Longitudinal and Seasonal Distribution of Benthic Invertebrates in the Little Lost River, Idaho

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ABSTRACT: A yearlong investigation of the Little Lost River, Idaho (five sites) was conducted to determine the environmental conditions and benthic invertebrate community composition of the stream and to discover factors responsible for distribution of the benthos. All chemical constituents measured showed a tendency to increase from headwaters to mouth. Stream temperatures ranged from 0-15 C near the headwaters and 0 to 22 C near the mouth. Chlorophyll *a* content of the periphyton was low (1-19 mg/m^2) following heavy winter ice cover and spring runoff, but attained relatively high levels (12-68 mg/m2) by the end of September. Allochthonous detritus levels were highest (64-96 g/m^2) near the headwaters; the lowest levels (16-24 g/m^2) were found in areas where the riparian vegetation was restricted largely to sagebrush and grass.

The study revealed a fauna comparable in richness to other Rocky Mountain streams. Sixty-two of the 68 taxa collected were insects. Ephemeroptera was the predominant group in terms of both species (29% of total) and number (62% of total). The most common species were *Rhithrogena robusta, R. hageni* and *Baetis tricaudatus* (Ephemeroptera); *Nemoura* sp., *Alloperla* sp. and *Isoperla fulva* (Plecoptera); and *Glossosoma* sp. and *Hydropsyche* sp. (Trichoptera). Mean number of invertebrates was between 1500 and 5000/m^2 at the various sites.

Local environmental conditions exerted a strong influence on the structure of the invertebrate community at the various locations in the river. Foremost among these were ice formation, temperature, volume of flow and food. Even though the volume of flow in the Little Lost River gradually recedes as it percolates into the substratum, the invertebrate community does not show a reversion to headwater conditions. Only 46% of the mayflies, 33% of the stone flies, 38% of the caddis flies and 14% of all others found in the headwaters also occurred near the downstream terminus and all of those were widely distributed in the river.

INTRODUCTION

The Lost Streams of Idaho constitute a unique set of isolated lotic environments located along a 146-km front in the Upper Snake River Valley of eastern Idaho (Andrews and Minshall, 1979). The streams originate in the Rocky Mountains bordering the Continental Divide and flow in a southeasterly direction to the edge of the Snake River Plain. The Snake River Plain is a high plateau built up of basalt lava flows erupted during the past several million years. The lava flows are very porous and streams contacting them disappear from the surface—hence the name, "lost" streams.

The present study involved a yearlong investigation of one of the Lost Streams, the Little Lost River (Fig. 1). The main objectives were to determine the species composition and longitudinal distribution of the benthic community of the Little Lost River and to see how these varied seasonally. This permitted placing the results of a more limited survey of all the Lost Streams in perspective and gave insights into the factors responsible for the macrodistribution of the benthic invertebrates.

DESCRIPTION OF THE LITTLE LOST RIVER AND COLLECTING SITES

Little Lost River arises in rugged mountainous terrain, near Mt. Borah, the tallest peak in Idaho (3750 m elev.), but soon enters a large glacial valley. Most of the streams entering the valley from side canyons sink into alluvium (up to 900 m deep in places) before reaching the river, except possibly during times of high runoff. The river disappears in an ephemeral playa, known locally as the "sinks," near the margin of the Snake River Plain and approximately 85 km from its source.

The stream lies at the northern edge of the Great Basin province. The climate is cool (mean annual temperature, 6C) and dry (30-76 cm/year). Summer temperatures rarely exceed 25C. About twice as much precipitation falls on the mountains as in the valley. Most of the stream flow comes from the mountains and originates as snowmelt. Sparse stands of coniferous trees characterize the mountains, while the vegetation of the valleys is largely sagebrush (*Artemisia tridentata*) and grass. Near the stream mouth, where it enters the Snake River Plain, some agricultural use occurs.

Five study sites were selected in riffle regions along the river from the headwaters to near Howe, Idaho (Fig. 1). Stream gradients ranged from 17.5 m/km near the source to 6.3 m/km near the overland terminus. The headwaters (Station 0) lie in Sawmill Canyon. The canyon is steep-walled, with mixed stands of douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus engelmanni*) on the slopes and

