with kind regards,
James

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Altitudinal zonation in a Rocky Mountain stream

By James V. Ward

With 27 figures and 9 tables in the text

Abstract

Gradients of physicochemistry, aquatic vegetation, and macroinvertebrates were investigated along the longitudinal profile of a pristine stream from alpine tundra to plains. Rhithron characteristics were maintained over nearly the entire stream course, with an abrupt transition to potamon thermal conditions in lower reaches. Aquatic angiosperms, absent from mountain sites, were abundant in the plains stream. Epilithon biomass exhibited a bimodal pattern with maxima in the headwaters (bryophytes) and plains (chlorophytes). Abundant species of epilithic algae were either euryzonal, or restricted to upper or lower sites. Total zoobenthos density and biomass exhibited three-fold and six-fold increases, respectively, from tundra to plains. The downstream increase in species diversity exhibited a sigmoid pattern. Zoobenthic species distributions are categorized into four major altitudinal patterns. A faunal discontinuity between the lower foothills and plains corresponds to the transition from rhithron to potamon conditions. Temperature, food, aquatic plants, and possibly biotic interactions appear important in structuring faunal patterns.

Contents

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1. Introduction

The gradient of environmental conditions that occurs as a function of altitude offers excellent opportunities to investigate factors which influence the diversity, composition, and abundance of stream organisms. Altitudinal stream zonation patterns have been extensively studied in Europe since THIENEMANN's work early in this century (THIENEMANN 1912, 1925). ILLIES & BOTOSANEANU (1963), and more recently HYNES (1970) and HAWKES (1975), have reviewed the zonation schemes resulting from investigations of longitudinal changes in the biotic and abiotic components of running waters. The river continuum concept (VANNOTE et al. 1980), developed in North America, perceives river systems as continuous resource gradients and therefore considers longitudinal changes as clinal rather than zonal.

The majority of longitudinal studies of running waters encompass only small elevation gradients (e.g., BERG et al. 1948), are limited in taxonomic scope (e.g., DÉCAMPS 1967) or study duration (e.g., ELGMORK & SAETHER 1970), or present difficulties in interpretation because of the confounding effects of impoundment (e.g., GAUFIN 1959) or pollution (e.g., BONAZZI & GHETTI 1977). Only a few investigators have conducted studies over large (>1000 m) elevation gradients that deal with the entire benthic fauna and give at least minimal consideration to downstream changes in environmental conditions (HARRISON & ELSWORTH 1958, OLIFF 1960, ILLIES 1964, WILLIAMS & HYNES 1971, KOWNACKA & KOWNACKI 1972, BRODSKY 1980, STARMÜHLNER 1984).

The St. Vrain River system in the Rocky Mountains of Colorado has ideal attributes for examining the longitudinal patterns of physicochemical conditions, flora, and fauna. The stream has a marked elevation gradient, dropping nearly 2000 meters in little more than 50 kilometers. Essentially pristine conditions prevail from its glacier-fed source in alpine tundra to the plains. The upper portion of the watershed is protected by its relative inaccessibility and its designation as a National Wilderness Area. A national forest, extending nearly to the plains, provides additional protection. Even the plains study location features a rocky substratum, high dissolved oxygen, and low nutrient levels, and contains a rich fauna providing no indication of adverse conditions. In addition, the stream remains free-flowing, having excaped the proliferation of dams that severely disrupt the natural longitudinal patterns in most lotic systems (WARD & STANFORD 1983). The lakes of the region have been described in detail (PENNAK 1958), and WARD (1975) examined bottom fauna-substratum relationships at a single location on a major tributary (North St. Vrain Creek).

Remarkably little previous research on stream zonation has been conducted in Colorado. DODDS and HISAW's (1925) pioneering study of the Ephemeroptera, Plecoptera, and Trichoptera of South Boulder Creek did not include other faunal components or aquatic plants, employed only qualitative sampling techniques, and did not include physical and chemical measurements (except temperature), and was limited to the period late June to early September. ELGMORK & SAETHER (1970) studied the invertebrates of the upper section of North Boulder Creek (above treeline), but their field collections were limited to four days in mid-July with no physical or chemical data other than temperature. KNIGHT & GAUFIN's (1966) altitudinal distribution study of a Colorado Western Slope drainage was limited to Plecoptera. ALLAN's (1975) study of the upper portion of a Western Slope stream was limited to the June through August period and did not include dipterans or non-insects. MECOM's (1972) investigation of an Eastern Slope drainage was limited to Trichoptera and employed only qualitative sampling.

Prior to the present investigation, a comprehensive study of the altitudinal zonation of a free-flowing stream from its glacier-fed source to the plains, including examination of physicochemical variables, macrophytes and epilithic algae, organic and inorganic sediment, and detailed analysis of the macroinvertebrate community, had not been conducted in North America. Documentation of ecological conditions as a function of altitude in a relatively undisturbed drainage will allow future assessment of the effects of pollution, stream regulation, and land use practices, as well as provide basic data of heuristic value.

The ensuing material begins with brief descriptions of the geological setting, terrestrial vegetation, and climate in order to place the study area in a watershed context. The primary purpose of the study is to examine the longitudinal gradients of biotic and abiotic factors, with special emphasis on the patterns of abundance, composition, and diversity exhibited by the macroinvertebrate community.

2. Geological setting, vegetation, and climate

The Rocky Mountains of western North America form an approximately 5,000 km long portion of the Cordilleran chain. The southern Rocky Mountain physiographic province, which includes all of the Colorado Rockies, contains numerous peaks which exceed elevations of 4,000 m (Rocky Mt. Assoc. Geol. 1972). The Front Range, in which the study stream is located, forms the easternmost unit of the Rocky Mountains. The Front Range was formed by the Laramide Orogeny of late Cretaceous and early Tertiary age. The present topography at upper elevations is due to stream incision in the late Tertiary and mountain glaciation processes during the Pleistocene, resulting in exposed Precambrian crystalline rocks (schists, gneisses, and granites). The lower foothills are primarily composed of sedimentary rocks of late Paleozoic and Mesozoic age. Sandstones, shales, and limestones underlie the Great Plains, the western edge of which is located at about 1,700 m elevation.

The Great Plains are dominated by grasslands with trees generally restricted to river valleys. Marr (1967) recognizes the following four climatic-climax vegetation regions on the Eastern Slope: (1) an open ponderosa pine *(Pinus ponderosa)* forest in the lower montane region (1800–2350 m; the foothills zone of other authors), (2) a more dense Douglas fir *(Pseudotsuga menziesii)*-ponderosa pine complex in the upper montane (2450–2750 m), (3) a dense spruce-fir *(Picea engelmannii-Abies lasiocarpa)* subalpine forest (2850–3350), and (4) an alpine tundra climax region of *Kobresia* meadows above about 3400 m. Ecotonal conditions characterize the gaps in elevation between climatic-climax regions. Marr defined the climatic-climax region by the conspicuous species occurring on sites of moderate exposure. North-facing and south-facing slopes as well as valley bottoms may have quite different species composition and densities. Stands of lodgepole pine *(Pinus contorta)* and aspen *(Populus tremuloides)* which may occur from about 2,600 m to over 3,050 m are successional stages following lumbering and fire. Descriptions of riparian vegetation at stream study sites are presented in the following section.

Annual precipitation averages 31 cm on the plains (1,509 m). At climatic-climax sites, Marr (1967) reported annual precipitation values of 51 cm for the lower montane, 53 cm in the upper montane, and 66 cm at subalpine and alpine sites. Mean annual air temperatures are 9 °C on the plains, 8 °C in the lower montane, 6 °C in the upper montane, 1 °C for the subalpine, and −4 °C for the alpine tundra.

Pleistocene glaciers extended from present-day cirques to about 2,440 m elevation (Richmond 1960). There were at least three Pleistocene glaciations; the last major glacial recession occurred about 7,000 years B.P. (Pennak 1963). Using stratigraphic evidence from lake and bog cores, Pennak determined that the present terrestrial vegetation has prevailed for the last 3,000 years during the Neoglaciation.

3. The study area

Middle St. Vrain Creek begins near the St. Vrain glaciers, which are tiny relicts of the Neoglaciation occupying the heads walls of cirques on the east side of the Continental Divide in northern Colorado. The stream originates at Lake Gibraltar, a cirque lake at 3,414 m elevation, and drops 1,870 m over a distance of 54 km. It begins as a first-order brook in alpine tundra, and is a fifth-order river in the lower reaches. No lakes or impoundments impede the stream's passage from tundra to plains. The highest gradient sections occur in the headwaters and in the lower foothills below the downstream extent of Pleistocene glaciation (Fig. 1). The upper three sites, in the high-gradient headwater region, were located within Pennak's (1958) alpine limnological zone. Three sites were within the montane limnological

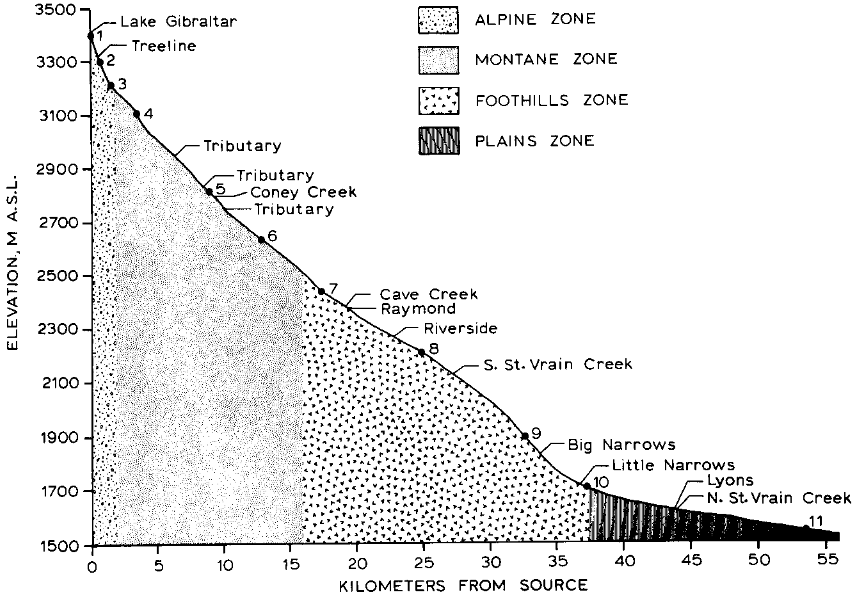

Fig. 1. Longitudinal profile of the St. Vrain River, Colorado, indicating confluence points of all second-order and larger streams. Arabic numerals indicate sampling sites. Limnological zones are based on PENNAK (1958). Big and Little Narrows are regions where the stream valley is constricted by steep canyon walls.

zone; four were in the foothills limnological zone; and the lowest site was within the plains limnological zone.

In the site descriptions that follow, a modification of the stream order system (STRAHLER 1957) has been adopted to account for tributaries of a lower stream order (which do not increase the stream order designation). For every tributary of lesser order, a superscript is added. If, for example, a first-order tributary enters the third-order stream, the designation is "3^1"; if a second-order stream (or two first-order streams) then enters, the designation becomes "3^3". This system essentially combines the widely used concept of stream order with the advantages conferred by link magnitude, which is the sum of all first-order streams (SHREVE 1966). First-order streams are those shown as permanent streams without tributaries on 7.5 minute topographic maps (scale 1:24000).

The upper five sites were reached on foot from the St. Vrain Glacier trail. The remaining sampling locations were accessible by road.

Site 1 (3,414 m a.s.l.; stream order 1) was located in alpine tundra on a north-facing slope above the upper limit of the krummholz (tree islands) ecotone region. True treeline lies at about 3,325 m elevation. The stream originates from the outflow of Lake Gibraltar, a cold monomictic cirque lake fed by the St. Vrain Glaciers (Fig. 2). During the first summer of the study approximately one-third of the lake

Fig. 2. Lake Gibraltar, the source of Middle St. Vrain Creek, and the Continental Divide.

was still ice covered on 7 August. The next year there was only a bare remnant of ice on 20 July. Snowfields extend a short distance into the water at all times. The outflow stream trickles through a talus slope of angular rock fragments for several meters before surfacing to coalesce into a well-defined channel. The stream at Site 1 was 60 cm wide and averaged 20 cm in depth. Width and depth measurements were determined in mid-September 1976, a relatively low water period.

The substratum at Site 1 was composed of bedrock, boulders, and angular rubble. Relatively few finer particles (gravel, sand, etc.) were present. Some glacial flour occurred in the fine fraction (see discussion under "Substratum"), but the glaciers are not active and the stream was extremely clear.

Dense stands of grasses, forbs, and low willow shrubs (*Salix* spp.) occurred along the edges of the stream, forming a nearly complete low canopy in most areas during summer.

Site 2 (3,304 m a.s.l.; stream order 2^1) was located a short distance below treeline. Stream width was about 3 m; depth averaged 14 cm. The substratum consisted of boulders and large angular rubble with little finer material. Subalpine fir and Englemann spruce grew on the stream banks, as did shrub willows, mosses, forbs, and grasses.

Site 3 (3,219 m a.s.l.; stream order 2^1) was located in a broad valley, and the stream was less shaded than at Sites 2 or 4. The stream was larger (6 m wide, 9 cm deep) than at Site 2, despite the same stream order designation, because of entering snowmelt carried by many small trickles not indicated on topographic maps. The substratum was primarily rubble (less angular than at upper sites) with sand, gravel, and some silt. The site was located in the spruce-fir forest (Fig. 3). Riparian vegetation consisted of a juniper shrub *(Juniperus communis)*, typical subalpine forbs, grasses, and sedges.

Fig. 3. Middle St. Vrain Creek during July at a location upstream from Site 3.

Site 4 (3,109 m a.s.l.; stream order 2^2) was located in spruce-fir forest within a high gradient section of a valley constricted by landslides from the precipitous faces of the mountains paralleling the stream. Conifer trees grew on the stream banks, although they did not form a complete canopy. Other riparian vegetation consisted of sparse willow shrubs, forbs, and a few grasses. The stream was sampled at a wide riffle (10 m averaging 13 cm deep) composed of rubble underlain by gravel and sand.

Site 5 (2,816 m a.s.l.; stream order 3^2) was located immediately upstream from an entering second-order tributary, Coney Creek. The stream section sampled was narrower (7 m, averaging 20 cm deep) than Site 4 with conifers forming a complete canopy. Banks were covered with moss; grasses and forbs were sparse. Rocky Mountain alder *(Alnus tenuifolia)*, not seen at higher elevations, and willows were the riparian shrubs at Site 5. Aspen *(Populus tremuloides)* first appear between Sites 4 and 5, but are very sparse and did not occur along the stream. This is in contrast to many drainage basins in Colorado, the upper portions of which have extensive stands of aspen. The substratum was similar to Site 4.

Site 6 (2,633 m a.s.l.; stream order 3^7), adjacent to Dick Campground, was the uppermost site where year-round sampling was possible. The stream was 14 m wide; depth averaged 15 cm. Aspen, Douglas fir *(Pseudotsuga menziesii)*, blue spruce *(Picea pungens)*, and lodgepole pine *(Pinus contorta)* first appear or become abundant near Site 6 as subalpine fir and Englemann spruce decline. Shrub willows, Rocky Mountain alders, and grasses occurred along the banks. The substratum consisted of rubble with gravel and sand, but little silt or clay.

Site 7 (2,438 m a.s.l.; stream order 3^7) was upstream from two groups of summer homes, Raymond and Riverside, clustered along Middle St. Vrain Creek. Stream width, depth, and substratum were similar to Site 6. The stream was generally well-shaded by the montane forest trees. Willows, alder, and birch *(Betula occidentalis)* formed a dense riparian shrub zone.

Site 8 (2,207 m a.s.l.; stream order 3^9) was located downstream from the hamlets of Raymond and Riverside. The stream flowed along one side of a narrow floodplain and was not as well-shaded as Site 7. Tree species near the stream included lodgepole pine, ponderosa pine, blue spruce, Douglas fir, aspen, and junipers *(Juniperus virginiana scopulorum)*. A dense riparian shrub zone similar to that of Site 7 was present. Stream width, depth, and substratum were similar to Sites 6 and 7.

Site 9 (1,890 m a.s.l.; stream order 4^1) was located well downstream from the confluence of South St. Vrain Creek, a third-order tributary. It was in an area of increasing gradient with steep canyon walls characteristic of the lower foothills. The stream had narrowed (8 m with a mean depth of 37 cm) and boulders and large rubble were common (Fig. 4). Considerably more sand was noted than at upper sites, primarily in areas out of the main current. This was the most difficult site to sample during high water. The forest vegetation was less dense than at Site 8, although riparian shrubs (willows, alder, birch) were abundant in some areas. Occasional blue spruce, cottonwood *(Populus)*, and willow trees occurred along the stream banks in this region.

Site 10 (1,701 m a.s.l.; stream order 4^2) was located where the stream valley began widening after flowing through a narrow canyon section. Vegetation was characteristic of the plains-foothills ecotone. Ponderosa pines and junipers were widely spaced and there was much bare ground devoid of even shrubs or herbaceous plants. The riparian vegetation was composed primarily of a narrow band of willow shrubs. Scattered cottonwood trees *(Populus sargentii)* were also present. The stream was still quite confined after flowing through the canyon section. The width and depth were similar to Site 9. There were fewer boulders, which were smaller than at Site 9, but otherwise the substratum was similar.

Site 11 (1,544 m a.s.l.; stream order 5) was located on the plains well below the village of Lyons and the confluence of North St. Vrain Creek (a fourth-order

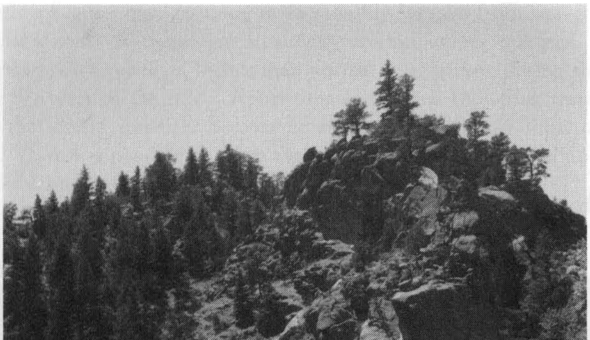

Fig. 4. The high gradient foothills section of St. Vrain Creek.

stream with a drainage area of about 310 km^2) with South St. Vrain Creek (drainage area 212 km^2). Stream width was 14 m; depth averaged 15 cm. Elm *(Ulmus americanus)* and cottonwood trees were scattered along the river. Willow shrubs were abundant in some sections. Grasses and forbs typical of the plains lined banks in most reaches (Fig. 5). Rubble was the predominant substratum, although localized areas of sand/gravel occurred between rocks. Fine sand and silt collected in and around macrophyte beds. Despite an upstream village, irrigation diversion and return flow, Site 11 had generally clear water with a rocky substratum, high dissolved oxygen, low nutrient levels, and a diverse fauna with major clean water elements. The U.S. Environmental Protection Agency (1972) concluded that an unpolluted aquatic environment of good water quality existed in the St. Vrain River between Lyons and Longmont, a town downstream from Site 11.

