

BOTTOM FAUNA-SUBSTRATE RELATIONSHIPS IN A NORTHERN COLORADO TROUT STREAM: 1945 AND 1974¹

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Abstract. A study of bottom fauna-substrate relationships conducted on North St. Vrain Creek, Colorado, USA in 1945 was repeated in 1974 to determine changes in the stream environment and in the community structure and standing crop of macroinvertebrates. The stream remains a clear, unpolluted trout stream with soft water of neutral pH. Despite differences in flow, temperature, and riparian vegetation, macroinvertebrate composition was similar to that of 1945; most differences can be attributed to normal year-to-year fluctuations and slight shifts in emergence periods. Total density was less on all substrata in 1974, which is attributed to the higher discharge. Total biomass was comparable except for lower values on bedrock in 1974.

Key words: Colorado; macroinvertebrates; standing crop; substrate; trout stream; watershed changes.

INTRODUCTION

One of the first investigations of bottom fauna-substrate relationships in streams of western North America was conducted during the summer of 1945 on North St. Vrain Creek, Colorado (Pennak and Van Gerpen 1947). Samples taken from sand, gravel, rubble, and bedrock substrata were compared on the basis of the density, biomass, and composition of the macroinvertebrate inhabitants.

During the summer of 1974, 29 yr later, I conducted a study on the same stretch of stream, using the methods of the original study with the following objectives in mind: (1) to determine to what extent the stream environment had been modified, naturally or anthropogenetically, during this period; and (2) to determine any changes which might have occurred in the macroinvertebrate community.

THE WATERSHED

The original 50-m stream section, at an elevation of 1,677 m in the northern Colorado mountains was relocated with the kind assistance of Professor Pennak. The stream itself appeared to have changed little from the original description: a foothills trout stream approximately 20 m wide with a variety of substrate types with rubble predominant. No rooted aquatic plants were present, and epilithic algae were poorly developed. However, a striking difference in streamside vegetation is apparent when the 1945 photograph is compared with the present view (Fig. 1).

North St. Vrain Creek above the study area drains 306 km². The headwaters originate in Rocky Moun-

tain National Park at elevations from 3,350 to 3,650 m. Numerous, small alpine lakes are associated with the headwater drainage area. Most of the remaining upstream area is in Roosevelt National Forest. The subalpine zone is predominantly a spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*) forest. Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) occur at lower elevations. The study area has a typical foothills vegetation, consisting of open stands of ponderosa pine (*Pinus ponderosa*) and occasional Colorado junipers (*Juniperus virginiana scopulorum*).

Land use patterns above the study area have changed little in the past 29 yr, largely due to the protection afforded by the national park and national forest. Most of the drainage area below the national park has a woodland land use classification (U.S. Soil Conservation Service 1973). Since established in the 1900's, Roosevelt National Forest has allowed only selective timber harvesting. Private woodlands are used mainly for homesites rather than wood production (Moreland and Moreland 1975).

The study site is located within rangeland, but in recent years there has been a general decrease in livestock grazing in the foothills and mountains of this area (Moreland and Moreland 1975). The absence of livestock in the immediate study area in recent years has apparently allowed the development of dense stands of riparian vegetation, primarily willow (*Salix exigua*) and Rocky Mountain alder (*Alnus tenuifolia*). The importance of streamside vegetation to macroinvertebrates has been emphasized by Hynes (1970) and Pennak (1971) among others; its increase in the study area, if indicative of upstream changes, may have had an effect on the macroinvertebrate community.

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FIG. 1. Views of North St. Vrain Creek, Colorado, in 1945 (upper) and 1974 (lower). Note increased riparian vegetation in 1974. The 1945 photograph was supplied by R. W. Pennak.

The stream above the study site flows in a steep-walled granitic canyon with dense riparian vegetation. Scattered homesites occur where the canyon broadens out 1.5 km above the study area and for a short distance upstream. The highway follows the canyon for only 3 km and the gravel road along the stream ends in another 4 km. From this point to the headwaters, the majority of the stream is inaccessible by road.

The only major change, other than increased streamside vegetation, known to have occurred above the study area was the construction of a 100-ha storage reservoir. Although the dam is 11 km above the study site, construction activities (1965–1969) must have had a considerable impact on the stream ecosystem. However, the substrate in 1974 did not differ noticeably from the 1945 description.

