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Macrohabitats of freshwater mussels (Bivalvia:Unionacea) in streams of the northern Atlantic Slope

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Abstract. The goal of this study was to predict the broad-scale (1–10 km) distributions of freshwater mussels from readily available macrohabitat descriptors. All six of the descriptors used (stream size, stream gradient, hydrologic variability, calcium concentration, physiographic province, and the presence or absence of a tide) had some predictive power, but stream size and tidal influence were the most effective predictors of mussel distributions. Unexpectedly, several mussel species typically occurred in calcium-poor waters, which I tentatively interpret as evidence that these species might not tolerate eutrophication. In general, the macrohabitat distributions of mussel species identified in this study correspond only moderately well to previously published, subjective assessments of mussel habitat use.

Key words: Unionidae, Margaritiferidae, bivalves, habitat, distribution, longitudinal succession, stream size, stream gradient, tidal influence, New York, Pennsylvania, discriminant analysis.

The distributions of North American freshwater mussels are known in much greater detail than those of other freshwater invertebrates because of the ease of collecting, identifying, and preserving these animals, and because of the long history of extensive collections by both amateurs and professionals. Thus, for many states and provinces, species lists of mussels are available for hundreds to thousands of sites. Naturally, the enormous literature on mussel distribution has led to a correspondingly large literature on the zoogeographical and ecological factors thought to have led to the observed distributional patterns. Zoogeographical factors exert strong controls on broad-scale distributional patterns, and seem now to be fairly well understood (e.g., Ortmann 1913, van der Schalie and van der Schalie 1950, Strayer 1987). A wide variety of ecological factors are commonly considered to be of importance, as well (e.g., Fuller 1974, McMahon 1991); however, the influence of these ecological factors rarely has been examined critically (but see van der Schalie 1938, Salmon and Green 1983, Strayer 1983, Strayer and Ralley 1993). The purpose of this paper is to use some of the extensive data now available on mussel distribution to describe quantitatively the habitats used by unionacean mussels in streams of the northern Atlantic Slope. My goals are both to provide accurate descriptions of mussel habitats and to test widely held assumptions about correlations between mussel distributions and environmental factors.

Critical examination of widely held beliefs about habitat use by freshwater mussels is especially important because information about habitat use is used to guide surveys and recovery programs for rare and endangered mussels. Erroneous information about habitat use obviously can impede these efforts. Of the 13 Atlantic Slope species that are the subject of this paper, one (*Alasmidonta heterodon*) is listed as endangered by the U.S. Fish and Wildlife Service (USFWS), and three others (*Alasmidonta varicosa, Lampsilis cariosa,* and *Lasmigona subviridis*) are listed as Category 2 species by USFWS (i.e., they are being considered for possible federal listing as threatened or endangered).

Ecological factors can influence mussel distribution on various spatial scales. In this paper, I am specifically concerned with ecological factors that affect mussel distribution on a scale of 1–10 km, which I will call a macrohabitat. Such macrohabitat factors often can be determined from analyses of maps or other published sources. An accompanying paper (Strayer and Ralley 1993) examines the influence of microhabitat (1–10 m) on mussel distribution.

Methods

My approach is to correlate mussel distribution within a zoogeographically uniform region with environmental factors that are widely considered to affect mussel distribution. The study area encompasses the entire Susquehan-

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na, Delaware, and Hudson River drainages, chiefly in Pennsylvania and New York. The mussel fauna in this region is well studied and relatively uniform, with no major zoogeographic discontinuities (Ortmann 1913, van der Schalie and van der Schalie 1950, Sepkoski and Rex 1974). Records of freshwater mussel distribution were taken from Ortmann (1919), Clarke and Berg (1959), and Harman (1970). Records from the Neversink River and its tributaries were taken from Strayer and Ralley (1991), and records from 31 sites in the Hudson River drainage were taken from Strayer (1987). Sites were either surveyed in the 19th century or are in rural areas without evidence of pollution-related loss of mussels. I omitted the remaining sites described by Strayer (1987) and Strayer and Ralley (1991) because of the possibility that their faunas were reduced by pollution or other anthropogenic impacts (see discussions on pp. 51–54 of Strayer (1987) and p. 24 of Strayer and Ralley (1991)). Therefore, 141 collecting sites were included in this analysis. All data are simply presence/absence data. Because I am concerned with the distribution of mussels from the northern Atlantic Slope zoogeographic province (van der Schalie and van der Schalie 1950), species in the Hudson River that arose from the Interior Basin (cf. Strayer 1987) are omitted from this analysis.

