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The Relationship of Leaf Processing Rates and Invertebrate Functional Groups to Stream Order in Northeastern Minnesota

Steven Norman Williams

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This thesis submitted by Steven Norman Williams in partial fulfillment of the requirements for the Degree of Master of Arts at St. Cloud State University is hereby approved by the final evaluation committee.

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Processing rates for aspen (*Populus tremuloides*) and red pine (*Pinus resinosa*) leaves were measured in first through fourth order streams in 1977. The purpose was to investigate the relationship between leaf processing rates and stream order designations.

Artificial leaf packs weighing 10 g were used to measure weight loss during two eight week periods; one during June and July the other during October and November. Processing rates between stream orders were not significantly different ($P>.05$) except for aspen leaves during the summer. Processing rates of aspen and red pine leaves were significantly more rapid ($P<.05$) in the summer than in the fall. Average processing coefficients for all stream orders combined were: aspen - 0.0212 in the summer and 0.0082 in the fall; red pine - 0.0026 in the summer and 0.0008 in the fall.

The invertebrates associated with the leaf packs were evaluated on a functional group basis. Collectors and filter feeders were the dominant functional groups at all stream orders on all dates. During both seasons shredders generally decreased with increasing stream order. In the summer, the ratio of shredders to collectors decreased with increasing stream order. In the fall the ratio was highest in first and third order streams; lowest in second order streams.

Key Words: Decomposition; detritus processing, leaf litter, stream order, *Populus*, *Pinus*, shredder, collector.

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Month Year

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INTRODUCTION

Allochthonous inputs provide the primary energy source for small, heterotrophic streams (Minshall 1967, Cummins et al. 1972 and 1973, Fisher and Likens 1972 and 1973). Nelson and Scott (1962) reported that in a Piedmont stream, 66% of the energy available to primary consumers was derived from allochthonous sources, primarily leaf materials. Vannote (1969) stated, "In woodland streams the allochthonous detritus input may support up to two-thirds of the annual energy requirements of primary consumers." Over 99% of the annual energy input to Bear Brook, New Hampshire was from allochthonous sources (Fisher and Likens 1973). Teal (1957) attributed 76% of the energy at the primary consumer level in Root Spring, Massachusetts to material of terrestrial origin, mainly leaf material.

Estimates of the amount of allochthonous matter entering streams have ranged from 1.37 to 5.0 $g/m^2/day$. Vannote (1969) estimated 1.37 g dry weight of particulate organic matter/m^2/day. Hynes (1970) found 1 kg/meter of bank length/yr (2.74 $g/m^2/day$ assuming a 1 meter wide stream) for a wooded valley stream; and Mathews and Kowalczewski (1969) and Kowalczewski (1970), 0.0489 $g/m^2/day$ for the River Thames. If only that area of the river under riparian vegetation is considered the calculation becomes 4.35 g/meter of bank length/day which is the same as small stream measurements. Fisher and Likens (1972) estimated 1.70 $g/m^2/day$ for Bear Brook, New Hampshire; and Petersen and Cummins

(1974) 5.0 g/m^2/day for a small stream in Michigan.

Cummins (1975) proposed a stream ecosystem model based on the concept of stream order. Stream order is an index of the position of a stream in the hierarchy of tributaries in a watershed (Horton 1945, Strahler 1957). First order streams are those which have no tributaries. When two first order streams meet a second order stream is formed. Two second order streams form a third order and so on. Lower order streams do not affect the order designation of higher order streams upon entry.

Stream ecosystems generally undergo a transition in invertebrate community structure and function as stream order increases (Cummins 1975). Small, heavily shaded, headwater streams rely on allochthonous material for the majority of their energy. These streams contain relatively large populations of shredding invertebrates capable of processing the large input of terrestrial organic matter, mainly leaf material. Shredders reduce coarse particulate organic matter (>1-4 mm) to fine particulate organic matter (<1 mm) which can be utilized by collector and filter feeding invertebrates. As stream order increases, allochthonous energy sources decrease in importance and instream primary production increases. This increase in primary production allows the development of a scraper community capable of utilizing this new food source.

Boling, et al. (1975) listed four major factors that contribute to detritus processing: 1) feeding by stream detritivores; 2) mechanical disruption by organisms burrowing through detritus; 3) weakening and attrition of detritus by microbial action; and 4) mechanical aggregation on obstacles and subsequent breakage by flowing water. Leaf processing has been measured in several ways. The method used by Petersen and Cummins (1974) and Reice (1974) allowed the loss of large leaf fragments while authors using mesh bags defined processed material as the size of material that would pass through a given mesh.

Processing rates are closely correlated with the types of detrital material entering a stream. Sedell, et al. (1975) found that hardwood leaves were colonized by microorganisms more rapidly than conifer leaves and therefore became available as a food source to invertebrates much sooner. Hart and Howmiller (1975) found higher invertebrate densities on leaves that were most rapidly conditioned by microorganisms. Woodall and Wallace (1972), working on several streams with different types of allochthonous inputs at the Coweeta Hydrologic Laboratory in North Carolina, felt that the vegetation on each watershed was the main factor affecting invertebrate species composition. They found that differences in the fauna of streams in four watersheds could be explained by the availability of food or case-making materials, both of which are controlled by watershed vegetation.

Hynes, et al. (1974) suggested that "the importance of leaf litter as a food for aquatic organisms probably lies in providing an energy source for microbial growth." Kaushik and Hynes (1968 and 1971) found that fungi were important decomposers of leaves. Nelson and Scott (1962) found the ratio of the weights of detritivores to detritus higher than the ratio of aquatic herbivores to plants. They felt that detritus feeders obtain a portion of their food in the form of bacteria or some bacterial metabolic product.

Microbial metabolism can account for the processing of leaf litter in the absence of invertebrates (Mathews and Kowalczewski 1969, Triska 1970), but a 20% increase in processing rates was reported when shredders were present (Petersen and Cummins 1974). Jones (1975) stated that "ingestion of material by other animals (shredders) and excretion as feces is thought to aid the decomposition process by producing a finely divided substrate which is more amenable to microbial attack." Short and Maslin (1977) found a significant increase in nutrient availability to collectors when shredders were present. They noted that an increase in phosphorus uptake by collectors occurred, "probably because of a reduction in particle size thereby increasing the amount of material available as food."

The purpose of this study was to investigate the relationships between leaf processing rates, stream order and invertebrate functional groups. The specific questions to be answered include:
1) Do leaf processing rates decrease with increasing stream order?;
2) Is there a relationship between leaf processing rates and invertebrate functional groups?; and 3) Do invertebrate functional groups conform to the stream order model proposed by Cummins (1975) which is discussed earlier in this paper?

STUDY AREA

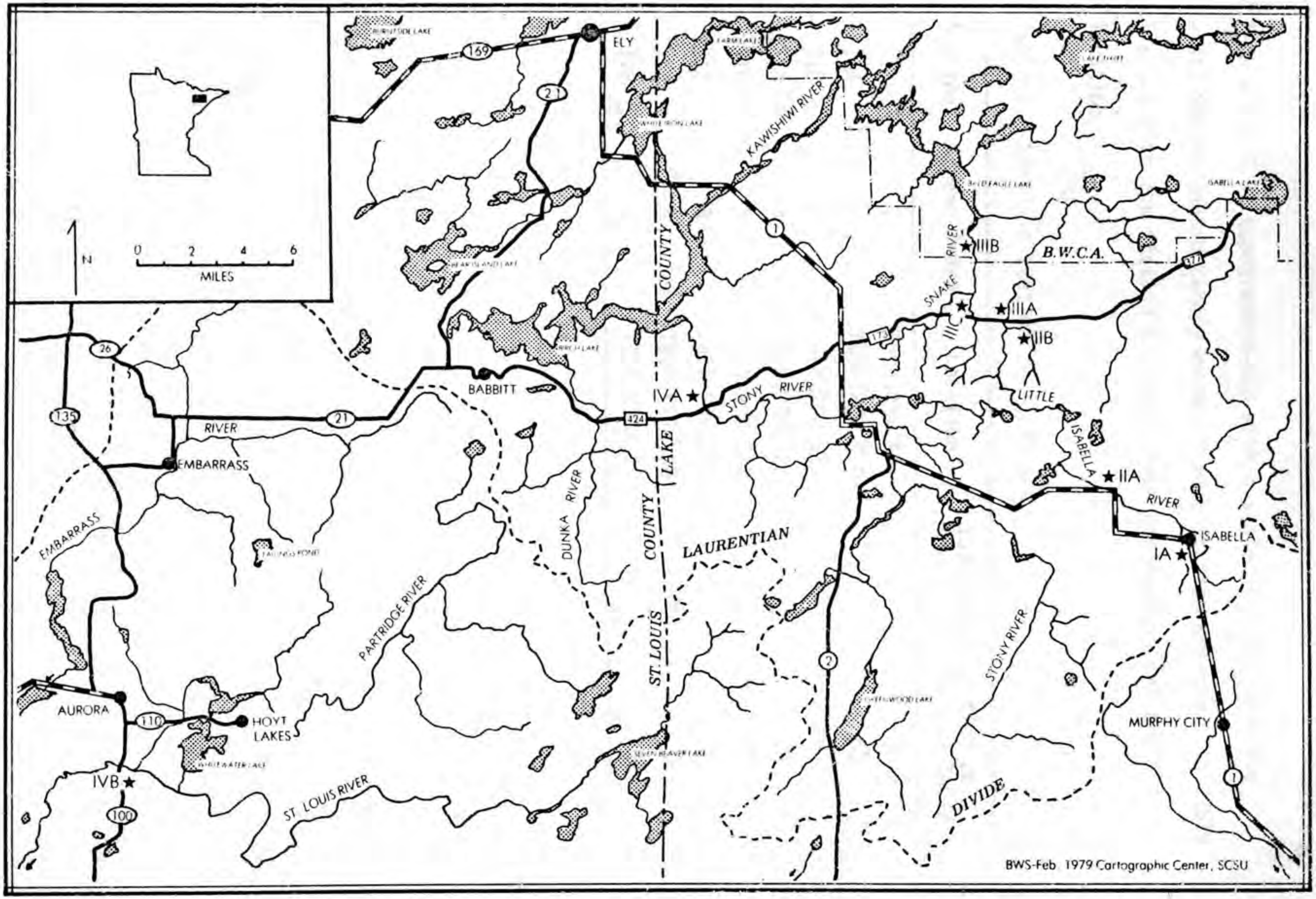
The Study Area was located in Lake and St. Louis Counties in northeastern Minnesota (Figure 1). This area is underlain by the Duluth Complex, a major rock unit of the Canadian Precambrian Shield (Green 1974). It generally consists of a feldspar rich gabbro overlain by unconsolidated surficial deposits of glacial till, peat, and lake and stream sediments (Veith, et al. 1976).

