

## Macroecology of a host-parasite relationship

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The larvae of freshwater mussels are obligate ectoparasites on fishes while adults are sedentary and benthic. Dispersal of mussels is dependent on the movement of fish hosts, a regional process, but growth and reproduction should be governed by local processes. Thus, mussel assemblage attributes should be predictable from the regional distribution and abundance of fishes. At a broad spatial scale in the Red River drainage, USA, mussel species richness and fish species richness were positively associated; maximum mussel richness was limited by fish richness, but was variable beneath that constraint. Measured environmental variables and the associated local fish assemblages each significantly accounted for the regional variation in mussel assemblages. Furthermore, mussel assemblages showed strong spatial autocorrelation. Variation partitioning revealed that pure fish effects accounted for 15.4% of the variation in mussel assemblages; pure spatial and environmental effects accounted for 16.1% and 7.8%, respectively. Shared variation among fish, space and environmental variables totaled 40%. Of this shared variation, 36.8% was associated with the fish matrix. Thus, the variation in mussel assemblages that was associated with the distribution and abundance of fishes was substantial (> 50%), indicating that fish community structure is an important determinant of mussel community structure. Although animals commonly disperse plants and, thus, influence the structure of plant communities, our results show a strong macroecological association between two disparate animal groups with one strongly affecting the assemblage structure of the other.

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Ecologists have long recognized the importance of dispersal in structuring plant communities, and insights about dispersal have contributed to multiple paradigms in ecology including succession, competitive exclusion, tropical species diversity, disturbance ecology, and plant/animal coevolution (MacArthur 1972, MacArthur and Wilson 1967, Futuyma and Slatkin 1973, Cody and Diamond 1975, Strong et al. 1984, Pickett and White 1985). Dispersal of offspring allows for colonization of new patches, decreases competition between offspring and parent, and in many cases ensures deposition of offspring in appropriate microhabitats (Howe and Smallwood 1982). Dispersal can enhance coexistence of multiple species by allowing otherwise inferior competitors to colonize new patches

(Grubb 1986, Hanski 1990, Shorrocks 1991) or through mass effects (Schmidha and Wilson 1985). A species may be absent from a patch not because of local biotic interactions or habitat conditions, but because none of its propagules have yet arrived at the patch. Such “colonization-limitation” (Tilman 1994) is an important determinant of community structure in sessile, benthic marine invertebrates (Connell 1985, Gaines and Roughgarden 1985, Menge and Sutherland 1987, Underwood and Fairweather 1989, Grosberg and Levitan 1992), in stream benthic communities (Townsend 1989, Palmer et al. 1996), and in many plant communities (Howe and Smallwood 1982, Tilman 1994).

A large proportion of plants in most communities are dispersed by animals (Howe and Smallwood 1982,

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Stapanian 1986). Examples include trees dispersed by frugivorous birds, mammals, and even fish (Howe 1977, Howe and Smallwood 1982, Sork 1987), nut caching and scatter hoarding by birds and mammals (Vander Wall and Balda 1977, Stapanian 1986, Platt and Hermann 1986), and herb dispersal by foraging ants (Beattie and Lyons 1975, Culver and Beattie 1980), turtles (Moll and Jansen 1995) and lizards (Valido and Nogales 1992). The resultant structure of these plant assemblages can be strongly influenced by the behavior patterns of the animal dispersers. For example, the distribution patterns of some understory fruiting shrubs in tropical forests are determined by the distributions of fruit-eating birds (Levy 1988), and *Opuntia* distributions in semiarid deserts are influenced by both rodent and ant seed predators (González-Espinosa and Quintana-Ascencio 1986).

Freshwater mussels (Bivalvia: Unionidae) have a complex life cycle in which the larvae (glochidia) are obligate, external parasites on the gills and/or fins of freshwater fish (Kat 1984, McMahon 1991). After excysting from the host tissue, juvenile mussels drop to the substrate and begin a benthic, sedentary existence. Both of these facts should have important implications for the distribution and abundance of mussels: initial colonization of mussels is totally dependent on the dispersal of the fish hosts, a regional process, but growth and reproduction should be governed by local environmental conditions and processes.

