INTERACTION OF SUBSTRATE PARTICLE SIZE AND OTHER HABITAT VARIABLES, AND THEIR RELATION TO THE MICRODISTRIBUTION OF BENTHOS IN A MONTANA SPRING-STREAM

by

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of

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in

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Dr. Gould —
Thanks for your suggestions!
I appreciate it!
Dick

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VITA

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He attended Pacific Lutheran University, Tacoma, Washington, from September 1961 to June 1965 and received a Bachelor of Science degree in biology.

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ABSTRACT

A detailed analysis was made of the interaction of substrate particle size and other habitat variables and their relation to the microdistribution of benthos in a Montana spring-stream. The 0.7 km headwater section was chosen to minimize variation in some of the factors (temperature, discharge, water chemistry, differential shading) which potentially may indirectly influence microdistribution. A sampler was designed to collect both the benthos and the substrate within 0.049 m^2. A total of 143 samples were collected biweekly over nine months. Each sample was processed to determine quantities of (1) each of the nine prominent insect genera in the stream, (2) each of the three macrophytes, and (3) substrate in each of 14 designated size-classes.

Data were processed using a computer-programmed multiple regression analysis. Independent variables included for each sample were the depth, microcurrent, specific location of the sample in the study area, three factors of time to compensate for seasonal variations, and several measures of substrate size distribution. The latter included percentiles, percentages in each size-class, shortness of the outer and inner quartiles and outer deciles, mode and mean substrate size, and sample weight. t statistics were used to determine the explanatory power of individual independent variables, while F statistics and F tests were used to determine the explanatory power of groups of variables.

The mean substrate distribution by percent weight was a bimodal curve with the much smaller mode corresponding to the smaller substrate sizes. The most significant substrate variables were those corresponding to the smaller sizes: the 10th and 25th percentiles (to 11 of the 13 insect taxa), the lowest percentile group (0.25th, 1st, 5th, and 10th percentiles; 9 taxa), and the shortness of the lower decile and lower quartile (6 taxa). Six insect taxa were significantly positively correlated to the moss (*Amblystegium noterophilum*), but the few significant relations found to the watercress (*Rorippa nasturtium-aquaticum*) and the pondweed (*Zannichellia palustris*) were negative.

It was deduced that the deposition with time of smaller substrate particles was a good indicator of a corresponding deposition with time of detritus and other food material. Those microhabitats physically most suitable to insects are those with at least some larger particles to provide stability and a greater variety of habitat space. It was further deduced that areas which contain larger particles and were also receptive to deposition of smaller particles promoted the development of a satisfactory food regime. This resulted from not only the deposition of food particles but also the availability of favorable substrate for growth of algae and macrophytes, and the resultant congregation of prey species. It was concluded that the precise distribution of food in microhabitats was both reflected by and affected by substrate size composition, and food was thus the most critical factor influencing the microdistribution of organisms in this stream.

INTRODUCTION

Previous studies on distributions of stream organisms can be grouped, in general, into those concerned with longitudinal distribution along a stream's course or between adjacent streams ("macrodistribution"), and distribution within limited, generally superficially homogeneous, portions of a stream ("microdistribution"). Microdistributional studies are of interest because organisms tend to be non-randomly distributed even within small areas of a single riffle (Needham and Usinger 1956). Such non-random distribution can be attributed to variation of environmental factors among microhabitats or to the behavior of the animals themselves (Allen 1959).

Environmental factors attributed to influencing macrodistribution of various organisms include erosion -- deposition (Moon 1939), water temperature (Ide 1935, Sprules 1947, Armitage 1961, Kamler 1965), chemical composition of the water (Ricker 1934, Armitage 1958), and aufwuchs concentration along a stream's course (Stadnyk 1971). While extremes of these factors beyond the limits of tolerance by organisms may limit distribution along a stream's course (Jaag and Ambühl 1964), the factors generally become minimally significant, and can be considered to exert uniform effect, within given small sections of a stream (Cummins 1964, Cummins and Lauff 1969). Environmental factors attributed to influencing microdistribution, researchers making significant contributions, and the organisms considered, are summarized in

Table 1.

Substrate size is frequently considered to be the most significant factor influencing microdistribution of stream benthos (Table 1) because it interacts with current velocity, plant growth, and food deposition, as well as provides suitable habitat space for foraging and protection. Cummins (1962, 1964, 1966), Cummins and Lauff (1969), and Thorup (1966) also state that the substrate size distribution at each sampling site can and should serve as the common denominator in ecological studies of stream benthos because it can readily and precisely be measured, as opposed to the continuous variety of microcurrents and precise location of food. In characterizing substrate size however, virtually all researchers (Cummins excepted) have used some form of phenotypic (superficial appearance) description of substrate as it varies from place to place, or at most, have measured only the largest particles. Since this type of analysis necessarily requires consideration of larger sections of a stream and thus says little about the precise substrate size composition where the organisms are collected, Cummins feels it is necessary to collect the substrate along with each individual sample to precisely assess its influence on microdistribution.

In addition, the specific factor or factors chosen for consideration in many stream benthic microdistributional studies have been considered in areas where variations in other factors potentially interacting and influencing microdistribution have been ignored. Allen (1959)

Table 1. Factors influencing microdistribution, researchers making significant contributions, and taxa considered. Su--substrate, C--current, F--food, D--depth, B--behavior, O--oxygen, Sh--shading, direct illumination.

Researchers	Factors	Taxa
Percival and Whitehead (1929)	Su	Invertebrata
Hunt (1930)	Su	selected Invertebrata
Moon (1939)	Su	Insecta
Wene and Wickliff (1940)	Su	Insecta
Linduska (1942)	Su	Ephemeroptera
Pennak and Van Gerpen (1947)	Su	Insecta, Hydracarina, Naididae (Oligochaeta)
Eriksen (1963, 1964)	Su	*Ephemera simulans, Hexagenia limbata* (Ephemeroptera)
Bell (1969)	Su	Insecta
Cummins and Lauff (1969)	Su	selected Insecta, *Helisoma anceps* (Gastropoda)
Hendricks, et al. (1969)	Su	Invertebrata
Kamler and Riedel (1960)	Su,C	Ephemeroptera, Plecoptera, Trichoptera
Lavandier and Dumas (1971)	Su,C	selected Invertebrata
Scott (1958)	Su,C,F	Trichoptera
Ulfstrand (1967)	Su,C,F,D	Ephemeroptera, Plecoptera, Trichoptera, Simuliidae (Diptera)
Allen (1959)	Su,C,B	*Pycnocentrodes* (Trichoptera), Parnidae (Coleoptera), Chironomidae (Diptera), *Potamopyrgus* (Gastropoda)
Egglishaw (1969)	Su,F[1],D	Invertebrata
Cummins (1964)	Su,F,B	*Pycnopsyche lepida, P. guttifer* (Trichoptera)

Table 1 (continued)

Researchers	Factors	Taxa
Sprules (1947)	Su,B	Insecta
Eriksen (1968)	Su,O	*Ephemera simulans*, *Hexagenia limbata* (Ephemeroptera)
Jaag and Ambühl (1964)	C,O	selected Ephemeroptera and Trichoptera
Egglishaw (1964)	F^2	Insecta and other Invertebrata
Buscemi (1966)	F^3	Insecta, Oligochaeta, Sphaeriidae (Pelecypoda)
Cushing (1963)	F^4	Ephemeroptera, Plecoptera, Trichoptera
Hughes (1966*a*)	Sh	Invertebrata
Hughes (1966*b*)	Sh	*Baetis harrisoni*, *Tricorythus discolor* (Ephemeroptera)

[1] plant detritus, moss, algae

[2] plant detritus

[3] organic seston and sediments

[4] plankton, suspended organic matter

suggests that a more promising approach is to study these factors over superficially more homogeneous areas, although it presents greater technical problems in making precise measurements and interpreting the results. Ulfstrand (1968) suggests that new experimental approaches are needed.

Consequently the purpose of my study was, first, to consider precisely the relationship of substrate particle size to benthos distribution within a superficially homogeneous section of a stream where the variability in many of the other factors, especially those which may potentially influence microdistribution indirectly, were minimized. Secondly, the purpose was to analyze in detail the interrelationships between all factors which appeared to vary significantly within the study area and their relationship to benthos distribution.

DESCRIPTION OF STUDY AREA

The headwaters of Blaine Spring Creek (45° 13' N, 111° 47-1/2' W) was selected for this study. It is a tributary of the Madison River (Missouri River drainage), 16.1 km south-southwest of Ennis, in Madison County, Montana. The stream is formed by the discharge from two adjacent springs (Figure 1). The water from both springs converges a short distance downstream and from here the stream flows southward to a point just north of the Ennis National Fish Hatchery where it is diverted underground. The study area selected was the 0.7 km section from below the springs (above the convergence) to just above the underground diversion. Elevation of the springs is 1701 m and the average gradient of the study area is 26 m/km. Average width and depth of the study area below the convergence are 5.4 m (range: 3.0-6.4 m) and 0.26 m (maximum: 0.51 m) respectively. Current velocity below the convergence averages 0.83 m/sec. Discharge from the springs is constant at 0.94 m^3/sec (unpublished records, Ennis National Fish Hatchery). However, small quantities of water are removed below the south spring above section 3 (Figure 1) for hatchery use, and from the reservoir near the middle of the study area (above section 6) for irrigation during the summer months.

Substrate particle sizes are well-diversified throughout the study area except at section 1. Except for occasional large cobble (128-256 mm), the largest particles consistently encountered are small

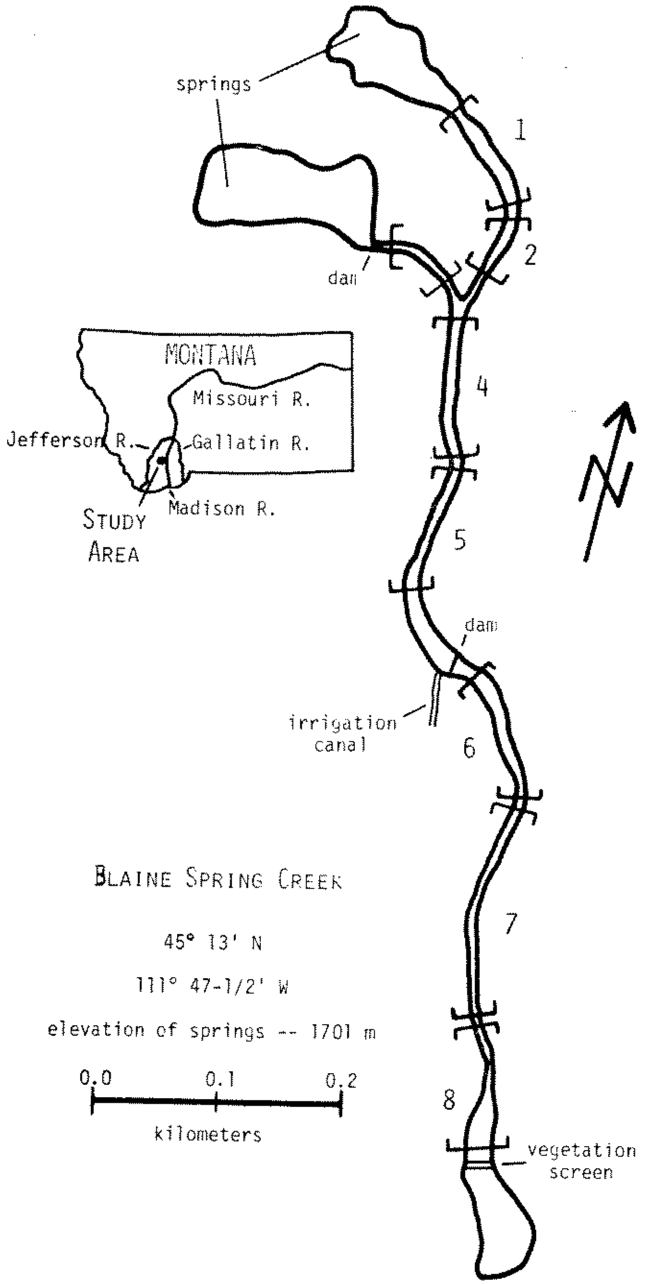


Figure 1. The headwater section of Blaine Spring Creek, Montana. The brackets indicate the eight sampling sections.

cobble (64-128 mm). Most of the substrate below the north spring (section 1) consists of layered marl and rubble, with progressively much less quantities downstream through section 2. No marl occurred within the remainder of the study area.

A preliminary survey of water chemistry using standard methods described by the American Public Health Association (1965) showed no differences in the quality of the water discharged from the two springs or longitudinally along the study area. Conductivity was 440 μmhos. The principal cations were calcium (2.7 me/ℓ) and magnesium (1.5 me/ℓ), with minor amounts of sodium (0.13 me/ℓ) and potassium (0.04 me/ℓ). The principal anions were bicarbonate (3.0 me/ℓ) and sulfate (1.3 me/ℓ), with a trace amount of chloride (0.05 me/ℓ). Variation of temperature both seasonally and downstream through the study area is minimal; the extremes measured during the sampling period (July 1969 - April 1970) were 13.0° (August 9, 1969) and 11.9°C (January 10, 1970).

The only deciduous vegetation along the stream within the study area was a few willows near the lower end. These did not appreciably shade the stream, and virtually no allochthonous detritus appeared in the samples. Vegetation within the stream itself was principally moss *(Amblystegium noterophilum)* and watercress *(Rorippa nasturtium-aquaticum)*, the latter being confined mainly near the shorelines. Small quantities of a horned-pondweed *(Zannichellia palustris)* and filamentous algae were also occasionally found. Most of the vegetation in the springs above the study area was removed by a hatchery crew on 15 September 1969, some of which probably drifted through the study area. Likewise, some of the vegetation from the study area itself was removed between 29 October and 11 November 1969.

The headwaters of Blaine Spring Creek were especially suitable for this study because, though there was considerable diversity of substrate particle sizes, there was minimal variation in some of the other factors (temperature, discharge, water chemistry, shading) which may at least indirectly influence microdistribution of benthos. In addition, the stages of development of the insects in this area had little variation within species, thus minimizing effects of differential behavior. Because the study area was a headwater section, no drift of organisms was possible from above, and it was speculated that more mature forms of many insects tended to drift out of the area.

METHODS AND MATERIALS

Field

A sampler designed by myself for this study (Figure 2) was used to simultaneously collect both the organisms and the substrate at each sampling site. It consisted of a metal cylinder mounted at one end through a circular plywood platform. A section of foam rubber with the same dimensions as the platform was glued to its bottom. A hole the same diameter as the cylinder was cut into the center of the foam. Two smaller cylinders were glued with epoxy into the larger cylinder opposite each other and slightly above the platform. A flange was attached with epoxy around one of the smaller cylinders to hold a net tied to it. The net used in this study had 36 threads/cm (<0.25 mm openings).

The principle of the sampler was to seal off a sampling site from the surrounding substrate and influence of the current. However, current was allowed to flow through the sampler through the two smaller cylinders to sweep dislodged suspended material into a net. A bucket with a tripod stand (Figure 2) was used to hold material scooped from within the sampler.

The study area was divided into 8 sections (Figure 1) to facilitate systematic sampling. One sample was collected from each section biweekly between mid-July 1969 and mid-April 1970. Specific sampling

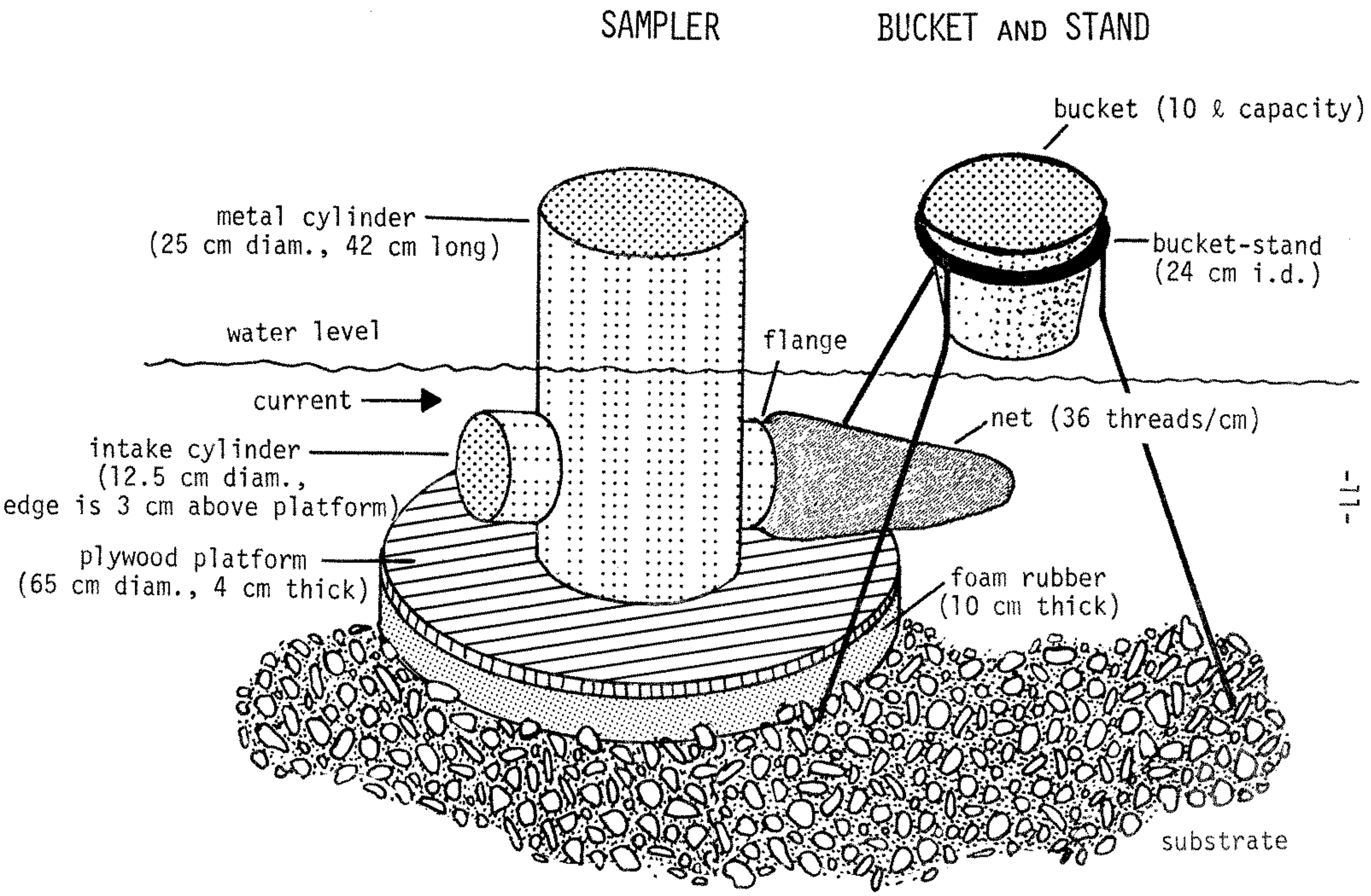


Figure 2. Sampler designed for this study.

sites within each section were selected using a biased-random procedure (Cummins 1962) to assure wide variation in both substrate size composition and amounts and species of vegetation. Once selected, a site was marked by placing the bucket-stand immediately downstream from it. Water temperature was measured at the site to the nearest 0.1°C with a laboratory thermometer. Current velocity was measured with a Leupold-Stevens midget current meter. Readings in number of revolutions for one minute were made 2 cm above the substrate by placing the end of the meter onto the stones or as close to the vegetation as possible at the center of the site. Depth was recorded from the scale on the current meter rod. All presampling operations were made by approaching the site from downstream.

The sampler was pressed into the water immediately upstream from the sampling site to compensate for its downstream drift. It was immediately seated on the sampling site by kneeling on the platform with one knee on either side of the main cylinder. Thus positioned, the platform abutted two legs of the bucket stand which prevented shifting of the sampler. The enclosed substrate was initially agitated and rubbed to dislodge the larger masses of vegetation and most of the invertebrates. These organisms, along with most of the finer suspended substrate material, were carried into the net. No attempt was made to dislodge all organisms at this time because it was desirable to complete the collection within a few minutes to avoid excessive erosion of the substrate from beneath the foam rubber. Substrate particles along with the remaining organisms were then scooped by hand from the sampler into the bucket. All loose substrate not exceeding a depth of about 15 cm was removed. Firmness of the substrate prevented removal to this depth in most cases however, and it was thus assumed that most organisms could not have penetrated beyond this point. After water in the sampler had cleared, the net was removed and placed in the bucket. The sampler was then taken from the stream followed by the sample.

Contents of the net and bucket for each sample were immersed in 5 percent formalin and stored separately to evaluate the efficiency of the agitation procedure in sweeping organisms into the net. Cobble too large for storage containers were scraped of organisms, placed in paper sacks and labeled.

Laboratory

The objectives of the laboratory procedures (Figure 3) were to determine the number of insects in each genus, the dry weights of each species of plant, and the weight of each size-class of substrate in each sample. Net and bucket portions of a sample were quantified separately. Since the net portions contained only fine substrate, it was possible to eliminate some of the intermediate steps shown in Figure 3. It was necessary to divide the bucket sample, which generally

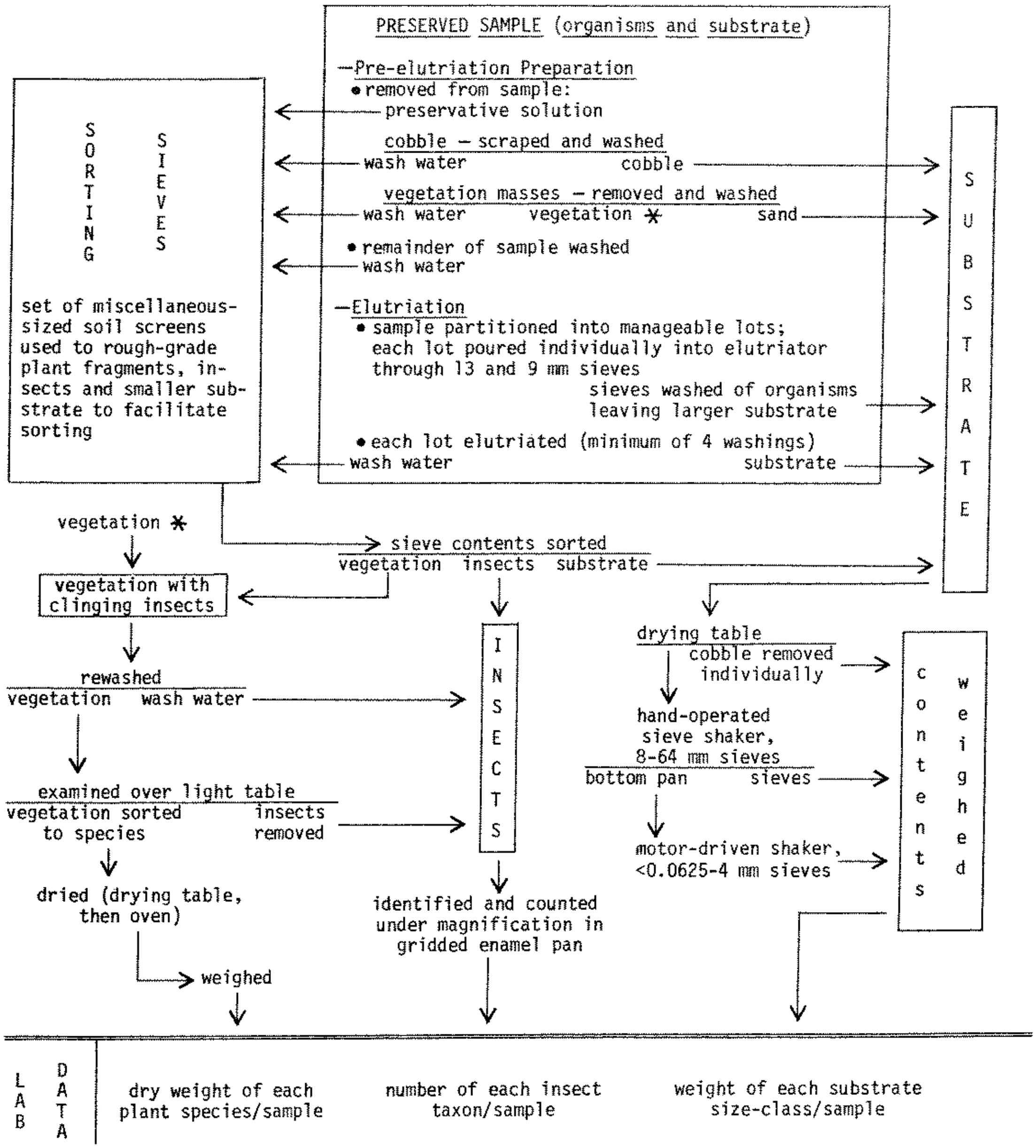


Figure 3. Lab procedures used in processing preserved samples to obtain the dry weight of each plant species, the number of insects in each taxon, and the weight of each substrate size-class.

contained 4 to 8 ℓ of substrate into smaller portions and process each separately.

