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Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*

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Abstract. We studied the microhabitats of six species of freshwater mussels, including two rare species of *Alasmidonta*, in the Neversink River, New York. In each of 270, 1-m² quadrats, we measured water depth, current speed, bottom roughness, spatial variation in current speed, distance to shore, presence or absence of macrophytes, presence or absence of an overhead canopy, the extent of patches of fine sediment, and sediment granulometry, as well as recording the mussels present. Mussel populations in the Neversink are dense (mean = 3.2/m²) and highly clumped. Stepwise discriminant analyses showed that current speed and spatial variation in current speed were the most useful predictors of the occurrence of mussels in quadrats. *Alasmidonta heterodon* was found most frequently at moderate current speeds and in quadrats that contained many patches of fine sediments. *Alasmidonta varicosa* occurred most frequently at moderate current speeds and in sediments with a high proportion of medium sands (0.25–1 mm). Nevertheless, the predictive power of discriminant models based on microhabitat variables is so low that we question the adequacy of a traditional microhabitat approach to unionacean ecology. We suggest that including geomorphological descriptors of the streambed or working at spatial scales of hundreds of metres might be more useful than a traditional microhabitat approach for predicting the distribution of freshwater mussels in streams.

Key words: Unionidae, *Alasmidonta*, freshwater mussels, endangered species, habitat, distribution, current speed, sediment particle size, streams, New York, discriminant analysis.

The rich, endemic unionacean fauna of North America has been badly damaged by human activities. Almost half of the native North American species are now either extinct (Turgeon et al. 1988), on the United States Fish and Wildlife Service (USFWS) Endangered Species List, or are proposed for listing by USFWS or treated as a Category 2 species (i.e., to be considered for listing) by USFWS (USFWS 1991). Even though many unionaceans have small and diminishing ranges, factors controlling the distribution and abundance of freshwater mussels are poorly known. Zoogeography (e.g., Ortmann 1913, van der Schalie 1945, van der Schalie and van der Schalie 1950) and gross organic or toxic pollution (e.g., Stansbery 1970, Fuller 1974, McMahan 1991) obviously influence the distribution of freshwater mussels, but the influence of other ecological factors is less clear. Nonetheless, ecological factors other than the large-scale or obvious factors mentioned above are cited frequently as being important to the distribution, abundance, or decline of unionaceans. For instance, nearly every general work on unionaceans (e.g., Ortmann 1919, Baker 1928, Clarke and Berg 1959, Clarke 1981a) describes the characteristic habitats of individual union-

acean species in terms of stream size, gradient, current speed, water depth, and the like. These habitat characterizations come from an enormous volume of primary literature on the natural history of unionaceans, but are based on informal impressions rather than on critical measurements. Habitat requirements of endangered unionaceans are likewise typically given in general, informal terms rather than by tested, quantitative parameters. For example, the habitats of the two rare species of *Alasmidonta* that are the subject of our study were given most recently as: "*A. varicosa* is usually found in rapids or riffles on rock and gravel substrates and also in sandy shoals. It is more abundant in small rivers and creeks . . ." (Clarke 1981b), and "[*A. heterodon*] lives on muddy sand, sand, and gravel bottoms in creeks and rivers of varying sizes, in areas of slow to moderate current and little silt deposition" (USFWS 1990).

The few careful tests of habitat use by unionaceans have had mixed success in confirming the widely used informal characterizations of unionacean habitats. In some regions, unionacean distributions on a scale of km are fairly well described by stream size and catchment characteristics (e.g., van der Schalie 1938, Stray-

TABLE 1. Environmental conditions encountered in sampling quadrats in the lower Neversink River.

Variable	Mean (range)
Distance from shore (m) ^a	6.1 (0.5-22.5)
Water depth (cm)	27.7 (0.4-104)
Roughness ^b	5.4 (0.5-28.1)
Current speed (cm/s)	11.8 (0.0-65.0)
Spatial variation in current speed ^c	6.3 (0.0-33.2)
Number of cores	1.0 (0-7)
% gravel (4-16 mm)	36.1 (0-94)
% coarse sand (1-4 mm)	21.9 (0-77)
% medium sand (0.25-1 mm)	34.8 (0-75)
% fine sand (0.062-0.25 mm)	5.5 (0-53)
% silt and clay (<0.062 mm)	1.6 (0-34)

^a Measured to the center of the quadrat.

^b Standard deviation of the five depth measurements per quadrat (see text).

