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Spatial and Temporal Patterns in Macrobenthic Stream Diversity¹

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The relationship between the characteristics of a stream community and sediments were studied for 1 yr in a small unpolluted river with a morainal substrate. Recognizable faunal assemblages were associated with silt or silt fill, sand or sand fill, and large boulders. The fauna in sediments of mean particle sizes coarser than sand but finer than boulders was characterized by a high variability due largely to temporal successions of morphologically related species. It was found that the number of species was directly proportional to mean particle size (in ϕ units) in spring when the sediments were well sorted, but the relationship broke down as the sediment interstices filled in. In late fall when the sediments were badly sorted, the number of species is perhaps more related to the sorting coefficient of the sediments. The relevance of these findings to studies of pollution is discussed.

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Nous avons consacré 1 a. à l'étude de la relation entre les caractéristiques d'une communauté fluviatile et celles des sédiments dans une petite rivière non polluée et à substrat de moraine. Des communautés fauniques reconnaissables sont associées au limon ou au limon interstitiel, au sable ou au sable interstitiel et aux gros blocs. La faune se trouvant dans les sédiments de particules plus grosses que le sable mais plus petites que les blocs est caractérisée par une haute variabilité, causée en grande partie par la succession dans le temps d'espèces morphologiquement apparentées. Le nombre d'espèces est directement proportionnel à la taille moyenne des particules (en unités ϕ) au printemps, au moment où les sédiments sont bien assortis. Cependant, cette relation ne tient plus à mesure que les interstices sédimentaires se remplissent. Tard en automne, quand les sédiments sont mal assortis, le nombre d'espèces est peut-être davantage lié au coefficient de classement des sédiments. Nous analysons l'application de ces constatations aux études de pollution.

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MOON (1939) wrote that, in a lake or stream, "by considering two factors, erosion and deposition, . . . it should be possible to devise a standard of comparison for diverse habitats." Many specific aspects of organism-substrate relationships have been studied in streams (Cummins 1966; Cummins and Lauff 1969), but the relationships between the diversity of stream substrates and the structure of the community have seldom been considered. The research presented here investigates the relationship of the stream community structure to substrate and changes in substrate characteristics in more detail than previous studies. An understanding of these relationships could result in better biogeographic comparisons of stream fauna and better sampling programs within streams by suggesting methods of sampling in a substrate-specific manner or by considering substrate to be one of the main factors affecting benthic distributions. Pollution- and disturbance-related studies could be refined by considering biological changes to be a direct result of substrate changes or by comparing the disturbed community to that which is expected. Also, the relationships between community structure, habitat structure, diversity, and stability are important theoretical considerations for the population ecologist.

Materials and Methods

The area of the Rat River that was sampled was an undisturbed, 100-m reach, 10-16 m wide, near Rosa, Manitoba (49°18'N, 96°52'W).

The word "sample" refers to animals or sediment collected from 1 ft² (929 cm²) of stream bottom with a 350- μ mesh Surber sampler. Sampling for the final analyses was approximately weekly from June 8 to August 22, 1971, then irregularly until October 8, 1971. Samples were taken again on February 11, 1972, and then on five occasions at approximately 10-day intervals from April 18 to June 3, 1972. On each date (total of 19), 10-20 samples were taken, depending on the number of visibly different substrate types. As the water level dropped, several substrate types were exposed and hence were not sampled. Nevertheless, an attempt was made to take a complete set of samples from silt, sand, pebbles, fine cobbles, coarse cobbles, riffles, and large rocks on all the sampling dates. Samples were taken to a depth of 8 cm where possible. The sampling site contained a sufficient variety of substrate types so that no area had to be redisturbed in sampling for at least 1 mo. The current usually was adequate to ensure that animals were easily washed into the net. In late summer, currents were created manually by washing water through the net. Samples were preserved in 10% formalin, washed in water after 2 days, and preserved in 70% ethanol. Benthic organisms were

identified in most cases to genus and keyed or numbered to species.

With each faunal sample, a sample of adjacent, similar-appearing sediment was taken or a description of the sediment made. Cores of fine substrate, 3-cm or smaller mean particle size, were sampled to a depth of 8 cm. In areas of coarser substrates, a 2-liter sample was taken monthly by pushing sediment into a plastic bag held under water. The substrate samples were stored frozen until analyzed. Boulders approximately 150 cm and larger were not collected but measured to obtain the mean diameter.