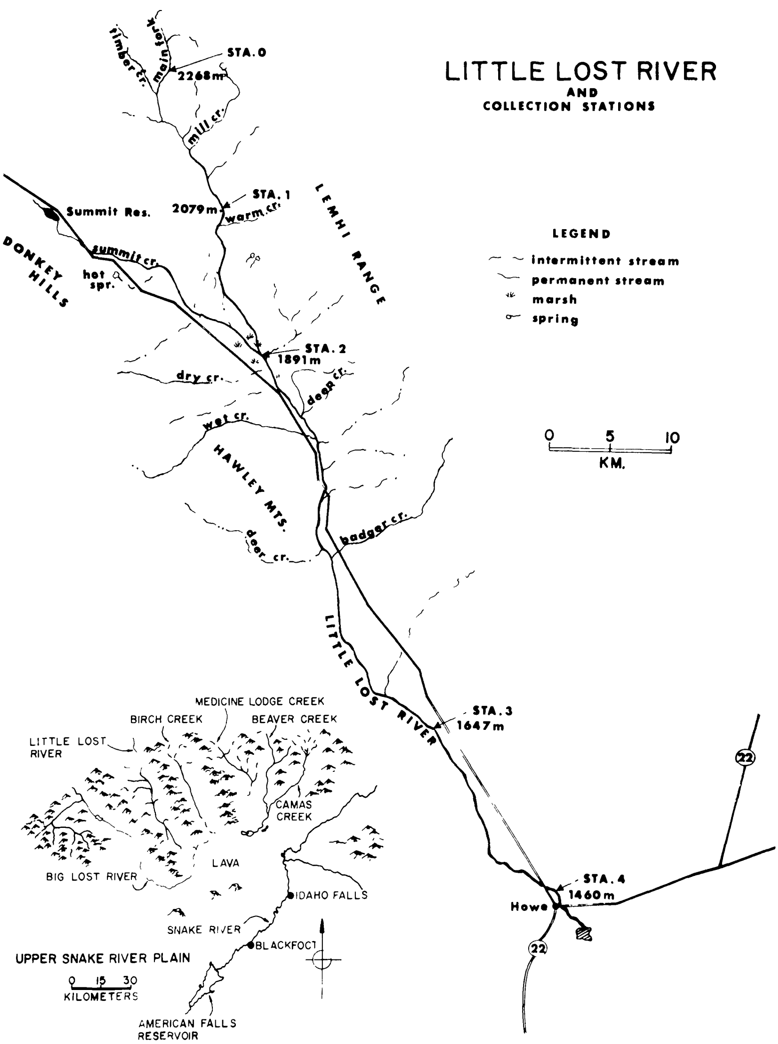

Fig. 1.—Drainage map of the Little Lost River, Idaho. Location and elevations of stations are indicated. The inset shows the location of the Little Lost River in relation to the other Lost Streams and the Snake River

growing along the river. Along most of this section conifers form a canopy over the river. The substrate consists of stones 10-30 cm in diam. Small pools, created by conifer trees that have fallen into the stream, are connected by riffles.

Station 1 is ca. 200 m upstream from the mouth of Sawmill Canyon. The riparian vegetation is dominated by balsam poplars (*Populus balsamifera*), many of which were killed by fire in 1963. River birch (*Betula fontinalis*) and willows (*Salix* spp.) are common, with crested wheat grass (*Agropyron cristatum*) forming most of the ground cover near the stream. The substratum is mostly stones 5-30 cm in diam, with some smaller material. The stream consists of riffles and only an occasional pool.

Station 2 is ca. 50 m below the confluence of the Little Lost River and Summit Creek and 12.1 km below the mouth of Sawmill Canyon. Below Sawmill Canyon the river loses as much as 50% of its flow to percolation into the alluvium. No trees occupy the banks in this area. The vegetation is dominated by sagebrush but includes crested wheat grass and *Poa* spp. The substratum consists of uniform stones ca. 5-12 cm in diam, with small sand deposits present in the meanders.

At Station 3, willows line the stream banks. The surrounding vegetation of the valley floor is a mixture of sagebrush, crested wheat grass, and rabbitbrush (*Chrysothamus nauseosus*). The substratum consists of alluvial gravels 2-10 cm in diam, with sand deposits at the meanders. Velocity was greater here than at any of the other stations, as was discharge. The latter is due to the inflow of several small, spring-fed creeks immediately upstream where the water table is forced to the surface by a large ridge extending from the Lemhi Mountains. Long nonturbulent runs and short riffles characterize this section of the stream.

Station 4 is 1.6 km upstream from where the river sinks. Roses (*Rosa woodsii*) and willows dominate the streamside, with balsam poplar and dogwood (*Cornus sericea*) occasionally present. The surrounding area is agricultural land, and during the irrigation season part of the river flow is diverted to nearby croplands. The substratum is smaller than at the other stations, averaging 2-5 cm in diam, with sand and silt mixed in with the rocks. Discharge here is less than at Station 3 because of water loss through infiltration.

METHODS

Benthic invertebrates and water samples were collected monthly. Qualitative benthos samples were taken with an aquatic dip net (1-mm mesh) over a wide variety of habitats. Quantitative samples were collected by using redwood trays 625 $cm^2 \times 9.5$ cm high, each containing 23 basalt rocks of similar size, shape and texture. These were placed within a riffle of each study area and were emptied monthly except when ice cover or high water prevented collecting. The trays were identical to those described by Minshall and Minshall (1977). They were removed by slipping a dip net (1-mm mesh) underneath each tray and quickly raising the net and the enclosed tray to the surface. In the subsequent processing of the material in the laboratory, a sieve having the same mesh as the netting that lined the bottom of the trays (263 μm), was used.