I considered six variables as potential predictors of freshwater mussel distribution: stream size, stream gradient, hydrologic variability, calcium concentration, physiographic province, and the presence or absence of a tide. All six have been suggested as influencing the distribution of mussels and other stream-dwelling animals, and all six often are available from published sources.

Stream size is well known to influence the distribution of freshwater mussels (e.g., van der Schalie 1938) and other stream-dwelling organisms (e.g., Hynes 1970, Vannote et al. 1980). I used the common logarithm of stream drainage area as a measure of stream size. The mean annual discharge (MAD, m^3/s) of a stream is closely related ($r^2 = 0.995$) to its drainage are (DA, km^2) by the following equation

$$MAD = 2.38 + 0.0156DA$$

for the 56 gage stations of the United States Geological Survey (USGS) in the study area (Ku et al. 1975, Loper et al. 1989, Firda et al. 1990, Kolva et al. 1990). The drainage area of each study site was estimated from data of Hoyt and Anderson (1905), Biesecker et al. (1968), Ku et al. (1975), Wagner (1981), Loper et al. (1989), Firda et al. (1990), and Kolva et al. (1990). In a few cases ($n = 17$) no published estimates of drainage areas were available, so I simply assigned the study site to one of five categories (cf. Fig. 4) based on rough estimates of drainage areas from maps. These sites were therefore omitted in the development of statistical models, but included in Fig. 4.

Stream gradient (=stream slope) is related to current velocity and substratum type, and is known to be of importance to the lotic biota (e.g., Hynes 1970). Stream gradient has received little attention from mussel ecologists, despite Altnoder's (1926) early suggestion that stream gradient affected the distribution of the pearl mussel *Margaritifera margaritifera* (cf. Young and Williams 1983), and the widespread belief that current velocity and substratum type are of paramount importance in determining the suitability of a habitat for freshwater mussels (e.g., Ortmann 1919, Clarke and Berg 1959, but see Strayer and Ralley 1993). I measured stream gradient on USGS 7½′ quadrangles for a stream reach of 4.8 km centered on the site where mussels were collected. Because stream gradient is strongly correlated with stream size (e.g., Hynes 1970), I used as a predictor variable the deviation of the gradient at a site from the average gradient of a stream of its size. To do this, I fitted an equation of the form

$$Y = a + b/X$$

to predict gradient from the common logarithm of drainage area as

$$G = -6.98 + (30.26/\log_{10}DA),$$

then calculated the deviation from the expected value as follows:

$$NEWGRAD = (G + 0.2) \div (-6.98 + (30.26/\log_{10}DA))$$

where NEWGRAD is the new predictor variable, G is the gradient in m/km, and DA is the drainage area in km^2.

The hydrology of a stream, particularly its susceptibility to spates and droughts, has been suggested to affect the distribution of mussels (Strayer 1983) and other organisms (e.g., Horwitz 1978, Poff and Ward 1989, Cobb et al. 1992).

TABLE 1. Frequency of occurrence of species of freshwater mussels in streams of the study area.

Species	Frequency
Elliptio complanata (Lightfoot)	80%
Strophitus undulatus (Say)	45%
Alasmidonta undulata (Say)	33%
Anodonta cataracta Say	30%
Lampsilis cariosa (Say)	26%
Lampsilis radiata (Gmelin)	21%
Alasmidonta varicosa (Lamarck)	21%
Lasmigona subviridis (Conrad)	16%
Anodonta implicata Say	8%
Ligumia nasuta (Say)	6%
Leptodea ochracea (Say)	5%
Alasmidonta heterodon (Lea)	4%
Margaritifera margaritifera (Linnaeus)	2%