The sediment samples were dry-sieved into 11 size-groups on an Endecott test sieve shaker with 10 sieves 63 μ -31.5-mm mesh size, each sieve having twice the mesh size of the one below it. Each sample was shaken for 6-10 min depending on the sample volume and degree of sorting of the sample. The sieves were then weighed. All rocks exceeding 48 mm diam were measured and then weighed. The Wentworth size classification (Wentworth 1922) was used. This consists of transforming the particle size in millimeters to $-\log_{10}$, known as ϕ (phi) units. Boulders are approximately -8ϕ , pebbles -5 to -2ϕ , sand $0-2 \phi$, and silt, approximately 3ϕ . Standard statistics in ϕ units, including mean, sorting coefficient (i.e. standard deviation), and skewness (median - mean \div sorting coefficient) were calculated for each sample (Inman 1952). The statistics on the larger, coarser sediment samples collected once a month were used as an estimate of the substrate parameters for similar-appearing samples in adjoining weeks. The measurements on the boulders were converted to comparable sediment parameters by using the mean diameter cubed instead of weight.

Current velocity, percent organic matter of the substrate, depth, and temperature also were measured with each sample. The current velocity was measured with an Hiroi Acoustic Current Meter (Model 2048), with a 12.7-cm propeller, at the sediment surface. Percent organic matter was calculated by determining the loss of organic carbon on combustion of a subsample of sediment at 540 ± 15 C for 1 h.

Mutual information analysis (Orloci 1968) was used to group 1) samples on the basis of similar species composition, and 2) species on the basis of similar occurrence patterns within all samples. These two sets of groups were then related to the environmental parameters. This method is conceptually and technically simpler than relating the distributions of more than 200 species in 271 samples to the environmental parameters. The technique is explained in Appendix A, since it has previously been used only in morphology (R. McV. Clarke unpublished data), in phytosociology (Orloci 1968; Williams et al. 1972) where the references to the technique are either excessively complicated or cross-referenced beyond ready understanding, and in benthic studies (Gregory and Loch 1973) where the proper technique is used but incorrectly described.

Included in the direct analysis (the grouping of samples) were all species that comprised more than 5% of all animals caught on any sampling date and

had at least 5% of the total species count on one sampling date. All species of which over 100 individuals were collected, as well as three of particular interest (*Hexagenia limbata*, *Stenonema nepotellum*, and *Perlesta placida*), were used in the grouping of species by inverse analysis. All species that comprised more than 1% of the individuals collected on each sampling date were used in the analysis of covariance and for the calculation of correlation coefficients. For these last statistics, sampling dates October 8, 1971 and February 11, 1972 were combined since only two samples were taken on February 11.

Results

The relationship between two sediment characteristics, mean particle size (MPS) and sorting coefficient (SC), changed during the sampling schedule (Fig. 1). In late fall and in early spring before peak flow, they were positively correlated; in midsummer they were not significantly correlated. Coarse sediments (-6 to -8ϕ) had uniform and low SC's all year. On dates when the correlation was high, fine sediments had a large SC or were badly sorted. On dates when the correlation was not significant, fine sediments had highly variable SC's and hence were sorted to varying degrees.

The direct analysis, which grouped 271 samples on the basis of species similarity, was arbitrarily truncated at the seven group level (Fig. 2) since these seven groups had more uninterrupted spatial and temporal characteristics at this level than at higher ones. These sample groups are plotted according to time of occurrence and MPS (Fig. 3). Each group containing between 16 and 71

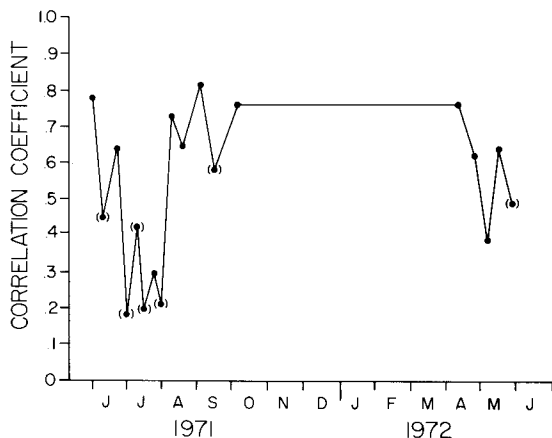


FIG. 1. Correlation coefficient between mean particle size and sorting coefficient of the sediments. Nonsignificant correlations ($P > .05$) have points in parentheses.

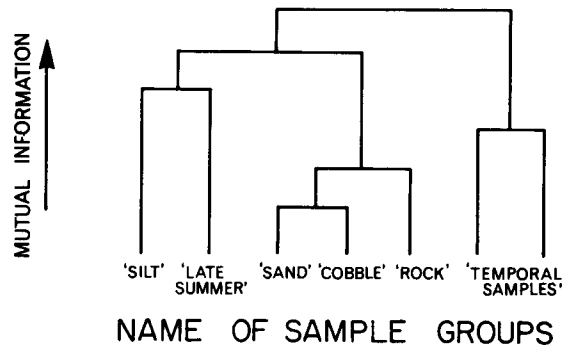


FIG. 2. Fusion pattern of the last seven sample groups in the direct mutual information analysis.

samples is named in the most appropriate descriptive terms.