WEATHER AND FLOW HISTORY

Air temperatures and precipitation data are from U.S. Weather Bureau records at the Longmont Station (1,510 m), 20 km below the study area; year-

round temperature and precipitation data are not available for the mountain areas (Moreland and Moreland 1975).

During the 30-yr period 1944–1974, mean air temperature at the Longmont Station was 9°C with annual means ranging from 8.3° to 11°C. Annual mean air temperatures were similar in 1945 and 1974 (8.6° and 9.4°C, respectively), as were means for June through August (18.9° and 20.5°C). Average temperatures for the immediately preceding years were also similar (8.7°C in 1944 and 8.9°C in 1973).

Annual precipitation averaged 32.8 cm from 1944–1975 with yearly totals ranging from 17.8 to 51.6 cm. Slightly less precipitation occurred during 1974 (32.3 cm) than 1945 (36.3 cm), although comparable amounts occurred from June through August of both years (11.8 and 11.6 cm). However, more than twice as much precipitation fell in June of 1974 as in 1945, including 5.1 cm of rain on 9 June. Precipitation was more evenly spread throughout the summer of 1945, and the daily maximum never exceeded 1.0 cm. The winter of 1973–74 was associated with a greater total snowfall (120.7 cm) than the winter of 1944–45 (87.1 cm). The year preceding the present study had a greater total precipitation (43.2 cm) than 1944 (28.2 cm).

Stream flow records are available only for the years preceding 1954, except for the discharge values calculated during the present study. The discharge from 1944 to 1953 averaged 2.7 m³/s (U.S. Geological Survey). The mean discharge during the 1945 water year (October–September) was 2.8 m³/s. The most recent flood preceding the original study occurred in June of 1941 with a discharge of 34.3 m³/s recorded on 22 June. A flood of comparable magnitude has not occurred since 1941; however, a heavy rainstorm in 1969, which filled the recently completely reservoir in a few days, would otherwise have resulted in severe downstream flooding (J. Cinea, Longmont City Engineer, *personal communication*).

METHODS

Sampling was conducted weekly from 18 June to 6 August, as in the original study. Current velocity and flow were determined with a WeathermeasureTM water current meter. Additional parameters were measured in 1974 to further assess the physical and chemical characteristics of the stream. Free and bound CO₂ were measured titrimetrically using phenolphthalein and methyl orange indicators. Hydrogen ion concentration was measured in the field with Hellige color disks and checked in the laboratory on a pH meter. Dissolved O₂ was determined by the standard Winkler method.

Each week three Surber samples were taken on each substrate type, resulting in a total of 96 samples.

TABLE 1. Abundance of macroinvertebrates on substrata of North St. Vrain Creek, Colorado. Symbols are as follows: + = <1.0/m², nd = not determined in 1945, * = taxa found only in 1945, ** = taxa found only in 1974

