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A PRELIMINARY STUDY OF THE TROPHIC RELATIONSHIPS OF THE LARVAE OF *BRACHYCENTRUS AMERICANUS* (BANKS) (TRICHOPTERA: BRACHYCENTRIDAE)

JOHN O. MECOM AND KENNETH W. CUMMINS[1]

Department of Biological Sciences, Northwestern University, Evanston, Illinois

INTRODUCTION

In recent years it has become increasingly apparent that studies concerning stream ecosystems have been severely hampered by a lack of knowledge of the trophic relationships of important benthic invertebrates. Whereas lotic ecologists have on occasion measured total organic matter in an attempt to estimate food material available to detritus feeders, relatively few have attempted to evaluate the tropic relationships of particular species (Cummins, 1962).

Although general qualitative information on the food habits of lotic invertebrates is available from a number of sources such as Wessenberg-Lund (1943) and Pennak (1953), quantitative trophic data for particular species is relatively scarce.

Hanna (1957) has cited papers dealing with the food of Trichoptera larvae. Most of the workers (*e.g.* Slack, 1936) have presented quantitative data in the form of number of individuals of a given species having a particular food material in the gut. Scott (1958) in his study of the Trichoptera of the River Dean attempted to correlate available food materials with those found with greatest abundance in the guts of six species of caddisfly larvae. Hanna (1957) using a technique for quantitation of individual gut contents determined the relative abundance of diatoms, Volvocales, Chlorococcales, desmids, and detritus and dead leaf material. His results are discussed in general terms on a seasonal basis for each of the four species studied.

The present study was undertaken to provide some preliminary information on the trophic relationships of the larvae of the caddisfly *Brachycentrus americanus*

[1]Present address: Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania.

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(Banks). These larvae are of particular interest because of the wide distribution of the species throughout the northern portion of North America (Ross, 1944). In addition, *B. americanus* larvae are frequently abundant in trout streams and undoubtedly serve as important food organism for trout species as do many Trichoptera (Ide, 1942). A new technique, described below, was employed to obtain quantitative information on food materials comprising larval gut contents and to arrive at an estimate of the relative abundance of food materials available.

Area of Study

Collections were made from eight Wisconsin streams. Plum Creek in Vilas County (Township 40 North, Range 11 East, Section 7) served as a collection site in the northern part of the state. Peterson Creek (T23N, R11E, S20), Comet Creek (T25N, R11E, S13), Crystal River (T21N, R11E, S11), and the Little Wolf River (T23N, R11E, S26) of Waupaca County, and the Tomorrow River (T24N, R10E, S30) of Portage County served as collection sites for central Wisconsin. Bluff Stream (T4N, R15E, S14) of Walworth County in southern Wisconsin was also collected. Plum Creek is a small rapidly-flowing, sandy bottom, meadow-type, brown trout stream; Comet Creek is a slow-flowing, sandy bottom, woodland, brook trout stream; the Little Wolf is an intermediate sized, sand and gravel bottom, brown and rainbow trout stream; the Tomorrow River is a small gravel-bottom brown trout stream; Bluff Stream is a small sand and clay bottom, brown trout stream. Samples were taken on the following dates (1962): Plum Creek, June 16; Peterson Creek, Comet Creek, and the Crystal River, June 11–12; Little Wolf River, April 21 and June 12; Tomorrow River, May 26; Bluff Stream, May 20.

Materials and Methods

The larvae were located with the aid of a plexiglas viewing box and hand picked from the stream bottom. Stream water samples (50 ml.) were collected in the immediate vicinity of the individual larva. Substrate samples such as leaves, twigs, pieces of bark, and mineral sediment were also taken from larval sites. In Spaulding Creek, where the population of *B. americanus* was particularly dense, observations of feeding larvae and photographs of the stream bottom were made.

The larvae were preserved in a mixture of 70 percent alcohol and formalin. (Nine parts alcohol to one part formalin.) The ventral surface of the animal was split from the region of the esophagus to the anus and the entire gut removed to a watchglass which contained 10 ml. of a two percent formalin solution. The gut contents were exposed by gentle pressure on the wall of the digestive tract and all tissue was removed with foreceps. The ten-ml. suspension of gut contents was then filtered through a 25 mm. type AA gridded millipore filter with a pore diameter of $0.8\,\mu$ using a vacuum pump and a microanalysis filter apparatus. (Millipore Filter Corporation, Bedford, Massachusetts). The millipore filter was then placed on a standard (3×1 in.) microscope slide to which one drop of cedarwood immersion oil had previously been added. The slide was allowed to dry for 12 hours and the filter was cleared with two drops of immersion oil. Gut analysis consisted of identification and enumeration of the organisms present in five randomly selected grid squares at a power of $100\times$. This technique of gut analysis has proven quite valuable in studies of the trophic relations of benthic macro-invertebrates. It is more rapid and allows better quantification than procedures previously employed. The method has the added advantage that a permanent record can be provided if the filters are permanently cleared and mounted in André medium (for preparation of André medium see Gottlieb, 1963).

