Production of *Brachycentrus spinae* Ross (Trichoptera: Brachycentridae) and its Role in Seston Dynamics of a Southern Appalachian Stream (USA)[1]

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ABSTRACT

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Brachycentrus spinae Ross had a univoltine life cycle similar to other *Brachycentrus* spp. Larvae hatched in May, developed through five instars, and pupated in March. Larval production, excluding silk secretions, was 260.686 mg AFDW m^{-2} yr^{-1}, and mean annual standing crop was 40.396 mg AFDW m^{-2}. Annual and cohort turnover ratios (Production/Biomass) were 6.4 and 6.0, respectively. Case construction (silk + detritus) was estimated at 256.2 mg AFDW m^{-2} yr^{-1}. Production attributable to five food types (animal, vascular plant detritus, amorphous detritus, filamentous algae, and diatoms) was calculated using literature derived values for assimilation and net production efficiencies. Animal food accounted for the majority of *B. spinae* production (61.71%), followed by amorphous detritus (25.08%). Annual food consumption by *B. spinae* was estimated at 2158.0 mg AFDW m^{-2}.

Seston data from Dryman Fork and *B. spinae* consumption estimates were used to calculate seston utilization. While larvae ingested only 0.00007% m^{-2} of total available summer seston, they selectively captured animal material, consuming 3.5 times the amount entering the study section. These data suggested that the animal component of the seston must be replaced every 400 m to support *Brachycentrus* feeding alone. While this species exerted a minor influence on seston quantity, its selective capture of high quality animal food could significantly alter seston quality.

Introduction

Species of the caddisfly genus *Brachycentrus* Curtis inhabit streams throughout North America. The larvae are omnivores, feeding predominantly on diatoms, filamentous algae, and detritus, as well as animal and plant material which they filter from the water or graze from the substrate (Gallepp 1974). Although the biology and behavior of several species have been investigated (Murphy 1919, Mecom and Cummins 1964, Gallepp 1974, 1977), the role of *Brachycentrus* spp. in stream energy flow and seston utilization is poorly understood.

Production studies of lotic caddisflies have become more numerous recently (e.g. Benke and Wallace 1980; Cudney and Wallace 1980), as have investigations examining the influence of filter feeding insects on stream seston (e.g. Ladle et al. 1972, McCullough et al. 1979). However, few authors have combined these analyses with the quantitative feeding studies necessary to obtain an elementary understanding of the functional role of these insects in stream ecosystems (Benke and Wallace 1980).

Our investigation dealt with *Brachycentrus spinae* Ross which inhabits streams of the Tennessee River basin in the southeastern United States. Our objectives were to: (1) determine the life history and production of *B. spinae* in a fourth order southern Appalachian stream; (2) investigate the trophic basis of production and annual food consumption, and (3) examine seston utilization by *B. spinae*.

Study Area

Dryman Fork is located in the Appalachian Mountains in Macon County, North Carolina (35° 3′ N, 86° 25′ W; Fig. 1), and is part of the headwaters of Coweeta Creek. Much of its drainage basin (567 ha) lies within the Coweeta Hydrologic Laboratory of the U.S. Forest Service. The lower 1.7 km of stream, where sampling was conducted, flows through a small mountain valley (ca. 405 ha) largely in private ownership. Land use here consists of forest, pasture, row crops, and gardens. However, throughout most of this area the fourth order stream is bordered by a dense growth of deciduous trees and shrubs, primarily *Alnus serrulata* (L.).

The stream ranges from 2.5–7.0 m in width ($\overline{X}$ = 4.65 m), 0.2–0.9 m in bankfull depth ($\overline{X}$ = 0.41 m), and has a gradient of 40 m km^{-1}. Substrate consists primarily of stones from 16 mm in diameter to large granitic outcrops, with 80% of the material between 6–50 cm in diameter. Water temperature ranged from 1.0–18.4°C between June 1978 and September 1979 with an annual mean of 11.4°C.