The area is divided into two major watersheds by the Laurentian Divide. Waters north of the Divide flow into Hudson Bay and waters south flow into Lake Superior.

The streams studied are permanent, relatively unimpacted streams that flow through a mixed coniferous-deciduous forest. They are generally of low gradient (0.8-4.7 m/km) and consist of long, slow stretches connected by short riffles. The water is characteristically soft (alkalinity 17-53 mg/l as $CaCO_3$), bog stained, with a pH ranging from 6.7-7.5. Riparian vegetation generally borders or covers the stream from May to September. The most common trees are alder (*Alnus* sp.), willow (*Salix* spp.), trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana*), and paper birch (*Betula papyrifera*).

A total of eight sample stations were established in the Little Isabella, St. Louis, and Stony River watersheds (Figure 1). These stations were located in riffles with mixed substrates of coarse sand, gravel, cobble, boulder, and ledgerock. Stream orders were selected

Figure 1. Study area showing location of sampling stations.



BWS-Feb. 1979 Cartographic Center, SCSU

from a U.S.G.S. topographic map with a scale of 1:62,500. The width and estimated canopy cover of each station are shown in Table 1 along with the station's stream order designation and specific location.

Table 1. Sampling station designations.

Station	Stream Order	Location	Estimated Width (m)	Estimated % Canopy Cover
I	1	T59N,R8W,S4	2	10
IIA	2	T60N,R9W,S30	6	60
IIB	2	T61N,R9W,S27	2	100
IIIA	3	T61N,R9W,S27	10	20
IIIB	3	T61N,R9W,S12	4	75
IIIC	3	T61N,R9W,S30	2	5
IVA	4	T60N,R11W,S8	12	0
IVB	4	T58N,R15W,S22	12	5

METHODS

Artificial leaf packs have been used to evaluate leaf processing in streams (Petersen and Cummins 1974, Reice 1974, Paul, Benfield and Cairns 1977). Leaves enclosed in mesh bags have been used by some authors to measure processing rates (Mathews and Kowalczewski 1969, Park 1974, Hart and Howmiller 1975), however, Petersen and Cummins (1974) suggested that complete processing would be hampered because of decreased microbial activity and the exclusion of large invertebrates. Petersen and Cummins (1974) and Reice (1974) used leaves fastened with nylon I bars to follow leaf pack processing. This allowed measurement of processing under near natural conditions. For this study processing is defined as the rate at which leaf material leaves a mesh bag (4 mm mesh size).

On 8 May and 28 September, 1977, trembling aspen (*Populus tremuloides*) and red pine (*Pinus resinosa*) leaves were collected, air dried, and frozen to prevent further degradation. Aspen leaves collected in September were picked from trees just prior to abcission, those collected in May had been on the ground approximately seven months. Red pine leaves collected on both dates had been on the ground an undetermined length of time. The September collection was timed so that the leaves would be in the same condition as those used in other studies. Leaves collected in May were partially processed because of leaching of water soluble components and were selected to provide information on leaves that normally enter streams during spring and early summer.

For this study leaves were enclosed in nylon mesh bags (mesh size 4 mm, Minnesota Fabrics Co., Minneapolis, MN). Aspen packs were constructed by loosely placing 10 g of leaves on a square of nylon mesh, drawing the edges together and binding with a nylon wire tie. This formed a circular bag approximately 10 cm in diameter (Figure 2). Red pine leaves were bound with a nylon wire tie to prevent whole leaves from slipping through the mesh. Ten gram packs were selected as the size which would provide a comparable processing rate through all seasons based on the findings of Reice (1974).

Prior to placement in streams, three packs of each species were selected at random to measure moisture content. Leaves were dried at 105°C for 24 hr (Weber 1973) and weighed to the nearest 0.1 g.

Leaf packs were tied to the upstream side of logs, (boards in the fall, Figure 3), anchored in the stream to simulate natural leaf pack formation. In May, leaf packs were placed in riffles at each station. Aspen packs were also placed in a pool at station IVB in May. In October, the sites were shifted slightly to areas of lower current velocity to reduce the variability in weight loss between individual leaf packs caused by water currents.

Twelve aspen packs were placed at each station on 26 May and 6 October, 1977. Three packs were removed from each station after 2, 4, 6 and 8 weeks in the summer. In the fall, aspen packs were collected after 1, 2, 4 and 8 weeks.

Figure 2. An aspen and red pine pack showing details of construction.


1
2
3
4
5
6
7
8
9
WESTCOTT

Figure 3. An aspen pack showing the method of anchoring leaf packs in the stream.

Similarly, in May, twelve red pine packs were used but only at four stations: one first order; two second order; and one fourth order. Three packs were collected from each station at two-week intervals. Because red pine processing rates were slow during the summer, only four packs were placed at each of the four stations in the fall and were left for the full eight weeks.

Leaf packs were randomly selected at the time of pickup and placed in plastic bags containing 100% ETOH. At the laboratory, the leaves were removed from the bag and rinsed with water to remove detritus and invertebrates. The leaves were dried at 105°C for 24 hr and weighed to the nearest 0.1 g. After the invertebrates had been sorted the remaining detritus was dried and the weight was added to that of the leaves. The amount of the detritus entering the bag from the stream was not significant.

Invertebrates were identified to genus, or the lowest level practical, and assigned to functional groups based on the classification by Merritt and Cummins (1978). To facilitate identification, chironomids were boiled in 5% KOH and mounted in CMCP-9AF.

Data Analysis

The following formula was used to calculate the percent dry weight of leaf material remaining:

$$\%R = W_{(tf)} / W_{(ti)} \times 100$$

where $W_{(tf)}$ is the amount of material remaining after a given time (t) and $W_{(ti)}$ is the initial weight of leaf material. This assumes a linear relationship which is helpful for comparing sites, seasons, and leaf species (Petersen and Cummins 1974).

Some authors have used an exponential decay model to describe weight loss (Fisher 1971, Petersen and Cummins 1974). This model assumes a constant loss of leaf material and was calculated using the formula:

$$\log_e [\%R / 100] = -kt$$

where %R is the percent of leaf material remaining after time (t) in days, and -k is the exponential decay (processing) coefficient which is computed using a least squares fit of the data.

Tests for significant differences in processing rates between summer and fall, and between riffle and pool samples at station IVB were performed using the Mann-Whitney test which is the non-parametric alternative to the *t*-test. This tests the hypothesis that two independent random samples were drawn from populations having the same parent distribution and the same medians. Differences in processing rates between stream orders were tested with the Kruskal-Wallis test which is a one way analysis by ranks. This tests the hypothesis that all samples came from the same population, and therefore there is no difference in mean level between several samples.

Invertebrate data were analyzed by calculating the relative abundance of taxa in each functional group and then the relative abundance of each functional group for each stream order. Dominant taxa were defined as those taxa which were present in the greatest number during a given season for each functional group.

RESULTS

Leaf Pack Processing

The mean percent of leaf material remaining for aspen and red pine leaves after eight weeks exposure is shown in Figures 4 and 5. The difference in the amount of leaf material remaining between stream orders was significant only for aspen leaves in the summer (Kruskal-Wallis test, $P<0.5$). The mean percent remaining for all stream orders combined was: aspen - 39.8% summer, 70.5% fall (Table 2); red pine - 81.9% summer, 95.4% fall (Table 3). In the summer, aspen packs were processed slowest in first order streams while in the fall processing rates were 20% faster in first order streams than other stream orders.

Figure 6 shows that the processing of aspen and red pine leaves was significantly more rapid in summer than fall (Mann-Whitney test, $P<0.05$). The average processing coefficient for aspen leaves for all stream orders combined was 0.0212 (0.0102 to 0.0280) in summer and 0.0082 (0.0055 to 0.0131) in fall (Table 2). The average processing coefficient for red pine for all stream orders combined was 0.0026 (0.0019 to 0.0033) in summer and 0.0008 (0.0007 to 0.0008) in fall (Table 3).

Figure 4. Mean percent of leaf material remaining with ranges for aspen after eight weeks exposure. (Data for first order streams during the summer are based on one leaf pack and ranges could not be included).

