Role of ecological factors and reproductive strategies in structuring freshwater mussel communities

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Abstract: Freshwater mussel community composition within two drainage basins in Alabama, U.S.A., was better explained by patterns of variability in the fish community and the type of strategy used by mussels for infecting host-fishes than by patterns of variability in microhabitat. Mussel species richness increased in a downstream direction, and large-stream sites were characterized by a distinctive faunal assemblage that was similar between drainages. In contrast, faunal composition of headwater sites varied widely between drainages. Patterns of mussel community variation were correlated with patterns of fish community variation but not with habitat. Densities of host-specialist mussels with elaborate host-attracting mechanisms and host-generalist mussels were independent of host-fish densities, and these mussels were present throughout the drainages. Densities of host-specialist mussels without elaborate host-attracting mechanisms were correlated positively with host-fish densities and were absent or rare in headwater and midreach streams. We propose that mussel species dependent on host-fish density are restricted to sites with stable numbers of hosts, but mussels not dependent on host-fish density are able to persist in areas with more unstable fish assemblages, such as headwaters.

Résumé : Nous avons constaté que la composition des communautés de moules d'eau douce de deux bassins hydrographiques de l'Alabama (États-Unis) s'explique mieux par la variabilité de la communauté ichtyenne et par le mécanisme par lequel les moules infectent leurs espèces hôtes que par la variabilité du microhabitat. La diversité taxinomique des moules augmentait quand on descendait les cours d'eau; les grands cours d'eau se caractérisaient par une communauté faunique particulière qu'on a retrouvée dans les deux bassins. Par contre, dans les eaux d'amont, la composition taxinomique des communautés variait beaucoup d'un cours d'eau à l'autre. Nous avons constaté que la variation taxinomique des communautés de moules était en corrélation avec celle des communautés ichtyennes, mais non avec l'habitat. La densité des populations de moules spécialisées ayant recours à des mécanismes complexes pour attirer leurs espèces hôtes et celle des populations de moules généralistes étaient indépendantes de l'abondance des poissons hôtes; ces deux types de moules étaient présentes partout dans les deux bassins versants. Quant à la densité des populations de moules spécialisées chez lesquelles aucun mécanisme complexe destiné à attirer les espèces hôtes n'a été mis en évidence, elle était en corrélation positive avec la densité des populations de poissons hôtes; ces moules étaient absentes ou rares dans les eaux d'amont et dans le cours moyen des cours d'eau. Nous pensons que les espèces de moules dont l'abondance dépend de la densité des populations de poissons hôtes sont confinées aux zones où les populations d'espèces hôtes sont numériquement stables, mais que les moules dont l'abondance est indépendante de la densité des populations de poissons hôtes peuvent persister dans les zones où les communautés ichtyennes sont instables, comme c'est le cas des eaux d'amont.
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Introduction

Increasingly, community structure of aquatic organisms is seen as the result of complex interactions of biotic and abiotic factors (Power et al. 1988). This view has grown from a large body of literature showing specific examples of deterministic and stochastic processes affecting a particular species or group of species at various spatial and temporal scales. Recent studies have begun to elucidate multifactorial mechanisms of community organization (Power 1990; Hart 1992; Jackson and Harvey 1993; Taylor et al. 1996), but there remains a general

dearth of ecosystem-level studies in which the relative contribution of diverse ecological variables at different scales can be assessed. Mechanisms of community structure of freshwater mussels are among the most poorly known of any widespread, conspicuous group of stream organisms. Much attention has been focused on mussels because of the alarming loss of species and populations in the twentieth century due to widespread habitat destruction (Williams et al. 1992). However, serious efforts have been made only recently to understand the basic ecological processes that determine distribution and abundance of mussel species (Salmon and Green 1983; Holland-Bartels 1990; Strayer 1993; Strayer and Ralley 1993; Strayer et al. 1994).

The North American freshwater mussel fauna is the most diverse on Earth (approximately 281 species), but many species appear to be similar in their response to factors usually thought to structure aquatic communities. In streams in the eastern United States, as many as 40 species can be found inhabiting a single riffle, but partitioning of habitat is often minimal (Holland-Bartels 1990; Strayer and Ralley

