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RELATIONS BETWEEN COMPLEX HYDRAULICS AND THE LOCALIZED DISTRIBUTION OF MUSSELS IN THREE REGULATED RIVERS

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ABSTRACT

A stratified random sampling design was used to examine the relations between selected hydraulic variables and the density of unionids at five sites on the Green, Licking, and Rough Rivers of Kentucky. We located the strata to ensure that samples occurred in a wide range of hydraulic conditions at each site. Eight 0.25 m^2 quadrat samples were collected from each 25 m^2 stratum. We measured mean water column velocity, depth, and substrate roughness before we sampled each quadrat. '*Fliesswasserstammtisch*' (FST) hemispheres were used to estimate shear stress. In all, we collected 798 individuals of 28 species of freshwater mussels. Simple hydraulic characteristics of our study sites were not correlated consistently with mussel density. For instance, water depth and mussel density were positively correlated in the Green River, negatively correlated in the Rough River, and not significantly correlated in the Licking River. In contrast, we found consistent negative correlations in all rivers between mussel density and complex hydraulic variables, such as shear velocity and FST hemisphere number. We believe that the limited recruitment observed in these rivers may have resulted from operation of upstream flood control dams that altered flow regimes seasonally. We suspect that the increased discharge during spring and early summer resulted in shear forces sufficiently high on mussel beds to prevent settlement of newly metamorphosed juveniles. Copyright © 2001 John Wiley & Sons, Ltd.

KEY WORDS: freshwater mussels; hydraulics; microhabitats; recruitment

INTRODUCTION

Freshwater mussels are among the most imperiled faunal groups in North America; 61 of the nearly 300 recognized species and subspecies are listed as endangered (US Fish and Wildlife Service, 1999). Moreover, populations of many other species have been extirpated or greatly reduced. The construction and operation of dams is one of the main causes of the declines in mussel populations (Hughes and Parmalee, 1999). Impoundments created by dams are often unsuitable habitats for many of the species that typically occupy riffle and shoal habitats (Isom, 1969; Petts, 1984). The loss of mussel populations below these impoundments has been attributed to the altered daily and seasonal discharge regimes, water temperatures and dissolved oxygen concentrations (Ahlstedt, 1983; Williams *et al.*, 1992; Layzer *et al.*, 1993; Tippit *et al.*, 1997). Frequently, mussel recruitment is limited or non-existent downstream of these impoundments. In some tailwaters, the lack of recruitment has been attributed to coldwater discharges that inhibit gametogenesis (Layzer *et al.*, 1993; Heinricher and Layzer, 1999). However, recruitment in tailwaters that have a more normal temperature regime is often limited as well; in these streams, it seems likely that mussel recruitment is affected by the altered hydrograph. Changes in stream discharge patterns may affect the abundance, distribution and movements of fishes that serve as hosts for the obligate parasitic larvae (glochidia) of mussels. Alternatively, the altered discharge pattern may directly affect the availability of suitable microhabitats for juvenile and adult mussels.

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Microhabitats of freshwater mussels have been described frequently in terms of simple hydraulic variables; however, water depth and velocity superficially define lotic habitats and explain little of the variation in the distribution of mussels (Holland-Bartels, 1990; Strayer and Ralley, 1993). Moreover, simple hydraulic variables are flow-conditional; measurements made at one discharge are of limited value for predicting suitable microhabitats for mussels at different discharges (Layzer and Madison, 1995). Simple hydraulic variables may be inadequate to describe mussel microhabitats because flow in lotic environments is three-dimensional; a fluid particle may travel longitudinally, laterally and vertically, and simple hydraulic variables do not describe this environment well. Flow conditions at a particular velocity could be laminar or turbulent, and these two conditions represent two completely different environments (Statzner *et al.*, 1988). Laminar flow is characterized by unidirectional flow; however, virtually all boundary layer flows of aquatic interest are turbulent (Nowell and Jumars, 1984; Carling, 1992). Moreover, flow is likely to be rough to turbulent, with no intact viscous sublayer if the bed consists of particles ≥ 8 mm in diameter (Carling, 1992). Variables that describe the boundary layer and the complexity of flow may describe mussel microhabitats more accurately. Complex stream hydraulic parameters that may be useful for describing mussel habitat include Reynolds number, Reynolds roughness number, Froude number, shear velocity, and shear stress (Statzner *et al.*, 1988). Layzer and Madison (1995) found that mussel densities were correlated with several complex hydraulic characteristics in a small headwater stream. In particular, shear stress was negatively correlated with mussel densities for a wide range (two orders of magnitude) of stream discharge. In this paper, we examine the relationships between several hydraulic variables, and the density of freshwater mussels in three regulated rivers.

