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V. Running waters

Trophic relationships in a small woodland stream[1]

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With 2 figures and 5 tables in the text

Introduction

Linesville Creek, a small woodland stream located in Crawford County in Northwestern Pennsylvania, has been under investigation for three years. In the course of a study aimed at delineating the factors which determine the microdistribution patterns of the macrobenthic invertebrates of the stream, extensive data have been gathered on the trophic relations of the species encountered in riffle habitats.

Various aspects of the trophic relations of stream invertebrates have been studied previously by a number of workers (LEATHERS 1922; WISSMEYER 1926; MUTTKOWSKI 1929; PERCIVAL and WHITEHEAD 1929; CAVENAUGH and TILDEN 1930; SLACK 1936; JONES 1950; WALSHE 1950; BADCOCK 1951; NAGAGAWA 1952; BROWN 1960, 1961 a, 1961 b; DEMORY 1961; HYNES 1961; CHAPMAN and DEMORY 1963; CUSHING 1963; DAVIS 1963; MINCKLEY 1963; CUMMINS 1964; MECOM and CUMMINS 1964; WARREN et al. 1964; CHAPMAN 1965; CUMMINS 1965) but as yet no one has completely defined the trophic structure of a lotic community.

It must be emphasized that the results described below represent an attempt to determine the ingestion food web of riffle areas in the stream. Undoubtedly when an assimilation food web is constructed it will be somewhat different. However, ingestion data must be gathered preliminary to assimilation studies and such data are of ecological interest. First, an ingestion food web for a stream community is probably a reasonable approximation of the assimilation food web and, second, the impact of a consumer on its food source is independent of assimilation, except in those few cases in which viable cells are released in the feces.

Methods

Field Samples

A five sample transect is collected each month from a riffle section of the stream. Each sample taken with a special riffle sampler, consists of all substrate materials down to a depth of 5 cm and a surface area of 900 cm^2. The sampling device, which is constructed of plexiglass with a foam rubber base is designed to shut off the current around the sampling area. All sediments and associated benthic organisms are removed from the sample area with a scoop and a 0.064 mm mesh dip net. Prior to the placement of the sampler, current velocity is measured at the substrate water interface with a

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pigmy current meter (CORBETT 1955). Before the sediments are removed, photographs of the substrate surface are taken and periphytic and bacterial samples are collected.

Periphytic algae available as a food source for primary macroconsumers are sampled with a scraping device fitted with a vacuum suction attachment (ROFF et al. 1965). Three 1 cm^2 areas are scraped from within the confines of the 900 cm^2 sample area. Ten to thirty ml of sediment are collected from each sample area in sterile bottles for bacterial analysis.

The benthic macroinvertebrates from the field samples are removed and sorted into species and age classes. Empirically determined weights for each species by size class are utilized to convert numbers to weights. A value of 5585 gram calories/gram dry weight (TRAMA 1957) is used to convert weights to energy equivalents.

Trophic Analysis

Most studies of stream trophic structure have been hampered by the lack of reliable quantitative methods. Rather than follow previous methods of approximation, the technique of MECOM and CUMMINS (1964) was employed. The contents of the entire digestive tract of one or more individuals in a given age class of a particular species are removed by microdissection. After the gut contents have been suspended in distilled water and dispersed with a magnetic stirrer, the material is drawn down on a Millipore filter (0.45 μ pore size). The number of guts and filter size (13 or 25 mm diameter) are selected to yield filters of suitable density for counting. Three food categories are enumerated.

1) Periphytic algae. Enumeration of the cells, identified to species in most cases, is continued until a total count of at least 100 cells has been achieved. Most counts consist of one to two rows across the center of the filter, although on occasion the entire filter must be counted. Based on the exact area of the filter counted, an estimate of the total numbers of each species on the filter is calculated. A value of 8.34×10^{-6} milligrams per cell is employed in the calculations of diatom dry weight. This value is based on the weight given by TRAMA (1957) for *Navicula minima* and adjusted to account for cells of greater weight than *N. minima*. A value of 3218 gm-cal/gm dry wt (TRAMA 1957) is used for diatom caloric conversions.