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Fig. 1. Qualitative (circles) and quantitative (triangles) freshwater mussel and fish sampling sites in the Sipsey Fork and Brushy Creek drainages, Alabama, U.S.A. Quantitative mussel sampling sites: 5 (lower Sipsey Fork), 8 (Borden Creek), 10 (Flannagin Creek), 15 (lower Brushy Creek), 21 (Rush Creek), 23 (Brown Creek), and 26 (upper Brushy Creek). Quantitative fish sampling sites: 5, 8, 10, 15, 21, and 23.
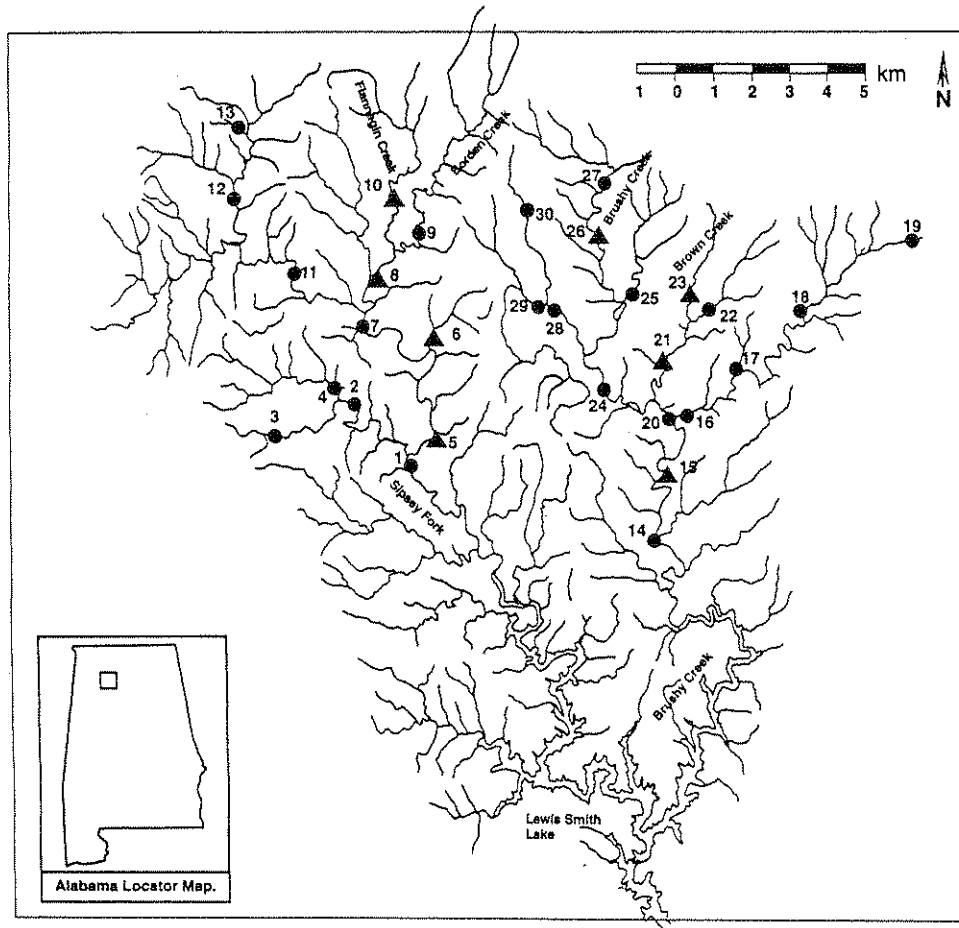
1993; Strayer et al. 1994), most species have similar feeding anatomies (Morton 1983; McMahon 1991), and predation on adult mussels is sporadic and localized in occurrence. In contrast, distributions and abundances of other macroinvertebrates and fishes are predictable from patterns of habitat and food resource usage by different species (Gorman and Karr 1978; Schlosser 1987a; Corkum 1989) and differential patterns of predation (Schlosser 1987b; Wooster 1994). Because larval mussels require a brief period as parasites on fishes to complete metamorphosis to juveniles, mussels show ecological attributes of both free-living and parasitic organisms. As a result, their distributions may be tied intimately to distributions of their host-fishes (Watters 1992). If the diverse North American fish fauna is viewed as a resource of potential hosts, freshwater mussels show striking resource partitioning.

Larvae of different mussel species range from generalists that use a taxonomically diverse range of fishes to strict specialists that metamorphose only on one or a few closely related fish species (see Watters 1994). Further, mussel species have evolved an array of strategies by which gravid females facilitate infection of a suitable host-fish with larvae (Dartnall and Walkey 1979; Kat 1984; Neves and Widlak 1988; Haag et al. 1995). Except for a few case studies (e.g., Smith 1985; Neves and Widlak 1988), the impact of specific characteristics of the

host-fish relationship on the distribution of mussels has not been examined.

We evaluated the relative usefulness of biotic and abiotic factors in explaining mussel community composition at different spatial scales within two similar drainage basins. First, we quantified patterns of mussel distribution and abundance within and between the two drainages. Second, we examined the relationship between physical habitat variables and mussel community composition. Third, we examined the relationship between fish and mussel community composition. Finally, we tested the relationships between densities of mussels with differing reproductive strategies and the densities of their respective host-fishes.

Study area

Sipsey Fork and Brushy Creek are tributaries of the Black Warrior River (Mobile Bay basin) in Lawrence and Winston counties, northwestern Alabama, U.S.A. The two watersheds are parallel, south-flowing drainages of similar size (Fig. 1). The streams were confluent approximately 15 km south of the study area, but their lower reaches were impounded by Lewis Smith Dam in 1961. These streams are on the Cumberland Plateau and are typical for this physiographic region, being

characterized by pool–riffle habitats and occupying deeply entrenched valleys.

These watersheds present an important opportunity for the study of community processes because the aquatic fauna may be relatively unmodified by humans. Mussel communities in much of North America have been modified extensively by water quality and physical habitat degradation in the last 100 years (Williams et al. 1992). In many streams, a significant proportion of the fauna has been extirpated, and the age structure of surviving species has shifted towards older individuals due to depressed recruitment (Parmalee et al. 1980). The Sipsey Fork and Brushy Creek drainages lie largely within William B. Bankhead National Forest and, other than sedimentation from timber harvest and road building, have escaped many of the perturbations to which most other watersheds in this region have been subjected. These mussel communities have experienced few species extirpations, have high species diversity, and have individuals in many age-classes for most species.

Methods

Mussel community

We generated qualitative species lists for 30 sites within the study area based on our field work and the results of a previous mussel survey of watersheds within Bankhead National Forest (McGregor 1992). In our field work and the 1992 study, sites were surveyed by snorkeling to find living mussels and by searching the shorelines for empty shells.

We quantified mussel community composition at seven sites: Sipsey Fork, lower Brushy Creek, Borden Creek, Rush Creek, Flannagin Creek, upper Brushy Creek, and Brown Creek (Fig. 1). Sites were chosen to represent an even, longitudinal progression from headwaters to larger streams in both watersheds (Fig. 1). At each site, we sampled 43–51 quadrats. We placed quadrats by laying a rope grid with numbered 1-m^2 cells over a reach of stream and selecting 25% of the cells using a random numbers table. We placed a 0.5-m^2 quadrat (with the exception of Rush Creek, where a 0.25-m^2 quadrat was used) in the center of each chosen cell, excavated substrate within the quadrat to a depth of 15 cm, and identified and enumerated all live mussels encountered. At each site, we sampled two to five reaches of 7–20 m in length that encompassed riffles, runs, or shallow pools. We did not sample sections of stream dominated by bedrock or deep, sluggish pools because these habitats typically yield low numbers of mussels. We conducted all mussel sampling from April to October 1993.

