences are similar among species (Strayer, 1981). Nevertheless, some species such as the spectaclecase (*Cumberlandia monodonta*) have very specific and consistent habitat preferences or requirements among streams (Stansberry, 1966). Also, under experimental conditions, some mussel species do show a preference for substrate type (Huehner, 1987; Bailey, 1989).

Habitats occupied by adults may reflect ontogenetic or seasonal requirements. Isely (1911) indicated that adult mussels are most abundant in the vicinity of, but not necessarily in, habitats optimal for the survival of juveniles. If so, typical measurements of the depth, velocity and substrate used by adults may be largely irrelevant to understanding the habitat requirements of juvenile mussels and the process of recruitment to existing beds. Moreover, because mussels are relatively sedentary components of the stream benthos (Isely, 1914; Matteson, 1955; Strayer, 1981), the timing of when habitat measurements are made may be crucial to understanding the habitat requirements of adults.

Larvae of most North American mussels are obligate parasites on fish. Thus recruitment to a localized mussel bed is dependent on the movements and habitats of their host fish. Cvancara (1970) suggested that fish hosts were a major factor in determining the distribution of mussels. Newly metamorphosed juveniles excysting from their host cannot control where they will settle. Coker *et al.* (1921) believed that the time of excystment was a critical period in the life history of mussels because juveniles may settle in unfavourable habitats or spates would dislodge others. Holland-Bartels (1990) suggested that high water velocities might displace settling juveniles before they can burrow or attach bissal threads to the substratum and, therefore, adult mussel distributions may reflect juvenile tolerances to current.

The stability of the substratum has often been suggested as an important factor in determining suitable mussel habitat (Parmalee, 1967; Cvancara, 1983; Strayer and Ralley, 1991). Stream channel degradation and aggradation below hydroelectric peaking projects have devastated mussel populations (Miller *et al.*, 1984; Layzer *et al.*, 1993). Mussel beds in highly stable, localized areas may be major centres for the dispersal and subsequent recruitment of other stream sections (Vannote and Minshall, 1982). Streambed scouring also appears to be a major cause of the failure of mussel reintroductions (Layzer and Gordon, 1993). In this paper, we examine how mussels are distributed with respect to simple hydraulic variables, host fish abundance, the available habitat of host fishes and complex hydraulic characteristics.

MATERIALS AND METHODS

Site description

Horse Lick Creek is a fourth-order tributary of the Rockcastle River in the upper Cumberland River drainage, Kentucky. The creek is unregulated and much of the catchment, including our study site, lies within a remote area of the Daniel Boone National Forest. Strip mining of coal in the lower catchment has impacted mussels; however, our study site was located several kilometers upstream of the degraded stream section (Layzer and Anderson, 1992).

Although there is no gauging station on Horse Lick Creek, the discharge is greatest in the winter and lowest in late summer, with an annual hydrograph typical of streams in this region. Daily discharge is highly variable because the deeply incised valley and limited floodplain result in rapid storm runoff.

Field measurements

Twenty-three permanent transects were established within the 230 m long study site. Transects were located across all hydraulic controls and all major habitat types (pools, riffles, runs), as well as transitional areas. The distances between transects varied from 6 to 25 m and depended on our perception of often relatively minor changes in channel morphology and hydraulic conditions. We used an unusually large number of transects to minimize the longitudinal extrapolation of measured and modelled hydraulic characteristics. Streambed elevations along each transect were surveyed to the nearest 3 mm and referenced to a common datum by the techniques described in Bovee and Milhous (1978). We measured the mean water column velocity and depth and recorded substrate type at intervals of 60 cm across each transect. The two most dominant substrate particle sizes (based on streambed coverage) were classified according to the following criteria; silt (<0·1 mm), sand (0·1–2 mm), gravel (3–75 mm), cobble (75–250 mm), boulder (>250 mm) and bedrock. These measurements and water surface elevations were taken at all transects for discharges of 0·03, 1·22, 2·18 and 9·35 m^3 s^{-1}. Additionally, one or more transects were gauged and water surface elevations determined at discharges of 0·06, 2·86 and 5·71 m^3 s^{-1}. Slope was calculated as the difference in water surface elevations of adjacent transects divided by the distance. We assigned a slope of 0·0001 when no measurable difference in water surfaces occurred.

Mussels were located by visually searching the entire study site. We used glass-bottom viewing buckets while wading in shallow areas and used snorkelling and scuba equipment to search deeper habitats. The location of each mussel was marked with a wire surveying flag; later, mussels were identified and measured. Water depth, velocity, substrate, study site segment (represented by a transect) and distance from the left ascending bank were measured. Over a six-day period, 30 person-days were expended to thoroughly search the entire site and record measurements.

Data analysis

Water surface elevations for each transect were determined from a combination of measured stage–discharge relationships and values predicted by the MANSQ subroutine of PHABSIM for flows ranging from 0·51 to 2·18 m^3 s^{-1}. Velocities in each cell for the simulated discharges were predicted by the IFG4 hydraulic model. Based on personal observations and substrate characteristics, we believe that the adult mussels moved little during the course of our study. Therefore, even though hydraulic conditions were modelled for entire cross-sections, only the predicted values for those cells wet at a discharge of 0·03 m^3 s^{-1} were used in developing frequency distributions of habitat availability and habitat use for mussels.

To determine the degree of similarity in microhabitat usage between pairs of species, we calculated proportional overlap values (Schoener, 1968):

$$O = 1 - 0.5 \sum_i^n |p_{ia} - p_{ib}|$$

where p_{ia} is the proportional use of microhabitat category i used by species a, and p_{ib} is the proportional use by species b.

Formulae in Statzner *et al.* (1988) were used to calculate Reynolds number (Re), shear stress (τ) and stream power per channel area (P_a) for each segment at a water temperature of 20°C. Froude number (Fr), mean water depth and velocity and stream width were obtained from the production run of MANSQ for measured and simulated discharges.