An elutriator was constructed for separating less dense material (invertebrates, plant fragments, and the occasional detritus) from the denser substrate. Its design was similar to that described by Lauff et al. (1961), except that a 64 mm rather than a 51 mm diameter drain spout was used, and the main column was extended an additional 15 cm above their specified 60 cm height. The largest substrate particles from the sample were first removed individually and scraped of vegetation and insects. Portions of a sample were then washed individually into the elutriator through 13 and 9 mm sieves to further cull out larger particles. The elutriation procedure used was similar to that described by Lauff et al., though after a few trials it was found more efficient to agitate the material at the bottom of the column not only with air injected through the bottom but also with a jet of water from the top which simultaneously filled the column. The sample portion was agitated, drained of the suspended material and reagitated a minimum of four times.

Five soil sieves were used to collect the suspended material from the elutriator and to roughly grade plant fragments and invertebrates for easier recognition and separation. Material on the larger sieves was washed into a gridded enamel pan, while that on the smaller sieves was washed into a flat-bottomed glass dish. Material in the dish was examined over a light table which consisted of an illuminated glass plate on which was drawn a 5 cm grid. The grids allowed the entire sample to be systematically examined a small portion at a time. Because of their small size, nearly all of the invertebrates in both the pan and the dish were removed with an aspirator. The aspirator was used with pipettes with tips of various constrictions depending upon the size of invertebrates being removed. Plant fragments were separated from the fine substrate particles unavoidably elutriated by carefully decanting the water and plants from both the pan and dish into a fine-mesh net.

The large masses of vegetation removed in the pre-elutriation procedures (Figure 3) plus fragments gathered in later sorting processes were teased apart over the light table to remove the remaining invertebrates and separate the plants into species (Table 2). Plants were placed on filter paper, dried initially over a drying table (metal trays placed over several light bulbs) and then in a drying oven at 100°C for 6 hours, and weighed.

The invertebrates were placed, a portion at a time, into a gridded enamel pan partially filled with water. The nine most numerous invertebrate taxa (Table 2) selected for counting were insects; all of the other insects and invertebrates combined numbered less than any of the genera counted. Because virtually all of the insects were small

Table 2. Taxa from Blaine Spring Creek analyzed in this study.

PLANTS

- Bryophyta (Musci)
  - -*Amblystegium noterophilum* (aquatic moss)
- Tracheophyta (Angiospermae)
  - -*Rorippa nasturtium-aquaticum* (watercress)
  - -*Zannichellia palustris* (horned-pondweed)

INSECTS

- Plecoptera (stoneflies)
  - Perlidae, Acroneurinae
    - -*Acroneuria pacifica*
  - Perlodidae and Nemouridae
    - -"other stoneflies"
- Trichoptera (caddisflies)
  - Hydroptilidae
    - -*Ochrotrichia* sp.
  - Rhyacophilidae
    - -*Rhyacophila* sp.
    - -*Glossosoma* sp.
- Ephemeroptera (mayflies)
  - Baetidae
    - Ephemerellinae
      - -*Ephemerella infrequens*
    - Baetinae
      - -*Baetis* sp.
    - Leptophlebiinae
      - -*Paraleptophlebia* sp.
- Coleoptera (beetles)
  - Elmidae
    - -*Optioservus* sp.

and relatively immature, it was necessary to examine the sample under 2X magnification while counting for positive recognition of genera. Also, because of the difficulty in recognizing and counting the immature stonefly nymphs in large quantities, all stoneflies other than *Acroneuria pacifica* were tabulated together. Most of these in the "other stoneflies" group (Table 2) were *Isoperla* sp. though *Nemoura* sp. occurred occasionally.

The substrate size classification used in this study (Table 3) was modified slightly after Cummins (1962, 1964), who in turn broadly modified the standard Wentworth classification of particle sizes. With the 2 mm class as the base, the minimum sizes of succeedingly larger and smaller classes are the function of the exponents 2 and 1/2 respectively. The phi (Ø) scale used to designate each class is the negative log to the base 2 of the minimum size of each class. Because sieve sizes 8, 16, and 32 mm were not locally available for this study, each of these corresponding minimum sizes for their respective classes was bracketed by sieves of adjacent sizes (Table 3).

The entire substrate sample was completely dried over the drying table. A 128 mm wire frame was used to sort out the larger from the smaller cobble. The remaining substrate sample was partitioned and shaken a small portion at a time in order not to overload the sieves. Each portion was first shaken through the four largest sieves (64-18.9 mm, Table 3) with a hand-operated portable sieve-shaker for 0.5

Table 3. Substrate size classification and sieves used. Substrate class terminology modified after Cummins (1962, 1964).

Substrate class	Particle size range (mm)	Phi scale	Sieves used	
			Size (mm)	U.S. Sieve Series no.
large cobble	128-256	-7	individual 128 mm wire square	
small cobble	64-128	-6	64	---
large pebble	32-64	-5	38.1 26.7	--- ---
small pebble	16-32	-4	18.9 13.3	--- ---
coarse gravel	8-16	-3	9.42 6.68	--- ---
medium gravel	4-8	-2	4.00	5
fine gravel	2-4	-1	2.00	10
very coarse sand	1-2	0	1.00	18
coarse sand	0.5-1	1	0.50	35
medium sand	0.25-0.5	2	0.25	60
fine sand	0.125-0.25	3	0.125	120
very fine sand	0.0625-0.125	4	0.062	230
silt and clay	<0.0625	5-9	bottom pan	

minutes. This period of shaking was adequate for sorting substrate through the sieves larger than 2 mm. The substrate collected in the bottom pan was then shaken through the next four sieves (13.3-4 mm) using the same procedure. The substrate then collected in the bottom pan (<4 mm) was shaken for 15 minutes through the remaining six sieves (2-0.062 mm) using a motor-driven sieve-shaker. The contents on each of the 14 sieves plus that in the final bottom pan (<0.062 mm) was weighed to three significant figures. The weights from the individual portions of the sample were summed to give the total weight per sieve for each sample. For those size categories where the sieves needed were not available (8, 16, and 32 mm), the total weights of the substrate on each pair of sieves used to bracket the minimum class size were partitioned (Table 12) according to the linear distance between the size of each sieve and the minimum class size.

Data analysis

A multiple regression analysis computer-programmed by Dr. Richard E. Lund of the Department of Mathematics, Montana State University, was used to evaluate the relationship between both macrophyte quantity (weight of each species and total weight) and insect numbers (tabulated according to class, orders, and genera), and the habitat parameters measured for each of the 143 samples (one sample of the 144 collected was discarded). In addition, the quantity of each of the three macrophytes was considered an independent variable in relation to the insect numbers, but as a dependent variable in relation to all of the other independent variables. The other independent variables included for each sample were: current velocity; depth; a dummy variable indicating whether or not filamentous algae was mixed with the macrophytes (in 15 of the 143 samples); linear, quadratic and cubic factors of time to account for seasonal variations; dummy variables representing each stream section to account for unrecognized variability longitudinally along the study section not accounted for by measured variables; and several measures of substrate size composition. The latter (though not all used in one regression model) were the percentage quantity in each size-class, percentiles (0.25, 1, 5, 10, 25, 50, 75, 90), the shortness of the inner quartile and the upper and lower quartiles and deciles in phi units, mean, mode size-class, and total substrate sample weight as a rough index to available habitat space. Statistics produced (see Table 16 for examples) were the variable means, simple and partial correlations, regression coefficients, standard errors, t and F values, intercept, R-squared, and *ANOVA* (analysis of variance).

The initial regression models programmed were used in conjunction with the correlation matrix of all variables to determine, first, if the group of independent variables used initially were significant, and second, to elucidate which of the variables were most significant

Successive models were developed eliminating those independent variables which were not significant to the majority of insect taxa. In some cases, variables were significantly correlated to various taxa when considered independently (simple correlation coefficients), but insignificant when considered with other independent variables in the multiple regression analysis. Correlation between the independent variables themselves is thus indicated. It would have been possible to develop refined models for each individual taxon had time and finances permitted. However, the t values are, in most cases, adequate indicators of significance for those variables included only in the initial models. In a few cases, t values for the same independent and dependent variable combination varied considerably between regressions, depending on the multi-colinearity of the independent variables included in the particular multiple regression models. Twenty-three different models were programmed before a final regression model was chosen as representative for the majority of insects. Most of these models were necessary to develop and refine parameters describing segments of the substrate-size distribution.

RESULTS

Correlation coefficient matrix

The correlation matrix (Table 4) lists the coefficients among all independent and dependent variables which were significant at the 5 percent level. Some of the significant correlations listed have little practical significance however. An example is the significant correlations of lower taxa to their corresponding higher taxa, of which, numerically, they may contribute a considerable portion. Several taxa were correlated to depth (Table 4), but only one to the current measurements. Correlation between depth and the current measurements near the level of the substrate was significant and negative. This is expected because the maximum current of deeper water generally tends to be proportionally further from the bottom.

Many taxa were significantly correlated to the percentage weights in the substrate size-classes and to the percentiles. The trend of the correlations within many of the taxa to the percentages was for significance in several adjacent size-classes, followed by one or two classes without significance, and finally followed again by classes with significance but coefficients with the opposite sign. The fact that several adjacent classes tend to be significantly correlated to taxa indicates that the degree to which the substrate was graded into classes was more than adequate. Many taxa were also significantly

es in the study
values in the
at the correla-
level; "n.a."
ationship was

A. noterophilum									
R. nasturtium-aquat.									
Z. palustris									
INSECTS									
Plecoptera									
A. pacifica									
other stoneflies									
Ephemeroptera	0.001								
E. infrequens	0.2707								
Baetis sp.									
Paraleptophlebia sp.									
Trichoptera									
Ochrotrichia sp.									
Glossosoma sp.									
Rhyacophila sp.									
Optioservus sp.									
depth									
current velocity									

Substrate			percentiles 10th	percentiles 25th	percentiles 50th	percentiles 75th	percentiles 90th	total weight	mode size-class
Substrate	percent weights	Ø(4)							
		Ø(3)							
		Ø(2)							
		Ø(1)							
		Ø(0)							
		Ø(-1)							
		Ø(-2)							
		Ø(-3)							
		Ø(-4)							
		Ø(-5)							
		Ø(-6)							
		Ø(-7)							
	percentiles	0.25th							
		1st							
		5th							
		10th							
		25th	9295						
		50th	7788	9045					
		75th	6362	7479	8844				
		90th	5790	6713	7704	9049			
	total weight		6005	-5763	n.a.	n.a.	n.a.		
	mode size-class		7276	5787	n.a.	n.a.	n.a.	-5475	

correlated to several adjacent percentiles, though there were no changes of sign here within taxa. Several taxa were significantly correlated, either positively or negatively, to the total sample weight, but there were few correlations to the mode size-class. The many significant correlations of both adjacent percentages and adjacent percentiles representing substrate distribution are expected; if it is accepted that current roughly grades substrate particles by distributing and redepositing them according to the interaction of eddy currents, turbulence and other factors, it would be highly unlikely to find the distribution of particles between adjacent size-classes to be random.

Multiple regression models

The *F* statistics of the initial regression models (regressions A and B, Tables 5 and 6) indicated that high significant relationships existed between the initial set of independent variables and nearly all of the taxa. In most cases, this relationship was significant at less than the 0.1 percent level. The only taxa not significant at the 5 percent level were 2 of the 3 species of macrophytes, *Rorippa nasturtium-aquaticum* (watercress) and *Zannichellia palustris* (pondweed), which together comprised only 3 percent of the total plant biomass (Table 14). Because these *F* statistics indicated high significance in the independent variables as a group, subsequent models were developed (Tables 5 and 6) to isolate and remove variables

Table 5. Independent variables included in regressions A-U.

Dependent variable notation:

1 - each plant genus
2 - plant genus data combined
3 - both no. 1 and no. 2
4 - each insect taxon: class, order, and genus
5 - insect class data only
6 - both no. 1 and no. 2
7 - both no. 3 and no. 4

REGRESSION	DEPENDENT VARIABLES	INDEPENDENT VARIABLES																																						REGRESSION
								Substrate																																
										percent weights															shortness of:					percentiles										
		moss	watercress	pondweed	algae	depth	current velocity	sample weight	mode Ø class	Ø(4)	Ø(3)	Ø(2)	Ø(1)	Ø(0)	Ø(-1)	Ø(-2)	Ø(-3)	Ø(-4)	Ø(-5)	Ø(-6)	Ø(-7)	Ø(2) + Ø(1)	Ø(0) + Ø(-1)	Ø(-2) + Ø(-3)	lower decile	lower quartile	inner quartile	upper quartile	upper decile	0.25th	1st	5th	10th	25th	50th	75th	90th	stream section	time (3)	
A	3				X	X	X	X	X				X	X	X	X	X	X	X	X	X												X	X	X	X	X	X	X	A
B	4	X	X	X	X	X	X	X	X				X	X	X	X	X	X	X	X	X												X	X	X	X	X	X	X	B
C	2				X	X	X																				X								X			X		C
D	5	X	X	X	X	X	X																				X								X			X		D
E	6																																					X		E
F	2				X	X	X	X	X																								X	X	X	X	X	X	X	F
G	5	X	X	X	X	X	X	X	X																								X	X	X	X	X	X	X	G
H	7																								X	X		X	X									X	X	H
I	5																									X		X										X	X	I
J	5																								X				X									X	X	J
K	4	X	X	X																		X	X	X									X	X				X	X	K
L	4	X	X	X																													X	X				X	X	L
M	4	X	X	X																		X	X	X														X	X	M
N	4	X	X	X																		X	X	X									X	X					X	N
O	4	X	X	X																													X	X					X	O
P	4	X	X	X																		X	X	X															X	P
Q	4	X	X	X						X	X	X	X																	X	X	X	X					X	X	Q
R	4	X	X	X						X	X	X	X																									X	X	R
S	4	X	X	X																										X	X	X	X					X	X	S
T	4	X	X	X																																		X	X	T
U	3									X	X	X	X																	X	X	X	X					X	X	U

Table 6. F statistics, the levels at which the null hypotheses are rejected, and the R^2 values for the dependent variables in each of the regressions. Independent variables for each regression are given in Table 5. f_1 is the degrees of freedom due to regression; f_2 the total degrees of freedom, is 142 for all regressions (N = 143).

Regression	Dependent variable	F statistic	P level	R^2
A	PLANTS	8.0478	<0.001	.6738
f_1 = 29	*Amblystegium noterophilum*	8.0558	<0.001	.6740
	Rorippa nasturtium-aquaticum	1.8390	<0.100	.3206
	Zannichellia palustris	1.0594	>0.250	.2138
B	INSECTS	6.5992	<0.001	.6575
f_1 = 32	Plecoptera	4.3382	<0.001	.5579
	Acroneuria pacifica	2.3046	<0.001	.4013
	other stoneflies	4.3338	<0.001	.5577
	Ephemeroptera	5.2945	<0.001	.6063
	Ephemerella infrequens	5.3844	<0.001	.6103
	Baetis sp.	1.6737	<1.050	.3275
	Paraleptophlebia sp.	4.1929	<0.001	.5495
	Trichoptera	2.7830	<0.001	.4474
	Ochrotrichia sp.	3.2563	<0.001	.4865
	Glossosoma sp.	3.3096	<0.001	.4905
	Rhyacophila sp.	3.4783	<0.001	.5029
	Coleoptera: *Optioservus* sp.	5.6545	<0.001	.6219
C	PLANTS	12.2716	<0.001	.5311
f_1 = 12				
D	INSECTS	5.8632	<0.001	.4092
f_1 = 15				
E	PLANTS	4.5807	<0.001	.1919
f_1 = 7	INSECTS	9.7220	<0.001	.3352

Table 6 (continued)

Regression	Dependent variable	F statistic	P level	R^2
F	PLANTS	9.7352	<0.001	.6148
f_1 = 20				
G	INSECTS	7.2488	<0.001	.5706
f_1 = 23				
H	PLANTS	13.7147	<0.001	.5802
f_1 = 14	*A. noterophilum*	12.5575	<0.001	.5787
	R. nasturtium-aquaticum	0.9581	>0.250	.0949
	Z. palustris	1.4447	<0.250	.1365
	INSECTS	13.1523	<0.001	.5899
	Plecoptera	8.1855	<0.001	.4724
	A. pacifica	2.4310	<0.005	.2100
	other stoneflies	8.2109	<0.001	.4731
	Ephemeroptera	11.4411	<0.001	.5558
	E. infrequens	11.9873	<0.001	.5673
	Baetis sp.	3.1277	<0.001	.2549
	Paraleptophlebia sp.	3.8970	<0.001	.2989
	Trichoptera	3.9236	<0.001	.3003
	Ochrotrichia sp.	4.4663	<0.001	.3282
	Glossosoma sp.	4.0886	<0.001	.3090
	Rhyacophila sp.	7.2051	<0.001	.4407
	Optioservus sp.	11.2995	<0.001	.5527
I	INSECTS	11.0738	<0.001	.5055
f_1 = 12				
J	INSECTS	13.8597	<0.001	.5613
f_1 = 12				
K	INSECTS	10.7927	<0.001	.6104
f_1 = 18	Plecoptera	6.6755	<0.001	.4921
	A. pacifica	2.7009	<0.001	.4949

Table 6 (continued)

Regression	Dependent variable	F statistic	P level	R^2
	other stoneflies	6.7495	<0.001	.4949
	Ephemeroptera	8.5805	<0.001	.5547
	E. infrequens	8.6570	<0.001	.5569
	Baetis sp.	2.2198	<0.005	.2437
	Paraleptophlebia sp.	6.3396	<0.001	.4792
	Trichoptera	4.3801	<0.001	.3887
	Ochrotrichia sp.	4.0265	<0.001	.3689
	Glossosoma sp.	3.9195	<0.001	.3626
	Rhyacophila sp.	5.4023	<0.001	.4395
	Optioservus sp.	9.2851	<0.001	.5741
L	INSECTS	12.7986	<0.001	.6019
$f_1 = 15$	Plecoptera	7.2232	<0.001	.4604
	A. pacifica	2.2775	<0.010	.2120
	other stoneflies	7.3026	<0.001	.4631
	Ephemeroptera	9.5773	<0.001	.5308
	E. infrequens	9.9936	<0.001	.5414
	Baetis sp.	2.4908	<0.005	.2273
	Paraleptophlebia sp.	6.1607	<0.001	.4212
	Trichoptera	4.8806	<0.001	.3657
	Ochrotrichia sp.	4.2584	<0.001	.3346
	Glossosoma sp.	4.4366	<0.001	.3438
	Rhyacophila sp.	6.5361	<0.001	.4357
	Optioservus sp.	11.2401	<0.001	.5704
M	INSECTS	9.0101	<0.001	.5336
$f_1 = 16$	Plecoptera	7.3418	<0.001	.4825
	A. pacifica	2.9412	<0.001	.2719
	other stoneflies	7.4288	<0.001	.4854
	Ephemeroptera	8.8505	<0.001	.5292
	E. infrequens	8.5225	<0.001	.5197
	Baetis sp.	2.1615	<0.010	.2154
	Paraleptophlebia sp.	6.8525	<0.001	.4653
	Trichoptera	2.2744	<0.010	.2241
	Ochrotrichia sp.	2.3614	<0.005	.2307

Table 6 (continued)

Regression	Dependent variable	*F* statistic	*P* level	R^2
	Glossosoma sp.	4.2445	<0.001	.3502
	Rhyacophila sp.	6.0375	<0.001	.4340
	Optioservus sp.	8.7234	<0.001	.5256
N	INSECTS	9.2802	<0.001	.4380
f_1 = 11	Plecoptera	5.9989	<0.001	.3350
	A. pacifica	2.5176	<0.001	.1745
	other stoneflies	6.0442	<0.001	.3367
	Ephemeroptera	9.0555	<0.001	.4319
	E. infrequens	9.6172	<0.001	.4468
	Baetis sp.	1.8531	<0.050	.1347
	Paraleptophlebia sp.	9.1846	<0.001	.4354
	Trichoptera	4.9797	<0.001	.2949
	Ochrotrichia sp.	4.1909	<0.001	.2603
	Glossosoma sp.	3.5960	<0.001	.2319
	Rhyacophila sp.	3.7791	<0.001	.2409
	Optioservus sp.	10.7008	<0.001	.4733
O	INSECTS	11.1781	<0.001	.4002
f_1 = 8	Plecoptera	8.2906	<0.001	.3311
	A. pacifica	2.6008	<0.001	.1344
	other stoneflies	8.3417	<0.001	.3324
	Ephemeroptera	11.4151	<0.001	.4053
	E. infrequens	12.3151	<0.001	.4237
	Baetis sp.	2.1027	<0.050	.1115
	Paraleptophlebia sp.	9.7213	<0.001	.3672
	Trichoptera	5.4607	<0.001	.2459
	Ochrotrichia sp.	3.9468	<0.001	.1907
	Glossosoma sp.	3.9866	<0.001	.1922
	Rhyacophila sp.	5.1944	<0.001	.2367
	Optioservus sp.	13.0011	<0.001	.4370
P	INSECTS	5.4765	<0.001	.2704
f_1 = 9	Plecoptera	6.0237	<0.001	.2896
	A. pacifica	2.9543	<0.001	.1666
	other stoneflies	6.0850	<0.001	.2917