As a measure of hydrologic variability, I used the 10-yr, 7-d low flow of a stream, expressed as a specific yield (L s^{-1} km^{-2}) by dividing by the area of the catchment. This measure was widely available for streams in the study area (Page and Shaw 1977, Eissler 1979) and is closely correlated ($r^2 = 0.85$) to another measure of flow variability, the ratio of the 98 percentile discharge to the 2 percentile discharge (cf. Richards 1990), by the following equation ($n = 35$):

$$\text{10-yr, 7-d low} = -0.0063 + 59.7 \cdot (\text{98 percentile}/\text{2 percentile})$$

Thus, low values of 10-yr, 7-d low flow indicate streams with highly variable hydrologic regimes. For 47 of the 141 study sites, there were no nearby reference data from Page and Shaw (1977) or Eissler (1979), so I had to omit estimates of hydrologic variability for these sites.

Calcium and long been regarded as critical to the distribution and abundance of mollusks (e.g., Boycott 1936, Clarke and Berg 1959), although some studies suggest its influence may be secondary to that of other factors (e.g., Lodge et al. 1987, Strayer and Ralley 1991). Calcium concentrations at the study sites were taken from Durfor and Anderson (1963), Biesecker et al. (1968), and Firda et al. (1990), or from unpublished data from the USGS or my laboratory.

Ortmann (1919) noticed that physiography seemed to influence the distribution of some species of mussels (cf. also Strayer 1983). To test the importance of physiography, I used the maps of Thompson (1966) and Berg et al. (1989) to divide the study area into five broad physiographic regions: coastal plains and lowlands provinces, the Piedmont province, plateaus of low relief (including the Glaciated Pocono Plateau, the Glaciated Low Plateau, and the Pittsburgh Low Plateau of Berg et al. (1989) and provinces F-2 through F-5 of Thompson (1966)), plateaus of high relief (the Mountainous High Plateau, the High Plateau, and the Allegheny Mountain province of Berg et al. plus C-1 of Thompson), and mountain provinces (the Appalachian Mountain province of Berg et al. plus F-1 of Thompson).

Variation in mussel community structure was summarized by detrended correspondence analysis (DCA, Hill and Gauch 1980). Relationships between mussel species richness and environmental variables were tested with stepwise multiple regression (PROC STEPWISE, SAS 1987) using the maximum r^2 method and $p = 0.15$ to enter or remove variables. I used analysis of covariance (ANCOVA) (PROC GLM, SAS 1987) to examine correlations between DCA axes and environmental variables. To test whether environmental variables were useful descriptors of mussel macrohabitats, I used stepwise discriminant analysis (PROC STEPDISC, SAS 1987) with $p = 0.15$ to enter or remove variables. Inspection of the data suggested that some of the relationships between species distributions and environmental factors might be nonlinear; in such cases, I tried forcing quadratic terms into the discriminant analyses. None of these nonlinear terms proved to be effective.

Results

Thirteen species of freshwater mussels from the northern Atlantic Slope are found in the study area (Table 1). Species richness is low, averaging only about three species per site, and reaching a maximum of only ten species (Fig. 1). Stepwise multiple regression identified stream size as the only useful predictor of species richness in non-tidal streams; species richness was slightly higher in tidal streams than in non-tidal streams (4.44 vs. 2.89 species, $p < 0.05$). Although stream size is a highly significant predictor ($p < 0.0001$) of mussel species richness, it accounts for only a small part of the variation in mussel species richness ($r^2 = 0.19$).

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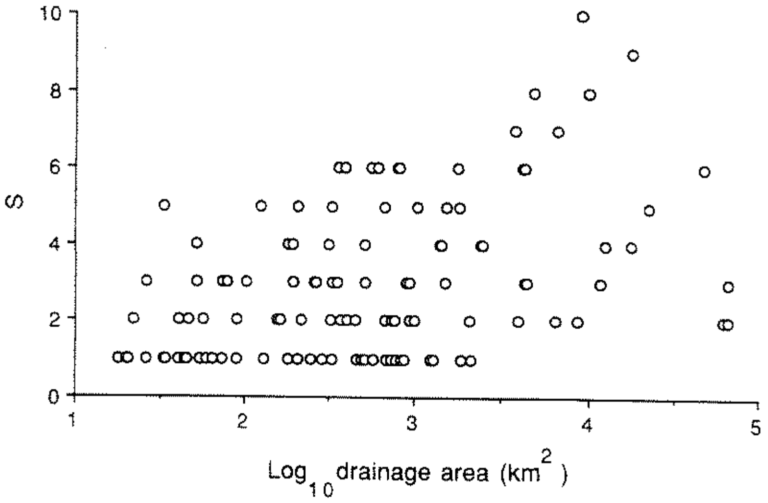