The St. Vrain River exhibited distinct rhithron characteristics (well-oxygenated, high current velocity, rocky substratum) throughout its length. There was, how-

Fig. 5. The plains sampling site at low water, showing the predominantly rubble substratum.

ever, an abrupt transition to potamon thermal conditions (sensu ILLIES and BOTOSANEANU 1963) at Site 11, while other rhithron characteristics were retained.

The fish fauna of mountain segments of St. Vrain Creek is primarily restricted to salmonids. Brown trout *(Salmo trutta)* and rainbow trout *(S. gairdneri)* predominate at lower and middle elevations, whereas brook trout *(Salvelinus fontinalis)* and cutthroat trout *(Salmo clarki)* occur in the upper reaches. In contrast, a relatively diverse fish fauna occurs in the plains river. PROPST (1982) recorded 16 species near the plains sampling site of the present study, comprised of cyprinids (10 species), catostomids and centrarchids (each with 2 species), and a percid *(Etheostoma nigrum)*. The only salmonids present were a few specimens of brown trout.

4. Methods and materials

The study extended over a 16-month period (June 1975 – September 1976). Sampling was conducted monthly throughout the study from the montane limnological zone (2,633 m) to the plains. The upper sites were only accessible during the summers due to the deep snowpack over the stream. An ice axe was required to procure samples at all locations sampled during winter, except the plains site. The majority of biotic and abiotic variables were sampled on each collection trip, resulting in 16 monthly samples from sites in the montane, foothills and plains zones. Variables less frequently sampled are so indicated.

Heavy snowpack resulted in higher than normal stream flow during the summer and autumn of the first year of the study. Approximately normal snowpack resulted in average runoff during the second summer. Because of an exceptionally low snowpack during the winter of 1980/81, it was possible to reach the base camp just below treeline (3,219 m) and procure samples through the ice in mid-January.

4.1 Chemical and physical parameters

Methods for field collection and laboratory analysis of physical and chemical variables followed Ward (1974). Maximum-minimum thermometers were installed at Sites 1, 4, 6, and 8 during the ice-free periods, and for the duration of the study at Site 11. A submersible recording thermograph was installed at Site 1 during the second summer. All thermometers were precalibrated.

Nitrate-nitrogen values were determined spectrophotometrically using chromotropic acid. The molybdate blue method was used in orthophosphate determinations.

Substratum samples were collected at Sites 1, 3, 6, 8, and 11 in July. An open cylinder was used to seal a section of bottom and the enclosed rubble and pebble were carefully removed. A smaller cylinder (5.3 cm diameter) was forced 5 to 8 cm into the substrate; metal plates were used to seal the ends of the cylinder and the sample was removed. This procedure was repeated at least five times at a site. In the laboratory, gravel (2–32 mm) was separated from finer materials by wet sieving. The substrate was ovendried at 60 °C to constant weight. The hydrometer method was used to separate the finer materials (<2 mm) into sand, silt, and clay fractions. The University Soil Testing Laboratory performed the substratum, nitrate, and phosphate analyses.

Continuous flow records (U.S. Geological Survey) were available only at a location 0.6 km downstream from the confluence of North and South St. Vrain Creeks. Discharge was estimated at Site 6 from current meter readings taken monthly during the open season. The current meter was carried to Site 1 to determine summer discharge at the stream source.

4.2 Sedimentary detritus

Sedimentary detritus was sampled on riffles at Sites 1, 3, 6, 8, and 11 during July when upper as well as lower sites were accessible. In addition, sedimentary detritus was collected from Site 8, the location thought to receive the greatest input of deciduous leaves, in October following the major period of leaf abscission at that elevation. An open cylinder was used to seal a section of stream bottom. Rubble-sized rocks were scrubbed and removed from the enclosure. The remaining substratum was disturbed and water was pumped with a hand-operated bilge pump through a 1,000 μm mesh net placed within a 50 μm mesh net. This process was continued until only clear water remained within the cylinder. Three such samples were taken across the riffle at each site. In the laboratory, the materials were separated into three particle sizes based on the longest dimension: 50–1,000 μm; 1–16 mm; and >16 mm. Living plant and animal matter was removed from each fraction under low magnification. Observations on the composition of the detritus were recorded and the samples were dried at 60 °C for a minimum of 48 hours until constant weight was attained. Samples were fired in a muffle furnace for 24 hours at 550 °C, a time period and temperature which minimizes carbonate loss (Petersen & Cummins 1974). According to Cummins (1966), weight loss on ignition is "the method of choice" for a single measure of sedimentary organic matter.

4.3 Epilithon

Epilithon, including algae, cyanobacteria, mosses, and liverworts with associated epiphytes and detritus, was collected from the upper surfaces of rubble-sized rocks. Qualitative samples were taken at various times during the study. In mid-August, riffles at each site were sampled using a timed scraping technique (WARD 1974). The percentage composition of the major components (moss, lichen, detritus, algae) was determined using a square Petri dish with a gridded bottom. A Sedgwick-Rafter counting cell was employed to estimate the percentage composition of the algal microphytes. The relative contribution of the algal phyla (including cyanobacteria) was obtained by counting the number of organisms present in five horizontal strips. This method was also used to determine the percentage composition of the species within each phylum, except Bacillariophyta (diatoms).

The diatoms were cleared of organic matter with 30% hydrogen peroxide, placed on heated coverslips, and the hydrogen peroxide was allowed to evaporate. The hot coverslips with adhering cleared valves were mounted on slides with Hyrax Mounting Medium. Five hundred valves per sample were counted at 1000X with a Leitz phase contrast microscope to determine the species and percentage composition.

Each sample (minus diatom subsample) was dried at 60°C until constant weight was attained, weighed, and fired in a muffle furnace at 550°C for 24 hours to obtain ash-free dry weight.

4.4 Macroinvertebrates

Macroinvertebrates were collected from rubble riffles at each site with Surber samplers enclosing 929 cm^2 of substratum. Six samples were taken at each site, three with a coarse-meshed (720 μm) sampler and three with fine mesh (240 μm), resulting in a total of 774 samples. While it is clear that a finer mesh is more efficient in retaining smaller individuals, fine mesh may be less efficient for collecting larger and more active animals (MACAN 1958, ZELT & CLIFFORD 1972). Use of two mesh sizes should thus maximize sampling efficiency, as well as provide comparative data. Within-site and between-site differences in substratum and current were minimized by confining sampling to rubble riffles, the predominant habitat type. Samples collected with different mesh were kept separate but the three samples from each mesh size were combined. Dry weight was determined by oven drying the animals at 60°C until constant weight was attained. No correction factor was applied to account for weight loss in preservative.

The adults of aquatic insects were collected by sweep netting and hand picking to provide additional taxonomic data. Some species designations are, of necessity, based on the distribution of immatures and adults. The remoteness of the upper sites and the comprehensive nature of the study precluded definitive associations of immatures and adults by rearing. Adults and immatures were stored in 80% ethanol.

5. Results and discussion

5.1 Chemical conditions

Dissolved oxygen was near saturation, as expected, at all mountain stream stations and exhibited no seasonal pattern (except as temperature influenced solubility coefficients). In Table 1 oxygen values are shown only for sites at which oxygen was determined on each sampling date. At Site 11, the plains station, the

Table 1. Mean values and ranges of physical and chemical parameters at study sites on the St. Vrain River, Colorado.

	Sampling Stations										
	1	2	3	4	5	6	7	8	9	10	11
Bound CO_2 (ppm)	3.0 (2.5–3.5)	3.5 (3–4)	3.5 (3–4)	4.9 (3.5–6.5)	5.9 (4–10)	7.1 (4.5–10.5)	7.8 (4.5–10.5)	8.2 (5.5–11)	9.0 (6–11.5)	10.1 (6–12)	30.4 (22–39)
pH (mode)	7.0	6.9	7.0	7.0	7.0	7.1	7.1	7.1	7.1	7.2	8.1
Temperature range (°C)	0–6	0–4.5	0–7.5	0–9	0–9.5	0–10.5	0–10	0–12	0–14.5	0–16	0–25
O_2 (ppm)	8.2	–	9.0	–	–	9.5	–	9.3	–	–	9.3
NO_3–N1) (ppm)	0.15	–	0.13	–	–	0.12	–	–	0.10	–	0.13
Orthophosphate1) (ppb)	<5	–	<5	–	–	<5	–	–	<5	–	<5
Total suspended (mg/l)	0.9 (0.7–1.2)	–	1.3 (1.2–1.3)	–	–	1.7 (0.2–6.7)	–	–	1.8 (0–4.8)	–	9.8 (2.3–32)
L.O.I.	0.4	–	0.5			0.7			0.5		2.0
Total dissolved (mg/l)	7.3 (6.4–8.8)	–	7.1 (6.4–7.8)	–	–	24.4 (13.6–34.3)	–	–	30.7 (19.2–37.9)	–	192.1 (130–309)
L.O.I.	2.7	–	2.5	–	–	9.2	–	–	11.2	–	42.4
Flow (m^3/sec)	–	–	–	–	–	–	–	–	–	–	3.33)
First summer	–	–	–	–	–	2.2	–	–	–	–	6.0
Second summer	0.072)	–	–	–	–	1.0	–	–	–	–	3.6

1) August. 2) July. 3) Annual mean and summer means at Site 11 are from U.S. Geological Survey records.

majority of oxygen values were also between 95 and 105% saturation. However, in June and July under conditions of low flow, warm water, dense beds of macrophytes and abundant algae, afternoon oxygen values were 122% and 129% saturation, respectively.

Modal pH values were circumneutral from alpine tundra to the lowest foothills site (Table 1), with little seasonal variation at a given site, a result of the low solubility of the metamorphic and igneous bedrock. The plains site exhibited a higher pH (8.1). The modal pH range over the various sites (6.9–8.1) was nearly identical to surface water pH modes (7.0–8.2) reported by Pennak (1958) for lakes of the region. The lakes, however, exhibited an abrupt pH increase between montane and foothills zones in contrast to the sharp increase in stream pH from the foothills to the plains (Fig. 6).

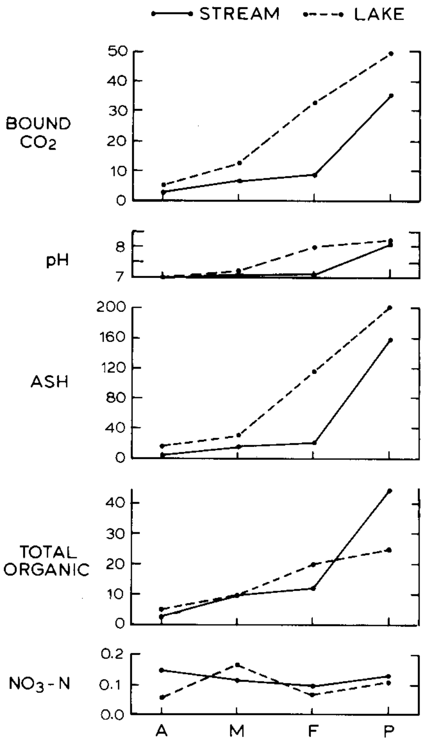

Fig. 6. A comparison of lake and stream chemistry in northern Colorado as a function of altitude. Mean values for lakes are based upon non-alkaline drainage lakes (Pennak 1958). Stream values are means from the present study at Site 1 in the alpine zone (A), Site 6 in the montane zone (M), Site 9 in the foothills zone (F), and Site 11 in the plains zone (P). Parameters are expressed in mg/l except pH for which modal units are shown.

Hardness (bound CO_2) values exhibited a three-fold increase from the alpine tundra (3.0 ppm) to the foothills stream site (9.0 ppm), with a marked increase at the plains location (30.4 ppm). The greatest increase in bound CO_2 for lakes occurred from the montane to the foothills zone (Fig. 6). Lakes exhibited somewhat harder water at a given altitude than the stream values of the present study. This difference is not unexpected since the rapidly moving stream water is in contact with the substratum for a relatively short period. Bound CO_2 values at a given stream site exhibited a distinct seasonal pattern. Low values during spring runoff were followed by a progressive increase through autumn and winter, with maxima in late spring prior to snowmelt.

Suspended matter means were very low at stream sites in the mountains and did not exhibit significant altitudinal differences (Table 1). Mean loss on ignition fractions ranged from 28% to 44% of the total suspended matter. Even the plains site exhibited a relatively low mean suspended matter value (9.8 mg/l), indicative of the generally clear water. Loss on ignition averaged 20% of total suspended matter indicating a greater proportion of suspended inorganics than at mountain stream sites. Suspended matter closely followed the flow pattern as expected. Higher flow during the first summer resulted in higher suspended matter values at all altitudes. For example, at Site 1 the mean for the first summer was 3.7 mg/l, whereas during the second summer the value was 1.0 mg/l. At Site 6 the summer means were 8.2 and 1.4 mg/l, respectively.

Total dissolved solids exhibited extremely low values at sites in the alpine zone with similar means at Site 1 and 3 (Table 1). Sites 6 and 9 in the montane and foothills zones exhibited values similar to each other, which were about three times greater than at alpine sites. It must be emphasized that values are not strictly comparable since means at alpine sites are based upon summer conditions, whereas montane, foothills, and plains sites represent averages of monthly samples for one year. Dissolved matter at the plains site was more than six times greater than at Site 9 in the foothills. Loss on ignition fractions were similar at mountain stream sites (35–38%), but lower (22%) at Site 11 on the plains. Differences in dissolved and suspended organic matter between mountains and plains are likely even greater than indicated, since only at the plains location would significant carbonate decomposition be expected to occur during firing. There was a general inverse relationship between discharge and total dissolved matter.

Suspended and dissolved fractions were combined in Figure 6 so that stream values can be compared with ash and total organic residue reported by PENNAK (1958) for lakes of the region. The small amount which plankton contribute to lake values allows comparisons to be made between lake and stream sites. The total organic matter progressively increased from alpine to plains lakes, whereas stream values exhibit an abrupt increase from foothills to plains sites. A four-fold increase in total ash values from alpine to the foothills stream sites is followed by a nearly eight-fold increase from foothills to plains. Lake waters exhibit a different pattern, the major increase in ash occurring between the montane and foothills zones. It appears that since stream gradients are high in the foothills, the low residue time of stream waters precludes major uptake of chemical species despite the greater solubilities of the rocks.

Pennak (1958) found nitrate-nitrogen results to "bear little relationship to limnological zones and altitude" for lakes of the region. Stream values were similar at all altitudinal zones (Fig. 6), even the plains site, although uptake by biota may be partly responsible (Hynes 1970).

Unlike nitrate-nitrogen, phosphate-phosphorus in lake waters of the region exhibited a considerable increase with decreasing altitude (Pennak 1958). At all stream sites sampled in the present study (Table 1), orthophosphate values were below the level of detection (<0.005 ppm), preventing comparisons with lakes of the region.

5.2 Temperature

Mean summer water temperatures varied from 2.3 °C (Site 1) to 20.8 °C (Site 11) the first year and from 3.8°C (Site 2) to 21.5°C (Site 11) during the second. The lower temperatures during the first summer are attributed to the higher discharge and prolonged period of snowmelt runoff. The thermal amplitude during the study period also exhibited a dramatic increase in the downstream direction (solid line of Fig. 7) with an especially marked change from Site 10 to Site 11. Because temperatures dropped to zero at all locations, the thermal amplitude is also the maximum temperature at a given site. Accurate diel temperature data are only available from summer thermograph readings at Site 1 where diel fluctuations ranged from 0.2°C to 1.1 °C. At other locations, the maximum observed diel ranges during the summer

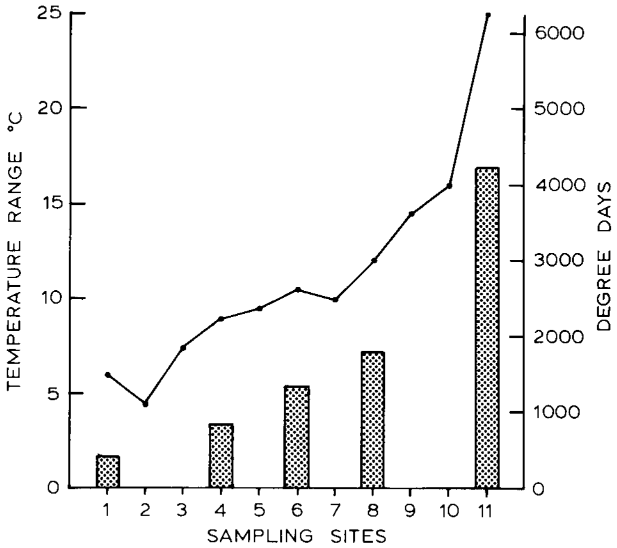

Fig. 7. Water temperature range (solid line) for the period of study at sites on St. Vrain Creek and estimated annual degree days (bars) at selected locations.

were 5°C at Site 3, which was well exposed to solar insolation by day and lacked a well-developed riparian vegetation to reduce heat loss by night; 7.5°C at Site 6; 9°C at Site 9; and 11.5°C at Site 11.

During June of the first summer the stream channel above Site 4 was covered with as much as 2 m of ice and snow. In contrast, the stream immediately above Site 4 was completely open by mid-June of the second summer, without even remnants of snow on the stream banks. The period of essentially complete ice cover lasted from November through March at Site 6, and from January to February at Sites 7 and 8. At Site 9 a narrow channel remained open during most of the winter even though the majority of the stream surface was ice covered from January through March. At Site 10 less than 50% of the stream surface was ice covered except in January. The plains site rarely had significant ice even on the edges except for a short period in January, allowing maximum-minimum thermometer readings to be taken for the duration of the study. At other sites these thermometers were removed during the period of ice cover.

Annual degree days (with 0°C as developmental zero) were estimated for selected sites. Values in Figure 7 are, however, only crude approximations based upon mean values derived from maximum-minimum thermometer readings (except Site 1 where a thermograph was installed) during the open season, with a temperature of 0°C assumed during the periods of ice cover at a given site (except Site 11).

Seasonal patterns of water temperature (Fig. 8) not only show the reduced amplitude of upstream reaches, but also demonstrate the tendency for seasonal maxima to occur later at upper sites.

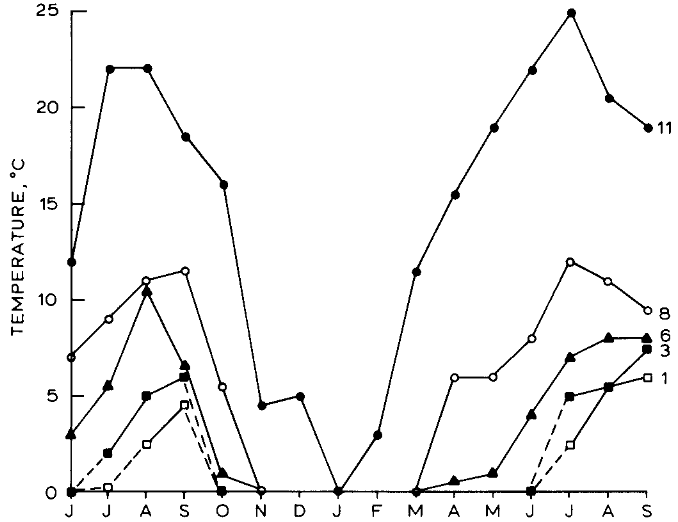

Fig. 8. Seasonal water temperature patterns at St. Vrain Creek sites (Arabic numerals) for the period of study. Dashed lines indicate extrapolated values at Site 1 and 3.

