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Food Habits and Ecology of Mayflies of the St. Maries River in Idaho[1]

B. R. GILPIN[2] and M. A. BRUSVEN[3]

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[2]Biology Department, Valley Center High School, Valley Center, Kansas 67147.

[3]Department of Entomology, University of Idaho, Moscow, Idaho 83843.

INTRODUCTION

Mayflies are an important and often abundant group of aquatic insects. They are widely distributed and adapted to both lentic and lotic environments. Until recently the food habits and ecology of many of the species have been largely unknown.

The order Ephemeroptera is composed of approximately 2,000 described species in the world with less than 20% of the nymphs known (Edmunds and Allen, 1966). The inability to identify the mayflies and particularly the nymphs has resulted in limited ecological studies for many of the species. The voluminous taxonomic work by Jensen (1966) provided keys and descriptions for indentifying Idaho mayflies and made this study possible.

Mayflies occupy an important place in the food chains of aquatic communities. Their ecological niche is primarily that of a herbivore, transforming plant tissue into animal tissue. They thus play an important role in the aquatic ecosystem by bridging the gap between primary production and secondary consumers. In addition, as members of the aquatic environment, their presence or absence may reflect water quality and general conditions of the environment.

This study was initiated in an effort to determine the food habits and ecology of mayfly nymphs so as to contribute fundamentally to a better understanding of food chains, environmental requirements and the micro- and macroecology of this important group of aquatic insects.

LIFE HISTORY

Mayflies represent a true aquatic order of insects with nearly their entire life spent in water. They occupy an important niche in the aquatic environment, existing principally as primary consumers. As herbivores they feed primarily on detritus, diatoms and algae; some nymphs, however, may be omnivorous or even carnivorous. The delicate nymphs are practically defenseless against their many aquatic predators. Protective coloration and/or withdrawal to secluded areas under rocks or cracks and crevices of rocks serve as their principal means of escape.

The life cycle of most mayflies is generally completed in one year. The number of molts during nymphal life is unknown for most species; however, it is estimated to be between 20 and 30. At the last nymphal molt, a subimago stage emerges from the water. This winged stage is very similar to the adult although not sexually mature. The final molt gives rise to the imago, a fully mature adult. The adults do not feed and live only a few days during which time mating and oviposition occur. After a short incubation period the eggs hatch giving rise to first instar nymphs.

STUDY AREA

This study was conducted on the St. Maries River in northern Idaho (Fig. 1-2) which has a drainage area of about 437 square miles and an average stream discharge of 520 cubic ft./sec. (Travis et al., 1964). The river courses through forested mountains of moderate relief and carries a light to moderate sediment load during spring run-off. Aside from silts, the upper portions of the river are largely unpolluted; the middle and lower portions receive sewage effluents from several small communities along the river. The stream habitats vary from fast riffles to deep pools (Fig. 2).

To more effectively study the food habits and ecology of the mayflies, 28 sampling stations were established from four regions of the St. Maries River (Fig. 1): 1) the West Fork of the St. Maries, stations 1-4; 2) the Middle Fork of the St. Maries, stations 5-17; 3) the middle St. Maries, stations 18-26 and 4) the lower St. Maries, stations 27-28.

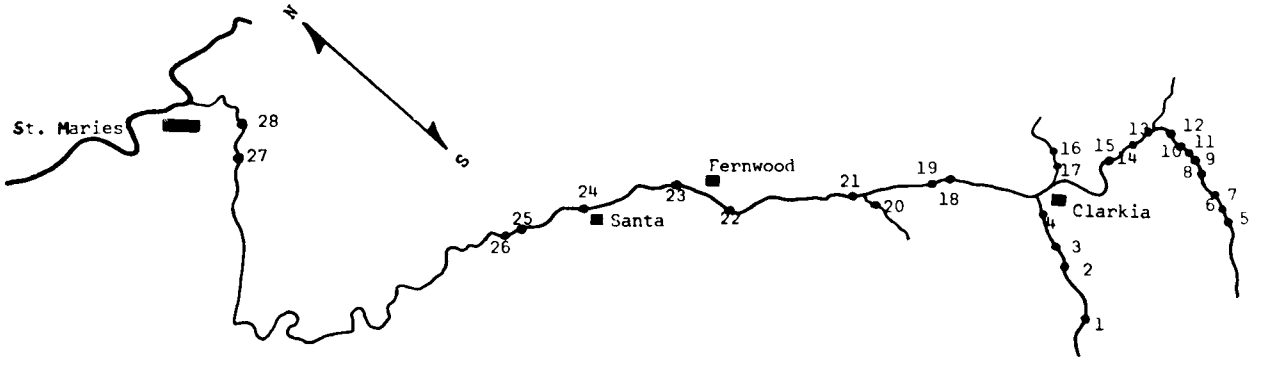

Fig. 1.—St. Maries River drainage with collecting stations identified by number.

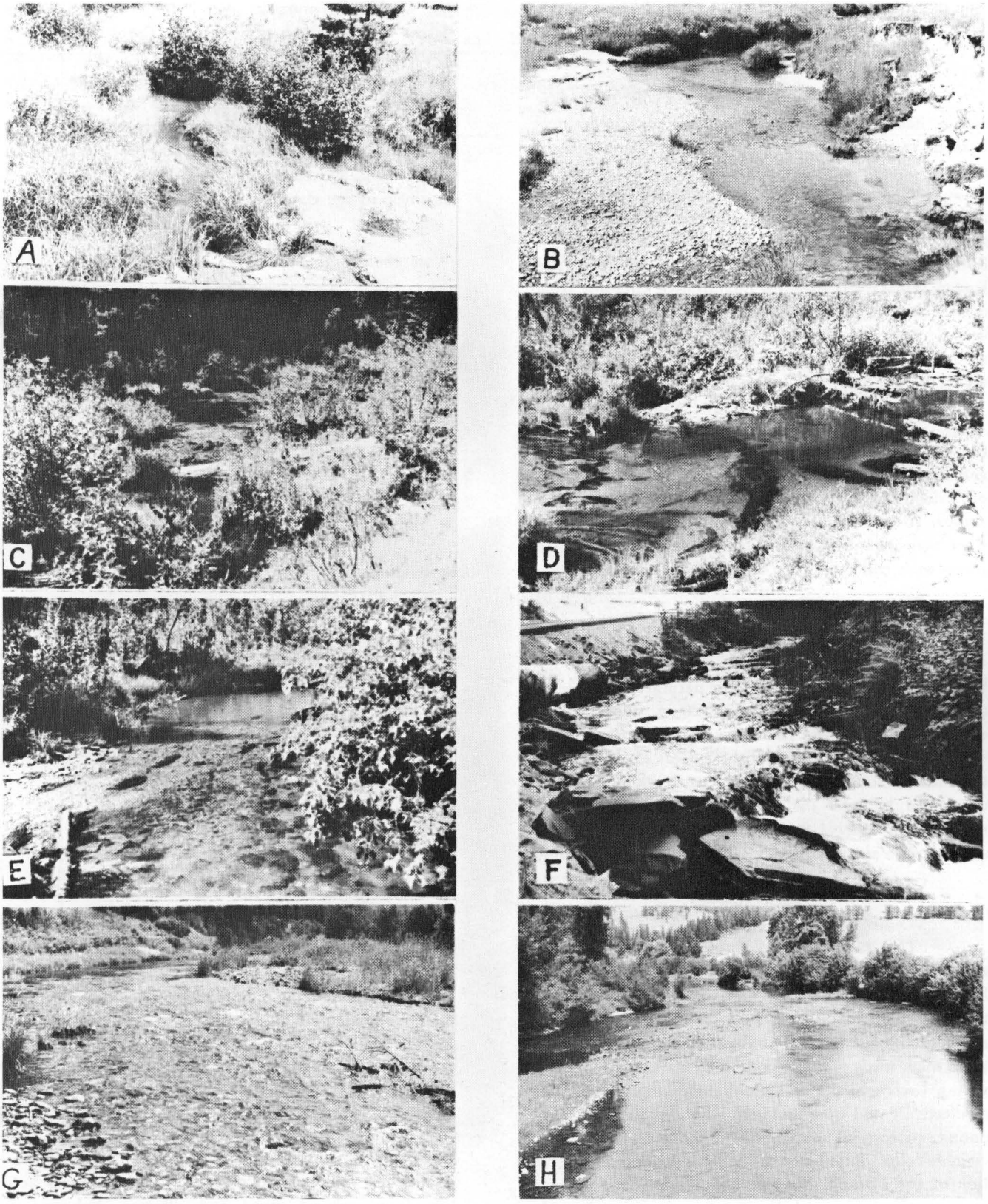

Fig. 2.–Stream habitats of the St. Maries River. A. Headwater pool, station 1; B. Slow riffle, station 4; C. Headwater riffle, station 7; D. Pool, station 5; E. Slow riffle, station 9; F. Moderate riffle, station 10; G. Fast riffle, station 18; H. Moderate riffle, station 24.