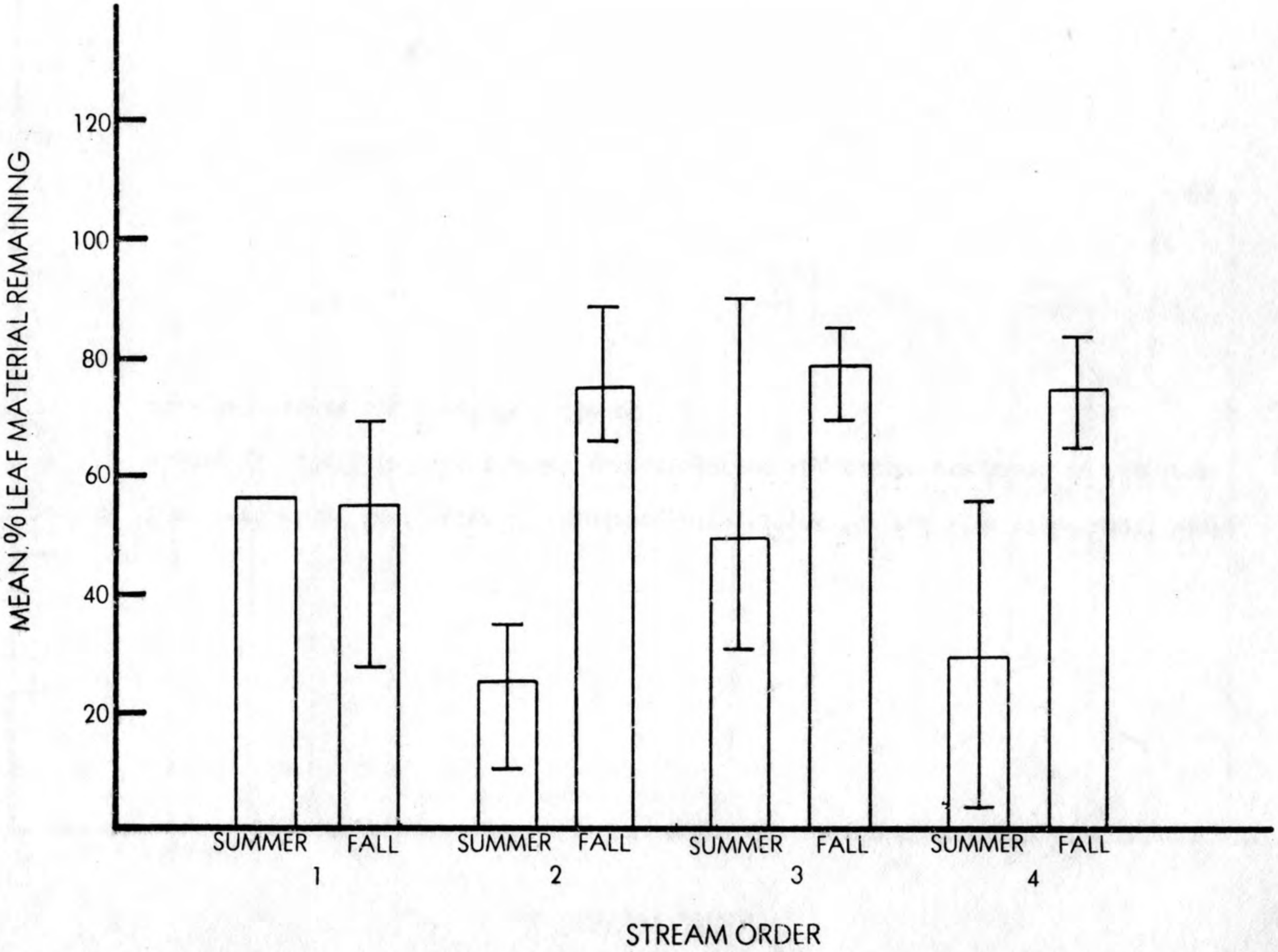

MEAN % LEAF MATERIAL REMAINING
120
100
80
60
40
20
SUMMER
FALL
SUMMER
FALL
SUMMER
FALL
SUMMER
FALL
1
2
3
4
STREAM ORDER

Figure 5. Mean percent of leaf material remaining with ranges for red pine after eight weeks exposure. (Data for first order streams during the summer are based on one leaf pack and ranges could not be included).