Taxon	Organisms/m ²							
	Sand		Gravel		Rubble		Bedrock	
	1945	1974	1945	1974	1945	1974	1945	1974
Ephemeroptera	40	52	312	174	450	167	260	46
<i>Ephemerella</i>	2	30	49	74	48	37	3	2
<i>E. g. grandis</i>	nd	0	nd	0	nd	2	nd	0
<i>E. inermis</i>	nd	8	nd	28	nd	24	nd	2
<i>E. (Dannella)</i>	nd	+	nd	0	nd	0	nd	0
<i>E. margarita</i>	nd	22	nd	43	nd	0	nd	0
<i>E. tibialis</i>	nd	+	nd	3	nd	11	nd	0
<i>Ameletus</i> sp.	+	4	+	+	2	0	0	0
<i>Baetis</i> (2 spp.)	2	5	12	24	59	33	41	11
<i>Pseudocloeon</i> sp.	36	11	240	62	261	43	212	32
** <i>Siphonurus</i> sp.	0	+	0	0	0	0	0	0
<i>Paraleptophlebia</i> sp.	0	0	2	5	30	4	0	0
** <i>Tricorythodes</i> sp.	0	+	0	1	0	0	0	0
<i>Epeorus albertae</i>	0	0	1	1	23	47	2	+
* <i>Heptagenia elegantula</i>	0	0	0	6	0	+	0	0
<i>Rhithrogena doddsi</i>	0	0	+	0	+	3	0	0
* <i>Stenonema</i>	0	0	2	0	4	0	0	0
* <i>Cinygmula</i>	0	0	4	0	22	0	2	0
Plecoptera	0	1	4	24	23	14	0	+
<i>Pteronarcella</i> sp.	0	0	2	+	10	5	0	0
* <i>Pteronarcys</i>	0	0	+	0	+	0	0	0
* <i>Nemoura</i> sp.	0	0	0	+	0	+	0	0
* <i>Diploperla</i> (<i>Isogenus</i>)	0	0	+	0	+	0	0	0
<i>Isoperla patricia</i>	0	0	0	0	4	2	0	0
* <i>Neoperla</i>	0	0	0	0	3	0	0	0
* <i>Atoperla</i>	0	0	+	0	2	0	0	0
* <i>Acroneuria pacifica</i>	0	0	0	0	0	+	0	0
* <i>Claassenia sabulosa</i>	0	0	0	0	0	+	0	0
* <i>Alloperla signata</i>	0	1	0	22	0	4	0	+
* <i>Hastaperla brevis</i> (?)	0	0	0	+	0	2	0	0
* <i>Paraperla</i>	0	0	+	0	4	0	0	0
Trichoptera	+	5	8	19	20	60	35	26
<i>Brachycentrus americanus</i>	+	2	1	+	6	20	33	9
<i>Micrasema</i> sp.	0	1	0	+	+	1	0	+
<i>Lepidostoma rayneri</i>	0	2	3	5	+	12	0	0
<i>Hydropsyche</i> sp.	0	0	+	0	7	18	+	12
* <i>Rhyacophila coloradensis</i>	0	0	0	0	0	0	0	1
<i>Agapetus taho</i>	0	0	2	+	3	7	0	0
<i>Psychomyia flavida</i>	0	0	0	0	0	0	+	+
<i>Agraylea</i> sp.	0	0	1	12	1	+	2	2
* <i>Helicopsyche</i> sp.	0	0	0	+	0	+	0	0
* <i>Athripsodes</i>	0	0	0	0	2	0	0	0
* <i>Oecetis</i>	0	0	0	0	+	0	0	0
* Odonata (Gomphinae)	0	0	0	0	+	0	0	0
Coleoptera	0	+	7	9	20	5	+	+
Elmidae ^a	0	+	7	9	20	6	+	+
** <i>Oreodytes</i> sp.	0	0	0	+	0	0	0	0
Diptera	150	27	222	18	90	19	254	63
<i>Atherix variegata</i>	0	0	+	+	3	1	0	0
* <i>Culicoides</i>	+	0	1	0	0	0	0	0
<i>Palpomyia</i> and <i>Bezzia</i>	1	+	9	0	7	0	+	0
* <i>Tanypodinae</i> ^b	0	+	0	1	0	0	0	0
Chironominae ^c	58	15	90	11	11	4	+	+
Orthocladiinae ^d	8	2	4	+	5	1	0	2
* <i>Diamesinae</i>	69	0	90	0	42	0	19	0
<i>Hexatoma</i> sp.	11	5	18	3	12	2	0	0
* <i>Erioptera</i> sp.	0	+	0	0	0	0	0	0
* <i>Pedicia</i> sp.	0	+	0	0	0	0	0	0
* <i>Protanyderus margarita</i>	0	+	0	+	0	0	0	0
<i>Simulium arcticum</i>	3	+	6	+	7	5	195	56
<i>Deuterophlebia coloradensis</i>	+	0	4	0	4	6	39	5
* <i>Hemerodromia</i> sp.	0	+	0	0	0	+	0	0
* <i>Chrysops</i> sp.	0	+	0	0	0	0	0	0
Oligochaeta	11	50	+	14	4	8	0	0
* <i>Eiseniella tetraedra</i>	0	49	0	14	0	7	0	0
* <i>Allolobophora chlorotica</i>	0	+	0	0	0	+	0	0
* <i>Naididae</i>	11	0	+	0	4	0	0	0
Hydracarina ^e	+	4	23	3	3	1	1	+
* Pelecypoda (<i>Pisidium</i> sp.)	0	1	0	0	0	0	0	0