Materials and Methods

Sampling

Larvae of *B. spinae* were obtained from samples collected for a larger study of net-spinning Trichoptera at six locations in Dryman Fork (Fig. 1, stations A-F). *Brachycentrus* occurred only at stations E and F. At each station a length of stream was marked off in 5 m intervals, and sample locations determined with randomly chosen coordinates. Four or five samples were taken semi-monthly in summer and monthly during other seasons from June 1978 to August 1979, totaling 82 samples per station. Samples were collected using a 52 cm wide drift net (230 μm mesh) with sheet metal panels attached to its anterolateral edges, similar to a Surber sampler. The net was anchored to the streambed, and the rocky substrate within a 50 cm × 50 cm (0.25 m^2) area upstream from the net opening was cleaned in front of the net to collect insects. Net contents were

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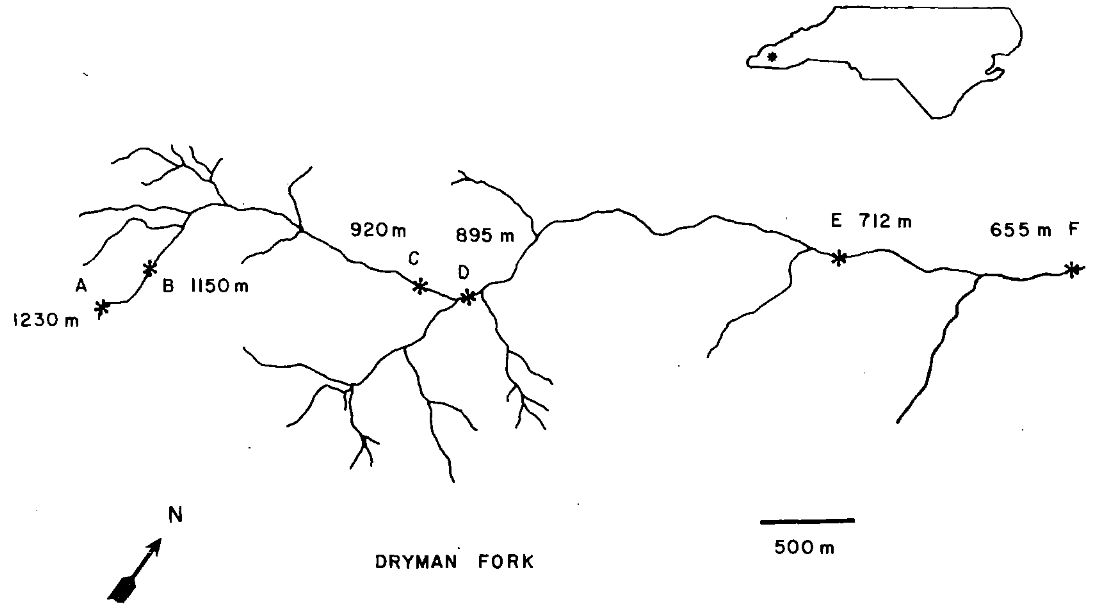

FIG. 1.—Map of Dryman Fork, Macon County, North Carolina, indicating sampling sites and their elevations.

preserved in a 6–8% formalin solution containing a small amount of Phloxine B dye, which facilitates laboratory sorting. Larval head capsule width at the eye level was measured to the nearest 20 μm with an ocular micrometer, and head width frequency histograms were constructed to separate the larval instars.

Production

Mean individual ash-free dry weights (AFDW) were determined for each instar from each station. Weights were based on a minimum of 10 larvae for a given instar and date. Larvae from preserved samples were placed in a drying oven (65°C) for 24 h, then transferred to a desiccator for 24 h. Individuals were then weighted on a Cahn 23® electrobalance to the nearest microgram and ashed in a muffle furnace (ca. 485°C) for one h. Final weights were obtained after the ash had desiccated for 24 h. Weights for each instar were obtained for all sampling dates on which it was present. Larval case weights were also determined using the same procedures.

