A COMPARATIVE SAMPLING STUDY OF BENTHIC INVERTEBRATE POPULATIONS IN A PRAIRIE STREAM

by

GENE LESLIE PETERSEN

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Approved by:

J. Richard Marzolf
Major Professor

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INTRODUCTION

The primary objective of the present study was to develop an effective quantitative sampling method for estimating densities and studying distributions of benthic macroinvertebrates in King's Creek, an intermittent tallgrass prairie stream. To evaluate the method results were compared to those obtained by sampling the same area with a widely used sampler. The comparison was made within a small uniform riffle to minimize sources of variation other than between sampling methods. The resultant extensive sampling of a single habitat allowed examination of microdistributional patterns and species associations at one point in time.

The validity of conclusions drawn from an ecological study depends in part on how well the data represent nature, thus, selection of methods deserves careful attention. Stream ecologists dealing with benthic invertebrates are confronted with a wide variety of sampling methods (Welch, 1948; Macan, 1958; Cummins, 1962; Southwood, 1966; Hynes, 1970; Edmondson and Winberg, 1971). The characteristics a sampler should have for a particular study depend on the objectives, the characteristics of the stream, the characteristics of the invertebrates under study, and the time and number of investigators available for sampling. Since no sampler is ideal for every purpose knowledge of the applicability of each method is essential for a wise choice. The strengths and limitations of the sampling methods commonly used in small, swift streams are discussed in Appendix A.

For estimating densities and studying distributions a sampler should ideally remove all benthic invertebrates within a specified volume of the stream bottom. The stovepipe sampler (Merritt, Cummins, and Resh, 1978), consisting of an open, toothed, cylinder, was chosen as having the greatest potential for accomplishing this with the coarse substrates and seasonally

variable current velocities of King's Creek. It can be used to remove entire units of substrate from the stream along with the associated fauna. After removal efficient means of separation can be utilized and analysis of the substrate for factors related to invertebrate distributions is possible. These advantages were felt to outweigh the relatively large amount of labor required per sample.

The best way to evaluate the relative effectiveness of two samplers is to directly compare the results obtained by sampling the same area with both. Despite this, few of the many samplers that have been developed have been carefully compared (Hynes, 1970). Comparisons that have been made have revealed differences in efficiency, variability, and selectivity among samplers (Macan, 1958; Albrecht, 1961; Hynes, 1961; Coleman and Hynes, 1970; Radford and Hartland-Row, 1971; Mason et al., 1973; Crossman and Cairns, 1974; O'Conner, 1974; Roby et al., 1978). A sampler comparison was considered an important preliminary step to further study, because no comparison of the stovepipe sampler with other methods has appeared in the literature and no quantitative sampling has been conducted previously on King's Creek or similar streams in the Kansas Flint Hills. The Surber sampler (Surber, 1937) was chosen as the standard for comparison because of its widespread use in other comparative studies (Albrecht, 1961; Radford and Hartland-Row, 1971; Kroeger, 1972; Crossman and Cairns, 1974; O'Conner, 1974; Roby et al., 1978) and statistical evaluations of sampling methods (Needham and Usinger, 1956; Gaufin et al., 1956; Harris, 1957; Chutter and Noble, 1966; Chutter, 1972).

High variabilities in the numbers and weights of individual taxa and the fauna as a whole have been noted since early quantitative studies of benthic invertebrates in streams (Needham, 1934; Mottley et al., 1939;

Leonard, 1939). For randomly distributed populations (i.e., each organism is equally likely to occur at every point in the environment) frequency distributions of counts follow a Poisson series, in which the variance is equal to the mean (Elliott, 1971). Departures from randomness can occur either towards uniformity (variance less than the mean) or aggregation (variance greater than the mean). Variances in benthic sampling data are often many times greater than the mean, even within quite uniform habitats (Needham and Usinger, 1956; Allen, 1959; Chutter and Noble, 1966), indicating that populations have aggregated distributions on a small scale. Aggregated distributions may be caused by environmental factors or behavioral interactions within or between species (Allen, 1959). If a physical factor is related to the observed aggregation it must be heterogeneous within the area sampled on a scale such that differences occur among sampling units. The animal may actively respond to these differences or be passively distributed by them.

The nature and degree of environmental heterogeneity depends on the scale of observation. Many physical and chemical factors (e.g., temperature and concentrations of ions) vary from stream to stream and along the stream continuum from headwaters to large river, but are nearly uniform in a small stretch of stream at one point in time. These may be important in determining the geographical range and longitudinal zonation of a species, but can have little effect on its small scale distribution. In riffles of swift streams oxygen concentration is high and nearly uniform within the upper few centimeters of the substratum. It is likely to affect only vertical distribution into the deep interstitial environment. Other factors, especially water depth, current velocity, substrate characteristics, and food densities, vary within small sections of streams as well as between

streams. They obviously vary between major habitat types, such as riffles and pools, but even within such superficially uniform habitats they are heterogeneous on the scale that stream bottoms are normally sampled. Benthic invertebrates are small enough to experience differences at this level of heterogeneity. By sampling a habitat at points visually selected to be as similar as possible rather than at points selected randomly or systematically Allen (1959) found that the coefficient of variation for total numbers of invertebrates was cut in half, but the variance was still significantly greater than expected for a random distribution. This suggests that unless behavioral interactions are causing aggregation, invertebrates are responding to environmental differences that are undetectable on the scale of human observation. Distributions on this scale are usually termed microdistributions.

Overwhelming evidence has accumulated that benthic invertebrates select favorable microhabitats. Current flow, nature of the sediments, and availability of food constitute the most likely variables influencing microdistribution (Ulfstrand, 1967; Reice, 1974; Cummins, 1975). The distributions of many species are related to current velocity (Allen, 1959; Chutter, 1969), especially those adapted to filter food particles from flowing water, such as the Simuliidae (Phillipson, 1956) and the net-spinning Trichoptera (Scott, 1958; Edington, 1968; Wallace, 1975). Even to species not directly dependent on it current flow has great indirect importance, because substrate characteristics and food distributions are determined by the transporting, sorting, and depositing of materials by the current. Thus, the density of a species may be correlated with current velocity at the surface even though this has little relationship to the flows of water experienced by individuals at different points within the substratum.

Cummins (1962, 1966) felt that substrate particle size could serve as a common denominator in the benthic ecology of streams. Studies involving qualitative substrate descriptions (Percival and Whitehead, 1929; Linduska, 1942; Pennak and Van Gerpen, 1947; Mackay, 1969), quantitative substrate particle size analysis (Cummins, 1964; Ericksen, 1964; Barber and Kevern, 1973; de March, 1976), laboratory substrate selection experiments (Cummins and Lauff, 1969), and in situ substrate colonization experiments (Wene and Wickliff, 1940; Minshall and Minshall, 1977) have all shown the relationship of substrate particle size to benthic invertebrate abundance, species composition, and diversity. Cordone and Kelley (1961) stress the detrimental effects of large deposits of erosional silt on benthic invertebrate populations. A light coating of silt has a positive effect on some species and a negative effect on others (Ellis, 1936; Cummins and Lauff, 1969; Rabeni and Minshall, 1977). Scott (1966) presents evidence that the size and distance apart of stones on the surface of a stream bed may be important in determining the density of some species. In addition to the inorganic substrate aquatic plants (Nelson and Scott, 1962; Minckley, 1963) and submerged wood (Hynes, 1970) can serve as substrates for stream invertebrates and have heterogenoous destributions.

Ulfstrand (1967) found that habitat types supporting an abundance of a particular species contained available foods that corresponded well with known food preferences and concluded that food supply is the factor most directly related to microhabitat selection. In samples from the natural stream bottom and substrate colonization experiments Egglishaw (1964, 1969) found the density of many species to be positively correlated with amounts of fine detritus, which is an important food source for many benthic invertebrates (Chapman and Demory, 1963; Cummins et al., 1966; Minshall, 1967;

Coffman et al., 1971; Cummins, 1973; Cummins et al., 1973; Fisher and Likens, 1973). Rabeni and Minshall (1977) explored the effects of various combinations of current velocity, substrate particle size, and amounts of detritus on the colonization of substratum-filled trays to determine whether a hierarchical pattern of factors affecting microdistribution exists. More organisms colonized a given substrate particle size in a riffle than in a pool and some species showed definite current preferences, but the overall effect of current velocity was minor in comparison to substrate particle size. The particle size that resulted in maximum colonization by most species was the size that collected the most fine detritus. When the amounts of detritus were experimentally equalized thare was no longer a substrate particle size preference. Thus, detritus-feeding invertebrates may colonize substrates on the basis of their capability to collect and store detritus.

Benthic invertebrates therefore appear to aggregate by selecting favorable microhabitats from a mosaic of interrelated environmental factors, food supply possibly being most directly important. Microhabitat preferences no doubt vary from species to species. The fact that distributional patterns of different species do not coincide is reflected by greater variabilities in numbers of each species than in total numbers of invertebrates (Leonard, 1939; Longhurst, 1959; Hynes, 1970). Although most benthic invertebrates are nonselective feeders (Cummins, 1973), ingesting a wide range of foods of appropriate dimensions, they fall into somewhat distinct categories of habit (adaptations for movement and maintenance of position) and feeding mechanism (Cummins, 1978). Habit categories are: swimmers, clingers, sprawlers, climbers, and burrowers; and feeding categories are: shredders (large particulate detritivores), collectors (small particulate detritus filterers and gatherers), scrapers (periphyton grazers), piercers (herbivores and car-

nivores), engulfers (carnivores), and parasites. Although each species probably has a different optimum microhabitat, species in the same habit and feeding functional groups might be expected to select similar microhabitats. If this is true their numbers in a set of sampling units should be positively correlated and cluster analysis should reveal distinct distributional groups corresponding to the functional groups. Extensive sampling of a single habitat, as in this study, allows a test of this prediction.

STUDY AREA

King's Creek is on the Konza Prairie Research Natural Area (KPRNA), a native tallgrass prairie located about 7 km south of Manhattan (Riley County) in the Flint Hills of Kansas. KPRNA was purchased by the Nature Conservancy in 1971 and 1977 and provided to Kansas State University for ecological research. The area encompasses 3487 hectares, 1637 of which are included in the King's Creek watershed (Fig. 1). A small portion of this area is riparian forest which extends upstream from the Kansas River along the stream margins. There are very few trees along most of the first and second order channels. Traveling downstream the vegetation in the immediate watershed gradually changes from prairie dominated by big bluestem (Andropogon gerardi), Indian grass (Sorgastrum nutens), and prairie cordgrass (Spartina pectinata) to forest dominated by hackberry (Celtis occidentalis), bur oak (Quercus macrocarpa), and chinquapin oak (Quercus muhlenbergia).

The area is characterized by shallow soils over sedimentary bedrock consisting of alternating strata of limestone and shale. Limestone outcroppings occur along the channel where the stream has cut through the bedrock strata. The streambed consists primarily of angular pieces of limestone and flint ranging in size from very fine sand (0.0625 mm) to large boulders (>256 mm). Silt and clay constitute a small percentage of the sediments, even in pools. A longitudinal profile of the stream beginning at the point marked with an asterisk in Fig. 1 is depicted in Fig. 2. The average gradient is 12.7 m km^{-1}, but there is a considerable decrease from the headwaters to the point where the stream leaves KPRNA. The stream has a typical riffle-pool arrangement with the frequency of pools increasing as gradient decreases.

Figure 1. King's Creek watershed on the Konza Prairie Research Natural Area.

