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SOME EFFECTS OF SPRING SNOWMELT RUNOFF ON AQUATIC INVERTEBRATE POPULATIONS IN A HIGH MOUNTAIN STREAM

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TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Page

CONTENTS OF APPENDICES

ABSTRACT

This study was an investigation of the abiotic and biotic factors acting on a community of benthic invertebrates in a high mountain stream during the spring snowmelt runoff period. All data used were collected in 1970. The study area was a 1 km section of Nash Fork Creek near 3,000 m in the Snowy Range, Wyoming.

The runoff began in mid-May when the discharge was 6 c.f.s. (.17 c.m.s.), rose erratically to a peak of June 25, at 125 c.f.s. (3.54 c.m.s.), then dropped through the rest of the summer. Water temperatures increased through the runoff from 0°C. in mid-May to 4.5-11.5°C. on June 25 and to 7-16°C. by July 21. The general snow cover over the stream present in mid-May was gone by June 4.

For each invertebrate species in the study area which could be separated, population estimates were made, size ranges were recorded, and when possible, hatching and breeding periods were noted. Of 30 species for which the life cycle could be defined, 6 were non-seasonal, 12 were slow seasonal, and 12 were fast seasonal, based on the system of Hynes (1970).

The median values for the total standing crop biomass were 3,600 mg per m^2 for June 1-4 and 5,980 mg per m^2 for July 27-29. These values were not different at the .05 level using the Mann-Whitney u-statistic.

Drift samples were taken between the benthos sampling periods. From the drift samples of June 12-13, 17-18, and 22-24, drift rates for all invertebrates together increased with the increase in discharge.

The same trend was found for the drift of oligochaetes and tipulid larvae considered separately.

In the daytime drift, the percentage of drifting oligochaete biomass which occurring as fragments was correlated with discharge (r = .9717).

The species which could be sorted with a live-sorting apparatus were considered as a group. The drift rates of this group increased with discharge through June 12-13 and 17-18 until the peak on June 22-24. They then decreased to lower levels on July 6-7 and 13-14, and finally increased, only at night, on July 21-22.

A net downstream loss of drifting invertebrates from the study area could not be confirmed.

A "Nocturnal Drift Index," which

$$= \frac{\text{Night Drift Rate} - \text{Day Drift Rate}}{\text{Night Drift Rate} + \text{Day Drift Rate}},$$

was correlated with water temperature (positive correlation) and discharge (negative correlation). For the multiple regression of the index on water temperature and discharge the coefficient of determination was .86. This was interpreted as showing an increase in behavioral drift with increasing water temperature, but an inhibition of behavioral drift with high discharge.

Samples taken to determine the percentage of drifting dead invertebrates contained 11 percent dead invertebrates.

Ratios of drift rate/benthos density were measured for a few species. The species most highly modified to resist current had the lowest drift/benthos ratios.

Predation on drifting invertebrates by fish was assumed to be a source of mortality. Also the rapid growth of the net-spinning *Arctopsyche* sp. larvae was taken to indicate that it was a very effective predator on drift during the runoff.

Adjustment of the life cycle was found to be a common means of adaptation to the runoff and was manifested in several ways:

1. The Diptera avoided exposing pupae to the peak of the runoff.
2. Many insect species were found to breed during the runoff. Of 30 selected species, 18 did breed, 4 (all fast seasonal species) were presumed not to breed, and the breeding period of 8 was not known.
3. Prolonged hatching of eggs and avoidance of hatching were recognized as runoff-survival strategies. Of 48 selected species, 5 were hatching only in the rising (June 1-24) phase, 6 only in the falling (July 6-29) phase, 21 species hatched in both phases, and 16 species did not hatch in either phase.

The coexistence of very similar congeneric species in the genera *Baetis*, *Alloperla*, *Nemoura*, *Paraleuctra*, and *Rhyacophila*, was hypothesized as possible because the congeners may have different runoff-survival strategies which vary in effectiveness due to the large yearly differences in the timing and severity of the runoff.

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INTRODUCTION

Variation in streamflow is a common feature of stream ecosystems. Any increase in volume flow will be accompanied by increased velocity and increased capacity to move bed materials and material washed into the stream. During the increase in streamflow organisms are faced with removal or redistribution of habitat and the physical hazards of the increased velocity and the moving bed materials.

It is known that populations of stream organisms may be drastically reduced following flash floods (Moffet 1936, Tarzwell 1937, Mottley 1939, Surber 1938, Sprules 1947). Floods following seasonal rains, although more predictable, do reduce benthic faunas (Stehr and Branson 1938, Oliff 1960, Allanson 1961, Chutter 1963). Anderson and Lehmkuhl (1968) found an increase in standing crop biomass during the period of fall rain freshets while some catastrophic drift was occurring. Some reduction of benthos was also found during the spring runoff period in Utah (Gaufin 1959) and in Montana (Logan 1963). A review of flooding effects is given by Hynes (1970).

Seasonal floods would seem to present a different situation to stream organisms than flash floods. Since seasonal floods are by definition more predictable, stream organisms have had a chance to develop adaptive strategies for withstanding their effects. The regularity of seasonal floods also makes it necessary that the organisms be able to cope with the flooding conditions.

In the Snowy Range of southeastern Wyoming the period of spring snowmelt brings the highest streamflow of the year to the mountain streams. This period of high discharge is rather prolonged and its timing is more or less predictable. Based on the assumption that the stream invertebrate communities present are adapted to surviving the spring snowmelt runoff period, this study is an effort to discover how survival in this period is accomplished in one such community.

The purposes of this study have been: 1) to describe seasonal changes in abiotic factors in the stream, 2) to define hazards to the invertebrate species posed by the runoff, 3) to describe adaptations by the species to the runoff (the adaptations considered are features of the life histories of the species, omitting the morphological adaptations to current which are well known) and 4) to determine if a reduction in community biomass due to runoff effects could be measured in the standing population and to see if that reduction could also be measured by the downstream loss of drifting invertebrates from the study area. The data for this study were collected in 1970.

In order to shorten this paper for publication, a chapter entitled "Invertebrate Species and Life Cycles" was deleted. This material can be obtained by contacting either the Water Resources Research Institute or the Department of Zoology at the University of Wyoming, Laramie, Wyoming 82071, or the author.

STUDY AREA DESCRIPTION

The study area (Figure 1) is a section of Nash Fork Creek in the Snowy Range, Albany County, Wyoming. The study area is approximately 1 kilometer in length, flowing southeast and extending from the confluence of Nash Fork Creek and Telephone Creek at 3,048 m. (10,000 feet) elevation, past the S.H. Knight Science Camp to the slower meandering meadow section below, at about 2984 m. elevation. Within this section one permanent stream, Sally Creek, joins from the right or south at about 3000 m elevation.

The stream flows through a mature subalpine forest of mixed Engelmann Spruce, *Picea engelmannii*, and Subalpine Fir, *Abies lasiocarpa*. U.S. highway 130 parallels the study area to the north, allowing access to the stream.

The streambed in the study area is 1009 meters in length. The mean stream width at the beginning and end of the study was 5.65 meters. The gradient of the streambed through the study area varies from 31% in the cascade section at the upper end of the study area to as little as .11% at the lower end. The stream profile is shown in Figure 2.

The bed materials vary from large boulders and bedrock in the steepest sections to sand and silt in a few quiet places. In the study area the primary substratum type is 12-24 cm rubble over smaller pieces of rubble, gravel and sand.

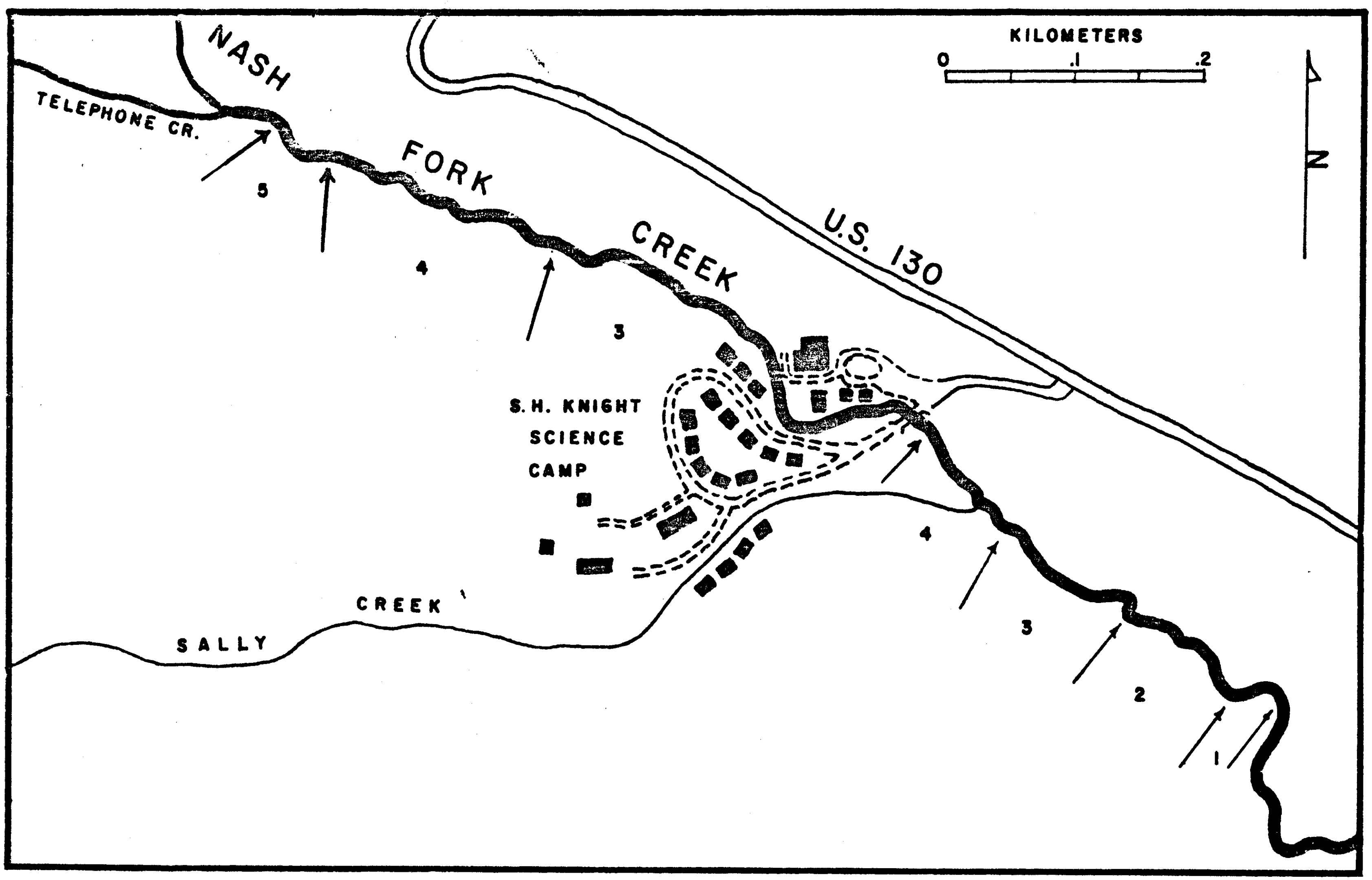


FIGURE I. STUDY AREA MAP

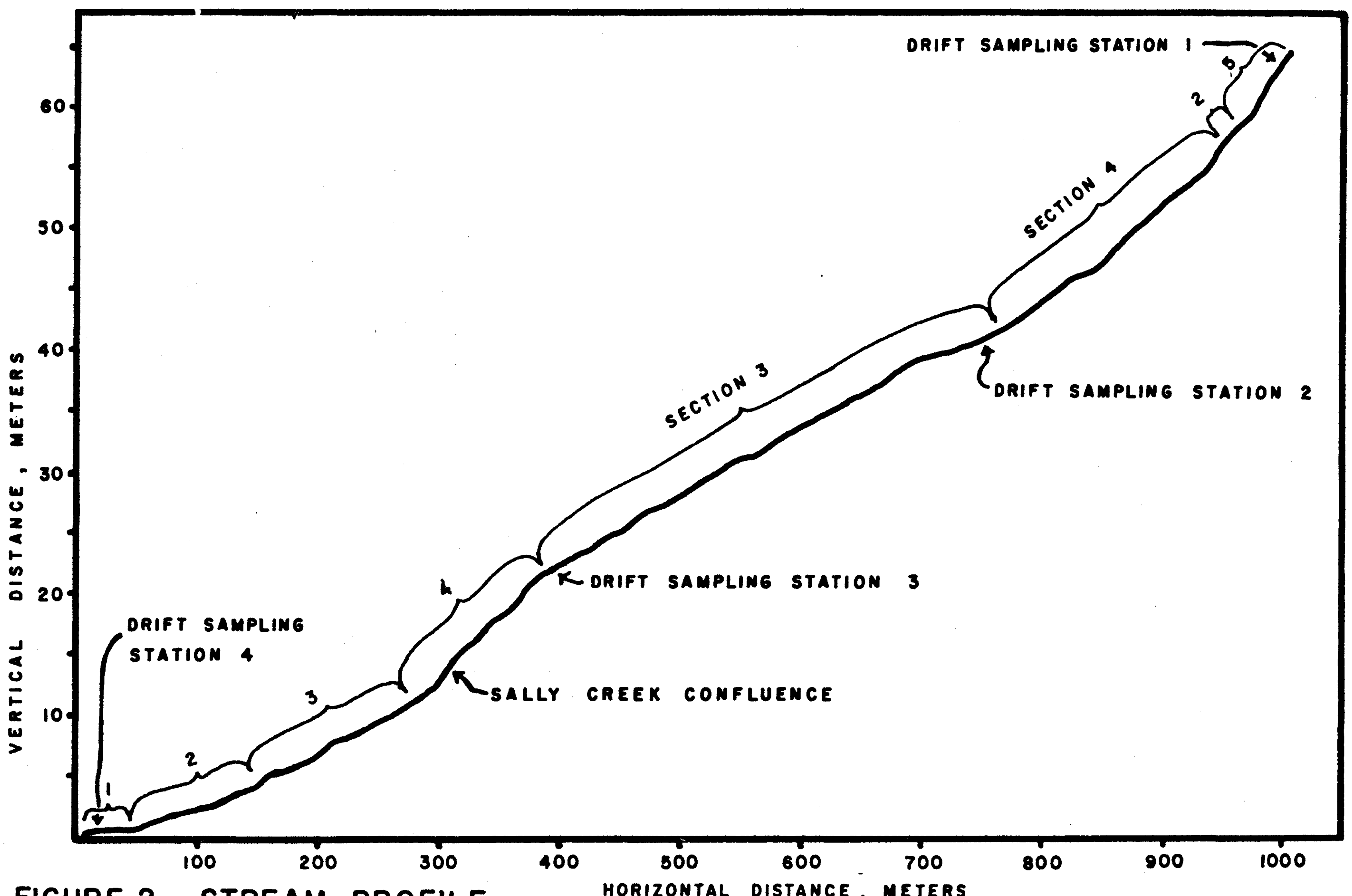


FIGURE 2. STREAM PROFILE

SEASONAL CONDITIONS IN THE STUDY AREA

The winter season is relatively long at the study area. Snowpack begins accumulating usually in October or November. After that time there is very little fluctuation in streamflow until some time in May when the runoff begins (Figure 3). The stream becomes mostly snow covered in the study area early in the winter, usually by mid-December. Certain locations in the stream tend to remain open, providing "windows" where algal growth continues. Water temperatures during the winter do not vary from 0°C. until the runoff begins.

In 1970 the streamflow began to increase on the 18th of May, when the mean flow was about 6 c.f.s. (0.17 c.m.s.). Streamflow increased almost daily, with interruptions due to cold weather until the peak on June 25 when the mean discharge at the study area was 125 c.f.s. (3.54 c.m.s.).

The daily hydrographs at the gaging station on Nash Fork above the study area (WRRI station 111.00) show considerable fluctuation in discharge, corresponding to the daily sequence of snowmelt (Figures 4 and 5). Because of the lag time involved between peak snowmelt and its influence on the hydrograph, the peak of the daily hydrograph arrives at the study area sometime after the peak of the snowmelt. During the runoff period, the daily peak generally arrives later each day, as the mean altitude of contributing snowmelt increases in the watershed. At WRRI station 111.00 on the 8th of June the peak of the daily runoff arrived near 17:00 hr., on June 18th at 18:00, and on June 25th the peak

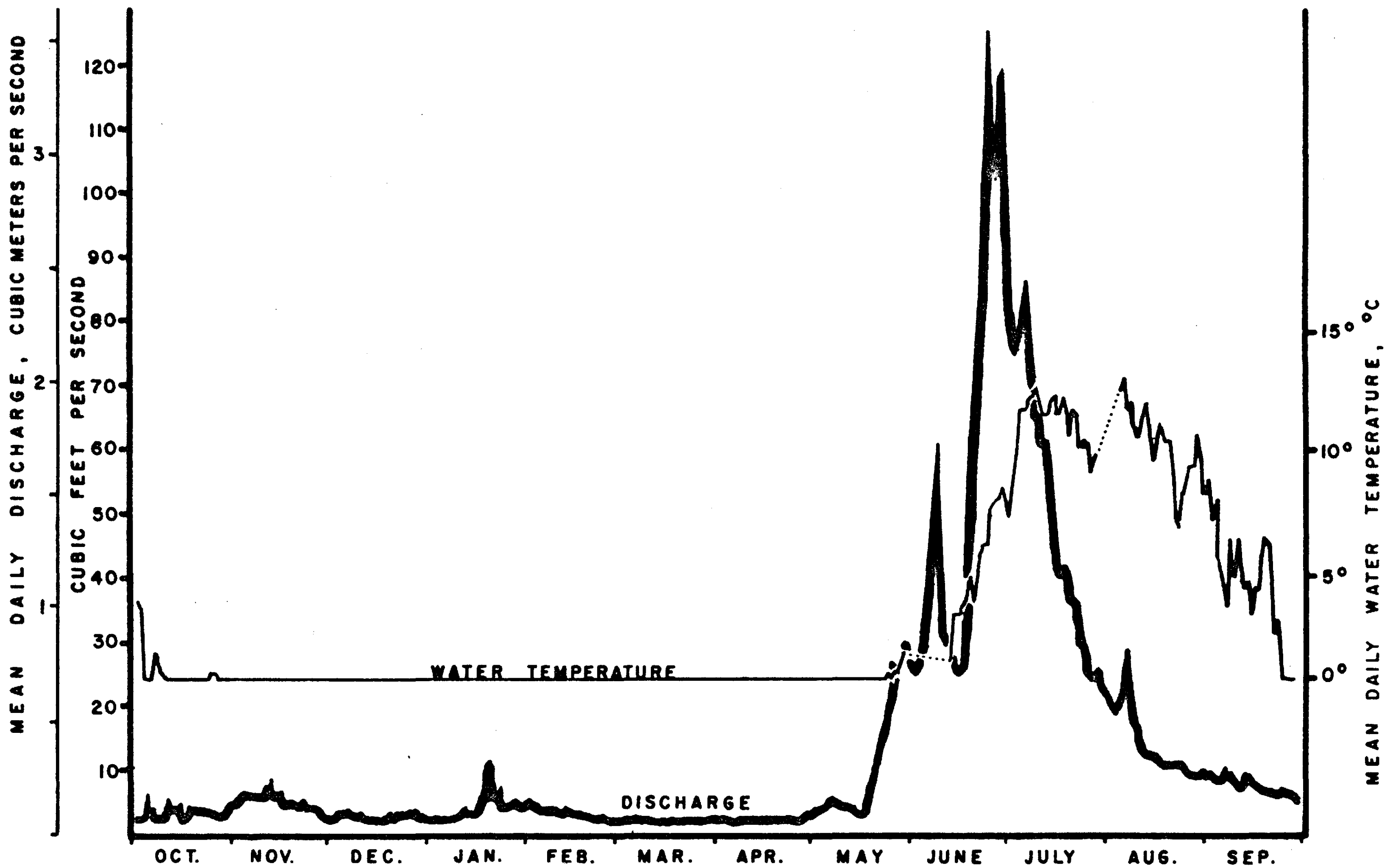


FIGURE 3. WATER TEMPERATURE AND DISCHARGE OF NASH FORK CREEK AT S.H. KNIGHT SCIENCE CAMP FOR WATER YEAR 1970; DISCHARGE ESTIMATED BY COMBINING DATA FROM W.R.R.I. STATIONS 111.00 AND 112.00