RESULTS

Abundance and spatial distribution

A total of 2004 mussels of 17 species, including the endangered *Pegias fabula* and *Villosa trabalis*, were collected (Table I). The mussel assemblage was dominated by *Elliptio dilatata*, *Medionidus conradicus* and

Table I. Numbers of each mussel species collected in each segment of the study site on Horse Lick Creek

Species																								Segment																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total
AL	1																							2
AM												1							1					5
AV	1	4				1			2							2	1	3	2	2				28
ED	7	24	23	9	9	37	10			1	2	18	85	68	74	119	72	67	82	46				763
LC	5	2	7	3		2	2				1		1	2	5	11	9	12	20	24	8			110
LF	2	3	4		2	2		1	1					1	1	2	5	3		2	5			30
LM	1		3	4	1								2	1	3	4	3	3	6	2				31
MC	8	3	18	3	9	19	5		3		1	13	44	35	40	85	40	29	25	40	1			422
PF		1				2			1				6	9	7	8	1	2	4			1		41
PO														1										3
PS								1								1		1						1
PY		1	7	2	1	2	1						6		5	6	8	9	7	10			1	67
SU																	1	1	1					3
TL																1	1			1				3
VI		4			1	1						1	6	6	9	12	7		7	2	1			56
VR		1														2	1			3			1	8
VT	9	15	11	6	7	21	6	1	3	1		10	37	31	49	84	38	38	34	28	3	1	1	431
All	33	58	74	27	29	87	24	2	10	1	4	43	187	154	200	343	190	169	189	160	18	1	1	2004
Area (m²)	97	486	217	145	105	128	77	76	138	84	156	202	67	41	75	94	67	37	84	68	316	90	40	2890

AL = *Actinonaias ligamentina*; AM = *Alasmidonta marginata*; AV = *Alasmidonta viridis*; ED = *Elliptio dilatata*; LC = *Lasmigona costata*; LF = *Lampsilis fasciola*; LM = *Lampsilis cardium*; MC = *Medionidus conradicus*; PF = *Pegias fabula*; PO = *Pleurobema oviforme*; PS = *Ptychobranchus subtentum*; PY = *Ptychobranchus fasciolaris*; SU = *Strophitus undulatus*; TL = *Toxolasma lividus*; VI = *Villosa iris*; VR = *Villosa trabalis*; VT = *Villosa taeniata*.

FRESHWATER MUSSELS   333

Table II. Product moment correlations between abundances of each species in each segment. (Only significant ($p < 0.05$) correlations are given (n.s. = not significant)

Species	ED	LC	LF	LM	MC	PF	PY	VI	VR	VT	All mussels
AV	0·67	0·44	n.s.	0·52	0·65	0·52	0·50	0·75	n.s.	0·78	0·72
ED		0·54	0·42	0·62	0·93	0·82	0·70	0·88	0·47	0·96	0·98
LC			n.s.	0·71	0·52	n.s.	0·81	n.s.	0·70	0·52	0·60
LF				n.s.	0·45	n.s.	0·60	n.s.	n.s.	0·43	0·45
LM					0·54	n.s.	0·69	0·54	n.s.	0·60	0·65
MC						0·76	0·68	0·84	0·64	0·97	0·97
PF							n.s.	0·83	n.s.	0·79	0·78
PY								0·47	0·65	0·66	0·74
VI									n.s.	0·88	0·88
VR										0·56	0·58
VT											0·99

AV = *Alasmidonta viridis*; ED = *Elliptio dilatata*; LC = *Lasmigona costata*; LF = *Lampsilis fasciola*; LM = *Lampsilis cardium*; MC = *Medionidus conradicus*; PF = *Pegias fabula*; PY = *Ptychobranchus fasciolaris*; VI = *Villosa iris*; VR = *Villosa trabalis*; and VT = *Villosa taeniata*.

V. taeniata; together, these three species comprised 81% of all mussels collected. Seven species were represented by less than 10 individuals. The longitudinal distribution of mussels was not random; 79% of the mussels occurred in segments 13 to 20 and there was no significant correlation ($p > 0.20$) between the number of mussels and the area of each segment. There was no difference among the 10 most common species in their longitudinal distributions; the numbers of most species in each segment were positively correlated with each other (Table II). The distribution of mussels across the width of each segment varied from being highly contagious in segment 19 to more uniform in segment 16 (Figure 1).

Microhabitats of mussels

Overlap values for the use of depth between all pairs of common species indicated similar usage of depth (Table III). Consequently, frequency distributions of depths used by all species were combined (Figure 2A).
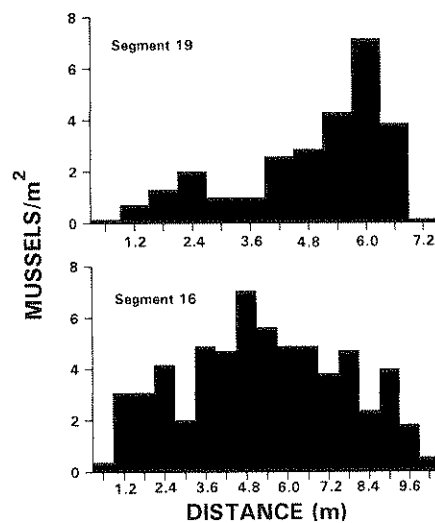

Figure 1. Density of mussels observed in two segments. Distance is from left ascending bank

Table III. Proportional overlap between pairs of most abundant ($n > 25$) species for use of depth at a discharge of $0.03\,\mathrm{m}^3\,\mathrm{s}^{-1}$

	ED	LC	LF	LM	MC	PF	PY	VI	VT	All species
AV	0.56	0.54	0.59	0.54	0.62	0.53	0.65	0.51	0.64	0.61
ED		0.75	0.63	0.73	0.89	0.72	0.77	0.65	0.86	0.93
LC			0.63	0.66	0.75	0.65	0.71	0.58	0.86	0.78
LF				0.62	0.68	0.62	0.61	0.59	0.72	0.71
LM					0.73	0.67	0.71	0.63	0.72	0.73
MC						0.70	0.83	0.63	0.90	0.93
PF							0.63	0.63	0.77	0.74
PY								0.58	0.87	0.80
VI									0.67	0.68
VT										0.91

AV = *Alasmidonta viridis*; ED = *Elliptio dilatata*; LC = *Lasmigona costata*; LF = *Lampsilis fasciola*; LM = *Lampsilis cardium*; MC = *Medionidus conradicus*; PF = *Pegias fabula*; PY = *Ptychobranchus fasciolaris*; VI = *Villosa iris*; and VT = *Villosa taeniata*.