We assigned stream order (Horton 1945; Strahler 1957) and link magnitude (Scheidegger 1965; Osborne and Wiley 1992) to all 30 qualitative sites using U.S. Geological Survey 7.5′ topographic maps. Link magnitude is the number of first-order segments upstream of a given point on a channel. This method accounts for subtle changes in stream size and discharge that have no influence on stream order and thus provides a more sensitive measure of hydrologic variation (Osborne and Wiley 1992). We examined relationships between species richness and stream size for all 30 qualitative sites by regressing species richness at each site on link magnitude. We log-transformed link magnitude to linearize the relationship (Sokal and Rohlf 1981).

We described patterns of community composition among sites using two methods: (1) pairwise similarity matrices were computed using Jaccard's index (species presence or absence, 25 qualitative sites, excluding five sites with no mussels) and Morisita's index (species abundance, seven quantitative sites), and sites were clustered by the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal 1973) and (2) principal components were

factored from the correlation matrix of individual species abundances in quadrats with mussels at the seven quantitative sites, and mean principal component scores (±2 SE) were calculated and plotted for each site.

Microhabitat

We characterized physical microhabitat at the seven quantitative sites during low water conditions in summer. At each quadrat, we measured water depth, current velocity, substrate composition, and the percentage (nearest 25%) of the quadrat covered by wood, vegetation, and leaf litter. We measured water depth and current velocity in the center of the quadrat using a meterstick and an electronic flowmeter (Marsh-McBirney Flo-mate, model 2000), respectively. We categorized substrate composition using a modified Wentworth scale (Cummins 1962) composed of (1) clay, (2) silt, (3) sand, (4) fine gravel, (5) coarse gravel, (6) cobble, (7) boulder, and (8) bedrock and estimated the percent area (nearest 25%) of the quadrat covered by each substrate category.

We described differences in habitat among sites. For all analyses, we deleted clay as a substrate category because of its low frequency of occurrence. We grouped continuous depth and current velocity measurements into six categories each and calculated the cumulative frequency of occurrence (ranked 0–4 for 0, 25, 50, 75, and 100% coverage) of each habitat category (substrates, wood, leaf, and vegetation) for each site. We used these to compute a Shannon–Wiener index of habitat diversity (H') for each site and a pairwise similarity matrix (Morisita's index) among the seven sites. We then clustered the sites as described for mussel abundances.

We examined relationships of habitat to patterns of mussel community composition among sites in two ways. First, we tested for correlation between the distance matrices for quantitative mussel sites and habitat variables for the same sites using the Mantel test with 20 000 permutations (Rohlf 1989). Second, we factored principal components from the correlation matrix of quadrat habitat variables for each mussel species and computed mean principal component scores (±2 SE) for each species to ordinate mussel species in habitat space (Moyle and Vondracek 1985). For this and a similar analysis for fishes, we used the broken-stick model (Jackson 1993) to evaluate the relative interpretability of the ordination results. Using this method, plots are considered to have interpretive value if observed eigenvalues exceed eigenvalues generated by the model.

Fish community

We compiled fish species presence/absence lists for 16 sites in the study area using our field data and collection records from the University of Alabama ichthyological collection. These sites overlapped with those for which mussel species lists were compiled. We clustered these sites as described for mussel presence/absence data.

We quantified fish community composition at six of the seven sites where quantitative mussel sampling took place (Fig. 1). Each site was sampled in October 1993 and April 1994 by electrofishing, and densities were quantified based on time shocked (25–53 min·site^{-1}· sample date^{-1}). We did not sample upper Brushy Creek for fishes. We sampled pools by placing a block net at each end and making two passes through the pool and riffles by placing a seine at the lower end of the riffle and shocking downstream to the net. We pooled results for the two sample dates to obtain a seasonal composite of the fish communities.

We described patterns of fish community composition among the six quantitative sites by computing pairwise similarity matrices using Jaccard's index (species presence or absence, 16 qualitative sites) and Morisita's index (species abundance, six quantitative sites), and sites were clustered as described for mussel community data.

We examined relationships between patterns of fish and mussel community composition using the same methodology used for comparing mussels with habitat. First, we tested for correlation (Mantel test, 20 000 permutations, Rohlf 1989) between the fish and mussel

Table 1. Mussel fauna of Sipsey Fork and Brushy Creek drainages, Black Warrior River system, Winston and Lawrence counties, Alabama, U.S.A.

Mussel species	Frequency of occurrence at qualitative sites with mussels ($n = 25$)
Anodontinae	
Strophitus subvexus	0.80
Ambleminae	
Pleurobema furvum	0.44
Elliptio arca	0.24
Quadrula asperata	0.24
Tritogonia verrucosa	0.20
Elliptio arctata	0.16
Lampsilinae	
Lampsilis perovalis	0.92
Villosa vibex	0.80
Villosa lienosa	0.64
Lampsilis straminea claibornensis	0.60
Ptychobranchus greeni	0.52
Medionidus acutissimus	0.44
Villosa nebulosa	0.44
Lampsilis ornata	0.20
Potamilus purpuratus[a]	0.04

[a]Found only in qualitative sampling.

distance matrices for 16 qualitative sites and between fish and mussel distance matrices for the six quantitative sites. Second, we factored principal components from the correlation matrix of fish species abundances at quantitative sites for each mussel species and computed mean principal component scores (±2 SE) to ordinate mussel species in fish community space (Moyle and Vondracek 1985).