2) Detritus. Detrital enumeration is accomplished by counting 10 fields at 400 $\times$ and measuring the diameter of all detrital particles counted. Whenever detrital fragments can be identified as vascular plant tissue, they are recorded as such. An empirically determined value of weight (3.03×10^{-2} mg) per unit area for vascular plant material collected in the field samples has been employed to convert the calculated total detrital area on a filter to an estimated weight. To convert the detritus complex to energy equivalents, a value of 4500 gm-cal/gm dry wt (a median value for vascular plant tissue) is used. Actually the detrital category, as defined in this study, includes not only dead plant and animal material but also the associated bacterial and fungal flora.

3) Animals. Each filter is scanned completely for animal fragments which are identified to species and age class whenever possible. An estimate, based on the occurrence of head parts, is made of the total number of individuals of each prey species ingested.

Primary Producers

Each preserved 1 cm^2 periphyton scraping sample is made up to a constant volume and subsamples are withdrawn for diatom counts and enumeration of the other algal groups. Subsamples to be counted for diatoms are cleaned with nitric acid and potassium dichromate and mounted in Hyrax (HOHN and HELLERMAN 1963). Counts of

other algal groups are obtained from Millipore filtered subsamples. Separate experiments are being conducted in order to estimate the rate of carbon fixation by the periphytic algae. The carbon-14 method in closed circulating chambers followed by gas-phase counting is being employed. Natural substrates from the stream bed are placed in the light and dark chambers and an electric motor maintains an internal rate of circulation approximating that in the stream (ROFF et al.).

Detrital Food

Although as yet no completely satisfactory technique has been devised for estimating relative amounts of available detrital material, standard bacterial plate counts have been made from steril bottle samples taken in each 900 cm^2 sample area. The assumption being made is that general bacterial activity will afford a rough index of the availability of detrital material. In addition, an organic fraction is measured in conjunction with the physical analysis of the sediments from field samples; this provides a rough estimate of the available vascular plant detritus of allochthonous origin.

Results and Discussion

Although samples from an entrie year have been collected, only data from the October 7, 1964 transect have been completely processed. The standing crops are given in Table 1. Samples 1 and 5 were taken from the stream margin, 3 from the center of the channel and 2 and 4 at intermediate positions. The standing crop increased from the margin of the riffle and was maximized at the center of the riffle which seems to be correlated with increased microhabitat diversity. In contrast, no clear-cut maximization of periphyton levels at the center of the channel was observed.

As representative trophic data, the results of gut analyses for the netspinning caddisfly *Hydropsyche slossonae* are shown in Table 2. Calculated total numbers, weights and calories of the diatom, detritus and animal categories in the guts of two age classes of *H. slossonae* are given in Table 3. Similar analyses have been made for the other species from the October transect.

In any study of the trophic relations of stream benthos it soon becomes apparent that the food web is extremely complex. This is apparent from Fig. 1 which shows only a portion of the food exchange pathways in a riffle area of Linesville Creek. Therefore, in order to express the riffle trophic structure, a technique has been used in which portions of each macrobenthic species are assigned, on the basis of gut analyses, to one of the trophic levels shown in Fig. 2.

For example the values given in Table 3 for food categories found in *H. slossonae* guts are converted to relative percents. These percentages are then used to determine the number, amount of biomass and calories of *H. slossonae* (that is the standing crop figure given at the top of Table 4) that should be assigned to each of the three trophic levels (Λ_2, Λ_2' and Λ_3, etc.). When this is done for each species represented in a given sample and totaled, the number, biomass and calories/m^2 to be assigned to each trophic level can be determined. The cal-