^a *Cleptelmis* sp. and *Zaitzevia* sp. in 1974.^b *Pentaneura* sp. in 1974.^c *Pseudochironomus* sp., *Parachironomus* sp., *Rheotanytarsus* sp., *Demicryptochironomus* sp., *Polypedilum* sp., *Paratendipes* sp., and *Micropsectra* sp. in 1974.^d *Eukiefferiella* sp., *Orthocladius* sp., *Cardiocladius* sp., and *Cricotopus* sp. in 1974.^e *Sperchon* sp. and *Lebertia* sp. in 1974.

Netting with comparable apertures (740 and 725 μm) was used in the two studies. As originally described, bedrock consisted of the surfaces of very large boulders; rubble consisted of pebbles and rocks with diameters ranging from 25 to 203 mm; coarse gravel consisted primarily of particles from 6 to 25 mm; very coarse sand consisted primarily of particles from 1.6 to 3.2 mm. Benthic samples were sorted in the field, and organisms were placed in 70% alcohol. Wet weights were determined on a balance after specimens had been placed on filter paper for 15 s, as was done in the original study.

RESULTS AND DISCUSSION

Flow, current, and water temperatures were somewhat different than during the summer of 1945. The mean discharge in 1945 ($6.4 \text{ m}^3/\text{s}$) was less than in 1974 ($8.0 \text{ m}^3/\text{s}$), as was the mean current velocity (0.8 and 1.0 m/s). Higher discharge values in 1974 were apparently a result of flow augmentation by summer cloudbursts, which were more frequent and of greater magnitude than in 1945. Water temperatures ranged from $9.4^\circ\text{--}17.8^\circ\text{C}$ in 1945, but only from $12^\circ\text{--}14.5^\circ\text{C}$ in 1974. Small unshaded streams are subject to short-term variations in water temperature (Edington 1966). The near absence of riparian vegetation in 1945 (if indeed a general upstream condition) may partially explain the wider temperature range found in the original study. Precipitation runoff from warm soils may increase stream temperature (Macan 1958); high precipitation in June 1974 associated with warm air temperatures may have caused the higher minimum stream temperature. Although the upstream reservoir releases deep water, it is unlikely that it exerts a significant effect on the water temperature of the study area since the dam is 11 km upstream, and since the water is considerably slowed by a small barrage (also present in 1945) a short distance below the dam.

Free CO_2 values of 1.0 ppm were consistently obtained, and bound CO_2 ranged from 4.5–5.0 ppm. Hydrogen ion concentration oscillated between 7.0 and 7.1. Dissolved O_2 was always $> 100\%$ saturated and exhibited a mean value of 10.1 ppm.

It appears that the stream environment was much the same as in 1945—a clear, unpolluted trout stream with soft water, neutral pH, and a mosaic of substrate types. Major differences were the greater development of riparian vegetation and the higher discharge in 1974.

Macroinvertebrate composition

Cummins (1966) provided a comprehensive review of the relationship of stream organisms to substrate type. No attempt will be made here to review the wealth of subsequent data on this topic.

Table 1 shows the abundance of macroinvertebrates on the four substrata in 1945 and 1974. More specific taxonomic determinations were often possible in the present study than in 1945; if so, the 1945 data are listed under the more specific taxon in Table 1. For example, the abundance data for *Isoperla* found in 1945 were placed under *Isoperla patricia*, the species found in 1974.