We predict that mussel distribution and abundance patterns should result from a hierarchy of constraints that includes historical effects, landscape-level influences, the availability of fish hosts, and local environmental conditions (Fig. 1). Partitioning the effects due to each level in the hierarchy is difficult. Historical and landscape effects will each contribute to the spatial structuring of mussel (and their fish hosts) distri-

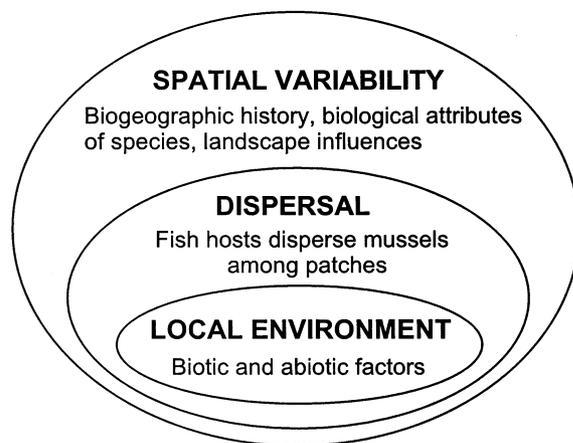


Fig. 1. Hypothesized hierarchy of constraints influencing mussel community structure.

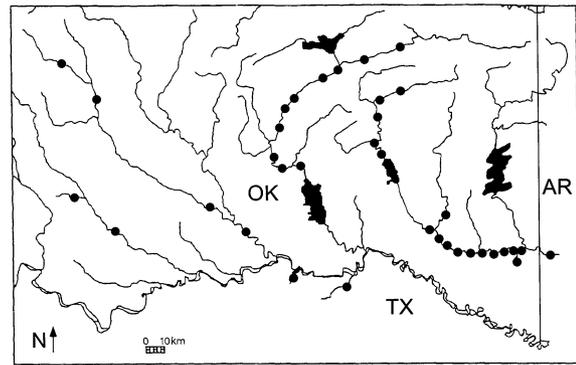


Fig. 2. Sampling locations.

bution and abundance patterns. Furthermore, the distribution and abundance of mussels and fish hosts, and local environmental characteristics, will show some degree of spatial autocorrelation. This spatial dependency arises from several potential sources including biological attributes of the organisms that may lead to nonrandom patterns of dispersion, physical attributes of the surrounding landscape that influence stream morphology, water chemistry and local habitat characteristics (Calow and Petts 1994), and historical constraints that determine regional species pools (Ricklefs 1989). Finally, fish and mussel assemblages are both likely to respond to local environmental factors. Thus, each level in the hierarchy is confounded by processes that are operating at other scales (Allen and Starr 1982).

Given this hierarchy of scale-dependent constraints, we hypothesize that mussel assemblage attributes should be predictable across large spatial scales from the regional distribution and abundance of fishes, and that this effect will be detectable above and beyond that due to spatial and environmental constraints. To test this prediction we sampled mussel and fish communities, and measured environmental variables, from 36 stream sites in the Red River drainage of the south central USA (Fig. 2). We analyzed our data using variation partitioning (Borcard et al. 1992, Pinel-Alloul et al. 1995, Aude and Lawesson 1998) to determine the simultaneous effects of fish distribution and abundance, abiotic environmental factors, and spatial location on the landscape, to mussel community structure. Because of the expected spatial dependencies in our data set, our null hypothesis predicted concordant patterns of variation across the sampling area for mussel and fish assemblages and measured environmental variables. However, after statistically accounting for spatial and environmental correlates of mussel distribution and abundance, any remaining correlation between fish and mussel assemblages supports our idea that fishes play an important role in determining mussel community structure.