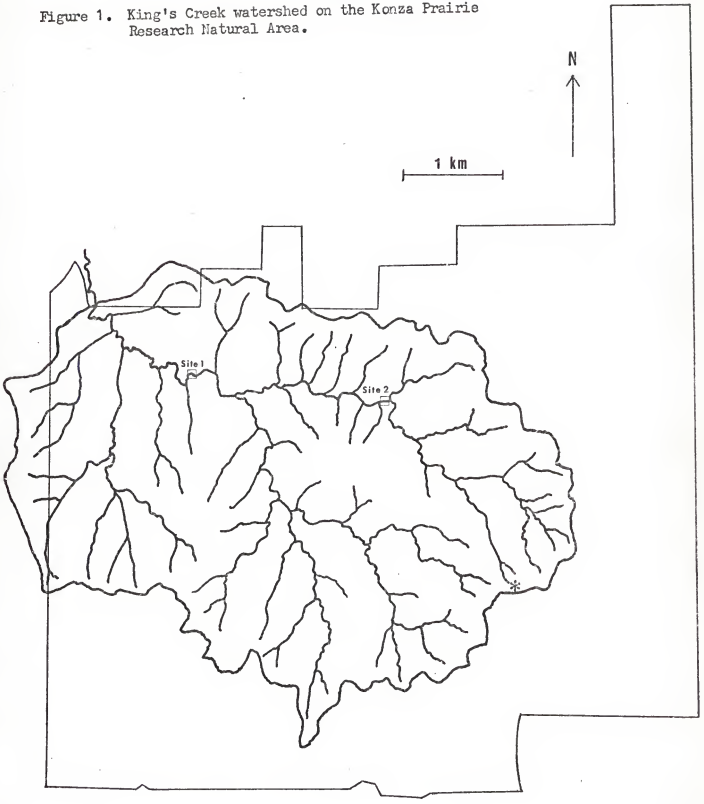
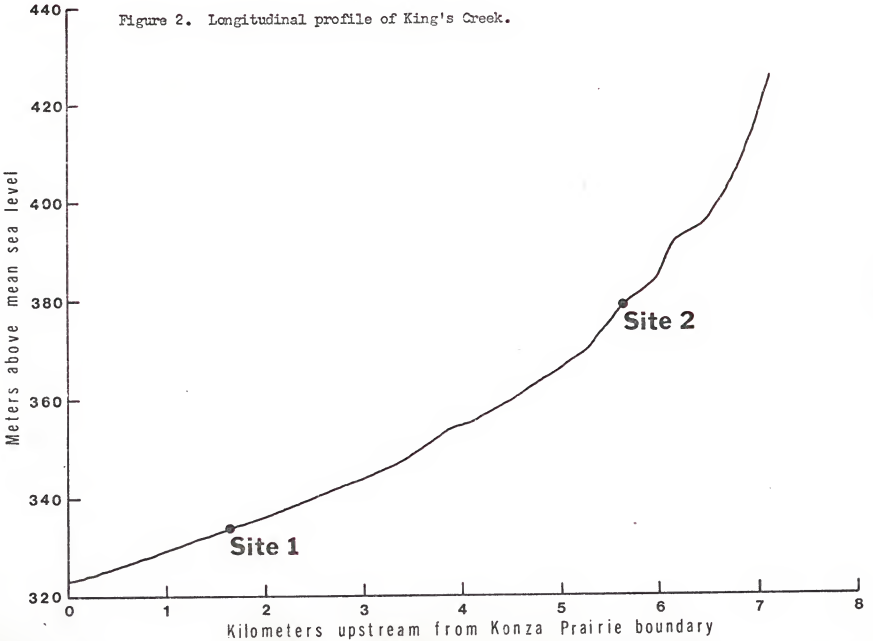


Figure 2. Longitudinal profile of King's Creek.



The portion of King's Creek within KPRNA is intermittant and although the period of record is short discharge has been extremely variable both seasonally and from year to year. The stream is spring fed and receives little surface runoff. Heavy rains, however, result in flash floods that scour the channel and cause major changes in the stream bed. The last major flood occurred in the summer of 1977 when the depth of water exceeded 5 meters in the lower part of the drainage. Piles of woody debris and sediments transported by the swift currents of the flood waters are evident far above the normally flowing channel. The stream flowed continuously below the second order channels from spring 1977 to summer 1978. The dry summer and fall of 1978 caused flow to cease in all but the lower kilometer of the main channel and a few small stretches below major springs or where the channel was impermeable. The stream remained in this condition from late August to the end of the year. Discharge during 1978 at the point where the stream leaves KPRNA varied from a high of approximately 200 liters sec^{-1} in spring to less than 5 liters sec^{-1} in fall.

The locations of the study sites are indicated in Figs. 1 and 2. Site 1 is a straight riffle about 40 meters long with quite uniform width, depth, and substrate. The canopy is closed over the stream at this point. At the time of sampling (15 June 1978) discharge was approximately 60 liters sec^{-1} and width, depth, and current velocity at the surface averaged 1.5 m, 10 cm, and 0.5 m sec^{-1}, respectively. Site 2 is a short riffle located 4.0 km upstream from site 1. Here the canopy is quite open. A spring enters a large pool immediately upstream. When site 2 was sampled (22 October 1978) flow at site 1 had ceased. Discharge, width, depth, and current velocity at site 2 were 0.6 liters sec^{-1}, 30 cm, 5 cm, and 5 cm sec^{-1}, respectively.

METHODS

Benthic invertebrate sampling

Both practical and theoretical considerations are involved in selecting the size of a sampler. For studying microdistribution a small sampler size is most suitable. The size should be related to the normal area of movement and the pattern of aggregation of the invertebrates under study (Cummins, 1975). It should be large enough so that the number of zero counts is small. Thus, the best size for studying distribution varies from species to species. For estimating density from a random distribution all sampler sizes are equally efficient (i.e., the relative amounts of sampling required for a given level of precision are equal). For aggregated distributions a small size is more efficient than a large one (Elliott, 1971). Less labor is required per sampling unit with a small sampler, so more units can be dealt with in the same amount of time. Small samplers, however, have greater perimeter error per unit area than large ones. The smallest size that can be used depends on how coarse the substrate is. In stony streams the sampler must be larger than most of the stones. The optimum size for this study was not obvious, so two sizes were compared. The area of the large stovepipe was 0.10 m^2, very close to that of the square foot Surber sampler (0.093 m^2). The small stovepipe was half this size (0.05 m^2).

The two stovepipe samplers were constructed of twelve-gauge steel rolled into cylinders and welded at the seams (all sampling equipment shown in Fig. 3). Both were 61 cm high. Teeth (1.3 cm long and spaced 5 cm apart) were cut into the bottom edge of each cylinder and bent alternately inward and outward at a slight angle to aid penetrating the substrate. Two holes were drilled opposite each other near the top edge so that an iron rod could be used to rotate the cylinders.

Figure 3. Photograph of stovepipe samplers, hand-operated pump, sorting tub, and Surber sampler.

The pump method was felt to be the most effective way to remove all invertebrates and fine material from the stovepipe samplers. A hand-operated bilge pump (Guzzler 600, Dart Union Co.) with a 2 inch hose was used for this purpose. A cloth tube filled with sand was packed around the outside of the stovepipe to restrict the flow of water under the sampler. In preliminary tests the pump frequently clogged with stones drawn through the hose. To alleviate this problem a ½ inch mesh screen was placed in the bottom of the sampler after scooping out the coarse substrate by hand. This allowed removal of the remaining fine material without drawing in particles so large as to clog the pump. Fifty strokes of the pump handle were found adequate to remove most silt and detritus, and presumably most of the invertebrates, from the small stovepipe. One hundred strokes were used with the large stovepipe.

After sampling in this manner the benthic invertebrates were contained within a large volume of substrate and water. To avoid transporting this large quantity of unsorted material back to the laboratory a sorting tub was devised for use in the field. The rectangular tub (46 cm x 61 cm) of galvanized sheet metal was constructed with a slanting bottom and an opening in the deep end (30 cm) leading to a 3.5 inch PVC pipe coupler. The coupler accepts a tube-shaped net with a short piece of PVC pipe attached at one end and the ring from a pint canning jar at the other. A removable ¼ inch mesh screen in front of the opening prevents particles larger than this from entering the net. The net is removable so the mesh size can be adjusted to suit the needs of the study. The jar is replaced for every sample. The first step of the sorting procedure is scooping the substrate from the stovepipe into a ½ inch mesh wire basket fitted in the sorting tub. The slurry of fine material and water is then pumped into the tub. The stones

in the wire basket are agitated and rinsed until clean and then removed from the tub. The remaining substrate is rinsed with stream water pumped through a 250μm mesh filter until the water is clear. Invertebrates, detritus, and fine inorganic particles are filtered from the water by the net and rinsed into the pint jar. The invertebrates in the jars may be hand-picked while alive or the contents may be preserved before picking. Thorough searching through the substrates from several samples taken with the small stovepipe revealed that the rinsing procedure was nearly 100% efficient for removing large invertebrates and greater than 90% efficient for removing Chironomidae larvae.

The sampler comparison was conducted in the riffle at site 1 on 15 June 1978. It was designed to maximize the probability of detecting differences in collection efficiency between samplers. A sample of twelve sampling units was collected with each stovepipe sampler and the Surber sampler. Although the riffle was quite uniform, the sampling units were grouped because high sampling variability was anticipated. Twelve points were selected randomly by means of a random numbers table and a group of three sampling units, one with each sampler, was collected starting at each point and moving in a line upstream. A space of 15 cm was left between the sampling units within the groups and one of the six possible orders in which the three samplers could be used was selected for each group by means of a random numbers table. Variability within the groups was expected to be less than that in the riffle as a whole, which would decrease the probability that differences among the density estimates of the samplers occurred by chance.

The Surber sampler used was equipped with a 1 mm mesh net. Large stones within the Surber frame were brushed to dislodge attached organisms. The

remaining substrate was thoroughly stirred to a depth of 10 cm with a garden trowel. The stovepipe samplers were bored into the substrate 10 cm and a 355 μm mesh net was used on the sorting tub. The Surber samples were also transferred to pint jars and all jars were filled with water, capped, and stored in the stream during sampling. They were then transported to the laboratory and refrigerated. The next day invertebrates were hand-picked from all samples and preserved for subsequent identification and enumeration.

Particulate organic matter sampling

A single sampling unit was collected with the small stovepipe sampler at site 2 on 22 October 1978 to evaluate the method's feasibility for estimating the quantity of organic matter in storage within the streambed. The stovepipe was bored into the substrate 10 cm and a 250 μm mesh net was used on the sorting tub. To collect particulate organic matter finer than this all water passing through the net in the rinsing procedure was collected in a large drum and the volume was brought up to 144 liters. A subsample of 1 liter was taken from this. After the invertebrates were hand-picked from the material in the jar the detritus was fractionated into the following size classes: greater than 2000 μm, 1000 - 2000 μm, 500 - 1000 μm, and 250 - 500 μm. The detritus less than 250 μm in the 1 liter subsample was fractionated into these size classes: 125 - 250 μm, 53 - 125 μm, and 0.45 - 53 μm. All detritus size fractions were dried in crucibles at 90°C, weighed, ashed at 550°C, for one hour and reweighed to determine ash-free dry weights. The small size classes were corrected for the concentrations of particulate organic matter in the rinse water.

Benthic invertebrate data analysis

Only the common taxa were included in the data analysis (except in

determining the number of taxa collected per sampling unit), because the precisions of estimates for the rare taxa were very low. The common taxa were arbitrarily defined as those with a mean of at least one per sampling unit for all three samplers. This eliminated all taxa with large numbers of zero counts. Before applying statistical methods the log (x+1) transformation was applied to the counts of the common taxa to fulfill assumptions of normality. The adequacy of this transformation for the data from this study is examined in Appendix B.

Two-way analyses of variance (Sokal and Rohlf, 1969), classified by sampler and group, followed by least significant difference (LSD) tests, were performed to determine if there were significant differences among samplers in the mean number of taxa per sampling unit and the mean density of each common taxon. The data for number of taxa were not transformed because they were approximately normally distributed. The counts of each common taxon for the small stovepipe and Surber samplers were adjusted to numbers per 0.10 m^2 before transformation so that the data for all samplers represented the same area of the stream bottom. Two-way analyses of variance were also performed classifying the data by sampler and order of the sampling unit within the group and by sampler and position across the stream's width (central 50% or either margin) to determine whether these two factors affected the numbers of any taxon collected. To examine the possibility of differences in selectivity between samplers the total numbers of each taxon were expressed as a percentage of the total fauna for each sampler.

Morisita's index of dispersion ($I_\delta = n(\Sigma(x^2) - x)/((\Sigma x)^2 - x)$) was used as a comparative measure of aggregation in the invertebrate distributions. It is a function of the number of sampling units, but if each sample con-

tains the same number of sampling units it is a good comparative index, because it is independent of the sample mean and total numbers (Elliott, 1971). The value of Morisita's index is one for a random distribution, less than one for a distribution more uniform than random, and greater than one for a distribution more aggregated than random. The maximum value, obtained when all individuals of a species are in the same sampling unit, is equal to the sample size (n=12 in this case). The significance of departure from randomness was assessed from the variance to mean ratio multiplied by (n-1), which is distributed approximately as Chi-square with n-1 degrees of freedom for a random distribution.