METHODS AND MATERIALS

Collecting Devices and Techniques

Mayfly nymphs were collected with an aquatic screen, hand net, drift net, Eckman dredge, cylindrical bottom sampler and by hand picking. Hand picking and an aquatic screen (26 x 36 in. made from 12 mesh copper screening fitted with wood handles) were used most extensively for qualitative collections from shallow riffles and pools. A cylindrical square-foot bottom sampler similar to that described by Waters and Knapp (1961) was used for quantitative sampling from riffle habitats. Where the river channel was too deep to use a screen or net, a 6 x 6 in. Eckman dredge was used. Insects were preserved in three-dram vials filled with 70% alcohol.

Algae were collected from the 28 stations on the St. Maries River during the months of June, July and August of 1967 and May of 1968 for the purpose of establishing a check list for mayfly food-habit studies (Gilpin et al., 1969). The free-floating algae were collected using a standard diatom net; attached forms were collected using a scraping technique.

Observational Methods

In order to study the microecology and behavior of mayfly nymphs in their natural environment, a triangular observation chamber (20 in. sides x 10 in. deep with a plexiglass bottom) was constructed. Steel stakes were inserted through the eyelets at each corner to facilitate stationary emplacement. Rocks were lifted or moved beneath the chamber in order to expose nymphs and observe their behavior. A diving mask and snorkel were also used for observation.

Stomach Analysis

The food habits of mayfly numphs were determined by stomach analysis. With the aid of a binocular microscope, the digestive tract (principally the mid-gut) was removed. A temporary slide was made of the gut contents by teasing the material from the lumen, mixing it with a drop of water and covering with a cover glass. The ingested material was evaluated qualitatively and quantitatively with the aid of a compound microscope fitted with an ocular grid and a variable-color illuminator base. Quantitative enumeration of the stomach contents was evaluated by volume on a relative basis, with the total composition in each stomach representing 100%. An ocular grid aided a quantitative evaluation of the contents. It is recognized, however, the method was subject to some error. When possible ingested algae were identified to genus and arthropods to order.

Mayfly nymphs were classified into 3 age classes differentiated primarily on the basis of wing development. Nymphs with little or no wing development were classified as age class one, nymphs with wing pads moderately developed as age class 2, and nymphs with wing pads fully or nearly fully developed as age class 3. Food habits analyses were restricted to the latter 2 age classes because of the small size and fragilness of age class one nymphs.

Stream Morphometrics

A modification of Wentworth's sediment classification (Welch, 1948) was used for describing bottom types (Table 1). Current speed was determined with a Midget Current Meter (Leupold and Stevens Instruments, Inc., Portland, Oregon) Water chemistry analyses were determined for total hardness, pH, dissolved oxygen and turbidity with a Hach Kit (Hach Chemical Company, Ames, Iowa).

TABLE 1

MODIFIED WENTWORTH'S SEDIMENT CLASSIFICATION

1.	Boulder: (more than 256 mm) more than 10"
2.	Large Cobble: (126-256 mm) 5-10"
3.	Small Cobble: (64-126 mm) 2 1/2-5"
4.	Course Pebble: (6-64 mm) 1/4-2 1/2"
5.	Fine Pebble: (1-6 mm)
6.	Sand: (0.062-1 mm)
7.	Silt: (0.004-0.062 mm)
8.	Clay: (less than 0.004 mm)
9.	Ooze: particulate organic and inorganic material

RESULTS AND DISCUSSION

The food habits, ecology, behavior and distribution of 31 species (2 of which represent species complexes) of mayflies from the St. Maries River were studied. The macro- and microecology were investigated with emphasis on physical factors such as bottom type, current speed and siltation. Behavior in relation to the microenvironment was also studied. The food habits were quantatively and qualitatively determined for all but one of the species (Table 3). All species were not of sufficient abundance to definitively evaluate their food habits. The food habits of species having fewer than 10 specimens analyzed are not dis-

Table 2. Morphometrics of 28 Stations on the St. Maries River in Idaho expressed as mid-summer averages for 1967 and 1968.

Stations	Size (yds)	Description	Bottom Type	Depth (in.)	Current speed (ft/sec)
West Fork					
1	2x20	slow riffle-pool	pebble; little or no siltation	6-18	0.5
2	3x15	moderate riffle	small cobble; lightly silted	8-10	1.8
3	2x6	pool	pebble; moderately silted	15-18	1.0
4	3x30	slow riffle	small cobble; lightly silted	6-10	1.1
Middle Fork					
5	4x10	pool	ooze	24-36	0.2
6	3x12	moderate deadfall riffle	small cobble; lightly silted	8-10	2.0
7	3x12	moderate riffle	small cobble; little or no siltation	6-10	2.0
8	3x5	fast riffle	small cobble; little or no siltation	10-12	2.4
9	3x9	slow riffle	pebble; lightly silted	8-10	0.8
10	3x20	moderate riffle	large cobble; little or no siltation	10-12	1.5
11	2x10	fast riffle	large cobble; little or no siltation	10-14	3.9
12	5x14	pool	pebble; lightly silted	14-18	1.4
13	4x8	fast riffle	boulder; little or no siltation	10-18	2.3
14	10x16	fast riffle	small cobble; little or no siltation	8-10	2.3

Table 2. Continued on next page

Stations	Size (yds)	Description	Bottom Type	Depth (in.)	Current speed (ft/sec)
15	7x14	moderate riffle	large cobble; lightly silted	10-12	2.0
16	7x7	backwater pool	ooze	18-24	0
17	6x25	moderate riffle	small cobble; little or no siltation	8-10	1.5
Middle St. Maries					
18	7x15	fast riffle	small cobble; little or no siltation	8-10	3.7
19	10x15	pool	large cobble; heavily silted	22-28	1.6
20	5x10	slow riffle	large cobble; moderately silted	6-10	1.3
21	30x25	fast riffle	large cobble; moderately silted	8-10	2.3
22	10x20	pool	large cobble; heavily silted	12-36	0.8
23	20x25	fast riffle	large cobble; moderately silted	6-18	2.7
24	40x30	moderate riffle	large cobble; moderately silted	8-10	2.0
25	7x20	fast riffle	boulder; lightly silted	12-36	2.7
26	20x30	sewage effluent pool	large cobble; heavily silted; detritus abundant	24-48	0.5
Lower St. Maries					
27	20x40	slackwaters	silt-mud	9-12	0.5
28	20x40	slackwaters	silt-mud	9-12	0.5

cussed in the subsequent section; however, notes on their ecology and distribution are given.

Station Morphometrics

Twenty-eight stations investigated during this study are morphometrically described (Table 2). The stations were selected on the basis of being representative of the numerous habitats of the river. The stations were evaluated for size, general description, bottom type, depth and current speed. The values represent mid-summer averages for 1967 and 1968. Season variations were most apparent for the flow regime and to some extent bottom type.

Species Food Habits and Ecology

Ameletus sp.

Food Habits: Nymphs fed primarily on detritus and diatoms. Detritus repesented 59.9%, diatoms and desmids 31.6%, filamentous algae 7.9%, and higher plants 0.6% of the material ingested (Table 3). Nymphs occurring on or around rocks in slow waters along the margins of the stream fed almost exclusively on diatom and detrital matter. Ingested material ranged from 60-85% detritus for nymphs occurring in moderately silted, detrital-covered pools and riffles. Nymphs living in more detrital-free habitats fed on larger amounts of diatoms and desmids. Filamentous algae were consumed regularly, but in small amounts. The relative composition of the food ingested was similar for age-class 2 and 3 nymphs.

Ecology and Behavior: Nymphs were collected from 16 of the 28 stations on the St. Maries River (Table 4). They were usually found in moderately-silted riffles and pools with bottom types of pebble to large cobble; occasionally they were found among submerged vegetation along stream margins. *Ameletus* sp. was the only mayfly collected from both slackwater stations 27 and 28. Here, nymphs were observed clinging to submerged brush, logs and pilings in the river. In shallow riffles they were observed clinging to sand and small pebbles. In slow to moderate riffles and pools, orientation was usually upstream on the tops and sides of rocks.