5.3 Substratum

Although all study sites were located on rubble riffles, the composition of finer materials varied somewhat between sites (Table 2). Gravel comprised over three-fourths of the substratum particles smaller than 32 mm in diameter at mountain stream sites; sand comprised from 11–19%. At the plains location, gravel comprised a smaller and sand comprised a greater proportion of the substratum. The greater clay fraction at headwater sites was likely a result of glacial flour deposits noted during sampling, which Pennak (1963) described as "greasy blue clay" from lake cores of this region. Large amounts of silts and clays accumulate at the base of rooted aquatic plant beds at the plains location, but substratum samples were not taken in depositional areas.

Table 2. Percentage composition of mineral substrate particles 32 mm or less in diameter from rubble riffles at St. Vrain Creek, Colorado.

Site	Gravel (2–32 mm)	Sand (0.0625–2 mm)	Silt (0.0039–0.0625 mm)	Clay (<0.0039 mm)
1	77.7	18.5	0.9	2.9
3	86.9	10.9	0.4	1.8
6	81.2	17.8	0.2	0.8
8	84.1	15.0	0.0	1.0
11	49.9	47.6	0.5	2.0

5.4 Sedimentary detritus

The standing crop of detritus in St. Vrain Creek (Table 3) was higher than summer values reported by Short & Ward (1981) for a stream at 2,410 m elevation in the same drainage basin. Especially surprising are the high values at sites of the alpine limnological zone. The general pattern shows a downstream decrease in benthic detritus during summer. Detritus standing crop at Site 11 in July (10.8 g/m^2) was much less than the August value (77.8 g/m^2) reported by Fisher (1977) for a river in the eastern deciduous forest.

FPOM (0.05–1 mm) comprised the majority of benthic detritus by weight at each site during summer (Table 3). The predominance of FPOM was especially pronounced at Site 1.

At the tundra location (Site 1) the majority of the coarse materials consisted of grass and sedge fragments. Conifer needles comprised most of the coarse materials at Sites 3, 6, and 8. Some seeds and fruits, deciduous leaf fragments, stem fragments, and woody twigs were also observed. At Site 11 deciduous leaf and stem fragments, seeds, fruits, and small pieces of wood were collected. No needles were observed in the detritus from the plains site.

Table 3. Mean percentage composition and standing crop of sedimentary detritus on rubble riffles during summer, St. Vrain Creek, Colorado.

Site	% Composition			g/m² AFDW
	0.05–1 mm	1–16 mm	>16 mm	
1	96	3	1	67.9
3	76	21	3	74.5
6	73	21	6	38.6
8	66	24	10	45.6
11	82	14	4	10.8

In mid-October the mean standing crop of sedimentary detritus at Site 8 was 134.7 g/m^2 AFDW. Deciduous leaf litter, mainly recently abscised whole leaves, comprised from 44% to 89% of total detritus. Small pieces of wood and conifer needles comprised the remainder of the coarse material (>1 mm), which collectively accounted for from 57% to 97% of total detritus.

5.5 Aquatic plants

Epilithic algae (including cyanobacteria), mosses, liverworts, lichens, and aquatic angiosperms were collected. Aquatic angiosperms occurred only at the plains location; mosses and liverworts occurred at all sites except the plains. Lichens were restricted to Sites 1 and 2.

Dense beds of *Elodea canadensis* and *Ranunculus aquatilis* occurred in the plains stream. These angiosperms commenced growth in May, reached maximum development in August, remained in good condition through October, then slowly declined until May of the next year. Certain macroinvertebrate species, not present at other sites, were associated with the aquatic angiosperms at Site 11.

Epilithon biomass exhibited a bimodal pattern as a function of altitude (Fig. 9). High values at the uppermost sites resulted from the great development of bryophytes. The large value at Site 11 resulted from dense growths of *Cladophora glomerata*. Lowest values occurred in the high gradient foothills location (Site 9). Algae made a relatively small contribution to total epilithon at the upper five sites where bryophytes predominated, but a significantly greater contribution beginning at Site 6 in the lower montane limnological zone. Detritus comprised from 5 to 60% of epilithon samples, but exhibited no apparent longitudinal pattern or any discernible relationship to sedimentary detritus.

Five phyla of "algae" (bacillariophytes, chlorophytes, chrysophytes, rhodophytes, cyanobacteria) were represented in epilithon samples. More than 94 species and varieties were identified (Appendix A). However, a few species comprised the vast majority of the cells of a given phylum at a site. The summer distribution and

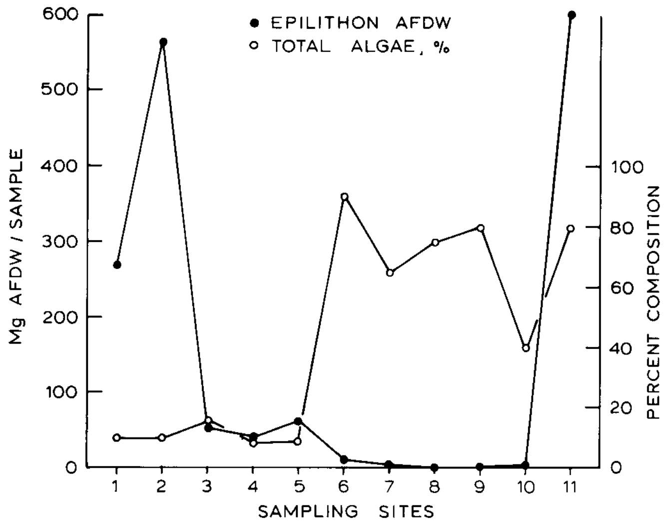

Fig. 9. Longitudinal patterns of epilithon ash-free dry weight (AFDW) and the relative contributions of algae (including cyanobacteria) to total epilithon.

relative abundance of species that comprised 10% or more of the organisms in their respective phyla at one or more sites are indicated in Table 4.

Bacillariophytes were most intensively studied, 63 species and varieties identified. Some, such as *Achnanthes lanceolata,* not only occurred over the entire altitudinal gradient, but were major components of the epilithic diatom flora at all sites. Other taxa were limited to upstream (e.g., *Diatoma anceps*) or downstream (e.g., *Nitzschia palea*) locations. A few diatom species were restricted to middle reaches of the study section (e. g., *Navicula exigua*), but none were major components of the epilithic diatom flora. Species normally considered lentic forms were more common in the lower reaches, as reported by Scheele (1952) for the diatom flora of the Fulda River, Germany. Based on an index of diatom diversity developed by Kawecka (1980) for European mountain streams, all sites in St. Vrain Creek contained low (31–70 species) or very low (<30 species) numbers of species. Although only a single habitat type (the upper surfaces of rubble-sized rocks) was examined in the present study, it appears that the diatom assemblage is taxonomically rather simple, especially considering the large elevation gradient traversed by the stream.

Chlorophytes were represented by 20 taxa, 6 of which comprised 10% or more of the green algae at a given site (Table 4). *Cladophora glomerata* comprised nearly 100% of the green algae at Site 11. *Ulothrix* was the most abundant green alga at the upper three sites, comprising nearly 100% of the green algae at Site 3. At sites 6–10 *Spirogyra* comprised from 50–100% of the chlorophytes collected.

Only two chrysophytes were collected. *Hydrurus foetidus* was confined to the upper sites in mid-August and was abundant (15% of total algae) only at Site 1. *Hydrurus* was, however, observed at all lower sites except the plains location during winter and spring. *Dinobryon,* the only other chrysophyte collected, was found only at Sites 10 and 11, but was not abundant.

Table 4. Distribution and relative abundance of common epilithic algae (including cyanobacteria) of St. Vrain Creek, Colorado (see text).

	Sites										
	1	2	3	4	5	6	7	8	9	10	11
Bacillariophyta											
Achnanthes lanceolata	1	1	1	2	4	1	1	1	1	1	1
A. minutissima	1	1	1	1	2	1	1	1	1	2	1
Cocconeis placentula	–	1	1	1	1	1	1	1	1	1	1
Cymbella ventricosa	1	2	1	1	1	1	1	1	1	1	1
Diatoma anceps	1	1	1	1	2	1	–	–	–	–	–
D. hiemale	1	1	1	1	1	1	–	1	–	–	–
D. hiemale var. *mesodon*	1	1	1	1	2	1	–	–	1	–	–
Frustulia rhomboides	–	1	–	1	–	1	–	–	1	–	–
Hannaea arcus	–	1	1	1	1	1	1	1	1	1	–
Melosira sp.	–	–	–	–	–	1	1	1	1	1	1
Navicula cryptocephala	–	–	–	–	1	1	1	1	1	1	1
Nitzschia palea	–	–	–	–	–	–	1	1	1	1	1
Chlorophyta											
Cladophora glomerata	–	–	–	–	–	–	–	–	–	–	6
Closterium spp.	1	–	–	–	1	1	–	1	–	1	1
Cosmarium botrytis	1	1	–	–	–	1	–	–	–	1	1
Microspora sp.	2	1	–	–	–	–	–	–	–	–	–
Spirogyra spp.	–	–	–	5	–	6	1	6	2	4	1
Ulothrix spp.	4	2	1	–	2	–	–	–	1	3	–
Chrysophyta											
Hydrurus foetidus	3	1	–	1	–	1	–	–	–	–	–
Cyanophyta											
Nostoc microscopium	–	–	–	–	–	–	–	–	–	–	1
Oscillatoria spp.	1	1	3	–	1	1	1	1	1	1	1
Phormidium spp.	3	5	5	4	4	2	1	2	1	1	1
Tolypothrix sp.	3	–	–	–	–	–	6	–	6	2	–
Rhodophyta											
Audouinella violaceae	–	–	–	–	1	–	–	–	–	–	–
Lemanea fucina	–	–	–	1	–	–	1	–	–	–	–

1 – Present but comprising less than 5% of the total algae at a site
2 – Taxa comprising 5–10% of the total algae at a site
3 – Taxa comprising 11–20% of the total algae at a site
4 – Taxa comprising 21–50% of the total algae at a site
5 – Taxa comprising 51–75% of the total algae at a site
6 – Taxa comprising >75% of the total algae at a site

Cyanobacteria were represented by seven taxa, four of which were abundant (Table 4). *Phormidium* was present at all sites, reaching greatest abundance at the upper five sites. *Tolypothrix* was extremely abundant at Sites 7 and 9, whereas at Site 8 the green alga *Spirogyra* comprised the majority of total algae.

Rhodophytes, represented by two species, were found at three sites in the middle reaches, but comprised less than 1% of the total algae.

The algae comprising the summer epilithon of the study stream may be grouped into species occurring over a wide range of altitude, species restricted to upper, and species restricted to lower sites. No species which comprised a major portion of the total algae were restricted to middle reaches. Except at the plains location, species which were abundant at a given site were found at several sites, rather than being restricted to one location. Although the smallest number of taxa (19) was recorded at Site 1 in alpine tundra, there was no discernible pattern of algal diversity along the longitudinal profile of St. Vrain Creek. The most diverse algal flora (44 species and varieties) occurred at Site 11 on the plains and at Site 6 in the middle reaches.

Surprisingly little work on the altitudinal distribution of stream algae has been conducted. To the writer's knowledge, the only comparable data are from the investigations of KAWECKA in the Tatra High Mountains of Poland (KAWECKA 1971) and the Rila Mountains of Bulgaria (KAWECKA 1974). The Rila Mountains study is of considerable interest in relation to St. Vrain Creek. The algae of the Bulgarian stream and the St. Vrain Creek were both sampled during August. Both studies sampled locations above timberline, throughout the forest zone, and in the plains section. Both studies sampled numerous stream sites over a considerable, and analogous, altitudinal gradient (8 sites from 1000–2000 m a.s.l. in the Rila Mountains; 11 sites from 1500–3400 m a.s.l. in the Rocky Mountains). Both mountain ranges are formed of crystalline rock. The downstream thermal gradient was greater in the Colorado stream which is glacier-fed than in the Rila Mountains stream. KAWECKA sampled a wider variety of habitat types at each site, which undoubtedly accounts for the greater number of taxa recorded (178 species and varieties vs. 94 in the present study). Considering the geographical locations of the two streams, the taxa collected were remarkably similar. All genera listed in Table 4 except *Audouinella* were also reported by KAWECKA (1974). Even at the species level, many of the algae were common to, and often abundant in, both drainages. It is not, however, possible to delineate distinct zones for the algal flora of the Rocky Mountain stream as KAWECKA did for the streams of the High Tatra and Rila Mountains.

A variety of factors may influence distribution of aquatic vegetation, although the design of the present study reduces the possible number of variables. Since all epilithon samples were collected from rubble riffles, current velocity and substrate were similar at all locations. Even at the lower gradient plains location, a sampling site was selected which had a relatively rapid current and a primarily rubble substratum. All epilithon samples were taken from the upper surfaces of rocks of similar sizes. While water hardness gradually increased downstream, annual mean values remained within the "soft" range except at the plains location. The pH was circumneutral at Sites 1 to 10, then increased to 8.1 on the plains. Water clarity was high even at the plains location. Based on limited sampling, the plant nutrients measured showed no apparent differences between sites.

Discharge, width, and depth did, of course, increase downstream, although all samples were taken from rocks in shallow water. Although most sites were well exposed to solar insolation, Site 1 where mosses predominated is on a north-facing slope and was shaded by a low canopy of alpine herbs and willow shrubs. Site 5, the only other location with a nearly complete canopy, was the site where diatoms reached their greatest relative abundance.

Except for the few exceptions noted above, temperature and dissolved solids were the only physicochemical factors to exhibit steep and consistent altitudinal gradients over the entire longitudinal profile of St. Vrain Creek. Even these distinct variations did not apparently influence such obviously euryokous species as *Achnanthes lanceolata,* which was collected at all sites and was relatively abundant at each location. Thermal differences explain the restricted distribution of some species. For example, oligotherms such as *Hydrurus foetidus* and *Diatoma anceps* (BLUM 1956, LOWE 1974) were restricted to upstream locations, at least in summer. The downstream increase in dissolved organics may explain the distribution pattern of the obligate heterotroph *Nitzschia palea* which, although eurythermal (LOWE 1974), is restricted to the lower reaches of St. Vrain Creek.

The absence of submerged angiosperms from Sites 1–10 undoubtedly relates to the short growing season, severe ice action, high gradient, and paucity of fine substratum materials at mountain stream sites.

5.6 Macroinvertebrates

More than 210 taxa of aquatic macroinvertebrates were identified from samples collected at the 11 sites (Appendix B). Many major groups were represented along the entire altitudinal gradient (Fig. 10). Three orders of insects, crustaceans, leeches, and snails were collected only from the lowermost sampling site on the plains.

Aquatic insects collectively contributed from 89–99% to total macroinvertebrate numbers and from 84–99% to total biomass at the different sampling sites. At mountain stream locations (Site 1–10) four orders of insects (Plecoptera, Trichoptera, Ephemeroptera, Diptera) comprised essentially the entire aquatic entomofauna (Fig. 11). Dryopoid beetles, virtually the only other insects present at mountain stream sites, accounted for only a small proportion of the total benthos. Triclads (Planariidae) were the most abundant non-insects, comprising 10% of total benthic biomass at the plains location and up to 8% at some mountain stream sites. Oligochaetes, nematodes, sphaeriid clams, and mites contributed little to the total benthos at any location.

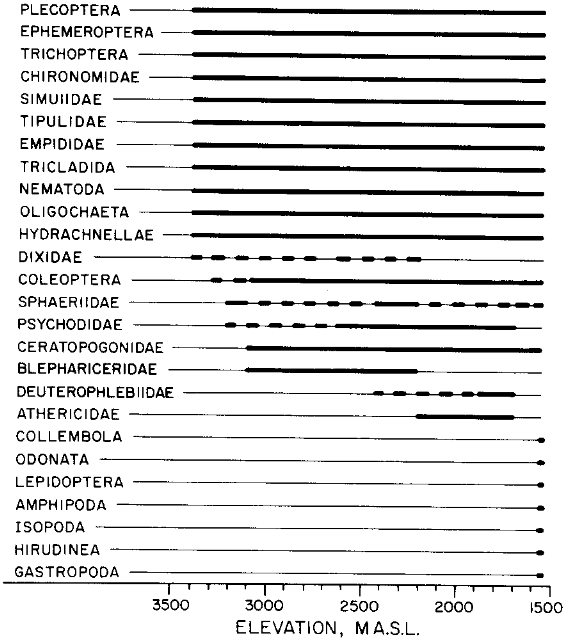

Fig. 10. The altitudinal distribution of major groups of macroinvertebrates along the course of the St. Vrain River.

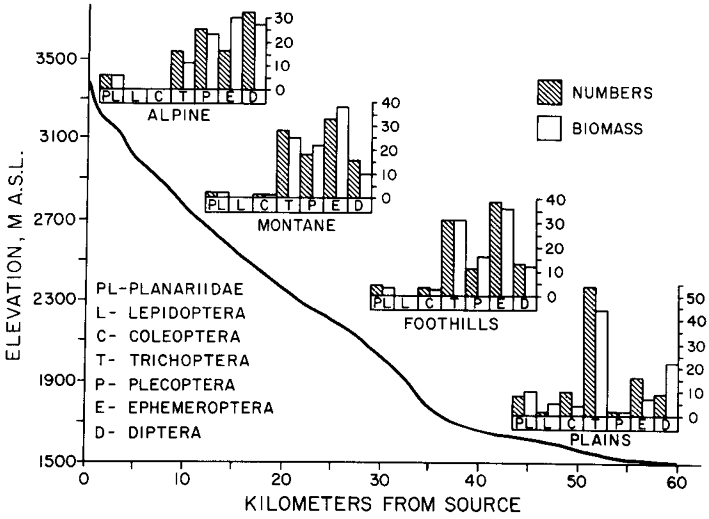

Fig. 11. The relative contribution (% composition) of macroinvertebrate groups that comprised at least 5% of total density or biomass at one or more sites along the course of the St. Vrain River. Values <1% are not indicated.

5.6.1 Abundance patterns

Total benthos exhibited trends of increasing density and biomass from the headwaters to the plains (Fig. 12). Numerical values were over three times greater and biomass values were nearly six times greater at the plains stream than at Site 1

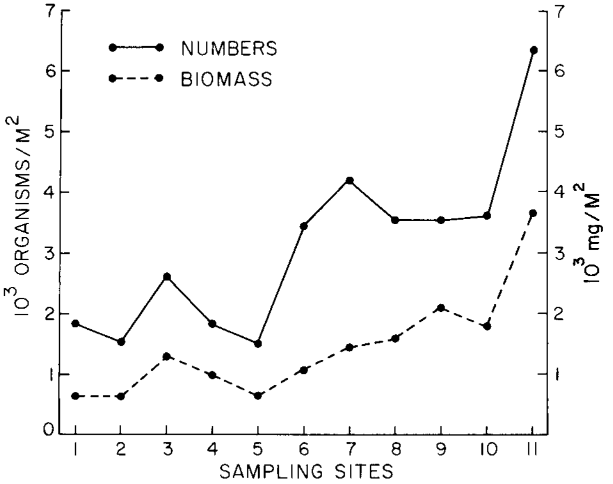

Fig. 12. The longitudinal patterns of total macroinvertebrate density and biomass.