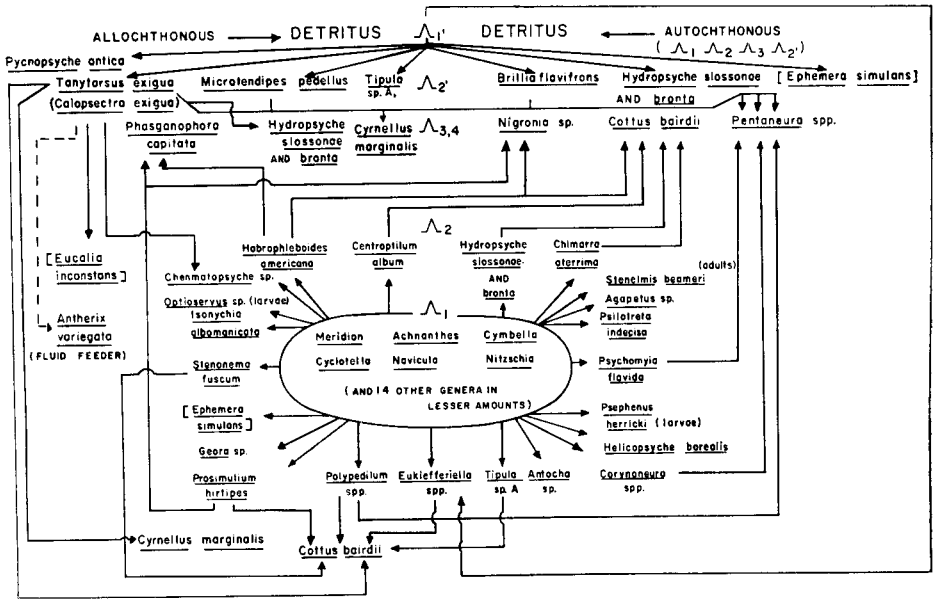

Fig. 1. A partial food web for riffle areas of Linesville Creek. Λ_1 = primary producers; Λ_1' = detritus; Λ_2 = primary consumers; Λ_2' = detrital consumers; $\Lambda_{3,4}$ = secondary consumer levels. Species in brackets are found only occasionally in riffle areas or live outside the riffle habitat but derive food from the riffle. The arrows indicate the flow of food to a given consumer.

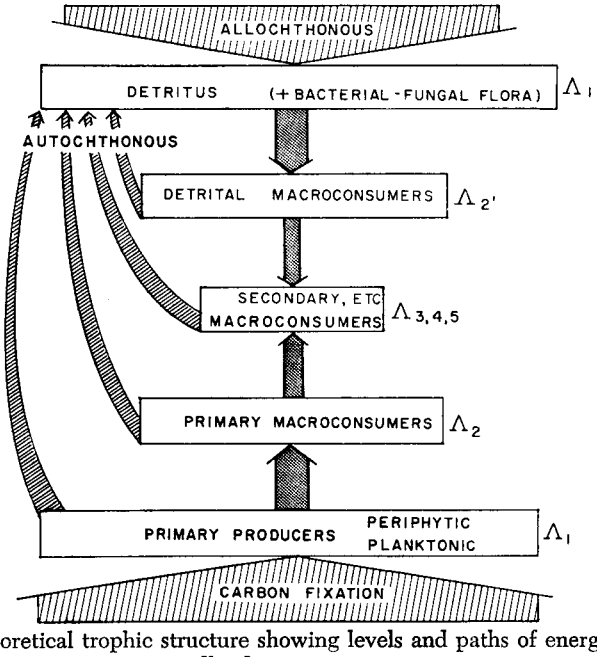

Fig. 2. Theoretical trophic structure showing levels and paths of energy flow in a woodland stream ecosystem.

Table 1. Standing crop of five — sample transect taken October 7, 1964, riffle area, Linesville Creek, Pennsylvania.

Taxon	Numbers/900 cm²				
	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5
Turbellaria					
Dugesia sp.		7	10		1
Oligochaeta	7	18		11	7
Mollusca					
Ferrissia rivularis	75	2	8	1	2
Physa sp.	1				1
Sphaerium sp.		1	1		1
Gyraulus sp.			8		
Acarina	2	12	104	28	7
Decopoda			1		
Orconectes sp.					
Plecoptera					
Acroneuria lycorias		2	6	1	
Chloroperla sp.			2		
Taeniopteryx maura		27	5	1	1
Ephemeroptera					
Stenonema fuscum	11	13	15	3	3
S. canadense	2	5	14	4	1
S. tripunctatum	8				
S. sp.*			3	5	
Isonychia albomanicata		2	7	1	1
Habrophleboides americana	7	44	54	31	18
Centroptilum album	5	8	24		2
Pseudocloeon sp.			2		
Caenis anceps	1				
Ephemera varia	2				
E. simulans			1		1
Unident. Ephemeroptera*				3	
Hemiptera					
Belastoma sp.	2				1
Ranatra fusca	1				
Microvelia sp.			1		
Megaloptera					
Nigronia sp.	1		1		2
Sialis sp.	1				
Trichoptera					
Hydropsyche bronta		17	46	30	15
H. slossonae		24	137	137	54
H. betteni		1	3	8	8
Cheumatopsyche sp.		89	227	123	43
Unident. Hydropsychids*			39	15	
Chimarra aterrima		44	48	48	46

Table 1 (continued).

