FEEDING HABITS OF WISCONSIN'S PREDOMINANT LOTIC PLECOPTERA, EPHEMEROPTERA, AND TRICHOPTERA[1]

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ABSTRACT

Feeding habits of nymphs or larvae of 101 species of Plecoptera, Ephemeroptera, and Trichoptera collected from Wisconsin's streams were determined by examining foregut contents. The percent by volume of animal, live vascular plant, filamentous algae, diatom, and detrital material recovered is reported. Plecoptera in the suborder Filipalpia were herbivore-detritivores, and most in the suborder Setipalpia were carnivores. Exceptions were *Isoperla bilineata* (Say), an omnivore, and *Isoperla signata* (Banks) and *I. slossonae* (Banks), both detritivore-herbivores. Except for omnivore *Ephemerella cornuta* Morgan, Ephemeroptera were detritivore-herbivores. Feeding habits of Trichoptera larvae were diverse. Species of Rhyacophilidae, Polycentropodidae, and Phyrganeidae were all carnivores, while Hydropsychidae, Leptoceridae, and Brachycentridae were generally omnivores. Species of Glossomatidae, Philopotamidae, Psychomyiidae, Hydroptilidae, Limnephilidae, Lepidostomatidae, Sericostomatidae, and Helicopsychidae were primarily detritivore-herbivores.

INTRODUCTION

To assess their roles in the aquatic ecosystem, feeding habits of 101 species of Wisconsin's most common Plecoptera, Ephemeroptera, and Trichoptera were studied. More than 1,500 specimens from 33 streams (Fig. 1) were dissected and percentages by volume of major food items were determined. Feeding habits for 70 species are reported for the first time.

MATERIALS AND METHODS

When possible, at least five specimens of each species were collected in early spring, late spring, summer, and fall, killed in 70 percent ethanol, and transferred to 3 percent formalin for preservation. Two solutions were necessary because preservation in ethanol resulted in plasmolysis of plant cells, while some insects regurgitated when placed directly into formalin. After head capsule widths were measured, specimens were dissected under water or 3 percent formalin. The intact foregut was removed and dissected further on a glass slide. A simple two-step sucrose medium (Dawson, 1956) was used to mount and preserve the gut contents.

A modification of techniques described by Mecom and Cummins (1964), Thut (1969), and Coffman *et al.* (1971), was used to characterize feeding habits. Five randomly-selected fields across the central portion of each mount were viewed with a compound microscope at 25, 100, or 250 magnifications. The lowest magnification that permitted the least prevalent food items to appear in every random field was chosen.

Approximate percent by volume of food items (animal, live vascular plant, filamentous algae, diatoms, and detritus) was recorded for each field. Since each coverslip was compressed to provide food items with roughly similar thicknesses, volumes were translated from area values although the authors realize that inaccuracies will occur in such extrapolations. Estimates were always made from least to most prevalent food items, with each value estimated to the nearest 10 percent. A preliminary scan was always