Nonparametric one-way analysis of variance was used to test for a difference in larval densities between stations. Differences in instar and case weights from stations E and F were tested using the Wilcoxon signed-ranks test. Since neither weights nor densities differed significantly between stations ($P>0.5$), these data were pooled for production calculations.

First and second instar *Brachycentrus* attach their cases to trailing vegetation (primarily exposed roots) along the bank (Murphy 1919) and were not adequately sampled by our methods. To obtain estimates of their densities we regressed the mean number of larvae per m^2 (from later dates) on time (Fig. 2). Both larval production and case construction were calculated by the instantaneous growth (IGR) method (Waters 1977) using densities obtained from the curve in Fig. 2. The date

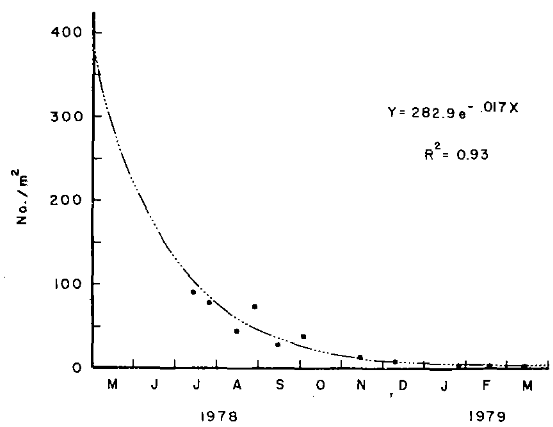

FIG. 2.—Larval mortality curve for *Brachycentrus spinae* Ross from Dryman Fork, Macon County, North Carolina, 1978–1979.

chosen for first instar density estimates was based on their initial appearance in the stream.

Gut analyses

Foregut analyses were conducted on the last three instars of *B. spinae* from Dryman Fork between 13 July 1978 and 17 February 1979. Slides for gut analysis were prepared using a modification of Cummins' (1973) membrane filter technique. Five food types were recognized: animal material, vascular plant detritus, fine amorphous detritus, filamentous algae, and diatoms. Individual fragments found in foreguts were outlined on paper using a compound microscope with a drawing tube. Projected areas of individual particles were measured from particle outlines with a Hewlett-Packard® 9864A digitizer interfaced to an HP 9825A desktop computer. Areas were used as an index of food volume in the gut. A total of 5330 particles was measured. Qualitative collections of late instar *B. spinae* for gut analyses were also made in Shope Fork from 1973–1975. This stream is another fourth order tributary of Coweeta Creek draining portions of the Coweeta Hydrologic Laboratory. The site of these collections is approximately 1.75 km north of the Dryman Fork site, at the entrance to the Coweeta Laboratory. Here Shope Fork is similar to Dryman Fork in size and substrate composition, but flows through an unshaded open meadow.

Differences in the proportions of each food type between instars, stations, and streams were tested using Chi-square contingency tables. Values of annual production and volumetric proportions of food types consumed by *B. spinae* were combined with literature derived bioenergetic data and used to calculate the amount of production attributable to each food type and annual food consumption (Benke and Wallace 1980).

Seston

Dryman Fork seston was sampled in July, September, and December 1978 and March, June, and August 1979. Four to 7 samples were taken from each station at each season. Miller high-speed plankton samplers were used to collect large particles (>234 μm dia.), and 22 liter carboys of stream water were collected to measure smaller materials. Seston was separated into seven size categories (see Table 5), and concentrations of each particle size class (mg AFDW liter^{-1}) were determined using the wet filtration method of Gurtz et al. (1980). The proportion of animal material in the seston was estimated by sorting animals from other materials and determining their concentrations (mg AFDW liter^{-1}) as for other seston. All subsequent discussion of seston data refers to organic material (AFDW).

Total streambed area between stations E and F during summer (5037 m^2) was calculated as the product of its length (1415 m) and average width (3.56 m). The mean width (see Study Area) was reduced by one m for this computation to account for low summer discharge and uninhabited streamside habitat. Total summer seston input to this section of stream was estimated by multiplying mean summer seston concentration at station E (average of July and September 1978 samples) by average discharge (1.1232 × 10^7 liters d^{-1}) and 92 days in July, August, and September. These quantities were used to calculate seston utilization by *B. spinae* in the study section.