Table 6 (continued)

Regression	Dependent variable	*F* statistic	*P* level	R^2
	Ephemeroptera	9.2134	<0.001	.3840
	E. infrequens	8.8341	<0.001	.3741
	Baetis sp.	1.7834	<0.100	.1077
	Paraleptophlebia sp.	11.0006	<0.001	.4267
	Trichoptera	1.9109	<0.100	.1145
	Ochrotrichia sp.	1.9223	<0.100	.1151
	Glossosoma sp.	3.9713	<0.001	.2118
	Rhyacophila sp.	4.4909	<0.001	.2331
	Optioservus sp.	8.0382	<0.001	.3523
Q	INSECTS	10.2887	<0.001	.6410
$f_1 = 21$	Plecoptera	6.7650	<0.001	.5400
	A. pacifica	3.6552	<0.001	.3881
	other stoneflies	6.7768	<0.001	.5405
	Ephemeroptera	7.9896	<0.001	.5810
	E. infrequens	8.5292	<0.001	.5968
	Baetis sp.	2.4604	<0.005	.2992
	Paraleptophlebia sp.	4.9704	<0.001	.4631
	Trichoptera	3.9764	<0.001	.4083
	Ochrotrichia sp.	4.5150	<0.001	.4393
	Glossosoma sp.	4.1377	<0.001	.4180
	Rhyacophila sp.	5.1926	<0.001	.4740
	Optioservus sp.	8.2728	<0.001	.5895
R	INSECTS	9.3471	<0.001	.5597
$f_1 = 17$	Plecoptera	7.1774	<0.001	.4940
	A. pacifica	3.5669	<0.001	.3266
	other stoneflies	7.2483	<0.001	.4964
	Ephemeroptera	8.9393	<0.001	.5487
	E. infrequens	9.3662	<0.001	.5602
	Baetis sp.	2.5991	<0.001	.2612
	Paraleptophlebia sp.	5.5921	<0.001	.4320
	Trichoptera	2.9005	<0.001	.2829
	Ochrotrichia sp.	3.7877	<0.001	.3400
	Glossosoma sp.	3.9388	<0.001	.3488

Table 6 (concluded)

Regression	Dependent variable	F statistic	P level	R^2
	Rhyacophila sp.	6.0338	<0.001	.4507
	Optioservus sp.	8.2998	<0.001	.5302
S	INSECTS	12.1375	<0.001	.6227
$f_1 = 17$	Plecoptera	8.2085	<0.001	.5275
	A. pacifica	3.1393	<0.001	.2992
	other stoneflies	8.1802	<0.001	.5266
	Ephemeroptera	9.7712	<0.001	.5706
	E. infrequens	10.3502	<0.001	.5847
	Baetis sp.	2.8685	<0.001	.2806
	Paraleptophlebia sp.	6.0072	<0.001	.4496
	Trichoptera	3.7011	<0.001	.3348
	Ochrotrichia sp.	4.1036	<0.001	.3582
	Glossosoma sp.	4.9216	<0.001	.4010
	Rhyacophila sp.	6.1458	<0.001	.4553
	Optioservus sp.	10.3592	<0.001	.5849
T	INSECTS	11.7654	<0.001	.5425
$f_1 = 13$	Plecoptera	9.5792	<0.001	.4912
	A. pacifica	2.3522	<0.001	.1916
	other stoneflies	9.6271	<0.001	.4924
	Ephemeroptera	11.3202	<0.001	.5329
	E. infrequens	11.8770	<0.001	.5448
	Baetis sp.	3.0737	<0.001	.2365
	Paraleptophlebia sp.	6.5330	<0.001	.3970
	Trichoptera	1.8195	<0.050	.1549
	Ochrotrichia sp.	2.1572	<0.025	.1786
	Glossosoma sp.	4.8246	<0.001	.3271
	Rhyacophila sp.	7.8333	<0.001	.4412
	Optioservus sp.	10.2772	<0.001	.5088
U	PLANTS	11.5782	<0.001	.6270
$f_1 = 18$	*A. noterophilum*	11.3335	<0.001	.6220
	R. nasturtium-aquaticum	1.4197	<0.250	.1709
	Z. palustris	1.2621	<0.250	.1548

insignificant to the majority of taxa. *F* tests between regressions (Table 10) were used to determine the significance of individual variables described by more than one parameter (substrate and stream section), and *t* statistics were used both to eliminate those independent variables described by only one parameter and to determine which of the several individual parameters used to describe the substrate distribution had the greatest significance.

Compilation of the significant *t* statistics (Tables 7 and 8) for variables which were significant in all of the regressions gives insight into which variables are significant to each taxon. But some caution should be exercised to avoid using the absolute frequency that specific variables appear as the sole basis of significance. *t* statistics should be evaluated in context with what other variables are included in specific regressions (Table 5). As mentioned earlier, the *t* values of parameters may vary considerably between regressions depending on whether correlated variables are used. For example, the use of one parameter to describe the relation of a variable with known significance to the dependent variable will likely produce a significant *t* value. However, if additional parameters are inserted which also significantly describe the relation by means of a similar variable (or variables), and the variables themselves are significantly correlated among each other, then the value of *t* statistics produced for any one parameter will generally be reduced, and some or all of these parameters may individually no

Table 7. Independent variables which were significant to each plant taxon at the $P = 0.05$ level ($t>[1.977]$).

Plant taxa	Independent variable	t value	Regression coefficient	Regression
Amblystegium noterophilum	depth	1.977	342.6	A
(moss)	percent wt., Ø[-4]	-2.414	-20.61	A
$\overline{X}_{\text{dry wt.}} = 429.2$ g/m^2	lower quartile	2.427	115.8	H
	upper quartile	-2.344	-188.0	H
	90th percentile	-2.551	-202.4	A
Rorippa nasturtium-aquaticum	current velocity	-2.128	-35.85	A
(watercress)	mode phi class	1.977	7.030	A
$\overline{X}_{\text{dry wt.}} = 9.018$ g/m^2	percent wt., Ø[-7]	2.962	2.518	A
	1st percentile	2.876	40.05	U
	5th percentile	-2.468	-35.04	U
	50th percentile	-2.152	-19.15	A
Zannichellia palustris (pondweed) $\overline{X}_{\text{dry wt.}} = 3.603$ g/m^2	none			
Combined weight of all three plant genera	current velocity	2.025	379.3	C
$\overline{X}_{\text{dry wt.}} = 441.8$ g/m^2		2.595	457.3	F
	percent wt., Ø[-4]	-2.289	-21.14	A
	lower quartile	6.504	156.8	H
	upper decile	-2.340	-187.4	H
	inner quartiles	-4.687	-128.3	C
	25th percentile	2.551	171.8	F
	50th percentile	5.321	110.2	C
	90th percentile	-2.492	-199.9	A
		-2.893	-235.1	F

Table 8. Independent variables which were significant to each insect taxon at the P = 0.05 level (t>[1.977]).

a) INSECTS ($\bar{X}_{no.}$ = 8454/m^2)

independent variable	t value	regression coefficient	regression
Amblystegium noterophilum	2.258	2.642	N
	3.082	3.430	O
	2.485	3.275	P
	2.669	3.170	R
	4.020	3.793	T
Rorippa nasturtium-aquaticum	-2.194	-25.22	K
	-2.470	-27.25	L
	-2.072	-25.01	M
	-2.240	-29.33	N
	-2.276	-29.40	O
	-2.103	-24.09	Q
	-2.100	-24.03	S
Zannichellia palustris	-2.212	-32.75	L
	-2.692	-38.84	Q
	-2.742	-39.64	S
depth	1.979	13,424	D
percent wt: $\phi(0) + \phi(-1)$	2.472	198.0	M
percent wt: $\phi(-2) + \phi(-3)$	-2.459	-154.3	N
	-2.032	-140.1	P
lower decile	4.976	2946	H
	5.123	1520	J
lower quartile	-2.892	-1750	H
	2.542	841.7	I
0.25th percentile	2.165	2569	S
10th percentile	4.041	2823	B
	4.363	3043	G
	4.805	2941	K
	5.011	2919	L
	5.658	3777	O
25th percentile	-2.594	-2072	K
	-3.272	-1766	L
	-3.968	-2446	O

Table 8 (continued)

b) Plecoptera ($\overline{X}_{no.} = 1626/m^2$)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	2.027	.7166	N
	2.473	.8078	O
	2.237	.8082	P
	2.142	.7859	R
	2.645	.7584	T
Rorippa nasturtium-aquaticum	-2.154	-9.196	B
	-2.375	-8.474	L
	-2.219	-7.841	M
	-2.162	-8.558	N
	-2.415	-9.155	O
	-2.264	-8.847	P
	-2.760	-10.31	Q
	-2.822	-10.35	R
	-2.703	-9.973	S
	-2.936	-10.55	T
percent wt: $\phi(0) + \phi(-1)$	2.142	59.70	K
	2.304	54.02	M
lower decile	2.587	500.3	H
10th percentile	2.031	383.0	L
	3.086	604.6	O
25th percentile	-2.311	-418.0	O

Table 8 (continued)

c) *Acroneuria pacifica* ($\overline{X}_{no.}$ = 43.45/m^2)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	2.189	.03134	B
	2.028	.02459	L
	2.044	.02274	N
	2.138	.02363	P
	3.380	.03596	T
sample weight	-2.056	-.005166	B
mode Ø class	-2.461	-13.77	B
percent wt: Ø(4)	1.996	16.47	R
percent wt: Ø(-4)	-2.629	-3.754	B
percent wt: Ø(-7)	-2.212	-3.015	B
percent wt: Ø(2) + Ø(1)	2.663	1.562	K
	2.719	.9535	M
	2.392	.7946	P
percent wt: Ø(-2) + Ø(-3)	3.210	2.008	K
	3.004	1.813	M
	2.327	1.389	N
	2.259	1.306	P
lower decile	2.036	14.18	H
upper quartile	2.233	20.90	H
10th percentile	-2.341	-31.31	S
25th percentile	-2.512	-27.99	B
50th percentile	2.128	29.74	B

Table 8 (continued)

d) Other stoneflies ($\overline{X}_{no.}$ = 1583/m^2)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	1.976	.6939	N
	2.427	.7873	O
	2.187	.7846	P
	2.104	.7639	R
	2.543	.7225	T
Rorippa nasturtium-aquaticum	-2.174	-9.213	B
	-1.985	-7.179	K
	-2.406	-8.515	L
	-2.256	-7.904	M
	-2.208	-8.680	N
	-2.455	-9.241	O
	-2.306	-8.947	P
	-2.757	-10.21	Q
	-2.823	-10.25	R
	-2.706	-9.914	S
	-2.945	-10.48	T
percent wt: Ø(0) + Ø(-1)	2.181	60.27	K
	2.375	55.22	M
lower decile	2.535	486.0	H
10th percentile	2.047	382.5	L
	3.084	600.1	O
25th percentile	-2.332	-419.0	O

Table 8 (continued)

e) Ephemeroptera ($\overline{X}_{no.} = 2108/m^2$)

independent variable	*t* value	regression coefficient	regression
percent wt: Ø(2) + Ø(1)	-2.429	-38.17	M
percent wt: Ø(0) + Ø(-1)	1.975	81.15	K
	2.425	85.35	M
percent wt: Ø(-2) + Ø(-3)	-2.046	-56.14	K
	-2.009	-54.33	M
	-2.410	-66.49	N
	-2.439	-67.55	P
lower decile	2.514	650.8	H
lower quartile	-2.297	-608.0	H
0.25th percentile	2.298	1227	S
10th percentile	2.664	762.4	K
	2.922	808.3	L
	3.335	969.2	O
25th percentile	-2.823	-723.3	L
	-3.138	-842.3	O

Table 8 (continued)

f) *Ephemerella infrequens* ($\overline{X}_{no.} = 1463/m^2$)

independent variable	*t* value	regression coefficient	regression
Rorippa nasturtium-aquaticum	-2.090	-9.800	K
	-2.142	-9.694	L
	-2.103	-9.850	M
	-2.198	-10.92	N
	-2.194	-10.62	O
	-2.095	-10.57	P
percent wt: Ø(0) + Ø(-1)	2.217	68.91	M
percent wt: Ø(-2) + Ø(-3)	-2.248	-53.49	N
	-2.095	-51.13	P
lower decile	2.877	630.7	H
lower quartile	-2.560	-573.4	H
0.25th percentile	2.286	1021	S
10th percentile	2.293	615.6	B
	3.154	787.1	K
	3.479	831.7	L
	4.032	1008	O
25th percentile	-2.948	-652.9	L
	-3.433	-793.0	O

g) *Baetis* sp. ($\overline{X}_{no.} = 414.1/m^2$)

independent variable	*t* value	regression coefficient	regression
none significant			

Table 8 (continued)

h) *Paraleptophlebia* sp. ($\overline{X}_{no.}$ = 230.0/m^2)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	3.223	.2564	B
	4.145	.2949	K
	4.828	.3413	L
	4.121	.2944	M
	3.251	.2035	N
	3.820	.2332	O
	3.349	.2089	P
	4.702	.3610	Q
	5.290	.3879	R
	4.654	.3475	S
	5.435	.3201	T
Rorippa nasturtium-aquaticum	2.328	1.653	K
	2.002	1.421	L
	2.068	1.427	M
	2.922	2.047	N
	2.482	1.758	O
	2.750	1.855	P
	2.056	1.507	R
depth	2.048	824.4	B
percent wt: Ø(0)	2.432	30.56	B
percent wt: Ø(-5)	2.027	14.44	B
percent wt: Ø(-7)	3.284	24.89	B
percent wt: Ø(2) + Ø(1)	-3.168	-6.478	M
	-2.427	-4.551	P
percent wt: Ø(0) + Ø(-1)	3.404	18.46	K
	3.537	16.20	M
	3.551	18.67	N
	3.799	16.59	P
lower decile	2.068	86.92	H
0.25th percentile	2.514	195.9	S
10th percentile	2.109	79.10	L
25th percentile	-2.230	-77.47	L
75th percentile	2.051	137.5	B

Table 8 (continued)

i) Trichoptera ($\overline{X}_{no.}$ = 915.4/m^2)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	-2.913	-.6541	B
	-3.595	-.9276	K
	-3.507	-.8690	L
	-3.086	-.8894	M
	-2.682	-.6282	N
	-2.187	-.4879	O
	-2.798	-.5757	Q
	-3.177	-.6656	S
Rorippa nasturtium-aquaticum	-2.122	-5.495	O
Zannichella palustris	-2.848	-7.636	B
	-2.066	-6.902	L
	-2.855	-7.337	Q
	-2.283	-6.241	R
	-2.591	-6.901	S
percent wt: Ø(2)	2.051	52.66	Q
	2.486	68.42	R
percent wt: Ø(2) + Ø(1)	2.235	18.43	M
	2.303	17.97	P
lower decile	4.574	489.5	H
lower quartile	-3.267	-357.3	H
10th percentile	3.608	443.0	B
	5.530	758.0	K
	5.086	668.5	L
	4.979	666.1	O
25th percentile	-2.746	-490.9	K
	-2.569	-312.9	L
	-2.982	-368.5	O

Table 8 (continued)

j) *Ochrotrichia* sp. ($\overline{X}_{no.}$ = 528.0/m^2)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	-2.692	-.5700	B
	-3.197	-.8413	K
	-3.054	-.7781	L
	-2.796	-.8052	M
	-2.154	-.5186	N
	-2.207	-.4317	Q
	-2.510	-.5045	S
Zannichellia palustris	-2.222	-5.620	B
	-2.098	-5.127	Q
sample weight	-2.230	-.08287	B
percent wt: $\phi(3)$	-2.087	-119.0	Q
	-2.205	-126.7	R
percent wt: $\phi(2)$	2.670	65.18	Q
	3.016	77.75	R
percent wt: $\phi(2) + \phi(1)$	2.642	21.78	M
	1.980	25.08	N
	2.899	22.71	P
lower decile	3.773	387.0	H
lower quartile	-2.143	-224.7	H
10th percentile	2.820	326.5	B
	4.941	690.7	K
	4.306	582.0	L
	4.102	570.6	O
25th percentile	-2.340	-426.8	K
	-2.169	-278.7	O
50th percentile	-2.464	-509.6	B

Table 8 (continued)

k) *Glossosoma* sp. ($\overline{X}_{no.} = 228.6/m^2$)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	-2.185	-.1336	L
	-2.997	-.1777	N
	-3.551	-.1989	O
	-2.836	-.1685	P
	-2.444	-.1588	Q
	-2.673	-.1693	S
	-3.520	-.1780	T
Zannichellia palustris	-2.058	-1.651	T
algae	2.331	201.0	B
lower decile	2.264	76.65	H
lower quartile	-2.990	-103.5	H
0.25th percentile	3.169	237.1	Q
	3.739	246.9	S
1st percentile	-2.181	-226.7	Q
	-2.725	-262.4	S
10th percentile	2.333	87.55	B
	2.060	66.81	L
	2.248	75.51	O
25th percentile	-2.219	-66.67	L
90th percentile	-2.197	-129.2	B

l) *Rhyacophila* sp. ($\overline{X}_{no.} = 158.8/m^2$)

independent variable	*t* value	regression coefficient	regression
Amblystegium noterophilum	2.279	.07802	O

Table 8 (concluded)

m) Coleoptera: *Optioservus* sp. $(\overline{X}_{no.} = 3805/m^2)$

independent variable	t value	regression coefficient	regression
Amblystegium noterophilum	2.251	1.661	B
	2.669	1.725	K
	2.822	35.18	L
	2.660	1.799	M
	3.894	2.365	N
	4.480	2.592	O
	3.966	2.641	P
	2.813	1.899	R
	5.034	2.708	T
Zannichella palustris	-2.195	-18.63	Q
	-2.251	-18.78	S
percent wt: $\phi(-2) + \phi(-3)$	-2.157	-70.28	N
lower decile	3.841	1306	H
upper decile	-2.455	-1433	H
10th percentile	3.697	1492	B
	3.322	1141	K
	3.264	1060	L
	4.429	1536	O
25th percentile	-2.551	-817.2	O

Table 9. Means of the dependent and independent variables computed from the mean values from each of the 143 samples. These means may be used in conjunction with the regression coefficients listed in Table 8.

Variable	Mean
INSECTS	8454/m^2
Plecoptera	1626/m^2
Acroneuria pacifica	43.45/m^2
other stoneflies	1583/m^2
Ephemeroptera	2108/m^2
Ephemerella infrequens	1463/m^2
Baetis sp.	414.1/m^2
Paraleptophlebia sp.	230.0/m^2
Trichoptera	915.4/m^2
Ochrotrichia sp.	528.0/m^2
Glossosoma sp.	228.6/m^2
Rhyacophila sp.	158.8/m^2
Coleoptera: *Optioservus* sp.	3805/m^2
PLANTS	441.8 g/m^2
Amblystegium noterophilum	429.2 g/m^2
Rorippa nasturtium-aquaticum	9.018 g/m^2
Zannichellia palustris	3.603 g/m^2
algae	present in 10.49% (15) of the samples
sample depth	0.2347 m
current velocity	0.4101 m/sec
sample weight	5936 g
mode phi class	Ø(-4.042)
lower decile shortness	2.858 Ø
lower quartile shortness	4.422 Ø
inner quartile shortness	2.776 Ø
upper quartile shortness	1.801 Ø
upper decile shortness	1.101 Ø

Table 9 (continued)

Variable		Mean	
		regressions A-P	regressions Q-U
percent weight in phi classes	4		.6904%
	3		2.751%
	2	7.329%	6.282%
	1	6.451%	5.775%
	0	6.676%	
	-1	4.840%	
	-2	6.199%	
	-3	10.01%	
	-4	18.94%	
	-5	25.45%	
	-6	13.30%	
	-7	.8196%	
	[2] + [1]	13.78%	
	[0] + [-1]	11.46%	
	[-2] + [-3]	16.12%	
percentiles	0.25		4.153 Ø
	1		2.995 Ø
	5		1.799 Ø
	10	.4246 Ø	1.003 Ø
	25	-2.217 Ø	-1.665 Ø
	50	-4.519 Ø	-4.415 Ø
	75	-5.611 Ø	-5.569 Ø
	90	-6.356 Ø	-6.319 Ø
stream sections		dummy variables (7) to account for the longitudinal variability in the stream sections (8)	
time	linear	9.538 (biweekly sampling dates numbered consecutively from 1 through 18)	
	cubic	117.9	
	quadratic	1635	

longer be significant. An *F* test (as described in Table 10) however, will still show significance of the group of parameters, just as the *t* statistic will indicate significance if only one parameter is used.

Substrate. Parameters used to represent substrate-size distribution in the initial regression models (regressions A and B, Tables 5 and 6) were the percentage weight in each of the size-classes Ø[-7] through Ø[1] (Ø[2] was omitted here due to the statistical necessity that the percentages do not total 100), the 10th, 25th, 50th (median), 75th and 90th percentiles, the mode size-class, and the total sample weight. In subsequent models (regressions C through P, Tables 5 and 6), various combinations of these plus additional parameters were used. These included the 50th (regressions C and D), and the 10th and 25th percentiles (regressions K, L, N, O) as the only percentiles included, the shortness of the inner quartile in phi units (regressions C and D), the shortness of the lower and upper quartiles and deciles both separately and together (regressions H - J), and the combined lower size-classes -- Ø[2] + Ø[1], Ø[0] + Ø[-1], Ø[-2] + Ø[-3] (regressions K, M, N, P). From these analyses it became evident that, while explanatory power over dependent variables was in independent variables describing the middle substrate size range and lesser power in the upper range (Tables 7 and 8), the stronger explanatory power was in those variables describing the smaller substrate sizes. The 10th and 25th percentiles and the shortness of the lower decile were significant to 11 of the 13 insect taxa; the lower quartile was significant to 6 taxa. Other substrate parameters were significant only occasionally.

The initial calculations of substrate parameters were based on data for the distribution in size-classes Ø[-7] through Ø[2] only. Though data were available for phi classes [3] through [5+], they were ignored because the mesh size of the sampler net (36 threads/cm) allowed some particles less than 0.25 mm (Ø[2+]) to pass through. However, considerable quantities less than this size were retained by the net and scooped out of the sampler by hand. Because the regressions models showed significance down to the smallest size-class (Ø[2]) included to this point, the size-class percentages were recalculated to include substrate in classes Ø[3] through Ø[5+]; the percentiles were recalculated and the 0.25th, 1st, and 5th percentiles were also determined. These revised data were used in subsequent regressions (regressions Q through U). It had to be assumed that this bias of the loss of some particles less than 0.25 mm was relatively proportional in all individual samples.

