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# The seasonal food habits of mayfly (Ephemeroptera) nymphs from three Alberta, Canada, streams, with special reference to absolute volume and size of particles ingested

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With 8 figures and 14 tables in the text

## Abstract

Food habits of mayfly (Ephemeroptera) nymphs from four sites of three Alberta, Canada, streams were studied from July 1975 to July 1976. An electronic counter was used to estimate total absolute volume and size of particles ingested. In respect to volume, detritus was the dominant material ingested by all 25 species. Generally, baetids and heptageniids consumed the greatest relative amounts of diatoms. *Drunella spinifera* populations were the only mayflies to consume large amounts of animal material. About two-thirds of all food items consumed by all populations consisted of particles less than 32 μm in diameter, and rarely were particles larger than 160 μm ingested. The relationship between total volume (in $\mu m^3$) of ingested material and total length of the nymph fitted an exponential function. Material consumed was dependent on availability in the microhabitat where nymphs fed. Most populations, or certain size classes within the population, could be placed, using multivariate analysis, in one of two major food habit regimes: surface feeders and interstitial feeders. Surface feeders consumed large amounts of diatoms, especially epilithic diatoms; these nymphs ingested high proportions of small particles, with total volume of consumed material being below average. Interstitial feeders consumed uniformly low proportions of predominantly epipelic diatoms; these nymphs ingested greater amounts of large particles. Seasonally, the detrital food base was often most important in late winter and spring. Diatom ingestion amongst surface feeders was often elevated in spring and autumn and could be related to larger epilithic diatom standing crops at these times. Average detrital ingestion was greatest in the boreal forest stream; whereas diatom ingestion was relatively most important near the spring-fed headwaters of the agricultural stream. Food-habit regimes (surface and interstitial feeders) are discussed in respect to the functional feeding group concept (i. e. shredders, collectors, etc.).

## Introduction

Most food habit studies of stream macroinvertebrates have been carried out on single streams located in forested temperate watersheds. Only infrequently have samples for gut analysis been collected throughout the year;

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and usually techniques are based entirely on microscopic examinations, which do not accurately estimate the size range of food particles and the total volume of material ingested.

We report here the results of a food habit study of mayfly (Ephemeroptera) nymphs from three different types of streams of west-central Alberta. We postulated that ingestion of different size food particles by different species, different populations of the same species, and different size classes within a population might be related to the nymphs' developmental stage or habitat or both. An electronic particle size counter was used to estimate particle size and volume of ingested food.

## Study area

### Bigoray River

The Bigoray River, part of the Arctic Ocean drainage, is a slow-moving brown-water stream located in the boreal forest of west-central Alberta (53° 31'N, 115°26'W). Dominant trees of the watershed are black spruce *(Picea mariana)* and willows (*Salix* spp.), with some stands of tamarack *Latrix laricina),* aspen poplar *(Populus tremuloides)* and balsam poplar *(Populus balsamifera).* Substrate in the study area consists almost entirely of fine particles, average particle size diameter being about 1.7 mm. Summer water temperatures did not exceed 18°C during the study period; winter temperatures were near 0°C for about 5 months. The stream froze over in late October 1975 and remained frozen until the first week of April 1976. Average summer base flow is 0.80 $m^3$/sec; average winter base flow is 0.14 $m^3$/sec (CLIFFORD 1978).

### Stauffer Creek

Stauffer Creek, part of the Hudson's Bay drainage, is a springfed stream flowing through agricultural land in west-central Alberta (52°12'N, 114°42'W). Vegetation of the watershed is characterized by grasses and sedges interspersed with willows and alders in low areas. Much of the watershed is cultivated for pasture, hay and cereal crops. There is extensive grazing in the watershed, especially in areas adjacent to the stream. Study site 1 was located 1.5 km downstream from the spring source. Discharge in this area is nearly constant at 0.2 $m^3$/second. Substrate at study site 1 consists mainly of small gravel, but there are several areas of fine sand and silt, which support dense beds of *Hippurus vulgaris.* Water at the source has a temperature of about 6°C; this has a stabilizing effect on water temperatures at site 1, and prevents winter freeze over.

Study site 2 was located 10.8 km downstream from the source. Substrate of this area consists mainly of medium size gravel. Site 2 has a more typical temperature regime for this latitude, exhibiting higher summer temperatures than at site 1; winter temperatures are near 0°C. Site 2 is ice-covered from the end of November to the first week of April. Discharge at site 2 fluctuates between 0.85 and 1.3 $m^3$/sec and is more variable and generally higher than site 1. This is due to the greater influence of surface runoff at site 2.

### Tay River

The Tay River, part of the Hudson's Bay drainage, is a foothills stream on the east slopes of the Rocky Mountains of west-central Alberta (52°03'N, 115°06'W). There is no evidence of logging or farming in the watershed; however, there are a few summer cottages immediately upstream of the sampling site. Substrate particle sizes range from medium sized cobbles to gravel. This type substrate was general throughout the stream, even in the deeper reaches, and is due to fast flow and high gradient. Winter water temperatures are not as low as for the Bigoray River and Stauffer Creek site 2. The winter of 1975–76 was mild, and the Tay River was ice-covered from about early December to mid-March; however, the riffle from which the samples were taken never completely froze over. Discharge varied from 0.5 $m^3$/sec to 2.0 $m^3$/sec, with peak flow, due to mountain snow melt and heavy rains in late June and early July 1976. Flow fluctuated more than in Stauffer Creek.

## Materials and methods

We sampled the four sites from early July 1975 until early August 1976 at about 3-week intervals. During winter, the sampling interval was lengthened to about 6 weeks.

### Flora

Changes in epilithic diatom standing crop were determined by collecting and preserving in 10% formalin between 5 and 10 rocks exposed at the substratum's surface. In the laboratory, diatoms were removed by scraping the entire surface of each rock with a stiff brush. The scrapings, along with the formalin in which the samples were stored, were deposited in a beaker and allowed to stand for 24 hours. During this period the diatoms settled and the formalin could be siphoned off. Each sample was then treated with a mixture of concentrated sulphuric acid and potassium dichromate to clear the frustules. The digestion agent was removed by a series of seven distilled water rinses using the same routine as for removal of the formalin preservative. Two subsamples from each cleared sample were placed uniformly on 22 mm diameter cover slips, dried at a low temperature on a hot plate, inverted, and mounted on a slide in a drop of Permount. Diatoms in a known area of each slide were then identified and counted.

Surface area of the rocks scraped was determined by covering each rock with aluminium foil. We were careful to cut off foil not in direct contact with the rock's surface. The foil was then removed, flattened and traced onto paper, and the surface area determined with a planimeter. Total surface area of the rocks scraped for each sample was arbitrarily reduced by 25% to compensate for the area not exposed to light and therefore not populated with diatoms.

Standing crop of diatoms was calculated by multiplying the diatom count of each subsample by a conversion factor and then taking the average value of two replicates. The conversion factor *(CF)* was

$$CF = \frac{Sc \times Vs}{ASs \times VSs \times Sr}$$

where $Sc$ = surface area of cover slip, $Vs$ = volume of diatom sample, $ASs$ = area of cover slip scanned, $VSs$ = volume of subsample, and $Sr$ = surface area of rocks minus 25%.

Dominant macrophytes of each site were also identified, and an estimate of percent coverage by each species determined. Significant growths of filamentous algae were also noted.

## Sampling of Ephemeropterans

Qualitative samples of mayfly nymphs were collected with a compound dip net consisting of a course 1 mm mesh inside a fine 210 $\mu$m mesh. Material collected in the coarse mesh consisted primarily of large nymphs (>2 mm) and organic debris. The fine mesh retained the smaller specimens, mineral material, and some fine organic debris. Both fractions were fixed in 70% ethanol to prevent regurgitation of stomach contents (COFFMAN 1967). The ethanol was immediately filtered off and the samples preserved in 15% formalin. If the number of mayflies in the fine fraction was greater than 2,000, the specimens were subsampled after flotation.

Mayflies from both the coarse and fine sample fractions were identified, counted, and separated into millimeter size classes based on measurement of total length (front of head to base of cerci). All specimens from the coarse fraction were counted and measured. Quadrants from the subsampled fine fraction were successively analyzed under a dissecting microscope at 6.4× until at least 300 specimens were counted. To associate mayfly nymphs with adult stages, required for species identification, mature nymphs were collected live and reared in the laboratory.

The mayflies from their respective streams were: Bigoray River (slow-moving, muskeg stream of the boreal forest) *Baetis tricaudatus, Callibaetis coloradensis, Centroptilum* spp. (Baetidae); *Paraleptophlebia debilis* and *Leptophlebia cupida* (Leptophlebiidae); *Caenis simulans* (Caenidae); *Siphlonurus alternatus* (Siphlonuridae); *Ephemera simulans* (Ephemeridae); *Stenacron canadense* (Heptageniidae); and *Siphloplecton basale* (Metretopodidae); Tay River (fast-flowing foothills stream) *Baetis persecutus* and *Pseudocloeon* sp. (Baetidae); *Paraleptophlebia* sp. (Leptophlebiidae); *Ameletus sparsatus* (Siphlonuridae); *Cinygmula mimus, Rhithrogena* sp., and *Epeorus* sp. (Heptageniidae); *Drunella flavilinea, D. spinifera, Ephemerella inermis,* and *Serratella tibialis* (Ephemerellidae); Stauffer Creek – Site 1 (upstream, springfed site of agricultural stream) *Baetis* spp. (Baetidae); *Cinygmula mimus* (Heptageniidae); *Ephemerella inermis, Serratella tibialis,* and *Drunella spinifera* (Ephemerellidae); Stauffer Creek – Site 2 (downstream site of agricultural stream) *Baetis* spp. and *Centroptilum* spp. (Baetidae); *Paraleptophlebia debilis* and *Leptophlebia cupida* (Leptophlebiidae); *Ephemera simulans* (Ephemeridae);

*Cinygmula mimus* (Heptageniidae); *Ephemerella inermis* and *Drunella spinifera* (Ephemerellidae).

## Stomach analysis

A stomach analysis sample consisted of stomach contents of a pooled sample for each 2 mm size class. Number of individuals used in a stomach analysis depended on total length of nymphs (from about 20 specimens for the 2–4 mm size class to 3 or 4 specimens for size classes of 8–10 mm and larger).

Stomach contents were removed from the specimens by microscopic dissection in a watch glass containing distilled water. Contents were removed either by splitting the specimen in the thoracic region and teasing the contents out of the digestive tract or by removing the gut intact before breaking the digestive tract and removing the material. Contents were removed from the watch glass with a micro-pipette and deposited in a clean vial containing approximately 20 ml of distilled water. Care was taken to remove only material present from the stomach and not pieces of body tissue.

Analysis of the pooled gut content samples was carried out using a combination of COFFMAN's (1967) membrane filter technique and an electronic particle counter. A problem with previous invertebrate stomach analysis techniques has been the inability to accurately quantify the volume of detrital material. All techniques relied upon a microscopic, two-dimensional estimate of food components. These techniques are adequate for materials having rigid and uniform shapes, such as diatoms and filamentous algae. However, for the detrital component, which is amorphous and greatly variable in its shape, a more accurate method was required. We used a Coulter Model TA II electronic particle counter to measure the total number and volume of ingested particles from each stomach contents sample. The counter provides a proportional breakdown of the total volume of material measured into size class channels. Mean volume of the particles recorded in each channel is exactly twice that of the preceding channel. It is therefore possible to calculate the number of particles measured in each size class channel. A particle size analysis range of 1.59–160 $\mu$m in diameter (2.09 to 2,196,000 $\mu m^3$) was adequate for mayfly stomach contents. Material with a diameter smaller than 1.59 $\mu$m was extrapolated to be less than 2% of the total, and particles larger than 160 $\mu$m were seldom encountered. Particle size analysis in this range required use of two aperture tubes on the particle counter: a 80 $\mu$m aperture tube measured particles with diameters from 1.59 $\mu$m to 8.0 $\mu$m, and a 400 $\mu$m tube measured particles from 8.0 $\mu$m to 160 $\mu$m.