FIG. 1. Species richness (S) of freshwater mussels in non-tidal streams of the study area, as a function of drainage area (DA, km^2). $S = 0.21 + 1.03 \log_{10}DA$, $r^2 = 0.19$, $p < 0.0001$.

of three species found primarily in tidal waters (*Anodonta implicata*, *Ligumia nasuta*, and *Leptodea ochracea*) from the other species (Fig. 2). ANCOVA shows that high scores on DCA axis 1 are correlated with large stream sizes ($F = 10.9$, $p = 0.0016$) and typically represent sites on lowland and piedmont physiographic provinces ($F = 3.3$, $p = 0.027$). High scores on DCA axis 2 represent sites with low calcium concentrations ($F = 9.1$, $p = 0.0037$), high hydrological variability ($F = 7.6$, $p = 0.0077$), and relatively high gradients ($F = 7.0$, $p = 0.01$). Although highly significant, these correlations between ordination scores and environmental variables are loose (r^2 of ANCOVA models = 0.27 for axis 1 and 0.31 for axis 2).

Species distributions

It is convenient to divide the species into five groups on the basis of their distributions. The first group includes generalist species whose distributions show no strong relationship to any of the environmental factors (Table 2). Included

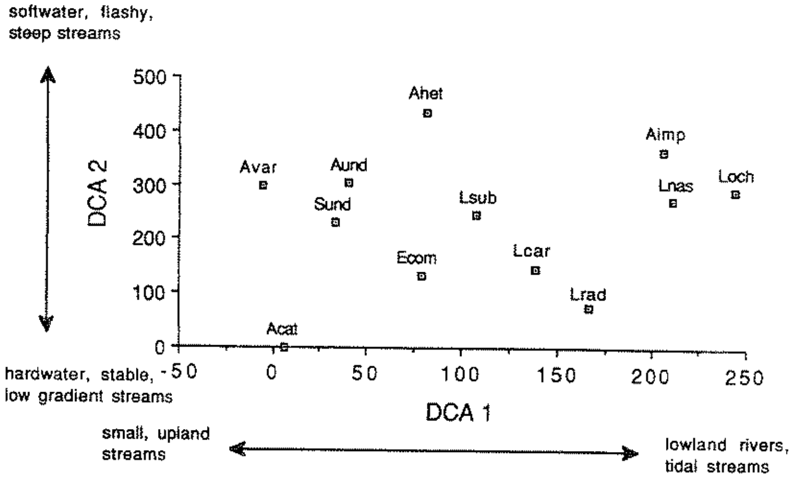

FIG. 2. Species scores on the first two DCA axes. Each species is identified by the first letter of its generic name and the first three letters of its specific name (cf. Table 1).

TABLE 2. Summary of results of stepwise discriminant analyses to predict the presence or absence of mussel species. Variables are listed in order of their appearance in a stepwise discriminant model. ASCC = average squared canonical correlation.

Species	Predictor	Partial *F*	ASCC	*p* (model)
Group 1				
Elliptio complanata	stream size	8.8	0.10	0.002
	physiography	4.0		
Alasmidonta undulata[a]	hydrology	2.0	0.14	0.01
	tide	6.7		
	calcium	3.1		
Anodonta cataracta	physiography	2.6	0.03	0.11
Strophitus undulatus	tide	5.6	0.11	0.013
	hydrology	3.4		
Lampsilis radiata	stream size	4.2	0.08	0.04
	physiography	2.3		
Group 2				
Anodonta implicata	tide	19.1	0.36	<0.0001
	calcium	9.0		
	hydrology	5.2		
	gradient	3.2		
Ligumia nasuta	tide	46.3	0.33	<0.0001
	physiography	6.1		
	stream size	3.5		
Leptodea ochracea	tide	170.0	0.55	<0.0001
Group 3				
Lampsilis cariosa	stream size	51.5	0.31	<0.0001
	physiography	2.3		
Group 4				
Lasmigona subviridis	hydrology	6.0	0.20	0.0009
	tide	9.0		
	gradient	2.4		
Group 5				
Alasmidonta heterodon	calcium	8.7	0.14	0.004
	gradient	3.1		
Alasmidonta varicosa	calcium	12.6	0.14	0.0007