The combined frequency distribution indicates a proportionally greater use of depths between 7 and 30 cm during base flow. Although this depth range occurred on only 44% of the study area, 72% of all mussels were found within this range during base flow. Depths >51 cm occurred over 22% of the study site, but only 3% of the mussels were found at these depths. However, if mussels did not move they all would occur at depths >51 cm during a discharge of $9.35\,\mathrm{m}^3\,\mathrm{s}^{-1}$ (Figure 2B). Suitability curves developed from these data are essentially non-overlapping (Figure 3).

At low discharge ($0.03\,\mathrm{m}^3\,\mathrm{s}^{-1}$), there was a limited range of velocities available; 91% of the study site had velocities $\leqslant 4\,\mathrm{cm\,s}^{-1}$ and the maximum velocity measured was $22\,\mathrm{cm\,s}^{-1}$. Most species occurred throughout the range of available velocities, but they tended to occur less frequently than expected in areas of no flow. Proportional overlap values between species indicated similar usage of available velocities (Table IV). The high overlap values between individual species for use of velocity and a composite use of velocity by all mussels indicate that the composite frequency distribution adequately describes use of velocity (Figure 4).

Disproportionate use of available velocities was evident at intermediate and at high discharges; 90% of all mussels occurred in velocities ranging from 71 to $150\,\mathrm{cm\,s}^{-1}$ even though only 54% of the study area that was wet at low flows had velocities within this range at a discharge of $9.35\,\mathrm{m}^3\,\mathrm{s}^{-1}$. The changes in the proportional use of velocities relative to availability result from the highly contagious distribution of mussels and differing rates of increase in velocities among individual cells as discharge increases. As in the case of water depth, suitability curves developed from these data would be non-overlapping.
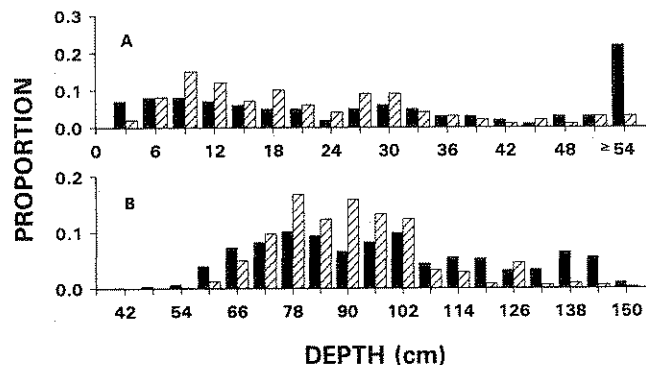

Figure 2. Proportional availability (solid bars) and use (hatched bars) of water depth by all mussels at a discharge of $0.03\,\mathrm{m}^3\,\mathrm{s}^{-1}$ (A) and at a discharge of $9.35\,\mathrm{m}^3\,\mathrm{s}^{-1}$ (B). Note difference in depth scale
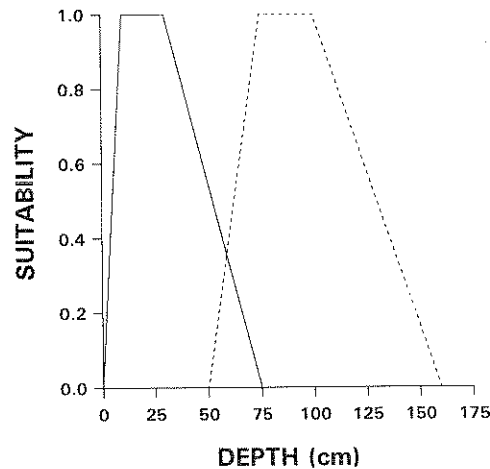
Figure 3. Preference curves of mussels for water depth at a discharge of 0·03 m³ s⁻¹ (solid line) and at a discharge of 9·35 m³ s⁻¹ (broken line)

Mussels used all sizes of substrate particles occurring on the study site; however, proportional use differed from availability (Table V). Although gravel comprised 13·7% of the area, 38·6% of all mussels occurred in gravel. Despite the disproportionately greater use of gravel, there was no significant correlation between mussel abundance and the amount of area covered by gravel in each segment. Unlike other species, few *Villosa iris* occurred in gravel, instead most *V. iris* were associated with cobble or boulders. In fact, nearly one-half of the *V. iris* were found under boulders or cobble. In contrast, only 2% of all other species were found under cobble- or boulder-sized particles. Overlap values for use of substrate were high among all species pairs, except for overlap between *V. iris* and other species (Table VI).

Complex hydraulic characteristics

Mussel densities were significantly correlated with several complex hydraulic key characteristics calculated for each segment at low flow (Table VII). Although the Froude number and Reynolds number were positively correlated with mussel densities at low flow, they were not correlated at higher stream discharges. In contrast, shear stress and stream power were negatively correlated with mussel densities for

Table IV. Proportional overlap between pairs of most abundant ($n > 25$) species for use of water velocity at a discharge of 0·03 m³ s⁻¹

	ED	LC	LF	LM	MC	PF	PY	VI	VT	All species
AV	0·73	0·75	0·75	0·84	0·83	0·72	0·85	0·77	0·86	0·80
ED		0·82	0·83	0·81	0·87	0·82	0·77	0·59	0·84	0·92
LC			0·84	0·87	0·86	0·74	0·81	0·62	0·79	0·87
LF				0·90	0·86	0·75	0·83	0·67	0·82	0·87
LM					0·89	0·74	0·85	0·70	0·86	0·81
MC						0·80	0·83	0·70	0·92	0·96
PF							0·72	0·57	0·75	0·80
PY								0·70	0·81	0·83
VI									0·75	0·67
VT										0·91

AV = *Alasmidonta viridis*; ED = *Elliptio dilatata*; LC = *Lasmigona costata*; LF = *Lampsilis fasciola*; LM = *Lampsilis cardium*; MC = *Medionidus conradicus*; PF = *Pegias fabula*; PY = *Ptychobranchus fasciolaris*; VI = *Villosa iris*; and VT = *Villosa taeniata*.