Once stomachs were dissected and placed in the vial of distilled water, 2 ml of a 50% glycerine solution (filtered through a 0.45 $\mu$m membrane filter to remove all particles) was added and shaken vigorously to dissociate the stomach particles. This process was aided by light sonication with an immersion type sonicator for 30 sec, which was sufficient to dissociate most large aggregates of particles without breaking the particles themselves. The sample was then diluted to 100 ml in a volumetric flask with a 0.9% NaCl electrolyte solution (membrane filtered) prior to being split into three fractions. One fraction was filtered onto a membrane filter and the other two used for electronic particle analysis. The amount of the sample partitioned into each fraction was noted in order to back calculate results to a per sample and per stomach basis.

The mounting technique of COFFMAN (1967) was used for the fraction filtered onto the 0.45 $\mu$m membrane filter. The filter was cleared in immersion oil at 35°C and then mounted in Permount. This portion of the sample was used for determining the number and kinds of diatoms contained in the stomachs, the volume of filamentous algae and sand grains present, and the presence or absence of animal material. Filter analysis consisted of an initial random scan at 100× for the presence of animal material, followed by scanning of a strip across the middle of the membrane at 1000×. All diatoms encountered during the high power scan were identified and counted as was the volume of filamentous algae. Mean diameter of all sand grains was also recorded and their volumes calculated, with the assumption their shape approximated a sphere. If the number of diatoms encountered in the 1000× scan was greater than 300, the scan was stopped before the complete diameter of the membrane was crossed. Number and taxa of diatoms, volume of filamentous algae, and volume of mineral material present in the initial stomach sample could then be calculated by knowing the area of membrane filter scanned, total membrane area, and portion of the sample filtered onto the membrane.

Efficiency of the membrane filter technique has been tested by GRAY & WARD (1979). They determined that gut material was randomly dispersed on the membrane and that confidence limits of 15% could be achieved on diatom counts from cleared filters.

The two remaining sample fractions were used for particle counter analysis. One was run through the 400 $\mu$m aperture tube and the other through the 70 $\mu$m tube. Prior to analysis in the Coulter Counter, both fractions were again diluted to 100 ml with filtered electrolyte, and the 70 $\mu$m fraction was filtered through a 25 $\mu$m filter to prevent aperture clogging.

Data drived from the three fractions of each stomach analysis sample were run through a Watfiv program developed by the authors. The program combined data from the 70 $\mu$m and 400 $\mu$m aperture tubes to calculate number and volume of particles in each size channel, along with the number of particles and total volume of material (expressed on a per stomach basis) for each gut sample. The relatively constant size of diatoms permitted volume of each diatom species to be calculated by taking length, width, and girdle width measurements of several individuals. Volume was determined by tracing to scale the frustule on graph paper, determining the surface area from the outline, and multiplying by girdle width. Total volume of diatoms ingested (of each diatom taxon) was calculated by multiplying the number per stomach (calculated from the membrane filter fraction) by the estimated volume. Volumes per stomach of filamentous algae and sand grains were also calculated.

Volume of detritus per stomach was derived by subtracting the volumes of filamentous algae, sand grains, and diatoms from the total volume of material determined by the Coulter Counter. Detritus was therefore defined as all remaining material present in a stomach other than diatoms, filamentous algae and sand grains. This included unrecognizable autochthonous and allochthonous organic material and recognizable

Table 1. Replicate stomach analyses of 10–12 mm *Siphlonurus alternatus* nymphs collected 25 June 1976 from the Bigoray River. C.V. is coefficient of variation.

| | Volume of Material ($\mu m^3 \times 10^{-6}$) Replicate | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | C.V. |
| Diatoms | 16.40 | 9.46 | 15.44 | 12.41 | 13.12 | 20.4 |
| Detritus | 992.60 | 709.20 | 829.80 | 660.00 | 606.70 | 20.3 |
| Mineral Particles | 4.49 | 5.11 | 3.03 | 1.12 | 2.42 | 49.6 |
| Filamentous Algae | 0.002 | 0.00 | 0.00 | 0.002 | 0.00 | – |

animal tissue. The animal fraction could usually be ignored because tissue fragment rarely occurred in any samples. Lastly, the program determined the proportion of each food component relative to the total.

Our technique could not be used for nymphs smaller than 2 mm because of insufficient gut material. Other methods also proved unreliable for very small nymphs; hence analysis of material consumed by specimens less than 2 mm in length is not presented.

Accuracy of the stomach analysis technique was tested by analyzing five replicate stomach analysis samples of 10–12 mm *Siphlonurus alternatus* nymphs collected on 25 June 1976. The reproducibility of the technique is good (Table 1).

## Results and discussion

### Relative abundance of ingested materials

Detritus was the major food item consumed by all ephemeropterans (Tables 2 and 3). Diatoms were second in importance, while filamentous algae and sand grains were usually detected in trace amounts. The very low con-

Table 2. Percentages of total volume of all ingested material composed of detritus and diatoms by Bigoray River and Tay River populations (all size classes) and ranges between size classes.

| | Detritus | | Diatoms | |
|---|---|---|---|---|
| | % Vol. | Range | % Vol. | Range |
| Bigoray River | | | | |
| *Baetis tricaudatus* | 74.1 | 54.9–85.6 | 20.9 | 5.2–46.7 |
| *Caenis simulans* | 95.3 | 94.4–96.4 | 4.2 | 2.2– 9.4 |
| *Callibaetis coloradensis* | 90.3 | 85.3–95.5 | 9.0 | 1.8–48.4 |
| *Centroptilum* spp. | 85.9 | 84.1–87.5 | 13.2 | 4.2–21.2 |
| *Ephemera simulans* | 94.8 | 91.0–96.8 | 3.9 | 0.7– 7.7 |
| *Leptophlebia cupida* | 96.6 | 95.7–97.9 | 2.8 | 1.1– 6.3 |
| *Paraleptophlebia debilis* | 95.6 | 95.1–95.9 | 3.0 | 1.9– 3.8 |
| *Siphlonurus alternatus* | 96.4 | 92.9–98.3 | 2.5 | 1.0– 6.5 |
| *Siphloplecton basale* | 95.2 | 94.0–96.8 | 3.1 | 1.2– 6.4 |
| *Stenacron canadense* | 96.5 | 95.6–97.4 | 3.2 | 2.0– 4.0 |
| Tay River | | | | |
| *Ameletus sparsatus* | 95.1 | 93.3–96.2 | 4.9 | 3.0– 9.1 |
| *Baetis persecutus* | 86.3 | 82.2–91.0 | 14.0 | 3.9–37.1 |
| *Cinygmula mimus* | 86.2 | 83.6–88.4 | 13.0 | 3.4–26.5 |
| *Epeorus* sp. | 83.6 | 79.7–88.6 | 14.9 | 7.9–35.3 |
| *Drunella flavilinea* | 92.9 | 85.1–97.6 | 7.2 | 1.4–20.3 |
| *Drunella spinifera* | 76.7 | 66.9–91.6 | 21.7 | 1.4–42.6 |
| *Ephemerella inermis* | 94.1 | 88.4–97.3 | 3.5 | 2.1– 7.0 |
| *Serratella tibialis* | 96.9 | 95.5–98.3 | 2.8 | 1.5– 4.2 |
| *Paraleptophlebia* sp. | 95.3 | 94.4–96.6 | 3.9 | 1.1– 9.8 |
| *Rhithrogena* sp. | 87.9 | 84.1–92.5 | 12.6 | 5.7–16.7 |

sumption of filamentous algae would indicate nymphs avoid this food resource, since occasionally these algae were very abundant in the study streams. Other workers (BROWN 1961; MOORE 1975; GRAY & WARD 1979) have also observed the phenomenon. Animal material was recorded in substantial quantities in only one *species, Drunella spinifera.*

Table 3. Percentages of total volume of all ingested material composed of detritus and diatoms by Stauffer Creek site 1 and site 2 populations (all size classes) and ranges between size classes.

| | Detritus | | Diatoms | |
|---|---|---|---|---|
| | % Vol. | Range | % Vol. | Range |
| Stauffer-1 | | | | |
| *Baetis* spp. | 77.0 | 72.4–79.3 | 21.2 | 10.0–65.7 |
| *Cinygmula mimus* | 69.8 | 52.6–79.1 | 25.4 | 11.1–82.3 |
| *Ephemerella inermis* | 90.5 | 88.8–93.7 | 8.7 | 4.7–14.6 |
| *Drunella spinifera* | 96.3 | 95.5–96.8 | 3.4 | 1.5– 4.8 |
| *Serratella tibialis* | 86.9 | 85.4–88.3 | 12.6 | 9.8–15.5 |
| Stauffer-2 | | | | |
| *Baetis* spp. | 70.5 | 45.4–83.3 | 20.6 | 0.2–84.4 |
| *Centroptilum* sp. | 84.5 | 82.3–86.5 | 15.2 | 12.8–19.0 |
| *Cinygmula mimus* | 92.6 | 91.9–93.1 | 6.9 | 3.1–10.7 |
| *Ephemera simulans* | 96.1 | 95.1–97.2 | 3.0 | 1.1– 6.7 |
| *Ephemerella inermis* | 94.0 | 92.1–96.1 | 5.7 | 0.5–29.6 |
| *Drunella spinifera* | 93.4 | 84.4–99.0 | 5.9 | 0.3–15.2 |
| *Leptophlebia cupida* | 93.2 | 91.2–95.4 | 6.1 | 1.3–22.8 |
| *Paraleptophlebia debilis* | 96.0 | 95.4–96.5 | 3.6 | 1.5– 8.6 |

**Diatoms**

Diatoms were the only significant food resource ingested other than detritus, and the relative importance of diatoms in the diet varied considerably between species, seasons, and sites. Generally, baetids and heptageniids consumed the greatest relative quantities of diatoms. Members of the Ephemerellidae varied considerably in overall consumption of diatoms. Representatives of Ephemeridae, Leptophlebiidae, Metretopodidae, and Siphlonuridae consumed almost entirely detritus, with diatoms usually representing less than 5% of the total gut contents.

