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THE FOOD HABITS AND ECOLOGY OF MAYFLIES  
OF THE ST. MARIES RIVER IN IDAHO

BY

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MASTER'S THESIS

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THE FOOD HABITS AND ECOLOGY OF MAYFLIES  
OF THE ST. MARIES RIVER IN IDAHO

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This thesis of Bobby Rex Gilpin for the Master of Science degree with a major in Entomology and titled "Food Habits and Ecology of Mayflies of the St. Maries River in Idaho" was reviewed in rough draft form by each Committee member as indicated by the signatures and dates given below and permission was granted to prepare the final copy incorporating suggestions of the Committee; permission was also given to schedule the final examination upon submission of two final copies to the Graduate School Office:

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## ABSTRACT

The food habits and ecology were studied for 31 species of mayfly nymphs from the St. Maries River in Idaho, during 1967 and 1968.

The nymphs were basically herbivores, feeding on variable amounts of detritus, diatoms and filamentous algae; insects were occasionally consumed. The feeding habits depended largely on the microhabitat of the nymph, e.g. riffle species generally fed more on filamentous algae and diatoms while pool-inhabiting nymphs fed largely on detritus. Age-class two and three nymphs usually fed on the same relative composition of food.

Nymphs of many mayfly species demonstrated similar microhabitat affinities, although the macrohabitats were often dissimilar. Bottom type and current speed were important factors limiting mayfly distribution.

A dendrogram was used to correlate station similarities biotically; several diverse habitats supported the same species.



## INTRODUCTION

Mayflies are an important group of aquatic insects which have a wide distribution and high adaptability. Until recently the food habits and ecology of many 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 lack of sufficient taxonomic keys has limited ecological studies for many species and particularly the nymphs.

In man's continued search for knowledge, he must seek deeper into the many subtle ecological relationships to understand the aquatic ecosystem. The nymphs of mayflies occupy an important place in the food chains of aquatic communities. Their ecological niche is primarily that of transforming plant tissue into animal. They thus play an important role in the aquatic ecosystem by bridging the gap between primary and secondary production.

This study on the food habits and ecology of mayfly nymphs will contribute fundamental knowledge to a better understanding of food chains, environmental requirements, microecology and behavior, pollutional relationships and to a basic biological understanding of this important aquatic insect group.

## REVIEW OF LITERATURE

The food habits and ecology of mayfly nymphs have been rather poorly documented in entomological literature. Much of the early work dealt with the life history and taxonomy of the adults.

Several taxonomic references on adult and nymphal mayflies bear special mention. Day (1963) and Berner (1959) contributed valuable keys to North American mayfly nymphs. Edmunds (1954), Edmunds and Allen (1957), Edmunds et al. (1963) and Allen and Edmunds (1961) contributed extensively to the taxonomy and ecology of mayfly nymphs. Through the efforts of G. F. Edmunds and his students at the University of Utah, valuable taxonomic and biological contributions have been made for western mayflies. S. L. Jensen (1966) recently completed a voluminous work on the mayflies of Idaho, providing invaluable information on their taxonomy and ecology.

Ecological contributions were made by several workers in the early 1900's. Morgan (1913) conducted studies on nymphal ecology and structure. Clemens (1913) reported on nymphal ecology and food habits of Heptagenia. In later studies, Clemens (1915, 1917) described the ecological requirements of Siphonurus and Chirotenetes.

Researchers of the 1920's and 1930's were largely concerned with the physical requirements of mayflies. Needham (1920) gave a general description and brief ecology of Rhithrogena mimus Eaton.

Dodds and Hisaw (1924) reflected on the behavior and morphological adaptations of mayfly nymphs in relation to their microhabitat. Neave (1930) reported on the migrations of Blasturus cupidus Say in selected habitats. Hora (1930) indicated current speed was an important limiting factor on nymphal distribution. Later, Ide (1935) demonstrated the effect of temperature on nymphal distribution in a stream. Studies on the biology of mayflies by J. G. Needham, J. R. Traver and Yin Chi Hsu (1935) summarized much of the early knowledge on North American mayflies and provided a basis for many of the later studies.

During the 1940's and early 1950's mayfly studies were still largely taxonomic-ecological, but with increased emphasis on mayflies in relation to the altered environment. Linduska (1942) indicated that the bottom type of streams is an important factor influencing the local distribution of mayfly nymphs. Berner (1950) recognized that the mayfly populations of a region were intimately related to the aquatic conditions of that region. By the early 1950's Ephemeroptera, Trichoptera and Plecoptera were being considered as possible pollution indicators. Gaufin and Tarzwell (1952) indicated that in evaluating aquatic organisms as indicators of pollution, caution must be used to evaluate all environmental factors.

Mayfly researchers of the late 1950's and 1960's contributed additionally to the ecology of mayfly nymphs. Most important of which are Lyman (1956), Edmunds and Allen (1957, 1966), Berner

(1957), Fremling (1960, 1964), Edmunds (1960), Leonard (1965), Leonard and Leonard (1962), Chapman and Demory (1963), Hughes (1966a, 1966b) and Swanson (1967).

## MATERIALS AND METHODS

### A. Drainage System

This study was conducted on the St. Maries River, an artery of the Spokane River Basin which is one of the important drainage systems in northern Idaho (Fig. 1). The St. Maries River has a drainage area of about 437 square miles and an average stream discharge of 520 cubic ft./sec. (Travis et al., 1964). The St. Maries River has its origin from two forks, the Middle Fork and West Fork which are confluent near Clarkia, Idaho. The river meanders northwest along a narrow valley floor and is confluent with the St. Joe River at the city of St. Maries, Idaho. Drainage waters subsequently flow into Coeur d'Alene Lake which in turn is drained via the Spokane River to the north.

The coniferous forest for the St. Maries River drainage is basically a Thuja-Tsuga-Pachistima association (Daubenmire, 1952).

The geology of the Middle and West Forks of the St. Maries River is the Pre-Cambrian belt series. The middle and lower St. Maries, from Clarkia downstream, grade into tertiary Columbia River basalt (Ross and Forrester, 1959).

The St. Maries River has several definable sources of pollution which are primarily restricted to the middle and lower regions of the river. The municipalities of Clarkia, Fernwood and Santa, Idaho, release raw sewage effluent into the river. Organic

enrichment is evidenced by increased abundance of algae and detritus. Pasture runoff and sawmill wastes also contribute minor sources of pollution.

The St. Maries River valley is principally an agricultural area; farming, ranching and lumbering provide the major economy.

To study more effectively the food habits and ecology of the mayflies, the St. Maries River was divided into four regions: 1) the West Fork of the St. Maries, 2) the Middle Fork of the St. Maries, 3) the middle St. Maries and 4) the lower St. Maries (Fig. 1).

#### West Fork

The headwaters of the West Fork originate in low undulating mountains approximately six miles southwest of Clarkia; the West Fork joins the Middle Fork near Clarkia. The adjoining mountains are covered primarily with Lodge-pole pine (Pinus contorta Dougl.), Douglas fir (Pseudotsuga menziesii (Poir.) Britt.) and Western red cedar (Thuja plicata D. Don.). Marginal stream vegetation consists primarily of Alder (Alnus sp.), particularly along the headwaters, Nut-grass (Cyperus sp.), Sedge (Carex sp.), Buttercup (Ranunculus sp.) and Bluegrass (Poa sp.). Stream velocities vary from 0.5 ft./sec. at the headwaters to 1.3 ft./sec. near the confluence. The bottom type of the riffles is principally pebble and small cobble. Stream depths range from 4 to 10 inches in riffles with intervening pools appreciably deeper (Fig. 2A, B).

### Middle Fork

The Middle Fork originates in moderately rugged relief approximately seven miles southeast of Clarkia. The adjoining slopes are covered primarily with Douglas fir (Pseudotsuga menziesii), Engelmann's spruce (Picea engelmanni (Parry) Engelm.), Western red cedar (Thuja plicata), Western hemlock (Tsuga heterophylla (Raf.) Sarg.), Western white pine (Pinus monticola Dougl.) and Grand fir (Abies grandis Lindl.). Marginal stream vegetation consists of Alder (Alnus sp.), Dogwood (Cornus sp.), Twin-berry (Lonicera sp.), False hellebore (Veratrum californicum Dur.) and Lady fern (Athyrium filixfoemina (L.) Roth.). The bottom types of the riffles are small and large cobble in depths of 6 to 18 inches; intervening pools range to three feet deep. Considerable deadfall is found in or spanning the river at the headwaters region. Stream velocities vary from 0.2 ft./sec. at the headwaters to 3.9 ft./sec. in the faster riffles (Fig. 2C-F).

### Middle St. Maries

This portion of the river occurs in a broad valley between the confluence of the Middle and West Forks near Clarkia and the slackwaters above the city of St. Maries. The size and character of this portion of the river changes markedly with the addition of waters from numerous tributaries. The adjoining slopes are covered primarily with Lodge-pole pine (Pinus contorta), Ponderosa pine (Pinus ponderosa Dougl.), Western white pine (Pinus monticola) and Subalpine fir (Abies lasiocarpa (Hook.) Nutt.). Marginal stream

vegetation consists of Alder (Alnus sp.), Willow (Salix sp.), Black cottonwood (Populus trichocarpa T. & G.), Horsetail (Equisetum sp.), Snowberry (Symphoricarpos sp.) and Stinging nettle (Urtica sp.). Riffle depths range from 6 to 36 inches with intervening pools up to 48 inches. Current velocities range from 0.5 ft./sec. in the slow-flowing pools to 3.7 ft./sec. in the faster riffles. The bottom types of the riffles are principally large cobble with increased abundance of boulders in the lower portions (Fig. 3G, H).

#### Lower St. Maries

This region is represented by slackwaters and extends from approximately six miles southwest of the city of St. Maries to the confluence of the St. Joe River. No riffles or turbulent waters occur in this section. The valley is quite broad with much marshy area adjacent to the river. The adjoining mountains are covered primarily with Lodge-pole pine (Pinus contorta), Ponderosa pine (Pinus ponderosa) and Western white pine (Pinus monticola). Marginal stream vegetation consists primarily of Alder (Alnus sp.), Black cottonwood (Populus trichocarpa) and several grasses. The bottom is of a silt-mud type with an abundance of decaying plant matter. Channel depths range from 9 to 12 feet.

Twenty-eight sampling stations were established along the St. Maries River and tributaries, four on the West Fork, 13 on the Middle Fork, 11 on the middle St. Maries and two on the lower St. Maries (Fig. 1). Station description and morphometrics are given on Table 4.



