Johnson
Brown
2000

The importance of microhabitat factors and habitat stability to the threatened Louisiana pearl shell, *Margaritifera hembeli* (Conrad)

Paul D. Johnson and Kenneth M. Brown

Abstract: *Margaritifera hembeli*, the Louisiana pearl shell, is a threatened mussel with a distribution limited to the headwaters of three tributaries of the Red River in central Louisiana, U.S.A. We assessed the role that several habitat characters played in determining its abundance and distribution. Pearl shell mussels were more common in second-order streams with elevated conductivity (≈0.04 mS/cm) and water hardness (8 mg/L). A discriminant analysis indicated that mussel density was related to water depth, substrate size, substrate compaction, and water velocity. Mussels were rare in deep, stagnant pools with silt-covered bottoms, and were more common in shallow, wide areas of streams with higher current velocities and in sediments with larger particle sizes. Mussel beds were also more likely to occur in sections of the stream where the substrate was more stable through time. These habitat associations may occur because individuals that recruit into, or later select, more stable microhabitats, have an advantage owing to the relatively long life cycle of this mussel. We suggest that the measurement of microhabitat characteristics can be important when evaluating habitat preferences and management plans for endangered mussel species in headwater streams.

Résumé : *Margaritifera hembeli* est une moule menacée dont la répartition est restreinte aux eaux d'amont de trois tributaires de la Rivière Rouge dans le centre de la Louisiane, É.-U. Nous avons évalué l'influence de plusieurs caractéristiques de l'habitat sur son abondance et sa répartition. Ces moules sont plus communes dans les eaux des ruisseaux de second ordre à conductivité (≈0,04 mS/cm) et à dureté (8 mg/L) élevées. Une analyse discriminante a révélé que la densité des moules est reliée à la profondeur de l'eau, à la taille des éléments du substrat, à la compaction du substrat et à la vitesse du courant. Les moules sont rares dans les cuvettes d'eau stagnante à substrat couvert de limon et elles préfèrent les eaux peu profondes dans les zones larges des ruisseaux où le courant est fort et où les sédiments contiennent des grosses particules. Les lits de moules se retrouvent aussi plus souvent dans les sections du ruisseau où le substrat est stable. Ces associations moules-habitat existent probablement parce que les individus qui s'établissent dans des microhabitats stables à leur naissance ou plus tard ont un avantage étant donné le cycle plutôt long de cette moule. Nous croyons que l'examen des caractéristiques du microhabitat est essentiel à l'évaluation des préférences d'habitat et à l'élaboration de programmes d'aménagement des espèces de moules menacées dans les ruisseaux d'amont.

[Traduit par la Rédaction]

Introduction

The relationships of freshwater mussel abundance and diversity to various habitat factors have been examined extensively because of the endangered status of the group (Williams et al. 1992; Neves et al. 1998). These factors include macrohabitat variables, such as degree of riparian cover (Morris and Corkum 1996), hydrological variability (Vannote and Minshall 1982; Di Maio and Corkum 1995; Layzer and Madison 1995), and drainage area and gradient (Strayer 1993), as well as microhabitat variables, such as current velocity, sediment size (Salmon and Green 1985; Way et al. 1989; Strayer and Ralley 1993), and water depth (Bronmark and Malmquist 1982; Stern 1983; Strayer 1993). For the most part, macrohabitat variables (e.g., those operating over the scale of kilometres versus metres) appear more important in predicting mussel diversity and abundance in larger rivers (Holland-Bartels 1990; Strayer 1993; Strayer et al. 1994; Di Maio and Corkum 1995; Morris and Corkum 1996).

In small drainages, microhabitat factors, such as sediment size, current velocity, and channel depth, can be important predictors of mussel distribution (Strayer 1981; Neves and Widlak 1987; Layzer and Madison 1995), but relationships can be complicated and correlations with mussel abundance or diversity can be low (Tevesz and McCall 1979; Strayer and Ralley 1993; Balfour and Smock 1995). However, in these small systems, macrohabitat variables may not vary considerably and microhabitat variables may be the only option available to evaluate habitat preference.

Margaritiferid bivalves are widely distributed across North America. *Margaritifera margaritifera*, the eastern pearl shell, occurs on the east coast from Newfoundland to Pennsylvania and in the headwaters of the Missouri River (Burch 1975). *Margaritifera falcata*, the western pearl shell, occurs in Pacific drainages from northern California to British Columbia