A surprising number of taxa were found only in 1945 (one asterisk on Table 1) or only in 1974 (two asterisks). This is especially striking for Plecoptera. Some differences can be explained by changes in emergence times, presumably as a result of the different temperature patterns of the 2 yr (Ide 1940). *Deuterophlebia*, for example, was much more abundant in 1945, but large numbers of empty pupal exuviae were found in 1974. *Pteronarcys* (although perennial) was not found in any of the samples in 1974, but last-instar nymphal exuviae were observed above the water level. This genus was rare in 1945, and in fact most taxa found in only 1 yr were rare (sometimes based on a single specimen) and are likely more indicative of sampling inadequacies than any real changes. A few taxa, however, exhibited considerable abundance 1 yr but were absent the other. *Eiseniella tetraedra*, abundant in 1974, was not reported in 1945. Permanent populations of this lumbricid earthworm are rarely found in unpolluted mountain streams (Ward 1974, *in press*), but are common in the mud banks at just about water level. If specimens were found in 1945, they were probably considered as accidentals. In the present study, considerable numbers were found on all substrata except bedrock. Whether high water washed specimens from the stream banks or permanent populations have been established (perhaps due to an increase in allochthonous organic matter) is difficult to ascertain from one summer's study. They did, however, exhibit a general decrease in abundance throughout the study (concomitant with decreasing flow), and none were found on rubble the last two sampling trips.

Alloperla signata was the most abundant stonefly in 1974 and was found on all four substrata, but was not reported in 1945. Different emergence times, confusion of early instars for *Paraperla* in 1945, or inadequate sampling of early instars may have been responsible. Large numbers of *A. signata* adults were collected in the willows with a sweepnet, and it is conceivable that the increase in streamside vegetation favors this stonefly.

Diamesinae were abundant on all substrata in 1945. It is difficult to account for their absence in the present study, and it may be that this represents a change in macroinvertebrate composition.

Figure 2 compares the relative percentage com-

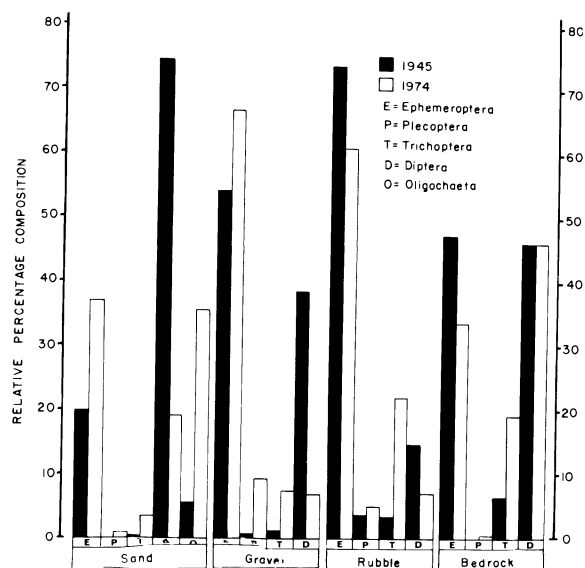


FIG. 2. Relative percentage composition by numbers of major bottom fauna taxa on four substrate types for North St. Vrain Creek, Colorado, 1945 and 1974.

position by numbers of major groups on the four substrata in 1945 and 1974. In 1945 on sand, dipterans (74.4%), ephemeropterans (19.8%), and oligochaetes (5.5%) comprised 99.7% of the macroinvertebrates; in 1974, these groups comprised 91.6% (19.2%, 37.0%, and 35.4%). Dipterans were considerably less important, and ephemeropterans were considerably more important in 1974, whether or not the lumbricid earthworms are included. There was a generally more even distribution of taxa on sand in 1974. The large amount of allochthonous plant material associated with sand in the present study and presumed differences in detrital particle size composition may have allowed colonization by

a greater variety of taxa. Unfortunately, no information on detritus is available from 1945. In 1974, 10 taxa were restricted to sand (Table 1). No taxa were listed as restricted to sand in 1945, although some likely would have been had more specific taxa been considered. A single specimen of *Ephemerella* (subgenus *Dannella*) was found on sand in 1974, the first confirmed report of *Dannella* west of the Mississippi River, and likely an undescribed species (R. K. Allen, *pers. comm.*).

On gravel, ephemeropterans (54.2%) and dipterans (38.6%) comprised 92.8% of the macroinvertebrates in 1945, but only 73.4% (66.5% and 6.9%) in 1974. Trichopterans were nearly six times more important, and plecopterans were more than 15 times more important on gravel in 1974. Ephemeropterans strongly dominated gravel in 1974, but compared to 1945, a generally more even distribution of taxa was observed. Only one rare taxon (*Oreodytes*) was restricted to gravel in 1974, and none were restricted to this substrate in 1945.