Finally, we tested the hypothesis that the abundance of a mussel species would be related to the density of its host-fishes. Our null hypothesis was that abundances of the mussel and host-fish would be independent; the alternative hypothesis was that the abundances of the mussel and fish host would be correlated positively. We established mussel/host-fish relationships using recent literature. These relationships were tested using one-tailed Pearson correlation analysis (SAS 1994). We tested the following mussel/host-fish pairs: *Lampsilis perovalis*/*Micropterus* spp. (Haag and Warren 1997), *Villosa* spp./Centrarchidae (Zale and Neves 1982; Neves et al. 1985; Haag and Warren 1997), *Medionidus acutissimus*/*Fundulus olivaceus*, *Etheostoma douglasi*, *Etheostoma whipplei*, *Percina nigrofasciata*, *Percina* sp. cf. *caprodes* (Haag and Warren 1997), *Pleurobema furvum*/*F. olivaceus*, *Campostoma oligolepis*, *Cyprinella callistia*, *Cyprinella venusta*, *Semotilus atromaculatus* (Haag and Warren 1997), *Ptychobranchus greeni*/*Etheostoma bellator*, *E. douglasi*, *P. nigrofasciata*, *P.* sp. cf. *caprodes* (Haag and Warren 1997), and *Strophitus subvexus*/host-generalist, including representatives of the families Fundulidae, Catostomidae, Cyprinidae, Centrarchidae, and Percidae (Haag and Warren 1997). We did not test relationships for *Elliptio arca*, *Elliptio arctata*, *Quadrula asperata*, or *Tritogonia verrucosa* because of an inavailability of host information for these species.

Results

Mussel community

Fifteen species of mussels were collected from streams in the study area, 14 of which were encountered in quadrat samples (Table 1). *Lampsilis ornata* and *Lampsilis straminea* were encountered only once and were excluded from all analyses except those discussed in this paragraph. During the early phases of field work, we did not distinguish *E. arca* from *E. arctata*; thus, we pooled the two species for all analyses. Species richness was associated positively with stream size (for all 30 qualitative sites: richness = 4.02 log(link No.), $P < 0.0008$, $R^2 = 0.40$; for seven quantitative sites: richness = 4.83 log(link No.), $P < 0.0001$, $R^2 = 0.94$; intercepts not significant, $P > 0.05$). Total density of mussels at the seven quantitative sites was not correlated with stream size (density with $\log_{10}$-transformed link magnitude, Pearson correlation coefficient $r = -0.1324$, $P < 0.78$), but relative abundances of individual species showed distinctive longitudinal patterns. Headwater sites were composed exclusively of species in the subfamilies Lampsilinae (*Villosa* spp., *M. acutissimus*, and *Lampsilis* spp.) and Anodontinae (*S. subvexus*), but the relative abundance of species in the subfamily Ambleminae (*Q. asperata*, *Elliptio* spp., *P. furvum*, and *T. verrucosa*) gradually increased in a downstream direction, composing 55 and 44% of the total at the lowermost sites in the Brushy and Sipsey drainages, respectively. Three lampsiline species (*L. ornata*, *P. greeni*, and *Potamilus pupuratus*) also were absent from headwater sites and increased in abundance in a downstream direction. No species were restricted to headwaters.

Phenetic classification of mussel species presence/absence data for the 25 qualitative sites with mussels produced three major clusters based primarily on stream size (Fig. 2a). The first two nodes separated four sites that were relatively depauperate (sites 9, 14, 30, and 27). These sites ranged from extreme headwaters (link magnitude 11, II order) to larger streams (link magnitude 272, V order), and the low diversity or unusual species composition at these sites was probably due to localized, anomalous stream conditions or inefficient sampling. The third node separated the remaining 21 sites into two groups: a cluster of large streams and a cluster of headwater to midreach streams. The large-stream cluster was composed of six V- and VI-order sites (link magnitude 158–405) on the lower reaches of Brushy Creek and Sipsey Fork. The headwater to midreach cluster was composed of 15 sites ranging from II to IV order (link number 8–143) that were distributed widely across the study area. Within this cluster, intradrainage proximity or stream size did not influence similarity as measured by species presence/absence.

Phenetic classification of the seven quantitative sites based on mussel species abundances revealed three clusters (Fig. 3a) describing differences in stream position and interdrainage patterns of species abundance. The first cluster was composed of large-stream sites (Sipsey Fork and lower Brushy Creek). These two sites were very similar in community composition (Morisita's index = 1.00). The remaining two clusters were composed of (1) headwater and midreach streams in the upper Sipsey Fork drainage (Borden and Flannagin creeks) and (2) headwater and midreach streams in the upper Brushy Creek drainage (Rush, Upper Brushy, and Brown creeks). Although these two clusters were distinct, they were more similar to each other than to the large-stream cluster.

Principal components analysis ordinating the seven quantitative sites by mussel species abundances separated sites into three groups (Fig. 4) that corresponded to the those identified by phenetic classification. Along the PC-I axis, sites were

