AN ABSTRACT OF THE THESIS OF

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Abstract Approved: Elmer J. Finck

A multitude of environmental factors influence the community structure of freshwater mussels. To determine which variables are most important in structuring mussel communities, and what species-environment relationships exist, I quantitatively sampled mussels at eight locations on the Neosho and Cottonwood rivers, and measured 20 physical and water chemistry variables. Using mussel abundance and biomass as dependent variables, Canonical correspondence analysis (CCA) showed that chemical (total hardness, alkalinity, pH, and total acidity) and stream size (stream width, water depth, and current velocity) variables constituted the main environmental gradient, while substratum formed a secondary gradient. Both CCA ordinations showed consistent species-environment relationships. Quadrula pustulosa, Quadrula quadrula, and Obliquaria reflexa were positioned nearer to the center of the ordination diagrams, suggesting these species may have little environmental preference. Amblema plicata, Leptodea fragilis, Potamilus purpuratus, Tritogonia verrucosa, and Truncilla donaciformis were positioned more toward the

periphery of the ordination diagrams, which suggests more specific environmental preferences. Water chemistry and stream size variables also accounted for the majority of significant correlations to the abundance and biomass of mussel species. Leptodea fragilis and Truncilla donaciformis were positively correlated with basic conditions, while A. plicata and O. reflexa were negatively correlated with basic conditions. Amblema plicata and Elliptio dilatata correlated positively with stream width and water depth. These data should form a basis for studies designed to determine causal factors in the population and community dynamics of freshwater mussels.

Fish are thought to be the main dispersal mechanism of unionid mussels, and thus should influence the amount of gene flow. To test predictions of genetic structure based on dispersal ability, I compared the genetic variability of O. pustulosa, a mussel species that is known to parasitize at least six species of fish, and O. reflexa, a mussel species that is thought to complete development without parasitism. I collected individuals from six locations on the Neosho and Cottonwood rivers, and measured genetic variability at 15 presumptive loci using starch gel electrophoresis. Although few significant differences were observed, O. pustulosa generally exhibited higher polymorphism, allelism, and heterozygosity, while O. reflexa had higher inbreeding among populations. Populations of O. reflexa that were closer in proximity were more genetically

similar, and genetic distance between Q. reflexa populations decreased farther downstream. There was no apparent geographic logic in similarity among populations of Q. pustulosa. These data give support to the hypothesis that fish affect the genetic structure of unionid mussels. As we increase our knowledge concerning the host species of freshwater mussels, more comparisons between species should be made to gain a better understanding of unionid evolution.

ECOLOGY AND GENETICS OF FRESHWATER MUSSELS IN THE NEOSHO AND COTTONWOOD RIVERS

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Community structure of freshwater mussels in the Neosho and Cottonwood rivers of Eastern Kansas

INTRODUCTION

Unionid mussels are a diverse and dominant faunal component of benthic communities in many riverine and lacustrine environments. They often comprise a major portion of the macroinvertebrate density or biomass (Mann 1964, Negus 1966, Fisher and Tevesz 1976, James 1985, Tevesz et al. 1985, Miller et al. 1986, James 1987, Hanson et al. 1988a, Nalepa and Gauvin 1988). Although a multitude of environmental variables are thought to influence the population dynamics and community structure of unionids, substratum type (Harman 1972, Stern 1983, Way et al. 1989, Holland-Bartels 1990), current velocity (Cvancara et al. 1966, Stern 1983, Way et al. 1989, Holland-Bartels, 1990), and water depth (Cvancara 1972, Haukioja and Hakala 1974, Hanson et al. 1988b, Huebner et al. 1990) are the most commonly addressed. The effects of substratum type, current velocity, and water depth on habitat selection may vary among species, with some having a wider tolerance than others (Huehner 1987). Unionids in general have broad habitat overlap (Strayer 1981), probably due to morphologic characteristics of the species (Tevesz and McCall 1979), or phenotypic plasticity of shell characteristics that are adapted to the environment (Kat 1982). In any case, it has been difficult to separate variables that most influence

their distribution and abundance, possibly because of variability among sites (Strayer 1981, Way et al. 1989). The overall species richness of unionids would predict habitat specialization, however they are much less habitat specific than marine bivalves (Tevesz and McCall 1979). This has certainly added to the difficulty in showing consistent species-environment relationships.

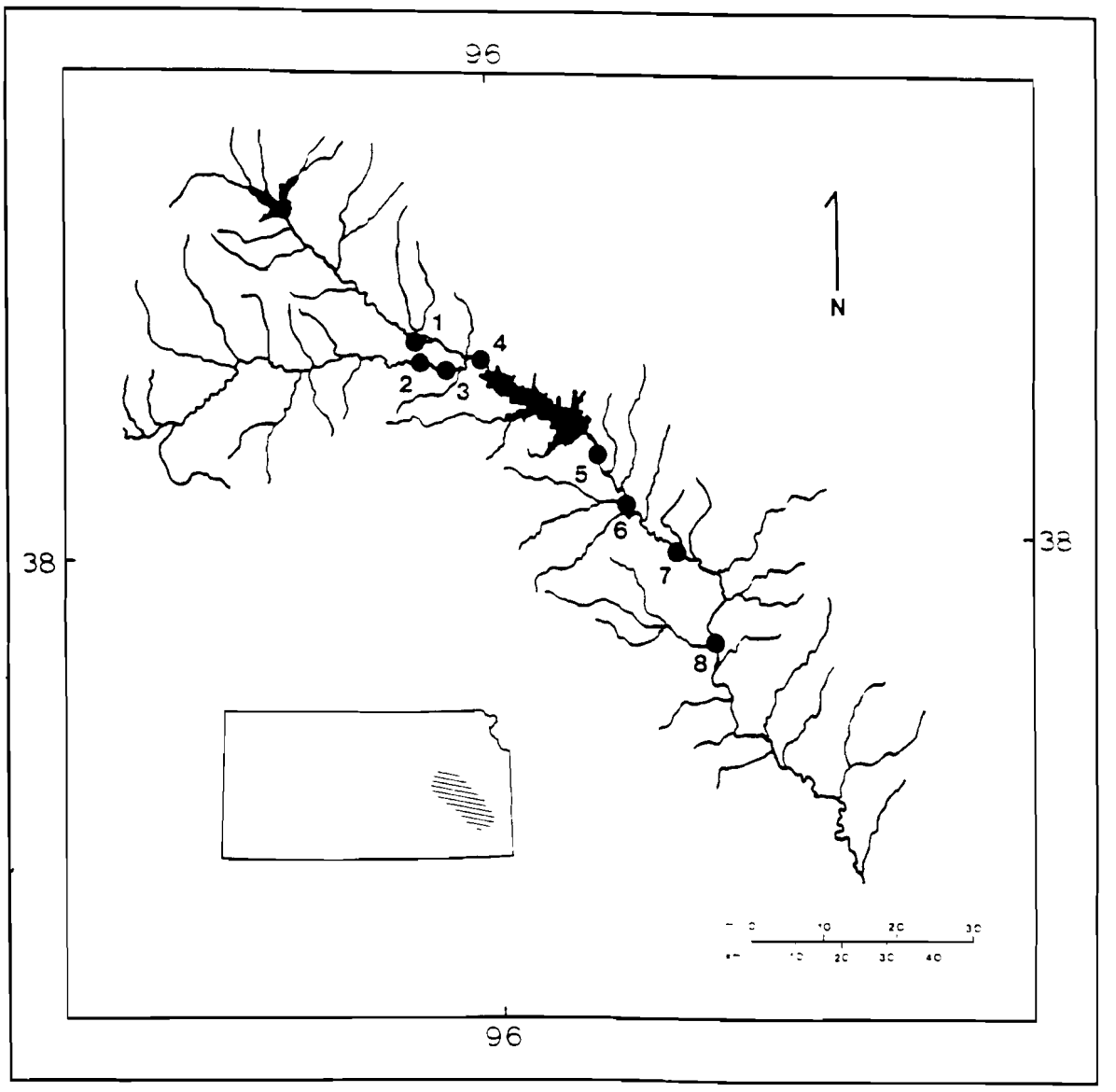
The potentially large number of factors that influence mussel community structure and the apparent similarity in habitat selection among species requires a conventional analytical method to discern species relationships to important abiotic elements. I used a multivariate approach in my study to 1) determine if substrate, current velocity, and water depth are the most important environmental variables in structuring unionid communities, and 2) determine what species-environment relationships exist for the mussel fauna of the Neosho and Cottonwood rivers in eastern Kansas.

MATERIALS AND METHODS

I systematically sampled mussels from 23 July - 20 September 1991 at eight locations on the Neosho and Cottonwood rivers in eastern Kansas (Fig. 1, Appendix 1). Using methods modified from Isom and Gooch (1986), I directed line transects perpendicular to the stream at 10 m intervals along the shore, and samples were taken at 5 m intervals along transects until 20 samples were obtained. The first sample point of each transect was staggered from 1 to 5 m from the shore, to evenly sample the nearshore portions of each site. This method was altered at site 7 where sampling was within 15 m from shore because the water became too deep to adequately sample beyond that point. At each sample point a 1 m^2 steel quadrat was dropped and the substrate was searched by hand for mussels. Given that sampling mussels in this manner is biased against small-sized species and juveniles (Van Cleave 1940, Haukioja and Hakala 1974, Miller and Payne 1988, Nalepa and Gauvin 1988), substrate was removed to a depth of 10 - 15 cm, placed in a 1.5 m^2 floating PVC quadrat with 6 mm mesh, and searched for small individuals. Mussels from each quadrat were placed in separate bags for transport back to the laboratory.

Physical and chemical variables were measured at each location. At each sample point I recorded substrate, classified as silt, mud, sand, gravel, rock, or a combination of these (Fisher and Tevesz 1976, Strayer 1981,

Figure 1. Location of study sites on the Neosho and Cottonwood rivers. Site numbers correspond to those in Appendix 1. State of Kansas (inset).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Tevesz et al. 1985), current velocity, measured with a manometer modified after Welch (1948), depth, temperature, and proximity to shore, classified as midstream or quarter nearest either shore. At each site I recorded stream width, and collected water samples to measure turbidity, dissolved oxygen, pH, alkalinity, total hardness, acidity, nitrate, phosphate, and sulfate using a Hach water chemistry kit. I measured all water chemistry variables in the laboratory except dissolved oxygen and pH which were recorded on location at each site.