The subsequent models developed (regressions Q through U, Tables 5 and 6) showed that the 0.25th through 10th percentiles as representatives of substrate distribution (Tables 7 and 8) were significant to the majority of taxa. To determine whether the percentiles or the size-class percentages had greater significance in relation to the other, both groups were excluded individually and simultaneously from what otherwise was the final regression model -- regression S (Tables 5, 6, 16). *F* tests (Table 10) indicated that the percentiles (0.25, 1, 5, 10) had far greater significance to virtually all of the insect taxa than did the size-classes regardless of whether or not the latter were included in the regression. Thus the 10th and 25th percentiles and the lower decile and quartiles were considered the best representatives of substrate distribution using the data excluding size-classes Ø[3] to Ø[5+], while the 0.25, 1st, 5th and 10th percentiles were the most significant representatives using data for all of the size-classes measured (Ø[-7] through Ø[5+]). No new regressions were computed with the additional data using the 10th and 25th percentiles or the lower decile and quartiles as the only substrate parameters, but it can reasonably be assumed that their significance would have changed little. The actual contribution by weight of size-classes Ø[3] to Ø[5+] compared to total sample weight was slight (2.75%) and thus altered the values of the original parameters only slightly.

Plants as independent variables. Regressions in which each of the plant species was considered an independent variable (Tables 5 and 6) indicated that each species was significantly correlated to several insect taxa (Table 8). Because the sign of the *t* values tended to be consistent within species but to vary among them, it was deemed undesirable to consider the total quantity of all three species combined as a single independent variable beyond the initial regressions.

Table 10. Tests of F between regressions. Refer to Table 5 for the complete set of independent variables included in each regression.

$$F_{(\text{reg. a - reg. b})} = \frac{(s.s._{a} - s.s._{b})/(f_{1\cdot a} - f_{1\cdot b})}{\text{residual } m.s.}$$

$s.s.$ = sum of squares due to regression f_1 = degrees of freedom $m.s.$ = mean square error

An alternate method for calculating F between any of the regressions in this study (Table 5) is to use the following formula with the R^2, N, and f values from Table 6.

$$F_{(\text{reg. a - reg. b})} = \frac{(R^2_{a} - R^2_{b})/(f_{1\cdot a} - f_{1\cdot b})}{(1 - R^2_{s})/(N - f_{1\cdot a} - 1)}$$

DISTRIBUTION POINTS OF F

P	$(f_{1\cdot a} - f_{1\cdot b})$					
	2	3	4	7	9	10
0.250	1.40	1.39	1.37	1.31	1.29	1.28
0.100	2.34	2.12	1.98	1.76	1.67	1.64
0.050	3.05	2.66	2.43	2.07	1.94	1.89
0.025	3.77	3.20	2.86	2.36	2.19	2.13
0.010	4.75	3.91	3.44	2.75	2.52	2.43
0.005	5.46	4.44	3.86	3.01	2.73	2.63
0.001	7.22	5.69	4.85	3.67	3.28	3.14

a) Significance of the shortness of lower and upper quartiles and deciles.

Regression Pair	H — I	H — J
Independent Variables Tested	lower and upper deciles	lower and upper quartiles
$(f_{1\cdot a} - f_{1\cdot b})$	2	2
INSECTS	13.17	4.46

Table 10 (continued)

b) Significance of the percent weights in the size-class combinations of Ø[2] + Ø[1], Ø[0] + Ø[-1], Ø[-2] + Ø[-3], the 10th and 25th percentiles, stream sections, and combination of the stream sections with the substrate parameters.

Regression pair	K - L	K - M	K - N	K - O	K - P
Independent Variables Tested	phi groups	percentiles	sections	sections, phi groups	sections, percentiles
$(f_{1 \cdot a} - f_{1 \cdot b})$	3	2	7	10	9
INSECTS	0.91	12.22	7.84	6.69	12.02
Plecoptera	2.58	1.18	5.48	3.93	5.49
Acroneuria pacifica	4.01	0.84	2.64	2.54	2.21
other stoneflies	2.60	1.16	5.55	3.99	5.54
Ephemeroptera	2.22	3.56	4.88	4.16	5.28
Ephemerella infrequens	1.45	5.19	4.40	3.73	5.68
Baetis sp.	0.90	2.33	2.56	2.17	2.48
Paraleptophlebia sp.	4.61	1.66	1.49	2.67	1.39
Trichoptera	1.55	16.69	2.72	2.90	6.18
Ochrotrichia sp.	2.24	13.58	3.05	3.50	5.55
Glossosoma sp.	1.13	1.07	3.61	3.30	3.24
Rhyacophila sp.	0.29	0.62	6.27	4.49	5.08
Coleoptera: *Optioservus* sp.	0.37	7.07	4.19	3.99	7.18

Table 10 (concluded)

c) Significance of percent weights in size-classes Ø[4], Ø[3], Ø[2], and Ø[1], and the 0.25th, 1st, 5th, and 10th percentiles.

Regression Pair	Q - R	Q - S	R - T	S - T
Independent Variables Tested	percentiles	phi classes	phi classes	percentiles
$(f_{1 \cdot a} - f_{1 \cdot b})$	4	4	4	4
INSECTS	6.85	1.54	1.22	6.65
Plecoptera	3.03	0.83	0.17	2.40
Acroneuria pacifica	3.04	4.40	6.27	4.80
other stoneflies	2.90	0.91	0.25	2.26
Ephemeroptera	2.33	0.75	1.09	2.75
Ephemerella infrequens	2.75	0.91	1.09	3.40
Baetis sp.	1.64	0.80	1.04	1.92
Paraleptophlebia sp.	1.75	0.76	1.92	2.99
Trichoptera	6.41	3.76	5.58	8.45
Ochrotrichia sp.	5.36	4.38	7.64	8.75
Glossosoma sp.	3.59	0.88	1.04	3.85
Rhyacophila sp.	1.34	1.08	0.55	0.81
Coleoptera: *Opticservus* sp.	4.36	0.34	1.43	5.73

Because each of the plant species tended to be significant to several insect taxa in the initial regressions, they were included in subsequent models as well as the final model chosen -- regression S (Table 16). The dummy variable inserted to note the occurrence of significant quantities of filamentous algae mixed with the higher aquatic plants (15 of the 143 samples) proved insignificant in initial models and was not included in subsequent regressions.

Other variables. The linear, quadratic and cubic factors of time inserted to adjust the regressions for seasonal variations were significant as determined from the individual t values (see Table 16). The dummy variables inserted to account for possible longitudinal variations along the study area not accounted for by measured variables were also significant as a group as determined from the difference in the F test between regressions K and N (Table 10b). Both the factors for time and stream section were thus included in most subsequent regressions, including the final model. (The sectional differences in substrate distribution for all samples are summarized in Table 13 and the sectional differences in plant biomass and insect numbers are summarized in Tables 14 and 15 respectively.)

Current velocity measurements included in regressions A through D, F and G, were significantly correlated only to the watercress and the total weight of all three plant species (Table 7). Depth was also significantly correlated to the watercress, but unlike current velocity, the correlation matrix also indicated several simple correlations of depth to other taxa. Because both variables were insignificantly correlated to other taxa in the regression analyses itself however, they were not considered beyond the initial regression models.

Plants as dependent variables. The independent variables which were significant to each plant taxa in those regressions (A, C, E, F, H, U, Table 5) in which the plants were considered as dependent variables are included in Table 7. Because the regressions subsequent to the initial ones were refined primarily for the insect taxa, no final model was developed exclusively for the plant taxa. However, the independent variables which were significant indicate that the trend with respect to substrate size was similar to that for most insect taxa. In general, significant negative relationships resulted for parameters representing larger substrate and significant positive relationships for parameters representing smaller substrate. This trend is generally typical for both the moss and the watercress, as well as for the combined plant biomass. No significant correlations to the pondweed, which contributed less than one percent of the total plant biomass (Table 14), resulted between any of the substrate or other parameters in any of the regression models.

Prediction of change in the quantity of organisms with changes in magnitude of the independent variables

Substrate. The mean substrate distribution curve (Figure 4a) determined by summing the individual sample percentages in each size-class (Table 13) is essentially bimodal. The low point between modes is at approximately Ø[-1] (2 mm) and the mode representing the larger substrate sizes peaks at nearly Ø[-5] (64 mm). The latter is about four times the magnitude of the broad mode at Ø[2] to Ø[0] (0.125-1.0 mm) representing the smaller sizes. To graphically represent the changes in taxa numbers as the four lowest percentiles (0.25, 1, 5, and 10) vary from the mean distribution, all four percentiles have been arbitrarily shifted by the same degree (Figure 4a). The corresponding quantitative changes predicted in the nine insect taxa which were significantly related to the percentiles in regression S (Table 10c) are represented in Figure 4b. All nine of these taxa show that as the substrate composition is proportionally distributed toward the smallest substrate sizes, predicted numbers increase. It would also be possible to demonstrate changes in taxa numbers with shifts of the percentiles to any other degree or even if changed individually by using the corresponding regression coefficients and mean values (Tables 8, 9, and 16).

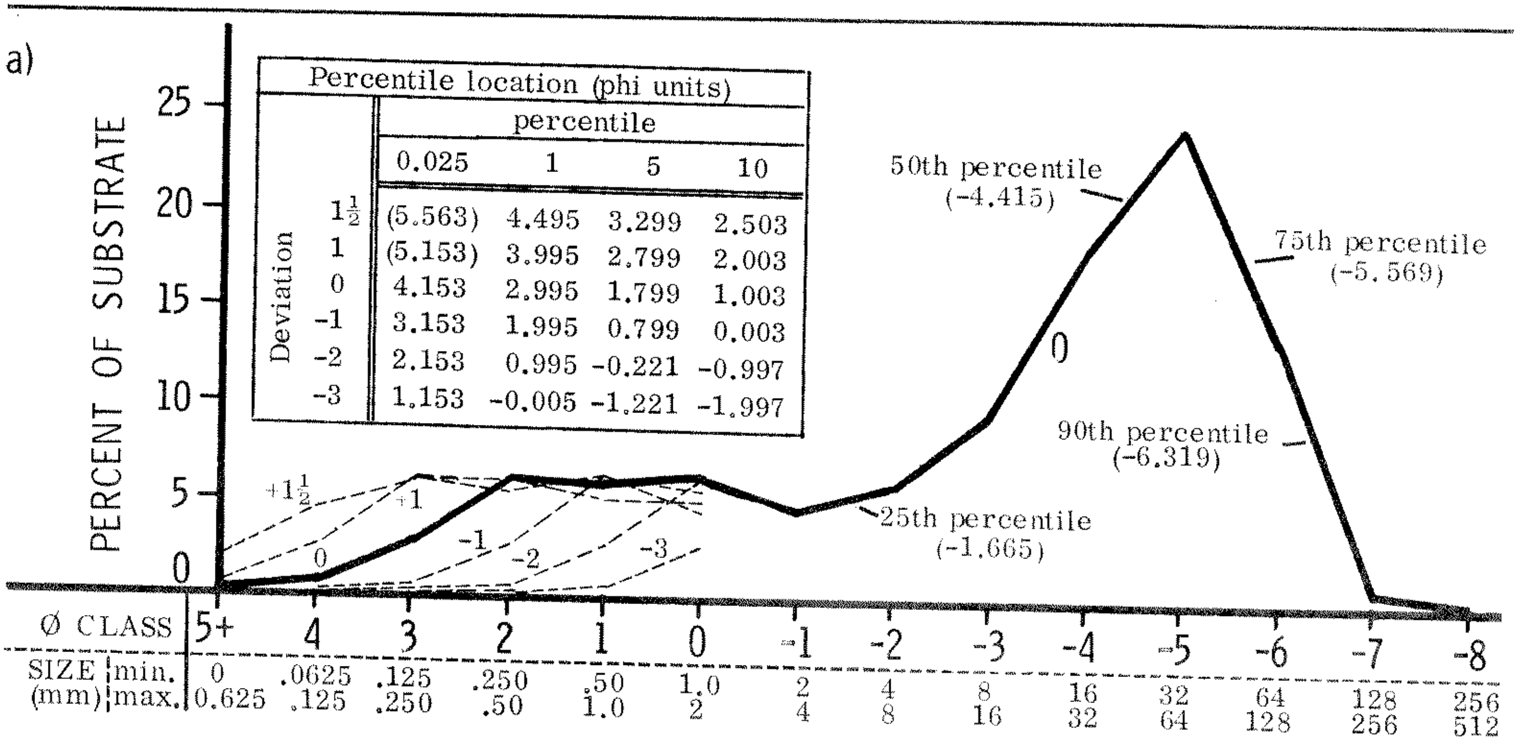
A similar trend toward greater numbers of insect taxa with

Figure 4. Deviation of the four lowest percentiles (0.25, 1, 5, 10) from their means and the predicted change in number of each insect taxon which was significant to these percentiles at the 5 percent level.

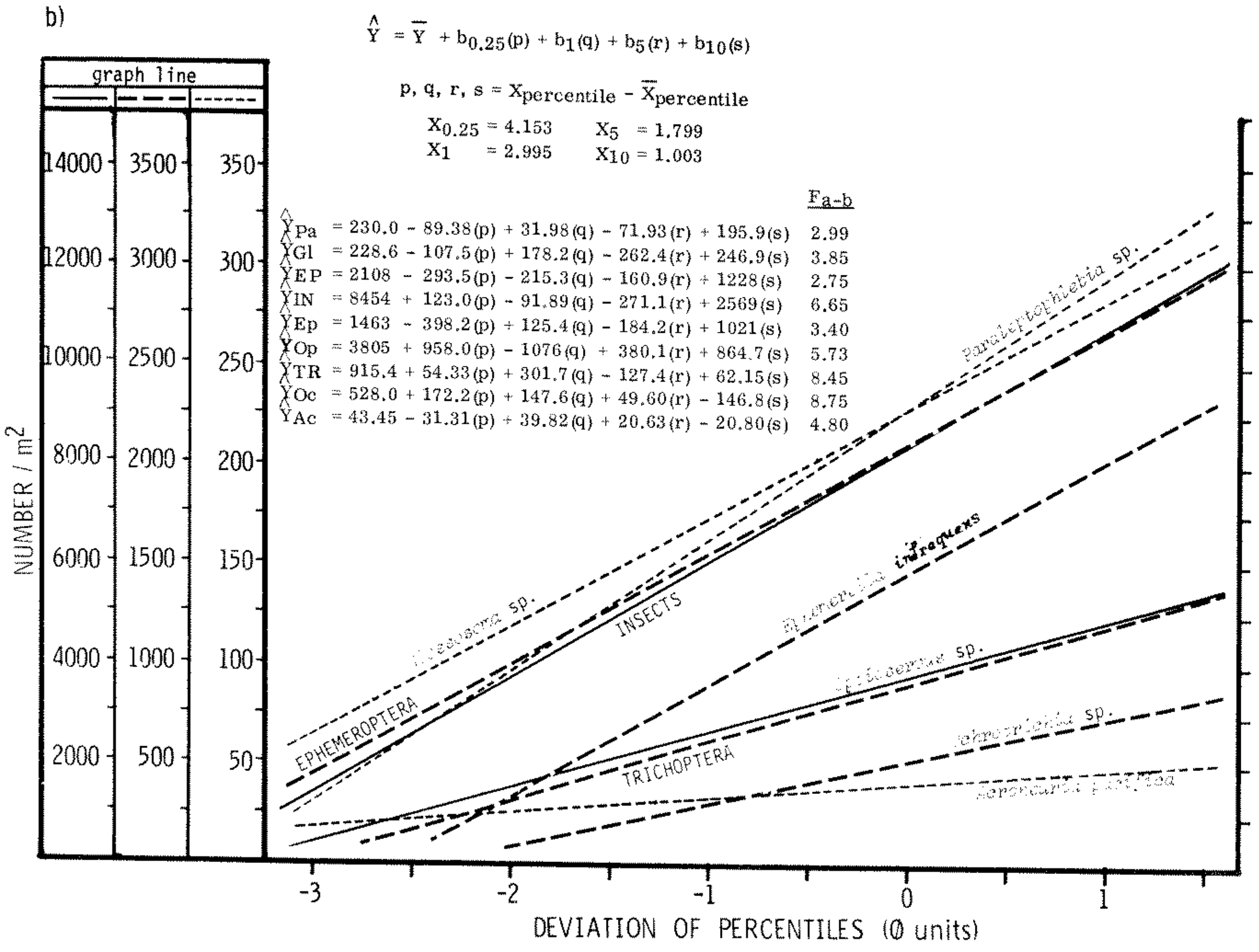
a) The mean substrate distribution ("0") determined by averaging the percent weights in each phi class from each of the 143 samples (Table 13). The curves of the hypothetical substrate distributions ($1\frac{1}{2}$, 1, -1, -2, -3) were calculated after shifting all four percentiles as a group by the amount in phi units indicated. All hypothetical distributions are well within ranges found in individual samples.

b) The predicted change in number of each insect taxon (9 of the 13 taxa) which were significant in the final model to changes in the four lowest percentiles. The F statistics are from Table 10c.

a)



	Percentile location (phi units)			
	percentile			
Deviation	0.025	1	5	10
1½	(5.563)	4.495	3.299	2.503
1	(5.153)	3.995	2.799	2.003
0	4.153	2.995	1.799	1.003
-1	3.153	1.995	0.799	0.003
-2	2.153	0.995	-0.221	-0.997
-3	1.153	-0.005	-1.221	-1.997



$$\hat{Y} = \overline{Y} + b_{0.25}(p) + b_1(q) + b_5(r) + b_{10}(s)$$

$$p, q, r, s = X_{percentile} - \overline{X}_{percentile}$$

$X_{0.25} = 4.153$ $X_5 = 1.799$

$X_1 = 2.995$ $X_{10} = 1.003$

	F_{a-b}
$\hat{Y}_{Pa} = 230.0 - 89.38(p) + 31.98(q) - 71.93(r) + 195.9(s)$	2.99
$\hat{Y}_{Gl} = 228.6 - 107.5(p) + 178.2(q) - 262.4(r) + 246.9(s)$	3.85
$\hat{Y}_{EP} = 2108 - 293.5(p) - 215.3(q) - 160.9(r) + 1228(s)$	2.75
$\hat{Y}_{IN} = 8454 + 123.0(p) - 91.89(q) - 271.1(r) + 2569(s)$	6.65
$\hat{Y}_{Ep} = 1463 - 398.2(p) + 125.4(q) - 184.2(r) + 1021(s)$	3.40
$\hat{Y}_{Op} = 3805 + 958.0(p) - 1076(q) + 380.1(r) + 864.7(s)$	5.73
$\hat{Y}_{TR} = 915.4 + 54.33(p) + 301.7(q) - 127.4(r) + 62.15(s)$	8.45
$\hat{Y}_{Oc} = 528.0 + 172.2(p) + 147.6(q) + 49.60(r) - 146.8(s)$	8.75
$\hat{Y}_{Ac} = 43.45 - 31.31(p) + 39.82(q) + 20.63(r) - 20.80(s)$	4.80

proportionally smaller substrate particles is noted in the other substrate parameters not included in the final regression model (Table 8). The most significant of these to the majority of taxa were the 10th and 25th percentiles and the lower deciles and quartiles, although other substrate parameters were occasionally significant. Similar predictions of numbers as given in Figure 4b can be made using the regression coefficients listed in Table 8 with the means listed in Table 9.

Examination of the parameters representing the smallest substrate sizes (the 0.25th through 10th percentiles, the smallest substrate classes, the lower decile -- Table 8) show that the signs of the regression coefficients of taxa significant to these variables are predominantly positive. Thus, greater numbers of insects are generally predicted when there is a relatively greater proportion of substrate in the size-classes from approximately Ø[2] to Ø[0]. However, examination of parameters representing the lower-middle substrate distribution (25th and 50th percentiles, shortness of the lower and inner quartile, percentages in the size-classes Ø[-1] through about Ø[4]), show that greater numbers of taxa are concurrently predicted when the distribution of substrate in this size range (about 2-16 mm) is proportionally toward the larger particles. The 11 regression coefficient pairs of the 10th and 25th percentiles (Table 8) corresponding to the significant taxa show that the coefficients for the 10th percentile are all positive while those for the 25th percentile are all negative.

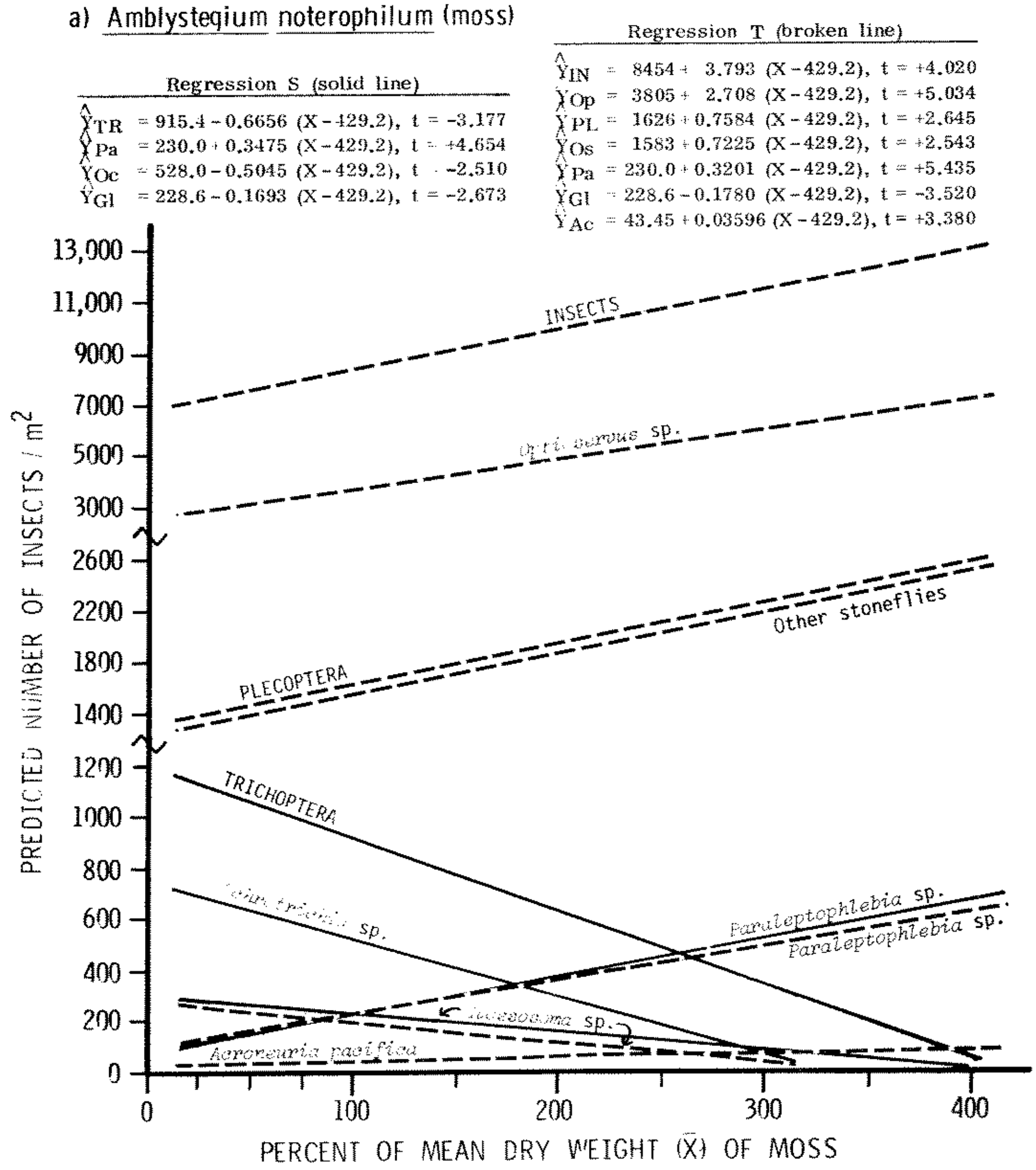
These percentiles lie on either side of the low point at about Ø[1] (Figure 4a) in the mean substrate distribution. Likewise, the same trend of opposite signs occurs for the six coefficient pairs of the lower decile and quartile. In summary, the greatest numbers in the insect taxa are predicted to be present when the substrate distribution by weight is distinctly low at about the Ø[-1] size-class, proportionally high between the size-classes from about Ø[2] to Ø[0], and proportionally high from beyond size-class Ø[1] to about Ø[4]. The significance of this aspect of the substrate distribution along with its relationship to other variables will be discussed later.