Water samples were obtained from the center of the stream, treated with 5 ml of chloroform, and returned to the laboratory for chemical analysis. The methods used are the same as those described by Minshall and Andrews (1973). Maximum-minimum recording thermometers were placed on the streambed inside sections of pipe and were read monthly. Discharge was calculated from stream velocity, depth and width. Velocities were measured with a small Ott C-1 current meter.

Chlorophyll *a* content of the periphyton was measured twice during the growing season. Chlorophyll extractions were made by immersing rocks from a 156 cm^2 area in 90% acetone. Extraction was carried out in black containers kept refrigerated during the 24-hr period. Spectrophotometric determination was with a Beckman DB-G Spectrophotometer, using the techniques and formula presented by Strickland and Parsons (1968).

Allochthonous leaf detritus from the substrate trays was examined in September and October 1970. The trays were in the stream 30 days prior to sampling. In the laboratory, leaf detritus was separated into coniferous and deciduous groups, identified, dried at 60C for 24 hr and weighed.

RESULTS

LIMNOLOGICAL PARAMETERS

Longitudinal variation in *p*H, specific conductance, total alkalinity, nitrate, phosphate, turbidity and discharge for the five stations of the Little Lost River are presented in Figure 2. Most of the constituents increased downstream, although the highest amounts usually were recorded at Station 3. Most streams increase their volume of flow downstream but the Little Lost River deviated from this pattern. After the stream leaves Sawmill Canyon, it rapidly loses water to the porous alluvium over which it flows; the same thing occurs again below Station 3.

Station 0 has the narrowest temperature range (0-15C). The maximum was reached in July, after which it decreased rapidly (Fig. 3). The elevation of Station 0 (2268 m), the extensive forest canopy along the stream and the canyon walls are responsible for this. In contrast, Station 2 had the greatest temperature range during the year (—1 to 24C) because of its full exposure. From December through March this station had ice cover, which attained a depth of 1 m. Both anchor ice and surface ice were present. The other accessible stations had only light ice cover or none at all.

DISTRIBUTION OF PLANT MATERIALS

Periphyton (as chlorophyll *a*) and allochthonous detritus standing crops were assessed as measures of potential food available for the invertebrate community. Chlorophyll *a* was lower in July than in September at all stations (Table 1) as a result of snowmelt runoff. Except for Station 0, which had high values due to a large amount of *Nostoc,* there was a progressive increase in chlorophyll *a* concentrations from headwaters to the mouth. Levels of deciduous detritus ranged from 19 to 128 g DW/m^2 (Fig. 4). Highest amounts were at Stations 1 and 3. Station 0 had mainly coniferous detritus; less than 10% was of deciduous origin.

LONGITUDINAL DISTRIBUTION OF INVERTEBRATES

Ephemeroptera.—Five species of mayflies were restricted to the headwaters (Table 2). Nine species extended from the headwaters onto the valley floor, and all but three of these occurred throughout the entire stream. Six species were taken only on the valley floor and were restricted to one or two sites

Rhithrogena robusta was the predominant mayfly at Station 0. *Rhithrogena hageni* replaced *R. robusta* as the predominant mayfly at Station 1 and was even more abundant than *Baetis tricaudatus,* which predominated at the remaining three stations. Eight species of mayflies were taken at Station 2 during the winter months, with an average of only one individual of each species taken per collection. However,

TABLE 1.—Chlorophyll *a* (mg/m^2) of the periphyton of the Little Lost River, Idaho