METHODS

We sampled five sites with relatively high mussel densities (> 12 m^{-2}), located on three rivers in Kentucky: two sites on the Green River, two sites on the Licking River and one site on the Rough River. Between 1969 and 1974, a dam was constructed on each of these rivers upstream of our sampling sites. These dams are operated by the US Army Corps of Engineers, primarily for flood control. Consequently, hydrographs for these rivers have lower peaks, but prolonged periods of moderately high discharge that occur from fall to late spring or mid-summer. All sites were sampled between 12 and 26 July 1995, when discharge was similar to pre-dam flows for July.

A stratified random sampling regime was used at each site to sample a diversity of hydraulic characteristics. The number of strata varied between sites, and reflected the variation in hydraulic conditions. Bedrock substrates and pools were excluded from sampling, because these areas are low quality mussel habitat. Four steel rods were inserted into the substrate to form the borders of strata that were sized to contain areas with seemingly similar hydraulic conditions. The strata were either 5 × 5 m or 8 × 3 m. In each stratum, tape measures were used to locate eight randomly selected pairs of coordinates to determine the placement of 0.25 m^2 quadrat frames. Water depth and mean water column velocity (at 0.6 depth) were measured in the center of each quadrat. Substrate roughness was determined by carefully fitting a 100 cm long chain (12 mm links) to the contours of the substrate. The substrate roughness (k) was calculated as $k = 100/d$, where d is the linear distance between the two ends of the chain (cm) after placement on the substrate. After roughness was estimated, a set of '*Fliesswasserstammtisch*' (FST) hemispheres was used to estimate shear stress. The FST hemispheres were of uniform size (diameter 7.8 cm), but varied in density (Statzner and Müller, 1989). The minor variations in weight of hemispheres of the same number have little effect on estimates of shear stress (Statzner *et al.*, 1991). In the field, a weighted platform (13 × 18 × 2 cm) was placed into the substrate, level with the stream bed. Two spirit levels mounted in the platform were used to make the platform horizontal. Using a standard release procedure, individual hemispheres were placed one at a time on the platform; the highest numbered (greatest density) hemisphere that moved was recorded. Mussels were collected by removing all substrate to a depth of about 10 cm from each quadrate, placing in a 6 mm mesh bag, and sorting by hand at stream side. All mussels were identified and returned to the stream. Formulae used to calculate Reynolds number (*Re*), Froude number (*Fr*), shear velocity (U_*) and Reynolds roughness number (Re_*) are listed in Appendix A.

RESULTS

A total of 798 mussels belonging to 28 species was collected in 184 quadrat samples. The species collected are typical of medium-sized rivers and most are widely distributed within the Ohio River basin (Table I). The mussel assemblage at each site was dominated by one to three species that constituted 64–85% of the mussels collected. All mussel species were combined for analysis, because the densities of the three dominant species in quadrats were highly correlated with the density of all mussels collected (all r-values ≥ 0.90). Overall densities varied from 3.1 to 6.2 mussels 0.25 m^{-2} among rivers (Table I). Mussel densities did not differ significantly between sites within rivers, and overall mussel density differed only between the Green and Rough Rivers (analysis of variance (ANOVA); Tukey's test, $p = 0.0004$).

Mean water column velocities and hemisphere numbers recorded were similar between sites within rivers (t-test, $p > 0.05$); however, the Green River sites differed in depth and the sites on the Licking River differed in substrate roughness (t-test, $p < 0.05$). Comparison of mean habitat variables (Table II) between