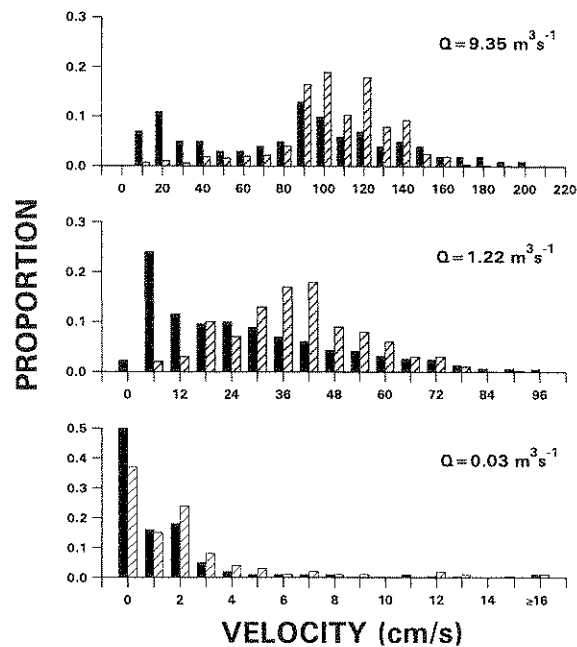J. B. LAYZER AND L. M. MADISON

Figure 4. Proportional availability (solid bars) and use (hatched bars) of mean water column velocities by all mussels at three discharges

stream discharges ranging from 0·03 to 2·18 m³ s⁻¹. Because these two complex hydraulic characteristics were highly correlated with each other at all discharges, only shear stress was analysed further. Values of shear stress determined at low discharge for each segment were highly correlated with shear stresses at all but the highest discharge (Table VIII).

Shear stress integrates depth and a velocity factor (product of g and s). If slopes remained constant and

Table V. Percentage composition of particle sizes and percentage usage by each species

Particle size category	Available	Species										All mussels
		AV	ED	LC	LF	LM	MC	PF	PY	VI	VT	
Silt	3·4	7·1	—	—	—	—	—	—	—	—	0·2	0·2
Sand	3·6	3·6	0·7	0·9	—	—	0·5	—	—	1·8	1·2	0·3
Sand–gravel	3·2	—	7·7	8·2	16·7	19·4	6·4	9·8	13·4	5·4	8·1	6·0
Sand-cobble	4·0	—	1·6	1·8	3·3	6·5	1·7	2·4	1·5	8·9	4·6	1·4
Sand–boulder	<0·1	7·1	0·1	0·9	3·3	—	1·7	—	—	14·3	3·7	2·0
Sand–bedrock	<0·1	—	—	—	—	—	1·0	—	—	—	0·2	0·1
Gravel	13·7	25·0	45·6	52·7	40·0	38·7	36·0	31·7	37·3	3·6	30·6	38·6
Gravel–cobble	36·7	32·1	33·0	27·3	26·7	32·3	32·0	43·9	31·4	19·7	28·1	31·1
Gravel–boulder	2·7	10·7	5·4	1·8	—	—	10·7	7·3	9·0	17·9	10·7	7·9
Gravel–bedrock	<0·1	—	0·3	0·9	—	—	—	—	—	—	0·2	0·4
Cobble	16·5	3·6	2·8	2·7	—	3·2	4·3	2·4	4·5	7·2	5·1	6·7
Cobble–boulder	10·8	10·7	2·1	2·7	10·0	—	5·5	2·4	3·0	21·4	7·0	4·7
Cobble–bedrock	<0·1	—	—	—	—	—	0·5	—	—	—	0·2	0·2
Boulder	4·2	—	0·3	—	—	—	—	—	—	—	—	0·1
Bedrock	1·0	—	0·1	—	—	—	—	—	—	—	—	0·1

AV = *Alasmidonta viridis*; ED = *Elliptio dilatata*; LC = *Lasmigona costata*; LF = *Lampsilis fasciola*; LM = *Lampsilis cardium*; MC = *Medionidus conradicus*; PF = *Pegias fabula*; PY = *Ptychobranchus fasciolaris*; VI = *Villosa iris*; and VT = *Villosa taeniata*.

Table VI. Proportional overlap between pairs of most abundant ($n > 25$) species for use of substrate

Species	Species									All mussels
	ED	LC	LF	LM	MC	PF	PY	VI	VT	
AV	0·68	0·61	0·65	0·60	0·79	0·69	0·72	0·57	0·79	0·75
ED		0·90	0·78	0·83	0·87	0·84	0·88	0·41	0·79	0·89
LC			0·80	0·79	0·80	0·76	0·82	0·39	0·77	0·82
LF				0·85	0·79	0·73	0·82	0·45	0·79	0·79
LM					0·79	0·79	0·87	0·38	0·75	0·81
MC						0·84	0·91	0·53	0·90	0·94
PF							0·86	0·43	0·81	0·83
PY								0·46	0·85	0·91
VI									0·61	0·52
VT										0·87

AV = *Alasmidonta viridis*; ED = *Elliptio dilatata*; LC = *Lasmigona costata*; LF = *Lampsilis fasciola*; LM = *Lampsilis cardium*; MC = *Medionidus conradicus*; PF = *Pegias fabula*; PY = *Ptychobranchus fasciolaris*; VI = *Villosa iris*; and VT = *Villosa taeniata*.