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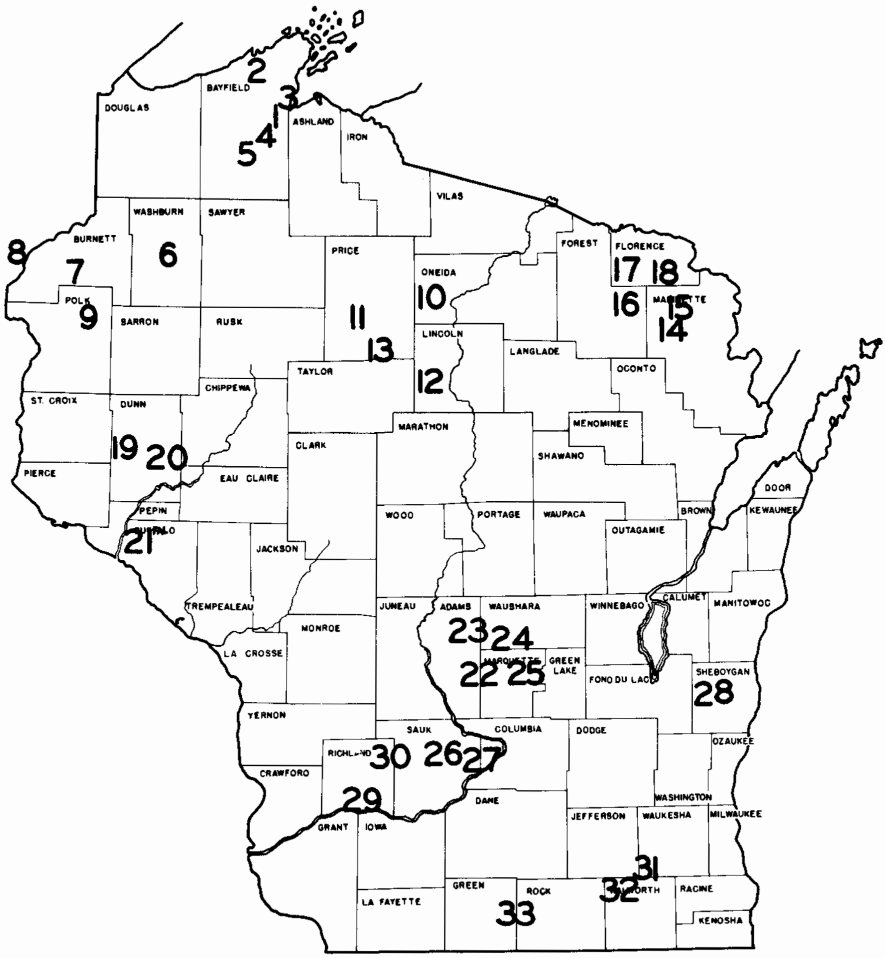

Fig. 1. Collection sites throughout Wisconsin.

1. Pine Cr.
2. E. Fk. Cranberry R.
3. Whittlesey Cr.
4. White R.
5. 18 Mile Cr.
6. Namekagon R.
7. Clam R.
8. St. Croix R.
9. McKenzie Cr.
10. Lit. Somo R.
11. Lit. Jump R.
12. Newood R.
12. N. Br. Levitt Cr.
14. Peshtigo R.
15. Sidney Cr.
16. Armstrong Cr.
17. Pine R.
18. Popple R.
19. Eau Galle R.
20. Rock Cr.
21. Spring Cr.
22. Lawrence Cr.
23. Big Roche Cri R.
24. Mecan R. #1
25. Mecan R. #2
26. Otter Cr.
27. Parfrey's Glen
28. Mullet R.
29. Wisconsin R.
30. Milancthon Cr.
31. Jericho Cr.
32. Bluff Cr.
33. Sugar R.

judicious to detect monophagous habits. Estimates of animal matter were sometimes categorized as percent by volume Plecoptera, Ephemeroptera, Trichoptera, Chironomidae, or other Diptera.

RESULTS

General feeding habits are summarized in Table 1. Where significant, seasonal differences and differences between streams are mentioned in the summaries below. Details of these differences and information on genera of algae consumed and streams sampled are reported by Shapas (1973).

PLECOPTERA

This relatively small order is roughly divided between herbivorous-detritivorous Filipalpia, and predatory Setipalpia. Early studies of feeding habits include those by Muttkowski and Smith (1921), Claassen (1931), Frison (1935), and Hynes (1941). More recently, food habits of Plecoptera have been studied by Minshall and Minshall (1966) in Kentucky, by Thut (1969) in Washington, and by Richardson and Gaufin (1971) in Utah and Colorado. We studied 21 species in seven families, and have summarized results in Tables 1 and 2.

PTERONARCIDAE–Both *Pteronarcys dorsata* (Say) and *Pteronarcys pictetii* Hagen are common in Wisconsin, but only mature male nymphs can be separated. Namekagon River nymphs that could be identified were *pictetii*, which fed primarily on detritus and diatoms as reported by Frison (1935). The small animal component (Chironomidae) may have been consumed inadvertently while feeding on allochthonous leaves.

TAENIOPTERYGIDAE–*Taeniopteryx nivalis* (Fitch) and *T. parvula* Banks were all detritivores. Both were classed as herbivores by Frison (1935), but some or all of Frison's *nivalis* could be *T. burksi* Ricker (Ricker, 1952; Harper and Hynes, 1971). *Taeniopteryx maura* (Pictet), however, was found by Coffman *et al.* (1971) to be mostly carnivorous in Pennsylvania.