Table I. Freshwater mussel species and numbers collected at each site

Species	Green River		Licking River		Rough River
	Site 1	Site 2	Site 1	Site 2	
Actinonaias ligamentina (Lamarck, 1819)	163	159	19	73	19
Amblema plicata (Say, 1817)	2	6	9	9	–
Cyclonaias tuberculata (Rafinesque, 1820)	3	12	13	1	–
Cyprogenia stegaria (Rafinesque, 1820)	2	1	–	–	–
Elliptio dilatata (Rafinesque, 1820)	11	3	39	32	2
Epioblasma triquetra (Rafinesque, 1820)	–	–	–	1	–
Fusconaia flava (Rafinesque,1820)	–	–	–	1	–
Fusconaia subrotunda (Lea, 1831)	–	–	–	3	–
Lampsilis cardium (Rafinesque, 1820)	–	–	3	–	–
Lampsilis ovata (Say, 1817)	5	1	–	–	–
Lasmigona costata (Rafinesque, 1820)	–	–	21	–	–
Leptodea fragilis (Rafinesque, 1820)	–	–	1	–	–
Ligumia recta (Lamarck, 1819)	–	1	1	–	–
Megalonaias nervosa (Rafinesque, 1820)	–	6	8	–	63
Obliquaria reflexa Rafinesque, 1820	–	–	3	–	–
Plethobasus cyphyus (Rafinesque, 1820)	–	1	–	–	–
Pleurobema sintoxia (Rafinesque, 1820)	4	6	–	2	–
Pleurobema cordatum (Rafinesque, 1820)	1	2	–	–	–
Potamilus alatus (Say, 1817)	–	2	–	–	–
Ptychobranchus fasciolaris (Rafinesque, 1820)	2	2	11	9	2
Quadrula metanevra (Rafinesque, 1820)	–	3	1	2	–
Quadrula nodulata (Rafinesque, 1820)	–	–	1	–	–
Quadrula pustulosa (Lea, 1831)	3	3	5	10	5
Quadrula quadrula (Rafinesque, 1820)	–	–	–	5	–
Strophitus undulatus (Say, 1817)	–	–	–	1	–
Tritogonia verrucosa (Rafinesque, 1820)	1	1	–	–	6
Truncilla donaciformis (Lea, 1828)	–	–	3	–	–
Truncilla truncata Rafinesque, 1820	1	–	–	–	7
Total mussels collected	198	209	138	149	104
Total samples taken	32	48	24	48	32
Overall density (mussels 0.25 m^{-2})	6.19	4.35	5.75	3.10	3.25
Species richness	12	16	15	13	7

Table II. Mean (range) values of hydraulic variables sampled for each river

River	k	U (cm s^{-1})	D (cm)	Re ($\times 1000$)	U_* (cm s^{-1})	Fr	Re_*	FST no.
Green	1.10 (1.00–1.23)	62 (26–113)	39 (15–76)	235 (81–570)	4.1 (1.6–7.2)	0.32 (0.12–0.54)	424 (160–784)	7.1 (3–12)
Licking	1.16 (1.05–1.37)	39 (8–86)	24 (6–37)	87 (10–260)	2.9 (0.7–6)	0.26 (0.07–0.55)	315 (72–730)	5.8 (3–10)
Rough	1.13 (1.03–1.27)	61 (12–103)	21 (5–46)	135 (9–294)	4.5 (1.0–7.2)	0.43 (0.11–0.84)	480 (111–824)	7.1 (3–10)

rivers indicated that mean water column velocity and hemisphere number were similar for the Green and Rough Rivers, but were lower on the Licking River (ANOVA; Tukey's test, $p = 0.001$). Depth and substrate roughness were similar for the Licking and Rough Rivers; however, sampling points on the Green River were significantly deeper (ANOVA; Tukey's test, $p = 0.0001$).

In each river, hemisphere number (FST no.) was highly correlated with most hydraulic variables (Table III). Mussel density was also negatively correlated with FST no., and with U, Fr, U_*, Re_*, for all rivers. The relation between mussel density and depth was not consistent among rivers. Mussel density and water depth were positively correlated in the Green River, negatively correlated in the Rough River, and not significantly related in the Licking River. Substrate roughness and mussel density were correlated only in the Rough River. Correlation coefficients between mussel density and U_*, and Re_* were nearly identical within each river. Because the correlation between U_* and Re_* approached unity in each river, and because U_* is used to calculate Re_*, only U_* was included in further analysis. Mussel densities were greater, but more variable, for lower values of most hydraulic variables, such as hemisphere number (Figure 1).

Mean values for mussel density and hydraulic variables were calculated for each stratum and analyzed, because of the likelihood of some mussel movement on a small scale; however, the reduction in sample

Table III. Product moment correlation coefficients ($r \times 100$) between habitat variables (data either raw or ln transformed) and mussel density for each river

Variable	Green River ($n = 80$)							Licking River ($n = 72$)						
	U	D	Re	Fr	U_*	Re_*	FST no.	U	D	Re	Fr	U_*	Re_*	FST no.
Mussel density	−39	51	NS	−48	−42	−41	−53	−64	NS	−49	−66	−65	−65	−59
U	–	NS	92	98	99	99	84	–	NS	88	95	99	99	74
D	–	–	52	−30	NS	NS	−37	–	–	61	−25	NS	NS	−31
Re	–	–	–	82	89	90	62	–	–	–	68	82	85	55
Fr	–	–	–	–	99	99	84	–	–	–	–	98	97	78
U_*	–	–	–	–	–	100	85	–	–	–	–	–	99	77
Re_*	–	–	–	–	–	–	85	–	–	–	–	–	–	75
	Rough River ($n = 32$)							All rivers ($n = 184$)						
Mussel density	−51	−51	−52	−37	−47	−43	−70	−35	27	−15	−44	−40	−40	−52
U	–	73	92	85	98	98	76	–	31	85	92	98	98	79
D	–	–	94	NS	59	58	69	–	–	73	−16	16	NS	NS
Re	–	–	–	59	84	83	78	–	–	–	59	77	75	59
Fr	–	–	–	–	93	93	65	–	–	–	–	97	97	77
U_*	–	–	–	–	–	99	74	–	–	–	–	–	99	81
Re_*	–	–	–	–	–	–	70	–	–	–	–	–	–	80