Table VII. Product moment correlations between complex hydraulic variables and observed mussel densities (data either raw or $\log_{10}$ transformed) at a discharge of $0·03 \, \mathrm{m^3 \, s^{-1}}$ (n.s. = not significant)

	Re	P_a	τ	Mussel density
Fr	0·70	n.s.	n.s.	0·41
Re		0·50	n.s.	0·55
P_a			0·90	−0·58
				−0·74

Table VIII. Product moment correlations between shear stress values at different stream discharges (n.s. = not significant)

Discharge $(\mathrm{m^3 \, s^{-1}})$	Discharge $(\mathrm{m^3 \, s^{-1}})$					
	0·51	0·68	0·85	1·22	2·18	9·35
0·03	0·90	0·92	0·89	0·88	0·80	n.s.
0·51		0·99	0·97	0·88	0·74	n.s.
0·68			0·99	0·93	0·82	n.s.
0·85				0·96	0·84	n.s.
1·22					0·93	0·56
2·18						0·73

the depth increased with an increase in discharge, then the shear stress should also increase. However, the relationship between shear stress and discharge varied among some segments due to differences in channel morphology (Figure 5). For segment 1, defined by a transect located at a hydraulic control, the shear stress was similar over the entire range of flows measured or modelled. In contrast, the shear stress in segment 10 declined precipitously at high discharge due to a 100-fold decrease in slope. Although the slopes for a few segments were sensitive to changes in discharge, the overall slope of the study site changed little between discharges of 0·03 and $9·35 \, \mathrm{m^3 \, s^{-1}}$. High shear stress was clearly associated with low mussel densities; however, the relationship between shear stress and density was more variable for shear stresses $<40 \, \mathrm{dyn/cm^2}$ (Figure 6).
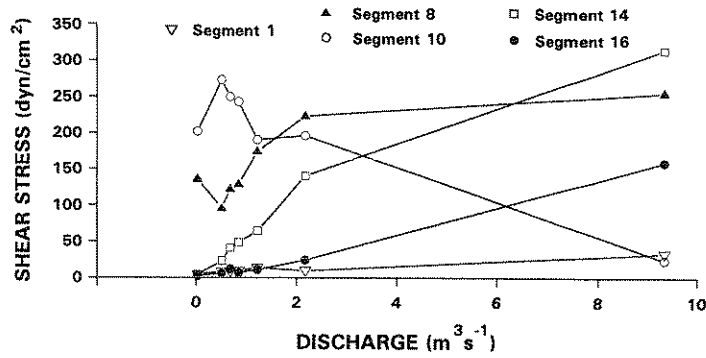
Figure 5. Relationship between shear stress and stream discharge for five segments

Mussel–host fishes relationships

Host fishes for all but one of the 17 mussel species occurring on the study site were determined from laboratory experiments or from published data (Table IX). There was no relationship between the known number of suitable host fish species and mussel abundance. For instance, Gordon *et al.* (1994) identified only rock bass (*Ambloplites rupestris*) as the host for *V. taeniata*, the second most abundant mussel species. In contrast, Luo (1993) identified 11 fish species, including several species that are abundant in Horse Lick Creek, as suitable hosts for *Lasmigona costata*, which comprised only 5% of the mussels present. Moreover, rock bass is a suitable host for at least six mussel species, yet the relative abundance of these species varied from 0·1 to 38%.

Comparison of mussel abundance with contemporary host fish abundances should be performed with caution because mussel abundance is based on recruitment in previous years. Most mussels found in Horse Lick Creek were probably 3 to 25 years old. Thus historical fish abundances could have been very different. In a concurrent study, Madison (1993) found that sculpins (*Cottus carolinae*), rainbow darters (*Etheostoma caeruleum*) and striped darters (*E. virgatum*) were the most abundant benthic fishes present on the study site. One or more of these three fishes serve as hosts for six mussels species (Table IX).
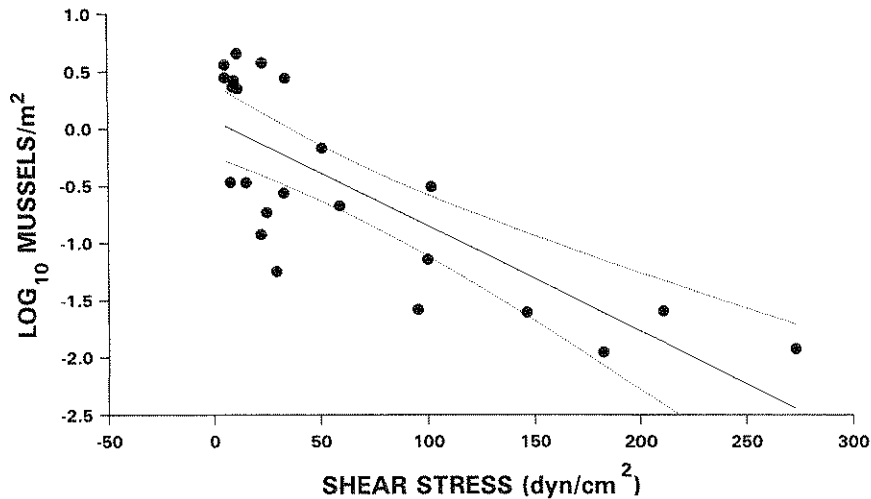
Figure 6. Relationship between mussel density and shear stress at a discharge of 0·51 $m^3 s^{-1}$. Dotted lines represent a 95% confidence band ($r = -0·9$)

Table IX. Mussel species and their host fish species that are known to occur in Horse Lick Creek