Baetidae – Diatom consumption by Stauffer 1 *Baetis* spp. accounted for nearly 15% of the total stomach contents throughout the year (Fig. 1). The only pronounced deviation occurred at the end of July when diatom consumption increased to 60%. Diatom ingestion in July occurred when diatom population levels were low. Seasonal diatom ingestion by *Baetis* populations of Stauffer 2 more closely approximated diatom standing crops (Fig. 4). Consumption was

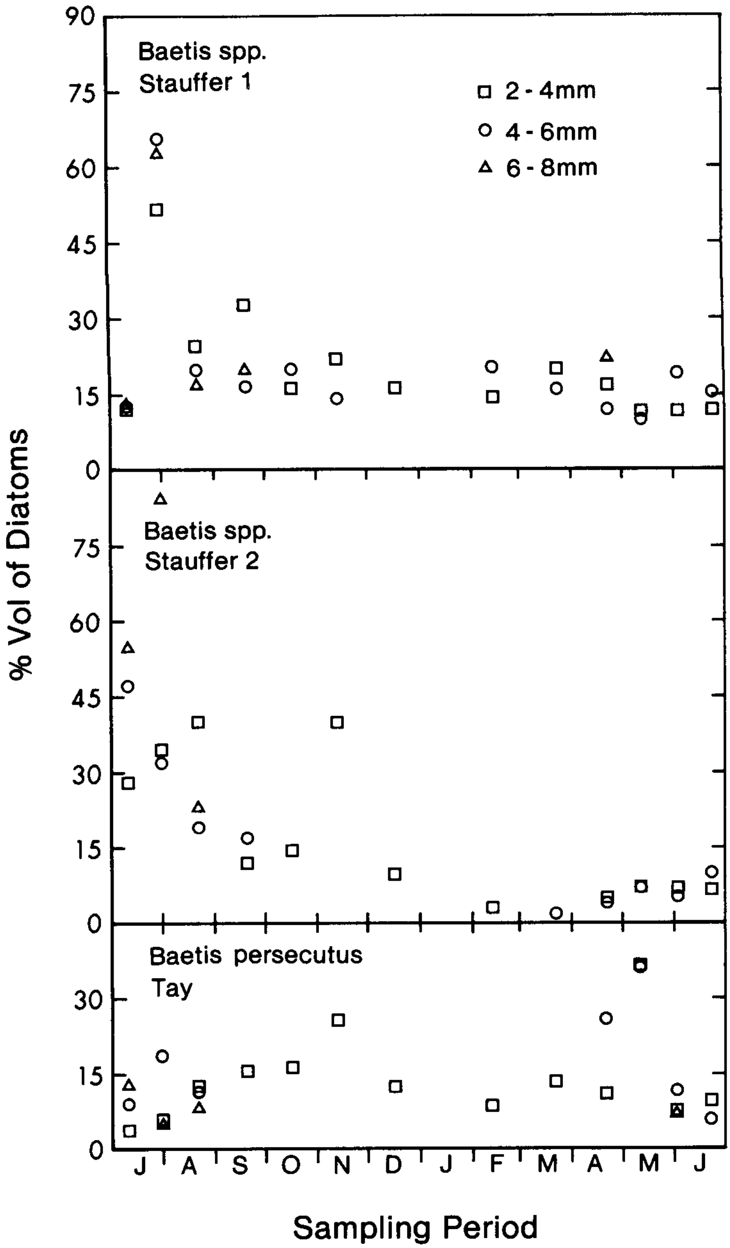


Fig. 1. Proportion of total ingested material composed of diatoms for the various size classes of *Baetis* spp. (Stauffer 1 and 2) and *Baetis persecutus* (Tay River) populations.

greater during summer and fall, then declined during winter and spring. *Baetis tricaudatus* populations from the Bigoray River had a diatom ingestion pattern that corresponded well to diatom population levels. Also, diatom ingestion by Tay River populations of *B. persecutus* (Fig. 1) corresponded to diatom abundance levels during summer and fall; however, a substantial spring increase in diatom consumption cannot be attributed to diatom availability.

The *Centroptilum* spp. are summer species and their life cycles were too short to discern seasonal ingestion patterns. The *Callibaetis coloradensis* population in the Bigoray River had a diatom consumption pattern that correlated well with diatom standing crops. Greatest ingestion (25% of total stomach contents) occurred during July.

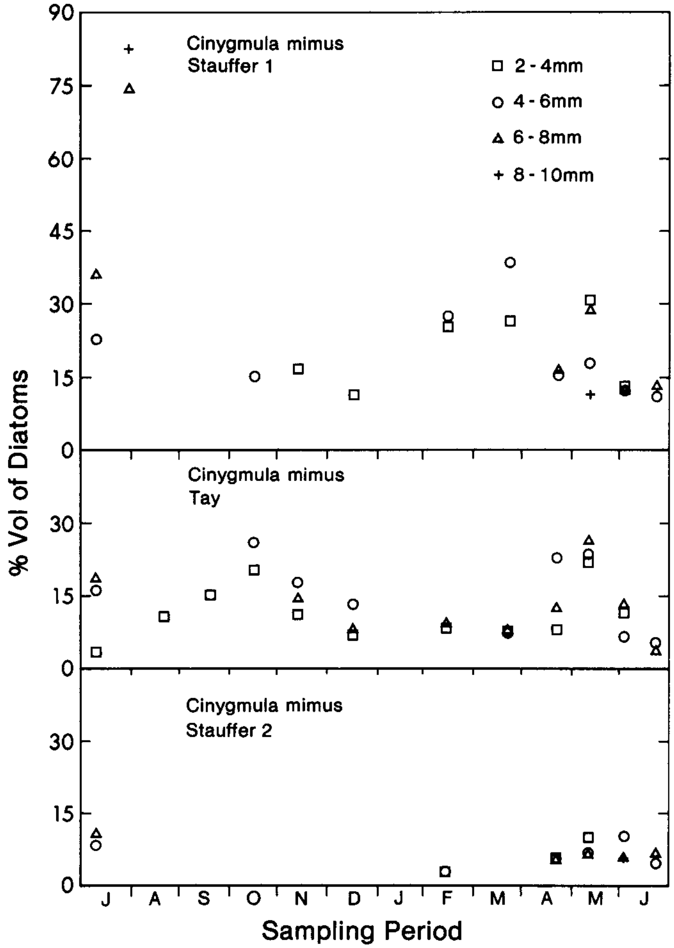


Fig. 2. Proportion of total ingested material composed of diatoms for the various size classes of *Cinygmula mimus* (Stauffer 1 and 2, and Tay River) populations.

Heptageniidae – Ingestion of diatoms by *Cinygmula mimus,* the most abundant heptageniid encountered, varied considerably between Stauffer Creek sites and the Tay River (Fig. 2). The greatest relative consumption of diatoms by any of the mayflies studied was exhibited by *C. mimus* nymphs of Stauffer 1, where diatoms accounted for 70 to 80% of the total ingested volume in late July, when the nymphs were mature. Diatom ingestion patterns of *C. mimus* populations were largely independent of diatom population levels at both Stauffer Creek sites. In contrast, ingestion of diatoms by *C. mimus* in the Tay River coincided well with standing crops.

The only seasonal pattern evident for *Epeorus* sp., found only in the Tay River, was elevated diatom consumption by nearly mature nymphs. *Rhithrogena* sp. nymphs were also collected from the Tay River, but seasonal patterns were lacking.

Ephemerellidae – Amongst ephemerellids, seasonal patterns of diatom ingestion varied considerably between species and locations. The *Ephemerella inermis* population of Stauffer 1 consistently exhibited a diatom consumption of about 10% of total stomach content throughout its life cycle (Fig. 3). At Stauffer site 2, *E. inermis* ate more diatoms during summer and fall when diatom standing crops were high; relative diatom ingestion decreased along with diatom populations during winter. The *E. inermis* population of Tay River ingested relatively low levels of diatoms.

Ingestion patterns of diatoms appeared independent of diatom standing crops for *Drunella flavilinea* and *Serratella tibialis* populations. Diatom consumption by *Drunella spinifera* was exceptionally variable, ranging from 2% to 45% of the material ingested. Ingestion patterns for *D. spinifera* nymphs from Tay River and Stauffer Creek generally coincided with diatom population levels, high during autumn and low during early spring.

Other Families – Amongst taxa with low overall diatom consumption, variability by season was not evident. These include populations of *Ephemera simulans* (Fig. 3), *Paraleptophlebia, Caenis simulans, Ameletus sparsatus, Siphlonurus alternatus, Stenacron canadense,* and *Siphloplecton basale. Leptophlebia cupida* populations from the Bigoray River (Fig. 3) ingested low quantities of diatoms throughout the year, whereas *Leptophlebia* populations from Stauffer-2 had elevated diatom consumption during October and November, coincident with a diatom bloom at that site.

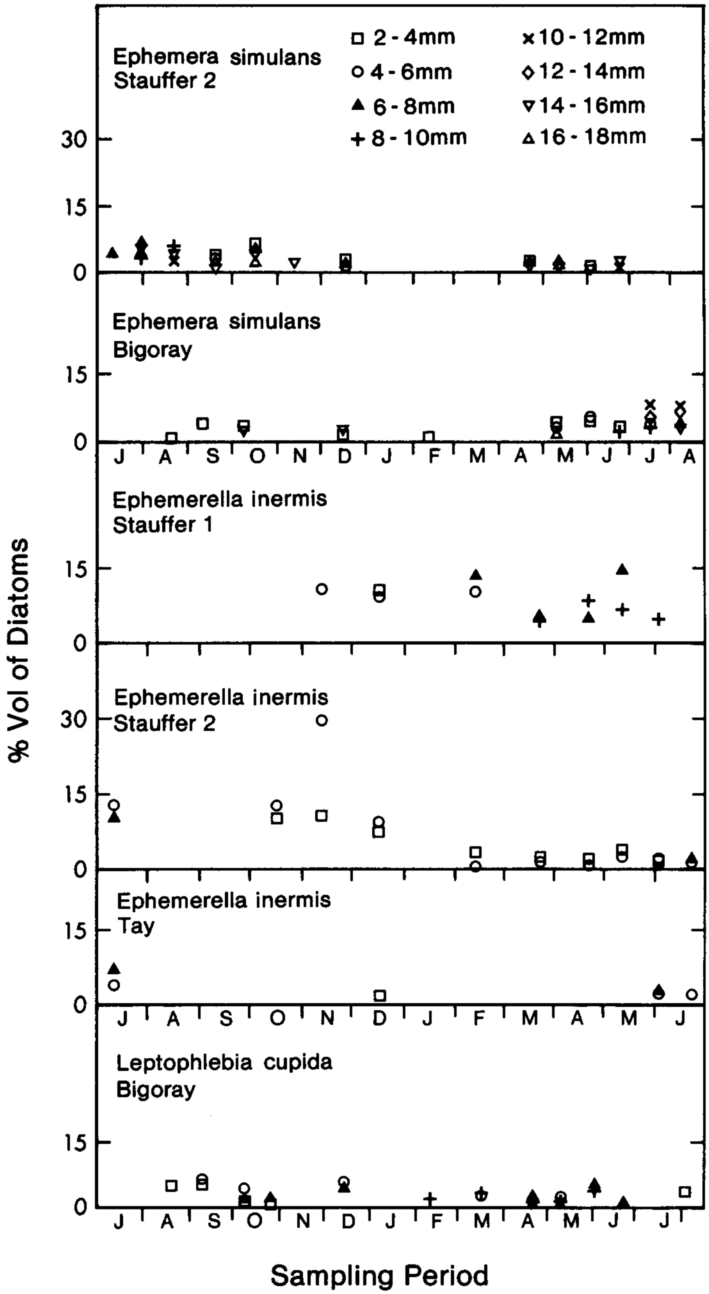


Fig. 3. Proportion of total ingested material composed of diatoms for the various size classes of *Ephemera simulans* (Stauffer 2 and Bigoray River), *Ephemerella inermis* (Stauffer 1 and 2, and Tay River), and *Leptophlebia cupida* (Bigoray River) populations.