Analysis of variance was performed for each of five environmental variables associated with samples in the seven groups (Table 1). If any environmental variables for a sample were estimated, rather than measured directly (see Methods), then they were not included in the calculations. Column 1 represents the lower, or the only, sediment size-class frequency peak (since sediment distributions were often bimodal). The measure of time was arbitrarily chosen to be the sampling date number (1-19). Two temporal peaks were calculated if there were two peak times of occurrence. The nature of significant differences was determined with Studentized Ranges (Snedecor and Cochran 1967) and are explained in the text below.

The "Silt" sample group (Fig. 3a) is unique on the basis of its large MPS or fine sediments ($MPS = -0.29 \phi$). These sediments generally were sorted poorly ($SC = 1.75$), had silt fill (low peak = 2.98ϕ), and probably were packed and offered few habitable interstices. This group spread into larger particles as the summer progressed and shrank again next spring. The species with the highest habitat diversity (Appendix A) in the pooled "Silt" samples were the mayflies *Ephemera simulans*, *Stenonema nepotellum*, an oligochaete, *Lumbriculus* sp., and the corixid *Cymatia* sp.

The "Late Summer" habitat type (Fig. 3a) is an extension of the silt habitat described above (Fig. 2). It is unique only on the basis of its time of occurrence. The silt-associated animals had moved into coarser sediments, probably due to reduced current velocities; *Heptagenia maculipennis*, a mayfly that was not found abundantly at any other time of the year, had the highest habitat diversity in this sample group. Other important

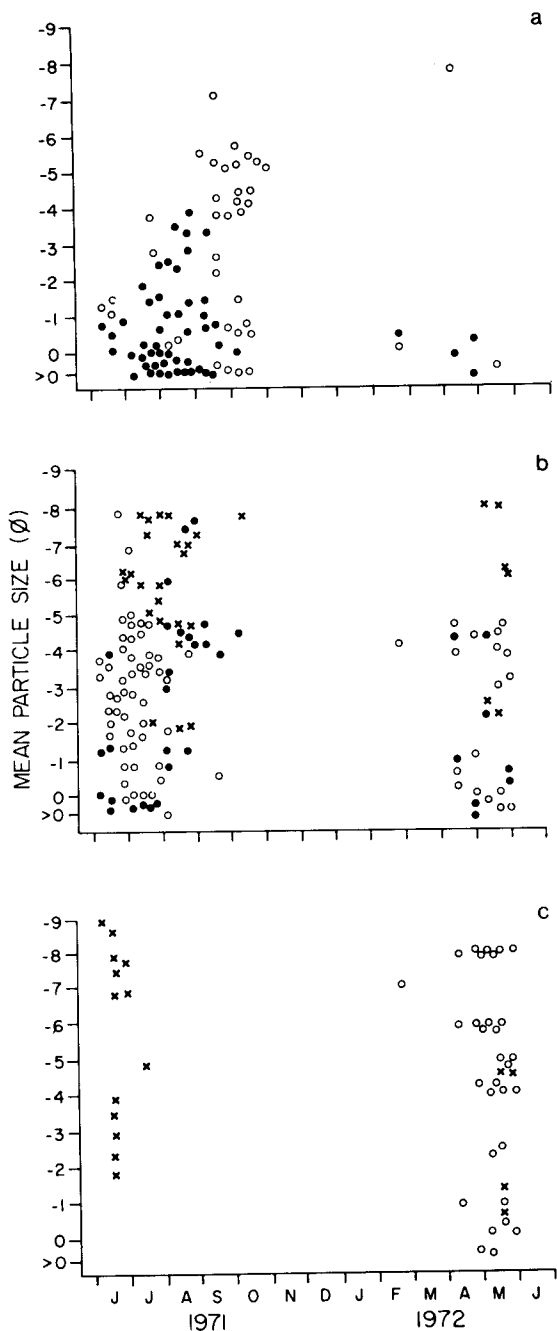


FIG. 3. Spatial and temporal orientation of the seven major sample groups identified by mutual information analysis. a, Orientation of "Silt" (●), and "Late Summer" (○) samples; b, orientation of "Sand" (●), "Cobble" (○), and "Boulder" (×) samples; c, orientation of "Temporal 1971" (×) and "Temporal 1972" (○) samples.

species were the beetle larvae *Stenelmis* spp., and the mayflies *Paraleptophlebia mollis* and *Hexagenia limbata*.