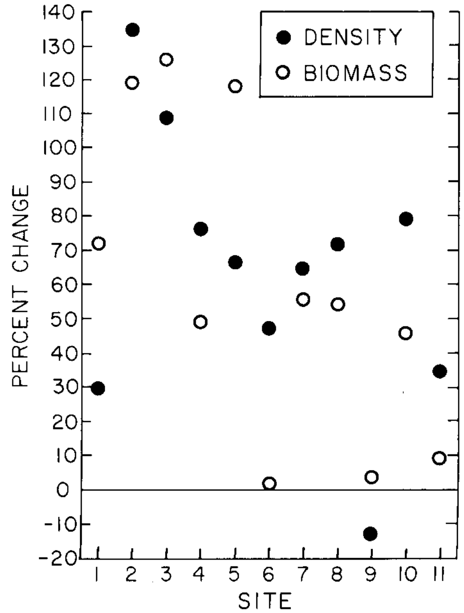

Fig. 13. The percent change in macroinvertebrate density and biomass values from the first summer (high discharge) to the second summer (normal discharge) of study.

in alpine tundra. The abundance peak at Site 3 is largely attributable to large populations of a single species of simuliid. The general pattern of abundance over the longitudinal profile is one of low values at the upper five sites, an increase in abundance from the lower montane through the upper foothills, a leveling of abundance in the high gradient lower foothills, followed by an abrupt increase at the plains site.

Because of an especially heavy snowpack the preceding winter, the first summer of study had a much higher discharge and an extended period of runoff compared to the second summer (see Table 1). Faunal abundance was correspondingly higher the second summer, except at Site 9 (Fig. 13). At several sites, mean density and biomass values were more than 50% greater the second summer, although reduced sampling efficiency under the high flow conditions of the first summer and a larger wetted perimeter undoubtedly account for some of these differences.

5.6.2 Diversity patterns

The downstream increase in macroinvertebrate species richness exhibits a generally sigmoid pattern (Fig. 14). Whereas only 34 species occurred at the

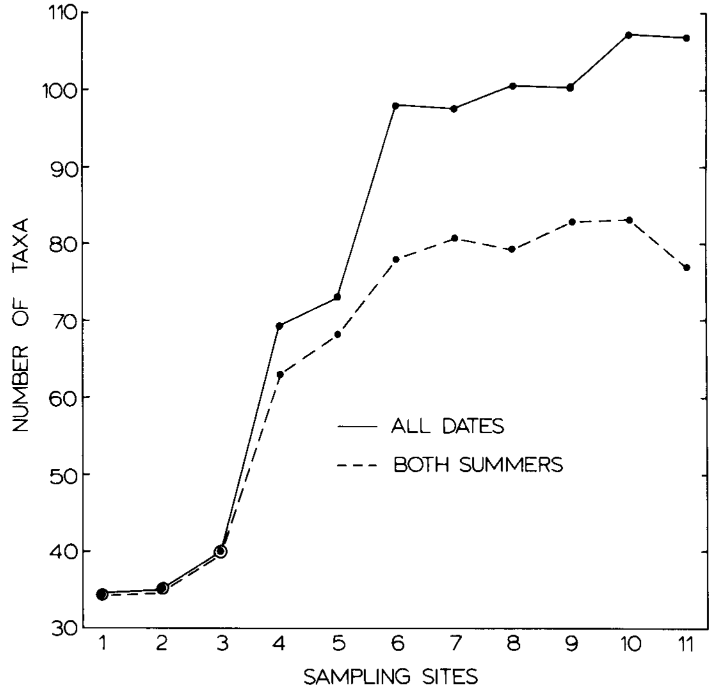

Fig. 14. The total number of macroinvertebrate taxa collected during the entire study and during the summers only, along the longitudinal profile of the St. Vrain River.

uppermost site, 106 taxa were identified from the plains stream. Total species richness is considerably depressed at middle and lower elevation sites if only summer data are utilized. Because the open season is so short at high elevations, it is unlikely that any common species were missed despite the fact that sampling was limited to summer periods at headwater sites. Samples collected through the ice in January 1981, when the headwaters were accessible due to an exceptionally low snowpack, did not yield additional species. However, the data from these mid-winter samples suggest that densities of winter stoneflies are higher at headwater locations than indicated from summer samples, presumably because many individuals emerge as soon as cracks appear in the ice.

At lower elevations where the open season is longer, certain abundant species of stoneflies may be missed entirely if sampling is restricted to the summer (cf. Ward 1984). Such species remain in egg diapause throughout the summer, hatch in autumn, grow primarily during winter and spring, and emerge well before maximum stream temperatures are attained (see Ward & Stanford 1982). The larger number of species of dipterans recorded from year-round as opposed to summer sampling at middle and lower sites is largely attributable to chironomids.

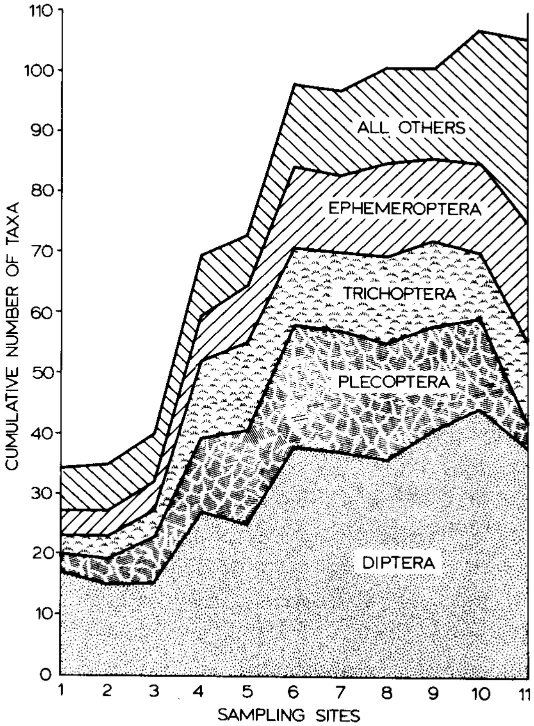

Fig. 15. The contributions of major groups to the total number of macroinvertebrate taxa collected.

Year-round versus summer sampling yielded appreciably more species of trichopterans only at mid-elevation sites. More than twice the number of species of coleopterans was recorded at Site 11 on the plains than were collected during the two summers. Ephemeropterans and non-insect groups exhibited summer species richness values as high or nearly as high as when data from all sampling dates are considered. These data suggest that summer sampling is sufficient to collect all common taxa of stream macroinvertebrates only at very high elevations, where the open season is limited to the "summer" period, or only for a very few groups such as ephemeropterans. It appears that year-round sampling may be necessary even to record all of the abundant species of most groups of macroinvertebrates in most mountain streams.

The same four orders of insects that accounted for the major portion of density and biomass at mountain stream sites collectively comprised the majority of the macroinvertebrate taxa (Fig. 15). Dipterans contributed more species than any other group at all sites, primarily because of the diverse chironomid fauna. The larger contribution of the "all others" category in the plains stream (Fig. 15) is due to an enhanced diversity of groups poorly represented at mountain stream sites (e.g., Coleoptera) and to the contribution of taxa by groups such as Odonata and Amphipoda that only occurred at Site 11 (see Fig. 10).

5.6.3 Macroinvertebrate composition

In this section the distribution and composition of major groups (Fig. 10) along the longitudinal profile of St. Vrain Creek will be examined in greater detail. Included are the taxonomic composition of each group, trends in the distributions of species comprising the group, and patterns of diversity and abundance collectively exhibited by them. For most groups, it is possible to approach this from the specific or at least generic level. The major exception is the Nematoda, for which no attempt was made to provide further identification. The abundance of nematodes was undoubtedly underestimated in this study since many (most?) specimens would have little difficulty passing through even the fine mesh (240 µm) used to collect samples. No attempt was made to collect neustonic organisms; the few that were accidently collected, mainly water striders (Gerridae, Veliidae), are not included in the data. A single corixid female collected from Site 10 was the only aquatic hemipteran encountered. Aquatic collembolans were found only at Site 11 where three individuals of *Isotomurus palustris*, a "secondary aquatic associate" according to WALTZ & MCCAFFERTY (1979), were collected.

Diptera. Dipterans were abundant along the entire stream gradient. The maxima in density and biomass at Site 3 (Figs. 16 and 17) are due largely to the massive development of the simuliid *Prosimulium onychodactylum* during the second summer. The biomass maximum at Site 11 is caused mainly by a tipulid of extremely large body size ($\bar{x}$ individual dry weight of fourth instar larvae of 96.6 mg) found only at that location.

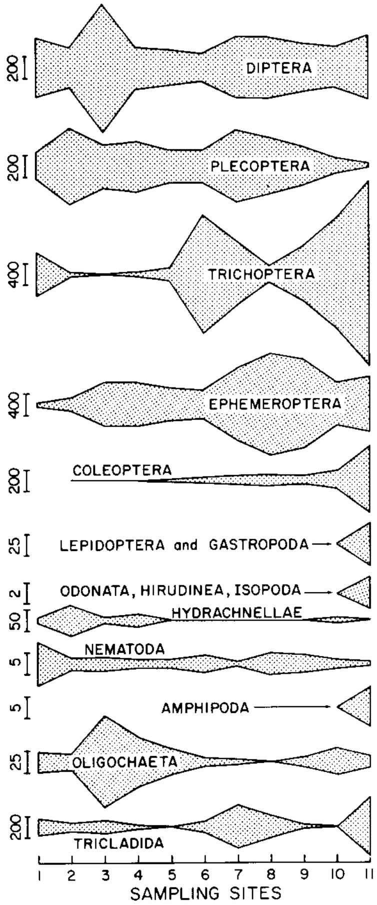

Fig. 16. Longitudinal density patterns for the major macroinvertebrate groups. Vertical scales indicate mean numbers of individuals per m^2. Values for Collembola, Hemiptera, and Sphaeriidae were too small to plot.

The chironomid fauna at each site contained more taxa than all other families of dipterans combined (Table 5). Chironomids also comprised the majority of total dipteran density at all sites, and biomass at some locations. Five subfamilies were represented (Table 6). The Orthocladiinae were the most diverse and abundant, as has been reported for other mountain streams (ELGMORK & SAETHER 1970, LAVILLE 1981) and, along with Diamesinae and Chironominae, had representatives along the entire stream profile. A very few Podonominae were collected, and only from sites in the middle reaches. Tanypodinae were found only at the lower six sampling sites. Although members of the Chironominae were generally restricted to lower elevation sites, the *Micropsectra* species complex was collected from all locations.

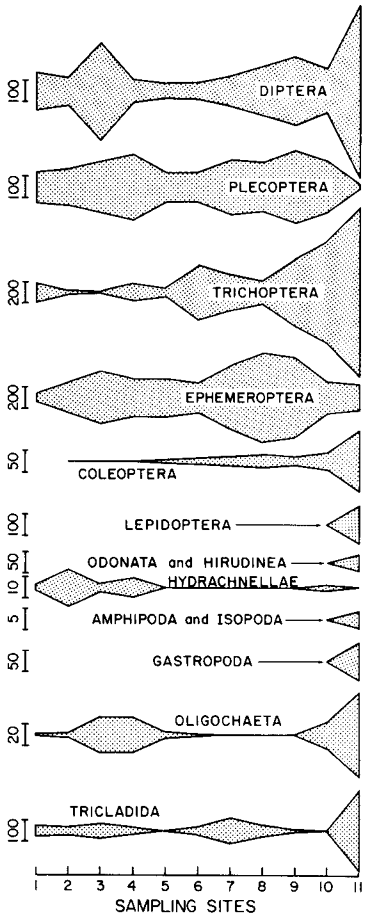

Fig. 17. Longitudinal biomass patterns for the major macroinvertebrate groups. Vertical scales indicate mean dry weights in mg per m^2. Values for Collembola, Hemiptera, Nematoda, and Sphaeriidae were too small to plot.

Orthocladius was the numerically dominant or co-dominant chironomid genus at all locations except 6, 7, and 8 where *Micropsectra* attained maximum abundance (see Appendix B). At sites in the alpine zone, *Orthocladius* shared dominance with other Orthocladiinae *(Eukiefferiella, Parorthocladius, Thienemanniella)* and *Diamesa*. At Site 11 on the plains *Orthocladius* and *Polypedilum* (Chironominae) were co-dominants. Another Orthocladiinae, *Tvetenia*, shared dominance with *Orthocladius* and/or *Micropsectra* at sites in the montane and foothills limnological zones.

Chironomid distributions at the species level show several interesting features, if rare species are excluded from consideration. There is no special headwater

Table 5. The number of taxa (S) in each family of Diptera and the percent contributed by each family to total dipteran density (D) and biomass (B) at each site[a].

Families		Sampling Sites										
		1	2	3	4	5	6	7	8	9	10	11
Chironomidae	S	12	12	14	19	17	25	22	20	25	28	27
	D	85	92	50	60	53	74	80	83	60	56	64
	B	88	70	41	39	17	24	55	38	24	21	19
Simuliidae	S	2	1	1	2	3	3	2	3	4	3	2
	D	6	6	44	20	35	9	4	2	5	13	21
	B	4	15	49	32	43	14	4	1	1	6	2
Tipulidae	S	1	1	1	2	2	3	6	6	6	7	6
	D	tr	tr	tr	3	tr	4	5	7	16	16	14
	B	tr	13	3	2	3	21	24	57	40	52	78
Athericidae	S	–	–	–	–	–	–	–	1	1	1	–
	D	–	–	–	–	–	–	–	tr	12	8	–
	B	–	–	–	–	–	–	–	tr	33	19	–
Blephariceridae	S	–	–	–	1	1	2	2	1	–	–	–
	D	–	–	–	tr	6	4	1	tr	–	–	–
	B	–	–	–	1	26	33	7	tr	–	–	–
Deuterophlebiidae	S	–	–	–	–	–	–	1	–	1	1	–
	D	–	–	–	–	–	–	tr	–	tr	tr	–
	B	–	–	–	–	–	–	tr	–	tr	tr	–
Ceratopogonidae	S	–	–	–	1	1	1	1	1	1	1	1
	D	–	–	–	tr	3	3	1	1	tr	tr	1
	B	–	–	–	tr	1	1	1	tr	tr	tr	tr
Dixidae	S	1	–	–	–	–	1	–	1	–	–	–
	D	tr	–	–	–	–	tr	–	tr	–	–	–
	B	tr	–	–	–	–	tr	–	tr	–	–	–
Empididae	S	1	1	1	2	1	2	2	2	2	2	2
	D	8	2	6	17	3	5	3	2	6	7	tr
	B	8	2	7	26	10	7	6	1	2	2	tr
Psychodidae	S	–	–	1	–	–	1	1	1	1	1	–
	D	–	–	tr	–	–	1	5	5	tr	tr	–
	B	–	–	tr	–	–	tr	4	2	tr	tr	–

[a] tr = <1%

Table 6. Number of species in each of the five subfamilies of chironomids found in St. Vrain Creek, Colorado.

	Sites										
	1	2	3	4	5	6	7	8	9	10	11
Diamesinae (8 species)	4	4	3	3	2	3	3	2	4	3	4
Podonominae (1 species)	–	–	–	1	1	–	1	–	–	–	–
Tanypodinae (4 species)	–	–	–	–	–	2	1	1	1	2	3
Orthocladiinae (24+ species)	7	7	10	14	13	18	15	15	16	16	14
Chironominae (9+ species)	1	1	1	1	1	2	2	2	4	7	6

association among chironomids. No species were restricted to Site 1, or to the alpine zone (Sites 1–3), and only one species was confined to the upper half of the longitudinal profile. Likewise, no common species were restricted to the middle reaches. Some species were restricted to the lower half of the stream and a few occurred only at Site 11 on the plains. Several species traversed the entire stream profile, occurring at all sites or missing from only one or two sites in the middle reaches. Other species occurred at all sites except the plains. Yet others occurred at all except the highest elevation site(s).

Two congeneric Diamesinae exhibited distinct non-overlapping distributions along the longitudinal profile of St. Vrain Creek. *Pagastia partica,* most abundant at Site 1, occurred from the stream source to Site 5; *Pagastia* cf. *sequax* occurred from Site 6 to the plains. In most other cases, however, congeneric species of chironomids occurred sympatrically at one or more sites. *Orthocladius (Euorthocladius)* sp. 2 and sp. 3 were both abundant at many of the same locations.

ELGMORK & SAETHER (1970), who conducted a mid-summer study of a glacier-fed stream near St. Vrain Creek, gave special attention to the chironomid fauna. The stream they studied originates at a higher elevation (3800 m a.s.l.) than St. Vrain Creek and the uppermost portion corresponds to THIENEMANN's (1954) "Gletscherbach" (glacier brook), a distinctive biotope with a distinctive chironomid fauna (KOWNACKA & KOWNACKI 1975), designated the Kryal Zone by STEFFAN (1971). The headwaters of St. Vrain Creek are epirhithral rather than kryal, however, lacking the distinctive kryon biocoenosis present at slightly higher elevations.

Other investigators have found distinctive patterns in the distribution of chironomids along the courses of mountain streams (KOWNACKA & KOWNACKI 1972, LAVILLE 1981). LAVILLE was able to identify species associations corresponding to crenon, epi-, meta-, and hyporhithron zones. The distribution of chironomids in St. Vrain Creek is less well defined. Abundant species, with some exceptions, tend to be widely distributed along the elevation gradient, rather than exhibiting zonal patterns. With the exception of *Pagastia partica,* the species able to develop high abundances in the harsh conditions of the alpine stream are those that occupy the entire or nearly entire stream profile. The general trend, therefore, is the addition of species downstream, without the loss of those present at higher elevations.

Simuliids occurred along the entire stream profile. They were most abundant at lower alpine-upper montane sites and at the plains location. Seven species of black flies in two genera were identified. *Simulium* first appeared in small numbers at Site 5 and generally increased in abundance with increasing distance downstream to attain density and biomass maxima at Site 11. Members of the genus *Prosimulium* occurred at all locations except Site 11. They were extremely rare in the lower foothills, abundant in the upper half of St. Vrain Creek, with maxima at Site 3 where *P. onychodactylum* mean density exceeded 500 individuals per square meter (Fig. 18). *P. travisi* occurred only at Site 1; *S. virgatum* was found only at Site 11.