^c Standard deviation of the five current measurements per quadrat (see text).

er 1983, 1993). Attempts to characterize the use of microhabitats (i.e., 0.1-10 m) by unionaceans have been less successful. In a careful study of an Ontario river, Salmon and Green (1983) reported significant differences in microhabitat attributes between areas with unionaceans and those without, and among areas occupied by different species of unionaceans. These authors found that water depth, current velocity, and streambed granulometry were useful in discriminating between areas with and without unionaceans, and among sites occupied by various species. Although the discriminant functions generated by Salmon and Green's (1983) study were statistically significant, their power to discriminate was not reported. Other studies (Tevesz and McCall 1979, Strayer 1981, Holland-Bartels 1990) also have identified statistically significant habitat characteristics but have emphasized the poor differentiation in habitat use among species and between areas with and without unionaceans.

The purpose of our study was to test whether widely accepted descriptions of unionacean microhabitat actually provided any power to predict where unionaceans would occur, and whether the microhabitat use that we could observe would correspond to microhabitat use reported in previously published, informal studies. The site of our study was the lower Neversink River in southeastern New York, which probably supports the world's largest remaining populations ($\sim 10^5$ individuals) of two

rare species of *Alasmidonta*. *Alasmidonta heterodon* is listed as endangered by USFWS, and *A. varicosa*, currently listed as a Category 2 species and apparently declining throughout its range, probably will soon be proposed for federal protection.

Study Area

The Neversink River rises on the southeastern slopes of the Catskill Mountains and flows south to join the Delaware River at Port Jervis, New York State. The catchment is largely forested, although the middle and lower parts support some agriculture and residential development. Flow from about 30% of the catchment is controlled by the Neversink Reservoir, which supplies drinking water to New York City.

The study area extends from the crossing of the aqueduct of the now-abandoned Delaware and Hudson Canal near Cuddebackville to the hamlet of Huguenot about 9 km downstream. This study area encompasses the known range of *A. heterodon* in the Neversink (Strayer and Ralley 1991). The Neversink here is about 40-m wide and mostly less than 1 m deep at base flow. A major tributary, the Basher Kill, enters the upper third of the study area. Stream gradient and particle size appeared to decrease in a downstream direction. The streambed was stony, with patches of sand and gravel. The water was clear and fairly soft (5-9 mg/L of calcium; Firda et al. 1990, Strayer and Ralley 1991). Further data on physical features are given in Table 1 and the accompanying text.

Methods

Our approach was to sample unionaceans and environmental conditions in quadrats widely dispersed in the study area to sample a wide range of conditions. We used a stratified random design to accomplish this. We divided the study area into three reaches: a high-gradient reach (1.4 km long) upstream of the Basher Kill, a high-gradient reach (2.8 km long) downstream of the Basher Kill, and a low-gradient reach (4.2 km long) even farther downstream. Within each reach, we established three study sites: a riffle, a run, and a pool. Because we could work only on land owned by cooperative landowners, these study sites were not randomly

chosen. The study sites were 100 m long and extended from one bank to the center of the river. We placed thirty quadrats in each study site according to the following procedure: we chose 10 random distances along the shore from 0 to 99 m, then picked three stratified random distances from shore at each of the ten chosen coordinates. Because we initially suspected (incorrectly) that unionacean densities were highest nearest the shore, we placed one quadrat 0.5–3.5 m from the shore, a second 4.5–6.5 m from the shore, and the third between 7.5 m from the shore and the center of the river.

Each quadrat was 1 m square, and was divided by nylon lines into 25 20 × 20-cm squares to facilitate the search for unionaceans. After placing a quadrat, we used a mask and snorkel to search each quadrat carefully for unionaceans, which we identified to species in the field. We did not excavate the substratum in our search, but we did look under all non-embedded stones small enough to be lifted. Typically, searching a quadrat took 30–45 minutes.

After searching for unionaceans, we took sediment samples and noted water depth, current speed, and the presence or absence of macrophytes and an overhead canopy. We used a 3.2-cm I.D. hand-held steel pipe to try to take sediment samples next to the 16 points in each quadrat where the nylon lines intersected. To estimate the extent of sediments fine enough to allow unionaceans to burrow, we recorded the number of the 16 points at which we successfully obtained cores. All cores taken within a quadrat were pooled, placed on ice immediately, then frozen. After thawing, these samples were dried at 60°C, then dry-sieved through a series of sieves (16 mm, 4 mm, 1 mm, 0.25 mm, and 0.062 mm). Following the suggestion of Buchanan (1984), sediments that contained more than 3% silt plus clay or which were conspicuously clumped were wet-sieved through a 0.062-mm sieve to remove silts and clays before dry-sieving. Because of the small volume of our samples, our statistical analysis omitted the 16-mm fraction.

