Food Habits of Stream Benthos at Sites of Differing Food Availability

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ABSTRACT: The food habits of 17 species of macroinvertebrates were examined and compared with the potential foods present in a small stream in northwestern Colorado. The majority of common species were small-particle herbivore-detritivores, but *Hesperophylax consimilis* and *Tipula commiscibilis* were large-particle detritivores. *Isoperla patricia* was the most common invertebrate predator. *Hydropsyche oslari* was eclectic in food habits, but was primarily a large-particle herbivore-detritivore with carnivory exhibited only by late instars. Only *Hydropsyche* and *Isoperla* showed significant size class differences in the composition of food ingested. No aquatic vascular plant material was identified in the gut contents of the species examined. Filamentous algae, although abundant at one location, were extensively utilized only as new growths or as decomposing fragments; however, epiphytic diatoms which extensively colonized algal filaments and vascular plant surfaces were an important food item. The use of t-tests following conversion of percentages to arcsin values showed that proportions of diatoms in the habitat and in the diets of macroinvertebrates were not significantly different. Nor did major dietary components differ significantly between sites despite considerable differences in food availability. Food ingested by herbivore-detritivores averaged 73% detritus, 22% diatoms and 5% filamentous algae. The similarity of food habits of herbivore-detritivores at different sites indicates that particle size, and possibly nutritive values, were the primary criteria determining food composition.

INTRODUCTION

Since Muttkowski and Smith's classic study (1929) of the food habits of aquatic insects in Yellowstone National Park, a number of other studies have been conducted in western North America. Most investigations have been concerned with particular groups of insects, specifically caddis flies (Thut, 1969; Rhame and Stewart, 1976), mayflies (Gilpin and Brusven, 1970) and stone flies (Sheldon, 1969; Richardson and Gaufin, 1971; Fuller and Stewart, 1977). Few studies have dealt with the food habits of a major portion of the total benthic fauna (Chapman and Demory, 1963; Koslucher and Minshall, 1973).

Stream invertebrates have been characterized as food generalists (Cummins, 1973). Food preferences have been explained largely on the basis of particle size or microhabitat selection rather than truly selective (*i.e.,* behavioral) feeding, although "conditioned" leaf material may be selected over leaves not yet colonized by microorganisms (Cummins, 1974).

The present study of Piceance Creek, a small stream in Colorado, was conducted to determine: (1) the food habits of the common macroinvertebrate species, and (2) the relationship between food ingested and food availability in the environment. Emphasis was placed on the relative contributions of filamentous algae and allochthonous organic material. A previous annual study (Gray and Ward, 1977) provided data on species composition and life cycles used in the selection of taxa for the present study.

DESCRIPTION OF THE STUDY AREA

Piceance Creek in Rio Blanco and Garfield counties in northwestern Colorado is a small tributary of the White River. The Piceance Basin is underlain by sedimentary rocks of the Green River Formation which contain extensive deposits of oil shale (keragenous marlstone), in addition to halite (NaCl), nahcolite ($NaHCO_3$) and gypsum ($CaSO_4$). The basin has a complex aquifer system which supplies 80% of the base flow of Piceance Creek (Weeks *et al.*, 1974).

Annual precipitation ranges from 30-51 cm, mostly as snow. Summer air temperature may exceed 40C, while winter temperatures of -40C have been recorded (Weeks *et al.*, 1974). Natural vegetation is composed of sagebrush (*Artemesia tridentata*) communities in valleys and on slopes and pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodland on ridges.

Two sampling sites from a previous basin-wide study (Gray and Ward, 1977) were selected for the subsequent investigation of food habits reported herein. Site PC-1 was located in the headwaters of Piceance Creek (2103 m elev.) ca. 1 km below several permanent springs. Consequently, conditions were relatively stable throughout the year, except during spring runoff. Riparian vegetation consisted primarily of sagebrush and various forbs and grasses. Although grazing is extensive along Piceance Creek, PC-1 was not greatly affected by livestock. Site PC-4 (1896 m elev.) was located directly below the confluence of Willow Creek, a small spring brook. Riparian vegetation consisted of rabbit brush (*Chrysothamnus* spp.), greasewood (*Sarcobatus vermiculatus*) and occasional willows (*Salix exigua*). This lower site was affected by grazing, irrigation return flows and, during winter, anchor and frazil ice.