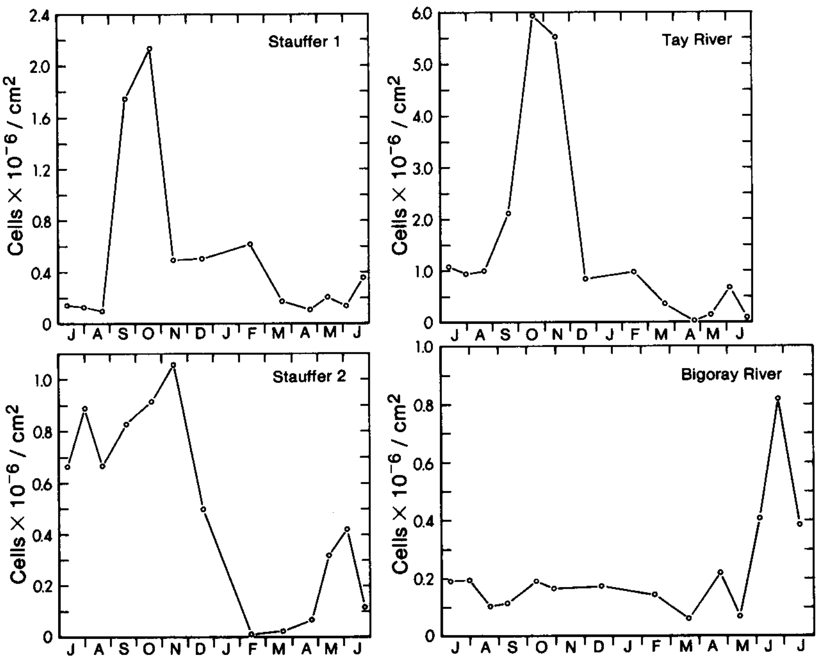


Fig. 4. Epilithic diatom sampling crops of the four study sites, 1975–1976.

## Animal material

*Drunella spinifera* was the only mayfly ingesting relatively large quantities of animal material. Nymphs of larger size classes, 6–8 mm and greater, contained substantial quantities of animal material, but it was not possible to quantify (by volume) the amount ingested. Most of the animal material consisted of insect head capsules, legs, and mouthparts, the only recognizable taxa being fragments of ephemeropteran nymphs and chironomid larvae. The large amount of animal material ingested would indicate *D. spinifera* nymphs are at least facultative predators, rather than incidental consumers of dead animal material. Even if predaceous, nymphs probably obtained considerable nutrition from the large quantities of detritus and diatoms consumed.

## Particle size and volume of ingested material

Mayfly nymphs ingested particles that were usually less than 160 μm in diameter; larger particles were rarely ingested, except for relatively large invertebrate tissue fragments. Particle size data of each sample were partitioned into four particle size classes (PSC) based on diameter categories: PSC-I = 1.6–32 μm, PSC-II = 32–64 μm, PSC-III = 64–101 μm, and PSC-IV =

101–161 μm. The proportion of total volume of consumed material made up of particles in each PSC range was calculated, and the average proportions for all populations of each site (all sampling dates and size classes combined) are shown in Table 4.

Table 4. Average percentage of volume material consumed in each of four particle size ranges by all populations of each site.

| Site | Particle Size Classes (μm) I (<32) | II (32–64) | III (64–101) | IV (101–161) |
|---|---|---|---|---|
| Bigoray River | 64.1 | 23.3 | 8.2 | 3.8 |
| Tay River | 67.9 | 16.8 | 9.2 | 6.1 |
| Stauffer-1 | 54.8 | 25.4 | 12.8 | 7.0 |
| Stauffer-2 | 69.4 | 16.7 | 9.1 | 4.8 |
| Average, all sites | 64.1 | 20.6 | 9.8 | 5.4 |

For the entire study, 64.1% of all food items consumed consisted of particles in PSC-I (32 μm diameter or less). Only 5% of the average volumes ingested was greater than 100 μm. Stauffer-1 populations consumed the relatively greatest amount of very large particles, and the Bigoray River populations consumed the smallest volume of very large particles. Baetids generally consumed above average proportions of small PSC-I size particles. *Cinygmula mimus*, *Rhithrogena* sp., *Ephemera simulans*, and *Paraleptophlebia debilis* populations also contained proportionally large quantities of small PSC-I particles. Nymphs of the other taxa consumed about average or less than average quantities of the small PSC-I particles. *Drunella spinifera* was the only species consuming large volumes of large particles (PSC-IV), the average percentages of PSC-IV particles being 20% (Stauffer-1 and -2).

There were seasonal trends in size of particles ingested for several taxa (Fig. 5). Of the 13 major taxa treated, 6 had a pronounced reduction in the ingestion of small particles during autumn; these were *Baetis* spp., *E. Simulans* and *D. spinifera* from Stauffer-2, *L. cupida* and *E. simulans* from the Bigoray River, and *C. mimus* from Stauffer-1. This trend may partially be accounted for by an autumn increase in the overall size of available detrital particles in the streams due to leaf fall. There was also a spring decline in small particle consumption amongst some of the *Baetis* spp., *C. mimus* and ephemerellids.

Volumes of ingested material by nymphs of a particular size class were statistically similar for the four sites. Average volume of material ($\mu m \times 10^{-6}$) ingested for nymphs of each size class (combining all populations of all sites) was 14.7 (2–4 mm), 57.1 (4–6 mm), 123.1 (6–8 mm), 216.1 (8–10 mm), 444.0 (10–12 mm), 687.5 (12–14 mm), 926.7 (14–16 mm), and 1155.0 (16–18 mm).

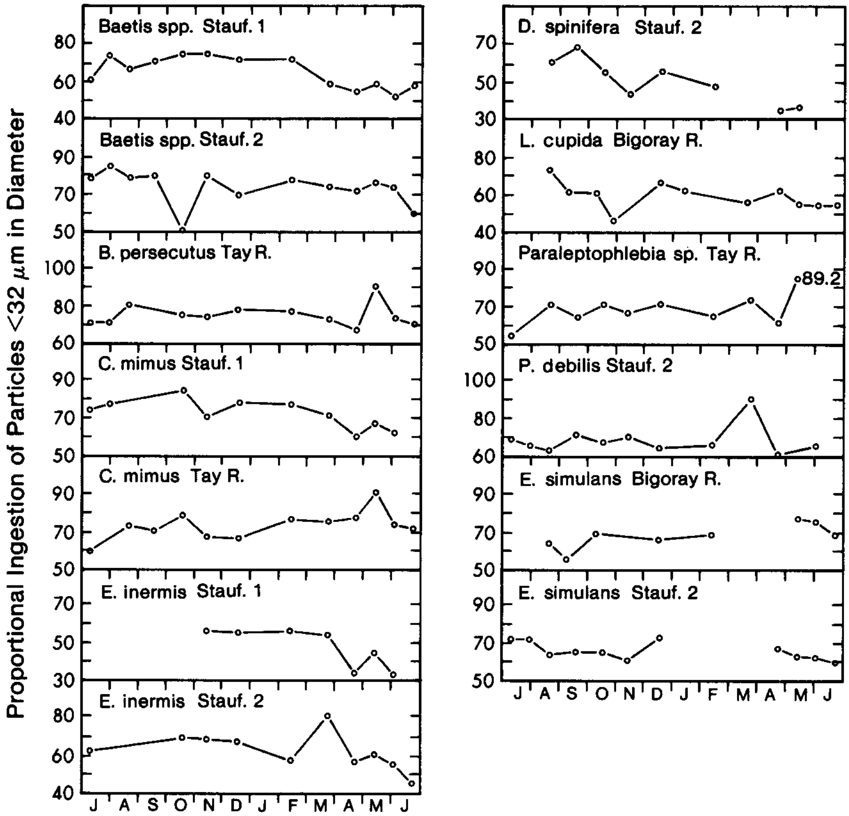


Fig. 5. Percentage ingestion of particles less than 32 μm in diameter by major taxa, 1975–1976.

The relationship between total volume ingested and total length of the nymphs fitted an exponential function, which in its linear form was

$$\log_e V = 1.988 + 0.357\,L\ (r^2 = 0.86,\ n = 119)$$

where $V$ is total volume of stomach contents, $L$ is the median total length of each size class, e.g. 3, 5, 7 mm, etc., and 1.988 and 0.357 are the regression line coefficients.

All baetids ingested low total volumes of material when compared to average volumes ingested for each size class. Generally *Leptophlebia* and *Paraleptophlebia* populations ingested above average volumes of material. *Caenis simulans* stomachs contained below average food volumes during the ice-free season and all specimens had empty guts during the winter months. *Caenis* was the only species that ceased feeding entirely during the winter. There were no consistent trends in regard to food volume and size class averages of food volume for the other species.

## Analysis of diatoms consumed

Relative abundance of the various diatom species ingested by each mayfly species was analyzed using multivariate methods. Cluster analysis was used to group mayfly species into clusters based upon similarities amongst species and relative abundances of diatoms ingested. Principal component analysis (PCA) was then utilized to distinguish the diatom species that were most important in defining each cluster. Details of the techniques are generally described by LEE (1971), SNEATH & SOKAL (1973), CLIFFORD & STEPHENSON (1975), and BOLAND (1976). The application to aquatic communities include studies by ROBACK et al. (1969), de MARCH (1976), BOLAND (1976), and SPRULES (1977).

Cluster and principal component analyses were carried out on stomach content data of each site for one sampling date each season. Ingested diatoms were analyzed separately by site, because of possible differences in diatom availability between sampling locations. We did not analyze stomach samples from more than one sampling date at one time, because seasonal changes in available diatom composition could mask any differential ingestion of diatom species. Sampling dates used in the analysis often varied between sites; this was necessary to maximize the number of populations and size classes that could be included in each multivariate analysis.

We used the multivariate analysis program entitled Clustan (WISHART 1975) for both cluster analysis and PCA. Data from Stauffer-2 on 10 July 1975 is used as an example. Data entered the computer as a matrix with rows representing size classes of mayfly populations (e. g. *Baetis* 2–4 mm) and columns representing proportional abundances of diatom species from the guts of each size class. Diatom species not accounting for 3% of the total number of diatoms consumed by at least one nymphal size class were excluded to increase normality of the data. Proportional data (instead of absolute cell counts) were used to prevent clustering of samples based on absolute quantity of each diatom consumed instead of on its relative abundance (CLARKE 1976). For example, a 4–6 mm *Baetis* nymph may consume twice as many *Achnanthes* as a 2–4 mm specimen; but the relative composition of *Achnanthes* with respect to all diatoms consumed may be similar for both samples.

Cluster analysis consisted of calculating a similarity matrix between samples using the Squared Euclidean Distance Method (SNEATH & SOKAL 1973). Clustering of samples was then done using WARD's Hierarchical Fusion Method (WARD 1963). For the Stauffer-2 example, the clustering procedure defined two major groups of gut samples (Fig. 6). Diatoms contained in the guts of all size classes of *Baetis* and *Ephemerella inermis* populations were similar and distinct from diatoms present in the guts of *Cinygmula mimus*, *Paraleptophlebia debilis* and *Ephemera simulans*.

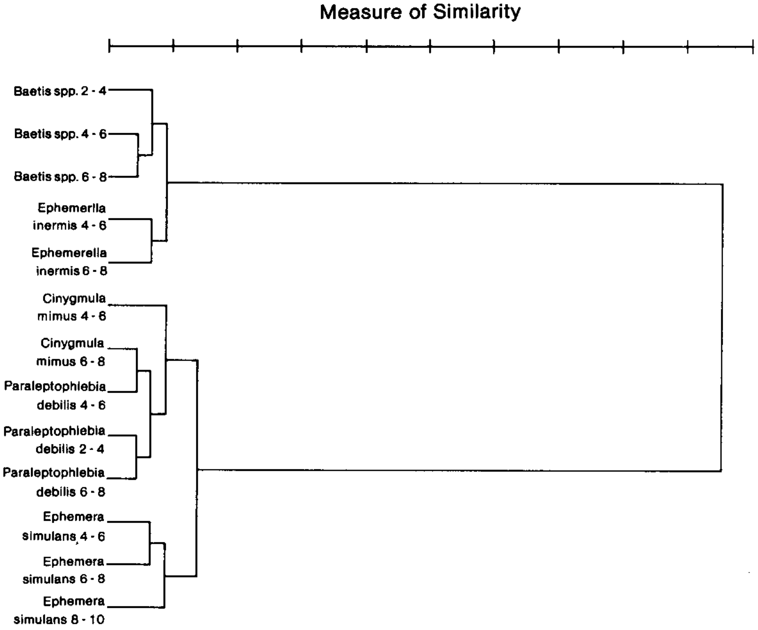


Fig. 6. Cluster analysis dendrogram of diatoms ingested by each mayfly size class analyzed 10 July 1975, Stauffer-2.