Correlation coefficients for all possible pairs of the common taxa were computed from the transformed data for each sampler to determine significant associations between taxa. The numerical taxonomy system of multivariate statistical programs (NT-SYS) (Rohlf et al., 1974) was used to perform cluster analyses on the correlation matrices by the unweighted pair-group method with arithmetic averages. The taxa are grouped in a hierarchical fashion with the level at which two groups connect determined by the mean of the correlation coefficients for all possible intergroup pairs of taxa. The first grouping in the analysis is between the two taxa with the highest correlation coefficient. Each subsequent grouping is determined by the highest correlation between any two remaining ungrouped taxa, any two groups already determined in the analysis, or any ungrouped taxon with any determined group. Cophenetic correlation coefficients (Sokal and Rohlf, 1962), the correlation coefficients between the elements of the correlation matrices and the corresponding cophenetic matrices, were computed to test for amounts of distortion in the cluster analyses. The cophenetic value for each pair of taxa is the level at which they are connected in the cluster

analysis. High cophenetic correlations indicate low distortion. The most distinct groups in each cluster analysis were found by subsets analysis. To be distinct by subsets analysis the lowest correlation coefficient between any two taxa within a group must be higher than the highest correlation coefficient between any taxon within the group and any taxon outside the group.

RESULTS

Benthic invertebrate fauna

The numbers of invertebrates found in the twelve sampling units taken with each sampler at site 1 are given in Tables 1 to 3. Counts of zero are left blank for clarity. Table 4 summarizes the data for all three samplers by giving density estimates (numbers/ m^2) for each taxon and the total fauna, and the mean number of taxa per sampling unit with each sampler. Standard deviations are given for all the means. The fauna is divided into thirty groups that do not necessarily correspond to species. These will be referred to as taxa for simplicity. The abbreviation sp. is used following a genus if it could not be identified further and there was no reason to suspect that more than one species was present.

The fauna was dominated by immature insects of which there were seventeen families representing seven orders. Odonata was represented by one individual of the family Coenagrionidae that was too small to identify further. Perlesta palida, the only species of Plecoptera, was present in low numbers. In the Ephemeroptera there were high densities of Stenonema tripunctatum and Choroterpes sp., moderate densities of Baetis sp., and two individuals of Caenis sp. Small larvae of Cheumatopsyche sp. were present in very high densities, dominating the Trichoptera. Polycentropus sp. and Chimarra sp. were present in low numbers. There were small numbers of larvae and adults of two genera of Dytiscidae (Acabus sp. and Bidessus sp.) and one genus of Elmidae (Stenelmis sp.) in the Coleoptera. The larvae and adults, although likely of the same species, were considered as separate taxa because of differences in morphology and ecology. Chironomidae dominated the Diptera and was the most numerous taxon collected. There were no doubt more than one species, but no attempt was made to separate them. The

Table 1. List of benthic invertebrates collected with the 0.05 m^2 stovepipe sampler at site 1.

Sampling unit number	1	2	3	4	5	6	7	8	9	10	11	12
Coenagrionidae	-	-	-	-	-	-	-	-	-	-	-	-
Perlesta palida	-	-	-	-	4	2	1	-	-	-	-	3
Stenonema tripunctatum	8	1	22	1	6	7	20	8	4	11	17	9
Choroterpes sp.	2	7	34	5	22	30	14	4	3	7	4	18
Baetis sp.	7	1	1	3	10	28	-	2	1	-	1	10
Caenis sp.	-	1	-	-	-	-	-	-	1	-	-	-
Cheumatopsyche sp.	30	-	41	5	185	209	1	23	-	1	-	104
Chimarra sp.	-	1	-	-	10	5	-	-	-	-	-	2
Polycentropus sp.	-	-	-	-	-	1	-	-	-	-	2	-
Agabus sp. (larvae)	-	-	-	-	-	-	-	-	-	-	-	-
Agabus sp. (adults)	-	-	-	-	-	-	-	-	-	-	-	-
Hydessus sp. (larvae)	-	4	1	-	-	-	-	-	1	2	3	1
Hydessus sp. (adults)	-	-	-	-	-	-	-	-	-	-	-	-
Stenelmis sp. (larvae)	-	-	-	-	1	2	2	-	-	1	-	2
Stenelmis sp. (adults)	3	1	-	-	-	1	-	-	-	-	-	-
Chironomidae (larvae)	62	117	43	75	41	120	32	20	71	26	18	62
Chironomidae (pupae)	10	6	6	9	4	6	3	3	2	1	1	1
Ceratopogonidae	2	4	-	3	-	1	4	5	2	-	-	4
Limnophora sp.	2	7	1	4	1	4	-	12	8	6	12	4
Hexatoma sp.	-	-	-	-	-	-	1	1	-	-	-	1
Simulium sp.	-	-	-	-	1	3	-	-	-	-	-	-
Sialis sp.	-	-	1	-	-	-	-	-	-	-	-	-
Asellus tridentata	3	-	-	1	7	3	-	2	-	1	2	-
Bactrurus hubrichti	2	-	4	-	-	-	-	-	-	-	-	1
Astascidae	1	-	-	1	-	-	-	1	2	1	4	-
Atractides sp.	10	1	1	5	-	9	1	2	7	4	2	10
Physa sp.	6	6	4	9	-	2	1	1	7	2	5	2
Ducesia sp.	-	-	1	-	-	-	-	1	-	-	-	-
Nais sp.	6	13	4	33	1	16	1	-	4	1	1	14
Nematomorpha	-	-	-	-	-	-	-	-	-	-	1	-
Total	154	170	164	154	293	449	81	85	113	64	73	248
Number of taxa	15	14	14	13	13	18	12	14	13	13	14	17

Table 2. List of benthic invertebrates collected with the 0.10 m^2 stovepipe sampler at site 1.

Sampling unit number	1	2	3	4	5	6	7	8	9	10	11	12
Coenagrionidae	-	-	-	-	-	-	-	-	1	-	-	-
Perlesta palida	-	-	-	-	1	-	2	-	-	-	-	-
Stenonema tripunctatum	28	5	29	6	18	18	63	7	5	20	86	22
Choroterpes sp.	18	7	32	14	2	46	20	15	10	6	16	11
Baetis sp.	8	2	5	-	15	24	1	2	2	1	1	6
Caenis sp.	-	-	-	-	-	-	-	-	-	-	-	-
Cheumatopsyche sp.	82	53	42	1	198	123	9	1	-	2	1	46
Chimarra sp.	-	-	-	1	5	1	-	-	-	-	-	-
Polycentropus sp.	-	-	-	-	3	-	-	-	1	1	-	-
Acabus sp. (larvae)	-	-	-	1	-	-	-	1	-	-	2	-
Acabus sp. (adults)	-	1	-	-	-	-	-	-	-	-	-	-
Bidessus sp. (larvae)	-	2	-	1	-	-	1	5	-	3	1	-
Bidessus sp. (adults)	-	-	-	-	-	-	-	-	-	1	-	-
Stenelmis sp. (larvae)	-	3	-	1	3	2	-	2	-	-	1	2
Stenelmis sp. (adults)	-	-	-	-	-	-	-	-	-	-	-	-
Chironomidae (larvae)	170	87	44	61	15	38	70	105	37	16	46	12
Chironomidae (pupae)	11	3	2	8	1	3	4	6	-	2	1	-
Ceratopogonidae	5	4	-	-	-	3	1	2	2	-	1	-
Limnophora sp.	5	5	6	3	2	17	2	23	11	6	18	6
Hexatoma sp.	-	-	-	-	-	1	1	-	-	-	-	3
Simulium sp.	-	-	-	-	3	-	-	-	-	-	-	-
Sialis sp.	-	-	-	-	-	-	-	-	-	-	-	-
Assellus tridentata	-	1	-	-	10	1	1	-	-	-	1	-
Isotrurus hubrichti	1	-	-	-	18	-	-	-	-	1	-	3
Astascidae	-	-	-	1	-	-	2	1	3	4	6	-
Atractides sp.	4	-	-	1	-	1	1	1	2	1	-	-
Physa sp.	5	13	-	16	-	1	4	5	-	6	-	7
Dugesia sp.	-	-	-	-	-	1	-	-	-	-	-	-
Nais sp.	3	4	1	3	1	6	19	17	1	2	2	2
Nematomorpha	-	-	-	-	-	-	-	-	-	-	1	-
Total	340	190	161	118	295	286	201	193	75	72	184	120
Number of taxa	12	14	8	14	15	16	16	15	11	15	15	11

Table 3. List of benthic invertebrates collected with the Surber sampler at site 1.

Sampling unit number	1	2	3	4	5	6	7	8	9	10	11	12
Coenagrionidae	-	-	-	-	-	-	-	-	-	-	-	-
Perlesta palida	-	-	1	-	-	-	-	-	-	-	-	-
Stenonema tripunctatum	13	3	18	-	21	19	28	5	9	2	5	5
Choroterpes sp.	6	7	32	2	16	40	2	12	9	-	4	2
Baetis sp.	11	-	-	1	6	7	-	4	2	-	1	2
Caenis sp.	-	-	-	-	-	-	-	-	-	-	-	-
Cheumatopsyche sp.	30	3	41	3	35	20	3	119	-	-	1	73
Chimarra sp.	-	-	2	-	-	-	-	-	-	-	-	-
Polycentropus sp.	-	-	1	-	-	-	-	-	-	-	-	-
Agabus sp. (larvae)	2	-	-	-	-	-	-	-	-	-	-	-
Agabus sp. (adults)	-	-	-	-	-	-	-	-	-	-	-	-
Ridessus sp. (larvae)	-	-	2	-	-	-	-	-	3	-	-	-
Ridessus sp. (adults)	-	-	-	-	-	-	-	-	-	-	-	-
Stenelmis sp. (larvae)	-	-	2	-	1	-	1	-	-	-	-	-
Stenelmis sp. (adults)	3	1	2	2	-	1	-	-	-	-	-	-
Chironomidae (larvae)	19	57	44	8	7	31	10	16	16	2	6	4
Chironomidae (pupae)	2	7	4	-	1	6	2	1	2	1	-	-
Ceratopogonidae	-	-	1	-	-	-	1	-	2	-	-	-
Limnophora sp.	5	5	4	2	-	6	2	11	9	3	-	11
Hexatoma sp.	-	-	-	-	1	-	-	-	-	-	-	-
Simulium sp.	-	-	-	-	-	1	-	2	-	-	-	1
Sialis sp.	-	-	-	-	-	-	-	-	-	-	-	-
Asellus tridentata	-	-	-	-	-	-	-	-	-	-	-	1
Bactrurus hubrichti	-	-	1	-	-	-	-	-	-	-	-	5
Astascidae	-	-	-	-	-	-	-	-	-	-	1	-
Atractides sp.	-	-	-	-	-	-	-	-	2	-	1	-
Physa sp.	28	29	10	4	4	23	3	6	-	1	-	8
Dugesia sp.	-	-	-	-	-	-	-	7	-	-	-	-
Nais sp.	7	3	16	5	-	3	3	4	1	-	5	1
Nematomorpha	-	-	-	-	-	1	-	-	-	-	-	-
Total	126	115	181	27	92	158	55	187	55	9	24	113
Number of taxa	11	9	16	8	9	12	10	11	10	5	8	11

Table 4. Mean density (numbers/ m^2) and standard deviation of each taxon with each sampler and mean number of taxa per sampling unit.