Both sampling sites were located on riffles of similar substrate composition (Mdϕ -4.6 and -5.3 on the linear phi-scale, Cummins, 1962) and exhibited similar temperature and *p*H ranges. Downstream increases in total dissolved solids, and dominant cations and anions resulted primarily from the natural geochemistry of the basin and secondarily from irrigation return flows. Detailed water chemistry and site descriptions are given in Gray and Ward (1977).

MATERIALS AND METHODS

Benthic macroinvertebrates were sampled monthly from October 1976 through May 1977, the major period of growth for the majority of the species examined. A metal core sampler, which enclosed an area of 325 cm^2, was used to take five replicate samples in a transect across a riffle at each site. The substrate was removed to a depth of 10 cm. The fine materials remaining within the core sampler were stirred vigorously and the suspended matter was collected in a net with 100 μm apertures. This latter procedure was continued for 5 min. Coarse materials previously removed were washed over the same net. Organisms were preserved in the field with 5% formalin and later transferred to 80% ethanol.

Periphyton was collected monthly by scraping the upper surfaces of several randomly selected rocks. Subsamples were examined with an ocular Whipple grid (as described below for gut contents) to estimate the percentage composition of detritus, diatoms, filamentous algae and total algae.

Sedimentary coarse particulate organic matter (CPOM) was collected in October, February and May using the core sampler. Materials retained by 1-mm mesh were separated into detritus, vascular plants, filamentous algae and total algae, and dried to constant weight at 60C.

Techniques for the analysis of food habits were modifications of those used by Mecom and Cummins (1964) and by Coffman *et al.* (1971). Two to five guts (foreguts and midguts) were dissected from each size class of each species on each date. Size classes were based on head capsule widths for most species. Total lengths were used to separate size classes of *Tipula, Limnophora* and tubificids. Only tubificids which exhibited no indication of fragmentation were used. Only full guts of each species were used. The gut contents were suspended in 15 ml distilled water and filtered through a millipore-type HA filter (25 mm diam, 0.45 μm apertures). Filtration was terminated while the filter was still damp. The filter was cleared with immersion oil and mounted on a microscope slide. For large samples, a subsample was withdrawn from the suspension (Brown, 1961). The percentage composition of food material was determined from areal measurements using an ocular Whipple grid. From 10 - 30 fields of view were examined at 200X or 400X, depending on the size and density of material.

During the previous year of study of the macroinvertebrate community (Gray and Ward, 1977), a preliminary examination of the food habits of nine species of aquatic insects was conducted to work out methods of food habit analysis and to subject the methods to statistical tests. The membrane filter method developed by Mecom and Cummins (1964) has been used by other investigators (*e.g.*, Coffman *et al.*, 1971; Koslucher and Minshall, 1973), but only Brown (1961) subjected his methods to rigorous statistical analysis. Therefore, the membrane filter method was subjected to statistical tests to determine if the material on the filter was randomly distributed, to determine the minimum count necessary for valid results and to place confidence limits on counts of particular items. In the first test, a filter prepared with the contents of three guts of *Baetis tricaudatus* (PC-4, May 1976) was used. Thirty-two random fields were counted at 500X (about 400 total items). By using the test for randomness of Pearson and Hartley (1966, Table 29c), it was determined that the three most abundant food items (detritus, total diatoms and *Navicula*) were randomly distributed (*e.g.*, for detritus: range/SD = 3.93). Using paired t-tests and chi-square tests, counts from 10 random fields (130 total items) were compared to total counts from all fields. No significant differences were found (*e.g.*, for detritus: t = 0.167, df = 40; $\chi^2 = 8.17$, df = 9). Confidence limits for a count of 130 items (95% level from t-tests) were $\bar{y} \pm 30\%$ for both detritus and diatoms.