Current speed and depth were measured at the center and four corners of each quadrat. We used a Marsh-McBirney 201M current meter to measure current speed 2.5 cm from the stream bottom. It was not logistically possible to measure current speed and depth at all 270 quadrats on the same day, but we did restrict these mea-

surements to days during which the water level in the river (as measured by a U.S. Geological Survey staff gage in the middle of the study area) was similar. The maximum stage difference on days on which we measured current speed and depth was less than 5 cm.

Quadrats within a site were visited in a haphazard order to avoid bias due to fatigue. Field work on each site was done in a period of 1–5 days of stable discharge. All field work was done between 13 June and 7 August 1991.

Some data were transformed prior to statistical analysis to reduce departures from normality. Current speeds and number of unionaceans per quadrat were \log_{10} -transformed, and the number of cores per quadrat was subjected to a square-root transformation (Elliott 1977). In addition to using the mean values of water depth and \log_{10} (current speed) for each quadrat as predictors, we used the standard deviation of these variables as estimates of the roughness of the streambed and the spatial variation in current speed, respectively.

Statistical methods such as discriminant analysis and multiple regression do not deal effectively with functions that peak at intermediate values. Inspection of the data showed that the response of some unionaceans to some variables was not linear, but rather peaked at intermediate values (cf. Fig. 2). Polynomial regression showed that unionacean occurrence was a significantly non-linear function of water depth and current speed. We therefore constructed new predictor variables for current speed and water depth simply as the absolute difference between the observed current speed or water depth and the value at which the frequency of unionaceans reached a maximum. That is, our analyses were based on the distance from an optimum current speed and water depth for each species.

Some authors (e.g., Salmon and Green 1983) have recommended running a principal components analysis (PCA) on granulometry data and using the PCA scores for subsequent statistical analyses. While these PCA scores have more desirable statistical properties than the original data, they also are more difficult to interpret. We ran our analyses on both the original granulometry data and on PCA scores derived from these data. Because the results of these two sets of analyses were closely congruent, we chose to present the more readily in-

TABLE 2. Unionaceans encountered in the 270 quadrats sampled.

Species	Total collected
<i>Elliptio complanata</i> (Lightfoot)	706
<i>Alasmidonta varicosa</i> (Say)	75
<i>Alasmidonta heterodon</i> (Lea)	43
<i>Strophitus undulatus</i> (Say)	27
<i>Anodonta implicata</i> Say	6
<i>Alasmidonta undulata</i> (Say)	1

terpretable results from the analyses of the granulometry data themselves.

Statistical analyses were run on two versions of our data set: the full set of predictor variables and a reduced variable set excluding granulometric variables. The sediments in the Never-sink are so rocky that we couldn't obtain any cores in 48% of our quadrats. By repeating our statistical tests on the data set without the granulometric variables, we were able to nearly double the sample size and greatly increase our power to detect relationships between mussel distribution and non-granulometric variables. Also, the values taken by the number of cores per quadrat could range from 0 to 7 in the reduced data set, but are restricted to 1 to 7 in the full data set. Therefore, we show results for statistical analyses both including and excluding granulometric variables (Tables 3-6).

Our chief goals were to predict the presence or absence of unionaceans in individual quadrats and to predict the number of unionaceans

in quadrats where unionaceans were present. We used stepwise discriminant analyses to develop statistical models to predict presence or absence of unionaceans based on our environmental measurements. These analyses were conducted using PROC STEPDISC in SAS (SAS 1987), using stepwise selection of variables at $p = 0.15$ to enter or remove variables. To predict the number of unionaceans per quadrat, we used PROC STEPWISE in SAS (SAS 1987) for stepwise multiple regression, choosing the maximum r^2 improvement technique. In addition, we tested for clumping of mussels using the variance-to-mean ratio as described by Elliott (1977).

Because we wanted to ensure that no environmental variables with useful predictive powers were overlooked, we ran a battery of other statistical tests (t -tests, ANOVA, ANCOVA, canonical and simple discriminant analyses) to identify useful predictor variables. None of these tests produced substantially different results from the stepwise discriminant analysis and stepwise multiple regressions, either in terms of the environmental variables identified as useful predictors or the statistical power of the resulting models, so we will not present these results here.

Results

Spatial distribution of unionaceans

We found six species of unionaceans in the study area (Table 2; cf. Strayer and Ralley 1991).