Taxon	Numbers/900 cm²				
	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5
Psychomyia flavida	126	7	37	17	
Polycentropus confusus					2
Cyrnellus marginalis	6	11	17	3	1
Helicopsyche borealis	15	12	19	61	66
Agapetus sp. (larvae)		123	136	102	33
A. sp. (pupae)			1	9	
Goera sp.		5	5		3
Neophylax nacatus (pupae)	1	1			
Pycnopsyche antica	4				1
Psilotreta indecisa		1	1	1	2
Hydroptilidae			10	1	
Coleoptera					
Psephenus herricki (lar.)	12	33	43	5	5
Ectoparia sp. (lar.)	3				1
Optioservus sp. (lar.)	4	78	102	39	14
O. sp. (adults)		3	4	2	2
Stenelmis beameri (lar.)		55		13	
S. beameri (adults)	7	1	4	5	4
Unident. elmids (lar.)*				1	
Unident. elmids (adults)				1	
Helichus sp. 1 (adult)					2
Dubiraphia sp. (adults)					13
Diptera					
Atherix variegata		8	14	31	3
Hemerodromia sp.	7	2	93	4	
Tabanus sp.					1
Antocha sp.	11	12	140	31	5
Palpomyia sp.			3	13	3
Simulium venustum		6	20	4	2
Simuliid pupae			1	2	2
Tipula sp. A					3
Total/900 cm² (exclusive of midges)	322	674	1416	795	383
Total/m²**	3574.2	7481.4	15717.6	8824.5	4251.3
Chironomid pupae		10	2	9	3
Pentaneura melanops group, sp. (p)					9
Brillia flavifrons		1			
Corynoneura sp.		13			2
Corynoneura taris		5			
Unk. genus near *Corynoneura*		6			
Cricotopus exilis		1			
Cricotopus junus		4			

Table 1 (continued).

Taxon	Numbers/900 cm²				
	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5
Eukiefferiella sp. near sp. 2		15			18
Unk. genus near *Eukiefferiella*		22			17
Hydrobaenus sp. near *paradorenus*		2			
Unk. genus near *Metriocnemus*		8			11
Cryptochironomus sp. B		1			
Limnochironomus modestus					
Microtendipes pedellus		21			1
Polypedilum scalaenum		1			2
Tanytarsus (= *Calopsectra*) *exigua*		39			20
Tanytarsus sp. near *pentatoma*		2			
Total Chironomids/900 cm²	—	151	—	—	83
Total Chironomids/m²**	—	1676.1	—	—	921.3
Total-all taxa/900 cm²	—	825	—	—	466
Total-all taxa/m²***	—	9157.5	—	—	5138.4

* Indistinguishable young stages or fragments.
** Calculated values.

culated values for *H. slossonae* are given in Table 4. As would be expected, the resulting trophic placement on the basis of numbers, weights and calories of the ingested items are different. If all food items are equally assimilable, then the importance of secondary consumption to *H. slossonae*, is much greater from the standpoint of energetics than it is when viewed in terms of the number of ingested items.

When periphyton cells/cm² values are expressed on a per meter square basis, the range is from 10^9/m² to 10^{12}/m² for the October 7 transect. Based on an average value of approximately 50,000 bacterial cells/ml of substrate and the weight of allochthonous vascular plant material recovered from the sediment samples, a very rough estimate of the detrital material available can be made.

By combining all the data for each sample of a given transect, an ingestion trophic structure can be constructed; an example is shown in Table. 5. The consumer data are based on trophic analyses of 170 macrobenthic individuals. When the consumer portion of the ingestion trophic structure is analyzed on the basis of weight or calories, the detrial consumer level constitutes about 30 %, the primary consumer level 30 % and the predator portion about 40 %. The latter estimate is minimal since fish (sculpins and darters) have not been included. The importance of detritus to the energy structure of a woodland stream is apparent and agrees well with the views expressed by HYNES (1963) and Ross (1963). Based

Table 2. Food Materials in the gut of *Hydropsyche slossonae;* October 7, 1964 Transect, Sample 5 (12 larvae, instar 3).