[a] The model presented was produced by forcing hydrology into the model despite its low F-value (p = 0.16); otherwise, the resulting model was not significant.

here are most of the common species of the Atlantic Slope fauna: *Elliptio complanata, Alasmidonta undulata, Anodonta cataracta, Strophitus undulatus,* and *Lampsilis radiata* (cf. Table 1).

The second group contains three species (*Anodonta implicata, Ligumia nasuta,* and *Leptodea ochracea*) whose distributions are closely tied to tidewaters (Table 2, Fig. 3). All three of these species may be found just above the head of tide in upland rivers (cf. Ortmann 1919, Strayer 1987, Strayer and Ralley 1991). In addition, *Ligumia nasuta* is very occasionally found in quiet waters well above the fall line (e.g., Strayer 1987). A complementary group of species is found less frequently in tidal waters than in upland sites (Fig. 3).

Species that are found more frequently in large rivers than in smaller streams constitute the third group. The chief representative of this group is *Lampsilis cariosa,* which is common in rivers that drain more than 1200 km², but much less frequent in smaller streams (Fig. 4). In addition, two of the generalist species (*Elliptio complanata* and *Lampsilis radiata*) are found somewhat more frequently in large streams than in small (Table 2, Fig. 4).

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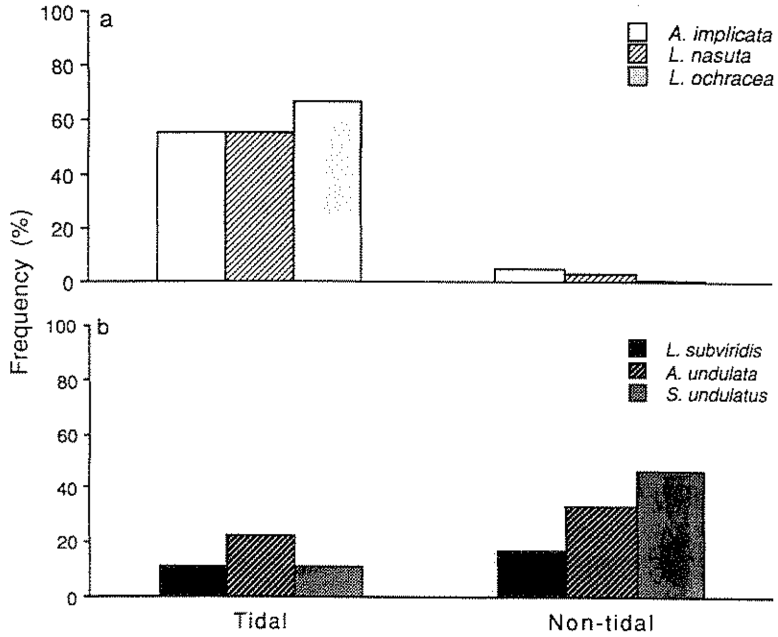

FIG. 3. Frequency of occurrence of mussels in tidal and non-tidal sites. a. Species typical of tidal waters. b. Species typical of non-tidal waters.

The fourth group contains species whose distribution is related most strongly to stream hydrology. The best example is *Lasmigona subviridis*, which is found much more frequently in streams with stable hydrographs than in those that are prone to spates or droughts (Fig. 5). Two of the generalist species (*Alasmidonta undulata* and *Strophitus undulatus*) are slightly more likely to occur in hydrologically stable streams than in flashy streams (Table 2).