In the laboratory I cleaned individual mussels with a brush to remove external periphyton. Soft tissue was removed, blotted with paper towel, and weighed to the nearest 0.1 g. To estimate individual dry mass, an additional 50 individuals representing nine species were collected separately. These animals were processed as above, placed on preweighed aluminum foil, and dried for 96hr in a non-convection oven at 60°C. These wet mass / dry mass data were used to formulate the regression equation, dry mass = -0.1007 + 0.2153(wet mass), in which dry mass could be predicted for all individuals.

Canonical correspondence analysis (CCA) was used to create a community ordination of correlations between species abundance and biomass and environmental data using CANOCO (Ter Braak 1988). This statistical procedure is a direct gradient analysis that produces CCA axes which are

linear combinations of environmental variables. The resulting species scores are parameters of response curves of species with respect to the ordination axis (Ter Braak 1988). Therefore, this method produces a picture of community structure in which sites, species, and environmental variables are represented and shows species-environment relationships. Sites and species are represented as points on the ordination diagram. For better display of the environmental gradient, and easier interpretation of the ordination diagram, sites were designated as Cottonwood River (sites 2 and 3), upper Neosho River (sites 1 and 4), and lower Neosho River (sites 5, 6, 7, and 8). Environmental variables in the ordination diagram are represented by arrows, which point toward the direction of the steepest increase of that variable, i.e., higher pH in the direction the arrow is pointing, lower pH in the opposite direction. The length of the arrows indicates the magnitude of correlations along the gradient, i.e., the higher the correlation of an environmental variable to the CCA axes, the longer the arrow. Eigenvalues are a measure of between site variability or separation of species distributions along the environmental axes, thus, high eigenvalues represent long environmental gradients.

Of the 21 species of mussels collected 13 occurred in < 5% of the samples (1 m^2 = 1 sample) and thus were eliminated from the analysis, because rare species, which are perceived

as outliers, may obscure the analysis of the overall data (Gauch 1982, Edds 1993). Significance of the overall ordination and individual axes were tested using a Monte Carlo permutation test. I also tested the relationship between species and environmental data using Pearson's product moment correlation analysis. Colinearity was detected for nitrate, sulfate and phosphate and are not discussed. Sequential Bonferoni adjustment (Rice 1989) was used to determine levels of significance of correlation coefficients.

RESULTS

Community Composition

A total of 315 individuals representing 21 species of unionid mussels was collected in 160 m^2 of sampling (Table 1). Mussels were found in 85% of the quadrats sampled. Quadrula pustulosa, Quadrula quadrula, Obliquaria reflexa, Leptodea fragilis, and Amblema plicata made up 71% of the total fauna. Four species, Truncilla donaciformis, Potamilus purpuratus, Elliptio dilatata, and Tritogonia verrucosa, composed between 3 - 6%, while the remaining 12 species accounted for 13% of the total fauna.

Mean density of mussels was 2 m^{-2} (range 0 - 8) and mean shell free biomass was 16.4 g m^{-2} (range 0 - 87.4 g). Species occurrence, density, and biomass were variable from site to site (Appendices 2 and 3). Quadrula pustulosa, Q. quadrula, and L. fragilis were the only species found at all sites, and 38% of the species were found at only one site. Seven species, Amblema plicata, E. dilatata, L. fragilis, O. reflexa, Q. pustulosa, Q. quadrula, and T. donaciformis, had the highest density at one or more sites (Appendix 2). Only five species, A. plicata, Lasmigona complanata, L. fragilis, Q. pustulosa, and T. verrucosa had the highest biomass at one or more sites (Appendix 3).

Community Ordination--Abundance

The overall community ordination and CCA axis 1 were both statistically significant (Monte Carlo test $P < 0.01$).

Table 1. Species[a] and number of unionid mussels collected in the Neosho and Cottonwood rivers.

Scientific name	Common name	Number collected
Amblema plicata	three ridge	36
Anodonta grandis	giant floater	1
Ellipsaria lineolata	butterfly	2
Elliptio dilatata	spike	11
Fusconaia flava	Wabash pigtoe	4
Lampsilis ovata	pocketbook	6
Lampsilis teres	yellow sandshell	1
Lasmigona complanata	white heelsplitter	7
Leptodea fragilis	fragile papershell	44
Obliquaria reflexa	threehorn wartyback	44

[a]Scientific and common names follow Turgeon et al. (1988)

Table 1. Continued.

Scientific name	Common name	Number collected
Pleurobema coccineum	round pigtoe	2
Potamilus ohiensis	pink papershell	1
Potamilus purpuratus	bleufer	11
Quadrula metanevra	monkeyface	9
Quadrula nodulata	wartyback	7
Quadrula pustulosa	pimpleback	55
Quadrula quadrula	mapleleaf	44
Strophitus undulatus	squawfoot	1
Tritogonia verrucosa	pistolgrip	10
Truncilla donaciformis	fawnsfoot	18
Truncilla truncata	deertoe	1

The first four axes had eigenvalues of 0.43, 0.22, 0.19, and 0.12 respectively, and accounted for approximately 82% of the variability in species distributions along the measured variables. CCA axes 1 and 2 explained 37% and 19% of the variation, respectively. CCA axis 1 had a gradient length of 3.96 standard deviations and represents a water chemistry - stream size gradient (Fig. 2). Environmental variables that were significantly correlated with CCA 1 were dissolved oxygen, pH, total acidity, alkalinity, total hardness, current velocity, stream type, and water depth (Table 2). Species that scored highest on CCA 1 were T. donaciformis, T. verrucosa, and L. fragilis, which were species most abundant in the Cottonwood River, and P. purpuratus, and A. plicata, which were species most abundant in the lower Neosho River (Fig. 2). Water chemistry and stream size variables also accounted for most of the significant correlations between individual species abundance and environmental variables (Tables 3 and 4). Abundance of L. fragilis and T. donaciformis was positively correlated with more basic conditions, while A. plicata and O. reflexa were negatively correlated with more basic conditions (Table 3). The abundance of A. plicata and E. dilatata was positively correlated with stream width and water depth (Table 4). CCA axis 2 was also significant ($P < 0.05$) and represents a substrate gradient (4.15 SD) (Fig. 2) with only the

Figure 2. Canonical correspondence analysis ordination diagram of axes 1 and 2 using species abundance. Squares = samples from the Cottonwood River (sites 2 and 3), circles = upper Neosho River (sites 1 and 4), triangles = lower Neosho River (sites 5, 6, 7, and 8). Arrows are the projection of environmental variables: TEMP = temperature, DO = dissolved oxygen, PH = pH, ACID = total acidity, ALK = alkalinity, HARD = total hardness, TURB = turbidity, DEPTH = water depth, CURR = current velocity, TYPE = stream type, WIDTH = stream width, PROX = proximity to shore, SILT = silt, SAND = sand, MUD = mud, GRAV = gravel, ROCK = rock. Species abbreviations: Ampl = Amblema plicata, Lefr = Leptodea fragilis, Obre = Obliquaria reflexa, Popu =Potamilus purpuratus, Qupu = Quadrula pustulosa, Ququ = Quadrula quadrula, Trve = Tritogonia verrucosa, and Trdo = Truncilla donaciformis.

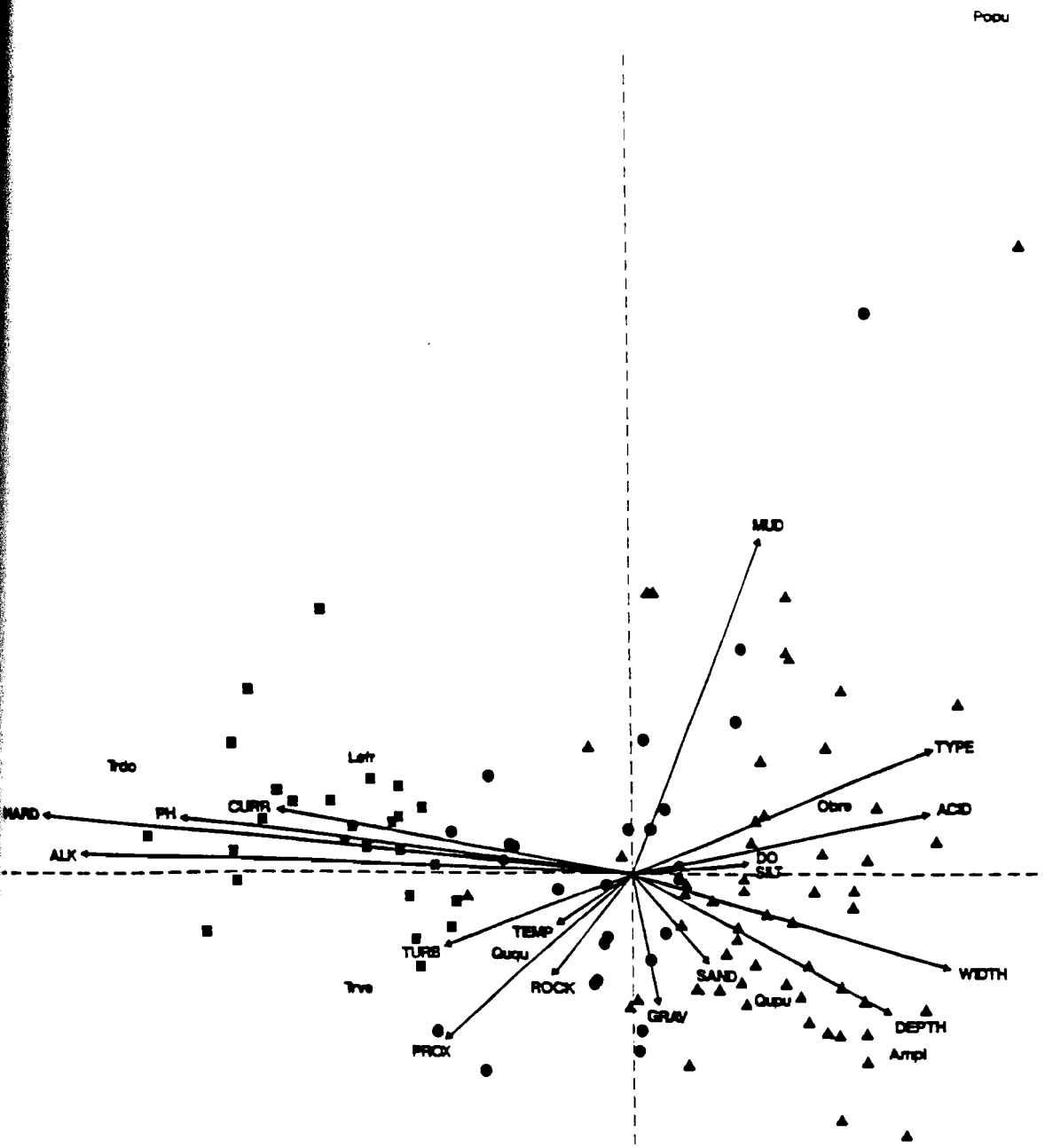
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Table 3. Correlation coefficients between water chemistry variables and species abundance of freshwater mussels from the Neosho and Cottonwood rivers. * P < 0.01, ** P < 0.001, *** P < 0.0001. Temp = temperature, DO = dissolved oxygen, Acid = total acidity, Alk = alkalinity, Hard = total hardness, Turb = turbidity.