Fig. 2. Phenetic classification of presence/absence data for (*a*) mussel assemblages at 25 sites and (*b*) fish assemblages at 16 sites in the Sipsey Fork and Brushy Creek drainages.
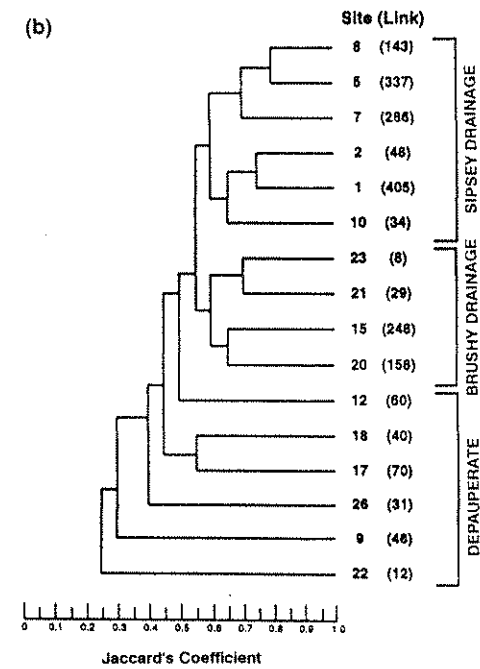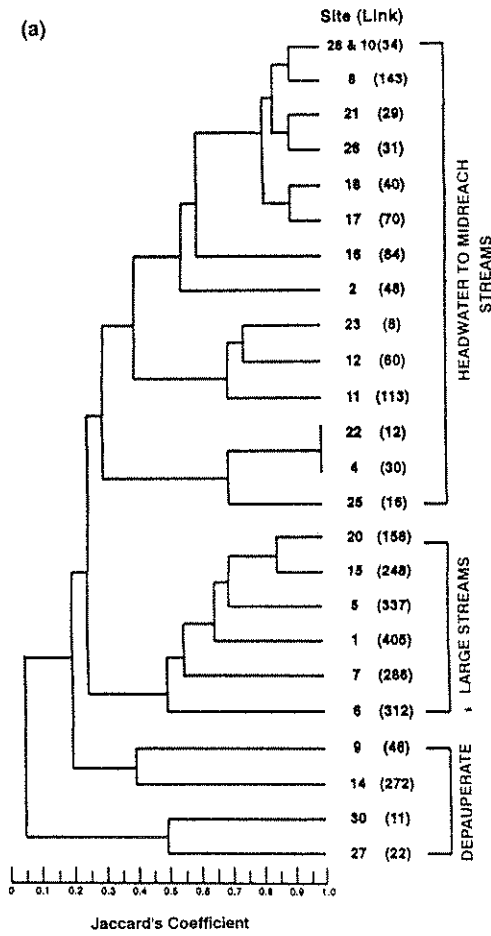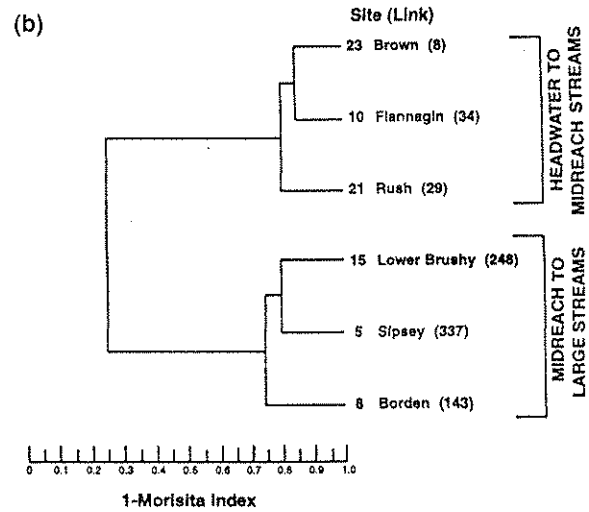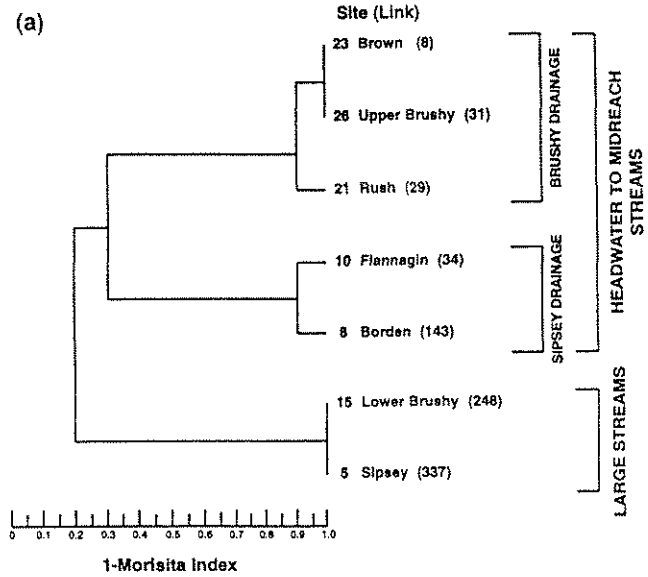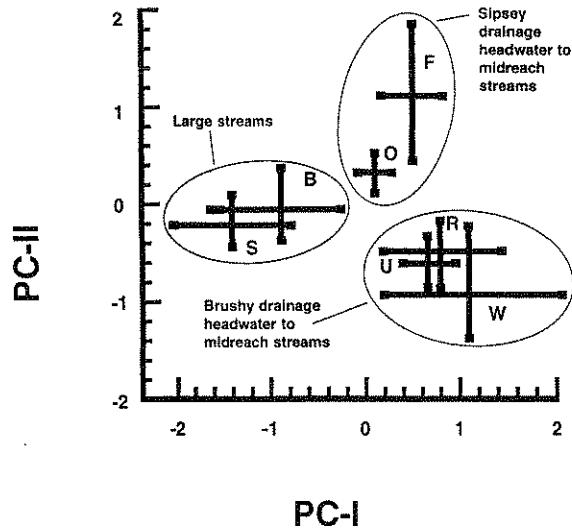
Fig. 3. Phenetic classification of species abundance data for (*a*) mussel assemblages at seven sites and (*b*) fish assemblages at six sites in the Sipsey Fork and Brushy Creek drainages.

ordered by stream size and were separated into two nonoverlapping groups (±2 SE): (1) large streams (Sipsey Fork and lower Brushy Creek, link magnitudes 337 and 248, respectively) and (2) headwater and midreach streams (Borden, Flannagin, Rush, Brown, and upper Brushy creeks, link magnitudes 8–143) (Fig. 4). Within each group, site standard errors overlapped widely. Magnitudes and polarities of loadings on the PC-I axis identified a large-stream faunal group that included *T. verrucosa*, *Elliptio* spp., *P. greeni*, and *P. furvum*, contrasted with a group of species more abundant in headwater streams, including *L. perovalis*, *S. subvexus*, *M. acutissimus*, and *Villosa* spp. The PC-II axis separated headwater and midreach sites into two nonoverlapping groups corresponding to intradrainage proximity: (1) sites in the upper