Food Material in Gut	Number Counted	Calculated Total Number in Gut	Relative % Abundance	Food Material in Gut	Number Counted	Calculated Total Number in Gut	Relative % Abundance
Achnanthes minutisima	28	6137.6	5.80	*Nitzschia frustulum*	4	876.8	0.83
A. deflexa	10	2192.0	2.67	*N. disapata*	2	438.4	0.41
A. linearis	7	1534.4	1.45	*N.* sp. A	1	219.2	0.21
A. lanceolata var. *rostrata*	1	219.2	0.21	*Nitzschia* Total	7	1534.4	1.45
A. girdle views	16	3507.2	3.31	*Cocconeis placentula*	6	1315.2	1.24
Achnanthes Total	**62**	**13590.4**	12.83	*Cyclotella meneghiniana*	4	876.8	0.83
Amphora affinis	2	438.4	0.41	*Melosira granulata*	4	876.8	0.83
A. ovalis	2	438.4	0.41	*Surirella angusta*	1	219.2	0.21
Amphora Total	**4**	**876.8**	0.83	Unident.	11	2411.2	2.28
Cymbella ventricosa	5	1096.0	1.04	Diatom Total	**122**	**26742.4**	25.25
C. naviculaformis	1	219.2	0.21				
C. microcephala	1	219.2	0.21	Detritus (Total Area			
C. sinuata	1	219.2	0.21	3.478 mm²)	85	76440.5	72.19
C. herbridica	1	219.2	0.21	Fungal Spores	3	2697.9	25.48
C. girdle view	2	438.4	0.41	Detritus Total	88	**79138.4**	74.74
Cymbella Total	**11**	**2411.2**	22.77	Animals	8	**8.0**	< 0.01
Gomphonema constrictum	1	219.2	0.21				
G. parvulum	2	438.4	0.41	Total Number of Items		105880.8	
G. angusta	1	219.2	0.21				
G. angusta var. *producta*	1	219.2	0.21	Total Number of Items			
Gomphonema Total	**5**	**1096.0**	1.04	Per Individual		7196.7	
Navicula gracilis	3	657.6	0.62				
N. minima	2	438.4	0.41				
N. sp. A	1	219.2	0.21	Diatom Total		385.8	5.36
N. sp. B	1	219.2	0.21	Detritus Total		6810.1	94.63
Navicula Total	**7**	**1534.4**	1.45	Animal Total		0.8	0.01

Table 3. Calculated totals of algal, detritus and animal fractions in the guts of *Hydropsyche slossonae*, expressed on a per individual basis; Transect taken October 7, 1964, data from sample 5.

Food Categories	Instar 3			Instar 4		
	Number	Dry Weight (mg × 10-3)	Gram-calories	Number	Dry Weight (mg × 10-3)	Gram-calories
Diatoms	385.8	3.217	0.010	1181.4	7.846	0.025
Detritus	6810.1	8.781	0,039	17073.4	14.047	0.063
Animals	0.8	19.000	0,106	2.5	0.115	0.001

Table 4. Trophic level placement of *Hydropsyche slossonae* (40 individuals of instar 3); October 7, 1964 Transect.

Trophic Level Assignment of *H. slossonae*	On basis of no. ingested items			On basis of wt. ingested items (mg)			On basis of gram cal. ingested items		
	Λ_2	Λ_2'	Λ_3	Λ_2	Λ_2'	Λ_3	Λ_2	Λ_2'	Λ_3
Relative % Ingestion	33.61	66.31	0.08	10.86	1.78	87.38	6.58	1.51	91.91
Number /m² Assigned	149.38	294.71	0.36						
mg/m² Assigned				24.13	3.91	194.18			
gm-cal/m² Assigned							81.66	18.74	1140.70

Λ_2 = primary macroconsumer;
Λ_2' = detrital macroconsumer
Λ_3 = secondary macroconsumer (and above).

Table 5. Empirical standing crop trophic structure for the fall community of Linesville Creek (sample 5, October 7, 1964 transect; Λ_2, Λ_2', and Λ_3, etc. based on ingestion data. Notation as in Table 4).