Nymphs of *Ameletus* sp. are excellent swimmers, swimming with darting speed and maneuverability unexceeded by most of the other mayflies studied. Nymphs were observed swimming upstream with relative ease in currents less than 0.5 ft./sec.; horizontal movements were also observed. Quick dorsoventral movements of the abdomen propel them through the water. The distance traveled depended on the degree of disturbance, current speed and nature of the bottom. The nymphs maintained swimming posture when disturbed and displaced downstream.

Age-class 3 nymphs were most abundant from early June to mid-July in the St. Maries River. Subimagos were collected in early April from the slackwaters of the St. Maries River. Jensen (1966) reported adult emergence from April to early August.

Baetis bicaudatus, Dodds

Food Habits: Nymphs fed primarily on detritus and diatoms with trace amounts of filamentous algae and higher plants. Detritus represented 57.4%, diatoms and desmids 34.2%, filamentous algae 6.6%, and higher plants 1.8% of the material ingested (Table 3). The nymphs inhabited the tops and sides of detrital and algae covered rocks. The maxillae of the nymphs are modified in the form of brushes which are used to sweep the detritus and diatoms from the substrate. Little food preference diversity was noted among the stations supporting *B. bicaudatus*. There was no significant differences in food preferences between age-class 2 and 3 nymphs.

Ecology and Behavior: Nymphs were collected from 16 of the 28 stations on the St. Maries River (Table 4). They were most commonly observed in relatively silt-free, moderate to fast-cobble riffles; however, nymphs were occasionally taken in moderately silted riffles. *B. bicaudatus* nymphs were never collected in waters polluted with sewage. *B. tricaudatus*, a closely related species, was occasionally collected from polluted situations. Dodds and Hisaw (1924) suggest that *B. bicaudatus*, because of its linear body and streamlined shape, represents one of the few mayfly nymphs that is almost perfectly adapted to fast currents ranging up to 10 ft./sec.

Orientation of *B. bicaudatus* nymphs was usually upstream on the tops of rocks; a few were observed on the sides and undersides of rocks. When disturbed from the front, the nymphs would detach and dart 3 to 6 in. downstream and establish a new position; disturbance from behind usually elicited slow forward movement. Nymphs of *B. bicaudatus* generally demonstrated greater swimming abilities than *B. tricaudatus*.

Age-class 3 nymphs occurred primarily from early June to early October.

Baetus parvus, Dodds

Food Habits: Nymphs fed primarily on detritus, diatoms and desmids. Detritus represented 53.4%, diatoms and desmids 33.8%, filamentous algae 7.5%, and higher plants 5.3% of the material ingested (Table 3). As with several mayflies, filamentous algae were not important constituents in their diet.

Table 3. Percentage composition of material ingested by mayfly nymphs.

INGESTED MATERIAL / Mayfly Spp.	Ameletus sp.	Baetis bicaudatus	Baetis parvus	Baetis tricaudatus	Centroptilum sp.	Cinygmula sp.	Epeorus albertae	Epeorus grandis	Epeorus longimanus	Ephemerella coloradensis
Division Chlorophyta										
Chaetophora sp.				0.3		0.1				2.9
Closterium sp.			0.1	0.1			0.1			
Cosmarium sp.	0.1	0.1		0.1		0.1	0.4			0.3
Microspora sp.				0.1					0.2	
Microthamnion sp.				0.2						
Mougeotia sp.	0.1					0.1				
Oedogonium sp.	0.1			0.4		0.1			0.2	1.4
Spirogyra sp.	0.3	0.4				0.2	0.3			
Stigeoclonium sp.	0.4			1.0		0.1	3.8		0.1	
Ulothrix sp.	0.6			0.9		0.7	1.2			
Misc. Desmids						0.1				
Division Chrysophyta										
Bumilleria sp.										
Diatoms	31.5	34.1	33.8	34.1	30.0	32.7	31.4	22.5	31.4	27.6
Division Cyanophyta										
Calothrix sp.				0.6						
Nostoc sp.										
Oscillatoria sp.	1.6	0.4	2.2	0.7	1.3	1.4			0.3	
Tolypothrix sp.										
Division Bryophyta										
Fontinalis sp.							0.3			
Misc. Materials										
Unident. algae	4.9	5.8	5.2	6.8	8.8	4.7	8.9	5.0	6.0	8.6
Detritus	59.9	57.4	53.4	52.3	58.1	57.0	52.7	72.5	61.1	50.7
Higher plants	0.6	1.8	5.3	2.4	1.8	2.7	0.3		0.7	
Unident. arthropods							0.6			
Insect Orders										
Ephemeroptera										7.1
Empty Stomachs	6	26	1	31	5	39	12	3	12	0
Stomachs with Contents	51	12	9	43	8	89	18	2	29	7
Total Mayflies Examined	57	38	10	74	13	128	30	5	41	7

Ephemerella doddsi	Ephemerella edmundsi	Ephemerella flavilinea	Ephemerella grandis	Ephemerella hecuba	Ephemerella hystrix	Ephemerella inermis & E. infrequens	Ephemerella margarita	Ephemerella spinifera	Ephemerella teresa	Ephemerella tibialis	Heptagenia criddlei	Paraleptophlebia bicornuta	Paraleptophlebia debilis	Paraleptophlebia heteronea & P. memorialis	Parameletus columbiae	Rhithrogena hageni	Rhithrogena robusta	Siphlonurus occidentalis	Tricorythodes minutus
2.2		1.4	0.5	1.1		0.4				1.0						0.1			
0.1		0.1	0.1	0.3						0.1	0.5								
			0.1	0.8						0.1	0.8	0.2							
0.7		0.2	0.7			0.4													
		0.1									0.1								
0.5		0.1	0.2	2.5		0.4	4.0			0.2	0.7							1.3	
1.3		2.3	0.6			0.4	8.5			1.0		0.2		0.2					
5.3		2.2	0.6	2.1	1.3	0.7			3.5	0.2	1.3					0.2			1.0
1.7		1.5	2.3	0.3		1.8				0.9					0.5	0.9			
0.4			0.1	0.1												0.9			
				0.2															
29.3	20.7	24.3	27.1	37.7	31.3	24.5	25.0	5.0	22.5	28.9	41.1	27.2	30.0	25.2	20.0	36.6	30.0	13.8	10.0
0.5			0.1	1.0															
						0.1													
3.0	1.7	0.8	3.9	0.7	7.5	1.3				0.5	0.5			0.3		0.6			
										0.2									
			0.2	0.2		0.2				0.5				0.9					
6.6	5.0	8.2	6.3	7.9	7.5	6.7	7.7		4.0	10.0	10.3	5.7	5.8	4.8	6.7	6.0	10.0	5.0	6.0
45.2	69.9	56.3	50.3	44.1	47.4	60.1	54.5	15.0	70.0	54.7	44.5	66.3	60.9	65.4	71.6	54.5	55.0	78.6	83.0
1.0	2.7	0.3	2.1	0.4	5.0	2.4	0.3			1.0	0.2	0.4	3.3	3.2	1.2	0.2	5.0	1.3	
2.2		1.0	4.6	0.6		0.4				0.6									
		1.2	0.2			0.2		80.0		0.1									
25	2	11	16	8	0	43	10	5	0	8	14	7	1	7	0	11	3	1	0
30	3	74	81	33	4	104	10	1	2	88	42	23	6	26	6	27	1	4	5
55	5	85	97	41	4	147	20	6	2	96	56	30	7	33	6	38	4	5	5

Table 4. Distribution of mayflies from 28 stations on the St. Maries River in relation to bottom sediments.