Mussel species	Host fish species	Reference
Actinonaias ligamentina	*Ambloplites rupestris* *Lepomis cyanellus* *Micropterus dolomieui*	Lefevre and Curtis (1910) Lefevre and Curtis (1912) Coker *et al.* (1921)
Alasmidonta marginata	*Hypentelium nigricans* *Ambloplites rupestris*	Howard and Ansen (1922)
Alasmidonta viridis	*Cottus carolinae*	Zale and Neves (1982a)
Elliptio dilatata	*Etheostoma caeruleum* *Ambloplites rupestris* *Cottus carolinae*	Luo (1993)
Lasmigona costata	*Ameiurus nebulosus* *Ambloplites ruprestris* *Campostoma anomalum* *Cottus carolinae* *Etheostoma caeruleum* *E. flabellare* *E. virgatum* *Fundulus catenatus* *Lepomis cynaellus* *L. megalotis* *Micropterus dolomieui*	Luo (1993)
Lampsilis cardium	*Micropterus dolomieui*	Coker *et al.* 1921
L. fasciola	*Micropterus dolomieui*	Zale and Neves (1982b)
Medionidus conradicus	*Etheostoma flabellare* *E. caeruleum* *E. virgatum*	Zale and Neves (1982b) Luo (1993)
Pegias fabula	*Etheostoma baileyi* *E. blenniodes*	Anderson and Layzer (unpubl. data)
*Pleurobema oviforme**	*Campostoma anomalum* *Cyprinella galactura* *Etheostoma flabellare*	Weaver *et al.* 1991
Ptychobranchus fasciolaris	Unknown	
P. subtentum	*Etheostoma caeruleum* *E. flabellare* *Cottus carolinae*	Luo (1993)
Strophitus undulatus	*Semotilus astromaculatus* *Lepomis cyanellus*	Baker (1928) Ellis and Keim (1918)
Toxolasma lividus	*Lepomis cyanellus* *L. megalotis*	Hill (1986)
*Villosa iris**	*Ambloplites rubestris* *Micropterus dolomieui*	*Zale and Neves (1982b)*
V. taeniata	*Ambloplites rubestris*	Gordon *et al.* (1994)
V. trabalis	*Etheostoma flabellare* *E. virgatum*	Layzer and Anderson (unpubl. data)

*Taxonomy of these species is uncertain; consequently, host fishes identified for upper Tennessee River populations may not be the hosts in Horse Lick Creek.
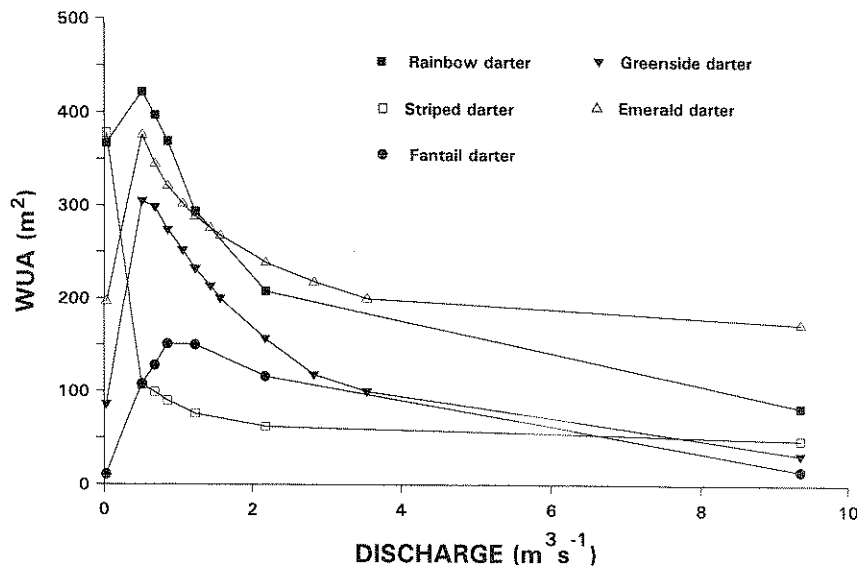
Figure 7. Relationship between discharge and weighted usable area (WUA) for five fish species that are hosts for *Pegias fabula* or *Medionidus conradicus*

Those six species includes the rarest, *Ptychobranchus subtentum*, and the most abundant, *Elliptio dilatata*, mussels present (Table I).

The maximum amount of weighted usable area (WUA) within the study site for hosts of *Pegias fabula*, greenside darters (*Etheostoma blennoides*) and emerald darters (*E. baileyi*), occurred at a discharge of $0.51 \, \text{m}^3 \, \text{s}^{-1}$ and remained relatively high for the flows commonly occurring ($\leqslant 2.18 \, \text{m}^3 \, \text{s}^{-1}$) during the time *P. fabula* released glochidia (Figure 7). The amount of WUA within each segment was not correlated ($p > 0.05$) with abundance of *P. fabula* for any flow modelled (Figure 8).

The relationship between WUA and discharge varied among fish hosts (rainbow darters, *E. caeruleum*; striped darters, *E. virgatum*; and fantail darters, *E. flabellare*) for *Medionidus conradicus*, but for all species the WUA was greatest at flows $\leqslant 1.22 \, \text{m}^3 \, \text{s}^{-1}$ (Figure 7). There was no significant correlation ($p > 0.05$) between the abundance of *M. conradicus* and WUA for any of its host species or the total WUA for all hosts in each segment (Figure 8). Although the WUA for all host fishes for *M. conradicus* was similar to the amount of WUA for both host species of *P. fabula*, *M. conradicus* was ten times more abundant than *P. fabula*.

DISCUSSION

A basic assumption of aquatic habitat simulation is that an organism will respond to changes in hydraulic conditions (Milhous *et al.*, 1989). This is a reasonable assumption for highly mobile species such as fish or many benthic organisms; however, for sessile organisms or those of limited mobility such as freshwater mussels, this assumption cannot be supported. On the contrary, most available information indicates that mussels move little in response to all but the most extreme changes in flow (Isely, 1914; Matteson, 1955; Strayer, 1981). In extreme cases of dewatering (Kaster and Jacobi, 1978; Samad and Stanley, 1986) or flow reductions (pers. obs.) mussels do move, but in an apparently random fashion rather than following receding water levels. In Horse Lick Creek, the large gravel–cobble substrate would prevent most movement, except for movement on top of the streambed.