Species	Variable						
	Temp	DO	pH	Acid	Alk	Hard	Turb
Amblema plicata	-0.115	-0.052	-0.340***	0.024	-0.291**	-0.252*	0.061
Anodonta grandis	-0.191	0.036	0.120	-0.014	0.061	-0.061	-0.028
Ellipsaria lineolata	0.026	-0.023	-0.170	-0.020	-0.068	-0.087	0.200
Elliptio dilatata	0.115	-0.164	0.000	-0.034	-0.114	-0.147	-0.034
Fusconaia flava	-0.010	-0.070	0.049	-0.023	-0.033	-0.101	-0.029
Lampsilis ovata	0.056	0.003	-0.199	0.059	-0.164	-0.146	0.108
Lampsilis teres	-0.191	0.036	0.120	-0.014	0.061	-0.061	-0.028

Table 3. Continued.

Species	Variable						
	Temp	DO	pH	Acid	Alk	Hard	Turb
Lasmigona complanata	-0.244**	0.076	0.081	-0.034	0.053	-0.101	-0.050
Leptodea fragilis	-0.007	0.024	0.258**	-0.259**	0.305***	0.298***	0.171
Obliquaria reflexa	-0.168	0.160	-0.152	0.137	-0.212	-0.284**	0.001
Pleurobema coccineum	-0.009	-0.023	-0.170	-0.020	-0.068	-0.087	0.200
Potamilus ohiensis	-0.019	-0.016	-0.120	-0.014	-0.048	-0.061	0.141
Potamilus purpuratus	0.016	0.014	-0.148	0.018	-0.144	-0.119	-0.110
Quadrula metanevra	0.039	0.047	-0.210	0.057	-0.163	-0.084	-0.079
Quadrula nodulata	0.035	0.067	-0.067	-0.201	0.004	-0.085	-0.081
Quadrula pustulosa	-0.066	0.057	-0.105	-0.098	-0.042	-0.172	0.108
Quadrula quadrula	0.051	-0.027	0.108	-0.185	0.173	0.135	-0.113

Table 3. Continued.

Species	Variable						
	Temp	DO	pH	Acid	Alk	Hard	Turb
Strophitus undulatus	0.080	0.036	0.060	-0.128	0.116	0.152	0.070
Tritogonia verrucosa	0.164	0.168	0.059	-0.139	0.129	0.227	-0.014
Truncilla donaciformis	0.040	-0.149	0.141	-0.117	0.238*	0.322***	0.172
Truncilla truncata	-0.191	0.036	0.120	-0.014	0.061	-0.061	-0.028

Table 4. Correlation coefficients between stream size variables and species abundance of freshwater mussels from the Neosho and Cottonwood rivers. * P < 0.01, ** P < 0.001, *** P < 0.0001. Depth = Water depth, Curr = current velocity, Type = stream type, Width = stream width, Prox = Proximity to shore.

Species	Variable				
	Depth	Curr	Type	Width	Prox
Amblema plicata	0.296***	-0.211	0.137	0.314***	-0.029
Anodonta grandis	0.093	0.004	0.028	-0.127	-0.061
Ellipsaria lineolata	0.022	-0.068	0.039	0.082	0.147
Elliptio dilatata	0.269**	-0.163	0.266	0.360***	-0.145
Fusconaia flava	0.193	-0.095	0.045	0.133	-0.032
Lampsilis ovata	0.050	-0.106	0.069	0.144	-0.014
Lampsilis teres	0.093	0.004	0.028	-0.127	-0.060

Table 4. Continued.

Species	Variable				
	Depth	Curr	Type	Width	Prox
Lasmigona complanata	0.075	-0.046	0.133	-0.145	0.079
Leptodea fragilis	0.040	-0.121	0.228	-0.007	-0.098
Obliquaria reflexa	0.052	0.059	0.026	-0.165	-0.065
Pleurobema coccineum	0.105	-0.039	0.039	0.082	-0.086
Potamilus ohiensis	-0.021	-0.028	0.028	0.058	-0.061
Potamilus purpuratus	0.012	-0.068	0.125	0.112	-0.124
Quadrula metanevra	0.066	-0.085	0.048	0.035	0.131
Quadrula nodulata	-0.055	-0.046	-0.002	0.067	0.071
Quadrula pustulosa	0.157	-0.180	0.039	0.073	0.076
Quadrula quadrula	-0.063	0.161	-0.150	0.037	0.177

Table 4. Continued.

Species	Variable				
	Depth	Curr	Type	Width	Prox
Strophitus undulatus	0.041	0.004	0.028	-0.035	0.104
Tritogonia verrucosa	-0.074	0.007	-0.106	-0.038	0.017
Truncilla donaciformis	-0.119	0.146	-0.138	-0.140	0.205
Truncilla truncata	0.069	0.004	0.028	-0.127	0.104

occurrence of mud and proximity to shore being significantly correlated with CCA 2 (Table 2). The only species that scored high on CCA 2 was P. purpuratus. There were also few significant correlations between species abundance and substrate variables (Table 5). Elliptio dilatata correlated negatively with sand and T. verrucosa correlated positively with rock (Table 5).

Community Ordination--Biomass

CCA axis 1 was significant (Monte Carlo test $P < 0.01$), although the overall ordination was not significant. The first four axes had eigenvalues 0.56, 0.38, 0.26, and 0.18 respectively, and approximately 90% of the variability in species biomass was explained by the first four axes combined. CCA axes 1 and 2 explained 36% and 25% of the variation respectively. As with the ordination using species abundance, CCA axis 1 shows a water chemistry - stream size gradient (Fig. 3) with a gradient length of 4.33 standard deviations. Environmental variables that were significantly correlated with CCA 1 were alkalinity, pH, total hardness, current velocity, stream type, stream width, and water depth (Table 2). Although there were fewer significant correlations between individual species biomass and environmental variables than with species abundance, these variables still accounted for the majority of significant correlations (Tables 6 and 7). Consistent with abundance, biomass of L. fragilis was positively correlated

Table 5. Correlation coefficients between substrate variables and species abundance of freshwater mussels from the Neosho and Cottonwood rivers. * P < 0.01, ** P < 0.001, *** P < 0.0001.

Species	Variable				
	Silt	Mud	Sand	Gravel	Rock
Amblema plicata	0.075	-0.085	0.011	0.084	-0.066
Anodonta grandis	0.096	-0.017	0.054	-0.256*	-0.048
Ellipsaria lineolata	-0.093	-0.024	0.077	0.035	-0.068
Elliptio dilatata	0.152	-0.040	-0.277**	-0.076	-0.115
Fusconaia flava	0.025	-0.028	-0.121	0.040	-0.079
Lampsilis ovata	0.038	-0.042	0.064	0.061	-0.045
Lampsilis teres	0.096	-0.017	0.054	-0.256*	-0.048
Lasmigona complanata	0.118	-0.040	0.013	0.058	-0.053

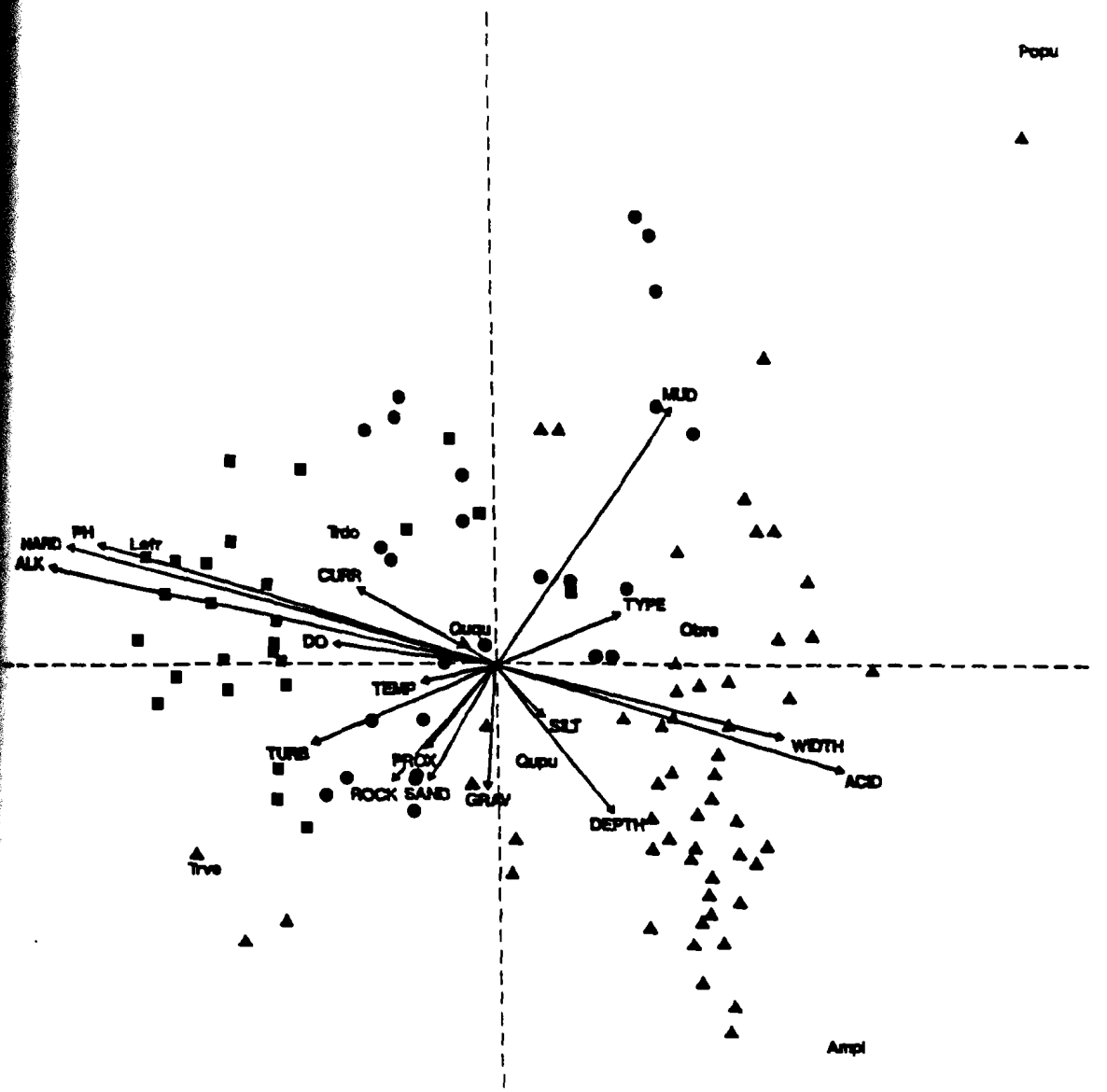
Table 5. Continued.