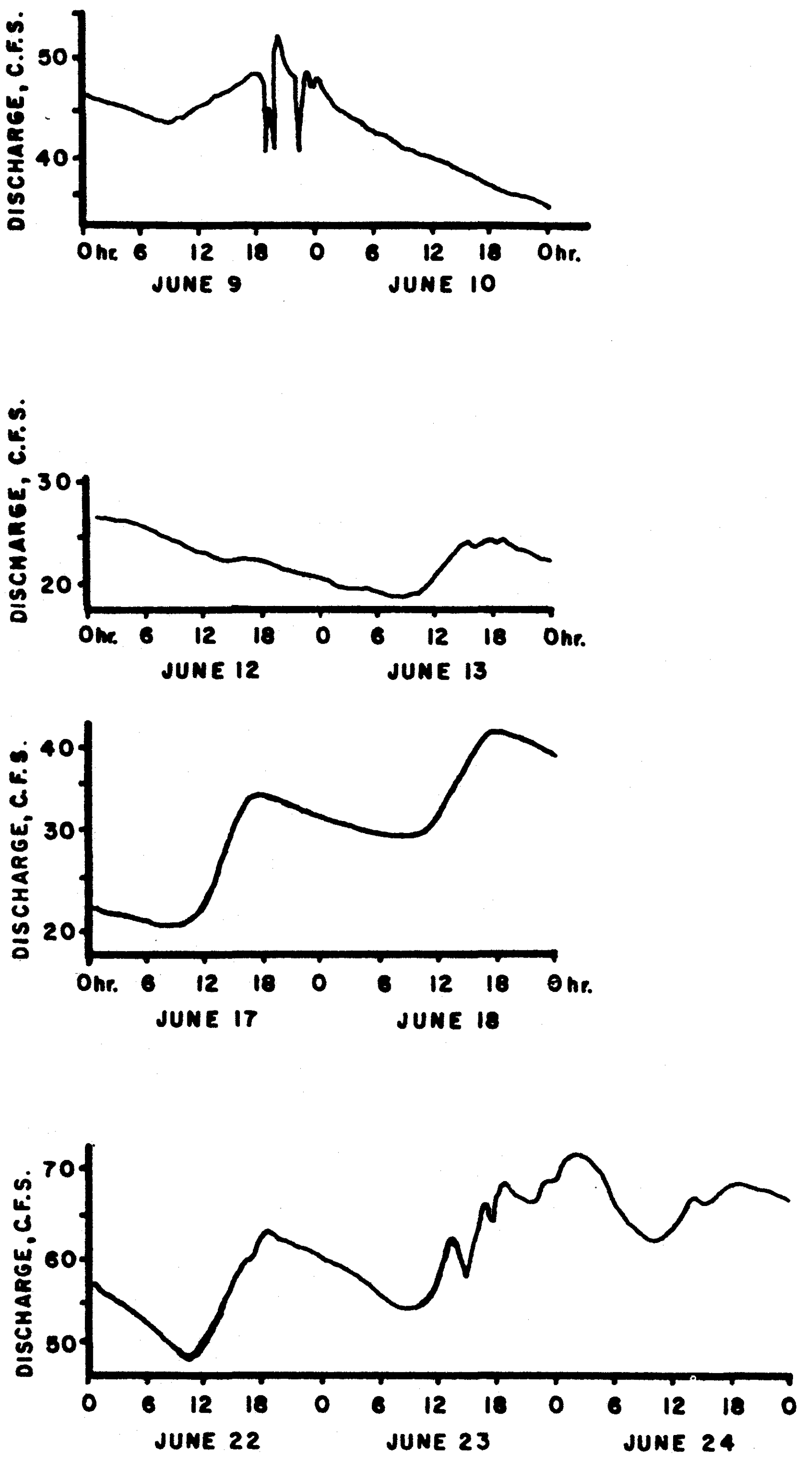


FIGURE 4. DAILY HYDROGRAPHS, W.R.R.I. STA. III.OO FOR JUNE DRIFT SAMPLING DATES

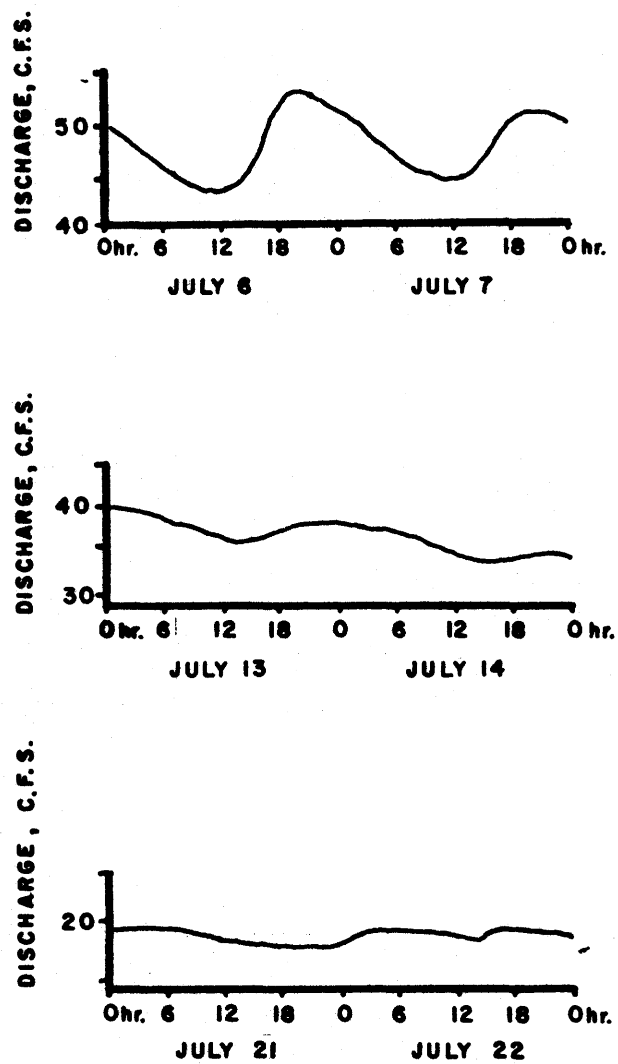


FIGURE 5. DAILY HYDROGRAPHS, W.R.R.I. STA. 111.00 FOR JULY DRIFT SAMPLING DATES

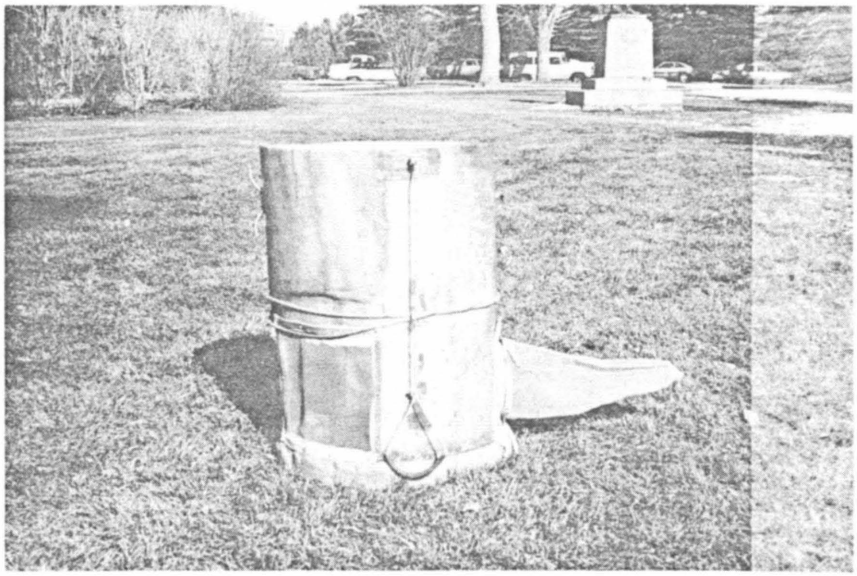


Figure 6. Side view of the benthos sampler

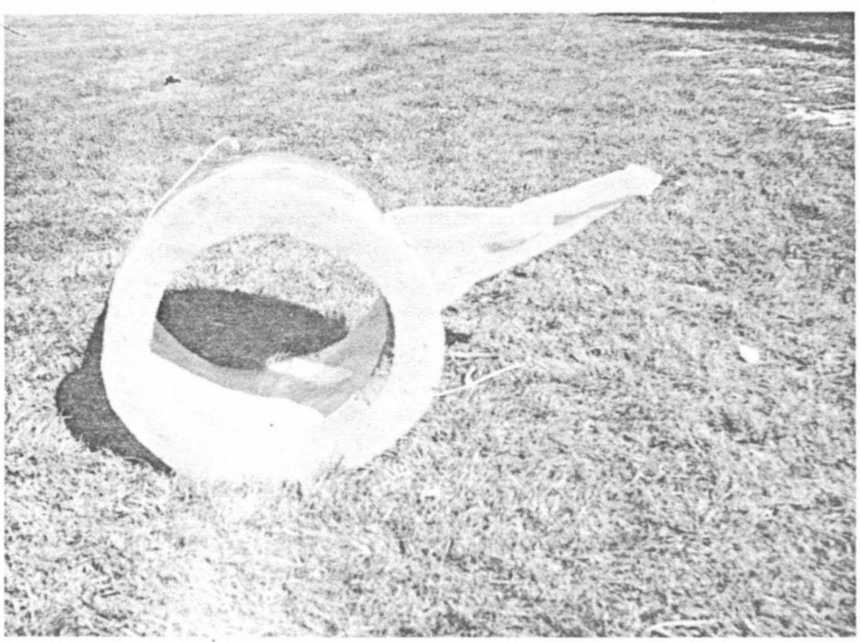


Figure 7. Bottom view of the benthos sampler

of the season's runoff occurred at about 17:40 M.S.T. On July 1 the daily peak arrived at 21:00, and by mid-July was arriving at 21:00 hr. After that time the peak was not well-defined.

Water temperature fluctuates similarly during the runoff, but follows the air temperature rather than the hydrograph. Daily mean temperatures and temperature ranges increase through the runoff period and into the mid-summer. In May during the early part of the runoff water temperature rose only a degree or so above 0°C. On June 25 the temperature range was 6°C. (4.5°-11.5°C.). On 21 July the range was 9°C. (7°-16°C.).

Snowcover over the stream begins to diminish with the beginning of the rise in streamflow. The areas where snow cover over the stream is deepest are the last to go, the snow usually breaking off in large chunks. These larger pieces of snow undoubtedly contribute to scouring of the streambed at this time.

METHODS

Benthos Samples

The benthos samples were taken with an enclosed sampler similar to that of Waters and Knapp (1961) but with several modifications (Figures 6 and 7). It is a sub-cylindrical frame built of fiberglass. The bottom opening is oval, enclosing an area of 0.1 m^2. The bottom edge has a plastic foam lip 6.5 cm thick by about 8 cm wide. The sampler is held against the substrate by the weight of the operator standing in the stirrups which are attached to either side of the sampler near the upper opening. The foam lining, compressed by the weight of the operator, forms a barrier to the enclosed organisms. A screen of nylon mesh (.505 mm mesh opening) covers two openings in the front or upstream side of the sampler, allowing water to enter the enclosure. A collecting net of the same material on the downstream side of the sampler screens the water leaving the enclosure. The collecting net is attached to the sampler by a separating zipper, allowing easy removal of the sample. The upstream face of the sampler is fitted with a rope cleat. This allows the sampler to be tied to an anchor point on the stream bank, for work in strong current.

The sampling procedure used is as follows. The operator places the sampler onto the streambed, secures the rope from the anchor point to the rope cleat, and steps into the stirrups.

Reaching into the enclosure the operator picks up each larger piece of rubble which can be moved, rubs the surface to dislodge the clinging organisms, then places the cleaned rock outside the sampler. When all of the larger stones have been removed, the remaining gravel, sand and silt are vigorously stirred with a stick for about 30 seconds. In locations where the current is not strong enough to wash the dislodged organisms into the collecting net, the water is forced through the net by "paddling" with the hands.

With this procedure completed the operator steps out of the stirrups. The sampler is lifted from the bottom by bracing it against the knees and swinging the bottom of the sampler forward, or upstream, in an arc, so that the water in the enclosure drains through the collecting net. Then the rope secured to the cleat is loosened.

Population Estimates

The population estimates were based on a benthos sampling plan using samples taken in a stratified series of transects. The study area was first divided into five sections based on the stream gradient. These areas were chosen by eye and the gradient was not measured until later when low water allowed better access. The gradient was then measured using a Brunton compass and steel tape.

The sections were chosen to be areas having the following ranges of gradients: section 1, 0-1.5% slope; section 2, 1.5-4.5% slope; section 3, 4.5-8% slope; section 4, 8-12% slope; section 5, more than 12% slope. The criteria were not strictly applied to each measured segment, but define the trend of the gradient over longer reaches of the stream. The sections are indicated in Figures 1 and 2.

The benthos samples were taken along transects across the stream.

The number of samples in a transect depended upon the width of the stream. The number of transects was limited to what could be sampled in a few days. The transects were chosen by picking a number from a random number table to designate a distance in paces from the downstream boundary of the section to be sampled. The sample locations are indicated in appendix A.

The plan was to take benthos samples for population estimates before and after the runoff. Because of the snow cover remaining over the stream when the runoff began, the early benthos series was not taken until all the stream was open. The first series was taken June 1-4, and so was not completed until 17 days after the hydrograph began to rise steadily. For convenience of interpretation, the late benthos series was taken when the stream flow had decreased to the same level (26 c.f.s.) as when the early samples were taken. This was July 27-29.

Drift Samples

Two types of net were used in the drift sampling (Figure 8). The first type of net used is a deep (about 1 meter) net with a small diameter (about 10 cm) mouth. This net was used to take samples in early June.

Near the peak of the runoff several samples were ruined because debris became lodged over the small net. The solution to this problem was to use nets with larger mouth area and take samples over a shorter period of time. The nets used were 0.1 meter^2 nets, also 1 meter deep.

Both nets were secured to a 0.1 m^2 frame held in place with metal

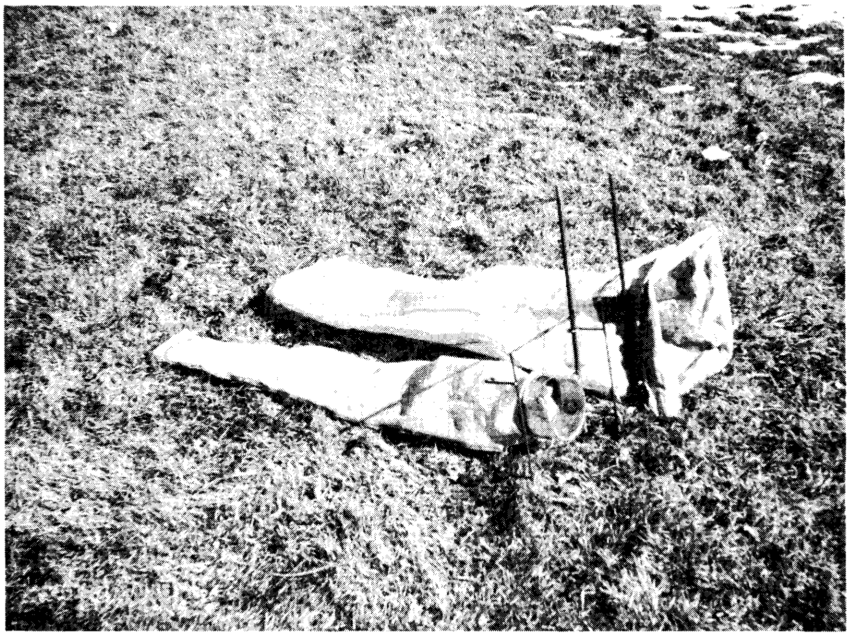


Figure 8. Two types of drift nets used in this study

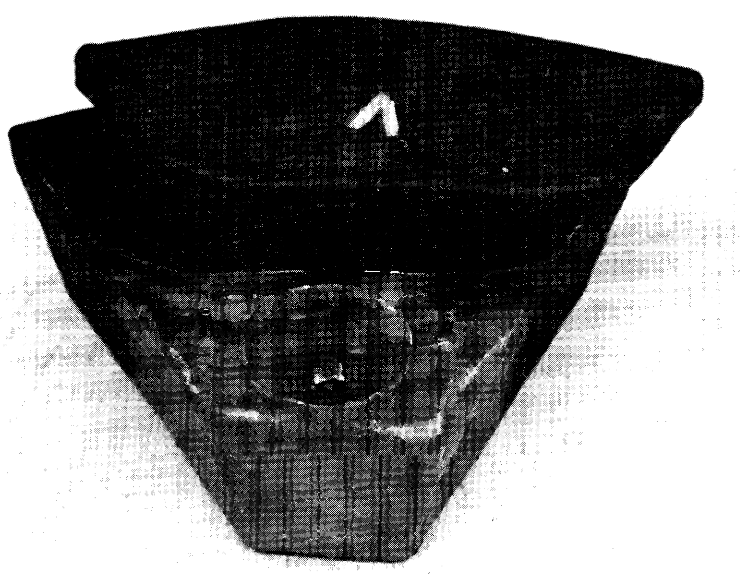


Figure 9. The live-sorting apparatus

rods driven into the substrate. The frames were also tied to an anchor point on the bank with a nylon line.

Volume flows through the drift nets were determined by measuring the velocity of the current entering the net mouth for one minute at the beginning and end of each sample. The flow meter used was a propeller-type recording flow meter (G.M. Mfg. & Inst. Corp. Model 466).

Drift samples were taken at four places in the study area (Figure 2). Samples were taken at stations 1, 2, 3 and 4 on June 9-10, 12-13, 17-18 and 22-23. After June 23 station 2 was no longer used. The remaining drift samples were taken on June 24 and July 6-7, 13-14 and 21-22. The earlier samples were taken with the small-mouthed nets for periods of approximately 12 hours, one at night and one in the day. The later samples were taken with the larger nets for approximately 40 minute periods three or four times during a 24 hour period.

Treatment of Samples

Benthos samples were killed immediately with a 10% formalin solution and stored. The organisms were removed from the samples later with the aid of a magnifying lamp and a white pan. The organisms were measured to the nearest 1 mm in length using a binocular dissecting microscope with a millimeter grid background.

Drift samples were left alive and allowed to sort in a live sorting apparatus. The live-sorting apparatus (Figure 9) has two chambers, one lighted and one dark, connected by a small orifice. The drift sample was placed in the dark chamber, from which many of the organisms crawled or swam through the orifice into the light chamber. The sorting procedure was allowed to continue from 6 to 18 hours. In most cases the organisms which did not move to the light chamber were killed and preserved with the remaining debris. These non-sorting fractions were later picked using the same technique as was used on the benthos samples, and the organisms were added to those live-sorted from the sample.

Some of the non-sorting fractions from July drift samples were unfortunately discarded. The organisms discarded were estimated by comparing the non-sorting and sorting fractions for those samples which were saved, and finding the percentage which did not live-sort. Only those species of which at least 50% of the individuals were found to live-sort were used in the results reported for the July drift samples. These organisms are given in Table 1.

Identification of the organisms was made as closely as possible, using published keys. In addition the stonefly collection was kindly identified by Dr. Arden Gaufin. A reference collection of those species which were distinguished in this study was made and constitutes a part of this paper.

Live Weight Estimation

Since the organisms in the samples were in preservative solutions for various lengths of time before tabulation, they were subject to weight loss as revealed by Howmiller (1972) and Stanford (1973). To compensate for this error, a system was used for estimating the live weight of the preserved organisms. This involved collecting live

Table 1. Organisms sortable with the light trap live-sorting apparatus.

Ephemeroptera

- *Rithrogena* spp.
- *Cinygmula* sp.
- *Epeorus longimanus*
- *Ameletus* spp.
- *Siphlonurus* sp.
- *Paraleptophlebia* sp.
- *Ephemerella doddsi*
- *E. coloradensis*
- *E. inermis*
- *Baetis* spp. A, B, C, D, E
- *Centroptilum* sp.

Plecoptera

- *Nemoura cinctipes*
- *N. oregonensis*
- *Nemoura* group 1
- *Nemoura* sp. 4
- *Paraleuctra occidentalis*
- *P. sara*
- *Eucapnopsis brevicauda*
- *Brachyptera* sp.
- *Arcynopteryx signata*
- *Alloperla borealis*
- *A. lamba*
- *A. lineosa*
- *A. autumna*
- *Isoperla fulva*
- *I. ebria*
- *Acroneuria pacifica*

Trichoptera

- Rhyacophila spp. 1, 2, 3, 4
  5, 7, 8, 9, 10
- *Arctopsyche* sp.
- Limnephilidae mixed species
- Lepidostomatidae species 1, 2,

Diptera

- Chironomidae larvae 2a, 2b, 12, 13
- Chironomidae mixed larvae

Acari, mixed species

individuals of as many species as possible, weighing them alive, then killing them in a preserving solution and measuring their length. The individual organisms were dried for about 10 seconds on a buchner filter, then placed in a pre-weighed vial which was then sealed with a rubber stopper. The individuals were weighed to the nearest 0.1 mg on an electronic balance (Sartorius Model 2400). After weighing, the individuals were killed in 10 percent formalin solution and measured to the nearest 0.1 mm over a 1 mm grid.