MAYFLY SPECIES	STATION AND BOTTOM								
	Peb/0	Sm-Cob/1	Slt-Peb/2	Sm-Cob/1	Ooze	Sm-Cob/1	Sm-Cob/0	Sm-Cob/0	Peb/1
	1	2	3	4	5	6	7	8	9
Ameletus sp.	x			x	x	x	x		x
Baetis bicaudatus			x	x		x	x	x	x
Baetis parvus									
Baetis tricaudatus	x	x	x	x	x	x	x	x	x
Centroptilum sp.				x					
Cinygmula sp.	x	x	x	x	x	x	x	x	x
Epeorus albertae		x	x	x					
Epeorus grandis									
Epeorus longimanus		x	x	x	x		x	x	x
Ephemerella coloradensis						x	x	x	x
Ephemerella doddsi							x	x	x
Ephemerella edmundsi						x	x	x	x
Ephemerella flavilinea		x	x	x	x	x	x	x	x
Ephemerella grandis	x	x		x	x	x	x	x	x
Ephemerella hecuba		x		x	x	x			
Ephemerella hystrix						x	x	x	
Ephemerella inermis and E. infrequens	x	x	x		x	x	x	x	x
Ephemerella margarita		x	x						x
Ephemerella spinifera	x					x	x	x	x
Ephemerella teresa		x		x					
Ephemerella tibialis	x	x	x	x	x	x	x	x	x
Heptagenia criddlei		x	x	x					
Heptagenia solitaria									
Paraleptophlebia bicornuta				x					
Paraleptophlebia debilis	x		x						
Paraleptophlebia heteronea and P. memorialis	x	x		x	x	x	x		
Parameletus columbiae									
Rhithrogena hageni		x	x	x	x	x	x	x	
Rhithrogena robusta								x	
Siphlonurus occidentalis									
Tricorythodes minutus				x					

Sediment Classification:

0–Little or no siltation
1–Lightly silted
2–Moderately silted
3–Heavily silted

Bldr–Boulder
Cob–Cobble
Peb–Pebble
Slt–Silt

Lg–Large
Sm–Small

SEDIMENTS

Lg-Cob/0	Lg-Cob/0	Peb/1	Bldr/0	Sm-Cob/0	Lg-Cob/1	Ooze	Sm-Cob/0	Sm-Cob/0	Lg-Cob/3	Lg-Cob/2	Lg-Cob/2	Lg-Cob/3	Lg-Cob/2	Lg-Cob/2	Bldr/1	Lg-Cob/3	Slt/3	Slt/3
10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
		x				x	x			x	x	x	x			x	x	x
x	x	x		x	x					x	x	x		x	x			
													x					
	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x		
						x							x		x			
x	x	x	x	x	x		x	x	x	x	x	x	x	x		x		
	x				x		x	x	x	x	x	x		x	x	x		
	x		x	x														
x	x	x	x	x	x		x	x	x	x	x	x	x	x	x			
x	x	x	x				x				x							
x	x	x	x	x	x			x	x		x		x	x				
x		x	x	x	x		x	x	x	x	x	x	x	x	x			
x	x	x	x	x	x		x	x	x	x	x	x	x	x	x			
							x		x	x	x	x		x	x	x		
x	x		x	x	x													
x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	
								x		x		x	x	x	x			
x	x		x				x											
								x							x	x		
x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x		
							x		x	x	x	x	x	x	x	x		
										x			x					
												x	x	x		x		
											x		x	x				
									x	x		x	x	x	x	x		
																		x
				x	x		x	x	x	x	x			x	x	x		
x	x			x	x		x	x			x							
											x							
												x				x		

Ecology and Behavior: *B. parvus.* was an uncommon mayfly of the St. Maries River, being collected from only station 23, a silty-cobble riffle (Table 4). Jensen (1966) indicated that nymphs of this species occur most commonly in warmer rivers and streams. Because of its rareness, microecological and behavioral information were not obtained.

Age-class 3 nymphs were collected during March in the St. Maries River. Jensen (1966) reported emergence from late June to late September.

Baetis tricaudatus **Dodds**

Food Habits: Nymphs fed primarily on detritus and diatoms. Detritus represented 52.3%, diatoms and desmids 34.3%, filamentous algae 11%, and higher plants 2.4% of the material ingested (Table 3). Nymphs were found primarily on the tops and sides of rocks in well-aerated riffles, feeding on detritus and algae collecting or growing in the porosities of rocks. Little food preference diversity was noted among the stations supporting *B. tricaudatuus.* Nymphs inhabiting silty pools had similar feeding habits to those inhabiting relatively silt-free riffles. Filamentous algae were consumed regularly but represented only a small percentage of the total material ingested. The food ingested was similar for age-class 2 and 3 nymphs.

Ecology and Behavior: Nymphs were widely distributed in the St. Maries River, being collected from 24 of the 28 stations (Table 4). They occurred from a variety of habitats. Bottom types ranged from small cobble to boulder, often with light to moderate accumulations of silt. Exclusion from 4 study stations, 10, 14, 27 and 28 might be explained on the basis of several ecological factors. Stations 27 and 28 were located in the slackwaters where channel depths ranged from 9 to 12 feet and where the bottom was principally silt and mud with considerable organic matter. These two stations supported a very low may fly population in general. Station 10 was a cascading white-water riffle, noticeably shaded by infringing conifers and with a bottom type of large, plate-like rocks. The combination of these factors is believed to have restricted this species in this habitat. Station 14 is believed to be a favorable habitat for this nymph since it manifests many of the physical features of other stations supporting the species. Its absence from this station was probably due to sampling.

B. tricaudatus is a small, round-bodied nymph moderately adapted for swimming. Nymphs were typically oriented in an upstream direction either on the sides or tops of rocks. Occasionally, nymphs were found in microeddies on the downstream side of rocks. On a few occasions, nymphs were observed clinging to *Prasiola* sheets, a green alga, and feeding on the epiphytic diatom stubble and detrital accumulations.

In swift water (3.0-3.9 ft./sec.), nymphs were observed clinging tenaciously to the rocks, bracing themselves against the forces of the current. The abdomen was observed to swing freely with the turbulence of the current. If disturbed from the front nymphs would dart backwards, tail first, reattaching on rocks several inches from their original position. When disturbed from behind the nymphs crawled slowly upstream.

B. tricaudatus is a multibrooded species having several age classes represented at any given time. Edmunds (1952), as reported by Jensen (1966), recorded adults being collected during every month except January in Utah. He reported emergence during all seasons at lower elevations.

Centroptilum **sp.**

Food Habits: Only 13 specimens of *Centroptilum* sp. were analyzed for food habits. The material ingested consisted of detritus 58.1%, diatoms and desmids 30%, filamentous algae 10.1%, and higher plants 1.8% (Table 3).

Nymphs were observed clinging to submerged vegetation, primarily filamentous algae, and feeding on the surface of the filaments and occasionally on the filaments themselves. The relative composition of the food ingested was approximately the same for age-class 2 and 3 nymphs.

Ecology and Behavior: *Centroptilum* sp. was an uncommon mayfly, found from 4 of the 28 stations on the St. Maries River (Table 4). Of the 4 stations, Station 16, a lentic habitat in the form of a backwater pool, supported the highest population and was the only station where the nymphs were collected more than once during the study. Nymphs occurring here were observed clinging to dense algae mates of *Spirogyra* and *Oscillatoria.* A few nymphs were observed under large porous lava boulders at station 25. No regular orientation pattern was discernable in relation to the current.

Age-class 3 nymphs occurred primarily during mid-June to late July in the St. Maries River. Jensen (1966) reported emergence from June to August.

Cinygmula **sp.**

Food Habits: Nymphs fed primarily on detritus and diatoms. Detritus represented 57%, diatoms and

desmids 32.9%, filamentous algae 7.4%, and higher plants 2.7% of the material ingested (Table 3).

Some food-preference diversity was noted among the stations supporting *Cinygmula* sp. Nymphs occurring in stations with a more silt-free bottom generally fed on larger amounts of filamentous algae and diatoms. The relative composition of the food ingested was approximately the same for nymphs of the age-class 2 and 3.

Ecology and Behavior: *Cinygmula* sp. was one of the most abundant and widespread mayflies in the St. Maries River, occurring in all but 4 of the 28 stations (Table 4). Nymphs showed a wide range of adaptability, occurring in slow gravel riffles to fast boulder riffles. Largest populations occurred in moderate to fast cobble riffles. The absence of *Cinygmula* sp. from station 16, 27 and 28 is believed due to unfavorable substrates consisting of mud and silt.

Cinygmula sp. is a medium-sized, dorsoventrally flattened nymph, capable of quick movements. Nymphs observed clinging to the tops and sides of rocks were oriented upstream; nymphs occurring beneath rocks were oriented primarily downstream. Occasionally nymphs were observed clustered in clumps of *Fontinalis.*

Age-class 3 nymphs occurred abundantly from early March to mid-July in the St. Maries River. Jensen (1966) reported variable emergence periods for this species.

Epeorus (Iron) albertae **(McDunnough)**

Food Habits: Nymphs of *E. albertae* are primarily detritus-diatom feeders. Detritus represented 52.7%, diatoms and desmids 31.9%, filamentous algae 14.2%, higher plants 0.6%, and arthropods 0.6% of the total food material ingested (Table 3). Filamentous algae were an important constituent in the diet of this species. Nymphs were usually found clinging to the tops and sides of silt and detrital-covered rocks and rocks having a rich growth of filamentous algae. Age-class 2 and 3 nymphs showed little diversity in their feeding habits.