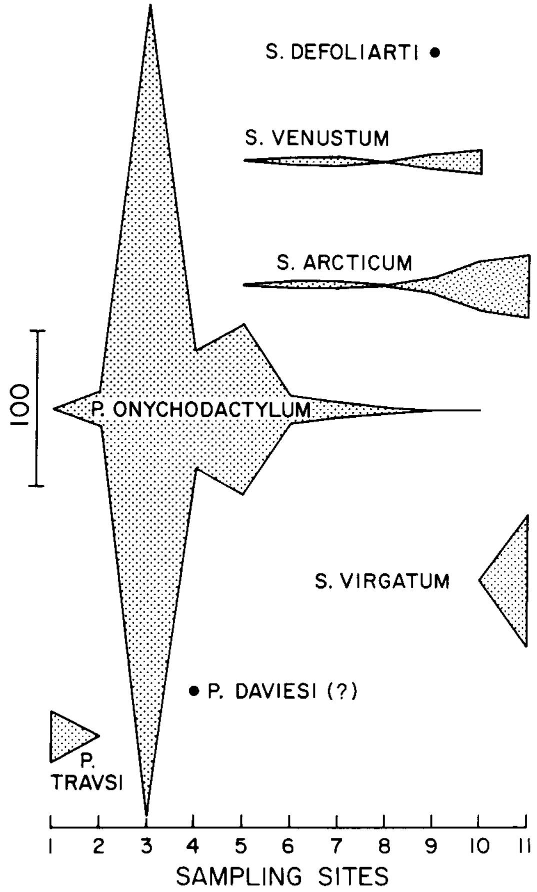

Fig. 18. Abundance patterns of the species of Simuliidae (*Simulium* and *Prosimulium*) along the longitudinal profile of the St. Vrain River. Vertical scale indicates mean number of organisms per m^2.

Temperature, current, and food are important factors in determining the distribution and abundance of black flies. In the River Endrick, Scotland, MAITLAND & PENNEY (1967) identified an upland stream association of simuliids comprised of cold stenotherms, and a riverine association thought to be favored by the richer conditions of the lower reaches. The distribution of black flies along the course of a French mountain river was attributed to the combined influence of temperature and current velocity (GAGNEUR 1976). WILLIAMS & HYNES (1971) reported a pronounced zonation of black flies in African mountain streams with nearly all species exhibiting rather restricted altitudinal limits. The restriction of species to particular altitudinal bands they attributed largely to temperature, rather than current or stream size, because species exhibited upward range extensions in the shorter and therefore warmer streams.

Tipulids occurred along the entire stream profile, but were poorly represented at the upper five sites. There is a downstream increase in the number of species, from a single species at each of the upper three sites to six species at the plains location. Abundance also exhibited a general downstream increase with tipulids comprising the majority of the total dipteran biomass at the lower four sites, attaining a mean value of 641 mg dry weight per square meter at the plains location.

Twelve species were identified during the study, none of which was found at all sites, although *Dicranota* sp., the only tipulid in the tundra stream, also occurred at Site 11 on the plains and at most of the intervening sites. The largest species, *Tipula* sp. 1 (prob. *T. commiscibilis*), was collected only from Site 11 on the plains. Most species were restricted to the lower half of the longitudinal profile. All common species except *Tipula* sp. 2 occurred at foothills sites, but not all of these extended their distribution to the plains.

Only one or two species were identified from each of the remaining dipteran families found in St. Vrain Creek. The snipe fly family Athericidae is represented by a single species, *Atherix pachypus*. *A. pachypus* was abundant at lower foothills sites, but did not occur in any other limnological zone.

The net-winged midges or Blephariceridae are restricted to the middle reaches of St. Vrain Creek, where the family contributed up to one-third of the dipteran biomass (Table 5). The most abundant species, *Agathon elegantula*, was sympatric with the rarer species, *Bibiocephala grandis*, at Sites 6, 7, and 8.

The Deuterophlebiidae or mountain midges are represented by a single species, *Deuterophlebia coloradensis*, in Colorado. A few specimens were collected from foothills sites. Larvae, which frequent the upper surfaces of submerged boulders and bedrock (Ward 1975), are most certainly underrepresented by the sampling method used in the present study.

Ceratopogonids occurred at all sites except those of the alpine zone, but were never abundant. All individuals appear to be a single species within the *Palpomyia/Bezzia* complex.

Dixid midges were only rarely encountered in samples from St. Vrain Creek. Larvae of lotic species of *Dixa* are most likely madicolous, occurring in the splash zone, and should probably be considered accidentals given the sampling methods of the present study.

Two genera of Empididae or dance flies were encountered. *Clinocera* occurred at all sites and was abundant at some locations. *Chelifera*, with the exception of one individual collected at Site 4, was restricted to the lower six sites.

The psychodid *Pericoma* sp. occurred sporadically from lower alpine to the lower foothills sites. Maximum abundance was attained at Sites 7 and 8.

Plecoptera. Stonefly abundance remained relatively constant from the headwaters to the foothills of St. Vrain Creek, whereupon values declined to very low levels at the plains site (Figs. 16 and 17). Plecoptera diversity exhibited a different pattern, with maximum species richness in the middle reaches (Fig. 19).

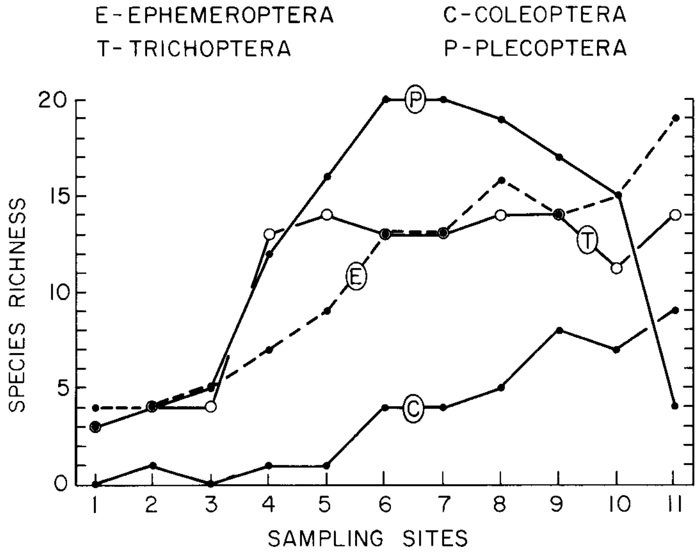

Fig. 19. The longitudinal pattern of species richness for the four most diverse non-dipteran insect orders.

Thirty-one species of Plecoptera were identified from the nymphal material collected during the study. Ward (1982) provided a list of the stonefly species found in St. Vrain Creek and their altitudinal limits, based on a partial data set (coarse mesh samples only). No additional species were identified from the 387 fine mesh samples (*Cultus aestivalis* was erroneously designated *C. pilatus*), but there were a few changes in species' distributions. Data from the additional samples filled gaps in the recorded distributions of some species and resulted in range extensions for some others (Appendix B is based on the entire data set). Presumed species' distributions have been constricted in a few instances because the additional samples failed to yield nymphs of species listed at a site because aerial adults were collected there. For example, because adults were collected from Site 10, *Isoperla quinquepunctata* was assumed to be a foothills species with marginal populations extending to the plains. The additional samples, however, failed to yield nymphal material from any but the plains site. *I. quinquepunctata,* which also occurs in cold springbrooks (Ward & Dufford 1979) and in the summer cool tailwaters below deep-release dams (Ward 1976a), is apparently restricted to the plains site by factors other than temperature.

No species of Plecoptera was restricted to sites in the alpine zone. The chloroperlid *Sweltsa borealis,* which occurred only at Sites 1–5, is the only headwater species among the Plecoptera. The other stoneflies collected from Site 1 (*Megarcys signata* and *Zapada oregonensis*) are euryzonal species found in all limnological zones except the plains.

Site 10 marks the lower distributional limits of a number of stoneflies. Some of these traverse all or nearly all of the stream course except the plains. Others are foothills species, found at Site 10 and usually one or two other foothills sites. A very few nymphs of some foothills species occur as accidentals at the plains location. *Triznaka signata,* however, is relatively abundant at and restricted to the lowermost foothills (Site 10) and plains (Site 11) locations.

A number of stoneflies, including some common species, are restricted to the middle reaches of St. Vrain Creek. *Taenionema nigripenne,* for example, was found only at Sites 6–8.

In summary, excluding rare species, the Plecoptera fauna is comprised of 6 euryzonal mountain species, 1 headwater species, 1 plains species, 2 foothills species, 4 middle reach species, 3 lower montane/foothills species, and 1 species that is common at both a mountain stream location (Site 10) and the plains (Table 7).

Table 7. Distribution of the Plecoptera, excluding rare species, of St. Vrain Creek, Colorado.

- Euryzonal mountain species
  - *Megarcys signata, Zapada oregonensis, Sweltsa coloradensis, Capnia confusa, Eucapnopsis brevicauda, Suwallia pallidula*
- Headwater species
  - *Sweltsa borealis*
- Plains species
  - *Isoperla quinquepunctata*
- Foothills species
  - *Pteronarcella badia, Claassenia sabulosa*
- Middle reach species
  - *Zapada cinctipes, Taenionema nigripenne, Capnia* sp., *Paraleuctra occidentalis*
- Lower Montane / foothills species
  - *Prostoia besametsa, Isoperla fulva, Malenka californica*
- Foothills / plains species
  - *Triznaka signata*

The distribution of Plecoptera in the Tatra and Carpathian Mountains (KAMLER 1967) exhibits several common features with the results of the present study. Neither study found stoneflies that were confined to the highest elevations; rather, those occurring at the uppermost sites tended to be species that traversed a large vertical range. In addition, the altitudinal pattern of Plecoptera diversity is similar to that of St. Vrain Creek, with high numbers of species in middle reaches, but few species at upper or lower sites. The species richness of Plecoptera determined by KNIGHT & GAUFIN (1966) for sites in the foothills and montane limnological zones of a Rocky Mountain drainage is also comparable to the pattern exhibited by the Plecoptera fauna of St. Vrain Creek, although there were major differences in the altitudinal distributions of several species common to both streams. Several investigators have stressed the primary importance of temperature in determining the altitudinal distribution of Plecoptera (DODDS & HISAW 1925, BRINCK 1949, KAMLER 1965, KNIGHT & GAUFIN 1966, RAVIZZA & RAVIZZA DEMATTEIS 1978). Whereas KNIGHT & GAUFIN (1966) consider temperature the major factor structuring the altitudinal distribution patterns of Plecoptera, they postulate, as does LILLEHAMMER (1974), that limited food resources at high elevations partly contribute to the low diversity of Plecoptera in the headwaters of high mountain streams.

Trichoptera. Caddisflies exhibited three progressively larger abundance peaks along the course of St. Vrain Creek (Figs. 16 and 17). A single species of limnephilid, *Allomyia tripunctata*(?), accounted for virtually the entire trichopteran standing crop at Site 1. *Rhyacophila* spp. and the limnephilid *Neothremma alicia* attained maxima at Sites 6 and 7 and are responsible for the abundance peak of the middle reaches. *Lepidostoma* sp., *Brachycentrus americanus*, *Hydropsyche oslari*, and *Glossosoma parvulum* attained maxima at Site 10, leading to the peak that culminated at Site 11 where the plains species, *Cheumatopsyche pettiti*, *Hydropsyche occidentalis*, *Nectopsyche stigmatica*, and *Helicopsyche borealis* developed extremely large density and biomass values. The altitudinal abundance patterns of some numerically dominant species and species complexes are shown in Figure 20.

Trichoptera species richness was low at alpine sites, increased markedly from Site 3 to Site 4, and stayed at about the same level over the remainder of the stream course (Fig. 19). Thirty-three species of caddisflies were identified. The species list and altitudinal limits reported by WARD (1981) from a partial data set (coarse mesh, year 1 only) require some emendation. Most changes involve vertical range extensions or filling gaps in distribution patterns. Site occurrences based on the presence of aerial adults were deleted if the entire data set failed to produce identifiable larvae of the species at that location. The limnephilid designated *Hesperophylax oreades*(?) based on ELGMORK & SAETHER (1970) is apparently *Psychoronia costalis* (WIGGINS 1977: 282). Specific identification of *Hydropsyche* larvae, formerly designated only at the generic level, clarified the distribution pattern of this important genus.

Three species of limnephilids comprised the entire trichopteran fauna at Site 1 (Appendix B). Unlike the plecopteran fauna of Site 1, which was comprised of euryzonal species at their upper altitudinal limits, the trichopterans were restricted to headwater sites. *Allomyia tripunctata*(?), by far the most abundant macroinvertebrate at Site 1, is truly a tundra stream species. *Allomyia* attains maximum density at the uppermost site and dramatically declines in abundance with increasing distance from the glacier-fed source (Fig. 20).

Several caddisflies, including some extremely abundant species, occurred only at the plains site. *Cheumatopsyche pettiti* and *Helicopsyche borealis* each had mean

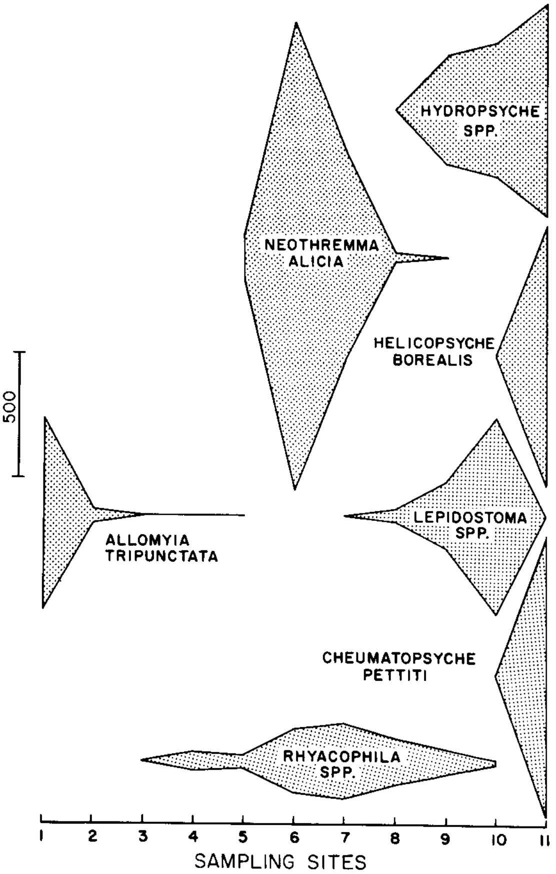

Fig. 20. Abundance patterns of some numerically dominant trichopteran species and species complexes. Vertical scale indicates mean number of organisms per m^2.

density values exceeding 1000 individuals per m^2, and neither species occurred at any mountain stream sites. Three species of *Nectopsyche* (one rare, one common, and one abundant) occurred sympatrically in the plains stream and all were collected only from that location.

With the exception of *Arctopsyche grandis* which extended upwards nearly to the alpine zone, members of the family Hydropsychidae were restricted to the lower foothills and plains. The five species of hydropsychids in St. Vrain Creek exhibited distributional patterns in general concordance with the longitudinal sequence reported by ALSTAD (1980) for the Provo River, Utah.

Seven species of *Rhyacophila* larvae were identified. All seven species cooccurred on the same riffles at Sites 4 and 5. However, each of the four abundant species, while occurring sympatrically at montane and upper foothills locations, attained density maxima at different sites (Fig. 21). The lower and upper distribu-

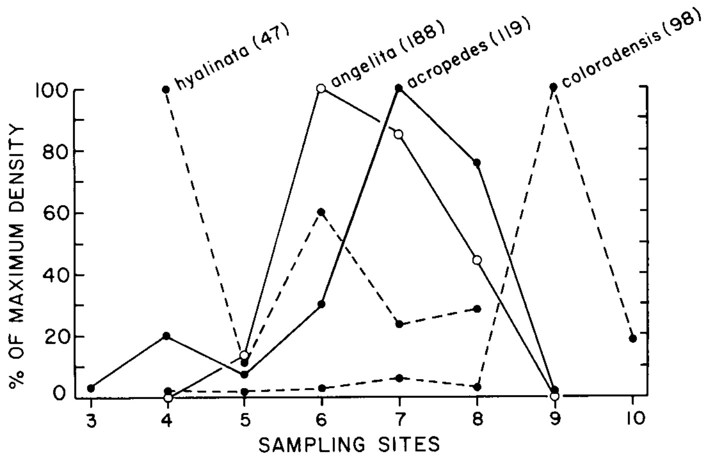

Fig. 21. The relative abundance distributions of the four most abundant species of *Rhyacophila* (Trichoptera). Numbers in parentheses indicate mean number of organisms per m^2 at the site of maximum abundance for that species.

tional limits of all seven species were at considerably higher elevations than in the Salmon River drainage (SMITH 1968), approximately six degrees of latitude farther north.

In summary, the altitudinal distribution pattern of the Trichoptera is more clearly defined than that of either the Chironomidae or the Plecoptera. The caddisfly fauna contains distinct headwater and plains elements, species restricted to the middle reaches, to montane sites, and to the foothills. Euryzonality is less well developed than in the chironomids or stoneflies. No species of caddisflies traversed the entire stream profile, although a few occurred at seven of the eleven sites. A marked faunal transition is apparent between the lower foothills and the plains. Eight species occurred only in the plains stream; Site 10 in the lower foothills marked the downstream distributional limit of several caddisflies.

Variations in the temperature regime as a function of altitude have been ascribed a major role in the zonation of Trichoptera (DÉCAMPS 1967, MECOM 1972). DÉCAMPS stresses the primary importance of the temperature range in determining Trichoptera distribution in running waters. Factors other than temperature that are major determinants of lotic caddisfly distribution patterns include food resources, chemical factors, current, and substratum (MACKAY & WIGGINS 1979).

Ephemeroptera. Mayfly abundance increased gradually throughout the alpine zone, remained at similar levels at all montane sites, attained maximum values at Site 8 in the middle foothills, thereafter declining to levels approximating those of montane sites (Figs. 16 and 17). Species from three families made major contributions to the abundance peak in the middle foothills: *Baetis tricaudatus* (Baetidae), *Epeorus longimanus* and *Rhithrogena hageni* (Heptageniidae), and *Drunella doddsi* and *D. grandis* (Ephemerellidae).

Ephemeroptera species richness exhibited a more or less continuous increase along the entire stream profile (Fig. 19), a pattern not unlike that reported by KAMLER (1967) for the mayfly faunas of Tatra and Carpathian mountain streams. Although a few species that were abundant at upper sites had lower limits in the foothills, the general pattern is the addition of species downstream without loss of those present at higher elevations. Twenty-eight species of mayflies were identified. The species distributions reported by WARD & BERNER (1980) from a partial data set (coarse mesh, year 1 only) require changes, including some of a nomenclatorial nature. Former ephemerellid subgenera have been elevated to genera by ALLEN (1980) and this is reflected in Appendix B. *Baetis intermedius* has been suppressed and placed in synonomy with *B. tricaudatus*, considerably extending the altitudinal range of this species. *B. parvus* has been suppressed and is now *B. hageni*. The species designated *Ameletus velox*(?) is actually *A. sparsatus*. The few other changes involve usually minor range extensions resulting from the additional data.

The Ephemeroptera fauna of St. Vrain Creek exhibits a longitudinal pattern differing from both Plecoptera or Trichoptera, although sharing some features with both groups. No mayflies were restricted to the headwaters; those that occurred at Site 1 are euryzonal species. Euryzonality was well developed among the mayfly fauna; seven species occurred at seven or more of the eleven sites. A diverse and distinctive assemblage of Ephemeroptera occurred in the plains stream. Nine species of mayflies were collected only from this location. *Tricorythodes minutus* was the most abundant of the plains mayflies. *T. minutus* finds favorable conditions in beds of aquatic angiosperms, which are frequently associated with warmer reaches of streams. However, *T. minutus* is a eurythermal mayfly that also occurs in cool lotic habitats containing higher aquatic plants (WARD 1974). Three species of *Heptagenia*, a warm-adapted genus from a largely cool-adapted family (Heptageniidae) occurred sympatrically at Site 11 and did not occur at mountain stream sites. However, the most abundant mayfly of the plains stream is *Baetis tricaudatus*, a species that extended to Site 4 in the upper montane zone.