Results

Larval Growth and Development

Brachycentrus spinae was univoltine in Dryman Fork (Fig. 3). Larvae hatched in May and developed synchronously through five instars. Fifth instars were first collected in late August and were present until March when they pupated. Larval growth (i.e., weight, y, vs. time, x) was linear during stadia I-IV ($y = 0.28 + 0.017x$; $r^2 = 0.92$), but exponential during the fifth stadium ($y = 0.98e^{0.308x}$; $r^2 = 0.98$). Mean AFDW of individual fifth instars increased from 1.825 mg in September to 11.548 mg by March (Table 1). Larval mortality followed a negative exponential pattern (Fig. 2) which was highly significant ($r = 0.96$, $P<0.005$) and is typical of aquatic invertebrates (Waters 1977).

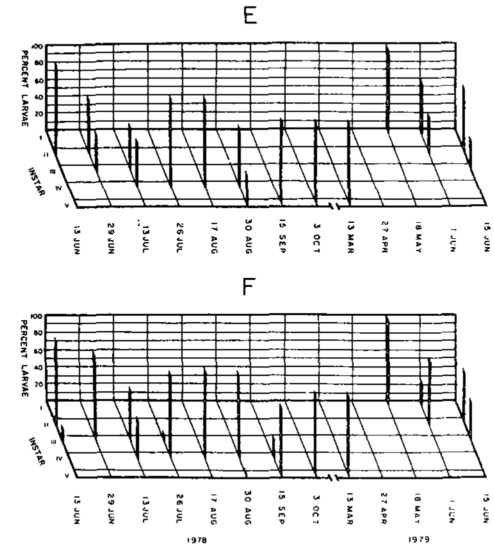

FIG. 3.—Instar distributions of larval populations of *Brachycentrus spinae* Ross from the two sampling sites in Dryman Fork, Macon, County, North Carolina, 1978–1979.

Table 1.—Mean individual weights (± standard error) of the five larval instars of *Brachycentrus spinae* from Dryman Fork, Macon County, North Carolina, 1978–1979 (mg ash-free dry weight).

Date	Instar	Weight (mg)
13 Jun	II	0.079±0.004
29 Jun	III	0.173±0.025
13 Jul	III	0.318±0.009
	IV	0.393±0.027
26 Jul	IV	0.883±0.051
17 Aug	IV	1.206±0.097
30 Aug	IV	1.805±0.084
15 Sep	V	1.825±0.174
3 Oct	V	3.199±0.246
14 Nov	V	3.557±0.339
7 Dec	V	4.631±0.531
27 Jan	V	6.853±0.854
17 Feb	V	8.477±1.540
13 Mar	V	11.548±1.109
18 May	I	0.021±0.001

Production

Production calculations using the IGR method are shown in Table 2. Mean weight on each date was calculated as the sum of products of each instar's mean weight and its relative frequency in the population (Table 1, Fig. 3). Annual production of *B. spinae* was 260.70 mg AFDW m^{-2}. Production estimates using the lower and upper 95% confidence bounds of the estimated mean densities (Table 2, col. 2) were 183.192 and 3[illegible].483 mg AFDW m^{-2}, respectively. Over 56% of annual larval production occurred during the summer

Table 2.—Instantaneous growth method production calculations for *Brachycentrus spinae* from Dryman Fork, Macon County, North Carolina, 1978–1979 (mg ash-free dry weight).