Similar tests were conducted using a filter prepared from the contents of two *Tipula commiscibilis* guts. Results were essentially the same as for *Baetis tricaudatus* (*e.g.*, for detritus: range/SD = 3.50; t = 1.70, df = 12; $\chi^2 = 2.18$, df = 3). Confidence limits (95% level) were $\bar{y} \pm 29\%$ for detritus and $\bar{y} \pm 23\%$ for diatoms.

In the present study, the number of items counted was increased to lower the range of confidence limits and the size of the count was adjusted to the diversity of items resulting in confidence limits of about $\bar{y} \pm$ 15-20% for detritus and total diatoms.

For *Isoperla patricia,* food habits analysis was primarily designed to determine the extent of carnivory. Confidence limits for single counts of prey items were determined from Pearson and Hartley (1966, Table 40).

RESULTS AND DISCUSSION

Faunal composition.—Forty-eight macroinvertebrate taxa were identified from Site PC-1, 44 from PC-4. Relatively few taxa comprised the majority of organisms at each site. Seventeen taxa were selected for examination of food habits with emphasis placed on the following six species common to both sites: the mayflies *Baetis tricaudatus* Dodds and *Ephemerella inermis* Eaton; the caddis flies *Hydropsyche oslari* Banks and *Hesperophylax consimilis* Banks; the stone fly *Isoperla patricia* Frison and the dipteran *Tipula commiscibilis* (Doane). With the exception of *B. tricaudatus,* which was more abundant at PC-1, these species comprised similar proportions of the benthic fauna at both sites.

In addition, food habits were analyzed for three species of the winter stone fly *Capnia* (*C. logana* Nebeker and Gaufin, *C. gracilaria* Claassen and *C. confusa* Claassen), the caddis fly *Glossosoma ventrale* Banks and the dipterans *Limnophora* sp., *Diamesa* sp. and *Eukiefferiella* sp. at PC-1; and the oligochaetes *Tubifex tubifex*

(O.F.M.) and *Limnodrilus hoffmeisteri* Claparede and the chironomids *Orthocladius* sp. and *Pseudodiamesa* sp. at PC-4.

Mean total density and biomass values at PC-1 for the period October-May were 3.1 X 10^4 organisms and 7.49 g dry weight per m^2. Values for PC-4 were 1.5 X 10^4 organisms and 9.17 g dry weight per m^2. The taxa examined for food habits comprised 61% of the total density and 89% of the total biomass at PC-1 and 74% of the total density and 86% of the total biomass at PC-4.

Composition of periphyton and CPOM.—The two sampling sites differed greatly in the composition of periphyton and sedimentary CPOM (Figs. 1 and 2). Diatoms

