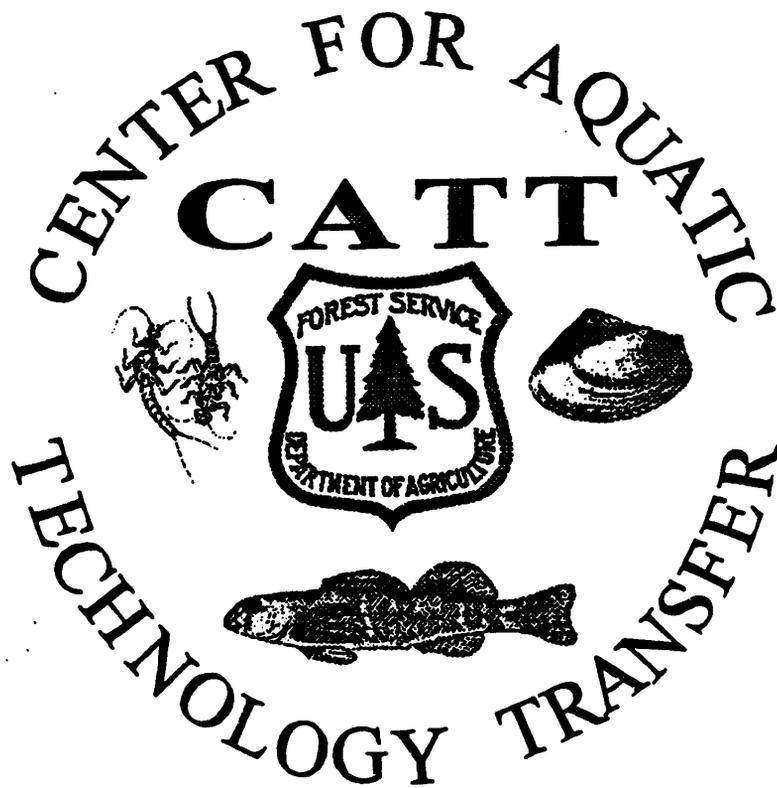


**Role of Ecological Factors and Reproductive Strategies
in Structuring Freshwater Mussel Communities**



**United States Department of Agriculture Forest Service
Center for Aquatic Technology Transfer
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United States Department of Agriculture Forest Service
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1000 Front Street
Oxford, Mississippi 38655

Wendell R. Haag
Biological Technician

and

Melvin L. Warren, Jr.
Team Leader
Terrestrial and Aquatic Fauna Team
Center for Bottomland Hardwoods Research
Southern Research Station

Submitted to:

April Hargis
Fishery Biologist
Alabama National Forests
Montgomery, AL

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² Headquartered at Virginia Tech, Blacksburg, VA 24061-0321

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

Wendell R. Haag and Melvin L. Warren, Jr.

USDA Forest Service, Southern Research Station, Forest Hydrology Laboratory, 1000 Front Street, Oxford, Mississippi 38655 USA

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Abstract

Freshwater mussel community composition within two drainage basins in Alabama, USA, 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 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 mid-reach 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.

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 20th 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 U.S., 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 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 in order 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, USA. 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 Sipsev 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

The 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: Sipsev 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-m² cells over a reach of stream and selecting 25% of the cells using a random numbers table. We placed a 0.5-m² quadrat (with the exception of Rush Creek, where a 0.25 m² 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 2-5 reaches of 7-20 meters 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-minute 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 5 sites with no mussels) and Morisita's index (species abundance, 7 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 flow-meter (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 from 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 PC 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.

The 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 ($25-53 \text{ min} \cdot \text{site}^{-1} \cdot \text{sample date}^{-1}$). 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, 6 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 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 PC 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 in press); Villosa spp./Centrarchidae (Haag and Warren in press; Zale and Neves 1982; Neves et al. 1985); Medionidus acutissimus/Fundulus olivaceus, Etheostoma douglasi, E. whipplei, Percina nigrofasciata, P. sp. cf. caprodes (Haag and Warren in press); Pleurobema furvum/F. olivaceus, Campostoma oligolepis, Cyprinella callistia, C. venusta, Semotilus atromaculatus (Haag and Warren in press); Ptychobranchnus greeni/Etheostoma bellator, E. douglasi, Percina nigrofasciata, P. sp. cf. caprodes (Haag and Warren in press); and Strophitus subvexus/host generalist, including representatives of the families Fundulidae, Catostomidae, Cyprinidae, Centrarchidae, and Percidae (Haag and Warren in press). We did not test relationships for Elliptio arca, E. arctata, Quadrula asperata, or Tritogonia verrucosa because of an inavailability of host information for these species.