Species	Variable				
	Silt	Mud	Sand	Gravel	Rock
Leptodea fragilis	0.102	-0.092	0.001	-0.109	-0.062
Obliquaria reflexa	0.003	-0.105	0.169	0.034	-0.021
Pleurobema coccineum	0.136	-0.024	0.077	0.035	-0.068
Potamilus ohiensis	0.096	-0.017	0.054	0.025	-0.048
Potamilus purpuratus	-0.021	0.146	-0.147	-0.072	-0.087
Quadrula metanevra	-0.098	-0.030	0.095	0.043	0.119
Quadrula nodulata	0.008	-0.037	0.012	-0.033	-0.048
Quadrula pustulosa	0.053	-0.068	0.011	0.028	-0.084
Quadrula quadrula	-0.068	-0.098	-0.189	0.034	0.067
Strophitus undulatus	0.096	-0.017	0.054	0.025	-0.048

Table 5. Continued.

Species	Variable				
	Silt	Mud	Sand	Gravel	Rock
Tritogonia verrucosa	-0.056	-0.055	-0.100	-0.011	0.251*
Truncilla donaciformis	-0.168	-0.060	-0.009	0.086	0.064
Truncilla truncata	0.096	-0.017	0.054	0.025	-0.048

Figure 3. Canonical correspondence analysis ordination diagram of axes 1 and 2 using species biomass. Squares = samples from the Cottonwood River (sites 2 and 3), circles = upper Neosho River (sites 1 and 4), triangles = lower Neosho River (sites 5, 6, 7, and 8). Arrows are the projection of environmental variables: TEMP = temperature, DO = dissolved oxygen, PH = pH, ACID = total acidity, ALK = alkalinity, HARD = total hardness, TURB = turbidity, DEPTH = water depth, CURR = current velocity, TYPE = stream type, WIDTH = stream width, PROX = proximity to shore, SILT = silt, SAND = sand, MUD = mud, GRAV = gravel, ROCK = rock. Species abbreviations: Ampl = Amblema plicata, Lefr = Leptodea fragilis, Obre = Obliquaria reflexa, Popu =Potamilus purpuratus, Qupu = Quadrula pustulosa, Ququ = Quadrula quadrula, Trve = Tritogonia verrucosa, and Trdo = Truncilla donaciformis.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with more basic conditions, while biomass of A. plicata was negatively correlated with pH (Table 6), biomass of E. dilatata was positively correlated with water depth and stream width, and A. plicata was positively correlated with water depth (Table 7). Again there were few significant correlations between substrate variables and species biomass (Table 8). Elliptio dilatata was negatively correlated with sand (Table 8). Species that scored highest on CCA 1 were L. fragilis and T. verrucosa, species which were most common in the Cottonwood and upper Neosho rivers, and P. purpuratus and A. plicata, species that were more common in the lower Neosho River. CCA 2 was also significant ($P < 0.05$) and seems to represent a substrate - water quality gradient (4.31 SD) (Fig. 3). Variables with significant correlations to CCA 2 were mud, rock, water depth, pH, alkalinity, and total hardness (Table 2). Species with high scores on CCA 2 were P. purpuratus and A. plicata.

Table 6. Correlation coefficients between water chemistry variables and species biomass of freshwater mussels from the Neosho and Cottonwood rivers. * P < 0.01, ** P < 0.001, *** P < 0.0001. Temp = temperature, DO = dissolved oxygen, Acid = total acidity, Alk = alkalinity, Hard = total hardness, Turb = turbidity.

Species	Variable						
	Temp	DO	pH	Acid	Alk	Hard	Turb
Amblema plicata	0.108	-0.026	-0.311***	0.009	-0.207	-0.202	-0.007
Anodonta grandis	-0.154	0.024	0.109	-0.015	0.058	-0.061	-0.015
Ellipsaria lineolata	0.032	-0.021	-0.139	-0.018	-0.048	-0.075	0.053
Elliptio dilatata	0.102	-0.128	-0.005	-0.033	-0.086	-0.136	-0.024
Fusconaia flava	0.051	-0.073	0.008	-0.021	-0.045	-0.086	-0.015
Lampsilis ovata	0.039	-0.018	-0.217	0.001	-0.107	-0.117	0.037
Lampsilis teres	-0.154	0.024	0.109	-0.015	0.058	-0.061	-0.015

Table 6. Continued.

Species	Variable						
	Temp	DO	pH	Acid	Alk	Hard	Turb
Lasmigona complanata	-0.199	0.048	0.089	-0.018	0.050	-0.099	-0.034
Leptodea fragilis	0.117	0.062	0.183	-0.377***	0.320***	0.410***	0.042
Obliquaria reflexa	-0.074	0.105	-0.143	0.118	-0.158	-0.219	0.067
Pleurobema coccineum	-0.006	-0.022	-0.150	-0.020	-0.052	-0.081	0.057
Potamilus ohiensis	-0.011	-0.017	-0.113	-0.015	-0.039	-0.061	0.043
Potamilus purpuratus	0.045	-0.002	-0.160	0.022	-0.130	-0.108	-0.054
Quadrula metanevra	0.089	0.035	-0.232	0.066	-0.161	-0.097	-0.043
Quadrula nodulata	0.045	0.035	-0.182	0.100	-0.140	-0.123	0.007
Quadrula pustulosa	-0.054	0.055	0.022	-0.134	-0.079	-0.074	-0.025
Quadrula quadrula	0.022	0.032	0.082	-0.198	0.178	0.136	-0.078

Table 6. Continued.

Species	Variable						
	Temp	DO	pH	Acid	Alk	Hard	Turb
Strophitus undulatus	0.071	0.024	0.053	-0.130	0.106	0.154	0.019
Tritogonia verrucosa	0.141	0.119	0.043	-0.111	0.105	0.208	-0.025
Truncilla donaciformis	0.048	-0.109	0.068	-0.050	0.153	0.216	0.007
Truncilla truncata	-0.154	0.024	0.109	-0.015	0.058	-0.061	-0.015

Table 7. Correlation coefficients between stream size variables and species biomass of freshwater mussels from the Neosho and Cottonwood rivers. * P < 0.01, ** P < 0.001, *** P < 0.0001. Depth = Water depth, Curr = current velocity, Type = stream type, Width = stream width, Prox = Proximity to shore.

Species	Variable				
	Depth	Curr	Type	Width	Prox
Amblema plicata	0.271**	-0.035	0.136	0.229	-0.007
Anodonta grandis	0.093	-0.006	0.028	-0.122	-0.061
Ellipsaria lineolata	0.017	-0.009	0.035	0.071	0.126
Elliptio dilatata	0.249*	-0.018	0.063	0.328***	-0.137
Fusconaia flava	0.173	-0.011	0.040	0.180	-0.070
Lampsilis ovata	0.047	-0.016	0.059	0.108	-0.051
Lampsilis teres	0.093	-0.006	0.028	-0.122	-0.061

Table 7. Continued.

Species	Variable				
	Depth	Curr	Type	Width	Prox
Lasmigona complanata	0.106	-0.014	0.090	-0.151	0.097
Leptodea fragilis	0.056	-0.026	0.074	-0.109	0.001
Obliquaria reflexa	0.020	0.038	0.230	-0.006	-0.125
Pleurobema coccineum	0.093	-0.009	0.038	0.076	-0.082
Potamilus ohiensis	-0.019	-0.007	0.028	0.057	-0.061
Potamilus purpuratus	0.021	-0.018	0.091	0.128	-0.096
Quadrula metanevra	0.113	-0.012	0.058	0.042	0.125
Quadrula nodulata	-0.088	-0.016	-0.062	0.073	-0.014
Quadrula pustulosa	0.080	-0.038	0.012	-0.011	0.093
Quadrula quadrula	-0.069	-0.025	-0.133	-0.004	0.174

Table 7. Continued.

Species	Variable				
	Depth	Curr	Type	Width	Prox
Strophitus undulatus	0.042	0.006	0.028	-0.032	0.102
Tritogonia verrucosa	-0.061	-0.020	-0.090	-0.028	-0.026
Truncilla donaciformis	-0.151	-0.017	-0.079	-0.087	0.174
Truncilla truncata	0.069	-0.006	0.028	-0.122	0.102

Table 8. Correlation coefficients between substrate variables and species biomass of freshwater mussels from the Neosho and Cottonwood rivers. * P < 0.01, ** P < 0.001, *** P < 0.0001.

Species	Variable				
	Silt	Mud	Sand	Gravel	Rock
Amblema plicata	0.073	-0.082	0.048	0.078	-0.029
Anodonta grandis	0.095	-0.017	0.055	-0.256*	-0.049
Ellipsaria lineolata	-0.082	-0.021	0.068	0.030	-0.061
Elliptio dilatata	0.159	-0.038	-0.255*	-0.056	-0.109
Fusconaia flava	-0.014	-0.024	-0.144	0.035	-0.069
Lampsilis ovata	0.021	-0.035	0.088	0.051	-0.101
Lampsilis teres	0.095	-0.017	0.055	-0.256*	-0.049
Lasmigona complanata	0.107	-0.035	0.056	0.050	-0.071

Table 8. Continued.