Plants as independent variables. Taxa which were significantly correlated to each of the three plant species (Table 8) in the final regression model, regression S (Table 16), and the predicted changes in numbers with changes in each plant's biomass are shown in Figure 5. *t* statistics from this model indicate that three insect taxa (Trichoptera, *Ochrotrichia* sp. and *Glossosoma* sp.) are negatively correlated to the moss (*Amblystegium noterophilum*), but one taxon (*Paraleptophlebia* sp.) is positively correlated. The model also indicated that three taxa (Insects, Plecoptera, and "other stoneflies") are negatively correlated to the watercress (*Rorippa nasturtium-aquaticum*) and three taxa (Insects, Trichoptera and *Optioservus* sp.) are negatively correlated to the pondweed (*Zannichellia palustris*). *t* statistics from regression T (Table 8) however, show a considerable difference (Figure 5) in the

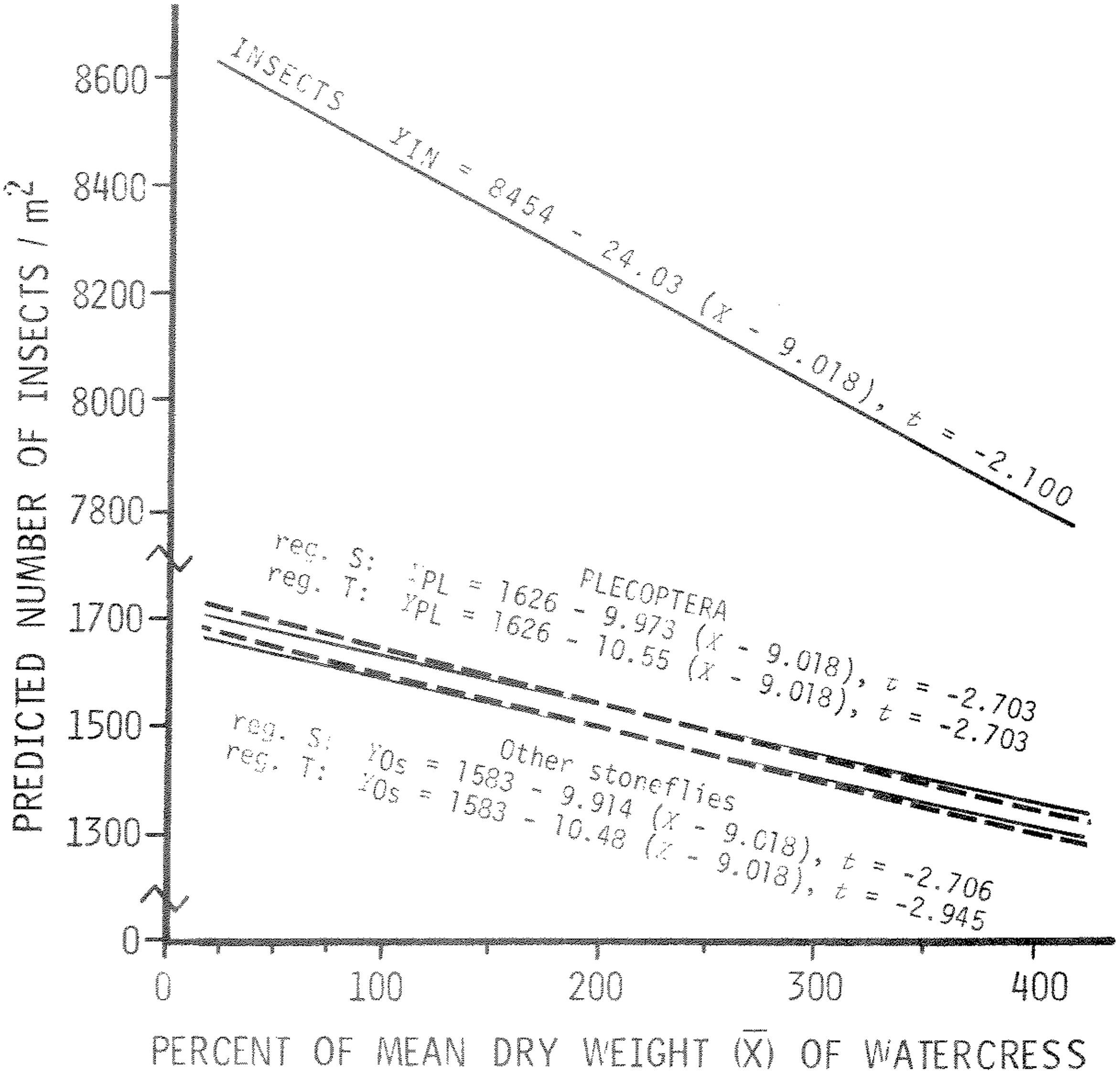
Figure 5. Predicted changes in the number of each insect taxon which was significantly related (5 percent level) to the quantity of each plant species in regression S (the final model) and regression T. The general regression formula is $Y_i = Y_i + b_i(X_p - X_p)$, where i refers to insect taxa and p to plant taxa. The regression coefficients and *t* statistics are from Table 8, and the plant and insect means from Table 9.

regression S -- solid line regression T -- broken line

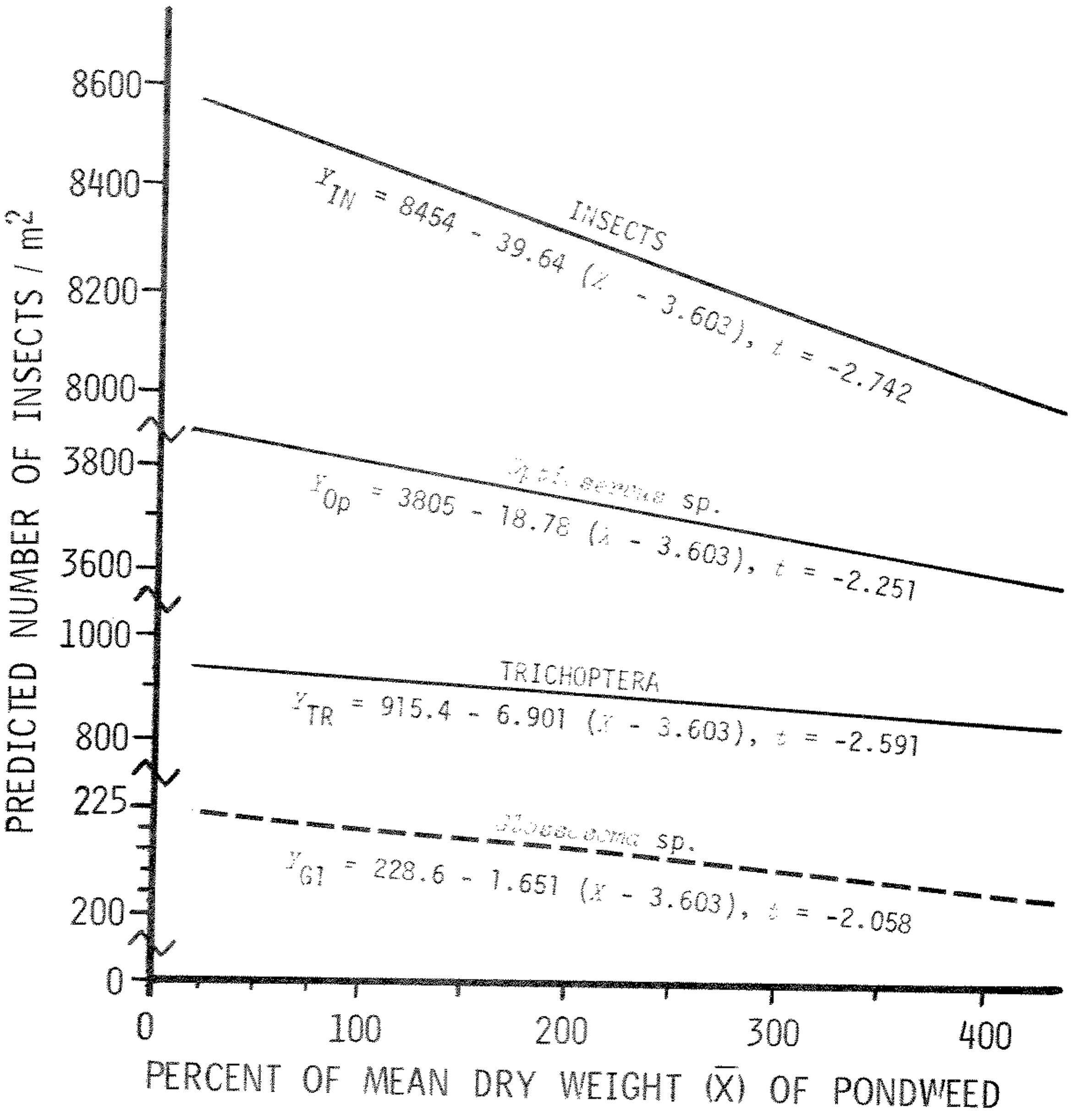
a) Amblystegium noterophilum (moss)



b) Rorippa nasturtium-aquaticum (watercress)



c) Zannichellia palustris (pondweed)



significant insect taxa and their predicted numbers to the plants. Six taxa (Insects, Plecoptera, *Acroneuria pacifica*, "other stoneflies", *Paraleptophlebia* sp. and *Optioservus* sp.) are now significantly correlated positively to the moss, while *Glossosoma* sp. is still negatively correlated to it. The only change in the correlations to the watercress is that the insect taxon is no longer significant to it. The three taxa significantly correlated negatively to the pondweed in regression S are no longer significant in regression T, but *Glossosoma* sp. is now significantly correlated negatively to pondweed in the latter regression. The considerable variation in the significance of the insects to the plants between these two regressions, and a rationale of which regression appears to be more appropriate, will be discussed later.

DISCUSSION

Evaluation of the results

The variables included in the multiple regression (Table 5) chosen as the final model, regression S (Table 16), accounted for over 62 percent ($R^2 = 0.6227$, Table 16a) of the variation in the insect taxon (the sum of all insect numbers). The R^2 statistics plus the F statistics (virtually all of which were significant at less than the 0.1 percent level) from all regressions (Table 6) indicates that a very substantial portion of the variation relating to the microdistribution of the insects was accounted for. Snedecor and Cochran (1967) state that, even when the variables included in a regression are statistically significant, it is not uncommon to find that the percentage of the variance of the dependent variable attributed to the regression is much less than 50 percent. Variation not accounted for in multiple regression analyses, according to Snedecor and Cochran, are due to variables not considered important, variables not feasible to measure, and unknown variables. Some of these possibilities as applied to this study will be mentioned later.

Substrate. The parameters representing the substrate size distribution (Tables 7 and 8) show that the greatest quantity of both insect and plant taxa are related to a bimodal substrate distribution by weight, similar to that represented by the mean distribution summed from the individual samples (Figure 4a). The 10th and 25th percentiles, the shortness of the lower decile and the lower quartile, and to a lesser extent the percentage weights in the appropriate size-classes (Table 8) show that 11 of the 13 insect taxa are significantly related to a distinct low point in the substrate distribution between the two modes. Further, greater numbers are related to an increase in the mode representing the smallest substrate particles (determined principally by the 0.25th, 1st, 5th, and 10th percentiles and the lower decile shortness, but also by the percentages in the corresponding size-classes). But concurrently, greater numbers are significantly related, though less strongly, to a rise toward the mode representing the larger substrate particles (determined principally by the 25th percentile and lower quartile, and to a much lesser extent by the higher percentiles and corresponding size-classes). Little significance was attributed to this mode, however, from near its peak (at about Ø[-5] toward the largest substrate particles. The fact that these two modes are simultaneously related to greater numbers in the insect taxa indicates that fewer numbers are predicted if the substrate is composed of particles by weight predominantly in the size ranges within either one or the other modes. The relationship that exists here, then, is one where the greatest numbers in most taxa are related to a bimodal distribution which consists of particles grossly grouped into both a larger (roughly Ø[-2] to Ø[-6], Figure 4a) and a smaller size group

(0[4] to 0[0]).

In the published research relating to associations between benthic fauna and substrate (Table 1), the general conclusion drawn is that greater numbers and diversity of organisms are associated with either larger substrate sizes or substrate compositions that are well-represented by all particle sizes. Hynes (1970) points out that areas with larger stones are generally more complex and are associated with greater diversity of fauna. In virtually all of the studies on substrate, only phenotypic descriptions of areas have been used, necessitating the consideration of sections of streams with gross, readily discernible differences. In general, smaller substrate sizes have been studied only in areas where they exist in a relatively homogeneous state, rather than in their proportion and relation to larger particles. The question which arises here then, is whether the results of this study conform to any of the above observations in previous studies, and what the significance is of the smaller particles. It is relatively easy to deduce why larger substrate particles are favorable for insect habitats. Included are available space for protection and foraging, stability, places for deposition of food, and greater variability of microcurrents. Larger particles were found to be significant to some extent in this study. The reasons why the smaller substrate particles were so much more significant will be considered with a discussion of the other variables after the latter have been considered individually.

Plants as independent variables. The results from the final regression model for plants as independent variables to the insect taxa showed that, with one exception (*Paraleptophlebia* sp. to *Amblystegium noterophilum*, Figure 5a), the few correlations that were significant between insect taxa and the plant species were negative. The plants themselves act as a habitat for many insects. They also provide them with food either directly, or indirectly by serving as a substrate for periphyton. In sorting the preserved samples in the laboratory, a strong relationship seemed to exist between insect numbers and the quantity of plants, especially the moss. This observation is substantiated by the very significant simple correlation (*c.c.* = 0.5533, Table 4) between the moss and the riffle beetle larva (*Optioservus* sp.), and between the moss and the insect taxon as well (*c.c.* = 0.3735). Thus, it initially seems surprising that there were virtually no significant positive correlations in the regression analyses between the insect taxa and the plants. This matter will likewise be discussed in context with the other variables after considering the other variables individually.

Other independent variables. The linear, quadratic, and cubic factors of time, included in most regressions including the final model, compensated for unavoidable seasonal variations in quantities of organisms during the 9-month sampling period. Some likely reasons for the significance of these factors include changes in habitat with maturity, emergence, and seasonal variation in the drift rate. These factors may have been minimized had it been practical to sample intensively over a short period of time. Cummins (1962), however, discourages against this, especially if autecological considerations are to be made.

The dummy variables inserted to account for potential variation between the eight stream sections from which one sample was taken biweekly proved significant. Consequently, they were used in most regressions including the final model to adjust for this bias. The fact that these variables proved significant indicates that there is probably some factor or factors not accounted for by the measured variables. One factor likely involved is the insect drift rate from section to section. Because the study area was a headwater section, no drift could enter the area from above. But it would be expected that progressively greater amounts of drift occurred downstream through the sections until the quantity leaving an area was equaled by the quantity entering it. Consequently, because of this factor alone, it would be expected that greater quantities of insects should occur at the lower stations than the upper, all other factors being equal. The total number of insects collected from each section with equal sampling effort (Table 14) show a wide variation in numbers among sections, with a definite bias toward greater density at the lower sections. This variation, however, must also be considered in context with the measured variables for each sample from each of the sections, as was done in the multiple regression analyses.

The current measurements made at each sampling site were insignificant to virtually all taxa. The only significant relationships of current in the multiple regression analyses were a positive correlation to *Amblystegium noterophilum* (moss) and a negative relation correlation to *Rorippa nasturtium-aquaticum* (watercress). The significant correlations above are logical since the moss was distributed on rocks in the main channel exposed to the faster currents, while the watercress occurred along the sides of the channel and thus in slower current.

The lack of significance of the current measurements to most taxa does not necessarily reflect the lack of importance of current, but probably to the method used. Though Cummins (1962) feels that a Leupold-Stevens current meter (used in this study) is suitable for microdistributional studies (readings can be taken 2 cm from the bottom), Eriksen (1966) considers that this and other devices, though better than those which measure average current, are of doubtful use because they cannot measure current among vegetation, under rocks, in crevices, in interstitial spaces or even at the boundary layers of surfaces where the organisms are found. Consequently, while no practical method yet exists to obtain an accurate index of current within the specific habitat of organisms, such data if available might have accounted for some of the unaccounted variation found in the regressions.

Though there were several positive simple correlations which were significant between depth and insect taxa (Table 4), there were virtually no significant relations found in the multiple regression analyses. The fact that there also was a significant simple negative correlation between depth and current measurements indicates that the accurate depth measurements probably served as an indicator for current measurement about as well as the current measurements themselves taken 2 cm above the substrate. The negative relationship is logical as the current at the bottom of streams tends to be proportionally slower as depth increases. While there were several significant simple correlations between taxa and depth but only one between taxa and current, only one significant t relationship occurred for depth, but two occurred for current (Table 8). This indicates that the depth measurements were likely correlated to one or more of the other variables used in the regressions which had greater significance to organism quantities. Depth is probably not a factor in limiting photosynthesis in this stream since most sampling depths were much less than 0.51 m (the maximum depth sampled) and turbidity at all times was extremely low.

Plants as dependent variables. As indicated earlier, some of the same significant relationships between the insect taxa and substrate parameters corresponded to those parameters significant to the plant taxa (Table 7). Significant parameters were mainly those representing the smallest particles. In processing the samples, an apparent relationship was noted between the quantity of the moss and the quantity of smaller substrate material ("sand") present in the samples. The simple correlations (Table 4) substantiate this observation; there are very significant positive correlations between the moss and the smaller substrate size-classes and also very significant negative correlations between the moss and the larger classes. Hence, since the smaller particles were also significantly correlated to all but one of the insect taxa, it can be concluded that the quantity of smaller substrate material was in some way related to the quantity of insects over and above that contributed by the moss itself. This interrelationship between the substrate, plant and insect quantities will be considered next.

Interrelationships of substrate, insect, and plant quantities. In the preceding discussions, the relationships of both plant and insect taxa to a substrate distribution similar to the mean distribution by weight (Figure 4a) were described. In addition, it was pointed out that the plants, notably the moss, were strongly correlated to the smaller substrate particles. But when the relative significance of both plants and smaller substrate particles was compared as they relate to the insect taxa, the characteristics of the substrate distribution were more important. Finally, it was questioned how these results relate to the observations of previous investigators, in which organisms have been associated, at least phenotypically, with the larger substrate particles. Unlike the more obvious benefits of larger particle sizes (such as stability, space for protection and foraging, places for food deposition, variety of microcurrents, and habitat of prey species), it is difficult to visualize a logical direct relationship of insects to smaller particles.

The mean distribution presented in Figure 4a is based on the percent weight in each size-class combined from the data of each individual sample. This distribution, however, can also be evaluated in terms of the estimated number of particles in each size-class (Table 11). The volume, and hence weight of particles of equal density, changes by a factor of eight when size is reduced or increased by a factor of two in the critical dimension (radius in this case since the particles were considered to be spheres for simplicity). Thus, while the actual weight of all particles in the size-classes decreases sharply at two places along the mean curve (Figure 4a) -- from about size class Ø[-5] to about Ø[-1] and again beyond class Ø[2] -- the actual number of particles increases here, though at a decelerated rate, with each successively smaller size-class. At points where the slope of the curve is negative, the rate of increase is accelerating (Table 11).

The highly negative slope of the distribution between Ø[-8] and approximately Ø[-5] and hence the rapid rise in particle numbers is attributed to the size limit of particles in the stream. (This area of the curve is somewhat similar to that of a standard normal

Table 11. The estimated weight of each particle and numbers of particles in each phi class for the mean substrate distribution (Figure 4a and Table 13). Calculations were based on the fact that median volumes of particles of any uniform shape in a phi class will change by a factor of 8 in any adjacent phi class. For simplicity, all particles were considered to be spherical and to have a specific gravity of 3. The median radii of the phi-class size ranges, rather than the radii of the median volumes, were used in the calculations in order to partially minimize the bias, especially in the larger size classes, of the non-random distribution of particles toward the minimum size in each class.

Phi class	Size range (mm)	Median particle weight (g)	Number of particles	Magnitude of change in particle numbers between adjacent phi classes	
				large → small	small → large
5	<0.0625	1.618×10^{-7}	1.082×10^{8}		
4	0.0625-0.125	1.294×10^{-6}	3.167×10^{7}	3.416	2.927×10^{-1}
3	0.125-0.25	1.035×10^{-5}	1.578×10^{7}	2.007	4.983×10^{-1}
2	0.25-0.5	8.283×10^{-5}	4.502×10^{6}	3.505	2.853×10^{-1}
1	0.5-1	6.626×10^{-4}	5.174×10^{5}	8.701	1.149×10^{-1}
0	1-2	5.301×10^{-3}	6.906×10^{4}	7.492	1.335×10^{-1}
-1	2-4	4.241×10^{-2}	6.395×10^{3}	10.70	9.260×10^{-2}
-2	4-8	3.393×10^{-1}	1.048×10^{3}	6.102	1.639×10^{-1}
-3	8-16	2.714×10^{0}	2.134×10^{2}	4.911	2.036×10^{-1}
-4	16-32	2.171×10^{1}	5.076×10^{1}	4.204	2.379×10^{-1}
-5	32-64	1.737×10^{2}	8.474×10^{0}	5.990	1.669×10^{-1}
-6	64-128	1.390×10^{3}	5.785×10^{-1}	14.65	6.827×10^{-2}
-7	128-256	1.112×10^{4}	4.329×10^{-3}	133.6	7.483×10^{-3}

distribution.) The slope of the curve from approximately 0[-5] to 0[-1] is quite highly positive and represents a relatively slow but uniform rise in particle numbers with successively smaller classes. The change of the slope back to negative and hence an acceleration in the increase in numbers of particles from classes 0[-1] to 0[2] represents the areas where the regression models indicated the greatest sensitivity in predicting taxa quantities. At the lower end of the distribution beyond about 0[2], the slope of the distribution again becomes positive, though estimated numbers of particles still increase but at a decelerated rate.