Trophic level		Number/m²*	Dry Weight Biomass (gm/m²)*	Killogram-Calories/m²*
Primary producers (periphytic only)	Λ_1	$4.6 \pm 1.2 \times 10^{10}$	387 ± 97	1245 ± 311
Detritus	Λ_1'	—	6.63 ± 1.66	26.5 ± 6.6
Primary macro-consumers	Λ_2	981.5 (19.0)	1.313 (31.8)	6.395 (27.7)
Detritial macro-consumers	Λ_2'	4187.0 (80.9)	1.228 (29.7)	7.255 (31.4)
Secondary, etc. macroconsumers	Λ_3	9.0 (0.1)	1,593 (40.9)	9.439 (40.9)

* Relative per cents of the macroconsumer levels shown in parentheses.

on an estimate of 2.5×10^6 algal cells ingested by all macrobenthic animals in sample 5 (October transect) and a periphyton standing crop of 4.6×10^{10}, the impact of grazing is less than 0.01 %. If the amount of algae in the gut represents that grazed in a 24 hour period, or even per hour, the impact on the periphyton community should be negligible.

The relative percents of the overall trophic structure of Linesville Creek is comparable to that reported by ODUM (1957) for Silver Springs, although the Linesville Creek absolute standing crop values for secondary consumers are about one fourth as large.

Original calorie measurements currently being made and computer analysis should enable the construction of a month-by-month trophic structure for Linesville Creek in the near future.

References

BADCOCK, R. M., 1952. Easter Meeting of the British Ecological Society. Work on Hydropsychidae. *J. Animal Ecol.*, **21**, 324.

BROWN, D. S., 1960. The ingestion and digestion of algae by *Chloeon dipterum* L. *Hydrobiol.*, **16**, 81—96.

— 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (PICTET) (Insecta, Ephemeroptera). *J. Anim. Ecol.*, **30**, 55—75.

— 1961. The morphology and functioning of the mouthparts of *Chloeon dipterum* and *Baetis rhodani*. *Proc. Zool. Soc. Lond.*, **136**, 147—176.

CAVENAUGH, W. J., and TILDEN, J. E., 1930. Algal food, feeding and case building habits of the larva of the midge fly, *Tanytarsus dissimilis* JOHANNSEN. *Ecol.*, **5**, 105—115.

CHAPMAN, D. W., 1965. The relative contributions of aquatic and terrestrial primary producers to the trophic relations of stream organisms. *Pymatuning Symp. in Ecology*, No. **4**, Univ. of Pittsburgh. In press.

CHAPMANN, D. W., and DEMORY, R. L., 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology*, **44**, 140—146.

CORBETT, D. M., 1955. Stream-gaging procedure. A manual describing methods and practices of the Geological Survey. *U. S. Geol. Surv. Water Supply Pap.* **888**, 1—245. (Pigmy information on p. 181, plate 21 A; current meters 168—184.)

CUMMINS, K. W., 1964. Factors limiting the microdistribution of larvae of the caddisflies *Pycnopsyche lepida* (HAGEN) and *Pycnopsyche guttifer* (WALKER) in a Michigan stream. *Ecol. Monogr.*, **34**, 271—295.

— 1965. A review and future problems in benthic stream ecology. *Pymatuning Symp. in Ecology*, **4**, Univ. Pittsburgh. In press.

CUSHING, C. E., 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. *Trans Amer. Fish. Soc.*, **92**, 216—219.

DAVIS, G. E., 1963. *Trophic relations of simplified animal communities in laboratory streams.* Ph. D. Thesis, Oregon State Univ., Corvallis. 87 pp.

DEMORY, R. L., 1961. *Foods of juvenile coho salmon and two insect groups important in the coho diet in three tributaries of the Alsea River, Oregon.* Unpubl. M. S. Thesis, Oregon State Univ., Corvallis.

HOHN, M. H., and HELLERMAN, J., 1963. The taxonomy and structure of diatom

populations from three eastern North American rivers using three sampling methods. *Trans. Amer. Microscop. Soc.*, **82**, 250—329.

HYNES, H. B. N., 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.*, **57**, 344—388.

— 1963. Imported organic matter and secondary productivity in streams. *Proc. Internat. Congr. Zool.*, **16**, 324—329.

JONES, J. R. E., 1950. A further ecological study of the River Rheidol. The food of the common insects of the main stream. *J. Animal Ecol.*, **19**, 59—174.

LEATHERS, A. L., 1922. Ecological study of aquatic midges and some related insects, with special reference to feeding habits. *U. S. Bur. Fish.*, **38**, 1—61.