Date	$\bar{X}$ # m^{-2}	(95% conf. int.)	$\bar{X}$ Weight (mg)	Standing Crop (mg m^{-2})	G*	Mean Standing Crop (mg m^{-2})	Production (mg m^{-2})
18 May	282.9	(182.6–406.7)	0.021	5.941			
1 Jun	226.8	(146.4–315.9)	0.057	12.928	0.9985	9.120	9.196
13 Jun	181.9	(121.1–254.6)	0.088	15.998	0.4343	14.463	6.281
29 Jun	138.5	(92.4–187.9)	0.173	23.960	0.6760	19.979	13.506
13 Jul	109.2	(75.0–148.7)	0.352	38.438	0.7103	31.199	22.161
26 Jul	87.5	(60.9–117.9)	0.940	82.250	0.9822	60.344	59.270
17 Aug	60.2	(42.7– 78.0)	1.206	72.601	0.2492	77.426	19.295
30 Aug	48.3	(34.5– 63.7)	1.796	86.747	0.3982	79.674	31.726
15 Sep	36.8	(26.5– 48.2)	1.821	67.103	0.1382	76.925	10.631
3 Oct	27.1	(19.7– 35.3)	3.199	86.693	0.5635	76.898	43.332
14 Nov	13.0	(9.5– 17.0)	3.557	46.241	0.1061	66.467	7.052
7 Dec	8.8	(6.4– 11.6)	4.631	40.753	0.2636	43.497	11.466
27 Jan	3.8	(2.7– 5.1)	6.853	25.015	0.3919	32.884	12.887
17 Feb	2.6	(1.8– 3.7)	8.477	22.040	0.2127	23.528	5.004
13 Mar	1.7	(1.2– 2.5)	11.548	19.632	0.3092	20.836	6.442
					0.2483@	9.816	2.437
				$\bar{X}$ = 43.089 mg m^{-2}		Annual Production = 260.686 mg m^{-2} yr^{-1}	

* G = ln(mean AFDW at end of an interval/mean AFDW at the beginning of the interval).
@ Final AFDW and density assumed to be 14.803 mg and 0.0 m^{-2}, respectively.

(July, August, and September), and fifth instars accounted for 31% of total production. The mean annual standing crop was 40.396 mg AFDW m^{-2}, the annual turnover ratio (TR = Production/Biomass) was 6.4, and the cohort TR was 6.0. Larval case construction (silk + detritus) was estimated at 256.2 mg AFDW m^{-2} yr^{-1} using the IGR method. Use of production methodology for these calculations is reasonable since larvae retain the same case throughout life and add to it as they grow.

Trophic Basis of Production

Production attributable to various foods can be estimated if three quantities are known: (1) volumetric proportions of food types consumed; (2) assimilation and net production efficiencies (AE and NPE, respectively) for various foods; and (3) annual production (Benke and Wallace 1980). Differences in the proportions of each food type ingested between instars and stations were not significant (P>0.05), so the data were pooled for subsequent calculations.

The relative importance of each food type to *B. spinae* in Dryman Fork was calculated as the product of the percentage of that type eaten and literature derived values (see Discussion) for AE and NPE (Table 3, cols. 1–4). Converting these relative values to percentages and multiplying each by annual production yield the actual amount of production attributed to each food (Table 3, cols. 5 and 6). Based on different assimilation efficiencies the most important food for *B. spinae* production in Dryman Fork was animal material, followed by amorphous detritus. Other foods accounted for only 13% of total production (Table 3).

Annual consumption of each food type was also calculated for *B. spinae* from Dryman Fork. The quotient of production from each food type divided by the product of its respective AE and NPE is annual consumption of that food (Table 3 cols. 6–8). Annual consumption of all food types by *B. spinae* was estimated at 2158.0 mg AFDW m^{-2}. Amorphous detritus comprised 60% of this figure and animal material 21%.