Species	Variable				
	Silt	Mud	Sand	Gravel	Rock
Leptodea fragilis	-0.010	-0.070	0.050	-0.008	-0.023
Obliquaria reflexa	-0.033	-0.095	0.126	0.037	-0.009
Pleurobema coccineum	0.127	-0.027	0.073	0.033	-0.065
Potamilus ohiensis	0.095	-0.017	0.055	0.025	-0.049
Potamilus purpuratus	-0.002	0.178	-0.138	-0.092	-0.084
Quadrula metanevra	-0.116	-0.035	0.113	0.050	0.115
Quadrula nodulata	-0.003	-0.037	0.019	-0.113	-0.100
Quadrula pustulosa	0.030	-0.050	-0.072	-0.019	-0.048
Quadrula quadrula	-0.067	-0.078	-0.175	0.004	0.074
Strophitus undulatus	0.095	-0.017	0.055	0.025	-0.049

Table 8. Continued.

Species	Variable				
	Silt	Mud	Sand	Gravel	Rock
Tritoqonia verrucosa	-0.035	-0.053	-0.110	-0.049	0.238
Truncilla donaciformis	-0.150	-0.053	-0.048	0.077	0.004
Truncilla truncata	0.095	-0.017	0.055	0.025	-0.049

DISCUSSION

The ordination analyses explained the structure of mussel communities well given the percent of variation in mussel distribution and biomass explained by the environmental variables. The high eigenvalues also indicate a strong environmental gradient (Verdonschot 1987, Verdonschot 1992a, 1992b). Environmental variables that were most strongly correlated to abundance and biomass of mussel species were chemical factors and stream size i.e., current velocity, stream width and water depth, while substrate seemed of secondary importance. This observation is supported by Cvancara and Harrison (1965) and Cvancara et al. (1966) where they showed water chemistry and stream velocity to be the main factors affecting mussel distribution. Water chemistry variables measured in concentration of calcium carbonate had the most distinct gradient and highest axis 1 scores (Fig. 2 and 3). Calcium carbonate would seem to be a likely candidate as a limiting factor of freshwater mussels given its importance in shell growth. Cvancara and Harrison (1965) suggested that total alkalinity was one of the main factors affecting mussel distribution in the Red River, North Dakota, and that high levels (Cvancara 1970) should be conducive to mussel propagation. However, species that were positively correlated with high calcium carbonate levels in my study were either thin shelled (L. fragilis) or small sized (T.

donaciformis), while species with more massive shells (A. plicata and O. reflexa) were negatively correlated with calcium carbonate levels. The opposite would be a more realistic scenario because thick shelled species should have higher calcium carbonate demands. In addition, it is highly unlikely that calcium levels were low enough to be limiting at any of the study sites, given that levels of total calcium ranges between 57 and 99 mg/l (Kansas Department of Health and Environment unpubl. data) within the entire Neosho River Drainage. Plus, relatively diverse unionid faunas occur in areas with lower calcium levels (Nalepa and Gauvin 1988). Strayer et al. (1981) and Huebner et al. (1990) concur that calcium levels as low as 2 - 3 mg/l are not limiting to mussel populations, although this is probably close to the lower limit (Huebner et al. 1990).

Strayer (1983) suggests that variables associated with surface geology and stream size such as current velocity are major factors influencing mussel distributions, and although chemical features of water vary with surface formations, they probably do not influence mussels. Stream size related factors exhibited a distinct gradient and correlated highly with axis 1 (Fig. 2 and 3). Species scores on axis 1 were related to these variables, and thus may indicate an association between the species and these variables. In general, the Neosho River has more large river characteristics (increased stream width and water depth)

farther downstream. Thus, species that favor large rivers, such as A. plicata, and P. purpuratus (Murray and Leonard 1962), tend to be more abundant, and thus the overall biomass of these species should be higher as well. In addition, unionid mussels often exhibit an increase in species richness with stream size (Strayer 1983, Pennak 1989). I did not observe an increase in species richness farther downstream (Appendix 2), although Frazier's data (1977) do show an increase in species richness from the headwater to near the Kansas-Oklahoma boarder. This difference may be due to the difference in the length of river that was sampled or in the sampling methodology.

The seemingly lesser importance of substrata on mussel abundance and biomass in my study is somewhat surprising given its traditional prominence as an important ecological factor. These data do not refute this importance, they only suggest that other factors may be more important, at least in these river systems. Possible reasons for this may simply be a result of the distinctness in the water chemistry/stream size gradient, variability of substrate was too high to detect a strong gradient, the range of substrate components was too low, or that characterization of substrate was not specific enough to detect its importance.

Separation of species in the ordinations using both abundance and biomass as dependent variables showed distinct relationships between species and environmental variables in

most cases. Species that lie in the center of the ordination diagrams are common in occurrence and may have their optima there or may be independent of the axes, while species that are less common lie at the periphery of the diagrams due to their specific environmental preference or due to chance (Verdonschot 1987, Verdonschot and Higler 1989, Verdonschot 1992a, 1992b). In both ordination diagrams, there were consistent species-environment relationships. Obliquaria reflexa, Q. pustulosa and Q. quadrula did not score high on the CCA axes, and were positioned closer to the center of both ordination diagrams than were the other species. These species, particularly Quadrula spp., are often locally abundant and seem to have a wide habitat tolerance with respect to substrate, water depth, and current velocity (Murray and Leonard 1962, Buchanan 1980, Oesch 1984). Amblema plicata, L. fragilis, P. purpuratus, T. verrucosa, and T. donaciformis scored higher on the CCA axes and were positioned toward the periphery of the ordination diagrams. The position of L. fragilis and A. plicata toward the periphery does not seem to be an artifact of rarity given their relatively high abundance, while rarity may be a factor for P. purpuratus and T. verrucosa. These species also tend to occupy a variety of substrates (Murray and Leonard 1962, Frazier 1977, Buchanan 1980, Stern 1983, Oesch 1984). Potamilus purpuratus is an exception because of its strong association

with mud substrate (Murray and Leonard 1962, Oesch 1984), a finding that was also apparent in my study. Some of these species, however, seem to be more specific with regard to water depth and current velocity, such as the association of A. plicata with deeper water (Murray and Leonard 1962, Frazier 1977), which is supported in my study, and the association of L. fragilis with low current velocity (Murray and Leonard 1962, Oesch 1984), a species that I found to be associated with swifter current.

Evaluation of ecological data using ordination techniques does not allow hypothesis testing, rather it is a hypothesis generating method (Gauch 1982, Leland et al. 1986, Verdonschot and Higler 1989). The use of CCA determined the major ecological gradients that may affect the distribution of unionid mussels, and there are many observations from my study that seem to be consistent with the present knowledge of habitat associations of these species. Ordination also showed more specific species-environment relationships, whereas before, only general conclusions of habitat associations could be drawn. These data should provide additional information for the design of studies to understand causal factors in population and community dynamics of unionid mussels in the central Great Plains.

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APPENDICES

Appendix 1. Specific locations of study sites on the Neosho and Cottonwood rivers, Kansas.

Site	Location
1	Neosho River, SW 1/4, SW 1/4, Sec. 33, T18S, R11E, Lyon Co. Kansas. 3.2 km N, 2.4 km E, Emporia.
2	Cottonwood River, SE 1/4, NW 1/4, Sec. 22, T19S, R11E, Lyon Co. Kansas. Within Emporia city limmits.
3	Cottonwood River, NE 1/4, SE 1/4, Sec. 28, T19S, R12E, Lyon Co. Kansas. 4.0 km S, 8.8 km E, Emporia.
4	Neosho River, NW 1/4, SW 1/4, Sec. 29, T19S, R13E, Lyon Co. Kansas. 0.8 km W, Neosho Rapids.
5	Neosho River, NW 1/4, SE 1/4, Sec. 23, T21S, R15E, Coffey Co. Kansas. 0.8 km N, 0.8 km E, Burlington.
6	Neosho River, NE 1/4, SE 1/4, Sec. 33, T22S, R16E, Coffey Co. Kansas. 0.4 km N, 2.4 km E, Leroy.
7	Neosho River, NE 1/4, NW 1/4, Sec. 33, T23S, R17E, Woodson Co. Kansas. 0.4 km E, Neosho Falls.
8	Neosho River, SW 1/4, NW 1/4, Sec. 32, T25S, R18E, Allen Co. Kansas. 1.6 km N, 2.0 km W, Humbolt.

Appendix 2. Mean density (no./m^2 ± SD) of freshwater mussels from eight locations[a] on the Neosho and Cottonwood rivers.

Species	Site							
	1	2	3	4	5	6	7	8
Amblema plicata	0.05 ± 0.22	0.05 ± 0.22	0	0	0.05 ± 0.22	0.55 ± 0.76	0.55 ± 0.94	0.55 ± 0.76
Anodonta grandis	0.05 ± 0.22	0	0	0	0	0	0	0
Ellipsaria lineolata	0	0	0	0	0	0	0.10 ± 0.31	0
Elliptio dilatata	0	0	0	0	0	0.55 ± 0.94	0	0
Fusconaia flava	0.05 ± 0.22	0	0	0	0	0	0	0.15 ± 0.49
Lampsilis ovata	0	0	0	0	0.05 ± 0.22	0.05 ± 0.22	0.15 ± 0.37	0.05 ± 0.22
Lampsilis teres	0.05 ± 0.22	0	0	0	0	0	0	0
Lasmigona complanata	0.20 ± 0.52	0	0	0.05 ± 0.22	0	0.05 ± 0.22	0.05 ± 0.22	0
Leptodea fragilis	0.40 ± 0.68	1.00 ± 1.08	0.25 ± 0.44	0.05 ± 0.22	0.15 ± 0.37	0.05 ± 0.22	0.10 ± 0.45	0.20 ± 0.70
Obliquaria reflexa	0.50 ± 0.89	0.10 ± 0.31	0	0.05 ± 0.22	0.40 ± 0.68	0.45 ± 0.51	0.55 ± 0.69	0.15 ± 0.37
Pleurobema coccineum	0	0	0	0	0	0	0.10 ± 0.31	0
Potamilus ohiensis	0	0	0	0	0	0	0.05 ± 0.22	0
Potamilus purpuratus	0.05 ± 0.22	0	0	0.05 ± 0.22	0	0.25 ± 0.64	0.05 ± 0.22	0.15 ± 0.49
Quadrula metanevra	0	0	0	0	0	0.30 ± 0.66	0.15 ± 0.49	0

[a] Locations correspond to those in Figure 1 and Appendix 1

Appendix 2. Continued.