Ecology and Behavior: *E. albertae* occurred in 14 of the 28 stations on the St. Maries River (Table 4). The species occurred primarily on the West Fork and the middle St. Maries. It is significant that *E. albertae* was generally absent or occurred in sparse numbers on the Middle Fork although several of the stations were superficially similar to those of the West Fork and middle St. Maries. Water temperatures averaged 4 to 5 degrees (F.) cooler on the Middle Fork, which may partially explain its absence. *E. longimanus* (Eaton), a closely related species, occurred abundantly throughout the river while *E. albertae* was generally restricted to the warmer regions. *E. longimanus* and *E. albertae* often occupied similar microhabitats on the West Fork and the middle St. Maries River.

Nymphs of *E. albertae* usually inhabitated the slower currents along the margins of the stream. They often occurred on the tops and sides of rocks orienting perpendicularly to the current. In faster riffles, as in station 10, nymphs were commonly found on the bottom of rocks and oriented in a downstream direction. In the pools of 2.5 to 3 feet deep, nymphs were generally observed on the tops of rocks with no particular orientation to current.

Age-class 3 nymphs occurred primarily from early July to mid August in the St. Maries River. Jensen (1966) reported July and August emergence in Idaho.

Epeorus (Iron) longimanus **(Eaton)**

Food Habits: Nymphs fed primarily on detritus and diatoms. Detritus represented 61.1%, diatoms and desmids 31.4%, fialmentous algae 6.8%, and higher plants 0.7% of the material ingested (Table 3). Chapman and Demory (1963) reported their diet to consist largely of diatoms and organic debris. Increased utilization of filamentous algae was noted from stations where it grew abundantly. Age-class 3 nymphs fed on approximately 10% more detritus than age-class 2 nymphs.

Ecology and Behavior: *E. longimanus* represented one of the most widely-distributed mayfly species, being found from 22 of the 28 stations on the St. Maries River (Table 4). It is well-adapted to a variety of habitats ranging from fast-cobble riffles to moderate-flowing, rocky pools. Habitats least preferred by *E. longimanus* were slow pebble riffles, backwater pools, and deep slackwaters. Also, *E. longimanus* was never collected near habitats polluted with sewage effluents.

E. longimanus was one of the more agile nymphs studied. It typically oriented upstream on tops of rocks which probably aided foraging on diatoms and detrital material deposited over the rocks. When the rocks were rotated, *E. longimanus* also rotated, maintaining an upstream orientation. On the underside of rocks, largest numbers were noted near the downstream side of rocks where larger detrital accumulations were deposited in microeddies.

Age-class 3 nymphs occurred primarily during August in the St. Maries River. Jensen (1966) reported emergence from late June to early September.

Epeorus (Ironopsis) grandis **(McDunnough)**

Ecology and Behavior: *E. grandis* was an uncommon mayfly occurring in only 3 of the 28 stations on the St. Maries River, all of which were located on the Middle Fork (Table 4). Fast-flowing cobble riffles were the principal habitats. Most of the nymphs occurred beneath rocks; a few were observed clinging to the sides of rocks among filamentous algae. No particular orientation was noted in relation to stream current.

Age-class 3 nymphs occurred primarily from early June to mid-July in the St. Maries River. Jensen (1966) reported emergence from June to August.

Ephemerella (Drunella) coloradensis **Dodds**

Ecology and Behavior: Nymphs were collected from 10 of the 28 stations on the St. Maries River, 9 of which occurred on the Middle Fork (Table 4). The cooler waters of the Middle Fork may have been a factor in their distribution.

The principal habitat of the nymphs was relatively silt-free, cobble riffles. Orientation was generally upstream on the tops and sides of rocks. In faster riffles they were commonly observed beneath rocks. They respond sluggishly when disturbed. Their dark coloration makes them difficult to see when residing on dark-colored rocks and may serve as protection against sight-feeding predators.

Age-class 3 nymphs occurred primarily from early June to mid-August in the St. Maries River. Allen and Edmunds (1962) reported emergence as late as September and early October.

Ephemerella (Drunella) doddsi **Needham**

Food Habits: Nymphs fed primarily on detritus, diatoms and desmids, and filamentous algae. Detritus represented 45.2%, diatoms and desmids 29.8%, filamentous algae 21.8%, arthropods 2.2%, and higher plants 1.0% of the material ingested (Table 3). Filamentous algae were important constituents in the diet of this species. This may be accounted for in part by their general occurrence in habitats supporting moderate to high filamentous algae development. The ingestion of arthropods is believed to be the result of random foraging activities rather than direct predation. Little food preference diversity was found among the stations supporting the nymphs. Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: Nymphs were collected from 14 of the 28 stations. Their distribution was limited to the Middle Fork and middle St. Maries, reaching greatest development in the Middle Fork (Table 4). Largest populations occurred in moderate to fast-flowing, silt-free riffles. Cobble was the preferred bottom type, but nymphs were occasionally taken from pebble and gravel riffles.

Nymphs of *E. doddsi* are morphologically adapted to moderate to swift-water habitats by virtue of their broad frontal shelf, contoured body and ventral adhesive disc. Nymphs were observed to inhabit the underside of rocks in sunlit areas and the tops and sides of rocks in shaded areas. Orientation on the bottoms of rocks was generally irregular while upstream orientation was common on tops of rocks. Their ability to cling to rocks was greatly enhanced by the large ventral disc. Their movements were generally sluggish when disturbed.

Age-class 3 nymphs occurred primarily from early June to mid-July in the St. Maries River. Jensen (1966) reported emergence from mid-June to mid-August.

Ephemerella (Caudatella) edmundsi **Allen**

Ecology and Behaviior: Nymphs were collected from 4 of the 28 stations on the St. Maries River, all of which were located on the upper portion of the Middle Fork (Table 4). Nymphs were generally found in pebble and cobble riffles of slow to moderate currents supporting an abundance of moss and algae. *Fontinalis*, a coarse moss, and *Prasiola*, a sheet-like alga, afforded excellent habitats for *E. edmundis* nymphs. Occasionally nymphs were found on the tops and sides of rocks.

Age-class 3 nymphs occurred primarily from early June to mid-July in the St. Maries River.

Ephemerella (Drunella) flavilinea **McDunnough**

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 56.3%, diatoms and desmids 24.4%, filamentous algae 16.8%, higher plants 0.3%, and arthropods 2.2% of the material ingested (Table 3). Filamentous algae were important constituents in the diet of this species. In stations 19, 20 and 23, 4 to 9% of their diet consisted of other mayflies. The relative composition of the food ingested was approximately the same for age-class 2 and 3 nymphs. Slight differences in composition were noted among different stations, however.

Ecology and Behavior: *E. flavilinea* was a widely distributed species occurring from 22 of the 28 stations

on the St. Maries River. *E. flavilinea* nymphs were collected from a variety of habitats, ranging from silty pools to boulder riffles. They were not collected near sewage effluents nor deep slackwaters (Table 4).

E. flavilinea is a medium-sized nymph closely related to *E. coloradensis.* Both species were often found in similar habitats; however, *E. flavilinea* extended into the warmer lower sections of the river while *E. flavilinea* was most commonly found in moderate to fast cobble riffles. Orientation was usually upstream on the tops and sides of rocks; however, a few were observed orienting downstream on the bottoms of rocks.

Age-class 3 nymphs occurred primarily from early June to mid-July in the St. Maries River. Jensen (1966) reported emergence in late July and August.

Ephemerella (Drunella) grandis **Eaton**

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 50.3%, diatoms and desmids 27.4%, filamentous algae 15.2%, arthropods 4.8%, and higher plants 2.3% of the material ingested (Table 3). Arthropods represented a small but significant part of their diet; it is believed that this was not the result of active predation. Little food preference diversity was found among the stations supporting this species. Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: *E. grandis* was a widely-distributed species occurring from 23 of the 28 stations on the St. Maries River. The only habitats not frequented by this species were the deeper pools, slackwaters, and habitats polluted with sewage effluents (Table 4). Nymphs generally showed affinities for habitats having protective cover as dead-fall, organic debris, *Fontinalis* clumps,and/or moderate to heavy algal development. In addition to vegetative affinities nymphs were often observed in the upper interstices of coarse gravel or on the tops, sides or undersides of rocks and logs. The nymphs are rather lethargic, moving slowly and methodically when disturbed. They have an exceptional ability to conceal themselves in stream debris and vegetation. Their coloration and dorsal spination are important adaptations providing excellent protective camouflage.

Age-class 3 nymphs occurred primarily from early March to mid-July. Allen and Edmunds (1962), as reported by Jensen (1966), recorded emergence from early June to early July.