The materials collected in an attempt to estimate the food available to larvae in the stream were analyzed following two procedures. A 20-ml. aliquot of the stream water sample was filtered and analyzed according to the procedure employed with gut contents. The analysis of attached organisms was achieved by gently scraping small fragments of debris, collected in the immediate vicinity of the larva, into ten ml. of distilled water. This material was filtered and analyzed as above.

A portion of the total number of samples taken from each stream site were selected for analysis. A water sample was filtered in conjunction with each gut analysis and two analyses of organic debris and sediment were completed for each site. Only data for terminal instar larvae have been presented; the numbers of larval guts analyzed from each stream collection were as follows: Spaulding Creek, 16; Tomorrow River, nine; Peterson Creek, eight; Plum Creek, eight; Comet Creek, seven.

RESULTS

B. americanus larvae collected from the Crystal River and Bluff Stream had sealed their cases for pupation and the digestive tracts were essentially clear of food materials. Samples taken from the Little Wolf River contained larvae of

TABLE I

Comparison of the Relative Abundance of Food Materials in Larval Gut, stream Water and Substrate Scraping Samples Taken in Comet Creek

Algal Genera and Other Food Items	Gut Analyses		Water Samples		Substrate Scrapings	
	$\bar{x}$ no.[a]	%	$\bar{x}$ no.	%	$\bar{x}$ no.	%
Navicula	16.0	70.8	7.1	65.7	20.3	72.5
Synedra	2.1	9.3	1.9	17.6	4.6	16.4
Gomphonema	1.8	8.0	0.4	3.7	1.0	3.6
Meridion	1.0	4.4	0.1	0.9	0.5	1.8
Microspora	0.6	2.7	0.3	2.8	0.3	1.1
Fragilaria	0.3	1.3	0.7	6.5	0.4	1.4
Melosira	0.1	0.4	0.1	0.9	0.4	1.4
Diatoma	0.1	0.4	0.1	0.9		
Tolypothrix	0.1	0.4				
Anabaena			0.1	0.9		
Vasc. plant frag.						
Animal fragments	0.5	2.2			0.5	1.8

[a]In all cases the mean number per grid square count is given.

B. numerosus (Betten). These animals had also sealed their cases for pupation. The digestive tracts were clear except for traces of *Navicula*, *Gomphonema*, *Synedra* and *Meridion*. Only the results from the actively feeding larvae taken in the Tomorrow River and Peterson, Spaulding, Comet and Plum Creeks have been presented.

Results of the analyses of larval gut contents, water samples and substrate scrapings are presented in Tables I–V according to stream collection site. In all instances the data are presented both as the mean number of each food item and as relative percents for comparative purposes. In each table, the algal food items have been ranked according to their relative densities in the larval digestive tracts. The predominance of diatom food (95.8 percent) in the diet of *B. americanus* larvae, as determined by gut analyses, is clearly shown in figure 1.

In Comet Creek, the Tomorrow River and Peterson Creek, *Navicula* and *Synedra* were the dominant food items encountered in larval gut analyses (Tables I–III) while Spaulding Creek samples revealed *Meridion* and *Navicula* were the most abundant food materials (Table IV). Larvae from Plum Creek had fed predominantly on *Melosira*, *Microspora* and *Synedra* (Table V). It should be noted that filamentous forms, such as *Melosira*, present a problem in gut analyses. Their trophic importance is often overestimated since they fragment easily and it is impossible to determine what constitutes one organism. The relative amounts