Results

The 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 L. 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 Elliptio 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 = $4.02 \log(\text{Link No.})$, $P < 0.0008$, $R^2 = 0.40$; for 7 quantitative sites: Richness = $4.83 \log(\text{Link No.})$, $P < 0.0001$, $R^2 = 0.94$; 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., Medionidus acutissimus, and Lampsilis spp.) and Anodontinae (S. subvexus), but the relative abundance of species in the subfamily Ambleminae (Quadrula asperata, Elliptio spp., Pleurobema furvum, and Tritogonia verrucosa) gradually increased in a downstream direction, composing 55% and 44% of the total at the lower-most sites in the Brushy and Sipsey drainages, respectively. Three lampsiline species (Lampsilis ornata, Ptychobranthus greeni, 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 4 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 twenty-one sites into two groups: a cluster of large streams and a cluster of headwater to mid-reach 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 mid-reach cluster was composed of 15 sites ranging from II- to IV-order (link number 8 to 143) that were distributed widely across the study area. Within this cluster, intra-drainage 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 inter-drainage 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 mid-reach streams in the upper Sipsey Fork drainage (Borden and Flannagin creeks) and, 2) headwater and mid-reach 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 PCI axis, sites were ordered by stream size and were separated into two non-overlapping groups (± 2 SE): 1) large streams (Sipsey Fork and lower Brushy Creek, link magnitudes 337 and 248, respectively) and, 2) headwater and mid-reach 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 PCI axis identified a large-stream faunal group that included Tritogonia verrucosa, Elliptio spp., Ptychobranthus greeni, and Pleurobema furvum, contrasted with a group of species more abundant in headwater streams, including Lampsilis perovalis, Strophitus subvexus, Medionidus acutissimus, and Villosa spp. The PCII axis separated headwater and mid-reach sites into two non-overlapping groups corresponding to intra-drainage proximity: 1) sites in the upper 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 PCII indicated that separation of headwater and mid-reach streams was due primarily to variation in abundance of four species. Upper Sipsey Fork streams were characterized by high densities of Villosa nebulosa

and V. lienosa, rarity or absence of S. subvexus, and lower densities of Lampsilis 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 structure. 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 intra-drainage 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 PCI axis (Fig 5a) did weakly separate species into the large- and small-stream faunal groupings seen in earlier analyses, however one species from each group (Medionidus acutissimus, small-stream group; Pleurobema furvum, large-stream group) overlapped widely with both clusters. The centroid for quadrats without mussels plotted within the small-stream group. Along the PCII axis,

Villosa lienosa was separated from all other species in association with high loadings for vegetation (Justicia americana) and silt; other species which showed highly variable abundances between drainages were not discriminated by habitat.