The "Sand" samples (Fig. 3b) were characterized by a low sediment size-class frequency peak different from all other samples (low peak = 0.94ϕ). The sediment samples ranged from pure sand to large rocks with sand fill. Samples in other groups generally had a silt fill (Table 1). This habitat type had a temporal and spatial distribution similar to both habitat types previously described; however, it always extended into slightly coarser sediments than the former. *Sphaerium* sp., a fingernail clam, was characteristic of these samples. Two Trichoptera, *Hydroptila* sp. and *Rhyacophila* sp., and the mayfly *Ephemera simulans*, which was also important in the silt habitat, were important in this habitat.

Two other sample groups, the "Cobble" and "Boulder" habitats, were both related to the "Sand" sample group (Fig. 2). The first of these, the cobble samples (Fig. 3b) had a high species diversity of $H' = 7.8$ (Appendix A) or contained 90 species. Its physical characteristics were mid-range, but it had a distinct time of occurrence (Table 1). It is of interest that a lower truncation level in this group gives four further significant temporal separations, as discussed below. The "Rock" sample group was characterized by coarse sediments ($MPS = -5.35 \phi$), low SC ($SC = 1.09$), and low depth (13.07 cm). Again, a lower truncation level yields two significantly different temporal separations, as discussed later. However, most species in the group occurred all year.

The two remaining sample groups are unique on the basis of their early spring occurrence. Both groups occurred in different years and in a range of medium and coarse sediments (Table 1). The 1972 spring was different from 1971 in that the blackfly larvae *Simulium* spp. were more abundant. The species in this habitat will be named in the next section.

The dendrogram of the inverse analysis, which grouped species on the basis of similar occurrence in samples (Table 2), was truncated at the 11 group level since this level allowed the faunal groups to be associated with the sample groups previously described. The distribution of all species agrees with the literature (de March 1974).

Four taxa, *Heptagenia maculipennis*, *Sphaerium* sp., *Simulium* spp., and *Pseudocloeon myrum*, were isolated in the analysis indicating that their distribution was not highly correlated with that of other species (Table 2).

The mayfly *Heptagenia maculipennis* occurred

TABLE 1. Means, standard errors, significance of differences, and nature of significant differences of several environmental variables in seven faunal groups.

	Low peak ϕ	MPS ϕ	Sorting coef (ϕ)	Depth (cm)	Time (sampling period)
Silt	2.89 ± 1.72	-0.29 ± 1.72	1.75 ± 0.55	24.94 ± 12.98	8.43 \pm 2.35
Late Summer	3.29 ± 1.98	-2.93 ± 2.70	1.51 ± 0.66	19.23 ± 11.87	10.88 \pm 3.32
Sand	0.94 ± 0.63	-2.44 ± 2.63	1.44 ± 0.54	26.00 ± 13.80	9.82 \pm 5.11
Cobble	2.53 ± 1.86	-2.69 ± 2.09	1.77 ± 0.56	27.73 ± 14.63	4.20 \pm 1.94 17.06 \pm 1.88
Boulder	3.56 ± 2.00	-5.35 ± 1.87	1.09 ± 0.53	13.07 ± 8.92	7.33 \pm 2.30 18.67 \pm .82
Temporal 1971	3.28 ± 1.75	-3.99 ± 2.53	1.44 ± 0.68	24.25 ± 16.06	1.42 \pm 1.16 17.75 \pm .50
Temporal 1976	4.05 ± 1.23	-4.14 ± 3.03	1.19 ± 0.57	26.03 ± 13.62	16.97 \pm 1.05
Estimated SE	1.71	2.32	0.56	13.32	2.74
Probability of significant differences	<0.01	<0.01	<0.01	<0.01	<0.01

in the greatest numbers in cobbles (-4.0 to -5.0 ϕ) in late August and in September. No other species showed a sediment preference in this size range at this time of the year, although several species showed preference for even coarser sediments.

Thirty samples with the most *Sphaerium* sp. (>30 in all cases), a fingernail clam, for which there was measured, not estimated, sediment data (see Methods) had particle size-class frequency peaks from 4.0 (-2 ϕ) to 0.5 mm (1 ϕ). Approximately one-half of these sediments had bimodal size-class frequency distributions, and the 4.0-0.5 mm peak was the smaller. Of 61 samples with no *Sphaerium* for which there was measured sediment data, 44 (72%) had particle size-class frequency peaks of less than 0.5 mm. *Sphaerium* was the dominant species only in the "Sand" habitat. *Sphaerium* probably has hydrological properties similar to particles of 0.5-4.0 mm, since it is usually less than 2 mm in size. Particles of this size will not go into suspension at normal stream current velocities, yet will shift slightly in a wide range of velocities (Inman 1949, fig. 2).