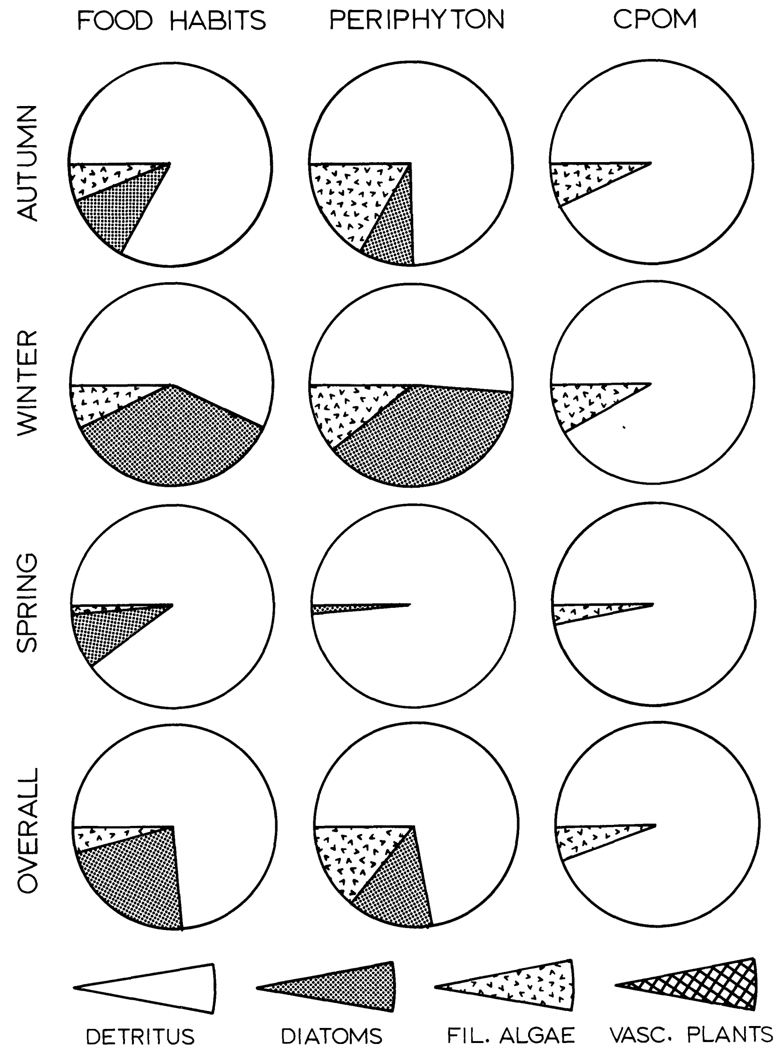

Fig. 1.—Mean percentage composition of major dietary components of herbivore-detritivores compared with the composition of these components in periphyton and coarse particulate organic matter (CPOM) at Site PC-1

were, however, present in the periphyton at both sites in nearly equal proportions (14-15%), and the species assemblages were also similar. Thirty-one taxa were recorded at PC-1, while 29 taxa were found at PC-4. *Navicula viridula* was the most abundant species at both sites throughout the study period. Other common species included *N. radiosa, N. rhynchocephala, Achnanthes lanceolata, A. minutissima* and *Cocconeis pediculus* (an abundant epiphyte on *Cladophora*). Seasonal abundance of diatoms differed at the two sites. At PC-1, peak abundance occurred in late winter prior to spring runoff. Peak diatom abundance at PC-4 occurred in the spring when runoff from snowmelt and irrigation activities brought considerable quantities of plant nutrients into the stream (Gray and Ward, 1977). The values for autumn at PC-4 (Fig. 2) are probably underestimates, since it was difficult to assess the abundance of epiphytic species on *Cladophora.*

A major difference in the periphyton communities at the two sites was the importance of filamentous forms, principally *Cladophora.* At PC-1, this green alga com-