The Fish Community

Fish community composition showed both longitudinal and inter-drainage 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. 2b): 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 Sipsy 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. 3b). 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 inter-drainage 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 PCI axis separated mussel species into two groups (Fig 5b) that corresponded to the large-stream and headwater to mid-reach faunal groups identified in previous analyses (Figs 3a and 4). Similarly, the PCII axis separated headwater and mid-reach species into two groups based on intra-drainage 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 mid-reach streams (Lampsilis perovalis, Villosa spp., Medionidus acutissimus, and Strophitus 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 (Pleurobema furvum and Ptychobranthus 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; Pyron and Taylor 1993; Ross 1986; Schlosser and Angermeier 1990). 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 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 to 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 and river redhorse 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 in press). 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 physico-chemical habitat specialists and availability of suitable habitat is an important factor in structuring communities. Although radically different habitats (e.g., wetlands vs. 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 were 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 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 non-displaying 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 Amblesinae 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 non-displayers. Displayers include members of the subfamily Lampsilinae in the genera Lampsilis, Villosa, Medionidus, Toxolasma, Ligumia, and possibly Epioblasma. In these genera, females display 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. Non-displayers include a large number of genera in the subfamily Ambleminae (in this study, Quadrula, Pleurobema, Elliptio, and perhaps Tritogonia) and lampsilines (in this study, Ptychobranthus, but perhaps about 10 other North American genera). Females of these genera may release larvae singly or in small packets which 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 (Strophitus subvexus); displaying host-specialists (Villosa spp., Lampsilis perovalis, and Medionidus acutissimus); and non-displaying host-specialists (Pleurobema furvum, Quadrula asperata, Elliptio spp., Tritogonia verrucosa, and Ptychobranthus greeni). We found that host-generalists and displaying host-specialists exclusively constituted headwater communities but also occurred in larger streams. Non-displaying 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 non-displaying host-specialists and their fish hosts (Table 2). This suggests that non-displaying 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 Sipsev Fork and Brushy Creek drainages is not easily explained by host-fish relationships or habitat. Although inter-drainage 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 offer compelling explanations 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 structure (Strayer 1983; Strayer 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.

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Table 1. Mussel fauna of Sipsev Fork and Brushy Creek drainages, Black Warrior River system, Winston and Lawrence counties, Alabama, USA.

Species	Frequency of occurrence at qualitative sites with mussels (n=25)
Anodontinae	
<u>Strophitus subvexus</u>	0.80
Ambleminae	
<u>Pleurobema furvum</u>	0.44
<u>Elliptio arca</u>	0.24
<u>Quadrula asperata</u>	0.24
<u>Tritogonia verrucosa</u>	0.20
<u>E. arctata</u>	0.16
Lampsilinae	
<u>Lampsilis perovalis</u>	0.92
<u>Villosa vibex</u>	0.80
<u>V. lienosa</u>	0.64
<u>L. straminea claibornensis</u>	0.60
<u>Ptychobranchnus greeni</u>	0.52
<u>Medionidus acutissimus</u>	0.44
<u>V. nebulosa</u>	0.44
<u>L. ornata</u>	0.20
<u>Potamilus purpuratus*</u>	0.04

* Species found only in qualitative sampling.

Table 2. Correlations of mussel abundance with abundance of fish hosts. r = Pearson's Correlation Coefficient, an asterisk (*) denotes significant correlation. Fish hosts for each mussel are given in footnotes.

Mussel species	r	P
Displaying host-specialists		
<u>Lampsilis perovalis</u> ¹	-0.3065	ns
<u>Villosa</u> spp. ²	0.6402	ns
<u>Medionidus acutissimus</u> ³	-0.7243	ns
Non-displaying host-specialists		
<u>Ptychobranchus greeni</u> ⁴	0.9161	<0.01*
<u>Pleurobema furvum</u> ⁵	0.9427	<0.01*
Host-generalists		
<u>Strophitus subvexus</u> ⁶	-0.5552	ns

¹ Micropterus spp.

² Centrarchidae

³ Fundulus olivaceus, Etheostoma douglasi, E. whipplei, Percina nigrofasciata, P. sp. cf. caprodes.

⁴ Etheostoma bellator, E. douglasi, Percina nigrofasciata, P. sp. cf. caprodes.

⁵ Campsotoma oligolepis, Cyprinella callistia, C. venusta, Semotilus atromaculatus, Fundulus olivaceus.

⁶ Catostomidae, Centrarchidae, Cyprinidae, Fundulidae, Percidae

Figure Legends

Figure 1. Qualitative (circles) and quantitative (triangles) freshwater mussel and fish sampling sites in the Sipsey Fork and Brushy Creek drainages, AL, USA. Quantitative mussel sampling sites include: 5 (lower Sipsey Fork); 8 (Borden Creek); 10 (Flannagin Creek); 15 (lower Brushy Creek); 21 (Rush Creek); 23 (Brown Creek); 26 (upper Brushy Creek). Quantitative fish sampling sites include sites: 5, 8, 10, 15, 21, and 23.

