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Environmental determinants of unionid clam distribution in the Middle Thames River, Ontario

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Seven unionid clam species were collected from 240 randomly allocated 0.5-m^2 quadrats in the Middle Thames River above Thamesford, Ontario. Five environmental variables were measured for each quadrat; the statistical procedure used was discriminant analysis on principal components of the data. Increased frequency of occurrence of clams (of all species) is associated with slow moving, shallow water but also with a relatively coarse substrate. Species of clams show separation along a similar water depth and velocity gradient.

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Sept espèces d'Unionidae ont été récoltées dans 240 quadrats de 0,5 m^2 répartis au hasard dans la rivière Middle Thames en amont de Thamesford, en Ontario. Cinq variables du milieu ont été mesurées à chaque quadrat; on a ensuite procédé à une analyse discriminante sur les composantes principales. La fréquence des moules (toutes les espèces) augmente lorsque l'eau est peu profonde et le courant faible et lorsque le substrat est relativement grossier. Les espèces se séparent selon un gradient semblable de profondeur et de vitesse de courant.

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Introduction

Many authors have observed that frequencies of occurrence of unionid clams are related to environmental factors, both in general and differentially among species. However, these observations usually relate to large-scale among-habitat patterns (e.g., among lakes or among different stretches of rivers). Although many lotic, and some lentic, habitats contain dense multispecies populations of unionids, there has been little success in demonstrating and quantifying within-habitat patterns that can be predicted from spatial patterns in environmental factors. Such microenvironment-related patterns might explain the ability of dense multispecies populations of unionids to coexist, even though they are filter feeding from what appears to be a common food resource. This study represents an attempt to determine the relationships between the distribution of unionid clams in the Middle Thames River and the spatial patterns of environmental factors.

Type of substrate may influence unionid species distribution (Baker 1928; Cvancara 1970; Harman 1972; Haukioja and Hakala 1974; and others). Indeed, the common names of some species reflect this perception. For example, the relatively thin-shelled *Anodonta grandis* ("the floater") can occur in semiliquid substrates of some oligotrophic lakes. However, Green (1971, 1972) found no substrate-related separation between *Anodonta grandis* and *Lampsilis radiatia* (the two most common lentic species) within or among 32 lakes in Manitoba, Saskatchewan, and northwestern Ontario. Rather the separation of these two species was on water chemistry variables, and primarily among lake regions of differing geology. Murray and Leonard (1962) and Parmalee (1967) concluded that, although some species are substrate specific, most tolerate a fairly wide range of bottom types. Coker *et al.* (1922) and Tudorancea (1972) considered associations of unionids with vegetation, and factors such as water depth and velocity have been mentioned by many authors.

Methods

The study area

The study area is in a 400 m stretch of the Middle Thames River 24 km east of London, Ontario, in a valley just above Thamesford. The river is 17–20 m wide at this point. For reference purposes when allocating samples, the study area was subdivided into 10-m intervals along both sides of the river. Groups of 10 such intervals were formed by running five lines, at 100-m intervals, across the river (Fig. 1).

Sampling design and field methods

Previous attempts at demonstrating within-habitat spatial separation of unionids related to microenvironment patterns in lotic communities have probably failed for three reasons: inadequate sample number, too crude measurement of environmental factors impinging on the organisms, and use of statistical methods (if any were used at all) inappropriate for demonstrating causal patterns. Here we have attempted to remedy these faults. Quantitative samples were allocated to be representative of the community within the study area. Sampling design and procedure were in common with a study of nest site selection by the longear sunfish *Lepomis megalotis peltastes* (Bietz 1981). The design consisted of six 0.5-m^2 quadrats randomly selected from 20 locations at each of 40