## Methods

### Sample sites

Mussels are long-lived organisms (life spans range to > 100 yr depending on the species (Bauer 1983, Heller 1990)), but many fishes are not. In disturbed systems there is the possibility that current mussel assemblages are the result of historical colonization events by fish no longer present in the area. To avoid this potential problem, we chose sample sites within the Red River drainage of the south central USA (Oklahoma, Texas and Arkansas, Fig. 2). It has been established that fish assemblages within this area have not changed significantly in the last few decades (Rutherford et al. 1992). There are also few extinctions or introductions of mussels documented for these rivers (Vaughn and Pyron 1995, Vaughn et al. 1996). We quantitatively sampled mussel and fish communities, and measured environmental variables, from 36 stream sites.

### Mussels and fishes

Relative abundance data for mussels were collected by hand-searching entire mussel beds for a standardized period of time. This is the favored technique for collecting information on mussel abundance, and is the only technique which can reliably be used to obtain estimates of total species richness and locate rare species (Kovalak et al. 1986, Cawley 1993, Vaughn et al. 1997, Strayer et al. 1997). Surveys were conducted by hand searching with the aid of Scuba-divers in deeper areas and by hand searches in shallow areas in the following manner: 1) a shoal was identified for surveying; 2) the entire area was searched by at least two people for one hour; 3) all mussels encountered were removed to shore; 4) all mussels were immediately identified; 5) mussels were put back in the water (alive) as close to where they were removed as possible. This technique is described in greater detail in Vaughn et al. (1997).

We sampled fishes at each site by seining for 45 min using a 1.5 × 4.6 m, 4.8 mm mesh seine, within, above, and below the surveyed mussel bed. Fish were preserved in 10% formalin and returned to the laboratory for identification.

### Environmental variables

We measured environmental variables either known or believed to be important to mussels and fishes (Vannote and Minshall 1982, McMahon 1991, Strayer 1993, Matthews 1998). At each of the 36 sites we recorded the distance of the site from entering upstream tributaries, elevation, stream gradient, and whether the site was above or below an impoundment (Fig. 2). We measured water temperature, pH, conductivity and dissolved oxy-

gen. We took five measures of water depth and current velocity across the mussel bed and calculated means and coefficients of variation. Two replicate water samples were collected, acidified to a pH of 2.0, frozen, and sent to a water quality laboratory for calcium determination. Three replicate substratum samples were collected at each site. These were brought back to the laboratory and allowed to dry. Samples were dry sieved, weighed, and individual proportions of samples assigned to the appropriate substratum size class (in mm) following Hynes (1970, p. 24) and Vaughn and Pyron (1995). We digitized the watershed boundaries upstream of each site from USGS 7.5 min quadrangle maps, and then used these data to calculate the total watershed area upstream of each site.

### Spatial variables

Spatial autocorrelation is a general statistical property of ecological data collected across geographic space (Legendre 1993); it presents a statistical problem for ecologists since autocorrelated data are not independent. Recently, there has been considerable improvement in methods that account for spatial autocorrelation (Dutilleul 1993, Legendre 1993, Cooper et al. 1997). To account for spatial autocorrelation in the mussel, fish and environment matrices, we considered the spatial location of the sampling sites in our analyses (Leduc et al. 1992, Legendre 1993, Magnan et al. 1994). We first obtained the latitude and longitude of each site from USGS maps and converted these data to Cartesian coordinates. Following Legendre (1990) and Magnan et al. (1994), we constructed a cubic trend surface polynomial that allowed us to estimate the parameters of a trend surface regression equation

$$Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3$$

where X and Y are orthogonal coordinates representing latitude and longitude, and Z is mussel abundance and distribution information in the form of ordination scores. Before computing the higher terms of the polynomial, we standardized the data to a mean of zero to reduce collinearity (Neter et al. 1984, Magnan et al. 1994). The resulting equation represents a geographic surface that describes how mussel assemblages vary over the matrix of X-Y coordinates. The X and Y terms define a plane and describe the simple, linear spatial patterns in the data. The quadratic, cubic and interaction terms model more complex spatial features on the landscape such as patches, peaks and valleys (Borcard et al. 1992, Legendre 1993, Borcard and Legendre 1994, Magnan et al. 1994).