NEMOURIDAE–Three species were examined and all were detritivore-herbivores. *Amphinemura delosa* (Ricker) was strictly a detrivore, while *Shipsa rotunda* (Claassen) and *Prostoia similis* (Hagen) also consumed some diatoms.

LEUCTRIDAE–Only *Leuctra ferruginae* (Walker) was studied. It was a detrivore with as much as half of the detritus composed of sand grains.

PERLIDAE–The four species studied were carnivores, which agrees with findings of Frison (1935), Coffman *et al.* (1971), and Tarter and Krumholz (1971). *Acroneuria lycorias* from the Popple River relied heavily on Trichoptera in the fall, Chironomidae and Plecoptera in early spring, and Ephemeroptera in late spring. *Paragnetina media* consumed mostly Chironomidae during fall and early spring, and Plecoptera during late spring.

PERLODIDAE–Nine of the 14 Wisconsin species of *Isogenoides* and *Isoperla* (Hilsenhoff and Billmyer, 1973) were studied. Six were carnivores, two herbivores, and one an omnivore. Carnivorous habits of *Isoperla clio* (Newman) as reported by Frison (1935) under *I. confusa* and Minshall and Minshall (1966) were confirmed, but our findings that *Isoperla bilineata* (Say) was omnivorous disagrees with Frison's (1935) statement that this species is a herbivore.

CHLOROPERLIDAE–*Alloperla* nymphs cannot yet be identified at the species level. Several that were near emergence were collected from Bayfield County streams, but only one contained food (larvae of Chironomidae) in its gut. *Hastaperla brevis* (Banks) was carnivorous, feeding on Chironomidae larvae. This sharply disagrees with Frison's statement (1935) that "the nymphs are herbivorous."

EPHEMEROPTERA

With few exceptions worldwide, mayfly nymphs must be considered as consumers of plant material in the form of diatoms, other algae and detritus. Most are either "collectors" or "scrapers" in Cummins' (1973) general feeding mechanism categories.

Table 1. Major dietary components of Wisconsin's noncarnivorous Plecoptera

Species	Percent by Volume				No.	Head Capsule Widths (mm)	Streams (Fig. 1)	Seasons*
	Animal	Filamentous Algae	Diatoms	Detritus				
Pteronarcidae								
Pteronarcys pictettii Hagen	5	2	45	48	6	2.8-5.4 mm	6	ES,F
Nemouridae								
Amphinemura delosa (Ricker)				100	6	0.7-0.9	3	LS
Shipsa rotunda (Claassen)			21	79	12	1.0-1.2	4,18	ES
Prostoia similis (Hagen)			27	73	20	0.8-1.1	13,18	ES
Leuctridae								
Leuctra ferruginea (Walker)				100	10	0.7-0.9	3	LS
Taeniopterygidae								
Taeniopteryx nivalis (Fitch)			11	89	7	1.0-1.5	31	F
Taeniopteryx parvula Banks			1	99	14	0.7-1.0	12,14,17	F
Perlodidae								
Isoperla bilineata (Say)	84		12	4	12	1.6-1.8	29	LS
Isoperla signata (Banks)	1	1	70	28	29	0.9-2.5	17,20	ES,F
Isoperla slossonae (Banks)			61	39	7	1.0-1.9	22	F

*ES = early spring; LS = late spring; S = summer; and F = fall.

Table 2. Major dietary components of Wisconsin's carnivorous Plecoptera

Species	Percent by Volume					No.	Head Capsule Widths (mm)	Streams (Fig. 1)	Seasons*
	Plecoptera	Ephemer-optera	Trich-optera	Chironomidae	Other Diptera				
Perlodidae									
Isogenoides frontalis (Newman)				50	50	8	1.6-2.6	17	F
	42	7		38	13	8	3.4-4.0	17	ES
Isoperla clio (Newman)	2	4		68	26	17	2.0-3.2	13,27	ES
Isoperla cotta Frison		11		67		9	0.7-1.7	13	LS
Isoperla dicala Frison		35		65		14	1.0-1.8	24,26	ES, LS
Isoperla frisoni (Illies)		2		98		9	1.4-1.9	1	LS
Isoperla transmarina Newman				75	25	9	1.0-2.5	10	ES
Perlidae									
Acroneuria lycorias (Newman)	9	16	67	8		10	1.7-5.5	18	F
	36	12	11	41		14	1.2-4.8	18	ES
		88		12		4	1.3-3.2	18	LS
Paragnetina media (Walker)		25		50	25	4	1.5-5.0	28	F
			20	80		10	3.3-5.4	28	ES
	50	15	10	25		4	2.0-3.4	28	LS
Perlesta placida (Hagen)	3	22	12	60	3	10	1.6-1.9	28	LS
Phasganophora capitata (Pictet)		29		54	17	8	2.2-3.3	17	ES,LS,F
Chloroperlidae									
Hastaperla brevis (Banks)				100		14	0.7-1.0	10,24	LS