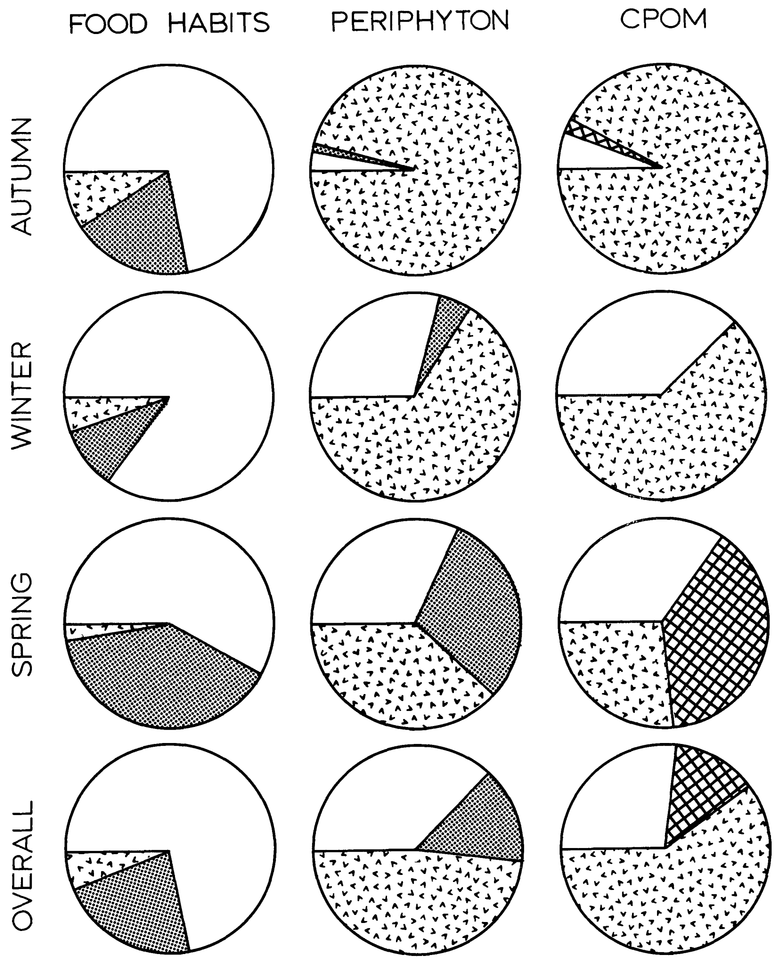

Fig. 2.—Mean percentage composition of major dietary components of herbivore-detritivores compared with the composition of these components in periphyton and coarse particulate organic matter (CPOM) at Site PC-4. Symbols same as Figure 1

prised 13% of the total periphyton and 6% of the total CPOM. It was usually present only as small, scattered growths, although a brief "bloom" occurred in November. At PC-4, *Cladophora* was very abundant, and other filamentous forms were also present (*Enteromorpha, Vaucheria* and *Rivularia*). Growths of these algae covered a large portion of the streambed from May through October, but were reduced in late autumn due to natural senescence and ice scour. Filamentous algae represented 63% of the total periphyton and 60% of the total CPOM at PC-4.

Although PC-1 was spring-fed, no aquatic vascular plants were present, likely due to scour during spring runoff and occasional flash floods in late summer. Both *Zannichellia* (pondweed) and *Rorippa* (watercress) were present at PC-4 and together represented 13% of the total CPOM.

Allochthonous material comprised an estimated 94% of the total sedimentary CPOM at PC-1, but only 27% at PC-4. The standing crops of allochthonous materials, however, were similar at PC-1 and PC-4 (means of 5.9 and 7.2 g dry wt/m^2, respectively), emphasizing the greater contribution of autochthonous materials at PC-4. Unlike woodland streams (*e.g.,* Coffman *et al.,* 1971; Fisher and Likens, 1973), leaf litter comprised a small portion ($<$ 5% total CPOM) of the allochthonous inputs at both sites. Most of the allochthonous organic matter was composed of small pieces of bark and twigs.

Food habits analyses.—The food habits of Piceance Creek macroinvertebrates are summarized in Table 1. The ensuing discussion will compare these results with published accounts for the same or similar species, will consider size class differences for selected taxa, differences in the diets of species common to both sites, and will compare the diets of herbivore-detritivores with food availability. In addition, an overall comparison will be made between the food habits of the benthic fauna of Piceance Creek and other extensively studied streams.

Based on Cummins' (1973) classification, *Baetis, Ephemerella, Capnia, Glossosoma, Limnophora,* all taxa of chironomids examined, and the tubificids were found to be small-particle herbivore-detritivores. The majority of particles ingested were less than 250 μm (usually less than 100 μm) in longest dimension, and were mainly composed of detritus and diatoms. Occasionally, however, filamentous algae were a significant component in the case of the chironomid *Pseudodiamesa* at PC-4 and for *Capnia* at PC-1 in November, when *Cladophora* made up 44% of the total *Capnia* diet.

Published studies indicate that the small-particle herbivore-detritivores of Piceance Creek are generally typical in the types and relative amounts of material ingested (Chapman and Demory, 1963; Gilpin and Brusven, 1970; Hynes, 1941; Koslucher and Minshall, 1973; Shapas and Hilsenhoff, 1976).

Tipula and *Hesperophylax* ingested primarily detrital particles greater than 1 mm in longest dimension and thus would be considered "shredders," or large-particle detritivores, under Cummins' (1973) classification. Although both species regularly consumed filamentous algae, this food item made up less than 20% of the total diet. Minckley (1963) found *Tipula nobilis* was primarily a grazer on moss and detritus, while Hall and Pritchard (1975) recorded diatoms and detritus in guts of *Tipula sacra.* Shapas and Hilsenhoff (1976) found that diatoms, detritus and lesser amounts of filamentous algae were the major foods of *Hesperophylax designatus.*

An unexpected result of the food habits studies was the similarity in consumption of filamentous algae at both sites despite the large differences in the abundance of algae. Of the six taxa common to both sites, only *Tipula* consumed more filamentous algae at PC-4 than PC-1, and even this difference was slight.

