# Altitudinal zonation in a Rocky Mountain stream

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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

# 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 tree-line), 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
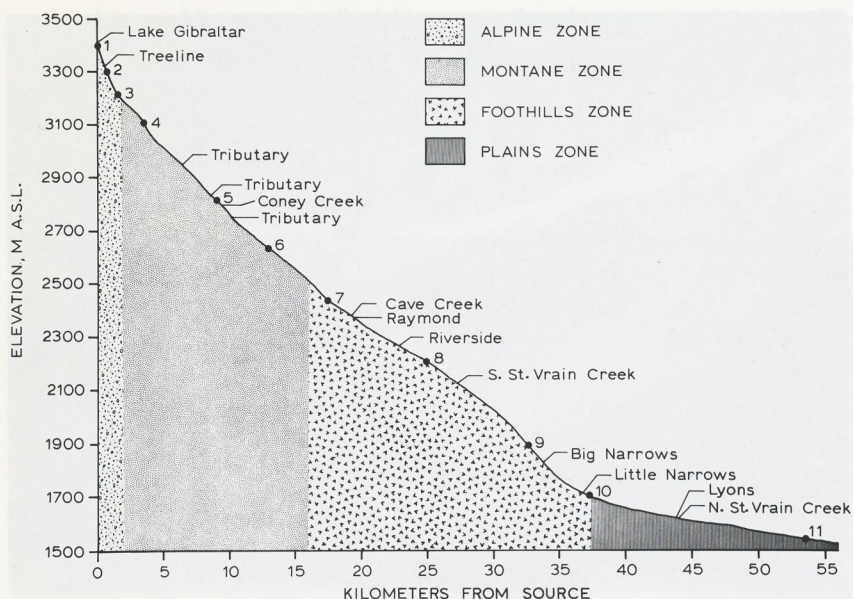
Fig. 1. Longitudinal profile of the St. Vrain River, Colorado, indicating confluence points of all second-order and larger streams. Arabic numerals indicate sampling sites. Limnological zones are based on PENNAK (1958). Big and Little Narrows are regions where the stream valley is constricted by steep 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 out-flow 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
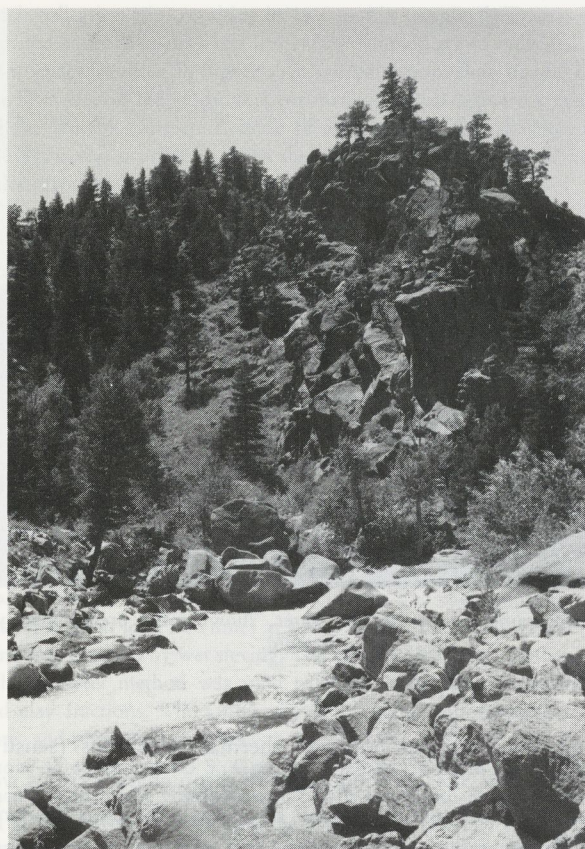
Fig. 4. The high gradient foothills section of St. Vrain Creek.

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 cm² 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 |
| $NO_3–N$[1] (ppm) | 0.15 | – | 0.13 | – | – | 0.12 | – | – | 0.10 | – | 0.13 |
| Orthophosphate[1] (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) | – | – | – | – | – | – | – | – | – | – | 3.3[3] |
| First summer | – | – | – | – | – | 2.2 | – | – | – | – | 6.0 |
| Second summer | 0.07[2] | – | – | – | – | 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).
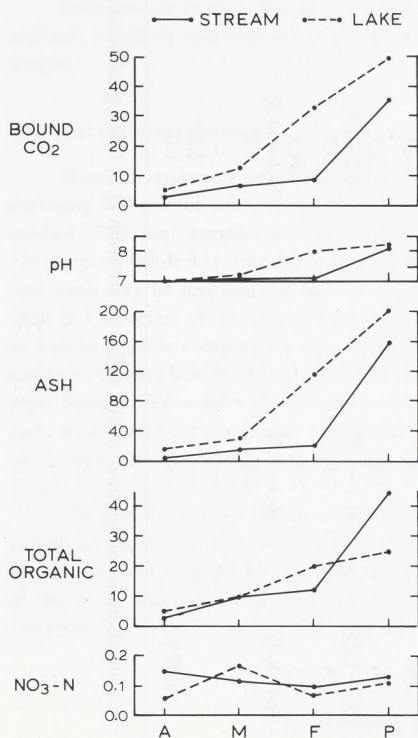


Fig. 6. A comparison of lake and stream chemistry in northern Colorado as a function of altitude. Mean values for lakes are based upon non-alkaline drainage lakes (Pennak 1958). Stream values are means from the present study at Site 1 in the alpine zone (A), Site 6 in the montane zone (M), Site 9 in 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
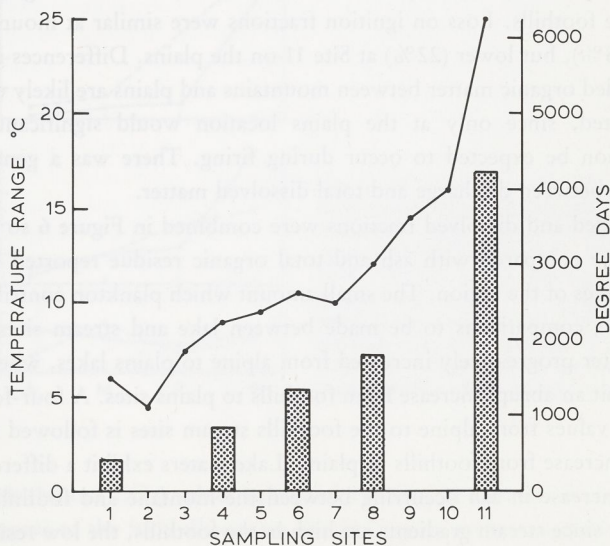


Fig. 7. Water temperature range (solid line) for the period of study at sites on St. Vrain Creek and estimated annual degree days (bars) at selected locations.

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.
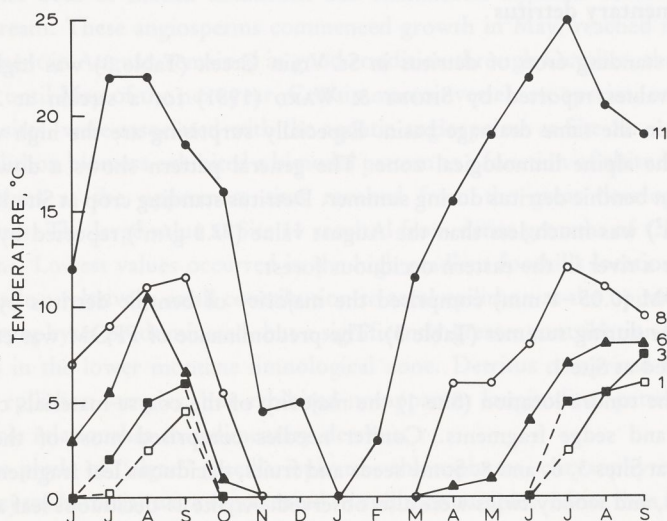


Fig. 8. Seasonal water temperature patterns at St. Vrain Creek sites (Arabic numerals) for the period of study. Dashed lines indicate extrapolated values at Site 1 and 3.

## 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/m² 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
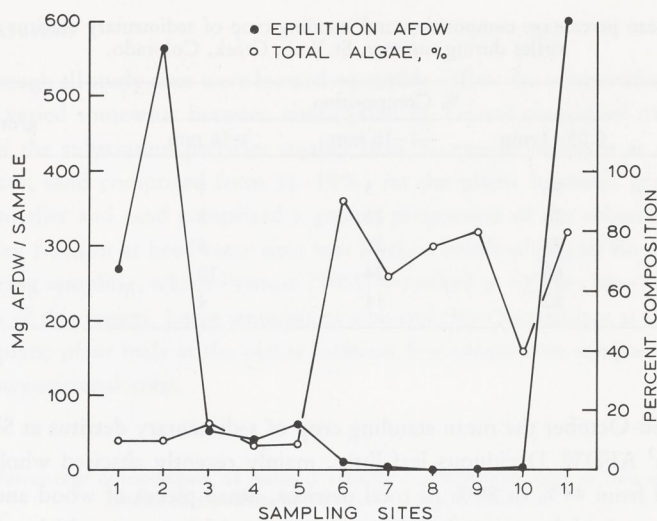
Fig. 9. Longitudinal patterns of epilithon ash-free dry weight (AFDW) and the relative contributions of algae (including cyanobacteria) to total epilithon.

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 | – | – | – | – | – | – |
| *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 sub-strate 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.
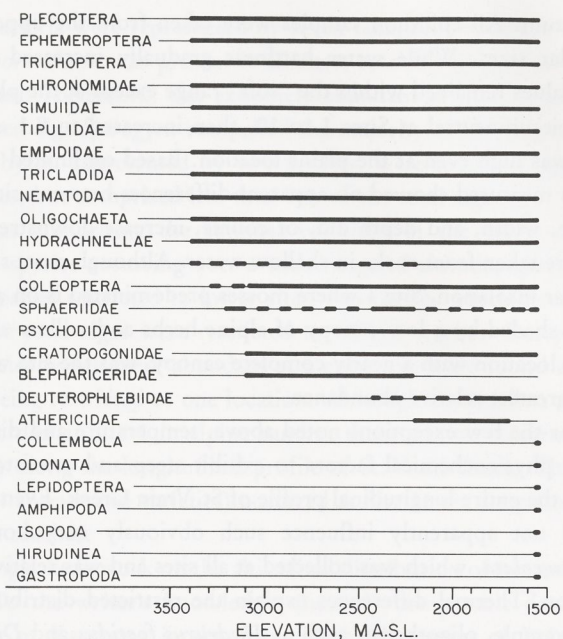
Fig. 10. The altitudinal distribution of major groups of macroinvertebrates along the course of the St. Vrain River.
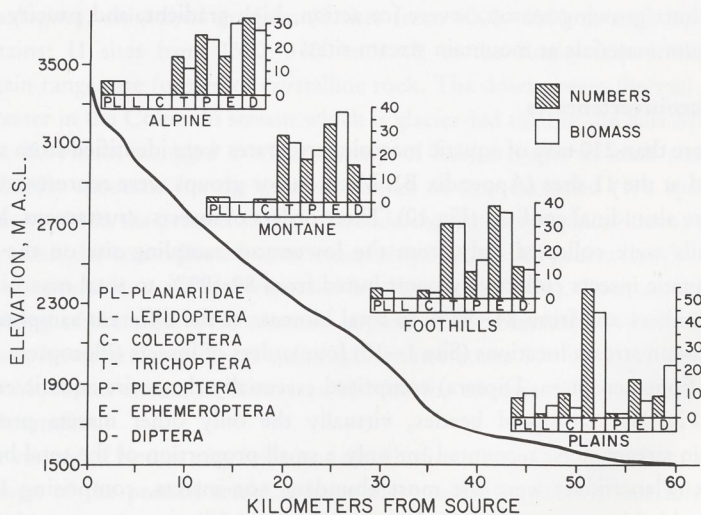
Fig. 11. The relative contribution (% composition) of macroinvertebrate groups that comprised at least 5% of total density or biomass at one or more sites along the course of the St. Vrain River. Values <1% are not indicated.

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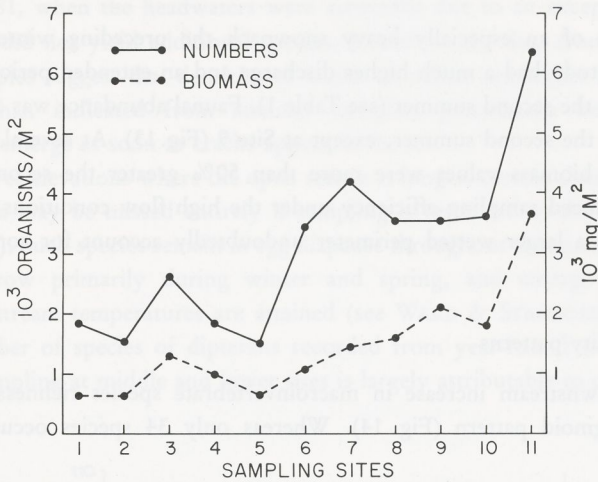
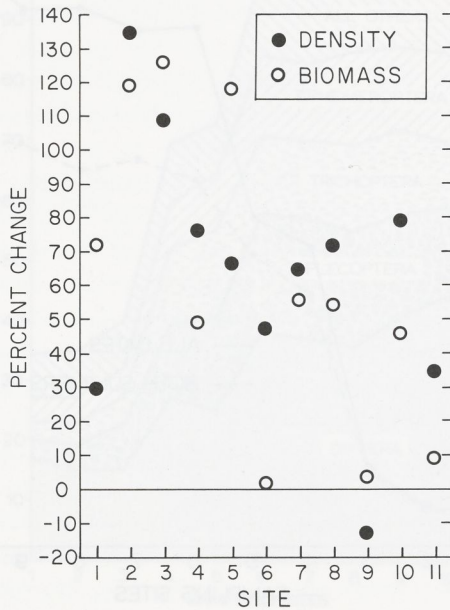Fig. 12. The longitudinal patterns of total macroinvertebrate density and biomass.