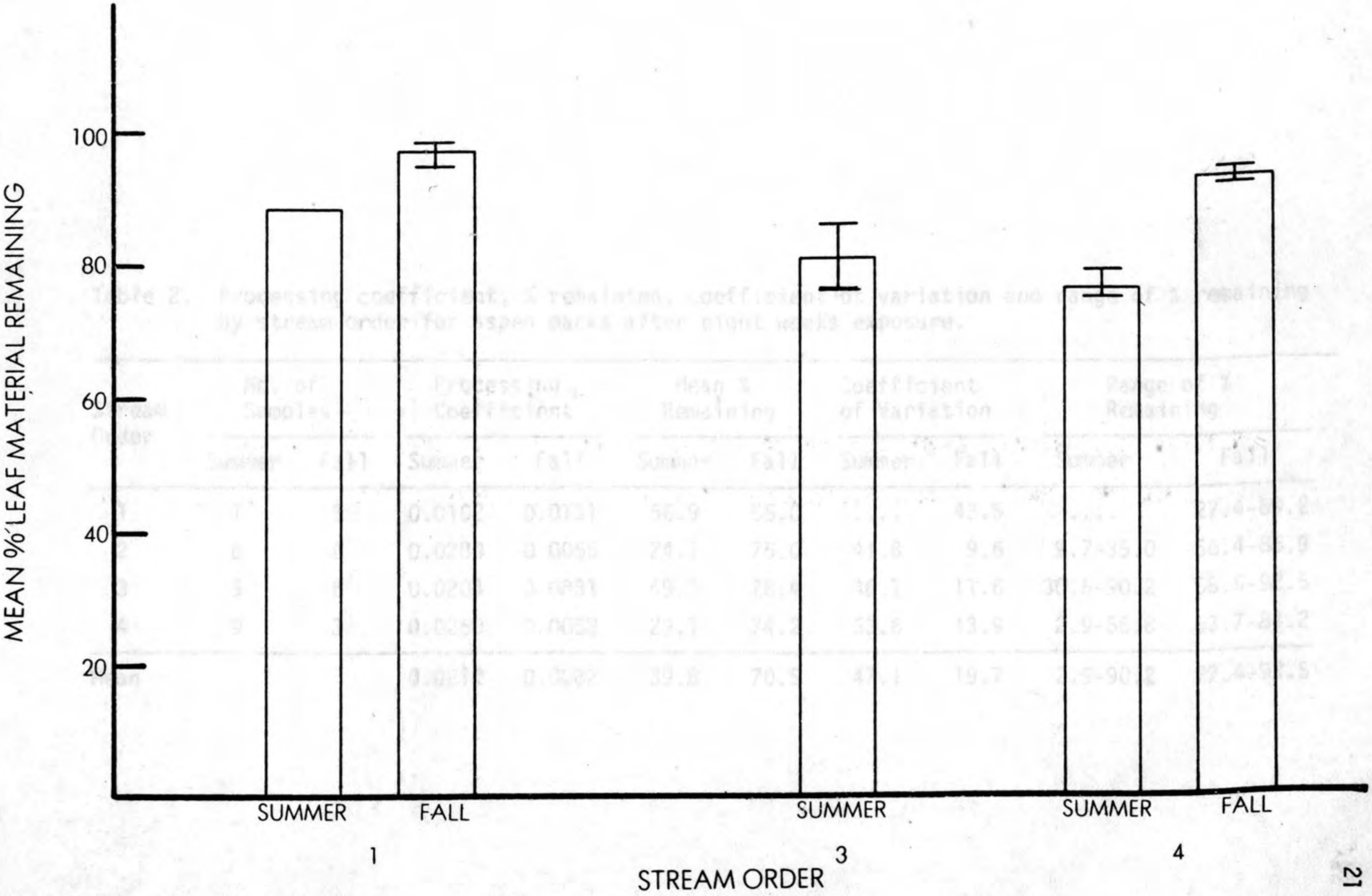

MEAN % LEAF MATERIAL REMAINING
100
80
60
40
20
SUMMER
FALL
SUMMER
SUMMER
FALL
1
3
4
STREAM ORDER

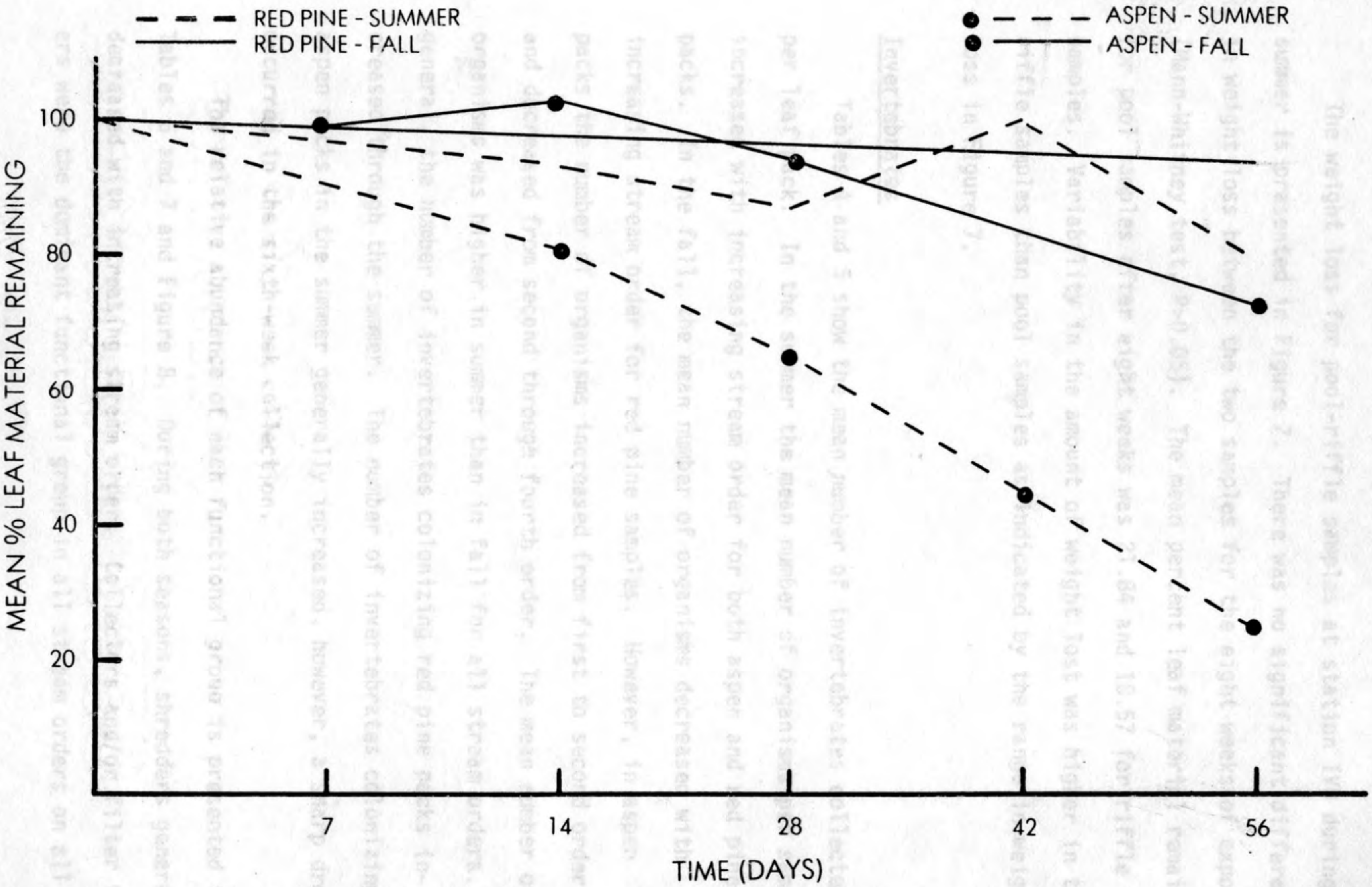
Table 2. Processing coefficient, % remaining, coefficient of variation and range of % remaining by stream order for aspen packs after eight weeks exposure.

Stream Order	No. of Samples		Processing Coefficient		Mean % Remaining		Coefficient of Variation		Range of % Remaining	
	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall
1	1	3	0.0102	0.0131	56.9	55.0	....	43.5	....	27.4-69.2
2	6	6	0.0280	0.0055	24.1	75.0	41.8	9.6	9.7-35.0	66.4-86.9
3	5	6	0.0204	0.0831	49.3	78.4	46.1	11.6	30.5-90.2	68.5-92.5
4	9	3	0.0260	0.0058	29.1	74.2	53.6	13.9	2.9-55.8	63.7-84.2
Mean			0.0212	0.0082	39.8	70.5	47.1	19.7	2.9-90.2	27.4-92.5

Table 3. Processing coefficient, % remaining, coefficient of variation and range of % remaining by stream order for red pine packs after eight weeks exposure.

Stream Order	No. of Samples		Processing Coefficient		Mean % Remaining		Coefficient of Variation		Range of % Remaining	
	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall
1	1	4	0.0026	0.0007	87.2	96.3	....	1.2	....	95.1-97.6
2	0	0	....	....	....	....	....	....	....	....
3	3	0	0.0033	....	81.5	....	6.1	....	76.1-86.1	....
4	3	4	0.0019	0.0008	95.5	2.7	2.7	0.4	75.6-79.4	95.1-95.7
Mean			0.0026	0.0008	81.9	95.4	4.5	0.8	75.6-86.1	95.1-97.6

Figure 6. Mean percent of leaf material remaining for all stream orders.


RED PINE - SUMMER
RED PINE - FALL
ASPEN - SUMMER
ASPEN - FALL
MEAN % LEAF MATERIAL REMAINING
100
80
60
40
20
7
14
28
42
56
TIME (DAYS)

The weight loss for pool-riffle samples at station IVB during the summer is presented in Figure 7. There was no significant difference in weight loss between the two samples for the eight weeks of exposure (Mann-Whitney test, $P>0.05$). The mean percent leaf material remaining for pool samples after eight weeks was 21.84 and 18.57 for riffle samples. Variability in the amount of weight lost was higher in the riffle samples than pool samples as indicated by the range in weight loss in Figure 7.

Invertebrates

Tables 4 and 5 show the mean number of invertebrates collected per leaf pack. In the summer the mean number of organisms per sample increased with increasing stream order for both aspen and red pine packs. In the fall, the mean number of organisms decreased with increasing stream order for red pine samples. However, in aspen packs the number of organisms increased from first to second order and decreased from second through fourth order. The mean number of organisms was higher in summer than in fall for all stream orders. In general, the number of invertebrates colonizing red pine packs increased through the summer. The number of invertebrates colonizing aspen packs in the summer generally increased, however, a sharp drop occurred in the sixth-week collection.

The relative abundance of each functional group is presented in Tables 6 and 7 and Figure 8. During both seasons, shredders generally decreased with increasing stream order. Collectors and/or filter feeders were the dominant functional group in all stream orders on all dates.

Figure 7. Mean percent of leaf material remaining for aspen packs at station IVB during the summer.

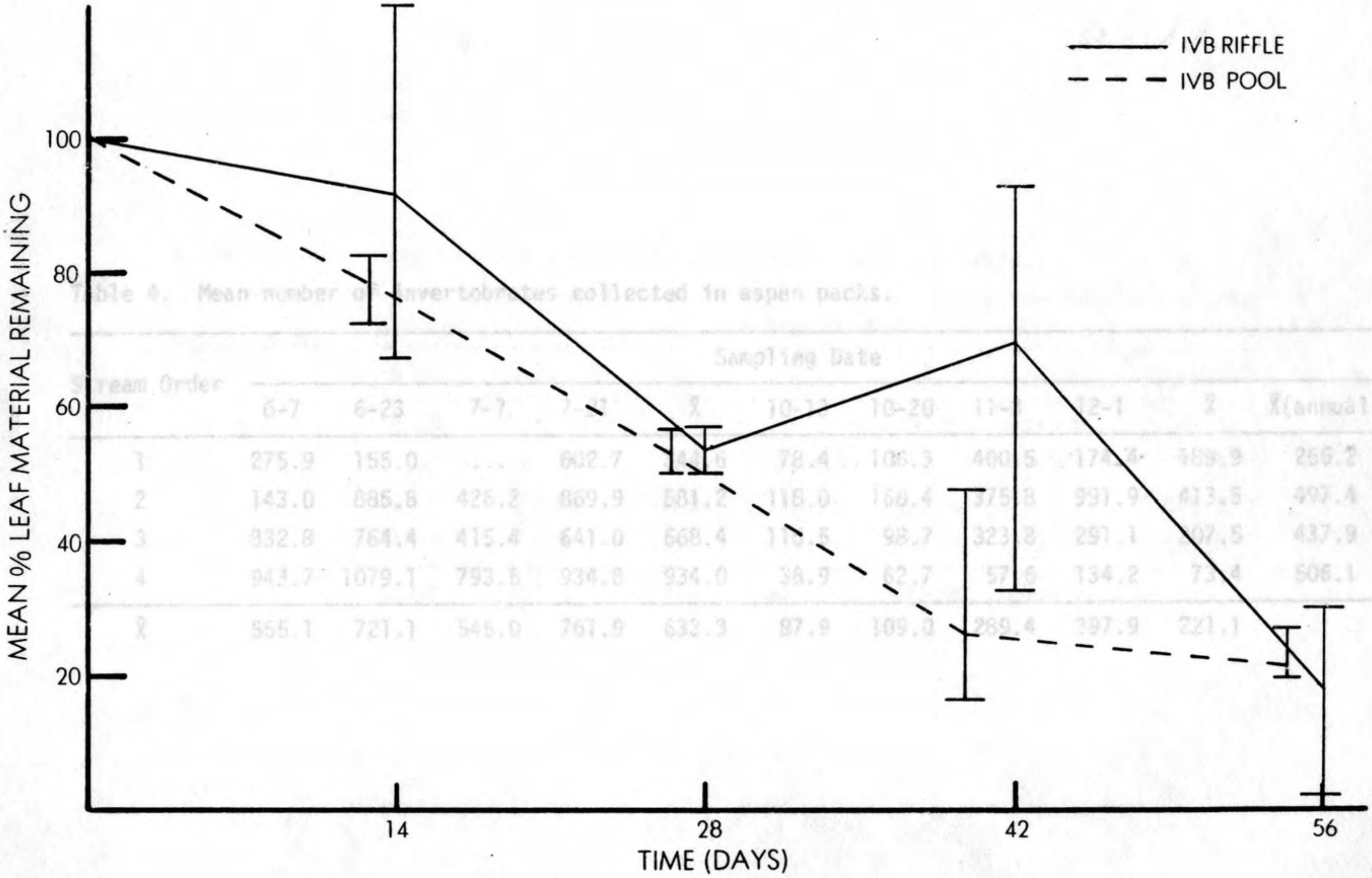

IVB RIFFLE
IVB POOL
MEAN % LEAF MATERIAL REMAINING
100
80
60
40
20
14
28
42
56
TIME (DAYS)

Table 4. Mean number of invertebrates collected in aspen packs.