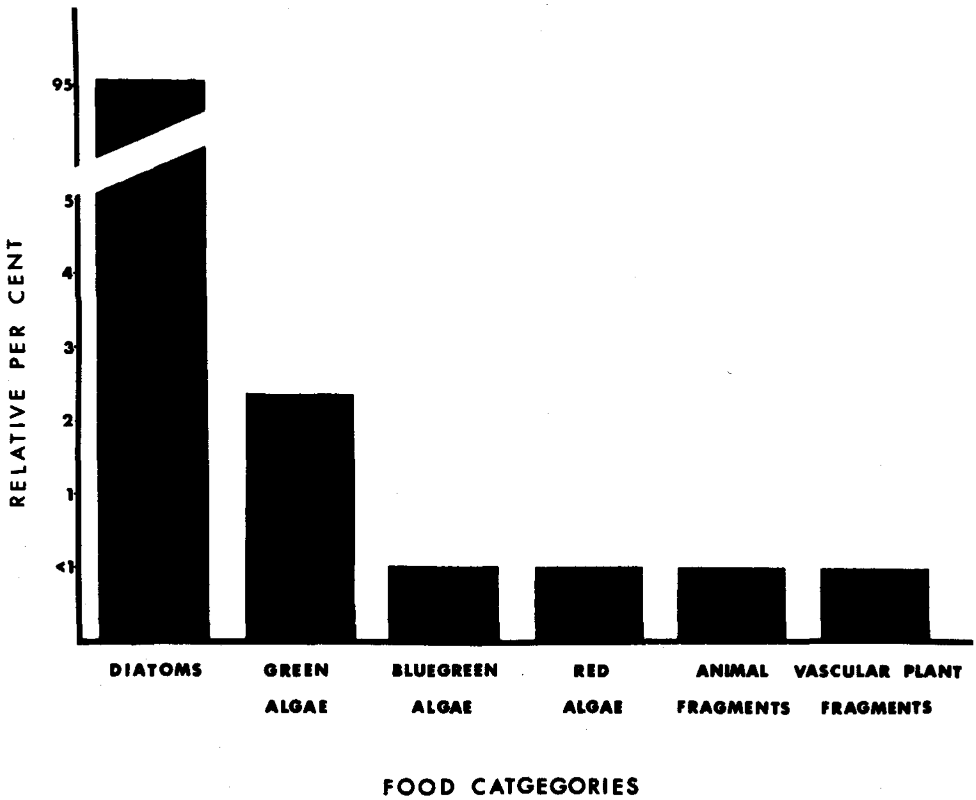

FIG. 1. A comparison of the relative abundance of food items ingested by *B. americanus* larvae.

of the seven dominant algal genera ingested by *B. americanus* larvae from the five streams are compared in figure 2.

The relative densities of food items in the larval digestive tracts and those in the environment, as estimated from water samples and substrate scrapings, were compared statistically (Kolmogorov-Smirnov one-sample test; Siegel, 1956) for each of the five streams. In each instance, the gut counts were compared separately to the water sample data and to the substrate scraping results. In all but two of these comparisons there was no statistically significant difference ($p > .20$) between the relative densities of food substances in the gut samples and those available in the environment as measured either by water samples or substrate scrapings.

The relative densities of algal genera were significantly different ($p < .01$) when the gut and scraping samples taken in Spaulding Creek were compared. Similarly the gut and water samples from Plum Creek were found to be significantly different ($p < .01$) when tested.

The Spaulding Creek analyses (Table IV) revealed that the relative density of *Meridion* in the gut samples was about three and one-half times more abundant in the scrapings than in the larval digestive tracts. Plum Creek data (Table V) showed a significant abundance of *Cocconeis* in the water samples (and to a lesser degree in the substrate scrapings) but an absence of this genus in the larval digestive tracts.