One species, *Rhithrogena robusta*, might be considered as restricted to middle reaches; however, *R. robusta* could also be described as a euryzonal species since it occurred from Sites 3–8. Several mayflies occurred only at sites in the lower half of St. Vrain Creek. Some of these also occurred in the plains stream, but for others, Site 10 marked the lower distributional limit. Two abundant species, both ephemerellids *(Drunella grandis, Serratella tibialis)*, occurred only in the foothills (1 *D. grandis* nymph was collected from Site 11). Figure 22 compares the distribution and abundance of some congeneric and confamilial species of mayflies. Members of the genera *Drunella*, *Ephemerella* (sensu stricto), *Attenella*, and *Serra-*

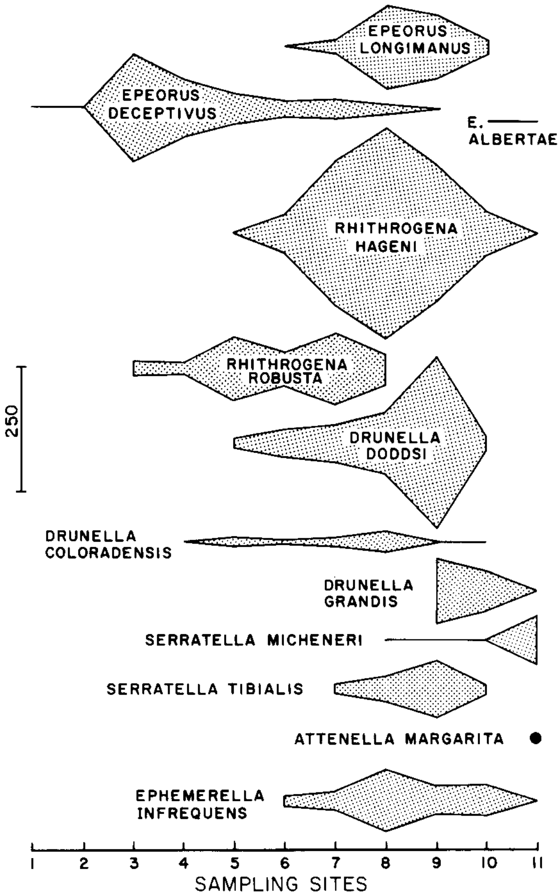

Fig. 22. Abundance patterns of some congeneric and confamilial species of Ephemeroptera. Vertical scale indicates mean number of organisms per m^2.

tella are closely related and were until recently all placed in the genus *Ephemerella* (sensu lato).

Several investigators have identified temperature as a primary, if not the primary, factor limiting the distribution of Ephemeroptera (Dodds & Hisaw 1925, Ide 1935, Kamler 1965, Brodsky 1980, Vannote & Sweeney 1980). Many of the mayflies of St. Vrain Creek are euryzonal; however, species occurring over a wide range of elevation do not necessarily encounter a proportionately wide temperature range. For example, *Epeorus deceptivus* traversed a 1524 vertical meter elevation gradient, yet was exposed to an annual temperature range of only 0–14.5°C at the warmest site.

Coleoptera. The diversity (Fig. 19) and abundance (Figs. 16 and 17) of coleopterans gradually increased downstream along the course of St. Vrain Creek.

The beetle fauna is comprised almost entirely of Elminthidae and Dryopidae. A very few individuals from other families were collected but only at foothills and plains sites. Beetles were absent from the tundra stream segment, but the elminthid *Heterlimnius corpulentus*, typically the only species in high elevation streams (BROWN & WHITE 1978) extended to Site 2 in the alpine zone (Fig. 23). Other species occurred only in the lower half of St. Vrain Creek. No common beetles were restricted to the plains stream, although three species attained maximum populations at the lowermost site.

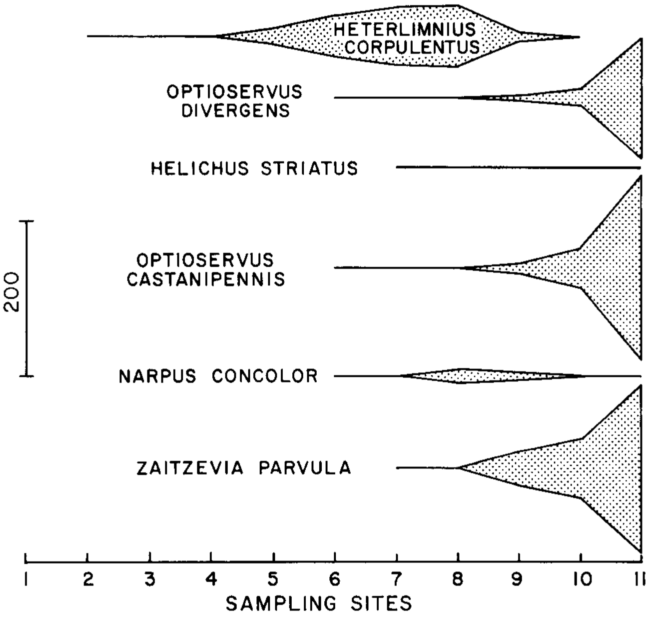

Fig. 23. Abundance patterns of dryopoid coleopterans. Vertical scale indicates mean number of organisms (adults and nymphs) per m^2.

A few researchers have conducted detailed examinations of the longitudinal zonation of lotic coleopterans (BERTHÉLEMY 1966, BERTHÉLEMY & LAUR 1975, WILLIAMS & HYNES 1971, SEAGLE & HENDRICKS 1982). Temperature appears to be an important factor determining zonation patterns in streams traversing extensive elevation gradients. SEAGLE & HENDRICKS (1982) suggest that downstream changes in food resources also play a role in the distribution of riffle beetles. They found the most diverse beetle assemblages in streams with well-buffered water and high levels of dissolved ions.

Odonata. Dragonflies and damselflies were not collected from any of the mountain stream sites. Three species, the anisopteran *Ophiogomphus severus* and the zygopterans *Argia vivida* and *Ishnura* sp., occurred in the plains segment, but none of these were abundant.

Lepidoptera. The aquatic moth *Petrophila longipennis* was restricted to the plains stream segment. As the generic name implies, *P. longipennis* is a rock-dwelling form. Larvae reside under a silk canopy which they typically spin over a slight depression in the surface of a rock. They feed on epilithic algae. First instar larvae lacked gills, whereas mature larvae possessed over 400 gills.

Hydrachnellae. The water mites collectively traversed the entire longitudinal profile of St. Vrain Creek, but were abundant only in the headwaters (Figs. 16 and 17). *Lebertia* sp. occurred from tundra to the plains. Three species of *Sperchon* exhibited overlapping though distinctive distributions: species A was restricted to the upper half of the stream course; species C occurred in the lower half; and species B extended from the tundra stream to Site 10 in the lower foothills. The number of species did not vary greatly as a function of altitude but was highest in the lower montane zone where the faunas from high and low altitudes overlap, a pattern also noted by YOUNG (1959). YOUNG conducted an extensive survey of the water mites of lentic and lotic habitats in north central Colorado, including the region and altitudinal gradient encompassed by the present study. He related altitudinal distribution patterns of stream species to changes in temperature and water chemistry. Distinct altitudinal zonation of water mites has also been reported for the European stream fauna (SCHWOERBEL 1964, VIETS 1966).

In addition to the water mites, a single individual from the family Trombidiidae was collected from the plains site. This specimen apparently represents an undescribed genus near *Podothrombium* (W. C. WELBOURN, Acarology Laboratory, Ohio State University, pers. comm.).

Oligochaeta. Nine species of oligochaetes from five families were identified from collections taken on rubble riffles (Appendix B). Oligochaetes exhibited abundance peaks at lower alpine/upper montane sites and in the lower reaches (Figs. 16 and 17). The tubificid *Limnodrilus hoffmeisteri* developed large populations at Sites 3 and 4 and was responsible for the high altitude maxima in density and biomass. *L. hoffmeisteri* was also a predominant species on stony substratum in the mountain region of a Danube tributary (BREZEANU et al. 1974). The abundance peak in the lower reaches resulted largely from the density maximum of *Lumbriculus variegata* at Site 10 and the biomass contributed by the large megadril *Eiseniella tetraedra* at Site 11. *L. hoffmeisteri* and the naidid *Nais simplex*, the only oligochaetes at headwater sites, occurred from tundra to the plains. *Tubifex tubifex* was found only at the plains site. The amphibious *E. tetraedra*, which occurred sporadically from upper montane sites to the plains, resides in mud banks along water courses and colonizes stream riffles under certain conditions (WARD 1976b).

WACHS (1967), who investigated the distribution of oligochaetes along the courses of the Fulda and Isar Rivers, concluded that water chemistry exerted little direct effect on the fauna, whereas substratum type and composition played major roles. LEARNER et al. (1978), who reviewed the biology of British Naididae, present a generalized longitudinal distribution for lotic species, which they feel is largely determined by current, substratum, vegetation, and temperature.

Tricladida. The two species of planarians occurring in St. Vrain Creek exhibited remarkably distinctive distributions. *Polycelis coronata* occurred at all mountain stream sites, whereas *Dugesia dorotocephala* was restricted to the plains stream. Not a single specimen of *Dugesia* was ever encountered in samples from mountain sites, nor was *Polycelis* ever found in the plains stream. *P. coronata* was the only species found by KENK (1952) in a brief survey of the triclad fauna of mountain streams and lakes of this region.

European planarians exhibit distinct altitudinal zonation patterns that are determined by temperature (reviewed by PATTEE et al. 1973), but such definitive data are generally unavailable for the North American fauna. *Polycelis coronata* is restricted to cold springs at low elevations (WARD et al. 1986), as is *Crenobia alpina,* the European species that extends to the highest elevations.

Hirudinea. A single species of leech, *Erpobdella punctata,* was identified during the study. According to HERRMANN (1970), *E.punctata* is the most abundant and widely distributed of the leeches found in lotic habitats in Colorado. Although he has records as high as 2500 m, in St. Vrain Creek *E. punctata* was restricted to the plains stream. HERRMANN (1970) found that low temperatures and high current velocities prevent most leeches from colonizing mountain streams.

Crustacea. Two amphipods and an isopod were identified, all of which were restricted to the plains stream (Appendix B). Amphipods occur in high mountain lakes, plains reservoirs, cold springs and regulated mountain streams in Colorado (PENNAK & ROSINE 1976, WARD 1974, WARD & DUFFORD 1979). They are, however, typically absent from high gradient mountain streams, apparently because they are not well adapted to resist strong currents. Only in habitats with relatively constant flow regimes such as springbrooks and streams below storage reservoirs, or where aquatic plants provide refuge from the current during spates and floods, are amphipods able to maintain populations in running waters of this region. Isopods are poorly represented in the Rocky Mountains and little is known regarding their ecological requirements.

Mollusca. With the exception of fingernail clams (Sphaeriidae), molluscs are poorly represented in Colorado waters (WARD et al. 1986). A very few species of unionid mussels have been reported from some plains rivers and reservoirs (BRANDAUER & WU 1978), but none occur even in the plains segment of St. Vrain Creek. A single species of sphaeriid clam, *Pisidium nitidium,* occurred sporadically in low numbers along the course of St. Vrain Creek. Populations of *Pisidium* are best developed in lakes or in the silted microhabitats of streams (WU 1978). The gastropods of St. Vrain Creek were represented by a single species of *Physa* that was common in the plains stream and was restricted to that location. The soft water and torrential nature of mountain stream sites is inimical to snails, whereas the harder water and development of angiosperms at Site 11 provide more suitable conditions.

6. Synthesis

A variety of interrelated factors may account for downstream changes in the composition, diversity, and abundance of lotic zoobenthos along stream courses. In this final section, an attempt is made to place the major findings of the study in perspective by examining generalized faunal patterns and factors that may contribute to longitudinal changes in the macroinvertebrates of the St. Vrain River.

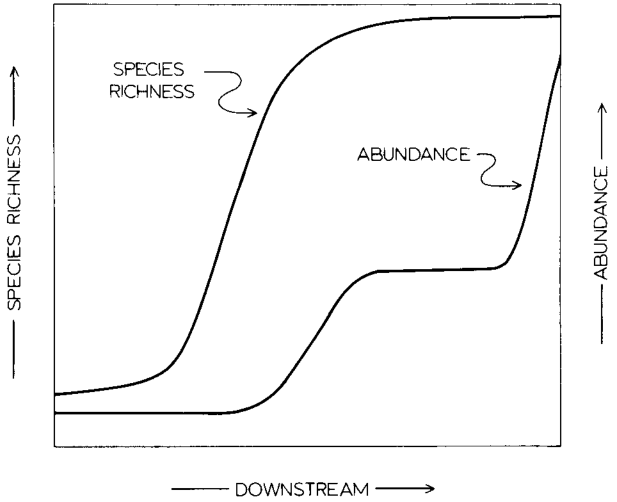

Fig. 24. Idealized altitudinal patterns of species richness and abundance for total zoobenthos.

The idealized downstream abundance pattern for total zoobenthos (Fig. 24) exhibits low values at the upper five sites, increases in the upper montane zone, plateaus in the lower montane and foothills, and markedly increases from Site 10 in the lower foothills to Site 11 on the plains. The idealized pattern of species richness for total zoobenthos exhibits a sigmoid form with low values in the headwaters, a marked increase in the mid-reaches, and an asymptote over the lower reaches.

Figure 25 shows the generalized forms of species richness curves exhibited by the major fauna components. With the exception of pattern 7, all groups shown occur at low diversity levels at high elevation sites. Pattern 7 is exemplified by groups such as lepidopterans, odonates, amphipods, isopods, leeches, and gastropods that are not found at mountain stream sites, occurring solely in the plains stream. Idealized pattern 5 is for mites and planarians, which maintain low levels of diversity along the entire stream profile. Most faunal groups, however, exhibit

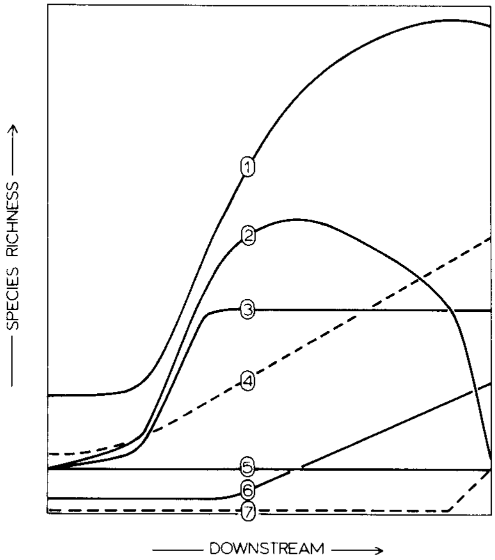

Fig. 25. Idealized types of species richness curves exhibited by the various faunal components (see text for details).

major downstream increases in species richness. Some of these begin increasing immediately, whereas others remain at low levels over several headwater sites. Patterns 4 (Ephemeroptera), 1 (Diptera), and 6 (Coleoptera) show progressively greater lag phases before the commencement of diversity increases. Rapid downstream increases in diversity, however, do not occur before the transition from the alpine to montane zones for any groups. Only plecopterans (pattern 2) exhibit declining diversity levels. Trichopterans (pattern 3) attain maximum species richness in the upper montane zone, then maintain similar levels over the entire remaining stream profile.

Zoobenthic species exhibit four major altitudinal distribution patterns (Table 8). Euryzonal species are those that occurred in the plains stream and traversed a large elevation gradient at mountain stream sites. This should not be confused with euryzonal mountain species (IID in Table 8) which traverse a large elevation gradient, but do not occur in the plains stream. Species of the lower reaches occur only at the plains and lower foothills sites. Plains species are those restricted to Site 11. Species were placed in the highest of the four abundance categories in Table 8 for which they achieved the prescribed density levels (based on grand means) at one or more sites. More than one-third of the species in the highest abundance category were restricted to the plains stream. Most of the remaining "very abundant" species were either euryzonal (type I) or mountain euryzonal (type IID). A few of them were restricted to the headwaters or mid-reaches, but none occurred solely in the lower reaches or foothills.

Table 8. The distribution of total zoobenthos according to the percentage of taxa (primarily species) contributing to each altitudinal pattern within each abundance category (see text for further information).

Altitudinal Patterns	% of Taxa by Abundance Category[a]				
	V	A	C	R	All Taxa
I. Euryzonal	18.2	40.0	32.4	11.0	22.5
II. Mountain	45.5	43.4	45.6	54.0	49.2
A. Headwaters	(9.1)	(0.0)	(5.9)	(7.0)	(5.7)
B. Mid-reaches	(9.1)	(6.7)	(8.8)	(17.0)	(12.4)
C. Foothills	(0.0)	(6.7)	(7.4)	(17.0)	(11.5)
D. Euryzonal (Mts.)	(27.3)	(30.0)	(23.5)	(13.0)	(19.6)
III. Lower Reaches	0.0	10.0	5.9	9.0	7.7
IV. Plains	36.4	6.7	16.2	26.0	20.6

[a] V (very abundant) 500+ org m^{-2}; A (abundant) 100–499 org m^{-2}; C (common) 10–99 org m^{-2}; R (rare) <10 org m^{-2}.

Faunal overlap between sites (Fig.26) was measured using WHITTAKER'S (1975) index of percentage similarity (Ps). The highest Ps values occur between adjacent sites, as expected. However, whereas Site 10 exhibits a 58.4% similarity with Site 9, a Ps value of only 17.8% is obtained when Site 10 is compared with Site 11.

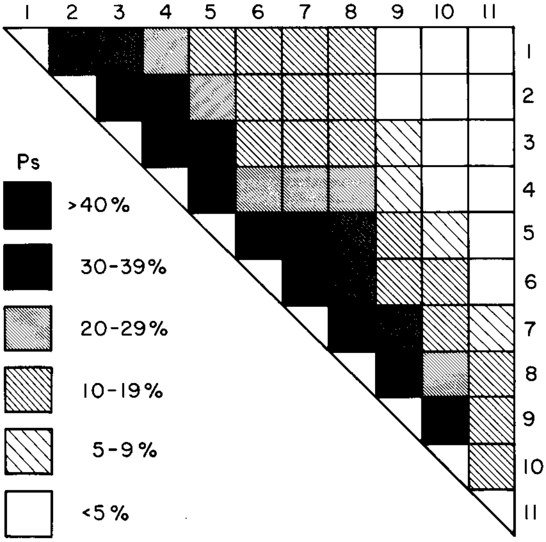

Fig. 26. Matrix of percentage similarity (Ps) between sampling sites based on total zoobenthic species.