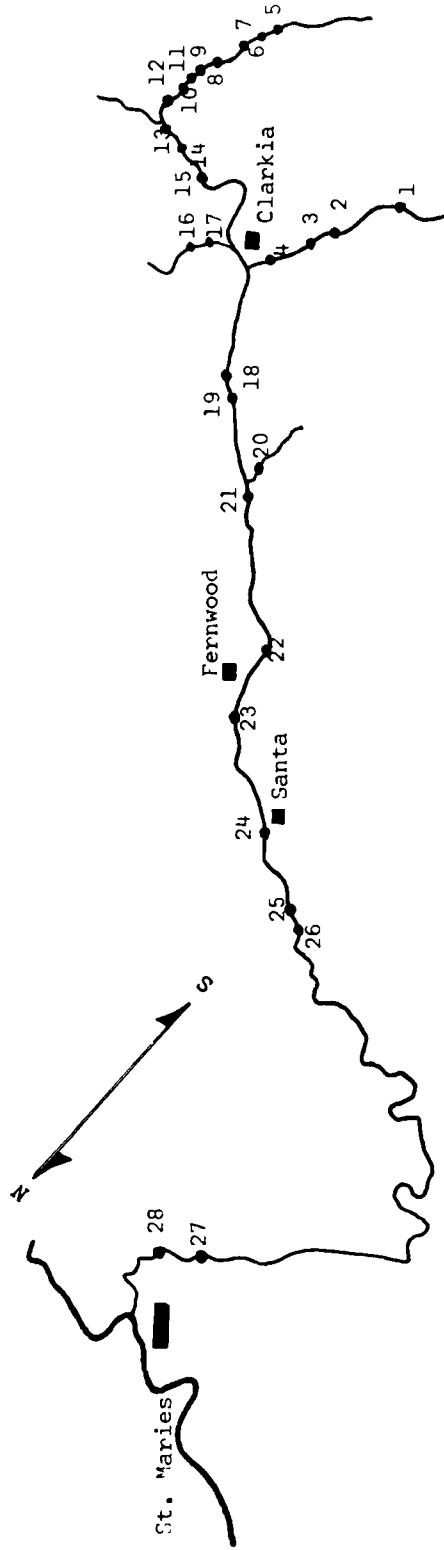


Figure 1. St. Maries River drainage with collecting stations identified by number.

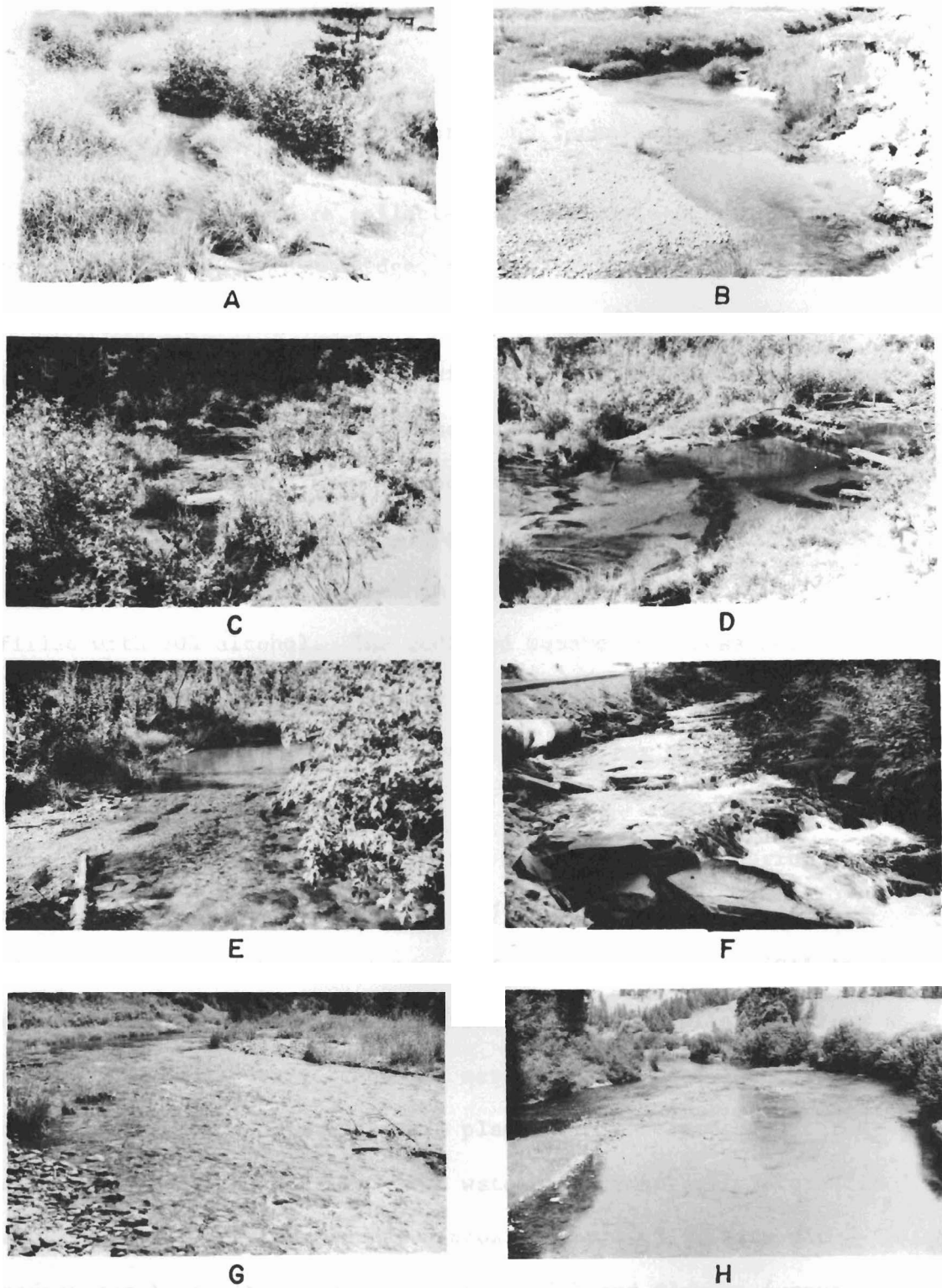


Figure 2. Stream habitats of the St. Maries River. A. Headwater pool, station 1; B. Slow riffle, station 4; C. Headwater riffle, station 7; D. Pool, station 5; E. Slow riffle, station 9; F. Moderate riffle, station 10; G. Fast riffle, station 18; H. Moderate riffle, station 24.

## B. Collecting Procedures and Techniques

Mayfly nymphs were collected using aquatic screens, hand nets, drift nets, Eckman dredge, modified Hess bottom sampler and by hand picking (Fig. 3B, D). Hand picking and the aquatic screen (26" x 36", 12 mesh copper screening with wood handles) were used most extensively for collecting mayflies in shallow riffles and pools. The screen was held in the current while upstream rocks were loosened and turned. Dislodged insects collecting on the screen were removed and stored in three-dram vials, partially filled with 70% alcohol. The modified square foot Hess bottom sampler was used for quantitative enumerations of mayfly populations. Where the river channel was too deep for screens and nets, a 6" x 6" Eckman dredge was used.

Algae were collected from the St. Maries River during the months of June, July and August, 1967 for the purpose of establishing a check list for subsequent food habits studies (Gilpin et al., in press). The free-floating algae were collected using a standard diatoms net; forceps and scraping were used for collecting the attached forms. Samples were placed in loosely capped three-dram vials, partially filled with water and temporarily stored in an illuminated refrigerator at approximately 5° C. Taxonomic references by Smith (1950), Prescott (1951) and Flowers (unpublished) served as the basis for identification of the algae.

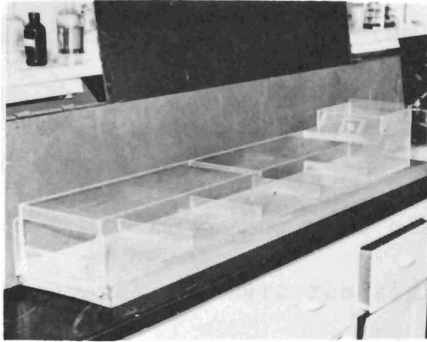
### C. Observational Methods

In order to study the microecology and behavior of mayfly nymphs in their natural environment, a triangular observation chamber, 20" on the sides by 10" deep with a Plexiglas bottom, was constructed (Fig. 3C). Steel stakes were inserted through the eye-lets at each corner to facilitate stationary emplacement. One corner of the chamber was pointed upstream to give greater stability against the current and to reduce turbulence. Rocks were lifted or moved beneath the chamber in order to expose nymphs and observe their responses. A diving mask and snorkel were also used to facilitate observation purposes.

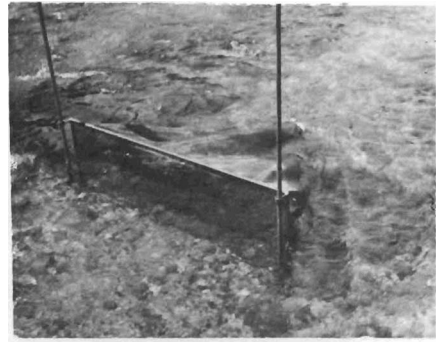
Laboratory observations were also made utilizing an artificial stream, 56" long, 8" wide, and 5" deep, made of 3/8" Plexiglas (Fig. 3A). A series of bottom types were established in divided sections of the artificial stream to simulate a variety of stream microhabitat conditions. Mayfly activities were observed from above and through the transparent sides of the stream.

### D. Stomach Analysis

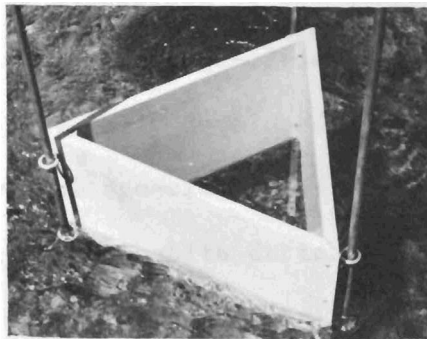
The food habits of mayfly nymphs were determined by stomach analysis. With the aid of a binocular microscope the digestive tract, principally the mid-gut, was removed (Fig. 3E, F). A temporary slide was made of the gut contents by teasing the material from the lumen, mixing it with a drop of water and covering with



A. Aquatic Stream



B. Modified Drift Net



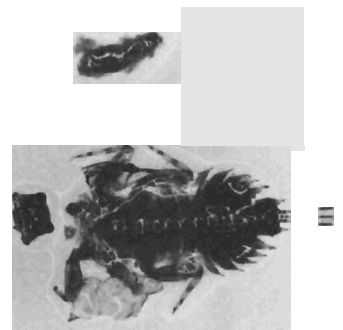
C. Observation Chamber



D. Modified Hess Sampler



E. Ephemerella hecuba



F. Ephemerella hecuba,  
dissected

Figure 3. Collecting apparatus and dissection techniques.

a cover glass. The ingested material was examined and identified with the aid of a compound microscope fitted with an ocular grid and a variable color-illuminator base.

