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John M. Payne

Utah State University

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INTERRELATIONSHIPS BETWEEN BENTHIC MACROINVERTEBRATES AND HABITAT IN A MOUNTAIN STREAM

by

John M. Payne

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Science

Approved:

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John M. Payne

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Interrelationships Between Benthic Macroinvertebrates and Habitat in a Mountain Stream

by

John M. Payne, Master of Science

Utah State University, 1979

Major Professor: Dr. John A. Kadlec
Department: Wildlife Science

A study to determine habitat differences of benthic macroinvertebrates was conducted on the upper Strawberry River, Utah. The investigation was part of a large scale project to determine minimum stream flow requirements for trout. The effects of time, habitat, depth and velocity on the distribution of benthic fauna were evaluated.

Samples of benthic invertebrates (146 total) were collected every 2 months at 8 stations on the river from November, 1975 through August, 1976. Representatives of 59 taxa were collected. Eight taxa comprised 90 percent of the mean annual community standing crop in numbers. Biomass was not dominated by any group of taxa. Community standing crop decreased from late Fall 1975 until early Summer 1976. The largest increase in standing crop occurred during August.

Prediction of benthic distribution through the use of depth and velocity categories was unsuccessful. Three-dimensional plots of the relative density of a taxon versus depth and velocity indicated the contagious nature of the animals' distributions but their preference for specific categories could not be demonstrated. The results suggested that macroinvertebrates could tolerate large variations in current and depth and that these physical factors are only indirectly related to faunal distribution.

Results of analysis of variance and covariance showed time to be the factor which influenced the distribution of most taxa (85%), followed by the time x habitat interaction (20%), velocity (18%), habitat (11%), and depth (9%). Comparisons in animal abundance were made between 4 riffles and 4 "pools". These two habitats did not differ significantly in substrate type or velocity, however depth did show significant differences. Results of nonparametric tests suggested that the majority of taxa migrated into "pools" during periods of snow, ice, and low flows, an indication that "pools" may provide refuge to macroinvertebrates during periods of stream dewatering and diversion.

(79 pages)

INTRODUCTION

Nature of the Problem

The development of water resources for domestic, industrial, and agricultural purposes in the intermountain west has led to impoundments, pollution, bank clearing, channelization, and, in the case of the Central Utah Project, diversion of head-water streams.

In response to the Central Utah Project, a study was undertaken by Utah State University to examine the ecological requirements of stream trout and to determine minimum flow requirements at all times of the year. To achieve this goal an ecosystem approach was undertaken. Individual studies were begun on periphyton, benthic macroinvertebrates, and fish. Physical factors such as temperature, discharge, and velocity, and chemical factors, such as alkalinity, pH, and hardness were monitored. Investigations also were begun on the formation of frazil and anchor ice and their potential effects on the stream communities (Kadlec 1975). The data collected from these studies were designed for use in the production of a computer simulation model for predicting the kinds of changes which would occur within the stream in reaction to man's perturbations. Initial field work was primarily aimed at the collection of basic information describing the structure of the ecosystem before dewatering. This thesis presents the baseline data collected on the benthic macroinvertebrates.

Objectives

Numerous physical, chemical and biotic factors regulate the occurrence and distribution of stream benthic invertebrates (Hynes

1970). General physical-chemical conditions, such as temperature, water quality, and dissolved oxygen, exert their influences over a wide area and may determine the macrodistribution of macroinvertebrate species (Cummins 1975). For example, temperature, water chemistry, and dissolved oxygen tend to operate in a homogeneous manner over localized areas of stream. They can, therefore, be ignored in microdistributional studies and attention may be directed to the heterogeneous conditions within a small area of stream bottom (Rabeni and Minshall 1977). Here, microdistributional patterns are influenced by certain factors that are quite varied, such as velocity, habitat, substrate particle size, turbulence, and food (Rabeni and Minshall 1977, Cummins 1975, and Hynes 1970).

Natural, unperturbed, headwater streams tend to have alternating deep and shallow areas--pools and riffles--as the major habitat types (Cummins 1964). Moon (1939) referred to this as the erosion-deposition concept: in places of fast flowing water all but the coarse substrate are washed away forming riffles and in areas of reduced current, depositional habitats or pools, fine sediments are deposited. Each species of macroinvertebrate, in accordance with its morphological and functional adaptations, selects one of these habitats in which to live (Odum 1971). Many studies have shown that benthic communities of pools and riffles differ in composition (Vannote 1976, Rabeni and Minshall 1977, Minshall and Minshall 1977, Kimble and Wesche 1975, Hynes 1970, Sprules 1941, and Shelford 1937). Both habitats must be sampled to determine distribution of all taxa that are present in a stream.

The erosion-deposition concept infers that current, depth and substrate are the principal factors that define pool and riffle structure. Many invertebrates have an inherent need for current, either for feeding purposes, or because their respiratory requirements demand it (Hynes 1970, Jaag and Ambuhl 1964). Edington (1968) found that the separation of larvae of net-spinning caddisflies into riffle and pool species was related to water velocity. Minshall and Minshall (1977) found three different relationships of invertebrate populations to current velocity. Some species increased in numbers as velocity increased, some species decreased, and a third type of response showed an optimum in mid-range, with the numbers tapering off on either side.

Water depth is also related to current velocity and may influence which habitats benthic animals prefer (Kamler and Reidel 1960 cited in Kimble and Weshe 1975). Kimble and Wesche (1975) and Hooper (1973) found that a depth of 0.3 m or less appears to produce higher numbers of organisms. Furthermore, as part of the general stream model that was developed for the overall study, Fowler (1977) incorporated the concept of a "depth-velocity category" for predicting suitable trout habitat in a stream. In Banks et al. (1974) several previous studies are cited as a basis for assuming that various species of fish at various stages of life tolerate specific ranges of depth and velocity. These conditions are referred to as the "depth-velocity category" of the habitat and may be measured in the field. Since depth and velocity are related to discharge through hydraulic relationships there exists the possibility of defining the abundance of any particular "depth-velocity category" as a function of discharge if we sufficiently understand the physical nature of the stream (Fowler 1977). It would be worthwhile, then, to classify macroinvertebrate habitat into depth by velocity categories also. Thus, if the width of a stream varies as through dewatering, the characteristic depths and velocities will exhibit changes, and the effects of these changes on macroinvertebrate distribution may be predictable.

The purpose of this study, therefore, was: (1) to assess the distribution of the benthic communities in pools and riffles of a headwater stream in terms of taxa and standing crop; (2) to determine any correlations between the distribution of invertebrates and physical factors of the stream environment such as depth and velocity; and (3) to suggest hypotheses about changes in invertebrate distribution due to alteration of habitat, depth, and current by reduced stream flow.

DESCRIPTION OF STUDY AREA

The Strawberry River is a small, clear headwater stream which originates from springs at an elevation of 3132 m (10,275 ft) on the southwest slope of the Uinta Mountains, Uinta National Forest, Wasatch County, Utah. The river flows 32 km (20 miles) south into Strawberry Reservoir and then 64 km (40 miles) east to Starvation Reservoir before flowing into the Duchesne River, a tributary of the Green River.

This study was conducted about 15 km upstream from Interstate Highway 40 (Heber to Duchesne, Utah). Four study sections (Figure 1), each 400 m long, were selected between 2500 m and 2601 m elevation to enable simultaneous manipulation of various stream flow levels (Kadlec, Wydoski and Fowler 1975). The study sections are from 500 m to 800 m apart and differ only slightly from one another physically (Table 1) and chemically (Kadlec and Fowler 1976).

The Strawberry River is fed by spring water and snow melt. The water temperature is cool through much of the year with the highest daily fluctuations during the summer months. The water is high in dissolved solids, most of which are in the form of calcium carbonate (mean total alkalinity 190 mg/l). The water is well buffered with an alkaline pH being maintained between 8.1 and 8.35.

Rolling hills surround the study stream. These are covered with quaking aspen (Populus tremuloides) and Engelmann spruce (Picea engelmanni), intermixed with blue spruce (P. pungens), Douglas fir (Pseudotsuga menziesii) and subalpine fir (Abies lasciocarpa). Big sagebrush (Artemisia tridentata) is abundant on the valley floor and

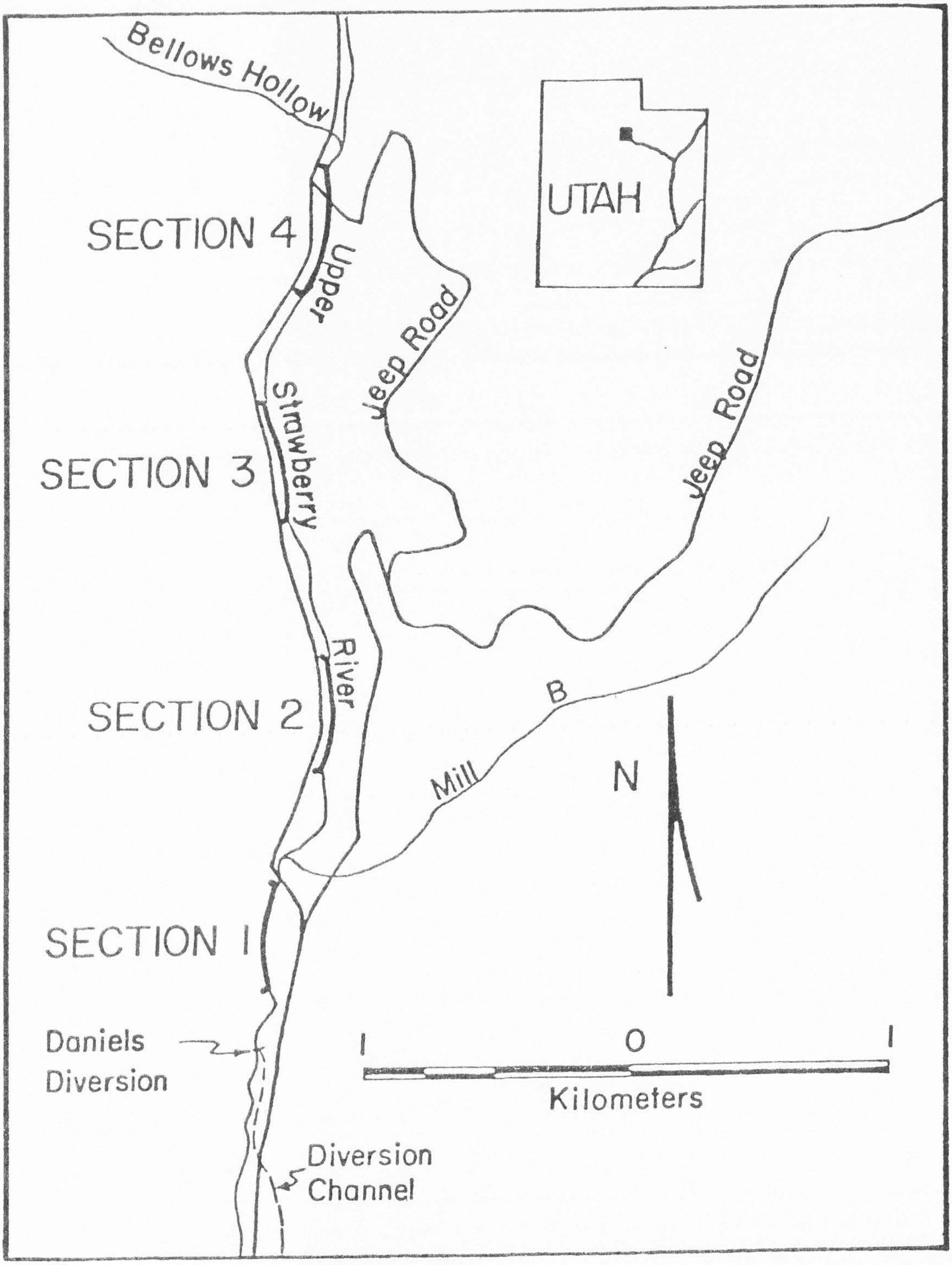

Figure 1. The four study sections on the upper Strawberry River.

Table 1. Physical parameters of the four 400 m study sections of the upper Strawberry River.

Section	Mean stream width (m)	Mean stream area (m^2)	Percentage slope	Average size of "pool" stones n = 10	Average size of riffle stones n = 10
1	3.44	1376	3.27	13.5 ± 6.8	8.9 ± 6.2
2	3.52	1408	2.90	10.3 ± 7.7	8.1 ± 5.4
3	3.35	1340	3.52	11.3 ± 5.7	13.0 ± 5.9
4	3.36	1344	3.44	19.8 ± 8.1	9.7 ± 7.2

south facing slopes. Pussy willow (*Salix wolfii*) is the most common shrub along the stream bank, sometimes forming a canopy over the stream. Various sedges and grasses add to the lush streamside vegetation.

Fluvial and adfluvial cutthroat trout composed 91% of the fish population in the upper Strawberry River (Valdez and Phillips 1976). Adfluvial spawners ascend 30 km from Strawberry Reservoir, and their progeny live sympatrically with the fluvial fish for their first 2 years of life. Mottled sculpin (*Cottus bairdi*), brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) were also present in the stream. Cutthroats in this stream were migratory, moving downstream in early winter and upstream in spring (Valdez and Phillips 1976). Many beaver (*Castor canadensis*) were present in the study area. Beaver dams were found above section 4 and a dam was also found between sections 2 and 3.

The habitat in all 4 sections is primarily an erosional type, interspersed with deep, pool-like pockets. However, the substrate in both riffles and "pools" is large cobble and small boulder (Cummins 1962), and cannot be used as a distinguishing characteristic between habitat types (Table 1). The distribution of stony material was constant for both "pools" and riffles and therefore was not a factor in the microdistributional study.

Classification and identification of habitats is difficult due to the subjectivity involved. The "pool" habitat of the upper Strawberry River does not have a substrate characteristic of the depositional habitat of Moon (1939). Visual observation of the "pool" bottoms, however, did show a layer of fine detritus that was not observed in riffle habitat. The "pools" therefore possessed properties of both pools and non-turbulent reaches or runs.

Anchor ice was first observed in the riffles during the November collection. Snow depth exceeded 2 m over the stream during the January and March collections. The summer was generally dry with occasional afternoon thundershowers. A heavy spring run-off resulting from mountain snowpack occurred during May and June.

MATERIALS AND METHODS

Selection of a Sampling Device

Most investigations of the benthos belong to one of two broad categories: extensive faunal surveys or intensive quantitative studies (Elliot 1971). The main objectives of a faunal survey are to discover which species are present, and to estimate the relative abundance of each species at different stations in the sampling area. Therefore, the sample at each location should cover a large area of bottom. The chief objective of quantitative studies is to estimate the total numbers per unit area for each species. The dimensions of the sampling unit for these purposes differs from the sample size of a faunal survey in that the smallest possible sampling unit should be used.

Deciding which method would best meet the objectives of both these studies is a difficult task. Quite often, a comparison of results from various benthic investigations is not possible because of the wide range of procedures employed. Much of the difficulty stems from the fact that a sampling device which is suitable for all types of habitat has yet to be developed. The sampler employed in this study was selected on the basis of a review of the literature. Samplers from all major categories (Macan 1959, Cummins 1962, Hynes 1970) were studied and the results of their collections compared statistically when possible (Payne 1976). I concluded that the wire basket filled with natural substrate (Crossman and Cairns 1974) performed better than any other available method for benthic studies of stony streams.

Collection of the Benthos

Benthic samples of macroinvertebrates were taken from the upper Strawberry River from September, 1975 through August, 1976. A riffle and "pool" were selected in each of the 4 study sections providing 8 sampling sites. Four baskets constructed of double layers of 1/4 inch wire mesh were placed laterally across the stream in each of the 8 sites, which allowed 32 baskets to be sampled during each collection period, 16 samples from the riffle habitat and 16 samples from the "pool" habitat. Each basket enclosed 0.25 m^2 and was 0.15 m deep. The size of the stream's substrate was the criterion which determined basket size (Table 1). Each basket was buried in the stream's substrate.

Successful sampling depended on the choice of a proper colonization period. Most studies employing samplers requiring colonization have allowed, on the average, a 1 month period between collections (Crossman and Cairns 1974, Benfield, Hendricks and Cairns 1974, Jacobi 1971, Mason, Anderson and Morrison 1967, Hester and Dendy 1962, Britt 1955, and Moon 1940). Rarely has the question of proper colonization time been addressed. However, Brooks (1972), in a study that evaluated a Hilsenhoff (1969) sampler, similar to the wire basket, found that seven weeks were required for the sampler to become fully colonized.

Frequency of sampling is important because of the differing life cycles of benthic invertebrates. Life cycles can be hemivoltine (e.g., Baetis), univoltine (most species), or multivoltine (e.g., Hesperoperla pacifica) (Usinger 1956). Even those species requiring the same length of time to complete their life cycles can emerge at different times of the year. Nemouridae and Capniidae, the winter stoneflies, emerge as adults from January to March (Gaufin et al. 1966) as opposed to most aquatic invertebrates which emerge during the summer months. Minshall (personal communication, March 1977) believes that for faunal surveys and quantitative studies, the minimum number of sampling periods on an annual basis should be 4 and should include the four seasons of the year.

Based on the above information I decided to allow a 2 month period for colonization of the baskets. This permitted 6 collections during a 1 year period and was considered a reasonable compromise between frequency of sampling and time required for processing the samples.