In the size range of particles having the greatest sensitivity for prediction of taxa numbers (0[-1] to about 0[3]), the number of particles necessary to make a significant change in the percent weight distribution becomes increasingly large (Table 11). Thus the significance attached to these size-classes by the regressions represents great sensitivity in minute changes in quantity. At the other extreme, one large particle added to a sample would change the percentage distribution considerably, yet could have little practical effect on microdistribution of taxa. Thus it is easy to see why the largest particles were far more erratic variables with regard to their actual significance and less reliable indicators of organism quantities. If an active process is at work in distributing the smaller particles individually (as will be discussed shortly), it is easy to see why the smaller particles have such significance when considering the magnitude of change in numbers of particles necessary to measurably alter the parameters (percentage by weight) used in this study.

In an area with uniform current velocity, both the size of the particle the current is capable of entraining (lifting and transporting) and the distance the particle can be carried is inversely proportional to the particle's size and weight. If a curve is plotted with the size, weight, or distance carried as the abscissa and the frequency as the ordinate, the curve will be concave and negative. In Blaine Spring Creek, where the discharge is stable the year around and periodic scouring thus does not occur, stream bottom disturbances which do occur result from the entraining of smaller particles and the shifting of larger particles as the latter lose support from around them. As the larger particles do shift, the smaller particles in the immediate area once sheltered by the larger particles (Hynes 1970) will now be subjected to greater influence of the current and possibly will become entrained. If the disturbed area has a good representation of all particle sizes (such as the mean distribution, Figure 4a), the smaller particles will be swept away in proportion to their size, the intensity of the current and the degree of turbulence. The resulting substrate distribution by weight will tend toward a unimodal curve skewed toward the larger particle sizes (like that depicted for the "-3" phi deviation of the four lowest percentiles in Figure 4a).

Redeposition of particles once entrained by the current is also inversely proportional to particle size and weight and proportional to current velocity under uniform conditions. Larger particles tend to break up uniform current flow, causing gradients from turbulence to quiescence, such as the dead-water areas typically found on the downstream sides of large stones (Jaag and Ambühl 1964). Areas of quiescence tend to be receptive to deposition of particles, though the particular mechanisms involved are not fully understood (Hynes 1970). If the areas which are receptive to deposition remain stabilized over a period of time, they will proportionally collect greater numbers of redeposited particles; if such areas contain a high proportion of larger particles, the redistribution of smaller particles in these microhabitats will shift the original distribution by weight from a skewed unimodal distribution to one which progressively becomes bimodal (similar to the mean distribution depicted in Figure 4a). The drop in the curve of the mean distribution beyond size-class Ø[3] toward the smallest particles is likely due to two factors. First, the majority of smallest particles picked up by the current will likely not settle out until the average current is reduced appreciably. Such areas did not occur in the stream sections sampled. Second, the mesh size of the sampler net allowed some particles in the size-classes beyond Ø[2] to pass through. This corresponds to the point in the mean distribution where the curve drops. The real distribution in this size range, if not continuing approximately level or upward, would at least not drop quite so rapidly.

The presence of smaller particles in areas with larger substrate, therefore, do not in any way appear to influence the benthos distribution directly. Rather it is an indication of both how long a microhabitat has remained stable and its receptivity to deposition of particles. Areas without large substrate particles will, of course, receive smaller particles too, sometimes in large quantities. But the regression models indicated that the smaller particles and to a lesser extent the larger particles were both related to benthos density. Further, the models showed that a dominance of smaller particles with few larger particles was less favorable for insect density. These microhabitats are those areas which are less complex (Hynes 1970), where little space and variety of habitat exists for organisms. On the other hand, areas with a dominance of larger particles are favorable for habitation, but the lack of smaller particles likely indicates that the area is either not receptive to deposition, or was recently disturbed and has not yet become fully colonized.

Areas receptive to deposition of substrate particles will also likely receive detritus and food organisms. Stable groups of stones will allow periphyton to develop on the upper surfaces. Higher aquatic plants are allowed to anchor and develop. It appears that once an area develops a satisfactory food regime, insects are attracted to it if other factors are not limiting. If larger substrate particles themselves were the principle factor to success in colonization, insects would immediately colonize these particles. Likewise, if current was the principle factor, insects should immediately colonize the larger stones which provide an infinite variety of microcurrents. But organisms tend to be found in areas where they are out of at least the direct influence of current, and in all but poorly oxygenated streams, the renewing of water around organisms does not appear to be critical (Ulfstrand 1967). Because the insects are strongly correlated to the smaller substrate particles which are deposited with time, the larger substrate and current factors do not appear to be of immediate importance here. The deposition of smaller particles reflects strongly on the development of a satisfactory food regime, which appears to be the principle factor in the development of favorable microhabitats for insects.

The microhabitats were especially sensitive to changes in quantities of smaller particles because it can be expected that the only particles carried by the current were those from erosion within the stream itself. The predictive value of this factor was enhanced by the fact that no materials were carried into the area from above, no feeder streams entered the area studied, and the discharge and thus velocity remained constant year around. Also, gross substrate variability in the stream areas was minimal, and phenotypically would have been considered uniform throughout as based on the descriptions of substrate contained in virtually all other studies of substrate-organism relationships.

The relationship of plants, especially the moss, which were also found correlated to smaller substrate particles have been ignored to this point. In those regressions where both the moss and the finer substrate particles were considered independent variables to the insect taxa, it was the substrate which was far more significant. Because strong simple correlations exist between moss and the smaller particles, it becomes evident that the moss itself acts similarly to the larger substrate by causing particles to settle from the current. Thus these particles are a dependent variable to the moss which itself becomes independent in this case. The initial presence of moss itself undoubtedly adds to the stability of the substrate underneath it. In addition, observations revealed that the moss itself anchors onto relatively large stones which in themselves tend to be more stable.

It is now evident that the smaller substrate particles contained in the samples were from the streambed itself within the complex of larger particles and from that collected by the moss. While its presence from both sources indirectly and ultimately reflects on a favorable food regime and thus does not alter the conclusions drawn previously about its significance, it does call for a different outlook on the relationship of moss as an independent variable to insects. This is especially true for the final model, regression S, where the strongest indicators of substrate (the lower percentile group which reflects on the size range of particles trapped by moss) were deliberately chosen, inadvertently further minimizing the significance of the moss. The only regression available where plants were considered independent variables to the insect taxa, but no substrate parameters were included, is regression T. A comparison of the *t* values of taxa significant to the plants in both regression T and regression S (the latter is the same as regression R with the lowest percentile group added) shows the following relationships (data from Table 8):

	INSECTS	Plecoptera	*Acroneuria pacifica*	other stoneflies	*Paraleptophlebia* sp.	Trichoptera	*Ochrotrichia* sp.	*Glossosoma* sp.	*Optioservus* sp.
reg S					4.654	-3.177	-2.510	-2.675	
reg T	4.020	2.645	3.380	2.543	5.435			-3.520	5.034

This phenomenon occurs, as mentioned earlier, because both the moss and the smaller substrate particles are individually significant to insects and both are also strongly correlated to each other. Note that, instead of the four taxa negatively correlated and one taxa positively correlated to the moss in regression S (Figure 5a), five taxa are positively correlated and one taxa negatively correlated in regression T. This now closely corresponds with the observations made while sorting the organisms. Consequently, since the smaller substrate particles collected by the moss and dependent on it could not have been analyzed separately from all other small particles, the significance of the moss to the insects was minimized in the analysis because the smaller substrate independent from the moss itself was so strongly related to insect density.

Autecological considerations. Though the approach of this study was synecological, some aspects of the autecological relationships should be noted here. From general observation it was noted that the moss (*Amblystegium noterophilum*) primarily inhabited areas of fast current whereas the watercress (*Rorippa nasturtium-aquaticum*) inhabited shorelines where the current was reduced, or other slower water areas not sampled. The current measurements in fact were significantly negatively correlated to the watercress, but not correlated to any other taxa. Microcurrents measured within sampled areas at the substrate level tended to vary considerably depending on precisely where the meter was placed and thus were inadequate measurements with respect to precise location of most taxa. However, gross currents in areas occupied by moss and areas occupied by watercress differed enough that they reflected on the overall range of the microcurrents measured. The pondweed (*Zannichellia palustris*) was not present in sufficient quantities in any of the sampled areas to make general observations on its relationship to current.

The elmid beetle larva, *Optioservus* sp., was the most strongly correlated to the moss of all insect taxa. Both the fact that it is a herbivore and is a clinging, non-swimming larva likely contribute to this habitat preference. Most numerous of the stoneflies collected from the stream was *Isoperla* sp., a carnivore. *Acroneuria pacifica*, another carnivore, was also collected though in small numbers compared to *Isoperla* sp. (Table 15). *Nemoura* sp., a herbivore, was present in small numbers compared to *Isoperla* sp. in those samples examined critically. Because both *Isoperla* sp. and *Nemoura* sp. were too small to separate readily in quantities even under magnification, it was necessary to tabulate them together as the "other stonefly" group. The stoneflies were strongly correlated (Table 4) to other insect taxa with the exception of *Glossosoma* sp. Though no analysis was made in this study of specific food habitats of the taxa from this stream, it is plausible that the carnivorous stoneflies were distributed within the microhabitats primarily in relation to location of suitable prey as long as other habitat requirements were not limiting.

Baetis sp. and *Paraleptophlebia* sp. are free-ranging mayfly genera which can cling to substrate in fast currents (Pennak 1953). *Ephemerella infrequens*, however, is more typically found clinging in crevices and undersides of stones. All three genera are herbivorous, feeding on algae and tissues of higher aquatic plants. Though no variables were significantly correlated to *Baetis* sp. in any of the regression analyses, this genus showed simple negative correlations to each of the percentiles. In addition, its relative numerical proportion at station 3 (Table 15), which contained the greatest proportion of large substrate particles (Table 13), was high. And, except for *Glossosoma* sp., its occurrence on those rocks scooped from the sampler was proportionally greater than any other insect taxon (see *The sampler used in this study* in the Appendix). This evidence plus the fact that nothing was correlated to it in the regression analysis reflects on its free-ranging behavior and ability to move quickly from place to place, thus allowing it to randomly disperse itself and inhabit more areas than any of the other taxa. *Paraleptophlebia* sp., on the other hand, showed significant correlation to the moss. *Ephemerella infrequens* showed significant negative correlation to the watercress, likely reflecting on its crawling behavior among stones.

Distinct differences were noted between *Glossosoma* sp. and the other two caddifly genera, *Rhyacophila* sp. and *Ochrotrichia* sp. *Glossosoma* sp., a stone case-builder which attaches its cases to undersides of larger stones, was negatively correlated in numbers to the other two genera. Consistent with its observed habitat, it showed the most distinct trend toward negative correlations to smaller substrate particles, and positive correlation to the larger particles. The other caddisflies showed a general though less distinct trend in the opposite direction. Also, *Glossosoma* sp. showed strong negative correlation to the moss in the simple correlation matrix (the only insect taxa to do so) and in the multiple regression analyses. *Ochrotrichia* sp. which uses sand particles for its purse-shaped case, tended to be negatively correlated to the plants. *Rhyacophila* sp., an entirely free-living and typically carnivorous caddisfly, was moderately correlated to the other insect taxa. As with the carnivorous stoneflies, this probably reflects on the significance of the food factor in their distribution.

Interaction of factors influencing microdistribution

From published research dating back to about the year 1930, and especially within the past decade, several factors have been attributed, or at least shown to be correlated, to microdistribution of organisms. The degree of significance attached to each factor is varied, due in part to the particular stream studied. Also, failure to recognize that factors tend to vary in parallel fashion because they are interrelated (Ulfstrand 1968) has also led to some of the discrepancy. Most researchers throughout the period, however, would be in agreement with the proposition stated by Cummins (1964) that, within the framework of certain factors which influence macrodistribution (distribution of organisms over grossly different sections of streams or even adjacent streams), other factors operate under the conditions imposed by those influencing macrodistribution to regulate localized distribution of organisms. As indicated in the introduction, those factors generally considered to exert a more uniform effect over gross sections of a stream include the direct or indirect effects of temperature, chemical properties of the stream, oxygen content, and altitude. Under this framework, factors attributed to producing the non-random distribution of benthos in localized areas (Table 1) are substrate characteristics, current velocity, food distribution, shading versus direct illumination, oxygen concentration when near minimal tolerance to organisms, and depth.

The interaction of habitat variables attributed to influencing microdistribution are complex, and the investigators listed in Table 1 and others have proposed various interactions of the particular factors they investigated with the benthos. Interactions of these factors plus those elucidated in this study are presented schematically in Figure 6. Because of the variability of different streams, not all of these may be significant or operable in each stream.

Interrelationships with substrate are perhaps the most varied (Figure 6). Substrate provides habitat space for foraging and protection against predators, a place for deposition of food substances, a place for periphyton growth and attachment of higher aquatic plants, and a place where the current is broken up into a variety of microcurrents and turbulence. Under special conditions, its character determines the success with which certain organisms can burrow into it and the corresponding

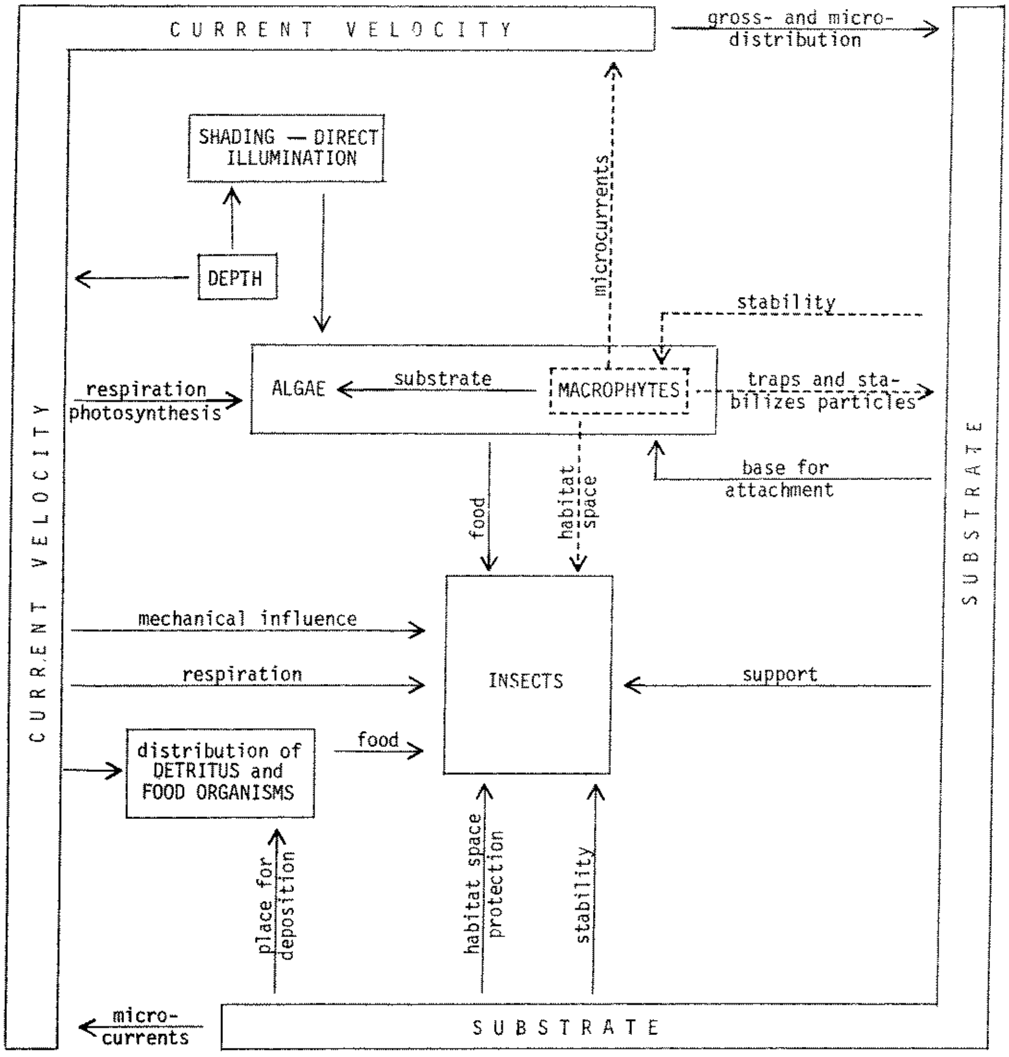


Figure 6. Interrelationships of habitat variables influencing the microdistribution of organisms.

quantity of oxygen that must be consumed (e.g. burrowing mayflies, Eriksen 1963, 1964). Also, the substrate is a place onto which caddisflies anchor cases or construct nets, and provides material from which to construct cases. Higher aquatic plants and detritus must be considered substrates in themselves as well as food sources for appropriate invertebrates.

Cummins (1962, 1964, 1966) and Cummins and Lauff (1969) have suggested that, of all the factors generally attributed to influencing microdistribution in streams (especially the three predominant ones -- substrate, current and food), substrate should be the basic denominator in stream benthic ecology. They, along with Moon (1939) and Thoroup (1966), point out that substrate not only interacts with most other factors (Figure 6). but it also is relatively easy to physically analyze compared to the others. The problem with previous studies on substrate is that, except for Cummins' (1964) work with two species of caddisflies, no researchers have made detailed analyses of the substrate precisely from where the organisms were collected. In most earlier studies, the phenotype (superficial appearance) of areas have been used to evaluate the effect of substrate on microdistribution. This type of approach necessitates the consideration of larger sections of streams than desirable to find habitats which are superficially different. The potential that other, perhaps unknown or unrecognized, factors will enter in is thus greatly increased. Most of the more recent studies have used more refined methods, generally either measuring the dimensions of the largest stone in the area, or one dimension of all the larger stones above a given size. The problem here is that much of the relatively larger material and all of the smaller particles are still ignored. In this study, critical grading of the substrate portion of the samples and detailed analysis of the data showed that superficially identical areas of substrate can differ considerably, and such differences can be related to variations in benthos density.

The macro- and micro-currents of a stream determine the size and distribution of particles, the distribution of detritus and other organic matter, and the renewing of water around organisms located in boundary layers or deadwater areas (Figure 6). Considerable attention was paid by researchers, especially in earlier publications, to the potential influence of the current in mechanically dislodging organisms from substrates where the full force of the current came into direct contact. According to these studies, this alleged influence was the basis of its significance over other effects of current shown in Figure 6. More recent concepts of boundary layers and turbulence (Jaag and Ambühl 1964, Eriksen 1966, Ulfstrand 1967) generally dismiss the older concept of the current's mechanical influence as a significant factor except under extreme conditions. It is now suggested that the boundary layer of relatively quiet water which extends above substrate particles is generally at least as high as the organism itself, and has little correlation to the current directly above it. The significance of reaeration by currents also may be over-emphasized. Ulfstrand (1967) points out that, unless a stream's oxygen concentration is near minimal tolerances, the concentration of oxygen anywhere within the habitat space of the organisms is well within limits and is not a critical factor in most streams. Thus the assessment from the most recent studies is that microcurrents themselves are of less significance than formerly attributed with regard to its mechanical influence and aeration. They still retain their significance in deposition of food and other particles to specific locations, and on a larger scale in determining the make-up of the substrate composition (Macan 1961).

The food factor is one that is often ignored, and in all but the most recent studies, has been neglected with regard to specific distribution of benthos. Ulfstrand (1967) points out that, of the three factors -- substrate, current, and food -- attributed to be most significant in all but special situations, substrate and current can probably be tolerated under sub-optimal conditions more readily than can food. Yet, the food factor is perhaps the most difficult to assess with regard to microdistribution since it would require determining specifically what organisms are feeding on and in which specific habitats. Use of laboratory streams in conjunction with field studies certainly appears to be a promising solution here.

Other factors occasionally are attributed to influencing microdistribution. Depth has occasionally been shown to be correlated, but static pressure is not a factor at shallow depths (Ulfstrand 1967). Correlation of depth to microdistribution is likely due to its own correlation to some other factors more directly related to the organisms, such as its effect on limiting light for algal growth or behavioral aspects such as emergence near shorelines. Hughes (1966*b*) found that for two species of mayfly nymphs, the effects of vegetative shading on microdistribution were due primarily to responses to light stimuli, rather than indirectly through influence on algal growth or temperature, or by deposition of allocthonous leaf detritus.

From their evaluation of the use of laboratory streams in the study of microdistribution, Cummins and Lauff (1969) suggested the concept of a hierarchy of factors which affect microdistribution. Ulfstrand (1967, 1968) similarly suggested that factor combinations, rather than single factors alone, must be considered, and urged that methods for analyzing these factors as a group be found. It is quite plausible, and demonstrated to some extent from the most recent published research and in this study, that the particular hierarchy is variable not only in different streams but within comparatively localized sections of the same stream. Anyone of the three principal factors -- substrate, food or current -- can be limiting no matter how favorable the conditions of the other two might be. If none are critically limiting, as would be expected in most situations, then the interaction of at least three factors should be considered to determine which is dominant.

Opinion varies as to which factor dominates overall within the interactions of factors. Each factor has its proponents, which reflects considerably on the specific stream systems with which the researchers are familiar. Among the more recent studies, Cummins (1962, 1966) favors the substrate factor, though he does not minimize the significance of food. Though this preference for substrate is related to the practical aspect that it is the only principle factor which can readily be measured in natural habitats, he as well as Thorup (1966) also note that substrate has many interrelationships with other factors of the environment. Scott (1958), Jaag and Ambühl (1964), and a majority of European researchers (Kamler and Riedal 1960) feel that the current is the most important factor, though this is based on the primary interactions of current with more direct factors (Figure 6). Jaag and Ambühl admit, however, that current is insignificant in the boundary layers which the organisms inhabit. Ulfstrand (1967) favors the food factor because, as mentioned above, it can be tolerated under sub-optimal conditions to a lesser degree than can current or substrate type. In my study, current appears to be the least significant of the three main factors at the immediate level of the organisms. In Blaine Spring Creek, the general current does not vary seasonally like most streams, and consequently does not have periods of greatly increased flow which can scour established habitats. Because this was a headwater section of the stream without vegetative shading, very little allocthonous detritus entered or was contributed here. Thus, current does not function to distribute organic matter other than relatively minor amounts released by the stream itself. Therefore, in the headwater section of Blaine Spring Creek, it is the interaction of the establishment of stable substrate with the development of a suitable food regime which appears to dominate. If these areas of stable substrate provide the minimal requirements for space and protection, it is the availability of suitable food sources which ultimately regulates microdistribution in this stream.