Mayfly nymphs were classified into three age-classes; food habits analysis were restricted to the latter two age-classes because the small size made dissections of age-class one nymphs difficult. Age-classes were 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 two, and nymphs with wing pads fully or nearly fully developed as age-class three. Differentiation of nymphal age-classes provides an opportunity for study of comparative food habits during nymphal development.

Ingested material was divided into six general categories: 1) diatoms and desmids, 2) filamentous algae, 3) unidentifiable algae, 4) higher plants, 5) arthropods and 6) detritus. The latter refers to organic and inorganic debris. Algae were identified to genus and arthropods to order where possible. In the presentation of results, unidentified and identified algae, exclusive of diatoms and desmids, are expressed collectively as a common percentage.

In addition to qualitative analysis, a quantitative analysis of the ingested material was made. Quantitative innumeration of the stomach contents was evaluated on a relative percentage basis, with the total composition in each stomach representing 100%. The use of an ocular grid facilitated quantitative evaluation of the stomach contents.

Food habits data was recorded on Fortran coding forms and transferred to punched cards for machine processing.

#### E. Stream Measurements

The length and width of the stations were measured by "stepping off" the desired distances. Where river depths were too great distances were estimated. The relative dimensions of the stations were variable, each reflecting, as much as possible, a homogenous habitat.

Bottom type classification used in this study (Table 1) represents a modification of Wentworth's classification of sediments based on particle size (Welch, 1948). The description of the bottom types was determined visually. The category of sediments that best reflected the condition of the station was used. It is acknowledged that for any station several sediment categories are present but many are of minor importance.

A Midget Current Meter<sup>1</sup> was used to record current speed. Current readings were taken at three to six points, equally spaced, across each station several times during the summers of 1967 and 1968. Readings were taken approximately two inches below the surface of the water.

Stream temperatures were recorded using a standard

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<sup>1</sup>Leupold and Stevens Instruments, Inc., Portland, Ore.

Centigrade thermometer. Temperatures were taken from the main channel of the stream wherever possible.

Water chemistry was performed for total hardness, pH, dissolved oxygen and turbidity using a Hach field testing kit<sup>1</sup>. Water chemistry analyses were made in August, 1967 and April and June 1968.

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<sup>1</sup>Hach Chemical Co., Ames, Iowa.



Table 1. Modified Wentworth's sediment classification.

- 
- 
1. Bedrock: sedimented rock masses
  2. Boulder: 10" or larger (256 mm)
  3. Large Cobble: 5-10" (126-256 mm)
  4. Small Cobble: 2 1/2-5" (64-126 mm)
  5. Pebble: 1/4-2 1/2" (4-64 mm)
  6. Gravel: (1-4 mm)
  7. Sand: (0.062-1 mm)
  8. Silt: (0.004-0.062 mm)
  9. Clay: (less than 0.004 mm)
  10. Ooze: particulate organic material
-

## RESULTS

### A. Introduction

The food habits, ecology, behavior and distribution of 31 species of mayflies from the St. Maries River were studied; two of which represented species complexes. A check list of the species is given in Table 6 (see Appendix). Species determinations were not made for nymphs of Ameletus, Centroptilum and Cinygmula because the taxonomy has not been fully resolved. Jensen (1966) studied the mayflies of Idaho and prepared keys for adults and nymphs of most species. This reference was used as the basis for identification of mayflies in this study. Confirmation of questionable material was made by Jensen. The macro and microecology were studied with emphasis on physical factors as bottom type, current speed and siltation. Behavior in relation to the microenvironment was also studied.

### B. Food Habits and Ecology

The food habits and ecology of mayfly nymphs of the St. Maries River were studied. Food habits and ecological relationships are important in understanding the aquatic ecosystem. Information was obtained regarding food types and amounts ingested, food types ingested in relation to microhabitats and the multiplicity of physical factors that influence distribution and

behavior of mayfly nymphs.

Food habits are recorded for all mayfly nymphs except Rhithrogena solitaria, a species rarely collected (Table 2). Analysis of a minimum of ten specimens of a species was considered necessary to establish food habits trends. Food habits of the following species were determined (Table 2), but are not discussed in this section because of insufficient numbers: Epeorus grandis, Ephemerella coloradensis, Ephemerella edmundsi, Ephemerella hystrix, Ephemerella spinifera, Ephemerella teresa, Heptagenia solitaria, Paraleptophlebia debilis, Parameletus columbiae, Rhithrogena robusta, Siphonurus occidentalis and Tricorythodes minutus.

Genus Ameletus Eaton

#### Food Habits

Ameletus nymphs fed primarily on detritus and diatoms. Detritus represented 59.9%, diatoms and desmids 31.6%, filamentous algae 7.9% and higher plants 0.6% of the material ingested (Fig. 4A, Table 2). Nymphs occurring on or around rocks in slow waters along stream margins fed almost exclusively on diatom and detrital accumulations on rock surfaces. Ingested material ranged from 60-85% detritus for nymphs occurring in moderately silted pool and riffle habitats. Nymphs living in more silt-free habitats fed on a higher percentage of diatoms. Filamentous algae were consumed regularly, but in relatively small amounts. The relative

composition of the food ingested was similar for age-class two and three nymphs.

#### Ecology and Behavior

Nymphs of Ameletus were collected from 16 of the 28 stations on the St. Maries River (Table 3). Nymphs were usually found in moderately silted riffles and pools with bottom types varying from pebble to large cobble; occasionally they were found along stream margins among submerged vegetation. Ameletus was the only mayfly collected from both slackwater stations, 27 and 28. Here, they were observed clinging to submerged brush, logs and pilings in the river.

Ameletus are round-bodied nymphs commonly found in slow to moderate riffles and pools and orientating upstream on the tops and sides of rocks. Nymphs were also observed clinging to sand and small pebbles in shallow riffles. Occasionally nymphs were found orientating downstream on the bottoms of lightly sedimented rocks.

Ameletus nymphs are excellent swimmers, swimming with darting speed and maneuverability unexceeded by most of the mayflies in the study. Nymphs were observed swimming upstream with relative ease in currents less than 0.5 ft./sec.; horizontal movements were also observed. Quick dorsoventral flexions of the abdomen propelled the nymphs 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 displaced.

Age-class three 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

The nymphs of B. bicaudatus 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 (Fig. 4B, Table 2). The nymphs inhabit the tops and sides of rocks which are generally covered with diatoms and other algae. The nymph's maxilla is modified in the form of a brush which is used to sweep the detritus and diatoms from the substrate. Little food preference diversity was noted among the stations supporting B. bicaudatus. There were no significant differences in food preferences between age-class two and three nymphs.

Ecology and Behavior

Nymphs of B. bicaudatus were collected from 16 of the 28 stations on the St. Maries River (Table 3). Nymphs commonly occurred in relatively silt-free, moderate to fast cobble riffles. Largest populations occurred in relatively silt-free habitats, although some nymphs were taken in moderately silted riffles. B. bicaudatus nymphs were never collected near the sewage outlet at Santa; however, B. tricaudatus, a closely related species, occurred

there. The macrohabitat of B. bicaudatus was generally similar to that of B. tricaudatus nymphs. It was suggested by Dodds and Hisaw (1924) that B. bicaudatus, because of its linear body and streamlined shape, represented 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 individuals were observed on the bottom of shallowly imbedded rocks. When disturbed from the front, nymphs would detach and dart three to six inches 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 three nymphs occurred primarily from early June to mid-July in the St. Maries River. Jensen (1966) reported emergence from late June to early October.

#### Baetis parvus Dodds

##### Food Habits

Nymphs of B. parvus 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 (Fig. 4C, Table 2). As with several mayfly nymphs filamentous algae was not an important constituent in their diet. The relative composition of the ingested material was similar to that of Baetis tricaudatus. Food preference diversity of B. parvus,

among different habitats, was impossible to evaluate because this insect had limited distribution.

#### Ecology and Behavior

B. parvus was one of the more uncommon mayflies of the St. Maries River, being collected from only station 23, a silty cobble riffle (Table 3). Jensen (1966) indicated that the 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 three 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 of B. tricaudatus were primarily detritus-diatom feeders. Detritus represented 52.3%, diatoms and desmids 34.3%, filamentous algae 11% and higher plants 2.4% of the material ingested (Fig. 4D, Table 2). Nymphs were found primarily on the tops and sides of small and large rocks in well aerated riffles, feeding on detritus and diatoms collecting or growing in the porosities of the rocks. Little food preference diversity was found among the stations supporting B. tricaudatus. 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. Age-class two nymphs had a slightly higher composition of diatoms than did age-class three nymphs; 37% and 33% of the materials ingested were diatoms respectively. Qualitatively the food ingested was similar for both age-classes.

#### Ecology and Behavior

B. tricaudatus nymphs were widely distributed in the St. Maries River, being found in 24 of the 28 stations (Table 3). They occurred in a variety of well aerated habitats. Bottom types ranged from small cobble to boulder, often with light to moderate accumulations of silt. Exclusion from four 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 9-12 feet and where the bottom was principally silt and mud with considerable organic accumulations. These two stations supported a very low mayfly 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 orientated in an upstream direction either on the sides or more commonly on tops of rocks. Occasionally, nymphs were found on the downstream side of rocks in the microeddies. In addition to center channel distribution, nymphs were sometimes collected near the margins of the stream where silt and debris accumulated. A few nymphs were observed crawling over gravel and pebbles in the slower riffles; movement was generally upstream. 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 and bracing themselves against the current with wide-spread legs. The abdomen was observed to swing freely with the turbulence of the current. If disturbed from the front, B. tricaudatus would dart backwards, tail first, catching hold on rocks several inches downstream from its 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. He reported that at lower elevations they emerge during all seasons.

Genus Centroptilum Eaton

Food Habits

Only 13 specimens of Centroptilum were analyzed for food habits. All the nymphs examined were taken from station 16, a backwater pool on Merry Creek which supported a moderate population. Only a few specimens were collected from other stations. The material ingested consisted of detritus 58.1%, diatoms and desmids 30%, filamentous algae 10.1% and higher plants 1.8% (Fig. 4E, Table 2).

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 two and three nymphs.