	0.05 m^2 Stovepipe		0.10 m^2 Stovepipe		Surber	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
Arthropoda						
Insecta						
Odonata						
Coenagrionidae	0	-	1	3	0	-
Plecoptera						
Perlidae Perlesta palida	17	28	2	6	1	3
Ephemeroptera						
Heptageniidae Stenonema tripunctatum	190	139	256	248	115	96
Leptophlebiidae Choroterpes sp.	250	223	164	122	118	136
Baetidae Baetis sp.	107	160	56	72	30	38
Caenidae Caenis sp.	3	8	0	-	0	-
Trichoptera						
Hydropsychidae Cheumatopsyche sp.	998	1497	465	618	294	394
Philopotamidae Chimarra sp.	30	61	6	14	2	6
Polycentropodidae Polycentropus sp.	5	12	4	9	1	3
Coleoptera						
Dytiscidae						
Dytiscinae Agabus sp. (larvae)	0	-	3	6	2	6
Agabus sp. (adults)	0	-	1	3	0	-
Hydroporinae Hidessus sp. (larvae)	20	27	11	16	4	11
Hidessus sp. (adults)	0	-	1	3	0	-
Elmidae Stenelmis sp. (larvae)	13	18	12	12	4	7
Stenelmis sp. (adults)	8	18	0	-	8	11
Diptera						
Chironomidae (larvae)	1145	687	584	456	197	185
Chironomidae (pupae)	87	62	34	34	23	25
Ceratopogonidae	42	38	15	17	4	7
Anthomyiidae Limnophora sp.	102	81	87	70	52	41
Tipulidae Hexatoma sp.	5	9	4	9	1	3
Simuliidae Simulium sp.	7	18	2	9	4	7
Neuroptera						
Sialidae Sialis sp.	2	6	0	-	0	-

Table 4. (continued)

	0.05 m^2 Stovepipe		0.10 m^2 Stovepipe		Surber	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
Crustacea						
Isopoda						
Asellidae Asellus tridentata	32	41	12	28	9	3
Amphipoda						
Gammaridae Bactrurus hubrichti	12	25	19	51	5	16
Decapoda						
Astascidae	17	24	14	20	1	3
Arachnida						
Hydracarina						
Hygrobatidae Atractides sp.	87	75	9	12	3	7
Mollusca						
Gastropoda						
Pulmonata						
Physidae Physa sp.	75	57	48	53	104	115
Platyhelminthes						
Turbellaria						
Tricladida						
Planariidae Dugesia sp.	3	8	1	3	6	22
Annelida						
Oligochaeta						
Plesiopora						
Naididae Nais sp.	157	194	51	62	43	47
Nematomorpha	2	6	1	3	1	3
Total	3413	2253	1862	856	1024	666
Number of taxa	14.2	1.7	13.5	2.4	10.0	2.7

larvae and pupae were placed in separate taxa. The Ceratopogonidae may also have been represented by more than one species. Other Dipterans were Limnophora sp., present in moderate densities, and Hexatoma sp. and Simulium sp., present in low densities. Neuroptera, the final order of insects, was represented by a single individual of the genus Sialis. Three orders of Crustacea were present in low densities. Only very young crayfish (Astascidae) were collected that could not be identified to genus. Adults in qualitative collections from King's Creek are of the genus Orconectes. Blind subterranean isopods (Asellus tridentata) and amphipods (Bactaurus hubrichti), usually found in caves, wells, and springs, were a surprising find in the riffle and possibly indicate the presence of a well-developed hyporheic fauna in the deep interstitial environment beneath the stream. Arachnids of the genus Attractides were in low abundance. Mollusca was represented only by snails of genus Physa. There were small numbers of planarians (Dugesia sp.) and moderate numbers of the small oligochaete Nais. Three horsehair worms (Phylum Nematomorpha) were collected.

Most sampling units contained less than half the total number of taxa. Eight taxa were present in fewer than five of the thirty-six sampling units. Only Chironomidae was present in all the sampling units. Stenonema tripunctatum and Choroterpes sp. were present in thirty-five units. Nine of the thirty taxa have means of at least one per sampling unit for all samplers and are included in the data analysis. These are Stenonema tripunctatum, Choroterpes sp., Baetis sp., Cheumatopsyche sp., Chironomidae larvae, Chironomidae pupae, Limnophora sp., Physa sp., and Nais sp. The standard deviations of the rare taxa are much larger in relation to the means than those of the common taxa (Table 4).

The numbers of the benthic invertebrates collected in the sample at

site 2 are given in Table 5. Seventeen taxa were collected, all of which were present in the samples at site 1. Density estimates based on one sampling unit are very imprecise but one very striking difference from the earlier samples was evident. Caenis sp. was the second most abundant taxon at site 2, whereas in all the samples at site 1 only two individuals were collected.

Sampler comparison

The results of the two-way analyses of variance performed on the transformed densities of the common taxa are given in Table 6. Differences among group means are significant ($P<.05$) for all taxa except Physa ($P=.11$) and Nais ($P=.42$). Thus, grouping the samples aided in detecting differences in efficiency among samplers because the within groups variance was small compared to the between groups variance for most taxa. The means for the first, second, and third sampling units within the groups are not significantly different ($P=.20$ to $.90$) for any taxon after removing the effects of sampler differences. By leaving 15 cm between the units within each group and moving upstream there appears to have been no interference of one sampling unit on the next.

The density estimates obtained with the Surber sampler are significantly ($P<.10$) less than those obtained with the small and large stovepipe samplers for seven and five taxa, respectively, and for total numbers. The small stovepipe yielded a significantly ($P<.10$) greater density than the large stovepipe for total numbers and two of the nine taxa. All other differences between sampler density estimates are nonsignificant ($P>.10$). For Chironomidae larvae and total numbers differences among all sampler means are significant ($P<.05$). For all three genera of mayflies (Stenonema, Choroterpes, and Baetis) and Limnophora the Surber sampler yielded signifi-

Table 5. List of benthic invertebrates collected with the 0.05 m^2 stovepipe sampler at site 2.

Coenagrionidae	6
Perlesta palida	1
Stenonema tripunctatum	2
Choroterpes sp.	18
Caenis sp.	91
Polycentropus sp.	12
Dytiscidae	1
Stenelmis sp. (larvae)	14
Stenelmis sp. (adults)	3
Chironomidae (larvae)	99
Ceratopogonidae	6
Limnophora sp.	5
Hexatoma sp.	11
Sialis sp.	1
Astascidae	1
Atractides sp.	7
Dugesia sp.	3
Nais sp.	1

Table 6. Significance levels for the two-way analyses of variance on transformed densities. (For the LSD tests **** indicates $P < .001$, *** indicates $P = .001$ to .01, ** indicates $P = .01$ to .05, * indicates $P = .05$ to .10, and NS indicates $P > .10$.)

Taxon	P for group differences in two-way analyses of variance	P for sampler differences in two-way analyses of variance	LSD tests for sampler means		
			0.05 m^2 Stovepipe	0.10 m^2 Stovepipe	Surber
Stenonema tripunctatum	0.0002	0.0099	20.67 NS	25.58 **	11.48
				***	
Choroterpes sp.	0.045	0.032	26.67 NS	16.42 *	11.84
				**	
Baetis sp.	0.0001	0.013	10.67 NS	5.58 *	3.05
				***	
Cheumatopsyche sp.	0.0001	0.58	99.83 NS	46.50 NS	29.42
				NS	
Chironomidae larvae	0.013	0.0001	116.17 ***	58.42 ****	19.73
				****	
Chironomidae pupae	0.0069	0.0002	8.67 ***	3.42 NS	2.33
				****	
Limnophora sp.	0.0091	0.10	10.83 NS	8.67 *	5.20
				*	
Physa sp.	0.11	0.23	7.50 NS	4.75 NS	10.41
				NS	
Nais sp.	0.42	0.13	15.67 NS	5.08 NS	4.60
				*	
Total numbers	0.0028	0.0001	341.33 **	186.33 ****	102.40
				****	

cantly (P=.001 to .10) lower densities than the stovepipe samplers, but the stovepipe estimates are not significantly different. The small stovepipe revealed a significantly ($P<.01$) higher density of Chironomidae pupae than the other two samplers, for which the difference is not significant. Only the difference between the small stovepipe and Surber sampler estimates is significant (P=.066) for Nais. No differences are significant for Cheumatopsyche and Physa. The mean numbers of taxa collected per sampling unit by the two stovepipe samplers are not significantly ($P>.40$) different, but the Surber sampler collected significantly ($P<.01$) fewer taxa than both stovepipes.

All of the common taxa except Stenonema and Physa exhibit a pattern in which the small stovepipe sampler yielded the highest density and the Surber sampler yielded the lowest density, although some of the differences were not significant. The precisions of density estimates for the rare taxa are low, but most follow the same pattern. Of the twenty-three taxa collected by every sampler seventeen show this pattern. If there were no differences in efficiency among the samplers an equal distribution of taxa among the six possible orders of means would be expected. Tested by Chi-square the observed pattern is highly significant ($P<.001$). Thus, overall, the small stovepipe removed the greatest number of benthic invertebrates per unit area and the Surber sampler removed the least.

The numbers of each taxon are expressed as a percentage of the total numbers for each sampler in Table 7. For all samplers the common taxa account for greater than 90% of the total numbers. The two stovepipe samplers yielded similar relative abundances for all taxa but Stenonema, which constitutes a considerably lower percentage with the small stovepipe. The Surber sampler exhibits two notable differences from the stovepipe samplers,

Table 7. The relative abundance (%) of each common taxon with each sampler.

Taxon	0.05 m^2 Stovepipe	0.10 m^2 Stovepipe	Surber
Chironomidae larvae	33.5	31.4	19.3
Cheumatopsyche sp.	29.2	25.0	28.7
Choroterpes sp.	7.3	8.8	11.6
Stenonema tripunctatum	5.6	13.7	11.2
Nais sp.	4.6	2.7	4.2
Baetis sp.	3.1	3.0	3.0
Limnophora sp.	3.0	4.7	5.1
Chironomidae pupae	2.5	1.8	2.3
Physa sp.	2.2	2.6	10.2
All other taxa	8.0	6.3	4.4
Total	100	100	100

a much lower Chironomidae larvae percentage and a much higher Physa percentage.

Table 8 gives an estimate of the amount of each size fraction of particulate organic matter stored within the streambed at site 2. The estimates represent the upper 10 cm of one square meter of the streambed. The total for all size classes is 1119 grams. The quantity of organic matter increases with each decreasing size class. The smallest class (0.45 - 53 μm) contains 71% of the total. The 53 - 125 μm and 125 - 250 μm classes contain 84% of the remainder.

Microdistributions and faunal associations

The values of Morisita's index are given in Table 9. The distributions of all taxa are significantly aggregated for all samplers ($P < .01$). Some taxa are clearly more aggregated than others. Baetis and Cheumatopsyche have consistently high values for all three samplers, whereas the values for Chironomidae larvae, Chironomidae pupae, and Limnophora are consistently low. The values for total numbers of invertebrates are generally lower than for most individual taxa. The index is quite constant among the samplers for Limnophora and total numbers. For other taxa there are considerable differences among samplers, but no consistent trend. For Baetis and Cheumatopsyche the index is similar for the large stovepipe and Surber samplers but higher for the small stovepipe, however, for Chironomidae larvae, Chironomidae pupae, and Physa the small stovepipe has lower values than the large stovepipe and Surber. Stenonema was most highly aggregated with the large stovepipe and Chloroperpes was most highly aggregated with the Surber sampler.

Correlation coefficients are consistently greater than 0.20 with all samplers for nine of the thirty-six possible pairs of common taxa. These are given in Table 10 with their levels of significance of difference from

Table 8. Estimates of particulate organic matter in storage at site 2.

Size Fraction (μm)	Ash-free dry weight (g/m^2 x 10 cm deep)	Percent
2000	6.5	0.6
1000 - 2000	10.1	0.9
500 - 1000	14.4	1.3
250 - 500	21.7	1.9
125 - 250	73.7	6.6
53 - 125	202.8	18.1
0.45 - 53	790	70.6
Total	1119	100

Table 9. Morisita's index of dispersion for the common taxa with each sampler.

Taxon	0.05 m^2 Stovepipe	0.10 m^2 Stovepipe	Surber
Stenonema tripunctatum	1.39	1.83	1.56
Choroterpes sp.	1.65	1.45	2.14
Baetis sp.	2.93	2.37	2.12
Cheumatopsyche sp.	3.05	2.60	2.62
Chironomidae larvae	1.31	1.42	1.76
Chironomidae pupae	1.26	1.63	1.66
Limnophora sp.	1.41	1.49	1.39
Physa sp.	1.23	1.95	2.15
Nais sp.	2.32	2.21	1.87
Total	1.39	1.19	1.38

Table 10. Correlation coefficients for pairs of taxa that were consistently associated (Numbers in parentheses are significance levels).