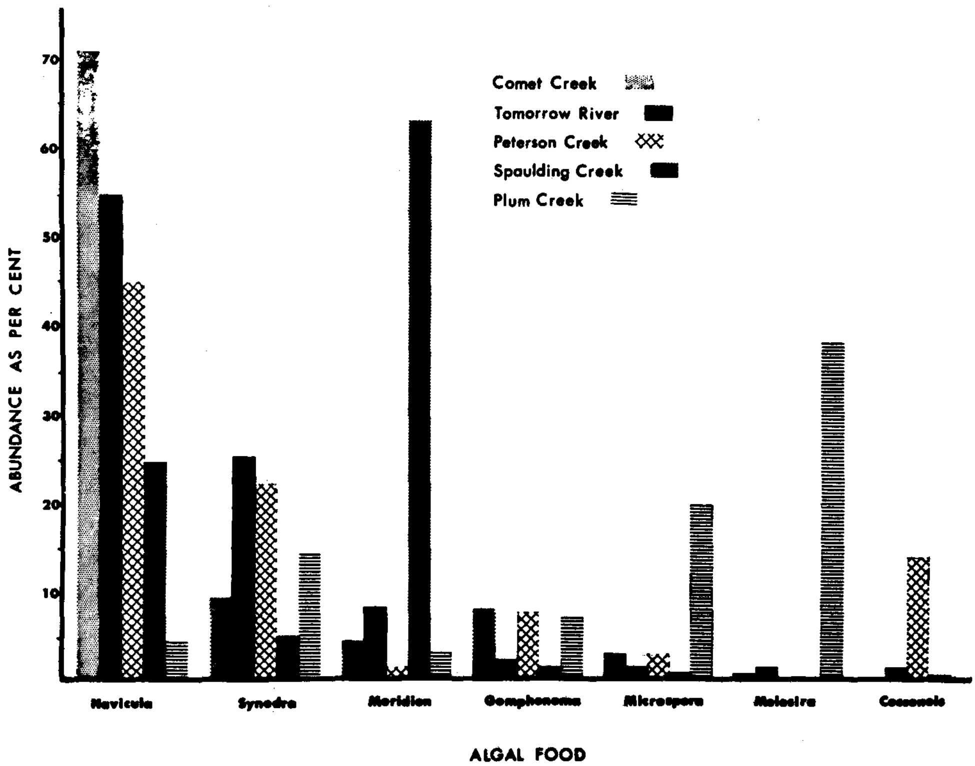

FIG. 2. A comparison of the relative amounts of seven dominant algal genera ingested by *B. americanus* larvae collected in five Wisconsin streams.

Along with the food items observed in *B. americanus* gut analyses, the sporozoan parasite *Gregarina* was encountered. About 25 percent of the larvae examined from the Tomorrow River and Comet, Peterson and Plum Creeks contained *Gregarina* parasites, with from one to three individuals per larva. Half of the larvae analyzed from Spaulding Creek contained *Gregarina* with the number of parasites varying from one to five.

DISCUSSION

The data presented indicate that terminal instar *B. americanus* larvae are predominantly diatom feeders. Although the importance of diatoms may have been overestimated because of their resistant nature relative to other food materials, the paucity of fragments of other algal groups, vascular plant and animal tissue does not warrant such a conclusion. The close correlation between diatom genera available, as measured by water samples and substrate scrapings, and those ingested by *B. americanus* larvae demonstrates the fortuitous nature of their feeding habits regarding this algal group.

TABLE II

Comparison of the Relative Abundance of Food Materials in Larval Gut, Stream Water and Substrate Scraping Samples Take in the Tomorrow River

Algal Genera and Other Food Items	Gut Analyses		Water Samples		Substrate Scrapings	
	$\bar{x}$ no.[a]	%	$\bar{x}$ no.	%	$\bar{x}$ no.	%
Navicula	5.2	54.7	4.6	45.1	70.5	55.7
Synedra	2.4	25.3	3.1	30.2	38.5	30.0
Meridion	0.8	8.4	1.0	9.8	6.1	4.8
Gomphonema	0.2	2.0	0.1	1.0	0.4	0.3
Fragilaria	0.1	1.1	0.2	2.0	1.0	0.8
Microspora	0.1	1.1	0.1	1.0	0.3	0.2
Anabaena	0.1	1.1	0.1	1.0	0.2	0.2
Cocconeis	0.1	1.1	0.9	8.8	7.9	6.2
Melosira	0.1	1.1	0.1	1.0	0.6	0.5
Oscillatoria					0.8	0.6
Pediastrum					0.1	0.1
Cymbella					0.4	0.3
Batrachospermum					0.1	0.1
Vasc. plant frag	0.1	1.1				
Animal fragments	0.3	3.1				

[a]See footnote, Table I.

TABLE III

Comparison of the Relative Abundance of Food Materials in Larval Gut, Stream Water and Substrate Scraping Samples Taken in Peterson Creek

Algal Genera and Other Food Items	Gut Analyses		Water Samples		Substrate Scrapings	
	$\bar{x}$ no.[a]	%	$\bar{x}$ no.	%	$\bar{x}$ no.	%
Navicula	11.7	45.0	2.7	46.6	64.3	63.3
Synedra	5.8	22.3	1.2	20.7	14.2	14.0
Cocconeis	3.7	14.2	0.6	10.4	5.8	5.7
Gomphonema	2.0	7.7	0.2	3.4	3.7	3.6
Cymbella	1.0	3.8	0.2	3.4	3.6	3.5
Microspora	0.7	2.7	0.2	3.4	3.8	3.7
Meridion	0.3	1.2	0.2	3.4	2.2	2.2
Fragilaria	0.3	1.2	0.2	3.4	2.0	2.0
Oscillatoria	0.1	0.4	0.2	3.4	1.3	1.3
Tabellaria	0.1	0.4				
Diatoma	0.1	0.4				
Anabaena	0.1	0.4	0.1	1.8	0.3	0.3
Stigeoclonium					0.3	0.3
Vasc. plant frag	0.1	0.4				
Animal fragments					0.1	0.1

[a]See footnote, Table I.