Although we did not measure *B. spinae* production in Shope Fork, we did obtain estimates of the relative importance of each food and its percent contribution to production (Table 4). While animal material and detritus

Table 3.—Calculations of the production attributed to each food type and the amount of food consumed by *Brachycentrus spinae* in Dryman Fork, Macon County, North Carolina, 1978–1979.*

	% Food Type in Foregut	AE	NPE	Relative Amt. to Product.	% Product. from each Food Type	Product. from each Food Type (mg m^{-2} yr^{-1})	AE × NPE	Amt. Food Consumed (mg m^{-2} yr^{-1})
Animal	21.3	0.7	0.5	7.46	61.714	160.879	0.35	459.653
Vascular Plant Detritus	11.2	0.1	0.5	0.56	4.636	12.085	0.05	241.696
Amorphous Detritus	60.6	0.1	0.5	3.03	25.083	65.387	0.05	1307.746
Filamentous Algae	3.9	0.3	0.5	0.59	4.843	12.624	0.15	84.162
Diatoms	3.0	0.3	0.5	0.45	3.725	9.711	0.15	64.740
							Total Consumption = 2157.997 mg AFDW m^{-2} yr^{-1}	

* Annual production = 260.686 mg AFDW m^{-2} yr^{-1}.

Table 4.—Foregut contents of the final three instars of *Brachycentrus spinae* and the percent of production attributable to each food type in Dryman and Shope Forks, Macon County, North Carolina.

	% of Total Area of Each Food Type*		% of Production Attributable to Each Food Type*	
	Dryman	Shope	Dryman	Shope
Animal	21.30	36.74	61.75	71.69
Detritus#	71.80	44.12	29.71	12.32
Filamentous Algae	3.90	9.12	4.88	7.64
Diatoms	3.00	10.03	3.73	8.36

* Differences between streams are significant ($P<0.02$).
# Vascular plant detritus and amorphous detritus combined.

were also the two most important foods in Shope Fork, the amounts consumed differed significantly between the two streams ($P<0.02$). Furthermore, larvae in Shope Fork consumed more filamentous algae and diatoms than those in Dryman Fork. This probably reflects greater primary production at the open, unshaded Shope Fork site.

Seston Utilization

We examined seston utilization by *B. spinae* using consumption data (Table 3) and seston data from station E (Table 5). Our attention focused on the summer months when over 56% of annual production (and consumption) occurred.

Mean summer seston concentration at station E was 1.645 mg AFDW liter^{-1} (Table 5), and total summer seston input to the 1.415 km stream section was estimated at 1699.851 kg AFDW. Annual food consumption by *B. spinae* in this section was 10.983 kg AFDW, with 6.178 kg AFDW (56.25%) consumed in summer.

During the summer *B. spinae* filtered only 0.36% (6.178 kg/1699.851 kg) of the total seston entering the study section at station E (Table 6). When smaller size fractions were excluded the percentage rose, but was still very low. Any food obtained by grazing would further reduce the seston utilization values. Considering only large material (>864 μm; 1.60% of total seston) the proportion captured increased to 22.7%.

In contrast, *B. spinae* selectively captured high quality animal material from the seston, consuming 3.5 times that entering the study section at station E (Table 6). Assuming all invertebrate drift was not returning to the substrate nor being regenerated, *B. spinae* feeding alone would consume all drifting invertebrates within a 400 m reach. Obviously this scarce material must be regenerated within the stream, which is consistent with Elliott's (1971) finding that invertebrate drift is regenerated over short distances. If prey invertebrates drifted a mean distance of 40 m (Elliott 1971), 10% would be captured by *B. spinae*.

Table 5.—Seston composition at station E of Dryman Fork, Macon County, North Carolina, based on samples from July and September 1978 (n = 12).

Size Fraction	Mean Concentration (mg l^{-1})	Percentage
> 5 mm	0.0065	0.40
864 μm–5 mm	0.0198	1.20
234 μm–864 μ	0.0426	2.59
106 μm–234 μm	0.1810	11.00
43 μm–106 μm	0.5218	31.72
25 μm–43 μm	0.2625	15.96
0.45 μm–25 μm	0.6108	37.13
	TOTAL = 1.645 mg l^{-1}	

Table 6.—Portion of total summer seston used by *Brachycentrus spinae* in Dryman Fork, Macon County, North Carolina, assuming various lower limits of particle size capture.