From these data a relationship between live weight and dead length was determined. The formula used is:

$$\text{weight} = \text{length}^3 \times \text{species constant "b"}$$

The species constants were determined from the linear regression formula:

$$Y = bX$$

$$\text{where "b"} = \frac{\Sigma XY}{\Sigma X^2}$$

$$Y = \text{weight, mg}$$

$$X = \text{length}^3\text{, mm}$$

This formula forces the regression through the origin (Steele and Torrie 1960) and was chosen since the regression line should be expected to go through the origin (the organism will have zero weight at zero length).

The length:weight relationships of species which could not be obtained alive were estimated by the following procedure. The length: weight relationships of preserved individuals from the original sampling of benthos or drift were determined as above for the live organisms. This was done for species for which the relationship had been established with live individuals. The difference between the live weight and dead weight relationships was taken to be due to weight loss in preservation. The percentage of weight loss found was used to adjust the dead weight:dead length relationships for similar species for which live specimens could not be found. Since these data were collected in November and December of 1973, many species present during the runoff were no longer available.

A few species were arbitrarily assigned "b" values determined for similarly-shaped species. This was done only for species for which too few individuals were collected or the individuals were too small to weigh with accuracy by the above procedure.

STANDING CROP BIOMASS CHANGES DURING THE RUNOFF PERIOD

The comparisons presented here are based on biomass rather than numbers. It is felt that biomass is the more easily understood parameter when discussing whole communities containing many species in a large range of sizes. An organism's effect on the rest of the community is assumed to be some function of that individual's size.

Mean standing crop biomass estimates for the early and late benthos sampling periods and the standard errors of the means are given in Table 2. Because of the large standard errors, the differences between the estimates could only be tested with non-parametric statistics. The Mann-Whitney U-statistic (Elliott 1971) was used to test differences between estimated median values of the standing crop biomass. The u-statistic is related to the median rather than the mean. The median values of standing crop biomass are also presented in Table 2, with the differences between the early and late estimates for each section indicated at the .05 level. Differences were found between the early and late estimates for sections 1, 2, and 5. The early estimate was larger for section 1 while the late estimates were larger for sections 2 and 5. The estimates for the entire study area were not different at the .05 level. Notice that for the entire study area estimates, the mean for the early samples was larger than for the late samples, but the median was not. This is probably due to the greater variation between samples in the early sampling period.

For each benthos sampling period, the difference between sections

Table 2. Mean numbers and weights per meter^2, standard errors of the means and median weights per meter^2 for invertebrate standing crops in each section of the study area for the early (June 1-4) and late (July 27-29) benthos sampling periods.

		MEAN				MEDIAN		
		Early		Late				
Section		mean	standard error	mean	standard error	early	late	different at .05 level
1.	n.	2,568	1,194	2,575	252			
	wt.	21,974 mg	10,921 mg	7,250 mg	594 mg	15,797 mg	7,266 mg	*
2.	n.	749	106	2,296	253			
	wt.	3,502 mg	751 mg	6,970 mg	1,068 mg	2,433 mg	5,948 mg	*
3.	n.	1,814	714	1,458	206			
	wt.	6,391 mg	1,993	5,253 mg	1,066 mg	4,174 mg	4,087 mg	
4.	n.	1,644	509	1,892	350			
	wt.	5,790 mg	1,845 mg	5,012 mg	2,755 mg	3,525 mg	3,462 mg	
5.	n.	80	65	2,100	270			
	wt.	271 mg	244 mg	2,882 mg	872 mg	45 mg	2,881 mg	*
entire	n.	2,250		1,790				
study area	wt.	6,309 mg		5,131 mg		3,601 mg	5,980 mg	

in the study area were tested. These results are shown in Table 3 (early) and Table 4 (late). Out of ten possible comparisons between sections, 5 were significantly different in the early sampling period. The estimates for section 1 were significantly larger than those for sections 2, 3 and 5, and the estimates for 2 and 4 were larger than for section 5. In the late sampling period the estimates for each section were much closer together. The only difference with statistical significance was section 1 vs. section 5, with section 1 being larger.

One factor contributing to the variation in the early benthos samples was probably the very restricted distribution of dense algal patches on the stream bed, corresponding to the "windows" in the snow cover during the winter. These algal patches contain concentrations of invertebrates. By the late benthos sampling period these patches of algae had been scoured away.

A second factor influencing the variation between early benthos samples could be the recent increase in streamflow above the steady winter level. The streambed margins, which recently had been dry, had had very little time to become colonized with algae or invertebrates, yet were included in the sampling. By the time of the late benthos sampling these marginal areas had had sufficient time to be colonized.

A third factor, applying only to section 1, was the scouring away of local silt concentrations and their dense chironomid fauna. These were present at the lower end of section 1 where ponding due to a beaver dam had affected the water level, creating quiet areas. The beaver dam washed out during the runoff, eliminating these habitats.

Although the statistical evidence is not conclusive, there is a

Table 3. Comparisons of median standing crop biomass estimates between sections for the early (June 1-4) benthos sampling period, based on tests of the U-statistic at the .05 level.

section	median standing crop biomass, mg per meter^2	comparison with other sections, * = difference at .05 level 1	2	3	4	5
1	10,790		*	*		*
2	2,430	*				*
3	4,170	*				
4	3,520					*
5	50	*	*		*	

Table 4. Comparisons of median standing crop biomass estimates between sections for the late (July 27-29) benthos sampling period, based on tests of the U-statistic at the .05 level.

section	median standing crop biomass mg per meter^2	comparison with other sections, * = difference at .05 level 1	2	3	4	5
1	7,270					*
2	5,950					
3	4,080					
4	2,740					
5	2,880	*				

general trend for the mean biomass to decrease with gradient, as indicated by the estimates for the separate study sections (the sections were defined by gradient). This is more marked for the early samples, probably because gradient is one factor in the snow cover over the stream. Since snow cover generally increased with increasing gradient, "window" areas for algal growth decreased correspondingly. The apparent exception of the low biomass in section 2 can be explained by the snow cover also since this section contains one area where a large snow drift accumulated.

DRIFT SAMPLES

All Drifting Invertebrates

Drift rates for all drifting invertebrates, including those not found in the benthos of the study area, are shown graphically in Figure 10. These are shown only for the three sampling periods for which the data were complete (data were incomplete for 9-10 June and all July sampling periods). The drift rates shown are the mean of the rates for all available stations. The sorting and non-sorting fractions are indicated.

Several trends are worth noting. Most of the increase with advancing season was in the non-sorting fractions. For the non-sorting fractions the night drift rates were greater than the day rates, but not remarkably so. The most striking characteristic was the large increase in the overall drift rates between 12-13 June and 22-24 June. Both the day and night drift rates for 22-24 June were more than 20 times those of 12-13 June. The difference in discharge was about 5 times. Since the peak stream discharge occurred on June 25, the 22-24 June drift samples must represent very nearly the peak of whatever catastrophic effects were occurring. As will be shown later, the discharge effect is not the only one to be considered.

Drifting Oligochaetes

Included within the non-sorting fractions are the drift rates for Oligochaetes. These rates, including the incomplete data from

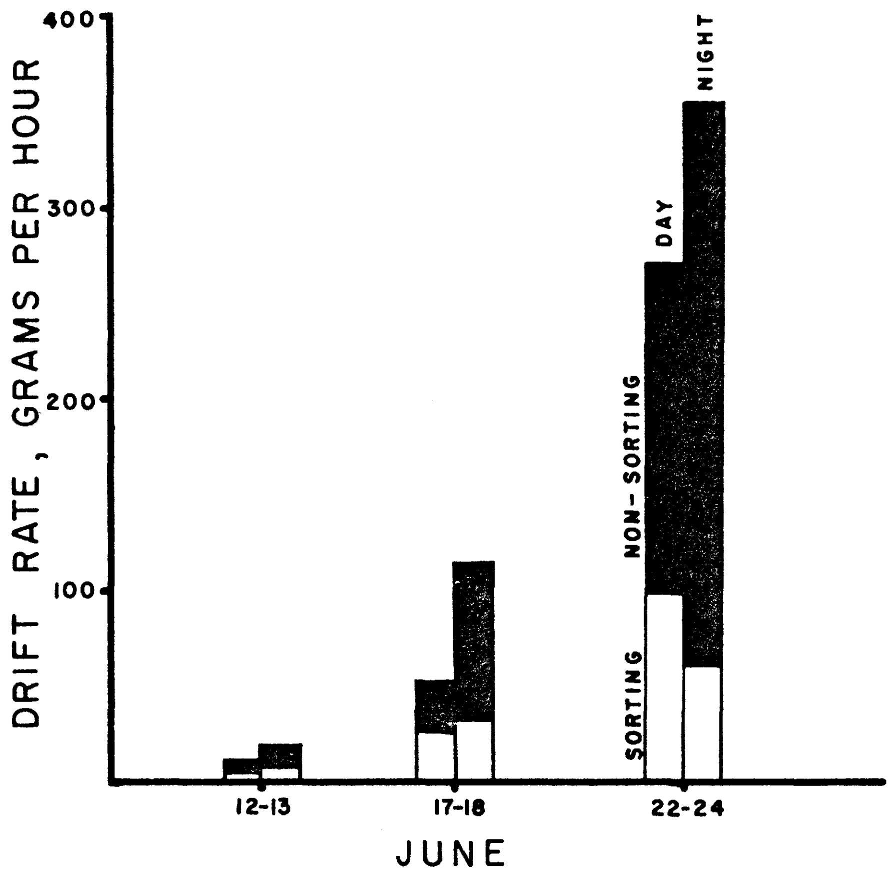


FIGURE 10. DAY AND NIGHT DRIFT RATES DURING JUNE FOR ALL DRIFTING INVERTEBRATES, INCLUDING SORTING AND NON-SORTING FRACTIONS

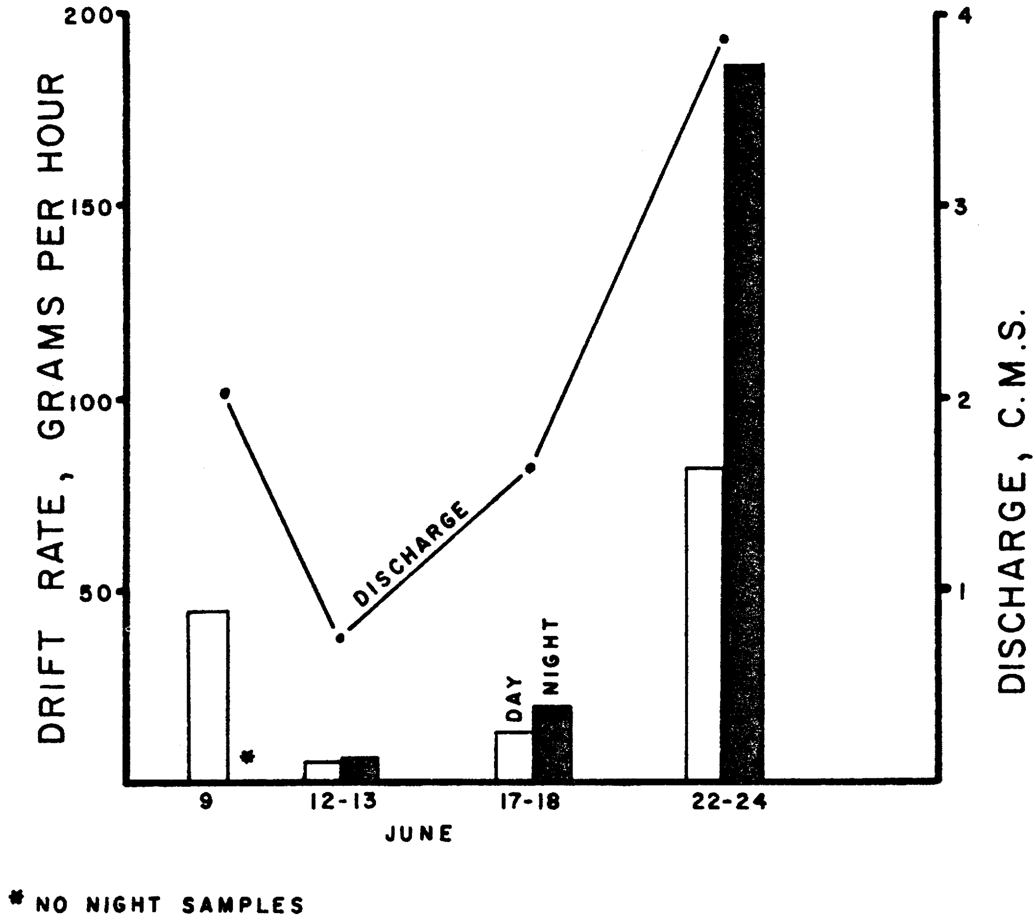


FIGURE 11. DAY AND NIGHT DRIFT RATES FOR ALL OLIGOCHAETA AND MEAN DAILY DISCHARGE

9-10 June are shown in Figure 11. Again the drift rate is seen to reflect changes in discharge. The relationship was non-linear. The night drift rate was higher than the day drift rate in all cases.

One point of interest is the occurrence of pieces of oligochaetes in the drift. The means by which they were broken is not known but two possibilities exist: 1) they were broken up by the grinding action of the substrate as it was moved by the current, or 2) they were broken up while drifting by abrasion against the substrate. Figure 12 shows the percent of drifting oligochaete biomass which was fragments in the diurnal samples. This relationship between the percentage as fragments and the discharge was apparently linear (Figure 13). The correlation coefficient is $r = .972$, and is significantly non-zero at the .05 level. The night data do not have the same close relationship to discharge. This difference between the day and night percentage fragment:discharge relationship is not understood. It could be related to the fact that the daytime samples were taken when the discharge was increasing while the night samples were taken when the discharge was falling.

Drift Tipulidae

The other major component of the non-sorting drift fraction was the Cranefly larvae (Tipulidae, Diptera). The combined drift rates for all drifting Tipulids are shown in Figure 14. Again the drift rates were related to discharge. The Tipulid drift rate was higher at night, much more so than with the Oligochaeta. Only one Tipulid fragment was found in the drift.

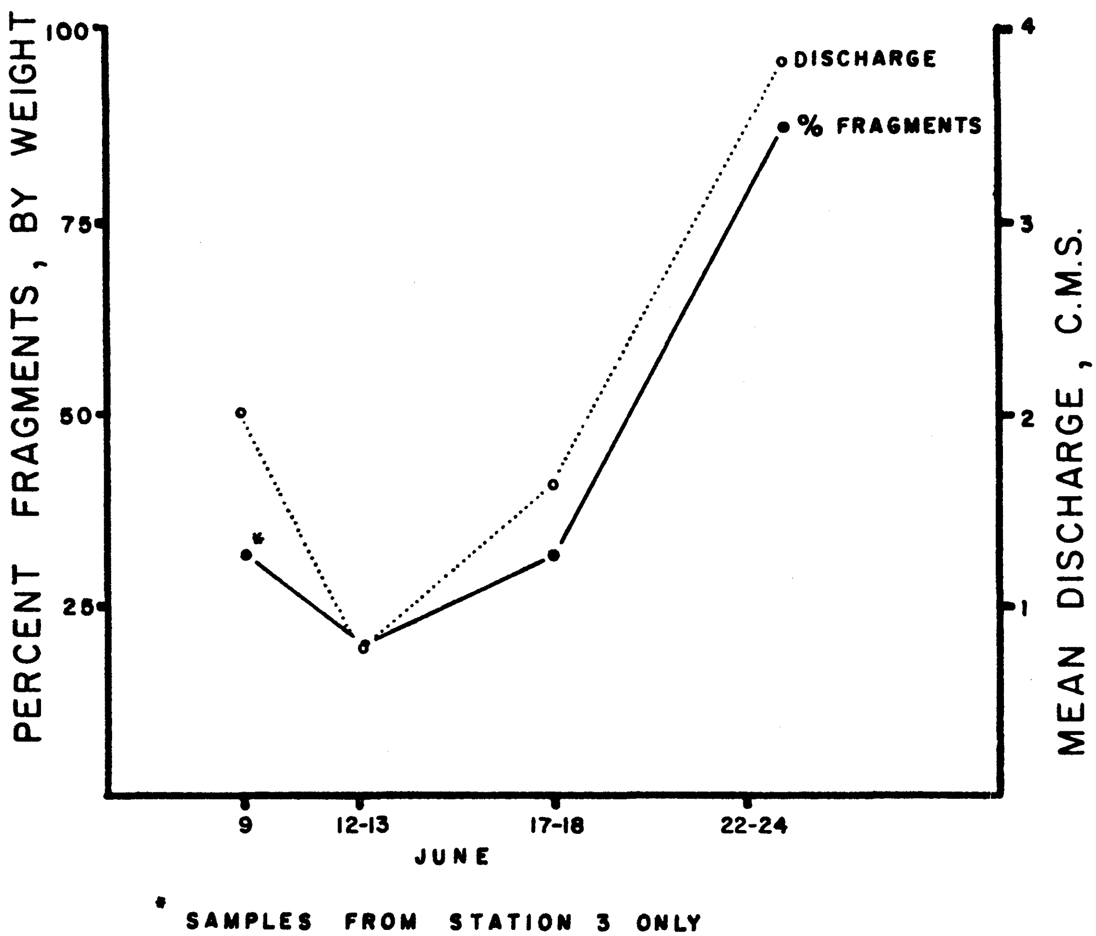


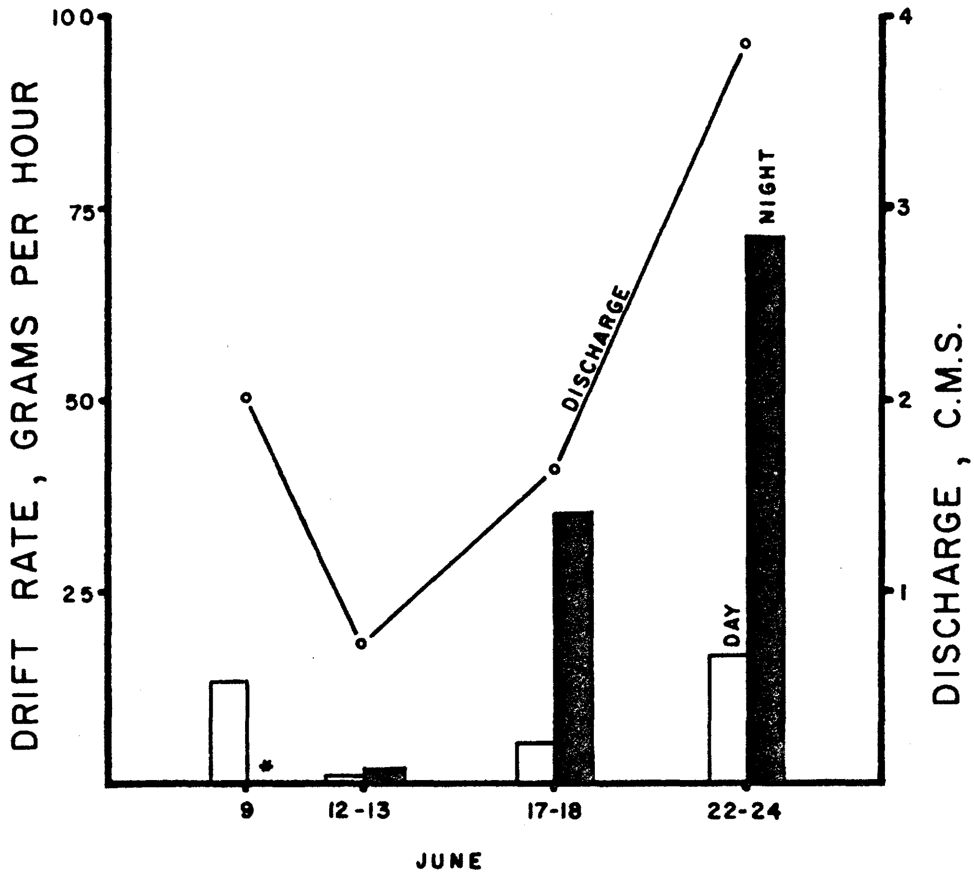
FIGURE 12. MEAN DAILY DISCHARGE AND PERCENT, BY WEIGHT, OF DRIFTING OLIGOCHAETES WHICH ARE FRAGMENTS

Drift of Live-Sorting Invertebrates

The live-sorting apparatus was used on all drift sampling dates as an aid to sorting. Since most of the non-sorting debris fractions were discarded after 24 June, the samples from after that date were handled differently. As detailed in the methods earlier, the number and weight totals for these organisms were estimated by adding the expected non-sorting percentage of each species to the amount recovered by the live-sorting procedure. The species for which this was done are listed in Table 1.

As a group these are the more active Arthropods. They include all the Ephemeroptera, most Plecoptera, most Trichoptera, the Chironomidae larvae, and the Acari. The "live-sortable" invertebrates will be discussed only as a unit, not broken down by species.