Species	Site							
	1	2	3	4	5	6	7	8
Quadrula nodulata	0	0	0.05 ± 0.22	0	0	0.05 ± 0.22	0.25 ± 0.64	0
Quadrula pustulosa	0.55 ± 0.89	0.25 ± 0.55	0.05 ± 0.22	0.30 ± 0.66	0.15 ± 0.37	0.30 ± 0.57	0.75 ± 0.79	0.40 ± 0.60
Quadrula quadrula	0.25 ± 0.55	0.30 ± 0.57	0.30 ± 0.47	0.65 ± 0.99	0.05 ± 0.22	0.15 ± 0.49	0.05 ± 0.22	0.45 ± 0.76
Strophitus undulatus	0	0.05 ± 0.22	0	0	0	0	0	0
Tritogonia verrucosa	0	0.25 ± 0.44	0	0.10 ± 0.31	0.10 ± 0.31	0.05 ± 0.22	0	0
Truncilla donaciformis	0	0.35 ± 0.67	0.35 ± 0.75	0.10 ± 0.31	0.05 ± 0.22	0	0.05 ± 0.22	0
Truncilla truncata	0.05 ± 0.22	0	0	0	0	0	0	0
Total	2.15 ± 2.35	2.35 ± 1.69	1.00 ± 1.40	1.35 ± 1.50	1.00 ± 1.17	2.80 ± 2.24	2.95 ± 2.14	2.10 ± 1.89
Number of species	11	8	5	8	8	12	14	8

Appendix 3. Mean shell free biomass (g/m^2 ± SD) of freshwater mussels from eight locations[a] on the Neosho and Cottonwood rivers.

Species	Site							
	1	2	3	4	5	6	7	8
Amblema plicata	1.16 ± 5.19	1.56 ± 6.95	0	0	0.67 ± 2.97	8.59 ± 13.30	7.75 ± 12.61	5.77 ± 8.68
Anodonta grandis	0.19 ± 0.83	0	0	0	0	0	0	0
Ellipsaria lineolata	0	0	0	0	0	0	0.44 ± 1.56	0
Elliptio dilatata	0	0	0	0	0	3.87 ± 7.01	0	0
Fusconaia flava	0.08 ± 0.34	0	0	0	0	0	0	0.99 ± 3.29
Lampsilis ovata	0	0	0	0	1.28 ± 5.70	1.22 ± 5.46	3.01 ± 7.81	0.34 ± 1.50
Lampsilis teres	0.28 ± 1.23	0	0	0	0	0	0	0
Lasmigona complanata	3.81 ± 11.03	0	0	0.46 ± 2.03	0	1.06 ± 4.72	0.40 ± 1.77	0
Leptodea fragilis	3.54 ± 6.16	24.28 ± 28.48	0.99 ± 2.35	1.13 ± 5.03	0.61 ± 2.46	0.72 ± 3.20	1.01 ± 4.52	1.96 ± 7.90
Obliquaria reflexa	0.93 ± 1.84	0.27 ± 0.83	0	0.14 ± 0.60	0.71 ± 1.63	1.29 ± 1.52	0.71 ± 1.15	0.34 ± 0.85
Pleurobema coccineum	0	0	0	0	0	0	0.35 ± 1.14	0
Potamilus ohiensis	0	0	0	0	0	0	0.19 ± 0.85	0
Potamilus purpuratus	0.43 ± 1.90	0	0	1.02 ± 4.56	0	5.60 ± 14.12	0.90 ± 4.00	3.22 ± 11.14
Quadrula metanevra	0	0	0	0	0	1.85 ± 4.50	0.40 ± 1.29	0

[a] Locations correspond to those in Figure 1 and Appendix 1

Appendix 3. Continued.

Species	Site							
	1	2	3	4	5	6	7	8
Quadrula nodulata	0	0	0.25 ± 1.12	0	0	0.26 ± 1.16	0.45 ± 0.97	0
Quadrula pustulosa	2.69 ± 4.57	1.33 ± 3.16	0.14 ± 0.60	1.66 ± 4.62	0.63 ± 1.60	0.78 ± 1.74	2.07 ± 2.57	1.38 ± 2.13
Quadrula quadrula	1.96 ± 4.61	1.87 ± 4.34	1.56 ± 2.70	5.56 ± 9.48	0.16 ± 0.72	0.92 ± 3.61	0.13 ± 0.56	1.96 ± 3.68
Strophitus undulatus	0	0.37 ± 1.63	0	0	0	0	0	0
Tritogonia verrucosa	0	4.32 ± 8.28	0	1.70 ± 5.32	2.10 ± 6.46	0.88 ± 3.91	0	0
Truncilla donaciformis	0	0.05 ± 0.10	0.11 ± 0.24	0.07 ± 0.24	0.02 ± 0.09	0	0.02 ± 0.09	0
Truncilla truncata	0.13 ± 0.56	0	0	0	0	0	0	0
Total	14.75 ± 18.63	34.03 ± 32.10	3.04 ± 4.70	11.70 ± 17.64	6.16 ± 8.45	27.01 ± 22.63	17.79 ± 15.26	15.94 ± 15.73

Effects of fish hosts on genetic variation in unionid mussels

INTRODUCTION

The genetic structure of populations is determined in part by the level of gene flow, which in turn is reflective of dispersal among populations (Slatkin 1985, 1987). Organisms that differ in their ability to disperse should therefore exhibit differences in genetic structure. Thus, species with limited ability to disperse will exhibit greater differentiation, which has been shown to be true in comparisons of species with contrasting life history characteristics that impose morphological (Zera 1981, Caccone 1985) or ecological (Caccone 1985, Liebherr 1988) restrictions on dispersal.

The freshwater mussel family Unionidae has a widespread geographic distribution (Taylor 1988). The richest fauna is in North America (Burch 1975) and includes 49 genera and 297 species and subspecies (Turgeon et al. 1988). Unionids are unique among bivalves in that they are, with few exceptions, obligate parasites on fish during the juvenile stage of the life cycle (Coker et al. 1921, Fuller 1974, Kat 1984). Dispersal is the most apparent advantage of this parasitic association, and host mediated dispersal has probably had profound effects on unionid distribution (Watters 1992) and evolution (Kat 1984).

In addition to fish being the main dispersal mechanism,

there is considerable variation in host specificity among unionids (Fuller 1974), although for the majority of species, hosts are not known. The unusual mode of host mediated dispersal coupled with inherent variation in host specificity poses obvious implications for the genetic structuring of unionid populations, and there is evidence that suggests the genetic structure of mussel populations may mirror the genetic structure of host populations (Markillie 1989).

Unionids can be placed in three general categories of host specificity: 1) host generalists-known to use several species of fish as hosts, 2) host specialist-known to use only one or very few species of fish as hosts, 3) facultative parasitism or no parasitism-ability to metamorphose into juvenile with or without a parasitic stage.

Obliquaria reflexa and Quadrula pustulosa are two species of widely distributed North American unionids that differ markedly in their development. Obliquaria reflexa is one of the few unionid species that is known to complete development from larvae to juvenile without a parasitic stage (Fuller 1974). Conversely, six species of fish are known to serve as hosts for Q. pustulosa, these are the shovelnose sturgeon (Scaphirhynchus platorynchus), white crappie (Pomoxis annularis), black bullhead (Ameiurus melas), brown bullhead (Ameiurus nebulosus), channel catfish

(Ictalurus punctatus), and flathead catfish (Pylodictus olivaris) (Fuller 1974). This suggests that O. pustulosa should possess a greater dispersal capacity and gene flow among populations than O. reflexa.

I used these two species to test predictions of genetic structure based on proposed dispersal abilities. If dispersal increases gene flow in O. pustulosa, its populations should exhibit: 1) higher numbers of alleles/locus, 2) higher levels of heterozygosity, 3) lower levels of inbreeding, and 4) less population subdivision than O. reflexa.