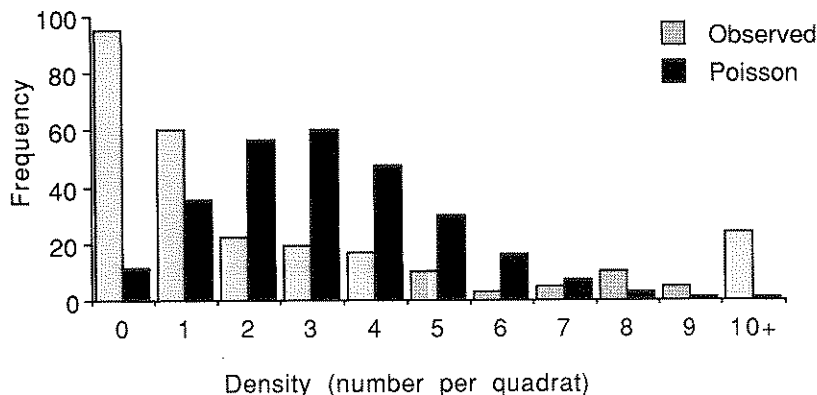


FIG. 1. Observed frequency of unionaceans in quadrats compared with expected frequency from Poisson distribution. The two distributions are significantly different ($p < 0.01$, χ^2 goodness-of-fit test, Elliott 1977, p. 45).

TABLE 3. Results of stepwise discriminant analyses to predict the presence or absence of unionaceans in individual quadrats, both with and without granulometric variables. ASCC = average squared canonical correlation.

	Order of entry	Variable	Partial F	$p(F)$	ASCC	p (model)
With granulometry ($n = 139$)	1	Current speed	18.5	<0.0001	0.12	<0.0001
	2	SD (current)	5.9	<0.02	0.16	<0.0001
	3	% medium sand	5.6	<0.02	0.19	<0.0001
Without granulometry ($n = 266$)	1	SD (current)	15.1	<0.0001	0.05	<0.0001
	2	Current speed	18.4	<0.0001	0.12	<0.0001
	3	Depth	7.1	<0.009	0.14	<0.0001
	4	Macrophytes	2.8	<0.10	0.15	<0.0001

Population density was high, with a mean of 3.2/m².

The distribution of unionaceans in the study area was highly clumped (Fig. 1). Clumping was apparent both among the nine study sites ($s^2/\bar{x} = 3.23$, $n = 9$, $p < 0.01$) and within six of the nine study sites ($s^2/\bar{x} = 2.14$ -20.49, $n = 30$, $p < 0.01$). Only at the three study sites with the lowest densities of unionaceans was the variance/mean ratio indistinguishable from random ($s^2/\bar{x} = 1.16$ -1.39, $n = 30$, $p > 0.05$).

Habitats used by unionaceans

Discriminant analyses to predict the presence or absence of unionaceans in individual quadrats were very highly significant (Table 3). The most useful discriminatory variables were cur-

rent speed and the spatial variation in current speed: unionaceans were found most frequently at intermediate current speeds (Fig. 2) and in areas of relatively uniform flow (Fig. 3). The only granulometric variable that had any discriminatory power was the percentage of medium sand (0.25-1.0 mm) in the sediments. High percentages of medium sand favored the occurrence of unionaceans. Finally, there was a hint of a negative association between unionaceans and macrophytes ($\chi^2 = 3.23$, $p = 0.07$).

Despite our ability to construct discriminant functions of very high statistical significance, our overall power to identify suitable habitats for unionaceans was low. This can be seen both in the low values of the average squared canonical correlation (ASCC) shown in Table 3, and perhaps more clearly in Figure 4a, in which

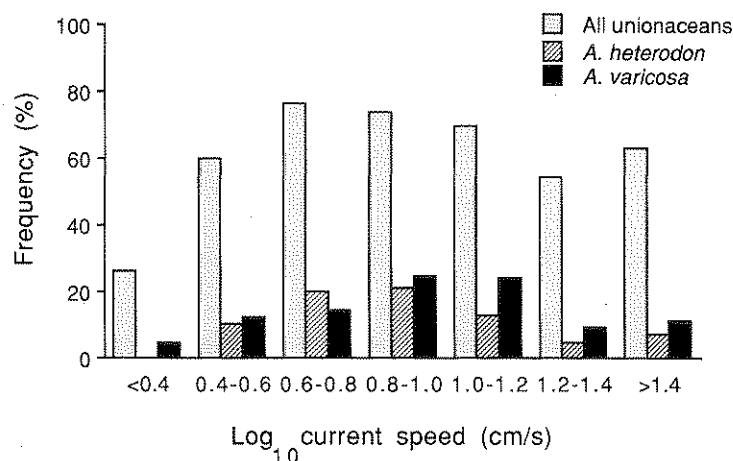


FIG. 2. Frequency of occurrence of all unionaceans, *Alasmidonta heterodon*, and *Alasmidonta varicosa* in relation to current speed.