The drift rates of the live-sortable organisms are shown in Figure 15. The data can conveniently be separated into two units. The first three dates are in the increasing discharge or rising phase of the runoff. The last three dates are in the decreasing or falling phase of the runoff. The rising phase was characterized by an increase, with discharge, of both day and night drift rates, the two approaching equality at the June 22-24 peak. After that time the drift rate dropped quite suddenly, more than did the discharge, and the drift became increasingly a nocturnal phenomenon. On the last drift sampling date, the drift rate at night had risen to its highest point, and nearly equaled the combined day and night drift rates at the peak of the runoff. Thus the drift rates of the live-sorting invertebrates in the late summer, when behav-



* NO NIGHT SAMPLES

FIGURE 14. DAY AND NIGHT DRIFT RATES FOR ALL TIPULIDAE AND MEAN DAILY DISCHARGE FOR JUNE DRIFT SAMPLING DATES

Drift of Live-Sorting Invertebrates

The live-sorting apparatus was used on all drift sampling dates as an aid to sorting. Since most of the non-sorting debris fractions were discarded after 24 June, the samples from after that date were handled differently. As detailed in the methods earlier, the number and weight totals for these organisms were estimated by adding the expected non-sorting percentage of each species to the amount recovered by the live-sorting procedure. The species for which this was done are listed in Table 1.

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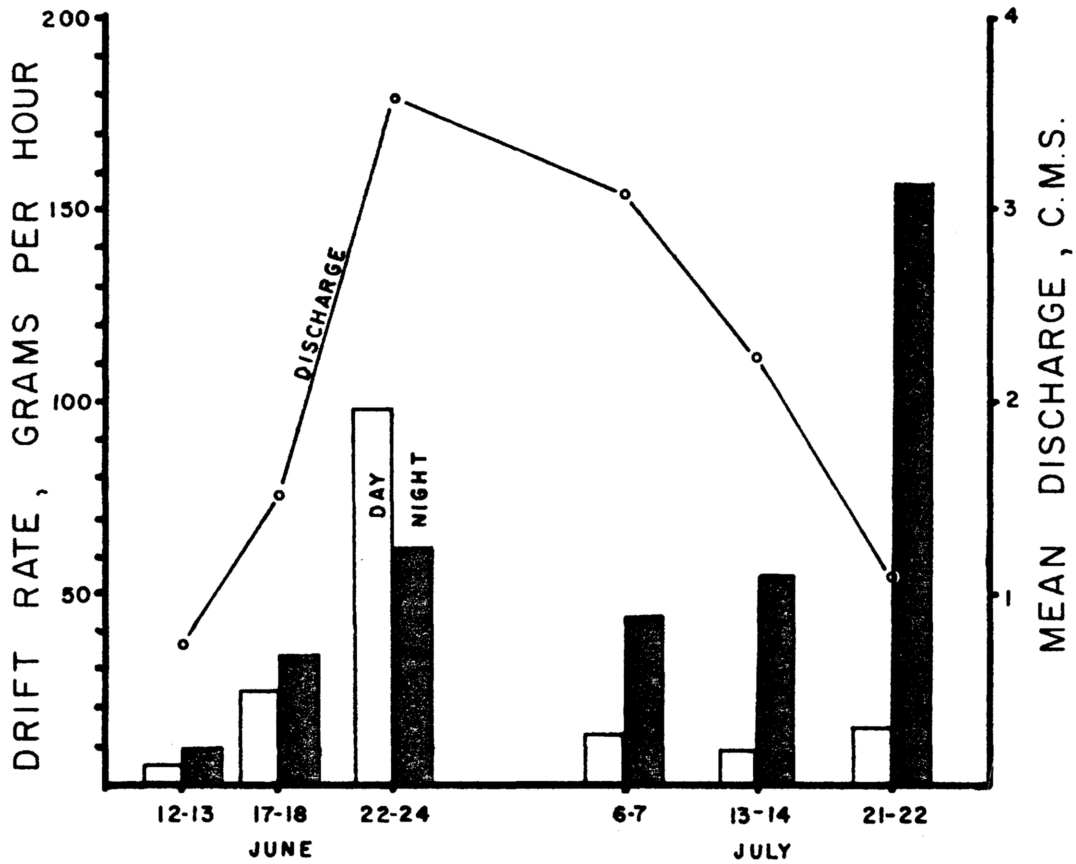

FIGURE 15. DAY AND NIGHT DRIFT RATES FOR ALL LIVE-SORTING INVERTEBRATES AND MEAN DAILY DISCHARGE FOR THE SAME PERIODS

ioral drift is probably the dominant source of drift, are as high as the drift rates at the peak of the runoff, when catastrophic effects are at their height.

Drift Rate Changes Between Stations

The changes in drift rate for the live-sorting invertebrates between sampling stations is illustrated in Figures 16 and 17. One of the objectives of this study was to measure the net loss of invertebrate biomass by drift from the study area, as the difference between incoming and outgoing drift rate. There was more often than not a net loss from the area according to the difference between drift rates at the upper (station 1) and lower (station 4) ends of the study area. However, the drift rates at the intermediate stations often decreased and definitely did not demonstrate a continuous trend of increase.

The changes in drift rate between stations must depend on several factors, such as predation on drifting organisms, the intensity of eroding conditions, and population densities in the immediate upstream areas. Other workers have found that drift rates increase through riffles and decrease through pools (Waters 1962b, Elliott 1967). Whether drift rates are increasing or decreasing through an area of streambed apparently depends on habitat and such biotic factors as presence of drift predators and species prone to drift. Since the upper and lower drift sampling stations represent the extremes of habitat found in the study area, it should not be surprising that drift rates were different at the two points. The fact that a net loss from the study area was often measured may only be because population densities were less at station 1

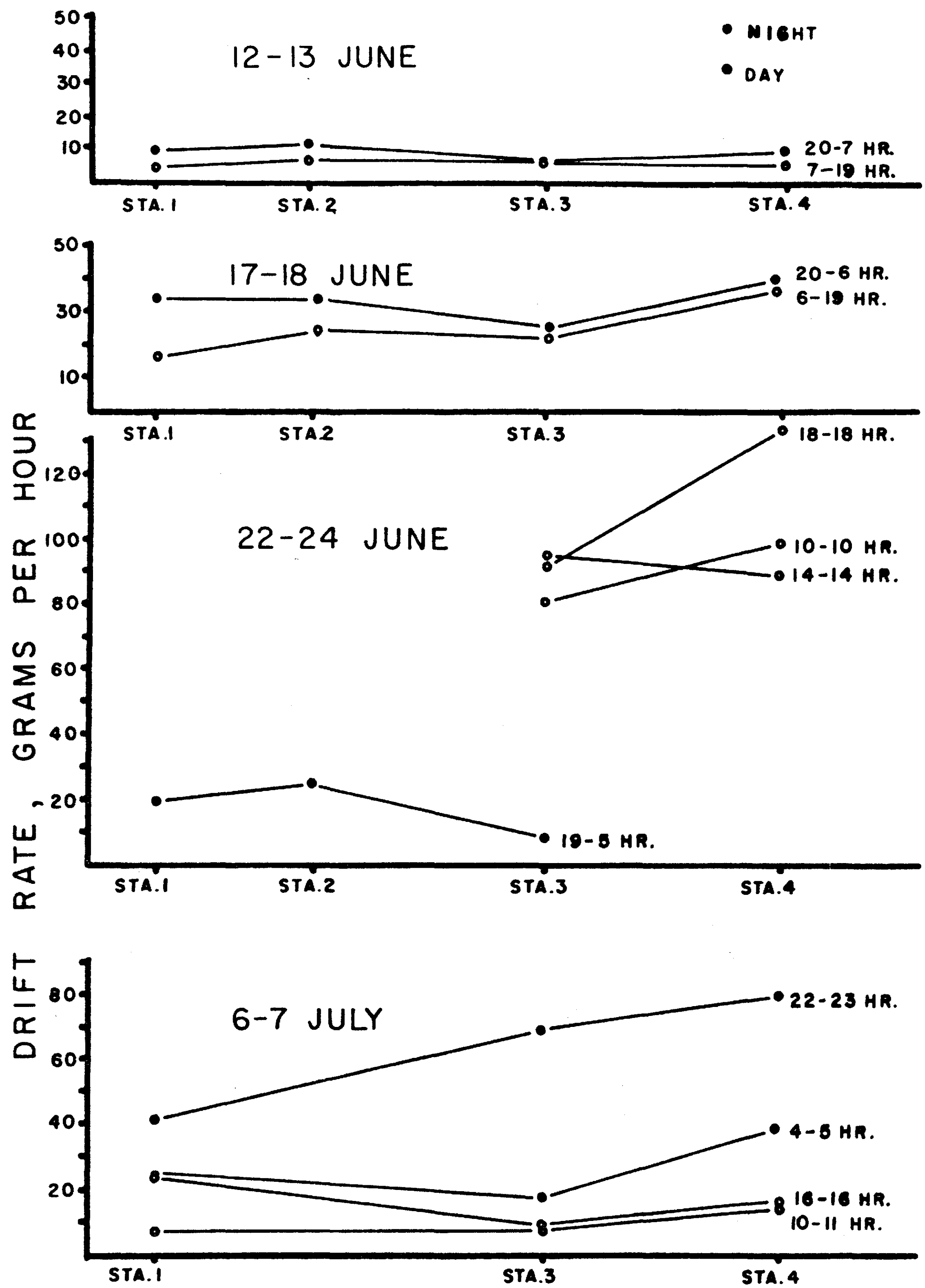

FIGURE 16. DRIFT RATE CHANGES BETWEEN ADJACENT DRIFT SAMPLING STATIONS FOR ALL LIVE-SORTING INVERTEBRATES; TIME IN 24-HR. STANDARD TIME

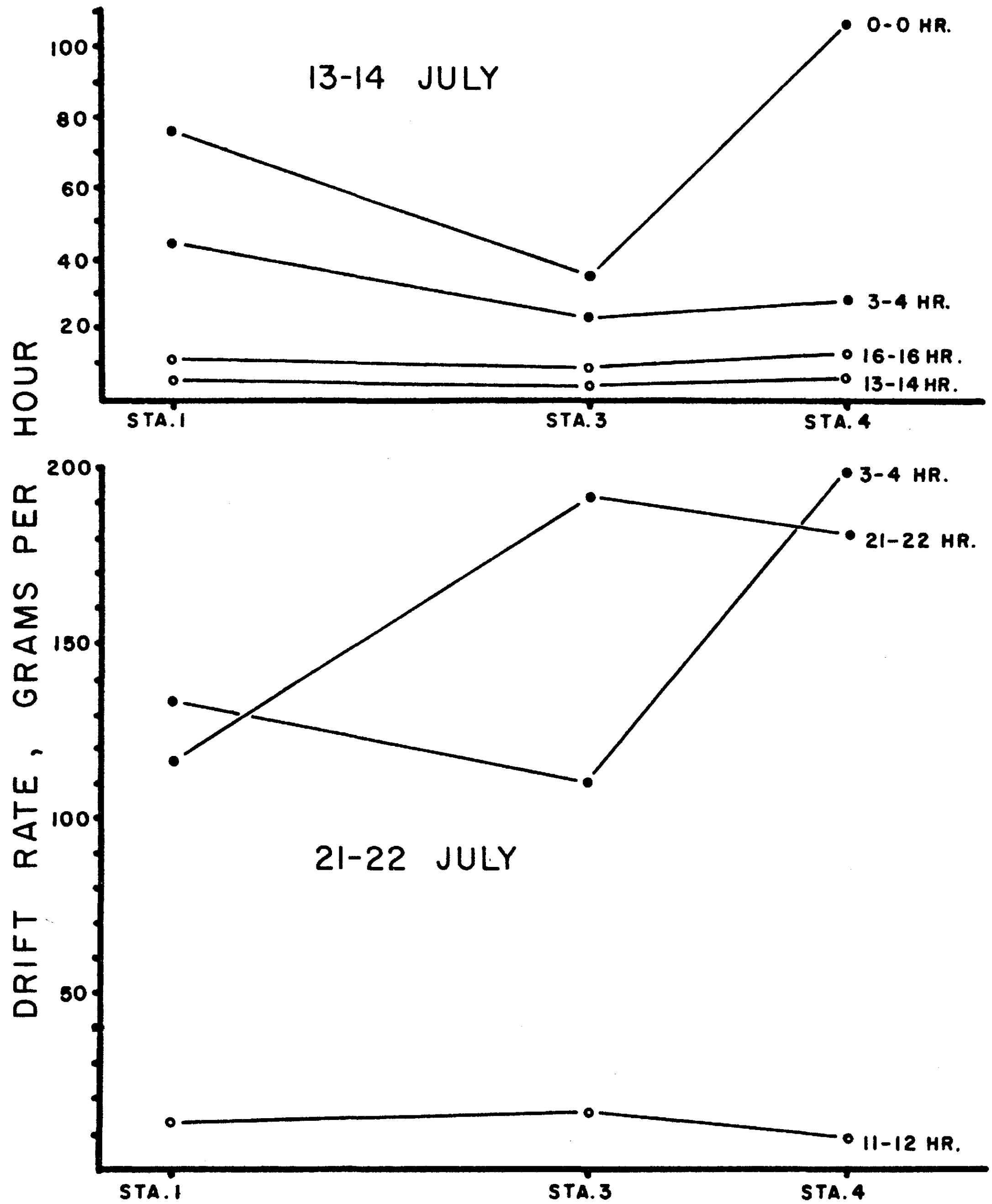

FIGURE 17. DRIFT RATE CHANGES BETWEEN ADJACENT DRIFT SAMPLING STATIONS FOR ALL LIVE-SORTING INVERTEBRATES; TIME IN 24-HR. STANDARD TIME

than at Station 4. Therefore, the possible net loss of invertebrates from the study area by drifting cannot be confirmed by the data collected. More extensive sampling would be necessary to confirm that net downstream loss of drifting individuals is a general feature of high mountain stream ecosystems. It seems likely that predators on drift would be utilizing the increased availability of these prey.

Catastrophic and Behavioral Drift

The terms "catastrophic and behavioral" drift as defined by Waters (1965) are useful in a conceptual sense, but they are difficult to apply to a description of data, as explained by Anderson and Lehmkuhl (1968). The use of these terms in description implies that the means by which the organisms entered the drift is known. In fact it would be very difficult to determine by direct means if individuals left the substrate by being washed away or if they released themselves purposefully. Thus, only indirect means can be used to estimate the relative influence of behavioral and catstrophic effects in generating drift.

Nocturnal Drift Rate Index

One possible way to approach behavioral drift is to consider the extent to which drift is nocturnal. Although behavioral drift of a few species occurs during the day, most examples of behavioral drift reported have been nocturnal (Waters 1962a). In the sorting-fraction drift (Figure 15) it is apparent that there was variation in the ratio of night to day drift rates. To quantify this relationship an index of nocturnal drift was devised:

$$\frac{\text{Night Rate - Day Rate}}{\text{Night Rate + Day Rate}} = \text{Nocturnal Drift Rate Index}$$

The index is +1 if all drift occurs at night, -1 if all drift occurs during the day, and 0 if the day and night rates are equal. The index was calculated for those drift sampling dates with both day and night samples and is shown in Figure 18. The calculation used drift rates based on biomass per 1000 m^3.

In the same figure are shown the daily mean water temperature and discharge. The index appears to be related to both parameters. The index is a reasonable mirror image of the discharge curve, but for most points also increases as the water temperature increases. For the regression of the index on discharge, the coefficient of determination is .177, and the correlation coefficient is -.421, which is not significantly non-zero at the .05 level. For the regression of the index on water temperature the coefficient of determination is .486, and the correlation coefficient is .696, which is also not significantly non-zero at the .05 level.

If we use the multiple regression model:

$$Z = M_1X + M_2Y + i$$

where: Z = Nocturnal Drift Index

X = water temperature, °C

Y = discharge, cubic meters per second

M_1 = regression coefficient for water temperature

M_2 = regression coefficient for discharge

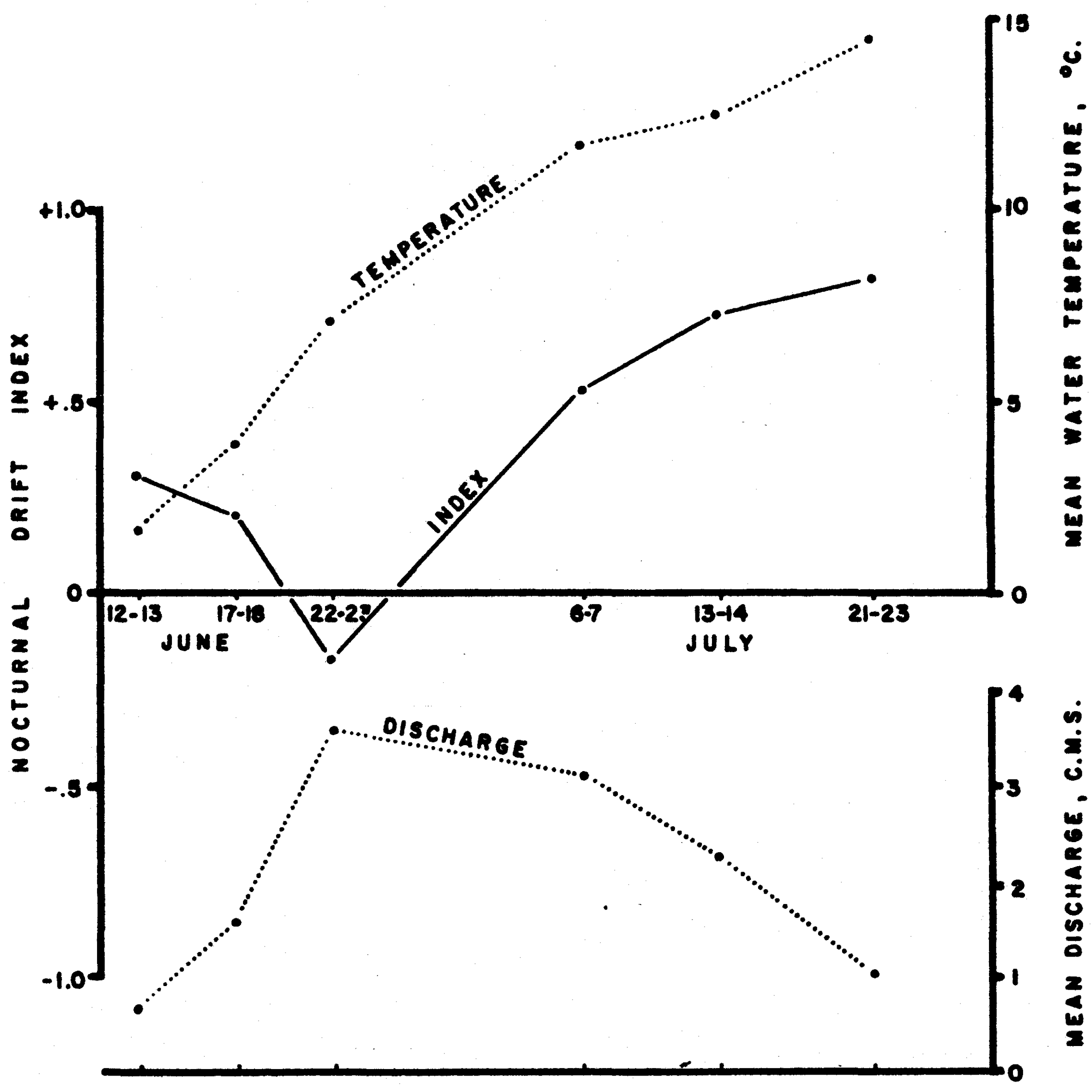

FIGURE 18. NOCTURNAL DRIFT INDEX, MEAN DAILY WATER TEMPERATURE, AND MEAN DAILY DISCHARGE FOR ALL DRIFT SAMPLING DATES WITH DAY AND NIGHT SAMPLES; INDEX BASED ON MEAN BIOMASS DRIFT RATE DATA FROM ALL AVAILABLE STATIONS

i = intercept

the regression of the index on both discharge and water temperature has a coefficient of determination of .86, which is the percent of the variation explained by the model:

$$Z = 0.0610\ X - 0.2034\ Y + 0.2984$$

Standard errors for the regression coefficients are:

S.E. (i) = .1871

S.E. (M_1) = .0159

S.E. (M_2) = .0713

M_1 is significantly non-zero at the .05 level. M_2 is significantly non-zero at the .05 level. The index is more closely related to water temperature, but discharge does contribute to the model, and both parameters together are a better estimator of the index than either is alone.

It should not be surprising that in these poikilothermous animals, an apparently behavioral phenomenon is related to temperature. During the falling phase of the runoff, the drift rates became more and more nocturnal as the temperature rose.

The index has a less-significant inverse relationship to discharge. The lowest index came at the highest discharge when catastrophic effects are presumed to have been highest. This can be interpreted as an indication that behavioral drift was suppressed by the high discharge catastrophic conditions. Perhaps the invertebrates were engaged in behavior not associated with behavioral drift. Elliott (1967) considered behavioral drift to be a phenomenon related to foraging activity. Perhaps the suppression of behavioral drift shown here results from the benthic invertebrates spending more effort in maintaining their positions rather than in foraging for food when discharge was high.