Two people removed each basket. One stood downstream of the basket with a 23 liter bucket. The entire contents of the basket (stones, detritus, silt, organisms, etc.) were removed from the stream and emptied into the bucket. The larger stones were individually scrubbed with a brush and placed back in the sample basket, which was re-embedded in its original location in the stream substrate. Using the sugar flotation technique (Anderson 1959), the organic material was separated from the remaining gravel and small stones by a series of sieves (the smallest with openings of 0.5 mm). The sample was then deposited in a 1 liter wide-mouthed plastic container and preserved in 10% formalin solution.

Table 2 is a diagrammatic representation of the sampling design. Each cell represents the actual number of baskets sampled. Because of spring run-off, samples were collected in June rather than in May.

Table 2. Experimental design for benthic analysis. 6 time periods, 4 locations, and 2 habitats produce 48 treatments. Each treatment contains the number of baskets sampled.

R = riffle   P = pool   n = 146

	1		2		3		4	
	R	P	R	P	R	P	R	P
Sep	4	4	4	4	4	3	4	4
Nov	4	4	3	4	1	3	4	4
Jan	1	1	1	1	1	1	1	1
Mar	4	4	4	4	4	3	4	4
June	3	1	1	4	4	1	3	3
Aug	4	4	4	3	2	4	4	4

The strong current from run-off resulted in the loss of 12 baskets. During January severe weather conditions and equipment failure caused only 1 basket from each sampling site to be collected. The loss of baskets at other times of the year was attributed to vandalism.

Laboratory Analysis of Benthic Invertebrate Samples

The preserved samples were rinsed with tapwater in a #60 Tyler sieve. The sample was then placed in a white enamel dissecting pan where the larger, easily recognized organisms were removed from the detritus with the aid of a 2X power magnifying lamp. The remaining sample, while being agitated, was poured through a subsampler (Walters 1969) providing 8 subsamples. The animals present in two of these subsamples were then separated from the detritus and, together with the larger, non-subsampled animals, keyed to their various taxa with the aid of a dissecting scope. The taxonomic keys used for identification were Wiggins (1977), Edmunds et al. (1976), Caucci and Nastasi (1975), Johannsen (1969), Gaufin et al. (1966), and Usinger (1956). Total numbers of each taxon found in each basket were then recorded.

Biomass was determined by taking the organisms out of formalin and placing them on filter paper in a Buchner funnel. The animals were then rinsed with distilled water and placed in a drying oven at 105°C for 4 hours (E.P.A. 1973). After cooling to room temperature while in the desiccator, the invertebrates were weighed on a Mettler H 51 analytical balance to four decimal places. All weights are listed in grams, dry weight.

Velocity and Depth Measurements

Measurements of water velocity were recorded upstream, downstream, and on top of each basket. The velocity readings (in ft/sec) were taken at the substrate-water interface with a Marsh-McBirney #201 electromagnetic current meter. The three readings per basket were combined to provide an average velocity per basket.

Depth measurements were taken by placing the end of a meter stick on the top center of the basket and recording the depth of water over the basket in centimeters. Velocity and depth readings were not taken for two of the six collection periods (September and January).

RESULTS

Community Composition

Representatives of fifty-nine taxa were collected (Table 3). Due to the scarcity of some organisms, 46 taxa were used in the analysis of numbers and 33 taxa were used in the analysis of biomass. These were organisms that were high in numbers, biomass, or both.

Two species of stoneflies previously reported (Gaufin et al. 1966) to be rare in Utah were very abundant in the study stream. Although common in the Northwest, *Brachyptera pallida* had never been collected in Utah and *Capnia uintahi* had been collected only from the upper Provo River, with intensive collecting throughout the rest of the state failing to locate this species elsewhere. Adults of *Capnia lemoniana* and *C. uintahi* were both collected, but they were indistinguishable in their nymphal stages. Their patterns of distribution are analyzed as one species and together are referred to in the text as *Capnia* spp.

Some of the rarer forms found in the study stream, such as Dytiscidae, Hydrophilidae, Corixidae, and Cyclopoda, were observed only once or twice. These are usually found in ponds and lakes and may have been washed downstream from beaver ponds. Ostracoda, Hydracarina, and Nematoda are included in the list of taxa studied, although generally they are considered to be microinvertebrates (< 3 mm at maturity; Cummins 1975). Because only the larger life stages of microbenthos were collected, the samples were not a good representation of the numbers present.

The remaining taxa, comprising the greatest percentage of organisms collected, belong to the order Insecta, with the exception of

Table 3. List of taxa observed in collections taken from the Upper Strawberry River, Utah during the period between September 1975 through August 1976.

EPHEMEROPTERA

Ameletus
Baetis
Cinygmula
Ephemerella coloradensis
Ephemerella doddsi
Ephemerella grandis
Ephemerella inermis
Epeorus longimanus
Paraleptophlebia
Rhithrogena

DIPTERA

*Antocha**
Ceratopogonidae
Chironomidae
Dicranota
Dolichopodidae*
Dixa
Empididae
Euparyphus
Hexatoma
Limnophora
Pericoma
Prosimulium
Ptychoptera
Tabanidae*
Tipula A & B
Unknown Tipulidae*

TRICHOPTERA

Arctopsyche
Hesperophylax
Hydroptilidae*
Limnephilus
Limnephilidae?
Unknown Limnephilidae*
Rhyacophila

PLECOPTERA

Alloperla pallidula
Arcynopteryx parallela
Arcynopteryx signata
Brachyptera pallida
Capnia lemoniana
Capnia uintahi
Hesperoperla (*Acroneuria*) *pacifica*
Isogenus aestivalis
Isoperla
Nemoura cinctipes
Unknown Perlodidae

COLEOPTERA

Elmidae
Dytiscidae*
Hydrophilidae*

MEGALOPTERA

Sialis

HEMIPTERA

Corixidae*

COLLEMBOLA

Entomobryidae*

MISCELLANEOUS AQUATIC TAXA

Cyclopoda*
Helobdella
Hydracarina
Nematoda*
Oligochaeta
Ostracoda
Pisidium
Dugesia

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*Taxa not used in analysis.

Dugesia, *Helobdella*, Oligochaeta, and *Pisidium*. They all are representative of the fauna of lotic waters, exhibiting the morpho-behavioral adaptations for living in a fast current.

Standing Crop

The arithmetic means of the numbers and biomass of organisms in each taxon were determined for the year, for each collection, and for each habitat per collection (Table 4-9). The annual mean standing crop in total numbers per m^2 was 8837 and in total biomass per m^2 was 3.276 g. Eight taxa (Chironomidae, *Baetis*, *Pericoma*, *Nemoura cinctipes*, *Cinygmula*, *Dugesia*, *Prosimulium*, and *Capnia* spp. comprised 90 percent of the annual mean standing crop in numbers and hereafter are referred to as the major taxa. Unlike standing crop in numbers biomass was not dominated by any group of taxa (Table 7). Only the caddisfly *Hesperophylax* had a much higher biomass (0.134 grams per basket) in comparison with the other taxa, which had on the average a mean annual biomass of 0.021 grams, and a range of 0.095 to 0.001 grams.

Numerical dominance for each member of the major taxa remained about the same during the one year period, except for *Prosimulium*, which was abundant only in the June collection. Chironomidae was always the most abundant taxon present (Table 5).

Community standing crop decreased from late Fall 1975 until early Summer 1976 (Table 5). In respect to the major taxa, this decrease was reflected in the standing crops of *Cinygmula*, *Pericoma*, *Capnia* spp. *Nemoura cinctipes* and *Dugesia*. *Baetis*, Chironomidae, and *Prosimulium* increased or remained about the same during this period (Table 5). There was an increase in community standing crop in June due to

*Table 4. Means, standard errors and maximum numbers of organisms per basket (.25 m^2) collected from the upper Strawberry River, Utah, over a one year time period (1975-76) and the standard deviations of the samples.

Taxa	Means and standard errors of the number of organisms per basket over a 1-year time interval	Maximum number of organisms per basket	Standard deviation
Chironomidae	922.7±98.1	6298	1185.3
Baetis	352.7±52.5	5995	634.2
Pericoma	208.5±30.9	2162	373.9
Nemoura cinctipes	201.8±31.2	2874	377.4
Cinygmula	118.3±13.8	1516	105.4
Dugesia	62.9±10.5	1120	126.4
Prosimulium	45.7±11.5	908	139.4
Capnia spp.	40.1± 7.4	664	89.1
Oligochaeta	35.7± 8.8	944	106.4
Hydracarina	23.0± 4.1	328	50.0
Alloperla pallidula	22.4± 3.5	348	42.7
Rhyacophila	19.5± 1.9	104	23.2
Paraleptophlebia	19.3± 2.3	173	27.2
Brachyptera pallida	15.1± 3.3	282	39.9
Ephemerella coloradensis	11.3± 1.7	112	21.0
Ostracoda	11.2± 2.5	216	30.8
Epeorus longimanus	8.7± 1.7	120	20.8
Ephemerella grandis	8.5± 1.6	132	18.9
Hesperoperla pacifica	7.6± .8	49	10.2
Limnophora	6.6± 1.4	117	16.5
Limnephilidae ?	6.6± 1.9	198	23.1
Arctopsyche	5.8± 1.8	195	22.2
Ephemerella doddsi	5.4± .9	76	10.3
Arcynopteryx	5.2± .7	41	6.5
Elmidae larva	5.2± 1.0	120	12.1
Ephemerella inermis	4.7± 1.2	83	14.5
Dicranota	4.4± .6	68	7.9
Ptychoptera	3.5± 1.3	184	15.9
Helobdella	3.4± 2.0	286	24.5
Hesperophylax	3.4± .6	42	6.6
Ameletus	3.3± .5	44	6.4
Unknown Perlodidae	2.9± .7	60	8.9
Euparyphus	2.3± .5	40	6.1
Limnephilus	2.1± .4	27	4.7
Ceratopogonidae	1.6± .3	32	4.1
Elmidae adult	1.6± .5	42	5.6

Table 4. Continued

Taxa	Means and standard errors of the number of organisms per basket over a 1-year time interval	Maximum number of organisms per basket	Standard deviation
Tipula B	1.6± .4	36	4.4
Arcynopteryx _signata_	1.2± .5	73	6.2
Empididae	.9± .2	16	2.6
Tipula A	.9± .2	18	2.1
Isogenus _aestivalis_	.4± .1	8	1.3
Pisidium	.4± .2	16	1.8
Sialis	.3± .1	5	1.0
Dixa	.2± .1	4	.8
Hexatoma	.2± .1	8	2.0
Rhithrogena	.1± .1	4	.6

Mean Standing Crop in Numbers/m^2/yr = 2837.228

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*Tables 5 and 6 list organisms in decreasing order according to their annual standing crop in numbers (Table 4).

Tables 8 and 9 list organisms in decreasing order according to their annual mean standing crop in biomass (Table 7).

Table 5. Mean standing crop in numbers per basket (.25 m^2) for each collection from the upper Strawberry River, Utah (1975-76).

Taxa	September	November	January	March	June	August
Chironomidae	796.9	742.4	521.4	632.3	493.6	1941.8
Baetis	149.4	206.4	480.5	266.3	314.6	789.6
Pericoma	360.6	166.7	15.8	46.5	11.7	449.6
Nemoura cinctipes	157.0	165.0	48.8	38.8	91.6	576.3
Cinygmula	66.2	186.2	101.8	84.7	167.8	117.1
Dugesia	18.3	36.6	4.5	10.3	88.8	189.4
Prosimulium	0.9	8.8	14.2	19.4	266.4	12.7
Capnia spp.	12.4	166.0	28.8	9.4	0.2	16.0
Oligochaeta	2.4	1.7	0	0.3	206.3	33.2
Hydracarina	10.6	9.2	0.1	2.6	52.5	57.2
Alloperla pallidula	37.9	19.8	8.0	10.9	45.6	8.6
Rhyacophila	13.4	24.8	8.5	7.5	41.3	22.0
Paraleptophlebia	40.7	11.8	0.8	5.4	20.6	33.0
Brachyptera pallida	0.1	12.7	29.8	31.8	10.0	14.9
Ephemerella coloradensis	0.6	8.4	4.6	15.3	31.2	9.5
Ostracoda	16.5	0.8	1.8	1.3	22.0	21.1
Epeorus longimanus	0	0.1	3.5	27.4	17.2	1.5
Ephemerella grandis	4.5	4.1	4.8	2.2	11.0	23.1
Hesperoperla pacifica	11.0	9.6	4.4	3.1	7.2	7.9
Limnophora	9.4	4.9	0.6	0.3	0.8	17.8
Limnephilidae ?	0.1	3.5	2.6	2.2	13.2	17.8
Arctopsyche	17.8	3.9	1.5	0.7	0.9	4.5
Ephemerella doddsi	4.6	6.1	12.9	6.4	2.4	4.7
Arcynopteryx parallela	3.8	10.6	16.6	4.1	3.2	1.2
Elmidae larva	1.4	2.2	0	0.8	21.5	7.0
Ephemerella inermis	0.5	0	0	0	0	23.1
Dicranota	2.4	4.4	0.4	1.1	12.4	5.9
Ptychoptera	9.8	2.7	0	1.2	0.2	3.2
Helobdella	12.6	1.6	0	1.2	0.2	0.8
Hesperophylax	6.7	0.5	0.1	1.4	4.8	4.8
Ameletus	2.3	6.5	2.6	3.0	0.8	3.6
Unknown Perlodidae	8.7	0.6	0	0.4	0.4	4.0
Euparyphus	0.9	0.5	0	0.4	2.2	8.2
Limnephilus	1.1	0.1	0.6	0.6	1.0	7.8
Ceratopogonidae	0.4	2.1	0	0.8	3.4	2.2
Elmidae adult	0.2	0.4	0	4.4	2.2	1.2
Tipula B	2.4	1.6	0.1	0	2.2	2.2
Arcynopteryx signata	3.1	1.1	1.4	1.2	0.2	0
Empididae	0	0	0	0.2	3.5	2.1
Tipula A	0.5	0.7	0.1	0	3.1	1.2
Isogenus aestivalis	0	0.4	0.4	1.0	0.6	0.1
Pisidium	0.3	0	0	0	0.8	1.0
Sialis	0.8	0.1	0	0.2	0	0.4
Dixa	0.1	0	0	0	0	0.7
Hexatoma	0	0	0	0	0.5	0.7
Rhithrogena	0	0	0	0.3	0.4	0
TOTAL MEAN STANDING CROP IN NUMBERS PER M^2	7117.2	7342.4	5287.2	4989.6	7922.0	17802.8

Table 6. Mean standing crop in numbers of organisms per basket (.25 m^2) for each habitat per collection from the upper Strawberry River, Utah (1975-76).

