

Longitudinal and seasonal distribution of macroinvertebrates and epilithic algae in a Colorado springbrook-pond system

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With 13 figures, 7 tables and an appendix in the text

Abstract

A study of a springbrook-pond system in the foothills of northern Colorado was undertaken to determine longitudinal and seasonal changes in the composition, abundance, and community structure of macroinvertebrates and epilithic algae. Light is the only variable which explains the seasonal patterns in epilithic algae which occurred in the otherwise constant environment of the spring source. There was a close relationship between annual mean biomass of epilithon and macroinvertebrate abundance at lotic sites. Indications of stressed conditions near the spring source (low diversity and equitability) are attributed to seasonal and diurnal thermal constancy. Total seston below the pond exhibited a pattern closely corresponding to seasonal patterns of common filter-feeders. The pond also contributed large amounts of detached vascular plants and drifting invertebrates to downstream reaches. Although macroinvertebrate density was similar on rubble and sand, biomass values were nearly three times greater on rubble. Highest coefficients of similarity were between macroinvertebrate assemblages on rubble and *Rorippa*; lowest values were between moss and sand. Some macroinvertebrate taxa occurred throughout the springbrook-pond system or colonized all lotic substrate types. Others were restricted to one site or one substratum. Some distinctive features of the Colorado springbrook fauna were noted.

Introduction

Running waters in general have received much less attention from ecologists than lakes (HYNES, 1970); non-thermal springbrooks have received even less. This is somewhat surprising since springbrooks offer exceptional opportunities to investigate ecological problems (ODUM, 1971). Considerable work has been done on springs in certain regions of Europe since THIENEMANN's (1906) original investigation. Danish springs, for example, have been intensively studied as indicated in the recent review by THORUP & LINDEGAARD (1977). However, only a few comprehensive, year-round studies have been conducted on non-thermal springbrooks in North America (NOEL, 1954; ODUM, 1957; TEAL, 1957; MINCKLEY, 1963; MINSHALL, 1968; TILLY, 1968; STERN & STERN, 1969). NOEL's study of a highly mineralized New Mexico springbrook was the only one of these conducted in western North America. An unpublished thesis (DUDLEY, 1953), the only previous investigation of the fauna and flora of Colorado springbrooks, is based upon a

study of less than one year's duration with a sampling scheme which prevents interpretation of longitudinal or temporal changes.

For this reason, a year-round ecological study of a Colorado springbrook was undertaken with an emphasis on longitudinal and seasonal changes in the composition, abundance, and community structure of macroinvertebrates and epilithic algae.

Site description

The springbrook is located at the base of the foothills (elev. 1597 m) of the Rocky Mountains in northern Colorado (40° 36' N, 105° 10' W). Water originates from four main sources which converge to form the main rheocrene (Fig. 1).

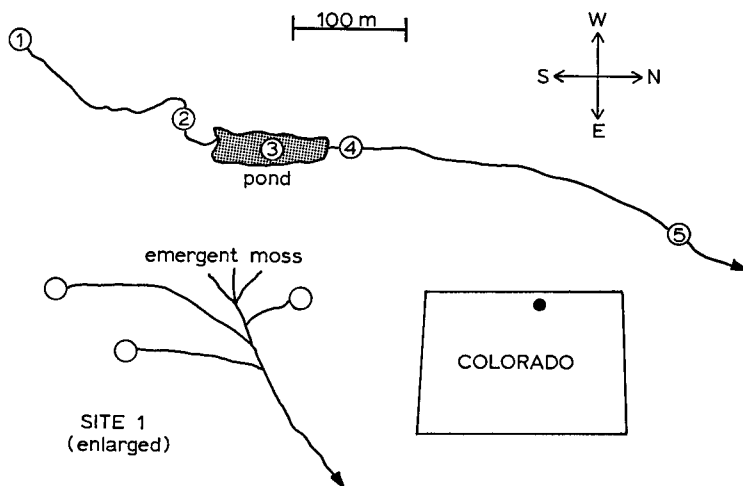


Fig. 1. Map of springbrook-pond system showing study locations (arabic numerals).

The three side channels were choked with watercress (*Rorippa nasturtium-aquaticum*); emergent moss (*Amblystegium*) predominated in the head region where more diffuse seepage occurred. Emergent angiosperms occurring in the source region included *Typha*, *Carex*, *Eleocharis*, *Scirpus*, and *Poaceae*. Willows (*Salix* spp.) were especially abundant on the north shore near the source. Various grasses and sedges occupied the opposite shore. *Veronica*, *Ranunculus*, *Chara*, *Catabrosa*, and *Potamogeton* grew in the channel. Cottonwood trees (*Populus*) occurred near the spring source and, along with willows, were scattered along most of the length of the study section. Plum (*Prunus americana*) grew on the east-facing slope of the hill from which the spring issued.

The bedrock is primarily sandstone with some limestone. The aquatic substrate was predominantly sand and organic silt. In areas of greater current, rubble formed an armor layer over gravel and sand. A clay hardpan occurred a few cm below the substrate surface in these riffle areas. Site 1 rubble samples were taken from a riffle below the convergence of the four main sources. At that point, the rheocrene was approximately 40 cm wide and 12 cm deep with *Berula* and *Rorippa* along the edges.

Site 2 was located on a rubble riffle above the pond about 180 m below Site 1. *Rorippa* grew sparsely along the edges, and some *Ranunculus* occurred in the channel.

Site 3 was located near the west shore of the pond half-way between the inlet and outlet. The substrate consisted of sand-gyttja. Submerged angiosperms, predominantly *Elodea canadensis*, formed dense populations. *Ceratophyllum demersum* and *Myriophyllum exalbescens* were less abundant. A cattail (*Typha latifolia*) marsh occurred at the upper end of the pond below Site 2. *Typha* and other emergents (*Carex*, *Eleocharis*, *Scirpus*) were also present along the edges. *Lemna minor* became abundant at times. The pond has an area of approximately 0.2 ha and a maximum depth of about 2 m.

Site 4 was a rubble riffle immediately below the pond. *Rorippa* was sometimes abundant along the edges, and dense beds of *Elodea* occurred in the channel at times. Other aquatic plants also occurred in lesser numbers.

Site 5 was located on a rubble riffle about 320 m below Site 4. Occasional sprigs of *Ranunculus* were the only higher aquatic plants at this lowermost site.

Methods

The study was conducted year-round from January 1974 through January 1975. Most parameters were sampled about every 28 days; those which were less frequently sampled are so indicated.

Physical and Chemical Parameters

Dissolved oxygen, pH, temperature, and flow were determined in the field. Dissolved oxygen was determined using the azide modification of the Winkler method. The pH was determined with a Hellige color comparator, temperature with a mercury field thermometer. Maximum-minimum thermometers were installed for 24 hours in January, March, June, and October at lotic stations. All thermometers were calibrated at 0 °C in an ice bath. Flow was determined at weirs above and below the pond.

Samples for free and bound CO₂, dissolved and suspended matter, and nitrate-nitrogen were transported to the laboratory in an ice chest. Free and bound CO₂ were determined titrimetrically by the phenolphthalein and methyl orange methods described by PENNAK (1949). Nitrate-nitrogen was determined on a Spectronic-20 Colorimeter (LIND, 1974). Suspended and dissolved matter were determined by filtration through cellulose discs with 0.45 μm apertures, and subsequent evaporation of one-liter water samples (WARD, 1974).

All pond measurements were taken just below the water surface. For the purposes of this study, the pond was considered primarily in relationship to its influence on the rheocrene. Although macroinvertebrates and physicochemical data were collected, no attempt was made to conduct a comprehensive investigation of the pond ecosystem.

Macroinvertebrates

Obtaining an adequate sample without depleting the fauna has been a serious problem in many springbrook studies (THORUP, 1970). The rich fauna of the springbrook in the present study allowed small but adequate samples to be taken about every 28 days without discernible effects on the fauna. At Site 1 macroin-

vertebrate samples were taken from (1) the rubble riffle, (2) watercress beds, (3) moss, and (4) sand. Rubble riffles were sampled with a Surber sampler which enclosed 929 cm² of substrate. At the riffle at Site 1 the sampler occupied virtually the entire stream width. Watercress was sampled by breaking off portions of the plant in the mouth of a net until approximately 100 grams of wet plant material, with contained invertebrates, was obtained. Care was taken to sample portions of plants which were completely submerged yet away from the substrate. Sand was sampled with an Ekman dredge which encloses an area of 232 cm². Emergent moss was sampled by taking three cores, each enclosing 38.5 cm².

Surber samples were taken from rubble riffles at all lotic stations. *Rorippa* and *Elodea* beds were also sampled at Site 4 below the pond. Macroinvertebrate drift was sampled four times during the study (March, June, September, December) to supplement bottom fauna investigations. Drift nets were installed at Sites 2 and 4, above and below the pond, for two hours following sunset and for two hours following sunrise to sample dawn and dusk peaks of drifting invertebrates (WATERS, 1962). Drift nets sampled approximately one-third of the total flow at both sites. Drift nets had apertures of 216 μm ; other netting used for macroinvertebrates had apertures of approximately 700 μm .

Pond benthos were sampled by taking 2 Ekman grab samples in water about 50 cm deep. Because of the dense submerged angiosperms, it was necessary to operate the Ekman grab manually in order to procure samples.

With the exception of a few distinctive Diamesinae, no attempt was made to key chironomids beyond the generic level. Since available keys did not adequately separate *Cricotopus* from *Orthocladius*, these two genera were considered as a complex in the present study.

Following identification and enumeration, the volume of major taxa was determined for each sample by displacement in graduated centrifuge tubes. A centrifuge tube with 0.01 ml graduations (developed for albumin and total protein analysis) was used for small volumes. Biomass (wet weight) was computed by conversion from volumetric measurements based on the conservative assumption of a specific gravity of 1.0. Biomass values of molluscs and trichopterans exclude shells or cases.

Species diversity values are based on the Shannon index with logarithms to base 2 (bits per individual). Equitability values were calculated from the table of LLOYD & GHELARDI (1964).

Zooplankton

Planktonic rotifers and crustaceans were collected from the pond, and from Sites 4 and 5 below the pond throughout the year by pouring ten liters of water through a plankton bucket with mesh apertures of about 50 μm . Identification and enumeration were made in a Sedgwick-Rafter counting cell.

Epilithon

Epilithon, associated epiphytes, and detritus were collected from the upper surfaces of rocks by a timed scraping technique described in WARD (1974). Five-minute samples were collected at all lotic sites except at Site 4 during November—January when the density of algae reduced sampling to two minutes.

The percentage composition of the algal microphyte-detritus component and the algal macrophyte component was determined concurrently using a square pet-

ri dish with a gridded bottom. A Sedgwick-Rafter counting cell was used to estimate the percentage composition of the algal microphytes and detritus. The relative contribution of the algal divisions 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 algal division, except Bacillariophyta.