Stream Order	Sampling Date										
	6-7	6-23	7-7	7-21	X̄	10-13	10-20	11-3	12-1	X̄	X̄(annual)
1	275.9	155.0	...	602.7	344.6	78.4	106.3	400.5	174.4	189.9	256.2
2	143.0	885.8	426.2	869.9	581.2	118.0	168.4	375.8	991.9	413.5	497.4
3	832.8	764.4	415.4	641.0	668.4	116.5	98.7	323.8	291.1	207.5	437.9
4	943.7	1079.1	793.5	934.8	934.0	38.9	62.7	57.6	134.2	73.4	506.1
X̄	555.1	721.1	545.0	761.9	633.3	87.9	109.0	289.4	397.9	221.1	

Table 5. Mean number of invertebrates collected in red pine packs.

Stream Order	Sampling Date						
	6-9	6-23	7-7	7-21	$\bar{X}$	12-1	$\bar{X}$(annual)
1	69.4	195.0	....	589.0	284.5	219.9	268.3
2	....	....	....	....	....	....	....
3	304.9	284.8	516.9	1195.7	575.6	....	575.6
4	312.9	736.3	550.8	823.7	605.9	90.23	502.8
$\bar{X}$	229.6	405.4	533.9	869.5	488.7	155.1	

Table 6. Functional group composition of aspen packs.

	Sampling Date															
Functional Group	6-9				6-23				7-7				7-21			
	Stream Order															
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Shredders	19.5	24.9	18.9	8.5	4.5	24.9	18.7	11.1	....	26.4	38.3	4.2	18.8	20.7	5.8	2.7
Collectors	22.4	34.3	24.9	29.6	37.2	37.1	28.8	31.8	....	36.7	28.5	29.6	48.5	19.9	27.2	25.9
Filter feeders	48.2	25.6	41.7	51.0	51.9	33.8	42.0	41.2	....	30.8	27.8	56.2	28.5	51.5	62.3	60.8
Predators	7.0	10.4	8.9	5.9	2.8	2.3	8.1	8.3	....	5.1	5.6	5.8	2.2	6.5	3.5	5.6
Scrapers	0.0	0.0	0.5	2.3	0.3	0.6	0.2	5.0	....	0.2	0.5	2.9	1.5	0.0	0.4	0.4
Piercing herbivores	0.0	0.0	0.0	0.0	0.0	0.2	0.3	0.6	....	0.5	0.0	0.5	0.2	0.7	0.0	0.0
Miscellaneous	2.9	4.7	5.4	2.4	3.5	1.3	1.9	2.4	....	0.9	0.0	0.6	0.3	0.8	0.7	4.7

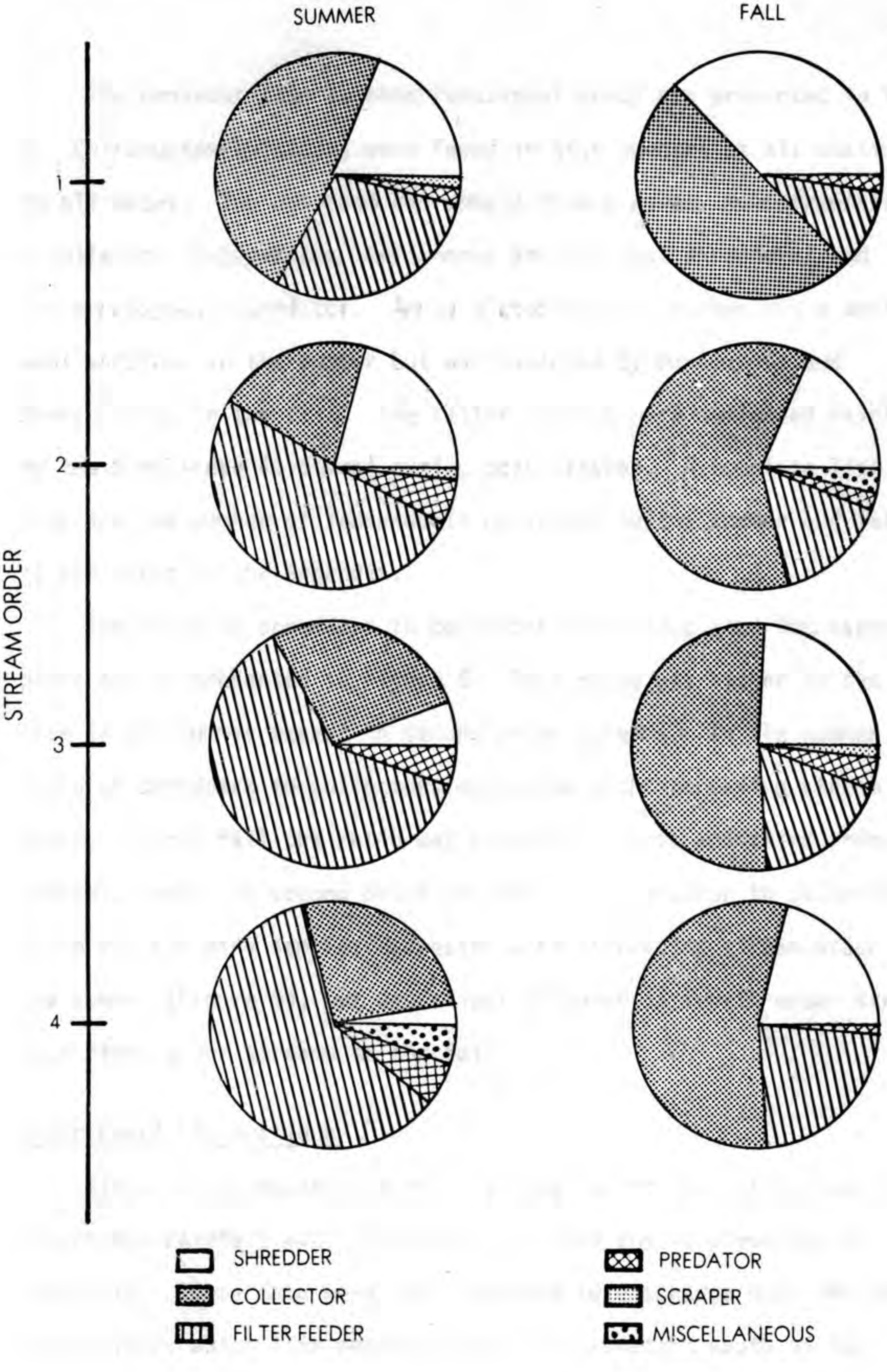
Table 6. Continued.

Functional Group	Sampling Date															
	10-13				10-20				11-3				12-1			
	Stream Order															
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Shredders	48.6	39.0	26.1	11.4	42.6	24.4	19.3	10.5	37.8	18.1	17.1	7.0	36.9	18.4	24.2	21.2
Collectors	12.4	34.2	22.0	68.4	18.6	39.5	47.9	66.8	30.2	55.5	40.6	55.3	50.5	63.6	52.0	55.0
Filter feeders	37.2	20.5	47.6	11.8	36.2	20.3	30.2	18.6	26.7	18.7	36.9	28.0	10.4	12.1	18.3	22.8
Predators	1.3	3.7	2.2	3.4	1.6	8.3	2.3	1.9	2.7	4.0	3.4	1.8	1.9	2.5	4.1	0.5
Scrapers	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.0
Piercing herbivores	0.0	0.4	0.3	3.2	0.0	0.1	0.0	0.5	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.5
Miscellaneous	2.1	1.8	1.4	1.9	0.9	7.2	0.3	1.3	2.3	3.6	2.0	7.8	0.2	3.4	1.5	0.3

Table 7. Functional group composition of red pine packs.

Functional Group	Sampling Date 6-9			6-23			7-7			7-21			12-1		
	Stream Order														
	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4
Shredders	18.8	5.0	7.7	16.9	13.1	7.7	....	5.8	6.4	32.6	2.1	4.5	29.3	....	30.3
Collectors	39.7	22.3	38.6	46.7	27.1	8.7	....	38.2	17.6	16.3	35.0	13.9	62.5	....	55.1
Filter feeders	20.8	56.8	43.3	13.3	43.4	73.2	....	42.5	72.9	50.7	49.3	75.0	5.9	....	8.9
Predators	19.1	14.2	6.4	20.5	13.2	9.2	....	6.4	3.0	0.5	8.2	5.9	1.4	....	3.0
Scrapers	0.0	0.0	0.7	0.0	0.7	0.0	....	0.3	0.0	0.0	0.0	0.0	0.0	....	0.0
Piercing herbivores	0.0	0.0	0.1	0.0	0.5	0.0	....	0.9	0.6	0.0	0.0	0.0	0.0	....	0.0
Miscellaneous	0.7	1.6	3.1	2.6	2.3	1.0	....	6.2	0.6	0.0	5.7	0.3	1.0	....	2.6

Figure 8. Invertebrate functional group composition of aspen packs after eight weeks exposure.