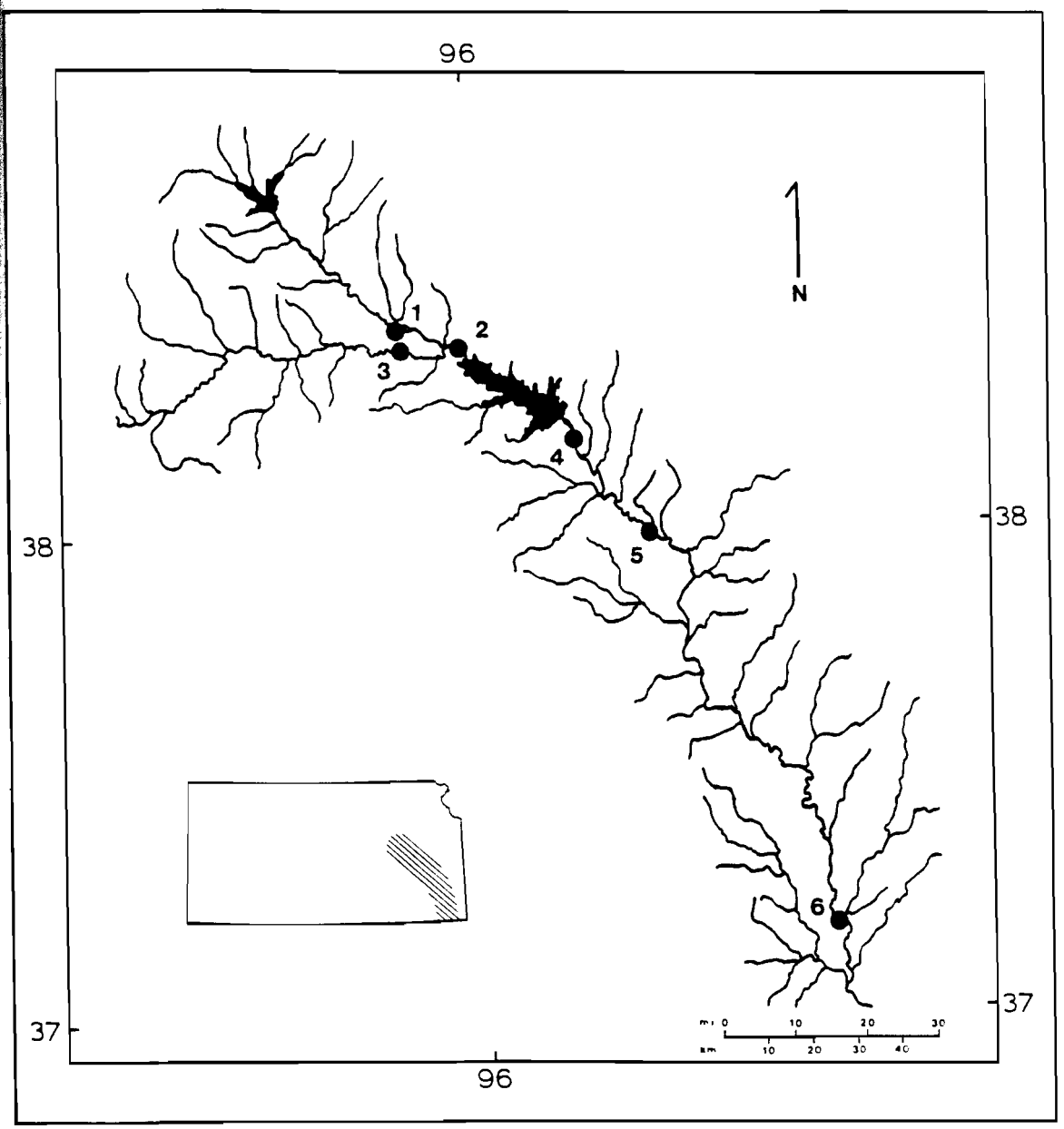
MATERIALS AND METHODS

I collected 10 specimens of Quadrula pustulosa and Obliquaria reflexa at six locations from the Neosho and Cottonwood rivers in eastern Kansas (Fig. 1) from July through September 1991: (1) Neosho River, SW 1/4, SW 1/4, Sec. 33, T18S, R11E, Lyon Co. Kansas, 3.2 km N, 2.4 km E, Emporia; (2) Neosho River, NW 1/4, SW 1/4, Sec. 29, T19S, R13E, Lyon Co. Kansas, 0.8 km W, Neosho Rapids; (3) Cottonwood River, SE 1/4, NW 1/4, Sec. 22, T19S, R11E, Lyon Co. Kansas, within Emporia city limits; (4) Neosho River, NW 1/4, SE 1/4, Sec. 23, T21S, R15E, Coffey Co. Kansas, 0.8 km N, 0.8 km E, Burlington; (5) Neosho River, NE 1/4, NW 1/4, Sec. 33, T23S, R17E, Woodson Co. Kansas, 0.4 km E, Neosho Falls; (6) Neosho River, NE 1/4, NW 1/4, Sec. 15, T33S, R21E, Labette Co. Kansas, 1.2 km N, 0.4 km E, Oswego.

I immediately returned live individuals to the laboratory where soft bodies were removed and stored at -60° C. Approximately 1.0 g of foot muscle was removed and homogenized with 1 - 3 ml grinding solution. I then placed the homogenate in 1.5 ml micro centrifuge tubes, centrifuged each for 1 minute, and stored them at -60° C.

Genetic variability was measured at 15 presumptive loci using horizontal starch gel electrophoresis. Enzymes assayed and number of loci were: esterase (EST), 1; glutamate dehydrogenase (GDH), 1; aspartate aminotransferase (AAT), 1 (formerly GOT); glucose-6-phosphate isomerase

Figure 1. Location of collecting sites on the Neosho and Cottonwood rivers. Sites correspond to those given in the text.


96
38
37
N
1
2
3
4
5
6
mi 0 10 20 30
km 10 20 30 40
96
38
37

(GPI), 1; glucose-6-phosphate dehydrogenase (G-6-PDH), 1; cytosol aminopeptidase (CAP), 1 (formerly LAP); malate dehydrogenase, (MDH), 2; purine-nucleoside phosphorylase (PNP), 1 (formerly NP); peptidase (PEP-gl), 1; phosphoglucomutase (PGM), 2; phosphogluconate dehydrogenase (PGDH), 1 (formerly 6-PGD); superoxide dismutase (SOD) 2. Tris citrate pH 8.0 was the buffer system and all gels were run for 8hr at 90v. Stain and buffer recipes follow Selander et al. (1971), Harris and Hopkinson (1976), and Murphy et al. (1990).

Allozyme data were analyzed using BIOSYS-1 computer package (Swofford and Selander 1981). Mean heterozygosity, percent polymorphic loci, and mean number of alleles per locus per population were calculated for each species. Differences in levels of heterozygosity and allelism between species were tested with a one tailed t-test. Genetic similarity (Rogers 1972) among populations was determined. The level of inbreeding within and among populations was assessed using Wright's (1965, 1978) F-statistics.

RESULTS

Of the 15 loci assayed, eight were polymorphic for Q. pustulosa and six for Q. reflexa (Table 1). The level of heterozygosity for both species was low, however, Q. pustulosa had higher overall values of mean heterozygosity and mean number of alleles per locus than Q. reflexa, but these were not significantly different (Table 2). Populations of Q. pustulosa generally had a higher percentage of polymorphic loci, number of alleles per locus, and mean heterozygosity than Q. reflexa. However, only at population four did allelism ($t=1.82$, $df=17$, $P<0.05$) and heterozygosity ($t=1.75$, $df=17$, $P<0.05$) differ significantly (Table 2).

Populations of both species were relatively similar. Average genetic similarity (Rogers 1972) was slightly higher for Q. reflexa (0.937) than for Q. pustulosa (0.925). Clustering of populations based on Rogers' (1972) genetic similarity showed populations of Q. reflexa that were closer in proximity were more similar, whereas clustering of populations of Q. pustulosa did not show geographic affinities (Fig. 2). Obliquaria reflexa also showed a general reduction in genetic distance between adjacent populations farther downstream, i.e., the genetic distance between populations 1 and 2 was much greater than populations 4 and 5 (Fig. 2). This trend was not apparent for Q. pustulosa.

Table 1. Allele frequencies of Quadrula pustulosa and Obliquaria reflexa from the Neosho and Cottonwood rivers.

		Quadrula pustulosa						Obliquaria reflexa					
Locus		1[a]	2	3	4	5	6	1	2	3	4	5	6
AAT	N	10	8	10	10	9	10	10	10	10	10	10	10
	a	0.900	1.000	1.000	1.000	1.000	1.000	0.900	1.000	0.900	1.000	1.000	1.000
	b	0.100	0	0	0	0	0	0.100	0	0.100	0	0	0
CAP	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	0.300	0.111	0.350	0.400	0.250	0.100	0	0	0	0	0	0
	b	0	0.111	0.200	0	0.050	0.250	0	0	0	0	0	0
	c	0	0.167	0.050	0	0.050	0	0	0	0	0	0	0
	d	0.300	0.056	0	0	0.150	0.250	0	0	0	0	0	0
	e	0.300	0.389	0.400	0.500	0.450	0.350	0	0	0	0	0	0
	f	0.050	0.111	0	0	0	0	0	0	0	0	0	0
	g	0	0.056	0	0	0	0	0	0	0	0	0	0
	h	0	0	0	0.050	0	0	0	0	0	0	0	0
	i	0	0	0	0	0.050	0.050	0	0	0	0	0	0
	j	0.050	0	0	0.050	0	0	0	0	0	0	0	0
	K	0	0	0	0	0	0	1.000	1.000	1.000	1.000	1.000	1.000
EST	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	1.000	1.000	1.000	1.000	1.000	1.000	0.900	0.900	0.950	0.900	1.000	0.950
	b	0	0	0	0	0	0	0.100	0.100	0.050	0.100	0	0.050
GDH	N	8	9	10	10	10	10	2	6	10	10	10	10
	a	1.000	1.000	1.000	1.000	1.000	1.000	0.500	0.917	1.000	1.000	1.000	1.000
	b	0	0	0	0	0	0	0.500	0	0	0	0	0
	c	0	0	0	0	0	0	0	0.083	0	0	0	0

[a] Numbers 1-6 correspond to collections localities in Figure 1 and text

Table 1. Continued.

Locus		*Quadrula pustulosa* 1	2	3	4	5	6	*Obliquaria reflexa* 1	2	3	4	5	6
G-6-PDH	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	0	0	0	0	0	0	1.000	1.000	1.000	1.000	1.000	1.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	0	0	0	0	0	0
GPI	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	0	0	0	0	0	0	1.000	0.750	0.950	0.900	0.850	1.000
	b	0	0	0	0	0	0	0	0.250	0.050	0.100	0.150	0
	c	1.000	0.778	1.000	0.950	1.000	1.000	0	0	0	0	0	0
	d	0	0.222	0	0.050	0	0	0	0	0	0	0	0
MDH-1	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	0	0	0	0	0	0	0	0.050	0	0	0.050	0
	b	0	0	0	0	0	0	1.000	0.950	1.000	1.000	0.950	1.000
	c	1.000	1.000	1.000	0.950	0.950	1.000	0	0	0	0	0	0
	d	0	0	0	0.050	0.050	0	0	0	0	0	0	0
MDH-2	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	1.000	1.000	1.000	1.000	1.000	1.000	0	0	0	0	0	0
	b	0	0	0	0	0	0	1.000	1.000	1.000	1.000	1.000	1.000
PEP-GL	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGDH	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	0	0	0	0	0	0	1.000	1.000	1.000	1.000	1.000	1.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	0	0	0	0	0	0

Table 1. Continued.

Locus		*Quadrula pustulosa* 1	2	3	4	5	6	*Obliquaria reflexa* 1	2	3	4	5	6
PGM-1	N	10	9	10	10	10	9	10	10	10	10	10	10
	a	0	0	0	0	0	0	0.950	1.000	0.900	1.000	1.000	1.000
	b	0	0	0	0	0	0	0.050	0	0.100	0	0	0
	c	0.150	0.111	0.150	0.100	0.050	0.167	0	0	0	0	0	0
	d	0.200	0.222	0.600	0.650	0.700	0.333	0	0	0	0	0	0
	e	0.650	0.667	0.250	0.250	0.200	0.500	0	0	0	0	0	0
	f	0	0	0	0	0.050	0	0	0	0	0	0	0
PGM-2	N	10	9	10	7	8	9	10	10	9	10	10	10
	a	0.350	0.222	0.100	0.286	0.125	0.278	0	0	0	0	0	0
	b	0.650	0.778	0.900	0.714	0.875	0.722	0	0	0	0	0	0
PNP	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	0	0	0	0	0	0	1.000	1.000	1.000	1.000	1.000	1.000
	b	1.000	0.889	0.900	1.000	1.000	0.900	0	0	0	0	0	0
	c	0	0.111	0.100	0	0	0.100	0	0	0	0	0	0
SOD-1	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.950	1.000	1.000	1.000
	b	0	0	0	0	0	0	0	0	0.050	0	0	0
SOD-2	N	10	9	10	10	10	10	10	10	10	10	10	10
	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 2. Measures of genetic variability in Quadrula pustulosa and Obliquaria reflexa from the Neosho and Cottonwood rivers.