Smallest Size Captured (μm)	% Used m^{-2}#	% Used Along 1.415 km of Stream
0.45	0.00007	0.36
25.0	0.00011	0.58
43.0	0.00015	0.77
106.0	0.00047	2.40
234.0	0.00170	8.67
864.0	0.00450	22.72
Animal Drift*	0.07100	358.85

* 0.0216% of total seston.
# To calculate percent used per linear meter of stream, multiply the tabulated value in this column by 3.56.

Discussion

The univoltine life cycle of *B. spinae* in Dryman Fork, with an extended fifth stadium and early spring pupation, was similar to other *Brachycentrus* spp. (Mecom and Cummins 1964). The only published study of brachycentrid production is that of DeCamps and LaFont (1974) in France on five *Micrasema* spp. Production of *B. spinae* was at the lower end of the range of values reported by these authors, 180–1800 mg dry wt m^{-2} yr^{-1}, but similar to values for other filter feeding caddisflies in small headwater streams (Benke and Wallace 1980). Silk used for case construction may account for 18–26% of the total AFDW of fifth instar *Sericostoma* larvae (Iversen 1979). Since our production calculations did not include silk secretions they undoubtedly yielded an underestimate for total organic production.

Studies of filter feeders in larger rivers, primarily hydropsychid caddisflies, report production in excess of 10–15 g m^{-2} yr^{-1} (Nelson and Scott 1962, Cudney and Wallace 1980). Benke and Wallace (1980) suggest that large differences in production between rivers and smaller headwater streams may be attributed to generally lower quality of particulate organic matter in the seston. Our results support this suggestion, as *B. spinae* production relied heavily upon high quality animal seston which was extremely scarce (0.0216% of total seston, Table 6). The question of food-limited filter feeder production in smaller headwater streams warrants further investigation into the role of food quantity and quality.

No bioenergetic studies exist for *Brachycentrus* spp., so we have followed the assumptions of Benke and Wallace (1980) for assimilation and net production efficiencies (Table 3). These authors provide a discussion of literature values and rationale for their selections.

Larvae of other *Brachycentrus* spp. are omnivores (Gallepp 1974, 1977), which was also true of *B. spinae*. Cummins (1973) found that algae, detritus, and animal material represent 80, 15, and 5%, respectively, of *B. americanus* (Banks) gut contents. Shapas and Hilsenhoff (1976) examined both *B. americanus* and *B. occidentalis* Banks and found that detritus, algae, and diatoms comprise > 90% of gut contents by volume, with animal material ≤ 8%. The higher proportion of animal material in *B. spinae* guts (21.3%) contrasted with these studies, but was similar to Murphy's (1919) findings for *B. nigrosoma* Banks (= *B. numerosus* (Say)). She states that the majority of gut contents in late instars is animal food such as mayfly nymphs, chironomids, small crustaceans, and water mites.

The variations evident in *Brachycentrus* gut contents may represent actual interspecific differences in food habits, or merely reflect food availability. Mecom and Cummins (1964) found close correlation between available food and gut contents of *B. americanus*, and we have shown how possible variation in food availability can result in significant intraspecific differences in feeding habits within the same watershed (Table 4). Low values reported for animal food may also be caused by its rapid assimilation. In any case, all *Brachycentrus* spp. studied ingest some animal material, and this may show the importance of intake of high-protein food during rapid growth in the final stadia (Anderson and Cummins 1979). The importance of animal food for production of stream benthos has been discussed by Benke and Wallace (1980).