Figure 2. Phenetic classification of presence/absence data for mussel assemblages at 25 sites (a) and fish assemblages at 16 sites in the Sipsey Fork and Brushy Creek drainages, AL, USA.

Figure 3. Phenetic classification of species abundance data for mussel assemblages at seven sites (a) and fish assemblages at six sites (b) in the Sipsey Fork and Brushy Creek drainages, AL, USA.

Figure 4. Principal components axes and mean scores (\pm 2SE) of quantitatively sampled sites ordinated by mussel species abundances. Capital letters indicate sampled site: "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); and "U", upper Brushy Creek (Site 26). Ellipsoids enclose sites whose standard errors overlapped on both axes.

Figure 5. Principal components axes and mean scores ($\pm 2SE$) of mussel species ordinated by microhabitat variables (a) and fish species abundances (b). Capital letters and numbers indicate mussel species: "A", Lampsilis perovalis; "B", Medionidus acutissimus; "C", Villosa nebulosa; "D", V. vibex; "E", Strophitus subvexus; "F", V. lienosa; "0", None; "1", Ptychobranthus greeni; "2", Pleurobema furvum; "3", Quadrula asperata; "4", Elliptio spp.; and "5", Tritogonia verrucosa. Ellipsoids enclose faunal groups identified by principal components loadings for analysis of mussel abundances among sites.