The fifth group includes species whose distribution is influenced by the calcium content of the water. This group contains *Margaritifera margaritifera* (Fig. 6), which is well known to prefer soft waters (e.g., Ortmann 1919, Bauer 1988), and also two or three species of *Alasmidonta* (Fig. 6), whose negative relationship with calcium was unexpected.

Discussion

Macrohabitat variables are useful predictors of mussel distribution in streams of the northern Atlantic Slope. The predictive power of macrohabitat variables varies widely, depending on the dependent and independent variables being considered (Table 2). For many species, though, the six macrohabitat variables considered in this study have much power to predict the presence or absence of a species (Figs. 3–6).

Stream size and the presence or absence of a tide were the most useful variables with which to describe mussel macrohabitat, but all of the environmental variables that I considered had some predictive value (Figs. 3–6, Table 2). Only one variable (stream gradient) had such limited predictive power that it might be considered to be ineffective.

My analysis suggests that two factors rarely considered in studies of unionacean distribution might be important in the study area. Following Horwitz's (1978) work on fish, I suggested that hydrological stability might help to determine mussel distribution in southern Michigan (Strayer 1983). The present study confirms that some mussel species are found more frequently in hydrologically stable streams than hydrologically flashy streams (Table 2, Fig. 5). This result raises the possibility that widespread anthropogenic alterations to stream hydrology may have contributed to the decline of mussels on the Atlantic Slope and elsewhere. Hydrology could affect mussels through many mechanisms (e.g., scouring mussels or sediments during spates; desiccation, thermal stress,

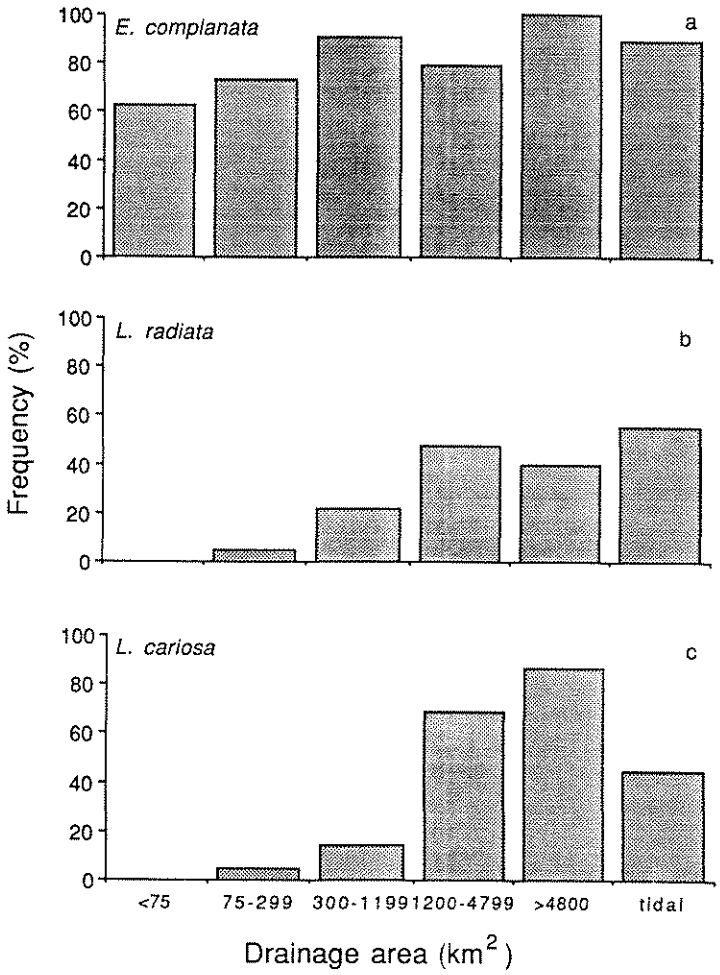

FIG. 4. Frequency of occurrence of mussel species as a function of stream size.

or exposure to mammalian predation during extreme low flows; cf. discussion of Poff and Ward 1989), but the importance of various mechanisms is not known.