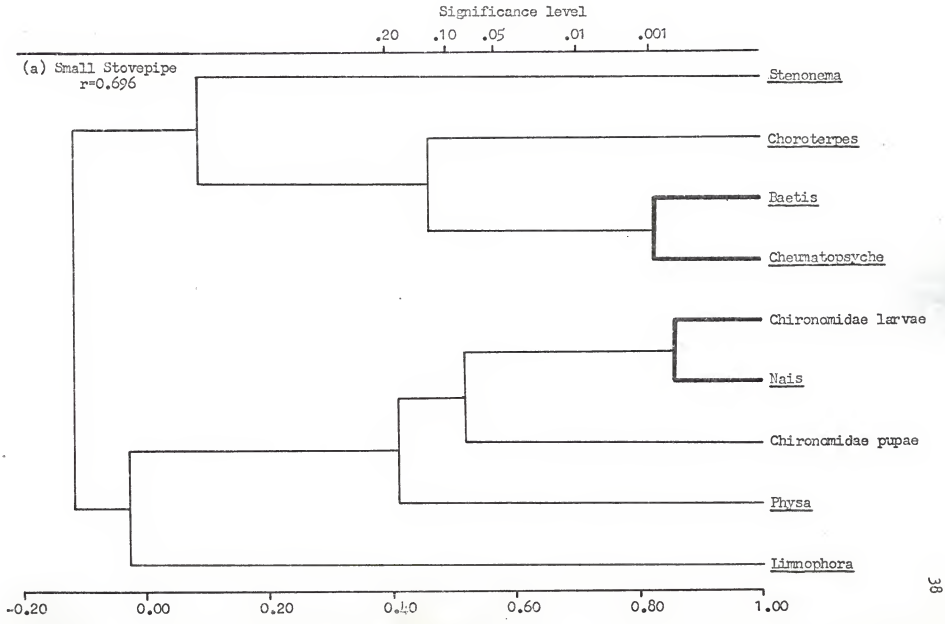
Taxon pairs	0.05 m^2 Stovepipe	0.10 m^2 Stovepipe	Surber	All samplers combined	Stovepipe samplers combined
Baetis - Cheumatopsyche	0.83 (0.0005)	0.82 (0.0012)	0.52 (0.086)	0.74 (0.0001)	0.83 (0.0001)
Chironomidae larvae - Chironomidae pupae	0.56 (0.061)	0.77 (0.0041)	0.82 (0.0012)	0.73 (0.0001)	0.68 (0.0001)
Chironomidae larvae - Nais	0.86 (0.0001)	0.52 (0.086)	0.61 (0.037)	0.58 (0.0001)	0.67 (0.0001)
Chironomidae larvae - Physa	0.38 (0.23)	0.28 (0.38)	0.62 (0.033)	0.20 (0.25)	0.31 (0.15)
Chironomidae pupae - Nais	0.48 (0.12)	0.54 (0.074)	0.22 (0.49)	0.43 (0.0091)	0.49 (0.017)
Chironomidae pupae - Physa	0.28 (0.38)	0.51 (0.093)	0.57 (0.054)	0.38 (0.023)	0.43 (0.038)
Nais - Physa	0.57 (0.054)	0.41 (0.19)	0.36 (0.26)	0.37 (0.027)	0.45 (0.028)
Stenonema - Choroterpes	0.32 (0.28)	0.28 (0.38)	0.56 (0.061)	0.47 (0.0043)	0.36 (0.087)

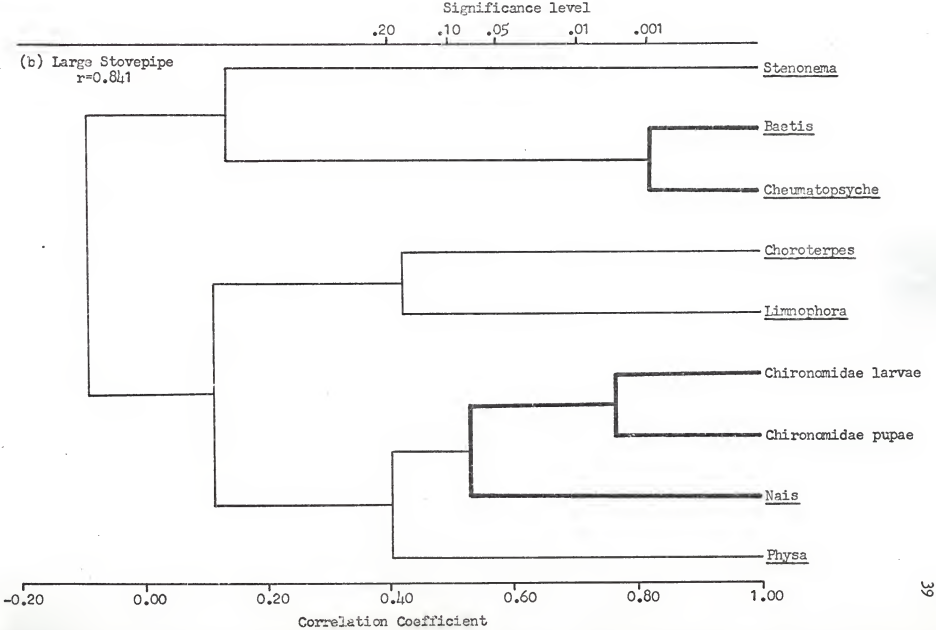
zero. Other pairs are significantly correlated with one sampler but far from significance for the other two. The coefficients for the two stovepipe samplers generally compare more closely to each other than to those for the Surber sampler. The only significant negative correlations are for the pairs Stenonema - Chironomidae larvae (r=-0.645) and Stenonema - Nais (r=-0.604) with the small stovepipe sampler. Limnophora showed no significant correlation with any taxon for any sampler.

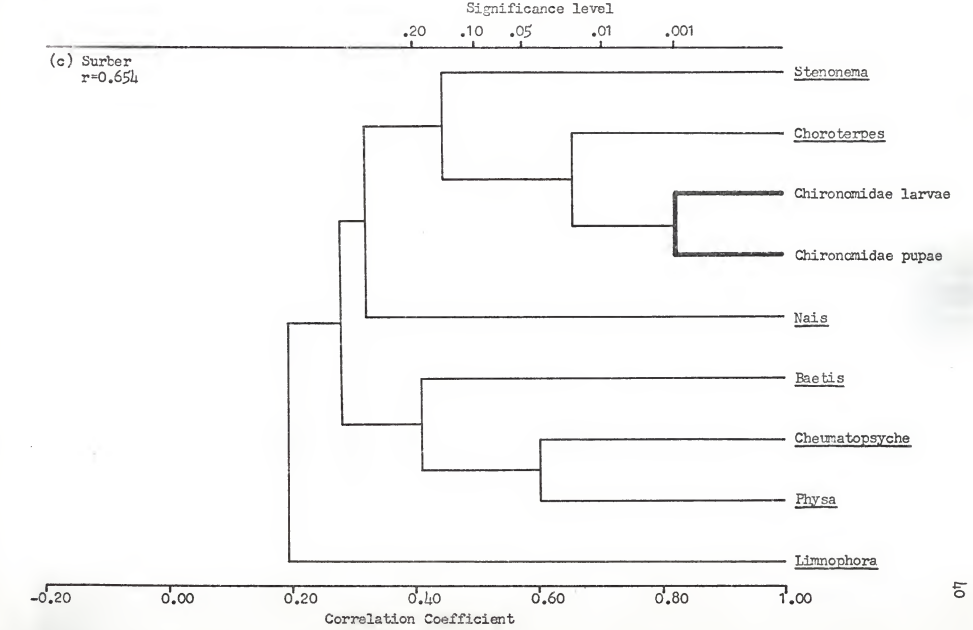
With a small sample size correlation coefficients must be high to be significantly different from zero. To increase sample size the data for all samplers were combined. The data for the two stovepipe samplers were also combined because their correlation coefficients are similar. The level of correlation necessary to meet the 5% level of significance is lowered from 0.576 for n=12 to 0.404 for n=24 and 0.330 for n=36. Table 10 also includes the correlation coefficients and levels of significance for the sampler combinations. The highest correlation coefficients for the combined data are for those pairs that are consistently high for all samplers. The most strongly correlated pairs are Baetis - Cheumatopsyche, Chironomidae larvae - Chironomidae pupae, and Chironomidae larvae - Nais.

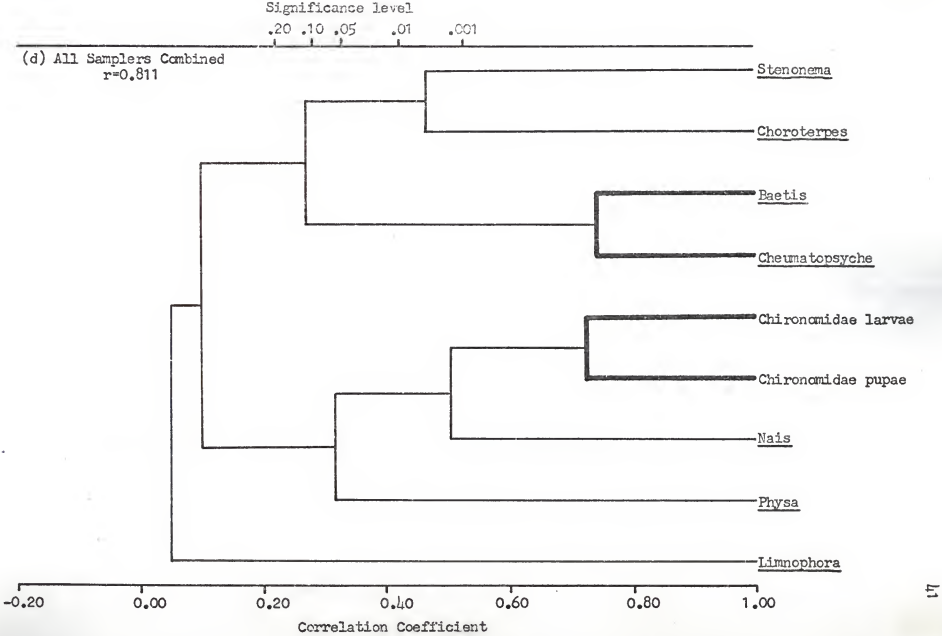
The results of the cluster analyses based on the correlation matrices for each sampler separately, all samplers combined, and the stovepipe samplers combined are presented as dendrograms in Fig. 4. The lower scales give the levels of correlation for the connections in the dendrograms. The upper scales give the significance levels corresponding to the correlation coefficients on the lower scales for the sample size of each dendrogram. These levels give some indication of the portion of each dendrogram that is unlikely to have resulted from chance associations. The connections made by bold lines signify those groups obtained by subsets analysis. Each of

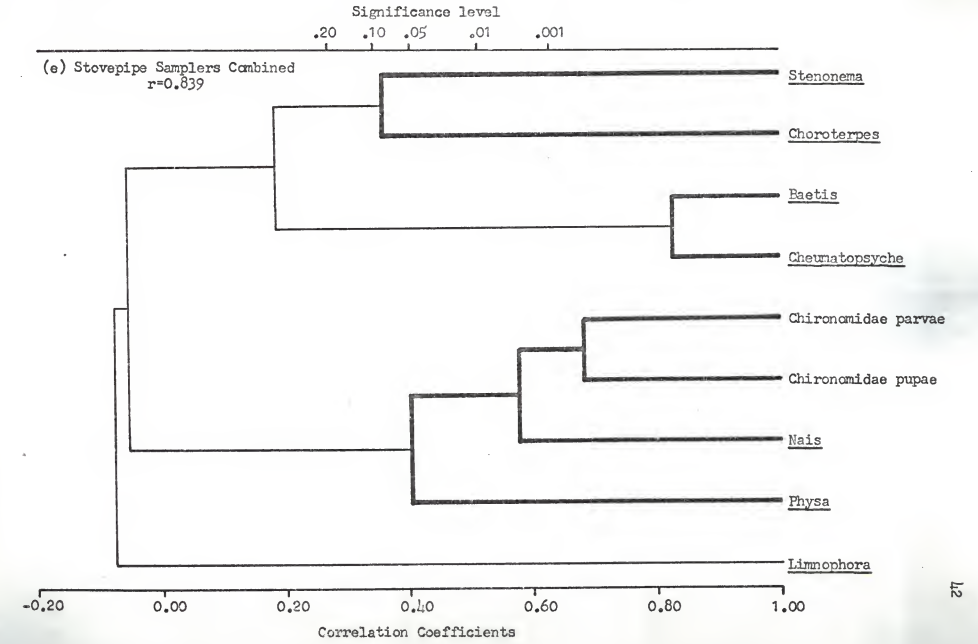
Figure 4. Dendrograms for the cluster analyses on the correlation matrices for (a) the small stovepipe sampler, (b) the large stovepipe sampler, (c) the Durber sampler, (d) all samplers combined, and, (e) the stovepipe samplers combined.


Significance level
.20
.10
.05
.01
.001
(a) Small Stovepipe
r=0.696
Stenonema
Choroterpes
Baetis
Cheumatopsyche
Chironomidae larvae
Nais
Chironomidae pupae
Physa
Limnophora
-0.20
0.00
0.20
0.40
0.60
0.80
1.00
Correlation Coefficient


Significance level
.20
.10
.05
.01
.001
(b) Large Stovepipe
r=0.841
Stenonema
Baetis
Cheumatopsyche
Choroterpes
Limnophora
Chironomidae larvae
Chironomidae pupae
Nais
Physa
-0.20
0.00
0.20
0.40
0.60
0.80
1.00
Correlation Coefficient


Significance level
.20
.10
.05
.01
.001
(c) Surber
r=0.654
Stenonema
Choroterpes
Chironomidae larvae
Chironomidae pupae
Nais
Baetis
Cheumatopsyche
Physa
Limnophora
-0.20
0.00
0.20
0.40
0.60
0.80
1.00
Correlation Coefficient


Significance level
.20 .10 .05 .01 .001
(d) All Samplers Combined
r=0.811
Stenonema
Choroterpes
Baetis
Cheumatopsyche
Chironomidae larvae
Chironomidae pupae
Nais
Physa
Limnophora
-0.20
0.00
0.20
0.40
0.60
0.80
1.00
Correlation Coefficient


Significance level
.20
.10
.05
.01
.001
(e) Stovepipe Samplers Combined
r=0.839
Stenonema
Choroterpes
Baetis
Cheumatopsyche
Chironomidae parvae
Chironomidae pupae
Nais
Physa
Limnophora
-0.20
0.00
0.20
0.40
0.60
0.80
1.00
Correlation Coefficients

these groups is very distinct from the rest of the fauna, suggesting that all of its members are distributed by the same causal mechanism. The cophenetic correlations are given for each dendrogram. The large stovepipe sampler has the highest cophenetic correlation (r=0.841), followed closely by the stovepipe samplers combined (r=0.839) and all samplers combined (r=0.811). For the small stovepipe and Surber samplers they are lower (r=0.696 and r=0.654, respectively), indicating greater distortion of the correlation matrices in the cluster analyses.