Blackfly larvae *Simulium* spp. occurred in large quantities (~ 600 per sample) in a narrow range of substrates (MPS = 6.3 ± 0.1 ϕ) in mid-May 1972 and in negligible numbers (total = 15) in 1971. The low habitat diversity of 3.73 bits indicates both low temporal and spatial diversity.

Pseudocloeon myrum was isolated solely on the basis of its early spring occurrence. It is the main species in both "Temporal" sample groups. Other early spring animals also occurred in the "Boulder" habitat (Table 2).

The segregation of many taxonomically and morphologically related species into different faunal groups (Table 2) is a notable aspect of the analysis. The segregation of two or more species into different groups means that the species usually did not occur in the same samples, or coexisted to a limited extent. The three Orthoclaudiinae occurred in three different spatial groups. The Baetidae (*Caenis* sp., *Pseudocloeon myrum*, *Baetis herodes*, *Baetis intercalaris*, and *Centropilum* sp.) occurred in different temporal groups (Table 2), the last four species accounting for possible divisions of the "Cobble" habitat. The Ecdyonuridae (*Stenonema nepotellum*, *Stenonema interpunctatum*, and *Heptagenia maculipennis*) were segregated into groups with different substrate characteristics, and also occurred in maximum numbers in spring, midsummer, and fall, respectively. Three Ephemeridae, *Ephemera simulans*, *Ephoron album*, and *Hexagenia limbata* were segregated into groups that differed significantly in time of occurrence.

Three large predaceous Plecoptera showed strong spatial separation or obvious separation on the basis of food habits. This is not shown with

TABLE 2. Data associated with last 11 groups of inverse mutual information analysis.

Species in group	Habitat diversity (bits)	Association with sample groups
<i>Hexagenia limbata</i> <i>Stenonema nepotellum</i> <i>Anacronyx</i> sp. (larva) <i>Orthocladinae</i> I <i>Procladius</i> sp. <i>Stenelmis</i> spp. (larva) <i>Paraleptophlebia mollis</i> <i>Heterelmis</i> sp. (larva)	8.76	"Late Summer" and "Silt"
<i>Sphaerium</i> sp.	6.67	"Sand"
<i>Baetis intercalaris</i> <i>Rhyacophila</i> sp. <i>Neocorixa</i> sp. <i>Phasganophora capitata</i> <i>Atherix</i> sp. <i>Pseudochironomus</i> sp.	6.83	"Cobbles" (early)
<i>Centroptilum</i> sp. <i>Orthocladinae</i> II	6.66	"Cobbles" (late)
<i>Baetis herodes</i> <i>Stenonema interpunctatum</i>	7.55	"Cobbles" (midsummer)
<i>Diplectrona</i> sp. <i>Pteronarcys</i> sp. <i>Paragnetina</i> sp. <i>Stenelmis</i> sp. (mature) <i>Hydropsyche</i> sp. <i>Perlesta placida</i> <i>Macronema</i> sp. <i>Hydroptila</i> sp.	8.27	"Boulders" and "Temporals"
<i>Pseudocloeon myrum</i>	5.25	"Temporals"
<i>Heptagenia maculipennis</i>	5.65	"Late Summer"
<i>Ephoron album</i> <i>Caenis</i> sp.	6.58	"Silt" (midseason)
<i>Hyallolela azteca</i> <i>Orthocladinae</i> III <i>Microtentipes</i> sp.	6.32	"Cobbles" (early spring)
<i>Lumbriculidae</i> I <i>Baetisca</i> sp. <i>Cymatia</i> sp. <i>Ephemera simulans</i>	6.51	"Silt" (early)
<i>Simulium</i> spp.	3.73	"Temporal 1972"

the given truncation level in the inverse analysis. Both *Perlesta placida* and *Paragnetina media* occurred in -4 to -6ϕ MPS sediments the whole year. However, *Paragnetina* was considerably larger than *Perlesta* so it is quite probable that the prey species were different. *Phasganophora capita* occurred in -3 to -4ϕ MPS sediments all summer long, and in smaller numbers in fall and winter, and probably also had different prey species. All three have several-year life cycles in

southern Manitoba. *Pteronarcys* sp. also lived in the coarsest sediments but it is herbivorous.

Three Hydropsychidae, which were grouped in the same "Boulder" habitat type, were temporally separated. The three species *Hydropsyche* sp., *Diplectrona* sp., and *Macronema* sp. occurred in peak numbers on June 8, July 6, and August 14, 1971, respectively. The difference in head size of the largest mature larvae (3.4, 1.9, and 1.5 mm, respectively), suggests different feeding

habits on the basis of different-sized mouth parts. *Hydropsyche* sp., the largest species, occurred earliest, when the current velocity was strongest and larger particles were in suspension; *Macronema* sp., the smallest, occurred latest, when smaller particles were in suspension. These three species are the basis of the possible divisions of the "Boulder" habitat.