Species of *Brachycentrus* and the closely related genus *Oligoplectrum* possess meso-and metathoracic legs highly specialized for filter feeding (Wiggins 1965). However, these legs also have raptorial characteristics, e.g., enlarged flattened femora with opposable tibiae and tarsi, and numerous short spines on their ventroposterior margins. Spines on the metathoracic legs of *B. spinae*, measured from SEM photomicrographs, had a mean length of 56 μm, and the distance between them was 2–10 μm (D. H. Ross, unpublished data). If the primary function of the spines was filtration of fine particles, one would expect more finer material (e.g. < 43 μm) to be captured than was indicated in Table 6. Gallepp (1974) considers the capture of particles < 250 μm by *B. americanus* unlikely. We believe the primary function of these specialized legs is to capture larger particles, e.g., animal material, and that the spines assist larvae in holding and manipulating prey. Algae and detritus may be ingested while larvae are grazing (Gallepp 1974). However, we consistently observed *B. spinae* with their cases attached to the substrate and legs extended in the filtering position, and Gallepp (1974) showed that filtering requires less energy expenditure than grazing. Therefore, these observations may partially account for the paucity of filamentous algae and diatoms in *B. spinae* guts.

The low seston utilization by *B. spinae* contrasted with some other lotic filter feeding insects, notably simuliids and hydropsychids. In certain localities these insects can remove an estimated 60–100% of the seston in distances of 0.6–9.2 km (Ladle et al. 1972; McCullough et al. 1979). Mean annual larval density of *B. spinae* in Dryman Fork (76.8 larvae m^{-2}) was much lower than densities in these other investigations. If brachycentrids had been as abundant as the filter feeders studied by McCullough et al. (1979), they would have removed 0.015% m^{-2} of the total seston, which is very close to the 0.01% m^{-2} reported by these authors.

Summary and Conclusions

We have attempted to summarize the role of *B. spinae* in "spiralling" organic materials in Dryman Fork (Fig. 4). Spiralling is a term used by Wallace et al. (1977) to describe material cycling that occurs in a stream reach, i.e., ingestion of materials by filter feeders, egestion into the detritus pool, and subsequent reingestion by organisms downstream. Only those matrials examined in our feeding analyses are shown.

While the impact of *B. spinae* on seston quantity was minimal (Table 6), this species may exert significant influence on seston quality. Larvae captured a significant portion of high-quality animal material from the seston, assimilated much of it, and egested the remainder as lower quality detritus. As Fig. 4 illustrates, *B. spinae* was a net producer of detritus, with egestion (feces) exceeding detritus ingestion by over 300 mg AFDW m^{-2} yr^{-1}. Benke and Wallace (1980) found that 6 species of net-spinning caddisflies in another Appalachian stream are also net producers of detritus.

Wallace et al. (1977) hypothesized that filter feeders play an important role in retardation and storage of organic inputs to stream ecosystems. *B. spinae* not only stored material through tissue elaboration (production), but also case construction. Case construction was 256

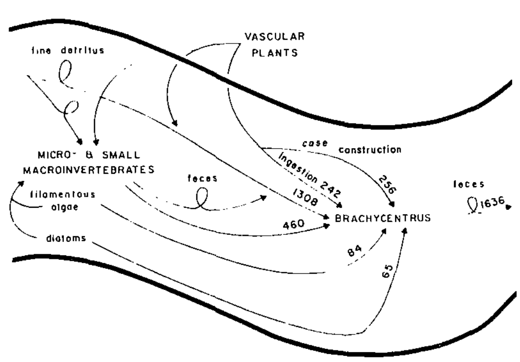

FIG. 4.—Role of *Brachycentrus spinae* Ross in "spiralling" organic matter in Dryman Fork. (All figures in mg AFDW m^{-2} yr^{-1}.)

mg AFDW m^{-2} yr^{-1}, almost equal to larval production. Silk secretions accounted for a portion of the cases, but the remainder represented other organic material stored within the stream reach. Sedell et al. (1978) discuss the influence of retention devices (e.g., boulders, woody debris, macrophytes, bed roughness) on particulate organic matter (POM) transport in streams. They consider filter feeding invertebrates to be an important biological retention device, and cite the necessity of developing retention indices for such devices. Whole guilds of filter feeders are capable of retaining significant amounts of POM (Ladle et al. 1972, McCullough et al. 1979). We have obtained rudimentary estimates of the amount of POM *B. spinae* removed from the seston, and while the role of this single species appeared minor, our studies suggested that the major effect of *B. spinae* is to alter the quality of seston rather than its quantity.

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