	Station				
	0	1	2	3	4
18 July 1970	13	2	1	9	19
28 September 1970	24	16	12	54	68

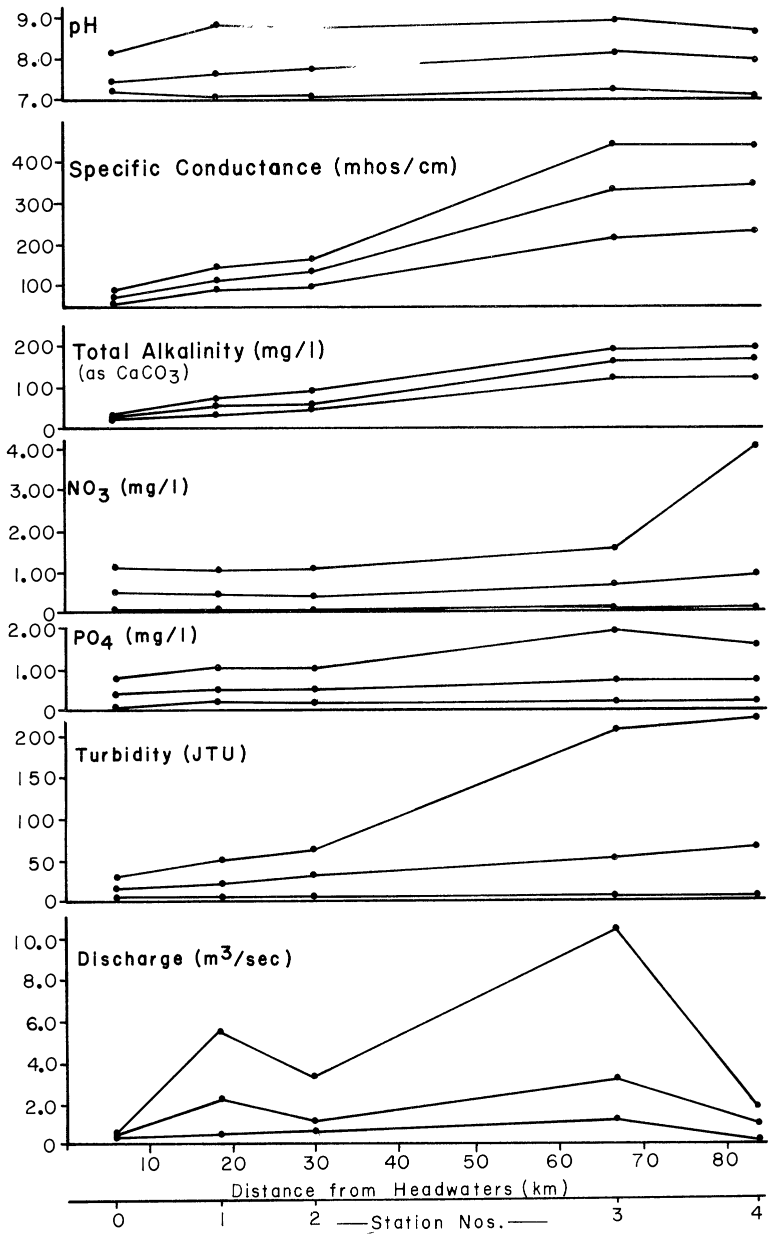

Fig. 2.—Summary of water quality and discharge conditions in the Little Lost River during the period November 1969 through October 1970. Mean, maximum and minimum values measured during the period are given

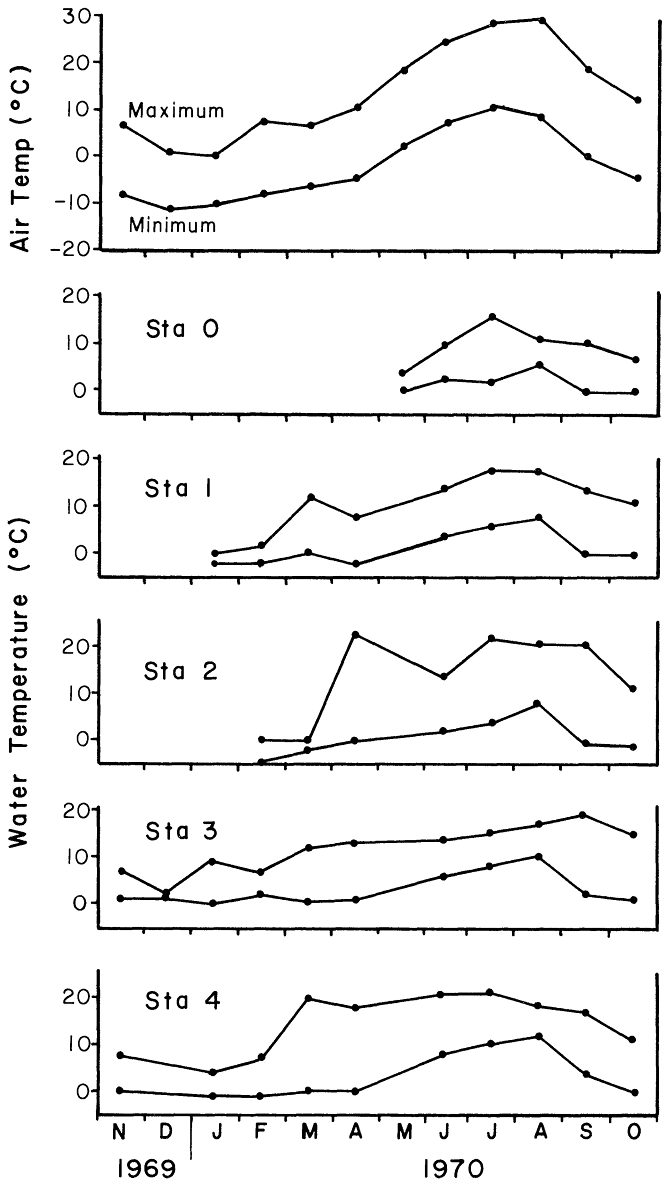

Fig. 3.—Air and weather temperature maxima and minima for the Little Lost River, Idaho. Air temperatures from U.S. Weather Bureau Station, Howe, Idaho, 0.5 km S of Station 4