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 to determine the species and percentage composition.

A Leitz phase contrast microscope and a Leitz orthoplan microscope, equipped with a Nomarski phase interference attachment, were utilized for algal identification.

Each sample (minus diatom subsamples) 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 (AFDW). There is negligible carbonate loss with this procedure (PETERSEN & CUMMINS, 1974).

Results and discussion

Physicochemical Analyses

The major importance of temperature on stream biota has been emphasized by IDE (1935), HYNES (1970), LEHMKUHL (1972), WARD (1974, 1976 a), among others. In addition to absolute values, the temperature pattern may have considerable influence on such things as life cycle phenomena. Aquatic invertebrates of temperate regions often depend on temperature fluctuations as environmental cues as is evidenced by the absence of many species in thermally constant habitats (WARD 1974, 1976 a, 1976 b). Springbrooks exhibit a gradient of decreasing thermal constancy downstream and are thus ideal habitats to study effects of temperature on biota.

Mean temperatures at Sites 1 (source) and 2 were virtually identical although seasonal fluctuations were greater at Site 2 (Table 1). Mean temperatures at the remaining sites, which were influenced by the pond (Site 3), were nearly identical to each other, but were slightly lower and had much greater ranges than the upper sites. Even Site 5, however, exhibited a relatively narrow annual temperature range (2—12 °C).

Diurnal fluctuations are influenced by cloud cover, wind, air temperature, turbidity, development of aquatic and riparian vegetation and other factors (MARTIN, 1972; EDINGTON, 1965; BOON and SHIRES, 1976). Since these factors may change from day to day, the data in Figure 2 are of only comparative value, and not precisely indicative of typical conditions during the months indicated. The pond dampened daily fluctuations in the stream below (Site 4) except during summer, a time of variable surface

Table 1. Physicochemical data¹ for springbrook-pond sampling sites.

Parameter	Sites				
	1 Source	2	3 Pond	4	5
Temperature (°C)	8.9 (8.0—10.0)	9.1 (7.0—11.1)	7.7 (3.0—12.0)	7.5 (3.0—11.1)	7.6 (2.0—12.0)
Free CO ₂ (ppm)	3.7 (2—6)	4.0 (2—8)	4.9 (4—8)	5.7 (4—6)	5.2 (4—8)
Bound CO ₂ (ppm)	29.5 (23.5—37.5)	33.0 (28.5—37.5)	33.4 (25.0—38.0)	37.5 (33.0—45.5)	36.2 (29.0—41.5)
O ₂ (ppm)	6.9 (4.7—9.1)	8.0 (8.4—9.4)	—	8.7 (6.7—10.6)	10.7 (9.0—11.9)
pH (median)	7.7 (7.3—8.0)	7.7 (7.5—7.9)	7.6 (7.4—8.1)	7.4 (7.3—8.1)	7.7 (7.3—8.0)
NO ₃ -N (ppm)	0.21 (0.16—0.29)	0.21 (0.12—0.30)	0.14 (0.06—0.23)	0.15 (0.09—0.21)	0.13 (0.06—0.23)
Flow (m ³ /min)	1.62 (0.78—2.46)	—	—	2.82 (1.32—5.28)	—
Suspended matter (mg/l)	0.9 (0—3.3)	19.0 (5.0—46.1)	6.2 (3.0—12.8)	5.9 (0.1—12.7)	13.4 (6.0—23.0)
L.O.I.	0.2 (0—1.1)	2.8 (0—6.6)	0.6 (0—2.8)	1.0 (0—3.3)	2.3 (0—6.9)
Dissolved matter (mg/l)	115.6 (80—145)	139.3 (116—158)	—	135.7 (100—150)	137.7 (101—153)
L.O.I.	32.5 (26.3—38.3)	38.3 (32.2—44.2)	—	41.6 (33.4—45.9)	41.7 (33.5—52.1)

¹ Annual means, range in parentheses.

temperatures. In English lowland ponds surface water temperatures in summer reached daily maxima which were higher than air temperatures (MARTIN, 1972).

All bound CO₂ means (Table 1) were within the "medium hardness" category of PENNAK (1971), although some within-site temporal variation occurred. The variations were likely a function of changes in flow, but no clear relationship with groundwater discharge was apparent.

Dissolved oxygen values were near or above saturation at all times at Sites 2 and 5. At Site 1, values ranged from 52 to 97% of saturation. Most of the year dissolved oxygen concentrations at the source were above 6.0 ppm. Low values occurred in November and December (4.7 and 4.8 ppm).

At Site 4 below the pond oxygen was normally near saturation, although saturation values of 76 and 77 % occurred in June and July, respectively.

Median pH values were comparable at all sites, varying from 7.3 to 8.1 throughout the study period.

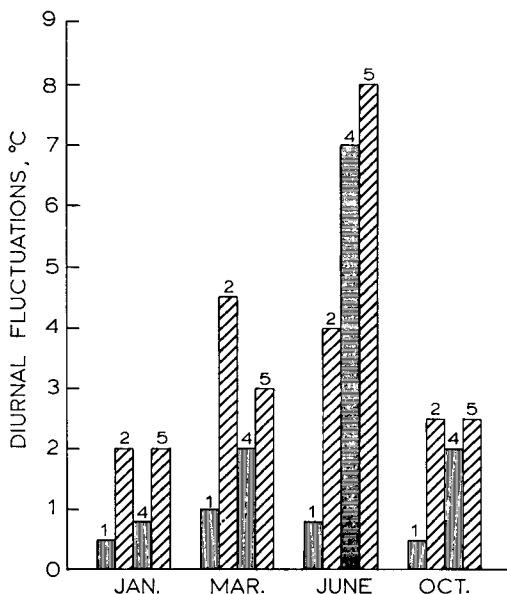


Fig. 2. Diurnal water temperature fluctuations at lotic sites during four seasons.

Nitrate-nitrogen values were comparable at all sites. Temporal variations were relatively slight and exhibited no discernible pattern.

Flow fluctuated somewhat, but was relatively constant compared with streams of this region which are not spring-fed. Additional groundwater entering the pond accounted for the larger discharge at Site 4.

Suspended matter was negligible at Site 1, increased at Site 2, was reduced by clarification at the pond and again increased at Site 5. The average percentage of total suspended matter lost on ignition ranged from 10—18 %.

Total dissolved matter was lowest at the source (115.6 mg/l) with slightly higher values, similar to each other, at the other stream sites. The average loss on ignition values ranged from 28 to 31 %.

Zooplankton

Zooplankton were collected about every 28 days to assess the trophic contribution of pond plankton to downstream reaches. Annual mean

density was 164 zooplankters/l in the pond, but only 37 and 10 zooplankters per liter were collected at Sites 4 and 5, respectively.

Several workers (e. g. CHANDLER, 1937; MÜLLER, 1956; RUTTNER, 1956; WARD, 1975 a) have investigated the downstream fate of lentic zooplankton. In all cases, rapid declines occurred downstream. Zooplankters, especially late instars of crustaceans, have been shown to avoid lake outflows (BROOK & WOODWARD, 1956), which likely accounts for the lower numbers at Site 4 than in the pond.

Simocephalus and *Chydorus* comprised the majority of the cladocerans which averaged 18 individuals/l in the pond. Site 4 samples contained only one-third the number of cladocerans found in the pond, Site 5 contained only 6 %.

The density of copepodid and adult cyclopoid copepods averaged 24/l in the pond. Only 4 % and 2 % remained at Sites 4 and 5, respectively. Nauplii density averaged 76/l in the pond, 17 % and 5 % of which remained at Sites 4 and 5, respectively.

A total of seven genera of rotifers was collected from the pond. *Notholca* was by far the most numerous. Rotifers averaged 45 individuals/l in the pond; 38 % remained at Site 4, 11 % at Site 5.

The relationships between seasonal abundance of zooplankton and filter-feeding invertebrates will be considered in a later section.

Epilithon

The term "epilithon" in a broad sense includes epilithic algae, associated epiphytes, and detritus.

Four algal divisions comprised the epilithic algae: Bacillariophyta, Chlorophyta, Cyanophyta, and Rhodophyta. The epiphytic algae belonged to Bacillariophyta, Chlorophyta, and Cyanophyta. Two genera of Euglenophyta were also recorded. Detritus and three divisions of algae (Bacillariophyta, Chlorophyta, and Cyanophyta) comprised the majority of the material collected (Figs. 3—6).

Bacillariophyta. The division Bacillariophyta was represented by 29 genera with 88 species (Appendix A). Diatoms exhibited maximum relative abundance during May at all sites. A spring diatom pulse is typical of temperate streams (HYNES, 1970).

Similar numbers of species of diatoms were found at Site 1 (55) and Site 2 (57) above the pond, and at Site 5 (52) the most downstream location. The greater number of species at Site 4 (69) was primarily due to the presence of lentic forms from the pond.

Diatoms were the predominant algae during late winter and early spring at Site 1 (Fig. 3). The spring source contained many of the species

ROUND (1973) listed as typical cold spring flora. *Fragilaria construens* was found only at Site 1; several other diatoms were collected only from Sites 1 and 2. *Achnanthes minutissima*, *A. lanceolata*, and *Navicula cryptocephala* were collected at all lotic sites.

Achnanthes spp., *Diatoma hiemale* var. *mesodon*, and *Cymbella* spp. were the predominant diatoms at the spring source (Fig. 7). The predominance of *Achnanthes* spp. throughout the year in springs has also been reported by other investigators (ROUND, 1973; SHERMAN and PHINNEY, 1971). *A. minutissima*, the most abundant *Achnanthes* species at Site 1, was also the most frequently collected diatom at Metolius Springs (SHERMAN and PHINNEY, 1971).

While *Cymbella* and *Achnanthes* exhibited maximum abundance during winter and spring, *Diatoma hiemale* var. *mesodon* was most prevalent in summer at Site 1 (Fig. 7). *D. hiemale* was present at other sites during the summer months, but was never as abundant as at Site 1.

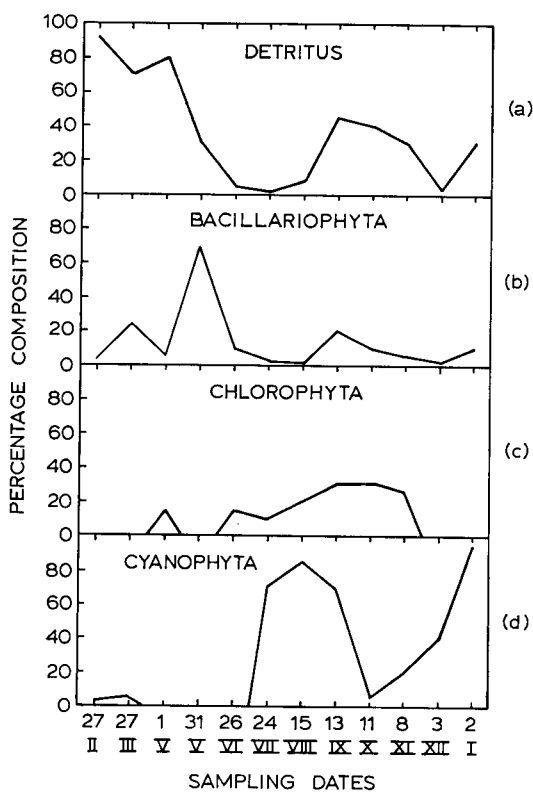


Fig. 3. Seasonal changes in the percentage composition of major epilithon components at Site 1.