*ES = early spring; LS = late spring; S = summer; and F = fall.

Table 3. Major dietary components of Wisconsin's lotic-water Ephemeroptera

Species	Percent by Volume				No.	Head Capsule Widths (mm)	Streams (Fig. 1)	Seasons*
	Animal	Filamentous Algae	Diatoms	Detritus				
Siphlonuridae								
Isonychia spp.			3	97	22	0.8-2.1	6	ES,LS,F
Siphlonurus alternatus (Say)			13	87	8	0.7-0.8	8	ES
Siphlonurus quebecensis (Provancher)			5	95	2	1.5-2.4	8	ES
Heptageniidae								
Epeorus vitrea (Walker)		13	9	78	10	2.5-3.1	16	LS
Heptagenia diabasia Burks				100	13	1.7-2.8	19	LS,F
Heptagenia hebe McDunnough		3	35	62	12	2.0-2.5	17,28	LS
Heptagenia lucidipennis (Clemens)				100	8	1.4-1.7	33	S
Heptagenia pulla (Clemens)			4	96	13	1.9-3.4	2	LS,F
Rithrogena impersonata (McDunnough)			26	74	16	1.1-2.6	5	ES,LS
Rithrogena jejuna Eaton			16	84	8	2.6-2.9	17	LS
Rithrogena sanguinea Ide			25	75	8	2.1-2.6	5	LS
Stenonema exiguum Traver			9	91	14	1.2-3.0	7	LS
Stenonema fuscum Clemens			17	83	37	1.1-3.8	11,26,31	ES,LS,F
Stenonema luteum Clemens				100	19	2.0-3.2	4,12	LS,S,F
Stenonema mediopunctatum (McDunnough)			15	85	13	1.5-3.7	28	LS,F
Stenonema rubrum (McDunnough)			17	83	12	2.2-2.7	24	LS
Stenonema terminatum (Walsh)			3	97	8	1.9-2.7	3	LS
Baetidae								
Baetis brunneicolor McDunnough			33	67	8	1.0-1.2	22	F
Baetis intercalaris McDunnough			54	46	8	1.0	24	LS
Baetis pygmaeus (Hagen)			12	88	2	0.8-1.0	7	LS
Baetis spinosis McDunnough			14	86	8	0.8-1.0	24	LS
Baetis vagans McDunnough			18	82	29	0.8-1.3	3	ES,LS,S,F
Pseudocloeon anoka Daggy			40	60	7	0.7-0.9	24	LS

Pseudocloeon carolina Banks		10	35	55	4	0.8-1.0	6	LS
Pseudocloeon dubium (Walsh)		1	48	51	8	0.8-1.0	8	LS
Pseudocloeon parvulum McDunnough			13	87	4	0.8	8	LS
Pseudocloeon punctiventris McDunnough			66	34	8	0.8-1.0	6	LS
Leptophlebiidae								
Leptophlebia sp.			26	74	8	2.1-2.6	7	ES
Paraleptophlebia mollis (Eaton)			1	99	21	0.9-1.5	16	ES,LS,F
Ephemerellidae								
Ephemerella aurivillii Bengtsson				100	7	0.7-1.0	2	F
			15	85	8	1.6-1.9	2	ES
		4	4	92	8	1.8-2.1	2	LS
Ephemerella catawba Traver			7	93	16	1.3-1.8	22	ES,LS
Ephemerella cornuta Morgan	40		8	52	8	1.5-1.8	5	LS
Ephemerella needhami McDunnough		5	24	71	8	1.2-1.5	24	LS
Ephemerella rotunda Morgan		1	10	89	19	0.6-1.6	24	ES,LS,F
Ephemerella subvaria McDunnough			13	87	6	1.1-1.4	16	F
	1	1	56	42	8	1.6-2.1	16	ES
Tricorythodes								
Tricorythodes sp.				100	3	0.9-1.1	9	F
Potomanthidae								
Potomanthus sp.			5	95	8	0.9-2.1	8	LS
Ephemeridae								
Ephemera simulans Walker			4	96	16	0.6-2.2	11	ES,F
Hexagenia limbata (Serville)			8	92	10	3.6-4.4	25	LS
Polymitarcidae								
Ephoron leukon Williamson			15	85	4	1.2-1.5	6	S
Baetiscidae								
Baetisca obesa (Say)			19	81	15	0.8-2.0	7,29	ES,F