Principal component analysis on these data involves calculation of a correlation matrix from which eigenvalues and eigenvectors were derived. Eigenvalues and eigenvectors summarize any variation in diatoms consumed in a more condensed form than the raw data matrix. The first 10 eigenvectors (rows) and corresponding eigenvalues for the Stauffer-2 example are presented in Table 5. The proportion of the total variance in the data that can be explained by each eigenvector is derived from the eigenvalue. The first eigenvector of the Stauffer example accounts for 40.80% of the total variance in diatom ingestion, the second 22.62%, and the third 12.57%. Each successive eigenvector accounts for a lesser proportion of the total variance. The first two eigenvectors usually explain most of the data variance; therefore they were the only ones analyzed.

Individual values of an eigenvector indicate the importance of each diatom species in accounting for the proportion of the variance explained by that eigenvector. For vector 1 in the example, *Fragilaria construens, F. leptostauron* var. *dubia, F. leptostauron* and *Achnanthes* spp. had high positive correlations with component one, while *Cocconeis placentula* had a high negative correlation. A bivariate plot can then be produced indicating the location of each stomach sample included in the analysis with respect to the first two principal components. Position of a stomach sample is determined by calculating its factor scores from the first and second eigenvectors. A factor score is a sum

Table 5. Principal components analysis of ingested diatoms for Stauffer-2 gut samples, 10 July 1975.

| | | Eigenvectors | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Eigenvalue | % Variance | *Fragilaria leptostauron* | *Fragilaria lepto-stauron* var. *dubia* | *Navicula* sp. A | *Cocconeis placentula* | *Fragilaria construens* | *Achnanthes* spp. | *Nitzchia* sp. B | Other species | *Navicula viridula* | *Navicula cryptocephala* |
| 4.08 | 40.80 | 0.39 | 0.39 | 0.17 | −0.49 | 0.39 | 0.28 | 0.15 | 0.39 | 0.03 | −0.13 |
| 2.26 | 22.62 | −0.32 | −0.07 | −0.23 | −0.07 | −0.03 | 0.32 | 0.57 | 0.13 | 0.33 | 0.54 |
| 1.26 | 12.57 | 0.10 | −0.25 | 0.69 | 0.04 | −0.37 | −0.04 | −0.14 | 0.40 | 0.32 | 0.18 |
| 1.07 | 10.72 | 0.05 | 0.26 | −0.30 | 0.01 | −0.16 | −0.46 | 0.09 | 0.12 | 0.68 | −0.34 |
| 0.55 | 5.49 | −0.08 | −0.42 | −0.21 | −0.00 | 0.22 | 0.54 | −0.45 | 0.03 | 0.40 | −0.27 |
| 0.41 | 4.10 | −0.42 | 0.44 | −0.06 | 0.09 | −0.50 | 0.38 | −0.09 | 0.30 | −0.21 | −0.29 |
| 0.18 | 1.80 | 0.47 | −0.34 | −0.48 | 0.14 | −0.23 | −0.03 | 0.08 | 0.51 | −0.29 | 0.01 |
| 0.12 | 1.16 | −0.50 | −0.02 | −0.09 | −0.10 | 0.39 | −0.40 | −0.32 | 0.52 | −0.12 | 0.19 |
| 0.07 | 0.72 | −0.27 | −0.40 | 0.23 | 0.06 | 0.17 | −0.08 | 0.55 | 0.12 | −0.12 | −0.59 |
| 0.00 | 0.00 | 0.12 | 0.26 | 0.11 | 0.84 | 0.37 | 0.12 | 0.06 | 0.15 | 0.08 | 0.05 |

of the proportionate abundance of each diatom species in the stomach sample times their corresponding component coefficient in the eigenvector.

The plot for the example indicates the first principal component to be along the horizontal axis and the second to be along the vertical axis (Fig. 7).

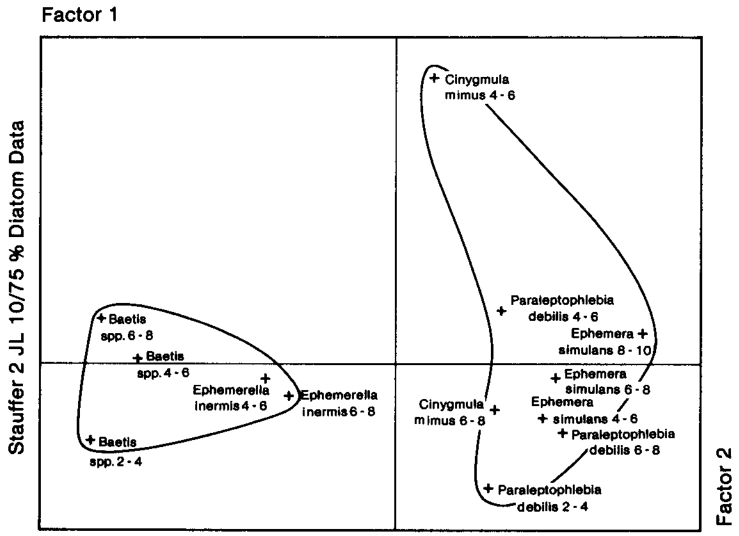


Fig. 7. First two principal components; location of each gut sample analyzed with respect to each indicated component, 10 July 1975, Stauffer-2.

The two components intersect at 0 with increasing positive values on one side of the intersection and negative values on the other side. The position of the 6–8 mm *Baetis* nymphs in the example indicates a large negative factor score for the first principal component and a small positive factor score on the second principal component. From this position, we inferred that diatom species with high negative values in eigenvector one were ingested by 6–8 mm *Baetis* spp. in high proportions, while diatoms with high positive values were not. A positive factor score for principal component two indicates that the positively correlated diatom species in eigenvector two were slightly more important. The stomach samples are grouped along factor one in a fashion similar to groupings produced by the cluster analysis. Clusters from the cluster dendrogram have been superimposed on the bivariate plot to compensate for distortions resulting from a change in dimensionality in the PCA (Sprules 1977).

In summary for the Stauffer-2 example, the first principal component accounts for most of the variance in diatoms ingested. This first component, along with the cluster analysis, divides the mayflies into two groups. One group includes all *Baetis* spp. and *Ephemerella inermis* stomach samples and is characterized by a high ingestion of *C. placentula*. The other group contains the remaining species and is characterized by a lack of *C. placentula* and an abundance of *Fragilaria construens, F. leptostauron* and *F. leptostauron* var. *dubia* in the guts. The second principal component further separates 4–6 mm *Cinygmula mimus* nymphs from other members of this group due to a relatively greater ingestion of *Nitzchia B, Navicula cryptocephala, N. viridula* and *Achnanthes* spp.

## Stauffer-1

Major clusters and diatoms most critical in defining each corresponding group are summarized in Tables 6 and 7. When the significant diatoms of each major group are analyzed for all seasons, a uniformity of diatom types is evident. General trends in size classes and species of ephemeropterans that occur in each group can also be detected; however, more seasonal variability occurs than with the diatoms.

Several workers have indicated that diatoms are relatively specific in their microhabitat selection. Although more work is needed in this area, major microhabitat partitions of some common stream diatom species have been determined (BLUM 1960; ROUND 1964). The major substrate habitats of diatoms in streams are defined as epilithic (stony substrate), epipelic (depositional substrate type) and epiphytic (attached to other plant material) (HYNES 1972). We used a literature-based microhabitat classification of diatoms (GUMTOW 1955; ROUND 1955, 1964; DOUGLAS 1958; BLUM 1960; HYNES 1972; HUTCHINSON 1975; MOORE 1976) to obtain microhabitat preferences of benthic stream diatoms relevant to our study. Only epilithic and epipelic diatoms were considered because most sampling was done in areas where these substrates predominate. A species is recorded as epipelic or epilithic if it achieves greatest relative abundance on that habitat type. Most species will likely be found incidentally in other habitats as well (HUTCHINSON 1975).

When diatom species characteristic of Group 1 (Tables 6 and 7) of Stauffer site 1 are compared with the habitat preference list, the frequently occurring species were considered mainly epilithic; e. g. *Cocconeis placentula, Achnanthes* spp., *Cymbella sinuata, Synedra* sp. Representatives of Group 2 are predominantly epipelic, e. g. *Fragilaria leptostauron, F. leptostauron* var. *dubia, F. construens,* and *Navicula* sp. Representatives of Group 3 are not as closely defined, although they appear to be mainly epipelic species.

If the dominant type of diatom ingested (epilithic or epipelic) is known, it is possible to predict where on the substrate the nymphs in question are feeding. Group 1 mayflies can be considered to feed in areas where epilithic diatoms are most abundant, which would include exposed areas of high current velocity such as upper substrate surfaces. Group 1 nymphs therefore have been classified as "surface feeders". Group 2 ephemeropterans represent species

Table 6. PC analysis summary of ingested diatoms for various size classes of nymphs, Stauffer 1.

| | 30 July, 1975 | mm | 14 November, 1975 | mm | 14 February, 1976 | mm | 23 April, 1976 | mm |
|---|---|---|---|---|---|---|---|---|
| group 1 | *Cinygmula mimus* | 6–8 | *Cinygmula mimus* | 2–4 | *Cinygmula mimus* | 4–6 | *Cinygmula mimus* | 4–6 |
| (surface feeders) | | 8–10 | | | *Baetis* spp. | 2–4 | | 6–8 |
| | *Baetis* spp. | 2–4 | | | *Cinygmula mimus* | 2–4 | *Baetis* spp. | 6–8 |
| | | 4–6 | | | | | | |
| group 2 | *Baetis* spp. | 6–8 | *Baetis* spp. | 4–6 | *Baetis* spp. | 4–6 | *Baetis* spp. | 2–4 |
| (interstitial feeders) | *Serratella tibialis* | 4–6 | | 2–4 | *Ephemerella inermis* | 6–8 | | 4–6 |
| | | 6–8 | *Ephemerella inermis* | 4–6 | | 4–6 | *Ephemerella inermis* | 8–10 |
| | | | *Serratella tibialis* | 6–8 | | | | 6–8 |
| group 3 (fluctuating) | | | *Drunella spinifera* | 6–8 | *Baetis* spp. | 2–4 | *Drunella spinifera* | 10–12 |

Table 7. Relevant diatom taxa defining ingestion clusters of Stauffer-1 mayflies (see text for further explanation).

| | 30 July, 1975 | 14 November, 1975 | 14 February, 1976 | 23 April, 1976 |
|---|---|---|---|---|
| group 1<br>(surface feeders) | *Achnanthes* spp. *<br>*Cocconeis placentula* *<br>*Synedra* sp. * | *Cocconeis placentula* *<br>*Achnanthes* spp. *<br>*Cymbella sinuata* * | *Cocconeis placentula* *<br>*Cymbella sinuata* *<br>*Achnanthes* spp. *<br>*Synedra* sp. A * | *Cymbella sinuata* *<br>*Cocconeis placentula* *<br>*Achnanthes* spp. * |
| group 2<br>(interstitial feeders) | *Fragilaria construens* +<br>*Fragilaria leptostauron* var. *dubia* +<br>*Fragilaria leptostauron* +<br>Other species | *Fragilaria leptostauron* +<br>*Fragilaria leptostauron* var. *dubia* +<br>*Fragilaria construens* + | *Fragilaria leptostauron* +<br>Other species<br>*Fragilaria construens* +<br>*Navicula* sp. B +<br>*Fragilaria pinnata* | *Fragilaria construens* +<br>*Fragilaria leptostauron* + |
| group 3<br>(fluctuating) | | *Navicula* sp. B +<br>*Nitzchia* sp. A +<br>*Cymbella cymbiformis* + | *Fragilaria leptostauron* var. *dubia* +<br>*Synedra* sp. A *<br>Other species<br>*Fragilaria leptostauron* + | *Navicula* sp. B +<br>*Fragilaria leptostauron* + |

* Epilithic species
\+ Epipelic species

feeding in areas with relatively higher epipelic diatom populations, namely interstices or the rock surfaces adjacent to them; these are called "interstitial feeders". Members of Group 3 do not fit either category; these nymphs may feed in either area and are referred to as "fluctuating".