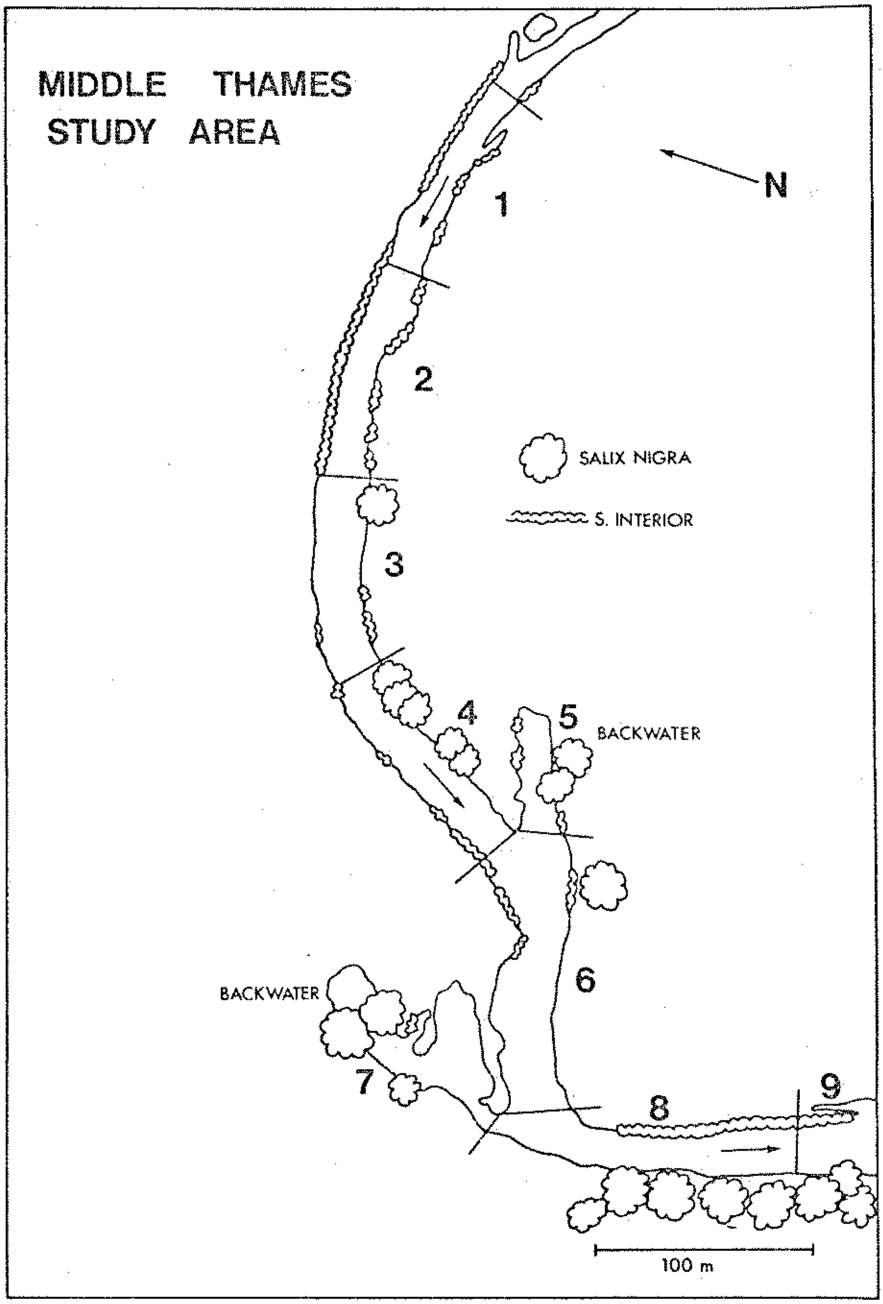

FIG. 1. The study area (taken from Keenleyside 1978 with permission).

sites that were randomly chosen from a grid covering the entire study area. Therefore 240 quadrats, each 0.5 m^2, were sampled.

For each sample five environmental variables were measured: water velocity, depth, substrate type, percentage vegetative cover, and distance to shore. All water velocity measurements were made on one day (with a pygmy current meter held just off the bottom); therefore they should be correct as relative among-quadrat values. Depth was measured at each of the four corners and in the center of a quadrat, and these five measurements were averaged to produce a single value for each quadrat. Depths were determined over the period July 5 to July 26, 1977, and were corrected to a standard water depth based on depth records over this period at three reference points in the study area. Two litres of substrate from the surface of each quadrat (approximately the top 10 cm) was sampled with a shovel. After removal of all clams, the sample was dry-sieved into 12 particle size classes ranging from 0.074 to 50.8 mm and the material in each of these classes was weighed. These 12 classes were later grouped into five classes: cobble, gravel, coarse sand, medium sand, and fine sand (after Folk 1968). Percentage vegetative cover was estimated by eye for each quadrat, and distance to the nearest shoreline was measured from the center of the quadrat. For additional details of procedures see Bietz (1981).

The unionid clam species were identified and representative specimens were sent to the National Museum of Canada for verification.