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
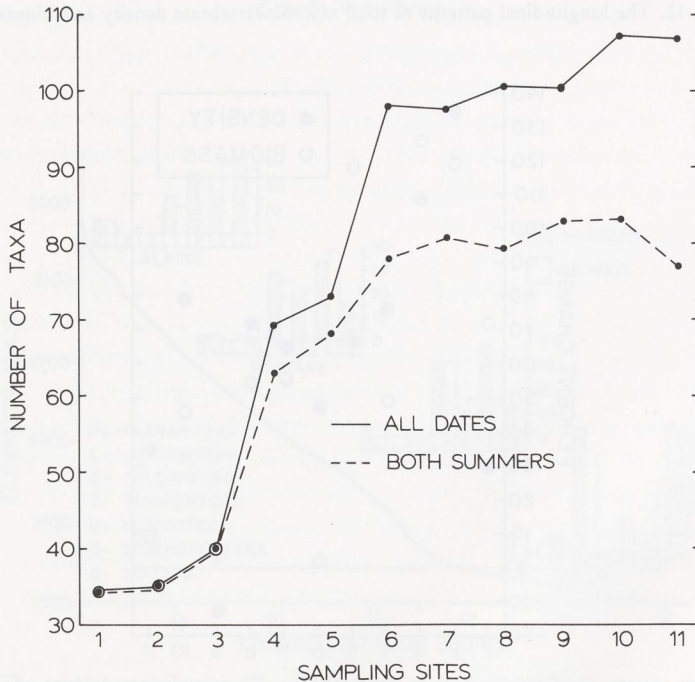


Fig. 14. The total number of macroinvertebrate taxa collected during the entire study and during the summers only, along the longitudinal profile of the St. Vrain River.

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.
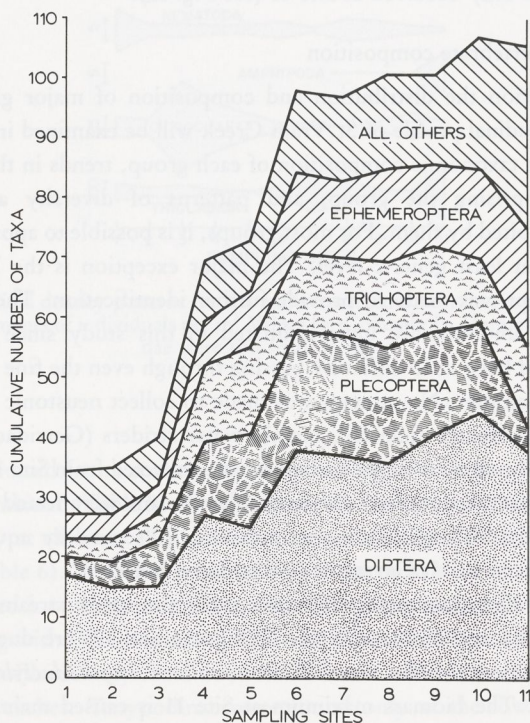


Fig. 15. The contributions of major groups to the total number of macroinvertebrate taxa collected.

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.
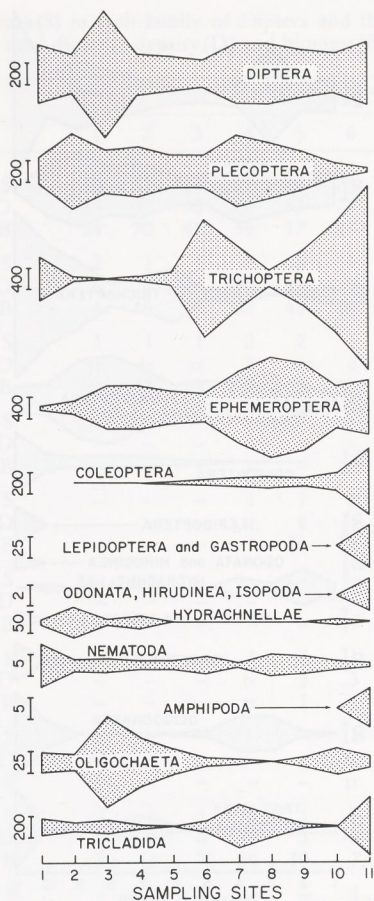
Fig. 16. Longitudinal density patterns for the major macroinvertebrate groups. Vertical scales indicate mean numbers of individuals per m². Values for Collembola, Hemiptera, and Sphaeriidae were too small to plot.

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.
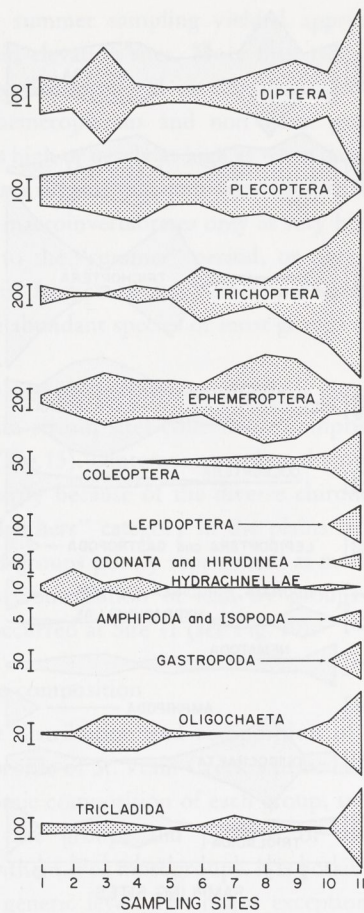
Fig. 17. Longitudinal biomass patterns for the major macroinvertebrate groups. Vertical scales indicate mean dry weights in mg per m². Values for Collembola, Hemiptera, Nematoda, and Sphaeriidae were too small to plot.

*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 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 |
| | D | 8 | – | 6 | 17 | 3 | 5 | 3 | – | 6 | 7 | tr |
| | B | 8 | 2 | 7 | 26 | 10 | 7 | 6 | 1 | 2 | 2 | tr |
| Psychodidae | S | – | – | – | – | – | 1 | 1 | 1 | 1 | 1 | – |
| | D | – | – | – | – | – | tr | 1 | 5 | 5 | tr | – |
| | B | – | – | – | – | – | 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.
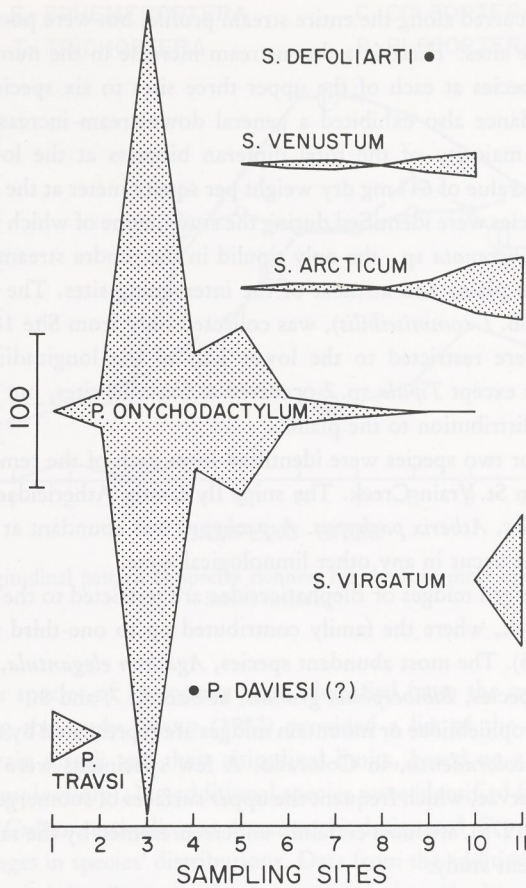
Fig. 18. Abundance patterns of the species of Simuliidae (*Simulium* and *Prosimulium*) along the longitudinal profile of the St. Vrain River. Vertical scale indicates mean number of organisms per m².

Temperature, current, and food are important factors in determining the distribution and abundance of black flies. In the River Endrick, Scotland, MAIT-LAND & 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).
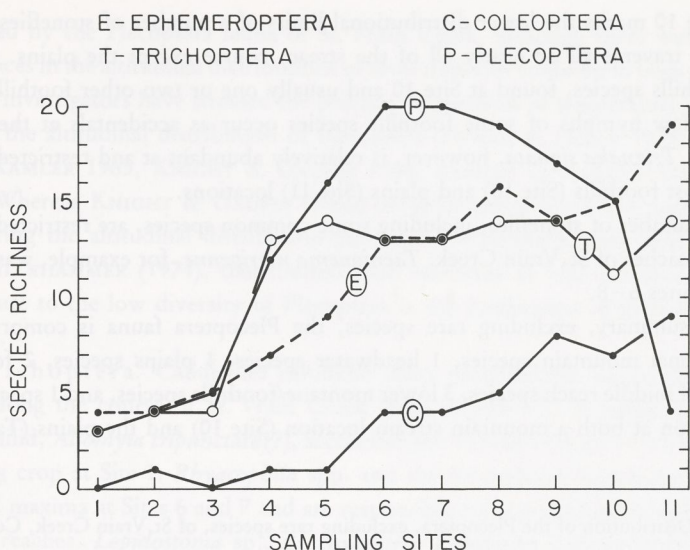
Fig. 19. The longitudinal pattern of species richness for the four most diverse non-dipteran insect orders.

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 deeprelease 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.

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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
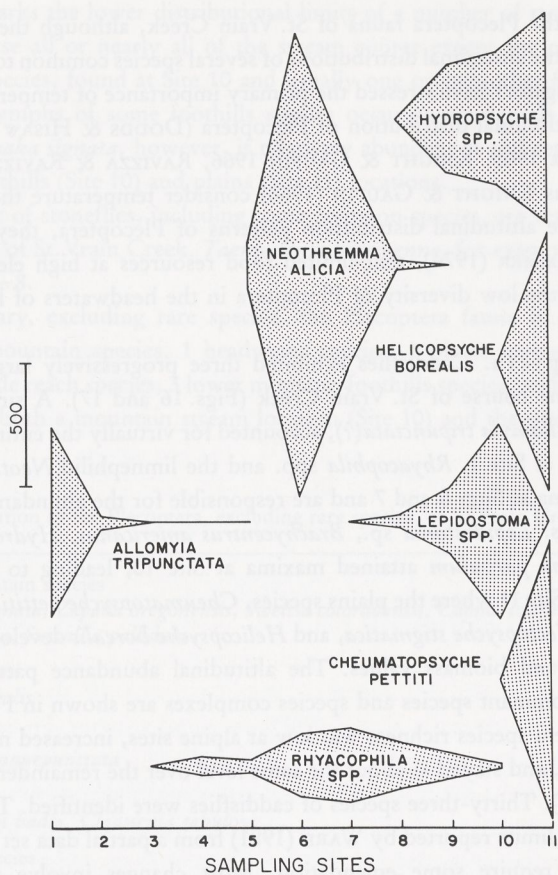
Fig. 20. Abundance patterns of some numerically dominant trichopteran species and species complexes. Vertical scale indicates mean number of organisms per m².

density values exceeding 1000 individuals per m², 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 co-occurred 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 m² 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.

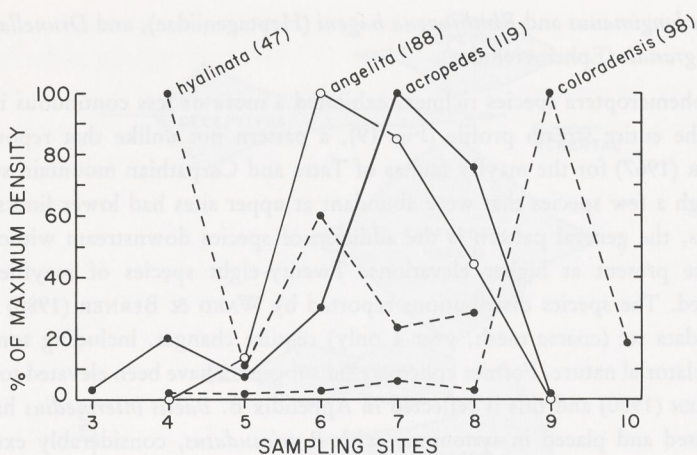In summary, the altitudinal distribution pattern of the Trichoptera is more clearly defined than that of either the Chironomidae or the Plecoptera. The caddisfly fauna contains distinct headwater and plains elements, species restricted to the middle reaches, to montane sites, and to the foothills. Euryzonality 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).

E p h e m e r o p t e r a. 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 synonymy 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-*
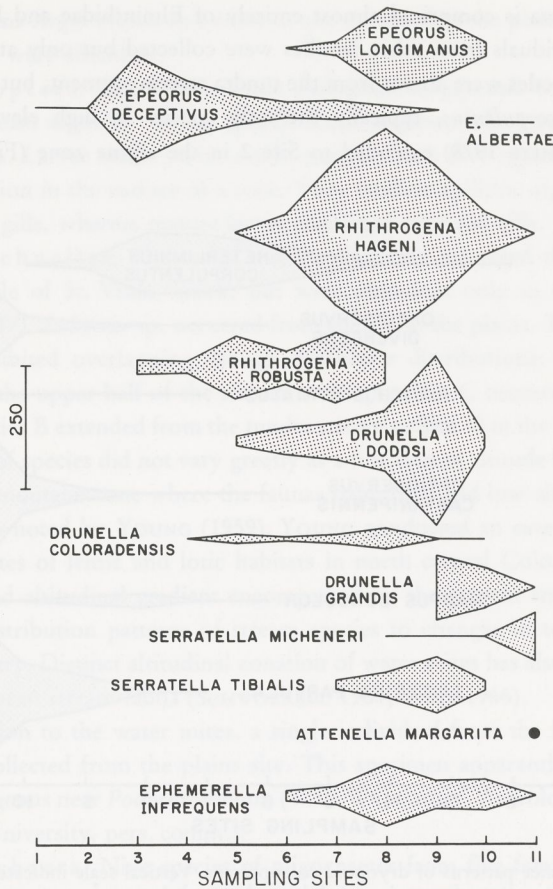
Fig. 22. Abundance patterns of some congeneric and confamilial species of Ephemeroptera. Vertical scale indicates mean number of organisms per m².