Taxa	September		November		January		March		June		August	
	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool
Chironomidae	136.4	1501.5	506.5	931.1	393.0	649.75	256.8	1032.9	611.7	349.1	1670.4	2195.1
Baetis	226.6	67.1	177.2	229.8	171.75	789.2	160.3	379.4	400.0	210.3	1046.1	550.1
Pericoma	288.4	437.6	93.1	225.5	2.0	9.5	10.7	84.6	10.0	13.8	584.1	323.9
Nemoura cintipes	174.7	138.1	164.1	165.7	45.5	52.0	37.7	40.0	91.9	91.3	738.5	424.9
Cinygmula	87.9	42.9	171.3	198.1	70.5	133.0	66.1	104.5	186.8	133.3	111.6	122.2
Dugesia	0.1	28.6	17.0	52.2	3.2	5.8	2.8	18.3	73.1	108.1	154.7	221.7
Prosimulium	1.1	0.7	11.9	6.3	17.5	11.0	16.4	22.7	203.5	348.2	18.2	7.6
Capnia spp.	8.2	16.9	146.2	181.8	21.0	36.5	13.7	4.8	0.4	0	8.1	23.3
Oligochaeta	0.1	4.9	0	3.0	0	0	0.2	0.3	266.4	132.9	36.0	30.5
Hydracarina	8.1	13.2	1.7	15.2	0.2	0	0.9	4.3	66.4	35.6	36.5	76.5
Alloperla pallidula	57.4	17.0	20.8	18.9	5.5	10.5	4.8	17.4	47.4	43.2	8.9	8.4
Rhyacophila	15.0	11.6	16.2	31.8	7.5	9.5	6.8	8.3	47.2	34.1	23.5	20.6
Paraleptophlebia	27.9	33.7	11.4	12.2	0	1.5	2.2	8.7	19.8	21.4	35.6	30.5
Brachyptera pallida	0	0.2	14.4	11.3	15.5	44.0	15.4	49.2	14.1	4.9	25.4	5.1
Ephemerella coloradensis	.25	1.1	1.8	13.6	1.5	7.8	9.8	21.2	45.5	13.6	11.1	8.1
Ostracoda	0	34.1	0.8	0.8	2.5	1.0	1.5	1.1	25.5	17.7	1.7	39.2
Epeorus longimanus	0	0	0.3	0	5.0	2.0	23.7	31.5	14.0	20.0	2.2	0.8
Ephemerella grandis	5.9	3.9	2.1	5.7	1.0	8.5	0.8	3.7	8.0	14.7	28.4	18.1
Hesperoperla pacifica	15.3	.4	4.7	13.4	1.2	7.5	1.0	5.3	10.0	3.9	4.8	10.8
Limnophora	2.6	16.8	0.4	8.5	1.0	0.2	0	0.5	1.4	0	20.0	15.7
Limnephilidae	0	0.1	0.7	5.8	1.8	3.5	0.7	3.8	15.8	10.0	3.8	30.8
Arctopsyche	33.8	0.8	6.6	1.7	2.5	0.5	1.1	0.2	1.5	0.1	9.1	0.2
Ephemerella coloradensis	6.6	2.5	3.2	8.5	5.5	20.3	4.4	8.5	3.1	1.7	4.6	4.7
Arcynopteryx parallela	1.3	6.5	9.2	11.7	13.2	20.0	2.4	5.8	4.4	1.8	2.0	0.5
Elmidae larva	0.7	2.3	0.8	3.3	0	0	0.3	1.4	26.9	14.9	7.8	6.3
Ephemerella inermis	0.5	0.5	0	0	0	0	0	0	0	0	33.1	13.8
Dicranota	3.7	1.1	6.2	3.0	0.2	0.2	0.4	1.8	14.1	10.3	5.0	6.8
Ptychoptera	12.5	6.9	0	4.9	0	0	0.1	2.5	0.2	0.1	0.6	5.6
Helobdella	0.1	26.1	0	2.8	0	0	0.1	2.3	0	0.4	0.3	1.3
Hesperophylax	8.8	4.5	0	0.9	0	0.2	0.4	2.3	4.5	6.2	6.4	3.3
Ameletus	0	4.8	1.1	10.8	0.8	4.5	2.1	3.9	0.4	1.1	3.4	3.7
Unknown Perlodidae	16.8	0	0.3	0.8	0	0	0.8	0	0.7	0	4.3	3.7
Euparyphus	0.8	1.1	0.4	0.6	0	0	0.3	0.5	2.4	1.8	9.7	6.8
Limnephilus	1.3	0.8	0.2	0.1	1.2	0	0.8	0.4	0.8	1.3	3.6	11.7
Ceratopogonidae	0.4	0.5	1.7	2.4	0	0	0.5	1.1	5.4	0.9	2.1	2.4
Elmidae adult	0.1	0.5	0	0.8	0	0	7.8	0.8	3.3	1.0	1.6	0.9
Tipula B	1.9	3.0	0.4	2.6	0.3	0	0	0	3.6	0.6	3.2	1.3
Arcynopteryx signata	5.6	0.4	2.2	0.2	0.5	0.2	0.5	1.9	0.3	0.1	0	0
Empididae	0	0.1	0	0	0	0	0.2	0.1	4.4	2.4	2.4	1.9
Tipula A	0.25	0.8	0.3	0.9	0	0.2	0	0.1	2.4	4.0	0.8	1.6
Isogenus aestivalis	0	0	0.6	0.3	0	0.8	1.7	0.9	0.7	0.6	0	0.3
Pisidium	0	0.6	0	0	0	0	0	0.1	0.7	0.9	1.1	0.9
Sialis	0.1	1.6	0	0.3	0	0	0	0.3	0	0	0	0.8
Dixa	0.1	0.1	0.1	0	0	0	0	0	0	0	1.1	0.3
Hexatoma	0	0	0	0	0	0	0	0	0.5	0.6	0.6	0.7
Rhithrogena	0	0	0	0	0	0	0.4	0.3	0	0.9	0	0
TOTAL STANDING CROP IN NUMBERS/m^2	4605.2	9764.0	5584.0	8749.2	3165.4	7318.6	2626.8	7510.8	8961.6	6651.2	18689.6	16973.6

Table 7. Means, standard errors and maximum biomass (grams, dry weight) of organisms per basket collected from the upper Strawberry River, Utah over a one year time period (1975-76) and the standard deviations of the samples. Each basket = 25 cm^2.

Taxa	Means and standard errors of the biomass of organisms per basket over a 1-year time interval (grams, dry weight)	Maximum biomass of organisms per basket	Standard deviation
Hesperophylax	.134± .029	.838	.204
Chironomidae	.095± .021	.716	.147
Baetis	.077± .02	.831	.140
Hesperoperla pacifica	.064± .017	.676	.117
Tipula A	.044± .011	.384	.079
Arcynopteryx parallela	.043± .01	.291	.071
Rhyacophila	.039± .007	.280	.048
Cinygmula	.038± .007	.208	.046
Dugesia	.034± .011	.525	.078
Nemoura cinctipes	.030± .004	.141	.03
Limnephilus	.026± .009	.322	.062
Alloperla pallidula	.024± .006	.158	.039
Prosimulium	.023± .011	.474	.078
Oligochaeta	.016± .005	.153	.032
Ephemerella grandis	.015± .01	.484	.071
Pericoma	.015± .004	.147	.027
Ephemerella coloradensis	.014± .005	.146	.032
Arcynopteryx signata	.012± .005	.204	.034
Arctopsyche	.010± .003	.084	.021
Limnophora	.010± .003	.110	.024
Brachyptera pallida	.008± .005	.251	.036
Ephemerella doddsi	.008± .002	.092	.016
Hydracarina	.008± .005	.232	.034
Capnia spp.	.006± .001	.037	.009
Ephemerella inermis	.005± .002	.069	.015
Paraleptophlebia	.005± .001	.025	.006
Ptychoptera	.004± .001	.053	.009
Elmidae larvae	.003± .002	.057	.011
Isogenus aestivalis	.003± .001	.039	.007
Hexatoma	.002± .001	.036	.006
Limnephilidae ?	.002±0	.003	.015
Elmidae adult	.001±0	.013	.003
Epeorus longimanus	.001±0	.011	.002

Table 8. Mean standing crop in biomass of organisms per basket (.25 m^2) for each collection from the upper Strawberry River, Utah (1975-76). (grams, dry weight).

Taxa	Sep	Nov	Jan	Mar	Jun	Aug
Hesperophylax	.347	.028	.004	.025	.201	.201
Chironomidae	.120	.126	.054	.100	.031	.138
Baetis	.034	.011	.036	.013	.105	.26
Hesperoperla pacifica	.071	.107	.048	.040	.027	.092
Tipula A	.065	.092	.001	.001	.048	.059
Arcynopteryx parallela	.004	.046	.144	.059	.004	0
Rhyacophila	.059	.040	.033	.025	.039	.038
Cinygmula	.035	.027	.024	.015	.033	.092
Dugesia	.025	.015	.004	.006	.099	.053
Nemoura cinctipes	.020	.051	.036	.031	.008	.035
Limnephilus	.047	.001	.005	.003	.013	.084
Alloperla pallidula	.032	.033	.005	.013	.059	.004
Prosimulium	.001	.001	.001	.005	.129	.002
Oligochaeta	.010	.019	0	0	.055	.012
Ephemerella grandis	.001	.005	.008	.005	.072	.002
Pericoma	.016	.051	.002	.014	.002	.006
Ephemerella coloradensis	0	.002	.001	.001	.011	.066
Arcynopteryx signata	.001	.015	.030	.020	.006	0
Arctopsyche	.013	.014	.007	.002	.015	.007
Limnophora	.025	.016	.001	.001	.0	.019
Brachyptera pallida	0	.001	.003	.035	.010	0
Ephemerella doddsi	.001	.004	.016	.011	.014	0
Hydracarina	.006	.002	0	0	.003	.034
Capnia spp.	.002	.021	.008	.005	0	.001
Ephemerella inermis	.001	0	0	0	0	.030
Paraleptophlebia	.010	.007	.001	.003	.005	.006
Ptychoptera	.011	.006	0	.002	0	0
Elmidae larva	0	.001	0	0	.006	.002
Isogenus aestivalis	0	.002	.002	.012	.001	0
Hexatoma	0	0	0	0	.007	.002
Limnephilidae ?	0	.004	.001	.002	.002	0
Elmidae adult	0	.001	0	.008	.010	.002
Epeorus longimanus	0	.001	0	0	.001	0
TOTAL BIOMASS IN GRAMS OF DRY WEIGHT/m^2	3.828	3.0	1.888	1.828	4.064	4.988

Table 9. Mean standing crop in biomass of organisms per basket (.25 m^2) for each habitat per collection from the upper Strawberry River, Utah (1975-76). (grams, dry weight)

Taxa	September		November		January		March		June		August	
	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool
Hesperophylax	.393	.302	0	.055	0	.008	.009	.041	.180	.222	.301	.1
Chironomidae	.046	.194	.041	.210	.019	.09	.025	.176	.040	.022	.116	.160
Baetis	.056	.011	.009	.014	.01	.062	.062	.021	.114	.096	.383	.138
Hesperoperla pacifica	.062	.081	.028	.186	.016	.08	.002	.078	.051	.003	.076	.108
Tipula A	.069	.061	.096	.088	0	.001	0	.002	.077	.020	.053	.064
Arcynopteryx parallela	0	.007	.046	.046	.147	.102	.027	.090	.006	.002	0	0
Rhyacophila	.034	.083	.03	.050	.034	.031	.002	.048	.034	.044	.035	.04
Cinygmula	.048	.023	.028	.027	.032	.015	.011	.109	.041	.024	.075	.110
Dugesia	.016	.034	.006	.025	.002	.007	.001	.012	.156	.041	.064	.041
Nemoura cinctipes	.020	.021	.054	.047	.033	.039	.029	.033	.009	.007	.054	.017
Limnephilus	.080	.014	.001	.002	.009	0	.004	.003	0	.027	.031	.137
Alloperla pallidula	.030	.033	.044	.022	.003	.007	.006	.021	.056	.063	.002	.005
Prosimulium	.001	0	.001	.001	.001	.002	.001	.008	.066	.193	.002	.003
Oligochaeta	.001	.019	0	.039	0	0	0	0	.045	.066	.006	.018
Ephemerella grandis	.001	.001	.004	.007	.002	.014	.001	.008	.023	.121	.002	.003
Pericoma	.013	.019	.023	.079	.001	.003	.025	.002	.003	.007	.006	
Ephemerella coloradensis	0	.001	0	.003	0	.001	.001	.002	.011	.012	.066	.067
Arcynopteryx signata	.001	.001	.028	.003	.055	.004	.009	.033	.012	0	0	0
Arctopsyche	.025	.002	.025	.003	.012	.002	.004	0	.029	.001	.014	0
Limnophora	.007	.044	.001	.030	0	.001	0	.003	.001	0	.017	.022
Brachyptera pallida	0	0	0	.001	.003	.004	.063	.007	.016	.004	0	0
Ephemerella doddsi	.001	.001	.002	.006	.007	.025	.009	.012	.014	.014	0	0
Hydracarina	.002	.010	0	.004	0	0	0	0	.004	.033	.005	.062
Capnia spp.	.002	.001	.015	.027	.005	.011	.006	.003	0	0	.001	.001
Ephemerella inermis	.001	.001	0	0	0	0	0	0	0	0	.037	.022
Paraleptophlebia	.009	.011	.008	.006	0	.001	.001	.005	.002	.008	.007	.005
Ptychoptera	.002	.020	0	.013	0	.001	0	.005	0	0	0	.001
Elmidae larva	0	.001	0	.001	0	0	0	0	.008	.004	.002	.001
Isogenus aestivalis	0	0	.033	.001	0	.005	.013	.012	.001	.002	0	.001
Hexatoma	0	0	0	0	0	0	0	0	.005	.009	.001	.004
Limnephilidae ?	0	0	.004	.004	.001	.001	0	.003	.001	.003	0	.001
Elmidae adult	0	0	0	.001	0	0	.014	.001	.018	.001	.003	.002
Epeorus longimanus	0	0	0	.003	.001	0	0	.001	.001	.002	0	0
TOTAL MEAN BIOMASS IN GRAMS OF DRY WEIGHT/m^2	3.68	3.984	1.988	4.016	1.572	2.228	.976	2.688	4.092	4.188	5.44	4.556

increases in numbers of *Prosimulium* and Oligochaeta. The largest increase for the community occurred during August. Highest numbers for all the major taxa except *Capnia* spp. and *Prosimulium* were found at this time (Table 5).

Habitat Preference

All taxa found in riffles were also found in "pools", with the "pool" habitat supporting a greater number of organisms in every collection. Judging by the mean numbers per basket for each habitat (Table 6), only a small percentage of taxa preferred the same habitat throughout the year. These animals preferred "pools" to riffles with only 1 taxon, the net-spinning caddisfly, *Arctopsyche* preferring riffles to "pools" throughout the year. Sampling indicated that the remaining taxa changed their habitat preference depending on the time of the year. The data suggest a pattern in which these organisms prefer riffle habitat during September, June and August and these same taxa then change their preference to "pools" during November, January and March. But the physical conditions changed at these times also which suggests the habitat preference may have stayed constant and only the location of the habitat changed.

As previously noted, discrimination between habitats based on substrate quality was not possible. Student's t-tests of the differences between the means of water velocities over the baskets of both habitats showed no differences for any collection (Table 10, Figure 2). The highest flows for both habitats were found during the summer months and low flows occurred during November and March.

Table 10. Measurements of water velocity over baskets at the substrate-water interface. R = riffle, P = pool, A-D = basket across the stream from west to east, M = missing basket.

Study sections and baskets	Velocity of water (cm/s) over baskets			
	November	March	June	August
1R				
A	0.0	2.9	55.0	M
B	1.5	0.0	M	38.1
C	10.1	0.0	37.1	30.5
D	8.1	8.9	53.9	36.6
1P				
A	0.8	0.0	8.1	11.2
B	3.9	1.1	M	13.7
C	9.1	2.1	M	15.7
D	1.7	3.1	M	7.1
2R				
A	M	1.9	M	27.5
B	3.5	5.7	M	19.3
C	8.2	3.8	M	26.9
D	0.0	0.0	14.8	11.2
2P				
A	6.0	6.6	15.8	9.6
B	15.1	14.7	22.9	26.4
C	5.2	11.6	27.4	22.3
D	4.8	8.1	38.6	17.3
3R				
A	M	6.6	11.7	M
B	M	4.0	21.3	15.8
C	0.2	0.5	24.9	M
D	M	2.5	37.6	15.7
3P				
A	M	M	M	1.0
B	0.7	0.2	M	3.0
C	1.3	0.7	40.1	3.5
D	1.9	1.0	M	6.1
4R				
A	0.0	2.8	M	1.0
B	5.3	27.9	31.5	11.7
C	1.5	14.0	44.7	21.8
D	3.6	0.0	38.6	15.3
4P				
A	5.7	0.1	38.1	6.6
B	4.9	7.0	M	12.2
C	6.7	8.7	27.5	13.7
D	8.4	7.9	25.4	15.2

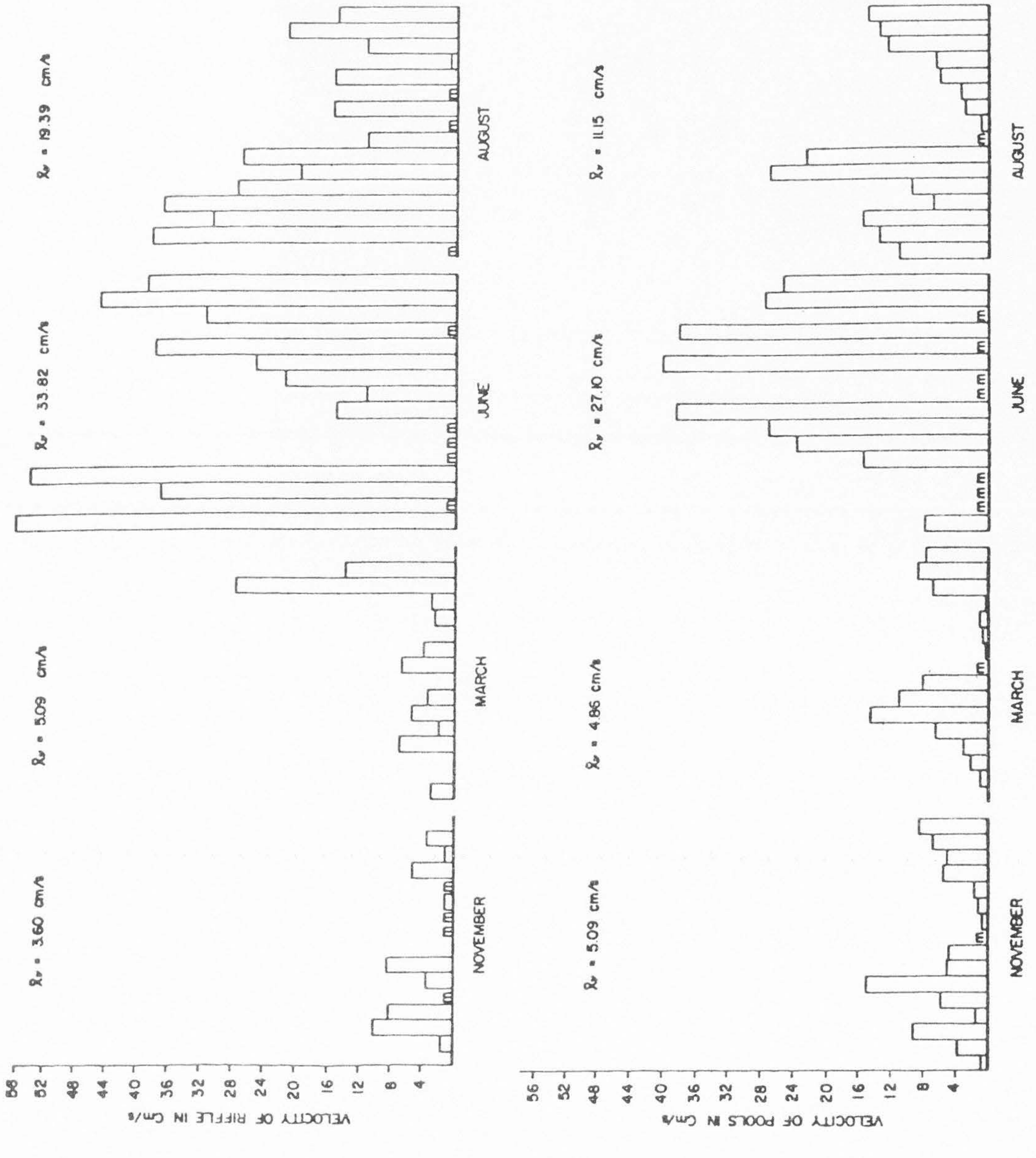

Figure 2. Velocity of water over baskets that were placed in riffles and pools of the upper Strawberry River, Utah. Measurements were taken November, 1975 and March, June, and August, 1976. m = missing basket.