Fig. 4. Principal components axes and mean scores (±2 SE) of quantitatively sampled sites ordinated by mussel species abundances. Sampled sites: S, lower Sipsey Fork (site 5); O, Borden Creek (site 8); F, Flannagin Creek (site 10); B, lower Brushy Creek (site 15); R, Rush Creek (site 21); W, Brown Creek (site 23); U, upper Brushy Creek (site 26). Ellipsoids enclose sites whose standard errors overlapped on both axes.
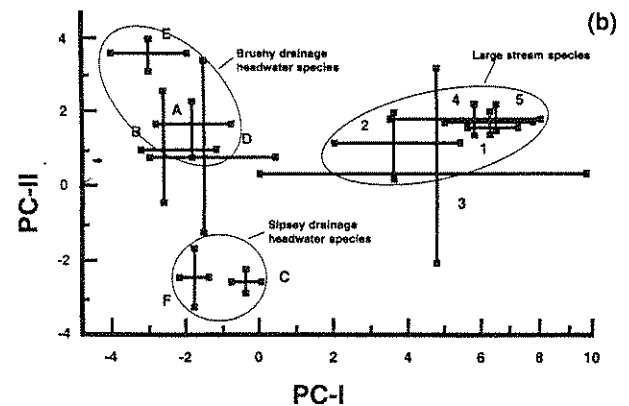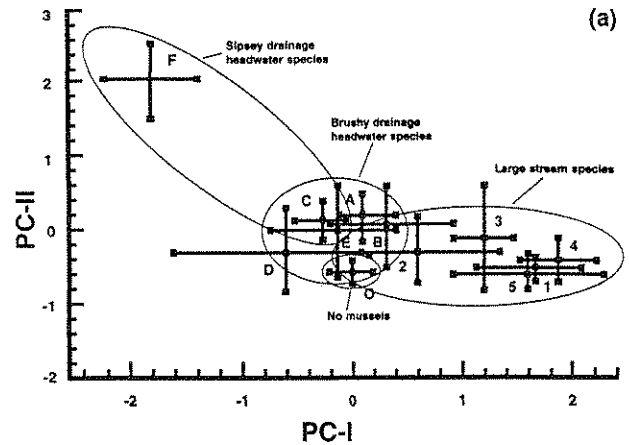

Fig. 5. Principal components axes and mean scores (±2 SE) of of mussel species ordinated by (*a*) microhabitat variables and (*b*) fish species abundances. Mussel species: A, *Lampsilis perovalis*; B, *Medionidus acutissimus*; C, *Villosa nebulosa*; D, *Villosa vibex*; E, *Strophitus subvexus*; F, *Villosa lienosa*; 0, none; 1, *Ptychobranchus greeni*; 2, *Pleurobema furvum*; 3, *Quadrula asperata*; 4, *Elliptio* spp.; 5, *Tritogonia verrucosa*. Ellipsoids enclose faunal groups identified by principal component loadings for analysis of mussel abundances among sites.

Sipsey Fork drainage (Borden and Flannagin creeks) and (2) sites in the upper Brushy Creek drainage (Rush, Brown, and upper Brushy creeks) (Fig. 4). Loadings on PC-II indicated that separation of headwater and midreach streams was due primarily to variation in abundance of four species. Upper Sipsey Fork streams were characterized by high densities of *Villosa nebulosa* and *Villosa lienosa*, rarity or absence of *S. subvexus*, and lower densities of *L. perovalis*; this pattern was reversed in streams in the upper Brushy drainage.

Microhabitat

Variation in microhabitat showed no distinct patterns in the drainages and showed little similarity to patterns of mussel community composition. Habitat diversity varied little among sites, ranging from 1.61 to 1.82. Habitat similarity among sites was high (>0.90), and phenetic classification did not reveal clusters based on either stream size or intradrainage proximity. Distance matrices for habitat and mussel abundance at the six quantitative sites were not correlated (Mantel $r = 0.2999$, $P > 0.05$).

Discrimination among mussel species based on habitat variables was weak. Principal components analysis of mussel species ordinated by habitat variables produced eigenvalues that did not exceed those of the broken-stick model, and thus was considered of questionable interpretive value. The PC-I axis (Fig. 5*a*) did weakly separate species into the large- and small-stream faunal groupings seen in earlier analyses; however, one species from each group (*M. acutissimus*, small-stream group; *P. furvum*, large-stream group) overlapped widely with both clusters. The centroid for quadrats without mussels plotted within the small-stream group. Along the PC-II axis, *V. lienosa* was separated from all other species in association with high loadings for vegetation (*Justicia americana*) and silt;

other species that showed highly variable abundances between drainages were not discriminated by habitat.

Fish community

Fish community composition showed both longitudinal and interdrainage patterns that were, in part, similar to patterns of mussel abundance. Phenetic classification of streams based on fish species presence/absence clustered the sites into three major groups (Fig. 2*b*): (1) a depauperate group with each site having 15 or fewer species (with the exception of Brushy Creek, site 22), (2) a group of sites in the Sipsey Fork drainage, and (3) a group in the Brushy Creek drainage. This distance matrix was not correlated with the distance matrix for mussel species presence/absence at the same sites (Mantel $r = 0.2382$, $P > 0.05$). Clustering of the six quantitative sites based on fish species abundances produced two groups of sites that corresponded only to stream size (Fig. 3*b*). However, this matrix was correlated with the distance matrix for mussel species

abundance at the same sites ($r = 0.4879$, $P < 0.05$), even though the fish matrix showed no interdrainage pattern, as seen for mussels.

Discrimination among mussel species based on associated fish species was strong and produced a pattern that was similar to patterns of variation in mussel community composition. Principal components analysis of mussel species ordinated by fish species produced eigenvalues that exceeded those of the broken-stick model, providing support for interpretation of this plot. The PC-I axis separated mussel species into two groups (Fig. 5b) that corresponded to the large-stream and headwater to midreach faunal groups identified in previous analyses (Figs. 3a and 4). Similarly, the PC-II axis separated headwater and midreach species into two groups based on intradrainage proximity (Fig. 5b) that corresponded to those identified previously (Figs. 3a and 4).