At Site 2 diatoms were less abundant than other algae (Fig. 4). *Achnanthes* spp., *Cymbella* spp. and *Nitzschia amphibia* were the predominant epilithic taxa throughout the year. The *A. lanceolata* maximum (8 November) was very similar to the time of its peak occurrence at Site 1. *A. minutissima* was most prevalent in the diatom community in autumn at Site 2, whereas at Site 1 a spring maximum was observed. *Cocconeis placentula*, a member of the epilithon which also occurred as an epiphyte on *Cladophora glomerata*, exhibited peak relative abundance values in January, February, and March.

Diatoms at Site 4 below the pond never comprised the major portion of the epilithon (Fig. 5). The *Achnanthes/Cymbella* complex was not as abundant throughout the year as at Sites 1 and 2, although combined they comprised 59%, 64%, and 52% of the diatom flora during February, March, and September, respectively. *Achnanthes minutissima* was the dominant species of that genus and was present during most of the year, reaching

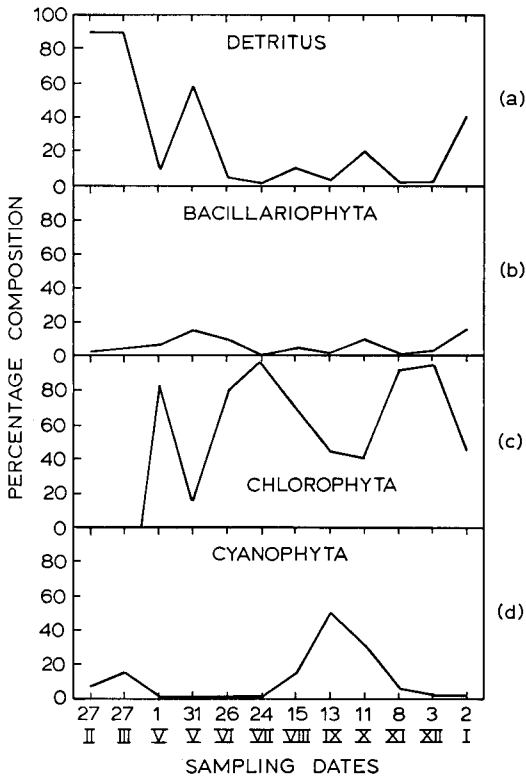


Fig. 4. Seasonal changes in the percentage composition of major epilithon components at Site 2.

a maximum in October. *Cymbella minuta* and *C. pusilla* were the major components of the *Cymbella* group. *Cymbella minuta* reached maximum relative abundance in February (49% of diatoms), as at Site 1. *C. pusilla* peaked in late May when it comprised 40% of the diatoms.

Nitzschia amphibia was the predominant diatom during most of the May through August period at Site 4. *Cocconeis placentula*, a cold-water form, was most prevalent during November, December, and January. The majority of the *Cocconeis* populations were epiphytic on *Cladophora glomerata*. *Rhoicosphenia curvata*, found only at Site 4, also had its greatest development as an epiphyte on *Cladophora glomerata*. This diatom was most numerous during December and January at which time *Cladophora* was also most abundant.

The *Achnanthes/Cymbella* complex was not as abundant in the total Bacillariophyta flora at Site 5 as at the other sites. However, major peaks in abundance were similar to Site 4. *Achnanthes minutissima* was the

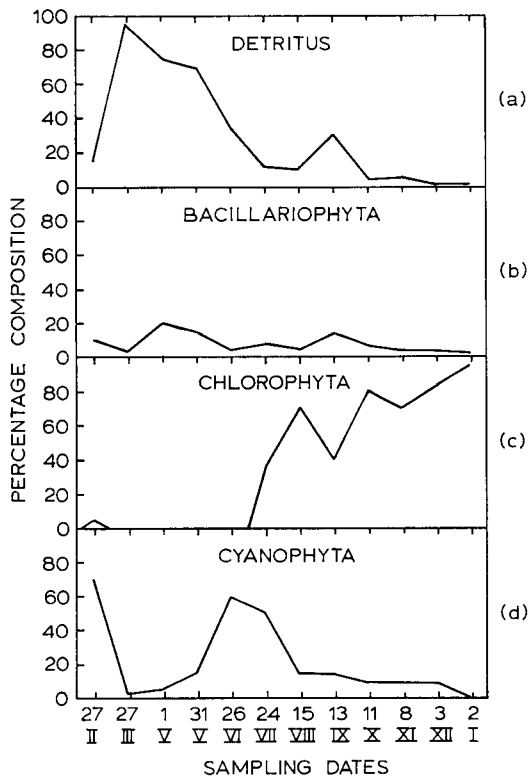


Fig. 5. Seasonal changes in the percentage composition of major epilithon components at Site 4.

dominant *Achnanthes* present as at all lotic sites. At Site 5, *Nitzschia amphibia* did not rank as high in the summer diatom flora as at Site 4. This alga reached maximum relative abundance in late March. *Cocconeis placentula* displayed a marked seasonal fluctuation at Site 5 with greatest development during the winter months. The dominance of this genus in the diatom flora corresponded to the dominance of *Cladophora* in the total algal community.

Chlorophyta. Chlorophytes were present throughout most of the year and at times comprised over 90% of the total algae (Figs. 3—6). The Chlorophyta formed the major portion of the total epilithon at all locations except Site 1 (annual means of 55%, 40%, and 45% at Sites 2, 4, and 5, respectively). At Site 1 green algae comprised 12% of the total epilithon. Chlorophytes present at lotic sites included *Characium*, *Chaetophora*, *Cladophora*, *Microspora*, *Oedogonium*, *Spirogyra*, *Stigeoclonium*, *Ulothrix*, and *Zygnema*.

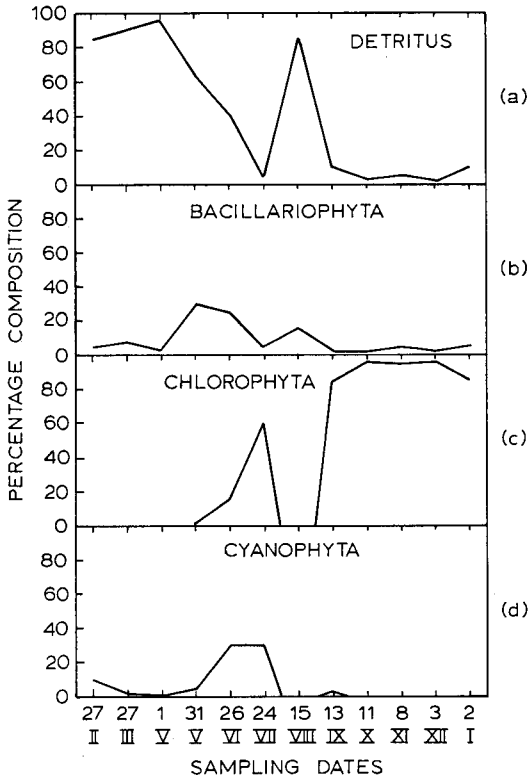


Fig. 6. Seasonal changes in the percentage composition of major epilithon components at Site 5.

Cladophora glomerata was the most numerous and widespread of the green algae. BLUM (1956) suggested that *C. glomerata* is the most abundant alga in lotic environments throughout the world. This alga was collected at all the sites and during all months except February and March. Many times throughout the year, *Cladophora* formed between 90—99 % of the green algae at a given site. At Site 1, its greatest development occurred during October and November. This alga represented 99+ % of the green algae present at Site 2 from 31 May through January, except December when *Oedogonium* comprised 90 % of the green algae. *Cladophora* was present at Site 4 from July through January with maximum development from November through January. It was collected at Site 5 from June through January (except August) with maximum development from October to December. However, *Cladophora* populations at Site 5 were never as extensive as at Site 4 immediately below the pond.

Ulothrix zonata, which occurred at all sites, reached maximum development at Site 1 during September when it comprised 90 % of the

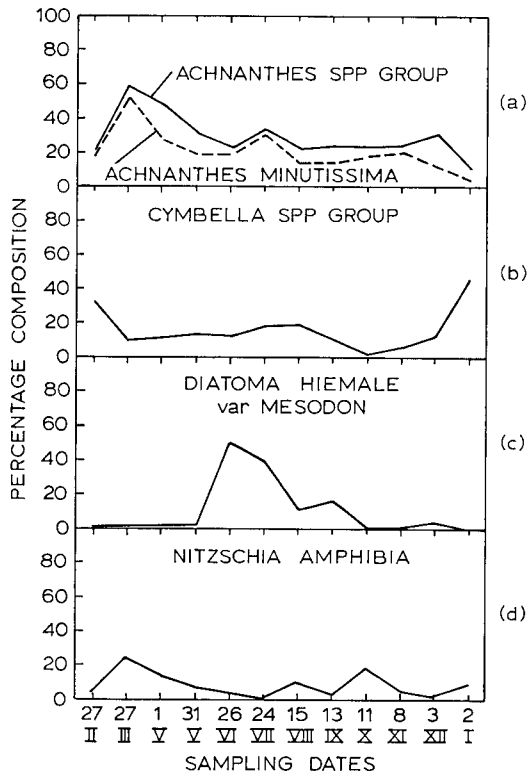


Fig. 7. Relative seasonal abundance of predominant diatoms at Site 1.

chlorophytes. BLUM (1956) indicated that *U. zonata* is a cold-water form. Rather than displaying a spring and summer pattern as described by SHERMAN & PHINNEY (1971), *U. zonata* exhibited fall and winter maxima in the present study.

The only other green alga which developed a large population was *Spirogyra*, which formed 70% of the green algal component at Site 4 during September. *Characium* was an epiphyte on *C. glomerata* during August and September at Site 4.

Cyanophyta. The blue-green algae exhibited marked seasonal fluctuations with peaks occurring in June, July, September, December, and February at various sites (Figs. 3—6). The abundance of blue-green algae at Site 2 during September and October was due to *Nostoc* colonies which comprised 99% of the cyanophyte flora.