Depth differed significantly between habitats (Table 11, Figure 3). Student's t-tests of the differences between the means of water depth over the baskets were significant for all collections (p = 0.1).

Statistical Analysis of the Effects of Time, Habitat, Depth and Velocity on Benthic Distribution

The results of the six collections from "pool" and riffle habitat were analyzed to determine the statistical significance of spatial and temporal dispersion of the standing crop estimates of the benthic populations. As is indicated by the standard deviation of the samples from the Strawberry River (Table 4), the variances are much larger than the means, a property of contagious distribution (Elliott 1971). Also, analysis of the frequency distributions for each taxon indicated a positive skewness for the distribution of all taxa for all collections. This is a property of a negative binomial, a mathematical model which best describes the parameters of contagious distribution (Elliott 1971). A contagious distribution appears to be the most common pattern of dispersal in stream invertebrates (Allan 1975, Chutter 1972, Chutter and Nobel 1966, Gaufin et al. 1956, Needham and Usinger 1956, Leonard 1939, and others).

Since clumped distributions violate the assumptions of parametric procedures (Neter and Wasserman 1974) a logarithmic transformation $[\ln(x+1)]$ was used in all cases to normalize the data. Plots of the arithmetic means vs. the variances indicated a dependence of the variance on the mean. Plots of the transformed means $[\ln(x+1)]$ vs. variance assured that the components of variance were independent of the mean and analysis of variance could be employed. Table 12 is a summary of this analysis.

Table 11. Measurements of water depth over the baskets. Negative numbers denote height of basket out of the water. R = riffle, P = pool, A-D = baskets across stream from west to east, M = missing basket.

Study section and basket	Depth of Water (cm) over baskets			
	November	March	June	August
1R				
A	-2.0	2.8	9.0	-13.0
B	1.8	7.9	M	7.0
C	9.6	12.7	18.0	5.0
D	13.4	7.5	18.0	5.0
1P				
A	9.0	5.4	25.0	6.5
B	19.0	7.3	M	9.0
C	18.7	8.8	M	14.5
D	21.7	9.5	M	16.5
2R				
A	M	-3.8	M	0.0
B	3.5	-4.5	M	7.5
C	5.4	-2.0	M	7.0
D	2.6	-4.0	13.0	-7.0
2P				
A	4.4	5.3	20.0	2.0
B	18.2	6.5	30.0	13.0
C	18.5	4.5	32.0	11.0
D	12.0	5.7	23.0	12.0
3R				
A	M	-8.3	6.7	M
B	M	3.2	12.7	5.0
C	5.7	0.0	7.3	M
D	M	0.0	7.2	1.0
3P				
A	M	M	M	23.0
B	51.0	41.9	M	28.0
C	65.0	49.3	28.5	26.5
D	67.7	53.5	M	20.0
4R				
A	-3.4	4.8	M	0.0
B	7.2	4.0	13.0	0.0
C	3.0	5.3	10.0	1.5
D	-4.7	-7.2	7.0	-7.5
4P				
A	10.3	1.0	12.0	-4.0
B	21.2	9.5	M	0.5
C	22.0	13.5	30.0	8.5
D	23.0	8.0	17.0	8.5

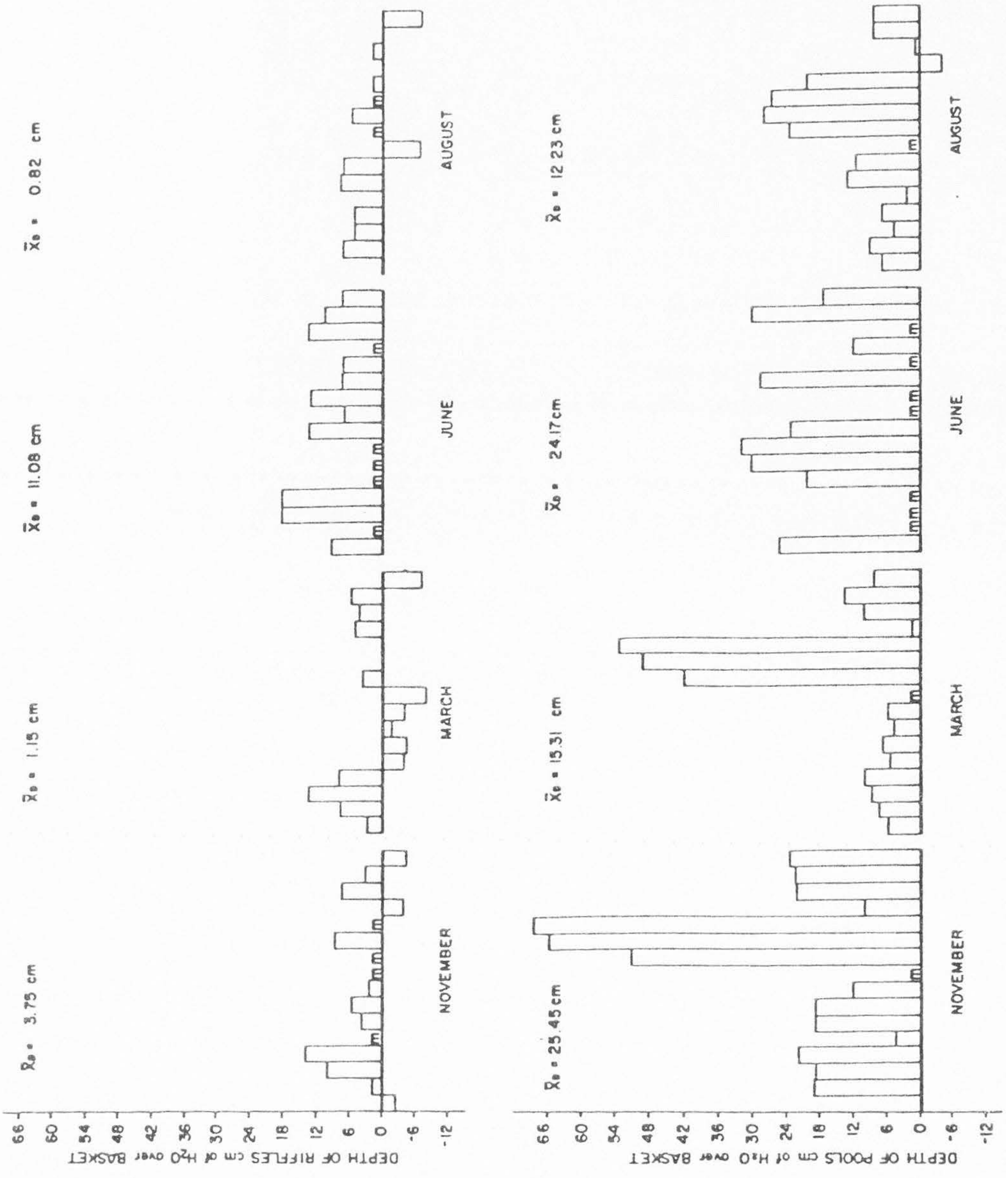

Figure 3. Depth of water over baskets that were placed in riffles and pools of the upper Strawberry River, Utah. Measurements were taken November, 1975 and March, June, and August, 1976. m = missing basket.

Table 12. Summary of F-tests on the means of the main effects and interactions for numbers of each taxon (6 collections). ***-P = .99, **-P - .95, *-P = .90.

Taxa	Habitat	Time	Time x Habitat
Chironomidae	**	***	**
Baetis		***	
Pericoma	*	***	
Nemoura cinctipes		***	
Cinygmula		*	
Dugesia		***	
Prosimulium		***	
Capnia spp.		***	
Oligochaeta		***	
Hydracarina		***	
Alloperla pallidula		***	
Rhyacophila		***	
Paraleptophlebia		***	
Brachyptera pallida		**	
Ephemerella coloradensis		***	**
Ostracoda	*	***	
Epeorus longimanus		***	
Ephemerella grandis		**	
Hesperoperla pacifica		*	**
Limnophora		***	
Limnephilidae ?		***	
Arctopsyche		***	*
Ephemerella doddsi		*	*
Arcynopteryx parallela		***	
Elmidae larvae		***	
Ephemerella inermis		***	
Dicranota		***	
Ptychoptera		**	

Table 12. Continued

Taxa	Habitat	Time	Time x Habitat
Helobdella			
Hesperophylax		***	*
Ameletus	*		
Unknown Perlodidae		**	*
Euparyphus		***	
Limnephilus		***	**
Ceratopogonidae			
Elmidae adult			
Tipula B		**	
Arcynopteryx signata			
Empididae		***	
Tipula A		***	
Isogenus aestivalis		*	
Pisidium			
Sialis		**	
Dixa	*	***	*
Hexatoma		*	
Rhithrogena			

Time was the most important factor affecting distribution of the benthos (Table 13). About 11 percent of the taxa had distributions which varied significantly with habitat, 18 percent varied significantly with velocity, 9 percent varied significantly with depth, and 20 percent varied significantly with the TxH interaction. The analysis of variance indicates that for the majority of taxa, there is no difference in abundance between riffles and "pools".

The differences in the means of numbers per basket for each taxon from both habitats (Table 6) suggest that more rhithrogenous fauna are migrating into the "pool" habitat during the winter months than are indicated by the analysis of variance (Table 12). This migration is further illustrated by a comparison of the plots of 4 taxa whose distributions did not vary significantly with the interaction term (Figures 4-7) with a taxon whose distribution was significant for the interaction (Figure 8) and with a taxon whose distribution varied significantly for habitat (Figure 9). Because of the linear nature of the ANOVA model and the high variation present, nonparametric statistics were used to further analyze the effects of the interaction term.

Taxa were assigned a + if the mean number per basket in a given collection was higher in the riffle habitat and a - if the average number per basket was higher in the pool (Table 14). Taxa that had zero counts for both habitats during any collection were not included. The totals indicate that more taxa were more abundant in the riffles during June, August and September collections and a much higher number of taxa were more abundant in the "pools" during November, January and

Table 13. Percentage of the community whose distributions showed significant differences and the percentage of the annual mean standing crop that their distribution represents.

Factors	% of Community significant	% of annual mean standing crop in numbers
Depth*	8.7	0.4
Velocity*	17.4	5.3
Habitat+	10.9	13.0
Time+	84.8	99.9
T x H+	19.6	11.0

*Analysis of Covariance

+Analysis of variance

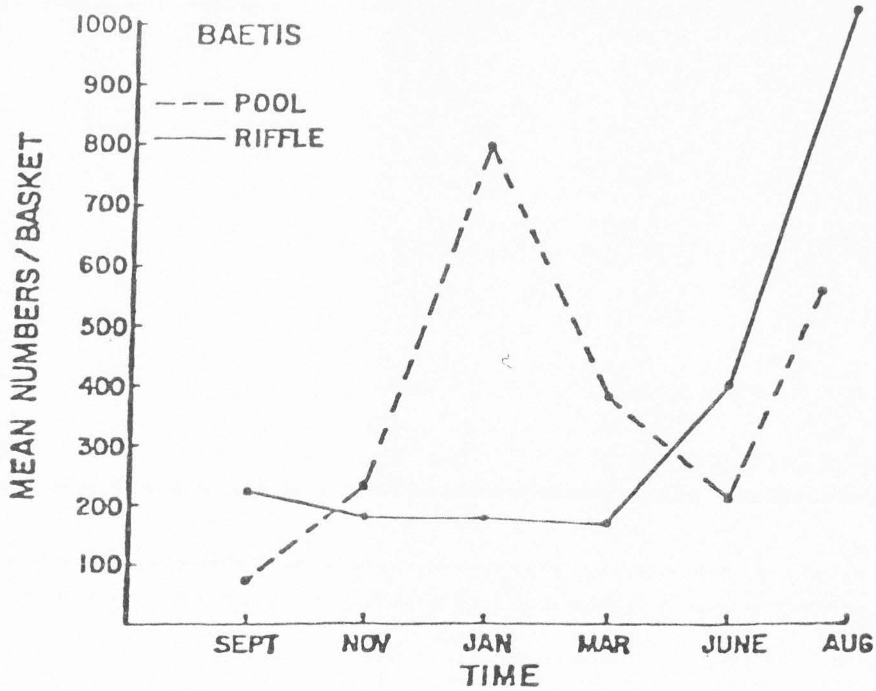

Figure 4. Mean numbers per basket of Baetis in pools and riffles of the upper Strawberry River, Utah, plotted against time. (1975-76).

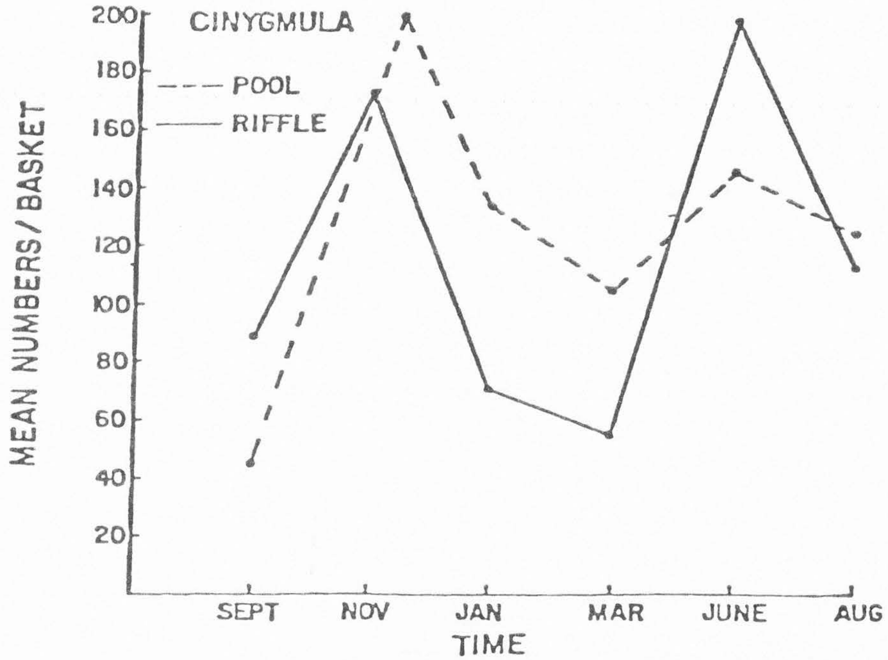

Figure 5. Mean number per basket of Cinygmula in pools and riffles of the upper Strawberry River, Utah plotted against time. (1975-76).

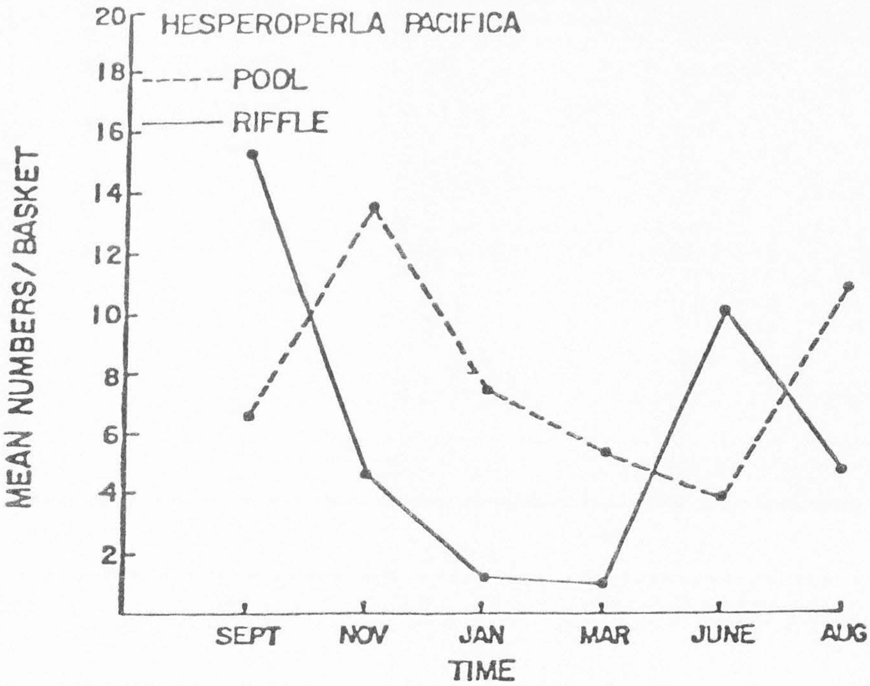

Figure 6. Mean numbers per basket of Hesperoperla pacifica in pools and riffles of the upper Strawberry River, Utah plotted against time. (1975-76).