Because streams are linear systems that often form complex drainage networks, we also accounted for the interconnections and potential dispersal pathways among sampling localities. The method we used was originally proposed by Kluge and Farris (1969) for phylogenetic analyses and was implemented by Magnan et al. (1994) to account for drainage connections among Canadian lakes. Each site was characterized by the sequence of nodes taken from the direct path between a given locality and the root of the hydrographic tree (confluence of the Little and Red Rivers). A locality-by-nodes matrix containing the numerical coding of the sites within the drainage network was then constructed according to Magnan et al. (1994). This matrix was added to the matrix of terms from the cubic trend regression model and the combined matrix was used in subsequent autocorrelation and variation partitioning procedures.

### Data analyses

For all sites we examined the relationship between fish species richness and mussel species richness. The significance of the resulting correlation coefficient was determined with a randomization procedure (Manly 1991). The dependent variable was randomized 5000 times and the observed correlation coefficient was compared to the distribution of those obtained from the randomization procedure.

Mussel, fish and environmental data were  $\log_{10}(X + 1)$  transformed. Then, we arranged the data into four matrices: mussel abundances by sites, fish abundances by sites, environmental variables by sites, and spatial variables (Cartesian coordinates and drainage network) by sites. Canonical correspondence analysis (CCA) (ter Braak 1986) is a direct gradient ordination technique that reduces multidimensional data to a few axes that are constrained to be linear combinations of the supplied predictor variables (ter Braak 1986, ter Braak and Verdonschot 1995). We used CCA to determine how well our fish, environment, and spatial matrices could each account for variation among mussel assemblages, and to partition shared and unshared variation among these three data sets.

For the above analyses, we first determined the effects of each predictor matrix on the mussel matrix. To avoid artificial increase in the explained variation due to chance (Borcard et al. 1992), we used a forward selection stepwise procedure which is a multivariate analog of the stepwise regression procedure (ter Braak 1990), to choose subsets of the variables that would best explain the mussel species abundance data. Variables were retained in the models if they had  $p$ -values  $< 0.15$ . This procedure is based upon a

permutation test, not partial  $F$ 's, and is used to eliminate at an early stage of the analysis variables that are strongly collinear or are clearly unrelated to the dependent matrix. The liberal significance level of 0.15 prevents the elimination of variables that may eventually prove useful in the simplified model (Legendre pers. comm.). This procedure was useful for eliminating redundancy and simplifying models, and was necessary for the fish matrix because there were many more predictor variables (fish species,  $N = 67$ ) than sites ( $N = 36$ ).

We used CCA calculated with PC-ORD (McCune and Mefford 1997) to determine how well our fish, environment, and spatial matrices could each account for variation among mussel assemblages. Eigenvalues for the first two axes of each of the three analyses were subjected to a Monte Carlo procedure to determine if the mussel and predictor matrices were associated (McCune and Mefford 1997). To test this hypothesis the rows of the predictor matrix were shuffled, destroying the relationship between the two matrices, but leaving the correlation structure within the predictor matrices intact. The shuffling procedure was done 5000 times and the eigenvalue was compared to the distribution of eigenvalues from the ordinations with the randomized data.

We then used CANOCO (ter Braak 1988) to partition the total variation in mussel assemblage structure into that due to spatial position of the sites, fish abundance and distribution, measured environmental variables, shared variation among the three data sets that could not be partitioned into independent effects, and unaccounted for variation. The variation partitioning procedure we used was described by Borcard et al. (1992), but modified to include three predictor matrices (Magnan et al. 1994, Pinel-Alloul et al. 1995).

We computed a correspondence analysis on the mussel species matrix to get the total inertia or sum of all eigenvalues, which represents a measure of total variation in the species abundance matrix (ter Braak 1986). Next we computed CCAs for each of the constrained models after removing the singular effects of each of the other two matrices, and the combined effects of the other two matrices. The results of the latter gave us the "pure" effect (as a percentage of variation accounted for) of each predictor matrix after dividing the inertia from each canonical analysis by the inertia from the correspondence analysis and multiplying by 100. Once all of the appropriate analyses were computed it was possible to determine the total variation accounted for in the mussel abundance matrix by all predictor matrices, the pure variation that each matrix contributed, and all of the possible combinations of shared variation among the matrices.