Nine genera of blue-green algae were identified during the study period. *Anabaena* was present at all sites but never was numerous. *Chamaesiphon incrustans* was an epiphyte on *Cladophora glomerata*. *Gloetrichia* comprised 90% of the cyanophycean standing crop at Site 1 in November and 99% at Site 2 in August. *Oscillatoria princeps* was the predominant blue-green alga at Site 1. Cyanophytes comprised the majority of the epilithon at Site 1 on several dates at which time *O. princeps* comprised 90% or more of the blue-green algae. *Phormidium* was found at all sites with greatest development occurring at Site 4. Other genera were numerically unimportant.

Euglenophyta. Euglenophyta was represented by only two genera: *Euglena* and *Phacus*. *Euglena* may form an epiphytic association with *Cladophora* (WHITTON, 1970); *Phacus* was probably a lentic form carried downstream from the pond.

Rhodophyta. The only representative of the division Rhodophyta was *Batrachospermum monoliforme*. This red alga has been associated with springs and spring-fed streams (ROUND, 1973; RIDER & WAGNER, 1972; YOSHIDA 1959). Only the *chantransia*-stage was collected during the present study; the gametophytes were not observed. The *chantransia*-stage, however, is perennial (RIDER & WAGNER, 1972), and plants were heavily monosporic on 30 May and 27 June. Since the monospores germinate into the *chantransia*-stage and fragmentation of the filaments has not been recorded in natural populations (YOSHIDA, 1959), monospore production is probably the means by which this alga maintains itself in the study stream. *Batrachospermum* was never a major component of the periphyton and was found only at Site 2. On 26 June the *Batrachospermum* mats supported a large epiphytic diatom community. *Diatoma vulgare* (73%) and *D. hiemale*

var. *mesodon* (15 %) comprised the majority of the epiphytic diatoms. The growth habit of both of these diatoms was a long chain of cells intermeshed with the *chantransia*-stage filaments and attached to these filaments at one end of the chain.

Epilithon Standing Crop

There was a general increase in epilithon standing crop from February into the summer months (Table 2, monthly means). The values dropped during late summer and autumn, then increased dramatically, reaching annual maxima in late autumn and winter. This latter increase was due to the presence of extensive *Cladophora* populations at Site 4. Filamentous chlorophytes often develop dense populations in the streams immediately below standing water (WARD, 1974). The comparatively high value for July was the result of the large *Oscillatoria princeps* population at Site 1. Biomass maxima occurred during the summer at Sites 1 and 2 above the pond, and in autumn and winter at the two downstream locations.

Table 2. Epilithon standing crop for the springbrook system.

Date	mg ash-free dry weight per 5-minute sample				
	Site 1	Site 2	Site 4	Site 5	Mean Monthly
27 II	4.8	1.8	8.7	6.3	5.4
27 III	8.2	5.0	3.9	9.2	6.6
1 V	9.2	26.5	8.9	0.8	11.4
31 V	14.9	4.5	11.7	5.1	9.0
25 VI	69.3	7.8	24.6	11.8	28.4
24 VII	305.3	4.6	26.8	19.2	89.0
15 VIII	26.0	17.1	58.7	0.1	25.5
13 IX	2.9	32.4	8.3	8.5	13.0
11 X	13.6	4.5	50.5	4.3	18.2
8 XI	14.5	15.2	664.8 ¹	23.7	179.5
3 XII	24.8	16.6	526.3 ¹	4.7	143.1
2 I	2.1	2.0	1086.8 ¹	6.7	274.4
Annual Mean	41.3	11.5	204.4	8.4	—

¹ Values obtained by multiplying 2-minute samples by 2.5.

The increase in ash-free dry weight (AFDW) from winter to summer cannot be solely attributed to an increase in water temperature. At Site 1 the temperature ranged from only 8—10 °C (Table 1), not a large enough fluctuation to explain the almost 7-fold increase in AFDW from February to June. Dissolved oxygen was lowest in November and December, but the

December AFDW was comparable to the August value (Table 2). None of the other variables which were recorded can be positively correlated with the seasonal fluctuations of the algal standing crop at Site 1. Light therefore appears to be a major factor controlling seasonal fluctuations at the spring source, an observation also supported by data from Metolius Springs (SHERMAN & PHINNEY, 1971). The influence of endogenous rhythms cannot, however, be discounted (HYNES, 1970). At downstream sites temperature exhibited more marked seasonal fluctuations which undoubtedly influenced seasonal changes in epilithon composition and biomass.

The spring source (Site 1) and Site 4 below the pond exhibited annual mean biomass values which are within the range found in unregulated mountain streams in Colorado (WARD, 1976 b). Epilithon biomass means at Sites 2 and 5 were considerably lower (Table 2). The higher value at Site 1 than at Site 2 was due to the large July *Oscillatoria princeps* populations, and to a greater standing crop of detritus.

Detritus formed the major portion of the "epilithon" over much of the year (Figs. 3—6). Low relative values during summer or autumn normally corresponded to increases in green or blue-green algae.

The high annual mean AFDW value at Site 4 was largely a result of the great development of *Cladophora glomerata* from November to January. The much lower epilithon biomass at Site 5 resulted primarily from the absence of a *Cladophora* "bloom." Chlorophytes comprised very similar proportions of the total epilithon at Site 4 (40 %) and at Site 5 (43 %). Cyanophytes, however, exhibited a three-fold greater relative abundance at Site 4 than at Site 5.

Macroinvertebrates

A summary of abundance and diversity data for the pond and for rubble riffles at lotic sites is presented in Table 3. Standing crop was much higher in the pond and at Site 4 below the pond than at other locations,

Table 3. Summary of macroinvertebrate parameters from rubble riffles and the pond.

Parameter	Sites				
	1 Source	2	3 Pond	4	5
Org/m ²	2512	1761	12,091	4120	1685
g/m ² (wet wt.)	48.3	56.4	103.2	136.9	34.7
Shannon index	1.8	2.7	3.0	3.7	3.5
Equitability	0.1	0.3	0.4	0.5	0.4

whereas Sites 1, 2, and 5 exhibited similar but lower values. Pelecypods, gastropods, oligochaetes, and leeches were responsible for the large standing crop (12,091 organisms and 103.2 g per m²) in the pond. *Baetis*, *Dugesia*, and gastropods comprised the majority of the fauna by numbers at Site 4, whereas by biomass *Tipula*, trichopterans, and gastropods were the most important. Values at lotic sites are similar to average numbers of organisms per m² of bottom reported by DUDLEY (1953) for four Colorado springbrooks.

The annual mean epilithon biomass values at lotic sites corresponded closely to the longitudinal pattern of macroinvertebrate abundance (Fig. 8).

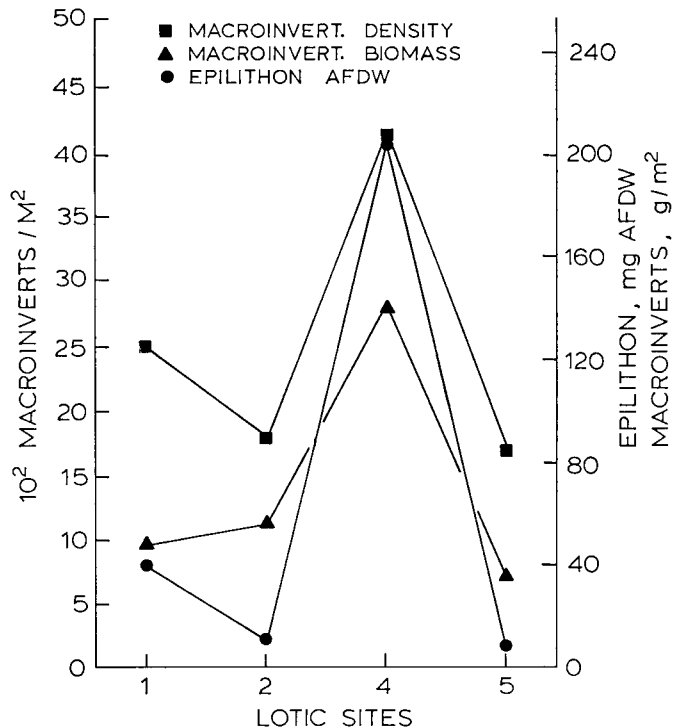


Fig. 8. Relationship between annual mean biomass of epilithon (per 5-minute sample) and macroinvertebrate abundance at lotic sites.

A close relationship between the abundance of algae and the total macroinvertebrate fauna is not normally apparent in streams (PENNAK, 1977), and, in fact, an inverse relationship may occur (HYNES, 1970). The relatively constant environment of the springbrook reduces the number of variables which might differentially affect algae and macroinvertebrates, although it is not clear whether this is a causal relationship or whether the

same conditions favor both groups. The inclusion of associated fine detritus in the "epilithon" totals would strengthen any trophic relationship with the invertebrate fauna.

Diversity and equitability exhibited a general downstream increase (Table 3). Shannon index values between 3.0 and 4.0 (WILHM, 1970) and equitability values greater than 0.5 (WEBER, 1973) characterize the macroinvertebrate communities in relatively natural streams. Diversity and equitability at the upper two sites indicate stressed communities. Site 1 exhibited especially low values. Reduced species diversity at the sources of springs has been reported by IDE (1935), SLOAN (1956), MINCKLEY (1963), and MINSHALL (1968), among others. MINSHALL (1968) found low diversity associated with large numbers of individuals at the source of woodland springbrook. The thermal conditions (temperature constancy, winter warm and summer cool conditions) of spring sources resemble the temperature regime below deep release dams, which has been postulated as responsible for the stressed macroinvertebrate communities of the receiving stream (WARD, 1974, 1976 a). Site 1 exhibited a seasonal range of only 2 °C (Table 1) and diurnal fluctuations of 1 °C or less (Fig. 2). SWEENEY (1976) reported reduced growth in certain stream organisms when exposed to constant temperatures. Such species would be at a competitive disadvantage near a springbrook source (WARD, 1976 a). Lethal and sublethal effects of constant thermal conditions on stream benthos have been dealt with in detail elsewhere and will not be elaborated here (WARD, 1976 a; LEHMKUHL, 1972). See WARD (1976 a, Fig. 2) for a conceptual model relating various thermal regimes to macroinvertebrate diversity. Suffice it to say that many temperate stream organisms are unable to complete their life cycles under constant thermal conditions, or are at a competitive disadvantage.

There are also other explanations for the low species diversity at spring sources. The absence of transport detritus from upper reaches limits the diversity and quantity of available food (also analogous to the situation below dams). Much of the species diversity in natural streams may be attributable to unpredictable temporal variations in environmental conditions which allow a relatively high degree of niche overlap (PATRICK, 1970). The constant conditions of springbrooks likely reduce niche overlap and community diversity, but allow the buildup of large populations of species able to tolerate such environments. In addition, year-round growth is possible for cold stenotherms.

Less-than-saturated dissolved oxygen values may have prevented some species from occurring at Site 1, but this is unlikely, since concentrations were above 6.0 ppm most of the year, and a substantial current was always present.