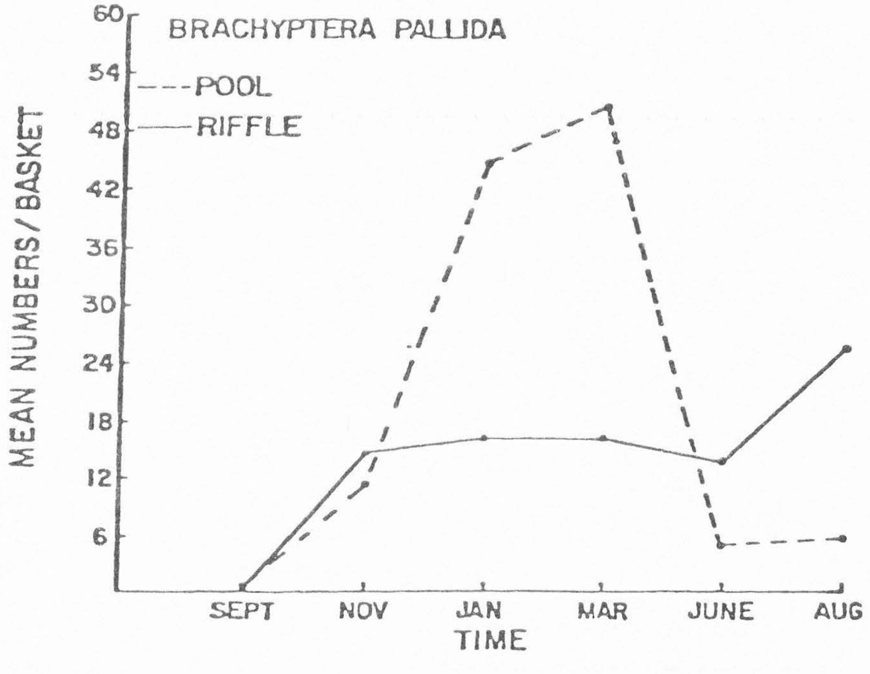

Figure 7. Mean numbers per basket of Brachyptera pallida in pools and riffles of the upper Strawberry River, Utah plotted against time. (1975-76).

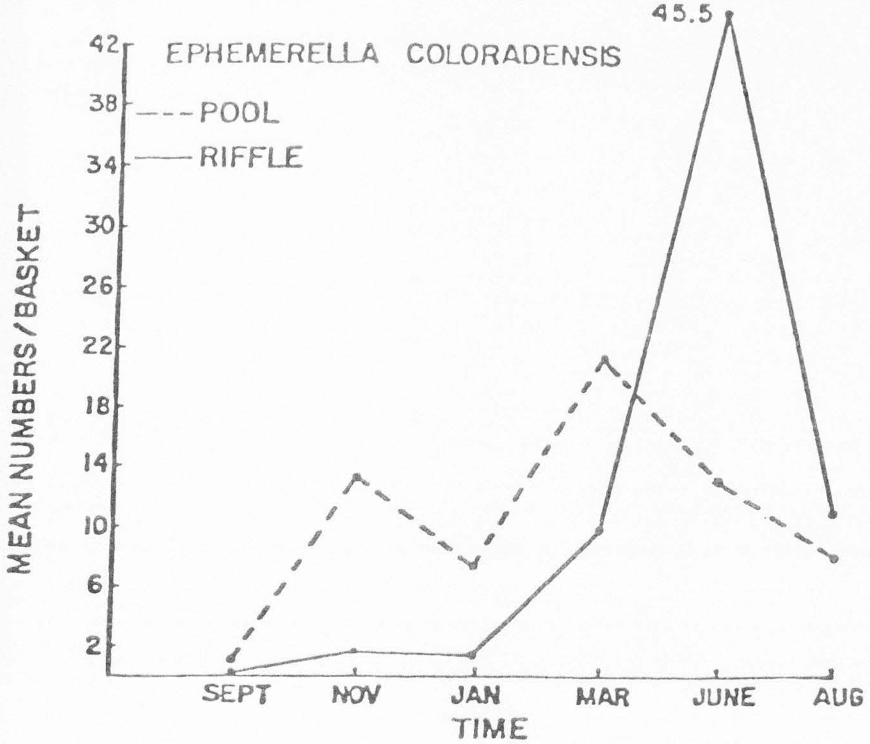

Figure 8. Mean numbers per basket of Ephemerella coloradensis in pools and riffles of the upper Strawberry River, Utah plotted against time. (1975-76).

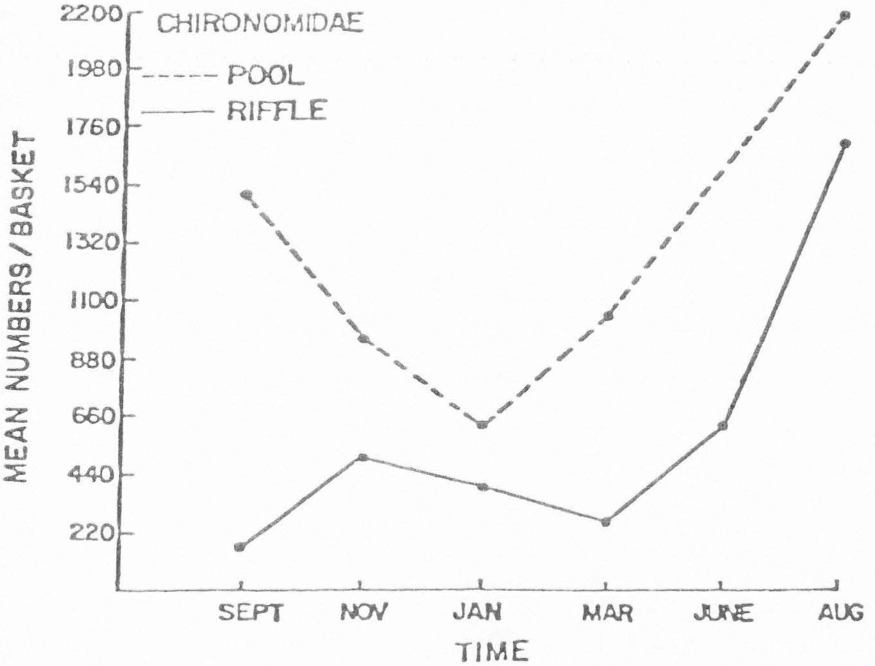

Figure 9. Mean numbers per basket of Chironomidae in pools and riffles of the upper Strawberry River, Utah plotted against time. (1975-76).

Table 14. Sign test for 24 taxa collected from the upper Strawberry River, Utah. + sign denotes that mean number of organisms per basket (.25 m^2) was higher in riffles; - sign denotes a higher mean number in "pools" for a given collection. The result of a Chi-square test on the totals is given.

Taxa	Sept	Nov	Jan	Mar	June	Aug
Baetis	+	-	-	-	+	+
Cinygmula	+	-	-	-	+	-
Ephemerella coloradensis	+	-	-	-	+	+
E. doddsi	+	-	-	-	+	-
E. grandis	+	-	-	-	-	+
Paraleptophlebia	-	-	-	-	-	+
Chironomidae	-	-	-	-	+	-
Tipula A	-	-	-	-	-	-
Limnophora	-	-	+	-	+	+
Pericoma	-	-	-	-	-	+
Prosimulium	+	+	+	-	-	+
Arctopsyche	+	+	+	+	+	+
Hesperophylax	+	-	-	-	-	+
Limnephilus	+	+	+	+	-	-
Limnephilidae ?	-	-	-	-	+	-
Rhyacophila	+	-	-	-	+	+
Alloperla pallidula	+	+	-	-	+	+
Arcynopteryx parallela	-	-	-	-	+	+
Brachyptera pallida	-	+	-	-	+	+
Capnia spp.	-	-	-	+	+	-
Hesperoperla pacifica	+	-	-	-	+	+
Nemoura cinctipes	+	-	-	-	+	+
Dugesia	-	-	-	-	-	-
Hydracarina	-	-	+	-	+	-
Total taxa more abundant in riffles/total taxa	13/24	5/24	5/24	3/24	16/24	15/24

x^2 statistic = 15.75 $x^2.01(5) = 15.1$

March. A chi-square test was performed on the totals and it was highly significant ($P < .01$).

The loss in degrees of freedom in analysis of covariance outweighed the reduction of experimental error (Table 15). With deletion of September and January collections fewer taxa showed significance for time and the time x habitat interaction (Table 16). Since September and January are two months when the animals demonstrate a changing preference in habitat (Table 14), the analysis of variance results which involved all 6 collections were a better evaluation of the effects of the qualitative variables on benthic distribution. However, since depth and velocity were significant for the distribution of some taxa (Tables 13 & 16), the results of covariant analysis can be used to show significance of the quantitative variables on spatial distribution of those taxa.

The principal use of concomitant variables in analysis of covariance is for reduction of experimental error and it is not a strong test of the effects of the variables themselves (Neter and Wasserman 1974), so further investigation on the effects of depth and velocity was conducted. Two-way tables using 3 categories of depth and velocity were constructed for each of the 4 collections, since depth and velocity are dependent on time (Appendix A, Tables 18-25). The observed and expected densities of animals per basket for each category were computed. Chi-square tests were then performed to test the hypothesis that the invertebrates were not found in any specific depth and velocity categories. The results of these tests on the densities of all 8 taxa for all 4 collections were found to be highly significant ($P = .005$).

Table 15. ANOVA model for the effects of time, habitat, and T x H on the distribution of benthic invertebrates using all six collections.

Source of Variation	df
Main Plot	
Location (replicates)	3
Habitat	1
Location x Habitat (Error A)	3
Split Plot	
Time	5
Time x Habitat	5
Location x Habitat x Time Location x Time (Error B)	30
Subsampling	144
TOTAL	191

Covariance model for the effects of depth, velocity, time, habitat, and T x H on the distribution of benthic invertebrates using only 4 of the 6 collections.

Source of Variation	df
Main Plot	
Location (replicates)	3
Habitat	1
Location x Habitat (Error A)	3
Split Plot	
Depth	1
Velocity	1
Time	3
Time x Habitat	3
Location x Habitat x Time Location x Time (Error B)	18
Subsampling	96
TOTAL	129

Table 16. Summary of F-tests on the means of the main effects and interaction and on the regression coefficients of the concomitant variables for numbers of each taxon (4 collections). ***-P = .99, **-P = .95, *-P = .90.

Taxa	Depth	Velocity	Habitat	Time	Time x Habitat
Chironomidae			*	***	**
Baetis		*			
Pericoma			*	***	
Nemoura cinctipes				***	
Cinygmula					
Dugesia				***	
Prosimulium		***		***	
Capnia spp.				***	*
Oligochaeta			*	***	***
Hydracarina				***	
Alloperla pallidula				***	
Rhyacophila	*	*			
Paraleptophlebia		*		**	
Brachyptera pallida					
Ephemerella coloradensis	*	*			***
Ostracoda			*	***	***
Epeorus longimanus			**	***	
Ephemerella grandis					
Hesperoperla pacifica			*		
Limnophora				***	
Limnephilidae ?					
Arctopsyche		***		***	
Ephemerella doddsi		***		***	
Arcynopteryx parallela				***	
Elmidae larva		*		*	
Ephemerella inermis				***	
Dicranota				***	
Ptychoptera			*		
Helobdella					
Hesperophylax	*			*	
Ameletus					
Unknown Perlodidae				*	
Euparyphus			*	***	
Limnephilus				***	***
Ceratopogonidae					
Elmidae adult					
Tipula B				*	
Arcynopteryx signata					
Empididae				**	
Tipula A					
Isogenus aestivalis					
Pisidium					

Table 16. Continued

Taxa	Depth	Velocity	Habitat	Time	Time x Habitat
Sialis				*	
Dixa	**		*	***	
Hexatoma					
Rhithrogena					

Rejection of the null hypothesis does not necessarily imply that the invertebrates are selecting specific depth and velocity categories. The observed densities could merely be a function of the nature of their distribution. To investigate this probability, the average density of organisms per basket was computed for each category and converted to relative density. Relative density was determined by equating the total numbers of a taxon per collection with 100% and then converting the numbers occurring in each category to the appropriate percentage. The relative density was then plotted against the respective category of depth and velocity (Figures 10-17) to depict trends towards a preferred depth and velocity category.

Interpretation of these graphs was difficult due to large differences in depth and velocity among the various collections. Obvious preferences for specific categories were demonstrated by only 3 taxa in only one collection. The densities of Cinygmula, Nemoura cinctipes, and Prosimulium for the August collection (Figures 13, 14, 16) indicated no preference among all 3 velocity categories but a clear preference for the lowest category of depth. These taxa showed no such preferences in other collections, nor did the collections of the remaining taxa. The graphs suggest that macroinvertebrates can tolerate large variations in depth and velocity. High density peaks seem to occur at random with respect to depth and velocity indicating another factor may be influencing their distribution.

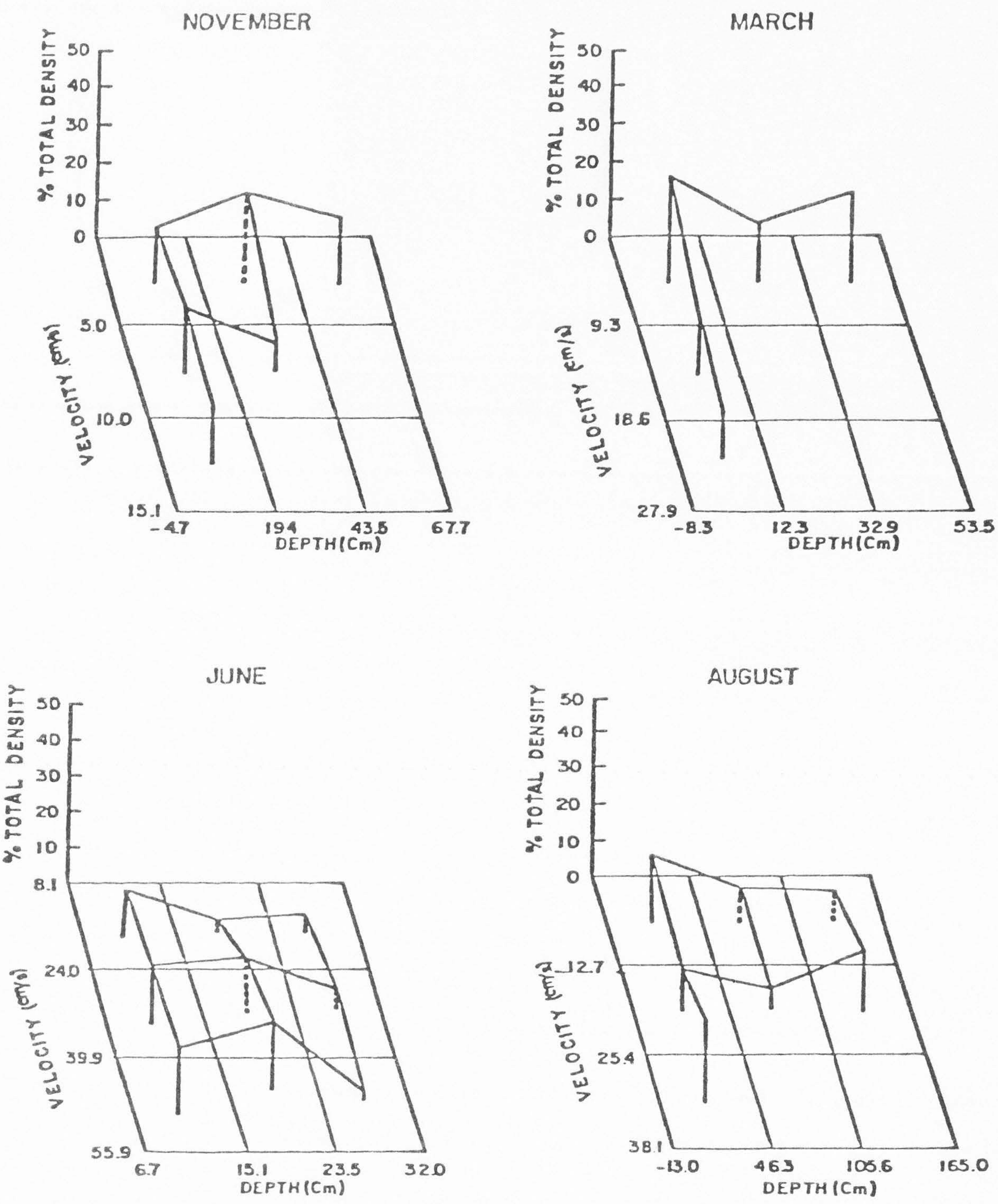

Figure 10. Relative density per basket of Chironomidae plotted against categories of depth and velocities for four collections from the upper Strawberry River, Utah. (1975-76).