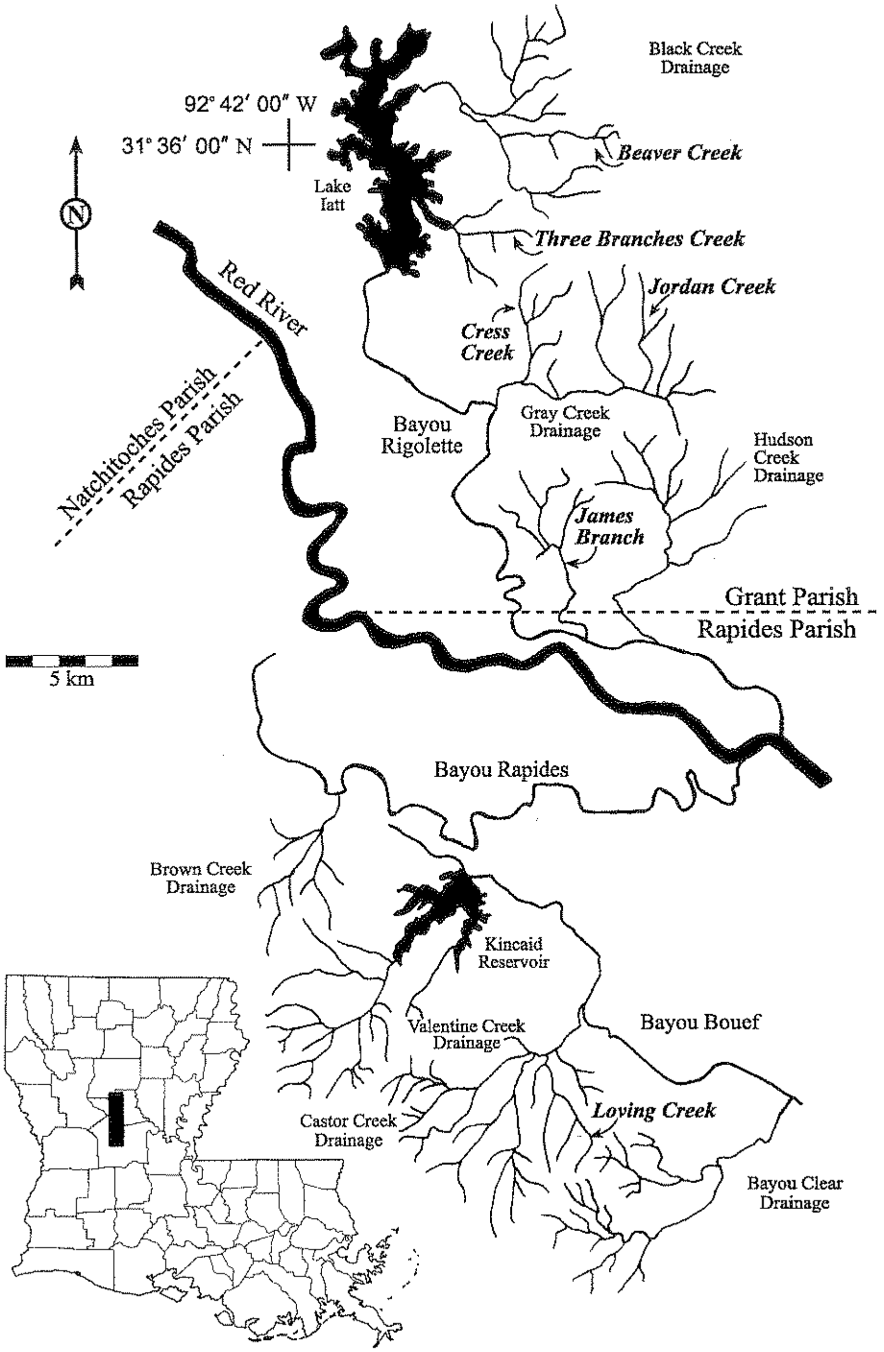
Received April 20, 1999. Accepted September 15, 1999.

P.D. Johnson. Southeast Aquatic Research Institute and Tennessee Aquarium, One Broad Street, P.O. Box 11048, Chattanooga, TN 37401-2048, U.S.A.
K.M. Brown.[1] Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1725, U.S.A.

[1] Author to whom all correspondence should be addressed (e-mail: kmbrown@lsu.edu).

Can. J. Zool. 78: 271–277 (2000)

Fig. 1. Map of the Bayou Rigolette, Bayou Rapides, and Bayou Bouef drainages in central Louisiana containing *M. hembeli.* Streams sampled are in boldface type and italic font. The inset of Louisiana indicates the location of the drainages in Grant Parish and Rapides Parish.



and southern Alaska (Clarke 1981). *Margaritifera marrianae*, the Alabama pearl shell, has a distribution limited to Escambia, Conecuh, and Monroe counties in Alabama (Shelton 1997). Each of these species, with the exception of *M. falcata* (Vannote and Minshall 1982), is restricted to small headwater systems.