Table 9 lists the numerically dominant and subdominant species for each site. In addition, species are shown that, while less abundant, are nonetheless characteristic of a given site or stream segment. The triclad *Polycelis coronata* is the only non-insect abundant enough to attain dominant or subdominant status, although several non-insects are distinctive components of the fauna of the plains stream. A few of the numerical dominants and subdominants are also characteristic of a particular stream segment. The limnephilid caddisfly, *Allomyia tripunctata,* is both a numerical dominant at Site 1 and a distinctive headwater species. All three dominant or subdominant species of Site 11 are also characteristic plains species, being restricted to that location. Most numerical dominants and subdominants, however, occupy a wide elevation range rather than being characteristic faunal components of a given stream reach. Some of the less abundant species, though not rare ones, are useful in identifying specific faunal assemblages or associations typical of a particular set of conditions. For example, the stoneflies *Claassenia sabulosa* and *Pteronarcella badia,* the mayfly *Drunella grandis,* and the dipteran *Atherix pachypus* typify conditions in the lower foothills. All of these species are reasonably abundant at and are largely restricted to Sites 9 and 10.

What environmental variables are responsible for the longitudinal faunal patterns in the St. Vrain River? The stream maintains a rocky substratum and is well oxygenated throughout its length. Sampling was confined to rubble riffles, the predominant bottom type, thus minimizing between-site differences in substratum and current. Some factors either did not vary (pH), or at least remained at low levels (bound CO_2, TDS) at all mountain stream sites, but exhibited dramatic increases from Site 10 in the lower foothills to Site 11 on the plains. Even temperature, which progressively increased downstream, exhibited the most marked change from foothills to plains. There is also a marked faunal discontinuity that occurs from the lower foothills to the plains. Many species, some of them extremely abundant, are restricted to the plains stream; Site 10 in the lower foothills marks the downstream limit of many other species.

It appears that temperature, food resources, aquatic plants, and possibly biotic interactions, are largely responsible for structuring downstream faunal patterns in the St. Vrain River. Each of these factors will be discussed in turn.

Temperature plays a major role in the distribution and abundance of lotic zoobenthos (Hynes 1970, Ward & Stanford 1982, Minshall et al. 1985, Ward 1985) and becomes especially important in stream systems such as the St. Vrain that traverse an extensive elevation gradient. Only the most cold-adapted species are able to establish populations in the headwaters of St. Vrain Creek, which remains ice-covered for 7+ months per year and where maximum summer temperatures do not exceed 6 °C. As annual degree days and the temperature range increase downstream, additional species find conditions suitable. The annual temperature range increased markedly from Site 10 (0–16 °C) to Site 11 (0–25 °C), resulting in a sharp transition from rhithron to potamon thermal conditions (sensu Illies & Boto-

Table 9. Numerical dominants and subdominants, and other distinctive components of the zoobenthos along the course of St. Vrain Creek, Colorado.

Site	Numerical Dominants	Numerical Subdominants	Other Distinctive Faunal Components
1	*Allomyia tripunctata*	*Orthocladius* sp. 3 *Zapada oregonensis*	*Prosimulium travisi* *Pagastia partica*
2	*Zapada oregonensis*	*Cinygmula* sp. *Parorthocladius* sp.	*Allomyia tripunctata*
3	*Cinygmula* sp. *Prosimulium onychodactylum*	*Zapada oregonensis*	
4	*Cinygmula* sp.	*Zapada oregonensis*	*Sweltsa borealis* *Rhyacophila* spp.
5	*Cinygmula* sp. *Neothremma alicia*	*Baetis bicaudatus*	*Sweltsa borealis* *Rhyacophila* spp. Agathon elegantula
6	*Neothremma alicia*	*Rhyacophila angelita*	*Agathon elegantula* *Taenionema nigripenne*
7	*Neothremma alicia*	*Polycelis coronata* *Rhithrogena hageni*	*Taenionema nigripenne*
8	*Baetis tricaudatus* *Rhithrogena hageni*	*Polycelis coronata*	
9	*Baetis tricaudatus* *Hydropsyche oslari*	*Drunella doddsi*	*Claassenia sabulosa* *Drunella grandis* *Pteronarcella badia* *Atherix pachypus*
10	*Lepidostoma* sp. *Hydropsyche oslari*	*Baetis tricaudatus* *Glossosoma parvulum*	*Claassenia sabulosa* *Drunella grandis* *Pteronarcella badia* *Atherix pachypus* *Brachycentrus americanus* *Triznaka signata* *Hydropsyche cockerelli*
11	*Cheumatopsyche pettiti* *Helicopsyche borealis*	*Hydropsyche occidentalis*	*Dugesia dorotocephala* *Tricorythodes minutus* *Baetis insignificans* *Heptagenia* spp. *Isoperla quinquepunctata* *Nectopsyche* spp. *Petrophila longipennis* *Simulium virgatum* *Tipula* sp. 2 *Physa* sp. *Hyallela azteca* *Crangonyx gracilis* *Asellus communis*

SANEANU 1963) corresponding to the distinct faunal discontinuity that is apparent from the lower foothills to the plains.

Thermal conditions in the plains stream eliminate most plecopterans and the cool-adapted species from other groups, while providing a suitable temperature regime for a diverse warm-adapted fauna. *Helicopsyche borealis,* for example, a numerical dominant in the plains stream, is a Nearctic representative of a tropical genus (WILLIAMS et al. 1983). In the St. Vrain River this caddisfly occurs only at the lowermost site, but a large population has also been located in a warm (25 °C) high elevation (3109 m) spring in the Colorado Rockies (WARD, unpubl.).

Aquatic vegetation also exhibits a marked transition from foothills to plains. Although bryophytes are best developed in the headwaters, they occur at all but the plains site. Conversely, aquatic angiosperms, absent from all mountain stream sites, were abundant in the plains stream. Beds of submerged angiosperms modify environmental conditions by increasing spatial habitat heterogeneity, providing current and prey refugia, serving as attachment sites for epiphytic algae, furnishing case-building materials, and generally altering the food base. Although qualitative sampling of the plant beds did not reveal additional species, the high macroinvertebrate diversity and abundance, and the restriction of certain faunal elements to Site 11 are attributable in part to the development of submerged angiosperms in the plains stream.

Autochthonous and allochthonous food resources varied along the longitudinal profile of the St. Vrain River and are partly responsible for shaping macroinvertebrate spatial patterns. Although a complete analysis of food resources was not undertaken in this study, seston and the summer distribution and abundance of epilithic algae and sedimentary detritus were examined along the stream course. It is possible, however, by examining the distribution of macroinvertebrate functional feeding groups (MERRITT & CUMMINS 1984) to gain some insight into the influence of downstream changes in food resources (Fig. 27).

Collector-gatherers, species that feed on fine sedimentary detritus, were relatively abundant at all sites. Scrapers, species that feed on attached algae and associated material (periphyton), were relatively abundant except at Sites 2 and 3. Detritivore shredders, macroinvertebrates that feed on coarse detrital particles, attained maximum development at Site 2 because of the large population of a stonefly shredder, but were virtually absent from the plains site. The bimodal relative abundance pattern of filter feeders, species that feed on particles suspended in the water column, largely reflects the large populations of black flies at lower alpine/upper montane sites and the progressive increase in hydropsychid caddisflies from the lower foothills to the plains. Other species of black flies and the caddisfly *Brachycentrus americanus* also contribute substantially to the development of filter feeders in the lower reaches. The contribution made by predators ranged from 6% to 24% at the various sites. Macrophyte herbivores, a composite of species that are plant piercers or that shred living plant tissue, are best developed in the head-

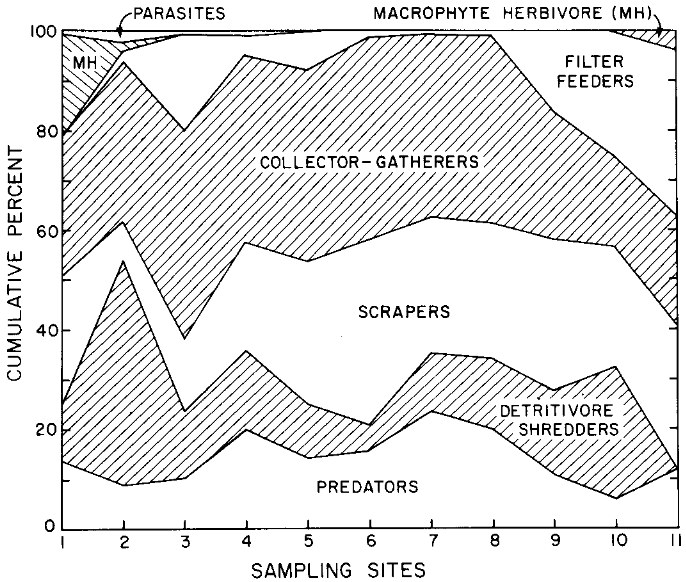

Fig. 27. Relative contributions of macroinvertebrate functional feeding groups (sensu Merritt & Cummins 1984) along the course of the St. Vrain River.

waters where bryophytes are abundant. Although macrophyte herbivores are also present at the plains site, it is perhaps not surprising that they are poorly represented there, since angiosperms are rarely utilized as a food source (when alive) by invertebrates of temperate streams (Hynes 1970, Minshall 1978, Gray & Ward 1979).

The only parasites identified among the macroinvertebrates are the nymphs of water mites that parasitize some species of aquatic insects.

The River Continuum Concept (Vannote et al. 1980) predicts downstream shifts in the relative abundance of functional feeding groups as food resources change along the longitudinal profile of river systems. According to this concept, shredders are abundant only in the headwaters; collectors (including filter feeders and gatherers) are important in all reaches, but are virtually the only non-predaceous invertebrates in the lower reaches; grazers are best developed in middle reaches; and predators are purported to maintain similar relative abundances along the entire stream profile.

The altitudinal distribution of functional feeding groups along the St. Vrain River exhibits little conformance with the River Continuum Concept, which is to be expected since the concept was derived primarily from studies of the deciduous forest streams of eastern North America. The increase of filter feeders in the lower reaches of the study stream and the virtual absence of detritivore shredders from the plains site are the only features that follow the predictions of the River Continuum Concept.

Biotic interactions may also contribute to the spatial distribution and abundance patterns of macroinvertebrates. Whereas the fish fauna of mountain stream segments is essentially restricted to salmonids that apparently do not play a major role in structuring macroinvertebrate communities (ALLAN 1982), a diverse assemblage of fishes occurs in the plains stream. The plains fishes are largely invertivores which collectively exhibit an array of food selectivity and feeding strategies (PROPST 1982), in contrast to salmonids that feed almost exclusively on drift. Some mountain species of invertebrates may be unable to maintain populations at the plains site because of the more intense fish predation. However, those zoobenthic species that have evolved under such conditions have developed predator avoidance mechanisms such as exploiting the prey refugia provided by the angiosperm beds.

Competitive displacement may truncate the range of temperature (or other factors) that a species could otherwise occupy in the absence of competitors (HYNES 1952, PATTEE et al. 1973, GÍSLASON 1982), and this may influence altitudinal distribution patterns along stream courses. Zonal boundaries are not normally determined by physical factors alone, but "correspond to values of the environmental variables at which the outcome of competition changes" (HUTCHINSON 1967). However, equilibrium conditions (sensu MACARTHUR 1960) are normally required for competitive displacement to occur. MINSHALL et al. (1985) postulate that temperate mountain streams alternate between equilibrium and non-equilibrium states with a periodicity that enables biotic interactions to become significant factors for relatively short-lived species such as aquatic insects. The extent to which biotic interactions influence altitudinal distribution patterns has received very little attention from stream ecologists and may provide a fruitful area for future research endeavors.

7. Summary

Altitudinal gradients of physicochemical factors, aquatic vegetation, and macroinvertebrates were investigated along the course (Fig. 1) of a pristine Rocky Mountain stream (Figs. 2–5) from its glacier-fed source in alpine tundra (3414 m a.s.l.) to the plains (1544 m a.s.l.). The St. Vrain River maintains a rocky substratum and is well oxygenated throughout its length. Sampling was confined to rubble riffles, the predominant bottom type (Tab. 2), to minimize between-site differences in substratum and current. A rhithron character prevailed over nearly the entire stream course, with an abrupt transition to potamon thermal conditions between the lower foothills and the plains (Figs. 7, 8). Chemical factors (Tab. 1) either did not vary (pH) or remained at low levels (e. g., bound CO_2, TDS) at all mountain stream sites, but dramatically increased from foothills to plains (Fig. 6), coincident with the transition from insoluble crystalline bedrock to highly soluble sedimentary strata. Fine particulate organic matter (FPOM, 0.05–1 mm) comprised the majority of the benthic detritus at all sites along the longitudinal profile during summer (Tab. 3). The predominance of FPOM was especially pronounced at the tundra site.

Aquatic angiosperms were restricted to the plains location; mosses and liverworts occurred at all sites except the plains. Epilithon biomass exhibited a bimodal pattern as a function of altitude (Fig. 9). High values at headwater sites resulted from the great develop-

ment of bryophytes. Dense growths of the filamentous chlorophyte *Cladophora glomerata* were responsible for high values in the plains stream. The 94 species and varieties of epilithic algae (Appendix A) did not form distinct zones, but may be grouped into (1) euryzonal species, (2) species restricted to upper sites, and (3) species restricted to lower sites. No species that comprised a major portion of the total algae (Tab. 4) were restricted to middle reaches.

Macroinvertebrates received the most intensive and comprehensive study. More than 210 taxa were identified (Appendix B). Many major groups were represented along the entire stream profile (e. g., Plecoptera, Ephemeroptera, Trichoptera, several families of Diptera, Tricladida, Hydrachnellae). However, three orders of insects, crustaceans, leeches, and snails were collected only from the plains stream (Fig. 10). Aquatic insects contributed 89–99% to total zoobenthos density and 84–99% to total biomass at the various sites (Fig. 11). Total abundance and species richness increased markedly from tundra to plains (Figs. 12, 14). Dipterans contributed more species than any other group at all sites (Fig. 15). Faunal abundance was depressed at most sites during the first summer of study, a time of abnormally high discharge and extended runoff (Fig. 13).

Longitudinal changes in the biomass (Fig. 16), density (Fig. 17), and diversity (Fig. 25) of the major taxa were examined. The major faunal components exhibited one of several types of species richness curves. Planarians and mites, for example, maintained low, relatively constant levels of diversity along the entire longitudinal profile; mayflies continually increased in diversity downstream; caddisfly diversity rapidly increased to attain a maximum level near the headwaters, which was maintained over the remainder of the longitudinal profile; stonefly diversity increased then dramatically decreased over the course of the St. Vrain River.

Taxonomic composition and species distribution and abundance patterns were analyzed for each major group of zoobenthos (Figs. 18–23, Tabs. 5–7). Species exhibit one of four types of altitudinal distribution patterns (Tab. 8): euryzonal (Type I), mountain (Type II with 4 subtypes), lower reach (plains and foothills – Type III), and plains (Type IV). Numerical dominants and subdominants, as well as less abundant distinctive faunal elements, were identified for each of the eleven sampling sites (Tab. 9).

The idealized abundance pattern developed for the zoobenthos of the St. Vrain River (Fig. 24) exhibits low values over the upper five sites, increases in the upper montane zone, maintains that level through the foothills, and markedly increases from the lower foothills to the plains. The idealized species richness pattern for total zoobenthos exhibits a sigmoid pattern (Fig. 24).

The headwaters of the St. Vrain River are epirhithral in nature with no evidence of the distinctive "Gletscherbach" (glacier brook) biocoenosis. A sharp faunal discontinuity between the lower foothills and the plains corresponds to the transition from rhithron to epipotamon conditions. Numerous species, including some extremely abundant ones, are restricted to the plains stream; the lower foothills marks the downstream limit of many other species. The percent similarity matrix (Fig. 26) further demonstrates the faunal break between Sites 10 and 11. Temperature, food resources (Fig. 27), aquatic plants, and possibly biotic interactions are ascribed major roles in structuring altitudinal faunal patterns.

8. Zusammenfassung

Höhenbedingte Unterschiede von physikalisch-chemischen Faktoren, Wasserpflanzen und Macro-Invertebraten wurden entlang dem Lauf (Abb. 1) eines natürlichen Rocky Mountain Flusses untersucht, beginnend mit der von einem Gletscher gespeisten Quelle in der alpinen Tundra (3414 m ü.M.) bis in das Flachland hinein (1544 m ü.M.). Die gesamte

Länge des St. Vrain Flusses weist ein felsiges Substrat auf und ist mit Sauerstoff gut angereichert. Stichproben wurden auf Stromschnellen mit dem vorherrschenden Bodentyp (Tabelle 2) beschränkt, um die Unterschiede zwischen Substrat und Strömung der verschiedenen Probestellen zu mindern. Ein Rhitron-Character war beinahe über den gesamten Flußverlauf vorherrschend, mit einem abrupten Übergang zu warmen Flußverhältnissen zwischen den Vorbergen und dem Flachland (Abb. 7, 8). Chemische Faktoren (Tab. 1) variierten entweder überhaupt nicht (pH) oder blieben bei niedrigen Werten (z.B. gebundenes CO_2, TDS) an allen Bergflußprobestellen, zeigten aber einen dramatischen Anstieg von den Vorbergen in die Ebene (Abb. 6), zusammentreffend mit dem Übergang von unlöslichem, kristallinem Flußbettgestein auf stark lösliche Sediment Strata. Feine organische Teilchenmaterie (FOT 0,05–1 mm) bildete den Hauptanteil des Gesteinschuttes am Flußboden an allen Probestellen entlang des longitudinalen Profils während des Sommers (Tab. 3). In der Tundra war das Vorherrschen der FOT besonders deutlich.

Angiosperme kamen nur an den Probestellen der Ebene vor; Moose und Lebermoose wurden an allen Probestellen mit Ausnahme der Ebene beobachtet. Epilithophyten-Biomassen zeigten eine Häufigkeitskurve als Funktion der Höhenlage (Abb. 9). Hohe Werte am Flußursprung sind der umfangreichen Entfaltung von Bryophyten zuzuschreiben. Dichtes Wachstum von haarfädigen Chlorophyten „*Cladophora glomerata*“ waren für die hohen Werte in dem Fluß innerhalb der Ebene verantwortlich. Die 94 Arten und die Vielfalt an Epilithophyten (Anhang A) bildeten keine distinktiven Zonen, sondern können in (1) verbreitete Arten, (2) Arten, die sich in den höheren Regionen befinden, und (3) Arten, die sich an den tiefer gelegenen Probestellen befinden, gruppiert werden. Keine der Arten, die den Hauptteil der gesamten Algen darstellen, waren auf die mittleren Regionen beschränkt (Tab. 4).