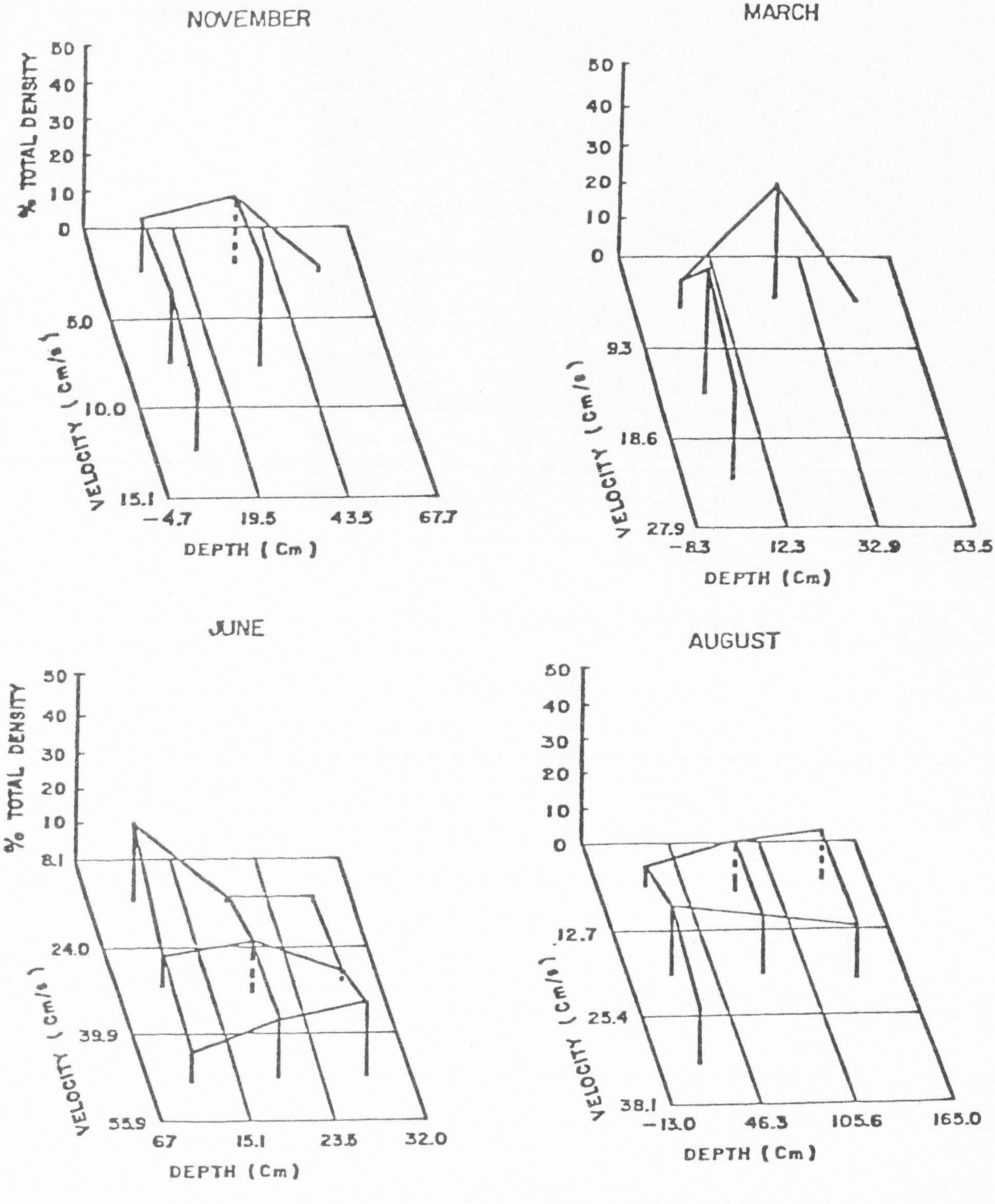

Figure 11. Relative density per basket of Baetis plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

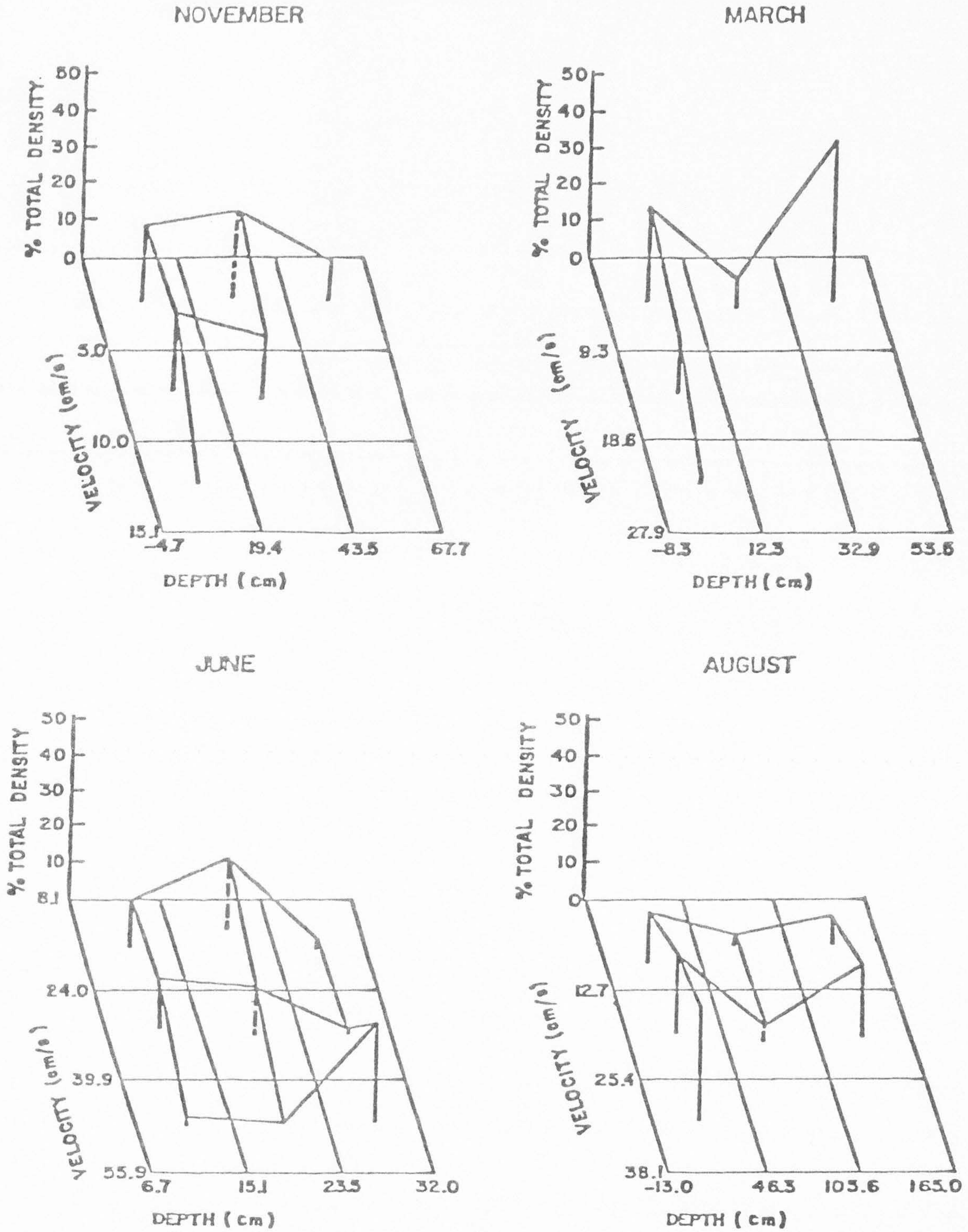

Figure 12. Relative density per basket of _Pericoma_ plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

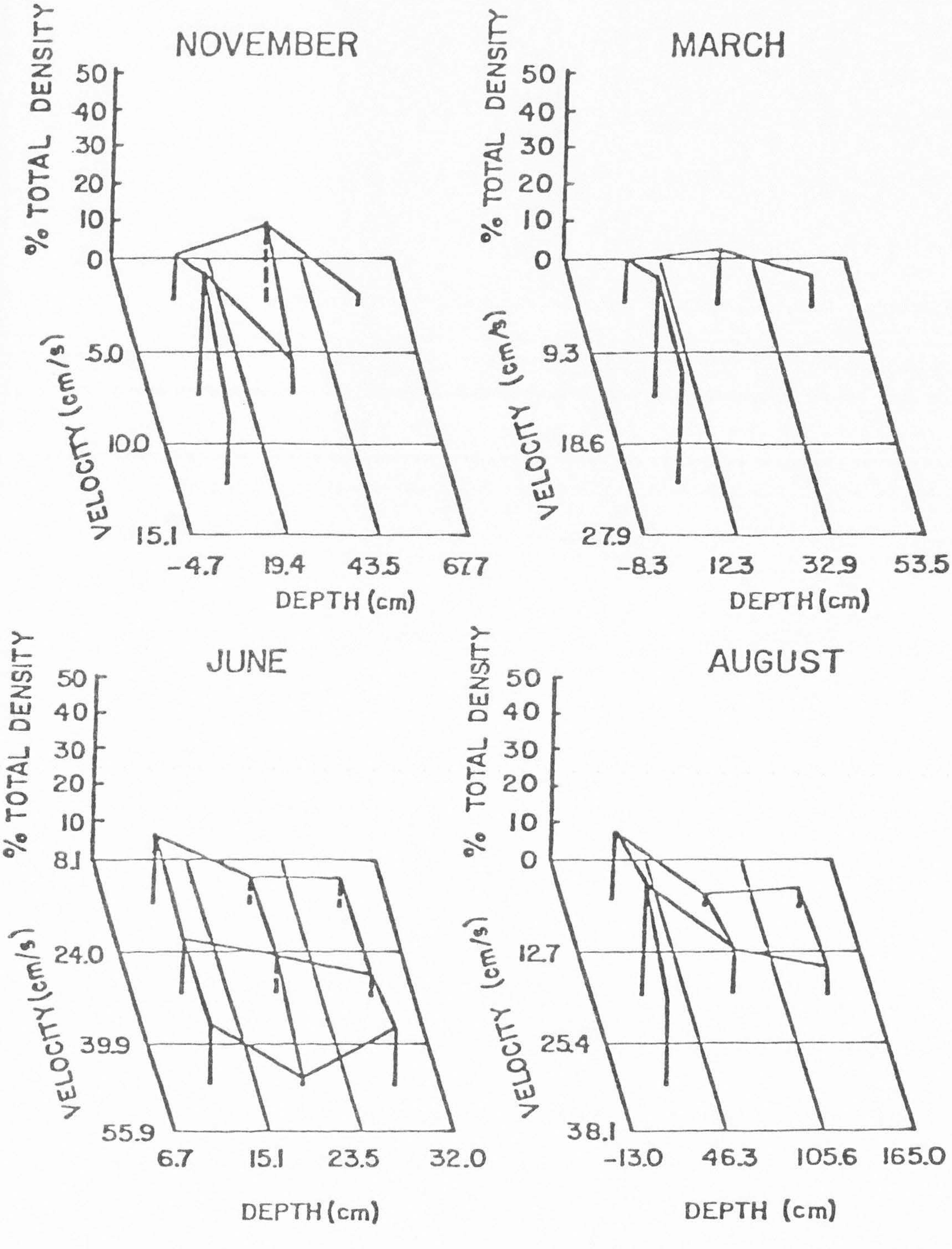

Figure 13. Relative density per basket of Nemoura cinctipes plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

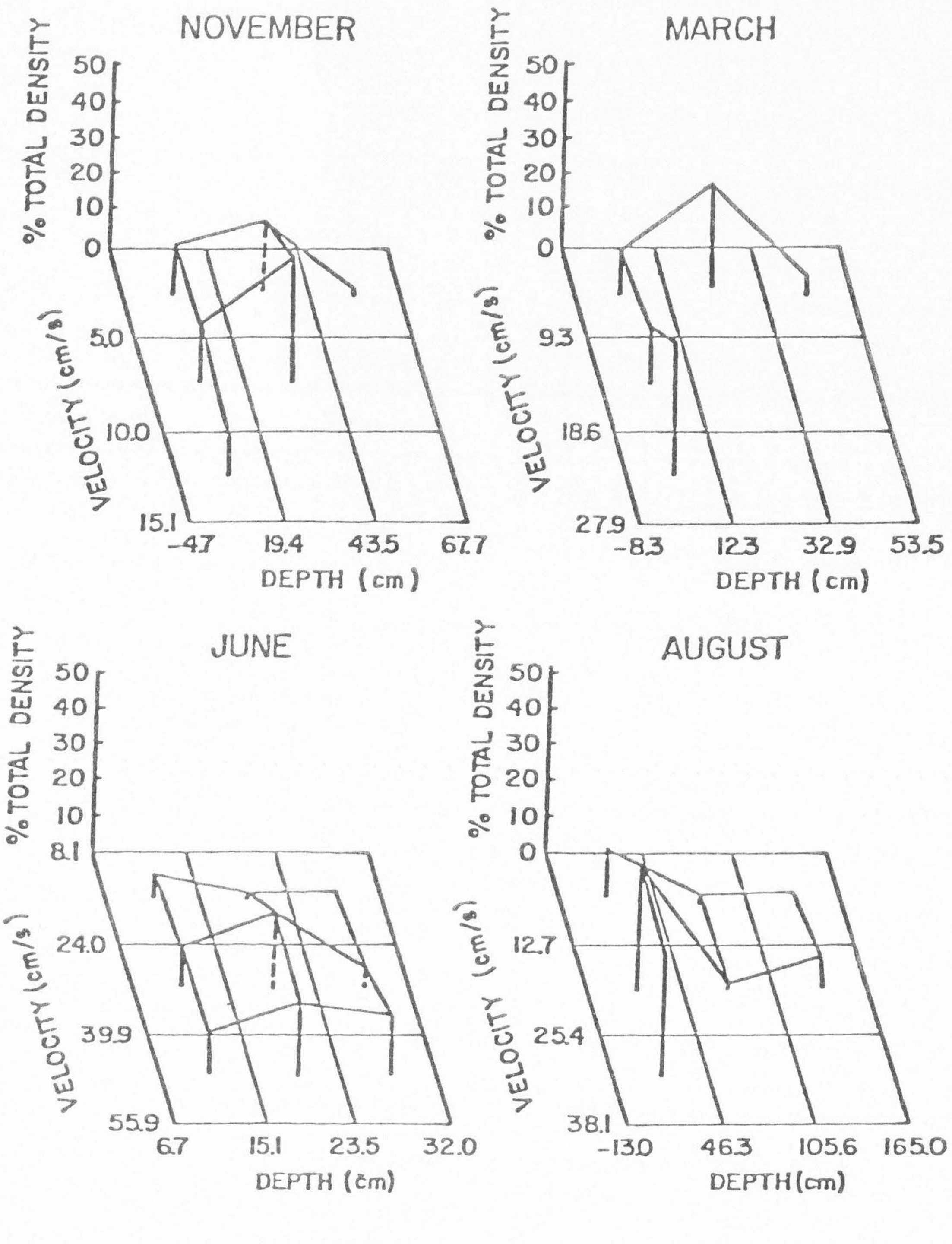

Figure 14. Relative density per basket of Cinygmula plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

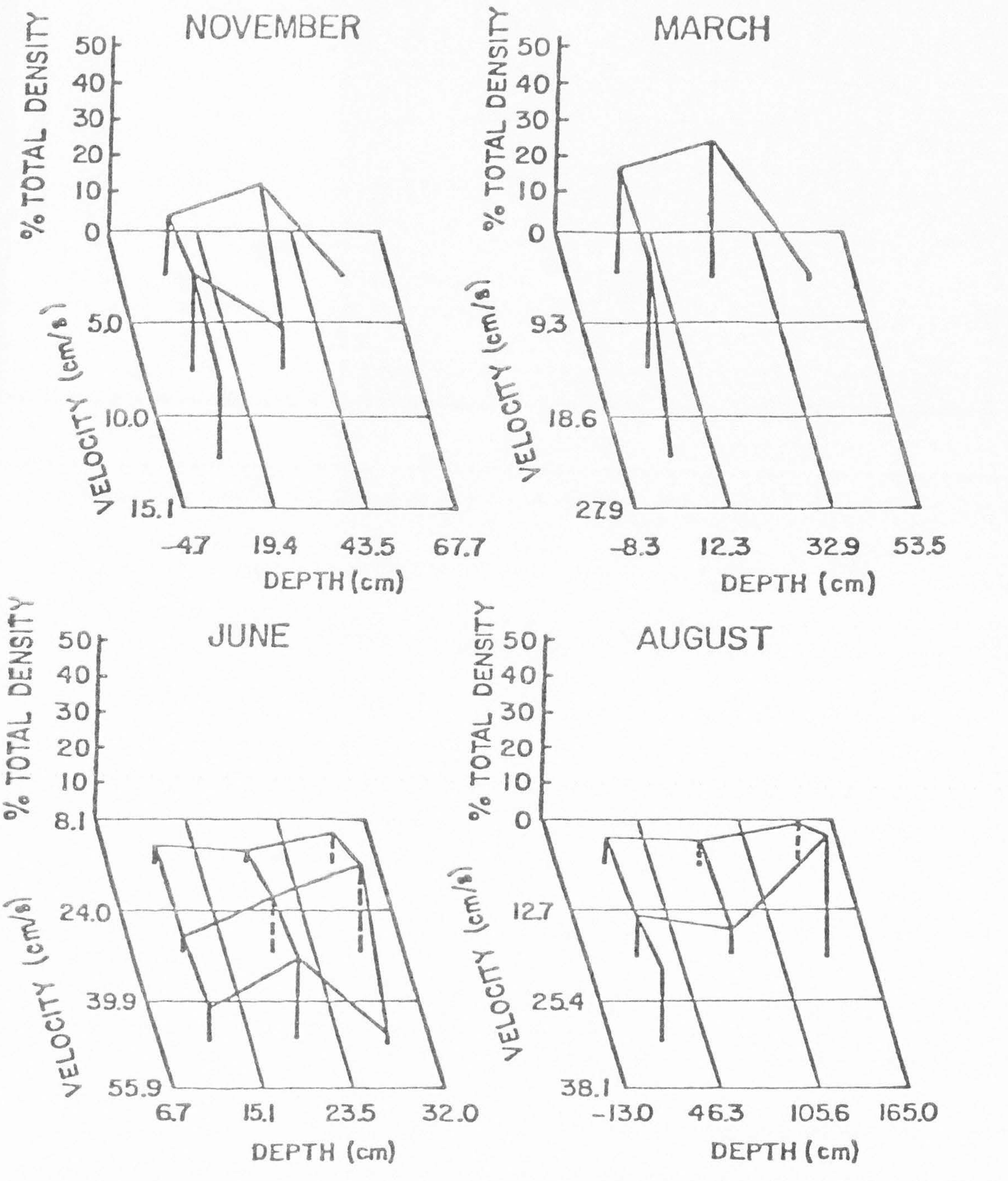

Figure 15. Relative density per basket of Dugesia plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