during the summer-autumn period 12 species were found here in much higher numbers. It appears that the harsh winter conditions, including anchor ice, had a detrimental effect on the mayflies but that by summer successful recruitment into the community had occurred by drift or through the hatching of eggs. The only mayfly restricted to Station 3 was *Ephemerella flavilinea,* which was taken only in March and April but in fairly high numbers. The only mayfly restricted to Station 4 was *Tricorythodes minutus,* a slower-water species. Most mayflies were absent or scarce from samples during June and July.

Plecoptera.—Distribution of the Plecoptera is similar to that of mayflies (Table 3). Of 16 species of stone flies, four were restricted to the canyon, eight were found in both canyon and valley, and four were found only at the lower end of the valley. Stone flies were important components of the aquatic community at Station 0, where they comprised 27% of the total number (*Nemoura* predominating), and also at Stations 2 and 4, where they comprised 12% of the total. *Arcynopteryx parallela* and *Pteronarcella badia* were the most numerous of those which were distributed along the length of the stream. These two species are eurythermal and also have a large altitudinal range in the Gunnison River, Colorado (Knight and Gaufin, 1966). The distribution indicated in Table 3 agrees with the findings of Knight and Gaufin on altitudinal range, except in the case of *Isoperla fulva* and *Claassenia sabulosa,* which were restricted to the lower end of the Little Lost River valley below 1647 m elevation.

Trichoptera.—Of 13 species of Trichoptera recorded (Table 4), four were restricted to Sawmill Canyon, and three of these were species of *Rhyacophila.* Another

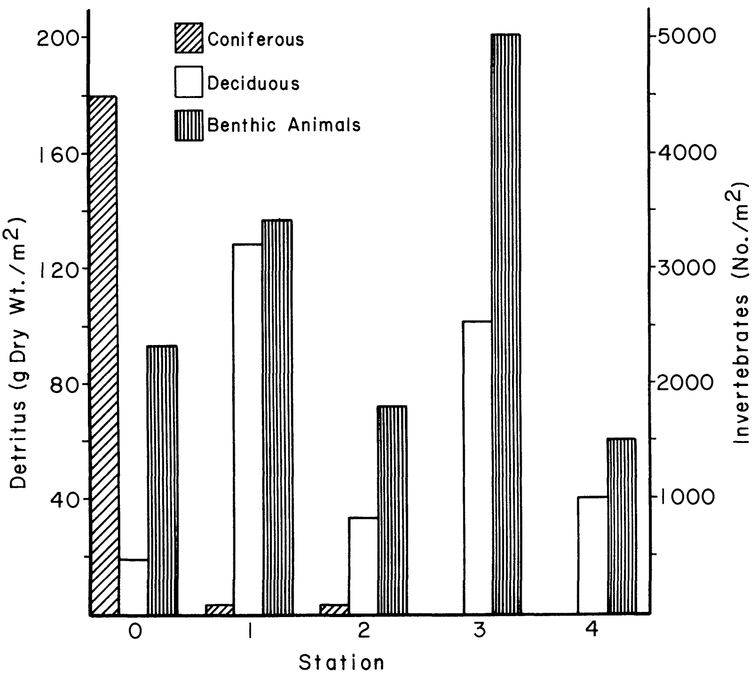

Fig. 4.—Allochthonous detritus of the Little Lost River, Idaho. The amount of conifer needles and cones (*Pseudotsuga, Pinus, Picea*) and deciduous leaves (*Betula, Salix, Populus, Alnus, Rosa*) found in artificial substrate trays during September and October 1970 is shown; the values for the 2 months are combined. The mean numbers of benthic invertebrates taken in the trays during the year also are presented

TABLE 2.—Distribution of the Ephemeroptera of the Little Lost River, Idaho. Table is based on monthly quantitative samples supplemented by qualitative dip net (=N) samples. Total number taken in substrate trays (625 cm^2) is listed by station. The number of samples at each site is indicated in parentheses