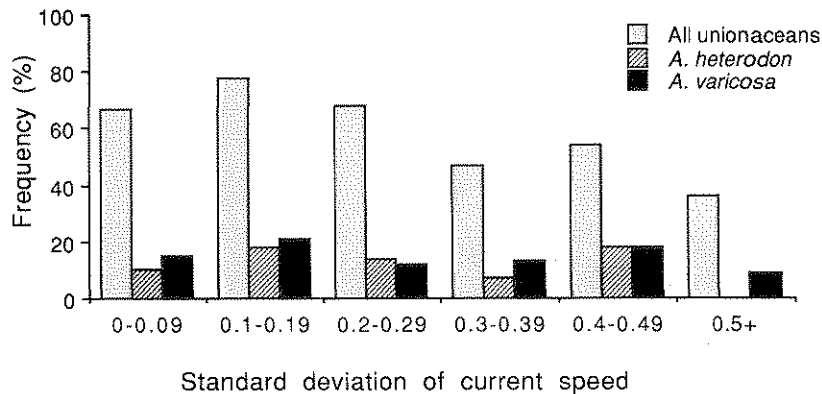


FIG. 3. Frequency of occurrence of all unionaceans, *Alasmidonta heterodon*, and *Alasmidonta varicosa* in relation to spatial variation in current speed.

we plot the occurrence of unionaceans along the two environmental axes that offer the best discrimination (Table 3).

The environmental variables we measured can also be used to predict the number of unionaceans per quadrat in those quadrats that contain unionaceans (Table 4). Depth, current speed, the proportion of fine sand, and the number of cores successfully taken were correlated with unionacean numbers, although the regressions in Table 4 account for little of the variation in unionacean numbers.

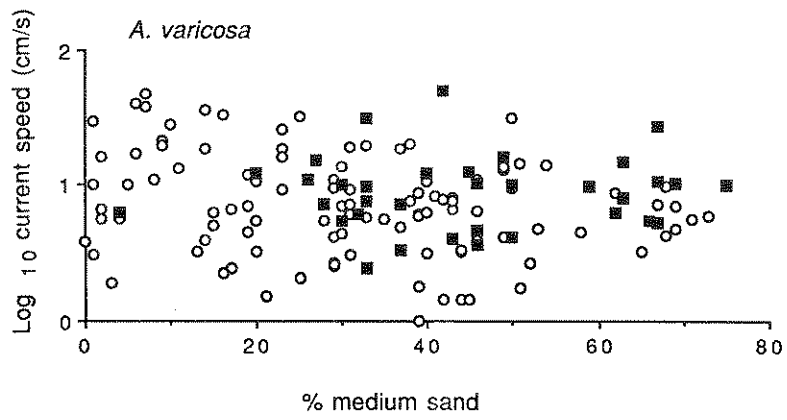
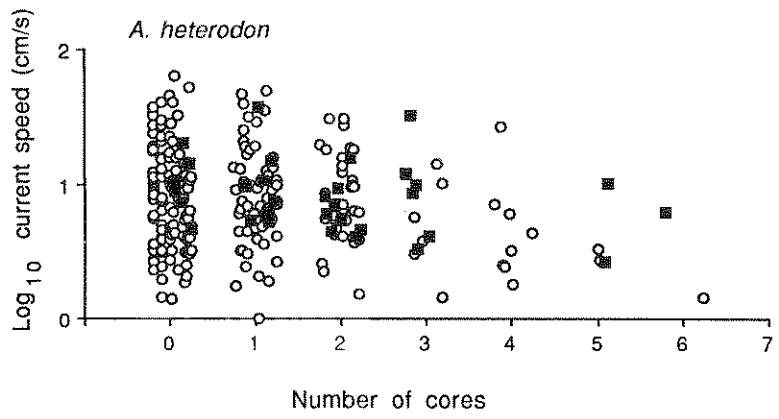
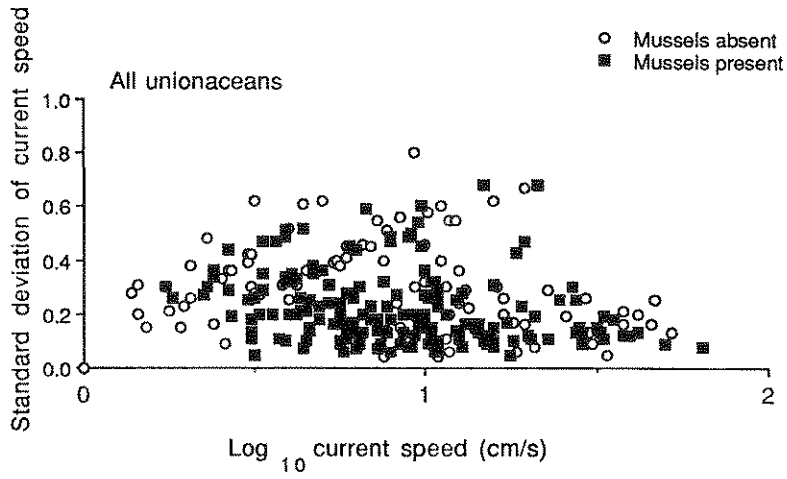
Differences among species in habitat use