Margaritifera hembeli is limited to 22 small headwater streams in central Louisiana, and its host fish is the brown madtom, *Noturus phaeus* (Johnson and Brown 1998). *Margaritifera hembeli* was separated from its congener *Margaritifera marrianae* in 1983 based upon internal anatomical differences (Johnson 1983). As a consequence, the known distribution of *M. hembeli* was limited to 10 streams south of the Red River, inside the Kisatchie National Forest in Rapides Parish in central Louisiana (Fig. 1). The revised distribution prompted the U.S. Fish and Wildlife Service to list the species as endangered in 1988. After we located the mussel in 12 additional streams in the Bayou Rigolette drainage, north of the Red River, in Grant Parish, Louisiana (Fig. 1), the status was revised to threatened in 1994.

In this study, we examine the relationship between microhabitat variables and the distribution of the threatened Louisiana pearl shell mussel. Our basic approach involves collecting quantitative data on habitat characters important for mussels in small streams (Salmon and Green 1985; Strayer 1993; Vaughn and Pyron 1995) and using a multivariate statistical technique, discriminant analysis, to judge their power in predicting mussel abundance in several of these streams.

Study area

Margaritifera hembeli is restricted to small second- and third-order streams in Grant Parish and Rapides Parish, Louisiana. These streams drain into two Red River tributaries (Bayou Rapides and Bayou Rigolette) and one historical tributary of the Red River (Bayou Bouef) (Fig. 1). *Margaritifera hembeli* is restricted to three small drainages in the upper section of Bayou Bouef in southwestern Rapides Parish. Bayou Rapides contains one drainage with mussels and Bayou Rigolette, in western Grant Parish and southern Winn Parish, contains four drainages with *M. hembeli*. Although tributaries in Bayou Rigolette were our primary focus, Loving Creek, in the Bayou Bouef drainage, was also examined (Fig. 1).

These headwater streams are slightly acidic, oligotrophic systems with low sediment organic content. The substrate is dominated by loose, fine, or very fine sand with infrequent patches of gravel and cobble. Streams are less than 5 m in width and less than 45 cm in depth. Stream gradients range from 1.9 to 6.1 m/km of stream in headwaters with mussels, and discharges range between 0.12 and 0.65 m^3/s. Riparian zones are dominated by secondary or primary growth of bald cypress (*Taxodium distichum*), American beech (*Fagus grandifolia*), black tupelo (*Nyssa sylvatica*), southern magnolia (*Magnolia grandiflora*), and long-leaf pine (*Pinus palustris*).

Materials and methods

Physicochemical factors

To determine if water quality affected mussel density, we examined seven physicochemical variables in five streams. Water quality variables were monitored on nine dates from July 1992 to February 1994. On each sampling date, water quality measurements were taken within a 6-h period at all sites. The same sampling site was repeatedly sampled through time at Beaver Creek and Jordan Creek (reported as high density streams for pearl mussels in Johnson and Brown 1998); James Branch and Loving Creek, sites with medium density; and Three Branches Creek, a site without mussels. Temperature (°C), dissolved oxygen (mg/L), specific conductivity (µS/cm), pH, and redox (mV) were recorded with a Hydrolab® Surveyor 3 water quality probe. Total hardness and free carbon dioxide concentration (mg/L) were determined with a Hach® kit. Differences in water quality variables among streams in the three mussel density categories were tested for with one-way analyses of variance and Tukey's a posteriori tests were used to compare differences in means among the three mussel abundance categories.

Microhabitat factors

The microhabitat analysis was conducted in five streams with mussels (Beaver Creek, Cress Creek (eastern branch), James Branch, Jordan Creek, and Loving Creek) and two streams without them (Cress Creek (western branch) and Three Branches Creek). Streams without mussels were in close proximity to streams with mussels and appeared to have similar habitats.

In each stream, channel width, mean channel depth, geometric mean sediment size, percent sediment organic content, mean sediment compaction, current velocity, and mussel density were determined at 11 locations at 100-m increments along a 1-km section. Because mussel beds (e.g., >20 mussels/m^2; Johnson and Brown 1998) were rarely located at the sampling points, identical measurements were recorded at a minimum of five mussel beds along the same 1-km section.

At each location, channel width was measured at base flow. Channel depth, current velocity, and sediment compaction were measured at five equidistant points across the channel and averaged. Because compacted sediments are more resistant to scouring, sediment compaction was measured with a Lang© penetrometer to determine if mussels prefer more stable sediments. Current velocity (cm/s) was recorded with a Montedoro–Whitney Model PVM-2A current meter, 2.5 cm above the substrate. A sediment core (volume ≈1500 cm^3, 10 cm wide × 15 cm deep) was collected from the channel center at each location, dried, and sifted through eight sieves (4, 2, 1, 0.5, 0.25, 0.125, 0.062, and <0.062 mm) following Buchanan (1984). Each sediment size class was weighed (mass in grams) and the geometric mean particle size calculated. Sediment size is inversely proportional to the geometric mean (e.g., a smaller mean indicates a larger mean particle size). An 8-cm^3 subsample of each core was ashed for 24 h at 550°C to determine percent organic content.