*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
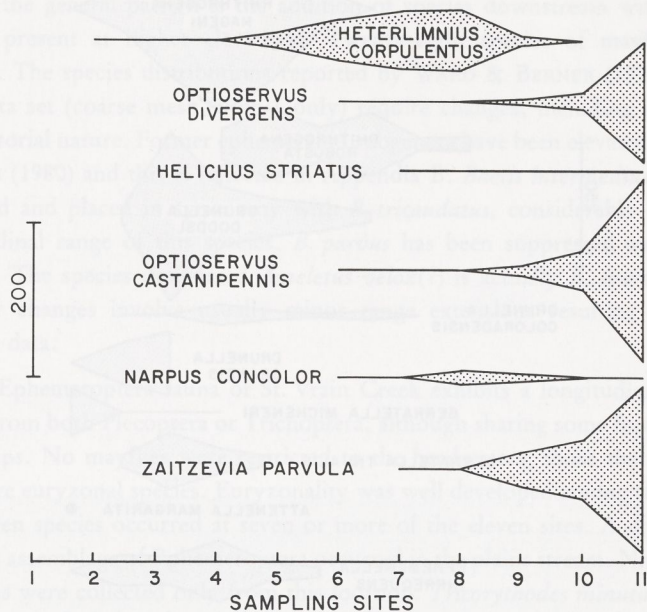


Fig. 23. Abundance patterns of dryopoid coleopterans. Vertical scale indicates mean number of organisms (adults and nymphs) per m².

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.

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.

O d o n a t a. 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.
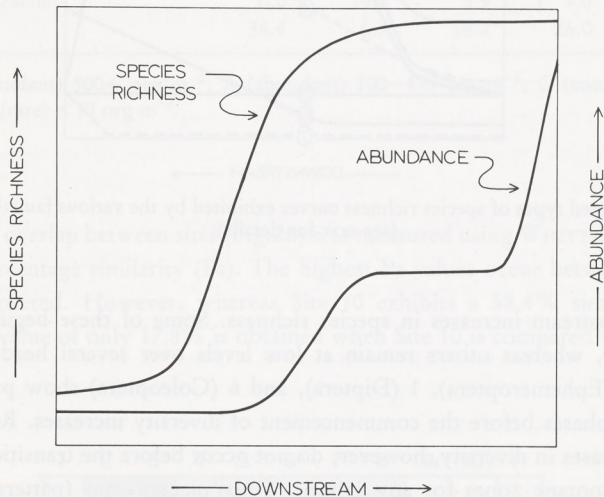


Fig. 24. Idealized altitudinal patterns of species richness and abundance for total zoobenthos.

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 head-waters, 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 gastro-pods 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
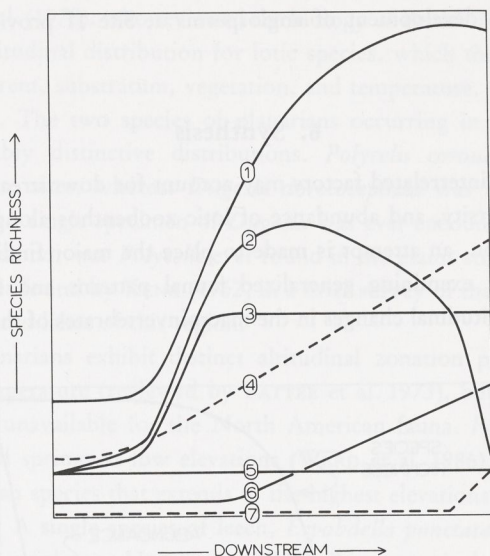
Fig. 25. Idealized types of species richness curves exhibited by the various faunal components
(see text for details).

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.
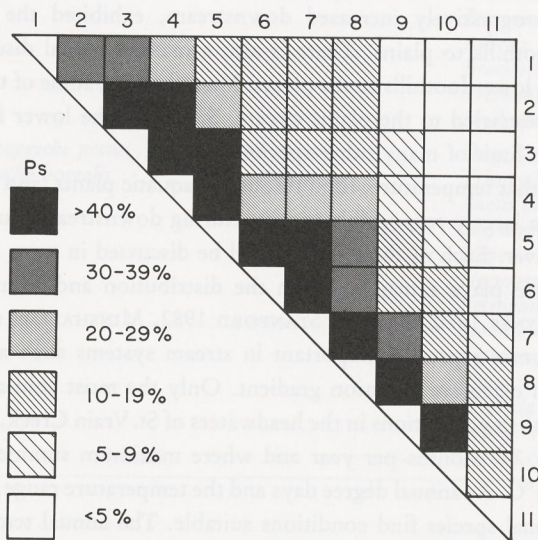


Fig. 26. Matrix of percentage similarity (Ps) between sampling sites based on total zoobenthic species.

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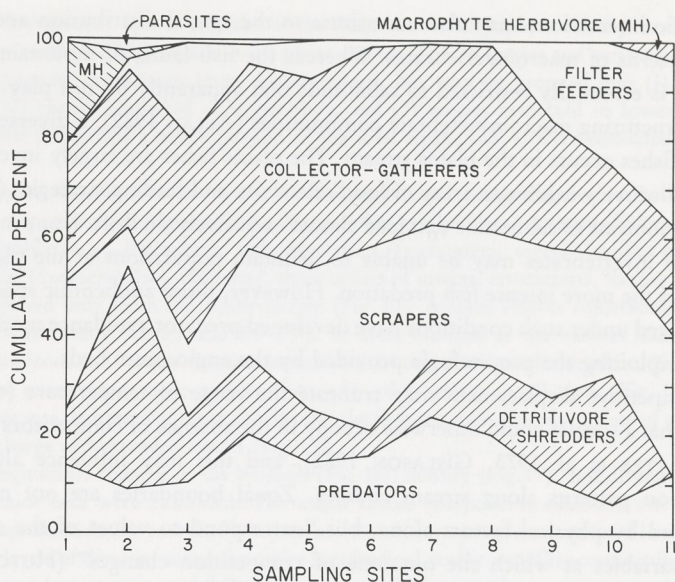
Fig. 27. Relative contributions of macroinvertebrate functional feeding groups (sensu MERRITT & CUMMINS 1984) along the course of the St. Vrain River.

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 an-
gereichert. Stichproben wurden auf Stromschnellen mit dem vorherrschenden Bodentyp
(Tabelle 2) beschränkt, um die Unterschiede zwischen Substrat und Strömung der verschie-
denen 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. gebun-
denes $CO_2$, 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 Teilchen-
materie (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-Bio-
massen 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) ver-
breitete 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). Wasser-
insekten 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 Schmelzwasser-
zuflusses 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.

# 9. Acknowledgements

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 | | | |
| 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 | |
| Sweltsa borealis | R | R | R | C | C | | | | | | |
| S. coloradensis | | R | C | C | C | C | A | A | C | | |
| Triznaka signata | | | | | | | | | | C | C |
| Paraperla frontalis | | | | | 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 | | |
| B. insignificans | | | | | | | | | | R | C |
| B. hageni | | | | | | | | | | | A |
| 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 | R | |
| E. longimanus | | | | | | | R | C | A | A | C |
| Heptagenia criddlei | | | | | | | | | | | R |

Appendix B   (continued 1)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Sampling Sites | | | | | | |
| *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

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *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 | | |
| *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 | | | | |
| *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 | C |
| *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 | | |
| 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 | R |
| 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 | |
| Rheocricotopus sp. | R | | | | C | C | C | C | R | | |
| Symposiocladius lignicola | | | | | | | R | | | | |
| Synorthocladius cf. semivirens | | | | | | | | | | | |
| Synorthocladius sp. | | | | | | | R | | | | |
| Thienemanniella sp. 1 | | | | R | R | R | R | R | | | |
| Thienemanniella sp. 2 | | | C | | | | | R | R | | |
| Tvetenia bavarica gr. sp. | R | C | 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 | 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 |
| **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 | R | | |
| *Optioservus castanipennis* | | | | | | R | | R | C | C | A |
| *O. divergens* | | | | | | R | | R | R | C | A |
| *Narpus concolor* | | | | | | R | R | C | R | R | A |
| *Zaitzevia parvula* | | | | | | R | | | C | C | A |
| *Helichus striatus* | | | | | | R | 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 | | | | |
| *Lebertia* sp. | R | C | R | R | | R | R | R | R | R | R |
| *Protzia* sp. | | | | | | | | | R | | |
| *Sperchon* sp. A | R | C | R | | | R | | | | | |
| *Sperchon* sp. B | R | C | R | C | | | | 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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# Disturbance and Fish Communities in Intermittent Tributaries of a Western Great Plains River

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Intermittent canyon tributaries of the Purgatoire River, Colorado, consist of isolated pools during long periods of low or no flow, which are punctuated during summer by intense flash floods lasting one to three days. Despite the frequent strong disturbances and limited opportunities for recolonization, we found fish in most permanent pools sampled along five tributaries. Of 11 native fishes in the river mainstem, five species penetrated an average of 6.6–9.1 km upstream in four drier tributaries; five others colonized only 0.3–1.0 km upstream; and one species was rare. Distribution of five species was different in the fifth tributary, which had more flow. Analysis of fish communities at sites sampled through time in four tributaries indicated that species composition and relative abundances remained relatively constant at three sites with deep complex pools but changed markedly at two sites with shallow simple habitat. This was probably because the latter offered little refuge from floods. We also found relatively variable species composition among pools along each tributary, little of which could be accounted for by drought, predation, or habitat complexity alone. We propose that differential effects of unpredictable floods in pools of varying habitat complexity, interacting with recolonization and recruitment, are sufficient to produce the spatial and temporal variation observed in tributary fish communities.

**D**ISTURBANCE is thought to play an important role in structuring communities of fishes and other organisms in streams (Karr and Freemark, 1985; Resh et al., 1988; Poff and Ward, 1989). Fishes inhabiting southwestern desert and western Great Plains streams are frequently exposed to disturbances from floods and droughts, and must persist in environments characterized by fluctuating flows (Meffe and Minckley, 1987; Minckley and Meffe, 1987), high natural turbidity (Cross and Moss, 1987; Matthews, 1988), and high temperatures (Matthews, 1987). Floods are especially detrimental in canyon reaches of western streams because fish cannot avoid displacement by escaping to floodplain refugia such as those often present in more mesic environments (Meffe, 1984; Minckley and Meffe, 1987). Adult fish must

maintain their position in the channel, or persist in microrefugia, and then recolonize and reproduce to sustain populations.

The response of western Great Plains stream fishes to disturbance is unknown because their ecology is relatively unstudied (Matthews, 1988). Thus, whereas floods were found to have little long-term effect on persistence of native species in southwestern desert (Minckley and Meffe, 1987), central Plains (Ross et al., 1985; Matthews et al., 1988), and Ozark streams (Matthews, 1986), fish in western Plains streams may respond differently. One reason is that, in contrast to the high proportion of endemic genera and species in southwestern desert streams (Minckley et al., 1986; Carlson and Muth, 1989), no species specifically adapted to harsh flow regimes occur in western Plains streams. This lack of endemics is probably largely a result of continuous faunal connections with the Mississippi and Red River basins (Cross et al., 1986). This contrasts with the long periods of isolation that promoted speciation in the Colorado River basin, for example. Species richness simply declines westward in Great Plains watersheds (Cross and Moss, 1987), and most fishes present are wide-ranging species preadapted to the harsh conditions that colonized from richer faunas to the east. Thus, the depauperate fauna that persists in harsh western canyon reaches is also likely to respond differently to disturbance than the richer fish communities of more mesic central Plains and Ozark streams.

Current theories hold that the ecology and life history of organisms reflect adaptations to characteristics such as frequency, intensity, and predictability of disturbance (Sousa, 1984; Schlosser, 1990; Poff and Ward, 1989). For example, if disturbances are too frequent or intense, colonizing species are expected to dominate the system (Grossman et al., 1982; Schlosser, 1987; Resh et al., 1988). Poff and Ward (1989) predict that fishes in "intermittent flashy" streams such as those we studied should be small, vagile, early maturing species with broad physiological tolerances that can withstand floods via behavioral or morphological adaptations. They also predict that communities will be depauperate, trophically simple, and have weak biotic interactions but that species persistence (sensu Connell and Sousa, 1983) will be high because of strong selection for flood and drought-resistant forms.

The purpose of this paper is to identify which factors related to disturbance affect fish community structure on a local scale in intermittent tributaries of a western Great Plains river. Resh et al. (1988) suggested this as one of the important questions to pose about the role of disturbance in shaping communities. We analyzed both spatial and temporal survey data to assess the relative importance of flash floods, droughts, vagility, and predation in influencing fish communities in isolated tributary pools and over longer stream reaches.

## STUDY AREA AND METHODS

The Purgatoire River is a seventh-order tributary of the Arkansas River in southeastern Colorado (for a detailed description, see Bramblett and Fausch, 1991). After descending from the Rocky Mountains to the Great Plains, it runs through Piñon Canyon, a remote canyon 60–1800 m wide and up to 150 m deep formed by sheer Cretaceous sandstone walls. Our study area included 10 intermittent tributaries that flow from the plains northwest of the canyon and downcut through smaller canyons or arroyos to the river (Fig. 1). Although the United States Army uses the adjacent plains for mechanized infantry training, track-driven vehicles are not permitted near the canyons; and thus far no effects on aquatic ecosystems have been detected. The United States Geological Survey (USGS) operates flow gauges on the river and five tributaries that have the greatest discharge (Fig. 1).