MECOM, J. O., and CUMMINS, K. W., 1964. A preliminary study of the trophic relationships of the larvae of *Brachycentrus americanus* (BANKS) (Trichoptera: Brachycentridae). *Trans. Amer. Microscop. Soc.*, **83**, 233—243.

MINCKLEY, W. L., 1963. The Ecology of a spring stream, Doe Run, Meade County, Kentucky. *Wildlife Monogr.*, **11**, 1—124.

MUTTKOWSKI, R. A., 1929. The food of trout stream insects in Yellowstone National Park. *Bull. New York State Coll. For., Roosevelt Wildlife Ann.*, **2**, 241—263.

NAGAGAWA, A., 1952. Food habits of hydropsychid larvae. *Jap. J. Limnol.*, **16**, 130—138.

ODUM, H. T., 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.*, **27**, 55—112.

PERCIVAL, E., and WHITEHEAD, H., 1929. A quantitative study of the fauna of some types of stream bed. *J. Ecol.*, **19**, 283—314.

ROFF, P. A., ROUGH, G. E., CUMMINS, K. W., and COFFMAN, W. P., 1965. *Methods for quantitative sampling and primary productivity measurements of periphytic stream algae.* In preparation.

ROSS, H. H., 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.*, **59**, 235—242.

SLACK, H. D., 1936. The food of caddis fly (Trichoptera) larvae. *J. Animal Ecol.*, **5**, 105—115.

TRAMA, F. B., 1957. *The transformation of energy by an aquatic herbivore, Stenonema pulchellum* (Ephemeroptera). Unpubl. Ph. D. Thesis, Univ. Mich.

WALSHE, B. M., 1950. The feeding habits of certain chironomid larvae (subfamily Tendipedinae). *Proc. Zool. Soc.*, **121**, 63—79.

WARREN, C. E., WALES, J. H., DAVIS, G. E., and DOUDOROFF, P., 1964. Trout production in an experimental stream enriched with sucrose. *J. Wildlife Managem.*, **28**, 617—660.

WISSMEYER, VON A., 1926. Nahrungsuntersuchungen bei Ephemeridenlarven. *Arch. Hydrobiol.*, **16**, 668—698.

Discussion

SCHMITZ: What fraction of detritus is derived from allochthonous material as compared with vascular plants from the stream?

CUMMINS: Vascular hydrophytes are essentially absent from the region of the stream under study.

MACIOLEK: Please comment on the relative digestibility or assimilation value of your primary food categories, diatoms, detritus and animals.

CUMMINS: We have no direct information on this as yet. Our approach will be to work out the ingestion food web first and then correct it to an assimilation food web based on laboratory tracer studies.

MACIOLEK: Do you enumerate diatoms in the guts by frustule or by protoplast within frustules?

CUMMINS: Enumeration is by frustules.

ILLIES: How do you distinguish, in the gut contents, those diatoms (living ones) which may have been eaten directly by the animal, from other diatoms which were taken into the gut by predation on diatom-eaters? Even in clearly predaceous animals (Perlidae for example), one finds large amounts of such secondary vegetarian food.

CUMMINS: At this point, we make no attempt to distinguish between directly and indirectly digested foods, unless the secondarily obtained food is still in the gut of the ingested prey — in that case the material is not counted. Eventually, it will be important to evaluate the assimilative importance of such secondarily obtained food.

REYNOLDSON: Your method of gut analysis would bias your data in the direction of arthropods and not include Mollusca and Platyhelminthes. Perhaps these are not important sources of prey in your case but might be in others.

CUMMINS: The two phyla are relatively unimportant in our stream but the problem has concerned us along with the question of the food of fluid feeding species. Techniques such as those which you have used with flatworms will have to be employed (chromatography, immunochemistry, tracers, etc.).

EGGLISHAW: Did you measure the total allochthonous plant material at each sampling site? We find that there is a close correlation between the amounts of benthic fauna and allochthonous plant material at sites in riffles. That you found the largest amounts of benthic fauna in midstream and the least amounts at the margins is probably due to greater amounts of plant detritus accumulating among the large stones in the center of the stream, as we have found in Scotland. It is very probable that the proportion of plant detritus in the food ingested by many species increases with increase in the amount of plant detritus at the site where these species occur.

CUMMINS: I agree that there is an important relationship between concentrations of allochthonous detritus and species densities. We do measure a gross organic fraction as a part of our sediment analysis procedure. We weigh this material and obtain calorie values whenever possible.