*ES = early spring; LS = late spring; S = summer; and F = fall.

The specific works detailing feeding habits of Ephemeroptera include studies by Morgan (1913) and Traver (1925) in New York, Muttkowski and Smith (1929) in Yellowstone Park area streams, Jones (1949, 1950) in Wales, Douglas (1958) in England, Gilpin and Brusven (1970) in Idaho and Coffman *et al.* (1971) in Pennsylvania.

Forty-two Wisconsin species are discussed here, with their general feeding habits summarized below and in Table 3.

SIPHLONURIDAE–*Isonychia* spp. and two species of *Siphlonurus* were analyzed. *Isonychia* spp., common in northern Wisconsin, were detritivores. Reports by Clemens (1917), Minckley (1963), and Coffman *et al.* (1971) have suggested omnivorous habits for this filter-feeding genus. Both *Siphlonurus alternatus* (Say) and *S. quebecensis* (Provancher) were highly detritivorous.

HEPTAGENIIDAE–Fifteen of the 21 species known to occur in Wisconsin were analyzed. All conformed to the herbivorous-detritivorous habits that have been generalized for the family.

BAETIDAE–Although primarily detritivores, a few species consumed large quantities of algae. This agrees well with work by Minckley (1963), Gilpin and Brusven (1970) and Coffman *et al.* (1971).

LEPTOPHLEBIIDAE–Nymphs of *Leptophlebia* sp. and *Paraleptophlebia mollis* (Eaton) were herbivore-detritivores, substantiating work of Morgan (1913), Traver (1925), and Coffman *et al.* (1971).

EPHEMERELLIDAE–Feeding habits of six Wisconsin species ranged from almost complete detritivory to omnivory. *Ephemerella catawba* Traver, *E. aurivillii* Bengtsson, and *E. rotunda* Morgan were mainly detritivores, while *E. needhami* McDunnough, and *E. subvaria* McDunnough also consumed significant numbers of diatoms. *E. aurivillii* substituted some detritus for diatoms and filamentous algae during spring. *E. subvaria* increased diatom intake four-fold from fall to spring, at the expense of detritus. *E. cornuta* Morgan was omnivorous, consuming about 40 percent by volume animal matter composed of Chironomidae and Ephemeroptera. Nymphs of *E. invaria* (Walker) and *rotunda* could not be separated (Allen and Edmunds, 1965) and are reported only as *rotunda.*

TRICORYTHIDAE–*Tricorythodes* nymphs cannot be identified to species. Nymphs from McKenzie Creek were entirely detritivorous.

POTOMANTHIDAE–*Potomanthus* sp. nymphs occur uncommonly in certain larger streams across the state, but cannot be identified to species. All were highly detritivorous, with a small porportion of ingested diatoms.

EPHEMERIDAE–*Ephemera simulans* Walker, an inhabitant of gravel riffles in northern Wisconsin, was primarily a detritivore. This observation disagrees with Coffman *et al.* (1971), who reported considerable feeding on animal material in Pennsylvania. The mud-inhabiting *Hexagenia limbata* (Serville) was also detritivorous.

POLYMITARCIDAE–*Ephoron leukon* Williamson was found uncommonly in Wisconsin's larger streams where nymphs were herbivore-detritivores.

BAETISCIDAE–*Baetisca obesa* (Say) ate mostly detritus, but occasionally high proportions of diatoms.