Green (1974) showed that another small group of predators, the Tanypodinae, were temporally separated in this study.

Correlation of the biological and environmental data (de March 1974) showed that MPS was the only environmental variable consistently associated with community characteristics, such as number of species, number of animals, or the diversity index H' . On 16 out of 18 sampling dates, the highest correlation was between the number of species (S) and MPS. Therefore, an analysis of covariance of 18 "S" vs. "MPS" regressions was performed.

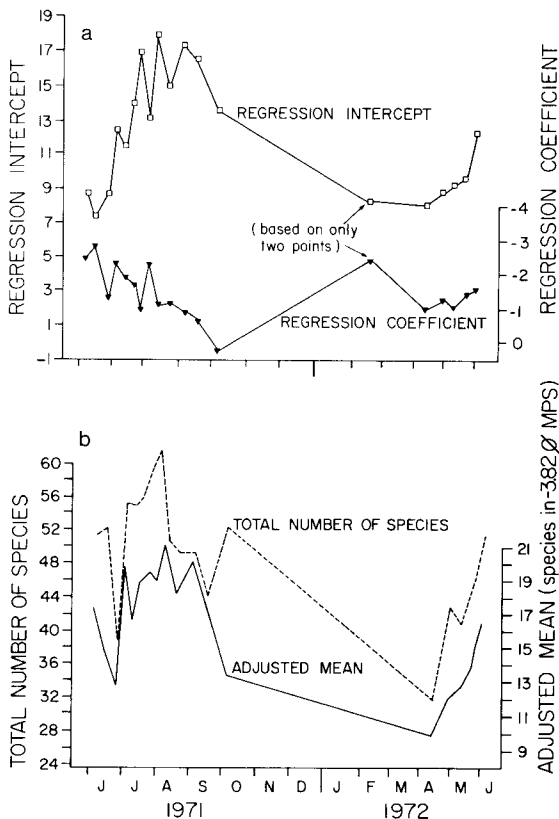


FIG. 4. a, Intercepts and regression coefficients of "number of species" vs. "mean particle size" regressions; b, total number of species and expected number of species at -3.82ϕ MPS.

In the analysis of covariance, the null hypothesis of the homogeneity of residual variances was rejected ($P \approx 0.025$). This probability value is borderline, but since heterogeneous variances primarily cause a lack of sensitivity (Cochran 1947), the results are presented, since these seem biologically meaningful.

The analysis indicated that there were significant differences between the adjusted means, slopes, and intercepts (P 's < 0.05) of the 18 samples. All three showed definite seasonal trends (Fig. 4a, b). The intercepts represent the number of species in 0.0ϕ MPS; the slopes represent the degree of response of S to MPS, and the adjusted means represent the number of species expected in -3.82ϕ MPS, the "average" sediment in the whole sampling program. The number of species varied seasonally (Fig. 4b); this is partially a sampling artifact resulting from the use of a relatively large mesh which missed many small instars. The adjusted mean is probably affected similarly. The correlation coefficients between S and MPS ranged from -0.86 to -0.11 on different dates, and are highly proportional to the slope. They are significant on all but three dates (August 14, September 16, and October 8, 1971). On three dates (September 16, October 8, 1971, and April 18, 1972), where the correlation is low or insignificant, S is significantly negatively correlated with the sorting coefficient (de March 1974).

Discussion

Although Fig. 1 shows that sediment characteristics change seasonally, a better explanation of the change is given by Inman (1949). My sampling scheme was biased in that it covered a wide range of mean particle sizes, but not necessarily a wide range of sorting coefficients, depths, and velocities. Hence, the correlations in Fig. 1 are biased and not based on an adequate amount of data. The range of current velocities that I sampled ($1.086-0.0 \text{ ms}^{-1}$) indicates that sediments from coarse pebbles to fine silt could have been lifted and deposited during the sampling season (Inman 1949, fig. 2) as current velocities and depths gradually decreased.

The changes in sediment characteristics are important to the fauna in two ways. First, if a species responds to a certain movable particle size, or to a current velocity, the location of the desirable habitat may change throughout the summer. Second, the number of available habitats in a certain area of stream may change. If any area is filled by progressively finer particles, the number of habitats decreases, and the number of

species may be reduced. Faunal responses of both types occurred in this study.

The direct and inverse mutual information analyses show that distinct fauna are associated with silt, sand, and boulders. All three sediments have unique hydrological and associated biological properties.