PROBLEMS FOR BENTHIC INVERTEBRATES CAUSED BY SCOURING

The large increase in stream discharge during the runoff holds at least three potential hazards for the benthic invertebrates: 1) physical damage, 2) displacement from suitable habitat, 3) vulnerability to predation while drifting.

Physical Damage

The movement of streambed materials by the force of the current can be a perilous situation for benthic invertebrates. The sliding, rolling, saltation and bouncing of pieces of bed material that occur with the highest discharges cause risk of injury to the organisms. The sizes of the moving bed materials relative to that of the invertebrates makes successful survival of an invertebrate from impact of all but the smallest substrate particles unlikely. Exceptions might be impact on appendages of the arthropods which can regenerate them. Mayflies and stoneflies with regenerated legs were found occasionally. Oligochaetes can perhaps regenerate after being broken. The cased Trichoptera larvae are probably protected by the case against abrasion from suspended sand. It is probably significant that the three most common cased Trichoptera larvae in the study area have relatively sturdy cases.

In this study some effort was made to determine what proportion of the drifting organisms were dead. Samples to determine the percentage of dead invertebrates in the drift were taken on June 27 and 29, near the peak of the runoff. The nets were left in only 10 minutes. The contents were carefully removed and taken to the lab immediately. There they were sorted by hand for 30 minutes only, even when more organisms remained. The information obtained gives a minimum estimate of the living proportion because the dead organisms were easier to pick from the sample, and some mortality due to handling of the samples was possible. The results are shown in Table 5.

Approximately 11% of the drifting invertebrates in these samples were dead. This sampling is too small to allow any conclusions about the vulnerability of any particular group to catastrophic death. However, it serves to illustrate that physical injury is a factor during the runoff.

Displacement From Suitable Habitat

Another problem for the benthic invertebrates during the runoff is displacement from suitable habitat. Two effects are possible, 1) dislodgement from the habitat, such as being swept off the substrate, and 2) removal of the habitat itself, such as the scouring away of patches of sand and silt by the current. These combined effects are the source of catastrophic drift.

Since all but a small percentage of drifting orgnisms are alive, as seen in Table 3, they are presumably capable of utilizing suitable habitat if they can find it. Organisms drifting out of the study area immediately are in a different habitat since the habitat immediately downstream is a low-gradient, meandering, silt, sand, and gravel habitat, with beaver dams present during many years. By drifting far enough, the organisms would eventually reach suitable habitat in the steeper gravel-

Table 5. Drifting organisms found alive and dead. Combined totals from three drift samples taken June 27 (1) and June 29 (2) at drift sampling station 2 (adult Diptera not included).

Organism	Number Alive	Number Dead
Rithrogena spp.	2	1
Cinygmula sp.	15	1
Epeorus longimanus	10	
Paraleptophlebia	4	1
Ephemerella doddsi	1	1
Ephemerella inermis	4	2
Baetis spp.	46	1
Nemoura spp.	7	
Alloperla spp.	3	
Arctopsyche larvae	1	
Rhyacophila spp. larvae	5	
mixed cased Trichoptera	5	
emerging Trichoptera adult	1	
Dytiscidae larvae	2	
Elmidae adults	3	
unidentified adult Coleoptera	1	
Tipulidae larvae	2	
Simuliidae larvae	8	2
mixed Chironomidae larvae	4	
mixed Chironomidae pupae	14	1
Heleidae pupae	1	
mixed Diptera larvae	6	
Acari	9	2
Oligochaeta	2	4 (includes 3 pieces)
Pisidium	1	1
Total	157	17

rubble-boulder habitat still further downstream. Lakes are other more serious hazards found within the watershed, but these are upstream in this particular case.

The removal of habitat by the current varies in its effect depending on the movability of the habitat. Attached macroscopic plants such as the alga Hydrurus foetidus and the moss Fontinalis sp. are lost completely once broken away from the substrate. Sand and silt become suspended and carried away especially during the rising phase of the daily meltwater surge, but are replaced by sand and silt from upstream. These materials are redeposited, but at different locations depending on the water level (Russell 1967). The gravel and smaller pieces of rubble which move by tumbling and sliding along the bottom move more slowly but it must be very hazardous for fragile organisms to occupy this habitat in these circumstances. The largest pieces of rubble move only at the highest discharges, and then probably slowly. So the problems which different benthic invertebrates face during the eroding phase of the runoff depend on what habitat they require.

Drift/Benthos Ratio

One approach to studying how organisms from different habitats are affected by catastrophic conditions is with drift rate/benthos density ratios. The ratio gives a relative measure of drift rates based on benthos population density. The procedure used was to divide the value of the mean daily drift rate for all available stations, in number per 1000 m^3, by the benthos density from the 1-4 June benthos samples in number per m^2. Ideally, the benthos population density and the drift would be measured at the same time, but this was not possible.

The time lag between the benthos estimate and the drift sampling makes the ratio impossible to interpret if there has been an unmeasured recruitment or loss of individuals from the population. Since recruitment of young or loss of adults was known to be occurring in most species populations, only a few species can be used here. The drift ratios for such selected species are shown in Figure 19.

The interpretation of the drift/biomass ratio data is speculative at this point; much more detailed information is needed to establish the reasons for the effects seen. With this disclaimer, a tentative interpretation of the drift/benthos data is offered.

The eight species selected have different habitat requirements and morphological adaptations. They can be put into three groups on the basis of those differences.

Rithrogena spp., *Ephemerella doddsi*, and *Ephemerella coloradensis* form one group. Small *Rithrogena brunnea* and *Rithrogena doddsi* could not be distinguished, so the data for these species are lumped. These four species are dorso-ventrally flattened. Except for *E. coloradensis* they have friction pads on the ventral side of the abdomen to increase resistance to the current. In the *Rithrogena* the gills form this structure. In *Ephemerella doddsi* the structure is a pad of fine bristles. The drift/benthos ratios of these mayflies are very low and nearly equal. Except for *E. coloradensis* they increase slightly with the discharge. These four all inhabit larger pieces of rubble. These larger pieces probably move relatively little during the high discharge. The strategy of clinging tightly to these rocks is very effective since it results in the lowest drift or displacement rates. Of these *E. coloradensis*,

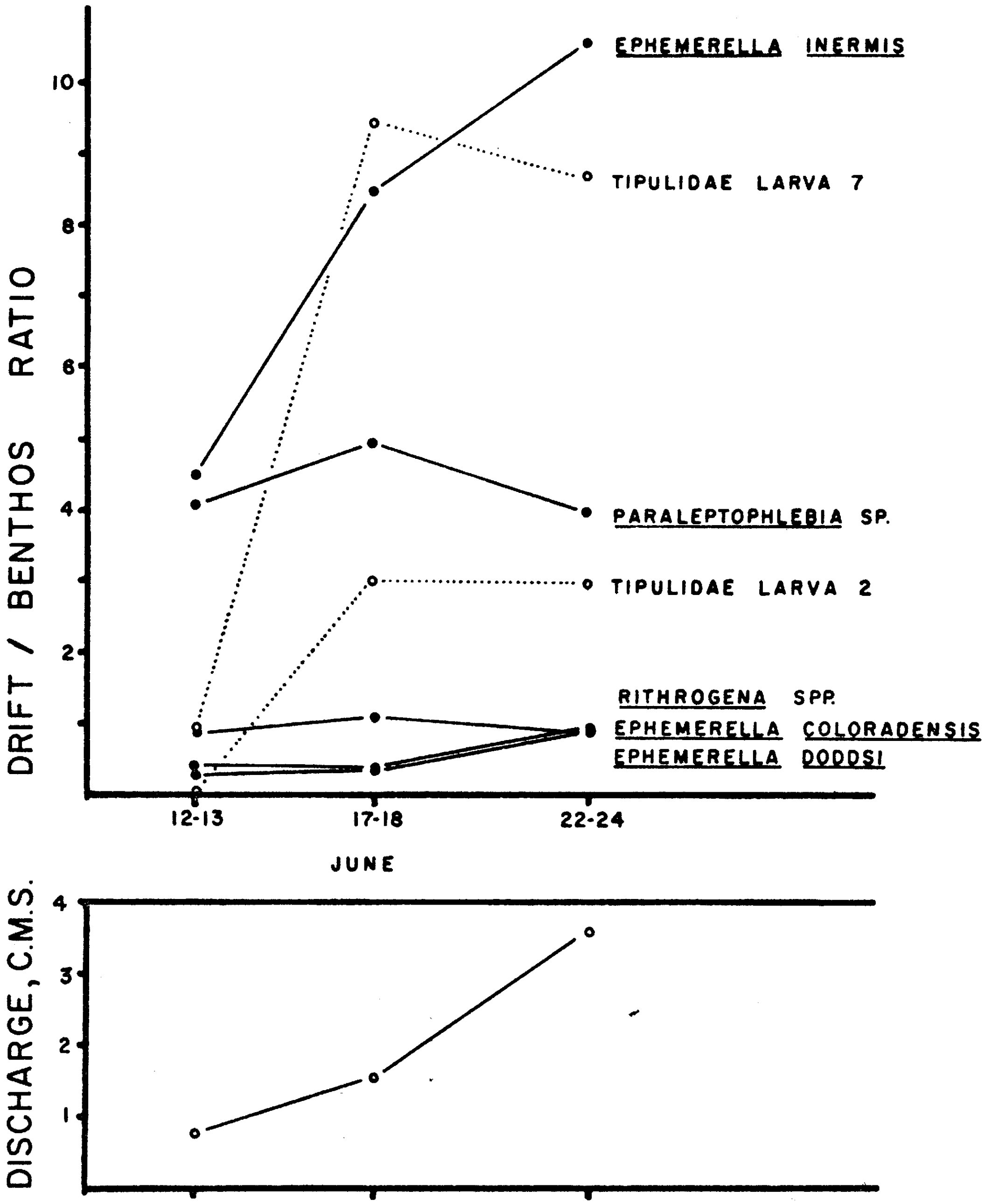

FIGURE 19. DRIFT / BENTHOS RATIOS FOR SELECTED SPECIES AND MEAN DAILY DISCHARGE FOR THREE DATES

which does not have a friction pad, has the highest drift/benthos ratio on the first two dates.

Tipulidae larvae 2 and 7 are burrowing forms, found where there are gravel and sand under larger rocks. They have no means to cling to rock surfaces and must rely on protection of overlying substratum. It is interesting that the drift/benthos ratios of these larvae show similar trends if different magnitudes. The trend is a very low ratio on the first date, and nearly equally high ratios on the last two dates, as if some plateau or equilibrium value were reached. Perhaps the habitat of underlying sand and gravel becomes vulnerable to scouring suddenly at the discharge level of the second sampling date. A reason for the ratio to not be much higher again, but only the same on the next sampling date when the discharge was higher, could be that displacement is related to the rate at which the habitat is being eroded. The latter is a function of the increase of the discharge over previous levels during the runoff as well as of the absolute discharge or velocity.

The remaining two species, Ephemerella inermis and Paraleptophlebia sp., form a third group. They are not particularly streamlined and probably inhabit protected areas in the stream. By comparison with the previous mayflies, their drift/benthos ratios are high. If the protected areas are becoming smaller or changing location with the rising discharge, these species would be forced to move, resulting in drift. Perhaps the drift/benthos ratios for Ephemerella inermis and Paraleptophlebia sp. here are some measure of the rate at which these "protected" locations are changing in location and size.

Predation on Drifting Organisms

A third problem for drifting organisms is the vulnerability to predation while drifting. Several fishes are common in the study area. The common native fish is the longnose sucker, *Catostomus catostomus* (Forster), which is abundant in the slower section below the study area and is present in the larger pools in the study area. The several trouts present in the study area are all introduced. In order of abundance these are: brook trout, *Salvelinus fontinalis* (Mitchill); brown trout, *Salmo Trutta fario* Linnaeus; rainbow trout, *Salmo gairdneri* Richardson, and occasional hybrids *Salmo gairdneri* X *Salmo clarki* (personal communication, Dr. George Baxter). No data on the predation of fishes on drifting invertebrates were taken in this study, but it is probable that all the fishes feed on drifting or displaced invertebrates to some extent.

The trouts are visual predators and prey best in the daylight. This probably contributes to the phenomenon of higher night drift rates both directly and in the evolution of the nocturnal behavioral drift.

Arctopsyche

Another likely predator of drifting invertebrates is *Arctopsyche* sp. The larvae capture their food in nets attached to the undersurface of large pieces of rubble. The effectiveness of this predator can be inferred from the remarkable pattern of growth. Length-frequency histograms for Arctopsyche are given in Figure 20. The life cycle lasts two years. Two year classes are present in the early benthos samples. By the time of the late benthos samples, the older larvae had matured and

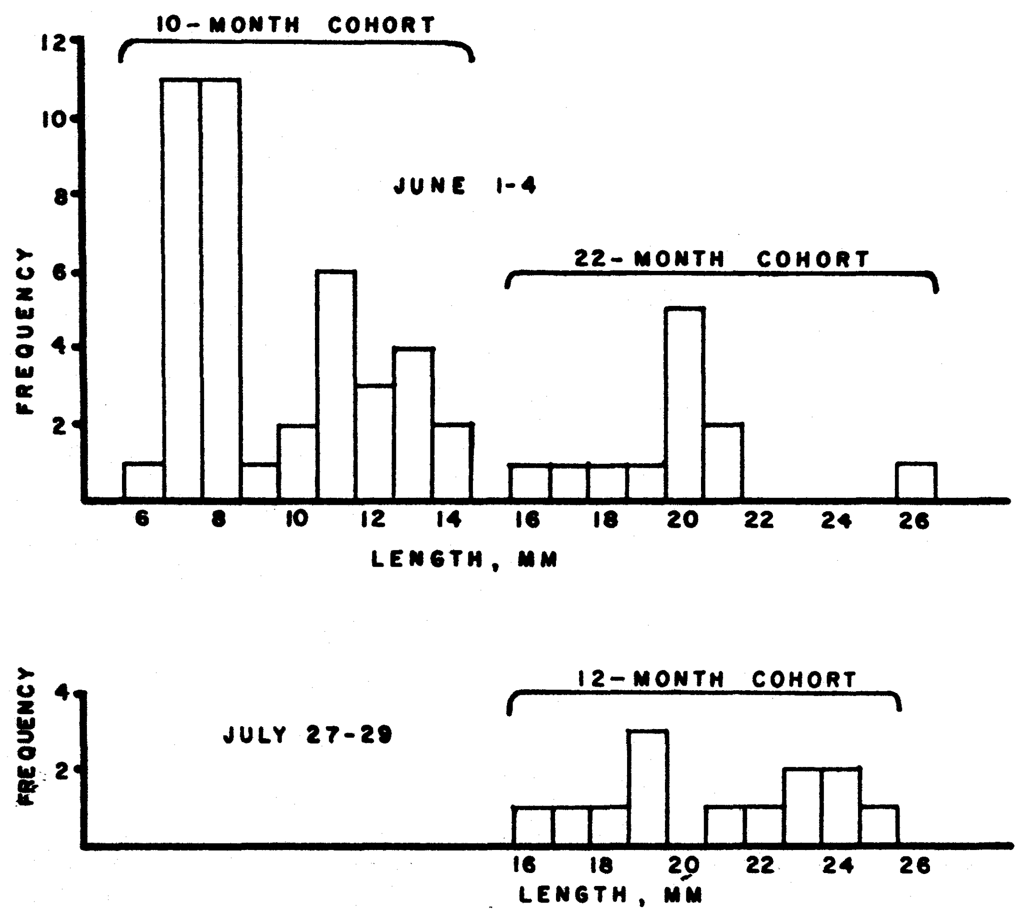

FIGURE 20. LENGTH-FREQUENCY HISTOGRAMS FOR ARCTOPSYCHE SP. LARVAE FROM THE EARLY AND LATE BENTHOS SAMPLING PERIODS

were not found. During the eight-week period the mean length of the younger year class grew from 10 1/2 mm to 20 1/2 mm. This represents a change in mean weight from 17.2 mg to 113.3 mg. The most remarkable fact is that this is essentially the same size as the older year class was eight weeks earlier in the early benthos samples. If this represents the usual pattern, then the larvae apparently do not grow for the next 10 months, until the next runoff.

The major part of the growth of this species is therefore taking place only during the runoff period. For a predator that feeds on drift to do well during the runoff is not a surprise. *Arctopsyche* is apparently a predator well-adapted to take advantage of the unique opportunities presented by the runoff.

SURVIVAL STRATEGIES DURING THE RUNOFF

Morphological Adaptation to Resistance of Current

Morphological adaptations are an obviously important part of adaptive strategy for coping with the runoff. The many structural adaptations employed to resist current are very well known and are really beyond the scope of this study. For an excellent discussion of these structures see Hynes (1970), Chapter VIII. Briefly, many devices are used by different species to reduce the force of the current, such as streamlining, spoiling devices and flattening, and to facilitate gripping of the surface, such as friction pads, suction discs, strong claws, and adhesive threads.

Adjustment of the Life Cycle

The relative predictability of the timing of the runoff period allows the possibility of adaptation by timing events in the life cycle to minimize catastrophic effects and to avoid exposing vulnerable stages. The most remarkable example of this is found in the Diptera. In the early benthos samples no Diptera pupae were found. In the late benthos samples many Diptera pupae in several families were present. Chironomidae larvae were found in 45 of the 52 early benthos samples, but no pupae. After the runoff Chironomid pupae were collected in 40 of 45 benthos samples. The same pattern holds for the other, less common, Diptera families.

The quiescent Diptera pupae would be vulnerable to the catastrophic effects of the rising phase of the runoff. Being attached to the substrate they would be subject to dislodgment or crushing when the bed materials move during the highest discharges. Also, because of the great increase in discharge and velocity, pupae adequately secured at the beginning of pupation might be inadequately secured later and be dislodged by the rising velocity. By waiting until after the runoff peak to pupate, individuals would have a reasonable assurance of not being dislodged by higher flows.

In the Trichoptera, another holometabolous order, pupae were present in both the early and late benthos samples. It would be of interest to know how the Trichoptera pupae have adapted to survive the rising phase of the runoff which the Diptera all seem to avoid.

In the other holometabolous order present, the Coleoptera, no pupae were found either before or after the runoff. The Elmidae pupate out of water under stones on the bank (Leech and Chandler 1968).

Many insect species breed during the runoff period. Both Gaufin (1959) and Logan (1963) attributed some decrease in benthos population densities during the runoff to emergence. The eggs are exposed to the effects of the runoff, although perhaps only to the later falling phase. Many stream insect eggs are known to be adhesive. The small eggs sticking to the rocks must be relatively safe during the runoff.

Since most insect species present were found to breed during the runoff, there must be some advantage to it. Table 6 summarizes some of the information on breeding during the runoff period and life cycle information of selected insect species. The expanded data are in

Table 6. Hynes' life cycle designation and summary of breeding period information for selected species of insects.

Order	Number of Species	Breed During the period	Life Cycle Designation
Ephemeroptera	4	yes	slow seasonal
	5	yes	fast seasonal
	3	no	fast seasonal
Plecoptera	5	yes	slow seasonal
	1	yes	fast seasonal
	1	no	fast seasonal
	1	?	non-seasonal
Trichoptera	2	yes	slow seasonal
	2	?	non-seasonal
Coleoptera	2	?	non-seasonal
Diptera	1	?	slow-seasonal
	1	yes	fast seasonal
	1	?	fast seasonal
	1	?	non-seasonal

Appendix F. The species used in the table meet the following criteria: 1) individuals were collected in both the early and late benthos samples, or at least 10 individuals were collected at some time in the benthos samples; 2) enough was known about the life cycle to assign it to one of Hynes' life cycle categories. The table shows that only four species out of 30 are definitely presumed not to breed during the period. Three of the four are the mayflies, Ephemerella coloradensis, Epeorus longimanus, and Cinygmula sp. These are all fast seasonal species, apparently breeding after August 1. Of the stoneflies listed, only Isogenus modestus, another fast seasonal species, is presumed not to breed during the period. The remaining species in the Trichoptera, Coleoptera, and Diptera, either do breed in this period or their breeding period is uncertain. To summarize, 18 species are known to breed, 4 are presumed not to breed, and for 8 species, the breeding periods are questionable. All those presumed not to breed in the period are fast seasonal species which undoubtedly breed in the late summer. Of the 12 slow seasonal species, 11 are known to breed during the period, and the remaining one is questionable. The breeding periods of all the non-seasonal species are not known.