## Results

Mussel and fish species richness were positively correlated across the 36 sites ( $r = 0.31$ ,  $p = 0.06$ ). This produced a triangular scatter pattern (Fig. 3) such that sites with high fish species richness had a wide range of mussel species richness values, but sites with low fish species richness never had high mussel species richness.

The forward selection procedure reduced our original data sets to three subsets of variables. Each of these subset matrices did a good job of predicting mussel assemblage structure, with significant eigenvalues ( $p \leq 0.05$ ) for at least one of the first two axes. Eigenvalues were as follows: fish axis 1 = 0.455,  $p = 0.076$ , fish axis 2 = 0.364,  $p = 0.003$ ; environment axis 1 = 0.372,  $p > 0.0006$ , environment axis 2 = 0.183,  $p = 0.002$ ; spatial axis 1 = 0.463,  $p > 0.06$ , spatial axis 2 = 0.38,  $p = 0.004$ .

When the variation in the mussel assemblage matrix was partitioned among fish, environmental, and spatial components, 79.3% of the variation in the mussel similarity matrix was accounted for (Fig. 4). This methodology also allowed us to estimate the shared variation among all combinations of the three predictor matrices. The pure fish component accounted for 15.4% of the variation in the mussel matrix. Pure spatial structure and pure environmental effects accounted for 16.1% and 7.8% of the variation in the mussel matrix, respectively. Shared variation that could not be partitioned into pure effects totaled 40% (Fig. 4). Of this shared variation, 36.8% was associated with the fish matrix. Thus, the variation in mussel assemblages that was explained by the distribution and abundance of fishes was substantial ( $> 50\%$ ).

## Discussion

The hierarchical nature of ecological patterns and processes appears to be a general ecological property

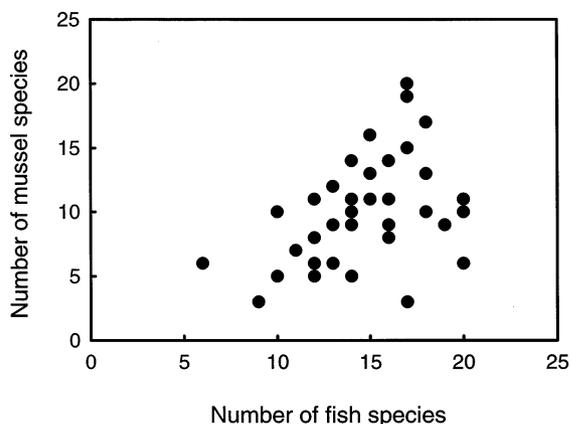


Fig. 3. The relationship between fish species richness and mussel species richness for the 36 sampling locations.

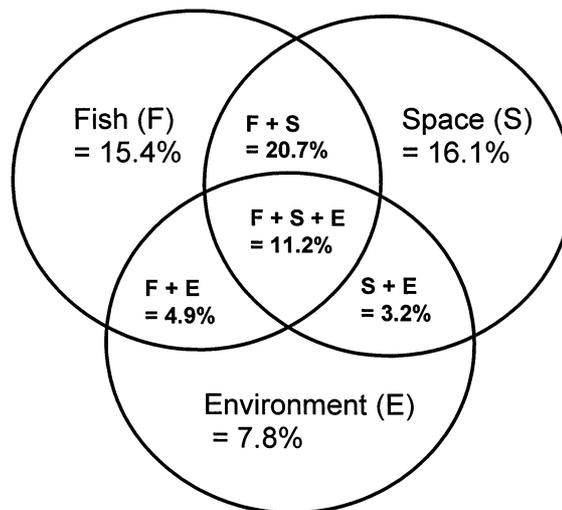


Fig. 4. Results of the variation partitioning procedure using canonical correspondence analysis. The total variation accounted for by the model was 79.3%, with 20.7% of the variation unexplained. Values shown in the diagram are the percentage of variation in the mussel matrix accounted for by fish, the environment, spatial structure, and shared variation among these components.