Station Elevation	0 2268m (5)	1 2079m (9)	2 1891m (7)	3 1647m (9)	4 1460m (10)
Ephemerella spinifera Needham	6	3	......	....	......
Epeorus grandis (McDunnough)	22	1	......	....	......
Cinygmula par (Eaton)	52	56	......	....	......
Baetis bicaudatus Dodds	46	38	......	....	......
Ephemerella hystrix Traver	3	25	......	....	......
E. doddsi Needham	14	256	16	....	......
Rhithrogena robusta Dodds	141	55	13	....	......
Ameletus velox Dodds	20	11	5	2	......
Cinygma sp.	48	13	15	2	11
Baetis tricaudatus Dodds	3	265	346	1297	192
Ephemerella grandis ingens McDunnough	2	42	11	37	2
E. inermis Eaton	71	197	20	399	43
Paraleptophlebia heteronea McDunnough	14	1	1	9	13
Rhithrogena hageni Eaton	2	456	41	112	4
Epeorus deceptivus (McDunnough)	......	....	9	....	......
Ephemerella coloradensis Dodds	......	....	1	....	......
E. tibialis McDunnough	......	....	8	....	......
E. flavilinea McDunnough	......	....	......	85	......
Ameletus oregonensis McDunnough	......	....	......	2	2
Tricorythodes minutus Traver	......	....	......	....	2
Total species 20	14	14	12	9	8
Total numbers	444	1419	486	1945	269

TABLE 3.—Longitudinal distribution and relative abundance of the stone flies (Plecoptera) of the Little Lost River, Idaho. Table is based on monthly quantitative samples supplemented by qualitative dip net (=N) samples. Total number taken in substrate trays (625 cm^2) is listed by station. The number of samples at each site is indicated in parentheses

Station Elevation	0 2268m (5)	1 2079m (9)	2 1891m (7)	3 1647m (9)	4 1460m (10)
Paraperla	4	......	......	......	......
Arcynopteryx signata (Hagen)	7	......	......	......	......
Acroneuria theodora Needham & Claassen	6	1	......	......	......
Brachyptera sp.	1	4	......	......	......
Nemoura sp.	141	36	17	......	......
Alloperla sp.	40	12	53	5	......
Isogenus sp.	1	21	1	19	26
Arcynopteryx parallela (Frison)	3	6	18	20	24
Pteronarcella badia (Hagen)	1	12	2	43	28
Isoperla patricia Frison	......	6	1	......	......
Capnia sp.	......	1	1	23	......
Acroneuria pacifica Banks	......	16	8	10	8
Isoperla fulva Claassen	......	......	......	159	43
I. mormona Banks	......	......	......	31	12
Claassenia sabulosa (Banks)	......	......	......	10	9
Pteronarcys californica Newport	......	......	......	1	2
Total species 16	9	10	8	10	8
Total numbers	204	115	101	321	152

member of that genus, *R. acropedes*, occurred along the length of the stream except at Station 2. *Arctopsyche grandis* and *Glossosoma* sp. were the only species found over the entire stream, but seven species extended from the canyon onto the valley floor. The most abundant taxon of Trichoptera was *Glossosoma* sp., which was numerous at all stations except Station 0. *Hydropsyche* sp. was quite numerous at Station 4. The least number of species (five) was at Station 2; the other stations each supported between seven and nine species. The fewest individuals were at Station 0.

Miscellaneous taxa.—Four groups of dipterans were widely distributed and numerous throughout the stream (Table 5). One beetle, *Agabus* sp., was restricted to Station 0. Another, *Dubiraphia* sp., was restricted to Station 1 and *Lara* sp. was restricted to Station 2. *Optioservus quadrimaculatus* and *Bidessus* sp., were more widely distributed, occurring at Stations 1 through 4. The snails *Gyraulis, Pisidium* and *Physa* were taken only at Stations 3 and 4. Only one amphipod, *Gammarus lacustris,* was taken in the trays, and this was at Station 4 in August.

SEASONAL OCCURRENCE OF INVERTEBRATES

Efforts to discern the seasonal occurrence of benthic invertebrates at each of the sites were complicated by sampling difficulties due to snow, ice cover and high water during winter and spring, especially at the upper stations (0-2). However, most of the 34 common species (>10 individuals at any site) were present at one or more stations during all seasons. A few species of Ephemeroptera and Plecoptera showed more restricted seasonal patterns (Table 6), including those apparently restricted to spring (*Ephemerella flavilinea*), summer-autumn (*Cinygma* sp., *Epeorus grandis*) and autumn-winter (*Capnia* sp.). It is noteworthy that there was no strong correlation between the season of occurrence of members of the latter group and their spatial distribution. However, a number of the species present during all seasons showed seasonal differences in abundances at the different stations. This is illustrated by a few selected cases in Figure 5. When all species were grouped according to their occurrence in winter-spring vs. summer-autumn, there was no substantial difference in the Shannon-Weiner index of species diversity (H′) between seasons or between sites (range 3.03-3.74) except at Station 2, which had a value of 3.77 in the summer-autumn period but only 2.80 in winter-spring. Species

TABLE 4.—Longitudinal distribution and relative abundance of the caddisflies (Trichoptera) of the Little Lost River, Idaho. Table is based on monthly quantitative samples supplemented by qualitative dip net (=N) samples. Total number taken in substrate trays (625 cm^2) is listed by station. The number of samples at each site is indicated in parentheses