Mussel densities were estimated at each of the locations by placing a 0.25-m^2 quadrat at 0.6, 1.6, 2.45, and 3.35 m (if channel width allowed) from the right channel margin, facing upstream. The substrate was visually examined and then gently searched by hand for mussels. There were a minimum of 37 individual quadrats recorded for each stream.

Mussel numbers (summed over all quadrats at each sampling location in the 1 km long section) were first grouped into three classes: none (n = 63), rare (≤2 individuals, n = 24), and common (>2, n = 12). The resulting 99 observations of six independent variables were used to separate the three density groups in a discriminant analysis (PROC CANDISC, SAS Institute Inc. 1988). A discriminant analysis constructs linear functions (discriminant functions or DFs) of the original variables that best separate mussel abundance classes in a discriminant space. It also estimates the predictive power of the original variables by the relative magnitude of their standardized discriminant coefficients. Wilk's λ indicates the power of the analysis in separating groups (smaller values indicate greater success). Separation of the groups is visualized by plotting centroids along the discriminant axes and the degree of overlap among groups is illustrated by drawing a line around the half of the discriminant scores that lies closest to the centroid. Normality of all independent variables was examined and geometric-mean particle size and current velocity data were log transformed. Percent organic content and sediment compaction rates were arcsine, square-root transformed before analysis.

Channel stability

We followed temporal changes in channel-bottom profiles at five sites in mussel beds at Loving Creek, James Branch, and Jordan Creek to assess the effects of channel stability on mussel abundance. Long-term channel stability can be quite important for these long-lived mussels (Vannote and Minshall 1982). We measured the distances to the channel bottom from a level line held above the water surface by two fence posts that were permanently placed into the stream bank. After a 1-year interval, the bottom profiles were remapped. We compared percent change in stream depth between points inside mussel beds versus those outside mussel beds for each profile with a t test after an arcsine, square-root transformation.

Results

Physicochemical variables

Streams differing in mussel abundance did not differ in average water temperature ($F_{[44]} = 0.10$, $p = 0.90$), dissolved oxygen concentration ($F_{[44]} = 0.003$, $p = 0.99$), or redox potential ($F_{[44]} = 0.35$, $p = 0.70$) but did differ in specific conductivity ($F_{[44]} = 9.37$, $p = 0.0004$), water hardness ($F_{[39]}$ =

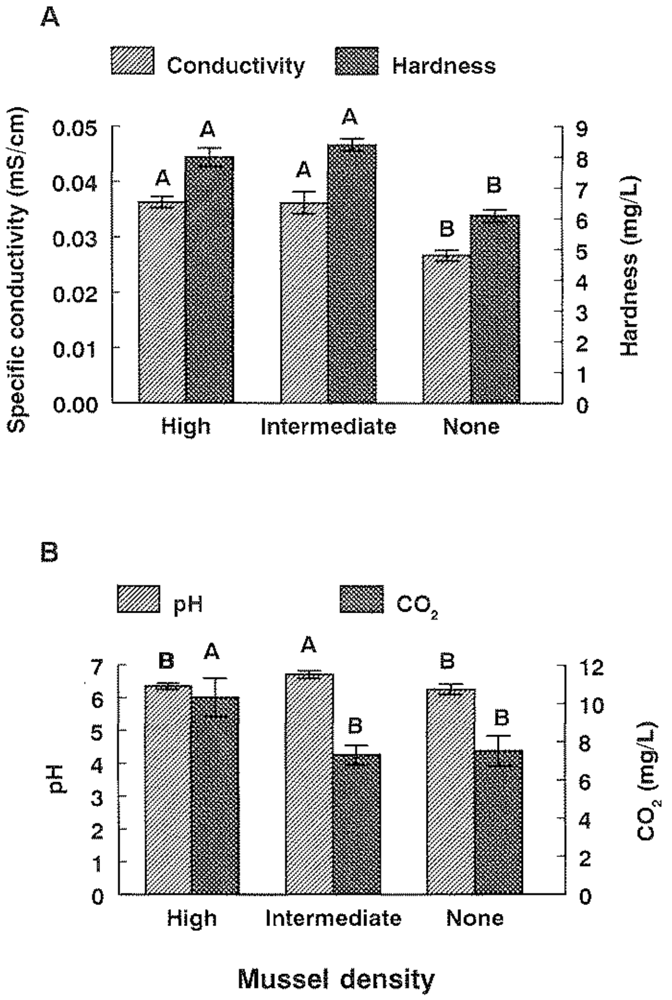


Fig. 2. Differences in several physicochemical variables among streams of divergent mussel abundance. Values are given as the mean ± SE. (A) Specific conductivity and water hardness. (B) pH and free carbon dioxide concentration. Similar letters above histograms indicate lack of significant differences based on Tukey's a posteriori tests.