The slow seasonal species, that is those which have immature stages present nearly all year but have a closely defined breeding period, may all be breeding during the runoff period. Several reasons why this strategy might be advantageous to the slow seasonal species are: 1) since the runoff period marks the beginning of the summer season when the water is open and warmer, individuals which hatch quickly find optimal growing conditions, 2) the potentially serious effects of downstream displacement of nearly mature individuals might be offset by the tendency of aerial adults to fly upstream (Roos, 1957), 3) in the life cycle, going from a vulnerable mature stage to a less vulnerable egg stage might be an advantage, 4) predators on breeding adults might be satiated by the availability of many species breeding during the same period.

Breeding during the rising phase of the runoff might have quite different consequences from breeding during the falling phase. Eggs laid during the rising phase would be subject to increasing discharges and eroding conditions while eggs laid during the falling phase would not. In many cases it is impossible to tell from the length-frequency data exactly in which phase the breeding is occurring and all that is known is that mature individuals were present in the drift during one period and were absent later. It would be useful to have more accurate information on the breeding periods.

Prolonged Hatching of Eggs

Hynes (1970) states that extended hatching of the eggs of stream insects is very common and suggests that this is insurance against loss of a generation, since newly-hatched individuals are more vulnerable to catastrophic conditions than are eggs. If, for whatever reasons, it is necessary for a species to have a hatching period which coincides with the runoff, that species needs some way for its newly hatched young to survive the catastrophic events associated with the highest discharges.

The peak of the runoff is predictable in its timing and severity only within broad limits. As shown in Table 7 the date of the peak

Table 7. Dates and amounts of instantaneous peak discharge for water years 1967-1972 at WRRI Station 106.00. (Data from Water Resources Series No. 28 and 32).

Year	Total Flow Acre-feet	Instantaneous Peak Discharge	Instantaneous Peak Date
1967	10052 a.f.	116 c.f.s.	June 21
1968	8829 a.f.	100 c.f.s.	June 20
1969	5942 a.f.	56 c.f.s.	May 27
1970	11043 a.f.*	204 c.f.s.	June 25
1971	15863 a.f.	247 c.f.s.	June 16
1972	11685 a.f.	225 c.f.s.	June 4

*January 1970 flows estimated

flow during the six years 1967-1972 varied from May 27 to June 25, and the instantaneous peak discharge varied from 56 c.f.s. to 245 c.f.s. Because of this uncertainty, what was good timing for hatching one year might be disastrous the next, and loss of a generation in the insects which breed only once in their life cycle could amount to extirpation. A possible strategy to fit these circumstances is redundancy of individuals provided by a hatching period extended long enough to avoid the worst conditions at some point.

The extent to which this redundancy strategy is used by species in the study area can be judged by the information in Table 8 (see Appendix G for the expanded data). Here the presence of individuals 1 or 2 mm in length is taken to indicate recent hatching. The information is taken from both benthos samples and drift samples. The species used are only insects for which young of that size could be recognized and of which at least ten individuals of any size were collected in the study area. The table presents data on the presence or absence of small young during the rising phase (June 1-24 samples) and the falling phase (July 6-29) samples.

The results show that indeed most species either avoid hatching during the runoff, or have an extended hatching period, that is they hatch during both the rising and falling stages. The five species which were found hatching only during the rising phase were not abundant, and their hatching later may have been missed by chance. It is very unlikely that the peak of the runoff would occur after July 6, from the streamflow data so far accumulated, so hatching during the July 6-29 period should be much safer.

Table 8. Presence of newly hatched individuals (1 or 2 mm.) in either drift samples or benthos samples during the rising (June 1-24) and falling (July 6-29) phases of the runoff. (For expanded data see Appendix F).

	Number of Species			
Group	rising	falling	both	neither
Ephemeroptera	1	4	8	1
Plecoptera	0	0	6	4
Trichoptera	2	0	4	5
Coleoptera	0	1	1	0
Diptera	2	1	3	6
Total	5	6	22	16

Redundancy and Community Structure

The term redundancy is used here to describe a strategy for survival for a species in which there is duplication of individuals in time or space. The individuals are vulnerable to severe conditions, but some duplicates survive by chance avoidance of the severe conditions either in time or in space. In the previous discussion of prolonged hatching of eggs, redundancy in time was apparent in the strategy of hatching over a long period, allowing some individuals to avoid hatching during the most severe period of the runoff. Examples of redundancy in space (the dispersal of individuals throughout the habitat to reduce the chance of extirpation) probably cannot be separated from the dispersion and spacing of individuals throughout habitats for other reasons, such as to facilitate food procurement.

Redundancy in another sense may be involved in a phenomenon that is not so much a strategy for individual species, but has an effect on community structure. Redundancy in this instance may help to explain the co-existence of a number of closely related species in time and space. In this benthic invertebrate community there are several examples of the co-existence of species which are closely related and have similar morphology and life cycles. The genus *Baetis* was represented by five very similar species. Among the stoneflies, there were four *Alloperla*, two of which are very similar, *A. borealis* and *A. lamba*. In the *Nemoura* there were five species, again two of which are very similar, *N. oregonensis* and *N. cinctipes*. There were two *Paraleuctra*, again very similar. In the Trichoptera, the genus *Rhyacophila* had five to eight species in the study area, several of which are similar in many ways.

It can be hypothesized that these are species which co-exist because of the uncertainty of the timing and severity of catastrophic events in the runoff period. They co-exist by having slightly different strategies for survival during the runoff period, such as in their timing of hatching or emergence.

The variation in the magnitude and timing of the peak discharge and the runoff period as a whole must be important factors in the survival of each species in the stream. Strategies for dealing with these factors will vary in their effectiveness from year to year. For this reason, species with slightly different strategies of hatching, emergence, etc., will vary in their survival from year to year. When one species suffers unusual mortality during the runoff, the scarcity of that species leaves an opportunity for a second species with otherwise similar life style to prosper. If the runoff conditions the next year were sufficiently different, perhaps the situation would be reversed, and the first species would be favored over the second. By this means, species might co-exist which under more stable conditions would not because of competitive exclusion.

A test of this hypothesis would involve very accurate determination of the hatching, emergence, and other strategically important features of the life cycles of these species, a monitoring of the variation in survival of the similar species in years with different runoff conditions and observation of relative survival of the congeners under stabilized streamflow.

This hypothesis cannot be supported by only one year of data and is only offered as one possible explanation of observations made in this study.

However, it is useful to end this discussion by asking if these similar species do represent species which are allowed to co-exist because of the uncertainty of the timing and severity of the spring snowmelt runoff.

SUMMARY

This study was an investigation of the abiotic and biotic factors acting on a community of benthic invertebrates in a high mountain stream during the spring snowmelt runoff period. All data used were collected in 1970. The study area was a 1 km section of Nash Fork Creek near 3,000 m, in the Snowy Range, Wyoming.

The runoff began in mid-May when the discharge was 6 c.f.s. (.17 c.m.s.), rose erratically to a peak on June 25, at 125 c.f.s. (3.54 c.m.s.), then dropped through the rest of the summer. Water temperatures increased through the runoff from 0°C. in mid-May to 4.5 - 11.5°C. on June 25 and to 7 - 16°C. by July 21. The general snow cover over the stream present in mid-May was gone by June 4.

Standing population estimates were made by taking benthos samples early (June 1-4) and late (July 27-29) in the runoff. The median values for the total standing crop biomass were 3,600 mg per m^2 for June 1-4 and 5,980 mg per m^2 for July 27-29. These values were not different at the .05 level, using the Mann-Whitney u-statistic.

Drift samples were taken between the benthos sampling periods. All drifting invertebrates together were studied on only three sampling dates, June 12-13, 17-18, 22-24. Drift rates for this group increased with the increase in discharge on these dates. The same trend was found for the drift of oligochaetes and tipulid larvae when considered separately.

Many fragments of oligochaetes occurred in the drift. In the day-

time drift the percentage of drifting oligochaete biomass occurring as fragments was correlated with discharge ($r = .9717$).

The species which could be sorted with a live-sorting apparatus were considered as a group. The drift rates of this group were studied during both June and July. The drift rates increased with discharge through June 12-13 and 17-18 until the peak on June 22-24. They then decreased to lower levels on July 6-7 and 13-14, and finally increased, only at night, on July 21-22.

A net downstream loss of drifting invertebrates from the study area could not be confirmed.

A "Nocturnal Drift Index," which

$$= \frac{\text{Night Drift Rate} - \text{Day Drift Rate}}{\text{Night Drift Rate} + \text{Day Drift Rate}},$$

was found to vary with the combined effects of water temperature (positive correlation) and discharge (negative correlation). For the multiple regression of the index on water temperature and discharge, the coefficient of determination was .86. This was interpreted as showing an increase in behavioral drift with increasing temperature, but an inhibition of behavioral drift with high discharge.

Samples taken to determine the percentage of drifting dead invertebrates contained 11 percent dead invertebrates.

Ratios of drift rate/benthos density were measured for a few species. The species most highly modified to resist current had the lowest drift/benthos ratios.

Predation on drifting invertebrates by fish was assumed to be a source of mortality. Also, the rapid growth of the net-spinning

Arctopsyche sp. larvae was taken to indicate that it was a very effective predator on drift during the runoff.

Adjustment of the life cycle was found to be a common means of adaptation to the runoff and was manifested in several ways:

1. The Diptera avoided exposing pupae to the runoff, as shown by the absence of pupae in the early benthos samples, although many were present in the late benthos samples.
2. Many insect species were found to breed during the runoff. Of 30 selected species, 18 did breed, 4 (all fast seasonal species) were presumed not to breed, and the breeding period of 8 was not known.
3. Prolonged hatching of eggs and avoidance of hatching were recognized as runoff-survival strategies. When the presence of 1-2 mm individuals was taken to indicate recent hatching, 5 species were hatching only in the rising (June 1-24) phase, 6 only in the falling (July 6-29) phase, 21 species in both phases, and young of 16 species were not found in either phase.

The coexistence of very similar congeneric species in the genera *Baetis*, *Alloperla*, *Nemoura*, *Paraleuctra*, and *Rhyacophila* was hypothesized as possible because the congeners may have different runoff-survival strategies which vary in effectiveness due to the large yearly differences in the timing and severity of the runoff.

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APPENDIX A

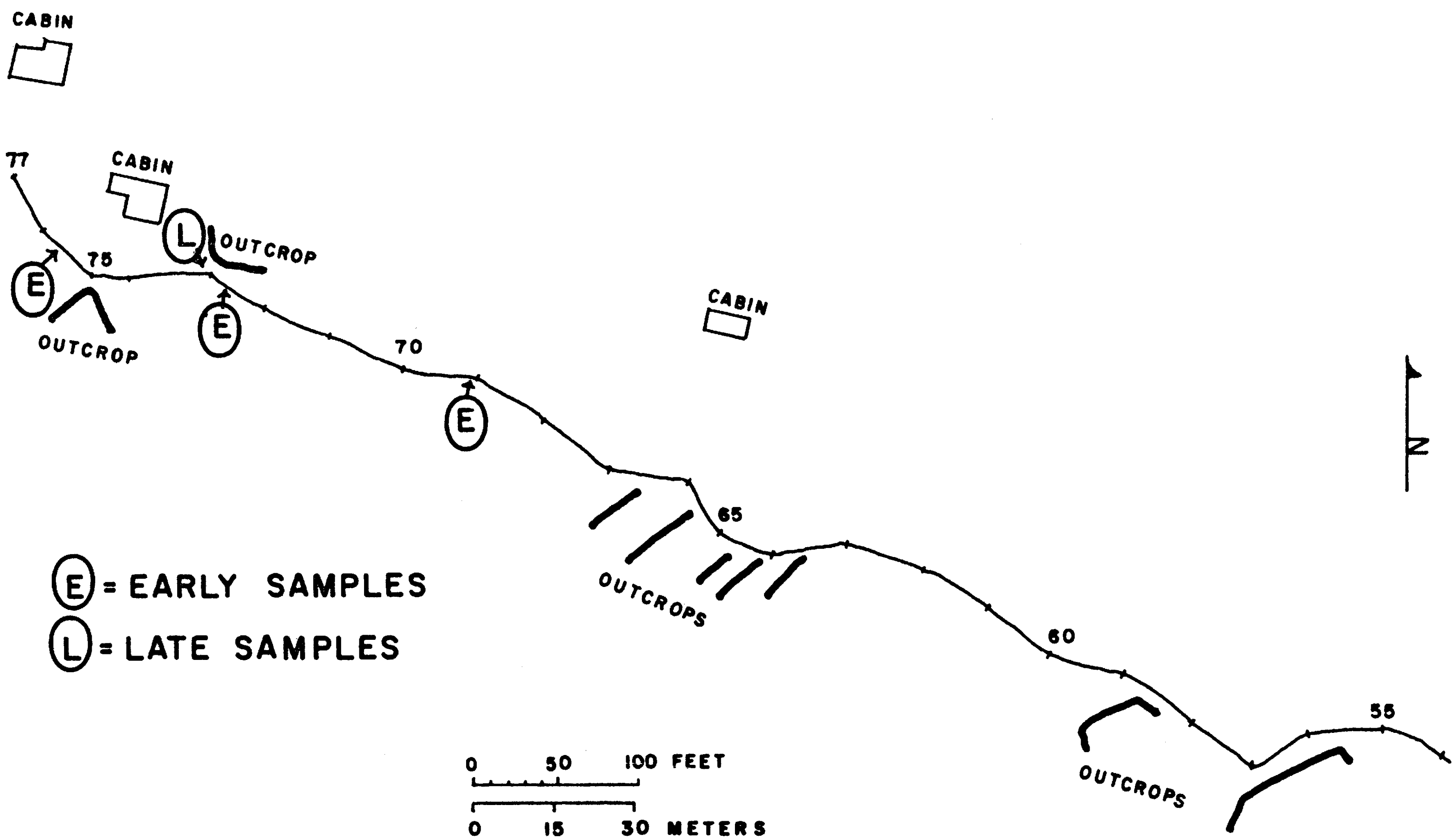
1970 Benthos Sampling Plan

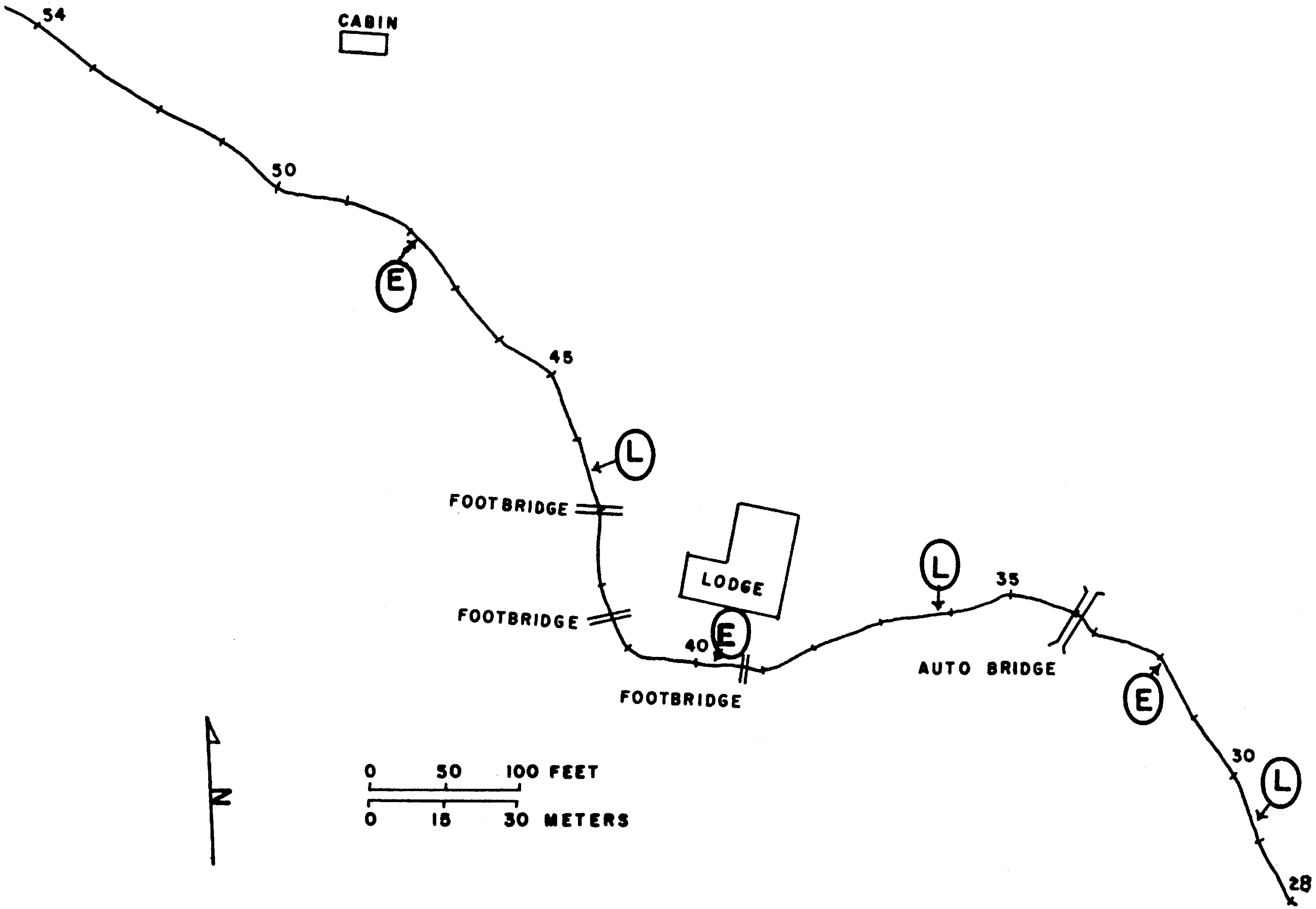
Early Benthos Samples

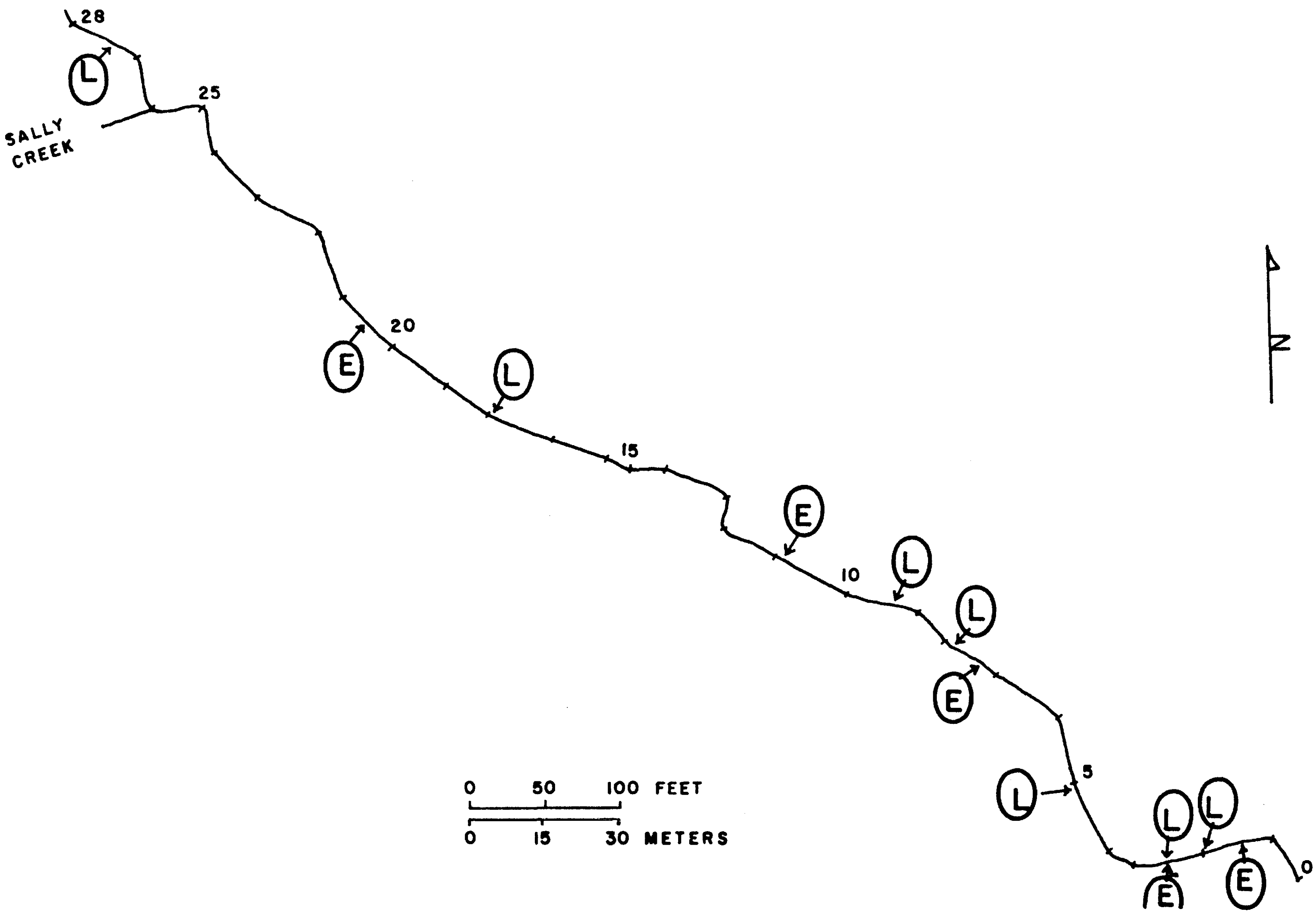
Date	Number of Samples	Study Area Section	Location on Map
1 June	2	1	2-3
2 June	6	1	1-2
2 June	4	2	7-8
2 June	5	2	10-11
4 June	6	2	72-73
2 June	5	3	20-21
3 June	7	3	39-40
3 June	5	3	47-48
3 June	4	4	31-32
3 June	5	4	69-70
4 June	3	5	75-76

Late Benthos Samples

Date	Number of Samples	Study Area Section	Location on Map
27 July	7	1	2-3
27 July	5	1	1-2
27 July	5	2	4-5
29 July	5	2	7-8
29 July	4	2	9-10
29 July	4	3	17-18
29 July	4	3	36-37
29 July	4	3	43-44
29 July	2	4	27-28
29 July	3	4	29-30
29 July	2	5	73-74


CABIN
CABIN
CABIN
77
75
70
65
60
55
L
OUTCROP
E
OUTCROP
E
E
OUTCROPS
OUTCROPS
N
E = EARLY SAMPLES
L = LATE SAMPLES
0 50 100 FEET
0 15 30 METERS


54
CABIN
50
E
45
L
FOOTBRIDGE
LODGE
L
35
FOOTBRIDGE
E
40
FOOTBRIDGE
AUTO BRIDGE
E
30
L
28
N
0 50 100 FEET
0 15 30 METERS


28
25
SALLY CREEK
20
15
10
5
0
L
E
N
0 50 100 FEET
0 15 30 METERS

APPENDIX B

Values of "b" used to back-calculate

the live weight of organisms

"b" values determined from live specimens killed in 10% formalin

Organism	"b"
Ephemerella doddsi	0.0405971
Ephemerella inermis	0.0245591
Paraleptophlebia sp.	0.0140818
Ameletus sp.	0.0165321
Rithrogena spp.	0.0261879
Baetis spp.	0.0190750
Belphariceridae larvae	0.474618
Diptera larva 7	0.0081674
Tipulidae larva 2	0.0233895
Chironomidae larva 12	0.0087972
Diptera larva 3	0.0072478
Nemoura oregonensis	0.0212403
Nemoura cinctipes	0.0205977
Arcynopteryx signata	0.0156683
Alloperla lamba	0.0091050
Alloperla borealis	0.0111782
Limnephilidae larva 1	0.0550450
Rhyacophila larva 1	0.0126701
Arctopsyche larvae	0.0131597
Lepidostomatidae larva 1	0.0381149

APPENDIX B (cont.)