Analysis of Stauffer-1 mayflies belonging to each group indicates that all size classes of *Cinygmula mimus*, on all dates analyzed, are surface feeders. Conversely, *Ephemerella inermis* and *Serratella tibialis* nymphs are consistent interstitial feeders. *Baetis* spp. size classes fluctuate between the two groups. *Drunella spinifera* always clustered separately as a third group, as did the 2–4 mm class of *Baetis* nymphs on 14 February 1976.

## Stauffer-2

Diatom associations at Stauffer-2 were similar to those of Stauffer-1 except for more frequent occurrence of epipelic diatom species in nymphs of the Group 1 clusters (Tables 8 and 9). This may be due to the greater diatom diversity at Stauffer-2 or to a lower current velocity and greater mean depth allowing more frequent occurrence of epipelic diatoms in surface habitats. In contrast to Stauffer-1, *Baetis* spp. were consistent members of the surface feeding group at Stauffer-2. Baetids were the only nymphs occurring entirely in this group. *Ephemerella inermis* nymphs were surface feeders during July and October, but interstitial feeders during February and April. *Leptophlebia* nymphs were primarily members of the surface group, except for the 2–4 mm nymphs on 14 February. *Paraleptophlebia debilis* size classes usually belonged to the interstitial group during summer and autumn, with a switch to the surface group by most size classes during spring and summer. *Ephemera simulans* nymphs were always interstitial feeders except for the 2–4 mm size class in April. *Cinygmula mimus* populations were consistently interstitial feeders, and this is in contrast to members of the Stauffer-1 population, which were surface feeders. *Drunella spinifera* nymphs occurred in all three groups.

## Tay River

Tay River surface feeders include all *Cinygmula mimus*, *Epeorus* sp., *E. inermis* and most *Baetis persecutus* nymphs (Tables 10 and 11). The summer species *Drunella flavilinea* and *Serratella tibialis* had members in both groups, with the very small nymphs tending to be mainly surface feeders. Interstitial feeders in the Tay River include *D. spinifera* and *Pseudocloeon* sp. for all samples analyzed. *Paraleptophlebia* and *Ameletus sparsatus* usually belonged to the interstitial group, but occasionally clustered out as surface feeders.

Table 8. PC analysis summary of ingested diatoms for various size classes of nymphs, Stauffer 2.

| | 30 July, 1975 | mm | 18 October, 1975 | mm | 14 February, 1976 | mm | 23 April, 1976 | mm |
|---|---|---|---|---|---|---|---|---|
| group 1 | *Baetis* spp. | 2–4 | *Baetis* spp. | 2–4 | *Paraleptophlebia debilis* | 4–6 | *Baetis* spp. | 2–4 |
| (surface feeders) | | 6–8 | *Ephemerella inermis* | 4–6 | *Baetis* spp. | 2–4 | *Cinygmula mimus* | 4–6 |
| | | 4–6 | *Leptophlebia* sp. | 2–4 | *Leptophlebia* spp. | 4–6 | | 2–4 |
| | *Ephemerella inermis* | 4–6 | *Ephemerella inermis* | 2–4 | | 6–8 | | 6–8 |
| | | 6–8 | *Leptophlebia* sp. | 4–6 | | | *Baetis* spp. | 4–6 |
| | | | | | | | *Drunella spinifera* | 10–12 |
| | | | | | | | *Ephemera simulans* | 2–4 |
| | | | | | | | *Paraleptophlebia debilis* | 4–6 |
| group 2 | *Cinygmula mimus* | 4–6 | *Paraleptophlebia debilis* | 4–6 | *Leptophlebia* spp. | 2–4 | *Drunella spinifera* | 8–10 |
| (interstitial feeders) | *Paraleptophlebia debilis* | 2–4 | *Ephemera simulans* | 16–18 | *Ephemerella inermis* | 4–6 | *Ephemerella inermis* | 6–8 |
| | *Cinygmula mimus* | 6–8 | | 14–16 | *Cinygmula mimus* | 2–4 | *Ephemera simulans* | 16–18 |
| | *Paraleptophlebia debilis* | 4–6 | | 10–12 | *Ephemerella inermis* | 2–4 | | 14–16 |
| | | | | 12–14 | *Paraleptophlebia debilis* | 6–8 | *Ephemerella inermis* | 2–4 |
| | | | | 2–4 | *Drunella spinifera* | 8–10 | *Ephemera simulans* | 12–14 |
| | | | *Paraleptophlebia debilis* | 2–4 | | | | 10–12 |
| | | | | | | | | 8–10 |
| group 3 (fluctuating) | *Cinygmula mimus* | 4–6 | *Drunella spinifera* | 8–10 | | | *Ephemerella inermis* | 4–6 |

Table 9. Relevant diatom taxa defining ingestion clusters of Stauffer-2 mayflies (see text for further explanation).

| | 30 July, 1975 | 18 October, 1975 | 14 February, 1976 | 23 April, 1976 |
|---|---|---|---|---|
| group 1<br>(surface feeders) | *Cocconeis placentula* *<br>*Navicula cryptocephala* + | *Synedra* sp. B *<br>*Gomphonema* sp. *<br>*Navicula* sp. A +<br>*Cymbella sinuata* * | *Cocconeis placentula* *<br>*Nitzchia* sp. A. +<br>*Cymbella cymbiformis* *<br>*Fragilaria leptostauron* + | *Achnanthes* spp. *<br>*Navicula* sp. B +<br>*Cocconeis placentula* *<br>*Fragilaria leptostauron* var. *dubia* + |
| group 2<br>(interstitial feeders) | *Fragilaria construens* +<br>Other species<br>*Fragilaria leptostauron* var. *dubia* +<br>*Fragilaria leptostauron* + | *Fragilaria construens* +<br>*Fragilaria leptostauron* var. *dubia* +<br>*Fragilaria leptostauron* +<br>*Navicula tripunctata* + | *Fragilaria construens* +<br>*Synedra* sp. A *<br>Other species<br>*Fragilaria pinnata* | *Gyrosigma* sp. +<br>*Fragilaria construens* +<br>*Synedra amphicephala* +<br>*Fragilaria leptostauron* + |
| group 3<br>(fluctuating) | *Nitzchia* sp. B +<br>*Navicula cryptocephala* +<br>*Navicula viridula* +<br>*Achnanthes* * | *Fragialria pinnata*<br>*Cymbella* sp. C *<br>*Navicula tripunctata* +<br>*Synedra* sp. A * | | *Fragilaria pinnata*<br>Other species<br>*Fragilaria leptostauron* var. *dubia* + |

* Epilithic species
\+ Epipelic species

Table 10. PC analysis summary of ingested diatoms for various size classes of nymphs, Tay River.

| | 10 July, 1975 | mm | 14 November, 1975 | mm | 14 February, 1976 | mm | 13 May, 1976 | mm |
|---|---|---|---|---|---|---|---|---|
| group 1 | Cinygmula mimus | 4–5 | *Cinygmula mimus* | 2–4 | *Cinygmula mimus* | 6–8 | *Baetis persecutus* | 4–6 |
| (surface feeders) | | 3–4 | | 4–6 | | 2–4 | | 2–4 |
| | | 6–7 | | 6–8 | *Baetis persecutus* | 2–4 | *Cinygmula mimus* | 4–6 |
| | *Epeorus* sp. | 5–6 | | | *Rhithrogena* sp. | 6–8 | | 6–8 |
| | | 7–8 | | | *Ephemerella inermis* | 2–4 | | 2–4 |
| | | 6–7 | | | *Cinygmula mimus* | 4–6 | *Drunella flavilinea* | 2–4 |
| | *Baetis persecutus* | 6–8 | | | *Ameletus sparsatus* | 4–6 | *Epeorus* sp. | 2–4 |
| | | 2–4 | | | *Paraleptophlebia* sp. | 4–6 | | |
| | *Drunella flavilinea* | 8–9 | | | | | | |
| | *Baetis persecutus* | 4–6 | | | | | | |
| | *Ephemerella inermis* | 6–8 | | | | | | |
| | *Cinygmula mimus* | 7–8 | | | | | | |
| | *Ephemerella inermis* | 4–5 | | | | | | |
| | *Cinygmula mimus* | 5–6 | | | | | | |
| | *Serratella tibialis* | 2–3 | | | | | | |
| | *Paraleptophlebia* sp. | 2–4 | | | | | | |
| group 2 | *Pseudocloeon* sp. | 2–4 | *Rhithrogena* sp. | 4–6 | *Paraleptophlebia* sp. | 6–8 | *Paraleptophlebia* sp. | 4–6 |
| (interstitial feeders) | | 4–6 | *Drunella spinifera* | 8–10 | *Ameletus sparsatus* | 10–12 | | 6–8 |
| | *Drunella flavilinea* | 6–8 | *Baetis persecutus* | 2–4 | | 12–14 | | |
| | *Serratella tibialis* | 4–6 | *Paraleptophlebia* sp. | 4–6 | | 8–10 | | |
| | | | *Rhithrogena* sp. | 6–8 | | 6–8 | | |
| | | | *Drunella spinifera* | 6–8 | *Paraleptophlebia* sp. | 2–4 | | |
| | | | *Ameletus sparsatus* | 8–10 | | | | |
| group 3 | | | *Paraleptophlebia* sp. | 2–4 | *Paraleptophlebia* sp. | 2–4 | | |
| (fluctuating) | | | | 4–6 | | | | |

Table 11. Relevant diatom taxa defining ingestion clusters of Tay River mayflies (see text for further explanation).

| | 10 July, 1975 | 14 November, 1975 | 14 February, 1976 | 13 May, 1976 |
|---|---|---|---|---|
| group 1<br>(surface feeders) | *Cymbella sinuata* *<br>*Gomphonema* sp. A *<br>*Cocconeis placentula* *<br>*Achnanthes* spp. *<br>Other species<br>*Navicula* sp. A +<br>*Navicula tripunctata* + | *Cymbella* spp. *<br>*Cocconeis placentula* *<br>*Cymbella sinuata* *<br>*Achnanthes* spp. * | *Cymbella sinuata* *<br>Other species<br>*Navicula* sp. A +<br>Gomphonema sp. A *<br>*Cymbella* spp. *<br>*Coccneis placentula* * | *Gomphonema* sp. A *<br>*Cocconeis placentula* *<br>*Cymbella* spp. *<br>*Cymbella sinuata* *<br>*Achnanthes* spp. *<br>Other species |
| group 2<br>(interstitial feeders) | *Navicula cryptocephala* +<br>*Synedra amphicephala* +<br>*Didymosphenia geminata*<br>*Cymbella* spp. +<br>*Navicula tripunctata* +<br>*Navicula* sp. A +<br>*Synedra* sp. B * | *Cymbella* spp. +<br>*Diatoma* sp. +<br>*Synedra amphicephala* +<br>*Navicula cryptocephala* +<br>*Fragilaria construens* +<br>*Synedra* sp. B *<br>*Nitzchia* sp. B + | *Achnanthes* spp. *<br>*Cymbella* spp. +<br>*Navicula tripunctata* +<br>*Didymosphenia geminata*<br>*Synedra* sp. B *<br>*Fragilaria construens* +<br>*Meridion circulare* *+<br>*Nitzchia* sp. B + | *Navicula* sp. A +<br>*Achnanthes* spp. *<br>*Fragilaria construens* +<br>*Cymbella* spp. +<br>*Synedra amphicephala* +<br>*Nitzchia* sp. B +<br>Other species<br>*Navicula cryptocephala* +<br>*Navicula tripunctata* + |
| group 3<br>(fluctuating) | | *Navicula tripunctata* +<br>*Navicula* sp. A +<br>Other species<br>*Cocconeis placentula* * | *Cocconeis placentula* *<br>Other species | |