Numerous studies have been conducted on *Hydropsyche* larvae, with the general conclusion that they are eclectic in food habits and highly variable in the extent of

TABLE 1.—Percentage composition of foods consumed by Piceance Creek macroinvertebrates. Symbols are as follows: a = detritus, b = diatoms, c = filamentous algae, d = animal, * = less than 1%. Numbers in parentheses in last column indicate number of size classes examined

Taxa and Site	Fall				Winter				Spring				Overall				Number examined
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	
Baetis tricaudatus																	65 (4)
PC-1	90	10	0	0	71	29	0	0	91	9	0	0	84	16	0	0	
PC-4	72	28	0	0	88	12	0	0	58	42	0	0	75	25	0	0	
Ephemerella inermis																	16 (3)
PC-1	----	----	----	------	----	----	----	------	98	2	--	------	98	2	0	0	
PC-4	88	12	0	0	92	8	0	0	68	31	1	------	82	18	*	0	
Isoperla patricia																	46 (5)
PC-1	0	0	0	100	5	1	1	93	0	0	0	100	2	*	*	98	
PC-4	40	23	0	37	0	0	0	100	0	0	0	100	13	8	0	79	
Hydropsyche oslari																	23 (4)
PC-1	----	----	----	------	41	24	32	3	88	10	2	0	64	17	17	2	
PC-4	74	8	18	0	69	13	18	0	63	37	*	0	69	19	12	0	
Hesperophylax consimilis																	12 (5)
PC-1	68	19	13	0	----	----	----	------	----	----	--	------	68	19	13	0	
PC-4	72	19	9	0	----	----	----	------	34	59	7	0	53	39	8	0	
Tipula commiscibilis																	32 (4)
PC-1	97	2	1	0	32	63	5	0	94	5	1	0	74	24	2	0	
PC-4	53	30	17	0	93	5	2	0	66	33	1	0	71	22	7	0	
Capnia spp.																	
PC-1	63	15	22	0	86	13	1	0	78	22	0	0	75	16	9	0	34 (4)
Glossosoma ventrale																	
PC-1	83	17	0	0	70	30	*	0	----	----	--	------	78	22	*	0	20 (2)
Limnophora sp.																	
PC-1	99	1	0	0	----	----	----	------	----	----	--	------	99	1	0	0	3 (1)
Eukiefferiella sp.																	
PC-1	----	----	----	------	33	63	4	0	----	----	--	------	33	63	4	0	10 (2)
Diamesa sp.																	
PC-1	----	----	----	------	46	54	0	0	----	----	--	------	46	54	0	0	8 (2)
Orthocladius sp.																	
PC-4	----	----	----	------	94	6	0	0	----	----	--	------	94	6	0	0	9 (2)
Pseudodiamesa sp.																	
PC-4	----	----	----	------	62	19	19	0	----	----	--	------	62	19	19	0	5 (1)
Tubificidae spp.																	
PC-4	----	----	----	------	88	12	0	0	----	----	--	------	88	12	0	0	5 (1)

carnivory (Crosby, 1975; Koslucher and Minshall, 1973; Rhame and Stewart, 1976; Wallace, 1974). In Piceance Creek, *H. oslari* was primarily a large-particle herbivore-detritivore. Although animals were occasionally found in the guts, they did not comprise more than 25% of the total diet on any occasion. Chironomidae were the animals most frequently consumed by *Hydropsyche* (80% of total animals ingested), with lesser numbers of *Baetis* (20%). Animals were consumed only by late instars, a tendency also noted by Crosby (1975). Significant dietary differences between size classes were noted only for *Hydropsyche* and *Isoperla.*

Isoperla patricia was the most common invertebrate predator in Piceance Creek. At PC-4, the only animals consumed were chironomids (72% of total animals ingested) and *Baetis* (28%). At PC-1, chironomids (78%) and *Baetis* (18%) were the dominant prey items with lesser numbers of *Capnia* (3%) and *Oligochaeta* (1%) also consumed. The reliance of *Isoperla* on small prey such as *Baetis* has also been reported by other investigators (Fuller and Stewart, 1977; Hynes, 1941; Richardson and Gaufin, 1971).