All values listed are significant ($p < 0.05$, NS = not significant).

sizes may have obscured some relations (Table IV). For instance, FST no. and mussel density were significantly correlated in the Green ($n = 10$) and Licking ($n = 9$) rivers, but not in the Rough River ($r = -0.76$; $p > 0.20$, $n = 4$). Nevertheless, compared with mean water column velocity and depth, most complex hydraulic variables proved to be more robust predictors of mussel density.

DISCUSSION

The hydraulic conditions that are most relevant to determining mussel distribution probably are those that characterize flows near the stream bed, because adult and juvenile mussels live within the substrate, and juveniles excysting from their hosts must settle to the bottom. Mussel density was related to some simple hydraulic variables in all rivers; however, no single variable was consistently related. Simple hydraulic variables that were the least descriptive of the density of mussels were substrate

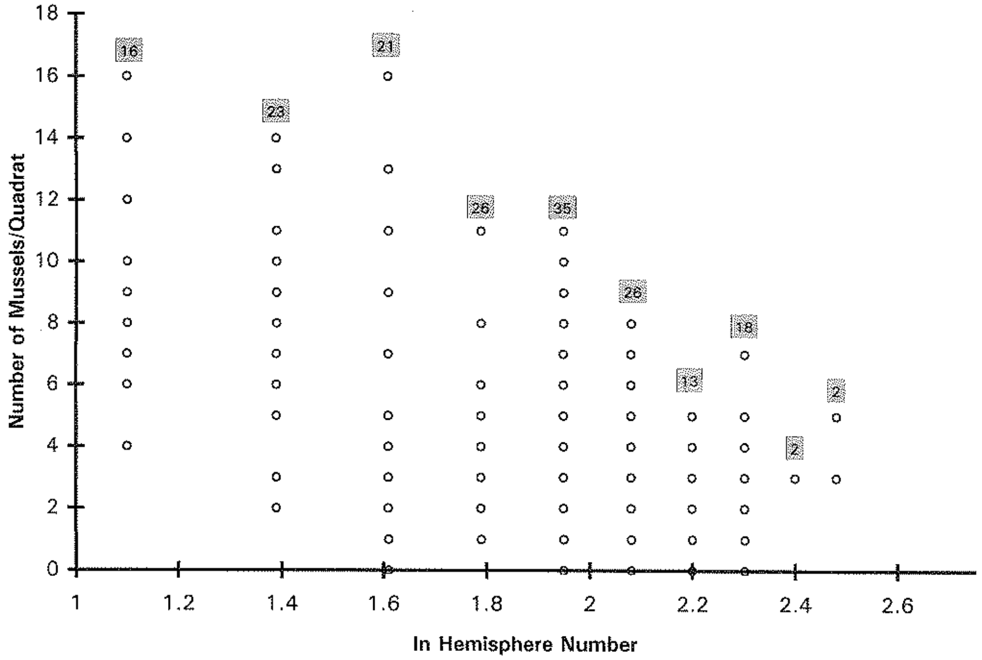

Figure 1. Relationship between the number of mussels and ln hemisphere number for all quadrats (0.25 m^2) sampled. The number of data points is less than the number of samples taken as a result of superimposition; numbers in boxes indicate the number of samples for each hemisphere number

Table IV. Product moment correlation coefficients ($r \times 100$) between mean mussel density and mean habitat variables per stratum (data either raw or ln transformed) in each river

River	n	U	D	Re	Fr	$U*$	FST no.
Green	10	NS	80	NS	−74	−63	−78
Licking	9	−87	NS	−73	−91	−89	−91
Rough	4	NS	NS	NS	−95	NS	NS
All rivers	23	−53	46	NS	−69	−60	−71

All values listed are significant ($p < 0.05$, NS = not significant).

roughness and depth. Although mussel density and mean velocity were negatively correlated in all rivers, the correlation was not significant when strata means were analyzed for the Green and Rough Rivers. In contrast, correlations between complex hydraulic variables and mussel density were more consistent and greater, especially when data from all rivers were combined. The relations between mussel density and those complex hydraulic variables that do not directly measure near-substrate flow conditions (Re and Fr) may not be consistent among streams or persist at all discharges. Mussel density and Froude number were negatively correlated in all rivers during our sampling; however, Layzer and Madison (1995) found that these variables were positively correlated at low flow, but were not significantly correlated at higher stream discharges.