The six species of unionaceans are positively associated in quadrats in the study area ($p < 0.001$ by the null association model of Schluter 1984). A stepwise discriminant analysis to discriminate among the five most common species of unionaceans on the basis of the environmental characteristics of the quadrats in which they were found was barely significant ($p = 0.049$), and was based on only one factor: current speed (Fig. 5).

TABLE 4. Results of stepwise multiple regressions to predict the number of unionaceans per quadrat in those quadrats that contain unionaceans.

	Order of entry	Variable	Partial F	$p(F)$	model r^2	p (model)
With granulometry ($n = 99$)	1	Current speed	6.4	<0.02	0.06	<0.02
	2	% fine sand	6.0	<0.02	0.12	<0.003
	3	Depth	2.7	<0.11	0.14	<0.003
Without granulometry ($n = 172$)	1	Depth	22.9	<0.0001	0.12	<0.0001
	2	Number of cores	7.2	<0.008	0.15	<0.0001
	3	Current speed	7.1	<0.009	0.19	<0.0001
	4	Canopy	4.1	<0.05	0.21	<0.0001
	5	SD (current)	2.4	<0.12	0.22	<0.0001

FIG. 4. Distribution of (a) all unionaceans, (b) *Alasmidonta heterodon*, and (c) *Alasmidonta varicosa* along the environmental axes identified by stepwise discriminant analyses as the most effective discriminators for each taxon. Each symbol shows the conditions found in one quadrat. In (b), the points are offset along the abscissa for clarity. For *Alasmidonta varicosa*, % medium sand and current speed provide the best 2-variable discriminant model, even though current speed does not appear in the final discriminant model (Table 6).



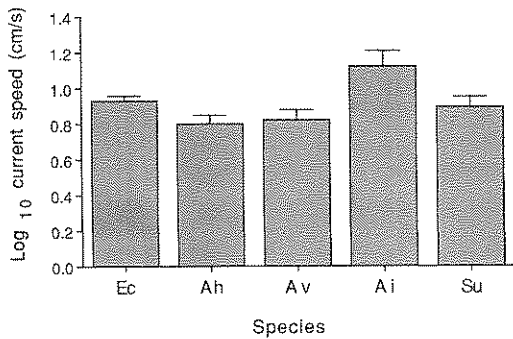


FIG. 5. Mean (+1 SE) current speed at which each of the five most common unionacean species were found. Ec = *Elliptio complanata*, Ah = *Alasmidonta heterodon*, Av = *Alasmidonta varicosa*, Ai = *Anodonta imbecilis*, Su = *Strophitus undulatus*.

Habitats of the *Alasmidonta* species

Alasmidonta heterodon was found most frequently in quadrats that contained many patches of fine sediments (Fig. 6; Table 5). It occurred most often at intermediate values of current speed (Fig. 2) and depth and tended to occur more frequently in areas of uniform flow than in areas of variable flow (Fig. 3). None of the other variables measured had any relationship with the occurrence of *A. heterodon*, either in a discriminant analysis (Table 5), or in univariate *t*-tests or contingency tables.

Despite our success in identifying three or four habitat variables that were related to the distribution of *A. heterodon*, our overall ability to predict the presence or absence of the species from a quadrat on the basis of habitat variables

was poor. The ASCC of the discriminant function was only 0.14, and a plot of the distribution of *A. heterodon* along our two most powerful discriminating variables (Fig. 4b) shows much overlap between quadrats with *A. heterodon* and those without.