Tributary canyons were searched for permanent pools capable of harboring fish. Most pools we sampled had aquatic and riparian vegetation and appeared permanent, although some canyons only had pools that appeared ephemeral. We also sampled these pools. The junior author made a broad spatial survey by sampling 51 sites during Sept.–Oct. 1987 and May–June 1988, most of which consisted of one isolated pool each. Seven of these sites, consisting of one or two connected pools (two pools at lower Van Bremer, lower Lockwood, and Red Rock) selected from those with the most complex habitat in each canyon, were designated as temporal sites (Fig. 1) and were sampled two to six times during seven sampling periods from fall 1983 to spring 1989. There were no barriers to fish dispersal, except for a small waterfall about 300 m downstream from the most upstream site in Taylor Arroyo.

Pools were approximately 3–8 m wide ($\bar{x} = 5.4$ m at temporal sites) and were isolated; hence, block nets were not used. Fish were captured

# 23: A Mountain River

J.V. WARD

## 23.1 INTRODUCTION

Mountain rivers are one of our most valued resources. The term, mountain river, conjures up visions of crystal-clear waters in a pristine setting. Indeed, most undisturbed running water segments occur in mountainous regions at high elevations. Mountain rivers share common features worldwide and have served as the primary site for the evolution of many lotic organisms. It is in such settings that the aquatic biota most clearly exemplify the remarkable adaptations to running water conditions. For the purposes of this chapter, the term 'mountain river' refers to running waters of high altitudes, the upper reaches of river systems. Although mountain rivers may extend downward to sea level in areas of recent coastal subsidence or in geologically youthful regions, such low elevation mountain rivers will be considered only briefly. The emphasis will be on high-gradient streams and rivers at high elevations in the temperate zone.

The ensuing material begins with the idealized features of mountain rivers, including typical environmental conditions, energy resources, biotic communities, and adaptations of the biota. This is followed by a general discussion of the types of running waters occurring at high elevations and their longitudinal patterns. The remainder of the chapter is devoted to the St. Vrain, an archetypical mountain river of the Colorado Cordillera.

## 23.2 GENERAL FEATURES OF MOUNTAIN RIVERS

### Environmental conditions

The high gradient (slope) of the typical mountain river, coupled with a highly irregular bed structure, results in rapid current and high turbulence. Consequently oxygen levels are near saturation and the stream water tends to be chemically and thermally homogeneous.

Only recently have lotic ecologists begun to characterize precisely the microcurrent regime near the surface of the streambed where many organisms reside (Wetmore *et al* 1990; Davis and Barmuta 1989; Nowell and Jumars 1984; Statzner *et al* 1988; see Chapter 5). Near-bed conditions may be hydraulically smooth (e.g. over flat sheets of bedrock) or hydraulically rough (over irregular stream bottoms). Under hydraulically smooth conditions there is a 'laminar sublayer' consisting of a thin zone of non-turbulent water above the bottom surface (Davis & Barmuta 1989; see Chapter 5). Under the hydraulically rough conditions that typify mountain streams and rivers, the near-bed current microenvironment is normally turbulent, although stable eddies may develop between closely spaced substrate particles as the current skims across the tops of those particles. Fluid dynamics depend not only on the spacing of substrate elements, but also on the height of individual particles above the streambed and 'relative roughness' (height of particles/water depth). In high-gradient riffles at low water, near-bed current patterns are extremely complex and high velocities occur close to the bed. None the less, the microcurrent regime of such riffles is highly heterogeneous and includes low-velocity microdepositional habitats. In addition, water velocities rapidly approach zero with increasing depth within the interstitial spaces of the hyporheic zone (Williams & Hynes 1974).

Mountain streams are 'erosional' habitats in

493

494

the sense that fine mineral particles tend to be eroded and transported downstream to 'depositional' habitats (e.g. lakes, lowland rivers). At smaller spatial scales, however, both erosional (e.g. riffles) and depositional (e.g. pools) habitats co-occur. None the less, coarse materials such as cobble (64–256 mm), pebble (32–64 mm), gravel (2–32 mm) and wood characterize the substrata of mountain streams and rivers (see Chapter 3). The composition and distribution of substrata within the channel are largely structured by physical processes related to the unidirectional flow of water interacting with basin geology and allochthonous organic debris (Keller & Swanson 1979; Bilby & Likens 1980). In old growth forests, wood debris may exert major controls on channel morphology (Harmon *et al* 1986) and the retention of organic matter (Bilby & Likens 1980; Speaker *et al* 1984). In contrast, wood debris plays a very minor role in streams above treeline where the source of wood is restricted to small riparian shrubs (e.g. *Salix* spp.). Tundra streams are often lined by willows and dense herbaceous vegetation, however, so relatively large standing crops of organic detritus may accumulate in the streambed during the growing season (Ward 1986).

High water clarity is a distinguishing feature of most mountain streams and rivers. Despite this, however, light for *in situ* primary production may be limiting. In densely forested headwater streams, the light available for autotrophic production is limited by canopy development. In exposed streams above treeline, autotrophic production is limited by low summer water temperatures and nutrient levels, and by the short growing season. Small rivers of middle elevations typically provide optimal conditions for instream primary production because of an open canopy, adequate levels of plant nutrients, and shallow, clear water.

Elevation exerts a primary influence on the temperatures of mountain waters through its influence on air temperatures, as reflected by the lapse rate (an average decrease in air temperature of about 6.5°C for every 1000-m increase in elevation). Stream temperatures tend to track air temperatures except when ice covered or during periods of snowmelt or spate (Ward 1985). Because groundwater temperatures approximate mean annual air temperatures, even mountain streams fed by groundwater are under the influence of the lapse rate. Factors related to insolation (aspect and canopy) can modify the influence of air temperature, as exemplified by the higher temperatures of some exposed streams above treeline compared with their canopied reaches at lower elevations (Ulfstrand 1968).

Typical river water is a dilute solution of calcium bicarbonate. The total dissolved solids (TDS) content of the world's rivers averages 120 mg $l^{-1}$ (Livingston 1963; see Chapter 4). The ionic content of the river generally increases downstream as the water ages and is contributed from an increasingly larger catchment (Hynes 1970). TDS values <50 mg $l^{-1}$ usually indicate drainage from igneous rock (Wetzel 1983). If the high elevation portion of the catchment consists of relatively insoluble crystalline bedrock, whereas soluble sedimentary strata occur at lower elevations, the downstream trend of increasing ionic strength is accelerated. Water hardness also tends to increase downstream in river systems. Therefore, mountain streams, unless originating as calcareous springs, are characterized by soft water of low ionic strength.

Because of the turbulent nature of high-gradient mountain streams, dissolved gases are well mixed and in equilibrium with the atmosphere. The decrease in gas solubility with increasing elevation (decreasing atmospheric pressure) is countered by the increase in solubility associated with the low temperature of the water.

### Energy resources

Both *in situ* primary production (autochthonous production) and allochthonous production derived from the surrounding landscape contribute organic matter to running waters (see Chapter 17). In high-gradient mountain streams bryophytes (mosses and lichens) and attached algae constitute the main photosynthetic organisms. The high current velocity and paucity of soft bottom sediment severely restricts or excludes floating or rooted angiosperms. Mountain rivers do not provide suitable conditions for the development of phytoplankton.

Much of the organic matter in mountain rivers is detritus of allochthonous origin and this is

especially marked in forested headwaters. In a canopied deciduous forest stream, leaf litter and other allochthonous detritus accounted for >99% of the annual energy budget (Fisher & Likens 1973). In coniferous forest streams examined by Naiman and Sedell (1979), more than 90% of the benthic detritus was wood. Mountain streams lacking fully developed canopies, such as alpine streams, depend to a greater extent on autochthonous production (Minshall 1978; Winterbourn *et al* 1981). For example, the fish fauna of high-gradient Andean headwaters above the forest consists mainly of algal-grazing catfishes (Lowe-McConnell 1987). The limited fauna inhabiting the sources of glacial-fed streams feed on wind-blown organic particles entrapped on the surface of the glacier and later released to the stream (Steffan 1971). Kohshima (1984) documented the occurrence of blue-green algae and bacteria in the meltwater drainage channels of a Himalayan glacier and in the guts of chironomid larvae.

## Biotic communities

The majority of organisms in high-gradient mountain rivers are benthic in the sense of being closely associated with the substratum. In contrast, organisms residing in the open water (plankton, nekton) or associated with the air—water interface (pleuston) are poorly represented, as are higher plants that require soft bottom sediments for rooting.

### Benthic community types

The benthic communities of running waters include biofilm assemblages, attached macrophytes, zoobenthos, hyporheos and bottom fishes. Biofilm, the organic layer that coats all solid surfaces, is a heterogeneous assemblage of attached algae, bacteria, fungi, protozoans and micrometazoans in a polysaccharide matrix (Lock *et al* 1984; see Chapter 15). In mountain streams, the primary sites of biofilm development are the surfaces of stones (epilithon) and submerged wood (epixylon). In addition to photosynthetic production, the biofilm is a major uptake site for dissolved organic matter, thereby adding to the food available to grazing fishes and invertebrates (Rounick & Winterbourn 1983).

Bryophytes are the primary attached macrophytes in many mountain rivers. Although not generally consumed as food, mosses and liverworts provide important physical habitat structure (Glime & Clemons 1972). The largely tropical attached angiosperms (Podostemaceae and Hydrostychaceae) are adapted to torrential mountain streams (Gessner 1955).

The distinctive and highly adapted zoobenthic community of high-gradient mountain streams is remarkably similar worldwide and is dominated by insects except in calcareous streams where crustaceans and molluscs are also abundant (Hynes 1970). For example, insects constitute more than 95% of total zoobenthos numbers in streams in the Rocky Mountains of North America (Ward 1975) and the Tien Shan Mountains of Asia (Brodsky 1980).

The hyporheic community consists of invertebrates that inhabit the interstitial spaces between sediment grains within the streambed and laterally under the banks (Williams & Hynes 1974; Pennak & Ward 1986; Stanford & Ward 1988; Danielopol 1989; see Chapter 11). The hyporheic community consists of selected components from the zoobenthic community that spend a portion of their lives in the hyporheic zone (e.g. early instars, diapausing nymphs) as well as permanent residents that are highly adapted for a hypogean existence. The few data available suggest that altitudinal distribution patterns of the hyporheos are at least partially decoupled from altitude, depending more on site-specific geomorphic features of the fluvial landscape (Ward & Voelz 1990).

Both resident and migratory fishes occur in mountain rivers. Migrants that spawn in the headwaters may come from lower riverine reaches (potamodromy), lakes (adfluvial), or the sea (anadromy). Catadromous eels (*Anguilla*) ascend rivers to complete growth and sexual maturity. Whereas most migratory species are nektonic, many resident fishes of mountain streams are truly benthic. Only the strongest swimmers, such as salmonids, can maintain a nektonic existence in high-gradient mountain streams.

## Adaptations of the biota

Running waters are physiologically richer than still waters (Whitford & Schumacher 1961; Hynes 1970) and lotic organisms have evolved various adaptations enabling them to inhabit high-gradient streams and take advantage of the benefits conferred by current. Morphological, behavioural and physiological adaptations often function in concert but are discussed under separate headings.

### Morphological adaptations

Sustained swimming is not commonly employed by the organisms of high-gradient streams. Only nektonic fishes, fusiform-shaped and elliptical in cross-section, are able to swim against the current for extended periods. Most fishes and other aquatic organisms use other adaptations to maintain position in fast water or to avoid the full force of the current.

Sessile forms use various means of attachment to anchor themselves to solid surfaces. Examples include algal holfasts, the rhizoids of mosses, the modified roots of attached angiosperms, and the salivary secretions used to affix the shelters of certain caddisflies and midges. Motile aquatic insects of mountain streams employ modified gills, hair fringes and hydraulic suckers to increase frictional resistance with the substratum. Dorso-ventral flattening of the body, well exemplified by heptageniid mayflies and water pennies (Psephenidae) may serve several functions. It enables organisms to feed on algae attached to the tops of rocks in rapid water, to move into cervices, and to be less vulnerable to predation. Many lotic invertebrates use hooks and claws to obtain purchase in rapid water. Riffle beetles (Elmidae), for example, crawl along the bottom using well-developed tarsal claws, quite in contrast to the nektonic beetles of lowland rivers that use hair fringes for swimming. Unlike most beetles, which are positively buoyant and must periodically renew air stores, the plastron of elmids frees them from surface visits, a dangerous and energetically expensive proposition for inhabitants of torrential streams (Ward 1992).

Benthic fishes of high-gradient mountain streams also exhibit a remarkable array of morphological adaptations (Allen 1969). They are dorsoventrally flattened or have an arched profile with a flat ventrum, in contrast to the laterally flattened fishes of lakes and lowland rivers. The paired fins tend to be positioned more laterally on the body and are more muscular than those of related slow water species. The pectoral fins may function as reverse hydrofoils; when the leading edge faces into the current, a negative pressure under the fin apresses the fish to the bottom. Bottom dwellers typically have reduced swim bladders and decreased buoyancy. Eyes are more dorsal, gill openings are more lateral, and the mouth of bottom dwellers is more ventral than in nektonic fishes. Benthic fishes of torrential streams exhibit various adaptations that serve to increase frictional resistance with the substratum. In Sculpins (Cottidae), the pelvic fins are far forward on the body and with the pectoral fins form a ventral friction device. A few other North American and European fishes exhibit friction devices similar to sculpins, but in African, Asian and South American torrential waters much more elaborate organs of attachment have been described (Hora 1930; Marlier 1953; Kleerekoper 1955). Fishes from several families have independently evolved mouth suckers or hydraulic discs near the mouth enabling them to attach very firmly to rocks.

### Behavioural adaptations

Because of the highly heterogeneous current regimes of torrential reaches, mobile organisms can exert choice over the current to which they are exposed. At the microspatial scale, organisms exhibit cryptic behaviour by moving into crevices or seeking refuge in moss tufts; others position themselves on rock faces. Even strong-swimming nektonic forms such as salmonids spend much time in areas of reduced current. Invertebrates poorly adapted to resist current are concentrated in the quieter margins, whereas other species are more abundant near the stream's centre (Needham & Usinger 1956). Differences in the morphological adaptations of congeneric fishes are consistent with their exposure to and ability to resist current (Mathews 1985). The more rheophilic dace, *Rhinichthys cataractae*, not only

occurs in faster current than its sympatric congener (*R. falcatus*), it also has a smaller swim bladder (Gee & Northcote 1963).