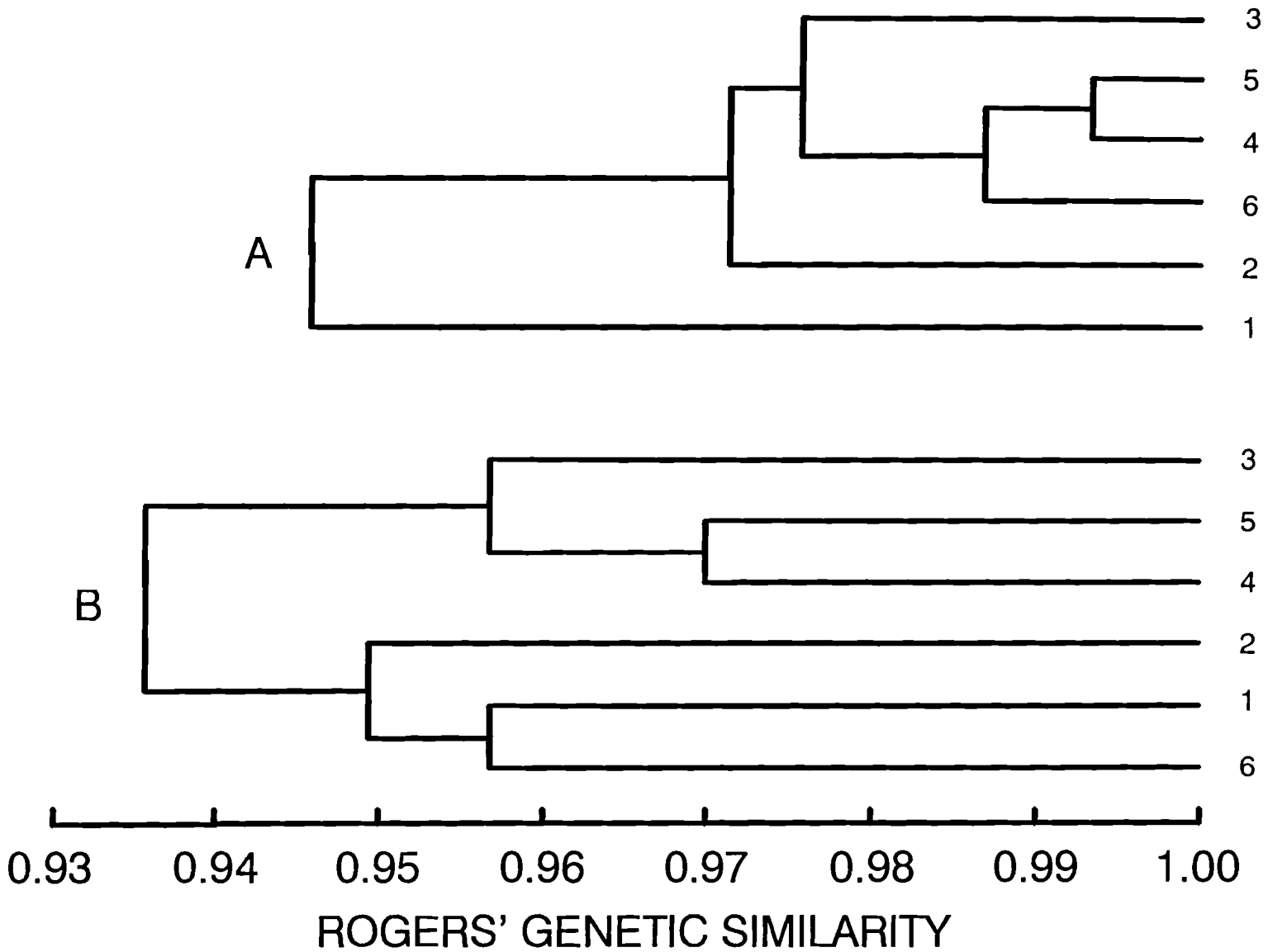
Population[a]	Quadrula pustulosa			Obliquaria reflexa		
	Mean alleles/ locus	% polymorphic loci	Mean heterozygosity	Mean alleles/ locus	% polymorphic loci	Mean heterozygosity
1	1.5(9.9)[b]	26.7	0.060	1.3(9.5)	26.7	0.020
2	1.7(8.9)	33.3	0.052	1.3(9.7)	26.7	0.038
3	1.5(9.9)	26.7	0.060	1.3(9.9)	33.3	0.033
4	1.5(9.5)	33.3	0.086	1.1(10.0)*	6.7	0.013*
5	1.7(9.6)	26.7	0.063	1.1(10.0)	13.3	0.027
6	1.5(9.8)	26.7	0.084	1.1(10.0)	6.7	0.007
All populations	2.2(57.6)	26.7	0.067	1.5(59.1)	13.3	0.023

[a] Population numbers correspond to those in Figure 1 and text

[b] Numbers in parentheses are mean sample sizes per locus

* Means between species are significantly different ($P<0.05$)

Figure 2. Phenogram of Rogers' (1972) genetic similarity among populations of (A) Obliquaria reflexa and (B) Quadrula pustulosa. Numbers 1-6 in the phenogram correspond to collection sites in Figure 1 and text.


A
3
5
4
6
2
1
B
3
5
4
2
1
6
0.93
0.94
0.95
0.96
0.97
0.98
0.99
1.00
ROGERS' GENETIC SIMILARITY

At comparable loci, the level of inbreeding was either higher for Q. pustulosa (GPI and PGM), or was relatively the same (AAT and MDH-1) between the species (Table 3). Overall inbreeding within populations (F_{is}) was higher for Q. pustulosa, while population subdivision (F_{st}) was higher for Q. reflexa (Table 3).

Table 3. F-statistics at all polymorphic loci of Quadrula pustulosa and Obliquaria reflexa from the Neosho and Cottonwood rivers.

	Quadrula pustulosa			Obliquaria reflexa		
Locus	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
AAT	1.000	1.000	0.085	1.000	1.000	0.069
CAP	0.292	0.337	0.063			
EST				0.273	0.298	0.035
GDH				0.745	0.884	0.388
GPI	0.773	0.809	0.158	0.006	0.099	0.094
MDH-1	-0.053	-0.017	0.034	-0.053	-0.017	0.034
PGM-1	0.474	0.545	0.135	-0.091	-0.026	0.060
PGM-2	0.429	0.455	0.045			
PNP	1.000	1.000	0.055			
SOD-1				-0.053	-0.008	0.042
MEAN	0.443	0.482	0.086	0.317	0.428	0.162

DISCUSSION

The observed trends in genetic structuring of Obliquaria reflexa and Quadrula pustulosa are in many cases consistent with predictions based on their dispersal abilities. The lack of significant differences, however, suggests that physical or biological factors other than fish may play a role in gene dispersal, or lack of it, in these species. For instance, even if glochidia of Q. pustulosa are being dispersed greater distances it does not necessarily mean that genes are being established, i.e., low recruitment. Mussels in general are patchy in distribution, and differences in population size and the distance between populations may affect gene flow. These could be addressed by comparing species with the same fish hosts, e.g., Potamilus ohiensis and Potamilus purpuratus, which parasitize white crappie and freshwater drum (Aplodinotus grunniens), or Truncilla truncata and Truncilla donaciformis, which parasitize sauger (Stizostedion canadense) and freshwater drum (Fuller 1974). Species that have low population density and or greater distance between populations, should display less gene flow among populations, and thus should exhibit lower heterozygosity and greater differentiation. Consistent with this prediction, Stiven and Alderman (1992) have shown that mussel species which are more common and have widespread distributions exhibit increased heterozygosity and

polymorphism than rarer species. Passive transport downstream may be preventing a large degree of local differentiation as seen in aquatic bacteria (McArthur et al. 1992), or the geographic range that was studied was too small to detect significant differences in genetic structure between the species. The fact that genetic distances was greater between upstream populations of Q. reflexa than populations farther downstream suggests that passive transport of individuals (and alleles) may be occurring, although, upstream populations of Q. reflexa had higher heterozygosity and polymorphism than downstream populations, which is contradictory. Concurrently, the fact that Q. pustulosa did not follow this same trend suggests that fish are playing a role in dispersal of this species.

The system of fish-mediated dispersal in unionid mussels is in many ways analogous to the pollination of plants by their animal visitors. Although in the latter it is gametes that are being dispersed rather than individuals, both systems may be dependent on animal dispersers. In plants, the mechanism of pollination greatly affects the level of genetic variability, i.e., higher levels of genetic subdivision in animal pollinated species than wind pollinated species (Hamrick et al. 1979, Loveless and Hamrick 1984). In the case of animal pollinated plant species, differences in pollen dispersal have been shown between hummingbirds and insects (Webb and Bawa 1983), and

between different species of hummingbirds (Linhart 1973, Linhart and Feinsinger 1980, Linhart et al. 1987) and insects (Primack and Silander 1975, Campbell 1985). Although Waser (1982) contends that dispersal distances do not differ among pollinators, larger pollinators, such as birds and bats, cause a greater reduction in subdivision due to higher rates of visitation and rare long distance dispersal (Loveless and Hamrick 1984).

If behavioral variation of plant pollinators affects the genetic structure, then behavioral variation in fish that serve as unionid hosts may also affect genetic structure. Some species of riverine fish are shown to move more than others. For instance, Funk (1955) has shown that channel catfish, freshwater drum, and white crappie are much more mobile than rock bass (Ambloplites rupestris), smallmouth bass (Micropterus dolomieui), spotted bass (Micropterus punctulatus), longear sunfish (Lepomis megalotis), and yellow bullhead (Ameiurus natalis). The size of fish may also influence the amount of movement. Smaller individuals of certain species are more sedentary than larger individuals, while in other species size does not seem to affect movement (Funk 1955). These data suggest that fish hosts that exhibit limited mobility may cause greater differentiation among mussel populations. In accordance with this prediction, Kat (1983) and Kat and Davis (1984) have shown that mussel species which have

anadromous fish hosts exhibit less differentiation than mussel species with hosts that are strictly freshwater. This prediction also applies to behavioral variation that occurs among fish that only inhabit freshwater. Host species that exhibit greater movement such as freshwater drum and white crappie (Funk 1955) may reduce subdivision among populations of mussel species that parasitize them, e.g., Leptodea fragilis, Potamilus alatus, P. purpuratus, and P. ohiensis (Fuller 1974), compared to mussel species whose hosts are more sedentary.

The results of my study lend support to the hypothesis that fish affect the genetic structure of freshwater mussels, although investigation for more conclusive evidence is needed. As we learn more about the hosts of freshwater mussels, comparisons between species should provide more information relative to the evolutionary mechanisms controlling this group.

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