Silt will deposit at a current velocity of 0.003 ms^{-1} , but will not resuspend until a considerably higher velocity of 0.60 ms^{-1} is reached (Inman 1949). Therefore, it is a stable habitat over a range of low current velocities. Fine organic matter has hydrological properties similar to silt, so that food is also available in this habitat. Factor analysis of all environmental variables (de March 1974) showed that organic matter was associated with finer particles and a low sorting coefficient. However, the number and type of animals that can live in or on silt is limited by the lack of interstices in silt. The direct analysis (Fig. 3a) showed that the "Silt" habitat was restricted to areas of fine particles in the spring, but extended into coarser particles during the summer. This is expected due to the sedimentation explained previously. Several of the species in this habitat (Table 2) are also common in lake bottoms, in which the "Silt" habitat exists all year. The presence of silt seems to be more important than mean particle size.

Sand is unique because of its instability. Coarse sand will deposit at a higher current velocity than silt, at 0.0156 ms^{-1} , but will resuspend at 0.2 ms^{-1} . Fine sand of 0.18 mm diam will suspend, tumble, and redeposit at velocities near 0.02 ms^{-1} . Therefore, sand occurs only in areas where the current velocity is in the appropriate narrow ranges. The direct analysis showed that the "Sand" habitat, like the "Silt" habitat, extended into areas of coarser particles during the summer (Fig. 3b). In fact, sand "preceded" silt into the coarser sediments as the current velocities gradually decreased. The fingernail clam, *Sphaerium* sp., with hydrological properties similar to sand, was widespread in this habitat. No other species was abundant exclusively in this habitat. I believe that other species shown to be associated with the "Sand" habitat, *Hydroptila* sp. and *Rhyacophila* sp., were dependent on slightly higher current velocities in sediments that contained the sand fill. These two species were grouped with other species dependent on higher current velocities (Table 2).

The "Boulder" habitat, or the tops of riffles (Langbein and Leopold 1968) are characterized by a unique physical stability which makes them a desirable habitat for stream fauna for several reasons. The size of boulders alone makes them a

desirable refugium for many large animals not included in this analysis: crayfish, turtles, and fish. Also, by virtue of their size, physical stability, and the nature of sediment sorting, the boulder habitat possesses a temporal stability of which many small invertebrates can take advantage. During the spring floods, current velocities were relatively reduced within the boulders. During the drier period in late summer, the small current that remained flowed through the boulders, since lines of boulders across the river essentially acted as dams for the remaining water. In midwinter, several habitats froze solid, but the boulder habitat was open due to turbulence. Several species that take advantage of this temporal stability have life cycles that last several years. Among these are *Pteronarcys* sp., a stonefly that may require 4 yr to mature; *Paragnetina* sp., another large stonefly; *Orconectes virilis*, a crayfish; a large dragonfly nymph, *Aeschna* sp. that may require 4 yr to mature; and several species of fish.

Besides containing these large and long-lived species, samples in the "Boulder" habitat always had a high species diversity, often as much as $H' = 5.0$ or $S = 43$. Species that were characteristic of other habitats were also found in the boulders, probably due to the fact that their particular requirements could be found within the heterogeneous boulder habitat.

The "Boulder" habitat extended into the "Cobble" habitat in early spring. Animals that depended on a high current velocity usually found only in boulders found their requirements in slightly finer substrates at that time.

All other habitats that contain sediments finer than boulders and coarser than sand are characterized by temporal faunal changes, which are probably related to physical changes. This is the "typical" stream habitat which is generally considered to be highly unpredictable (Needham and Usinger 1956) and is the most unpredictable in this study.

This lack of predictability is due primarily to the temporal succession of taxonomically related insects within the "Cobble" habitat. This type of succession was also found by Grant and MacKay (1969) who concluded that ecological separation among morphologically and trophically similar species is produced by staggering the times of occurrence of the species.

The results of the covariance analysis give a partial predictive model for the number of species in a particular sediment at a particular time in the form of the following equation,

$$S(t) = a(t) \text{ MPS} + b(t) \text{ SC} + c(t) \quad (1)$$

where $S(t)$ = number of species occurring at a

particular time; $a(t)$, $b(t)$, and $c(t)$ are empirically derived constants, MPS = mean particle size of sediments, and SC = sorting coefficient of the sediments. The constants are determined primarily by the sediments available, the species pool, and the sediment changes during the summer.