The dendrograms for the two stovepipe samplers compare closely. In both cases Chironomidae larvae, Chironomidae pupae, Nais, and Physa are grouped together although the order in the hierarchy differs. Within this group Chironomidae larvae, Chironomidae pupae, and Nais form a distinct grouping by subsets analysis with the large stovepipe, but only the first-order Chironomidae larvae - Nais grouping is distinct with the small stovepipe. Baetis and Cheumatopsyche form a distinct group with both samplers. The two stovepipe dendrograms differ mainly in the grouping of Choroterpes and Limnophora.

The Surber sampler dendrogram differs considerably from those of the stovepipe samplers. The only distinct group by subsets analysis is Chironomidae larvae - Chironomidae pupae. Nais and Physa are not associated with the Chironomidae larvae - Chironomidae pupae group and the first-order Baetis - Cheumatopsyche group is lacking. The major differences between the Surber and stovepipe dendrograms are caused by the high correlations between Cheumatopsyche and Physa (r=0.602) and Choroterpes and Chironomidae larvae (r=0.740), which are very low or slightly negative with the stovepipe samplers. The high Cheumatopsyche - Physa correlation causes Physa to group with Cheumatopsyche rather than the Chironomidae larvae- Chironomidae pupae

group and causes Baetis to group with Cheumatopsyche at a lower level. The high Choroterpes - Chironomidae larvae correlation causes Nais to group with the Chironomidae larvae - Chironomidae pupae group at a lower level than Choroterpes and Stenonema.

Although the levels differ slightly, the network of groupings in identical in the dendrograms for all samplers combined and the stovepipe samplers combined. They compare closely to those for the large and small stovepipes separately. The portion of the dendrogram unlikely to have resulted from chance associations is greatest with all samplers combined, but by excluding the Surber sampler more groups are distinct by subsets analysis. With the all sampler combination the Baetis - Cheumatopsyche and Chironomidae larvae - Chironomidae pupae groups are distinct. With the stovepipe sampler combination the Stenonema - Choroterpes group and the entire Chroonomidae larvae - Chironomidae pupae - Nais - Physa group are distinct along with the Baetis - Cheumatopsyche group. Limnophora can be considered to be a distinct group with one member. All the distinct groups of the stovepipe sampler combination but Stenonema - Choroterpes have within group connections below the 5% level of significance. The Stenonema - Choroterpes group with the all sampler combination, although not distinct, is connected below the 1% level of significance.

The cluster analysis on the stovepipe data therefore indicates that at the time the riffle at site 1 was sampled the common taxa were associated in four quite distinct groups: the Stenonema - Choroterpes group, the Baetis - Cheumatopsyche group, the Chironomidae larvae - Chironomidae pupae - Nais - Physa group, and the Limnophora group. The patterns of aggregation support these groups. Baetis and Cheumatopsyche are both very highly aggregated and more variable with small sampler size. Chironomidae larvae,

Chironomidae pupae, and Physa are all less highly aggregated and more variable with large sampler size. Stenonema and Choroterpes had similar intermediate levels of aggregation. Limnophora was the only taxon whose distribution was affected by position across the stream's width.

Various sources were used to place the taxa of each group in the habit and feeding mechanism categories of Cummins (1978) (Table 11). The cluster analysis groups correspond quite well to these categories. Both Stenonema and Choroterpes have flattened morphologies and cling to the under surfaces of rocks. They feed by sweeping and scraping algae and detritus from surfaces. Most lotic Chironomidae burrow in the substrate and construct discrete tubes, feeding primarily on fine detritus. They generally pupate within their burrows, the pupal stage lasting only a few days (Oliver, 1971). Nais is also a burrower and detritus feeder. Of the common taxa Limnophora is the only predator and it is in a group by itself. The associations that do not fit well with the functional group categories are the association of Physa with Chironomidae larvae, Chironomidae pupae, and Nais and the association of Baetis with Cheumatopsyche.

Table 11. Habit and feeding mechanism categories for the taxa of each group determined by cluster analysis.

Cluster analysis groups	Taxon	Habit category	Feeding mechanism category
Group 1	Stenonema	Clingers (flattened)	Collectors (gatherers), scrapers
	Choroterpes	Clingers (flattened)	Scrapers, collectors (gatherers)
Group 2	Baetis	Swimmers, clingers	Collectors (gatherers), scrapers
	Cheumatopsyche	Clingers (fixed retreat)	Collectors (filterers)
Group 3	Chironomidae larvae	Generally burrowers (tube dwellers)	Generally collectors (gatherers)
	Chironomidae pupae	Inactive	Nonfeeding
	Nais	Burrowers	Collectors (gatherers)
	Physa	Clingers, climbers	Scrapers collectors (gatherers)
Group 4	Limnophora	Burrowers	Engulfers (predators)

DISCUSSION

Sampler comparison

The conditions of depth, current, and substrate at site 1 were nearly ideal for proper functioning of the Surber sampler. Invertebrates were carried into the net well with minimal backwash, little inorganic material entered the net, and there was no erosion around the frame. Thus the stovepips samplers were clearly superior in collection efficiency under conditions in which the Surber sampler efficiency was maximal. The stovepipe samplers are efficient under a wide range of conditions. The Surber sampler is completely ineffective at low current velocities as at site 2, where the small stovepipe sampler functioned very well. The Surber cannot be used to collect the substrate for analysis and only rough estimates of particulate organic matter larger than the mesh of the net are possible. The method for collection of particulate organic matter with the stovepipe samplers added a few minutes per sampling unit but seemed to be very effective. The results indicate that a very large proportion of the organic matter stored within the streambed is of very small particle sizes, which have been neglected by many studies that have examined detritus concentrations in the substrate.

The major advantages of the Surber sampler were its compactness and speed and ease of operation. The stovepipe method involves several pieces of heavy equipment, which is definitely a disadvantage if it is necessary to walk long distances. Only one operator was required for the Surber and each sampling unit was collected in five to ten minutes. The stovepipe method worked best with three to four operators and required fifteen to twenty minutes per sampling unit. The Surber sampler is of value in preliminary sampling to get a quick picture of densities and relative abundan-

ces of the common taxa, but for quantitative estimates of density, biomass, and production and for studying distribution the advantages of the stovepipe sampler clearly outweigh the disadvantages.

The overall underestimation of density by the Surber sampler was probably due mainly to incomplete removal of the fauna from the substrate. Care was taken to sample to the same depth with all samplers, but rinsing the substrate within the sorting tub was much more efficient for removing invertebrates and detritus than stirring it within the stream. This source of error probably affected all taxa about equally except for perhaps Physa. The much higher relative abundance of Physa with the Surber sampler may indicate a shortcoming of the sorting tub. It was designed to separate low density organic material from the dense substrate. Dense invertebrates like Physa may be more efficiently separated by the swift current of the stream. The lower relative abundance of Chironomidae with the Surber sampler is probably the result of many of the small larvae passing through the larger mesh size of the Surber net. Decreasing the mesh size results in greater backwash with the Surber sampler, but has no effect on the sorting tub except for slightly increasing the time required for the sorting procedure.

Although for many taxa the differences between the density estimates of small and large stovepipes were not significant, the small stovepipe was more efficient overall. Since the samples were collected in exactly the same way the most likely explanation is that the sorting procedure was less efficient with the large stovepipe. The volume of substrate collected with the small stovepipe was more manageable in the sorting tub and easier to rinse free of silt and detritus. A larger sorting tub would probably increase sorting efficiency for the large stovepipe sampler . The greater

relative abundance of Stenonema with the large stovepipe is difficult to explain since the other taxa, including the mayflies, were collected in similar percentages. Two of the large stovepipe sampling units contained more than twice as many Stenonema as all other sampling units with all samplers (Tables 1 to 3). These abnormally high concentrations resulted in both the high relative abundance and high index of dispersion of Stenonema with the large stovepipe. Besides being more efficient the small stovepipe collected as many taxa per sampling unit, required less time to collect and sort each sample, and gave density estimates as precise as those for the large stovepipe. The large stovepipe was easier to bore into the substrate because of its greater weight and larger basal area. No stones were encountered larger in area than the small stovepipe in sampling the riffle at site 1. In areas like this the small sampler size appears superior but for sampling areas with coarser substrates the larger size would be preferable.

The stovepipe samplers were clearly more efficient than the Surber sampler, but the proportion of the total fauna collected by the stovepipes is unknown. Although there is no way to be sure how the counts obtained compared with the actual numbers present, the rinsing procedure with the small stovepipe appeared to be at least 90% efficient and it would seem that few invertebrates within the area of the cylinders could escape transfer into the sorting tub. The total invertebrate densities and number of taxa in this study were quite low compared to most published studies, but this does not necessarily indicate that the sampling methods were inefficient relative to other studies, because invertebrate faunas vary greatly from stream to stream and spatially and temporally within a single stream. The low densities obtained represent only a single riffle of a particular intermittant prairie stream at one point in time and could be due to many causes

other than sampler inefficiency. The efficiencies of the stovepipe samplers can perhaps be best judged by comparing the densities collected by them to that collected by the Surber sampler, for which the efficiency relative to total numbers has been estimated. Kroeger (1972) found that 10 cm deep substrate samples collected from a riverbed below a reservoir immediately after the flow of water had been stopped contained 3.6 times the density of invertebrates collected with a Surber sampler in the same area when the water was flowing. A drift net and migration trap showed no movement of the fauna with the receding water and the substrate samples were searched very carefully, so they likely represented the actual densities very closely. In this study the small and large stovepipe samplers, respectively, collected 3.3 and 1.8 times the number of invertebrates collected per unit area by the Surber sampler. This suggests that the small stovepipe estimates closely approached the actual densities in the stream.

Microdistributions and faunal associations

When studying the distribution of organisms with a quadrat-type sampler the results are influenced by the size of the sampler. The quadrat is merely an arbitrary area of the habitat rather than a discrete natural unit with some biological significance. For aggregated populations the variance is greatest when sampler size corresponds to the average size of clumps of organisms (Elliott, 1971). If sampler size is very small or large in relation to the scale of aggregation the distribution will appear random or uniform depending on whether the clump size is constant or variable and how the organisms within the clumps and the clumps themselves are distributed. Aggregation was detected by both sampler sizes for all the common taxa in this study, suggesting that the scale of clumping was not very small or large in relation to the range of sampler sizes used. Examination of the

data shows that the high and low counts appear to be quite randomly distributed among the sampling units for each sampler; thus the variation in the results do not reflect a distinct large scale habitat difference. The fact that differences among group means are significant for most taxa shows that aggregation can also be detected on a scale large enough to include three sampling units, but since variation within these groups is also high the sampler sizes are probably nearer the scale of clumping. Differences in the level of aggregation detected by different sampler sizes may be related to the scale of clumping in the populations. Taxa with lower indices of dispersion for the small stovepipe than the larger samplers (Chironomidae larvae, Chironomidae pupae, and Physa) may be clumped on a scale nearer 0.10 m^2 than 0.05 m^2. Taxa like Baetis and Cheumatopsyche may be clumped on a scale nearer the smaller area. The scale of clumping depends on the scale of heterogeneity in the factor causing the clumping and the scale of response to the factor by the animals. Differences in the scale of clumping between taxa can be expected since the invertebrates differ in size, mobility, and the factors to which they are responding. The range of sampler sizes used seems to be near the average clump size for the invertebrates within this riffle, and thus near the optimum size for studying microdistribution. Although all benthic invertebrates are mobile to some degree their short term distributions are probably fairly stable on this scale.