In 1945, on rubble, ephemeropterans (73.7%) and dipterans (14.7%) comprised 88.4% of the macroinvertebrates; in 1974, these groups comprised only 67.9% (60.8% and 7.1%). Trichopterans were the second most abundant taxon in 1974 (22%), being seven times more important than in 1945. In 1974, six taxa were restricted to rubble; in 1945, seven taxa were restricted to this substrate.

On bedrock, ephemeropterans (47.2%) and dipterans (46.1%) comprised 93.3% of the macroinvertebrates in 1945. In 1974, these groups comprised 79.7% (33.6% and 46.1%). It is interesting that dipterans comprised exactly the same percentages on bedrock in 1945 and 1974. Trichopterans were more important in 1974 (19.2%) than in 1945 (6.4%). In 1974, two trichopterans were restricted to bedrock compared to one trichopteran in 1945.

TABLE 2. Biomass of major taxa for 1974 and mean biomass and density values for 1945 and 1974, North St. Vrain Creek, Colorado. Values in parentheses exclude lumbricid earthworms

Taxon		Biomass (mg/m ²) wet weight			
		Sand	Gravel	Rubble	Bedrock
Ephemeroptera		153	670	1,395	127
Plecoptera		4	113	87	2
Trichoptera		30	36	1,046	362
Coleoptera		0.3	12	8	0.2
Diptera		443	766	236	182
Oligochaeta		1,548	734	657	0
Hydracarina		3	2	0.6	0.4
Pelecypoda		13	0	0	0
Mean biomass (g/m ²)	1945	0.6	1.3	2.5	1.7
	1974	2.2(0.6)	2.3(1.6)	3.4(2.8)	0.7(0.7)
Mean density (organisms/m ²)	1945	202	575	610	551
	1974	141(91)	261(247)	274(266)	136(136)

Standing crop

Biomass values for major taxa in 1974 and mean biomass and density values for both years are shown in Table 2. The poor standing crop in the North St. Vrain was emphasized in the original paper, but the density of macroinvertebrates was even lower in 1974. This can be attributed to the higher flow in 1974, which was 13.6 m³/s (slightly greater than bankfull) at the beginning of the study and averaged 8.0 m³/s (as opposed to 6.4 m³/s in 1945). Similar numbers of organisms were found on rubble, gravel, and bedrock in 1945, but sand was considerably poorer. In 1974, sand contained relatively greater numbers of organisms and bedrock relatively fewer than in 1945. If the lumbricid earthworms are considered as accidentals, a relative abundance pattern similar to 1945 is shown for the four substrata. The paucity of organisms on bedrock in 1974 supports the idea of high water limiting the fauna, since organisms (e.g., *Simulium*) commonly found on bedrock are especially favored by low, relatively constant flow, which was apparently the situation in 1945.

Except for bedrock, biomass values were higher in 1974, primarily due to *Eiseniella tetraedra*. The addition of lumbricid earthworms from the stream banks during high water represented a considerable input of potential food material which may be of some importance in the economies of unproductive streams. If earthworms are eliminated, the same or similar biomass values are found for the 2 yr, except for lower values on bedrock in 1974. The similar biomass values both years, coupled with lower densities in 1974, would be explicable if development rates were higher in 1974 due to the different temperature pattern. Earlier warming in 1974 may have precipitated earlier development and more rapid growth of some species than in 1945, even though mean temperatures were similar and higher temperatures were reached in 1945 (Hartland-Rowe 1964, Langford 1971). Langford (1971) suggests that onset of hatching for some species is related to the date on which a certain absolute temperature is reached rather than to degree day summations. He found that nymphs of some stream insects may be considerably larger 1 yr than the next and attributes this to temperature variation between years. However, without detailed temperature data preceding and during the sampling periods of both years, this remains speculative. Another explanation is that the productive capacity of the stream has increased somewhat and that under conditions of lower, more constant flow, an increase in numbers would result in biomass values higher than in either year.

Considering the time span, the normal year-to-year fluctuations in macroinvertebrate numbers and composition, the increase in riparian vegetation, the differences in temperature and flow regimes, and the construction of an upstream reservoir, the macroinvertebrate community changed remarkably little from 1945 to 1974.

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