Relationships between mussel and host-fish abundances varied among mussel species (Table 2). Abundances of mussels that were widespread within the drainages and characteristic of headwater to midreach streams (L. perovalis, Villosa spp., M. acutissimus, and S. subvexus) were not correlated with abundances of their fish hosts. Within this group, two distinct modes of host use and attraction were represented. Strophitus subvexus is a host-generalist; the other three lampsiline species are host-specialists that possess mantle modifications used ostensibly to lure a fish to the gravid female. Abundances of species restricted to larger streams (P. furvum and P. greeni) were correlated positively with abundances of fish hosts. Both of these species are host-specialists but do not have mantle modifications.

Discussion

Community composition of freshwater mussels in the study area showed two important patterns: (1) species richness increased in a downstream direction and the faunas of large-stream sites were characterized by similar, distinctive assemblages and (2) faunal composition of headwater sites varied widely among sites in different drainages. Distribution and abundance of free-living animals are usually thought to be controlled by three broad factors: food availability, predation intensity, and physical habitat requirements (Connell 1975; Angermeier and Karr 1983; Power et al. 1988). Diverse marine bivalve communities are structured by food resource partitioning, predation pressures, competition for space, and distinct differences in habitat usage among species (Purchon 1977; Hughes and Griffiths 1988; McGrorty et al. 1990). Likewise, stream fish communities often are structured by a similar suite of factors (Angermeier and Karr 1983; Moyle and Vondracek 1985; Ross 1986; Schlosser and Angermeier 1990; Pyron and Taylor 1993). However, for diverse freshwater mussel communities, these factors do not offer satisfactory explanations of observed patterns in distribution and abundance.

Partitioning of food resources is an important component of community structure in marine bivalves. Marine bivalve communities may be composed of representatives of several subclasses and orders and show great diversity in feeding strategies (e.g., suspension and deposit feeding, boring, and carnivory) (Morton 1983; Allen 1985). In contrast, North American freshwater mussel communities are composed of members of a single order (Unionoida) and, with the exception

Table 2. Correlations (r, Pearson's correlation coefficient) of mussel abundance with abundance of fish hosts.

Mussel species	r	P
Displaying host-specialists		
Lampsilis perovalis[a]	–0.3065	ns
Villosa spp.[b]	0.6402	ns
Medionidus acutissimus[c]	–0.7243	ns
Nondisplaying host-specialists		
Ptychobranchus greeni[d]	0.9161	<0.01*
Pleurobema furvum[e]	0.9427	<0.01*
Host-generalists		
Strophitus subvexus[f]	–0.5552	ns

Note: *Significant correlation; ns, not significant. Fish hosts for each mussel are given in the footnotes.

[a]Micropterus spp.

[b]Centrarchidae.

[c]Fundulus olivaceus, Etheostoma douglasi, Etheostoma whipplei, Percina nigrofasciata, Percina sp. cf. caprodes.

[d]Etheostoma bellator, Etheostoma douglasi, Percina nigrofasciata, Percina sp. cf. caprodes.

[e]Campsotoma oligolepis, Cyprinella callistia, Cyprinella venusta, Semotilus atromaculatus, Fundulus olivaceus.

[f]Catostomidae, Centrarchidae, Cyprinidae, Fundulidae, Percidae.

of five species in the Margaritiferidae, are members of a single family (Unionidae). Although detailed dietary information about freshwater mussels is lacking, anatomical or behavioral modifications that would suggest the presence of food resource specialization have not been documented.

In general, predation pressure on molluscs in freshwater is thought to be low compared with marine systems (Vermeij and Dudley 1985). Many marine predators are adapted strictly for molluscivory, and marine bivalves have an array of shell modifications and behaviors to thwart predation. In contrast, freshwaters have few molluscivorous species (despite exceptions such as freshwater drum (Aplodinotus grunniens) and river redhorse (Moxostoma carinatum) with crushing molariform pharyngeal teeth), and freshwater bivalves lack the antipredator shell and behavioral modifications seen in marine bivalves (Vermeij and Dudley 1985; Vermeij 1993). Although larval mortality is high (Young and Williams 1984) and little is known about juvenile mortality, adult freshwater mussels are long-lived organisms with low annual mortality (Negus 1966; Bauer 1987). Adult mussels may be subject to size- and species-selective predation from muskrats (Hanson et al. 1989; Neves and Odum 1989; Watters 1995). However, muskrat predation is sporadic and localized (personal observation), and muskrats do not occur in many areas that support diverse mussel faunas. In our study area, we observed no mortality from muskrats, and molluscivorous fishes are rare or absent.

Many freshwater animals as well as marine bivalves are strict physicochemical habitat specialists, and availability of suitable habitat is an important factor in structuring communities. Although radically different habitats (e.g., wetlands versus streams) may support different mussel species assemblages, habitat and environmental variables poorly predict presence and abundance of mussel species within a stream reach or a drainage (Holland-Bartels 1990; Strayer and Ralley 1993; Strayer et al. 1994). We found that, in general, species were not discriminated by habitat. Mussel populations in our study were usually sparse, and quadrats with no mussels were

not distinguished by habitat variables from quadrats inhabited by mussels (Fig. 5a), suggesting that space or suitable habitat was not limiting. Adult mussels have broad niche widths for habitat (Tevesz and McCall 1979), and Strayer et al. (1994) questioned the usefulness of focusing on these mechanisms in studies of mussel ecology.

Although mussel species show little obvious specialization in feeding, antipredator defenses, or habitat, there is striking partitioning of host-fish resources among species. The majority of the life of a mussel is spent as a free-living organism, but as larvae, mussels are inexorably dependent on the host-fish. In this way, mussels show characteristics of parasitic organisms in which an important resource base is the host (Price 1990). The niche concept as applied to mussel species must therefore encompass variables related to the host as one of the most important dimensions.