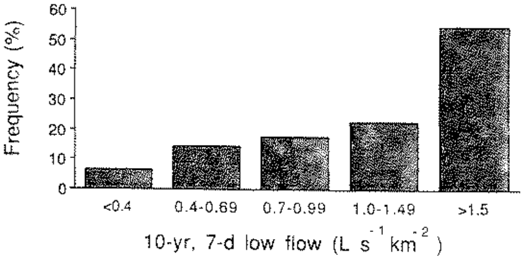

FIG. 5. Frequency of occurrence of *Lasmigona subviridis* in streams as a function of hydrologic stability.

More surprisingly, in trying to test the hypothesis that mussels prefer streams rich in calcium, I found that four species of mussels occur most frequently in calcium-poor streams (Table 2, Fig. 6). The limitation of *Margaritifera margaritifera* to soft waters has been known for a long time (e.g., Ortmann 1919, Bauer 1988), but the negative correlations between calcium concentration and the distribution of the three species of *Alasmidonta* were unexpected. As it seems unlikely that a high concentration of calcium itself is deleterious to *Alasmidonta* species, a factor correlated with calcium concentration probably is responsible for determining the distribution of these species. Bauer's intensive work on the ecology of *Margaritifera margaritifera* in Germany suggests that the responsible factor

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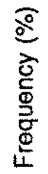

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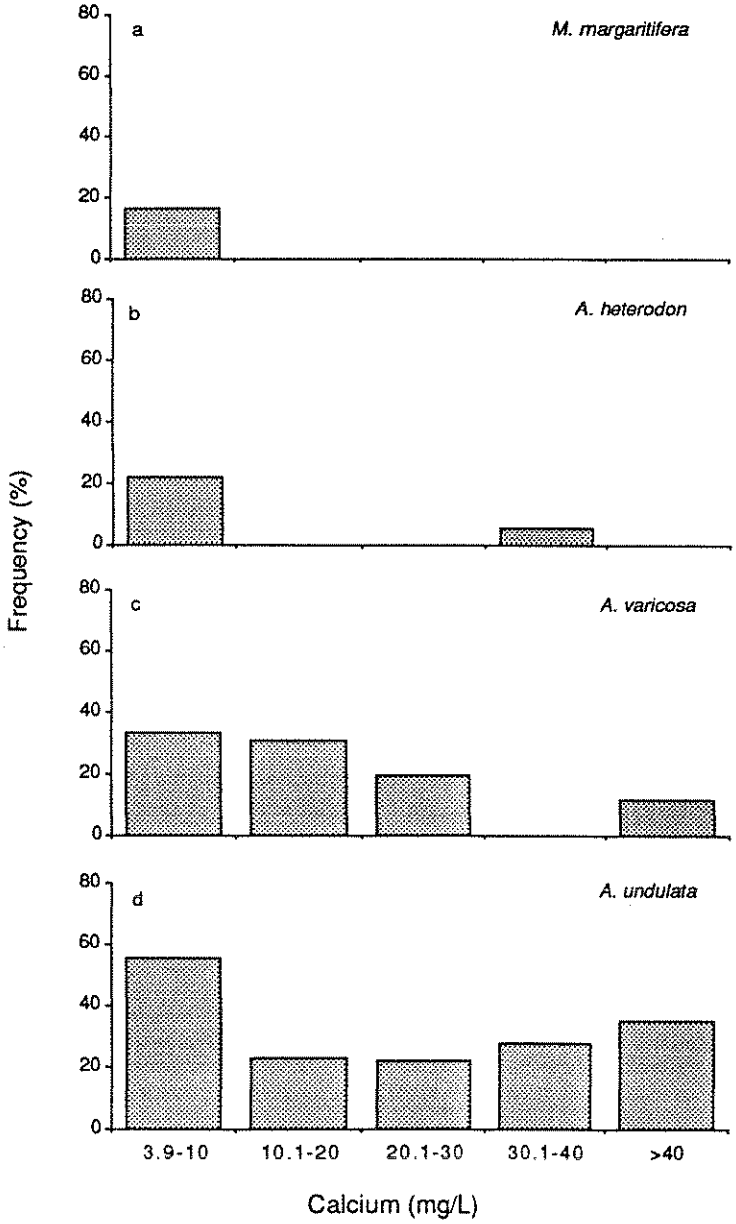