* Epilithic species
\+ Epipelic species

## Bigoray River

Data interpretation is more complicated for Bigroay River mayflies, because sampling was not restricted to a riffle area. We also sampled in emergent shoreline vegetation and slow water areas. Cluster and PCA, as at the other sites, nevertheless resulted in two main groups, with predominantly epilithic diatoms in guts of Group 1 nymphs and epipelic diatoms in nymphs of Group 2 (Tables 12 and 13). Higher aquatic plants are very common in this slow-moving stream (CLIFFORD 1978). And the possibility of ingestion of epiphytic diatoms must also be considered for Bigoray River mayflies. It is sometimes difficult to differentiate between epilithic and epiphytic diatom species because the same species often inhabit both substrate types (ROUND 1964; HUTCHINSON 1975). Some diatoms from Bigoray River nymphs, classified as epilithic, may have been from epiphytic habitats. Surface feeders from the Bigoray River therefore include grazers on rock surfaces and also aquatic macrophytes. Bigoray River surface feeders include *Baetis tricaudatus, Centroptilum* sp., *Paraleptophlebia debilis, Siphloplecton basale,* and *Stenacron canadense. Callibaetis coloradensis* nymphs were also in Group 1 except for the 4–6 mm nymphs of the 30 July 1975 sample. The *Caenis simulans* and *Ephemera simulans* populations were entirely in Group 2. *Leptophlebia cupida* and *Siphlonurus alternatus* specimens were also interstitial feeders except for a few large *L. cupida* and very small *S. alternatus* nymphs.

# Functional feeding groups

## Classifications

Our food habitat data can be used to classify each mayfly population according to the functional feeding group concept, i.e. shredders, scrapers, gathering-collectors, filtering-collectors, piercers, and predators (CUMMINS 1973; CUMMINS & KLUG 1979). Most populations were in the scraper or gathering-collectors categories; however, predators and filtering-collectors populations were also discernible (Table 14).

Of our four food habit parameters, the dominant type of diatom consumed proved the most valuable for defining functional groups. Scrapers were considered to feed on the surface and upper sides of rocky substrates or on macrophytes; therefore a predominance of epilithic and epiphytic diatoms would be expected in their stomach contents. Populations defined as surface feeders most often classified into the scaper category.

Mayflies defined as interstitial feeders usually fitted nicely into the collector category. Included in this group would be nymphs feeding in areas of reduced current, such as dead water spaces between rocks, on lower surfaces of the

Table 12. PC analysis summary of ingested diatoms for various size classes of nymphs, Bigoray River.

| | 30 July, 1975 | mm | 10 October, 1975 | mm | 20 March, 1976 | mm | 14 May, 1976 | mm |
|---|---|---|---|---|---|---|---|---|
| group 1 (surface feeders) | *Stenacron canadense* | 8–10 | *Callibaetis coloradensis* | 2–4 | *Siphloplecton basale* | 14–15 | *Callibaetis coloradensis* | 4–6 |
| | *Centroptilum* sp. | 2–4 | | 4–6 | | 13–14 | | |
| | *Baetis tricaudatus* | 4–6 | | 6–8 | | 11–12 | *Leptophlebia cupida* | 6–8 |
| | | 2–4 | | 8–10 | | 16–17 | *Callibaetis coloradensis* | 6–8 |
| | *Centroptilum* sp. | 6–8 | | | | 15–16 | | 10–12 |
| | *Paraleptophlebia debilis* | 6–8 | | | | | *Siphlonurus alternatus* | 2–4 |
| | *Centroptilum* sp. | 4–6 | | | | | *Leptophlebia cupida* | 12–14 |
| | | 8–10 | | | | | *Callibaetis coloradensis* | 8–10 |
| | *Paraleptophlebia debilis* | 4–6 | | | | | *Siphloplecton basale* | 16–18 |
| | | | | | | | *Leptophlebia cupida* | 10–12 |
| | | | | | | | *Siphloplecton basale* | 14–15 |
| | | | | | | | | 13–14 |
| group 2 (interstitial feeders) | *Siphlonurus alternatus* | 10–12 | *Ephemera simulans* | 14–16 | *Leptophlebia cupida* | 6–7 | *Leptophlebia cupida* | 8–10 |
| | | 8–10 | *Leptophlebia cupida* | 6–8 | | 10–12 | | 5–6 |
| | | | | 2–4 | | 7–8 | *Ephemera simulans* | 20–22 |
| | *Callibaetis coloradensis* | 4–6 | *Siphlonurus alternatus* | 8–10 | | 5–6 | *Caenis simulans* | 4–6 |
| | | | *Ephemera simulans* | 2–4 | | 3–4 | *Ephemera simulans* | 2–4 |
| | | | | | | 8–9 | | 4–6 |
| | | | *Siphlonurus alternatus* | 10–12 | | 9–10 | | |
| | | | *Leptophlebia cupida* | 4–6 | | | | |

Table 13. Relevant diatom taxa defining ingestion clusters of Bigoray River mayflies (see text for further explanation).

| | 30 July, 1975 | 10 October, 1975 | 20 March, 1976 | 14 May, 1976 |
|---|---|---|---|---|
| group 1 (surface feeders) | *Achnanthes* spp. * | *Epithemia* sp. B * | *Achnanthes* spp. * | *Synedra* sp. A * |
| | *Cocconeis placentula* * | *Fragilaria* sp. + | *Diploneis* sp. + | Other species |
| | *Epithemia* sp. B * | *Cymbella sinuata* + | *Fragilaria leptostauron* + | *Nitzchia* sp. C + |
| | *Nitzchia* sp. B + | *Cyclotella* sp. A + | *Cyclotella* sp. A + | *Cyclotella* sp. B + |
| | | *Gomphonema* sp. A * | | *Meridion circulare* * + |
| | | *Epithemia* sp. A * | | |
| group 2 (interstitial feeders) | *Synedra* sp. A * | *Gyrosigma* sp. + | *Nitzchia* sp. A + | *Diploneis* sp. + |
| | *Nitzchia* sp. C + | *Nitzchia* sp. B + | Other species | *Epithemia* sp. C * |
| | Other species | *Achnanthes* spp. * | *Synedra* sp. A + * | *Surirella* sp. + |
| | *Navicula cryptocephala* + | *Navicula cryptocephala* + | *Cocconeis placentula* + | *Stauroneis* sp. + |
| | *Fragilaria leptostauron* + | | *Navicula* sp. A + | *Cymbella* sp. C + |
| | *Navicula pupula* + | | *Nitzchia* sp. C + | *Nitzchia* sp. A + |
| | *Navicula tripunctata* + | | *Epithemia* sp. C * | |

* Epilithic species
+ Epipelic species

rocks, and fine-grained depositional substrata common in pools and along stream margins. Epipelic diatom communities predominate in these habitats and therefore are reflected in the material consumed.

The type of diatoms ingested by members of the predator category were variable. Possibly, this is due to *D. spinifera* nymphs obtaining prey from various microhabitats, assuming the diatoms ingested are derived from incidental ingestion along with the prey or from the gut tract of the prey.

Quantity of diatoms consumed also was valuable in defining functional groups. With a few exceptions, nymphs defined as scrapers tended to consume more diatoms than did collectors. This agrees with the premise that diatoms are relatively more abundant on exposed surfaces than in interstices (BADCOCK 1949). Fluctuations in diatom consumption by scrapers probably reflect the seasonality of epilithic standing crops. The greater dependence on detritus by interstitial feeders would reflect a low diatom standing crop and a high detrital accumulation in interstitial and depositional habitats.

Particles ingested by mayfly nymths of our study ranged in size from 1.6 to 160 $\mu$m in diameter. For the entire study, 65.4% of the volume of food items consisted of particles in PSC-I (32 $\mu$m or less.). Most material ingested by all taxa is therefore in the ultrafine particulate organic matter category.

Scrapers consumed a greater proportion of PSC-I particles, whereas gathering-collectors often ingested greater proportions of larger PSC-III and IV particles. Size of particles ingested differentiated gatherers from filter feeders. *Ephemera simulans*, a burrowing filter feeder, consistently ingested above average volumes of small $< 32$ $\mu$m particles. Particle sizes ingested by the predator *D. spinifera* were consistently above average, reflecting the ingestion of large animal tissue fragments.

Relative total volume of material consumed can also be related to the four functional feeding groups. Compared to the study average, most scrapers ingested below average quantities of material by volume, whereas most gatherers ingested above average quantities. Filter feeders consumed below average quantities of food items.

One factor favoring larger gut volume amongst gatherers is the size of particles ingested. Gatherers ingested proportionally more large detrital particles. A specific volume of large detrital particles has a smaller total surface area than an equal volume of small particles. Therefore, the total colonizing microflora, presumably the major nutritional component of detritus, would be greater per unit volume of small particles. Consequently, nymphs ingesting large detrital particles would have to ingest greater volumes of detritus than nymphs (scrapers) ingesting small detrital particles to derive the same nutritional value. The filter feeder *E. simulans* consumed below average quantities of material, but this may be compensated for by the small mean size of particles.

Table 14. Trophic classification.

| Species | Seasons | Site | Type of diatom ingestion | Average % diatom ingestion | Relative total volume ingested | Relative consumption of particles $<32\ \mu m$ in diameter | Trophic classification according to MERRITT & CUMMINS (1978) |
|---|---|---|---|---|---|---|---|
| I. Scrapers | | | | | | | |
| *Baetis* spp. | all | Stauffer 1 | S & I | 21.2 | – | + | CG, S |
| *Baetis* spp. | all | Stauffer 2 | S | 20.6 | – | + | CG, S |
| *Baetis persecutus* | all | Tay River | S | 14.0 | – | + | CG, S |
| *Baetis tricaudatus* | all | Bigoray River | S | 20.9 | – | + | CG, S |
| *Callibaetis coloradensis* | all | Bigoray River | S | 9.0 | – | + | ? |
| *Centroptilum* sp. | all | Bigoray River | S | 13.2 | – & + | + | CG, S |
| *Centroptilum* sp. | all | Stauffer 2 | ? | 15.2 | – | + | CG, S |
| *Cinygmula mimus* | all | Stauffer 1 | S | 25.4 | – | + | CG, S |
| *Cinygmula mimus* | all | Tay River | S | 13.0 | – | + | CG, S |
| *Epeorus* sp. | all | Tay River | S | 14.9 | – | + | CG, S |
| *Leptophlebia cupida* | all | Stauffer 2 | S | 6.1 | – | + | CG |
| *Ephemerella inermis* | S & F | Stauffer 2 | S | 12.9 | – | AVG | CG, S, E |
| *Rhithrogena* sp. | all | Tay River | S & I | 12.6 | + | + | CG, S |
| *Stenacron canadense* | all | Bigoray River | S | 3.2 | + & – | + | CG, S |
| II. Collectors | | | | | | | |
| A. Gatherers | | | | | | | |
| *Ameletus sparsatus* | all | Tay River | I | 4.9 | – | – | CG |
| *Caenis simulans* | all | Bigoray River | I | 4.2 | – | – | CG |
| *Cinygmula mimus* | all | Stauffer 2 | I & S | 6.9 | + | + | CG, S |
| *Ephemerella inermis* | all | Stauffer 1 | I | 8.7 | + | – | CG, S, E |
| *Ephemerella inermis* | W & S | Stauffer 2 | I | 1.9 | + | – | CG, S, E |
| *Ephemerella inermis* | all | Tay River | S | 3.5 | – | – | CG, S, E |