SUMMER
FALL
STREAM ORDER
1
2
3
4
SHREDDER
COLLECTOR
FILTER FEEDER
PREDATOR
SCRAPER
MISCELLANEOUS

The dominant taxa in each functional group are presented in Table 8. Chironomids (Diptera) were found in high numbers at all stations on all dates. The dominant chironomid genera were: *Eukiefferiella*, a collector; *Polypedilum, Cricotopus* and *Brillia*, shredders; and *Conchapelopia*, a predator. Among plecopterans, *Leuctra* was a dominant shredder in the summer but was replaced by *Paracapnia* and *Taeniopteryx* in the fall. The filter feeders were dominated mainly by the Simuliidae (Diptera) during both seasons. A complete list of taxa and the number of individuals collected during summer and fall is presented in the Appendix.

The ratio of shredders to collectors was calculated for aspen packs and is presented in Figure 9. This ratio was higher in the fall than in the summer except in second order streams. In the summer, the ratio of shredders to collectors decreased with increasing stream order. In the fall the ratio was highest in first and third order streams; lowest in second order streams. The shredder to collector ratio for red pine samples decreased with increasing stream order in the summer (Figure 9), but was slightly higher in fourth order streams than first order streams in the fall.

Water Level Fluctuations

Since discharge data were not available for the Little Isabella watershed, rainfall was plotted against time and is presented in Figure 10. These data were then compared to discharge data for the Dunka River, which lies approximately 24 kilometers south of the

Table 8. Dominant taxa in each functional group.

	Summer	Fall
Shredders	*Polypedilum* (D)	*Paracapnia* (P)
	Cricotopus (D)	*Brillia* (D)
	Lepidostoma (T)	*Taeniopteryx* (P)
	Leuctra (P)	Filipalpia (P)
Collectors	*Eukiefferiella* (D)	*Eukiefferiella* (D)
	Orthocladinae (D)	Orthocladinae (D)
	Micropsectra (D)	*Ephemerella* (E)
	Parametriocnemus (D)	Leptophlebiidae (E)
Filter feeders	Simuliidae (D)	Simuliidae (D)
	Hydropsychidae (T)	*Rheotanytarsus* (D)
	Hydropsyche (T)	Tanytarsini (D)
	Tanytarsus (D)	*Tanytarsus* (D)
Scrapers	*Physa* (G)	*Physa* (G)
	Pseudocloeon (E)	*Pseudocloeon* (E)
Piercing herbivores	*Ithytrichia* (T)	*Hydroptila* (T)
	Oxyethira (T)	*Oxyethira* (T)
Predators	*Conchapelopia* (D)	*Conchapelopia* (D)
	Atherix variegata (D)	*Atherix variegata* (D)
	Setipalpia (P)	Setipalpia (P)
	Hydracarina	*Isoperla* (P)

(P) Plecoptera, (T) Trichoptera, (D) Diptera, (E) Ephemeroptera, (G) Gastropoda

Figure 9. Ratio of shredders to collectors after eight weeks of exposure. (Collectors include both collector and filter feeder functional groups).

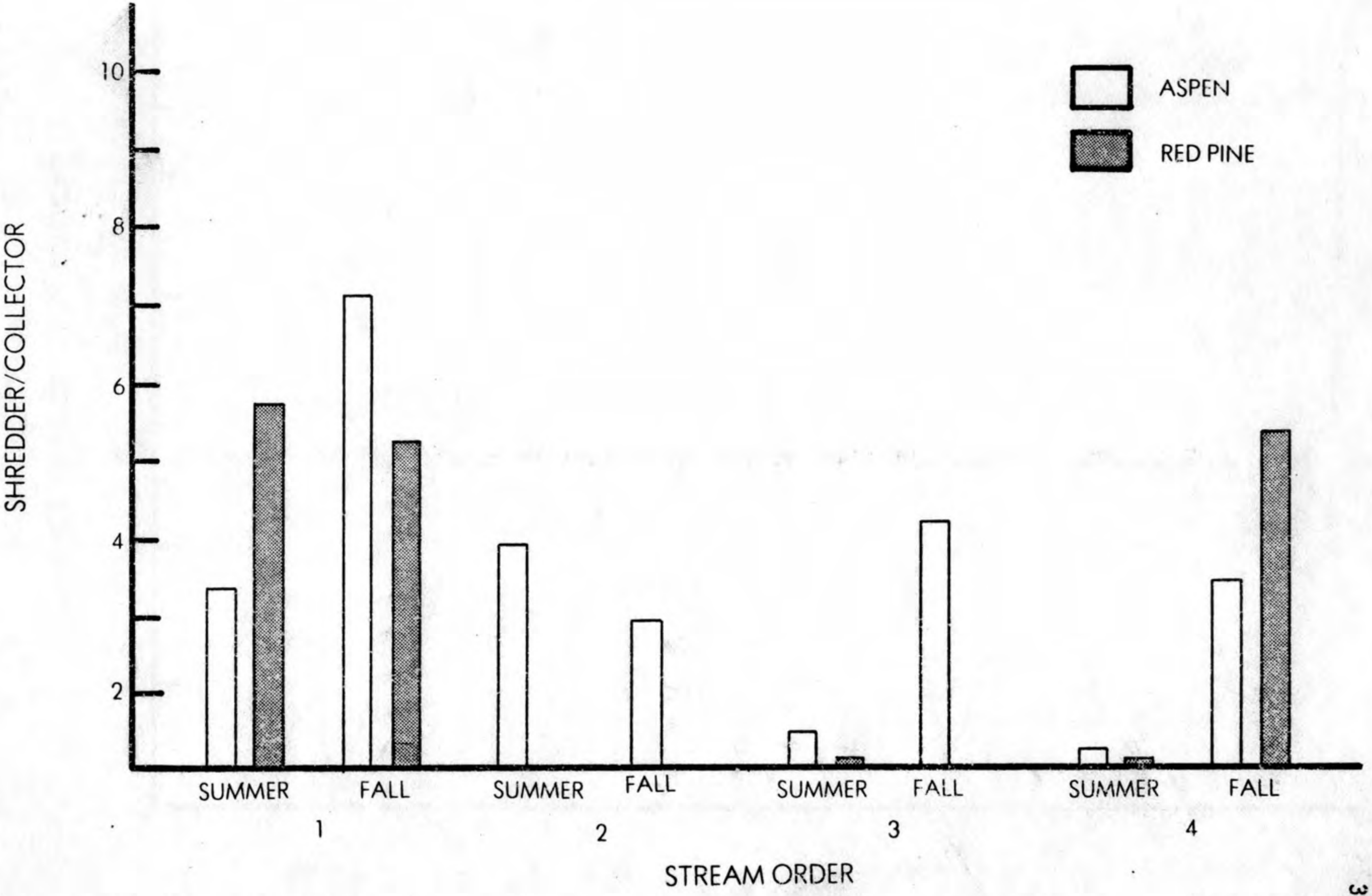
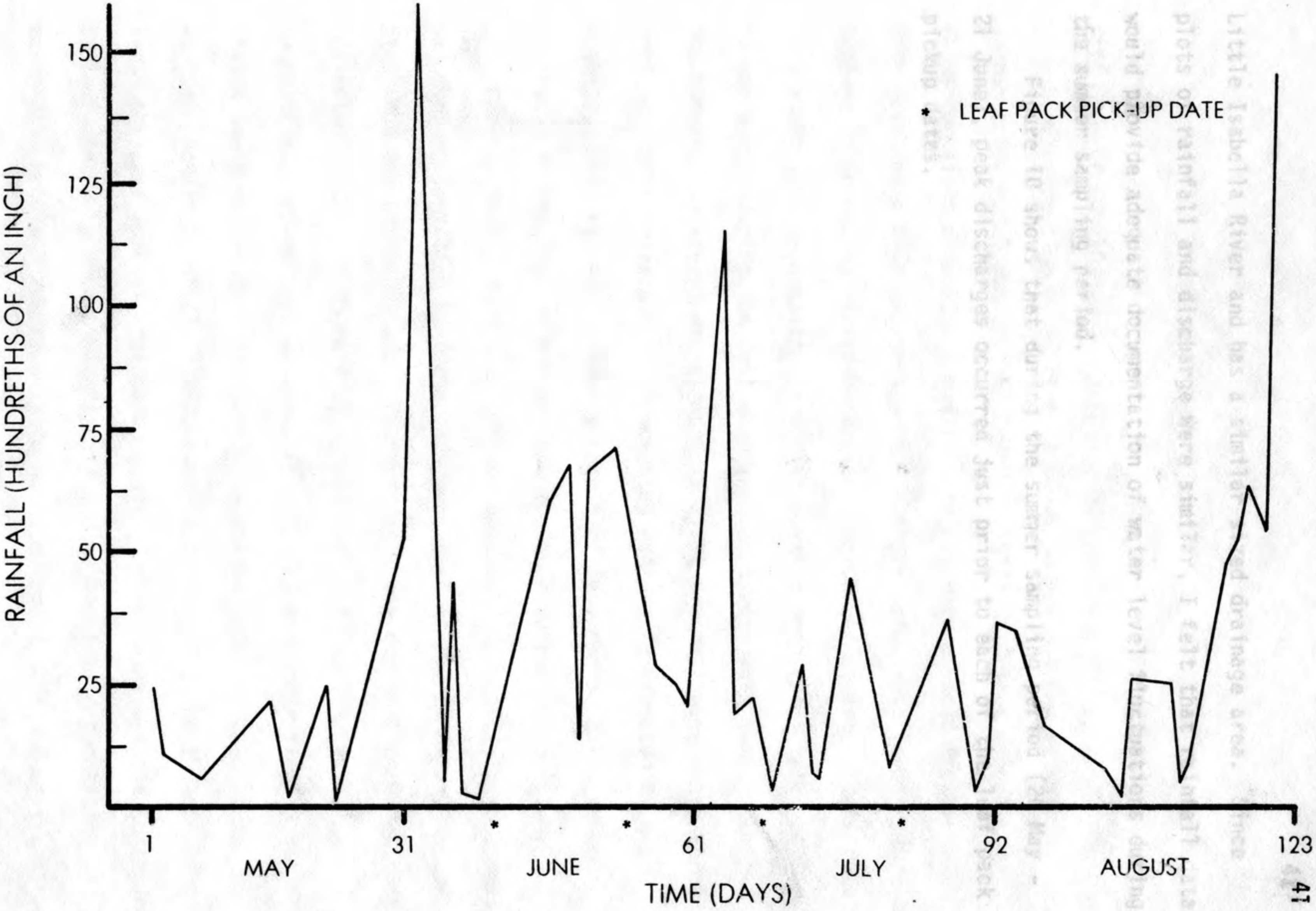