Many environmental variables were associated with the occurrence of *A. varicosa* (Table 6). The strongest associations were with the percentage of medium sand (0.25–1.0 mm) in the sediment, the number of cores successfully taken, water depth, and current speed. *Alasmidonta varicosa* was found in areas having high values of the first two of these variables and intermediate values of the latter two variables (Figs. 2, 6). There also is a suggestion of a negative association between *A. varicosa* and aquatic macrophytes ($\chi^2 = 7.22$, $p = 0.007$). As was the case for *A. heterodon*, our ability to predict the occurrence of *A. varicosa* on the basis of even the most effective pair of these environmental predictors is very limited (Fig. 4c).

Discussion

Our results can be interpreted in two different ways. First, we were able to show that some readily measurable environmental variables are correlated with the distribution and abundance of unionaceans. One could thus argue that an analysis of unionacean microhabitats is a useful exercise. Some of the variables identified as predictors in our analysis have for some time been suspected to influence the distribution of unionaceans. For instance, the appearance of water depth and current speed as predictors is

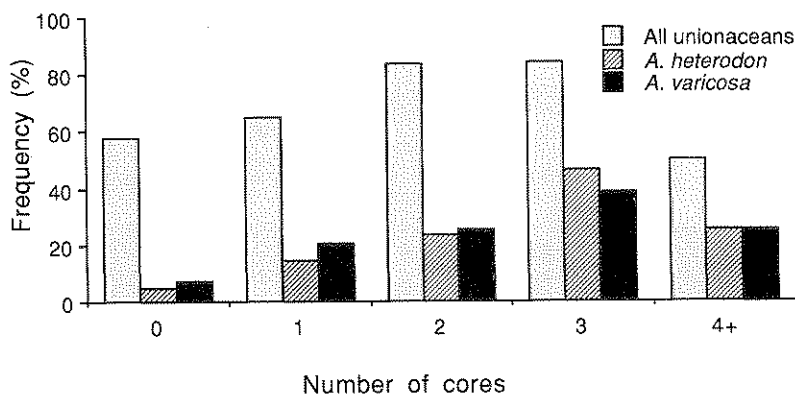


FIG. 6. Frequency of occurrence of all unionaceans, *Alasmidonta heterodon*, and *Alasmidonta varicosa* in relation to the number of cores taken in each quadrat.

TABLE 5. Results of stepwise discriminant analyses to predict the presence or absence of *Alasmidonta heterodon* in individual quadrats. ASCC = average squared canonical correlation.

	Order of entry	Variable	Partial F	p(F)	ASCC	p (model)
With granulometry (n = 139)	1	Depth	7.5	<0.007	0.05	<0.007
	2	Number of cores	4.9	<0.03	0.08	<0.003
	3	Current speed	5.7	<0.02	0.12	<0.0005
Without granulometry (n = 266)	1	Number of cores	22.5	<0.0001	0.08	<0.0001
	2	Current speed	10.2	<0.002	0.11	<0.0001
	3	Depth	5.2	<0.03	0.13	<0.0001
	4	SD (current)	2.8	<0.10	0.14	<0.0001

not surprising in light of the long tradition of using these factors to describe unionacean habitats (e.g., Ortmann 1919, Clarke and Berg 1959). Other variables that often have been used to describe unionacean habitats and were shown to have some significance as predictors in the Neversink include the presence or absence of macrophytes, distance from shore, and certain aspects of sediment granulometry. It is worth noting, however, how ineffective the granulometry of the sediment was, in general, in predicting the distribution or abundance of unionaceans, considering that nearly all previous workers concerned with unionacean distribution have emphasized grain size. Even where we did show granulometry to be important, our results do not always correspond to the conclusions of earlier authors. For example, *A. varicosa* is nearly always described as preferring gravelly sediments (e.g., Ortmann 1919, Clarke and Berg 1959), but our study shows that it occurred

most frequently in fine to medium sands in the Neversink (Table 6).

In contrast, two other factors identified in our study as related to the distribution and abundance of unionaceans are rarely mentioned in previous works on unionacean ecology. Chief among these is the number of cores per quadrat, a measure of the extent of patches of fine sediments presumably suitable for unionaceans to burrow in. This variable appears to be especially important in determining the distribution of the two rare species of *Alasmidonta* (Fig. 6; Tables 5, 6), and may be worthy of further investigation, for two reasons. First, many rivers, especially in the northeastern United States, are rocky like the Neversink. Unionaceans in these streams may be limited in part by the number and distribution of small, protected patches of fine sediments. Second, although it has long been known that excessive sediment loads to streams may damage unionacean populations

TABLE 6. Results of stepwise discriminant analyses to predict the presence or absence of *Alasmidonta varicosa* in individual quadrats. ASCC = average squared canonical correlation.