Macroinvertebrate Composition

In this section, a general discussion of the macroinvertebrate composition of different sites will be followed by a more specific discussion of common taxa. A total of 101 taxa from 46 families were collected during the study. Four taxa were collected only in drift samples. Insects comprised the majority of the fauna at most locations and on most substrata except the pond and Site 4 below the pond where molluscs, oligochaetes, and planarians were abundant.

The total number of taxa collected from rubble riffles increased only slightly downstream (Table 4). However, despite a relatively large number

Table 4. Number of taxa collected from the pond and rubble riffles at lotic sites.

Taxon	Sites				
	1	2	3 (Pond)	4	5
Ephemeroptera	1	1	1	5	6
Plecoptera	2	1	0	2	1
Trichoptera	3	4	1	4	8
Diptera	17	13	8	12	12
Odonata	1	2	1	0	1
Hemiptera	0	0	1	1	1
Coleoptera	2	5	3	3	2
Gastropoda	4	3	4	4	5
Pelecypoda	1	2	2	1	1
Hirudinea	0	1	2	1	1
Tricladida	1	1	1	1	1
Amphipoda	1	1	1	1	1
Oligochaeta	3	2	2	3	3
Total	36	36	27	38	43

of taxa on rubble riffles above the pond, most species were rare and one or two species comprised the vast majority of the total organisms (Fig. 9). This was especially evident at Site 1 where the most abundant species [*Baëtis tricaudatus*(?)] comprised over 70% of the total organisms. Several dipterans (e. g., Empididae) were restricted to the source and, although rare, comprised an appreciable percentage of the total taxa on rubble at Site 1 (Table 4). At Sites 4 and 5 below the pond the two most abundant species comprised less than half of the total organisms. The pond (Site 3) contained fewer total species than lotic sites.

Some general differences are noted between macroinvertebrates on different substrata at the same site (Table 5). Care must be exercised when comparing density and biomass data, since rubble and sand values are

areal based, whereas macroinvertebrates on plants are related to the volume of plant tissue (see table legend).

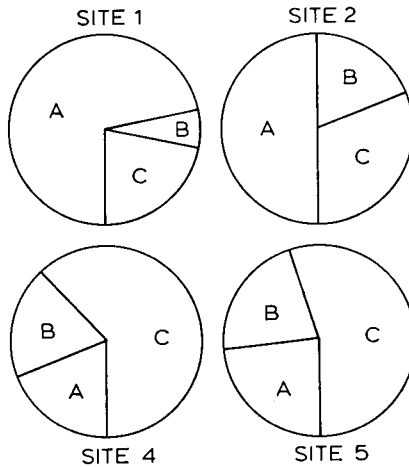


Fig. 9. The percentage of the total macroinvertebrate fauna comprised by the most abundant species (A), the next most abundant (B), and all the remaining species (C).

Table 5. Number of taxa and abundance of macroinvertebrates collected from various substrata at Sites 1 and 4. Density and biomass (wet weight) values are per m² rubble and sand; per 1,000 ml of plant tissue for moss, *Rorippa*, and *Elodea*.

Taxon	Site 1				Site 4	
	Rubble	Sand	<i>Rorippa</i>	Moss	Rubble	<i>Elodea</i> / <i>Rorippa</i>
Ephemeroptera	1	1	2	1	5	2
Plecoptera	2	0	1	1	2	0
Trichoptera	3	1	2	2	4	2
Diptera	17	16	6	16	12	11
Odonata	1	0	3	0	0	1
Hemiptera	0	0	0	0	1	2
Coleoptera	2	1	3	7	3	3
Gastropoda	4	2	2	1	4	4
Pelecypoda	1	1	1	1	1	0
Hirudinea	0	0	0	0	1	0
Tricladida	1	1	1	1	1	1
Amphipoda	1	1	1	0	1	1
Oligochaeta	3	3	1	2	3	0
Total Taxa	36	27	23	32	38	27
Density	2512	2569	1549	2316	4120	2155
Biomass	48.3	12.3	11.8	10.3	136.9	20.6

At Site 4 watercress was sampled from the beginning of the study through early May. From late May to mid-August aquatic plants were too sparse to sample. *Elodea* beds were sampled in September and October. In November watercress again became abundant and was sampled for the remainder of the study. Despite the fact that *Elodea* beds were sampled only twice at Site 4 versus seven times for *Rorippa*, their macroinvertebrate fauna was very similar. Since most differences were based on rare occurrences of a few species, macroinvertebrates collected from *Rorippa* and *Elodea* at Site 4 are combined in Table 5.

While macroinvertebrate density values were similar on rubble and sand at Site 1, biomass was three times greater on rubble. This is due to the predominance of small organisms (chironomids and oligochaetes) in sand. Macroinvertebrates on watercress and moss exhibited similar biomass values at Site 1, although somewhat higher densities occurred on moss. Macroinvertebrate density values on plants at Site 4 were comparable to Site 1. Biomass was greater at Site 4 primarily due to the large numbers of gastropods below the pond. Macroinvertebrate standing crop on rubble below the pond was much higher than at Site 1, partly due to the contribution of organisms from the pond by drift.

Rubble contained the largest number of total taxa. Watercress at Site 1 contained the fewest macroinvertebrate taxa, primarily a result of the low diversity of dipterans.

The percentage composition of major taxa at various sites and on various substrata is presented in Fig. 10.

Ephemeroptera. A total of nine genera of mayflies was collected during the study. *Baëtis tricaudatus*(?) occurred at all locations, except the pond, and was collected from all substrata. *Baëtis* was the only mayfly at Sites 1 and 2, except for a few *Callibaëtis nigrinus* collected from watercress near the source. *Baëtis* was the most abundant organism on rubble at all sites and on watercress at Site 1. In Rold Kilde, a Danish spring, *Baëtis rhodani* was the most abundant organism on stony bottom (THORUP & LINDEGAARD, 1977). *Baëtis* was most abundant on rubble in North St. Vrain Creek, Colorado, but also occurred on all other substrata studied (WARD, 1975 b). *Baëtis* is a most ubiquitous genus occurring in extreme habitats unoccupied by other mayflies (EDMUNDS, JENSEN & BERNER, 1976).

Callibaëtis nigrinus was the sole mayfly in the pond. Single specimens were collected from rubble at Sites 4 and 5; a few individuals colonized watercress at the source and at Site 4 below the pond.

Heptagenia sp. was the only other mayfly of any abundance and it was restricted to Site 5. The remaining mayflies were collected in small numbers (single specimens in some cases) only on rubble at Sites 4 and 5.

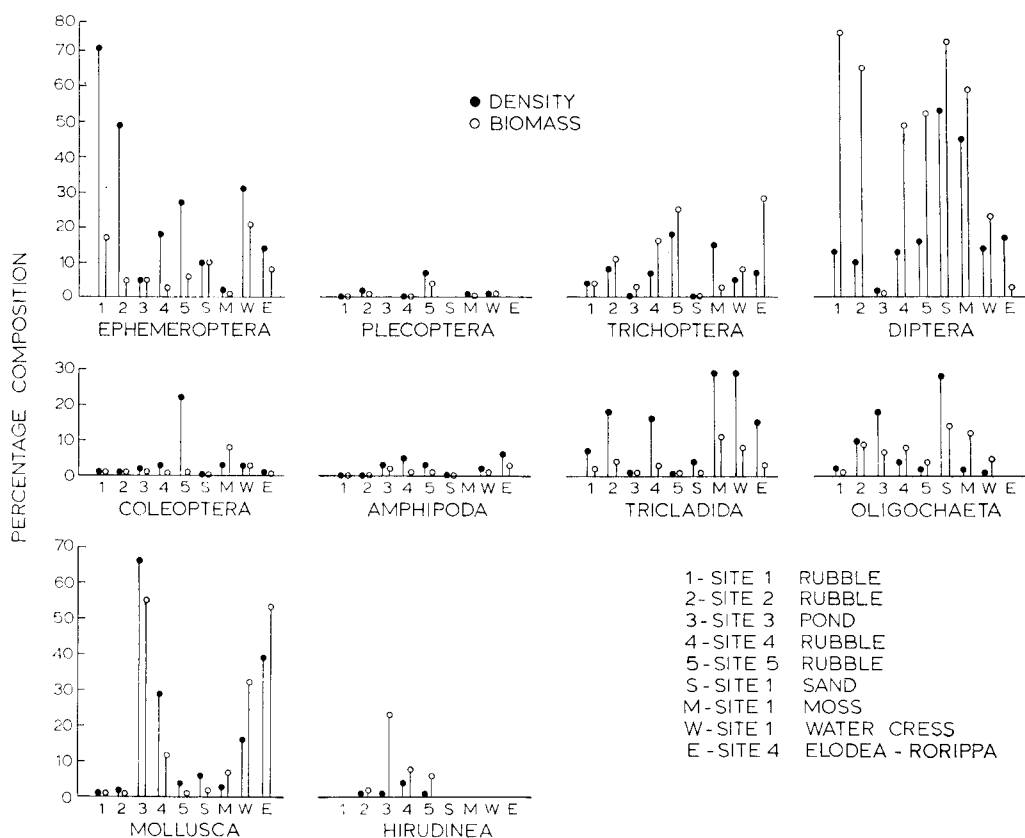


Fig. 10. Percentage composition (annual means) of major taxa at various sites on various substrata.

Heptageniidae, *Ephemerella inermis*, and *Tricorythodes* were restricted to the lowest site.

Ephemeropterans were numerically the most important group at Sites 1, 2, and 5 on rubble and on watercress at Site 1 (Fig. 10). *Baëtis* comprised 71% of the total fauna on rubble at Site 1.

Plecoptera. Only two genera of stoneflies were collected. None occurred in the pond or on sand at Site 1. Although *Amphinemura* sp. occurred on watercress and moss at the source, no stoneflies were found in plant beds at Site 4. *Isoperla patricia* occurred on rubble at all lotic stations. Plecopterans comprised only a minor portion of the macroinvertebrates in the study section (Fig. 10). Greatest abundance occurred at Site 5 where *I. patricia* comprised 4% and 7% of the total fauna by biomass and density, respectively.

Trichoptera. A total of eight genera of caddisflies was found in the study section. Due to difficulties in separating larval limnephilids (even at the generic level), immatures from each site were placed in rearing chambers. Rearing was successful except with pond specimens. Immatures from the pond were identified as *Hesperophylax*, although a species designation was not possible. *Hesperophylax incisus* occurred at all stream sites. *Hesperophylax* occurred on all substrata except sand. *Limnephilus frijole* only occurred at Site 5 (based on identification of adults and pupae) where it was found with *H. incisus*. Since it was not possible to separate larvae with certainty, the two genera are considered together (*Hesperophylax/Limnephilus*) for purposes of diversity calculations; in distribution data, it is assumed that *Limnephilus* occurred only at Site 5. *Hydroptila* sp. occurred on all substrata and at all locations except the pond. It was the only caddisfly which occurred on sand. *Hydroptila* developed large populations on moss and along with *Hesperophylax* was the only trichopteran to colonize plant beds. *Hydropsyche* sp. occurred rarely at Site 2 and was most abundant at Site 5. *Hydropsyche* was displaced by *Cheumatopsyche* below the pond, but both genera occurred at Site 5. A similar distribution of the two genera occurred below a surface-release reservoir in central Colorado (WARD & SHORT, 1978). Downstream drift of seston undoubtedly accounts for the abundance of hydropsychids at sites below the pond. There was a general downstream increase in the number of taxa of trichopterans (Table 4); all genera found in the study section occurred at Site 5. Caddisflies reached their greatest relative abundance at Sites 4 and 5 (Fig. 10), primarily due to *Hesperophylax/Limnephilus* and hydropsychids.