During January of the preceding year, five distinct size classes of *Isoperla patricia* occurred simultaneously at PC-1 (Fig. 3). This allowed a comparison of food habits of different size nymphs under identical conditions. Increased size resulted in greater carnivory, and consumption of larger prey, a tendency previously noted by Fuller and Stewart (1977) and Winterbourn (1974). The animal prey of larger nymphs primarily consisted of *Capnia* and *Baetis,* whereas early instars preyed mainly on small chironomids. In Piceance Creek, *I. patricia* has an extended hatching period

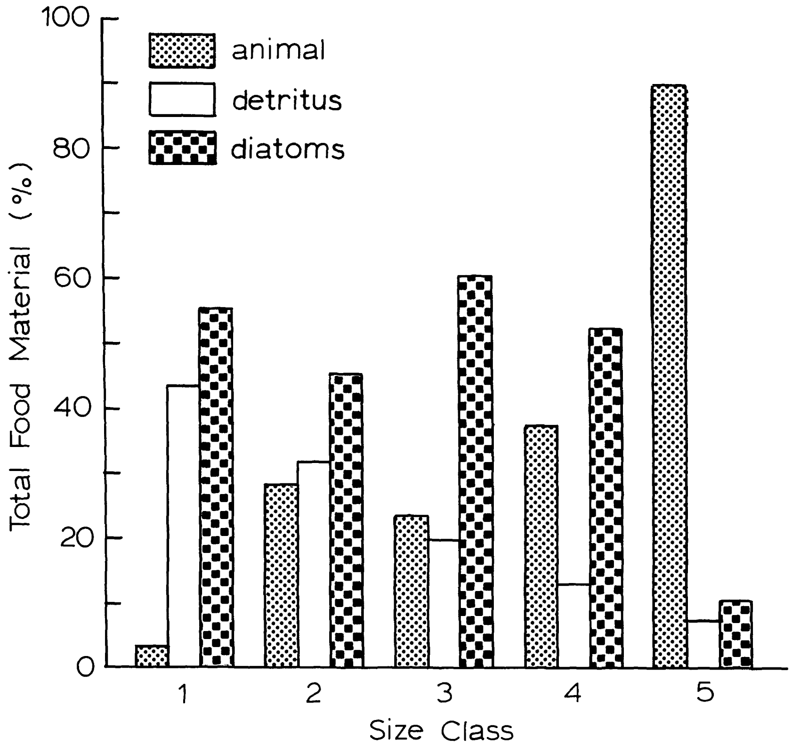

Fig. 3.—Percentage composition of foods of five size classes of *Isoperla patricia* nymphs at PC-1, January 1976

(mid-August to early January) which, combined with differences in food habits between instars, would serve as a mechanism to reduce intraspecific competition and allow more efficient utilization of the habitat.

Differences in the diets of taxa common to both sites were generally small. There was a slight tendency for organisms at PC-4 to consume more diatoms. This even applied to *Isoperla* and may be related to a lower density of prey items in the habitat (Fahy, 1972).

Seasonal changes in food habits of herbivore-detritivores are indicated in Figures 1 and 2. Composition of major food categories in the diets generally reflected the composition of periphyton and sedimentary CPOM at PC-1. At PC-4, however, composition of the diets was greatly different from that of the potential foods, especially with respect to filamentous algae (Fig. 2). Overall, diets at both sites were similar despite considerable differences in food availability, suggesting that the species studied are less opportunistic than generally suggested (*e.g.,* Cummins, 1973).