Statistical analysis

The null hypothesis of a random distribution of clams over a homogeneous environment was tested by comparing the distribution of abundance to a Poisson distribution. A discriminant analysis (DA) was then performed to test the null hypothesis of similar environment at locations with and without clams (regardless of species), and to describe any environmental differences. Finally we used DA to test and describe environmental differences among clam species, as in the multivariate niche analysis of Green (1971). Preceding each DA, principal components analysis (PCA) was applied to the environmental data both for transformation and interpretation purposes. As a transformation PCA has several virtues (see Green 1979). First, it can reduce the number of original variables while minimizing the loss of information in doing so. Second, the new variables produced by PCA (the "PC scores") are uncorrelated and therefore a stepwise DA can validly be done. Third, as a consequence of the central limit theorem the new variables represented by the PC scores will tend to be more normally distributed than were the original variables.

The results of a PCA can in themselves be of value for interpretation of spatial environmental variation, especially when environmental variables have high spatial correlation as they do in a stream. Any attempt to identify PC's after the first (PC_1) as real, independent factors should be made with caution, however, because the PCA model of uncorrelated components related to the original variables in a linear and additive manner is often unrealistic for ecological data (see Green and Vascotto 1978; Green 1979; and references cited therein). They may safely be interpreted as statistically independent components of the data with empirical relationships to the original variables, and this will suffice for our purposes.

We first performed PCA on the substrate data, which consisted of percentages by weight in five size classes. PCA is particularly effective in the analysis of data comprising percentages in several categories (Gower 1967; Green 1979). The denominator used to calculate the percentages (here the total weight of substrate sampled from a quadrat) does not vary greatly among samples, which is necessary to ensure that poorly behaved ratio variables are not produced (Atchley *et al.* 1976; Green 1979). A subset of the PC's from this analysis was then used, along with the other habitat variables, in a subsequent PCA, which generated PC scores that were used in the discriminant analyses (DA's). This two-step PCA could have been done in one step. However, interpretations of results from the first PCA (on the substrate data only) seemed to be of value.

The number of samples in the DA for the "clams versus no clams" analysis is equal to the number of quadrats, whereas in the DA for the "among-species" analysis it is equal to the number of species occurrences in quadrats. Therefore the PCA sequence had to be carried out separately for each of the two analyses.

Results

The species and their frequency of occurrence are listed in Table 1. Of the 240 quadrats, 126 contained clams. Clams were distributed nonrandomly ($\chi^2_{(4df)} = 36.2$).

Locations with clams versus locations without clams

Of the four possible PC's from the PCA on the five substrate variables (Table 2), the first three accounted for 95% of the variation and were used for further analysis. The PCA on all seven habitat variables (Table 3) yields seven PC's. The first (PC_1) is fine to coarse substrate composition; PC_2 is vegetative cover associated with deep, slow-moving water; PC_3 is distance from shore, unrelated to anything else; PC_4 is vegetative cover in shallow riffle-type areas; PC_5 is depth and water velocity increasing together; PC_6 and PC_7 are uninterpretable and account for less than 1% of the variation. A stepwise discriminant analysis results in one discriminant function (only one is mathematically possible), and three of the PC's contribute significantly to the discrimination between the locations with and without clams (Table 4). Interpretations of their contributions to the discrimination follow.

Increasing values of PC_5, representing deep, fast water, cause a larger negative contribution to the discriminant vector (discriminant function (DF) coefficient for $PC_5 = -0.68$), which moves the discriminant score (DS) value in the direction of the "no clams" group centroid. Increasing values of PC_4, representing vegetated shallower areas, cause a larger positive contribution to the discriminant vector (DF coefficient for $PC_4 = 0.44$), which moves the DS value in the direction of the "with clams" group centroid. Increasing values of PC_1, representing substrate with a lower proportion of cobble relative to finer materials, cause a larger negative contribution to the discriminant vector (DF coefficient for $PC_1 = -0.44$), which moves the DS value in the direction of the "no clams" group centroid. In summary, clams are most often found in vegetated shallow areas with low current, but their occurrence is also biased toward substrates with a substantial component coarser

TABLE 1. Species of unionid clams collected in the study area

Species	No. of individuals in all 240 samples (each 0.5 m^2)
Villosa iris Lea	108
Elliptio dilatata Raf.	64
Strophitus undulatus Say	16
Fusciona flava Raf.	13
Alasmidonta calceola Lea	12
Lampsilis radiata Gmelin	2
Pleurobema cordatum coccineum Conrad	1