Ecology and Behavior

Centroptilum was an uncommon mayfly, found in only four of the 28 stations on the St. Maries River (Table 3). Of the four stations, station 16, a backwater pool, was the only station where the nymphs were collected more than once during the study. Nymphs of Centroptilum occurring here were observed clinging to dense mats of Spirogyra and Oscillatoria filaments. This was a lentic habitat with a mud bottom and having a rich growth of algae. A few specimens were found living on the bottom of large porous lava boulders at station 25; no regular orientation pattern was discernable in relation to the current.

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

Genus Cinygmula McDunnough

#### Food Habits

Nymphs of Cinygmula 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 (Fig. 4F, Table 2).

Some food preference diversity was noted among the stations supporting Cinygmula. Nymphs occurring in stations with a more silt-free bottom generally fed on a greater percentage of filamentous algae and diatoms. In stations 8 and 15, nymphs fed on 5-10% filamentous algae as Oscillatoria, Ulothrix and Chaetophora. The relative composition of the material ingested varied with the microhabitat of the nymphs. Stations as 4, 10 and 18 supported nymphs feeding on as much as 75% detritus; the percentage of detritus ingested in stations 8 and 15 averaged 54%. The relative composition of the food ingested was approximately the same for nymphs of age-class two and three.

#### Ecology and Behavior

Cinygmula was one of the most abundant and wide-spread mayflies in the St. Maries River, occurring in all but four of the 28 stations (Table 3). Nymphs showed a wide range of adaptability

occurring in slow gravel riffles to fast riffles with boulder or cobble bottoms and often moderately silted. Largest populations occurred in moderate to fast, cobble riffles. The absence of Cinygmula was expected from stations 16, 27 and 28 because of the mud and silt bottoms and a general lack of coarse sediments and rocks. The bottom type of station 25 was principally lava boulders containing numerous porosities; nymphs of Cinygmula were most abundant and commonly found on smooth surfaced rocks.

Cinygmula is a medium sized nymph adapted for quick maneuverability over rocks and debris. Nymphs were typically found clinging to the tops and sides of rocks and orientating upstream; occasionally they were found crawling in clumps of Fontinalis. Several nymphs were observed orientating downstream on the bottoms of lightly silted rocks.

Age-class three nymphs occurred abundantly from early March to mid-July in the St. Maries River. Jensen (1966) reported that several species may occur in the state, with variable emergence times.

#### 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 (Fig. 4G, Table 2). Filamentous algae were

an important constituent in the diet of this species. The nymphs were usually found clinging to the tops and sides of silt and detrital covered rocks which often had a growth of filamentous algae. Age-class two and three 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 3). The species occurred primarily on the West Fork and the middle St. Maries. It is significant to note that E. albertae was generally absent or occurred in sparse numbers on the Middle Fork, even though several of the stations were superficially similar to those of the West Fork and middle St. Maries. Water temperatures averaged 4-5° cooler on the Middle Fork which may, in part, explain its absence. E. longimanus, a closely related species, was found abundantly throughout the river while E. albertae was generally restricted to the warmer regions. Nymphs of E. longimanus and E. albertae were often found occupying similar microhabitats on the West Fork and the middle St. Maries River.

Nymphs of E. albertae usually inhabited the slower currents along the margins of the stream. They often occurred on the tops and sides of rocks and orientated perpendicularly to the current. In faster riffles, as in station 10, nymphs were commonly found on the bottoms of rocks and orientated in a downstream direction. In the pools of 2.5 to 3 feet deep, nymphs were generally observed on the tops of rocks and were variously

orientated to the current.

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

#### Epeorus (Iron) longimanus (Eaton)

##### Food Habits

Nymphs of E. longimanus fed primarily on detritus and diatoms. Detritus represented 61.1%, diatoms and desmids 31.4%, filamentous algae 6.8% and higher plants 0.7% of the material ingested (Fig. 4H, Table 2). 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 three nymphs fed on approximately 10% more detritus than nymphs of age-class two.

##### Ecology and Behavior

E. longimanus represented one of the more widely distributed mayfly species, being found in 22 of the 28 stations on the St. Maries River (Table 3). It is well adapted to a variety of habitats ranging from fast-cobble riffles to moderate-flowing, rocky pools. According to Edmunds (1957), E. longimanus is found in moderately fast streams at elevations between 5,000 and 10,000 feet. All E. longimanus nymphs collected from the St. Maries River were at elevations below 5,000 feet. Habitats least preferred by E. longimanus were slow pebble riffles, backwater pools

and deep slackwaters. Also, E. longimanus was never collected near the sewage effluent at Santa, Idaho.

E. longimanus was one of the more agile nymphs collected. It was typically found orientating upstream on tops of rocks and downstream on the bottoms of rocks. Upstream orientation on tops of rocks probably aided foraging on diatoms and detrital material deposited over the rocks. When the rocks were rotated, E. longimanus also rotated, maintaining its upstream direction. On the underside of rocks, largest numbers were noted near the downstream side where larger detrital accumulations were deposited in microeddies. This perhaps provided a more readily available source of food. When disturbed, nymphs of E. longimanus would retreat to other rocks and seek seclusion.

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

#### Epeorus (Ironopsis) grandis (McDunnough)

##### Food Habits

Food habits were not summarized for E. grandis because of insufficient material.

##### Ecology and Behavior

E. grandis was an uncommon mayfly occurring in only four of the 28 stations on the St. Maries River, all of which were located on the lower half of the Middle Fork (Table 3). Cold, fast-flowing

riffles with bottom types of large and small cobble were the principal habitats.

Most of the nymphs collected were on the bottom of rocks; a few were observed clinging to the sides of rocks and in close proximity to algae filaments. No particular orientation pattern was noted in respect to stream currents.

Age-class three 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

##### Food Habits

Food habits were not summarized for E. coloradensis because of insufficient material.

##### Ecology and Behavior

E. coloradensis nymphs were collected from ten of the 28 stations on the St. Maries River, nine of which occurred on the Middle Fork (Table 3). 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. They were observed orientating upstream on the tops and sides of rocks in moderate flowing riffles and often on the underside of rocks in faster waters; their orientation was primarily upstream. They responded slowly and sluggishly when disturbed. Their dark coloration makes them difficult to see when



living on darker rocks and may serve as a protective adaptation from predators.

Age-class three nymphs occurred primarily from early July to mid-August in the St. Maries River. Emergence was reported by Allen and Edmunds (1962) as late as September and early October.

Ephemerella (Drunella) doddsi Needham

Food Habits

Nymphs of E. doddsi fed primarily on detritus and filamentous algae. Detritus represented 45.2% of the material ingested, diatoms and plants 1.0% (Fig. 4I, Table 2). Filamentous algae was an important constituent in the diet of this species. This may be accounted for in part, by the fact that the nymphs generally inhabited well aerated riffles having moderate growths of algae. Because the nymphs generally demonstrated a low tolerance to bright light, it is surmised that they fed on algae covered rocks after emerging from seclusion during the shaded or dark hours of the day. 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 two and three nymphs fed on approximately the same relative composition of food.

Ecology and Behavior

Nymphs of E. doddsi 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 3). Largest populations occurred in moderate to fast-flowing, silt-free riffles. Riffle bottom types were generally of small and large cobble, but occasionally pebble and gravel.

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

Age-class three 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

##### Food Habits

Food habits were not summarized for E. edmundsi because of insufficient material.

##### Ecology and Behavior

E. edmundsi nymphs were collected from four of the 28 stations on the St. Maries River, all of which were adjacent to one another and located in the upper Middle Fork (Table 3). Nymphs

were generally found in pebble and cobble riffles of slow to moderate currents and having an abundant growth of moss and algae. Fontinalis, a coarse moss, and Prasiola, a sheet-like alga afforded excellent habitats for E. edmundsi nymphs. Most of the nymphs were observed living on Fontinalis and/or Prasiola and orientating upstream. A few nymphs were observed feeding on Prasiola. Occasionally, E. edmundsi nymphs were found on the tops and sides of rocks.

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

#### Ephemerella (Drunella) flavilinea McDunnough

##### Food Habits

The nymphs of E. flavilinea 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 (Fig. 4J, Table 2). Filamentous algae were an important constituent in the diet of this species. In stations 19, 20 and 23, 4-9% of their diet was other mayflies. The relative composition of the food ingested was approximately the same for age-class two and three nymphs; slight changes in composition were noted among different stations, however.

##### Ecology and Behavior

E. flavilinea was a widely distributed species occurring in

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. No specimens were collected near the Santa sewage effluent, station 26, or the two slackwater stations, 27 and 28 (Table 3).

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 sections of the river while E. coloradensis frequented the colder Middle Fork. E. flavilinea was most commonly found in moderate to fast riffles with bottom types of small and large cobble. Nymphs were usually observed orientating upstream on the tops and sides of rocks. Occasionally E. flavilinea nymphs were found on the bottoms of small cobble rocks and usually orientated downstream.

Age-class three 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 of E. grandis 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 (Fig. 4K, Table 2). Arthropods were occasionally ingested; it is believed that this was not the result

of predatory tendencies. Little food preference diversity was found among the stations supporting the species. Age-class two and three nymphs fed on approximately the same relative composition of food.

#### Ecology and Behavior

E. grandis was a widely distributed species occurring in 23 of the 28 stations on the St. Maries River. The only habitats not frequented by this species were the pools of stations 3 and 16, the sewage effluent of station 26 and the slackwaters (Table 3). E. grandis nymphs generally showed affinities for habitats containing protective cover as dead-fall, organic debris, Fontinalis clumps and/or moderate to heavy algal growths. Many of the nymphs were observed living in Fontinalis clumps or clinging to filaments of algae and other submerged vegetation. A few nymphs were observed clinging to the tops or sides of rocks; occasionally they were found on the underside of rocks and logs. The comparatively large nymphs of E. grandis were slow and methodical in their movements. They have an exceptional ability to conceal themselves in stream debris and vegetation. The dark coloration and dorsal spination of this nymph is an important morphological adaptation providing excellent protective camouflage.

Age-class three 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 of E. hecuba 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% (Fig. 4L, Table 2). 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 and Paraleptophlebia which occupied similar microhabitats. Little food preference diversity was found among the stations supporting the nymphs. Age-class two and three 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 3). The nymphs typically inhabited the underside of rocks in moderate to lightly silted riffles and pools; occasionally nymphs were observed clinging to the tops of rocks. Orientation was irregular in both cases. 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 sort of defensive mechanism rather than retreating. If the nymph dislodges from its substrate, it drifts downstream while flexing its

abdomen regularly. Downstream displacement is usually several feet from its original position.

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

Ephemerella (Caudatella) hystrix Traver

Food Habits

Food habits were not summarized for E. hystrix because of insufficient material.