	Order of entry	Variable	Partial F	p(F)	ASCC	p (model)
With granulometry (n = 139)	1	% medium sand	10.5	<0.002	0.07	<0.002
	2	Macrophytes	3.4	<0.07	0.12	<0.0005
	3	% fine sand	2.7	<0.11	0.14	<0.0004
	4	Depth	3.7	<0.06	0.15	<0.0003
	5	Number of cores	2.2	<0.15	0.16	<0.0002
Without granulometry (n = 266)	1	Depth	14.5	<0.0002	0.05	<0.0002
	2	Number of cores	9.5	<0.003	0.08	<0.0001
	3	Current speed	6.1	<0.02	0.11	<0.0001
	4	Macrophytes	3.5	<0.07	0.12	<0.0001
	5	Distance from shore	2.6	<0.11	0.12	<0.0001

(e.g., Ellis 1936, Fuller 1974), potential detrimental effects of reducing the sediment load to a river have not been considered. Fluvial geomorphologists have shown (e.g., Leopold et al. 1964, pp. 454-457) that the reduced sediment loads caused by impoundment result in downcutting of the river bed and a loss of fine materials from the river bed for long reaches downstream of the dam. Impoundment thus could destroy unionacean habitat by removing the patches of fine sediment from the river bed for long reaches below dams, at least in stony rivers. A possible example of this is given by Clarke's (1986) observation that all but one species of unionacean have been eliminated in recent years from the Connecticut River, which is extensively impounded.

The other variable that might be worth studying further is spatial variation in current speed, which was a significant correlate of unionacean distribution and abundance in several models (Tables 3-5; Fig. 3). We know of no previous suggestions that this factor might affect unionacean distribution (but see Hubert and Rahel [1989] for a parallel example for fish); although it is possible to imagine several mechanisms, we have no evidence of the ways in which it might exert its effects.

An alternative interpretation of our results emphasizes the consistently low power of our models to predict the occurrence and density of unionaceans. The r^2 of our best models fell in the range of 0.1-0.2, leaving unexplained the greater part of the observed variation in unionacean distribution and abundance. The low predictive power of our statistical models is especially disturbing considering that we made quantitative measurements in a large number of quadrats of most of the microhabitat features that have been suggested to be of importance to unionaceans.

Our results reinforce the conclusions of previous authors (e.g., Tevesz and McCall 1979, Strayer 1981, Holland-Bartels 1990) that physical aspects of microhabitats are of limited use in predicting the occurrence and species composition of unionaceans in running waters, and raise serious doubts about the utility of using such an approach to predict the distribution and abundance of unionacean species. Unless microhabitat models more effective than ours can be developed, it hardly seems worthwhile to measure and describe unionacean microhabi-

tats in terms of such traditional variables as current speed, and sediment granulometry.

What alternative approaches might be used to develop more powerful models for assessing unionacean habitats? The microhabitat approach could simply be extended by considering variables not usually measured by unionacean ecologists. For example, more sophisticated descriptors of the streambed based on fluvial geomorphology (e.g., Leopold et al. 1964, Richards 1982) might allow a better understanding of the dynamics of the streambed habitat at a time scale relevant to the long-lived unionaceans. Vannote and Minshall (1982) already have shown that sediment stability may be of critical importance, for instance (see also Young and Williams 1983). Alternatively, the considerable small-scale variation in unionacean communities (e.g., Fig. 1) might be abandoned as being practically unpredictable, in favour of predictive models on larger spatial scales. Unionacean communities might be more easily predictable at scales of km rather than at scales of m (e.g., van der Schalie 1938, Strayer 1983, 1993). Fisheries biologists have been developing models of habitat suitability based on physical features on scales of tens to hundreds of metres (e.g., Layher and Maughan 1985, Wesche et al. 1987, Hubert and Rahel 1989); similar models might be developed for unionaceans. Finally, there is the dismaying possibility that lotic unionacean communities are not predictable from easily measurable variables, but instead are controlled by hard-to-measure phenomena such as ephemeral, mm-scale conditions during glochidial settlement or transient biological interactions such as the abundance, activity, and immune status of host fishes during critical infective periods. As we suggest above, however, several promising lines of attack could be pursued before attempts to develop predictive models of unionacean distribution and abundance are abandoned.

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