10
8
6
4
2
SHREDDER/COLLECTOR
ASPEN
RED PINE
SUMMER
FALL
SUMMER
FALL
SUMMER
FALL
SUMMER
FALL
1
2
3
4
STREAM ORDER

Figure 10. Inches of rainfall recorded at the Little Isabella ranger station during 1977.


RAINFALL (HUNDRETHS OF AN INCH)
150
125
100
75
50
25
* LEAF PACK PICK-UP DATE
1
31
61
92
123
MAY
JUNE
JULY
AUGUST
TIME (DAYS)

Little Isabella River and has a similar sized drainage area. Since plots of rainfall and discharge were similar, I felt that rainfall data would provide adequate documentation of water level fluctuations during the summer sampling period.

Figure 10 shows that during the summer sampling period (26 May - 21 June), peak discharges occurred just prior to each of the leaf pack pickup dates.

DISCUSSION

Leaf Pack Processing

Leaf processing rates in this study do not conform to the stream order model proposed by Cummins (1975). If leaf processing rates correlate with stream order, then the rate of leaf degradation should decrease with increasing stream order because of larger populations of shredding invertebrates in lower order streams. Data from this study show no significant differences in processing rates between stream orders during the fall when shredders were most abundant. In the summer, processing was slowest in first order streams where shredders were most prevalent and processing rates were expected to be highest. This was most likely a result of less mechanical breakage of leaves in the smaller streams due to lower current velocities.

Cummins (1975) felt that initial processing of conditioned leaves was through ingestion by large shredders such as *Pteronarcys* (Plecoptera) and the Limnephilidae (Trichoptera). The dominant shredder taxa collected in this study were all small particle feeders (e.g. *Polypedilum, Cricotopus, Leuctra, Paracapnia*) and their feeding activities could not account for the large weight loss, especially in summer. Benfield, et al. (1977) suggested that, "in the absence of large shredder species, the major route of processing was the softening of leaf tissue by microbial activity and subsequent fragmentation by mechanical breakage due largely to water currents." Field observations, and the higher coefficients of variation for weight loss in the summer indicate that water level fluctuations and subsequent changes in current velocity could account for the rapid processing rates.

The slower processing rates and decreased variability for red pine leaves during both sampling periods can be attributed to the longer period of time required for conditioning of conifer leaves. Different leaf species become conditioned by microbial activity at different rates resulting in differential rates of invertebrate colonization (Sedell, et al. 1975, Boling, et al. 1975). This is also supported by the present study. Greater numbers of invertebrates were present in the aspen packs than in the red pine packs during the first four weeks. This differential rate of microbial conditioning allows a continuous addition of new food sources to the invertebrate community (Petersen and Cummins 1974).

The mean processing coefficient for aspen leaves for the fall period is near that reported by Petersen and Cummins (1974). The summer mean processing coefficient for aspen leaves is an order of magnitude higher than their reported fall values. The lack of reported data for leaf processing for the summer makes further comparisons impossible. The higher summer processing rates in this study for both leaf species can probably be attributed to greater mechanical disruption as a result of higher current velocities in the summer.

Several other factors may have contributed to the higher processing rates in the summer including temperature, higher invertebrate numbers in the leaf packs, and the condition of the leaves. Aspen leaves used in the summer were on the ground approximately seven months prior to collection and water soluble compounds had already been leached from the leaves.

Invertebrates

The colonization of leaf packs by invertebrates increases with time as the leaves become conditioned by bacteria and fungi (Sedell, et al. 1975). Data from this study generally support this conclusion (Tables 4 and 5). An exception was noted for aspen packs in the summer where the number of invertebrates increased during the first four weeks but decreased from four to six weeks. The increase during the first four weeks is a result of greater microbial conditioning of the leaves. The decrease between the fourth and sixth week might be explained by two factors: 1) higher current velocities that resulted from increased stream flow may have caused greater instability in the aspen packs, forcing invertebrates to leave the packs and drift downstream; and 2) emergence of one or more cohorts of dominant species without replacement by the next cohort. The increase in the number of invertebrates in aspen packs from six to eight weeks was a result of the addition of new genera not previously collected, and more individuals in those genera that had declined during the previous two weeks.

The greater stability of red pine packs that resulted from the different method of construction of these packs lessened the adverse effects of higher current velocities. The mean number of invertebrates colonizing red pine packs in the summer increased throughout the eight weeks.

The mean number of organisms per sample increased with increasing stream order in the summer for both aspen and red pine packs. This increase may be a result of greater population size and a greater number of species in higher order streams. More favorable habitat for colonization and greater physical stability in higher ordered streams probably led to larger invertebrate populations.

In the fall, the mean number of organisms per sample generally decreased with increasing stream order, indicating that a factor other than physical stability of the environment was determining the density of the invertebrates. Petersen and Cummins (1974) stated that "a large portion of the aquatic insect community has become synchronized to the autumnal input of leaf material." The greater input of leaves to small, headwater streams in the fall results in higher shredder populations in these streams.

The change in dominant taxa between seasons is a result of specific life cycles that are related to changes in physical factors such as temperature, photoperiod, and specific food sources. The taxa that occurred as dominants during both seasons generally have extended emergence periods, multiple generations per year or several species with different hatching and emergence periods within a genus.

RECOMMENDATIONS

1. Additional studies of leaf processing rates should include data on physical factors such as temperature, current velocity, pH and invertebrate biomass to determine the single and joint effects of these parameters on leaf processing.
2. A larger data base is needed, including a greater number of stations and more leaf packs per station, to determine the true relationship between leaf processing rates and stream order.
3. The relationship between invertebrate functional groups and stream order warrants further study. This form of analysis may provide a relatively easy method of classifying streams but further documentation of this method of analysis is necessary.
4. A standard methodology for investigation of detritus processing in aquatic habitats is needed if future studies of community function are to be of value.
5. More information on invertebrate food habits would facilitate the placing of organisms into functional groups.

LITERATURE CITED

Benfield, E. F., D. R. Jones, and M. F. Patterson. 1977. Leaf pack processing in a pastureland stream. Oikos 29:99-103.

Boling, R. H., Jr., E. D. Goodman, J. A. VanSickle, J. O. Zimmer, K. W. Cummins, R. C. Petersen, and S. R. Reice. 1975. Toward a model of detritus processing in a woodland stream. Ecology 56:141-151.

Cummins, K. W. 1975. The ecology of running waters theory and practice. Pages 277-293 *in* D. B. Baker, W. B. Jackson, and B. L. Prater, eds. Proc. Sandusky River Basin Symposium. Tiffin, Ohio. U.S. Gov't. Printing Office 1976-653-346.

Cummins, K. W., J. J. Klug, R. G. Wetzel, R. C. Petersen, K. F. Suberkropp, B. A. Manny, J. C. Wuycheck, and F. O. Howard. 1972. Organic enrichment with leaf leachate in experimental lotic ecosystems. Bioscience 22(12):719-722.

Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Fisher, S. G. 1971. Annual energy budget of a small forest stream ecosystem, Bear Brook, West Thornton, New Hampshire. Ph.D. Thesis. Dartmouth College, Hanover, N.H. 97 pp.

Fisher, S. G., and G. E. Likens. 1972. Stream ecosystems: organic energy budget. Bioscience 22:33-35.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43:421-439.

Green, J. C. 1974. Geology of the copper-nickel deposits of Minnesota. Naturalist 25:1-3.

Hart, D. D., and R. P. Howmiller. 1975. Studies on the decomposition of allochthonous detritus in two Southern California streams. Verh. Internat. Verein. Limnol. 19:1665-1674.

Horton, R. E. 1945. Erosional development of streams and their drainage basins. Bull. Geol. Soc. Amer. 56:275-370.

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

Hynes, H. B. N., N. K. Kaushik, M. A. Lock, D. L. Lush, Z. S. J. Stocker, R. R. Wallace, and D. D. Williams. 1974. Benthos and allochthonous organic matter in streams. J. Fish. Res. Board Can 31:545-553.