Ephemerella (Timpanoga) hecuba **(Eaton)**

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 44.1%, diatoms and desmids 38.9%, filamentous algae 15.8%, higher plants 0.6%, and arthropods 0.6% (Table 3). Filamentous algae were an important constituent in the diet of this species. Although the microhabitats of *E. hecuba* generally had large amounts of detrital matter, the amount ingested was relatively low when compared to nymphs of *Cinygmula* sp. and *Paraleptophlebia* sp. which occupied similar microhabitats. Little food preference diversity was found among the stations supporting the nymphs. Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: *E. hecuba* occurred in 12 of the 28 stations on the St. Maries River (Table 4). The nymphs typically inhabited areas of moderately-silted pebbles and rocks. Orientation was generally irregular in relation to the current. *E. Hecuba* is a well-camouflaged, pubescent nymph which usually has large amounts of silt covering its body.

Mature nymphs of *E. hecuba* are large and dorsoventrally flattened. When disturbed they raise their abdomens as a defensive mechanism rather than retreating for cover. If dislodged from the substrate, nymphs were observed to drift downstream flexing their abdomens as a means of rudder control. Downstream displacement was usually several feet. Nymphs are relatively lethargic and not easily disturbed.

Age-class 3 nymphs occurred primarily from early July to mid-August in the St. Maries River. Jensen (1966) reported that little is known about the biology and emergence patterns of the adults in Idaho.

Ephemerella (Caudatella) hystrix **Traver**

Ecology and Behavior: *E. hystrix* was a relatively uncommon mayfly, occurring from 8 of the 28 stations on the St. Maries River, all of which were located on the Middle Fork (Table 4). Nymphs were usually found in moderate to fast riffles clinging to moss *(Fontinalis)* and algae *(Prasiola).* The vegetative microenvironments of the nymphs afforded excellent concealment. Occasionally nymphs were observed clinging on the downstream sides of large cobble or crawling slowly among the pebbles and gravel of the stream bottom. Orientation to the stream current was usually irregular.

Age-class 3 nymphs occurred primarily from early June to mid-July in the St. Maries River. Jensen (1966) reported emergence in late June and early July.

Ephemerella (Ephemerella) inermis **Eaton** and *E. (Ephemerella) infrequens* **McDunnough**

Food Habits: *E. inermis* and *E. infrequens* are considered together because the nymphs could not be satisfactorily separated. Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 60.1% of the material ingested, diatoms and desmids 24.5%, filamentous algae 12.2%, higher plants 2.6%, and arthropods 0.6% (Table 3). Filamentous algae were an important constituent in the diets of these species. Food preference diversity was variable among the stations. Filamentous algae were moderately consumed in most riffle habitats; higher plants and arthropods were frequently ingested in pool habitats. Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: Nymphs occurred in 25 of the 28 stations on the St. Maries River being found from a wide variety of habitats ranging from heavily-silted pools to fast-flowing boulder riffles (Table 4). Nymphs were most commonly observed on the tops and sides of submerged logs and rocks in slow to moderate riffles. Occasionally nymphs were found clinging to moss *(Fontinalis)* or other submerged vegetation. Orientation of the nymphs to the current was generally irregular.

Age-class 2 and 3 nymphs occurred primarily from early June to July in the St. Maries River. Jensen (1966) reported *E. inermis* may be multibrooded, as the adults have been collected from late May to early September; adults of *E. infrequens* have been reported from June to September (Allen and Edmunds, 1965).

Ephemerella (Attenuatella) margarita **Needham**

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 54.5% of the material ingested, diatoms and desmids 25%, filamentous algae 20.2%, and higher plants 0.3% (Table 3). Filamentous algae were utilized to a greater extent than most of the other species studied. On several occasions nymphs were observed feeding on the stubble-like algae growing on surfaces of rocks. Feeding was done by moving the head in a series of forward to back motions. Little food preference diversity was noted among the stations supporting the nymphs. Age-class 2 and 3 nymphs fed on about the same relative composition of food.

Ecology and Behavior: Nymphs were collected from 9 of the 28 stations on the St. Maries River, 6 of these were located on the middle St. Maries (Table 4). Nymphs usually occurred along the margins of slow, moderately-silted, cobble riffles, and in close association with algae or other submerged vegetaion. Occasionally, they were found in shallow pools on the bottoms of detrital-covered rocks. Orientation was generally upstream on tops of rocks. If disturbed nymphs would quickly dislodge and drift several inches downstream before reattaching to a suitable substrate.

Age-class 3 nymphs occurred primarily during August in the St. Maries River. Allen and Edmuns (1961) reported *E. margarita* adults occurring from July to late August in Idaho.

Ephemerella (Drunella) spinifera **Needham**

Ecology and Behavior: *E. spinifera* was a relatively uncommon mayfly occurring in 9 of the 28 stations on the St. Maries River, most of which were located on the Middle Fork (Table 4). Nymphs were commonly observed clinging to moss *(Fontinalis)* Orientation in relation to stream current was generally irregular.

E. spinifera is a spiny nymph, blending well with its environment. Dorsal spination provides an excellent surface for the accumulation of silt and algae, rendering the nymph less conspicuous to predators.

Age-class 3 nymphs occurred primarily from early June to mid-August in the St. Maries River. Jensen (1966) recorded emergence from late July to early September.

Ephemerella (Serratella) teresa **Traver**

Ecology and Behavior: *E. teresa* was an uncommon mayfly occurring in 5 of the 28 stations on the St. Maries River, most of which were located on the middle St. Maries (Table 4). Nymphs usually occurred in moderate-flowing, light to moderately-silted cobble riffles; occasionally nymphs were found in faster riffles. Nymphs were commonly observed clinging to the tops and sides of rocks. Orientation to current was usually upstream.

Age-class 2 and 3 nymphs occurred primarily during mid-July in the St. Maries River and would suggest a late summer or early fall emergence. Jensen (1966) reported the biology of the adults unknown.

Ephemerella (Serratella) tibialis **(McDunnough)**

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 54.7%, diatoms and desmids 29.1%, filamentous algae 14%, higher plants 1.5%, and arthropods 0.7% of the material ingested (Table 3). Food preference diversity varied among the stations supporting *E. tibialis* nymphs. The diversity generally varied with the availa-

bility of the different food items. Where larger amounts of filamentous algae were present, they were generally fed on to a greater degree.

Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: *E. tibialis* was one of the most widespread mayfly species, occurring in 25 of 28 stations on the St. Maries River. It was not recorded for stations 16, 27 and 28 (Table 4). Its near universal occurrence would indicate a wide range of adaptability. Largest populations occurred in slow to moderately-flowing cobble riffles having little or no siltation. Jensen (1966) reported this species occurring in most moderately-flowing streams and at all elevations in Idaho.

E. tibialis nymphs were commonly observed clinging to the tops and sides rocks, orienting upstream. Infrequently they were found on the undersides of rocks and crawling and clinging to mats of algae or moss. Nymphs clinging to the surfaces of the rocks were often observed moving their body up and down in "push-up" fashion. This behavior probably had a respiratory function by increasing the water flow around the gills.

Age-class 3 nymphs occurred primarily from early June to mid-August in the St. Maries River. Jensen (1966) reported emergence from early July to mid-September.

Heptagenia criddlei McDunnough

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 44.5%, diatoms and desmids 42.4%, filamentous algae 12.9%, and higher plants 0.2% of the material ingested (Table 3). In habitats having heavy algal growths as in stations 3, 22, 23 and 25, filamentous algae were most extensively utilized. Habitats having less filamentous algae but more detritus resulted in nymphs feeding more extensively on the latter. Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: Nymphs occurred in 12 of the 28 stations on the St. Maries River, 8 of which were located on the middle St. Maries (Table 4). Nymphs were usually found in moderately-flowing, lightly-silted cobble riffles. Nymphs of *H. criddlei* were generally observed on the tops and downstream sides of rocks. Orientation was generally irregular. Extensive algal development was usually present on the inhabited rocks.

H. criddlei nymphs are dorsoventrally flattened and demonstrate a unique mobility in slow currents. Nymphs swim from rock to rock by means of gliding motion. Up and down flexions of the abdomen in conjunction with leg movements propel the nymphs.

Age-class 3 nymphs occurred primarily from early June to mid-August in the St. Maries River. Jensen (1966) reported emergence from mid-June to late September.

Heptagenia solitaria McDunnough

Ecology and Behavior: *H. solitaria* was an uncommon mayfly, occurring in only 2 of the 28 stations on the St. Maries River, stations 19 and 22 (Table 4). The principal habitat of the nymphs was moderately-silted, detrital-covered pools or runs. Nymphs were most abundant on the underside of moderately-silted cobble; infrequently nymphs were observed clinging to the tops of rocks. Orientation in relation to the stream current was generally irregular. Few microecological and behavioral observations were made because of limited distribution and extremely low population.