17.12, $p < 0.0001$), pH ($F_{[44]} = 4.44$, $p = 0.02$), and free CO$_2$ concentration ($F_{[44]} = 4.79$, $p = 0.01$). Differences in conductivity, water hardness, and pH are probably biologically significant as streams with high or intermediate mussel densities had higher average water quality means than the stream without mussels (Fig. 2).

Microhabitat variables

The stream-channel microhabitat analysis was successful at separating the three mussel-abundance categories (Table 1). The first discriminant function separated sites with mussels from locations where mussels were absent (Fig. 3) and explained 80% of the variation among groups (squared canonical correlation = 0.21). Channel width, current velocity, and sediment compaction were positively related to mussel abundance (Table 1, Fig. 3). The negative relationship of the particle size index to mussel density again indicates (see Materials and methods) that mussel density and mean sediment size are positively correlated. Mussel density was only weakly associated with sediment organic content and channel depth. The second discriminant function explained the remaining 20% of the variation and had a lower squared canonical correlation of 0.06. Average values for habitat characteristics in each of the streams are given in Table 2.

Channel stability

At four of the five sites studied, the percent change in stream-bottom profile was significantly greater in areas of the channel without mussels than with mussels. Specifically, the percent change was significantly greater outside of the beds at Loving Creek, site 1 ($t = 3.2$, $p < 0.005$, df = 15; Fig. 4); Loving Creek, site 2 ($t = 2.3$, $p < 0.025$, df = 18); Jordan Creek, site 1 ($t = 2.57$, $p < 0.025$, df = 16); and James Branch ($t = 2.9$, $p < 0.010$, df = 12). The only site that did not show significant differences was Jordan Creek, site 2 ($t = 1.33$, $p < 0.10$, df = 15).

Discussion

Physicochemical variables

Our results suggest that Louisiana pearl shells are more likely to be found in small headwater streams with harder water and circumneutral pH values. Although also characteristic of headwater streams, other pearl shells are known to inhabit streams with higher dissolved oxygen levels, lower calcium concentrations, and that are nutrient limited and moderately acidic (Bauer 1992). In fact, Strayer (1993) found that low calcium levels were the best microhabitat predictors of *M. margaritifera* abundance in northeastern U.S. streams, although the relationship appeared indirect since these mussels were common in oligotrophic streams and eutrophication is associated with increased Ca^{2+} levels. Increased eutrophication has certainly reduced the range of pearl shells in both Europe and North America (Young and Williams 1983; Bauer 1988; Strayer 1993). Although we acknowledge that the single stream without mussels (Three Branches Creek) where water quality was monitored could be anomalous, we think that these small woodland streams in Louisiana have such soft water (specific conductivity <0.050 mS/cm) that calcium content may be a limiting factor for shell deposition, explaining the positive relationship between abundance and water hardness.

Microhabitat variables

Our data indicate that the abundance of *M. hembeli* is positively associated with several microhabitat variables. The multivariate model provided a convenient way of quantifying the type of habitats where mussels were likely to be found. Mussels were rare in deep pools that characteristically had slower flowing water and silty bottoms. Shallow, wide areas, with well-compacted substrate, or infrequent patches of larger gravel substrate, all with good flow, evidently provided more suitable microhabitats.

Other studies also suggest the importance of microhabitat variables for margaritiferids. For example, current velocity is important (Stober 1972; Vannote and Minshall 1982; Bauer 1987) and positive relationships between substrate size and abundance also occur for *M. margaritifera* (Young and Williams 1983; Bauer 1992), *M. falcata* (Stober 1972; Vannote

Table 1. Results of discriminant analysis using stream microhabitat variables to separate mussel density categories.

	Standardized coefficients						
	Proportion of variation	Channel width	Particle size	Organic content	Sediment compaction	Channel depth	Current velocity
DF_1	80%	0.51	–0.42	0.04	0.56	–0.01	0.36
DF_2	20%	0.15	0.67	–0.60	0.7	0.43	–0.02

Note: Standardized discriminant coefficients for both discriminant functions (DF) are given, along with Wilk's λ, its significance, and the proportion of the variation among groups explained by each DF. Wilk's $\lambda = 0.75$; $F = 2.32$; $p = 0.008$.

Fig. 3. Plot of mussel abundance group centroids, separated in a discriminant analysis by microhabitat variables. The outlines include the half of the discriminant scores that lie closest to the centroids and indicate the amount of overlap among the three groups. The relative importances of the original microhabitat variables in separating the groups, based on the values of standardized discriminant coefficients, are given in Table 1.