It is not surprising that mussels have no apparent adaptation to tract changes in flow. In lotic systems, short-term but often substantial fluctuations in flow resulting from precipitation would change the
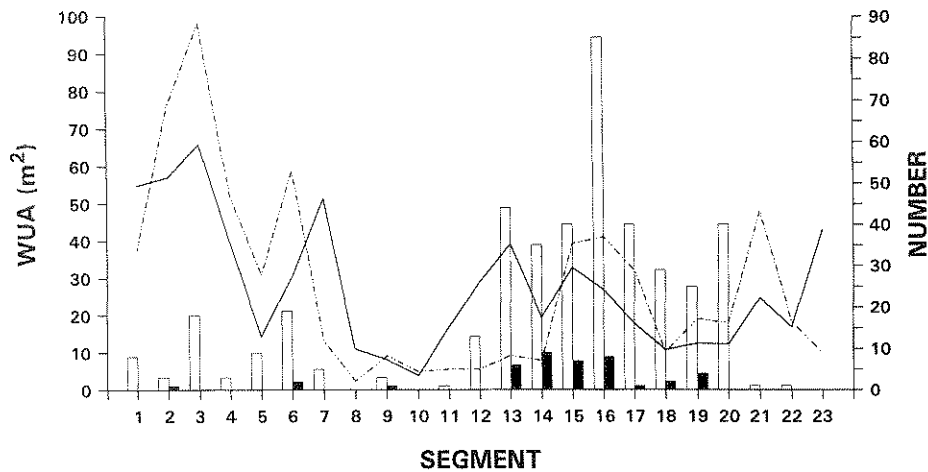
Figure 8. Numbers of *Pegias fabula* (solid bars) and *Medionidus conradicus* (open bars) and total weighted usable area (WUA) for hosts of *P. fabula* (broken line) and for hosts of *M. conradicus* (solid line) for each segment at a discharge of $0.51 \, m^3 \, s^{-1}$

hydraulic conditions faster than mussels could move. Thus under unsteady flow conditions, mussels might expend a considerable amount of energy and time if they attempted to respond to changes in flow. This does not mean that hydraulic conditions do not influence mussel distributions. Hydraulic features have frequently been related to mussel distributions in other studies (Salmon and Green, 1983; Holland-Bartels, 1990; Strayer and Ralley, 1993). Similarly, mussels in Horse Lick Creek were not distributed proportionally among all depths and velocities for any flow measured or modelled. A further indication that simple hydraulic variables were important in determining the distribution of mussels in Horse Lick Creek was the disproportionate change between low and intermediate discharges in the mean water column velocities for locations with and without mussels. During base flow ($0.03 \, m^3 \, s^{-1}$), 50% of the study site had no measurable current and 37% of the mussels were found at zero velocity; however, at a discharge of $1.28 \, m^3 \, s^{-1}$, 38% of the site that was wet at low flow had velocities $\leq 12 \, cm \, s^{-1}$ but 95% of the mussels occupied areas of higher velocity. These higher velocities may be important for delivering food, successful spawning or providing suitable microhabitat conditions for host fishes.

Unfortunately, associations between simple hydraulic conditions and mussel distributions are flow-conditional—that is, measurements (and calculated preferences) of simple hydraulic variables made at one discharge are of limited value in predicting suitable microhabitats for mussels at different discharges. Because the ability to predict mussel abundance and distribution based on microhabitat measurements has been poor, even at discharges similar to the flow at which measurements were made, Strayer and Ralley (1993) questioned the value of using simple hydraulic characteristics to describe microhabitats. Because these characteristics are flow-conditional, we agree that they have limited predictive power. In contrast, complex hydraulic variables, because of their relative constancy over a wide range of flows, are of greater value in predicting mussel distributions. We suggest that shear stress is a primary factor in determining the suitability of a location for juvenile settlement.

The coexistence of species and factors influencing the relative abundances of species within an assemblage have been the focus of much research (see Pianka, 1983). The coexistence of mussels in Horse Lick Creek is particularly interesting in the light of the fact that most species used similar habitats and there was no widespread partitioning of host fishes, though partitioning of the same host species may occur on a seasonal basis. Coexistence and the relative abundances of mussels may be maintained by the partitioning of food particle sizes or largely driven by stochastic processes such as hydraulic conditions during or shortly after juvenile excystment. We speculate that the rarity of some species, particularly *V. trabalis*, is governed by hydraulic conditions. Because of regulations restricting the collecting and handling of endangered species, we did not

attempt to determine the gametogenic cycle of *V. trabalis*. However, based on our field observation in Buck Creek, a nearby Cumberland River tributary, we have reached some tentative conclusions regarding when this species releases glochidia. During our numerous sampling trips to Buck Creek, we had great difficulty in locating specimens of *V. trabalis*, except in the months of December to February. During this time period, we frequently found *V. trabalis* lying on top of the substrate or only partially embedded. Moreover, all of the individuals that we found during the winter were gravid females, suggesting that their exposure was related to releasing glochidia. We have observed similar behaviour by other species in other seasons; presumably, the behaviour is related to attracting host fishes.

If, indeed, *V. trabalis* releases glochidia primarily during the winter, the high stream discharges typical of this season may result in high shear stresses on the existing mussel beds and thereby limit recruitment. Perhaps the recruitment of *V. trabalis* is contingent on below-normal stream discharges. In contrast, *Medionidus conradicus*, which shares two host species with *V. trabalis*, 'exposes' itself primarily in May and June. The relatively low discharge and concomitant low shear stress on existing mussel beds during this period may be chiefly responsible for the abundance of *M. conradicus* in Horse Lick Creek.

Determining the 'correct' equations to calculate shear stress and other complex hydraulic characteristics can be perplexing. For instance, Statzner *et al.* (1988) present three formulae for estimating each of several key hydraulic variables. Each of these equations requires different methods of collecting data. Although the values of individual key hydraulic characteristics calculated by these equations sometimes differed greatly, Statzner *et al.* (1988) found that each method produced significant correlations with insect abundance. Two of the methods of calculating complex hydraulic characteristics require measuring or visually estimating streambed roughness. Although we visually classified substrate particle sizes, our categorization probably did not reflect streambed roughness because of the variable shape of larger particles in Horse Lick Creek. We classified particles based on estimates of their length and width and thus the area of streambed covered, but we did not account for particle thickness and, consequently, height above the surrounding streambed material. All particles categorized as cobble or boulder by this method would not have had the same contribution to streambed roughness because of their highly variable thickness. Some of these particles were essentially large slabs 1–3 cm thick, whereas the thickness of other particles was similar to their length and width.