Statistical analyses of the percentage values were performed using a conversion of percentages to arcsin values (angular transformation) (Hall and Pritchard, 1975). Using Student's t-tests, comparisons were made between the percentages of diatoms and filamentous algae in the foods consumed, and in the periphyton and CPOM. In addition, a comparison was made between the overall food composition for all species examined at the two sites. At PC-1, the proportions of diatoms and filamentous algae in the habitat and in the diets were not significantly different ($P>0.50$). Diatom percentages in the food and in the periphyton at PC-4 were also not significantly different ($P = 0.40$). However, a significant difference ($P<0.01$) was found between the percentage of filamentous algae in the diets and that in the periphyton, or that in the CPOM. Differences between the overall food percentages at PC-1 and PC-4 were not significant ($P>0.60$).

These results indicate that detritus and diatoms were ingested in nearly equal proportion to their abundance in the habitat. The data from PC-4, however, indicate that filamentous algae were not consumed in proportion to their relative abundance in the stream.

The consumption of filamentous algae (primarily *Cladophora*) was observed to be limited by the extent of carbonate deposits on the filaments, the density of epiphytic diatoms (*Cocconeis* spp.) and the size of the individual filaments. Carbonate deposits were extensive on living growths of *Cladophora,* particularly in late autumn prior to senescence, and the mechanical difficulty in ingesting such filaments is a likely reason for limited uptake (Brown, 1961). *Cladophora* filaments which were consumed nearly always had a dense covering of epiphytic diatoms, and large numbers of *Cocconeis* in a gut were indicative of grazing on *Cladophora.* During late autumn, the *Cladophora* growths were in a state of decline with large amounts detaching from the "mats" and entering the sedimentary detrital pool. At PC-4, consumption of *Cladophora* was highest during the autumn (Fig. 2), suggesting that fragmentation of the filaments facilitated consumption.

Another factor which may indirectly contribute to the relatively small amounts of *Cladophora* consumed is the low energy content of this alga. Dichromate oxidation indicated a caloric content of 1.63 ± 0.68 kcal/g algae, whereas allochthonous organic matter had a caloric value of 3.28 ± 0.46 kcal/g (dry weight).

Despite its abundance at PC-4, no aquatic vascular plant material was found in the guts of the species examined, and there was no evidence of grazing on living plants. Koslucher and Minshall (1973) also reported a virtual absence of living vascular plant tissue in the diets of stream invertebrates despite the availability of this potential food in the habitat. *Tipula, Hesperophylax* and *Hydropsyche* would seem capable of ingesting such material, the caloric content (2.99 kcal/g dry weight) of which was comparable to allochthonous detritus. It has been suggested that mechanical difficulty in digesting the tissue is the main factor limiting consumption (Brown, 1961).

The similarity of overall food habits of herbivore-detritivores at PC-1 and PC-4 indicates that particle size, and possibly nutritive value, were the primary criteria determining consumption by macroinvertebrates. However, the nutritional value of *Cladophora* cannot be accurately estimated given the mechanical difficulty of ingesting this alga and the fact that epiphytic diatoms colonize the filaments.

The overall composition of food ingested by Piceance Creek herbivore-detritivores was 73% detritus, 22% diatoms and 5% filamentous algae, which is comparable to results of other studies. Chapman and Demory (1963) found that herbivore-detritivores in two Oregon streams with large terrestrial inputs consumed 40% algae and 60% detritus. Koslucher and Minshall (1973), whose study sites on Deep Creek, Idaho-Utah, like PC-4 had large standing crops of filamentous algae, found that herbivore-detritivores consumed 60% detritus, 39% diatoms and 1% filamentous algae. The similarity of these values, in spite of the different organic inputs from allochthonous and autochthonous sources, supports the important role of particle size in food composition. It also suggests that diverse stream systems have similar particle size distributions regardless of the source of the detritus.

For *Tipula,* and other shredder species which are capable of exploiting a larger particle-size range (thus more food types), the nutritive value of the food has an apparent important role. As Cummins (1974), among others, has indicated, leaf CPOM itself contains relatively little nutritive value for macroinvertebrates until colonized by microorganisms. We suggest that filamentous algae can also serve as a substrate for organisms which enhance its nutritive content, in particular, epiphytic diatoms.

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