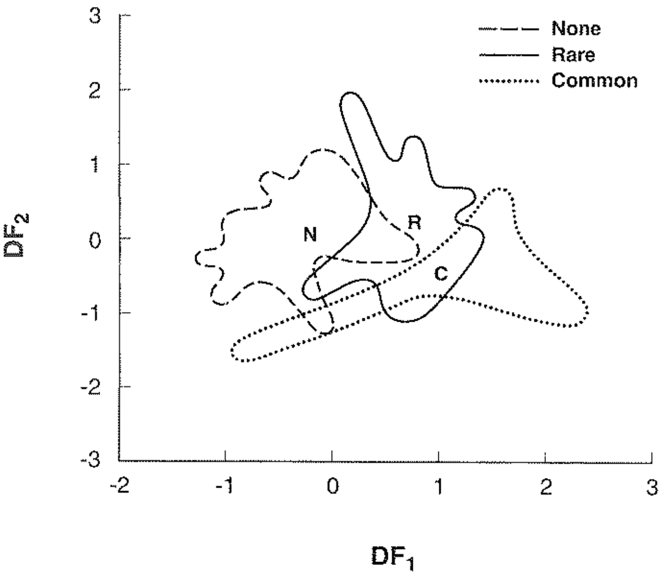
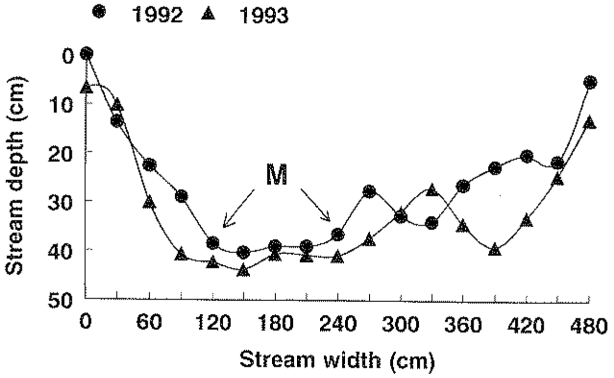


Fig. 4. A cross section of the stream bottom of Loving Creek showing the change in the channel bottom over a 1-year period. The letter M indicates the position of the mussel bed in the channel.



and Minshall 1982), as well as for *Arkansia wheeleri* (Vaughn and Pyron 1995). Layzer and Madison (1995) suggested that shear stress also limits juvenile mussel settlement and survival on a microhabitat scale.

Substrates with large particles evidently increase microhabitat stability. Cobbles or boulders lower chances of mussel dislodgement during spates (Vannote and Minshall 1982). Our data on temporal variation in channel morphology suggest channel stability is important. At three profile sites without mussels, reference posts were eliminated by spates. In general, certain mussels may have evolved adaptations to high and turbulent flow, as mussel assemblages differ between rivers with constant versus unpredictable flow (Di Maio and Corkum 1995).

These studies and our sampling results suggest that *M. hembeli* is either selecting or surviving better in areas that are stable over long intervals. Alternatively, it is possible that larger pearl mussel beds contribute to substrate stability because their high densities reduce sediment transport. At any rate, gravel–cobble substrate is rare in these Louisiana headwater streams, making it unlikely that mussels were associated with these substrates by chance alone. Habitat selection could occur, as *M. hembeli* was frequently observed crawling along the stream bottom with tracks several metres long. At Jordan Creek, an entire bed of pearl shells (≈1000 individuals) moved 7 m upstream in a 1-year period after a spate reshaped the channel, dropping the water level.

Our success in predicting the abundance of pearl shells is somewhat unique, as most investigators have had little success predicting the distributions of individual mussel species in large rivers with microhabitat variables (Holland-Bartels 1990; Strayer 1993; Strayer and Ralley 1993; Strayer et al. 1994; Haag and Warren 1998). Studies in larger rivers also have indicated that endangered species, although always rare, occur in highly diverse mussel beds (Vaughn and Pyron 1995; Hornbach et al. 1996). Even in another headwater stream, Balfour and Smock (1995) had little success in predicting the microdistribution of *Elliptio complanata* with physicochemical variables. However, discriminant analyses were successful in predicting the abundance of the endangered Quachita rock-pocketbook (*Arkansia* [*Arcidens*] *wheeleri*) and the threatened Neosho mucket (*Lampsilis rafinesqueana*) in Oklahoma rivers, based on microhabitat variables such as water hardness, depth, sediment stability, macrophyte abundance, and co-occurring mussel diversity (Vaughn and Pyron 1995; Vaughn 1998).

Although microhabitat variables appear important to the distribution of adult *M. hembeli*, juvenile mussel distributions could still be influenced by differences in other factors, such as host fish distributions (Watters 1992; Haag and Warren 1998) or spates (Layzer and Madison 1995). For example, the presence of young mussels (<5 cm shell length) is positively related in Louisiana pearl shells to the abundance of the fish host *Noturus phaeus* (Johnson and Brown 1998).

Table 2. Values (mean ± SE) of microhabitat variables used as predictor variables in the discriminanat analysis for five streams containing *M. hembeli* and two streams without mussels.