Diptera. More kinds of dipterans were collected than any other major group (Table 5). A total of 46 taxa was identified during the study. The family Chironomidae accounted for 19 taxa; nine different tipulids were identified; specimens from ten other families were collected. The most diverse dipteran assemblage occurred on rubble at Site 1 (17 taxa). A total of 16 taxa was collected from sand (primarily chironomidae) and from moss.

Dipterans comprised the majority of the total macroinvertebrate biomass on rubble at all locations (Fig. 10). They comprised the majority of biomass and density on sand and moss. Their paucity in the pond is surprising.

Four species of *Simulium* were identified (from pupae), all of which occurred sympatrically at Site 5. Black flies were most abundant on rubble at Site 4, likely due to contributions of seston from the pond. THORUP (1974) found a successive distribution of species of Simuliidae downstream

from the source of a Danish springbrook. In the present study, *S. latipes* was the only species identified at Site 1. At Site 4 below the pond *S. nr vittatum* was the only species found. At Site 5 the above two species were rare, the predominant simuliid being *S. hunteri*.

Nine tipulids were identified during the study. *Tipula* sp. A was collected from all sites and substrata except the pond. Other taxa were generally rare and restricted in distribution. *Limonia* was restricted to moss at Site 1 where it occurred in large numbers. No tipulids were found in the pond. Tipulids comprised the majority of the dipteran biomass (nearly 100% on rubble) at all sites except the pond and on all substrata except plants below the pond.

A total of 19 chironomid genera was collected, including *Odontomesa fulva* which was found only in drift samples. The greatest number of taxa occurred in the pond, on rubble and plants below the pond, and in sand. Sand contained dense populations of *Prodiamesa olivacea* which was found no where else. *Pseudodiamesa pertinax* was restricted to Site 4 where large numbers were collected from aquatic plants. Diamesinae are characteristically cold stenotherms usually restricted to much higher elevations in Colorado.

Tanypodinae were represented by two genera; only *Procladius* occurred in any numbers and only in sand where it was the second most abundant organism.

Orthocladiinae occurred at all sites and colonized all substrata examined. The *Cricotopus/Orthocladius* complex was the most numerous.

A total of six genera of the subfamily Chironominae was identified. Chironominae were absent or rare except in the pond and in sand at Site 1. *Chironomus* was restricted to the pond.

Dipterans from nine other families were collected, most of them in small numbers. The stratiomyiid *Euparyphus* was the second most abundant organism on moss at Site 1.

O d o n a t a. A few specimens of four genera of the zygopteran family Coenagrionidae were collected. The only one of numerical importance was *Ischnura* which exhibited an annual mean of 232 org/m² in the pond.

H e m i p t e r a. Hemipterans (*Hesperocorixa* and *Notonecta*) were not found on any substrata above the pond and were numerically insignificant at other locations. Even in the pond they constituted less than 1% of the density or biomass of the macroinvertebrates. However, their low representation may be due in part to avoidance of sampling equipment.

C o l e o p t e r a. A diverse assemblage of larval and adult beetles from six families was collected. With the exception of a single specimen, elmid

beetles (*Optioservus*) were restricted to rubble at Sites 4 and 5. *Optioservus* was second in abundance to *Baetis* at the most downstream site. The most diverse coleopteran assemblage occurred on moss (Table 5). The dytiscid *Deronectes* exhibited an annual mean of 189 org/m² in the pond. Coleopterans were relatively unimportant except at Site 5 and on moss (Fig. 10).

Mollusca. A total of five species of snails and one genus of fingernail clam (*Pisidium*) was collected in the study section. *Pisidium* was collected at all sites and from most substrata. *Pisidium* was the most abundant organism in the pond, comprising 40 % of the total fauna. Mean annual density was 3,751 org/m².

Physa occurred at all sites and on all substrata examined, and was the only snail collected from moss. It was the second most abundant organism in the pond and on rubble at Site 4. At least one species of *Lymnaea* occurred at all sites and on all substrata except moss. *Gyraulus* was generally restricted to the pond and Site 4 below the pond. In the pond gastropods were the most abundant major taxon, comprising 35 % and 39 % of the fauna by density and biomass, respectively. Gastropods also constituted the majority of the macroinvertebrate numbers at Site 4 below the pond. The abundance of snails in springbrooks is quite different from the situation in mountain streams in Colorado, which are generally devoid of gastropods due to rapid and fluctuating current, soft water, and the absence of rooted aquatic plants.

Mollusca in toto clearly dominated the fauna of the pond and plant beds below the pond. They were also the most abundant organisms on rubble at Site 4 and they constituted the majority of the biomass on watercress at Site 1.

Hirudinea. *Erpobdella punctata* and *Helobdella stagnalis* were the only leeches collected. Both species are widespread in Colorado, occurring in lentic and lotic waters, including springbrooks (HERRMANN, 1970). *H. stagnalis* was restricted to the pond; *E. punctata* occurred at all sites except the source and developed the largest populations at the pond and Site 4. Despite the maximum density below the pond, no specimens were collected in plant beds, which thus provided a refuge for the snails upon which they prey.

Tricladida. *Dugesia dorotocephala* was the only planarian collected and it occurred at all sites on all substrata examined. *D. dorotocephala* was the second most abundant organism on rubble at Sites 1 and 2 and on watercress at the source and Site 4. It was the most abundant species on moss. THORUP & LINDEGAARD (1977) list

D. gonocephala as the most abundant organism on submerged macrophytes, but on emergent mosses it comprised less than 1 % of the total fauna.

A m p h i p o d a. *Hyalella azteca* was the only amphipod found, and it was collected from all sites and all substrata except moss. This was surprising since amphipods (*Gammarus pulex*) were the most abundant organism on emergent moss in a Danish spring, and moss provided an especially important microhabitat for young amphipods (THORUP & LINDEGAARD, 1977). Although amphipods may be the most abundant organisms in springbrooks in eastern North America, *H. azteca* comprised less than 5 % of the fauna except at Site 4 where the greatest numbers were found in plant beds.

While no other amphipods were collected during the present study, in September 1977 several subterranean amphipods were collected from the source which are similar to those recently described from a nearby spring (WARD, 1977). Their taxonomic status is being investigated.

O l i g o c h a e t a. Members of three families of oligochaetes were collected. The Naididae *Pristina* occurred at all sites, being most abundant in the pond and on sand at the source. It was the most abundant organism on sand and with chironomids constituted 70 % of the fauna. Tubificids were essentially restricted to the pond where they were second to molluscs in numerical abundance.

The large lumbricid earthworm, *Eiseniella tetraedra*, occurred at all lotic sites and on all substrata except plant beds at Site 4. Largest numbers occurred on rubble below the pond. This amphibious species is found in mud banks of Colorado mountain streams, but permanent aquatic populations (not accidentals swept in by high water) are apparently restricted to lotic reaches with reduced flow fluctuations (WARD, 1975 b, 1976 b).

Table 6 summarizes the distribution of common genera which occur in one or more of the categories indicated. Rare taxa are excluded since the chances of finding them at only one site or on only one substratum are disproportionately high. Therefore, there is not a category for genera restricted to the pond even though three (*Chironomus*, *Chrysops*, and *Helobdella*) were found only at Site 3. They were not abundant enough to be certain that they were even primarily restricted to the pond. Taxa listed as "primarily restricted to the pond and Site 4" are considered lentic forms, since they were most abundant in the pond, and were absent or rare above the pond and at the lowest site.

A surprising number of genera occurred in the pond and at all lotic sites (Table 6). An additional six genera colonized all stream locations but were not found in the pond.

Table 6. Categorization of macroinvertebrate distribution patterns and common genera¹ contained therein.

Occurred at all sites:

Hesperophylax, Physa, Lymnaea, Pisidium, Dugesia, Hyalella, Pristina

Occurred at all sites except pond:

Baetis, Tipula, Eiseniella, Isoperla, Hydroptila, Eukiefferiella

Primarily restricted to pond and Site 4:

Callibaetis, Dicrotendipes, Gyraulus, Tubificidae

Occurred on all lotic substrata examined:

Physa, Dugesia, Hydroptila, Baetis, Tipula, Procladius, Cardiocladius, Deronectes

Restricted to rubble:

Heptagenia, Isoperla, Glossosoma, Hydropsyche, Cheumatopsyche, Simulium, Optioservus, Hexatoma

Restricted to sand:

Prodiamesa, Stictochironomus

Restricted to moss:

Limonia, Pericoma

Restricted to source:

Diamesa, Paranais, Limonia, Pericoma

Restricted to sites below pond:

Heptagenia, Cheumatopsyche, Pseudodiamesa

¹ Genera except Tubificidae.

Eight genera were collected from all lotic substrata; another eight were restricted to rubble; two chironomids were taken only from sand; and two dipterans were restricted to moss.

The coefficient of JACCARD (1902) was utilized to further investigate the differences in composition of macroinvertebrates on the four substrata at Site 1 (lower left values in Table 7). However, JACCARD's coefficient is based only upon presence or absence of taxa and did not sufficiently discriminate between samples. Percentage similarity (WHITTAKER, 1975) combined presence/absence data with relative abundance and proved to be more sensitive to macroinvertebrate composition differences on the various substrata (upper right values in Table 7). The lowest percentage similarity (PS) value was between sand and moss. This was the only pair which the JACCARD index differentiated. Rubble and watercress exhibited the highest PS; moss and watercress also exhibited high values. Other pairs exhibited intermediate percentage similarity. THORUP and LINDEGAARD (1977) also

Table 7. Similarity of macroinvertebrate composition of four substrata at Site 1 using the coefficient of JACCARD and percentage similarity (see text).

	Rubble	Sand	Moss	Watercress
rubble	—	24.1	21.4	45.5
sand	.419	—	14.3	27.3
moss	.396	.349	—	44.7
watercress	.415	.400	.410	—

compared faunal composition on various substrata of Danish springs using percentage similarity. They found very low PS between stony bottoms and emergent moss (no sandy areas were present), and relatively high PS values between stony bottom and submerged vegetation.