TRICHOPTERA

Since most Trichoptera larvae cannot presently be identified to species, it is no surprise that feeding habit data for this order are generally lacking. Studies to date indicate a diversity of feeding habits, with shredders, collectors, and predators all being found (Cummins, 1973). Lloyd (1921) described general feeding habits of many species of North American caddisfly larvae; Slack (1936) revealed similar information for caddisflies of England; Ross (1944) spoke in general terms for a few Illinois species; Jones (1950) detailed feeding habits of many species from Wales; Scott (1958) performed gut dissections on species from England; and Coffman *et al.* (1971) reported on inhabitants of Linesville Creek, Pennsylvania.

Of approximately 275 species of Trichoptera in Wisconsin, 38 were dissected for feeding habit analysis. Results are listed below and in Table 4.

RHYACOPHILIDAE–Although most species are apparently carnivorous, Thut (1969) reported an omnivore and a herbivore from Washington. Both *Rhyacophila acropedes* Banks and *R. vibox* Milne were carnivorous in Wisconsin.

GLOSSOSOMATIDAE–Larvae of *Glossosoma* spp. and *Protoptila* spp. were scrapers, consuming subequal portions of diatoms and detritus. This agrees in general with work presented by Cummins (1973).

PHILOPOTAMIDAE–These net-spinning, filter-feeding larvae appear to select against animals and large particles. *Chimarra aterrima* Hagen and *Dolophiloides distinctus* (Walker) behaved similarly, consuming roughly twice as much detritus as diatoms. With *aterrima*, a slight increase in ingested diatoms at the expense of detritus occurred between spring and summer. Apparently, *aterrima* ingests a diet that mirrors stream suspended matter (Williams and Hynes, 1973).

PSYCHOMYIIDAE–Like the Philopotamidae, larvae of this family are net-spinning, small particle filter-feeders. Only *Psychomyia flavida* Hagen was examined, and it consumed subequal amounts of detritus and diatoms. Coffman *et al.* (1971) reported almost exclusive algal feeding for this species in Pennsylvania.

POLYCENTROPIDAE–The net-spinning larvae were almost exclusively carnivorous in Wisconsin, agreeing with work by Coffman *et al.* (1971), Winterbourn (1971), and Hynes (1972).

HYDROPSYCHIDAE–Because larvae of several species remain unknown, identifications at the species level must be considered tentative. Most are filter-feeding net-spinners, although grazing and prey-stalking may occur. Wisconsin species were generally omnivorous. The variability of feeding habits is illustrated by *Hydropsyche betteni* Ross, which was reported as primarily carnivorous by Coffman *et al.* (1971), a diatom feeder by Minckley (1963), and an omnivore in this paper. *H. slossonae* consumed subequal quantities of diatoms from fall through late spring, although amounts of other materials were variable.

HYDROPTILIDAE–Larvae are probably scrapers, although their feeding habits have received little attention. Two Wisconsin species *Agraylea multipunctata* Curtis and *Leucotrichia pictipes* (Banks) were herbivorous, consuming diatoms, filamentous algae, and detritus. Minckley (1963) reported similar data for *A. multipunctata.*

PHRYGANEIDAE–Larvae of most species are shredding herbivores (Cummins, 1973), although carnivores are known (Winterbourn, 1971). *Ptilostomis* spp. from the Mecan River No. 2 were exclusively carnivorous.

LIMNIPHILIDAE–Shredding and scraping are apparently the major modes of food gathering in this family (Cummins, 1973). Most Wisconsin species examined relied heavily on detritus for food, with scrapers (*Hesperophylax* and *Neophylax*) consuming larger proportions of diatoms. The diatom component in *S. designatus* was shifted during spring in favor of increased filamentous algae intake.

LEPTOCERIDAE–Larvae have been classified as shredders, scrapers, and prey-swallowing predators (Cummins, 1973). *Ceraclea ancylus* (Vorhies), *Nectopsyche candida* (Hagen), and *N. sp. a* Ross were all omnivorous in Wisconsin, while *Oecetis avara* (Banks) was decidedly carnivorous.

LEPIDOSTOMATIDAE–Cummins (1973) classifies the larvae as shredders. *Lepidostoma sp.* consumed primarily detrital plant tissue in Wisconsin.