TABLE 2. Principal component vectors for PCA on substrate data, in the "clams versus no clams" analysis

Variable	PC$_1$	PC$_2$	PC$_3$	PC$_4$
Cobble	−0.96	−0.06	−0.18	0.04
Gravel	0.51	−0.54	0.66	0.07
Coarse sand	0.92	−0.01	−0.26	−0.27
Medium sand	0.87	0.17	−0.36	0.30
Fine sand	0.08	0.88	0.46	−0.01
Cumulative percent of variation	55.7	77.9	95.3	100

TABLE 3. Principal component vectors for PCA on all habitat data, including three substrate PC's, in the "clams versus no clams" analysis

Variable	PC$_1$	PC$_2$	PC$_3$	PC$_4$	PC$_5$
Mean depth	−0.17	0.79	0.19	−0.34	0.44
Water velocity	0.16	−0.75	0.35	0.30	0.43
Distance to shore	−0.11	0.29	0.91	0.12	−0.25
Vegetative cover	−0.13	0.62	−0.22	0.74	0.10
Substrate PC$_1$	0.99	0.12	0.02	−0.01	0.00
Substrate PC$_2$	0.99	0.12	0.02	0.00	0.00
Substrate PC$_3$	0.99	0.12	0.02	0.00	−0.01
Cumulative percent of variation	43.4	67.7	82.7	93.6	100

TABLE 4. Summary of discriminant analysis results from the "clams versus no clams" analysis

Discriminating variables	Change in Rao's V	Significance (α)	Discriminant vector
PC$_5$	9.5	<0.01	−0.68
PC$_4$	4.1	0.04	0.44
PC$_1$	4.2	0.04	−0.44
PC$_2$	3.3	0.07	−0.39

Groups	Locations with clams	Locations without clams
Group centroids in reduced space	0.22	−0.34

than gravel. Since low-current shallow areas in rivers tend to have medium to fine rather coarse substrates, this optimization must often represent a compromise among environmental factors. Distance to shore per se (PC$_3$) appears to be irrelevant, as does presence of vegetation and low water velocity at greater depths (PC$_2$).

Among different species locations

In the "among-species analysis" the results of the PCA on the substrate variables are similar (Table 5). Again the PCA on all habitat variables yields seven PC's (Table 6). These PC's are somewhat different because they are based on data from only those locations where clams are present (which are in effect weighted by the number of species present: see Discussion). In the "among-species" stepwise DA, the first discriminant function (DF$_1$) is based on two PC's (PC$_5$ and PC$_7$) that significantly contribute to the discrimination among clam species (Table 7). There are no other DF's that are a function of significantly discriminating PC's.

Increasing values of PC$_7$, representing greater depth and water velocity, cause a larger positive contribution to the discriminant vector (DF coefficient for PC$_7$ = 0.66), which moves the DS toward larger positive values. Increasing values of PC$_5$, representing vegetated shallow areas relatively close to shore and with sandy substrate, also cause a larger positive contribution to the discriminant vector (DF coefficient for PC$_5$ = 0.64), which moves the DS toward larger positive values. The species' group centroids on the DF$_1$ axis are in Table 7.

The best "among-species" discriminator (PC$_7$) is similar to the best "clams versus no clams" discriminator (PC$_5$). The second best "among-species" discriminator (PC$_5$) is similar to the combined second and third best "clams versus no clams" discriminators (PC$_4$ and PC$_1$). However, in the "among-species" analysis shallow vegetated areas are associated with sandy substrates and closeness to shore, all in one PC that describes the natural out-from-shore gradient, whereas in the "clams versus no clams" analysis one PC represents shallow-with-vegetation while a different PC represents *coarseness* of substrate.

TABLE 5. Principal component vectors for PCA on substrate data, in the "among-species" analysis

Variable	PC$_1$	PC$_2$	PC$_3$	PC$_4$
Cobble	−0.98	0.05	0.14	0.08
Gravel	0.58	0.21	−0.78	0.08
Coarse sand	0.94	−0.11	0.23	−0.22
Medium sand	0.86	−0.23	0.35	0.28
Fine sand	0.24	0.93	0.28	0.02
Cumulative percent of variation	59.8	79.2	95.3	100

TABLE 6. Principal component vectors for PCA on all habitat data, including three substrate PC's, in the "among-species" analysis