(Menge and Olson 1990, Rahel 1990, Levin 1992). In our system, each level of the hierarchy (Fig. 1) contributed to the variability in mussel community structure across the geographic region. Untangling the independent effects of each hierarchical level is difficult. Mussel and fish assemblages both respond to the environment. Furthermore, mussel and fish assemblages, and the environment are each expected to show some degree of spatial autocorrelation. Therefore, some difficulty in separating the effects of spatial structure, fish assemblages and the environment is expected; we cannot reveal effects of fishes that are correlated with spatial and environmental effects in the same way that genetic and environmental effects are difficult to partition in studies of IQ (see Taylor and Gotelli 1994).

Variation partitioning allowed us to statistically account for the spatial structure that occurred in the sampled mussel and fish assemblages and in the measured environmental variables. Similarly, we were able to account for measured environmental effects on fish and mussel matrices, making it more likely that any remaining pattern between mussels and fishes would have biological significance. However, fish effects may simply be a surrogate for unmeasured environmental variables, and both fish and environmental effects may, in part, be masquerading as spatial effects. To determine the importance of these complex interactions, we further partitioned the variation in mussel assemblage structure into that due to the pure effects of the three predictor matrices, and the shared effects due to possible combinations of the three predictor matrices. Pure

fish and spatial effects each accounted for more than twice as much of the variation in mussel assemblages as the measured environmental variables (Fig. 4). While 40% of the variation in mussel assemblages was confounded, shared fish effects (36.8%) and shared space effects (35.1%) were almost double that of shared environmental effects (19.3%).

The spatial structuring of communities poses the problem of the relative contribution of different factors whose interaction often results in an overlaid effect in space (Borcard et al. 1992). Our analyses of spatial variation included two kinds of spatial variables: interconnections among drainages (locality-by-nodes matrix) and geographic location (polynomial of  $x$  and  $y$  coordinates). Interconnections among drainages are important because they represent dispersal pathways for host fish. Reducing the spatial complexity of the drainage basin to a polynomial of  $x$ - $y$  coordinates may at first seem inappropriate for riverine organisms. However, the surrounding terrestrial landscape has a large influence on stream structure and function and thus the distribution of stream organisms (Allan 1995). Furthermore, a given Euclidian distance across one section of a landscape (e.g. 2 km across a mountain) may represent very different environmental conditions than the same distance across a different section of the landscape (e.g. 2 km across a flood plain). Our analyses showed that geographic location and drainage interconnections both are affecting mussel distribution and abundance.

The large amount of variation in mussel assemblage structure explained by both pure and shared spatial components is not surprising given the spatial scale of our study, which spans several river systems and biogeographic boundaries. The variation in mussel community structure explained by spatial location on the landscape reflects colonization history and available species pools of both mussels and fishes, unmeasured environmental variation that is autocorrelated with landscape, and local biotic interactions and processes that have lead to nonrandom distribution patterns (beyond that of colonization via fish hosts) (Schluter and Ricklefs 1993).

Nonetheless, while spatial location, as expected, affected mussel assemblage structure, our analysis revealed a strong association between mussel assemblages and fish assemblages, with pure and shared fish effects associated with > 50% of the variation in mussels. We can conclude that the distribution and abundance of fishes is an important determinant of mussel community structure. Our results do not, however, allow us to make predictions about effects of individual fish species on mussels. We examined the whole fish community, regardless of whether they were carrying glochidia or not. For these rivers, and for most systems, we do not know the fish-host requirements for the majority of mussel species (< 20%) (McMahon 1991, Watters 1994), and the validity of many proposed relationships

is questionable (Hoggarth 1992). The specific host-parasite relationships in our system have not yet been determined, and causality in that sense is not implied here. However, we predict that as such knowledge is gained it will only improve our ability to detect important fish-host constraints on mussels.