Ecology and Behavior

E. hystrix was a relatively uncommon mayfly occurring in eight of the 28 stations on the St. Maries River, all of which were located on the Middle Fork (Table 3). Nymphs were usually found in moderate to fast riffles clinging to submerged vegetation of Prasiola and Fontinalis. The vegetative microenvironments of the nymphs afforded good concealment from predators. Occasionally nymphs were observed clinging on the downstream sides of large cobble or crawling slowly among the finer sediments of the stream bottom. Orientation to the stream current was usually irregular.

Age-class three 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<sup>1</sup>

Food Habits

E. inermis and E. infrequens 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% (Fig. 4M, Table 2). Filamentous algae was an important constituent in the diet of these species. Food preference diversity was variable among the stations. Filamentous algae was moderately consumed in most riffle habitats; higher plants and arthropods were frequently ingested in the pool stations. Age-class two and three nymphs fed on approximately the same relative composition of food.

Ecology and Behavior

E. inermis and E. infrequens nymphs occurred in 25 of the 28 stations on the St. Maries River. The nymphs were found in a wide variety of habitats ranging from heavily silted pools to fast flowing, boulder riffles (Table 3). Nymphs were commonly observed living on the tops and sides of submerged logs and rocks in slow to moderate riffles; riffle habitats supported the largest populations. Occasionally nymphs were found clinging to Fontinalis

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<sup>1</sup>E. inermis and E. infrequens are considered together in this study because of the inability to satisfactorily separate the nymphs taxonomically. Jensen (1966) indicated both species may occur in the same habitats.



clumps or other submerged vegetation. Orientation of the nymphs to the current was generally irregular.

Age-class two and three 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.

Ephemerella (Attenuatella) margarita Needham

Food Habits

E. margarita 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% (Fig. 4N, Table 2). Filamentous algae were utilized to a much greater extent by E. margarita nymphs than by many of the species studied. On several occasions nymphs were observed feeding on the stubble-like algae growing on surfaces of rocks. Feeding was done with the mandibles and maxillae while the head was moved with a forward to back motion. Little food preference diversity was found among the stations supporting the nymphs. Age-class two and three nymphs fed on about the same relative composition of food.

Ecology and Behavior

Nymphs of E. margarita occurred in nine of the 28 stations on the St. Maries River, six of which were located on the middle St. Maries (Table 3). Nymphs usually occurred along the margins of slow, moderately silted, cobble riffles and in close proximity to

algae or other submerged vegetation. Occasionally, they were found in shallow pools on the bottom of silted rocks. Their orientation was generally upstream on tops of rocks. If disturbed, the nymphs would quickly dislodge and drift several inches downstream before reattaching to a suitable substrate.

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

#### Ephemerella (Drunella) spinifera Needham

##### Food Habits

Food habits were not summarized for E. spinifera because of insufficient material.

##### Ecology and Behavior

E. spinifera was a relatively uncommon mayfly occurring in nine of the 28 stations on the St. Maries River, most of which were located on the Middle Fork (Table 3). Nymphs usually occurred along the stream margins of moderate to fast cobble riffles. Nymphs were commonly observed clinging to submerged vegetation as Fontinalis, but occasionally were found under large rocks. Orientation in relation to stream current was generally irregular.

E. spinifera is a spiny nymph, blending well with its microenvironment. The dorsal spination of the nymph provides an excellent surface for the accumulation of silt and algae which makes it less conspicuous to predators and makes it appear as part

of the substrate.

Age-class three 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

Food Habits

Food habits were not summarized for E. teresa because of insufficient material.

Ecology and Behavior

E. teresa was an uncommon mayfly occurring in only five of the 28 stations on the St. Maries River, most of which were located on the middle St. Maries (Table 3). Nymphs usually occurred in moderate flowing, light to moderately silted cobble riffles; occasionally nymphs were found in faster riffles. E. teresa nymphs generally inhabited the central channel of moderate flowing riffles and the margins of faster riffles. Nymphs were commonly observed clinging to the tops and sides of rocks; orientation to the stream current was usually upstream.

Age-class two and three 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 is unknown.

Ephemerella (Serratella) tibialis (McDunnough)

Food Habits

E. tibialis 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 (Fig. 40, Table 2). Filamentous algae was an important constituent in the diet of this species. Food preference diversity varied among the stations supporting E. tibialis nymphs. Nymphs from different habitats were generally quite versatile in their feeding habits, utilizing a variety of filamentous algae and varied amounts of detritus and diatoms. Nymphs generally fed on filamentous algae to a higher degree in stations supporting an abundance of it. Age-class two and three 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 the 28 stations on the St. Maries River. It was not recorded for stations 16, 27 and 28 (Table 3). Its near universal occurrence would indicate a wide range of adaptability. Slow to moderate flowing, cobble riffles with little or no siltation supported largest populations. Jensen (1966) reported this species occurring in most moderately flowing streams and at all elevations in Idaho.

E. tibialis were commonly found clinging to the tops and sides of rocks with upstream orientation. Several nymphs were

found on the undersides of rocks. Occasionally nymphs were observed clinging or crawling among Prasiola and Fontinalis; foraging probably took place on the plants' surfaces. When positioned on the downstream side of rocks, nymphs were observed performing a "pumping" action, moving their body up and down in push-up fashion, an activity which probably increased the water flow around the gills.

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

#### Heptagenia criddlei McDunnough

##### Food Habits

H. criddlei 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 (Fig. 4P, Table 2). In habitats having heavy algal growths as in stations 3, 22, 23 and 25, greater amounts of filamentous algae were ingested. Habitats having less filamentous algae and more detritus supported nymphs feeding more extensively on the latter. Age-class two and three nymphs fed on approximately the same relative composition of food.

##### Ecology and Behavior

H. criddlei nymphs occurred in 12 of the 28 stations on the St. Maries River, eight of which were located on the middle St.

Maries (Table 3). Nymphs were usually found in moderately flowing, cobble riffles with light to moderate siltation. Nymphs of H. criddlei were generally observed on the tops and downstream sides of rocks; their orientation was generally irregular. Extensive growths of algae were usually present on the inhabited rocks. A few nymphs were found on the underside of rocks in moderately silted pools with cobble bottoms.

H. criddlei are dorsoventrally flattened nymphs which have unique mobility in slow currents. Nymphs were capable of swimming from rock to rock using a gliding motion; up and down flexions of the abdomen and forward to back movements of the legs help propel the nymphs.

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

#### Heptagenia solitaria McDunnough

##### Food Habits

Food habits were not summarized for H. solitaria because of insufficient material.

##### Ecology and Behavior

H. solitaria was an uncommon mayfly, occurring in only two of the 28 stations on the St. Maries River, stations 19 and 22 (Table 3). The principal habitat of the nymphs was moderately silted, cobble pools or runs. The nymphs were usually found in the

center channel of the pools, but occasionally along the margins. Most of the nymphs inhabited the underside of moderately silted cobble; less frequently, nymphs were observed clinging to the tops of rocks. Orientation of the nymphs in relation to the stream current was generally irregular. Relatively few microecological and behavioral observations were made because of limited distribution and low populations.

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

#### Paraleptophlebia bicornuta (McDunnough)

##### Food Habits

P. bicornuta 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% (Fig. 4Q, Table 2). Large amounts of silt, numerous diatoms and detritus were generally present in their microhabitat. Filamentous algae were not an important constituent in the diet of this species. Little feeding diversity was found among the stations supporting the nymphs. Relative composition of the food ingested was approximately the same for age-class two and three nymphs.

##### Ecology and Behavior

P. bicornuta nymphs occurred in five of the 28 stations on the St. Maries River (Table 3). Nymphs were usually found in

warmer, slow-flowing cobble riffles with moderate to heavy siltation. Largest populations occurred at station 26 which was heavily polluted with sewage effluent.

P. bicornuta was generally found on the bottoms of large cobble rocks partially covered with biodepositional accumulations. Orientation was generally irregular in relation to stream currents. Nymphs showed moderate agility when disturbed but usually confined their movements to a single rock.

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

#### Paraleptophlebia debilis (Walker)

##### Food Habits

Food habits were not summarized for P. debilis because of insufficient material.

##### Ecology and Behavior

P. debilis was an uncommon mayfly, occurring in five of the 28 stations on the St. Maries River, three of which were located on the middle St. Maries (Table 3). The nymphs occurred primarily in warmer, moderate flowing cobble riffles with moderate to heavy siltation. Nymphs of P. debilis were usually found on the underside of rocks, but occasionally on the tops and sides of rocks.

P. debilis nymphs were occasionally observed inhabiting the same microhabitat as P. bicornuta. Both species appeared to have



similar physical requirements; neither species was collected from the Middle Fork.

Age-class three 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)<sup>1</sup>

#### Food Habits

P. heteronea and P. memorialis 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 (Fig. 4R, Table 2). In stations with dead-fall or with abundant over-hanging vegetation, nymphs fed on greater amounts of higher plants. Age-class two and three nymphs fed on approximately the same relative composition of food.

#### Ecology and Behavior

P. heteronea and P. memorialis nymphs occurred in 13 of the 28 stations on the St. Maries River (Table 3). Nymphs were usually found in slow to moderate flowing cobble riffles with moderate siltation. Nymphs of P. heteronea and P. memorialis were generally observed clinging to the tops and sides of rocks; orientation to the stream current was usually upstream.

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<sup>1</sup>P. heteronea and P. memorialis are considered together in this study because of the inability to satisfactorily separate the nymphs taxonomically.

Age-class three 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

#### Food Habits

Food habits were not summarized for P. columbiae because of insufficient material.

#### Ecology and Behavior

P. columbiae was an uncommon mayfly, occurring in five of the 28 stations on the St. Maries River; one of which was located in the slackwaters (Table 3). 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 orientating upstream. Nymphs found in the slackwater areas were clinging to submerged brush, logs and pilings in the river and were found in coexistence with Ameletus nymphs, however, the latter were more abundant.

Like Ameletus, P. columbiae are round-bodied nymphs, but exhibited less mobility and maneuverability than Ameletus nymphs.

Age-class three nymphs of P. columbiae occurred primarily from early June to mid-July in the St. Maries River. Nymphs were collected only during early March in the slackwaters. Edmunds (1957), as reported by Jensen (1966), indicated nymphal life is completed within 16 to 22 days or less. Female imago deposit the

eggs during mid-June; hatching occurs shortly after the snow melts the following May.

Rhithrogena hageni Eaton

Food Habits

R. hageni 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% (Fig. 4S, Table 2). 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 two and three nymphs.