Age-class 3 nymphs occurred primarily during early June in the St. Maries River. Jensen (1966) reported emergence from June to September.

Paraleptophlebia bicornuta (McDunnough)

Food Habits: Nymphs fed primarily on detritus and diatoms. Detritus represented 66.3% of the material ingested, diatoms and desmids 27.4%, filamentous algae 5.9%, and higher plants 0.4% (Table 3). Little feeding diversity was noted among the stations. The composition of the food ingested was approximately the same for age-class 2 and 3 nymphs.

Ecology and Behavior: Nymphs occurred in 5 of the 28 stations on the St. Maries River (Table 4). Nymphs were usually found in slow-flowing, detrital-covered cobble riffles. Largest populations occurred at station 26, which was heavily polluted with sewage effluent. The microenvironment was generally the underside of rocks; the intergravel spaces and surfaces of the rocks were usually filled or covered with detritus. Orientation was generally irregular in relation to the stream current. Nymphs showed moderate agility when disturbed, but usually confined their movements to a single rock.

Age-class 3 nymphs occurred primarily during August in the St. Maries River. Jensen (1966) reported emergence from mid-September to mid-October.

Paraleptophlebia debilis **(Walker)**

Ecology and Behavior: *P. debilis* was a relatively uncommon mayfly, occurring in 5 of the 28 stations on the St. Maries River, 3 of these located on the middle St. Maries (Table 4). Moderate flowing cobble riffles with an abundance of detritus were preferred habitats. Nymphs usually occurred on the underside of rocks, but occasionally on the tops and sides and in gravel and detrital filled interstices.

P. debilis and *P. bicornuta* nymphs occasionally were observed together. Both species have similar physical requirements; neither species was collected from the Middle Fork.

Age-class 3 nymphs occurred primarily during August in the St. Maries River. Jensen (1966) reported emergence from late August to late October.

Paraleptophlebia heteronea **(McDunnough)** and *P. memorialis* **(Eaton)**

Food Habits: *P. heteronea* and *P. memorialis* are considered together because of the inability to satisfactorily separate the nymphs. Nymphs fed primarily on detritus and diatoms. Detritus represented 65.4%, diatoms and desmids 25.2%, filamentous algae 5.3%, and higher plants 4.1% of the material ingested (Table 3). In stations with dead-fall or with abundant overhanging vegetation, nymphs fed on greater amounts of higher plants. Age-class 2 and 3 nymphs fed on approximately the same relative composition of food.

Ecology and Behavior: Nymphs occurred in 13 of the 28 stations on the St. Maries River (Table 4). Nymphs were usually found in moderately-silted, slow to moderate-flowing cobble riffles. Nymphs of *P. heteronea* and *P. memorialis* were generally observed clinging to the tops and sides of rocks. Orientation to stream current was usually upstream.

Age-class 3 nymphs occurred primarily from early March to mid-June in the St. Maries River. Jensen (1966) reported emergence of both species from early June to early August.

Parameletus columbiae **McDunnough**

Ecology and Behavior: *P. columbiae* was an uncommon mayfly, occuring in 5 of the 28 stations on the St. Maries River, one station being located in the slackwaters (Table 4). Nymphs occurred primarily in the slower, moderate-to-heavily silted cobble riffles and pools. Most of the nymphs were observed clinging to the tops and sides of rocks and orienting upstream. Nymphs occurring in the slackwater were observed clinging to submerged brush, logs, and pilings in the river, and were found in coexistence with nymphs of *Ameletus* sp. Like *Ameletus* sp., nymphs of *P. columbiae* are round-bodied, but exhibit less mobility than the former.

Age-class 3 nymphs of *P. columbiae* occurred primarily from early June to mid-July in the St. Maries River. Edmunds (1957), as reported by Jensen (1966), indicated nymphal life is completed within 16 to 22 days or less. Female imagos deposit the eggs during mid-June; hatching occurs shortly after the snow melts the following May.

Rhithrogena hageni **Eaton**

Food Habits: Nymphs fed primarily on detritus, diatoms, and filamentous algae. Detritus represented 54.5% of the material ingested, diatoms and desmids 37.5%, filamentous algae 7.8%, and higher plants 0.2% (Table 3). Little food preference diversity was found among the stations supporting the nymphs. The relative composition of the food ingested was approximately the same for age-class 2 and 3 nymphs.

Ecology and Behavior: *R. hageni* was a widely-distributed mayfly occurring in 17 of the 28 stations on the St. Maries River (Table 4). Nymphs occurred primarily in slow to moderate-flowing, lightly silted cobble riffles. The preferred microenvironment was generally the undersides of rocks.

Age-class 3 nymphs occurred primarily from mid-March to mid-June in the St. Maries River. Jensen (1966) reported emergence from mid-June to August.

Rhithrogena robusta **Dodds**

Ecology and Behavior: *R. robusta* was a relatively uncommon mayfly, occurring in 7 of the 28 stations on the St. Maries River; 5 of these were located on the Middle Fork (Table 4). The nymphs occurred primarily in relatively silt-free, moderate-to-fast cobble riffles. The population of *R. robusta* was consistently low in all habitats. Nymphs were usually observed on the undersides of rocks in the faster currents; however, they occasionally were observed on the tops and sides of rocks.

Age-class 3 nymphs occurred primarily from early March to early June in the St. Maries River.

Siphlonurus occidentalis **Eaton**

Ecology and Behavior: *S. occidentalis* was one of the most uncommon mayflies, occurring from only station

21, a slow-flowing cobble riffle (Table 4). Nymphs were generally observed clinging to *Fontinalis* along the stream margins, infrequently on the tops of moderate to heavily-silted rocks. Edmunds (1960) reported fresh water lakes, pools and slow-moving silted streams as the preferred habitat of *S. occidentalis.*

Age-class 3 nymphs occurred from June to early August in the St. Maries River. Jensen (1966) reported emergence from mid-May to mid-October.

Tricorythodes minutus **Traver**

Ecology and Behavior: *T. minutus* was an uncommon mayfly, occurring from only 3 of the 28 stations on the St. Maries River (Table 4). Nymphs were generally observed clinging to the tops and sides of rocks, occasionally to submerged vegetation. Because of their small size and limited distribution, few behavioral observations were made.

Food Habits—General

The composition of the ingested food for most of the mayfly nymphs was largely determined by the available food. Jones (1949) reported that most herbivorous mayflies fed on algae if abundant, and if not, would feed on some standby food. He noted that *Ephemerella* sp. nymphs fed on *Ulothrix*, a green alga when it was plentiful, but turned to *Fontinalis*, a moss, when algae were scarce. Seasonal changes in food habits were noted by Chapman and Demory (1963). Nymphs of the St. Maries River utilized 3 primary food types, detritus, diatoms, and filamentous algae. Spring and summer nymphs usually fed on higher amounts of algae, which reached their best development during these periods; late-summer and fall nymphs fed more on detritus. Several species as *Baetis bicaudatus*, *Baetis tricaudatus*, and *Paraleptophlebia bicornuta* were relatively consistent in their feeding habits during the year.

The type of food available in a lotic environment is influenced by the depth of the stream, current speed, water chemistry, bottom type, light conditions, etc. If algae were adapted to a particular microhabitat, they were usually fed upon by the herbivorous nymphs of that microhabitat. Fast currents in the center channel of station 8 and 10 supported various algae as diatoms, desmids, and *Nostoc* while *Ulothrix* and *Spirogyra* occurred predominately along the stream margins. Slower riffles as stations 20 and 24 commonly supported *Ulothrix*, *Oscillatoria*, and *Oedogonium* Most of the mayflies occurring in these respective stations or micohabitats within these stations fed on these algae; however, detritus almost universally represented the principal ingested material.

Mayfly nymphs of the St. Maries River were almost totally herbivorous with detritus, the particulate organic matter, most commonly utilized. The lowest percentage of ingested detritus was by *Ephemerella hecuba* and *Heptagenia criddlei* (Table 3). Both species occupied moderate to heavily silted habitats and both ingested greater amounts of diatoms and filamentous algae than other nymphs occupying the same or similar microhabitats. *Cinygmula* sp. and *Paraleptophlebia* spp. nymphs inhabiting the same or similar habitats ingested detritus at an average of 10% higher than *E. hecuba* and *H. criddlei.* Nymphs of *Paraleptophlebia* spp. ingested the largest amounts of detritus, ranging as high as 66% (Table 3). The food habits were generally variable among the species occupying the same or similar habitats. This is believed to be greatly influenced by their morphology, nature of the mouth parts, and physiological needs.