Behavioural drift, the downstream transport of benthic organisms by current, is a functional attribute of running waters, although whether drift entry is passive or active is contentious (Allan *et al* 1986; Brittain & Eikeland 1988). The colonization-cycle hypothesis has been proposed as a drift compensation mechanism for aquatic insects with a winged adult stage (Müller 1982); upstream flight by ovigerous females prevents faunal depletion of the headwaters and provides a means of exploiting different habitats during different seasons or lifecycle stages. Upstream migration within the water has been documented for a variety of stream invertebrates (Söderström 1987).

Another behavioural adaptation to torrential conditions is employed by black fly larvae (Simuliidae), which use silk threads as 'life-lines', enabling them to regain their original position if displaced accidently or to avoid a predator (Wotton 1986). Certain caddisflies add mineral particles to their cases to increase ballast, especially before the quiescent pupal stage.

## Respiratory physiology of aquatic insects

Aquatic insects perhaps best exemplify, through their respiratory physiology, the special conditions of high-gradient mountain streams. Insects tend to be the most abundant and diverse metazoans in such habitats; entire orders of insects evolved in cool headwater streams; and a great deal is known of their respiratory physiology, which has common features with other faunal groups characteristic of high-gradient mountain streams (e.g. salmonid fishes; Allen

1969). The fauna of high-gradient mountain streams evolved in an environment — cool, turbulent, oxygen-saturated waters — that does not necessarily require special physiological adaptations. Adaptive radiation occurred later as lowland rivers and lentic habitats were colonized (Ward & Stanford 1982). It is, in fact, the lack of adaptations that is most striking when the respiratory physiology of insects from cool lotic waters is considered and contrasted with related forms from more stagnant waters (Table 23.1).

Insects from running waters generally, and high-gradient headwaters in particular, are unable to regulate oxygen consumption, which varies directly with the oxygen concentration of the medium (dependent-type respiration). In addition, insects from running waters tend to have high metabolic rates, are intolerant of low oxygen levels, and generally lack the ability to use ventilatory movements to enhance oxygen uptake. Insects and other animals with an evolutionary history tied to mountain streams have had little or no selective pressures to develop adaptations to low oxygen conditions. Obligatory rheophiles, while able to survive temporary oxygen deficits in moving water, succumb in still water even at high concentrations of oxygen (Philipson 1954; Hynes 1970).

Temperature is also intimately related to the respiratory physiology of aquatic insects. For example, onset of death occurred at an oxygen concentration 2.4 times higher when stonefly nymphs were held at 15.6°C than at 10°C (Knight & Gaufin 1964). The cold stenothermous nature of mountain stream animals probably relates as much to high oxygen requirements as it does to low temperature (Hynes 1970).

**Table 23.1** Contrasting features in some general respiratory characteristics of insects in running and standing waters

| Characteristic | Standing waters | Running waters |
| --- | --- | --- |
| Type of respiration | Independent[a] | Dependent[a] |
| Oxygen consumption | Low | High |
| Tolerance of low oxygen concentration | High | Low |
| Ventilatory movements | Well developed | Poorly developed[b] |

[a] See text for definition; [b] well developed in case- and tube-dwelling forms.

498

## Longitudinal patterns

Spatial changes in abiotic and biotic variables along the course of river systems have long attracted the attention of river ecologists (e.g. Shelford 1911; Thienemann 1912). Illies (1961) proposed a universal zonation scheme for running waters based on the rather sudden transition in zoobenthic community composition that corresponded to fish zonation patterns (Müller 1951) and to shifts in factors such as temperature and current. The most marked faunal changes occurred at the lower end of the salmonid zone; areas upstream from this point were designated 'rhithral', those below were designated 'potamal'. Rhithral was defined as the upper reaches where the annual range of monthly mean water temperatures does not exceed 20°C, dissolved oxygen levels are continuously high, the substratum is predominantly coarse, the current is turbulent, and the water is clear (Table 23.2). The annual range of monthly mean water temperatures in the potamal commonly exceed 20°C, oxygen levels are low at times, finer substratum materials are abundant, the current is less turbulent, and water clarity is lower. Illies and Botosaneanu (1963) expanded the zonation scheme to include an upper krenal zone for streams originating as springs (summer-cool, winter-warm). Steffan (1971) added yet another upper zone, the kryal, to encompass streams arising from the meltwater of glaciers and permanent snowfields ($T_{max} < 4°C$). The distinctiveness of the biota of the major zones has focused on differences in temperature regimes. Statzner and Higler (1986) proposed that stream hydraulics also play an important role in structuring zonation patterns (see Chapters 3 and 11).

The river continuum concept (RCC), developed in North America (Vannote *et al* 1980), perceives the downstream changes along rivers from a clinal rather than a zonal perspective (see Chapter 17). According to the RCC, river systems are longitudinal resource gradients along which stream organisms are predictably structured. This conceptual model was initially formulated for undisturbed deciduous forest streams with headwaters that are fully canopied by riparian vegetation and dominated by groundwater. The upper reaches are, therefore, light-limited heterotrophic systems (allochthonous leaf litter providing the major energy source) with temperature, discharge, and chemical regimes that are relatively stable and predictable (Table 23.3). As the canopy opens in the middle reaches, where the water is shallow and remains clear, primary production is maximized and autotrophy prevails ($P/R > 1$). The stream is no longer buffered by a dense canopy or groundwater dominance, and environmental heterogeneity reaches a maximum (e.g. diel amplitudes of temperature). The large volume of

**Table 23.2** Idealized features of the four major zones of river systems as interpreted from the zonation perspective

| | Major zones | | | |
|---|---|---|---|---|
| | Kryal | Krenal | Rhithral | Potamal |
| Temperature | $< 4°C$ | Summer-cool, winter-warm | $T_{max} > 4°C \leq 20°C$ | $T_{max} > 20°C$ |
| Transparency | Clear or turbid | Clear | Clear | Turbid |
| Substratum | Coarse | Fine to coarse | Coarse | Fine |
| Oxygen | Saturated | Variable | Saturated | Periodic deficits |
| Gradient | High | Variable | High | Low |
| Plankton | Absent | Absent | Absent | Present |
| Algae | Absent | Variable | Epilithon, Epixylon | Epipelon, Epiphyton |
| Bryophytes | Absent | Variable | Abundant | Sparse/absent |
| Rooted plants | Absent | Abundant | Sparse/absent | Variable |
| Zoobenthos | *Diamesa, Prosimulium* | Non-insects/insects | Insects predominate | Insects/non-insects |
| Fish fauna | Absent | Variable | Rheophilic | Limnophilic |

**Table 23.3** Idealized features of the three reaches of river systems as interpreted from the perspective of the river continuum concept (as initially formulated)

|  | River reaches | | |
|---|---|---|---|
|  | Upper | Middle | Lower |
| Temperature | Cool, low amplitude | High amplitude | Moderate amplitude |
| $P/R$ | <1.0 | >1.0 | <1.0 |
| Energy source | Terrestrial detritus | *In situ* PP* | Transport detritus |
| Bottom light | Low | High | Low |
| Nutrient availability | Low | High | Low |
| Attached algae | Sparse | Abundant | Sparse |
| Submerged angiosperms | Absent | Abundant | Sparse |
| Plankton | Absent | Absent | Present |
| Leaf litter | Abundant | Sparse | Negligible |
| Invertebrates | | | |
| Shredders | Co-dominant | Rare | Absent |
| Collectors | Co-dominant | Co-dominant | Dominant |
| Grazers | Sparse | Co-dominant | Absent |
| Predators | Low | Low | Low |
| Fish fauna | Cool-water invertivores | Piscivores and invertivores | Planktivores and bottom feeders |
| Environmental heterogeneity | Low | High | Low |
| Biotic diversity | Low | High | Low |

* PP = primary production

water in the lower reaches reduces environmental heterogeneity. The lower reach river is again heterotrophic ($P/R < 1$), being light limited by reduced water transparency and greater depth. The RCC stresses the interdependence of organic resources and invertebrate functional feeding groups, and how these change along the continuum. Criticisms of the RCC (e.g. Winterbourn *et al* 1981; Barmuta & Lake 1982) stem only partly from the fact that not all rivers are expected to exhibit the structural and functional features of undisturbed deciduous forest streams exemplified by Vannote *et al* (1980). The river continuum should be perceived as a 'sliding scale', whereby adjustments are made to accommodate different climatic/vegetational/hydrological settings (Minshall *et al* 1983) or anthropogenic disturbances (Ward & Stanford 1983). A more basic difficulty relates to the essentially deterministic nature of the RCC model, since many lotic ecologists view stream communities as stochastic phenomena (e.g. Grossman *et al* 1982; Reice

1985). In addition, interactions between the channel and adjacent floodplain and aquifer systems should be fully integrated into any holistic perspective of river ecosystems (Ward 1989).

## 23.3 THE ST VRAIN: AN ARCHETYPICAL MOUNTAIN RIVER

The St Vrain River, a major tributary of the South Platte River system, rises on the eastern slope of the Continental Divide in the Southern Rocky Mountain Physiographic Province (Fig. 23.1). The confluence of the north and south branches, fourth-order segments, occurs at the village of Lyons at the base of the foothills. The catchment above this point (the mountain catchment) encompasses 522 km². The headwaters of the North St Vrain lie within Rocky Mountain National Park; the headwaters of the middle and south branches are in the Indian Peaks Wilderness area. Much of the remaining catchment is in National
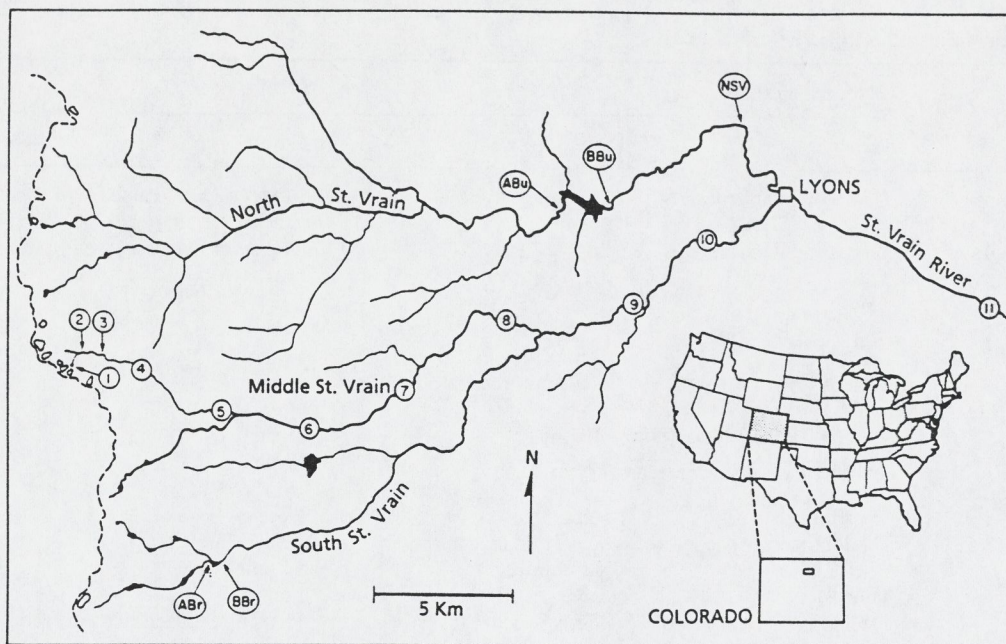
**Fig. 23.1** The St Vrain River Basin showing the 11 sampling sites along the elevation gradient and other sampling locations referred to in the text. The dashed line along the western margin is the Continental Divide, along the eastern side of which are shown extant cirque glaciers. The village of Lyons is located at 40°13′N latitude and 105°16′W longitude.

Forest land. Research has been conducted at the sites shown in Fig. 23.1 (Ward 1975, 1981, 1982, 1984, 1986, 1987; Ward & Berner 1980; Ward & García de Jalón 1991). Studies conducted at the site on the North St Vrain (NSV), in the foothills above Lyons at 1677 m a.s.l., dealt with macroinvertebrate distribution patterns on various natural substrata. The influence of a deep-release storage impoundment on downstream conditions was examined by studying stream sites above (ABu, 1951 m) and below (ABu, 1890 m) Buttonrock Reservoir. The influence of a surface-release storage impoundment, Brainard Lake, located in the headwater of the South St Vrain, was examined from studies conducted at sites ABr (3153 m) and BBr (3146 m).

The most intensive and extensive research, the results of which provide the focus for the remainder of this chapter, was conducted at the 11 sites (arabic numerals in Fig. 23.1) located along the longitudinal river profile (see p. 504). From site 1, a first-order alpine tundra stream at 3414 m

a.s.l., the pristine Middle St Vrain drops precipitously to site 11 on the Great Plains (1544 m) in less than 55 km. The plains river segment from Lyons to site 11 has a relatively high gradient (15.9 m km$^{-1}$), a rocky substratum, is well oxygenated, and has good water quality, thereby providing an interesting contrast with the mountain river (sites 1–10).

### Bedrock geology and glacial history

At the sources of the St Vrain River system there are 16 mountain peaks exceeding 4000 m and the largest extant glaciers in Colorado (Madole 1969). Above the foothills the exposed bedrock is largely igneous and metamorphic rock of Precambrian age, consisting primarily of the gneisses and schists of the Idaho Springs formation and Longs Peak–St Vrain granite. The lower foothills are composed of sedimentary rocks of the late Paleozoic and Mesozoic.