The two instances of a discrepency between the relative densities of diatoms available and those encountered in gut-counts probably represent some shift in availability rather than true selective feeding. It seems that larvae collected in Spaulding Creek were gathering more food from the water than by grazing on periphyton. Free-floating *Meridion* was more readily available to these larvae than the attached *Synedra* whereas about as much *Navicula* was being displaced by the stream current as was remaining associated with the periphyton (Table IV).

TABLE IV

Comparison of the Relative Abundance of Food Materials in Larval Gut, Stream Water and Substrate Scraping Samples Taken in Spaulding Creek

Algal Genera and Other Food Items	Gut Analyses		Water Samples		Substrate Scrapings	
	$\bar{x}$ no.[a]	%	$\bar{x}$ no.	%	$\bar{x}$ no.	%
Meridion	22.3	63.3	2.2	44.0	10.4	18.4
Navicula	8.7	24.7	1.8	36.0	11.2	19.9
Synedra	1.8	5.1	0.4	8.0	18.7	33.2
Fragilaria	0.6	1.7			5.2	9.2
Gomphonema	0.4	1.1	0.2	4.0	4.3	7.6
Microspora	0.2	0.6	0.1	2.0	0.6	1.1
Tabellaria	0.2	0.6				
Anabaena	0.1	0.3	0.2	4.0	0.2	0.4
Arthrospira	0.1	0.3				
Cocconeis	0.1	0.3			4.0	7.1
Spirogyra	0.1	0.3				
Oscillatoria	0.1	0.3	0.1	2.0	0.8	1.4
Batrachospermum	0.1	0.3				
Diatoma frag	0.1	0.3				
Cymbella					0.5	0.9
Melosira					0.3	0.5
Vasc. plant frag	0.1	0.3				
Animal fragments	0.1	0.3			0.2	0.4

[a]See footnote, Table I.

TABLE V

Comparison of the Relative Abundance of Food Materials in Larval Gut, Stream Water and Substrate Scraping Samples Taken in Plum Creek

Algal Genera and Other Food Items	Gut Analyses		Water Samples		Substrate Scrapings	
	$\bar{x}$ no.[a]	%	$\bar{x}$ no.	%	$\bar{x}$ no.	%
Melosira	2.7	38.6	1.3	13.0	9.6	36.1
Microspora	1.4	20.0	0.5	5.0	1.3	4.9
Synedra	1.0	14.3	1.4	14.0	4.8	18.0
Gomphonema	0.5	7.1	0.2	2.0	0.2	0.8
Navicula	0.3	4.3	1.7	17.0	1.6	6.0
Fragilaria	0.3	4.3	0.7	7.0	1.1	4.1
Meridion	0.2	2.9	0.6	6.0	1.3	4.9
Oscillatoria	0.1	1.4	0.4	4.0	2.3	8.6
Nodularia	0.1	1.4				
Cocconeis			2.4	24.0	3.9	14.7
Cymbella			0.5	5.0	0.3	1.1
Anabaena			0.2	2.0	0.1	0.4
Vasc. plant frag	0.1	1.4				
Animal frag	0.2	2.9	0.1	1.0	0.1	0.4

[a]See footnote, Table I.

The data indicate that Plum Creek larvae were feeding predominantly by grazing. Apparently the large displacement of *Cocconeis* by the stream current, compared to the relative amount remaining attached to the substrate, sufficiently reduced the availability of this form that it was not detected in the gut samples (Table V). A selective rejection of *Cocconeis* seems unlikely since it was taken readily by *B. americanus* larvae in other streams (Fig. 2).