The genus *Baetis* was a common and abundant mayfly occurring in moderate-to-fast cobble riffles (Table 4). *B. bicaudatus* is considered by Nielson (1950) to be one of the better adapted mayflies to fast currents. Ninety-one percent of the material ingested by nymphs of this species was detritus and diatoms (Table 3). *B. tricaudatus*, a closely-related species, fed on approximately 86% detritus and diatoms and occupied a wider range of habitats. The latter species fed on approximately 10% filamentous algae. *Ameletus* sp. had similar feeding habits as *Baetis* but generally occupied slower riffles and pools (Table 4). Nielson (1950) reported round-bodied nymphs as *Baetis* and *Ameletus* having mouth parts morphologically adapted for feeding on rock-surface accumulations. The sweeping action of the comb-like maxillae is used to brush detritus and diatoms from the surface of the rock. Orientation of nymphs of both species was usually upstream, thus permitting the currents to augment the effectiveness of the maxillae during feeding.

Nymphs as *Epeorus albertae*, *Ephemerella doddsi*, *E. flavilinea*, *E. grandis*, *E. hecuba*, *E. inermis*, *E. infrequens* and *E. tribialis* ingested trace amounts of arthropods, principally other insects (Table 3). The amounts were consistently small and did not represent a major part of their diets. Arthropod ingestion was probably accidental; none of the species studied consistently fed on arthropods. True round-bodied nymphs as *Ameletus* sp., *Baetis* spp., and *Centroptilum* sp. were never recorded as feeding on arthropods (Table 3).

The food habits were determined primarily for age-class 2 and 3 nymphs because of the greater facility for dissection. Most species analyzed indicated that food habits were essentially the same for both age classes. However, age-class 3 nymphs of *Epeorus longimanus* and *Heptagenia criddlei* fed more on

detritus than age-class 2 nymphs. This may be partly explained by their life cycles; age-class 3 nymphs of these species were abundant during late summer when detritus was more abundant.

Ecology and Behavior—General

In addition to biological factors, many physical factors of the environment influence the distribution, ecology, and behavior of mayfly nymphs. Hora (1930) reported that the principal factor influencing distribution was current speed. Later Ide (1935) concluded that the general distribution of mayflies is limited primarily by temperature differences, but local distribution may be affected by biological factors and other physical factors. Linduska (1942) reported that the bottom type was perhaps the most important factor influencing distribution. Based on findings from this study, we believed a combination of factors and not a single factor influence distribution. Most notable of these factors are water velocity, bottom type, light intensity, and water chemistry in addition to biotic factors as food availability and intra- and inter-specific interactions.

Nymphal anatomy greatly influences nymphal behavior and orientation, particularly with respect to stream current and substrate. Round-bodied nymphs as *Ameletus* sp. and *Baetis* spp. were commonly found orienting upstream on the tops and sides of rocks and pebbles in riffles of moderate velocity, their bodies offering little resistance to the passing currents. Dorsoventrally flattened nymphs as *Cinygmula* sp. and *Epeorus* spp. were generally observed clinging to the sides of rocks in riffles of moderate to fast velocity. In slower riffles they were frequently observed on tops of rocks. Orientation was generally irregular in both cases. It should be acknowledged that the little-known characteristics of the rock-water interface undoubtedly influence in an important way the microecology and behavior of rock-dwelling mayflies. The lack of instrumentation and general difficulty in studying the ecological implications of this region have relegated ecologists to principally macroecological investigations.

Although this study was not principally pollution oriented, the sewage effluents contributed by several small communities seemed to warrant investigation. Station 26, a sewage effluent pool near Santa, Idaho, was established to reflect mayfly-pollution relationships. The cobble of this station was largely imbedded in the gravels and finer sediments and covered with detritus. Several species of mayflies frequented this station (Table 4), but only 3, *Paraleptophlebia bicornuta*, *P. heteronea* and *P. memorialis*, had consistently high populations. Human sewage apparently had little adverse effect upon these mayflies. Their diet consisted largely of detritus from decomposing sewage. The greatest limiting factor to most of the other species of mayflies in this habitat is believed to be the detrital-covered bottom, rendering the rocks and intergravel spaces inaccessible or otherwise uninhabitable. The water chemistry for this station was not appreciably different from other stations. (Table 5).

Many mayfly nymphs from the St. Maries River had a wide distribution while others were more restrictive (Table 4). Nymphs as *Baetis tricaudatus*, *Cinygmula* sp., *Epeorus longimanus*, *Ephemerella flavilinea*, *E. grandis*, *E. inermis*, *E. infrequens*, and *E. tibialis* reflected the former condition, although their densities were variable. *Baetis tricaudatus*, although having a wide distribution, reached its greatest development in the colder, unsilted riffles of the Middle Fork. Many of the species were more specific in their micohabitat selection. *Epeorus grandis* occurred only in the cold, relatively unsilted riffles of the Middle Fork as did *Ephemerella edmundsi*. Nymphs as *Paraleptophlebia bicornuta* and *Heptagenia solitaria* preferred the slow, silty, detrital-covered riffles and pools of the middle St. Maries. Largest populations of nymphs generally occurred in relatively silt-free, moderately flowing cobble riffles. *Ephemerella tibialis* and *Cinygmula* sp. usually represented the largest population in this type of habitat and were also the most widely distributed mayflies of the river.

Water Chemistry

Chemical analysis of the St. Maries River was performed for total hardness (ppm $CaCO_3$)hydrogen ion concentrations (pH), dissolved oxygen, and turbidity (Table 5). Analyses were made with a Hach field kit. Turbidity was measured in Jackson Turbidity Units. Analyses were performed at 5 locations, the West Fork, Middle Fork, upper middle St. Maries, lower middle St. Maries and the slackwaters. Samples were taken in August, 1967 and April and June, 1968. Analysis of the slackwaters was taken only during August, 1968.

Total hardness (ppm $CaCO_3$) was relatively consistent for the two Forks and the upper middle St. Maries. Station 26, a sewage effluent habitat, varied from 10 to 30 ppm $CaCO_3$. Dissolved oxygen ranged from 8 to 11 ppm throughout the river. Hydrogen ion concentration in the river was relatively consistent for samples taken during April and August; the post-runoff samples during June were slightly lower, ranging from 7.0 to 7.7. Turbidity (J.T.U.'s) of the river was zero except near station 26 and the slackwater which was recorded as 15 in August.

The water chemistry of the St. Maries River was relatively consistent during the various sampling periods. It is believed that differences in the 4 chemical characters of the water were not of sufficient magnitude to influence the distribution of mayflies.

SUMMARY

The food habits and ecology of 12 genera and 31 species of mayflies from the St. Maries River were studied. Nymphs of the St. Maries River were basically herbivorous, feeding largely on detritus, diatoms, and filamentous algae. Food habits for most species varied little from habitat to habitat. Intermediate stage and older age-class nymphs usually had similar feeding habits.

The distribution of mayfly nymphs of the St. Maries River was variable. Species such as *Cinygmula* sp. and *Ephemerella tibialis* had a wide distribution, adapting to a variety of habitats while *Epeorus grandis*, *Centroptilum* sp., and *Heptagenia solitaria* had limited distributions. We believe conditions of the microhabitats greatly influence mayfly distribution.

Different mayflies generally had different environmental requirements. Nymphs such as *Paraleptophlebia bicornuta*, *P. heteronea*, and *P. memorialis* had strong affinities to habitats having considerable detritus, while nymphs of *Epeorus grandis* and *Ephemerella edmundsi* frequented more silt and detrital-free habitats. The principal physical factors influencing the distribution of mayflies on the St. Maries River are believed to be bottom type and current speed. Moderately-flowing, lightly-silted cobble riffles supported the largest populations of mayfly nymphs.

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Table 5. Water Chemistry Analysis from Five Locations on the St. Maries River.[1]

Location	Total Hardness (ppm $CaCO_3$)	Dissolved O_2 (ppm)	pH	Turbidity (JTU's)[2]
West Fork				
April 1968	20	10	8.3	0
June 1968	20	10	7.7	0
August 1967	20	9	8.9	0
Middle Fork				
April 1968	10	11	8.4	0
June 1968	10	10	7.0	0
August 1967	20	8	8.9	0
Upper Middle St. Maries				
April 1968	20	11	8.6	0
June 1968	10	10	7.1	0
August 1967	10	8	8.9	0
Lower Middle St. Maries				
April 1968	30	10	8.6	0
June 1968	10	9	7.2	0
August 1967	25	8	8.8	15
Slackwaters				
August 1968	20	10	8.7	15

[1]Analysis made with Hach field kit.

[2]Jackson Turbidity Units.