Four major glaciations occurred in this region:

Pre-Bull Lake, Bull Lake, Pinedale and the Neo-glaciation (Madole 1969; White 1982). Pre-Bull Lake deposits are sparse and their ages are uncertain. Bull Lake glaciers, also of uncertain age, extended 13 km down the South St Vrain Valley to 2700 m, 15 km down the Middle St Vrain Valley to 2580 m, and 14 km down the North St Vrain Valley to 2400 m (White 1982). Pinedale glaciers advanced to nearly the same elevations as Bull Lake glaciers and Pinedale till now covers 90% of the glaciated areas. Pinedale glaciation began more than 30 000 years BP; the glaciers began retreating from their outermost positions about 14 000 years ago, receding to the cirques about 10 000 years BP. There is no evidence of glaciers or perennial snowfields in the Front Range during the Altithermal maximum (c. 7500–6000 BP). During the last 6000 years there have been several minor advances of cirque glaciers, collectively termed the Neoglaciation, the most recent of which occurred from 300 to 100 years BP. Extant glaciers are tiny and are confined to north- and east-facing cirques along the Continental Divide (Fig. 23.1).

Mountain valleys, formed by stream incision in the early Tertiary, are broad and U-shaped at higher elevations, but are narrow and deep below the maximum extent of Pleistocene glaciation. The Neoglacial ice remnants are not active, so that even streams originating directly from these cirque glaciers contain clear water.

### The climate/vegetation gradient

Climatic conditions and terrestrial vegetation communities change dramatically along the steep elevation gradient (Marr 1961; Peet 1981). The continental climate is subject to extreme fluctuations. At higher elevations, appreciable snowfall can occur during all months of the year and high winds are common. Mean values of climatological data from five locations along the elevation gradient are shown in Table 23.4.

The forest vegetation of the mountain landscape can be illustrated as a community mosaic, with gradients of moisture-topography superimposed on the elevation gradient (Fig. 5 in Peet 1981). Dry foothill locations are typified by open ponderosa pine (*Pinus ponderosa*) woodlands. More mesic or higher elevation foothill sites exhibit higher tree densities and the addition of Douglas fir (*Pseudotsuga menziesii*). Dense stands of lodgepole pine (*Pinus contorta*), a post-fire successional species, occur at many middle elevation sites. Lodgepole pine is succeeded by Douglas fir at lower mid-elevations and by Engelmann spruce (*Picea engelmannii*) and sub-alpine fir (*Abies lasiocarpa*) at higher mid-elevation sites. In the subalpine zone, Engelmann spruce and subalpine fir are successional and climax forest co-dominants, except on the driest sites where limber pine (*Pinus flexilis*) occurs. Alpine tundra begins at approximately 3500 m elevation.

Site 1 on Middle St Vrain creek (Fig. 23.1) is located in alpine tundra on a north-facing slope where treeline extends only to 3325 m elevation. A small cirque lake, fed by the St Vrain Glaciers, is the source for the stream. During the summer, lush tundra vegetation, consisting of low willow shrubs (*Salix*) and herbs, forms a nearly complete canopy over portions of the first-order stream.

**Table 23.4** Long-term climatological data means from five locations along the eastern slope of the Front Range, Colorado

| | Elevation (m a.s.l.) | | | | |
| --- | --- | --- | --- | --- | --- |
| | 1603 | 2195 | 2591 | 3048 | 3750 |
| Annual air temperature (°C) | 8.8 | 8.3 | 5.6 | 1.7 | −3.3 |
| Daily minimum temperature (°C) | – | 1.4 | −0.8 | −4.4 | −7.3 |
| Daily maximum temperature (°C) | – | 14.6 | 12.1 | 6.9 | −0.2 |
| Annual precipitation (cm) | 40 | 58 | 58 | 77 | 102 |
| Days per year >0°C (days) | 135 | 125 | 104 | 59 | 47 |

From Barry (1973) and Peet (1981).

502

Willows (*Salix* spp.) occur in the riparian zone along the entire elevation gradient (sites 1–11). Rocky Mountain alder (*Alnus tenuifolia*) is an important riparian species at middle elevations, where it co-occurs with willows and Rocky Mountain birch (*Betula occidentalis*). Scattered cottonwood trees (*Populus sargentii* and *P. angustifolia*) occur in the stream corridor in the foothills and lower montane and extend on to the plains.

### Physicochemical gradients

The St Vrain is a snowmelt river (*sensu* Poff & Ward 1989). Although the magnitude of snowmelt runoff varies between years, the temporal pattern is predictable (Fig. 23.2). Dissolved oxygen is near saturation at all mountain stream sites. Oxygen supersaturation is observed at the plains site, where dense macrophyte beds and filamentous algae occur. Summer values of nitrate-nitrogen ranged from 0.10 to 0.15 mg l$^{-1}$ with no discernible altitudinal pattern. Orthophosphate levels are below detection limits (5 µg l$^{-1}$).

Other physicochemical variables exhibit longitudinal patterns (Fig. 23.3). Water temperature maxima ($T_{max}$) exhibit a progressive downstream increase. Because the water temperature drops to 0°C at all sites, $T_{max}$ is also the annual temperature range. At the highest elevations the stream is
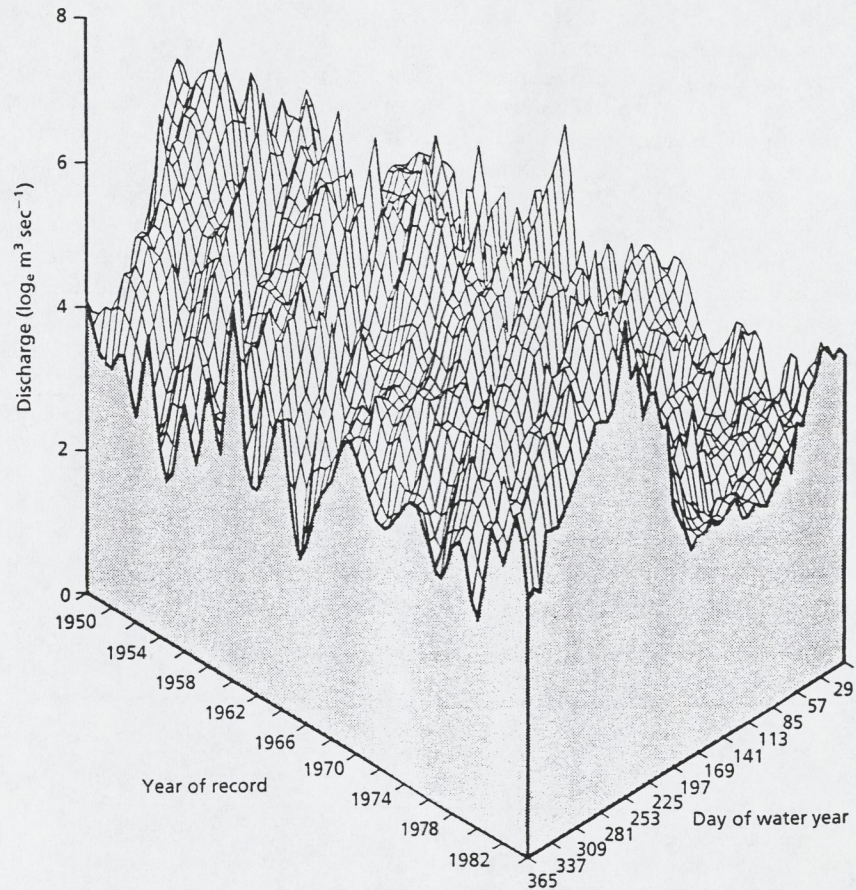


**Fig. 23.2** Long-term hydrograph based on daily mean discharge records from a location 0.6 km downstream from the confluence of the north and south branches of the St Vrain River. Year of record is the water year, 1 October–30 September.
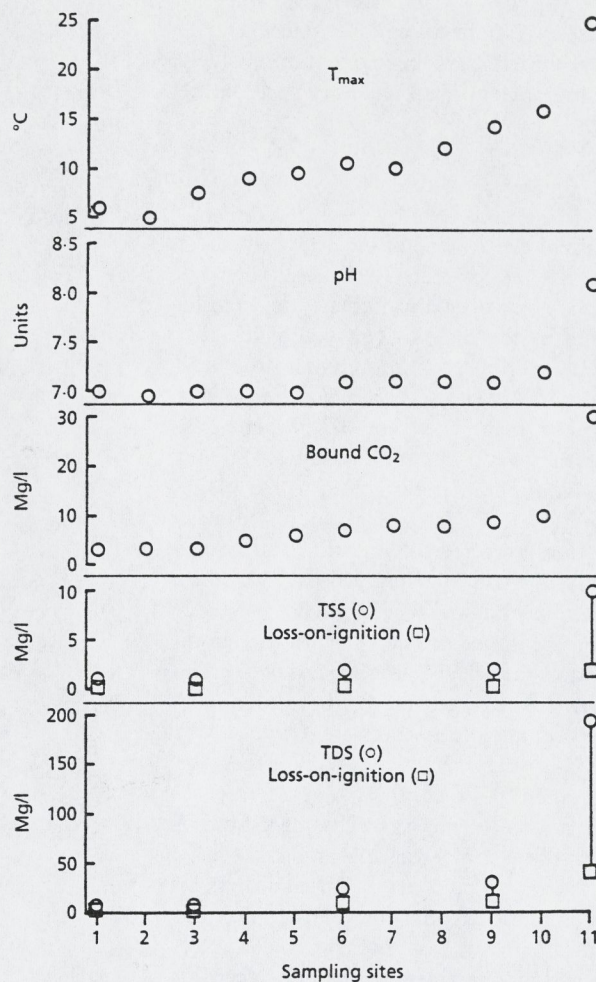
**Fig. 23.3** Longitudinal patterns of maximum temperature, pH, bound carbon dioxide (methyl orange alkalinity) and total suspended and dissolved solids (showing loss-on-ignition fractions) along the course of the St Vrain River.

snow covered for more than half the year, whereas site 11 drops to 0°C for only a short period in January when ice forms only along the edges. Annual thermal summation estimates range from 450 degree-days (>0°C) at site 1 to 4220 degree-days at site 11. Values of the remaining variables in Fig. 23.3 increase only slightly from the tundra to the lower foothills, then abruptly increase to the plains site.

All sampling sites were located on rubble riffles to minimize between-site differences in bed materials. In the smaller mineral fraction (<32 mm), gravel predominates (78–87%) in the mountain river. Sand (62.5 μm to 2 mm) and gravel are equivalent in the plains river. Silts (3.9–62.5 μm)

and clays (<3.9 μm) constitute <3% of the smaller size fraction at mountain and plains sites. During summer, fine particles (0.05–1 mm) constitute the majority of the sedimentary detritus (66–96%) on riffles at mountain and plains locations. Coarse detritus reflects the terrestrial vegetation, with grass and sedge fragments common in the tundra stream, conifer needles at middle elevations, and sparse deciduous plant detritus in the plains river.

### Biotic gradients

The distribution and abundance patterns of aquatic flora, fishes and zoobenthos are included

in this section. Emphasis will be placed on the zoobenthos, which have been most intensively studied. General trends and idealized patterns are emphasized.

## Aquatic flora

The biomass of the attached flora attains greatest values in the headwaters, where bryophytes (mosses and liverworts) and lichens are well developed, and in the plains river, where the filamentous chlorophyte *Cladophora glomerata* proliferates (Fig. 23.4(a)). Aquatic lichens were collected only from the two headwater sites, whereas bryophytes occur at all mountain stream locations. *Cladophora* is restricted to the plains river. At mid-elevation sites, where biomass levels are low, a variety of epilithic microalgae predominate. Distribution patterns of individual taxa are best demonstrated with diatoms (Bacillariophyta), the most intensively studied group (63 species and varieties). Some species of diatoms occur at all sites along the elevation gradient (e.g. *Achnanthes lanceolata*); others are found only in upper (e.g. *Diatoma anceps*) or lower reaches (e.g. *Nitzschia palea*). No common species are restricted to middle elevations. The algal flora of the St Vrain River, however, does not exhibit the distinct zonation patterns demonstrated by Kawecka (1974) for streams of the High Tatra and Rila mountains. Aquatic angiosperms are restricted to the plains river, where dense beds of *Elodea canadensis* and *Ranunculus aquatilus* occur from July through October.

## Fish fauna

Salmonid fishes occupy the entire elevation gradient and extend a short distance into the plains river (Ellis 1914; Propst 1982). Cut-throat trout (*Oncorynchus clarki*), the only indigenous salmonid of this region, is now confined to high elevation tributaries, having been largely displaced by introduced species. Brook char (*Salvelinus fontinalis*) now occupies the same headwater habitat as cut-throat trout. Rainbow trout (*Oncorynchus mykiss*) is planted in most accessible reaches of Colorado streams. Brown trout (*Salmo trutta*) is more tolerant of warmer
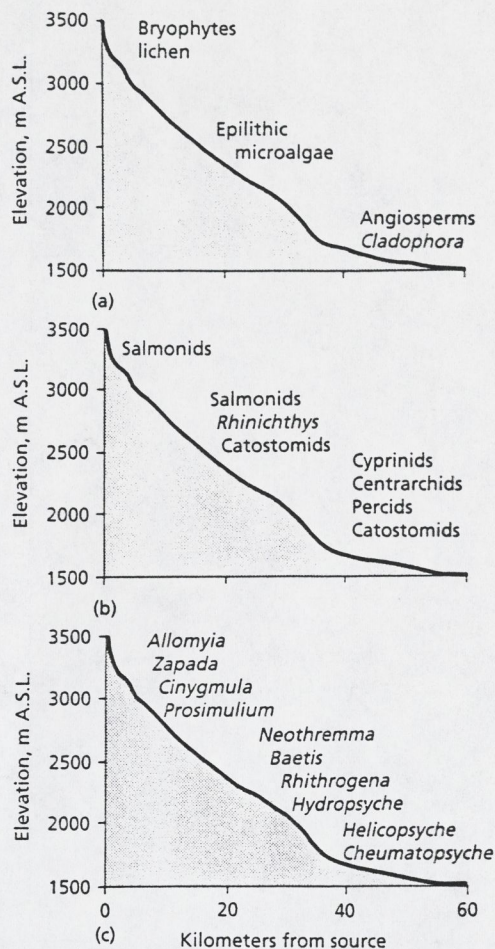


**Fig. 23.4** The long profile of the St Vrain River showing dominant floral and faunal components of the headwater, middle elevation, and plains river segments. (a) Aquatic flora. (b) Fish fauna. (c) Zoobenthic fauna.

waters than most salmonids and extends from mid-elevations downward on to the plains. A depauperate fish fauna characterizes Front Range river systems (Fig. 23.4(b)). Sculpins (Cottidae), typically co-dominant with salmonids in high-elevation segments, are historically absent from the eastern slope of Colorado. Two catostomids (*C. catostomus* and *C. commersoni*) and the long-nose dace (*Rhinichthys cataractae*) are the only other fishes commonly encountered in mountain streams of this region. A somewhat richer fauna occurs in the plains river where Propst (1982)

recorded 16 species of fishes, mainly cyprinids (ten species, including *R. cataractae*), but also including the two catostomids, two centrarchids, a percid, and (rarely) brown trout.