On a broad scale, hydrological stability is a determining factor in mussel distributions (Strayer, 1983, 1993; Di Maio and Corkum, 1995). However, factors influencing the localized distribution and structure of mussel assemblages are not fully understood. Nonetheless, there is increasing evidence that hydraulics play a significant role, operating at both the adult and the juvenile stages. Vannote and Minshall (1982) suggested that periodic scouring events determine the age structure of a mussel bed. They found that beds located in areas that were protected from scouring associated with flood events contained older individuals, while those beds that were unprotected and susceptible to the scouring effects of major floods were composed of younger mussels—presumably representing recruitment since the last flood. Strayer (1999) demonstrated that mussel beds in two rivers in New York occurred primarily in areas that provided refuge from scouring during high-flow events. We agree with this hypothesis; the beds we studied were likely present prior to flow regulation, and, thus, had been exposed to naturally occurring flood events. Although this 'refuge hypothesis' explains the persistence of beds over the course of decades, it offers little insight on the cause of the within bed patchiness we observed (0–16 mussels quadrat^{-1}), and the near absence of recruitment. This patchiness may be related to localized differences in shear forces. Layzer and Madison (1995) suggested that shear stress was a major factor in determining where juveniles settled. The consistently significant correlations between hemisphere number, shear velocity and mussel density that we found supports this hypothesis. Clearly, the level of shear stress that would preclude settlement of small, suspended particles (i.e. juveniles < 0.35 mm) is far less than that necessary to induce bed-load movement.

The juvenile stage is often the most sensitive time in the life cycle of aquatic organisms. Undoubtedly, mortality of juvenile mussels must be high at the time of excystment from their hosts, because the juveniles have no control over host fish location at the time of excystment; consequently, juveniles may settle in unsuitable habitats. Further, above-normal stream discharge may create near-bed hydraulic conditions that preclude juveniles from settling in otherwise favorable habitats, i.e. established mussel beds. Thus, recruitment may be possible only during times of low shear forces on mussel beds. In streams regulated for flood control, such times may be limited to late summer, and sporadically at other times during years of low precipitation. The mussel beds we sampled contained few ($< 2\%$) young mussels. In particular, the populations of *Actinonaias ligamentina* were composed almost entirely of large (> 110 mm long) old individuals that may well have been recruited to the mussel beds before the dams were constructed (1969–1974). In contrast, recruitment of *A. ligamentina* in the Clinch River, an unregulated stream, occurred during this time period (Ahlstedt and Tuberville, 1997). Unlike the mussel beds studied by Vannote and Minshall (1982), the mussel beds we studied did not seem to be centers for dispersal; in other, unrelated sampling in these rivers, we also found few young *A. ligamentina* in other beds. Thus, we believe that regulation of these rivers was a major factor limiting recruitment of some species, especially *A. ligamentina*. Specifically, the unnaturally high discharge during the spring and early summer could result in high shear forces on mussel beds at the precise time that we would expect juvenile excystment by most lampsiline species, such as *A. ligamentina*. Recruitment of amblemine species may be less affected by river regulation, because excystment of their juveniles occurs later in the summer, when discharge is similar to pre-dam conditions. In fact, more recent sampling of another mussel bed in the Green River resulted in the collection of several juveniles of most amblemine species present, but few young *A. ligamentina* (Layzer, unpublished data).

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APPENDIX A. SYMBOLS AND FORMULAE FOR HYDRAULIC VARIABLES

Derived from Statzner *et al.* (1988)

Simple hydraulic variables

D	Depth of sample (cm)
g	Acceleration owing to gravity (cm s^{-2})
k	Substrate roughness
U	Mean water column velocity (cm s^{-1})
v	Kinematic viscosity (cm^2 s^{-1})

Complex hydraulic variables

Fr	Froude number (dimensionless)
Re	Reynolds number (dimensionless)
Re_*	Reynolds roughness number (dimensionless)
U_*	Shear velocity (cm s^{-1})

Formulae

$Fr = U(gD)^{-0.5}$

$Re = UDv^{-1}$

$Re_* = U_* k v^{-1}$

$U_* = U[5.75 \log_{10}(12Dk^{-1})]^{-1}$

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