FIG. 6. Frequency of occurrence of mussel species as a function of calcium concentration of streamwater.

may be plant nutrients. Bauer (1988, 1992, Bauer et al. 1980) found that the fertility of a stream (i.e., its calcium, phosphate, and especially nitrate content) helps to determine the growth, survivorship, and reproduction of *M. margaritifera*. My results suggest a similar deleterious effect of eutrophication on the *Alasmidonta* species. This effect is consistent with the observation of declining populations of these species over broad areas of their ranges, which have been subjected to enrichment from agricultural fertilizers, domestic wastes, and nitrate-rich acidic precipitation. More detailed analysis of the effects of eutrophication on *Alasmidonta* species might therefore be fruitful.

My results provide only limited support for

TABLE 3. Supposed habitat use by unionacean species in the study area (summarized from Ortmann [1919], Clarke and Berg [1959], and Harman [1970]) compared with the results of the present analysis.

Species	Supposed use	This study
Margaritifera margaritifera	soft waters	soft waters
Elliptio complanata	ubiquitous	larger streams, widespread
Alasmidonta heterodon	unknown	softwater, high gradient streams
Alasmidonta undulata	smaller streams and rivers (Ortmann); large streams (Harman)	hydrologically stable, soft, non-tidal waters
Alasmidonta varicosa	smaller streams and rivers with high gradients	soft waters
Lasmigona subviridis	smaller streams and rivers	hydrologically stable, non-tidal streams
Anodonta cataracta	small streams on lowlands or piedmont	most frequent (slightly) in lowland or piedmont streams
Anodonta implicata	coastal streams	tidal waters
Strophitus undulatus	smaller streams and rivers	non-tidal, hydrologically stable streams
Ligumia nasuta	tidal and other quiet waters	tidal waters
Leptodea ochracea	tidal and coastal waters	tidal waters
Lampsilis cariosa	medium to large rivers, especially those of high gradient	larger streams
Lampsilis radiata	medium to large rivers and tidal waters	larger streams

previously published descriptions of mussel macrohabitats (Table 3). For many species, including three of the four rare species in the study area, the observed macrohabitat use was quite different from those published previously. In general, it appears that earlier authors overemphasized the importance of stream size in determining mussel distribution in the northern Atlantic Slope region. Although stream size plays a dominant role in determining mussel distribution in other regions (e.g., van der Schalie 1938, Strayer 1983), its influence is relatively weak in the study area (Fig. 4, Table 2). Only *Lampsilis cariosa* shows a strong response to stream size.

The mismatch between my results and those of earlier authors can be explained in at least two ways. First, this study applied quantitative analyses to an extensive data set, while previous workers relied on their impressions based (however insightfully) on more limited data sets. Therefore, my analysis could be more objective and more powerful statistically. On the other hand, earlier workers were able to take into account their impressions of the abundance of each species at their collecting sites, a factor I could not consider because even crude, semi-quantitative estimates of abundance are published only rarely by malacologists. For instance, while *Lasmigona subviridis* was found as frequently in large rivers as in smaller streams, Ortmann (1919) noted "the specimens found by myself in larger rivers generally were few".

In general, it appears that macrohabitat variables are less effective in controlling mussel community structure in the study area than in Michigan streams, where only two master variables (stream size and surface geology) are associated with most of the variation in mussel community structure (van der Schalie 1938, Strayer 1983). The comparative ineffectiveness of macrohabitat variables in northern Atlantic Slope streams suggest that other, unmeasured variables or smaller scale processes exert important effects on the mussel community in this region more frequently than they do in Michigan.

Nevertheless, by considering a few simple macrohabitat variables, I was able to circumscribe the distributions of mussels in streams of the northern Atlantic Slope (precisely in some cases), call into question the accuracy of many

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previously published habitat descriptions, and identify some usually overlooked variables (hydrological stability and *low* calcium concentrations) as useful predictors and fruitful subjects for future research. Because it often is possible to obtain such macrohabitat variables from the literature at relatively low cost, I believe that macrohabitat analyses will often be useful in studies of mussel ecology.

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