Variable	PC$_1$	PC$_2$	PC$_3$	PC$_4$	PC$_5$	PC$_6$	PC$_7$
Mean depth	0.79	0.12	−0.04	0.15	−0.38	−0.19	0.39
Water velocity	−0.78	0.33	0.12	−0.09	0.10	0.28	0.41
Distance to shore	0.39	0.71	−0.02	−0.26	−0.28	0.41	−0.18
Vegetative cover	0.47	0.05	0.37	−0.65	0.43	−0.17	0.08
Substrate PC$_1$	0.47	−0.56	0.34	0.18	0.10	0.54	0.05
Substrate PC$_2$	0.38	0.15	0.71	0.14	0.53	0.13	0.97
Substrate PC$_3$	0.14	0.53	0.49	0.58	0.31	−0.12	−0.06
Cumulative percent of variation	28.6	46.6	61.3	74.3	85.6	94.7	100

TABLE 7. Summary of discriminant analysis results in the "among-species" analysis, for DF$_1$

Discriminating variables	Change in Rao's V	Significance (α)	Discriminant vector
PC$_7$	18.9	0.01	0.66
PC$_5$	17.1	0.02	0.64
PC$_3$	13.3	0.06	0.50

Groups (species)	Group centroids in reduced space	Description of environmental gradient
Lampsilis radiata	1.02	Nearshore, sandy,
Elliptio dilatata	0.79	vegetated, shallow,
Strophitus undulatus	0.73	edge of channel
Fusciona flava	0.19	
Pleurobema cordatum	−0.25	Mid-channel, coarse,
Alasmidonta calceola	−0.31	little vegetation,
Villosa iris	−0.42	deeper flat bottom

Discussion

Statistical analysis considerations

In the "clams versus no clams" analysis the discrimination is between two groups, one of which is the location at which no clams were present. There is danger that such a group characterized by absences may be heterogeneous (Green 1979), since absence could have diverse causes. For example, both extremes of the substrate particle size gradient, or of the depth gradient, could be unsuitable for clams. Examination of our data suggests that we do not have this problem. In any case the effect would probably be a loss of power in our ability to discriminate between the groups, which would be a conservative bias.

A different problem is that the observations on the environmental variables from a given quadrat enter the "among-species analysis" data for each species that is present in the quadrat. Therefore, some observations in different "species groups" are not independent. The effect of this on the test is not known, but it seems logical that it would make the groups look more similar than they really are. If that is the case then again there would be a conservative bias.

Ecological results

The out-from-shore gradient in this as in most rivers is one of increasing depth, decreasing vegetation, and coarser substrates. In the Middle Thames River the different unionid species occur in somewhat different distributions along this gradient. Ignoring species, the clams occur most frequently in the shallow, slow-current, more vegetated areas, but with a preference for coarser substrates if they can be found within tolerable depth and current regimes. Shallow areas with slow, steady current, often partially vegetated, and with a sandy substrate, are probably optimal for lotic unionids because minimal turbulence is combined with a steady food supply and a minimum of silt (Parmalee 1967; Murray and Leonard 1962). Also slower currents may enhance reproduction by unionids by making fertilization of eggs more certain (Evermann and Walton 1918). However, when the river is in flood, shallow, slow-current areas become deep, fast-current areas. Clams may be more firmly imbedded in substrates with a substantial component of cobble and other coarser than gravel material (Harman 1972). Therefore, patches of coarser substrate in shallower areas are preferred habitat. Both frequency of occurrence of clams and separation of species are related to quite small principal components of the environmental variables, whereas some much larger PC's are not important (Tables 4, 7). This indicates that the environmental patterns that are relevant to unionids, and perhaps to other biota as well, are not necessarily the patterns we can easily see and quantify.

The distribution of species along an environmental gradient has been described for many other habitats such as the marine intertidal zone. The lotic environment is of course a highly unstable one, and this stretch of the Middle Thames River in particular is subject to both very low and to turbulent high water levels. Therefore, one cannot expect lotic unionid species to show temporally stable microhabitat niche differentiation such as is seen in the tide level zonation of marine littoral communities. Unionid species would be expected to utilize mobility more than physiological tolerance as an adaptation. A barnacle, say, does not have that option. One of us (R.H.G.) has observed, on a number of occasions and in various habitats, *Lampsilis radiata* actively dispersing in apparent response to changing water level, and *Anodonta* spp. displaying strong patterns of seasonal depth variation.

In summary, despite inevitable and frequent disruption by the temporal variability of most lotic environments, a spatial pattern of microhabitat differentiation by unionid species can be discerned.

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