## Zoobenthic fauna

Insects dominate the zoobenthos, constituting 89–99% of the densities, 84–99% of the biomass, and 79–93% of the taxa at the 11 sites. The numerically dominant species at each site are all insects (Fig. 23.4(c)) from only four orders: Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies) and Diptera (true flies). Additional orders (Odonata, Lepidoptera, Collembola) were collected from the plains river, and aquatic beetles (Coleoptera) occur at low densities at sites 2–11. Some non-insect groups are widely distributed along the elevation gradient (nematodes, oligochaetes, mites, planarians); others are confined to site 11 on the plains (amphipods, isopods, snails, leeches).

Zoobenthic abundance is low in the headwaters, increases from the montane to the upper foothills, levels off in the high-gradient foothills segment, and markedly increases in the plains river (Fig. 23.5). In the tundra stream (site 1), zoobenthic density averages 1856 organisms $m^{-2}$ and biomass averages 652 mg dry weight $m^{-2}$. In the plains river, mean values are 6355 organisms and 3646 mg $m^{-2}$.

Zoobenthic diversity exhibits a sigmoid pattern along the elevation gradient (Fig. 23.5). From a total of 210 taxa, 34 occur at site 1, and 106 at site 11. The major faunal components exhibit one of the seven species richness curves illustrated in Fig. 23.6. Pattern number 7 is for those groups that are absent from the mountain river. The other six patterns all exhibit low species richness in the headwaters. Pattern 5 organisms (planarians, mites) maintain low levels of diversity along the entire gradient. Mayfly diversity (pattern 4) progressively increases downstream over most of the river's course. Dipterans (pattern 1) and beetles (pattern 6) show progressively greater lag phases before the start of diversity increases. Caddisfly species richness (pattern 3) reaches maximum values in the upper montane zone, then remains at similar levels over the remaining sites. Only stoneflies (pattern 2) exhibit declining diversity downstream.

Zoobenthos occurring in the tundra stream include a few special headwater elements, but most abundant species are euryzonal forms. The two
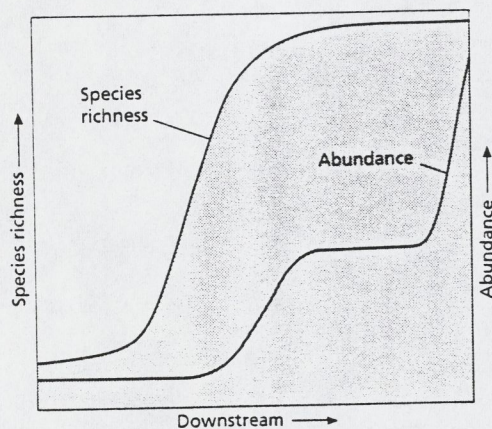


**Fig. 23.5** Idealized altitudinal patterns of species richness and abundance for total zoobenthos along the course of the St Vrain River (from Ward 1986; ©1986 by E. Schweizerbart'sche Verlagsbuchhandlung).
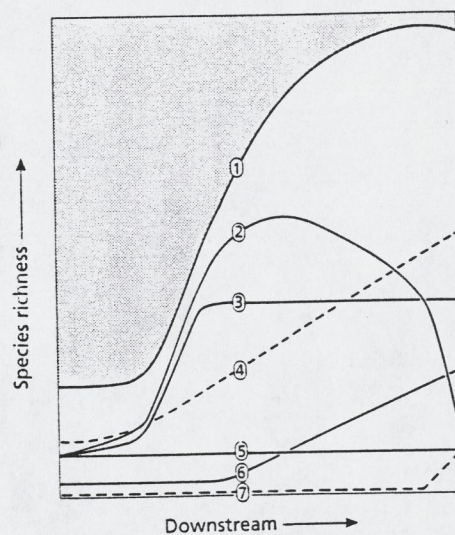


**Fig. 23.6** Idealized types of species richness curves exhibited by the various faunal components along the course of the St Vrain River. See text (from Ward 1986; ©1986 by E. Schweizerbart'sche Verlagsbuchhandlung).

506

most abundant stoneflies at site 1, for example, extend downstream to site 10 (*Megarcys signata*) or site 9 (*Zapada oregonensis*). The addition of species downstream, without loss of those present at higher elevations, generally characterizes the chironomid midge fauna, mayflies, beetles and oligochaetes. Even in these groups, however, many species do not extend their range into the plains river. Conversely, many species that occur at site 11 are not found at any mountain site. Euryzonality is less well developed in the caddisfly fauna, which contains distinct headwater (e.g. *Allomyia tripunctata*) and plains elements (e.g. *Heliopsyche borealis*) as well as species restricted to middle elevations (e.g. *Neothremma alicia*). The two planarians of the St Vrain River exhibit remarkably distinct distributions, with *Polycelis coronata* occurring at all mountain sites, but not in the plains river to which *Dugesia dorotocephala* is restricted.

## 23.4 SUMMARY AND CONCLUSIONS

A rhithral character prevails along the elevation gradient of the St Vrain River from sites 1–10,

followed by a rather abrupt transition to potamal conditions at site 11. This is best exemplified by the sharp faunal discontinuity between sites 10 and 11. Site 10 in the lower foothills marks the downstream distribution limit of many zoobenthic species. Conversely, numerous species of the plains river segment, including some of extreme abundance, do not penetrate the mountain river. Faunal overlap between adjacent mountain stream sites (along the diagonal in Fig. 23.7) is high. Even the tundra stream (site 1) exhibits a relatively high overlap (39.2%) with site 2 located below treeline. Site 10 exhibits a 58.4% faunal similarity with site 9, but only a 17.8% overlap with site 11, the plains river.

The St Vrain River, although glacial fed, lacks the distinct kryon biocoenosis present at slightly higher elevations in an adjacent drainage (Elgmork & Saether 1970). Rhithral conditions extend to the headwater of the Middle St Vrain. Some rhithral features are maintained even at the plains site (coarse substrata, relatively high gradient and turbulence, well oxygenated water of high transparency). What factors then are responsible for the spatial patterns of zoobenthos observed along the course of the St Vrain River?
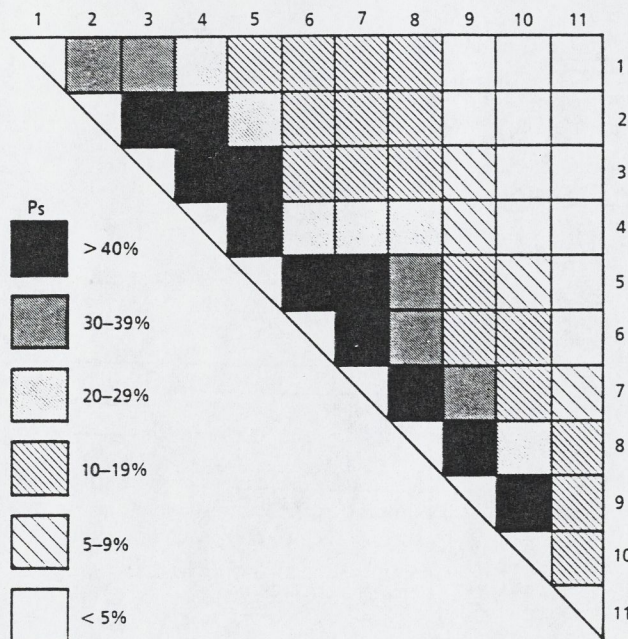


Fig. 23.7 Matrix of percentage similarity (Whittaker 1975) between sampling sites based on total zoobenthic species (from Ward 1986; ©1986 by E. Schweizerbart'sche Verlagsbuchhandlung).

Many researchers have espoused changes in temperature as a major, if not primary, factor responsible for the altitudinal changes in zoobenthic communities (e.g. Dodds & Hisaw 1925; Kownacka & Kownacki 1972; Brodsky 1980). Both the universal zonation scheme proposed by Illies and Botosaneanu (1963) and the river continuum concept of Vannote *et al* (1980) ascribe an important role to the thermal regime. The low faunal diversity at the highest elevation of the St Vrain is largely attributable to temperature (including 7+ months of ice and snow cover, $T_{max} \leq 6°C$, <500 annual degree-days), as only the most cold-adapted forms can tolerate such extreme thermal conditions. Additional species appear downstream as the thermal amplitude expands and degree-days increase. Even at site 10 in the lower foothills, after descending more than 1700 m in elevation, the annual temperature range is only 0–16°C. At site 11, however, the plains river inhabitants are exposed to an annual range of 0–25°C. Because the zoobenthos of mountain streams tend toward cold stenothermy, it is not surprising that site 10 marks the lower elevation limit of many species and that there is a sharp transition from rhithron to potamon elements between the lower foothills and the plains. A diverse and distinct warm-adapted fauna occurs in the plains river.

Factors other than temperature also contribute to the distinctive nature of the plains fauna. Beds of aquatic angiosperms, absent from the mountain river, increase habitat heterogeneity, provide current refugia and protection from predation, supply case-building materials, and serve as attachment sites for epiphytic algae. Site 11 exhibits similarities with the autotrophic middle reaches of the river continuum (see Table 23.3), given the high amplitude temperature regime, the open canopy, the relatively shallow and clear water, the abundant algae and angiosperms, and the high levels of environmental heterogeneity and biotic diversity. Additional factors that may have structured the plains zoobenthic community include the presence of a more diverse, and largely invertivorous, fish fauna (Propst 1982), and invertebrate predator–prey and competitive interactions that differ from those occurring in the mountain river.

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508

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510

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- Next fall
- Disturbance
- Nutrient cycles
- Non-native ( mysids = text)
- pred-prey

*Larval Fish Laboratory*

**Colorado State University**

# MEMORANDUM

**To:** Fishery Faculty and Graduate Students; Dr. Cook
**From:** Darrel Snyder
**Date:** 11 December 1991

**Subject: Survey of Electrofishing Experiences, Observations and Recommendations**
(please attach responses)

Name: _____     Date: _____

1.    Please describe the nature and extent of your electrofishing experience? (supervisor, crew leader, crew member?)

Please also distribute copies to your graduate students with electrofishing experience (copies were already given to grad. students with offices in the Larval Fish Lab area (Rm 33x).

3.    What species and size groups have you sampled or monitored with electrofishing gear?

4.    What electrofishing equipment and techniques have you used? (Type of gear, manufacturere and model, typical operational configuration and settings, special procedures or hints for optimum operation.)

5.    Describe observations of adverse or injurious effects on fish or other aquatic organisms (physical appearance, abnormal behavior, or mortalities to target fish, non-target fish (note species); please note specific electrical field conditions and equipment configurations and settings under which these injuries were observed if you can remember or have access to that information.) If you very rarely or have never observed electrofishing injuries, please say so.

6     Based on your experience, what recommendations would you offer for optimal electrofishing efficiency while minimizing injury to fish? (Procedures, settings, dos and don'ts).

7     Please read the attached text abstracted from a draft report still in preparation for researchers in the Lower Colorado River Basin. Please relate your response, thoughts, oversights, or criticisms on the content. Consider sections I (broadened to cover fish in general) and II of the recommendations in regard to our own use of electrofishing techniques. Do we need to establish Departmental or University policy on electrofishing gear, use, and training? Would it be appropriate for fishery faculty to consider the matter of injury to fish and establishment of such policy later this winter or early spring?

*Larval Fish Laboratory*

# MEMORANDUM

**Colorado State University**

**To:** Fishery Faculty and Graduate Students; Dr. Cook
**From:** Darrel Snyder
**Date:** 11 December 1991

**Subject:** **Survey of Electrofishing Experiences, Observations and Recommendations**
(please attach responses)

Name: _____          Date: _____

1. Please describe the nature and extent of your electrofishing experience? (supervisor, crew leader, crew member?)

2. What environments and under what environmental conditions have you sampled with electrofishing gear? (Rivers, streams, lakes or reservoirs; habitats; time of year, day or night, water temperatures, conductivities, other environmental conditions you consider important.)

3. What species and size groups have you sampled or monitored with electrofishing gear?

4. What electrofishing equipment and techniques have you used? (Type of gear, manufacturere and model, typical operational configuration and settings, special procedures or hints for optimum operation.)

5. Describe observations of adverse or injurious effects on fish or other aquatic organisms (physical appearance, abnormal behavior, or mortalities to target fish, non-target fish (note species); please note specific electrical field conditions and equipment configurations and settings under which these injuries were observed if you can remember or have access to that information.) If you very rarely or have never observed electrofishing injuries, please say so.