Site	Location	Channel width (cm)	Channel depth (cm)	Current velocity (cm/s)	Geometric mean substrate size (mm)	% sediment organic content	Penetrometer compaction (kPa)
Beaver Creek	Channel	331.2±21.5	22.6±2.1	1.3±0.1	0.063±0.006	1.57±0.03	668.2±224.2
	Mussel beds	392.7±6.7	8.3±1.6	4.5±1.7	0.068±0.012	2.80±0.15	1118.9±244.8
Cress Creek (eastern branch)	Channel	313.4±26.8	17.4±2.0	6.3±1.5	0.085±0.005	0.50±0.06	501.1±121.2
	Mussel beds	406.1±55.3	21.6±1.1	2.6±0.1	0.081±0.008	0.62±0.02	835.2±160.2
James Branch	Channel	287.1±14.7	14.6±2.7	2.0±0.6	0.091±0.007	0.43±0.06	686.5±141.8
	Mussel beds	249.9±31.5	10.4±0.8	5.0±1.9	0.110±0.003	0.78±0.02	965.6±205.9
Jordan Creek	Channel	380.5±22.0	23.2±5.3	2.5±0.7	0.103±0.006	0.39±0.03	359.2±89.2
	Mussel beds	420.9±29.2	13.5±2.3	4.7±0.5	0.233±0.013	1.14±0.01	940.5±180.7
Loving Creek	Channel	358.6±13.2	20.4±1.3	4.1±0.3	0.069±0.002	0.55±0.01	533.1±82.4
	Mussel beds	422.6±17.0	21.5±1.8	4.3±0.6	0.086±0.011	0.82±0.02	752.8±164.7
Cress Creek (western branch)	Control	328.1±10.7	13.9±2.2	4.6±1.1	0.063±0.037	0.76±0.02	874.1±286.1
Three Branches Creek	Control	276.1±25.1	14.1±2.9	1.9±0.5	0.059±0.008	0.73±0.01	592.6±93.8

The knowledge that microhabitat variables are important for *M. hembeli* in these small headwater streams will help conserve populations. Shallow, broad sections of streams with stable substrates need to be conserved, rather than silty, stagnant pools or areas subject to hydrological instability. Such microhabitats are being used, for example, to transplant individuals when natural beds are in danger from man-made channel alterations like bridge replacements (K.M. Brown, personal communication).

Acknowledgements

The Louisiana Natural Heritage Foundation provided money through the Endangered Species program to initiate the study and the U.S. Forest Service provided the majority of the funding. Jason Curole and Joe Nehlig helped with the fieldwork and Dr. Marianne Hollay assisted with the sediment statistical analysis. Emlyn Smith, of the U.S. Forest Service, provided assistance with the Bayou Rigolette mussel survey. Finally, we owe special thanks to Gary Lester and Steve Shively of the Louisiana Natural Heritage Program for their invaluable assistance with several aspects of this project.

References

Balfour, D.L., and Smock, L.A. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca:Unionidae) in a headwater stream. J. Freshwater Ecol. **10**: 225–268.

Bauer, G. 1987. Age structure, age specific mortality rates and population trends of the freshwater pearl mussel *Margaritifera margaritifera* in North Bavaria. Arch. Hydrobiol. **98**: 523–532.

Bauer, G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in central Europe. Biol. Conserv. **45**: 239–253.

Bauer, G. 1992. Variation in the life span and size of the freshwater pearl mussel. J. Anim. Ecol. **61**: 425–436.

Bronmark, C., and Malmquist, B. 1982. Resource partitioning between unionid mussels in a Swedish lake outlet. Holarct. Ecol. **5**: 389–395.

Buchanan, J.B. 1984. Sediment analysis. *Edited by* N.A. Holme and A.D. McIntyre. Methods for the study of marine benthos. 2nd ed. Blackwell Press, Oxford. pp. 41–65.

Burch, J.B. 1975. Freshwater unionacean clams (Mollusca: Pelecypoda) of North America. Malacological Publications, Hamburg, Michigan.

Clarke, A.H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ont.

Di Maio, J., and Corkum, L.D. 1995. Relationship between spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. Can. J. Zool. **73**: 663–971.

Haag, W.R., and Warren, M.L., Jr. 1998. Role of ecological factors and reproductive strategies in freshwater mussel communities. Can. J. Fish. Aquat. Sci. **55**: 297–306.

Holland-Bartels, L.E. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. J. N. Am. Benthol. Soc. **9**: 327–335.

Hornbach, D.J., March, J.G., Deneka, T., Troelstrup, N.H., and Perry, J.A. 1996. Factors influencing the distribution and abundance of the endangered winged mapleleaf mussel *Quadrula fragosa* in the St. Croix river, Minnesota and Wisconsin. Am. Midl. Nat. **136**: 278–286.