Macro-Invertebraten wurden am intensivsten und umfassendsten untersucht. Mehr als 210 Taxa wurden identifiziert (Anhang B). Viele der Hauptgruppen kamen entlang des Flußprofils vor (z.B. Plecoptera, Ephemeroptera, Trichoptera, verschiedene Gattungen der Dipteren, Tricladidae, Hydrachnellae). Jedoch drei Insektenarten, Crustaceen, Blutegel und Schnecken wurden nur aus dem Fluß im Bereich der Ebene gesammelt (Abb. 10). Wasserinsekten trugen 89–99% zu der Zoobenthosdichte und 84–99% zu der Gesamtbiomasse an den verschiedenen Probestellen bei (Abb. 11). Die Gesamtfülle und der Artenreichtum stieg von der Tundra in die Ebene auffallend an (Abb. 12, 14). An allen Probestellen steuerten Diptera mehr Arten bei als irgendeine andere Gruppe (Abb. 15). Während des ersten Sommers der Untersuchung war die Menge der Fauna an den meisten Stellen beschränkt, da dies mit dem Zeitpunkt einer anormal hohen Wasserführung und eines langwährenden Schmelzwasserzuflusses zusammentraf (Abb. 13).

Longitudinale Änderungen in der Biomasse (Abb. 16), Dichte (Abb. 17) und Vielfalt (Abb. 25) der Haupttaxa wurden untersucht. Die Hauptkomponenten der Fauna zeigten Artenreichtumskurven für charakteristische Typen. Planarien und Milben zum Beispiel bewahren geringe, verhältnismäßig konstante Vielfaltsdurchschnitte entlang dem gesamten longitudinalen Profil; stromabwärts nahmen Ephemeriden laufend an Vielfalt zu; die Vielfalt der Köcherfliegen nahm zu, bis sie einen maximalen Durchschnitt schon in der Nähe des Flußursprungs erreichte, der über den Rest des longitudinalen Profils aufrechterhalten blieb. Die Vielfalt an Plecopteren nahm anfangs zu und dann drastisch über den gesamten Lauf des St. Vrain Flusses ab.

Eine klassifizierte Zusammensetzung, die Artenverteilung sowie Vielfaltsregeln der Arten wurden für jede Hauptgruppe des Zoobenthos bestimmt (Abb. 18–23, Tab. 5–7). An höhenbedingten Verteilungsanordnungen gehören die Arten jeweils einem von vier Typen (Tab. 8) an: verbreitet (Typ I), gebirgig (Typ II mit 4 untergeordneten Typen), niedrigere Bereiche (Ebene und Vorberge – Typ III) und Ebene (Typ IV). Zahlenmäßig dominante und subdominante als auch häufige, charakteristische Faunaelemente wurden für jede der elf Probestellen ermittelt (Tab. 9).

Das idealisierte Vielfaltsmuster, das sich für das Zoobenthos des St. Vrain Flusses ergab (Abb. 24), zeigt niedrigere Werte im Vergleich mit den oberen fünf Probestellen, Zunahmen in der oberen Gebirgszone, den gleichen Wert in den Vorbergen und markante Zunahmen von den niederen Vorbergen bis in die Ebene hinein. Die idealisierten Artenreichtumsmuster für das gesamte Zoobenthos weisen ein S-förmiges Bild (Abb. 24) auf.

Der Flußursprung des St. Vrain ist von Natur aus epirithral und zeigt keine Anzeichen der charakteristischen „Gletscherbach"-Biocoenose. Eine scharfe Diskontinuität der Fauna zwischen den niederen Vorbergen und der Ebene stimmt mit dem Übergang von Rhitron zum Epipotamon überein. Zahlreiche Arten, darunter einige sehr häufig vorkommende, sind auf den Flußabschnitt der Ebene beschränkt; die niederen Vorberge markieren die Grenze stromabwärts für viele andere Arten. Eine prozentuale Ähnlichkeitsmatrix (Abb. 26) zeigt weiterhin den Bruch in der Fauna zwischen den Probestellen 10 und 11. Temperatur, Nahrungsquellen (Abb. 27), Wasserpflanzen und mögliche biotische Wechselwirkungen werden als die Hauptfunktionen in der Gliederung der höhenbedingten Struktur der Fauna betrachtet.

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Appendix A. Summer distribution of epilithic algae (including cyanobacteria) at sampling sites along the longitudinal profile of St. Vrain Creek. Presence at a site indicated by +.

	Sites										
	1	2	3	4	5	6	7	8	9	10	11
Phylum Bacillariophyta											
Achnanthes lanceolata	+	+	+	+	+	+	+	+	+	+	+
A. lanceolata var. *rostrata*	+	+	+								
A. lanceolata var. *dubia*									+		+
A. minutissima	+	+	+	+	+	+	+	+	+	+	+
Asterionella formosa										+	
Amphora sp.		+		+							
Cocconeis placentula		+	+	+	+	+	+	+	+	+	+
C. rugosa			+	+	+						
Cyclotella meneghiniana							+				+
Cymbella affinis		+	+	+	+	+	+	+	+	+	+
C. turgida					+	+	+				
C. ventricosa	+	+	+	+	+	+	+	+	+	+	+
Denticula sp.		+		+		+					
Diatoma anceps	+	+	+	+	+	+					
D. hiemale	+	+	+	+	+	+		+			
D. hiemale var. *mesodon*	+	+	+	+	+	+			+		
D. vulgare							+	+			+
Epithemia sorex											+
Eunotia pectinalis		+				+				+	
Fragilaria capucina				+		+		+	+	+	+
F. construens	+	+		+							
F. crotonensis		+							+	+	
F. leptostauron			+	+							
F. pinnata				+							
F. vaucheriae				+	+	+		+		+	
Frustulia rhomboides		+		+		+			+		
Gomphoneis herculeana									+		
Gomphonema acuminatum			+	+						+	+
G. angustatum						+		+	+		+
G. constrictum						+			+		
G. olivaceum	+			+		+		+	+		+
G. parvulum						+	+	+		+	+
Hannea arcus		+	+	+	+	+	+	+	+	+	
H. arcus var. *amphioxys*		+	+	+	+	+	+		+		
Melosira sp.						+	+	+	+	+	+
M. varians										+	+
Meridion circulare		+		+			+				
Navicula sp. 1	+	+									
Navicula sp. 2		+	+	+	+	+	+				
Navicula sp. 3					+		+	+	+	+	+
N. cryptocephala					+	+	+	+	+	+	+
N. exigua					+	+					
N. pupula			+								
N. radiosa			+	+	+	+		+	+	+	+
N. tripunctata					+	+					+
N. viridula											+
Neidium affine											+
Nitzschia sp. 1		+									
Nitzschia sp. 2		+	+	+	+	+	+				

Appendix A (continued)

	Sites										
	1	2	3	4	5	6	7	8	9	10	11
Nitzschia acicularis				+	+	+	+	+	+	+	+
N. apiculata						+			+	+	
N. dissipata		+				+			+		
N. palea							+	+	+	+	+
Pinnularia sp. 1					+						
Pinnularia sp. 2						+				+	+
Stauroneis smithii				+							
Surirella angustata						+					
S. ovata											+
Synedra rumpens		+				+		+			
S. ulna			+	+		+	+	+	+	+	+
Tabellaria fenestrata						+					
T. flocculosa						+					
Phylum Chlorophyta											
Ankistrodesmus falcatus										+	+
Bulbochaete sp.											+
Cladophora glomerata											+
Closterium sp. 1	+				+	+		+			
Closterium sp. 2					+	+		+		+	+
Cosmarium sp. 1										+	+
C. botrytis	+	+				+				+	+
Haematococcus lacustris (aplanospore)	+										
Hyalotheca sp.								+		+	
Microspora sp.	+	+									
Oedogonium sp.										+	+
Pediastrum duplex										+	
Scenedesmus quadricauda										+	+
Selenastrum westii											+
Spirogyra spp.				+		+	+	+	+	+	+
Staurastrum sp.										+	+
Staurastrum paradoxum										+	
Stigeoclonium sp.										+	
Ulothrix spp.	+	+	+		+				+	+	
Phylum Chrysophyta											
Dinobryon sp.											+
Hydrurus foetidus	+	+		+		+					
Phylum Cyanobacteria											
Anabaena spp.		+	+	+		+	+	+	+	+	+
Chamaesiphon incrustans							+			+	+
Merismopedia punctata											+
Nostoc microscopium											+
Oscillatoria spp.	+	+	+		+	+	+	+	+	+	+
Phormidium spp.	+	+	+	+	+	+	+	+	+	+	+
Tolypothrix sp.	+						+		+	+	
Phylum Rhodophyta											
Audouinella violaceae					+						
Lemanea fucina				+			+				

Appendix B. Macroinvertebrate taxa collected from sampling sites along the longitudinal profile of St. Vrain Creek and their abundance based on means from total individuals collected (all dates and mesh combined). Four abundance categories are used: R (rare) <10; C (common) 10–99; A (abundant) 100–499; and V (very abundant) 500 or more organisms per m^2.

	Sampling Sites										
	1	2	3	4	5	6	7	8	9	10	11
Plecoptera											
Amphinemura sp.							R	R	R	R	
Malenka californica						R	C	R	R	R	
Prostoia besametsa					R	C	A	A	A	C	
Zapada cinctipes				R	R	C	C	R	R		
Z. frigida								R			
Z. oregonensis	A	V	A	A	C	C	C	C	R		
Taenionema nigripenne						C	C	R			
Capnia confusa			R	R	C	R	R	R	R	R	
Capnia sp.				R	C	C	R				
Eucapnopsis brevicauda				R	R	C	A	C	R	R	
Utacapnia sp.					R	R		R			
Paraleuctra occidentalis				R	C	R	R				
P. vershina							R	R	R		
Pteronarcella badia									C	C	
Pteronarcys californica										R	
Isoperla fulva						R	R	R	C	C	
I. quinquepunctata											C
I. sobria						R	R	R			
Cultus aestivalis				R	R	R	R	R			
Diura knowltoni						R		R	R		
Pictetiella expansa					R						
Kogotus nonus					R	R	R	R			
Megarcys signata	C	C	C	C	C	C	C	C	R	R	
Skwala parallela									R	R	R
Hesperoperla pacifica					R	R	R		R	R	
Claassenia sabulosa									C	C	R
Suwallia pallidula				R	R	C	C	C	C	R	
Sweltsa borealis	R	R	R	C	C						
S. coloradensis		R	C	C	C	C	A	A	C	C	
Triznaka signata										C	C
Paraperla frontalis				R		R	R				
Ephemeroptera											
Ameletus sp.	C	C	C	C	R	C	R	R			
Ameletus sparsatus						R		R	R	R	
Baetis bicaudatus	R	C	C	C	A	C	A	A	C		C
B. insignificans										R	A
B. hageni											R
B. tricaudatus				R	C	C	A	V	V	A	V
Callibaetis sp.											R
Pseudocloeon sp. 1								C	C	C	R
Pseudocloeon sp. 2											R
Cinygmula sp.	C	A	V	V	A	A	A	A	R	R	
Epeorus albertae										R	R
E. deceptivus	R	R	A	A	C	C	C	C	R		
E. longimanus						R	C	A	A	C	
Heptagenia criddlei											R

Appendix B (continued 1)

	Sampling Sites										
	1	2	3	4	5	6	7	8	9	10	11
H. elegantula											R
H. simplicioides											R
Rhithrogena hageni					R	C	A	A	A	C	R
R. robusta			R	C	A	C	A	C			
Choroterpes inornata(?)											C
Paraleptophlebia heteronea						R	R	C	C	C	R
Drunella coloradensis				R	C	R	C	C	R	R	
D. doddsi					C	C	C	A	A	C	
D. g. grandis									A	C	R
Ephemerella infrequens						C	C	A	C	C	R
Attenella margarita											R
Serratella micheneri								R		R	A
S. tibialis							C	C	A	C	
Tricorythodes minutus											A
Trichoptera											
Rhyacophila acropedes			R	C	R	C	A	C	R		
R. angelita				R	C	A	A	C	R		
R. coloradensis				R	R	R	R	R	C	C	
R. hyalinata				C	R	C	C	C			
R. tucula				R	R	R					
R. verrula				R	R						
R. vocala group				R	R	R	R	R	R		
Ecclisomyia maculosa		R	R	R			R				
Psychoronia costalis (?)	R	R	R	R		R					
Allomyia tripunctata (?)	V	C	R	R	R						
Limnephilus sp.											R
Neothremma alicia					A	V	V	C	R		
Oligophlebodes minutus				R	R			R	R		
Psychoglypha sp.	R	R		R							
Lepidostoma veleda					R	R	C	C	R	R	
Lepidostoma sp.							R	C	A	V	R
Amiocentrus sp.											R
Brachycentrus americanus							R	R	C	A	R
Micrasema sp.						R	R	R			
Arctopsyche grandis				R	R	C	R	R	C	C	
Cheumatopsyche pettiti											V
Hydropsyche cockerelli										C	
H. occidentalis											V
H. oslari								R	A	A	C
Agapetus boulderensis									R	C	
Glossosoma parvulum					R	R	R	R	C	A	C
Nectopsyche diarina											R
N. gracilis											C
N. stigmatica											A
Oecetis avara										R	C
Ochrotrichia sp.										R	R
Helicopsyche borealis											V
Dolophilodes aequalis					R	R			R		

Appendix B (continued 2)

	Sampling Sites										
	1	2	3	4	5	6	7	8	9	10	11
Diptera											
Chironomidae											
Boreoheptagyia sp.									R		
Diamesa sp. 1	R	R	C	C	R	R	R		C	R	C
Diamesa sp. 2	R										
Diamesa sp. 3											C
Pagastia partica	C	R	R	R	R						
P. cf. *sequax*						R	R	R	R	R	R
Potthastia sp.		R									
Pseudodiamesa sp.	R	R	C	R		R	R	R	R	R	R
Lasiodiamesa sp.				R	R		R				
Brillia modesta				R	C	C	R	R	R	R	R
Corynoneura sp.				R	R			R	R	R	R
Cricotopus sp. 1					R	R	R	R	R	R	R
Cricotopus sp. 2											C
Diplocladius sp.				R		R					
Eukiefferiella prob. *claripennis*	C	R	R	R		R	R	C	C	C	C
E. devonica gr. sp.			R	R		R	R	R	R	R	C
E. potthasti gr. sp.				R					R		
Heterotrissocladius sp.				R		R	R	C	R	R	R
Krenosmittia sp.					R	R	R			R	
Lopescladius sp.						R					C
Orthocladius (Euorthocladius) sp. 1		R	R		R	R	R				C
Orthocladius (Euorthocladius) sp. 2	A	C	C	C	R	R	C	R	R	R	C
Orthocladius (Euorthocladius) sp. 3	A	C	A	C	C	R	R	R	C	R	R
Orthocladius sp.		R	C	R	R		R	C	C	C	C
Parametriocnemus sp.	R	C	R	R	R	C	R	C	C	C	R
Parorthocladius sp.	R	A	C	C	C	R	C	C	R	R	
Rheocricotopus sp.	R				C	C	C	C	R	R	
Symposiocladius lignicola						R					
Synorthocladius cf. *semivirens*										R	
Synorthocladius sp.						R					
Thienemanniella sp. 1				R	R	R	R	R	R	R	
Thienemanniella sp. 2			C					R	R		
Tvetenia bavarica gr. sp.	R		C	C	C	C	C	C	C	C	R
Ablabesmyia sp.										R	
Pentaneura sp.											C
Procladius sp.						R					R
Thienemannimyia gr. sp.						R	R	C	R	C	R
Micropsectra spp.	R	C	C	C	C	C	A	A	C	C	R
Paratendipes sp.											R
Phaenopsectra sp.							R				
Polypedilum fallax gr. sp.										R	
P. scalaenum gr. sp.						R		R	C	C	C
Rheotanytarsus sp.									R	R	R
Robackia sp.										R	R
Stempellinella sp.									R	R	
Tribelos sp.										R	R

Appendix B (continued 3)

	Sampling Sites										
	1	2	3	4	5	6	7	8	9	10	11
Simuliidae											
Prosimulium daviesi (?)				R							
P. onychodactylum	R	C	V	C	A	C	C	R	R	R	
P. travisi	C										
Simulium arcticum					R	R	R	R	C	C	C
S. defoliarti									R		
S. venustum					R	R	R	R	C	C	
S. virgatum											C
Tipulidae											
Antocha sp.								R	C	C	
Dicranota sp.	R			C	R	R	C	R	R	R	C
Gonomyia (?) sp.											R
Hesperoconopa sp.						R	R	R	R	R	
Hexatoma sp. 1					R	R	C	C	C	C	R
Hexatoma sp. 2										R	R
Limnophila sp.							R	R	R	R	C
Ormosia sp.				R							
Pedicia sp.										R	
Rhabdomastix sp.							R	R	R		
Tipula sp. 1		R	R				R				
Tipula sp. 2											C
Ceratopogonidae											
Palpomyia/Bezzia sp.				R	R	R	R	R	R	R	R
Dixidae											
Dixa sp.	R					R		R			
Psychodidae											
Pericoma sp.			R			R	C	C	R	R	
Deuterophlebiidae											
Deuterophlebia coloradensis							R		R	R	
Athericidae											
Atherix pachypus								R	C	C	
Blephariceridae											
Agathon elegantulus				R	C	C	R	R			
Bibiocephala grandis						R	R	R			
Empididae											
Clinocera sp.	C	R	C	C	R	R	C	R	C	C	R
Chelifera sp.				R		R	R	R	R	R	R
Coleoptera											
Heterlimnius corpulentus		R		R	C	C	C	C	C	R	
Optioservus castanipennis						R		R	C	C	A
O. divergens						R		R	R	C	A
Narpus concolor						R	R	C	R	R	R
Zaitzevia parvula							R		C	C	A
Helichus striatus							R	R	R	R	R
Helichus sp.									R		
Helophorus sp.											R
Paracymus sp.											R

Appendix B (continued 4)

	Sampling Sites										
	1	2	3	4	5	6	7	8	9	10	11
Tropisternus sp.											R
Haliplus sp.											R
Hydroscapha sp.									R		
Bidessus subtilius										R	
Collembola											
Isotomurus palustris											R
Lepidoptera											
Petrophila longipennis											C
Odonata											
Ophiogomphus severus											R
Argia vivida											R
Ishnura sp.											R
Hemiptera											
Corixidae female										R	
Oligochaeta											
Eiseniella tetraedra				R	R		R			R	R
Limnodrilus hoffmeisteri	C	C	A	C	C	R	R	R		R	R
Tubifex tubifex											R
Lumbriculus variegata					R	R	R	R	R	C	
Haplotaxis gordioides					R		R	R	R	R	
Nais communis								R		R	R
N. simplex	R	R	R	R	R	R			R	R	R
Ophiodonais serpentina										R	R
Amphichaeta leydigi										R	
Acarina											
Atractides sp.						R	R			R	
Lebertia sp.	R	C	R	R		R	R	R	R	R	R
Protzia sp.								R			
Sperchon sp. A	R	C	R	R		R					
Sperchon sp. B	R	C	R	C		R		R	R	R	
Sperchon sp. C					R	R	R	R		R	R
Trombidiidae sp.											R
Tricladida											
Polycelis coronata	A	C	A	C	R	C	A	A	C	R	
Dugesia dorotocephala											V
Nematoda spp.	C	R	R	R	R	R	R	R	R	R	R
Hirudinea											
Erpobdella punctata											R
Amphipoda											
Crangonyx gracilis complex											R
Hyallela azteca											R
Isopoda											
Asellus communis											R
Gastropoda											
Physa sp.											C
Pelecypoda											
Pisidium nitidium (?)			R	R			R	R			R

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