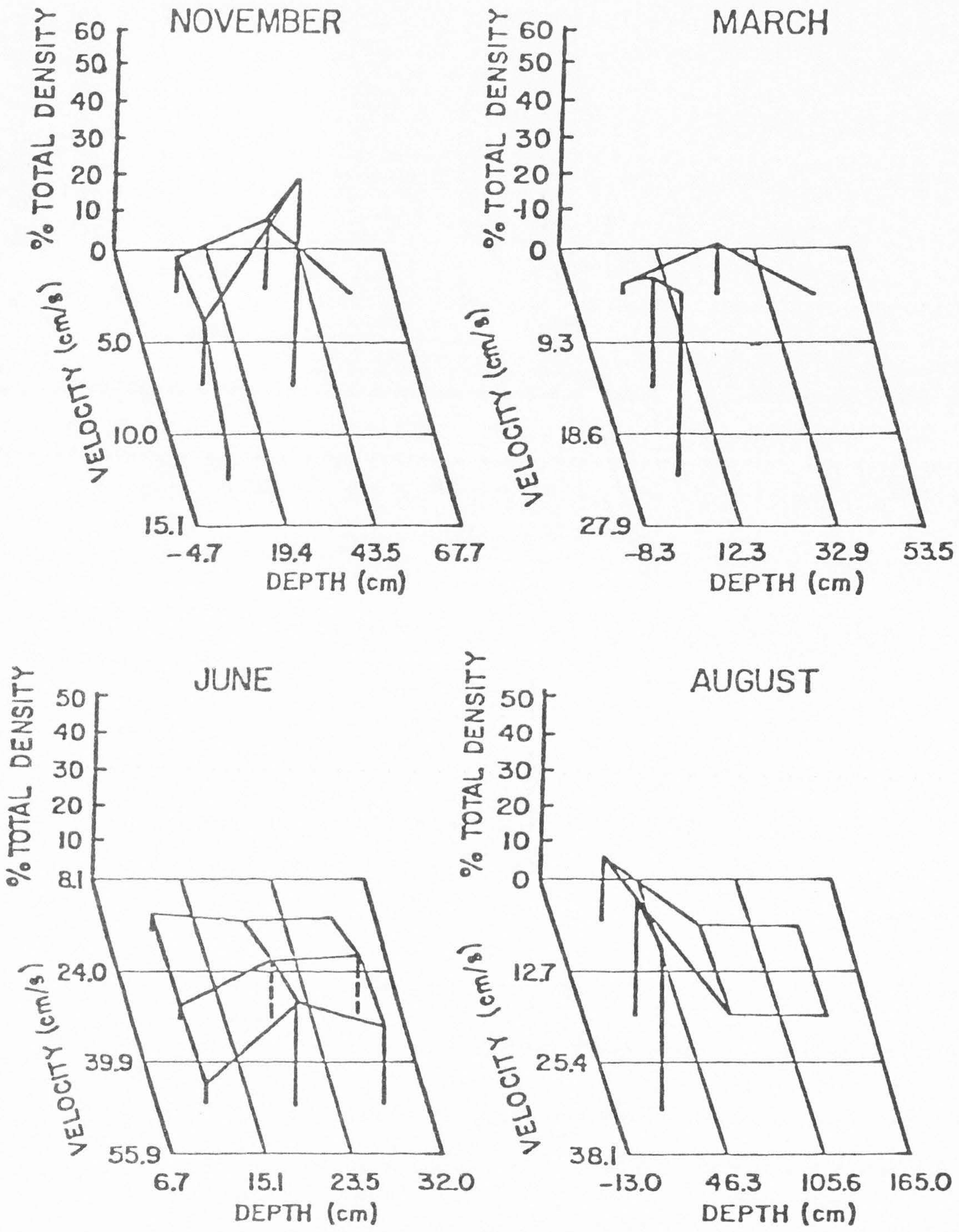

Figure 16. Relative density per basket of Prosimulium plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

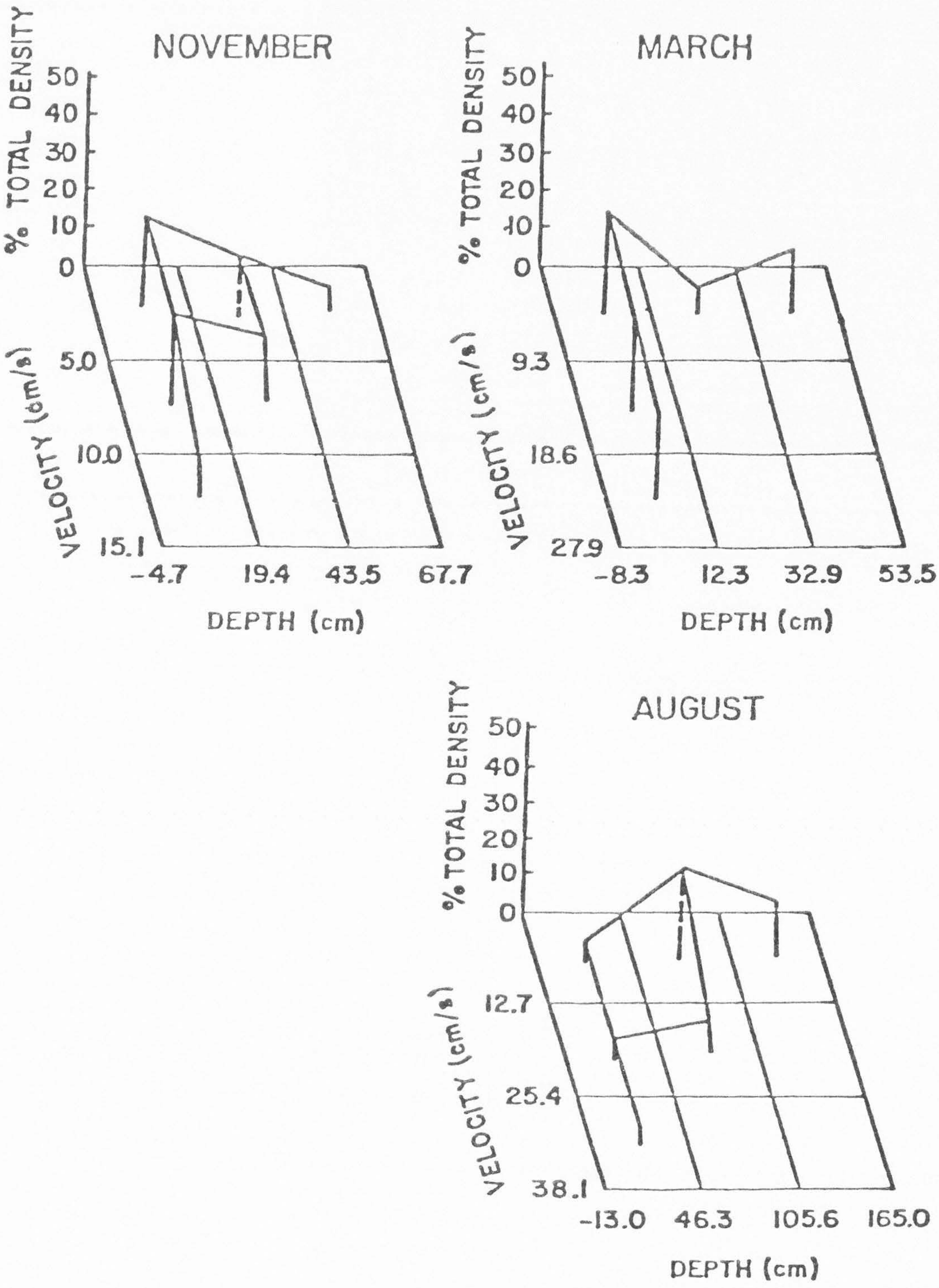

Figure 17. Relative density per basket of Capnia spp. plotted against categories of depth and velocity for four collections from the upper Strawberry River, Utah. (1975-76).

DISCUSSION

Depth and Velocity Categories

Attempts to develop depth and velocity categories which would predict the distribution for the major taxa were unsuccessful. Although highly significant differences of abundance among depth and velocity categories were found by Chi-square analysis, the plots of animal densities failed to demonstrate any preferred class of current and depth that would be useful for management purposes. Differences were probably the result of the contagious distribution of the animals over a wide range of velocities and depths. In some cases (*Baetis*, Figure 11 and *Pericoma*, Figure 12) the highest densities of a taxon were found in the lowest and highest categories of depth and velocity for the same collection.

Since the correlative evidence is weak, the possibility exists that the relationship is only indirect. Macan (1974) states that there is no direct effect of current unless the bottom is unstable, when agility, or some other ability that enables the animal to avoid the dangers of a shifting bottom may influence its distribution. Minshall (personal communication, September 1976) believes that food is a major determinant for microdistribution of benthic invertebrates. Because the distributions of a certain percentage of the taxa were significant for depth and velocity and some general trends were indicated by the plots of their densities vs. depth and velocity, the possible use of these two factors should not be ruled out as a method for predicting benthic distribution. Future studies that combine depth and velocity with the amounts of detritus and primary production present in the sampling area are recommended.

Spatial Dispersion due to Time and Habitat, and Their Interaction

Time. The important effect of time (Table 13) on the distributions of the majority of taxa was probably due to the nature of an insect's life cycle. Most of the adult stages leave the stream upon emergence; the egg and pupal stages were not considered. During the January and March collections adult specimens of *Brachyptera pallida*, *Capnia* spp. and *Nemoura cinctipes* were found in large numbers on the snow alongside the stream. These stoneflies were among the most numerous of all taxa studied. Their emergence was reflected in the community standing crop (Table 5) which decreased during this period of time.

Mortality may also have caused a decrease in standing crop during the winter months, although this is difficult to assess on a community basis because different life cycles were involved. Most of the taxa considered, however, had univoltine life cycles with emergence and egg deposition occurring during the summer months (Wiggins 1977, Gaufin et al. 1966, Usinger 1956). Mean individual weights suggested that the large increases in standing crop for August were a result of the recruitment of young. Successive increases in growth and smaller population estimates indicated mortality to be a factor, together with the emergence of the winter stoneflies, in reducing the standing crop of the community. *Baetis* was the only taxon that did not decrease during this time, but actually had its second highest population estimate during January, the other peak occurring in August. This could be a result of a bivoltine life cycle. According to Edmunds et al. (1976) many species of Baetis have two generations per year, a summer brood developing in about three months and an overwintering brood taking a longer time.

Habitat. That only 11% of the taxa showed distributions differing significantly with habitat (Table 13) was partly explained by the lack of difference in velocity between habitats (Figure 2). This similarity in current for both habitats is reflected in the nature of the substrate. The absence of significant differences in abundance between "pools" and riffles was probably due to their similar substrate. This supports the finding of other studies (Minshall and Minshall 1977, Barber and Kevern 1973, Elgmork and Saether 1970, Hynes 1961, Macan 1957, Noel 1954, Jones 1949, Pennak and van Gerpen 1947, Linduska 1942, and Percival and Whitehead 1929) which showed that the substrate is a major factor controlling patterns of spatial dispersion in benthic invertebrates. The dipterans Chironomidae, Pericoma, and Dixa, plus the ephemeropteran Ameletus, and the Ostracoda differed in distribution between habitats. These organisms preferred "pools" to riffles at all collection times. Edmunds et al. (1976) characterize the nymphal habitat of Ameletus as rocky pools on the sides of boulders and, although they are strong swimmers, they seek quieter water before coming to rest on the bottom. One species has been observed only between and behind small stones at the water's edge, where the nymphs were well protected from the slightest current. Usinger (1956) states that the common habitats of Pericoma is saturated mud and sand at stream margins, and moss and algae floating on still or slow-moving streams; that the larvae of Dixa always occur along the downstream margin of rocks or floating branches; and that most members of the Chironomidae prefer soft, silty sediments on which they are dependent for building their tubes. Hickman (1967) describes members of the Ostracoda as living on the bottom substratum, often in the ooze. Some species are found on sandy bottom and others on soft mud.

It appears that all of these organisms would prefer a depositional habitat rather than an erosional one. Depth differed significantly between habitats (Figure 3). The distribution of stony material was the same; the "pools" had a layer of detritus that was not noticeable in the riffles. Much more time was required to sieve the basket contents from the "pools" than the riffles because of the fine particulate detritus present. Since current regimes were essentially the same, the absence of layered detritus from the riffles may be a function of turbulence, with the "pool" habitat having a more laminar flow at the substrate-water interface. This qualitative difference in detritus, together with differences in depth and turbulence may have been the factors responsible for the habitat preference of those taxa whose distribution varied significantly with habitat.

Time x habitat. The means of the numbers of animals per basket for each habitat indicated that most of the taxa were changing habitat preferences at the same time of the year. This trend was further supported by the results of the sign test and chi-square test (Table 14). These trends were not observed for the taxa whose distributions were significant for habitat.

The question, then, is why this trend occurs. Anchor ice was most prevalent during the November collection and was observed only in the riffles. Snow depth over the stream during January and March exceeded 2 m with snow and ice penetrating through the water column and into the substrate of the riffles but not through the pools. The basket sampler depends on re-colonization between collection periods and a failure to do so would lead to fewer animals being collected. If the community standing crop for each collection is divided into separate standing crop estimates for each habitat (Table 17). the ratio of riffle organisms to "pool" organisms is low during September, November, January, and March and high during June and August with a correlation with flow of 0.95. The evidence suggests that reduced flow may have prevented invertebrate drift in the riffle areas but not movement into the "pools" from the riffles above.

This same evidence also refutes the argument that decreased sampling efficiency was responsible for lower standing crop estimates during the winter months. If this were true then the percentage of animals in the "pools" should also decrease as it did in the riffles, but this was not the case.

Anchor ice begins to form on riffles, first on the upstream faces of larger stones, spreading to cover much of the bottom and may extend into the pools (Hynes 1970). There is little evidence in the literature to support the idea of snow and ice preventing movement of benthic fauna. This may be the result of the difficulties encountered in sampling invertebrate drift when large amounts of snow cover the

Table 17. Total mean standing crop in numbers per m^2 and in biomass per m^2 (grams, dry weight) per habitat for each collection from the upper Strawberry River, Utah (1975-76). R = riffle P = pool.

	September		November		January	
	R	P	R	P	R	P
Numbers	4605	9764	5584	8749	3165	7318
Biomass	3.68	3.98	1.99	4.02	1.57	2.23
% total numbers	32	68	39	61	30	70
Ratio of riffle organisms to pool organisms	.47		.64		.43	

	March		April		August	
	R	P	R	P	R	P
Numbers	2626	7510	8961	6651	18,689	16,973
Biomass	0.98	2.69	4.09	4.19	5.44	4.56
% total numbers	26	74	57	43	52	48
Ratio of riffle organisms to pool organisms	.35		1.35		1.10	

r = .95 x = ratio of riffle organisms to pool organisms
y = velocity of water over baskets

stream. Pearson and Kramer (1972) in their study on Temple Fork at 1988 m in the Bear River Mountains of Northern Utah and Maciolek and Needham (1951) in their winter studies on Convict Creek at 2,000 m in the Sierra Nevada both observed that anchor ice formed in the riffles at night, dammed the pools and reduced the rate of flow. Each day it melted and broke up, greatly increasing the rate of flow, and the scouring action of the ice detached benthic animals and increased the amount of drift. Benson (1955) reported reduction of insect population in a Michigan stream following severe anchor ice conditions and Mecom (1970) also reported the reduction of larval populations of two caddisflies following anchor-ice conditions.

Anchor ice and large amounts of snow fall, which are common at the higher elevations where headwaters are found, could be acting synergistically in creating intolerable conditions for riffle fauna, producing an exodus to the deeper, more predictable habitat of the pool.

It must not be overlooked that other factors besides those considered in this study (competition, predation, temperature, dissolved oxygen, etc.) affect the distribution of invertebrates inhabiting running waters. For example, the significance of the oxygen concentration below which a species cannot live is obvious, but more common and less easy for the ecologist to evaluate is the concentration in which a species cannot fully exert itself (Macan 1974). Stream invertebrates have evolved in an environment which has selected for a very narrow tolerance range for dissolved oxygen.

Low levels of oxygen concentration in the riffle during the winter may then be a cause for movement into a more suitable habitat.

If the reason for switching habitats is a mechanical one, such as the reduction of flow due to snow and ice, it may be possible to make interpretations pertinent to the effects of removing water from the stream on the distribution of benthic invertebrates. In any reduced flow regime, the width of the stream will decrease, reducing the area of the riffle. Usually the pool will not be affected as much because depth does not decline as much as stream width. McClay (1968) reported significant differences in numbers of aquatic insects in a test riffle before and after a 75 percent dewatering. Pearson et al. (1970) found that the maximum production of aquatic insects is controlled by water velocity through the riffle and the total amount of riffle area. "Pools", in a sense, may then become a "limiting factor" for invertebrates, and may provide refuge for the animals during periods of low water.