B. americanus larvae observed in the field had their cases fastened to the substrate (such as cobbles or submerged vegetation) and facing into the current. In many instances such larvae were observed protruding from their cases exposing the head and thorax with the legs extended in a "fishing" posture. When larvae in the "fishing" position were fed in the field they readily took midge larvae or other *B. americanus* individuals that had been removed from their cases. This feeding response was not observed when fragments of vascular hydrophytes or pieces of *Batrachospermum* were presented. *B. americanus* larvae were not seen actively grazing in a manner characteristic of periphyton feeders. Since these larvae fasten their cases to the substrate, however, the grazing is probably accomplished in a limited region near the front of the case; in order to obtain a fresh grazing site the larvae probably free the case, move to a new location and attach the case. The present observations agree well with those of Lloyd (1921).

Both grazing and "fishing" could account for the abundance of diatoms taken by *B. americanus* larvae since they were abundant in both water samples and substrate scrapings. Although the free-floating materials may reflect only the abundance of forms attached to the substrate that are utilized as food, actual feeding on suspended matter is indicated by the Spaulding Creek data (Table IV) as well as field observations of "fishing" larvae. The small amounts of animal material taken by *B. americanus* larvae are probably obtained by "fishing".

Slack (1936) reviewed the various concepts relating trichopteran larval morphology to feeding habits. For example, larvae having setal brushes on both mandibles are normally phytophagus, those with a setal brush on the left mandible only are usually omnivorous and larvae lacking mandibular brushes are carnivorous. The mandibles of *B. americanus* (Pl. I) are stout and blunt with four denticles. There is a setal brush on the medial surface approximately midway along the dorsal margin of each mandible. In addition, there are two long setae at the lateral, ventral corner of each mandible.

The eyes occupy an anteromedial position on the lateral margins of the head. The suggestion that such a location is indicative of omnivorous food habits (anteriorly located eyes being typical of carnivores and a posterior position typical of herbivores) is not substantiated by the very predominantly phytophagous larvae of *B. americanus.*

The thoracic legs of the larvae are sparsely endowed with setae, except for a fringe on the ventral margin of the femur and trochanter of the prothoracic legs (Pl. I). This setal fringe may well function in filtering material from the water. No other special morphological adaptations were detected relative to a "filter feeding" habit. It is hoped that future laboratory experiments and field observations will clarify further the relationships between morphology and feeding mechanisms in *B. americanus* larvae.

The technique of trophic analysis utilized in the present study seems preferable to merely recording the number of larvae that contain a particular food item. For example, all the *B. americanus* larvae examined contained both *Navicula* and *Fragilaria*, but there is little doubt that *Navicula* was the more important food

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EXPLANATION OF PLATE I

FIG. 3. Right prothoracic leg of *B. americanus* larva, lateral aspect showing setal fringe (arrow); ×35.
FIG. 4. Left prothoracic leg, medial aspect showing setal fringe on femur (upper arrow) and trochanter (lower arrow); ×92.
FIG. 5. Left prothoracic leg, lateral aspect showing setal fringe (arrow); ×41.
FIG. 6. Setal brush of left mandible (arrow); ×246.
FIG. 7. Right mandible, medial aspect showing setal brush (arrow); ×115.
FIG. 8. Right mandible, dorsal aspect showing setal brush (arrow at left) and pair of setae (arrow at right); ×123.

PLATE I

source. In the present procedure, the entire gut content is drawn onto a filter of known surface area so that the total amount of food contained in the digestive tract can be counted directly or estimated from partial counts.

The question regarding the relationship of ingestion to the assimilation of food materials remains unanswered by the present approach but it is hoped that tracer techniques can be employed to provide the necessary data. The problem of evaluating the nutritional role of ingested food should also be dealt with. Smirnov (1962) has shown that although two species of vascular hydrophytes are ingested by larvae of the caddisfly *Phryganea grandis* L. they differ significantly with regard to meeting the animal's nutritional requirements.

Finally, further analyses are required to determine the food habits of *B. americanus* larvae during the subterminal instars. More larvae need to be examined, particularly from other streams.

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SUMMARY

1. The food of *Brachycentrus americanus* (Banks) larvae collected from five streams in Wisconsin is described. Water samples and substrate scrapings were collected in the immediate vicinity of larvae sites in an attempt to estimate the availability of food materials.

2. A new method for analysis of the gut contents, as well as water samples and substrate scrapings, is described.

3. The larvae of *B. americanus* from all collection sites were found to be primarily diatom feeders with small amounts of other algal groups, vascular plant tissue and animal fragments also represented in the guts.

4. A close correlation between the food substances available and those found in larval digestive tracts, indicated that the genera of diatoms ingested were determined primarily by their relative abundance in a given stream.

5. The relationships between larval morphology and trophic habits are discussed.

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