Drift

Since the intent of the drift studies was not to intensively study drift patterns, but rather to provide data to supplement bottom fauna investigations, only pertinent results will be presented.

Below the pond drift rates of macroinvertebrates were over ten times greater than at Site 2 (numerically and gravimetrically). Much of the difference can be attributed to large amounts of living plants, and associated organisms, in drift samples below the pond. At both sites, the majority of plants and detritus in drift occurred in morning samples in June. At Site 2 the 21 g (dry weight) in the two-hour morning sample in June was almost exclusively fine plant detritus. In contrast, at Site 4 not only was the amount much greater (138 g), but large pieces of living *Elodea* comprised the majority of the sample. Drifting plants at Site 4 also explain the large numbers of organisms not normally encountered in drift samples, such as gastropods. Despite larger amounts of plant material in morning drift, a slightly greater number of aquatic animals occurred in night than in morning samples at both sites. Aerial adults and terrestrials were rare in drift samples with the exception of large numbers of adult *Callibaetis nigrinus* in June samples below the pond. *Baëtis*, *Dugesia*, and chironomids accounted for the majority of drifting animals above the pond. Gastropods, coleopterans (primarily *Deronectes* larvae), and *Hyalella azteca* comprised the majority of the drift fauna below the pond.

Seasonal Patterns of Abundance

Seasonal abundance patterns are largely a reflection of the seasonal trends of the predominant organisms. This is especially true at the upper sites, since a few taxa comprise the vast majority of organisms (Fig. 9).

Baëtis was the most abundant taxon on rubble at all lotic sites and on watercress at the source. On rubble at Site 1 (Fig. 11 a) the abundance of *Baëtis* exhibits numerous seasonal peaks and similar patterns occur at Sites 2 and 4. At Site 5, however, two distinct abundance peaks are apparent (Fig. 11 b), a large spring peak and a smaller peak in autumn. In addition, at Site 1, nymphs with black wing pads were collected throughout the year supporting multivoltinism. *Callibaëtis nigrinus*, the only mayfly in the pond, had a distinctly univoltine life cycle (Fig. 11 c) with emergence occurring in May and June.

Dugesia dorotocephala was a major component of the fauna on rubble at Sites 1, 2, and 4 and on moss and submerged plants. In all cases, major abundance peaks occurred in winter and autumn (Fig. 11 d). Minor variations did not appear to be a function of the distance from the spring source.

Tipula larvae were large, fourth instars often exceeding 5 cm in length and 0.5 cm in diameter. They were collected from all sites and substrata

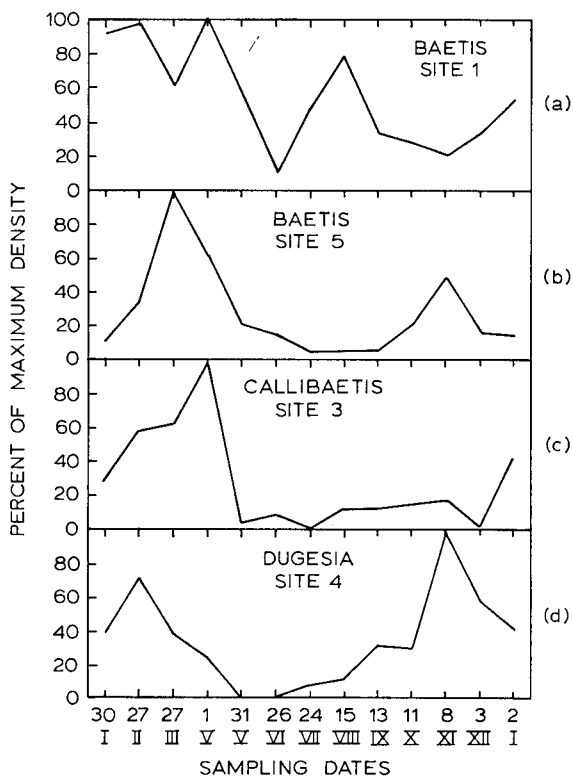


Fig. 11. Seasonal changes in macroinvertebrate taxa expressed as percent of maximum density.

except the pond and were numerically abundant on rubble at Sites 1 and 2. Because of their large size, they comprised over 97% of the dipteran biomass on rubble at all lotic sites. Their seasonal pattern at Site 1 (Fig. 12 a) showed a general decrease in numbers from winter through summer, at which time only fourth instar larvae remained. Specimens were then absent for one or two months. In autumn, specimens (primarily first instars) again appeared in samples and their numbers and size increased as growth and recruitment occurred.

Four taxa comprised 80% of the macrobenthos in the pond (Figs. 12 b—d, 13 a). *Pisidium* and *Physa* exhibited similar seasonal patterns with maximum numbers in late summer and autumn. *Gyraulus* and Tubificidae also exhibited late summer peaks, but maximum numbers occurred in December and January, respectively. Tubificidae and *Pisidium* which were absent or rare in drift samples did not occur in large numbers below the pond. *Gyraulus* and *Physa* were abundant in drift samples and at Site 4. At

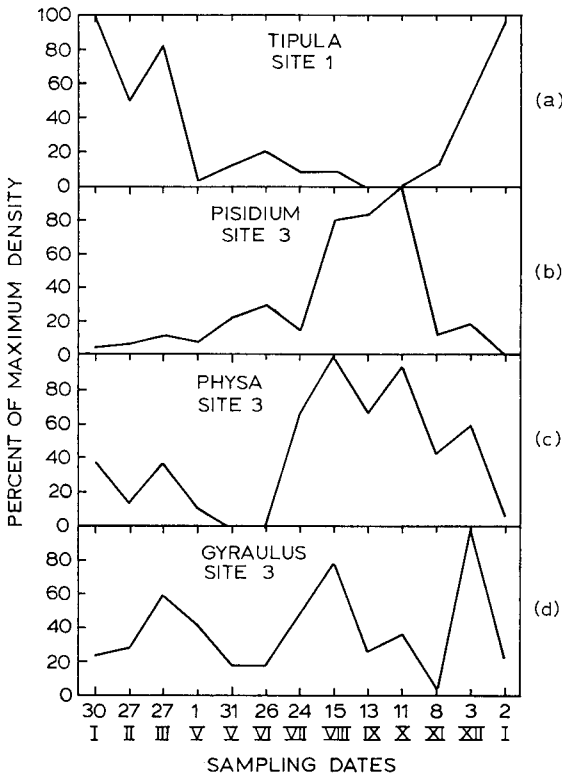


Fig. 12. Seasonal changes in macroinvertebrate taxa expressed as percent of maximum density.

Site 4 *Physa* exhibited a seasonal pattern similar to the pond population, although late summer and autumn peaks were delayed one month. On watercress at Site 1 the major peak occurred in October. At Site 4, *Gyraulus* exhibited a seasonal pattern similar to the pond population, although the late March peak was the largest.

The naidid oligochaete *Pristina* was the most abundant organism on sand at the source. Greatest abundance occurred in December (Fig. 13 b).

Cheumatopsyche and *Simulium* were major filter-feeders at Site 4 below the pond. *Cheumatopsyche* occurred primarily in late winter and spring, whereas maximum numbers of *Simulium* occurred in late summer (Fig. 13 c). The seasonal abundance of zooplankton at Site 4 (Fig. 13 d) exhibits a pattern similar to the combined abundance of *Cheumatopsyche* and *Simulium*, although the *Cheumatopsyche* maximum occurs at a period of low zooplankton density. The total seston maximum, however, does correspond to the maximum *Cheumatopsyche* density (Fig. 13 d).

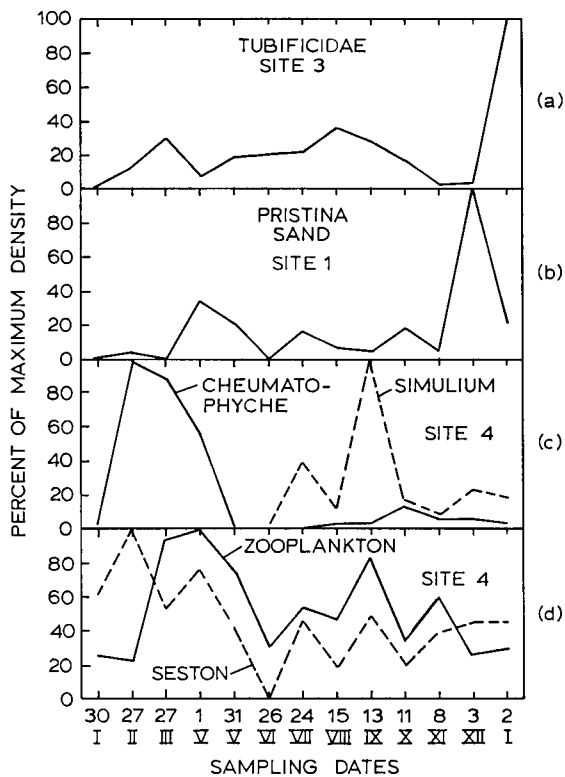


Fig. 13. Seasonal changes in macroinvertebrate taxa, total zooplankton, and seston expressed as percent of maximum density.

Comparisons with Eastern North American Springbrooks

Although the biota of springbrooks is generally similar world-wide, some distinct differences were noted between the invertebrates of the Colorado springbrook and the fauna of springbrooks in eastern North America.

The predominance of crustaceans reported for eastern springbrooks (e.g., MINCKLEY, 1963) was not apparent in the present study. One or more species of *Gammarus* is normally very abundant in eastern springbrooks. *Hyaella azteca* occurred in the Colorado springbrook, but was never abundant. Isopods, so often abundant in eastern springbrooks, were not encountered, a fact also noted by DUDLEY (1953) in her study of Colorado springbrooks. However, these differences do not necessarily apply to western springbrooks generally. NOEL (1954) found *Gammarus fasciatus* (previously unreported in the western U.S.) in a New Mexico springbrook, and DAVIDSON & WILDING (1943) reported isopods in a spring in Oregon. Decapods were not encountered in the present study, but have been reported from eastern springbrooks.

MINCKLEY (1963) notes the paucity of aquatic insects near the source of Doe Run, a springbrook in Kentucky. The mayfly *Baëtis* comprised over 70 % of the total macroinvertebrates at Site 1 of the Colorado springbrook and was the most abundant organism on rubble at all lotic sites.

The caddisfly *Rhyacophila* has been collected in eastern springbrooks, but although numerous species occur in Colorado streams, not a single specimen was encountered in the Colorado springbrook.

Despite these notable exceptions, there are more similarities than differences between the fauna of the Colorado springbrook and springbrooks in eastern North America. Some differences may be accounted for by the lesser contribution of terrestrial leaf litter to the Colorado springbrook compared to springbrooks of the Eastern Deciduous Forest. Other differences can be attributed to historical zoogeographic factors, such as the poorly developed crayfish fauna of Colorado, or to the substitution of different forms of a typical faunal group (*Dugesia dorotocephala* in Colorado vs. *Phagocata gracilis* or *P. velata* in eastern North America). Additional studies of a variety of Colorado springbrooks are clearly indicated.