Ecology and Behavior

R. hageni was a widely distributed mayfly, occurring in 17 of the 28 stations on the St. Maries River (Table 3). Nymphs occurred primarily in slow to moderate-flowing, lightly-silted, cobble riffles and occasionally in shallow pools. Nymphs of R. hageni were generally found clinging to the undersides of rocks.

Age-class three 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

Food Habits

Food habits were not summarized for R. robusta because of insufficient material.

### Ecology and Behavior

R. robusta was a relatively uncommon mayfly, occurring in seven of the 28 stations on the St. Maries River, five of which were located on the Middle Fork (Table 3). The nymphs occurred primarily in relatively silt-free moderate to fast cobble riffles. The population of R. robusta was consistently low in all habitats. R. robusta nymphs were usually found on the bottoms of rocks in the faster currents of the river. Occasionally, nymphs were observed on the tops and sides of rocks orientated upstream.

Age-class three nymphs occurred primarily from early March to early June in the St. Maries River. Jensen (1966) reported that little is known about the biology of the adults.

### Siphonurus occidentalis Eaton

#### Food Habits

Food habits were not summarized for S. occidentalis because of insufficient material.

### Ecology and Behavior

S. occidentalis was one of the most uncommon mayflies, occurring only in station 21, a slow-flowing cobble riffle (Table 3). A few late instar nymphs were collected from an overflow pool adjacent to station 25 during early June. Nymphs were generally observed clinging to Fontinalis along the stream margins. Occasionally nymphs were observed clinging to the tops of moderate to heavily silted rocks. Edmunds (1960) reported fresh water

lakes, pools and slow moving, silted streams as habitats of S. occidentalis.

Age-class three 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

##### Food Habits

Food habits were not summarized for T. minutus because of insufficient material.

##### Ecology and Behavior

T. minutus was an uncommon mayfly, occurring in only three of the 28 stations on the St. Maries River (Table 3). Station 4, a slow flowing cobble riffle, supported the largest population. Nymphs of T. minutus were generally found clinging to the tops and sides of rocks, occasionally to submerged vegetation along stream margins. Because of their small size and limited distribution, few behavioral observations were made.

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

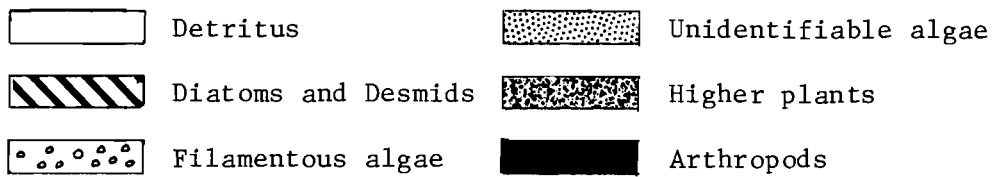
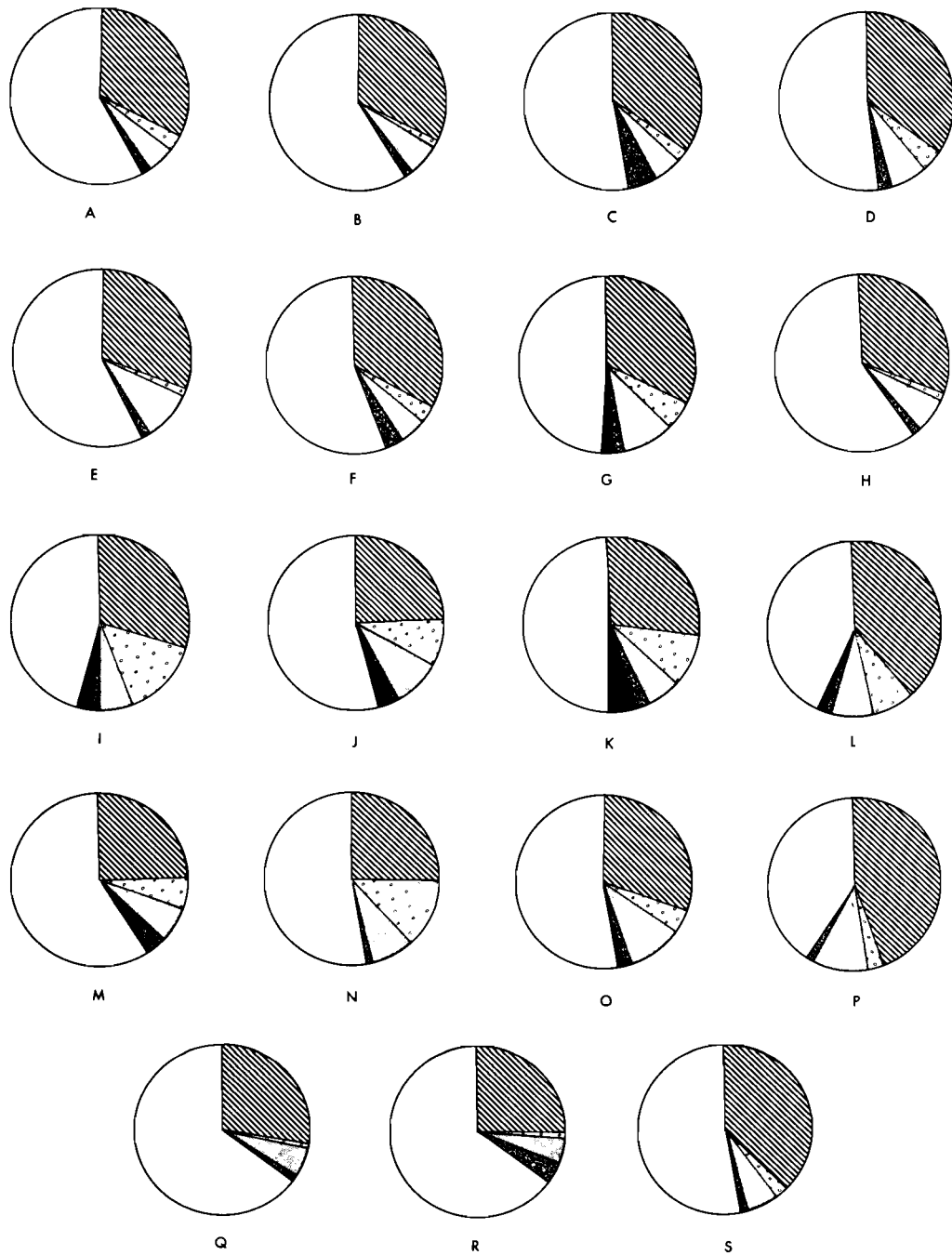
Explanation of Figure 4.

- A. Ameletus sp.  
Detritus: 59.9%  
Diatoms and Desmids: 31.6%  
Filamentous algae: 3.6%  
Unidentifiable algae: 4.3%  
Higher plants: 0.6%
- B. Baetis bicaudatus  
Detritus: 57.4%  
Diatoms and Desmids: 34.2%  
Filamentous algae: 0.8%  
Unidentifiable algae: 5.8%  
Higher plants: 1.8%
- C. Baetis parvus  
Detritus: 53.4%  
Diatoms and Desmids: 33.9%  
Filamentous algae: 2.2%  
Unidentifiable algae: 5.2%  
Higher plants: 5.3%
- D. Baetis tricaudatus  
Detritus: 52.3%  
Diatoms and Desmids: 34.3%  
Filamentous algae: 4.2%  
Unidentifiable algae: 6.8%  
Higher plants: 2.4%
- E. Centroptilum sp.  
Detritus: 58.1%  
Diatoms and Desmids: 30.0%  
Filamentous algae: 1.3%  
Unidentifiable algae: 8.8%  
Higher plants: 1.8%
- F. Cinygmula sp.  
Detritus: 57.0%  
Diatoms and Desmids: 32.9%  
Filamentous algae: 2.7%  
Unidentifiable algae: 4.7%  
Higher plants: 2.7%
- G. Epeorus albertae  
Detritus: 52.7%  
Diatoms and Desmids: 31.9%  
Filamentous algae: 5.3%  
Unidentifiable algae: 8.9%  
Higher plants: 0.6%  
Arthropods: 0.6%
- H. Epeorus longimanus  
Detritus: 61.1%  
Diatoms and Desmids: 31.4%  
Filamentous algae: 0.8%  
Unidentifiable algae: 6.0%  
Higher plants: 0.7%
- I. Ephemerella doddsi  
Detritus: 45.2%  
Diatoms and Desmids: 29.8%  
Filamentous algae: 15.2%  
Unidentifiable algae: 6.6%  
Higher plants: 1.0%  
Arthropods: 2.2%
- J. Ephemerella flavilinea  
Detritus: 56.3%  
Diatoms and Desmids: 24.4%  
Filamentous algae: 8.6%  
Unidentifiable algae: 8.2%  
Higher plants: 0.3%  
Arthropods: 2.2%
- K. Ephemerella grandis  
Detritus: 50.3%  
Diatoms and Desmids: 27.4%  
Filamentous algae: 8.9%  
Unidentifiable algae: 6.3%  
Higher plants: 2.3%  
Arthropods: 4.8%

Explanation of Figure 4. (Continued)

- L. Ephemerella hecuba  
Detritus: 44.1%  
Diatoms and Desmids: 38.9%  
Filamentous algae: 7.9%  
Unidentifiable algae: 7.9%  
Higher plants: 0.6%  
Arthropods: 0.6%
- M. Ephemerella inermis  
and E. infrequens  
Detritus: 60.1%  
Diatoms and Desmids: 24.5%  
Filamentous algae: 5.5%  
Unidentifiable algae: 6.7%  
Higher plants: 2.6%  
Arthropods: 0.6%
- N. Ephemerella margarita  
Detritus: 54.5%  
Diatoms and Desmids: 25.0%  
Filamentous algae: 12.5%  
Unidentifiable algae: 7.7%  
Higher plants: 0.3%
- O. Ephemerella tibialis  
Detritus: 54.7%  
Diatoms and Desmids: 29.1%  
Filamentous algae: 4.0%  
Unidentifiable algae: 10.0%  
Higher plants: 1.5%  
Arthropods: 0.7%
- P. Heptagenia criddlei  
Detritus: 44.5%  
Diatoms and Desmids: 42.4%  
Filamentous algae: 2.6%  
Unidentifiable algae: 10.3%  
Higher plants: 0.2%
- Q. Paraleptophlebia bicornuta  
Detritus: 66.3%  
Diatoms and Desmids: 27.4%  
Filamentous algae: 0.2%  
Unidentifiable algae: 5.7%  
Higher plants: 0.4%
- R. Paraleptophlebia heteronea  
and P. memorialis  
Detritus: 65.4%  
Diatoms and Desmids: 25.2%  
Filamentous algae: 0.5%  
Unidentifiable algae: 4.8%  
Higher plants: 4.1%
- S. Rhithrogena hageni  
Detritus: 54.5%  
Diatoms and Desmids: 37.5%  
Filamentous algae: 1.8%  
Unidentifiable algae: 6.0%  
Higher plants: 0.2%

Figure 4. Food composition of principal mayfly nymphs of the St. Maries River.