Johnson, P.D., and Brown, K.M. 1998. Intraspecific variation in the life history of the Louisiana pearl shell mussel *Margaritifera hembeli*. Freshwater Biol. **40**: 317–330.

Johnson, R.I. 1983. *Margaritifera marrianae*, a new species of Unionacea (Bivalvia: Margaritiferidae) from the Mobile–Alabama–Coosa and Escambia river systems, Alabama. Occasional papers on molluscs. Mus. Comp. Zool. (Harv. Univ.) Annu. Rep. **4**: 299–304.

Layzer, J.B., and Madison, L.M. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. Regul. Rivers Res. Manag. **10**: 329–345.

Morris, T.J., and Corkum, L.D. 1996. Assemblage structure of freshwater mussels (Bivalvia: Unionidae) in rivers with grassy and forested riparian zones. J. N. Am. Benthol. Soc. **15**: 576–586.

Neves, R.J., and Widlak, J.C. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. Am. Malacol. Bull. **5**: 1–7.

Neves, R.J., Bogan, A.E., Williams, J.D., Ahlstedt, S.A., and Hartfield, P.W. 1998. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. *In* Aquatic fauna in peril: the southeastern perspective. *Edited by* G.W. Benz and D.E. Collins. Spec. Publ. No. 1, Southeast Aquatic Research Institute, Chattanooga, Tenn. pp. 43–85.

Salmon, A., and Green, R. 1985. Environmental determinants of unionid clam distribution in the middle Thames River, Ontario. Can. J. Zool. **61**: 832–838.

SAS Institute Inc. 1988. PC-SAS user's manual: statistics. SAS Institute, Cary, N.C.

Shelton, D.N. 1997. Observations on the life history of the Alabama pearl shell *Margaritifera marrianae* R.I. Johnson, 1983. *In* Conservation and management of freshwater mussels II: Initiatives for the future, November 1995. *Edited by* K.S. Cummings, A.C. Buchanan, C.A. Mayer, and T.J. Naimo. Upper Mississippi River Conservation Committee, Rock Island, Ill. pp. 26–27.

Stern, E.M. 1983. Depth distribution and density of freshwater mussels (unionidae) collected with scuba from the lower Wisconsin and St. Croix rivers. Nautilus, **97**: 36–42.

Stober, Q.J. 1972. Distribution and age of *Margaritifera margaritifera* (L.) in a Madison river (Montana, U.S.A.) mussel bed. Malacologia, **11**: 343–350.

Strayer, D.L. 1981. Notes on the microhabitats of unionid mussels in some Michigan streams. Am. Midl. Nat. **106**: 411–415.

Strayer, D.L. 1993. Microhabitats of freshwater mussels (Bivalvia: Unionacea) in streams of the northern Atlantic slope. J. N. Am. Benthol. Soc. **12**: 236–246.

Strayer, D.L., and Ralley, J. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. J. N. Am. Benthol. Soc. **12**: 247–258.

Strayer, D.L., Hunter D.C, Smith L.C., and Borg, C.K. 1994. Distribution, abundance, and roles of freshwater clams (Bivalvia: Unionidae) in the freshwater tidal Hudson River. Freshwater Biol. **31**: 239–248.

Tevesz, J.S., and McCall, P.L. 1979. Evolution of substratum preference in bivalves (Mollusca). J. Paleontol. **53**: 112–120.

Vannote, R.L., and Minshall, G.W. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. Proc. Nat. Acad. Sci. U.S.A. **79**: 4103–4107.

Vaughn, C.C. 1998. Determination of the status and habitat preferences of the Neosho mucket in Oklahoma. Report to the Oklahoma Department of Wildlife Conservation, Oklahoma Natural Heritage Inventory and Oklahoma Biological Survey, Norman.

Vaughn, C.C., and Pyron, M. 1995. Population ecology of the endangered Ouachita rock-pocketbook mussel, *Arkansia wheeleri* (Bivalvia: Unionidae), in the Kiamichi River, Oklahoma. Am. Malacol. Bull. **11**: 145–151.

Watters, G.T. 1992. Unionids, fishes and the species area curve. J. Biogeogr. **19**: 481–490.

Way, C.M., Miller A.C., and Payne, B.S. 1989. The influence of physical factors on the distribution and abundance of freshwater mussels (Bivalvia: Unionidae) in the lower Tennessee river. Nautilus, **103**: 96–98.

Williams, J.D., Warren, M.L., Cummings, K.S., Harris, J.L., and Neves, R.J. 1992. Conservation status of freshwater mussels of the United States and Canada. Fisheries, **18**: 6–22.

Young, M., and Williams, J. 1983. Redistribution and local recolonization by the freshwater pearl mussel *Margaritifera margaritifera*. J. Conchol. **31**: 225–234.