The decrease in the ability of this equation to predict the number of species in late summer is related to sediment changes and accompanying changes in habitat heterogeneity. In spring, current velocities are typically high, the particles of all sizes are well sorted, and the sediment types are distinct. A large number of habitats are available, all differing in available footholds and exchange rates of oxygen and food. A great variety of niches exists in coarse substrates and a small variety in finer substrates. Hence, in early spring the number of species is highly correlated with habitat heterogeneity as indicated by MPS. As the interstices of substrates fill in with progressively finer particles during the summer, the habitat heterogeneity is gradually reduced starting from the finest sediments and moving gradually into coarser sediments. MPS becomes less efficient in predictions of the number of species since the fill is of importance. At this time, sorting of sediments is perhaps a better indicator of the number of species.

The results presented do not deny the extreme importance of response by a species to current velocity. However, in terms of a sampled area of stream bottom, the measurement of current velocity at an arbitrary point in or on the sample is essentially meaningless since many microhabitats exist within the sample (Cummins 1966). A close examination of sediments, however, is an indication of present and past current conditions. Nevertheless, the current velocity measured with the 5-in. (12.7 cm) propellor at the surface of the sediments tended to be proportional to MPS on many dates, especially in the early spring (de March unpublished data). The addition of SC and depth to the correlation between MPS and current velocity often increased the multiple correlation coefficient significantly.

Although the use of diversity indices has provided some information in studies of pollution in rivers and streams, the relationships in equation (1) are potentially more informative, and based on a firmer theoretical background in terms of both mathematics and population ecology. Since information content is the information analogue to the metric measure of variance (Kullback 1968), and since the latter is usually proportional to the total number of animals and to the number of samples in untransformed species count data (Taylor 1953), the measurement of only the

number of species is sufficient as an indicator of community richness and is also more subject to statistical treatment than is a diversity index. A river that has been changed or polluted could be examined in terms of equation (1), and changes in the shape or slope of the regressions would be of primary importance. The constants in the curve would be determined by sampling only at the most important times of the year. A different $c(t)$ would be found for both silt and sand. If a finer mesh were used for sampling, it is possible that the temporal dependence in equation (1) would be eliminated or reduced since the number of species may be close to constant all year (Mundie 1970). Also, if no pretreatment values are available, the estimation of the potential number of species by using sediment data and constants from streams in a similar geographic area is probably more accurate than by using diversity indices, a method that assumes that a certain number of species and type of species-abundance curve is normal in a stream.

The stream community is an excellent system for the study of factors underlying faunal diversity. Many of the principles and ideas described by MacArthur (1972) for biogeographic patterns apply to the stream on a smaller, more manageable scale. Faunal diversity is related to habitat heterogeneity, stability, and perhaps to history and productivity. Unfortunately, these factors are not independent from each other in this study, but this is not necessarily true for all other streams. The effect of competition as a determinant of diversity cannot be assessed from this study, since the fauna has evolved to minimize competition between closely related species and also between predators. One can only speculate on the importance of predation in determining diversity at this point.

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Appendix A

Williams and Lambert (1966) and Williams et al. (1972) found that several grouping techniques based on information statistics were more desirable than any grouping technique based on metric measures, especially in situations where sample structure more than the numbers in different taxa are of interest.

The information content formula used in this study was:

$$I = N \log_2 N - \sum_{i=1}^s N_i \log_2 N_i = \sum_{i=1}^s N_i \log_2 \frac{N_i}{N}$$

where I = information content, N = the total number of animals in the sample, N_i = the number of individuals of the i^{th} species, and s = the number of species. I/N gives the common diversity index H' (Pielou 1966). The mutual information content, ΔI , between two samples is simply the information content of the pooled samples minus the information contents of the two samples individually. The best formulation for use by the computer is formula (4) in Orloci (1968).

The grouping of species by this technique is called inverse mutual information analysis (Williams and Lambert 1961). This technique is based on the "habitat diversity" rather than on the information content of the species collection. The habitat diversity per individual (Levins 1968) of a species is:

$$\log_2 B = \sum_{j=1}^h \frac{N_j}{N} \log_2 \frac{N_j}{N}$$

where $\log_2 B$ = habitat diversity, N_j = the number of individuals in habitat j , N = the total number of individuals, and h = number of habitats.

In this paper, B rather than $\log_2 B$ was a measure of habitat diversity per individual.

The grouping technique with either formula consists of consecutively combining samples or species that have the smallest mutual information value when combined. A truncation level is chosen by terminating the combinations at any point.

It is theoretically correct to use information formulae that use logarithms of factorials ($\log N!$) rather than logarithms of simple numbers (Pielou 1966). According to Williams et al. (1972) which formula is used is not important in classificatory work since both are positive convex functions. Stirling's approximation to the logarithm of factorials can be used for large numbers only; however, the changeover from logarithms of factorials to the approximation at an arbitrary point causes meaningless fusions since the two forms may differ by an order of magnitude. If Stirling's approximation is used for all estimates the pattern of fusions is similar to that using simple logarithms.