Heterlimnius larvae	0.0133652
Planaria	0.0160365

"b" values determined from preserved specimens with estimated weight loss added

Organism	"b"
Ephemerella coloradensis	0.0254658
Epeorus longimanus	0.0264418
Cynigmula sp.	0.0182725
Alloperla lineosa	0.0089867
Isoperla fulva	0.0173310
Eucapnopsis brevicauda	0.0090104
Paraleuctra sara	0.0059898
Nemoura group 1	0.0193124
Rhyacophila larva 2	0.0085904
mixed Trichoptera pupae	0.0326433
Lepidostomatidae larva 2	0.0226216
mixed Simuliidae pupae	0.0551977
Simuliidae larva 2	0.0209497
Tipulidae larva 7	0.0076482
mixed Chironomidae pupae	0.0246947
Bezzia sp.	0.0022863
Cleptelmis larvae	0.0079578
Pisidium	0.226177

APPENDIX B (cont.)

Arbitrarily Assigned "b" Values

Alloperla autumna	0.0089867
mixed unidentified *Alloperla*	0.0091050
Isogenus modestus	0.0156683
Isoperla ebria	0.0156683
Paraleuctra occidentalis	0.0052122
Centroptilum sp.	0.0191750
mixed Ephemeroptera adults	0.0191750
Rhyacophila spp. 3, 4, 5, 6 7, 8, 9 10	0.0126701
Limnephilidae larvae 2-12	0.0226216
unidentified Trichoptera larvae	0.0226216
Glossosoma larvae	0.0226216
Agapetus sp. larvae	0.0226216
Lepidostomatidae larvae 3-4	0.0226216
Chironomidae larvae	0.0087972
Tipulidae larvae 1, 5, 9, 10, 13, 14	0.0076482
Tipulidae larvae 3, 4, 8, 11, 12	0.0233895
Chironomidae adults	0.0246947
Empididae pupae	0.0246947
unidentified Diptera pupae	0.0246947
unidentified pupae	0.0246947
Simuliidae adults	0.0551977
unidentified Diptera larvae 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	0.0072478
Diptera larva 9	0.0072478
Nematomorpha	0.0007621

APPENDIX B (cont.)

Siphlonurus sp.	0.0165321
unidentified *Ephemerella* sp.	0.0245591
ant	0.0246947
Homoptera adults	0.0246947
unidentified Dytiscidae larvae	0.0131869
unidentified Hemiptera nymphs	0.0246947
unidentified Humenoptera adults	0.0246946
Collembolla	0.0246947
Nemoura species 4	0.0205977
Brachyptera sp.	0.0193124
unidentified Plecoptera	0.0193124
small Oligochaeta	0.0022863
Belphariceridae pupae	0.0474618
Dytiscidae larva 1	0.0131869
Staphilinidae adult	0.0723054
Physa sp.	0.2226177
unidentified Coleoptera larvae 4, 5, 9	0.0133652
Planorbidae	0.2226177
Lireopeidae larvae	0.0087972
Coleoptera larva 4	0.0131869
Syrphidae larvae	0.0072478
Dixa sp.	0.0087972
Amphizoa larva	0.0723054
Spider	0.0246947
Dolichopodidae larva 1	0.0072478
Millipede	0.0156683
Chaoborinae larva	0.0087972
Culicidae larva	0.0087972
Coleoptera larva 6	0.0133652
aphid	0.0246947
Tipulidae adult	0.0076482

APPENDIX B (cont.)

Miscellaneous Formulas

Eiseniella	=	$(\pi)(r^2)$(length, mm)(1.502)
Acari	=	0.303 mg
Elmidae adult 2	=	0.75 mg
Dytiscidae adult 1	=	0.7 mg
fish larvae "b"	=	0.00696676
fish eggs	=	$4/3\ \pi r^3$

APPENDIX C - Early

Mean number and weight per meter^2 estimates in each study section for the early (June 1-4) benthos sampling period. Upper figure is number; lower figure is weight.

Species	study area sections 1	2	3	4	5	all section weighted mean
Rithrogena spp.	33.8	56.7	57.1	92.2	3.3	63.49
	271.2 mg	420.4 mg	375.9 mg	589.8 mg	29.9 mg	422.97 mg
Cinygmula sp.	123.8	158.0	200.0	251.1	0	196.85
	51.8 mg	65.3 mg	98.6 mg	93.1 mg	0	86.47 mg
Epeorus longimanus	6.3	16.7	5.9	23.3	0	12.00
	1.5 mg	4.5 mg	1.2 mg	6.5 mg	0	3,10 mg
Ameletus spp.	32.5	0.7	4.7	2.2	0	4.54
	284.9 mg	2.4 mg	29.0 mg	18.8 mg	0	32.96 mg
Paraleptophlebia sp.	6.3	0.7	43.5	33.3	0	31.15
	13.6 mg	0.6 mg	44.4 mg	47.9 mg	0	35.75 mg
Ephemerella doddsi	140.0	44.0	39.4	41.1	3.3	43.83
	1429.1 mg	493.8 mg	460.9 mg	393.0 mg	46.4 mg	458.93 mg
Ephemerella coloradensis	10.0	6.0	4.1	4.4	0	4.60
	2.6 mg	1.5 mg	0.8 mg	2.0 mg	0	1.30 mg
Ephemerella inermis	60.0	5.3	11.2	8.9	0	11.76
	198.4 mg	22.4 mg	34.2 mg	40.5 mg	20.5 mg	41.18 mg
Baetis species A	10.0	5.3	1.2	6.7	0	3.62
	23.1 mg	10.4 mg	2.8 mg	4.2 mg	0	5.13 mg

APPENDIX C (cont.) - Early Benthos Samples

Species	1	2	3	4	5	all section weighted mean
		study area sections				
Baetis species C	0	0.7	0	2.2	3.3	0.82
	0	0.4 mg	0	5.3 mg	4.1 mg	1.64 mg
Baetis species D	0	1.3	2.4	3.3	0	2.27
	0	1.2 mg	1.8 mg	2.5 mg	0	1.76 mg
Baetis species E	0	0	0	0	0	0
	0	0	0	0	0	0
Centroptilum sp.	0	0.7	16.5	3.3	0	9.23
	0	0.3 mg	2.2 mg	1.3 mg	0	2.43 mg
Nemoura cinctipes	0	2.7	37.1	30.0	0	27.03
	0	6.5 mg	33.1 mg	64.1 mg	0	34.84 mg
Nemoura oregonensis	0	5.3	31.2	27.8	0	23.88
	0	5.7 mg	76.7 mg	43.0 mg	0	50.78 mg
Nemoura group 1	8.3	4.0	14.1	16.7	0	12.73
	4.2 mg	0.9 mg	4.5 mg	5.4 mg	0	4.02 mg
Nemoura species 2	0	0	1.2	1.1	0	0.89
	0	0	1.1 mg	1.5 mg	0	0.95 mg
Paraleuctra spp.	2.5	6.0	7.1	10.0	0	7.23
	3.2 mg	5.9 mg	13.2 mg	11.0 mg	0	10.59 mg
Eucapnopsis brevicauda	11.3	29.3	50.6	20.0	0	35.52
	12.0 mg	31.4 mg	51.3 mg	19.0 mg	0	35.94 mg

APPENDIX C (cont.) - Early Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Branchyptera sp.	0	2.7	0.6	10.0	0	3.40
	0	11.1 mg	4.2 mg	38.8 mg	0	16.94 mg
Arcynopteryx signata	0	2.7	2.4	0	0	1.57
	0	382.2 mg	378.7 mg	0	0	245.55 mg
Isogenus modestus	1.3	0.7	1.8	1.1	0	1.34
	2.5 mg	0.7 mg	3.7 mg	0.6 mg	0	3.60 mg
Isoperla fulva	10.0	3.3	5.9	10.0	3.3	6.72
	114.5 mg	22.0 mg	31.5 mg	65.5 mg	12.5 mg	42.39 mg
Alloperla borealis	12.5	20.7	60.0	14.4	0	37.49
	97.0 mg	75.5 mg	264.2 mg	65.3 mg	0	165.20 mg
Alloperla lamba	16.3	10.7	20.0	14.4	3.3	16.34
	80.1 mg	38.9 mg	97.9 mg	52.0 mg	15.5 mg	72.96 mg
Alloperla lineosa	0	0	0	0	0	0
	0	0	0	0	0	0
Alloperla autumna	0	0.7	1.2	0	0	0.69
	0	1.3 mg	3.0 mg	0	0	1.67 mg
mixed small Alloperla	17.5	43.3	55.9	100.0	0	62.18
	16.0 mg	32.7 mg	54.1 mg	62.5 mg	0	49.51 mg
Acroneuria pacifica	0	11.3	12.9	33.3	0	17.16
	0	67.9 mg	8.48 mg	636.7 mg	0	224.83 mg

APPENDIX C (cont.) - Early Benthos Sample

Species	study area sections 1	2	3	4	5	all section weighted mean
Rhyacophila larva 1	1.3	18.7	41.8	30.0	3.3	31.91
	8.1 mg	160.9 mg	388.6 mg	195.2 mg	14.5 mg	271.61 mg
Rhyacophila larva 2	15.0	46.7	68.8	78.9	0	63.30
	26.3 mg	54.4 mg	74.3 mg	65.2 mg	0	63.98 mg
Rhyacophila larva 3	0	0.7	2.0	10.0	0	3.69
	0	1.8 mg	1.3 mg	11.5 mg	0	4.05 mg
Rhyacophila larva 4	0	0	0	0	0	0
	0	0	0	0	0	0
Rhyacophila larva 5	0	0.7	2.4	6.7	0	3.08
	0	0.1 mg	0.5 mg	2.3 mg	0	0.88 mg
Rhyacophila larva 7	0	1.3	1.2	4.4	0	1.80
	0	9.5 mg	13.4 mg	23.9 mg	0	14.54 mg
Rhyacophila larva 8	0	0	0	0	0	0
	0	0	0	0	0	0
Rhyacophila larva 9	0	0	0	0	0	0
	0	0	0	0	0	0
Rhyacophila larva 10	2.5	0	9.4	4.4	0	5.96
	1.3 mg	0	1.5 mg	0.7 mg	0	2.16 mg
Glossosoma sp.	0	1.3	0	1.1	0	0.50
	0	5.1 mg	0	3.1 mg	0	1.91 mg

APPENDIX C (cont.) - Early Benthos Samples

Species	study area section 1	2	3	4	5	all section weighted mean
Anagapetus	0	0	0	0	0	0
	0	0	0	0	0	0
Psychomyiidae larvae	0	0	0	0	0	0
	0	0	0	0	0	0
Arctopsyche sp.	6.3	13.3	7.6	22.2	0	12.09
	28.9 mg	333.1 mg	99.4 mg	1001.8 mg	0	371.46 mg
Limnephilidae species 1	266.3	4.7	10.6	5.6	0	19.66
	1269.6 mg	32.1 mg	46.5 mg	23.3 mg	0	92.36 mg
Platycentropus sp.	0	0	1.2	0	0	0.58
	0	0	13.6 mg	0	0	6.80 mg
Ecclisomyia sp.	18.7	0	0.6	0	0	0.91
	382.0 mg	0	9.7 mg	0	0	18.41 mg
Lepidostomatidae species 1	5.0	6.0	24.7	16.7	6.7	18.21
	12.2 mg	19.9 mg	87.9 mg	54.2 mg	4.4 mg	62.62 mg
Lepidostomatidae species 2	2.5	2.7	4.7	3.3	0	3.76
	19.4 mg	17.4 mg	30.2 mg	30.1 mg	0	26.71 mg
mixed Trichoptera pupae	0	1.3	3.5	8.7	0	4.08
	0	48.9 mg	98.7 mg	189.4 mg	0	102.65 mg
Bidessus sp. (Dytiscidae) adult	0	0	0	1.1	0	0.30
	0	0	0	0.8	0	0.22 mg

APPENDIX C (cont.) - Early Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Heterlimnius sp. adults	0	0.7	0	0	0	0.10
	0	1.3	0	0	0	0.19 mg
Heterlimnius sp. larvae	176.3	11.3	8.2	4.4	3.3	10.60
	229.0 mg	27.3 mg	36.1 mg	10.1 mg	5.6 mg	35.47 mg
Cleptelmis sp. adults	0	0	4.7	2.5	0	2.95
	0	0	4.3 mg	1.9 mg	0	2.21 mg
Cleptelmis sp. larva	61.3	6.0	220.6	54.4	0	128.60
	37.4 mg	3.6 mg	101.2 mg	25.2 mg	0	59.60 mg
Tipulidae larva 2	20.0	1.3	1.8	2.2	0	2.59
	4668.2 mg	508.3 mg	507.8 mg	233.9 mg	0	605.46 mg
Tipulidae larva 7	2.5	2.7	3.5	2.2	0	2.87
	14.8 mg	13.1 mg	25.8 mg	6.7 mg	0	17.32 mg
Tipulidae larva 8	0	0	0	1.1	0	0.30
	0	0	0	5.6 mg	0	1.52 mg
Blephariceridae larvae	0	4.7	1.2	1.1	0	1.58
	0	162.3 mg	55.8 mg	70.2 mg	0	70.82 mg
Simuliidae larva 2	0	6.0	18.2	74.4	10.0	30.53
	0	7.5 mg	32.5 mg	153.7 mg	38.9 mg	60.40 mg
Chironomidae larva 2a	5.0	1.3	0	0	0	0.43
	1.2 mg	0.2 mg	0	0	0	0.08 mg

APPENDIX C (cont.) - Early Benthos Samples

Species	study area section 1	2	3	4	5	all section weighted mean
Chironomidae larva 2b	0	1.3	283.5	2.2	0	142.39
	0	0.01 mg	40.1 mg	0.2 mg	0	20.08 mg
Chironomidae larva 12	0	0	0	0	0	0
	0	0	0	0	0	0
Chironomidae larva 13	72.5	53.3	357.1	162.2	6.7	233.68
	96.1 mg	39.3 mg	75.9 mg	70.6 mg	7.3 mg	67.48 mg
mixed unidentified	1102.5	30.0	132.9	146.6	0	160.98
Chironomidae larvae	10643.0 mg	21.4 mg	69.4 mg	126.1 mg	0	558.99 mg
mixed unidentified	0	0	0	0	0	0
Chironomidae pupae	0	0	0	0	0	0
Bezzia sp. larvae	78.0	16.7	28.2	14.5	0	24.19
	81.0 mg	14.9 mg	24.3 mg	11.9 mg	0	21.38 mg
Diptera larva 2	0	0	0	2.2	0	0.60
	0	0	0	12.2 mg	0	3.30 mg
Diptera larva 3	65.0	18.7	26.5	27.8	0	26.67
	1498.0 mg	61.3 mg	88.4 mg	70.2 mg	0	141.86 mg
Diptera larva 4	3.8	3.3	1.8	4.4	0	2.75
	5.9 mg	4.5 mg	2.4 mg	6.2 mg	0	3.81 mg
Diptera larva 5	0	0	0.6	0	0	0.29
	0	0	0.5 mg	0	0	0.27 mg

APPENDIX C (cont.) - Early Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Diptera larva 6	102.5 820.9 mg	2.7 5.7 mg	12.4 12.6 mg	6.7 5.6 mg	0 0	13.06 27.01 mg
Acari	1.3 0.4 mg	0 0	3.0 0.8 mg	0 0	0 0	1.52 0.46 mg
Pisidium sp.	109.0 389.0 mg	15.3 28.0 mg	1.2 1.2 mg	3.3 5.9 mg	0 0	8.88 24.16 mg
Polycelis coronata	1.3 39.6 mg	6.7 13.3 mg	0 0	3.3 5.3 mg	0 0	9.18 3.22 mg
Eiseniella sp.	5.0 135.1 mg	5.3 243.2 mg	7.6 1107.0 mg	8.9 998.3 mg	3.3 2.5 mg	7.36 965.39 mg
Sparganophilus sp.	5.0 111.6 mg	10.7 40.0 mg	16.5 1256.5 mg	21.1 167.0 mg	10.0 36.0 mg	10.96 679.52 mg
unidentified small Oligochaetes	7.5 5.6 mg	2.0 0.5 mg	20.0 5.3 mg	15.6 2.1 mg	0 0	14.84 3.56 mg
Baetis species B	16.3 7.0 mg	19.3 7.5 mg	50.0 18.4 mg	72.2 23.3 mg	10.0 3.3 mg	48.37 17.04 mg

APPENDIX C - Late Benthos Samples

Mean number and weight per meter^2 estimates in each study section for the late (July 27-29) benthos sampling period. Upper figure is number; lower figure is weight.