### C. Mayfly Distribution

Table 3 reflects in a composite manner a check list of mayfly species, their distribution and substrate relationships for the 28 stations on the St. Maries River. Some species had a wide distribution, being found in a variety of habitats, while others were more restrictive and found in only a few habitats. Table 3 also reflects the heterogeneity of the mayfly population for the different stations.

### D. Station Morphometrics

In order to relate the physical features of the stream with the distribution, microecology and behavior of mayfly nymphs, a morphometric analysis was made of the 28 stations (Table 4). The stations were analyzed for size, stream character (i.e. pool, riffle, etc.), bottom type, stream depth and current speed. The stream measurements represent average conditions for the months of May through August 1967 and 1968.

### E. Dendrogram

Sneath's method of clustering by single linkage, as outlined by Sokal and Sneath (1963) for establishing taxonomic relationships, was used in designing the dendrogram. Analogous methods and variations of this method have been used by plant ecologists

Table 3. Distribution of mayflies in relation to stations, bottom type and siltation.

Mayfly SP.	STATIONS																															
	Peb-Grav/0	Sm-Cob/1	Silt-Grav/2	Sm-Cob/1	Ooze	Sm-Cob/1	Sm-Cob/0	Peb-Grav/1	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Grav/1	Bldr/0	Sm-Cob/0	Sm-Cob/0	Ooze	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0	Sm-Cob/0			
Ameletus sp.	X																															
Baetis bicaudatus																																
Baetis parvus																																
Baetis tricaudatus																																
Centroptilum sp.																																
Cinygmula sp.																																
Epeorus albertae																																
Epeorus grandis																																
Epeorus longimanus																																
Ephemerella coloradensis																																
Ephemerella doddsi																																
Ephemerella edmundsi																																
Ephemerella flavilinea																																
Ephemerella grandis																																
Ephemerella hecuba																																
Ephemerella hystrix																																
Ephemerella inermis and E. infrequens																																
Ephemerella margarita																																
Ephemerella spinifera																																
Ephemerella teresa																																
Ephemerella tibialis																																
Heptagenia criddlei																																
Heptagenia solitaria																																
Paraleptophlebia bicornuta																																
Paraleptophlebia debilis																																
Paraleptophlebia heteronea and P. memorialis																																
Parameletus columbieae																																
Rhithrogena hageni																																
Rhithrogena robusta																																
Siphonurus occidentalis																																
Tricorythodes minutus																																

Bottom Type-Siltation Classification

- 0 - Little or no siltation
  - 1 - Lightly silted
  - 2 - Moderately silted
  - 3 - Heavily silted
- Bldr = Boulder
  - Cob = Cobble
  - Grav = Gravel
  - Ig = Large
  - Peb = Pebble
  - Silt = Silt
  - Sm = Small

Figure 5. Dendrogram of mayfly-algae-station relationships.

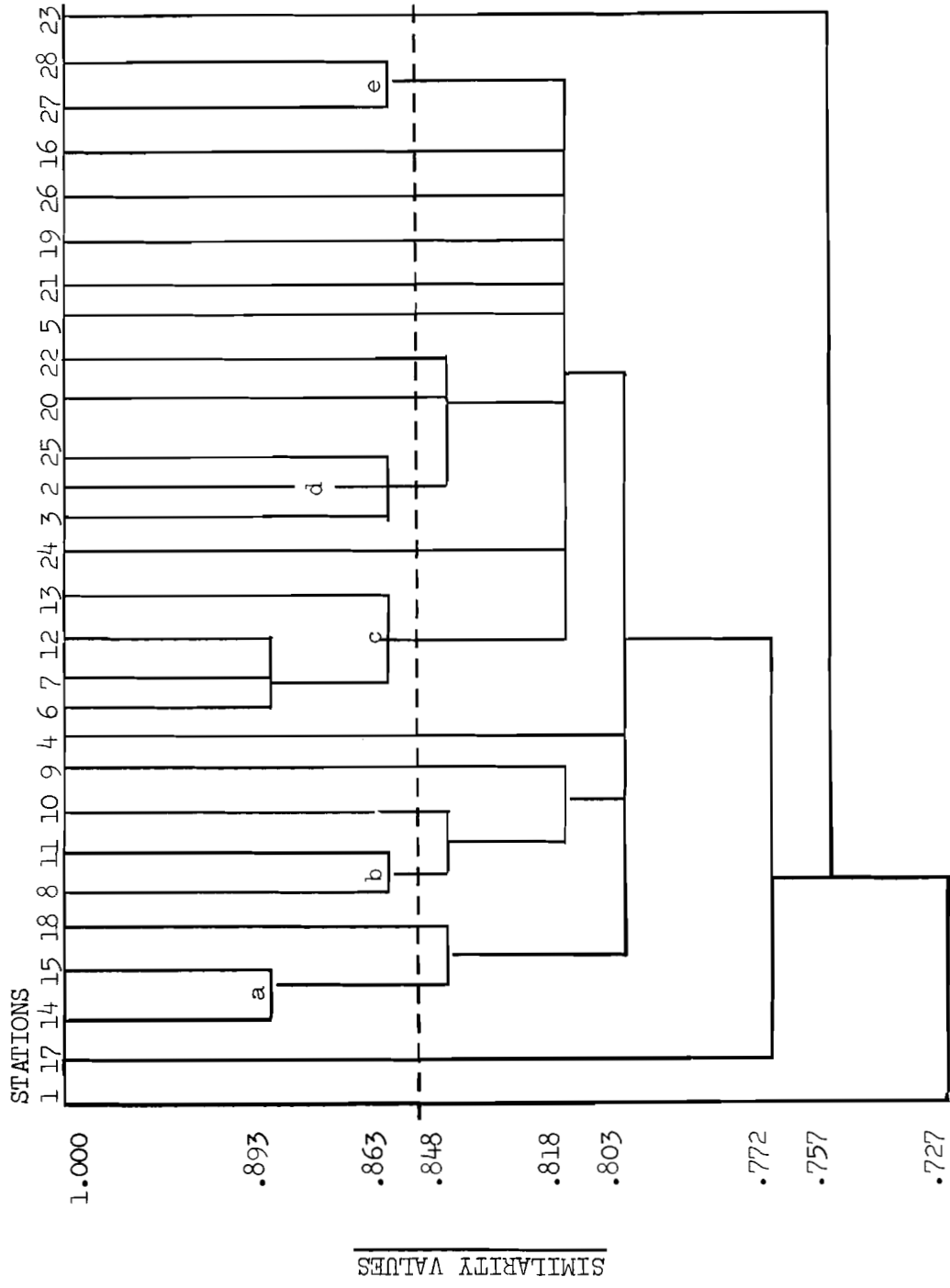


Table 4. Station Morphometrics.<sup>1</sup>

Stations	Size (yds.)	Description	Bottom type	Depth (in.)	Current Speed
West Fork					
1	2x20	Slow riffle-pool	Pebble-gravel; little or no siltation	6-18	0.7 ft./sec. to 0.3 ft./sec.
2	3x15	Moderate riffle	Small cobble; lightly silted	8-10	1.8 ft./sec.
3	2x6	Pool	Silt-gravel; moderately silted	15-18	1 ft./sec.
4	3x30	Slow riffle	Small cobble lightly silted	6-10	1.1 ft./sec.
Middle Fork					
5	4x10	Pool	Ooze	24x36	0.2 ft./sec
6	3x12	Moderate dead-fall riffle	Small cobble; lightly silted	8-10	2.0 ft./sec.

<sup>1</sup>Mid-summer averages for 1967 and 1968.

Table 4. (Continued) Station Morphometrics.

Middle Fork (cont.)					
7	3x12	Moderate riffle	Small cobble; little or no siltation	6-10	2.0 ft./sec.
8	3x5	Fast riffle	Small cobble; little or no siltation	10-12	2.4 ft./sec.
9	3x9	Slow riffle	Pebble-gravel; lightly silted	8-10	0.8 ft./sec.
10	3x20	Moderate riffle	Large cobble; little or no siltation	10-12	1.5 ft./sec.
11	2x10	Fast riffle	Large cobble; little or no siltation	10-14	3.9 ft./sec.
12	5x14	Pool	Gravel, lightly silted	14x16	1.4 ft./sec.
13	4x8	Fast riffle	Boulder; little or no siltation	10-18	2.3 ft./sec.
14	10x16	Fast riffle	Small cobble; little or no siltation	8-10	2.3 ft./sec.

Table 4. (Continued) Station Morphometrics.

Middle Fork (cont.)					
15	7x14	Moderate riffle	Large cobble; lightly silted	10-12	2 ft./sec.
16	7x7	Backwater pool	Ooze	18-24	0 ft./sec.
17	6x25	Moderate riffle	Small cobble; little or no siltation	8-10	1.5 ft./sec.
Middle St. Maries					
18	7x15	Fast riffle	Small cobble; little or no siltation	8-10	3.7 ft./sec.
19	10x15	Pool	Large cobble; heavily silted	22-28	1.6 ft./sec.
20	5x10	Slow riffle	Large cobble; moderately silted	6-10	1.3 ft./sec.
21	30x25	Fast riffle	Large cobble; moderately silted	8-10	2.3 ft./sec.
22	10x20	Pool	Large cobble; heavily silted	12-36	0.8 ft./sec.

Table 4. (Continued) Station Morphometrics.

Middle St. Maries (cont.)					
23	20x25	Fast riffle	Large cobble; moderately silted	6-18	2.7 ft./sec.
24	40x30	Moderate riffle	Large cobble; moderately silted	8-10	2 ft./sec.
25	7x20	Fast riffle	Boulder; lightly silted	12-36	2.7 ft./sec.
26	20x30	Sewage effluent- pool	Large cobble; heavily silted	24-48	0.5 ft./sec.
Lower St. Maries					
27	20x40	Slackwaters	Silt-mud	9-12 ft.	0.5 ft./sec.
28	20x40	Slackwaters	Silt-mud	9-12 ft.	0.5 ft./sec.



(Williams and Lambert, 1959; Harberd, 1960; Orloci, 1967 and Webb et al., 1967).