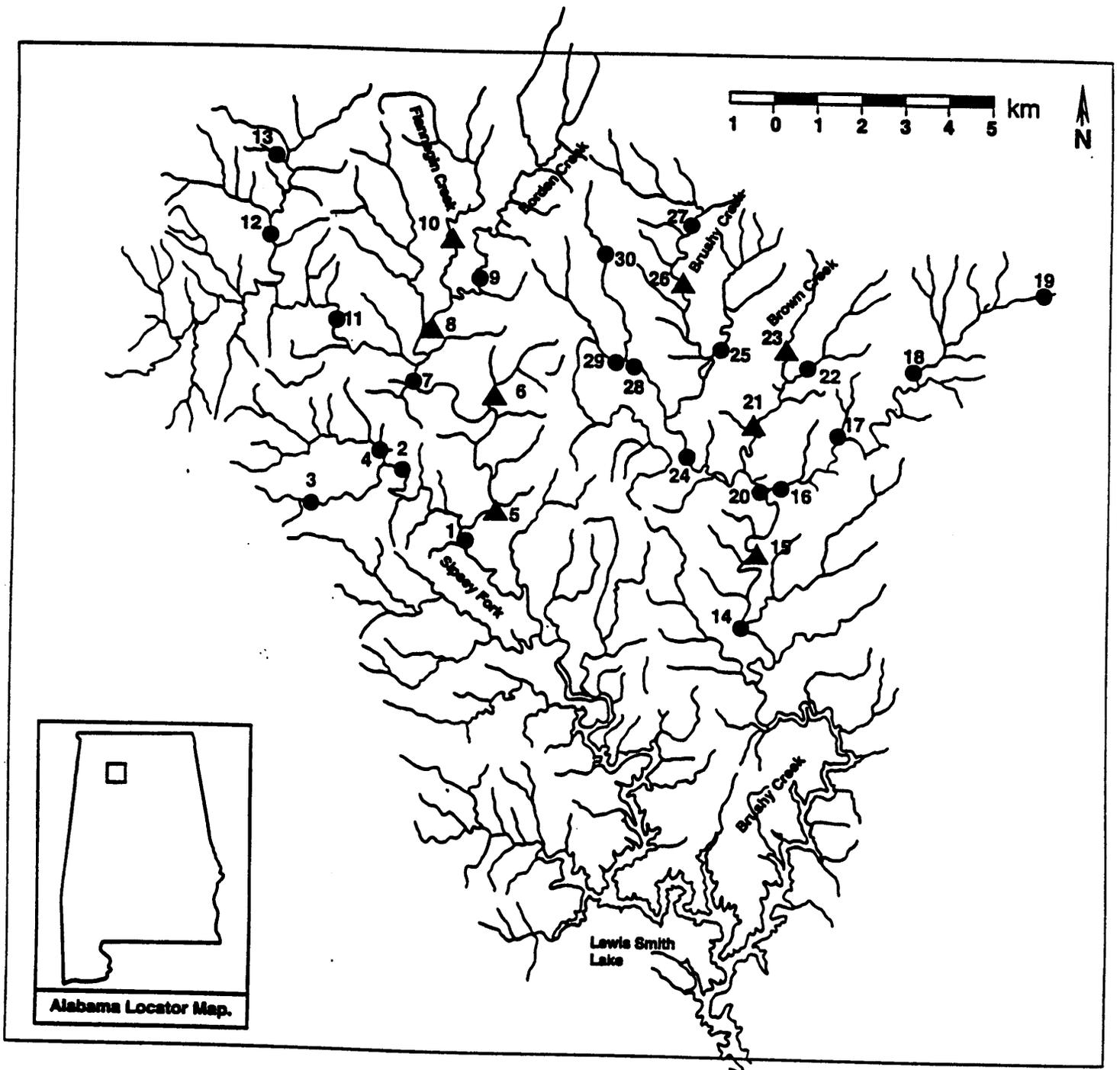


FIG 1

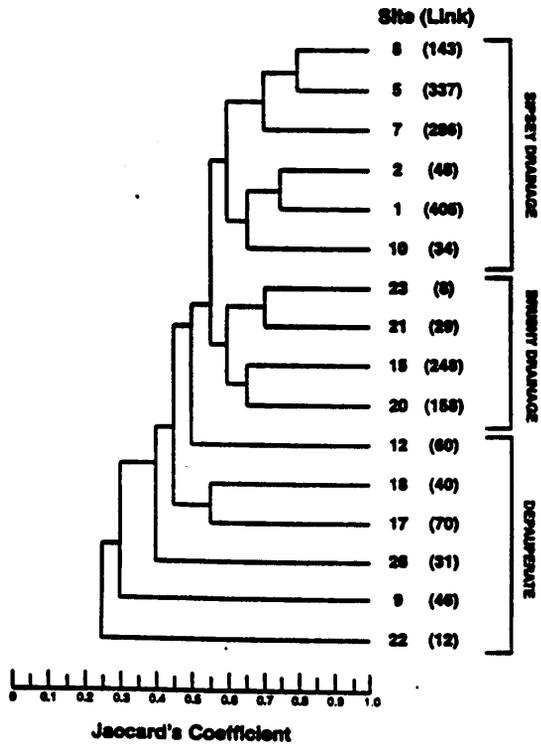