The study showed that a detailed analysis of substrate size composition as suggested by Cummins (1962, 1964, 1966), Cummins and Lauff (1969) and Thorup (1966) can be used to elucidate its effects on microdistribution. Secondly, this study integrated all recognized and measured variables with each other and related their influence to microdistribution. Eriksen (1966) makes the plea that, because gross measurements of the environment are of little value to the understanding of the microenvironment, the parameters within the microhabitats of the given organisms must be determined. Admittedly, the stream in this study was chosen to minimize variability of factors typically more variable in most other streams to reduce the complexity of analysis. However, Allen (1959) suggests that the proper approach to such studies is to choose a stream with minimal variation in all but the prime factor to be considered.

A logical follow-up to this study could involve several aspects. First, it would be interesting to analyze the results from carefully placed trays of variously graded substrate within the stream studied to determine if the original distribution of substrate particles does evolve with time in the manner hypothesized. Second, it would be interesting to apply the methods of analyses used in this study, namely the integration of all potential variables with a multiple regression analysis, to a stream which has more variation in other factors than found here. And third, it would be interesting to analyze the distribution of organisms in laboratory streams where the magnitude of the various factors could be carefully controlled, and the movements of organisms directly observed.

APPENDIX

APPENDIX

The sampler used in this study

Data compiled separately from the net and bucket portions of the sampler (see Methods and Materials) show that the following percentages of each taxon were obtained from each portion:

	net	bucket
PLANTS	72.85	27.15
A. noterophilum	72.57	27.43
R. nasturtium-aquat.	82.08	17.92
Z. palustris	80.14	19.86
INSECTS	71.12	28.88
Plecoptera	75.28	24.72
A. pacifica	71.31	28.69
other stoneflies	75.39	24.61

	net	bucket
Ephemeroptera	70.77	29.23
E. infrequens	72.92	27.08
Baetis sp.	59.48	40.52
Paralepto-phlebia sp.	84.29	15.71
Trichoptera	57.59	42.41
Ochrotrichia sp.	72.54	27.46
Glossosoma sp.	20.92	79.08
Rhyacophila sp.	52.23	47.77
Coleoptera:		
Optioservus sp.	72.90	27.10

No deliberate attempt was made to dislodge all of the organisms into the net, as it was desirable to complete the sampling process within the shortest possible period of time. Even so, over 70 percent of both plant and insect quantities were collected in the net. With a little more effort, however, it should be possible to dislodge virtually all of the organisms by thoroughly scraping and rubbing all rocks before placing them in the bucket. Also, some vegetation was deliberately placed into the bucket rather than being allowed to flow into the net if its presence would have tended to clog the net. This sampler (Figure 2) has the advantage over a Surber-type in that no backwash due to the resistance to flow can occur around the sides, thus preventing the escape of organisms. Though weights on the platform were not used while sampling in the study area, the sampler was modified so that bricks could easily be added as needed to both sides of the platform to give it greater density and stability in swifter or deeper water.

A recent publication by Mundie (1971) describes a sampler designed for use by aquatic biologists (especially those interested in substrate size distributions), as well as by fish biologists and geomorphologists. The frame is rectangular with a tapered portion extending from one side to be pointed into the current to minimize resistance. Current can be regulated to reduce backwash with a sliding gate at the end of the tapered section. A coarse net is inserted inside a finer net on the downstream side of the sample. This system roughly grades the contents and allows retention of finer particles than otherwise would be possible without causing backwash. In use, the sampler is placed on the substrate and gravel is piled around it to prevent materials or current from escaping underneath. An optional frame with the same shape as the sampler bottom can be implanted into the streambed and the substrate inside allowed to recolonize before placing the sampler on it.

The advantages of Mundie's sampler is the streamlined design and use of the double net. The method of sealing the sampler at the bottom, however, seems questionable, especially for use in a stream such as the one I sampled. Though Mundie's method of piling substrate around the edges may work well with finer substrate material, more difficulty would occur in trying to seal it in coarse substrate. It would not appear to be adequate where it is desired to retain all substrate particles. Mundie states that this method is superior to those types of samplers using a strip of foam rubber, apparently meaning a narrow strip around the perimeter. My sampler (Figure 2) uses a section of foam rubber which is 20 cm wide from the edge of the opening in the middle to the edge of the platform. It presented no problem whatever during the study in preventing the current from flowing underneath the foam rubber itself.

In evaluating the two samplers, it would appear that the basic design of Mundie's sampler, which does offer some advantages (though mine was thoroughly adequate for purpose it was designed) could be adapted to a platform such as on my sampler. In fact, it would seem possible to adapt it so that a platform with the attached foam rubber could be added or removed as desired, thus retaining the advantages of both designs.

Multiple regression analyses in stream benthos studies

In virtually all studies which have been conducted on the microdistribution of stream organisms, a certain variable or variables were chosen for study and others were generally ignored. Graphs or simple correlations were chosen in most cases to demonstrate the relationship which existed between an independent variable and the dependent variable.

The most thorough analysis of factors found in all the studies on microdistribution was that made by Egglishaw (1969) who derived partial deviations from the relationships of the insect numbers to the amount of detritus, the sample depth and the length of the largest stone in the sampling area. The fallacy with simpler analyses is that variables operating within the habitat are not considered to be related to each other or if the relationships are recognized, they are ignored. Relationships certainly do exist (Figure 6) and certain variables may parallel other variables which have a more direct relationship to the actual organisms considered (Ulfstrand 1967). A multiple regression analysis, however, compensates for relationships between related variables by holding each of the independent variables at its mean while other variables are analyzed. Several examples exist in the study to demonstrate this where the results from the simple correlation matrix differ considerably from results obtained in the multiple regression analyses.

This approach also allows for compensation of unavoidable variations which are not of direct concern in a study. In this study, time and section variables were included respectively to compensate for seasonal variation and unmeasured variation between the sections sampled. Another use of multiple regression analyses is the determination of which of several variables or groups of variables describing the basic source of variation have the greatest relation to independent variables. In this study, substrate was described by several variables to determine which most adequately described the influence of the distribution. Since all of these variables were correlated as expected to each other, the significance of any one parameter was diffused over all parameters. In such a circumstance, it is possible that few or none of the parameters will individually show significant t statistics. However, an F test (Table 10) on the group of parameters in question will determine whether the group as a whole has significance, just as the t statistics will indicate significance if only one parameter is used.

The multiple regression analyses indicated why organisms should be divided into the lowest taxa possible for analysis. For example, results for the plant species and the caddisfly genera were often opposite between the lowest taxa. Analysis of the higher taxa in both cases frequently showed that the opposite effects of lower taxa tended to cancel each other out, resulting in apparent insignificance of certain variables.

Table 12. The partitioning of the weights of the substrate on those sieves which were used to bracket those size ranges [Ø(-2) to Ø(-5)] where the specific sieves needed were not available.

Phi class	Size range (mm)	Percent assigned to each phi class by the sieves used	Sieve used (mm)
-1	2-4	100	2.00
-2	4-8	100	4.00
		48.2	6.68
-3	8-16	51.8	
		100	9.42
		48.2	13.3
-4	16-32	51.8	
		100	18.9
		46.5	26.7
-5	32-64	53.5	
		100	38.1
-6	64-128	100	64.0

Table 13. Percentages of substrate in each phi class for each of the 8 stream sections. Data is based on the percentages of substrate contained in each individual sample. Size ranges of phi classes are listed in Table 3.

Phi class	Section								All samples combined
	1	2	3	4	5	6	7	8	
5	.2328	.3322	.1578	.2682	.3733	.5117	.2150	.2667	.2949
4	.8250	.5867	.1311	.3124	.7878	1.435	.4628	.9617	.6904
3	3.810	2.819	.3211	1.220	2.531	6.508	1.499	3.212	2.751
2	7.454	7.868	1.027	4.730	5.985	15.08	3.390	4.634	6.282
1	4.267	9.102	2.416	6.823	6.337	8.777	4.100	4.439	5.775
0	6.226	8.375	4.622	8.221	5.572	6.236	5.521	4.688	6.168
-1	5.999	5.046	4.312	5.641	4.822	3.295	3.902	3.592	4.569
-2	7.685	5.742	6.274	7.211	7.464	3.638	4.732	5.262	5.993
-3	15.38	7.696	10.41	9.764	11.98	6.432	7.643	8.734	9.755
-4	19.96	18.33	19.64	20.08	21.72	14.13	17.78	17.05	18.58
-5	20.33	26.88	25.90	26.66	21.80	20.82	31.11	25.00	24.80
-6	7.833	7.226	24.78	9.072	9.803	10.47	19.65	19.29	13.55
-7	0.000	0.000	0.000	0.000	.9078	2.672	0.000	2.867	.8115

Table 14. The total dry weight in grams of the individual plant genera and their combined weight collected from each of the eight stream sections during this study (regular type), the dry weight per square-meter (parentheses), the percentage distribution of each taxon relative to the other taxa within each section (italics), and the percentage distribution within each taxon relative to the other stream sections (brackets). A total of 18 -- 0.049 m^2 samples were processed for stream sections 1-3 and 5-8 during the study period. For section 4, where only 17 samples were used, the total weight indicated for each group is adjusted upward by 18/17 to make comparisons between sections.

Plant taxon	Stream section								Mean per section	Total
	1	2	3	4	5	6	7	8		
PLANTS	162.8 (184.6) *100.0* [5.213]	471.2 (534.3) *100.0* [15.09]	115.2 (130.6) *100.0* [3.689]	305.5 (346.4) *100.0* [9.782]	284.2 (322.2) *100.0* [9.100]	713.3 (808.7) *100.0* [22.84]	611.4 (693.2) *100.0* [19.58]	459.4 (520.9) *100.0* [14.71]	390.4 (442.6) *100.0* [12.50]	3123 (442.6) *100.0* [100.0]
Amblystegium noterophilum	148.0 (167.8) *90.91* [4.889]	452.7 (513.3) *96.07* [14.96]	113.2 (128.3) *98.26* [3.740]	283.6 (321.5) *92.83* [9.369]	274.2 (310.9) *96.48* [9.058]	699.6 (793.2) *98.08* [23.11]	610.2 (691.8) *99.80* [20.16]	445.9 (505.6) *97.06* [14.73]	378.4 (429.0) *96.93* [12.50]	3027 (429.0) *96.93* [100.0]
Rorippa nasturtium-aquaticum	14.76 (16.73) *9.066* [21.34]	18.53 (21.01) *3.933* [26.79]	1.990 (2.256) *1.727* [2.877]	1.670 (1.893) *.5466* [2.414]	4.460 (5.057) *1.569* [6.448]	13.17 (14.93) *1.846* [19.04]	1.270 (1.440) *.2077* [1.836]	13.32 (15.10) *2.899* [19.26]	8.650 (9.807) *2.215* [12.50]	69.17 (9.807) *2.215* [100.0]
Zannichellia palustris	.04000 (.04535) *.02457* [.1511]	0.000 (0.000) *0.000* [0.000]	0.000 (0.000) *0.000* [0.000]	20.22 (22.93) *6.619* [76.36]	5.480 (6.213) *1.928* [20.69]	.5400 (.6122) *.07570* [2.039]	0.000 (0.000) *0.000* [0.000]	.2000 (.2268) *.04354* [.7553]	3.310 (3.753) *.8479* [12.50]	26.48 (3.753) *.8479* [100.0]

Table 15. The total number of insect taxa collected for each of the eight stream sections during this study (regular type), the numbers per square-meter (parentheses), the percentage distribution of each taxon relative to the other taxa within each section (italics), and the percentage distribution within each taxon relative to the other stream sections (brackets). A total of 18 -- 0.049 m^2 samples were processed for stream sections 1-3 and 5-8 during the study period. For section 4, where only 17 samples were used, the total number indicated is adjusted upward by 18/17 to make comparisons between sections.

Insect taxon	Stream section								Mean per section	Total
	1	2	3	4	5	6	7	8		
INSECTS	2290 (2596) *100.0* [3.831]	10,846 (12,297) *100.0* [18.14]	2983 (3382) *100.0* [4.990]	7466 (8465) *100.0* [12.49]	5995 (6796) *100.0* [10.03]	12,156 (13,782) *100.0* [20.34]	7906 (8964) *100.0* [13.23]	10,133 (11,489) *100.0* [16.95]	7472 (8472) *100.0* [12.50]	59,775 (8472) *100.0* [100.0]
Plecoptera	224.0 (254.0) *9.782* [1.945]	1983 (2248) *18.28* [17.22]	700.0 (793.7) *23.47* [6.078]	1593 (1806) *21.34* [13.83]	1210 (1372) *20.18* [10.51]	2441 (2768) *20.08* [21.20]	1563 (1772) *19.77* [13.57]	1802 (2043) *17.78* [15.65]	1440 (1632) *19.27* [12.50]	11,516 (1632) *19.27* [100.0]
Acroneuria pacifica	29.00 (32.88) *1.266* [9.446]	76.00 (86.17) *.7007* [24.76]	27.00 (30.61) *.9051* [8.795]	34.00 (38.55) *.4554* [11.07]	25.00 (28.34) *.4170* [8.143]	38.00 (43.08) *.3126* [12.38]	33.00 (37.41) *.4174* [10.75]	45.00 (51.02) *.4441* [14.66]	38.38 (43.51) *.5137* [12.50]	307.0 (43.51) *.5137* [100.0]
other stoneflies	195.0 (221.1) *8.515* [1.740]	1907 (2162) *17.58* [17.01]	673.0 (763.0) *22.56* [6.004]	1559 (1768) *20.88* [13.91]	1185 (1344) *19.77* [10.57]	2403 (2724) *19.77* [21.44]	1530 (1735) *19.35* [13.65]	1757 (1992) *17.34* [15.67]	1401 (1589) *18.75* [12.50]	11,209 (1589) *18.75* [100.0]
Ephemeroptera	501.0 (568.0) *21.88* [3.360]	2709 (2357) *19.17* [13.94]	753.0 (853.7) *25.24* [5.050]	2159 (2448) *28.92* [14.48]	1850 (2098) *30.86* [12.41]	2683 (3042) *22.07* [17.99]	1977 (2241) *25.01* [13.26]	2908 (3297) *28.70* [19.50]	1864 (2113) *24.94* [12.50]	14,910 (2113) *24.94* [100.0]

Table 15 (continued)

Insect taxon	Stream section								Mean per section	Total
	1	2	3	4	5	6	7	8		
Ephemerella infrequens	176.0 (199.5) *7.686* [1.699]	1649 (1870) *15.20* [15.92]	320.0 (362.8) *10.73* [3.089]	1561 (1770) *20.91* [15.07]	1250 (1417) *20.85* [12.07]	2189 (2482) *18.01* [21.13]	1381 (1566) *17.47* [13.33]	1832 (2077) *18.08* [17.69]	1295 (1468) *17.33* [12.50]	10,358 (1468) *17.33* [100.0]
Baetis sp.	78.00 (88.44) *3.406* [2.664]	132.0 (149.7) *1.217* [4.508]	326.0 (369.6) *10.93* [11.13]	400.0 (453.5) *5.358* [13.66]	402.0 (455.8) *6.706* [13.73]	333.0 (377.6) *2.739* [11.37]	430.0 (487.5) *5.439* [14.69]	827.0 (937.6) *8.161* [28.24]	366.0 (415.0) *4.898* [12.50]	2928 (415.0) *4.898* [100.0]
Paralepto-phlebia sp.	247.0 (280.0) *10.79* [15.22]	298.0 (337.9) *2.748* [18.36]	107.0 (121.3) *3.587* [6.593]	197.0 (223.4) *2.639* [12.14]	198.0 (224.5) *3.303* [12.20]	161.0 (182.5) *1.324* [9.920]	166.0 (188.2) *2.100* [10.23]	249.0 (282.3) *2.457* [15.34]	202.9 (230.0) *2.715* [12.50]	1623 (230.0) *2.715* [100.0]
Trichoptera	673.0 (763.0) *29.39* [10.40]	795.0 (901.4) *7.330* [12.28]	548.0 (621.3) *18.37* [8.465]	866.0 (981.9) *11.60* [13.38]	532.0 (603.2) *8.874* [8.217]	1159 (1314) *9.534* [17.90]	946.0 (1073) *11.97* [14.61]	955.0 (1083) *9.425* [14.75]	809.3 (917.5) *10.83* [12.50]	6474 (917.5) *10.83* [100.0]
Ochrotrichia sp.	432.0 (489.8) *18.86* [11.64]	486.0 (551.0) *4.481* [13.10]	156.0 (176.9) *5.230* [4.204]	217.0 (246.0) *2.907* [5.847]	197.0 (223.4) *3.286* [5.309]	874.0 (990.9) *7.190* [23.55]	677.0 (767.6) *8.563* [18.24]	672.0 (761.9) *6.632* [18.11]	463.9 (525.9) *6.208* [12.50]	3711 (525.9) *6.208* [100.0]
Glossosoma sp.	239.0 (271.0) *10.44* [14.61]	283.0 (320.9) *2.609* [17.30]	216.0 (244.9) *7.241* [13.20]	426.0 (483.0) *5.706* [26.04]	183.0 (207.5) *3.053* [11.19]	79.00 (89.57) *.6499* [4.829]	95.00 (107.7) *1.202* [5.807]	115.0 (130.4) *1.135* [7.029]	204.5 (231.9) *2.737* [12.50]	1636 (231.9) *2.737* [100.0]

Table 15 (concluded)

Insect taxon	Stream section								Mean per section	Total
	1	2	3	4	5	6	7	8		
Rhyacophila sp.	2.000	26.00	176.0	223.0	152.0	206.0	174.0	168.0	140.9	1127
	(2.268)	(29.48)	(199.5)	(252.8)	(172.3)	(233.6)	(197.3)	(190.5)	(159.7)	(159.7)
	.08734	*.2397*	*5.900*	*2.987*	*2.535*	*1.695*	*2.201*	*1.658*	*1.886*	*1.866*
	[.1775]	[2.307]	[15.62]	[19.79]	[13.49]	[18.28]	[15.44]	[14.91]	[12.50]	[100.0]
Coleoptera: *Optioservus* sp.	892.0	5989	982.0	2849	2403	5873	3420	4468	3360	26,876
	(1011)	(6790)	(1113)	(3230)	(2724)	(6659)	(3878)	(5066)	(3809)	(3809)
	38.95	*55.22*	*32.92*	*38.16*	*40.08*	*48.31*	*43.26*	*44.09*	*44.97*	*44.97*
	[3.319]	[22.28]	[3.654]	[10.60]	[8.941]	[21.85]	[12.73]	[16.62]	[12.50]	[100.0]

Table 16. Computer data of the final multiple regression model — regression S. All means are raw data based on the individually sampled area — 0.049 m^2. Regression coefficients *(b)* used in the generalized regression formula $(Y_x = \bar{Y}_x + b_1(X_1 - \bar{X}_1) + b_2(X_2 - \bar{X}_2) + \cdot \cdot \cdot + b_n(X_n - \bar{X}_n))$ should be multiplied by 20.37 (0.049 m^2 x 20.37 = 1 m^2) if insect or plant quantity is likewise converted to quantity per square meter. One exception is when the plant and insect quantities are both converted and the plants are independent; in this case, the regression coefficient to be used is as given. t = 1.977 when P = 0.05 with 142 degrees of freedom.

a) INSECTS ($\bar{X}_{no.}$ = 415.0)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed t value
A. noterophilum		21.07	.5799E-01	.7385	1.137	.6494
R. nasturtium-aquat.		.4427	-.1846	-24.03	11.44	-2.100
Z. palustris		.1769	-.2382	-39.64	14.46	-2.742
percentiles	0.25th	4.153	.1901	126.1	58.24	2.165
	1st	2.995	-.1402E-01	-13.31	84.86	-.1568
	5th	1.799	-.4662E-02	-4.511	86.53	-.05212
	10th	1.003	.9512E-02	6.040	56.79	.1064
dummy variables for stream section variability		.0000	-.4536	-279.0	49.04	-5.690
		.0000	.2042	114.4	49.03	2.332
		.0000	-.2986	-178.1	50.93	-3.498
		-.6993E-02	.3824E-01	21.34	49.88	.4279
		.0000	-.1579	-85.18	47.63	-1.788
		.0000	.3292	193.9	49.76	3.897
		.0000	.4676E-01	26.71	51.04	.5233
time	linear	9.538	-.5151	-268.2	39.92	-6.719
	quadratic	117.9	.4793	29.56	4.842	6.105
	cubic	1635	-.4342	-.9030	.1675	-5.390

intercept = 579.9 R squared = 0.6227   std. error $(s_{y,x})$ = 210.1

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	.910560E+07	535623	12.1375
Residual	125	.551622E+07	44129.7	
Total (n = 143)	142	.146218E+08		

Table 16 (continued)

b) Plecoptera $(\bar{X}_{no.} = 79.84)$

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed t value
A. noterophilum		21.07	.8790E-01	.3618	.3667	.9866
R. nasturtium-aquat.		.4427	-.2350	-9.973	3.690	-2.703
Z. palustris		.1769	-.1332	-7.007	4.662	-1.503
percentiles	0.25th	4.153	.9646E-01	20.35	18.78	1.083
	1st	2.995	-.5811E-01	-17.81	27.37	-.6508
	5th	1.799	.1399	44.07	27.90	1.579
	10th	1.003	-.1414	-29.24	18.31	-1.597
dummy variables for stream section variability		.0000	-.3314	-62.10	15.81	-3.927
		.0000	.1215	21.63	15.81	1.368
		.0000	-.1547	-28.75	16.42	-1.750
		-.6993E-02	.3826E-01	6.886	16.09	.4281
		.0000	-.7856E-01	-13.53	15.36	-.8811
		.0000	.2284	42.08	16.05	2.623
		.0000	.2945E-01	5.422	16.46	.3294
time	linear	9.538	-.4914	-81.19	12.87	-6.308
	quadratic	117.9	.4961	9.973	1.561	6.387
	cubic	1635	-.4624	-.3150	.5403E-01	-5.831

intercept = 127.8 R squared = .5275   std. error $(s_{y,x})$ = 67.74

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	640351.	37667.7	8.20848
Residual	125	573610.	4588.88	
Total (n = 143)	142	.121396E+07		

Table 16 (continued)

c) *Acroneuria pacifica* ($\bar{X}_{no.}$ 2.133)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	.1264	.1874E-01	.1315E-01	1.425
R. nasturtium-aquat.		.4427	-.4007E-01	-.5932E-01	.1323	-.4483
Z. palustris		.1769	-.5925E-01	-.1109	.1672	-.6636
percentiles	0.25th	4.153	-.1344	-1.021	.6734	-1.516
	1st	2.995	.9196E-01	1.013	.9813	1.033
	5th	1.799	.1721	1.955	1.001	1.953
	10th	1.003	-.2049	-1.537	.6567	-2.340
dummy variables for stream section variability		.0000	-.6089E-01	-.3863	.5670	-.6821
		.0000	.2596	1.703	.5669	3.005
		.0000	.6700E-01	.4421	.5889	.7508
		-.6993E-02	-.2541E-01	-.1639	.5768	-.2842
		.0000	-.1414	-.8794	.5508	-1.596
		.0000	-.1352	-.8781	.5754	-1.526
		.0000	-.4946E-01	-.3268	.5902	-.5536
time	linear	9.538	-.2976E-01	-.1537	.4616	-.3329
	quadratic	117.9	.7822E-01	.4911E-01	.5599E-01	.8772
	cubic	1635	-.9480E-01	-.2063E-02	.1937E-02	-1.065

intercept = .6648   *R* squared = .2992   std. error (sy,x) = 2.429

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	314.902	18.5236	3.13928
Residual	125	737.574	5.90059	
Total (n = 143)	142	1052.48		