In general, published studies relating environmental variation to mussel distributions demonstrate a decreasing ability to predict where mussels will occur as the scale of observation decreases. At a geographic scale, one can predict whether or not mussels will occur in a system based on large-scale geological and hydrological factors combined with biogeographic history (Vannote and Minshall 1982, Strayer 1987). For example, mussels are generally believed to be most successful in stable, sand-gravel mixtures and are generally absent from substrata with heavy silt loads (McMahon 1991). Substrate type and stability are ultimately determined by surface geology which regulates hydrology, slope and turbidity of streams (Strayer 1983). At a regional scale (1–10 km), Strayer (1993) attempted to predict the distributions of mussels from macrohabitat descriptors (stream size, stream gradient, hydrologic variability, calcium concentration, physiographic province and tidal influence) within three northeastern USA river systems. At this scale of analysis, all of these variables had some predictive power, with stream size and tidal influence the most effective predictors of mussel distributions. At a local scale, Strayer and Ralley (1993) then used discriminant analysis to analyze the microhabitat preferences (scale of 1 m<sup>2</sup>) of mussels within a single tributary of one of the drainages studied above. At this scale, the power of the discriminant models to predict where mussels would occur was very low. Other studies have also reported that there are often few discernable habitat differences between stream reaches with and without mussels (Strayer 1981, Holland-Bartels 1990, Vaughn and Pyron 1995). A criticism of these local-scale studies is that they have characterized microhabitats based on static properties (e.g. sediment size) while dynamic properties (e.g. sediment stability) may be more important to mussels (Strayer et al. 1994, Di Maio and Corkum 1995).

Studies that have attempted to predict mussel distributions based strictly on fish-host distributions have also been unsuccessful. For example, Bauer et al. (1991) were unable to explain the distribution of three species of unionids in 39 Bavarian streams based on the distributions of 12 potential host fish species in the system. Strayer et al. (1994) examined the distributions of three unionid species in the Hudson River estuary. Two of these mussel species shared a migratory fish-host species (*Alosa* sp.) and reproduced at different times of the year. Strayer et al. (1994) concluded that it was therefore unlikely that the patchy distribution of mussels they observed was caused by a patchy distribution of fish hosts.

Our data help explain why local habitat variables are such poor predictors of mussel distribution; mussel distributions should be the result of local habitat conditions as well as fish-host environmental preferences and behavior. Thus, mussel species may occupy a range of habitats because they are deposited there by their fish hosts, but growth and reproduction may be optimized only under the most favorable habitat conditions. For example, most unionid species can be found on a number of different substrate types, but growth rates of individuals in these habitats can be quite different (Kat 1982, Hinch et al. 1986, Kesler and Bailey 1993). This should have effects on fitness, since body size and fecundity are correlated in unionids (Downing et al. 1993). The opposite situation should also hold true; habitat that appears "optimal" for mussels, may not contain mussels because the area has not been used by fish hosts. This has been proposed as a reason for the rarity of some species of mussels with apparently broad habitat tolerances (Vaughn and Pyron 1995).

The mussel communities studied here represent a guild of sedentary, filter-feeders on seston (McMahon 1991), which is floating by them in the current. Recent studies of freshwater mussels have demonstrated that spatial and food-resource competition is either not occurring or is negligible in importance (Brönmark and Malmqvist 1982, Bauer et al. 1991, but see Kat 1982). These studies, combined with observations that mussels are highly spatially aggregated (Downing and Downing 1992), suggest that competition for spatial resources may not be important in structuring mussel communities. Mussel assemblage structure may instead reflect differences in colonization potential among mussel species. Abundant, widespread mussel species may use either more common, widespread fish species as hosts, use more than one fish species as a host, or both. Indeed, the widespread distribution of freshwater bivalves that do not have a parasitic stage (families Sphaeriidae and Corbiculidae) relative to unionids may reflect fundamental differences in their capacity for dispersal (Kat 1984). These are hypotheses that need to be tested.