The best sampler size for measuring association between taxa by correlation of numbers is the size that best detects aggregation since a large range of densities will be sampled. The sampler sizes in this study should therefore be effective for detecting microdistributional associations of taxa. The associations must be interpreted in terms of the range of habitats sampled. If the whole stream was sampled all of the common taxa of

this study would probably be strongly associated as riffle taxa. Since a uniform riffle was sampled the associations represent microhabitat associations. Associations should be best detected with samplers that most nearly collect all of the invertebrates within each sampling unit, thus the stovepipe dendrograms are probably more reliable than the Surber dendrogram. The Surber dendrogram definitely shows least separation of the major groups. The slopes of the regression of one taxon on another will differ in some cases between the Surber and stovepipe samplers because the Surber collected some taxa in different proportions than the stovepipes. Combining the data in these cases could decrease the correlation. This effect is obvious for the Chironomidae larvae - Physa pair, for which the correlation coefficient for all samplers combined is considerably less than all the single sampler correlations. The dendrogram for the stovepipe samplers combined is probably most reliable, despite the fewer degrees of freedom than with all samplers combined, because the stovepipe samplers had similar results and were more efficient than the Surber sampler.

If the distribution of Chironomidae larvae is at all stable the larvae and pupae should be highly associated. The high Chironomidae larvae - Chironomidae pupae correlations for all samplers suggest that the methods do detect real associations. The taxa appeared to group on the basis of feeding mechanisms and modes of existance with two exceptions. Physa seems to have little in common with the burrowers of the group (Chironomidae and Nais). It is the most weakly associated member of the group and may represent a chance association. Baetis and Cheumatopsyche are also quite different but form the most highly associated group in the study ($P < .0001$ for both combinations of samplers). Although they are in different habit and feeding categories they do have some other similarities. Both are among

the few aquatic insects whose terrestrial adults enter the water to oviposit. Most individuals of both taxa were quite small, so the association could be due to selection of similar sites for oviposition. Another similarity is that both have a direct current requirement. Cheumatopsyche is a net-spinning caddisfly that captures its food from flowing water. Baetis is a streamlined swimming mayfly with high oxygen requirements that is usually found on top of rocks in the highest current velocities (Rabeni and Minshall, 1977).

Every sampling unit within the riffle at site 1 was probably potentially available habitat for every taxon. Negative associations would be expected only if one taxon behaviorally excluded another or if the environmental factors determining distribution were negatively correlated. The lack of negative correlations suggests that neither of these situations were occurring in this study. The groups determined by cluster analysis were independently distributed. Each taxon may tend to concentrate where its food supply is densest, thereby obtaining the most food per unit time. The food resources for the different functional groups of feeders may have been independently distributed, resulting in the independently distributed functional groups of invertebrates. Benthic invertebrates seem to partition food mainly by the methods they use to obtain it and the microsites in which they feed rather than by qualities of the food. Streams are unstable environments with a low diversity of food types but they are physically very heterogeneous. The coexistence of a large number of species may be possible primarily because of microhabitat specialization.

The relationships suggested by the data from this study were very likely real in this particular instance, but they may not be general to other streams, other habitats within this stream, or even this habitat at

other times of the year. The composition, density, and diversity of the fauna, life history stages of the species present, and complexity and stability of the habitat are probably all important in determining the distributional patterns of the populations present. Intraspecific and interspecific competition and predation may vary in importance depending on the circumstances. Catastrophic influences, such as floods, probably eliminate any natural grouping of the fauna for some time. Combining the approach used in this study with the study of factors related to the distribution of benthic invertebrates in streams may help to elucidate the causal mechanisms of small scale community structure under different conditions.

APPENDIX A

Macan (1958) recognized five categories of methods for sampling benthic invertebrates in swift, stony streams: (1) collection by hand; (2) colonization of units of natural or artificial substrate; (3) boxes or cylinders that enclose an area of the stream bottom; (4) stationary nets into which dislodged organisms are washed; and, (5) shovel samplers that are pushed through the substrate. These categories will be used in discussing the advantages and disadvantages of the major types of methods. In streams with substrates of silt or sand samplers such as grabs, dredges, and corers can also be used but their use is very limited in high gradient streams.

Most hand collection methods involve lifting individual stones from the stream. Standardized methods of hand collection, such as five minute collections of stones in front of a net (Macan, 1958), have been used for rough faunal comparisons but are poor quantitative methods. Errors are introduced through variation in the area of habitat sampled, subjective bias by the collector, and selectivity for certain taxa. The only advantage to this method is its speed.

Trays filled with natural substrate were first used by Moon (1935, 1940) to investigate the movements of the benthic fauna in the littoral zone of a lake. Wone and Wickliff (1940) examined the effects of substrate particle size and the surrounding habitat on the colonization of substrate filled baskets in a stream. An artificial substrate sampler of hardboard plates was designed by Hester and Dendy (1962) for use as a standard sampler in water quality investigations. A wide variety of substrate colonization samplers have been devised since. They have been especially appealing to investigators of benthic invertebrates as indicators of water quality because results are often less variable than with conventional sampling

methods (Crossman and Cairns, 1974). However, as Cummins (1962, 1966, 1975) points out, colonization samplers do not necessarily provide quantitative estimates for the fauna within the surrounding stream bottom. They are most valuable for use in controlled experiments examining the effects of different variables on selective colonization (Egglishaw, 1964; Coleman and Hynes, 1970; Townsend and Hildrew, 1976; Rabeni and Minshall, 1977).

A shovel sampler consists of a cutting edge in front of a frame with netting that is pushed down into the substrate and upstream for a fixed distance (Allen, 1940; Macan, 1958). A coarse net collects stones and gravel and prevents them from entering and damaging a fine net. Such samplers can be adapted for use in deep water (Usinger and Needham, 1956), but the depth of penetration into the substrate is limited. Shovel samplers do not work well on rough stream bottoms and considerable losses of organisms can occur around the mouth of the net if the current velocity is too high or low because the substrate is disturbed greatly.

The simplest method involving the use of a stationary net is standardized kicking upstream from a hand held net (Hynes, 1970). The chief advantage of this method is its speed. Morgan and Egglishaw (1965) found that it yielded quite consistent results, but Frost et al.(1971) evaluated the technique and found that less than 20% of the fauna was collected. The results were affected by many factors, including duration of sampling, kicking intensity, complexity of community, behavior of fauna, net mesh, and current velocity. The method cannot be considered strictly quantitative. The Surber sampler (Surber, 1937) is a more quantitative version of the same basic method. A square foot frame with sides marks an area upstream from a net. The substrate within the frame is thoroughly brushed and disturbed to dislodge organisms which are then carried into the net by the

current. The Surber sampler has become the most widely used stream bottom sampling method. Little equipment is required, samples can be taken rapidly, and preliminary sorting is accomplished right in the stream. There are also numerous drawbacks to the method. If there is little or no current organisms are not washed into the net. If current velocity is high organisms are lost by backwash around the edges. The finer the mesh of the net the more serious the backwash problem. With a coarse net many small invertebrates pass through. Other sources of error are loss of organisms under the frame, entrance of drifting organisms into the net, incomplete removal of the fauna from the substrate, edge errors in coarse substrates, erosion around the frame in swift currents, and limitations concerning the depth of water and depth within the substrate that can be sampled.

The Surber sampler has been modified in various ways to overcome some of these difficulties. Hess (1941) designed a cylindrical sampler with a base of 3/4 inch strap iron that could be turned a short distance into the bottom to prevent escape of organisms under the frame. The front of the cylinder was constructed of 1/6 inch hardward cloth to prevent entrance of material from upstream and the rear was made of canvas with an opening leading to a fine net. The backwash problem was reduced with these modifications. Waters and Knapp (1961) improved this design further by enclosing the entire cylinder with 471 μm mesh netting, and using a removable collection bag at the end of the net. Lane (1974) prevented the escape of small invertebrates and reduced the backwash problem by using a Surber sampler with two nets, the inner net of 1 mm mesh and the long outer net of 250 μm mesh. Screen-bottomed catch bottles were attached to the ends of both nets. Mundie (1971) utilized removable double nets (600 μm and 50 μm) on a streamlined floorless box sampler with a narrow adjustable inlet at the upstream

end. The sampler is placed on the bottom and a shoulder of gravel is built up around the outside. The current entering the sampler can be controlled and all material coarser than 50 μm can be removed up to depths of 10 to 30 cm.

Other box samplers have been devised that do not make use of the current to wash animals into a net. Needham (1934) pushed a square foot box into the streambed, washed off enclosed rocks in a bucket, and sieved the enclosed water after stirring the finer sediments. Whitley (1962) used a similar approach for sampling mud-bottomed streams. A sheet metal cylinder was pushed into the bottom, water was baled out, and the substrate scooped into containers. Both of these methods are of limited application in stony streams. Coffman et al. (1971) applied this idea to riffle habitats by using a plexiglass box with a base to which foam rubber was attached. Two collectors kneeled on the flange on opposite sides of the sampler, shutting off the current. Sediments and invertebrates were removed to a depth of 5 cm by hand, with a trowel, and with a fine mesh dip net. Some fine material and small invertebrates that settle into the interstices of the substrate below are missed. Cummins (1964) turned an 8.5 cm diameter cylinder into the substrate, forced a steel plate under it, and removed the entire contents. This is not practical for a larger sampler. Wilding (1940) described a brass cylinder sampler (1 ft^2) with teeth attached to the lower margin to aid in penetration of stony stream bottoms. Coarse materials were removed and placed in a container. The remaining material was agitated and a closely fitting perforated cylinder (0.04 mm holes) with a rotary leaf valve in the bottom was inserted in the first cylinder with the valve open. The valve was then closed, the cylinder removed, and the contents sieved. Before the inner cylinder was devised a 2 inch suction pump was

used to remove the remaining animals with the water (Davidson and Wilding, 1943), but the investigators felt that excessive time was required to rid the samples of silt. Merritt, Cummins, and Resh (1978) portrayed a flow diagram for detailed analysis of stream bottom samples collected with a toothed cylinder (Wilding or stovepipe sampler) and a bilge-type hand pump. Such samplers have the advantage that the inorganic substrate and organic matter in storage can be removed to a desired depth along with the fauna for analyses of factors related to distribution. Drawbacks are the bulk of equipment and relatively high labor per sample, difficulty in penetrating rough stream bottoms, and loss of organisms in swift currents caused by downward eddies from placing the sampler.

Net mesh and depth of sampling are two factors greatly affecting the reliability of results that have caused problems in most samplers and rendered the results of most studies incomparable. Jonassen (1955) showed that by reducing the sieve mesh from 0.6 to 0.2 mm the numbers of Chironomids and Oligochaetes collected from lake bottom samples were increased by 100 to 600%. Barber and Kevern (1973) obtained similar results in a river, increasing total invertebrate numbers by 95 to 325% by changing from a 0.50 to 0.25 mm sieve. Most samplers do not collect microinvertebrates at all, but many have severly underestimated the small individuals of what are normally termed macroinvertebrates as well. The problem has been that decreasing mesh size has resulted in increasing other losses and sampling labor. The box and cylinder samplers that do not sort the fauna with the current are most promising for eliminating this problem. A number of recent studies (Coleman and Hynes, 1970; Radford and Hartland-Row, 1971; Hynes, 1974; Williams and Hynes, 1974; Hynes, et al., 1976) have shown that normal surface-dwelling benthic invertebrates can occur in considerable num-

bers down to depths of at least 70 cm beneath the surface of stream substrates. Maximum densities often occur at a depth near 10 cm, which is deeper than most samplers penetrate. The great amount of labor involved in deep sampling methods makes reasonable sample sizes impractical, and the relationship of the deep-dwelling fauna to the community existing at the water-substrate interface is not known. Perhaps the best solution to this problem is to attempt to sample efficiently to a depth of at least 10 cm in quantitative studies and to collect a few samples with deep sampling methods to give a rough picture of vertical distribution in the stream studied. The depth used in a study should always be carefully controlled and specified so that the portion of the habitat sampled is clear.

APPENDIX B

Parametric statistical tests are based on the assumption that the data are from a population with a normal frequency distribution. Two properties included in this assumption that are important when testing for differences between means are that the variance is independent of the mean and that the components of the variance are additive. The frequency distributions of data from aggregated populations are positively skewed and in most sampling data the mean and variance tend to increase together. The application of methods based on the normal distribution to such data can result in erroneous conclusions, especially with small sample sizes. The alternatives are nonparametric methods applied to rankings of the data in which no assumptions are made about the distribution of the population, and parametric methods applied to a mathematical transformation of the data that fulfills the assumption of normality. The latter alternative was chosen because the study was designed for application of two-way analyses of variance and correlation coefficients. An analysis of variance tests the hypothesis that different treatment means are equal with the assumptions that the population is normally distributed and the variances for all means are equal. A correlation coefficient gives an estimate of how well changes in one variable can be predicted from changes in another based on the assumption that the populations form a bivariate normal distribution.