Though we used our classification of particle sizes to describe mussel microhabitats in the more traditional way, we question the utility of such an exercise for streams with a highly heterogeneous mixture of particles ranging from sand to cobble. Many headwater streams in the Cumberland River drainage and elsewhere have such a mixture. In these streams, a problem in the use of substrate to describe microhabitat arises when mussels are found, and commonly so, between or behind cobbles and boulders in small deposits of sand or gravel. Clearly, mussels require small particles for burrowing, but the presence of the large particle, which has the greater influence on near-bottom hydraulics, may in fact determine the suitability of the location for a mussel. Therefore, although measures of streambed roughness are desirable for calculating complex hydraulic characteristics, the simple classification of substrate in streams such as Horse Lick Creek is of limited value.

Shear stress, calculated by the method we used, is a composite measure of the drag effect in a stream segment (Carling, 1992). This method may be inappropriate for calculating the shear stress to describe mussel habitat in large streams where mussel beds rarely span the width of the river; however, in small streams such as Horse Lick Creek, it may be the most appropriate method. Although we argued that adult mussels move little, particularly in heterogeneous substrates, some movement of juveniles is likely. In the laboratory, recently metamorphosed juveniles are active (pers. obs.) and, in the field, juveniles occupy different habitats to adults (Isely, 1911; Neves and Widlak, 1987). Thus either through active or passsive means juveniles move to nearby adult habitats. Consequently, the shear stress measured for a small ($\leqslant 25$ m) stream segment may determine the suitability of the segment for juvenile settlement, survival, growth and eventual use by adults.

The use of shear stress and other complex hydraulic characteristics offers the most promising approach for describing and predicting mussel habitats; however, much additional research is needed to refine the methodology and to determine the most appropriate formulae for estimating these variables in different

sizes and types of streams. For instance, the spatial and temporal variation in shear stress in larger streams affected by peaking hydropower operations (Gore *et al.*, 1994) clearly requires a different approach to that we used.

INSTREAM FLOW RECOMMENDATIONS

To determine the instream flow needs of freshwater mussels in regulated streams, we recommend an approach that incorporates modelling both simple and complex hydraulic characteristics. The traditional application of PHABSIM for simulating the available habitat for mobile organisms at various stream discharges does not indicate how the location of this habitat may change with a change in discharge. Such information, however, is available in some subroutines of PHABSIM, but it is not in a format suitable for modelling mussel habitat. We believe that the high correlations between shear stress and mussel density reflects recruitment during the juvenile stage. Undoubtedly, other abiotic and biotic factors such as food availability influence the suitability of an area for mussels. Until all factors governing the distribution of mussels have been elucidated, we recommend that attempts to provide adequate instream flows for mussels are restricted to providing suitable hydraulic conditions over existing beds as opposed to providing suitable conditions in segments where mussels are scarce or absent.

In Horse Lick Creek, few mussels occurred in water <6 cm deep during low flows. Although the significance of water depth is unclear, similar depth limitations have been noted in other studies in small streams (Starnes and Bogan, 1982; Layzer, unpubl. data). This apparent limitation of depth probably varies with stream size and perhaps among mussel beds within a stream. Therefore, we recommend that minimum depths are determined during low flows on a site-specific basis. Furthermore, we believe that such minima should be viewed as temporary maintenance depths. Although many mussels were found in areas of zero flow, such conditions cannot be considered conducive to maintaining species that occur only in lotic habitats. The low-flow conditions under which our data were collected probably do not persist for prolonged periods in unregulated streams, except during a drought. Therefore, in the case of Horse Lick Creek, we would recommend velocities $\geqslant 2$ cm s^{-1} over existing mussel beds based on the clear preferences demonstrated by mussels during low flow (Figure 4). Again, we suggest that such minima are based on site-specific data. We are concerned that no flow conditions might be viewed as suitable for temporary maintenance in regulated streams, particularly downstream of peaking hydroelectric projects, which have no flow conditions during portions of most days throughout the year. We suspect that such frequent occurrences of no flow would be detrimental to mussel populations.

Although we found no clear relationship between the availability of host fish habitat and mussel abundance, the importance of providing an adequate habitat for host species cannot be dismissed. Perhaps there were sufficient numbers of host fishes and enough suitable habitat for them throughout the study site to ensure successful mussel reproduction. More likely, the lack of a demonstrable relationship between the host fish habitat and mussel density resulted from the fact that some segments containing a great amount of host habitat also had high shear stress values. Consideration of the host habitat may be more critical in other streams where some mussels utilize hosts that typically exhibit upstream spawning migrations. If these migrations occur during glochidial release periods, the movements of infested host fish may be crucial for mussel dispersal and the maintenance of upstream populations. Clearly, flows suitable for host migrations and spawning must be maintained, but this may first require identifying host species. Hosts have been identified for only about 25% of the mussels in North America. Moreover, even for species with identified hosts, all potential hosts may not be known. A literature review indicated that hosts were known for only 12 of the 17 mussel species on our study site. However, based on our fish collections and general knowledge of the icthyofauna of the region, we judged that the known hosts for three species either did not occur in Horse Lick Creek or were of such rarity that they could not be effective hosts. Consequently, we and others (Table IX) initiated laboratory studies and subsequently identified new hosts (that occur in Horse Lick Creek) for these three species and for four other species that lacked host information. The process of identifying host species is laborious, but we believe that it must be done on a site-specific basis unless it is judged that

the occurrence and abundance of known hosts are adequate to account for the distribution and abundance of mussels.

In regulated streams where the discharge may exceed normal seasonal flow regimes, we recommend that considerable emphasis is placed on minimizing the shear stress over existing mussel beds. We recognize that the widespread use of shear stress as a measure of habitat suitability for mussels requires much more research in a variety of stream types and sizes. In the interim, we recommend that the shear stress not exceed $50\,\mathrm{dyn\,cm^{-2}}$ on existing mussel beds. We also emphasize that this recommendation is based only on shear stress values calculated by the equation we used; other formulae will probably result in very different shear stress values. Nonetheless, we hope that future research will incorporate several methods for determining shear stress and, perhaps, determine the most appropriate formula to use.

ACKNOWLEDGEMENTS

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