Table 14. (cont.)

| Species | Seasons | Site | Type of diatom ingestion | Average % diatom ingestion | Relative total volume ingested | Relative consumption of particles < 32 μm in diameter | Trophic classification according to MERRITT & CUMMINS (1978) |
|---|---|---|---|---|---|---|---|
| *Drunella flavilinea* | all | Tay River | S & I | 7.2 | – | – | ? |
| *Serratella tibialis* | all | Stauffer 1 | I | 12.6 | + | – | CG, S, E |
| *Serratella tibialis* | all | Tay River | S & I | 2.8 | + | – | CG |
| *Leptophlebia cupida* | all | Bigoray River | I & S | 2.8 | + | – | CG |
| *Paraleptophlebia debilis* | all | Bigoray River | S | 3.0 | + | AVG | CG |
| *Paraleptophlebia* sp. | all | Tay River | F | 3.9 | – | + | CG |
| *Paraleptophlebia* sp. | all | Stauffer 2 | I | 3.6 | + | + | CG |
| *Pseudocloeon* sp. | all | Tay River | I | 6.1 | – | AVG | S, CG |
| *Siphlonurus alternatus* | all | Bigoray River | I | 2.5 | + | – | CG, S, E |
| *Siphloplecton basale* | all | Bigoray River | S | 3.1 | + | – | ? |
| B. Filterers | | | | | | | |
| *Ephemera simulans* | all | Bigoray River | I | 3.9 | – | + | CG, E |
| *Ephemera simulans* | all | Stauffer 2 | I | 3.0 | – | + | CG, E |
| III. Predators | | | | | | | |
| *Drunella spinifera* | all | Stauffer 1 | F | 3.4 | – | – | CG, S, E |
| *Drunella spinifera* | all | Stauffer 2 | S-I-F | 5.9 | + & – | – | CG, S, E |
| *Drunella spinifera* | all | Tay River | I | 21.7 | + & – | – | CG, S, E |

S = surface diatoms; I = interstitial diatoms; – = below average; + = above average; C = collector; G = gatherer; F = filterer; S = scraper; E = engulfer

### Species and functional feeding groups

Inclusion of a population in one of the functional feeding categories means most specimens on most dates met the criteria in question. However, shifts from one food habit category to another, either by season or by size class, occurred frequently and will be discussed later. Scrapers were dominated by members of the Baetidae and Heptageniidae (Table 14). Baetids have frequently been observed to prefer exposed surface habitats in relatively fast water (GILPIN & BRUSVEN 1970; EDMUNDS et al. 1976; CORKUM et al. 1977). Gatherers include most ephemeropterans considered crawlers and burrowers, which often inhabit interstitial or depositonal habitats (EDMUNDS et al. 1976). The major families with representatives in the gathering-collector group were Ephemerellidae, Leptophlebiidae, Caenidae, and Siphlonuridae. *Ephemera simulans* was the only filter feeder and *Drunella spinifera* the only predator.

## Seasonal and spatial variation in food habits

### Seasonal variation

The functional feeding classification represents consensus feeding habits of populations considered over the entire study period, but food habits of many populations often varied with the season or life cycle stages.

One seasonal occurrence was a fluctuation in the relative number of diatoms ingested. This was most evident among populations defined as scrapers, e.g. *Baetis* spp., *Cinygmula mimus* and *Ephemerella inermis*. Amongst these populations, peak diatom consumption often occurred during spring or autumn or both, correlated with peak epilithic standing crops and the optimal growth periods for many univoltine winter mayflies. The winter mayflies usually hatch during late August or early September and grow rapidly until ice-cover, usually in November. As water temperatures rise in spring, growth resumes with nymphs maturing during late spring or summer. Elevated ingestion of a high energy food resource, e.g. diatoms, during these major spring and autumn growth periods may be an important factor in life-cycle strategies for scraper feeding species (MINSHALL 1978). Ingestion of detritus by collectors was usually uniform throughout the year.

There were seasonal differences in the size of particles consumed for many mayflies. Interstitial feeders, especially, often consumed a greater proportion of large particles during autumn, when leaf-fall occurs, and presumably the largest detrital particles are to be found in the stream. Relatively smaller particles are consumed by interstitial nymphs after the ice goes out in spring.

COFFMAN et al. (1971) and CUMMINS (1973) noted elevated quantities of detritus from guts of small specimens, and this phenomenon was also observed for some mayfly species of our study, especially populations of *Baetis* spp. and *C. mimus.* When young nymphs first appeared in late summer or early autumn, gut analysis frequently indicated a collector feeding regime with a corresponding high detrital ingestion rate. As the season progressed, diatom consumption often increased, coincident with a shift to surface feeding. Hatching probably often takes place in the interstices; therefore an interstitial feeding regime amongst early instar nymphs seems reasonable (Coffman et al. 1971).

There were changes in feeding habits of mature nymphs. Food was never found in nymphs of the last nymphal instar (characterized by dark wing pads). A reduced volume of ingested material by late instar nymphs was also frequently observed, e.g. *Rhithrogena* sp., *S. canadense, P. debilis,* and *L. cupida.* Some populations, notably *Baetis* spp. from Stauffer-1, *C. coloradensis, E. inermis, L. cupida,* although exhibiting a reduced total volume of food consumed as they matured, actually increased relative diatom ingestion during the late (but not last) nymphal instars.

## Spatial variation

There were differences in mayfly food habit patterns between the three streams, particularly with respect to relative ingestion of detritus and diatoms (Tables 2 and 3). Detrital ingestion can be considered the difference between percent diatom ingestion and 100 percent, since mineral matter and filamentous algae were insignificant (Fig. 8).

Overall, diatom ingestion was highest at the springfed site of the agricultural stream (Stauffer-1), intermediate in the fast-flowing foothills stream (Tay River), and lowest in the slow-moving muskeg stream (Bigoray River),

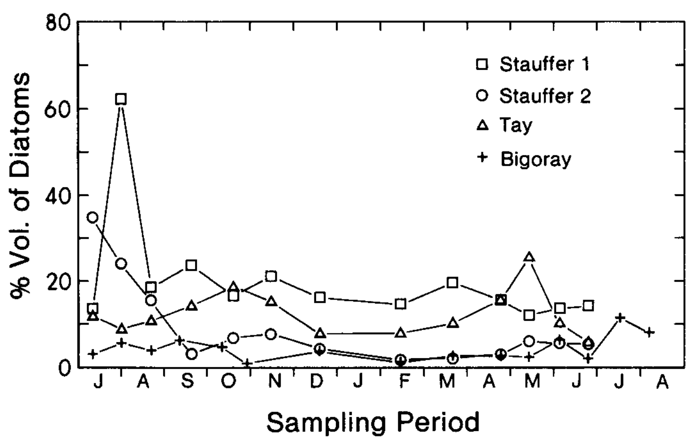


Fig. 8. Seasonal total consumption of diatoms by all populations of each site, 1975–1976.

where diatoms usually made up less than 5% of all ingested material. Mayflies of the downstream site of the agricultural stream (Stauffer-2) also exhibited a very low average diatom ingestion, except during summer and early autumn.

## Summary

Nymphal mayfly food habits were studied in three Alberta, Canada, streams; total absolute volumes and particle sizes ingested were estimated using an electronic counter.

Detritus was the major food item consumed by all ephemeropterans (Tables 2 and 3).

Baetids and heptageniids consumed the greatest amount of diatoms (Figs. 1 and 2); *Drunella spinifera* populations were the only mayflies to consume significant amounts of animal material.

Nymphs ingested particles that were usually less than 160 µm in diameter; about two-thirds of all food items consisted of particles less than 32 µm in diameter (Table 4). There was a tendency for smaller particles to be ingested in autumn (Fig. 5).

Volumes of ingested material by nymphs of a particular size class were similar for the four study sites. The relationship between total volume ingested and total length of nymphs fitted an exponential function.

Relative abundance of the various diatom species ingested by each mayfly species was analyzed using multivariate techniques. Populations or size classes within populations could be placed into one of two major food habit regimes: surface feeders and interstitial feeders (Tables 6–13).

The detrital food base was often most important in late winter and spring; whereas diatom ingestion amongst surface feeders was often elevated in spring and autumn and could be related to large epilithic diatom standing crops at these times (Figs. 4 and 8).

Average detrital ingestion was greatest in the boreal forest stream; diatom ingestion was relatively most important near the spring-fed headwaters of the agricultural stream (Fig. 8).

The food habit regimes, as determined by multivariate techniques, are discussed in respect to the functional feeding group concept (Table 14).

## Zusammenfassung

Die Nahrung von Eintagsfliegenlarven (Ephemeroptera) wurde an vier Stellen in drei Bächen in Alberta, Kanada, von Juli 1975 bis Juli 1976 untersucht. Das Gesamtvolumen und die Größe der Nahrungsteilchen wurden mit einem elektronischen Zählgerät bestimmt. Bei allen 25 Arten bildete Detritus den volumenmäßig größten Anteil der Nahrung.

Gewöhnlich fraßen die Baetiden und Heptageniiden den verhältnismäßig größten Anteil an Diatomeen. Die einzigen Eintagsfliegen, die große Mengen an tierischem Material fraßen, waren Populationen von *Drunella spinifera.* Ungefähr zwei Drittel der Nahrung aller Populationen bestand aus Teilchen mit einem Durchmesser von weniger als 32 µm, und Teilchen mit einem Durchmesser von über 160 µm wurden selten aufgenommen. Das Gesamtvolumen der aufgenommenen Nahrung (in $\mu m^3$) kann als eine Exponentialfunktion der Länge der Larven dargestellt werden. Die Art der Nahrung hing von dem Angebot des Mikrohabitats ab. Die meisten Populationen oder bestimmte Größenklassen innerhalb einer Population konnten durch eine mathematische Analyse als Oberflächen-Weidegänger oder Interstitial-Weidegänger eingeordnet werden. Die

Oberflächen-Weidegänger fraßen große Mengen an Diatomeen, besonders epilithische Arten. Diese Larven fraßen einen großen Anteil kleiner Teilchen, und das Gesamtvolumen der Nahrung lag unter dem Durchschnitt. Die im Interstitial sich ernährenden Tiere fraßen durchweg niedrige Anteile an Diatomeen, die meist epipelisch waren; diese Nymphen fraßen größere Mengen an größeren Nahrungsteilchen. Gegen Ende des Winters und im Frühjahr bildete Detritus oft den wichtigsten Bestandteil der Nahrung. Der Anteil der Diatomeen in der Nahrung der Oberflächen-Weidegänger war im Frühjahr und Herbst oft größer und hing von dem höheren Bestand an epilithischen Diatomeen während dieser Zeiten ab. Die durchschnittliche Detritusaufnahme war im Waldbach am größten, während Diatomeen in der Quellregion des Baches im landwirtschaftlichen Gebiet von verhältnismäßig großer Bedeutung als Futter waren. Die Art der Futteraufnahme – von der Oberfläche oder im Interstitial – wird mit Hinsicht auf die funktionalen Ernährungsgruppen diskutiert (z. B. Schaber, Sammler).

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