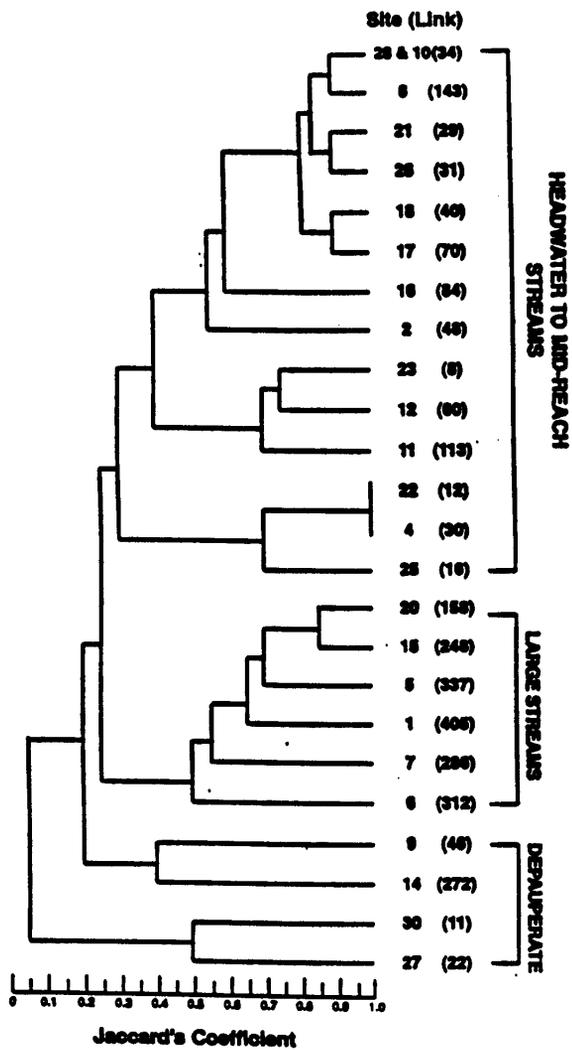
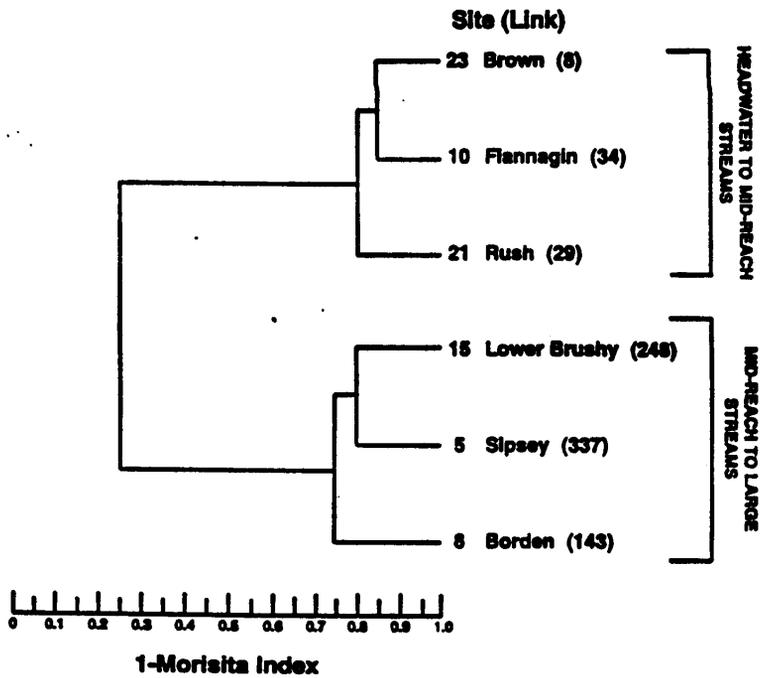