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Appendix A

Bacillariophyta distribution at lotic sites (+ indicates present).

	Site 1	Site 2	Site 4	Site 5
<i>Achnanthes affinis</i>	+	+	+	+
<i>Achnanthes clevei</i>	+	+		
<i>Achnanthes lanceolata</i>	+	+	+	+
<i>Achnanthes linearis</i>	+	+		
<i>Achnanthes minutissima</i>	+	+	+	+
<i>Achnanthes saxonica</i>		+	+	
<i>Amphora ovalis</i>			+	
<i>Amphora perpusilla</i>	+	+	+	+
<i>Anomoeoneis vitrea</i>		+		
<i>Asterionella formosa</i>			+	+
<i>Caloneis lewigii</i>			+	
<i>Caloneis ventricosa</i> var. <i>alpina</i>			+	
<i>Cocconeis pediculus</i>	+	+	+	+
<i>Cocconeis placentula</i>	+	+	+	+
<i>Cymbella cistula</i>			+	
<i>Cymbella minuta</i>	+	+	+	+
<i>Cymbella prostrata</i>	+	+		
<i>Cymbella pusilla</i>	+	+	+	+
<i>Cymbella sinuata</i>	+	+	+	+
<i>Cymbella tumida</i>	+	+	+	
<i>Denticula elegans</i>		+		
<i>Diatoma hiemale</i> var. <i>hiemale</i>			+	
<i>Diatoma hiemale</i> var. <i>mesodon</i>	+	+	+	+
<i>Diatoma tenue</i> var. <i>elongatum</i>			+	
<i>Diatoma vulgare</i>		+	+	+
<i>Diploneis elliptica</i>	+	+		+
<i>Epithemia sorex</i>		+	+	+
<i>Epithemia turgida</i>			+	
<i>Eunotia curvata</i>			+	
<i>Fragilaria brevistriate</i>			+	
<i>Fragilaria capucina</i>			+	
<i>Fragilaria construens</i>	+			
<i>Fragilaria crotonensis</i>			+	
<i>Fragilaria leptostauron</i>	+	+		
<i>Fragilaria pinnata</i> var. <i>lancettula</i>	+	+		
<i>Fragilaria vaucheriae</i>	+	+	+	+
<i>Frustulia rhomboides</i>				+
<i>Gomphonema acuminatum</i>			+	+
<i>Gomphonema angustatum</i>	+	+	+	+
<i>Gomphonema brebissonii</i>		+	+	
<i>Gomphonema clevei</i>	+		+	
<i>Gomphonema olivaceiodes</i>			+	
<i>Gomphonema olivaceum</i>	+	+	+	+
<i>Gomphonema parvulum</i>	+	+	+	+
<i>Gomphonema subclavatum</i>	+	+	+	+

<i>Gomphonema truncatum</i>	+	+	+	
<i>Gomphoneis herculeana</i> var. <i>robusta</i>			+	
<i>Gyrosigma acuminatum</i>			+	+
<i>Hannaea arcus</i>	+			+
<i>Melosira varians</i>			+	+
<i>Meridion circulare</i>	+	+		
<i>Navicula</i> sp.	+	+	+	+
<i>Navicula bacillum</i>			+	
<i>Navicula cryptocephala</i>	+	+	+	+
<i>Navicula cuspidata</i>		+	+	+
<i>Navicula elginensis</i>	+			
<i>Navicula exigua</i>	+	+	+	+
<i>Navicula exigua</i> var. <i>capitata</i>	+	+	+	+
<i>Navicula minima</i>	+	+	+	
<i>Navicula parvulum</i>				+
<i>Navicula pelliculosa</i>	+	+	+	+
<i>Navicula pupula</i>	+	+	+	+
<i>Navicula pupula</i> var. <i>capitata</i>	+	+		
<i>Navicula rhynchocephala</i>	+	+	+	+
<i>Navicula salinarum</i>	+	+	+	+
<i>Navicula tripunctata</i>	+	+	+	+
<i>Navicula viridula</i>	+	+	+	+
<i>Neidium binode</i>			+	+
<i>Nitzschia</i> sp.	+	+	+	+
<i>Nitzschia acicularis</i>	+	+	+	+
<i>Nitzschia amphibia</i>	+	+	+	+
<i>Nitzschia dissipata</i>	+	+	+	+
<i>Nitzschia fonticola</i>	+	+	+	+
<i>Nitzschia hungarica</i>	+	+	+	+
<i>Nitzschia linearis</i>	+	+	+	+
<i>Nitzschia palea</i>	+	+	+	+
<i>Nitzschia sigmoidea</i>			+	
<i>Opephora martyi</i>	+	+	+	+
<i>Pinnularia intermedia</i>				+
<i>Pinnularia rupestris</i>	+			
<i>Rhoicosphenia curvata</i>			+	
<i>Stauroneis smithii</i>	+	+		
<i>Surirella angustata</i>	+	+	+	+
<i>Surirella ovalis</i>	+	+	+	+
<i>Surirella ovata</i>				+
<i>Synedra parasitica</i> var. <i>subconstricta</i>			+	
<i>Synedra rumpens</i>	+	+	+	+
<i>Synedra ulna</i>	+	+	+	+

Summary

A one-year study of a Colorado springbrook-pond system was undertaken to determine longitudinal and seasonal changes in the composition, abundance, and community structure of macroinvertebrates and epilithic algae. Lotic sam-

pling sites (Fig. 1) were established on rubble riffles at Site 1 (spring source) and Site 2 above the pond, and at two downstream locations (Sites 4 and 5). Other substrata (sand, moss, *Rorippa*, and *Elodea*) were also examined.

Bacillariophyta and *Oscillatoria princeps* were the major components of the epilithon at the spring source, whereas Chlorophyta predominated at other lotic sites (Figs. 3—6). Predominant members of the diatom flora exhibited distinct seasonal patterns; at the spring source (Fig. 7) light is the only variable which would explain the seasonal fluctuations. There was a close relationship between annual mean biomass of epilithon and macroinvertebrate abundance at lotic sites (Fig. 8).

Macroinvertebrate diversity exhibited a general downstream increase (Table 3). Diversity and equitability values at the source indicated a moderately stressed community, which is attributed largely to the seasonal and diurnal temperature constancy (Table 1, Fig. 2). A few taxa comprised the majority of total organisms (Fig. 9), and largely determined seasonal abundance patterns (Figs. 11—13). Total seston below the pond exhibited a seasonal pattern closely corresponding to temporal changes in the predominant filter-feeding invertebrates (Fig. 13).

The relative composition of major taxa differed greatly between sites and substrate types (Fig. 10). Although macroinvertebrate density was similar on rubble and sand, biomass values were nearly three times greater on rubble (Table 5). Faunal abundance was comparable on the plant substrata, although somewhat higher macroinvertebrate biomass occurred in plant beds below the pond. The lowest coefficients of similarity were between macroinvertebrate assemblages on moss and sand; highest values were between rubble and *Rorippa* (Table 7).

Seven macroinvertebrate taxa occurred at all sampling sites; six others were collected from all lotic sites but were absent from the pond (Table 6). Some genera were restricted to one site or one substrate type; others were collected from all lotic substrata.

Although the biota of springbrooks is generally similar world-wide, some distinctive features of the Colorado springbrook were noted.

Zusammenfassung

Eine einjährige Studie eines Quellrinnsal-Teichsystems wurde in Colorado unternommen, um Änderungen stromabwärts und saisonale Änderungen in der Zusammenstellung, Menge und Struktur der Lebensgemeinschaften von Macro-Invertebraten und Epilithophyten festzustellen. Probestellen für Quellrinnsale (Abb. 1) wurden festgelegt: Stelle 1, an Stromschnellen (Quellenursprung), Stelle 2, oberhalb des Teiches und an zwei Stellen stromabwärts (Stellen 4 und 5). Andere Substrate (Sand, Moos, *Rorippa*, und *Elodea*) wurden auch untersucht.

Bacillariophyta und *Oscillatoria princeps* waren die Hauptvertreter der Epilithophyten am Quellenursprung, während Chlorophyta an den anderen Quellrinnsalstellen vorherrschten (Abb. 3—6). Die vorherrschenden Mitglieder der Diatomen-Flora zeigen klare saisonale Normen; Licht ist die einzige Variable, die die saisonalen Schwankungen am Quellenursprung (Abb. 7) erklären würde. Ein enger Zusammenhang bestand zwischen der einjährigen durchschnittlichen Biomasse der Epilithophyten und dem Überfluß an Macro-Invertebraten an den Quellrinnsalstellen (Abb. 8).

Die Artendiversität der Macro-Invertebraten zeigt stromabwärts eine allgemeine Zunahme (Tabelle 3). Artendiversität und Gleichartigkeitswerte am Quellen-

ursprung weisen auf eine unter mäßigem Druck stehende Lebensgemeinschaft hin, welcher größtenteils der saisonalen und täglichen Temperaturkonstanz zugeschrieben werden kann (Tabelle 1, Abb. 2). Einige wenige Taxa enthielten die Mehrheit der gesamten Organismen (Abb. 9) und bestimmten größtenteils die saisonalen Abundanzverhältnisse (Abb. 11—13). Das Gesamt-Seston unterhalb des Teiches wies eine saisonale Norm auf, die genau den zeitlichen Änderungen bei den vorherrschenden filtrierenden Invertebraten (Abb. 13) entsprach.

Die relative Zusammensetzung der Haupttaxa war sehr unterschiedlich zwischen den Probestellen und den Substrattypen (Abb. 10). Obwohl die Besiedlungsdichte der Macro-Invertebraten in Geröll und Sand ähnlich war, übertrafen die Biomassewerte des Gerölls die des Sandes beinahe dreifach (Tabelle 5). Die Besiedlungsstärke der Fauna war mit dem Pflanzensubstrat vergleichbar, obwohl eine etwas höhere Biomasse von Invertebraten im Pflanzenbett unterhalb des Teiches vorkam. Die geringste Ähnlichkeit bestand zwischen Macro-Invertebraten-Ansammlungen auf Moos und Sand, die größte Ähnlichkeit zwischen Geröll und *Rorippa* (Tabelle 7).

Sieben Macro-Invertebraten Taxa kamen an allen Probestellen vor; sechs andere wurden von allen Quellrinnalen eingesammelt, waren aber im Teich nicht vorhanden (Tabelle 6). Einige Gattungen waren auf eine Stelle oder Substrattypen beschränkt; andere wurden an allen Quellrinnal-Substraten zugelassen.

Obwohl die „Biota“ von Quellrinnalen im allgemeinen überall in der Welt ähnlich beschaffen sind, wurden einige charakteristische Merkmale des Colorado Quellrinnals festgestellt.

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