Station Elevation	0 2268m (5)	1 2079m (9)	2 1891m (7)	3 1647m (9)	4 1460m (10)
Neothremma sp.	6	......	......	......	......
Rhyacophila vaccua Milne	3	......	......	......	......
R. hyalinata Banks	1	1	......	......	......
R. vepulsa Milne	N	1	......	......	......
R. acropedes Banks	25	9	......	22	6
Parapsyche elsis Milne	10	36	19	6	......
Glossosoma sp.	3	99	113	154	106
Arctopsyche grandis (Banks)	N	31	14	7	2
Hydropsyche sp.	....	9	9	43	203
Drusinus sp.	....	8	......	3	......
Brachycentrus occidentalis Banks	....	31	......	25	37
Lepidostoma sp.	....	......	2	1	1
Limnephilus sp.	....	......	......	......	1
Total species 13	8	9	5	8	7
Total numbers	48	225	157	261	356

richness also was reduced from 32 to 15 at Station 2 but showed little or no change at the other sites. These differences are attributed largely to the severe ice conditions at Station 2 since the effect of spring runoff, the other catastrophic event occurring during the winter-spring period, should have been similar at all stations.

CONCLUSION

The benthic invertebrate fauna of the Little Lost River is composed mostly of insects; 62 of the 68 taxa belonged to this class. Ephemeroptera was the predominant group in terms of both species (29% of the total) and numbers (62% of total),

TABLE 5.—Longitudinal distribution and relative abundance of various benthic taxa of the Little Lost River, Idaho. Table is based on monthly quantitative samples supplemented by qualitative dip net (=N) samples). Total number taken in substrate trays (625 cm^2) is listed by station. The number of samples at each site is indicated in parentheses

Station Elevation	0 2268m (5)	1 2079m (9)	2 1891m (7)	3 1647m (9)	4 1460m (10)
Turbelleria	14	......	......	N	....
Agabus sp. (Coleoptera)	1	......	......	......	....
Heleidae (Diptera)	2	......	1	N	....
Hydracarina	1	......	......	1	....
Simulium (Diptera)	2	1	32	97	....
Tipula (Diptera)	1	14	2	3	....
Chironomidae (Diptera)	15	163	101	192	94
Dicranota sp. (Diptera)	....	8	4	2	1
Optioservus quadrimaculatus (Horn) (Coleoptera)	....	6	8	27	28
Bidessus sp. (Coleoptera)	....	N	1	2	1
Pericoma sp. (Diptera)	....	8	1	......	....
Dubiraphia sp. (Coleoptera)	....	5	......	......	....
Sialis sp. (Neuroptera)	....	......	3	......	....
Hyalella azteca (Saussure) (Amphipoda)	....	......	......	3	....
Gyraulus sp. (Mollusca)	....	......	......	1	7
Pisidium sp. (Mollusca)	....	......	......	3	4
Physa sp. (Mollusca)	....	......	......	N	5
Lara sp. (Coleoptera)	....	......	......	......	11
Gammarus lacustris Sars (Amphipoda)	....	......	......	......	1
Total taxa 19	7	8	9	13	9
Total Diptera	19	194	141	294	95
Total all others	16	11	12	37	57

TABLE 6.—Common species which were absent from collections during one or more seasons. A dash indicates times for which no sample was obtained

		Winter			Spring		Summer			Autumn		
	Site	D	J	F	M	A	J	J	A	S	O	N
Isoperla mormona	3	X	....	X	X	X	—	....	....	....	....	—
	4	....	....	....	....	X	X	....	....	....	....	....
Ephemerella flavilinea	3	....	....	....	X	X	—	....	....	....	....	—
Nemoura sp.	0	—	—	—	—	—	X	X	X	X	X	—
	1	—	—	....	X	....	....	X	X	X	X	X
	2	—	—	—	—	....	....	....	X	X	X	X
Cinygma sp.	0	—	—	—	—	—	X	X	X	....	X	—
	1	—	—	....	....	....	....	X	X	....	....	....
	2	—	—	—	—	....	....	X	X	....	X	....
	3	....	....	....	....	....	—	X	....	....	....	—
Epeorus grandis	0	—	—	—	—	—	....	X	....	X	X	—
	1	—	—	....	....	....	....	....	X	....	....	....
Capnia sp.	1	—	—	X	....	....	....	....	....	....	....	....
	2	—	—	....	....	....	....	....	....	....	X	....
	3	X	X	X	....	....	—	....	....	....	X	—