BRACHYCENTRIDAE–The omnivorous larvae alternate between grazing and filter-feeding with their legs (Gallepp, 1974). *Brachycentrus americanus* (Banks) and *B. occidentalis* Banks, which often occur together in Wisconsin, are apparently opportunistic omnivores. *Micrasema rusticum* (Hagen) and *M. wataga* Ross probably spend more time grazing, as more filamentous algae and diatoms were found in their guts than in *Brachycentrus* spp.

SERICOSTOMATIDAE–Based only on three dissections, *Agarodes distinctum* (Ulmer) larvae appeared to be shredder-detritivores in Wisconsin.

HELICOPSYCHIDAE–Dissections of *Helicopsyche borealis* (Hagen) larvae revealed a diet of diatoms and detritus, substantiating reports by Coffman *et al.* (1971).

Table 4. Major dietary components of Wisconsin's lotic-water Trichoptera

Species	Percent by Volume					No.	Head Capsule Widths (mm)	Streams (Fig. 1)	Seasons*
	Animal	Live Vascular Plant	Filamentous Algae	Diatoms	Detritus				
Rhyacophilidae									
Rhyacophila acropedes Banks	100					9	1.0-1.4	1,2,3	LS
Rhyacophila vibox Milne	100					8	1.0	27	ES
Glossosomatidae									
Glossosoma spp.				46	54	8	0.6-0.7	26	ES
Protoptila spp.				62	38	10	0.3	24	LS
Philopotamidae									
Chimarra aterrima Hagen				31	69	8	1.0-1.3	31	F
				28	72	8	1.0-1.1	31	ES
				46	54	4	1.0-1.3	31	S
Dolophiloides distinctus (Walker)				28	72	8	1.0-1.3	13	LS
Psychomyiidae									
Psychomyia flavida Hagen				47	53	6	0.7-1.0	(5 streams)	LS
Polycentropidae									
Neureclipsis sp.	94			2	4	16	1.0-1.2	7	ES,F
Polycentropus cinereus Hagen	100					9	1.1-1.4	8,29	LS
Hydropsychidae									
Diplectrona modesta Banks	44			4	52	8	1.4-1.5	27	ES
Hydropsyche betteni Ross	14		—	66	20	8	0.8-1.4	28	F
	32			36	32	6	0.8-1.5	28	ES
Hydropsyche orris Ross	2	2	2	41	45	8	1.1-1.6	29	LS
Hydropsyche simulans Ross	26	4		29	41	8	1.4-2.1	8	LS
Hydropsyche slossonae Banks	20			23	57	8	1.2-1.4	22	F
	7			23	70	8	1.3-0.5	22	ES
	13		19	27	41	8	1.2-1.5	22	LS
Parapsyche apicalis (Banks)	79			21		8	1.7-1.9	15	ES
Potamyia flava (Hagen)				43	57	8	1.2-1.4	29	LS
Hydroptilidae									
Agraylea multipunctata Curtis			6	40	54	7	0.2-0.3	31	LS
Leucotrichia pictipes (Banks)				80	20	5	0.2	24	ES

Phryganeidae									
Ptilostomis spp.	100					6	1.4-2.2	25	ES,F
Limnephilidae									
Hesperophylax designatus (Walker)				76	24	8	1.0-2.2	22	F
			4	76	20	8	1.5-1.6	22	ES
			45	35	20	4	1.5-1.6	22	LS
Hydatophylax argus (Harris)			13		87	8	1.6-2.6	9,10,26	LS
Limnephilus sp.		14		9	77	7	1.6-1.7	25	LS
Nemotaulius hostilis (Stevens)				19	81	10	1.7-2.5	24,32	ES,F
Neophylax concinnis McLachlan			3	45	52	12	0.6-1.1	26,27	ES
Neophylax fuscus Banks			4	64	32	8	0.9-1.1	28	ES
Neophylax oligius Ross			1	43	56	8	0.9-1.0	26	ES
Pycnopsyche sp.			4	50	46	8	1,7-2.2	24	ES
Leptoceridae									
Ceraclea ancylus (Vorhies)	20			6	74	5	0.8-0.9	12	ES
Nectopsyche candida (Hagen)	43		21	20	16	8	0.7-0.9	29	LS
Nectopsyche sp. a. Ross	52			4	44	7	0.5-0.8	7	LS
Oecetis avara (Banks)	100					4	0.7-1.0	22	ES
Lepidostomatidae									
Lepidostoma sp.				14	86	8	0.8-0.9	22	ES
Brachycentridae									
Brachycentrus americanus (Banks)				41	59	8	0.7-1.2	22	F
	2	3	5	35	55	8	1.0-1.2	22	ES
	8		27	21	44	8	0.9-1.2	22	LS
Brachycentrus occidentalis Banks	3			20	77	8	1.0-1.3	22	F
				11	89	8	1.0-1.2	22	ES
Micrasema rusticum			7	59	34	8	0.5-0.7	26	ES
Micrasema wataga Ross			45	35	20	8	0.8-1.0	22	LS
Sericostomatidae									
Agarodes distinctum (Ulmer)				13	87	3	0.7-1.9	24	F
Helicopsychidae									
Helicopsyche borealis (Hagen)				61	39	8	0.6-0.7	24	LS