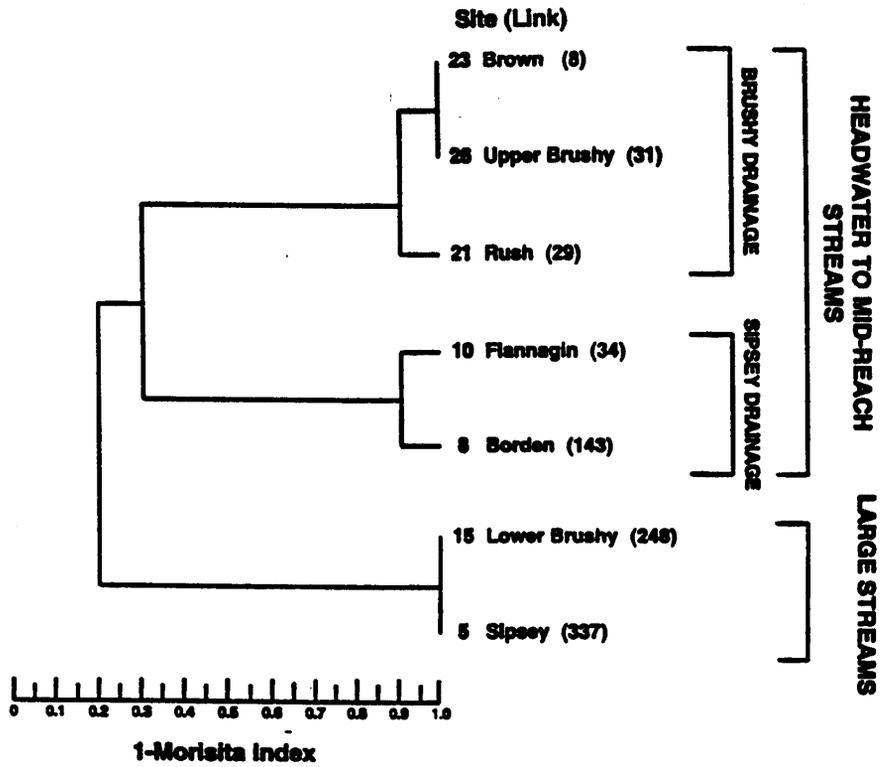
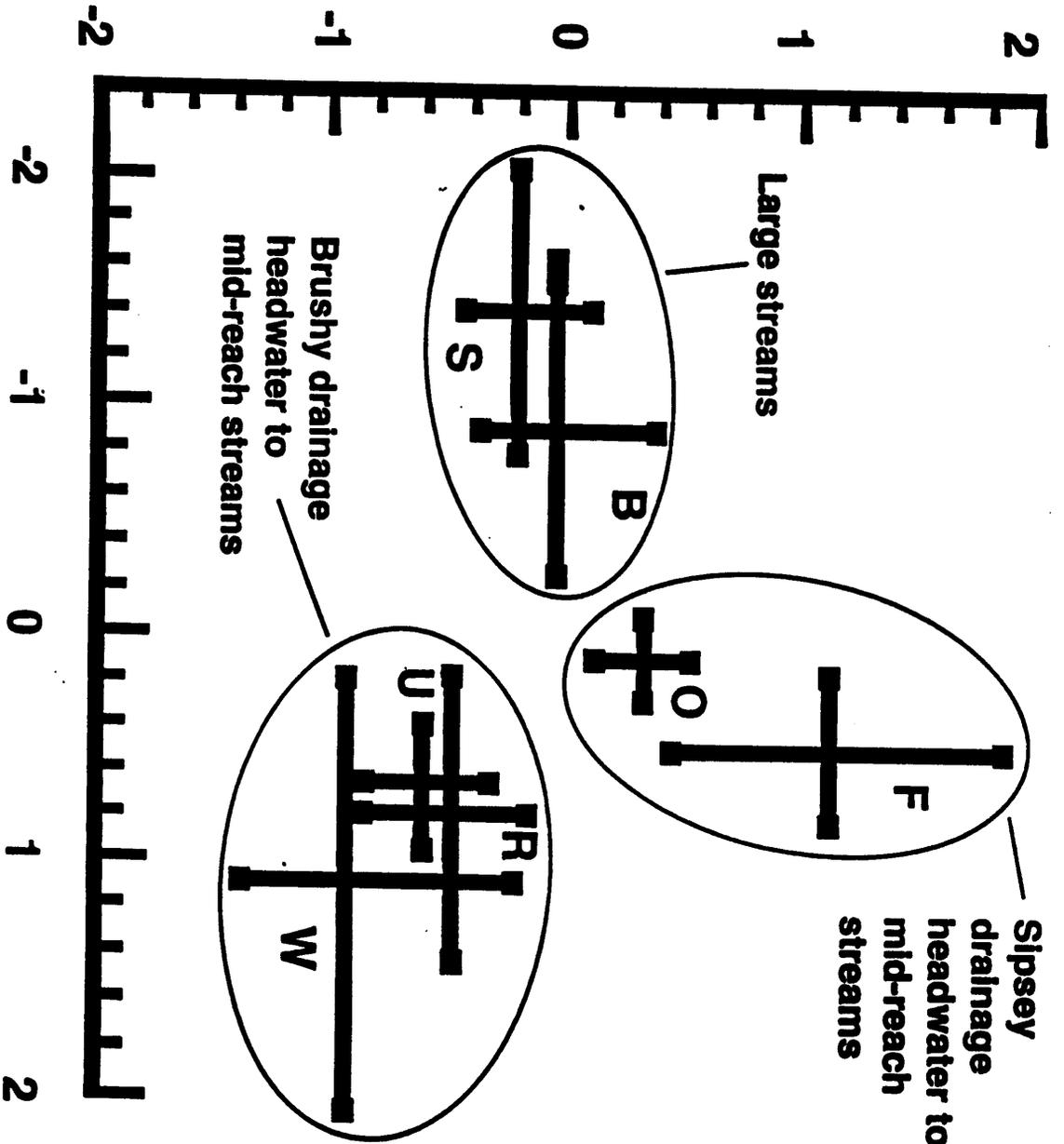


Fig 2a



PC-II



PC-I

FIG. 4