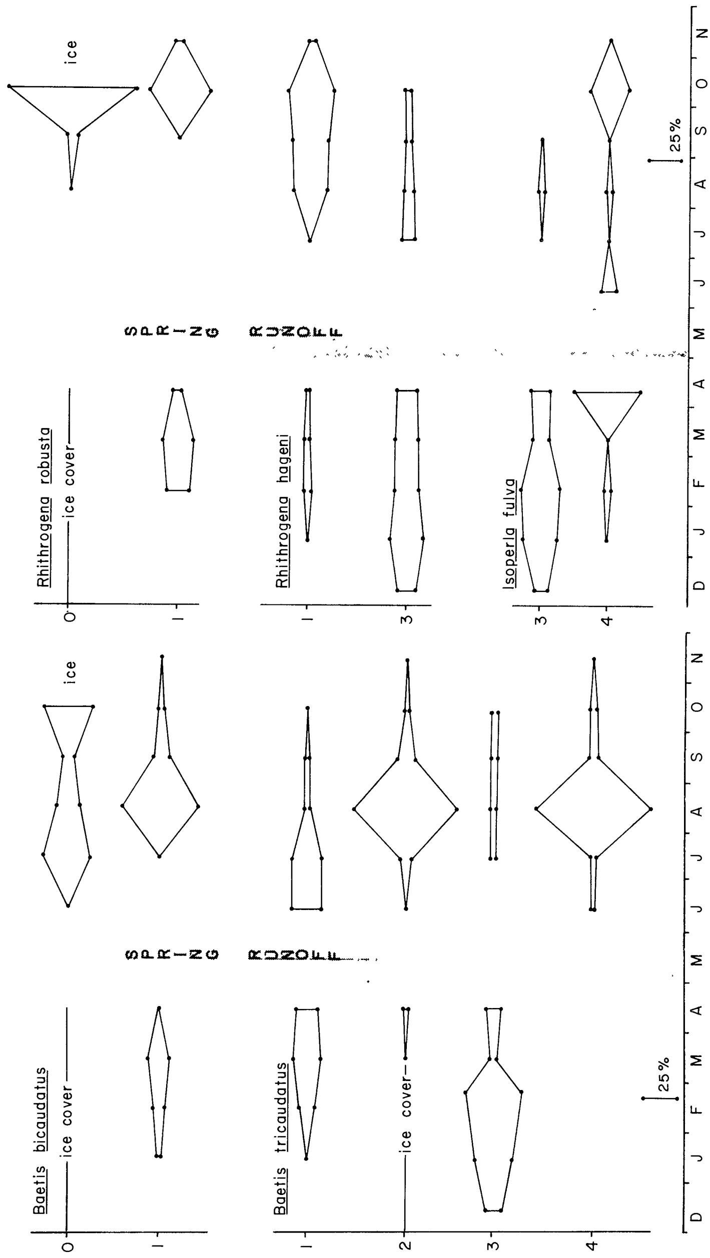

Fig. 5.—Seasonal variations in the abundance of selected species at different stations in the Little Lost River

although some variation occurred between stations. For example, at Station 3 the number of Plecoptera species was greater than Ephemeroptera and at Station 4 the total number of Trichoptera individuals was more. Mean numbers of invertebrates ranged from $1500/m^2$ at Station 4 to $5000/m^2$ at Station 3 (Fig. 4). These findings do not support the notion of an impoverished fauna in the Little Lost River (DeCosta, 1966).

Total number of individuals and numbers per species varied along the river and seasonally between sites even when the same species was present at several locations. Furthermore, there was no definite pattern of progressive changes in the numbers of species or individuals in the longitudinal distribution of invertebrates within the stream, normally associated with decreases in elevation (Gaufin, 1959; Knight and Gaufin, 1966). These observations suggest that community structure itself is dynamic and readily adjusts to local environmental conditions. This appears to be due to the strong influence of local conditions such as ice formation at Station 2 and substantial decreases in discharge at Stations 2 and 4. For example, there was a fairly strong linear correlation between total numbers and mean annual discharge ($r^2=0.82$).

A moderate correlation (linear model $r^2=0.58$; parabolic model $r^2=0.65$) existed between the total number of invertebrates and the amount of detritus. But the relationship was no better than that found for chlorophyll *a* ($r^2=0.65$ for both models). Thus, the longitudinal variations may be explained partly by the amount of food present, but it is not possible to determine from the present data whether food type has any effect.

The Lost Streams are peculiar in that they do not increase progressively in size from headwaters to mouth. Instead, they gradually decrease in size before totally disappearing from the epigean environment. In one sense then, the streams might be thought of as flowing downhill for a time and then returning toward a headwater condition. The invertebrate community in the headwaters was similar to that at the mouth in terms of diversity (H′) (3.74 vs. 3.51). But species richness was greater in the headwaters (38 vs. 32), and there was no return to the community composition of the headwaters as the volumes of flow gradually became similar. Instead, most of the species found in the headwaters were gradually replaced downstream. Only 46% of the mayflies, 33% of the stone flies, 38% of the caddis flies and 14% of all others found at Station 0 also occurred at Station 4; all of these were widely distributed throughout the river. Based on the known biology of the species involved, these shifts appear to be due to substantial differences in degree days between the two sites (ca. 1510 vs. 3160).

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