*ES = early spring; LS = late spring; S = summer; and F = fall.

DISCUSSION

The gut analysis technique used is a departure from the recent vogue in Millipore filtration as pioneered by Mecom and Cummins (1964). While use of Millipore filters in detailed nutritional studies is without question advantageous, their use for general feeding habit determination can generate misinformation. Dispersal of gut contents through shaking or sonication prior to filtration can result in disruption of prey gut walls allowing plant matter to be mistaken for carnivore food items (Coffman *et al.*, 1971). Oil clearing and permanent mounting of the filter can also have drastic morphological effects on algae.

In both types of gut analysis, many items are undoubtedly missed due to differential digestion rates, and some are simply listed in incorrect categories. Cummins (1973) logically assumes that items digested most rapidly, and hence seldom observed in gut contents, may actually have high nutritional significance for the consumer. Such items probably include certain soft-bodied Diptera, Oligochaeta, and fragile Ephemeroptera. Improper categorization often occurs with live vascular plants, which can rarely be distinguished from detrital plant tissue, and with prey gut contents which may not be associated with the prey and thus are mistaken for the predator's ingesta.

Cummins (1973) describes five major feeding mechanisms (shredding, collecting, scraping, sucking, and prey-swallowing), which adequately cover all North American aquatic insect taxa. Food items used by Wisconsin's lotic-water inhabitants can be conveniently partitioned into animal material, live vascular plants, diatoms, other algae (mostly filamentous forms), and detritus.

The category of detritus is in urgent need of further definition, for its constitution varies considerably from season to season and stream to stream. Detritus, as used in this paper and others, encompasses a conglomeration of mostly unrecognizable material, including allochthonous and autochthonous decaying plant debris, dead animals, insect exuviae, consumer fecal matter, aquatic fungi, mineral matter, and associated microflora. We clearly need to know more about a material which is eaten by such a large proportion of insect species.

The significance of sand grains in aquatic insect guts remains conjectural. Some detritivores were found with guts almost exclusively filled with sand grains, a material with no nutritional value alone. With some insects, mineral particles may serve as a gastric mill for food abrasion. Richardson and Gaufin (1971) found sand only in foreguts of *Pteronarcys californica* nymphs, and believe that it is used for grinding food, after which it is regurgitated. On the other hand, ingestion could be incidental and regurgitation necessary to prevent injury to soft mid- and hindgut tissues. Cummins (1973) suggested value of mineral material to aquatic insects by virtue of its adsorbed organic material and associated bacteria.

Describing feeding habits of aquatic insects is complicated by their generalized feeding capabilities. Indeed, food may never become the factor limiting kinds of insects present in a stream, since within certain broad limitations, most species can use a variety of material for nutrition (Hynes, 1972). This ability to use a range of materials probably encourages exploitation of the aquatic environment and reduces effects of conditions that may limit the availability of certain food items, but it also confounds efforts to pin distinct trophic labels on customers.

Since significant feeding niche variations may occur among even the most closely allied species, feeding studies must be performed at the species level. As emphasized by Hynes (1972) and Cummins (1973), however, the most important factor in feeding habitat determinations may be local conditions, for they do indeed beget local results. This realization must be clear in our minds when we interpret feeding habit data from a variety of sources.

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