There is supporting evidence from other studies that the distribution of fish is critical to mussel assemblage structure. Extirpation of mussels from several river systems and from river stretches above dams has been linked to the disappearance of the appropriate fish hosts (Kat and Davis 1984, Watters 1995) and mussel species have also reinvaded rivers when their fish host was reintroduced (Smith 1985). Recently Haag and Warren (1998) found that the mussel community structure within two drainage basins in Alabama, USA, was better explained by the pattern of variability in the fish community and by the type of strategy used by mussels for infecting host fishes, than by patterns of variability in the microhabitat. Watters (1992) examined richness data for 37 rivers within the Ohio River drainage and

found that the number of mussel species was directly related to the number of fish species present and, to a lesser extent, the drainage area. However, Watters was unable to account for the fact that fish and mussels may be showing similar but independent responses to environmental conditions, which could lead to spurious correlations. His patterns indicated that correlations between fish diversity and mussel diversity were strongest for large rivers, while for smaller streams, mussel diversity was better correlated with drainage area. He attributed this to the transient nature of fish assemblages in smaller streams, but did not quantify this. There is some evidence suggesting that fish assemblages in small streams are more transient than assemblages in larger streams (Schlosser 1987), although this pattern is not well documented and may not occur in some stream systems (Taylor et al. 1996).

Our data are consistent with Watters (1992), but at a finer scale. He compared richness patterns for entire drainages, while our data are for localities within one large river system. At this scale we also found a positive correlation between mussel species richness and fish species richness. More interesting, however, is the pattern of variation present. The relationship (Fig. 3) is roughly triangular with all points falling below a diagonal line that defines the maximum mussel species richness for a site. Sites with high fish species richness had a wide range of mussel species richness values, but sites with low fish species richness never had high mussel species richness. This pattern suggests that two constraints are affecting the distribution of mussels. First, local mussel species richness is constrained by the number of available fish hosts. Because of this constraint, maximum mussel species richness at sites must decrease with decreasing fish species richness at sites. This "boundary" is, of course, probabilistic (Brown 1995). It is possible for points to occur above the boundary, but if suitable fish hosts are not available for the mussel species present, some will be doomed to local extirpation (shifting the point downwards). Additionally, environmental constraints may further limit mussel species richness at any given locality, which is why areas with high fish species richness can have a wide range of mussel species richness values.

Since mussel assemblages are constrained by the distribution and abundance of fish hosts, by implication, dispersal should be an important limiting factor to mussel communities. This idea is supported by distributional (Vaughn 1997) and genetic (Berg et al. 1995) evidence that at least some species of mussels exist as metapopulations, where regional processes can be as or more important than local factors in determining assemblage structure (Holt 1994). This has important implications for not only our understanding of how mussel communities are structured, but for conservation biology and management as well. Genetically-fixed dispersal behavior may become a liability when habitat

deteriorates (Davis and Howe 1992) and this appears to be what is happening to freshwater mussels worldwide (Bogan 1993). Freshwater mussels have declined over the past century at the same time that river fragmentation has greatly increased (Benke 1990, Zwick 1992, Bogan 1993, Allan and Flecker 1993, Dynesius and Nilsson 1994). In rivers, fragmentation has not only decreased available local habitat for mussels, it has exponentially increased the difficulty of dispersal between local habitat patches because dams and channelization impede the movement of host fish or alter their normal behavior (Neves and Angermeier 1990, Watters 1995). In many cases, the remaining, declining mussel populations in such systems are similar to Harrison's (1991) concept of a "non-equilibrium metapopulation" in which recolonization is insufficient to balance extinction. Conservation of mussel species may be critically linked to preserving dispersal pathways for fish hosts between local habitat patches suitable for mussels.

Species diversity and dynamics in communities depend not only on local interactions, but on regional processes such as the dispersal of individuals (as adults or propagules) between local patches. By focusing only on local habitat features and processes such as competition and predation, many ecological studies have underestimated the contribution of regional scale processes to local distribution patterns (see Ricklefs and Schluter 1993, Edwards et al. 1994, Brown 1995, Palmer et al. 1996). While ecologists have long recognized the importance of dispersal in structuring plant communities, we suggest that dispersal also often plays an important role in structuring animal communities. Our results show a strong macroecological association between two disparate animal groups with one strongly affecting the assemblage structure of the other. For many animals dispersal may be as critical a limiting factor as local habitat conditions.

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