If a sample is large enough for the counts to be placed in a frequency distribution an adequate transformation can be chosen by testing its fit with known frequency distributions for which specific transformations apply. For small sample sizes as in this study a general transformation must be chosen from the relationship of variance to mean. For samples from distinctly aggregated populations in which the variance is many times greater

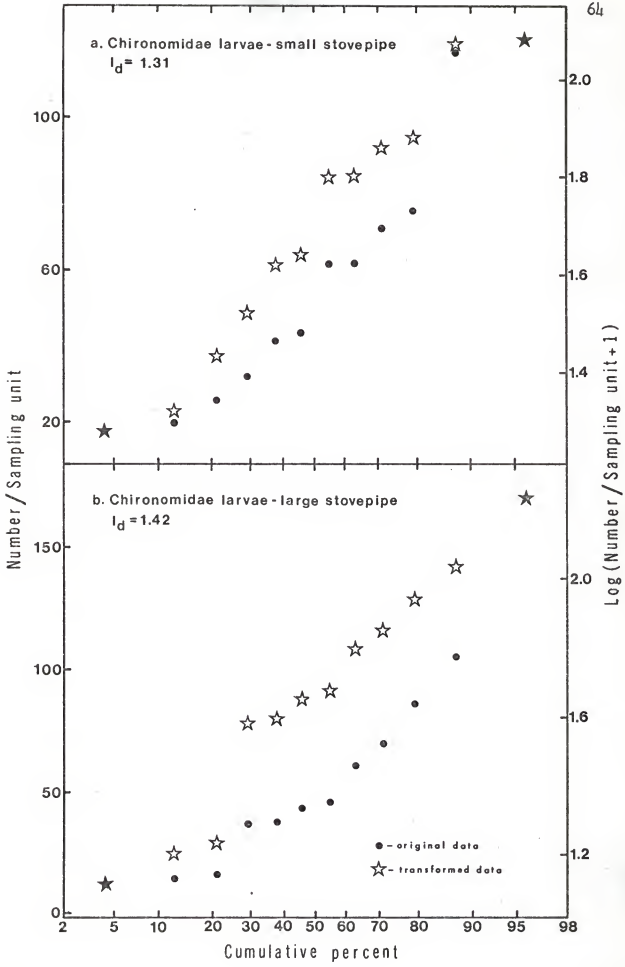
than the mean the most useful transformation is the logarithm transformation (Southwood, 1966; Elliott, 1971). If counts of zero are present a constant, usually one, must be added to the counts first. The variances are significantly greater than the means for all the common taxa in this study so the log (x+1) transformation was applied to the counts.

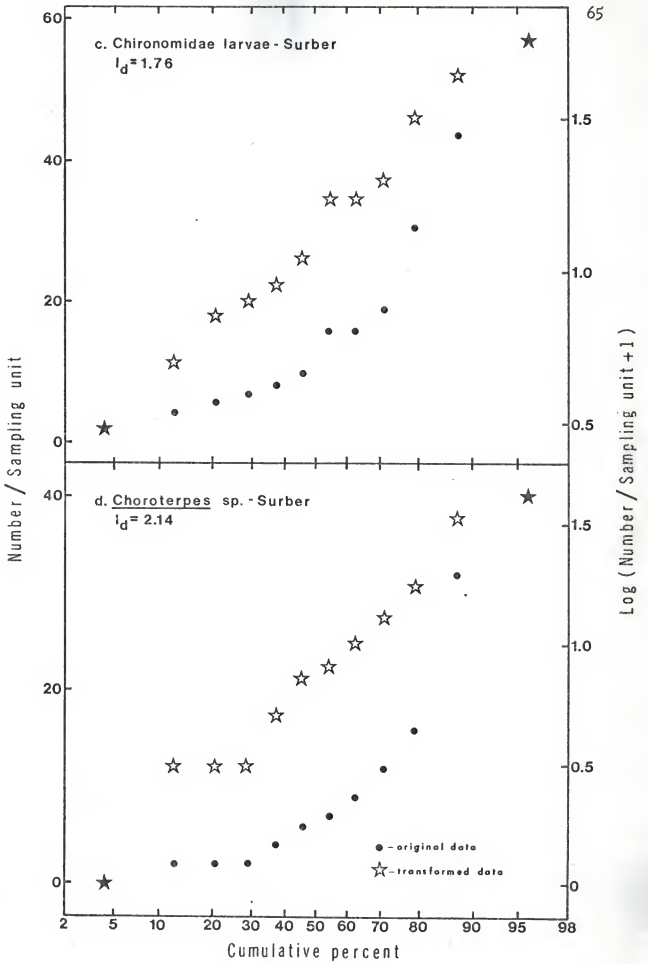
Normally distributed data plotted on a probability scale give a straight line (Southwood, 1966). If the distribution is positively skewed (i.e., the population is aggregated) the points form a concave curve. To test the adequacy of the transformation for normalizing the data the original and transformed counts for six of the samples covering a wide range of aggregation (Morisita's index values of 1.31 to 3.05) were plotted on a probability scale (Fig. 5). In each case a straight line fits the plot of the transformed data better than that of the original data. The transformation appears most adequate in the middle of the range of aggregation.

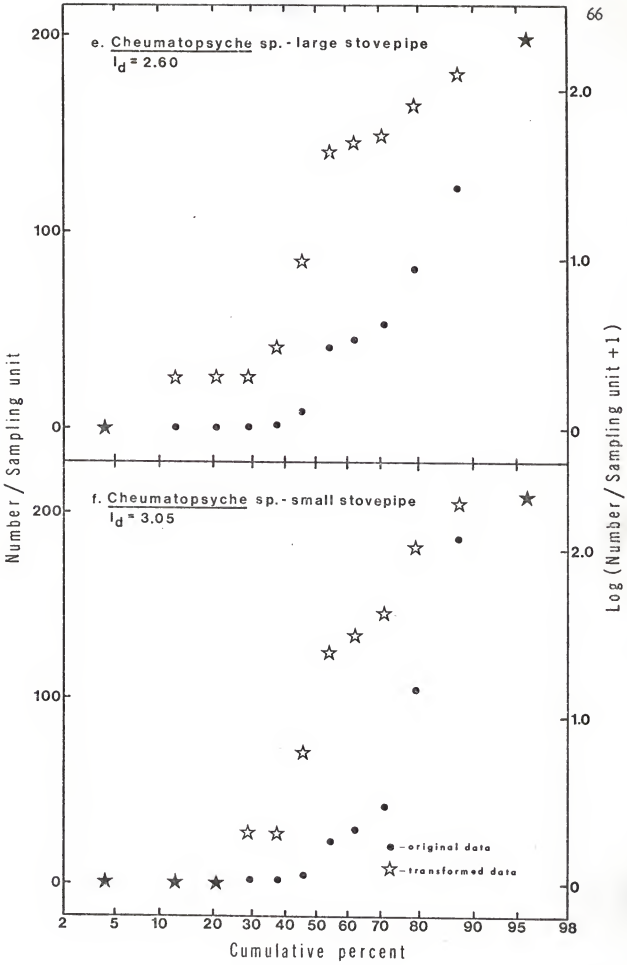
The variance tends to increase with the mean for most taxa. Taking all the data for the common taxa together the logarithms of the means and variances are highly correlated ($r=0.91$), despite differences in how the different taxa are distributed. The logarithms of the means and variances of the transformed data are not significantly correlated ($r=0.12$). With the original data F-tests reveal significant differences ($P<.05$) between the highest and lowest variances for most taxa as estimated by different samplers. All differences are nonsignificant ($P>.20$) for the variances of the transformed data. The transformation therefore appears adequate for fulfilling the requirements of independent means and variances and equal variances among treatments. This also insures that the components of the variances are additive.

In order for the analyses of variance to test for significant differ-

Figure 5. The original and transformed data for six taxa plotted on a probability scale.


a. Chironomidae larvae - small stovepipe
I_d = 1.31
b. Chironomidae larvae - large stovepipe
I_d = 1.42
Number / Sampling unit
Log (Number / Sampling unit + 1)
Cumulative percent
● - original data
☆ - transformed data
0
50
100
150
20
60
100
1.2
1.4
1.6
1.8
2.0
2
5
10
20
30
40
50
60
70
80
90
95
98


c. Chironomidae larvae - Surber
I_d = 1.76
d. Choroterpes sp. - Surber
I_d = 2.14
Number / Sampling unit
Log (Number / Sampling unit + 1)
Cumulative percent
● - original data
☆ - transformed data
60
40
20
0
65
1.5
1.0
0.5
0
2
5
10
20
30
40
50
60
70
80
90
95
98


e. Cheumatopsyche sp. - large stovepipe
I_d = 2.60
f. Cheumatopsyche sp. - small stovepipe
I_d = 3.05
Number / Sampling unit
Log (Number / Sampling unit + 1)
200
100
0
2.0
1.0
0
● - original data
☆ - transformed data
2
5
10
20
30
40
50
60
70
80
90
95
98
Cumulative percent

ences among sampler density estimates it was necessary to adjust the counts so that they all represented the same area of the stream bottom since different sampler sizes were used. All counts were adjusted to numbers per 0.10 m^2, the area of the large stovepipe sampler. This was a minor adjustment for the Surber sampler counts but the counts for the small stovepipe sampler were doubled. Doubling the counts increases the variances by a factor of four. This would result in errors in the analysis of the adjusted data because of large violations of the assumption of equal variances. After the log (x+1) transformation is applied to the adjusted data, however, the variance is changed from the variance of the transformed unadjusted data by a factor of less than 1.5 in all cases. In no case does it become significantly different from the variance of the transformed data for the other two samplers, so errors caused by the adjustment are minimal.

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A COMPARATIVE SAMPLING STUDY OF BENTHIC INVERTEBRATE POPULATIONS IN A PRAIRIE STREAM

by

GENE LESLIE PETERSEN

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A quantitative sampling method for estimating densities of benthic invertebrates in streams was developed and evaluated in King's creek, an intermittant stream on the Konza Prairie Research Natural Area near Manhattan, Kansas. The sampling equipment consists of an open, toothed cylinder (stovepipe sampler) that is bored into the streambed, a hand operated bilge pump that removes water, invertebrates, and fine sediments, and a sorting tub that separates invertebrates and detritus from the inorganic sediments in the field. Stovepipe samplers of two sizes (0.05 m^2 and 0.10 m^2) were compared to the Surber sampler, the most widely used method, by sampling a small, uniform riffle. The comparison was made with twelve randomly located groups of sampling units, each group consisting of one sampling unit collected with each sampler to a depth of 10 cm in the sediments. Nets used on the Surber sampler and the sorting tub for the stovepipe samplers were of 1 mm and 355 μm mesh size, respectively.

A total of thirty taxa were collected, many of which were rare. The small stovepipe, large stovepipe, and Surber samplers revealed mean total densities of 3413, 1863, and 1024 invertebrates per square meter, respectively, all of which were significantly different ($P < .05$). Of the twenty-three taxa collected by every sampler seventeen showed the pattern of highest density with the small stovepipe and lowest density with the Surber sampler ($P < .001$ by Chi-square). The Surber sampler yielded densities significantly ($P < .10$) less than those obtained with the small and large stovepipes for seven and five taxa, respectively. The small stovepipe estimates were significantly ($P < .10$) greater than those of the large stovepipe for two taxa. The Surber sampler collected significantly ($P < .01$) fewer taxa per sampling unit than both stovepipe samplers, for which the difference was not significant ($P > .40$). Underestimation of densities by

the Surber sampler was due primarily to incomplete removal of the fauna from the sediments and passage of small invertebrates through the net. The greater volume of sediments collected with the large stovepipe resulted in decreased sorting efficiency relative to the small stovepipe. Particulate organic matter was collected from a single sampling unit with the small stovepipe and fractionated into seven size classes ranging from 0.45 to 2000μm. Total ash-free dry weight was 1119 grams per square meter to a depth of 10 cm in the sediments. The smallest class (0.45 - 53μm) contained 71% of the total and the 53 - 125μm and 125 - 250μm classes contained 84% of the remainder.

From the extensive data obtained from the comparison microdistributional patterns and species associations were examined. All taxa were highly aggregated, but there were differences between taxa in level of aggregation and scale of clumping. Correlation coefficients were computed for the counts of all possible pairs of the nine most common taxa. A cluster analysis performed on the correlation matrix for the combined data of the stovepipe samplers revealed four distinct groups of taxa: (1) Stenonema - Choroterpes; (2) Baetis - Cheumatopsyche; (3) Chironomidae larvae - Chironomidae pupae - Nais - Physa; and, (4) Limnophora. The members of these groups corresponded well with distinct categories of feeding mechanism and mode of existence.