Jones, J. G. 1975. Heterotrophic microorganisms and their activity. Pages 141-154 *in* B. A. Whitton ed. River ecology. Univ. California Press, Berkeley.

Kaushik, N. K., and H. B. N. Hynes. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. J. Ecol. 56:229-243.

Kaushik, N. K., and H. B. N. Hynes. 1971. The fate of the dead leaves that fall into streams. Arch. Hydrobiol. 68:465-515.

Kowalczewski, A. 1970. The leaf litter as a food source of aquatic organisms in the river Thames. Pol. Arch. Hydrobiol. 17(30): 133-134.

Mathews, C. P., and A. Kowalczewski. 1969. The disappearance of leaf litter and its contribution to production in the River Thames. J. Ecol. 57:543-552.

Merritt, R. W., and K. W. Cummins. 1978. Ecological tables *in* An introduction to the aquatic insects of North America. Kendall/ Hunt Publ. Co., Dubuque, Iowa. 441 pp.

Minshall, W. G. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology 48(1): 139-149.

Nelson, D. J., and D. C. Scott. 1962. Role of detritus in the productivity of a rock outcrop community in a Piedmont stream. Limnol. Oceanogr. 7:396-413.

Park, D. 1974. On the use of the litter bag method for studying degradation in aquatic habitats. Int. Biodeterior. Bull. 10(2):45-48.

Paul, R. W., Jr., E. F. Benfield, and J. Cairns, Jr. 1977. Effects of thermal discharge on leaf decomposition in a river ecosystem. Paper presented at the 20th International Association of Theoretical and Applied Limnology Meetings, Copenhagen, Denmark. 16 pp.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biol. 4:343-368.

Reice, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology 55:1271-1282.

Sedell, J. R., F. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verh. Internat. Verein. Limnol. 19:1617-1627.

Short, R. A. and P. E. Maslin. 1977. Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. Ecology 58:935-938.

Strahler, A. N. 1954. Quantitative geomorphology of erosional landscapes. Compt. Rend. 19th Intern. Geol. Congr., Sec. 13: 341-354.

Teal. J. M. 1957. Community metabolism in a temperate cold spring. Ecol. Monogr. 27:283-302.

Triska, F. S. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream. Ph.D. Thesis. Univ. Pittsburgh. 189 pp.

Vannote, R. L. 1969. Detrital consumers in natural systems. Pages 20-23 *in* The stream ecosystem. Tech. Rpt. No. 7. Institute of Water Research, Michigan State Univ.

Veith, D. L., M. G. Pojar, W. A. Ryan, and S. K. Hakomaki. 1976. The Regional Copper-Nickel Study technical assessment program. Naturalist 27(34):14-21.

Weber, C. I. 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. U.S. Environmental Protection Agency. 670/4-73-001.

Woodall, W. R., Jr., and J. B. Wallace. 1972. The benthic fauna in four small Southern Appalachian streams. Am. Midl. Nat. 88:393-407.

APPENDIX

List of taxa and number of individuals collected.

	Summer	Fall
Shredders		
Plecoptera		
Pteronarcidae		
Pteronarcys	8.0	1.0
Nemouridae (unidentified)	0.3	2.3
Amphinemura	25.0	0.7
Leuctridae (unidentified)	85.7	
Leuctra	107.2	
Capniidae	7.3	
Allocapnia	59.3	
Paracapnia		402.5
Taeniopterygidae		
Taeniopteryx		250.5
Filipalpia (suborder)	30.0	186.0
Trichoptera		
Limnephilidae (unidentified)	0.3	2.7
Grammotaulius	1.0	0.3
Pycnopsyche		1.0
Nectopsyche	1.3	
Platycentropus		0.5
Lepidostomatidae		
Lepidostoma	122.5	124.1
Diptera		
Tipulidae (unidentified)	1.3	1.0
Tipula	1.7	6.2
Chironomidae		
Cricotopus	1084.0	100.2
Polypedilum	1794.9	20.8
Brillia	12.3	329.2
Endochironomus		0.5
Collector - gatherers		
Ephemeroptera		
Heptageniidae (unidentified)	37.0	1.3
Stenacron		1.0
Stenonema (rubrum, fuscum, rivulicolum)	20.3	22.8
Baetidae (unidentified)	150.3	23.3
Baetis (flavistriga, frondalis, hageni)	183.5	31.5
Heterocloeon	4.0	

	Summer	Fall
Ephemeroptera (cont)		
Leptophlebiidae (unidentified)	199.3	271.1
Paraleptophlebia (debilis)	46.9	4.7
Leptophlebia		35.8
Ephemerellidae		
Ephemerella	153.5	277.6
Tricorythidae		
Tricorythodes	264.5	
Caenidae (unidentified)	0.3	
Caenis	141.0	
Polymitarcidae		
Ephoron album	0.3	
Trichoptera		
Brachycentridae		
Micrasema	6.0	10.7
Leptoceridae		
Ceraclea	6.3	0.5
Coleoptera		
Elmidae (unidentified)	42.0	2.7
Stenelmis	21.0	
Dubiraphia	1.5	0.3
Macronychus	1.7	
Optioservus	35.6	16.5
Diptera		
Tipulidae		
Antocha	0.3	0.3
Chironomidae		
Orthocladinae (subfamily)	1294.2	1039.4
Thienemanniella	43.3	17.2
Diplocladius		74.5
Rheocricotopus	347.3	37.9
Cardiocladius	98.0	
Trissocladius		1.1
Eukiefferiella	1357.9	1284.7
Parametriocnemus	419.9	216.9
Psectrocladius	23.3	1.5
Chironomini (tribe)	162.8	3.4
Stictochironomus	2.1	
Tanytarsini (subfamily)		
Micropsectra	447.9	8.8
Amphipoda		
Hyallela azteca	20.2	1.7
Oligochaeta	147.5	3.1
Decapoda	2.7	
Isotomidae		
Isotoma	0.3	

	Summer	Fall
Filter feeders		
Ephemeroptera		
Siphlonuridae		
Isonychia	4.7	
Trichoptera		
Philopotamidae (unidentified)	728.5	0.7
Chimmara (socia, obscura)	761.8	0.8
Dolophilodes	67.2	0.3
Psychomyiidae (unidentified)	13.7	
Psychomyia		0.3
Polycentropodidae		
Neureclipsis	38.8	0.7
Hydropsychidae (unidentified)	1650.1	15.1
Cheumatopsyche	374.6	47.0
Hydropsyche (betteni, cuanis, slossonae, simulans, bifida)	1630.7	76.0
Macronema (zebratum)	305.7	
Brachycentridae		
Brachycentrus (numerosus)	43.8	2.7
Diptera		
Simuliidae (unidentified)	2648.0	947.3
Simulium	141.5	
Chironomidae		
Chironominae (tribe)		
Tanytarsini (subfamily)	672.1	109.6
Tanytarsus	946.7	85.8
Rheotanytarsus	406.6	128.1
Chironomini (subfamily)		
Microtendipes	80.7	
Pelecypoda		1.0
Sphaeridae	1.0	
Scrapers		
Ephemeroptera		
Baetidae		
Pseudocloeon	45.5	0.3
Leptophlebiidae		
Choroterpes (basilis)	34.0	
Coleoptera		
Psephinidae		
Ectopria	0.3	

	Summer	Fall
Gastopoda	4.0	
Physa	84.3	0.3
Ferrissia	1.3	
Piercing herbivores		
Trichoptera		
Hydropilidae (unidentified)	2.7	0.3
Hydroptila	3.7	4.0
Agraylea		0.7
Orthotrichia		0.3
Oxyethira	14.7	1.0
Mayatrichia (ayama)	10.0	
Neotrichia	0.3	
Ithytrichia	16.5	
Predators		
Plecoptera		
Setipalpia (suborder)	37.5	27.3
Perlidae (unidentified)	24.2	12.0
Acroneuria	30.6	2.3
Perlesta (placida)	6.7	
Phasganophora (capitata)	1.3	
Paragnetina	6.3	
Perlodidae (unidentified)	0.3	
Isoperla	3.0	18.1
Trichoptera		
Rhyacophilidae		
Rhyacophila	1.7	4.7
Leptoceridae		
Oecetis	5.5	
Polycentropodidae		
Nyctiophylax	1.3	
Odonata		
Anisoptera		
Calopterygidae	1.8	
Calopteryx	3.0	
Zygoptera	1.0	0.3
Cordulegasteridae		0.3
Cordulegaster		0.5
Gomphidae	9.5	0.8
Aeshnidae	2.5	0.3
Macromiidae	0.3	

	Summer	Fall
Megaloptera		
Corydalidae	4.0	
Coleoptera		
Dytiscidae	6.7	1.2
Hydraenidae	1.0	
Gyrinidae	9.3	
Diptera		
Tipulidae		
Dicranota	0.3	1.7
Ceratopogonidae		
Palpomyia group	26.6	0.3
Chironomidae		
Tanypodinae (subfamily)	16.2	11.6
Conchapelopia	791.7	96.2
Nilotanypus	15.1	
Zavrelimyia	1.2	
Chironomini (tribe)		
Parachironomus	0.7	
Empididae	1.0	
Rhagionidae		
Atherix variegata	79.3	27.7
Tabanidae	11.4	
Nematoda	2.2	
Hirudinea	7.3	0.3
Hydracarina	34.5	0.3