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# IMPACTS OF ELECTROFISHING ON FISH

Darrel E. Snyder

Larval Fish Laboratory
Colorado State University
Fort Collins, Colorado 80521

**Tentative Introduction and Recommendations**
DRAFT — December 2, 1991

Prepared for

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## Introduction

Electrofishing, a valuable sampling technique in North America for four decades, is in a state of flux. The field is expanding with new equipment, applications, and understanding but contracting with increased concern for comparability of data and safety of operators and fish. In some situations it is even being switched off to prevent adverse impacts on fish. Much effort has been expended during the past couple decades on improvements in equipment and techniques for safer operation, flexibility, and increased capture range and efficiency. But recent investigations by Sharber and Carothers (1988, 1990), Holmes et al. (1990), and Meyer and Miller (1991, In Press) have documented substantial injury to the spine (often over 40% and sometimes much more) to certain species of fish using relatively modern equipment and pulsed direct current waveforms. The problem is real and appears to be wide spread. Renewed concern about potential electrofishing injury has prompted biologists or managers in several agencies to take a closer look at the situation in their own waters. It has led at least one agency, the Alaska Department of Fish and Game, to impose a moratorium on use of the technique in waters containing large rainbow trout (Holmes et al. 1990; Reynolds, pers. com.). This concern is also the motivation for this review of electrofishing injury and its potential effect on endangered species in the Lower Colorado River Basin. While most of the existing data on injurious effects pertains to salmonids, especially rainbow trout, implications for other species are serious.

Why this sudden recognition of a potential problem?  Probably because we have come to expect some injury, and perhaps mortality, as a by-product of most fish collection techniques, and because the electrofishing injuries of immediate concern are often *not externally obvious*.  If captured fish appear to recover sufficiently to swim away and there are no notable external injuries (perhaps other than "brand" or "burn" marks -- mostly a hemorrhaging of skin capillaries or local expansion of melanophore pigment, now recognized as often being associated with spinal injuries), we typically consider the fish "unharmed" and assume they will continue to grow and behave normally.  Many biologists across the country now acknowledge that the situation may be otherwise, at least for some species.  For example, a special session was conducted on the matter during the July 1991 meeting of the Western Division of the American Fisheries Society in Bozeman, Montana; a workshop was also planned for spring 1991 in Hull, England, but was cancelled due to the Iraqi conflict).  Other biologists, including Nehring (1991, abstract) and Schneider (In Press), minimize the likely occurrence and significance of these injuries by noting that years of electrofishing have not had a detrimental effect on the specific populations they manage or monitor.  In these situations, if such injuries do occur in notable numbers, perhaps the question is not so much one of resource reduction but quality.  Observations to date suggest that most fish with electric-field induced spinal injuries, unless particularly severe, do survive.  For some of these fish, the injury will result in permanently bent backs or related deformities; for others, old injuries may only be detected in x-rays or upon dissection, possibly on a fisherman's dinner table.

The questions generated by this concern are many, but primarily what species and size groups are affected, to what degree and using what equipment and techniques, and what can be done to eliminate or minimize the problem?  The immediate concern centers on spinal compression fractures, dislocations, and related internal hemorrhages and tissue damage.  But broader questions are also being considered or re-examined -- effects on physiology, stress levels (can a fish with a broken back not be stressed?), behavior, growth, and reproduction, and the mechanisms involved in causing the injury.  Many of these are not new questions; spinal injury has long been associated with AC (alternating current) fields.  But in spite of the electrofishing's prominent role in fishery research and management, well-designed investigations in response to these questions are scarce, often very limited in scope (frequently a by-product of another investigation), and difficult to compare because of differing gear, techniques, environmental conditions, fish, and terminology.

Our current knowledge of electrofishing practice, theory, and effects on aquatic organisms is well represented in three European books by Vibert (1967), Cowx and Lamarque (1990), and Cowx (1990).  These books comprise the published reports and papers of special FAO (Belgium, 1966) and EIFAC (European Inland Fisheries Advisory Council; England, 1988) symposia.  A Russian book on electrofishing by Sternin et al. (1972; English translation 1976) complements these with detailed information from Soviet research and summaries from world literature not found elsewhere (e.g., a suggested approach for standardizing the description of fish responses in electric fields and tables on fish response thresholds and electrofishing injuries and mortalities -- unfortunately without references).  Unfortunately, the matter of electrofishing injury and mortality received little attention in these major symposia and books, aside from the need to minimize or eliminate the zone of tetany around the anode.  Also, new revisions or refinements of hypotheses regarding the nature and mechanisms involved in fish response to electric fields are being developed (i.e., the "Bozeman Paradigm" of Norman Sharber relating fish responses to various phases of epilepsy, presented at the 1991 special session on electrofishing injuries mentioned above).

Perhaps it is time for a concerted, well-funded, national (if not international) effort to better document electrofishing effects and injuries, mechanisms, response thresholds, and means for optimizing capture efficiency while minimizing injury for at least the species targeted or frequently captured by electrofishing techniques.  Such a coordinated effort will probably require sponsorship and leadership from a federal agency with a vested interest (e.g., Bureau of Reclamation, Fish and Wildlife Service), a consortium of state, federal, or international (FAO) agencies, and (or) major professional organizations such as the American Fisheries Society.  We must understand the problem, the factors involved, and how, if possible, to control them.  If injury is a problem and we cannot adequately reduce the extent of electrofishing injury to target or incidental species, we must abandon or severely limit use of these detrimental techniques and seek less damaging alternatives.  As fishery biologists, this is our ethical

responsibility to the fish and other aquatic organisms we manage, study, or protect, the populace we serve, and ourselves. If we do not take the initiative and accept the responsibility, it will likely be forced upon us by an informed (or at least partially informed) portion of the public we serve.

**Recommendations for Electrofishing Policy and Research:**

I. Minimize electrofishing of or in the vicinity of endangered species until response thresholds and susceptibility to injury are determined in controlled experiments with hatchery-reared stock or it can otherwise be adequately demonstrated that current or new electrofishing techniques will not harm the endangered species of concern .

A. Institute a moratorium on new sampling programs using electrofishing unless critical to the recovery effort and less potentially damaging alternative collection techniques are not available.

B. If effective, less potentially damaging, alternative sampling techniques are available for programs currently relying on electrofishing and if their use will not jeopardize critical comparisons with past data, replace electrofishing techniques with the alternatives.

C. If electrofishing remains the capture technique of choice, either because it is less potentially damaging to the target species, or because abandonment of electrofishing as used in the past would jeopardize critical comparisons with past data:

1. Update electrofishing equipment and techniques, including specimen handing protocol, to assure the least likely harm to captured fish based on the latest available information.

   a. Abandon use of AC electrofishing gear and techniques except when all fish are to be preserved or killed and uncaptured injuries or mortalities are not a concern (as when eradicating fish and perhaps certain other aquatic organisms from a particular body of water or habitat).

   b. Since straight DC (direct current) fields are generally considered less injurious to fishes than PDC (pulsed direct current), consider use of this current when its greater power requirements or more limited effective field than with PDC are not a problem.

   c. When using PDC systems, use waveforms, pulse frequencies or patterns, pulse durations and power levels identified as causing the least damage while still maintaining adequate capture efficiency. Square waves with pulse frequencies of about 30 Hz or less or Coffelt's CPS (complex pulse system, trademark) are currently recommended in this regard, but much research is still needed on these and alternative currents.

   d. Operate electrofishing systems with the largest practical anode(s) and lowest effective power settings to minimize or eliminate the zone of full tetany near the anode. Effective settings will ultimately be determined in controlled experiments to determine response threshold levels for the target fish. While spinal injuries may not be specifically induced or increased in the zone of tetany, the chances for electrocution, respiratory disfunction, and other potentially injurious conditions are increased.

2. Institute, if not already done, a standardized procedure to document each electrofishing operation including output parameters and measures of local conductivity, water temperature, and field strength (voltage gradient at specified distances from the anode) as well as detailed observations on injuries or abnormal behavior (all species).

3. Provide for the time, materials, and facilities for preservation (icing and freezing or fixation) and subsequent (or on-site) documentation of the nature and extent of injuries of mortalities and severely injured fish which are not likely to recover and survive (a representative subsample should suffice in the case of large numbers). Standardized documentation should include photographs, autopsies, x-rays if possible, and standard terms or codes for description of recurring injuries (e.g., descriptors for spinal injuries agreed upon during the electrofishing session of the 1991 meeting of the Western Division of the American Fisheries Society).

II. Assure the safe and proper use and functioning of electrofishing equipment, associated gear (e.g., boat operation), and techniques. If national or state guidelines to this end are available and sufficient, they should be adopted and closely followed (the guidelines currently available through the U.S. Fish and Wildlife Service may need updating; Canada has recently published such a set of guidelines).

A. If not already required, at least the electrofishing team leaders should be properly trained and certified in the theory and practice of electrofishing equipment and techniques. An appropriate course and certification program is available through the Fisheries Academy of the U. S. Fish and Wildlife Service at Leestown, West Virginia; the course, currently instructed by Kolz and Reynolds is normally offered at least twice a year at various locations throughout the country. This or alternative courses should be frequently updated to provide the latest information on equipment and techniques for minimizing adverse effects (e.g., injury) on fish and other aquatic organisms.

B. Other electrofishing team members should be trained, if not certified, in the proper use of electrofishing gear and techniques for the specific sampling program; each should be prepared to handle emergencies or usual circumstances.

C. All team members must be adequately trained (certified) in first aid and CPR.

D. Recertification in electrofishing, first aid, and CPR should be required on a periodic basis both as a refresher and to assure the latest information.

III. Sponsor research:

A. To determine the field strength thresholds for field perception (twitch, possibly defining the outward extent of potential spinal injuries) and effective electrofishing responses (e.g., taxis and narcosis and/or tetany) for endangered and other target or typically captured fishes. These thresholds should be determined in DC and selected PDC currents at various conductivities and temperatures within and perhaps beyond the ranges likely to be encountered in the field. Initial orientation of the fish in the field should also be considered and test organisms frequently checked with x-ray to help define the factors and conditions involved in and controlling spinal injury. Finally, behavior for each species when first perceiving the electric field should be documented (e.g., rapid swimming, dropping to cover, etc.). This information will be used to define optimal electrofishing fields and techniques for the target species.

B. To test in controlled experiments the relative effectiveness of existing and potential improvements in PDC currents for generating desirable electrofishing responses and minimizing spinal injuries. Experimental currents might consider variations in pulse form, frequency, width, and pattern (these various characteristics of pulsed currents are believed to affect species differently, e.g., some catfish appear to be very sensitive to even small, barely perceptible, pulsed currents). The importance of voltage spikes at the leading edge of square-waves might also be considered (if found to be a problem, electronics will be needed to better "cleanup" the waveforms tested or used in practice).

C. To develop better electrode systems designed to eliminate or further minimize the tetanizing zone and adjust to optimum size for water conductivity changes. Possibilities might include:

1. Floating spherical cap or hemispherical electrodes suspended from a frame with vertical guides and a hydraulic unit to raise the electrodes when traveling between sites.

2. Floating hemi- or quarter cylinder, or horizontal plate with adjustable insulative cover to change amount of electrode exposed depending on conductivity levels and specific generating and control equipment used (adjustment might be controlled automatically by "black box" described below).

3. Protective, non-conductive grids around electrodes to prevent fish from directly contacting the electrodes or, in the case of smaller electrodes, entering the zone of tetany immediately around the electrode.

4. Inclusion of an underwater light integrated in the anode to improve capture efficiency when electrofishing at night. The light should attract certain species (hopefully the target species) to the electric field and perhaps reduce number of fish taking flight away from the effective field and anode.

D. To determine the feasibility and help develop continuous in-situ conductivity, temperature, and voltage-gradient sensors mounted at specific locations on or distances from the anode(s) (and perhaps the cathode) to continuously monitor these parameters and allow automatic or manual adjustments to account for changes in conductivity and field strength.
   1. Adjustments would be based on parameters necessary to generate and maintain optimal effective fields for specific species of specific sizes.
   2. The sensor array might also include other useful parameters such as water depth. The latter might help define the extent or range of the effective electrical field.
E. To determine the feasibility and help develop automated output control via a built-in "black box" (computer) using in-situ sensor input to control output and maintain optimal fields for target fishes (based on experimentally determined thresholds for taxis, narcosis and injury minimization. User would input desired field strength (e.g., voltage gradient, current density, or power density at position of sensor) or perhaps specify the target species and size range (black box would use an appropriate lookup table to determine optimal field strength based on experimentally determined thresholds).
   1. An automated compensation system would be able to instantaneously adjust control box output in response to sudden changes in conductivity and or temperature, as when encountering effluent from a tributary or man-made source, as well as changes in the field resulting from changes in channel configuration, substrate conductivity, and varying distances between anode and cathode when one or both are not rigidly fixed in position (as when suspended from a boom or manipulated by hand).
   2. The system would maintain constant fields in vicinity of the anodes or a constant effective field size or range (channel configuration information, e.g., water depth, might be necessary for the latter). This should help minimize otherwise uncontrollable changes in the field that might make the field either less effective or more injurious to the target fish.
   3. The black box could also warn users when settings for target species will jeopardize the welfare of other species or size groups.
   4. It might also provide a continuous visual diagram of current waveform and parameters (oscilloscope) and approximate effective field size and shape (computer display screen).
   5. It should also dramatically improve the comparability of data based on catch per unit effort by accounting for a large number of variables and maintaining constant effective fields that can be replicated in various bodies of water (probably within specific conductivity ranges). Effective fields would be those of similar size adjusted automatically for differences in conductivity and temperature as well as changes in threshold levels for the target fish as conductivity and temperature change.
   6. The system would automatically shutdown whenever problems develop or the system cannot compensate for changes. This will prevent damage to the generator/control box system, damage to fish by fields beyond those optimally defined, and operation of the system when electrical conditions are unsafe. The black box might be able to identify the source of the problem and suggest steps to remedy the problem (e.g., change electrode size to....).

IV. Sponsor or help sponsor the establishment of a portable (trailer based) or non-exclusive fixed-site testing laboratory for the research and testing recommended under items III A and B. These facilities should be developed and used in collaboration with commercial producers of electrofishing equipment and other experts in the field of electrofishing and electrofishing electronics (e.g., Reynolds, Novotny, Priegel, Kolz, and perhaps some European experts). X-ray equipment and film development facilities should be included in the laboratory.

V. Sponsor the field testing of the various results from the above research and development efforts and new equipment and currents developed elsewhere. The possibility of portable onsite X-ray equipment should be investigated. This would allow many captured fish to be examined for spinal injuries without sacrificing the specimens and eliminate the need to kill, freeze, and transport fish for analysis.

5