Table 16 (continued)

d) other stoneflies ($\bar{X}_{no.}$ = 77.71)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	.8396E-01	.3430	.3642	.9420
R. nasturtium-aquat.		.4427	-.2352	-9.914	3.664	-2.706
Z. palustris		.1769	-.1320	-6.896	4.630	-1.489
percentiles	0.25th	4.153	.1019	21.37	18.65	1.146
	1st	2.995	-.6183E-01	-18.82	27.18	-.6926
	5th	1.799	.1347	42.12	27.71	1.520
	10th	1.003	-.1350	-27.71	18.19	-1.523
dummy variables for stream section variability		.0000	-.3316	-61.71	15.70	-3.930
		.0000	.1128	19.93	15.70	1.269
		.0000	-.1581	-29.19	16.31	-1.790
		-.6993E-02	.3944E-01	7.050	15.97	.4413
		.0000	-.7399E-01	-12.65	15.25	-.8296
		.0000	.2344	42.96	15.94	2.696
		.0000	.3144E-01	5.749	16.35	.3517
time	linear	9.538	-.4932	-81.04	12.78	-6.339
	quadratic	117.9	.4968	9.924	1.551	6.400
	cubic	1635	-.4626	-.3130	.5366E-01	-5.833

intercept = 127.1 *R* squared = .5266 std. error *(sy,x)* = 67.28

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	628398	37023.4	8.18017
Residual	125	565750	4526.00	
Total (n = 143)	142	.11951E+07		

Table 16 (continued)

e) Ephemeroptera ($\overline{X}_{no.}$ = 103.5)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	.3722E-01	.2132	.5120	.4164
R. nasturtium-aquat.		.4427	-.1277	-7.419	5.152	-1.440
Z. palustris		.1769	-.9507E-01	-6.951	6.510	-1.068
percentiles	0.25th	4.153	.2013	60.26	26.22	2.298
	1st	2.995	-.1849E-01	-7.900	38.21	-.2067
	5th	1.799	-.2425E-01	-10.57	38.96	-.2712
	10th	1.003	-.5034E-01	-14.41	25.57	-.5635
dummy variables for stream section variability		.0000	-.2882	-74.29	22.08	-3.365
		.0000	.2684E-01	6.626	22.07	.3002
		.0000	-.2187	-57.47	22.93	-2.506
		-.6993E-02	.7398E-01	18.63	22.46	.8294
		.0000	-.7804E-02	-1.872	21.45	-.08726
		.0000	.1922	49.07	22.40	2.190
		.0000	-.9576E-02	-2.461	22.98	-.1071
time	linear	9.538	-.6161	-157.2	17.97	-8.746
	quadratic	117.9	.5351	15.44	2.180	7.082
	cubic	1635	-.4543	-.4301	.7544E-01	-5.701

intercept = 297.1   *R* squared = .5706   std. error *(sy,x)* = 94.59

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	.148620E+07	87423.6	9.77119
Residual	125	.111838E+07	8947.07	
Total (n = 143)	142	.260458E+07		

Table 16 (continued)

f) *Ephemerella infrequens* ($\overline{X}_{no.}$ = 71.83)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed value
A. noterophilum		21.07	-.4309E-01	-.2064	.4280	-.4822
R. nasturtium-aquat.		.4427	-.1397	-6.795	4.307	-1.578
Z. palustris		.1769	-.8916E-01	-5.446	5.442	-1.001
percentiles	0.25th	4.153	.2003	50.12	21.92	2.286
	1st	2.995	-.2531E-01	-9.044	31.94	-.2831
	5th	1.799	.1691E-01	6.157	32.57	.1890
	10th	1.003	-.8153E-01	-19.55	21.38	-.9145
dummy variables for stream section variability		.0000	-.3049	-66.07	18.46	-3.579
		.0000	.5975E-01	12.35	18.45	.6692
		.0000	-.2321	-51.13	19.17	-2.667
		-.6993E-02	.6550E-01	13.78	18.78	.7339
		.0000	-.3401E-01	-6.823	17.93	-.3805
		.0000	.2537	54.91	18.73	2.932
		.0000	.2590E-01	5.565	19.21	.2896
time	linear	9.538	-.6225	-133.6	15.02	-8.892
	quadratic	117.9	.5333	12.85	1.823	7.049
	cubic	1635	-.4492	-.3545	.6306E-01	-5.621

intercept = 257.9 *R* squared = .5847 std. error *(sy,x)* = 79.07

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	.110015E+07	64714.9	10.3502
Residual	125	781564	6252.51	
Total (n = 143)	142	.188172E+07		

Table 16 (continued)

g) *Baetis* sp. ($\overline{X}_{no.}$ = 20.33)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	.4215E-01	.7210E-01	.1529	.4716
R. nasturtium-aquat.		.4427	-.1020	-1.764	1.538	-1.147
Z. palustris		.1769	-.6003E-01	-1.307	1.943	-.6723
percentiles	0.25th	4.153	.5992E-02	.5245	7.829	.06699
	1st	2.995	.3663E-01	4.675	11.41	.4098
	5th	1.799	-.1393	-18.30	11.63	-1.573
	10th	1.003	.1109	9.528	7.635	1.248
dummy variables for stream section variability		.0000	-.1876	-14.08	6.592	-2.135
		.0000	-.1136	-8.426	6.591	-1.278
		.0000	-.8137E-01	-6.249	6.846	-.9128
		-.6993E-02	.4656E-01	3.495	6.706	.5212
		.0000	.4365E-01	3.128	6.404	.4885
		.0000	.6099E-02	.4562	6.689	.06819
		.0000	-.2004E-01	-1.538	6.862	-.2241
time	linear	9.538	-.2241	-13.79	5.366	-2.570
	quadratic	117.9	.2208	1.648	.6509	2.531
	cubic	1635	-.2056	-.5292E-01	.2252E-01	-2.349

intercept = 44.45 R squared = .2806 std. error (sy,x) = 28.24

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	38891.2	2287.72	2.86853
Residual	125	99690.3	797.522	
Total (n = 143)	142	138582		

Table 16 (continued)

h) *Paraleptophlebia* sp. ($\overline{X}_{no.}$ = 11.29)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed t value
A. noterophilum		21.07	.3843	.3475	.7467E-01	4.654
R. nasturtium-aquat.		.4427	.1344	1.139	.7513	1.517
Z. palustris		.1769	-.1868E-01	-.1983	.9493	-.2089
percentiles	0.25th	4.153	.2194	9.615	3.824	2.514
	1st	2.995	-.5659E-01	-3.531	5.572	-.6337
	5th	1.799	.2471E-01	1.570	5.682	.2763
	10th	1.003	-.1047	-4.388	3.729	-1.177
dummy variables for stream section variability		.0000	.1605	5.855	3.220	1.818
		.0000	.7489E-01	2.703	3.219	.8397
		.0000	-.2382E-02	-.8907E-01	3.344	-.02664
		-.6993E-02	.3690E-01	1.352	3.275	.4128
		.0000	.5205E-01	1.823	3.128	.5828
		.0000	-.1699	-6.299	3.267	-1.928
		.0000	-.1706	-6.488	3.352	-1.936
time	linear	9.538	-.3171	-9.799	2.621	-3.739
	quadratic	117.9	.2570	.9453	.3180	2.973
	cubic	1635	-.1817	-.2272E-01	.1100E-01	-2.065

intercept = -5.279 R squared = .4496   std. error (sy,x) = 13.79

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	19431.3	1143.02	6.00717
Residual	125	23784.4	190.275	
Total (n = 143)	142	43215.7		

Table 16 (continued)

i) Trichoptera ($\overline{X}_{no.}$ = 44.94)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	-.2733	-.6656	.2095	-3.177
R. nasturtium-aquat.		.4427	.2131E-01	.5023	2.108	.2383
Z. palustris		.1769	-.2258	-6.901	2.664	-2.591
percentiles	0.25th	4.153	.2543E-01	3.051	10.73	.2844
	1st	2.995	-.3576E-01	-6.255	15.64	-.4000
	5th	1.799	.8282E-01	14.81	15.94	.9292
	10th	1.003	.2279E-01	2.667	10.46	.2549
dummy variables for stream section variability		.0000	-.1660	-17.01	9.035	-1.882
		.0000	-.1471	-15.02	9.033	-1.663
		.0000	-.9510E-01	-10.02	9.383	-1.068
		-.6993E-02	.3884E-01	3.994	9.191	.4346
		.0000	-.1922	-19.21	8.777	-2.189
		.0000	.1467	15.20	9.168	1.658
		.0000	.2238	24.14	9.404	2.567
time	linear	9.538	-.2462	-20.89	7.354	-2.840
	quadratic	117.9	.2845	2.960	.8921	3.317
	cubic	1635	-.2928	-.1057	.3087E-01	-3.423

intercept = 81.82 *R* squared = 0.3348 std.error (sy,x) = 38.71

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	94257.0	5544.53	3.70106
Residual	125	187261.	1498.09	
Total (n = 143)	142	281518.		

Table 16 (continued)

j) *Ochrotrichia* sp. ($\overline{X}_{no.}$ = 25.92)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	-.2191	-.5045	.2010	-2.510
R. nasturtium-aquat.		.4427	.8205E-01	1.861	2.022	.9205
Z. palustris		.1769	-.1552	-4.487	2.555	-1.756
percentiles	0.25th	4.153	-.6251E-01	-7.208	10.29	-.7002
	1st	2.995	.1452E-01	2.435	15.00	.1623
	5th	1.799	.4234E-01	7.246	15.29	.4738
	10th	1.003	.7511E-01	8.453	10.04	.8421
dummy variables for stream section variability		.0000	-.9019E-01	-8.775	8.667	-1.012
		.0000	-.1281	-12.52	8.665	-1.444
		.0000	-.8513E-01	-8.599	9.001	-.9553
		-.6993E-02	-.1311	-13.04	8.817	-1.479
		.0000	-.1862	-17.84	8.419	-2.119
		.0000	.1483	14.74	8.795	1.676
		.0000	.2523	26.30	9.021	2.915
time	linear	9.538	-.2336	-18.95	7.055	-2.686
	quadratic	117.9	.2761	2.748	.8558	3.211
	cubic	1635	-.2880	-.9955E-01	.2961E-01	-3.362

intercept = 77.44 *R* squared = 0.3582 std. error *(sy,x)* = 37.13

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	96171.1	5657.12	4.10356
Residual	125	172324.	1378.59	
Total (n = 143)	142	268495.		

Table 16 (continued)

k) *Glossosoma* sp. ($\overline{X}_{no.}$ = 11.22)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed *t* value
A. noterophilum		21.07	-.2326	-.1693	.6332E-01	-2.673
R. nasturtium-aquat.		.4427	-.1014	-.7259	.6371	-1.139
Z. palustris		.1769	-.1618	-1.476	.8050	-1.834
percentiles	0.25th	4.153	.3171	12.12	3.243	3.739
	1st	2.995	-.2368	-12.88	4.726	-2.725
	5th	1.799	.1602	8.746	4.819	1.815
	10th	1.003	-.1476	-5.278	3.162	-1.669
dummy variables for stream section variability		.0000	-.1968E-01	-.6009	2.731	-.2200
		.0000	.1236	3.802	2.730	1.393
		.0000	-.1395	-4.467	2.836	-1.575
		-.6993E-02	.3564	11.85	2.778	4.265
		.0000	-.5494E-01	-1.632	2.652	-.6151
		.0000	-.7541E-01	-2.343	2.771	-.8455
		.0000	-.1033	-3.299	2.842	-1.161
time	linear	9.538	-.5654E-01	-1.407	2.223	-.6331
	quadratic	117.9	-.1794E-02	-.5409E-02	.2696	-.02006
	cubic	1635	.2626E-01	.2740E-02	.9329E-02	.2937

intercept = 4.273 *R* squared = 0.4010 std. error *(sy,x)* = 11.70

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	11448.5	673.443	4.92159
Residual	125	17104.3	136.834	
Total (n = 143)	142	28552.8		

Table 16 (continued)

1) *Rhyacophila* sp. ($\bar{X}_{no.}$ = 7.797)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed t value
A. noterophilum		21.07	.1931E-01	.8175E-02	.3787E-01	.2159
R. nasturtium-aquat.		.4427	-.1471	-.6333	.3810	-1.662
Z. palustris		.1769	-.1718	-.9384	.4814	-1.949
percentiles	0.25th	4.153	-.8571E-01	-1.865	1.939	-.9619
	1st	2.995	.1314	4.189	2.826	1.482
	5th	1.799	-.3653E-01	-1.178	2.882	-.4087
	10th	1.003	-.2404E-01	-.5085	1.891	-.2689
dummy variables for stream section variability		.0000	-.3856	-7.629	1.633	-4.672
		.0000	-.3265	-6.305	1.633	-3.862
		.0000	.1585	3.043	1.696	1.794
		-.6993E-02	.2689	5.184	1.661	3.121
		.0000	.1475E-01	.2616	1.586	.1649
		.0000	.1496	2.803	1.657	1.692
		.0000	.5994E-01	1.141	1.700	.6713
time	linear	9.538	-.3558E-01	-.5290	1.329	-.3980
	quadratic	117.9	.1194	.2168	.1612	1.344
	cubic	1635	-.1407	-.8865E-02	.5579E-02	-1.589

intercept = 0.9808E-01 R squared = 0.4553   std. error (sy,x) = 6.995

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	5112.45	300.732	6.14575
Residual	125	6116.67	48.9333	
Total (n = 143)	142	11229.1		

Table 16 (concluded)

m) Coleoptera: *Optioservus* sp. ($\overline{X}_{no.}$ = 186.8)

Independent variable		Mean	Partial correlation	Regr. coef.	Std.error regr.coef.	Computed t value
A. noterophilum		21.07	.1123	.8291	.6564	1.263
R. nasturtium-aquat.		.4427	-.9628E-01	-7.143	6.605	-1.082
Z. palustris		.1769	-.1973	-18.78	8.345	-2.251
percentiles	0.25th	4.153	.1122	42.45	33.62	1.263
	1st	2.995	.3405E-01	18.66	48.99	.3809
	5th	1.799	-.9418E-01	-52.83	49.95	-1.058
	10th	1.003	.1273	47.03	32.78	1.435
dummy variables for stream section variability		.0000	-.3689	-125.6	28.31	-4.438
		.0000	.3044	101.1	28.30	3.573
		.0000	-.2418	-81.89	29.40	-2.786
		-.6993E-02	-.2535E-01	-8.164	28.79	-.2835
		.0000	-.1623	-50.56	27.50	-1.839
		.0000	.2631	87.56	28.72	3.049
		.0000	-.1182E-02	-.3892	29.46	-.01321
time	linear	9.538	-.3469E-01	-8.942	23.04	-.3881
	quadratic	117.9	.3795E-01	1.187	2.795	.4246
	cubic	1635	-.4817E-01	-.5215E-01	.9671E-01	-.5392

intercept = 73.19 R squared = 0.5849   std. error (sy,x) = 121.3

ANALYSIS OF VARIANCE FOR THIS REGRESSION

Source	*d.f.*	*S.S.*	*M.S.*	*F* Value
Due to Regression	17	.258942E+07	152319.	10.3592
Residual	125	.183796E+07	14703.7	
Total (n = 143)	142	.442738E+07		

LITERATURE CITED

Allen, K. R. 1959. The distribution of stream bottom faunas. Proc. New Zealand Ecol. Soc. 6: 5-8.

American Public Health Association. 1965. Standard method for the examination of water and wastewater including bottom sediments and sludges. 12th ed. Amer. Publ. Health Assoc. Inc., New York. 769 p.

Armitage, K. B. 1958. Ecology of the riffle insects of the Firehole River, Wyoming. Ecology 39: 571-580.

Armitage, K. B. 1961. Distribution of riffle insects of the Firehole River, Wyoming. Hydrobiologia 17: 152-174.

Bell, H. L. 1969. Effect of substrate types on aquatic insect distribution. J. Minnesota Acad. Sci. 35: 79-81.

Buscemi, P. A. 1966. The importance of sedimentary organics in the distribution of benthic organisms, p. 79-86. *In* K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman [ed.]. Organism-substrate relationships in streams. Spec. Publ. No. 4, Pymatuning Laboratory of Ecology, Univ. Pittsburgh. 145 p.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Amer. Midl. Nat. 67: 477-504.

Cummins, K. W. 1964. Factors limiting the microdistribution of larvae of the caddisflies *Pycnopsyche lepida* (Hagen) and *Pycnopsyche guttifer* (Walker) in a Michigan stream (Trichoptera: Limnephilidae). Ecol. Monogr. 34: 271-295.

Cummins, K. W. 1966. A review of stream ecology with special emphasis on organism-substrate relationships, p. 2-51. *In* K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman [ed.]. Organism-substrate relationships in streams. Spec. Publ. No. 4, Pymatuning Laboratory of Ecology, Univ. Pittsburgh. 145 p.

Cummins, K. W., and G. H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. Hydrobiologia 34: 145-181.

Cushing, C. E., Jr. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. Trans. Amer. Fish. Soc. 92: 216-219.

Egglishaw, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33: 463-476.

Egglishaw, H. J. 1969. The distribution of benthic invertebrates on substrata in fast-flowing streams. J. Anim. Ecol. 38: 19-33.

Eriksen, C. H. 1963. The relation of oxygen consumption to substrate particle size in two burrowing mayflies. J. Exp. Biol. 40: 447-453.

Eriksen, C. H. 1964. The influence of respiration and substrate upon the distribution of burrowing mayfly naiads. Verh. Internat. Verein. Limnol. 15: 903-911.

Eriksen, C. H. 1966. Benthic invertebrates and some substrate-current-oxygen interrelationships, p. 98-115. *In* K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman [ed.]. Organism-substrate relationships in streams. Spec. Publ. No. 4, Pymatuning Laboratory of Ecology, Univ. Pittsburgh. 145 p.

Eriksen, C. H. 1968. Ecological significance of respiration and substrate for burrowing Ephemeroptera. Can. J. Zool. 46: 93-103.

Hendricks, A., W. M. Parsons, D. Francisco, K. Dickson, D. Henley, and J. K. G. Silvey. 1969. Bottom fauna studies of the lower Saline River. Texas J. Sci. 21: 175-187.

Hughes, D. A. 1966*a*. Mountain streams of the Barberton area, Eastern Transvaal. Part II. The effect of vegetational shading and direct illumination on the distribution of stream fauna. Hydrobiologia 27: 439-459.

Hughes, D. A. 1966*b*. The role of responses to light in the selection and maintenance of microhabitat by the nymphs of two species of mayfly. Anim. Behav. 14: 17-33.

Hunt, J. S. 1930. Bottom as a factor in animal distribution in small streams. J. Tennessee Acad. Sci. 5: 11-18.

Hynes, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto. 555 p.

Ide, F. P. 1935. The effect of temperature on the distribution of the mayfly fauna of a stream. Univ. Toronto Stud., Biol. Ser. 39: 9-76.

Jaag, O., and H. Ambühl. 1964. The effect of the current on the composition of biocoenoses in flowing water streams. Int. Conf. Water Pollut. Res., London, Sept. 1962. Pergammon Press, New York. p. 31-49.

Kamler, E. 1965. Thermal conditions in mountain waters and their influence on the distribution of Plecoptera and Ephemeroptera larvae. Ekol. Polsk. 13: 378-414.

Kamler, E., and W. Riedel. 1960. A method of quantitative study of the bottom fauna of Tatra streams. Polsk. Arch. Hydrobiol. 21: 95-105.

Lauff, G. H., K. W. Cummins, C. Eriksen, and M. Parker. 1961. A method for sorting bottom fauna samples by elutriation. Limnol. Oceanogr. 6: 462-466.

Lavandier, P., and J. Dumas. 1971. Microrepartition de quelques especes d'invertebres benthiques dans des ruisseaux des Pyrenees centrales. [Microdistribution of benthic invertebrates in streams of the Central Pyrenees.] Ann. Limnol. 7: 7-23. [In French, English summary].

Linduska, J. P. 1942. Bottom types as a factor influencing the local distribution of mayfly nymphs. Can. Entomol. 74: 26-30.

Macan, T. T. 1961. A review of running water studies. Verh. Internat. Verein. Limnol. 14: 587-602.

Moon, H. P. 1939. Aspects of the ecology of aquatic insects. Trans. Brit. Entomol. Soc. 6: 39-49.

Mundie, J. H. 1971. Sampling benthos and substrate materials down to 50 microns in size, in shallow streams. J. Fish. Res. Bd. Canada 28: 849-860.

Needham, P. R., and R. L. Usinger. 1956. Variability in the macrofauna of a single riffle in Prosser Creek, California, as indicated by the Surber sampler. Hilgardia 24: 383-409.

Pennak, R. W. 1953. Fresh-water invertebrates of the United States. Ronald Press Co., New York. 769 p.

Pennak, R. W., and E. D. Van Gerpen. 1947. Bottom fauna production and physical nature of the substrate in a northern Colorado stream. Ecology 28: 42-48.

Percival, E., and H. Whitehead. 1929. A quantitative study of the fauna of some types of stream-bed. J. Ecol. 17: 282-314.

Ricker, W. E. 1934. An ecological classification of certain Ontario streams. Univ. Toronto Stud., Biol. Ser. 37: 7-114.

Scott, D. 1958. Ecological studies on the Trichoptera of the River Dean, Cheshire. Arch. Hydrobiol. 54: 340-392.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames. 593 p.

Sprules, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Univ. Toronto Stud., Biol. Serv. 56: 1-81.

Stadnyk, L. 1971. Factors affecting the distribution of stoneflies in the Yellowstone River, Montana. Unpublished Ph.D. dissertation, Montana State Univ., Bozeman. 36 p.

Thorup, J. 1966. Substrate type and its value as a basis for the delimitation of bottom fauna communities in running waters, p. 59-74. *In* K. W. Cummins, C. A. Tryon, Jr., and R. T. Hartman [ed.]. Organism-substrate relationships in streams. Spec. Publ. No. 4, Pymatuning Laboratory of Ecology, Univ. Pittsburgh. 145 p.

Ulfstrand, S. 1967. Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams. Oikos 18: 293-310.

Ulfstand, S. 1968. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae). Oikos 19: 167-190.

Wene, G., and E. L. Wickliff. 1940. Modification of a stream bottom and its effect on the insect fauna. Can. Entomol. 72: 131-135.