Mussel species show great variation in host-fish specificity and in strategies for infecting fishes with larvae and can be divided into at least three major groups: host-generalists, displaying host-specialists, and nondisplaying host-specialists. Host-generalists use as hosts fish species in many different families and feeding guilds (Trdan and Hoeh 1982; Watters 1994). Generalists include many species in the subfamily Anodontinae (including the genera *Anodonta*, *Pyganodon*, *Utterbackia*, *Strophitus*, and others) and possibly some members of the Ambleminae and Lampsilinae (Watters 1994). Host-generalists broadcast prodigious numbers of larvae that encounter a host in a passive manner (Dartnall and Walkey 1979) or release larvae bound in long mucous webs that entangle potential fish hosts (Kat 1984). Host-specialists use a small number of fish species that are usually in the same family and (or) feeding guild (Watters 1994). Among host-specialists, there are two distinct strategies for increasing chances of host parasitization: displayers and nondisplayers. Displayers include members of the subfamily Lampsilinae in the genera *Lampsilis*, *Villosa*, *Medionidus*, *Toxolasma*, *Ligumia*, and possibly *Epioblasma*. In these genera, females have modified mantle margins (Kat 1984) or present larvae in attached external structures (Haag et al. 1995), both of which mimic food items of fishes and are thought to attract host-fishes to the gravid female mussel. Nondisplayers include a large number of genera in the subfamily Ambleminae (in this study, *Quadrula*, *Pleurobema*, *Elliptio*, and perhaps *Tritogonia*) and lampsilines (in this study, *Ptychobranchus*, but perhaps about 10 other North American genera). Females of these genera may release larvae singly or in small packets that mimic fish food items, but they are distinguished by a lack of modified structures that serve to attract hosts to the gravid female.

Patterns of host-fish use and infestation strategy among mussel species may explain some of the patterns of mussel distribution and abundance in our study streams. Representatives of the three major host strategies are present in our system: host-generalists (*S. subvexus*), nondisplaying host-specialists (*P. furvum*, *Q. asperata*, *Elliptio* spp., *T. verrucosa*, and *P. greeni*), and displaying host-specialists (*Villosa* spp., *L. perovalis*, and *M. acutissimus*). We found that host-generalists and displaying host-specialists exclusively constituted headwater communities but also occurred in larger streams. Nondisplaying host-specialists were restricted to larger streams. Headwater fish communities are usually persistent in composition but more temporally variable in

abundance than downstream communities (Schlosser 1982; Moyle and Vondracek 1985; Freeman et al. 1988; Schlosser 1990). Host-generalists and displaying host-specialists may be able to inhabit headwaters because their infestation strategies release them from a density-dependent relationship with host-fishes. Release from density dependence occurs through use of a taxonomically broad host-fish array or by attracting host-fish species of variable densities to the gravid mussel before release of larvae. In support of this, we found no correlation in host-fish and mussel abundance among host-generalists and displaying host-specialists (Table 2). In contrast, we found positive correlation of abundances of nondisplaying host-specialists and their fish hosts (Table 2). This suggests that nondisplaying host-specialists show a density-dependent relationship to host-fishes, an advantageous mechanism to increase chances of infestation of specific host-fishes where host-fish abundances are less variable (i.e., large streams) and a disadvantage for persistence in habitats with highly variable fish abundances (i.e., headwaters). At the scale of the drainage basin, longitudinal patterns of mussel species distribution and abundance are linked closely to dynamics of host-fish relationships.

Variation in species abundance at headwater sites between the Sipsey Fork and Brushy Creek drainages is not easily explained by host-fish relationships or habitat. Although interdrainage patterns of community composition were similar between fishes and mussels, patterns of variation in fish communities between drainages were, in part, caused by species that were restricted to one drainage or the other. However, no mussel species were restricted to one drainage. Differences in fish communities also were influenced by variation in abundance of species common to both drainages, but abundances of mussel species in headwaters are uncorrelated with host-fish densities. Similarly, headwater mussel species were not discriminated based on habitat variables, even though each drainage was characterized by a unique species assemblage (Fig. 5a). Neither host-fish availability nor habitat offers a compelling explanation for observed differences in mussel community composition among headwater sites.

Variation among headwater mussel communities may be the result of stochastic processes associated with unstable headwater habitats (Schlosser 1982). Small-scale variation in mussel density has been attributed to the distribution of stable substrates (Vannote and Minshall 1982) but, at larger scales, stream size is the most consistent predictor of mussel community composition (Strayer 1983, 1993), despite attempts to relate other habitat variables to observed patterns (Strayer 1993; Strayer et al. 1994). Studies of stream fishes give strong evidence of decreasing upstream–downstream gradients in natural environmental variability (Schlosser 1990). For mussels, more stable downstream conditions may allow deterministic processes such as density-dependent mussel/host-fish relationships to influence community structure, while wide fluctuations in flow regime and habitat stability may largely influence community structure in headwaters.

Mussel communities should be viewed as the result of complex interactions of biotic and abiotic factors operating differentially on different spatial and temporal scales as well as on species with different life history strategies. At the scale of a drainage basin, mussel distributions and abundances may be influenced by dynamics of mussel/host-fish relationships. At

smaller scales, stochastic variation in biotic and abiotic factors as well as local physical heterogeneity may preclude manifestation of deterministic mechanisms and produce unpredictable species assemblages and abundances. Several important aspects of freshwater mussel ecology such as food use and juvenile mortality remain poorly known. However, there are currently no compelling arguments for the existence of strong differential predation among species, and niche width for food and habitat use appears to be broad for many species. Concomitant with broadening of use of these resources is a narrowing of niche width at the dimension of the fish host. The diverse radiation of North American freshwater mussels may have occurred in concert with opportunities for intense exploitation and partitioning of the diverse host-fish resource.

Acknowledgments

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