Species	study area sections 1	2	3	4	5	all section weighted mean
Rithrogena spp.	46.7	90.7	60.0	4.0	0	46.55
	395.2 mg	392.9 mg	463.0 mg	28.2 mg	0	314.87 mg
Cinygmula sp.	215.0	155.0	65.8	64.0	0	82.89
	1022.7 mg	613.3 mg	237.8 mg	238.5 mg	0	320.52 mg
Epeorus longimanus	51.7	102.9	118.3	36.0	10.0	86.71
	69.9 mg	223.5 mg	573.3 mg	353.5 mg	84.2 mg	421.31 mg
Ameletus spp.	5.8	11.4	0	20.0	0	7.37
	21.1 mg	35.2 mg	0	65.3 mg	0	23.85 mg
Paraleptophlebia sp.	17.5	5.7	5.0	18.0	0	9.02
	6.9 mg	6.7 mg	2.5 mg	8.4 mg	0	4.84 mg
Ephemerella doddsi	4.2	12.1	27.5	2.0	5.0	16.44
	250.0 mg	355.1 mg	690.8 mg	0.1 mg	1.6 mg	405.02 mg
Ephemerella coloradensis	5.0	10.7	2.5	0	0	3.06
	49.2 mg	96.8 mg	43.0 mg	0	0	37.96 mg
Ephemerella inermis	10.8	3.6	1.7	2.0	0	2.40
	120.7 mg	60.1 mg	17.5 mg	25.1 mg	0	29.93 mg
Baetis species A	315.8	133.6	74.2	120.0	40.0	105.1
	359.8 mg	120.4 mg	117.9 mg	164.1 mg	97.7 mg	253.4 mg

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weight mean
Baetis species B	8.3	14.3	21.7	38.0	10.0	70.44
	6.7 mg	10.3 mg	8.8 mg	8.0 mg	0.9 mg	8.50 mg
Baetis species C	282.5	302.9	103.3	240.0	40.0	175.63
	224.1 mg	233.9 mg	74.5 mg	231.0 mg	112.0 mg	148.62 mg
Baetis species D	257.5	471.4	452.5	322.0	685.0	422.23
	338.5 mg	590.0 mg	505.8 mg	383.2 mg	554.6 mg	479.15 mg
Baetis species E	0	2.1	0	0	0	0.35
	0	5.1 mg	0	0	0	0.75 mg
Centroptilum sp.	139.2	86.4	16.7	74.0	0	47.47
	214.9 mg	139.2 mg	23.9 mg	109.1 mg	0	71.85 mg
Nemoura cinctipes	0	4.3	1.7	0	0	1.46
	0	1.3 mg	0.3 mg	0	0	0.33 mg
Nemoura oregonensis	4.2	8.6	12.5	0	0	7.70
	2.4 mg	4.3 mg	7.8 mg	0	0	4.64 mg
Nemoura group 1	0	0	0	0	0	0
	0	0	0	0	0	0
Paraleuctra spp.	0	5.0	2.5	2.0	0	2.53
	0	5.2 mg	1.4 mg	0.3 mg	0	1.53 mg
Eucapnopsis brevicauda	0	0	0	0	0	0
	0	0	0	0	0	0

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weight mean
Brachyptera sp.	0	0	0	0	0	0
	0	0	0	0	0	0
Arcynopteryx signata	10.0	9.3	9.2	2.0	0	6.95
	10.3 mg	10.4 mg	7.6 mg	0.3 mg	0	5.86 mg
Isogenus modestus	2.5	0.7	0	2.0	0	0.76
	72.8 mg	11.2 mg	0	41.7 mg	0	16.28 mg
Isoperla fulva	1.7	0	0	0	0	0.076
	46.2 mg	0	0	0	0	2.11 mg
Alloperla borealis	146.7	75.0	29.2	42.0	0	43.70
	422.1 mg	259.4 mg	120.1 mg	217.5 mg	0	177.34 mg
Alloperla lamba	0	0.7	0	0	0	0.105
	0	6.5 mg	0	0	0	0.959 mg
Alloperla lineosa	32.5	32.1	8.3	16.0	0	14.72
	143.5 mg	118.6 mg	28.8 mg	82.3 mg	0	60.73 mg
Alloperla autumna	15.8	7.1	2.5	10.0	0	5.73
	53.8 mg	30.0 mg	7.7 mg	38.5 mg	0	21.16 mg
mixed unidentified Alloperla	75.8	143.3	56.7	252.0	0	88.53
	108.5 mg	113.9 mg	51.1 mg	222.0 mg	0	76.07 mg
Acroneuria pacifica	10.8	9.3	5.0	2.0	0	4.90
	96.6 mg	73.2 mg	5.6 mg	3.4 mg	0	17.43 mg

APPENDIX C (cont.) - Lage Benthos Samples

Samples	study area sections 1	2	3	4	5	all section weighted mean
Rhyacophila larva 1	13.3 53.7 mg	18.3 59.2 mg	19.2 173.1 mg	6.0 99.5 mg	10.0 291.9 mg	14.49 135.27 mg
Rhyacophila larva 2	20.0 14.5 mg	71.4 36.4 mg	42.5 19.3 mg	42.0 21.3 mg	0 0	44.04 21.41 mg
Rhyacophila larva 3	0 0	0 0	0 0	2.0 0.7 mg	5.0 0.5 mg	0.72 0.20 mg
Rhyacophila larva 4	0 0	1.4 55.4 mg	0 0	0 0	5.0 109.5 mg	0.39 12.16 mg
Rhyacophila larva 5	0.8 0.3 mg	1.4 0.8 mg	9.2 46.5 mg	4.0 6.2 mg	0 0	5.91 25.02 mg
Rhyacophila larva 6	1.7 10.0 mg	0 0	0.8 1.3 mg	2.0 1.6 mg	0 0	1.03 2.10 mg
Rhyacophila larva 8	0 0	0 0	0.8 7.7 mg	0 0	0 0	0.42 3.85 mg
Rhyacophila larva 9	0 0	0 0	0 0	0 0	10.0 173.3 mg	0.36 6.34 mg
Rhyacophila larva 10	0 0	0 0	0 0	0 0	0 0	0 0
Glossosoma sp.	0 0	0.7 0.1 mg	0.8 0.15 mg	0 0	0 0	0.52 0.094 mg

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Anagapetus ? sp.	0	0	0	0	0	0
	0	0	0	0	0	0
Psychomyiidae sp.	0	0	1.7	0	0	0.83
	0	0	0.6 mg	0	0	0.28 mg
Arctopsyche sp.	0.8	8.6	3.3	0	0	2.97
	133.4 mg	1018.6 mg	352.8 mg	0	0	332.37 mg
Limnephilidae larva 1	0	0	0	0	0	0
	0	0	0	0	0	0
Pycnopsyche sp.	1.7	0	0	0	0	0.076
	10.1 mg	0	0	0	0	0.46 mg
Lepidostomatidae larva	0	0	2.1	6.0	5.0	3.05
	0	0	0.8 mg	6.2 mg	1.5 mg	2.11 mg
Lepidostomatidae sp. 1, pupa	0	0.7	0	0	0	0.105
	0	3.4 mg	0	0	0	0.500 mg
Lepidostomatidae larva 2	0	0	0	0	0	0
	0	0	0	0	0	0
mixed Trichoptera pupae	5.0	4.2	7.5	6.0	0	6.23
	76.7 mg	152.2 mg	208.0 mg	102.9 mg	0	155.99 mg
Heterlimnius sp. adults	0	0	0.8	0	0	0.42
	0	0	3.9 mg	0	0	1.93 mg

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Heterlimnius sp. larvae	58.3	27.1	18.3	44.0	0	27.74
	93.8 mg	49.3 mg	32.4 mg	43.3 mg	0	39.45 mg
Cleptelmis sp. larvae	12.5	2.9	27.5	16.0	0	19.06
	6.8 mg	1.6 mg	14.5 mg	6.1 mg	0	9.44 mg
Tipulidae larva 2	8.3	10.7	6.7	6.0	0	6.91
	1486.2 mg	1033.0 mg	888.0 mg	1485.2 mg	0	1066.04 mg
Tipulidae larva 5	0.8	0.7	0.8	0	0	0.56
	59.0 mg	7.3 mg	26.1 mg	0	0	16.81 mg
Tipulidae larva 7	0	0	0	0	0	0
	0	0	0	0	0	0
Blephariceridae pupae	0	0.7	0.8	0	0	0.65
	0	33.9 mg	39.5 mg	0	0	30.72 mg
Simuliidae larva 1	6.7	20.0	38.3	180.0	125.0	75.74
	8.8 mg	35.0 mg	37.8 mg	108.4 mg	232.7 mg	62.30 mg
Simuliidae larva 2	1.7	24.3	9.2	46.0	110.0	24.72
	1.6 mg	148.2 mg	63.4 mg	208.7 mg	563.1 mg	130.73 mg
Simuliidae larva 4	0	0	0	0	10.0	0.37
	0	0	0	0	45.3 mg	1.66 mg
Simuliidae larva 5	0	0	0	0	5.0	1.83
	0	0	0	0	30.3 mg	0.74 mg

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Simuliidae larva 6	0	0	0	0	5.0	0.18
	0	0	0	0	2.9 mg	0.10 mg
Simuliidae larva 7	0	0	0	0	25.0	0.91
	0	0	0	0	8.2 mg	0.30 mg
Prosimulium sp. pupae	14.1	40.0	2.5	6.0	0	9.41
	75.2 mg	199.1 mg	22.8 mg	34.6 mg	0	53.56 mg
Simulium sp. pupae	1.7	1.4	1.7	0	0	1.12
	2.5 mg	2.1 mg	0.7 mg	0	0	0.79 mg
Chironomidae larva 2a	0	0.7	0	0	0	0.11
	0	0.2 mg	0	0	0	0.025 mg
Chironomidae larva 2b	5.8	1.4	0	4.0	0	1.56
	3.5 mg	0.6 mg	0	0.3 mg	0	0.32 mg
Chironomidae larva 12	74.2	60.0	29.2	38.0	65.0	39.47
	256.7 mg	214.2 mg	87.6 mg	113.1 mg	190.5 mg	400.22 mg
Chironomidae larva 13	5.8	2.9	8.3	14.0	0	8.64
	3.8 mg	2.0 mg	4.1 mg	4.9 mg	0	3.83 mg
mixed unidentified	498.3	105.7	102.5	156.0	840.0	162.56
Chironomidae larvae	372.5 mg	90.9 mg	86.6 mg	67.6 mg	323.1 mg	104.92 mg
mixed unidentified	95.0	67.8	28.0	92.0	40.0	54.46
Chironomidae pupae	246.7 mg	92.5 mg	69.9 mg	113.0 mg	14.9 mg	85.38 mg

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
Bezzia sp. larvae	5.8	0	0.8	4.0	0	1.76
	5.8 mg	0	0.4 mg	3.1 mg	0	1.31 mg
Diptera larva 1	0.83	0	0	0	0	0.038
	4.40 mg	0	0	0	0	0.201 mg
Diptera larva 2	0.83	0	0	0	0	0.038
	1.30 mg	0	0	0	0	0.059 mg
Diptera larva 3	0.83	0	0.83	0	0	0.45
	8.72 mg	0	0.75 mg	0	0	0.58 mg
Diptera larva 4	0	0	0.83	0	0	0.42
	0	0	1.30 mg	0	0	0.64 mg
Empididae pupa 1	1.7	0	0	0	0	0.07
	3.9 mg	0	0	0	0	0.17 mg
Acari	1.7	0.7	1.7	6.0	0	2.74
	0.5 mg	0.4 mg	0.5 mg	1.8 mg	0	0.83 mg
Pisidium sp.	8.3	0	0	6.0	0	2.00
	36.7 mg	0	0	4.0 mg	0	2.76 mg
Eiseniella sp.	4.2	3.6	2.5	6.0	0	6.09
	363.8 mg	43.3 mg	63.2 mg	431.8 mg	0	171.54 mg
Sparganophilus sp.	5.0	5.0	2.5	22.0	0	8.17
	27.0 mg	11.3 mg	3.5 mg	63.6 mg	0	21.90 mg

APPENDIX C (cont.) - Late Benthos Samples

Species	study area sections 1	2	3	4	5	all section weighted mean
unidentified small	7.5	15.0	0.8	0	0	2.76
Oligochaetes	9.2 mg	2.7 mg	0.4 mg	0	0	1.01 mg

APPENDIX D

A Tentative Key to the Nymphs of the Subfamily Baetinae (Ephemeroptera) in Nash Fork Creek, Albany County, Wyoming

1. Bases of antennae much closer together than width of labrum . . . . <u>Centroptilum</u> sp.

— Bases of antennae about as far apart as width of labrum 2

2. Middle tail minute. . . . . <u>Baetis</u> B

— Middle tail longer 3

3. Dark paired markings on abdominal tergites distinct except in nymphs less than 2.5 mm long; middle tail short, never more than 1/6 the length of the laterals or more than 0.9 mm . . . . <u>Baetis</u> D

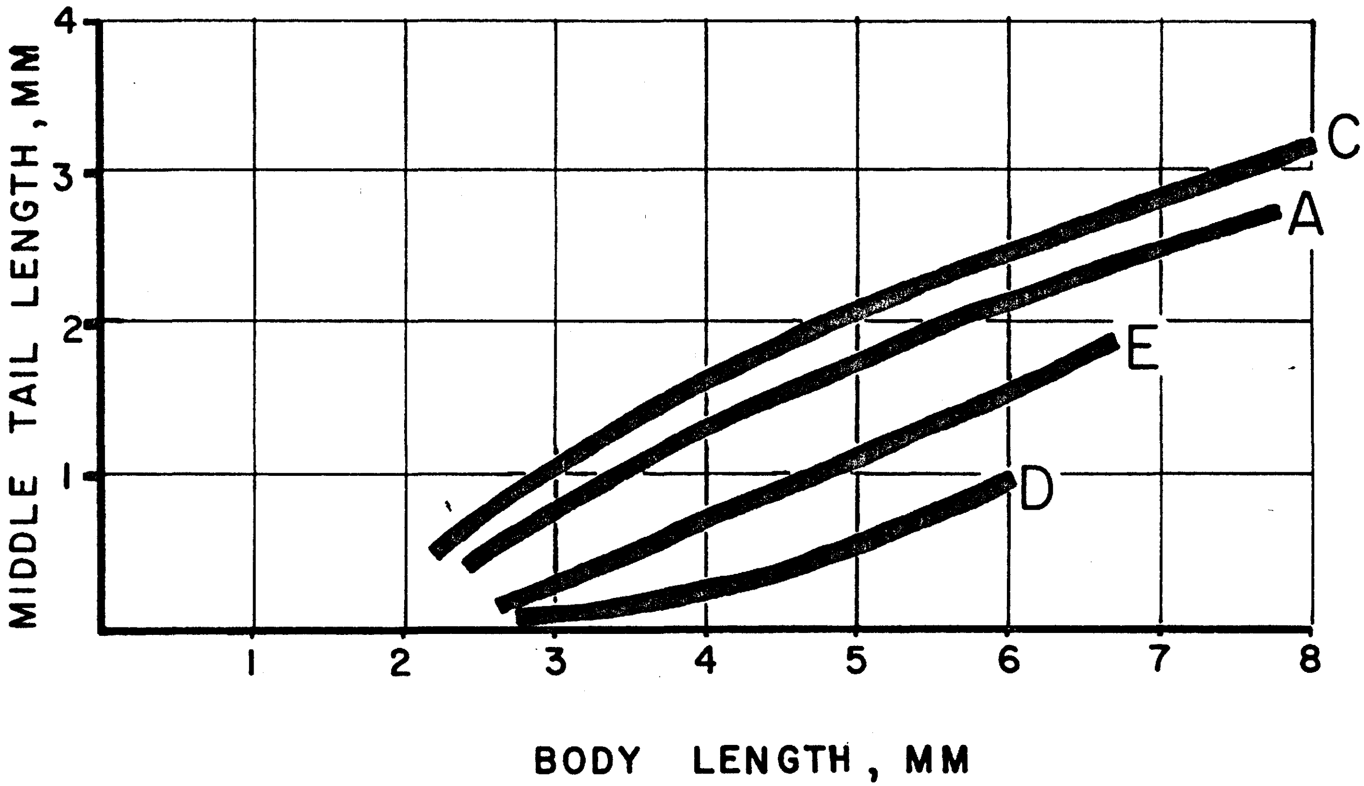
— Dark paired markings on abdominal tergites fainter; middle tail longer than 1/6 the length of the laterals in larger nymphs 4

4. Abdominal tergites with no markings or at least extremely faint markings; body rather uniformly brownish; middle tail of mature nymphs about 1/4 the length of the laterals . . . . <u>Baetis</u> A

— Abdominal tergites with more noticeable paired dark markings 5

5. Length of middle tail about 1/2 the length of the laterale in mature nymphs . . . . <u>Baetis</u> C

— Length of middle tail about 3/10 the length of the laterals in mature nymphs . . . . <u>Baetis</u> E



BODY LENGTH VS. MIDDLE TAIL LENGTH IN <u>BAETIS</u> A,C,D,E

APPENDIX E

A Tentative Key to Larvae of the Genus *Rhyacophila* (Trichoptera) in Nash Fork Creek, Albany County, Wyoming

1. Abdominal gills present 6
__ Abdominal gills absent 2
2. Laterally-projecting spur on anal leg minute or absent . . 3
__ Laterally-projecting spur on anal leg larger 4
3. Laterally-projecting spur on anal leg absent; no proleg-like projections on abdomen . . . . *Rhyacophila* 10
__ Minute laterally-projecting spur present on anal leg; abdominal segments 2-8 with double, smooth, proleg-like projections from each ventro-lateral corner . . . . *Rhyacophila* 9
4. Laterally-projecting spur on anal leg as long as or longer than the anal claw, extending beyond the end of the anal leg; color pale yellow; common . . . . *Rhyacophila* 2
. . . . . rare, (may be synonymous) . . . . . *Rhyacophila* 8
__ Laterally-projecting spur on anal leg shorter than anal claw 4
5. Laterally-projecting spur on anal leg about 2/3 the length of the anal claw; at least the larger individuals have a <u>single</u> smooth proleg-like projection on each ventro-lateral corner of abdominal segments 2-8; dorsum of head with a dark mottled pattern . . . . *Rhyacophila* 7
__ Laterally-projecting spur on anal leg shorter; no proleg-like projections on abdominal segments, but ventro-lateral margins bulge slightly; a dark spot on dorsal posterior portion of head . . . . *Rhyacophila* 3
6. Abdominal gills not branched; mesothorax with one pair of gills, metathorax with two pair, abdominal segments 1-7 with 4 pair; some darker spots on dorsum of head . . . . *Rhyacophila* 4
__ At least some abdominal gills branched 7

APPENDIX E (cont.)

7. Abdominal gills with three or less branches; gills on first abdominal segment 2-branched; all gill branches about 1/2 the length of abdominal setae; smaller and darker than #1. . . . . Rhyacophila 5

__ Abdominal gills 5-20 branched; gills on first abdominal segment with at least 6 branches; some gill branches 1/6 as long as setae; abundant . . . . <u>Rhyacophila</u> 1

APPENDIX F

Hynes' life cycle designation and summary of breeding period information for selected species of insects.

Species	breed during the period	life cycle classification
Rithrogena brunnea	yes	slow seasonal
Cinygmula sp.	no	fast seasonal
Epeorus longimanus	no	fast seasonal
Paraleptophlebia sp.	yes	slow seasonal
Ephemerella doddsi	yes	slow seasonal
Ephemerella coloradensis	no	fast seasonal
Ephemerella inermis	yes	slow seasonal
Baetis sp. A	yes	fast seasonal
Baetis sp. B	yes	fast seasonal
Baetis sp. C	yes	fast seasonal
Baetis sp. D	yes	fast seasonal
Centroptilum sp.	yes	fast seasonal
Nemoura cinctipes	yes	slow seasonal
Nemoura oregonensis	yes	slow seasonal
Nemoura group 1	yes	fast seasonal
Paraleuctra occidentalis	yes	slow seasonal
Arcynopteryx signata	yes	slow seasonal
Isogenus (Kogotus) modestus	no	fast seasonal
Isoperla fulva	yes	slow seasonal
Acroneuria pacifica	(?)	non-seasonal
Rhyacophila sp. 1	(?)	non-seasonal
Arctopsyche sp.	(?)	non-seasonal
Lepidostomatidae sp. 1	yes	slow seasonal
Limnephilidae sp. 1	yes	slow seasonal

APPENDIX G

Presence of newly hatched individuals (1 or 2 mm) in either drift samples or benthos samples during the rising phase (June 1-24) or the falling phase (July 6-29) of the runoff. R = rising phase only, F = falling phase only, B = both phases, N = present in neither phase.

Species	R	F	B	N
Rithrogena spp.			X	
Cinygmula sp.			X	
Epeorus longimanus			X	
Ameletus spp.			X	
Paraleptophlebia sp.			X	
Ephemerella doddsi		X		
E. coloradensis	X			
E. inermis				X
Baetis sp. A		X		
Baetis sp. B			X	
Baetis sp. C		X		
Baetis sp. D			X	
Baetis sp. E		X		
Centroptilum			X	
Nemoura cinctipes			X	
Nemoura oregonensis			X	
Nemoura group 1			X	
Paraleuctra occidentalis				X
Paraleuctra sara				X
Eucapnopsis brevicauda				X
Brachyptera sp.				X
Arcynopteryx signata			X	

APPENDIX G (cont.)

Species	R	F	B	N
Isoperla fulva			X	
Acroneuria pacifica			X	
Rhyacophila sp. 1			X	
Rhyacophila sp. 2			X	
Rhyacophila sp. 3			X	
Rhyacophila sp. 4				X
Rhyacophila sp. 5	X			
Rhyacophila sp. 7				X
Rhyacophila sp. 10	X			
Arctopsyche sp.				X
Limnephilidae sp. 1				X
Lepidostomatidae sp. 1			X	
Lepidostomatidae sp. 2				X
Heterlimnius sp.		X		
Cleptelmis sp.			X	
Tipulidae sp. 2				X
Tipulidae sp. 7				X
Blephariceridae sp. 1				X
Simulium sp.		X		
Prosimulium sp.			X	
Chironomidae sp. 2a	X			
Chironomidae sp. 2b			X	
Chironomidae sp. 13			X	
Bezzia sp.				X
Diptera larva 3	X			
Diptera larva 4				X
Diptera larva 6				X
Total	5	6	22	16