The context in which the habitat designation of "pool" was used for this study applies only to small headwater streams with the pool and riffle structure as described by Hynes (1970). This kind of "pool" habitat is not applicable to larger order streams that have deeper pools, riffles, and reaches. In these larger streams a reach is described as an intermediate condition between a riffle having turbulent waters and a pool which is comparatively deep and slow flowing (Luedtke et al. 1976). The pool habitat of small headwater streams approximates the habitat of the reach in larger streams except in length, the reach being much longer. The results of this study have indicated that reduced flow does have a considerable impact on the distribution and movement of macroinvertebrates, and that pockets of deeper water are necessary to minimize the effects of this impact. Since these pockets of deeper water are common to the headwater streams which are being considered for diversion and are providing refuge for the benthic animals in periods of low water, preservation of the quality and quantity of these habitats should be considered in any dewatering scheme.

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APPENDICES

APPENDIX A

Depth and Velocity Categories and Chi-square Analysis on the Distribution of the Major Taxa

Tables 18-25

Each category contains the observed and expected numbers of organisms and the mean density per basket of organisms for that category (heavier print).

TABLE 18

CHIRONOMIDAE

NOVEMBER

DEPTH (cm)

VELOCITY (cm/s)	-4.7–19.4	19.4–43.5	43.5–67.7	TOTAL
0–5.0	7128 7768 648.00	2240 1412 1120.00	2499 2119 833.00	11,867
5.0–10.0	6104 4943 872.00	700 1412 350.0	—	6804
10.0–15.1	396 1412 687.00	—	—	396
TOTAL	13,628	2940	2499	n=19,067

$\chi^2 = 1969.19$ $\chi^2_{.005(5)} = 16.75$

MARCH

DEPTH (cm)

VELOCITY (cm/s)	-8.3–12.3	12.3–32.9	32.9–53.5	TOTAL
0–9.3	15,422 17,069 701.00	750 1264 375.00	1815 1897 605.00	17,987
9.3–18.6	1257 1897 419.00	—	—	1257
18.6–27.9	354 632 354.00	—	—	354
TOTAL	17,033	750	1815	n=19,598

$\chi^2 = 709.68$ $\chi^2_{.005(4)} = 14.86$

JUNE

DEPTH (cm)

VELOCITY (cm/s)	6.7–15.1	15.1–23.5	23.5–32.0	TOTAL
8.1–24.0	1413 1481 471.00	75 494 75.00	248 987 124.00	1736
24.0–39.9	3145 2468 629.00	1962 1481 654.00	636 987 318.00	5743
39.9–55.9	1304 987 652.00	961 494 961.00	128 494 128.00	2393
TOTAL	5862	2998	1012	n=9872

$\chi^2 = 2193.03$ $\chi^2_{.005(8)} = 21.96$

AUGUST

DEPTH (cm)

VELOCITY (cm/s)	-13.0–46.3	46.3–105.6	105.6–165.0	TOTAL
–12.7	23,870 21,343 2170.00	1120 1940 1120.00	1020 1940 1020.00	26,010
12.7–25.4	11,760 15,522 1470.00	728 1940 728.00	1990 1940 1990.00	14,478
25.4–38.1	15,780 11,642 2830.00	—	—	15,780
TOTAL	51,410	1848	3010	n=56,268

$\chi^2 = 3029.66$ $\chi^2_{.005(6)} = 18.55$

TABLE 19 BAETIS

NOVEMBER

DEPTH (cm)

VELOCITY (cm/s)	-4.7–19.4	19.4–43.5	43.5–67.7	TOTAL
0–5.0	1991 2270 181.00	528 413 264.00	52 619 17.30	2571
5.0–10.0	1792 1444 256.00	776 413 388.00		2568
10.0–15.1	432 413 216.00			432
TOTAL	4215	1304	52	m=5571

X^2=989.48 X^2.005(5)=16.75

MARCH

DEPTH (cm)

VELOCITY (cm/s)	-8.3–12.3	12.3–32.9	32.9–53.5	TOTAL
0–9.3	2904 5863 132.00	1778 533 889.00	20 800 6.67	4702
9.3–18.6	2808 800 936.00			2808
18.6–27.9	752 267 752.00			752
TOTAL	6464	1778	20	m=8262

X^2=11,083.06 X^2.005 (4)=14.86

JUNE

DEPTH (cm)

VELOCITY (cm/s)	6.7–15.1	15.1–23.5	23.5–32.0	TOTAL
8.1–24.0	1886 944 622.00	37 315 37.00	145 630 72.50	2048
24.0–39.9	1400 1574 280.00	1194 944 398.00	284 630 142.00	2878
39.9–55.9	326 630 163.00	451 315 451.00	592 315 592.00	1369
TOTAL	3592	1682	1021	m=6295

X^2=2243.69 X^2.005(8)=21.96

AUGUST

DEPTH (cm)

VELOCITY (cm/s)	-13.0–46.3	46.3–105.6	105.6–165.0	TOTAL
–12.7	4103 8692 373.00	744 790 744.00	924 790 924.00	5771
12.7–25.4	9120 6321 1140.00	972 790 972.00	812 790 812.00	10,904
25.4–38.1	6240 4740 1040.00			6240
TOTAL	19,463	1716	1736	22,915

X^2=4204.12 X^2.005 (6)=18.55

TABLE 19 BAETIS

NOVEMBER

VELOCITY (cm/s) \ DEPTH (cm)	-4.7 – 19.4	19.4 – 43.5	43.5 – 67.7	TOTAL
0 – 5.0	1991 2270 181.00	528 413 264.00	52 619 17.30	2571
5.0 – 10.0	1792 1444 256.00	776 413 388.00		2568
10.0 – 15.1	432 413 216.00			432
TOTAL	4215	1304	52	m=5571

X^2=989.48 X^2.005(5)=16.75

MARCH

VELOCITY (cm/s) \ DEPTH (cm)	-8.3 – 12.3	12.3 – 32.9	32.9 – 53.5	TOTAL
0 – 9.3	2904 5863 132.00	1778 533 889.00	20 800 6.67	4702
9.3 – 18.6	2808 800 936.00			2808
18.6 – 27.9	752 267 752.00			752
TOTAL	6464	1778	20	m=8262

X^2=11,083.06 X^2.005 (4)=14.86

JUNE

VELOCITY (cm/s) \ DEPTH (cm)	6.7 – 15.1	15.1 – 23.5	23.5 – 32.0	TOTAL
8.1 – 24.0	1886 944 622.00	37 315 37.00	145 630 72.50	2048
24.0 – 39.9	1400 1574 280.00	1194 944 398.00	284 630 142.00	2878
39.9 – 55.9	326 630 163.00	451 315 451.00	592 315 592.00	1369
TOTAL	3592	1682	1021	m=6295

X^2=2243.69 X^2.005(8)=21.96

AUGUST

VELOCITY (cm/s) \ DEPTH (cm)	-13.0 – 46.3	46.3 – 105.6	105.6 – 165.0	TOTAL
12.7	4103 8692 373.00	744 790 744.00	924 790 924.00	5771
12.7 – 25.4	9120 6321 1140.00	972 790 972.00	812 790 812.00	10,904
25.4 – 38.1	6240 4740 1040.00			6240
TOTAL	19,463	1716	1736	22,915

X^2=4204.12 X^2.005(6)=18.55

TABLE 21 NEMOURA CINCTIPES

NOVEMBER

DEPTH (cm)

VELOCITY (cm/s)	-4.7–19.4	19.4–43.5	43.5–67.7	TOTAL
0–5.0	1617 1813 147.00	424 330 212.00	44 494 14.70	2085
5.0–10.0	1330 1153 190.00	794 330 397.00	——	2124
10.0–15.1	240 330 120.00	——	——	240
TOTAL	3187	1218	44	m=4449

$\chi^2 = 1162.32$ $\chi^2_{.005(5)} = 16.75$

MARCH

DEPTH (cm)

VELOCITY (cm/s)	-8.3–12.3	12.3–32.9	32.9–53.5	TOTAL
0–9.3	726 854 33.00	177 78 88.50	42 116 14.00	945
9.3–18.6	148 116 49.30	——	——	148
18.6–27.9	110 39 110.00	——	——	110
TOTAL	984	177	42	m=1230

$\chi^2 = 330.13$ $\chi^2_{.005(4)} = 14.86$

JUNE

DEPTH (cm)

VELOCITY (cm/s)	6.7–15.1	15.1–23.5	23.5–32.0	TOTAL
8.1–24.0	164 275 54.70	7 92 7.00	31 183 15.50	202
24.0–39.9	483 458 96.60	531 275 177.00	84 183 42.00	1098
39.9–55.9	212 183 106.00	176 92 176	144 92 144.00	532
TOTAL	859	714	259	n=1832

$\chi^2 = 653.50$ $\chi^2_{.005(8)} = 21.96$

AUGUST

DEPTH (cm)

VELOCITY (cm/s)	-13.0–46.3	46.3–105.6	105.6–165.0	TOTAL
–12.7	3850 6338 350.00	21 576 21.00	32 576 32.00	3903
12.7–25.4	7208 4609 901.00	44 576 44.00	232 576 232.00	7484
25.4–38.1	5322 3457 887.00	——	——	5322
TOTAL	16,380	65	264	n=16,709

$\chi^2 = 5193.73$ $\chi^2_{.005(6)} = 18.55$

TABLE 22 CINYGMULA

NOVEMBER

VELOCITY (cm/s) \ DEPTH (cm)	-4.7–19.4	19.4–43.5	43.5–67.7	TOTAL
0–5.0	1518 2051 138.00	440 373 220.00	72 559 24.00	2030
5.0–10.0	2429 1305 347.00	180 373 90.00	—	2609
10.0–15.1	396 373 198.00	—	—	396
TOTAL	4343	620	72	n=5035

$\chi^2=1644.21$ $\chi^2_{.005(5)}=16.75$

MARCH

VELOCITY (cm/s) \ DEPTH (cm)	-8.3–12.3	12.3–32.9	32.9–53.5	TOTAL
0–9.3	1564 1864 71.10	165 169 82.50	130 254 43.30	1859
9.3–18.6	579 254 193.00	—	—	579
18.6–27.9	188 85 188.00	—	—	188
TOTAL	2331	165	130	n=2626

$\chi^2=649.57$ $\chi^2_{.005(4)}=14.86$

JUNE

VELOCITY (cm/s) \ DEPTH (cm)	6.7–15.1	15.1–23.5	23.5–32.0	TOTAL
8.1–24.0	765 503 255.00	99 168 99.00	188 336 94.00	1052
24.0–39.9	1050 839 210.00	420 503 140.00	140 336 70.00	1610
39.9–55.9	460 336 230.00	17 168 17.00	216 168 216.00	693
TOTAL	2275	536	544	n=3355

$\chi^2=606.29$ $\chi^2_{.005(8)}=21.96$

AUGUST

VELOCITY (cm/s) \ DEPTH (cm)	-13.0–46.3	46.3–105.6	105.6–165.0	TOTAL
12.7	1199 1290 109.00	12 117 12.00	24 117 24.00	1235
12.7–25.4	1328 938 166.00	40 117 40.00	42 117 42.00	1410
25.4–38.1	756 704 126.00	—	—	756
TOTAL	3283	52	66	n=3401

$\chi^2=439.32$ $\chi^2_{.005(6)}=18.55$

TABLE 23 DUGESIA

NOVEMBER

VELOCITY (cm/s) \ DEPTH (cm)	-4.7 – 19.4	19.4 – 43.5	43.5 – 67.7	TOTAL
0 – 5.0	362 402 32.90	108 73 54.00	0 110	470
5.0 – 10.0	382 256 54.60	46 73 23.00	—	428
10.0 – 15.1	89 73 44.50	—	—	89
TOTAL	833	154	0	m=987

$\chi^2=206.27$ $\chi^2_{.005(5)}=16.75$

MARCH

VELOCITY (cm/s) \ DEPTH (cm)	-8.3 – 12.3	12.3 – 32.9	32.9 – 53.5	TOTAL
0 – 9.3	253 226 11.50	29 21 14.50	1 31 0.33	283
9.3 – 18.6	36 31 12.00	—	—	36
18.6 – 27.9	0 10	—	—	0
TOTAL	289	29	1	m=319

$\chi^2=46.11$ $\chi^2_{.005(4)}=14.86$

JUNE

VELOCITY (cm/s) \ DEPTH (cm)	6.7 – 15.1	15.1 – 23.5	23.5 – 32.0	TOTAL
8.1 – 24.0	132 266 44.00	33 89 33.00	159 178 79.50	324
24.0 – 39.9	203 444 40.60	435 266 145.00	432 178 216.00	1070
39.9 – 55.9	160 178 80.00	214 89 214.00	8 89 8.00	382
TOTAL	495	682	599	n=1776

$\chi^2=956.50$ $\chi^2_{.005(8)}=21.96$

AUGUST

VELOCITY (cm/s) \ DEPTH (cm)	-13.0 – 46.3	46.3 – 105.6	105.6 – 165.0	TOTAL
– 12.7	1243 2085 113.00	104 190 104.00	176 190 176.00	1523
12.7 – 25.4	1400 1516 175.00	113 190 113.00	528 190 528.00	2041
25.4 – 38.1	1932 1137 322.00	—	—	1932
TOTAL	4575	217	704	n=5496

$\chi^2=1546.02$ $\chi^2_{.005(6)}=18.55$

TABLE 24 PROSIMULIUM

NOVEMBER

DEPTH (cm)

VELOCITY (cm/s)	-4.7 – 19.4	19.4 – 43.5	43.5 – 67.7	TOTAL
0 – 5.0	67 97 6.09	12 18 6.00	0 26	79
5.0 – 10.0	80 61 11.40	72 18 36.00	—	152
10.0 – 15.1	6 18 3.00	—	—	6
TOTAL	153	84	0	n=237

$\chi^2=213.20$ $\chi^2_{.005(5)}=16.75$

MARCH

DEPTH (cm)

VELOCITY (cm/s)	-8.3 – 12.3	12.3 – 32.9	32.9 – 53.5	TOTAL
0 – 9.3	158 427 7.18	76 39 38.00	0 58	234
9.3 – 18.6	236 58 78.70	—	—	236
18.6 – 27.9	132 19 132.00	—	—	132
TOTAL	526	76		n=602

$\chi^2=1480.89$ $\chi^2_{.005(4)}=14.86$

JUNE

DEPTH (cm)

VELOCITY (cm/s)	6.7 – 15.1	15.1 – 23.5	23.5 – 32.0	TOTAL
8.1 – 24.0	253 799 84.30	2 266 2.00	140 533 70.50	395
24.0 – 39.9	535 1332 107.00	1377 799 459.00	1080 533 540.00	2992
39.9 – 55.9	364 533 182.00	908 266 908.00	668 266 668.00	1940
TOTAL	1152	2287	1888	n=5327

$\chi^2=3496.32$ $\chi^2_{.005(8)}=21.96$

AUGUST

DEPTH (cm)

VELOCITY (cm/s)	-13.0 – 46.3	46.3 – 105.6	105.6 – 165.0	TOTAL
– 12.7	104 140 9.45	0 13	0 13	104
12.7 – 25.4	133 102 16.60	0 13	0 13	133
25.4 – 38.1	132 76 22.00	—	—	132
TOTAL	369	0	0	n=369

$\chi^2=111.94$ $\chi^2_{.005(6)}=18.55$

TABLE 25 CAPNIA SPP.

NOVEMBER

DEPTH (cm)

VELOCITY (cm/s)	-4.7 – 19.4	19.4 – 43.5	43.5 – 67.7	TOTAL
0 – 5.0	2255 1823 205.00	240 331 120.00	160 497 53.30	2655
5.0 – 10.0	1372 1160 196.00	296 331 148.00	—	1668
10.0 – 15.1	151 331 75.50	—	—	151
TOTAL	3778	536	160	n=4474

$\chi^2=496.23$ $\chi^2_{.005(5)}=16.75$

MARCH

DEPTH (cm)

VELOCITY (cm/s)	-8.3 – 12.3	12.3 – 32.9	32.9 – 53.5	TOTAL
0 – 9.3	231 208 10.50	5 19 2.50	20 28 6.67	256
9.3 – 18.6	28 28 9.33	—	—	28
18.6 – 27.9	9 9 9.00	—	—	9
TOTAL	268	5	20	m=293

$\chi^2=15.14$ $\chi^2_{.005(4)}=14.86$

AUGUST

DEPTH (cm)

VELOCITY (cm/s)	-13.0 – 46.3	46.3 – 105.6	105.6 – 165.0	TOTAL
– 12.7	116 176 10.50	60 16 60.00	36 16 36.00	212
12.7 – 25.4	62 128 7.75	20 16 20.00	88 16 88.00	170
25.4 – 38.1	82 96 13.70	—	—	82
TOTAL	260	80	124	n=464

$\chi^2=766.59$ $\chi^2_{.005(6)}=18.55$

APPENDIX B

Recent Changes in the Taxonomic Names of Some Species of Plecoptera

Recent Changes in the Taxonomic Names of Some Species of Plecoptera

Names Used in Text	*Recent Changes
Alloperla pallidula	Suwallia pallidula
Arcynopteryx parallela	Skwala parallela
Brachyptera pallida	Taenionema pallidum
Capnia lemoniana	Utacapnia lemoniana
Nemoura cinctipes	Zapada cinctipes

*Bauman, R. W., A. R. Gaufin and R. F. Surdick. 1977. The Stoneflies (Plecoptera) of the Rocky Mountains. Memoirs of the American Entomological Society No. 31:208 p.