In addition to a purely physical evaluation of the stations, it was believed important to evaluate and compare stations biologically. To do this, a dendrogram was designed (Fig. 5) to reflect similarities and dissimilarities based on the presence or absence of different algae and mayflies among the stations. Stations having a common biota of algae and mayflies would reflect similarities by a common clustering of percentage relationships. The criterion for admission of a station to a cluster is based on the highest percentage similarity with a station of that cluster. By lowering the percentage for admission, more stations could be admitted to the cluster with the resulting relationships becoming more obscure.

Station clusters (a, b, c, d and e) above similarity value .855 were selected for analysis and discussion. Other levels or values could have been selected; however, based upon the resultant clustering, this level was believed to be most meaningful.

#### F. Water Chemistry

Chemical analysis of the St. Maries River was performed for total hardness (ppm  $\text{CaCO}_3$ ), hydrogen ion concentration (pH), dissolved oxygen and turbidity (Table 5). Analyses were performed at five 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 in 1968. Analysis of the slackwaters was taken only during August, 1968.

Table 5. Water chemistry analysis from five locations on the St. Maries River.<sup>1</sup>

	West Fork			Middle Fork			Upper middle St. Maries			Lower middle St. Maries			Slackwaters Aug. (1968)
	Apr.	Jun.	Aug.	Apr.	Jun.	Aug.	Apr.	Jun.	Aug.	Apr.	Jun.	Aug.	
Total Hardness (ppm CaCO <sub>3</sub> )	20	20	20	10	10	20	20	10	10	30	10	25	20
Dissolved O <sub>2</sub> (ppm)	10	10	9	11	10	8	11	10	8	10	9	8	10
pH	8.3	7.7	8.9	8.4	7.0	8.9	8.6	7.1	8.9	8.6	7.2	8.8	8.7
Turbidity (JTU's) <sup>2</sup>	0	0	0	0	0	0	0	0	0	0	0	15	15

<sup>1</sup>Water chemistry analysis were taken in August, 1967, and April and June in 1968. Analysis of the slackwaters was taken only during August, 1968.

<sup>2</sup>Jackson Turbidity Units.

## DISCUSSION

### A. General

Mayflies represent a truly aquatic order, with nearly their entire life spent in water. They occupy an important niche in the aquatic environment serving as food for fishes and other aquatic animals. Mayfly nymphs are principally primary consumers, transforming plant tissue into animal. They fulfill the requirements of a basic herbivore feeding 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 cracks and crevices of rocks serve as their principle means of escape.

Most mayfly nymphs live from one to two years. The number of molts during nymphal life is unknown for most species; however, it is estimated between 20 and 30. At the last nymphal molt, a subimago stage emerges from the water; a stage very similar to the adult although not sexually mature. The final molt produces the imago, a fully mature adult. The imagos live only a few days, during which time mating and oviposition occur. The adults do not feed. After a short incubation period the eggs hatch and the first instar nymph emerges.

## B. Food Habits

The composition of the ingested food for most of the mayfly nymphs was largely determined by the type of food available in their microenvironment. 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 fed on Ulothrix when it was plentiful, but turned to Fontinalis when algae were scarce. Nymphs of the St. Maries River utilized three primary food types, detritus, diatoms and filamentous algae. Spring and summer nymphs usually fed on higher amounts of algae, which bloom primarily during these periods. Late summer and fall nymphs depend more on detritus. Chapman and Demory (1963) reported that the food habits change seasonally. To a degree this was true for some of the species studied in the St. Maries River, although based on phenological changes during the spring and summer, several species as Baetis bicaudatus, Baetis tricaudatus and Paraleptophlebia bicornuta were relatively consistent in their feeding habits.

The type of food available in a lotic environment is influenced by the depth of the stream, current speed, bottom type and various other subtle physical factors to which the nymphs are biologically and physically attuned. If algae are adapted and grow in a particular microhabitat, they are usually fed upon by the herbivorous nymphs of that microhabitat. Fast currents in the center channels of stations 8 and 10 (Table 4) supported various

algae as diatoms, desmids and Nostoc while Ulothrix and Spirogyra occurred predominately along the margins. Slower riffles as stations 10, 20 and 24 (Table 4) commonly supported Ulothrix, Oscillatoria and Oedogonium. Mayflies occurring in these stations or microhabitats within these stations fed on these algae; however, detritus almost universally represented the principal material in the gut.

Mayfly nymphs of the St. Maries River were almost totally herbivorous, with detritus, the particulate organic and inorganic stream debris, being most commonly utilized. The lowest average percentage of detritus was ingested by Ephemerella hecuba and Heptagenia criddlei (Fig. 4L, P, Table 2). Both nymphs occupied moderate to heavily silted habitats and both ingested a higher percentage of diatoms and filamentous algae than other nymphs occupying the same or similar microhabitats. Cinygmula and Paraleptophlebia nymphs inhabited the same or similar habitats as E. hecuba and H. criddlei (Table 3); however, both nymphs ingested detritus at an average of 10% higher than the latter species. Nymphs of Paraleptophlebia ingested the highest percentage of detritus, 65-66% (Fig. 4Q, R, Table 2). It was apparent in many cases the food habits were variable among nymphs of different species occupying the same or similar habitats.

The genus Baetis is often a common and abundant mayfly in moderate to fast cobble riffles (Table 3). B. bicaudatus is considered by Nielson (1950) to be one of the better adapted mayflies

to fast current. Nymphs fed largely on detritus and diatoms (91%) even though the environment appeared to be relatively detrital free (Fig. 4B, Table 2). 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 had similar feeding habits as Baetis but generally occupied slower riffles and pools (Table 3). Nielson (1950) reported that the round-bodied nymphs as Baetis and Ameletus have mouth parts morphologically adapted for feeding on rock-surface accumulations. The sweeping action of the comb-like maxillae, brushes detritus and diatoms from the rocks into the mouth. Orientation of nymphs of both species was usually upstream, thus permitting the currents to augment the effectiveness of the maxillae.

Nymphs as Epeorus albertae, Ephemerella doddsi, E. flavilinea, E. grandis, E. hecuba, E. inermis, E. infrequens and E. tibialis ingested trace amounts of arthropods, principally other insects (Table 2). The percentages were consistently small and did not represent a major part of the diet; ingestion was probably accidental. None of the species studied consistently fed on arthropods.

The food habits were reflected primarily for age-class two and three nymphs because of the greater ease in dissection. Most species analyzed indicated that food habits were essentially the same for both age-classes. However, age-class three nymphs of

Epeorus longimanus and Heptagenia criddlei fed more on detritus (up to 10%) than age-class two nymphs. This may be partly explained by their life cycles; age-class three nymphs of these genera were abundant during late summer when detritus was more abundant.

### C. Ecology and Behavior

In addition to biological factors, many physical factors influence the distribution 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 other physical and biological factors. Linduska (1942) reported that the bottom type was perhaps the most important factor influencing distribution. He concluded that since the nature of the bottom can so profoundly affect the current speed, the current speed as such, would be of secondary importance in distribution. He also noted that an irregular stream bottom affords many places of greatly reduced velocity so that even where surface velocity is fast, species seemingly not morphologically adapted to an area may inhabit such situations. Based on findings from this study it is believed that a combination of factors and not a single factor influences distribution. It is probable that many other physical factors are also involved to a lesser or greater degree such as light, stream size, siltation and



water chemistry along with biotic factors as food availability and intra and interspecific relationships.

Nymphal morphology and stream microhabitat, most important of which includes stream current and substrate, greatly influenced nymphal behavior and orientation. Round-bodied nymphs as Ameletus and Baetis were commonly found on the tops of rocks in moderate riffles and orientating upstream. These nymphs offered little resistance to the passing currents. When inhabiting the slower riffles and pools, the nymphs were observed swimming from rock to rock, primarily downstream. Dorsoventrally flattened nymphs as Cinygmula and Epeorus, were generally observed clinging to the sides and bottoms of rocks where stream velocities were moderate to fast. In slower riffles they were observed on tops of rocks. Orientation was generally irregular in both cases. It is interesting to note that the food habits of round and flat-bodied nymphs in the St. Maries River varied little in composition of detritus and diatoms. Flat-bodied nymphs fed on slightly higher amounts of filamentous algae and higher plants. Arthropods were not recorded as being ingested by any of the round-bodied forms as Ameletus, Baetis and Centroptilum (Table 2).

Although pollution was not a principal point of consideration in this study, the sewage effluent contributed by several small communities seemed to warrant study. Station 26 was a sewage effluent pool near Santa, Idaho and was established to reflect mayfly-pollution relationships. The stream bottom of this

station consisted of large cobble, heavily covered with biodebris; water depths ranged from one to three feet. Several species occurred at this station (Table 3), however, only three species, Paraleptophlebia bicornuta, P. heteronea and P. memorialis had consistently high populations. Human sewage had little effect upon these mayflies. The greatest limiting factor appeared to be the gross alteration of the bottom with detritus. Water chemistry analysis for that station (Table 5) and other stations was not appreciably different.

Many mayfly nymphs in the St. Maries River had a wide distribution while others were more restrictive (Table 3). Nymphs as Baetis tricaudatus, Cinygmula, Epeorus longimanus, Ephemerella flavilinea, Ephemerella grandis, Ephemerella inermis, Ephemerella infrequens and Ephemerella tibialis reflected the former condition, although population numbers 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 microhabitat selection. Epeorus grandis occurred only in the cold unsilted riffles of the Middle Fork as did Ephemerella edmundsi. Nymphs as Paraleptophlebia bicornuta and Heptagenia solitaria preferred the slow silty riffles and pools of the middle St. Maries. The distribution of the nymphs indicated that detrital accumulations and the general bottom types are important physical factors of their micro-environment.

Largest populations of mayfly nymphs generally occurred in moderately-flowing, cobble riffles, relatively free of detrital accumulations. Ephemerella tibialis and Cinygmula usually represented the largest populations in this type of habitat; they were also the most widely distributed mayfly nymphs of the river.

In addition to the physical interrelationships of station habitats with mayflies (Table 4), biotic relationships were reflected with the aid of a dendrogram (Fig. 5). The dendrogram represents station similarities based on the presence or absence of mayflies and algae. An arbitrary line, having a similarity value of .855, was established to separate the more highly correlated with the less correlated stations. Stations correlated below this value reflect divergent similarities. By using additional biotic or abiotic factors, the degrees of similarity among stations may tend to be reinforced or possibly changed.

Several stations were highly correlated with one another so as to form clusters on the dendrogram. These stations were 14 and 15 (cluster a), 8 and 11 (cluster b), 6, 7, 12 and 13 (cluster c), 3, 2 and 25 (cluster d) and 27 and 28 (cluster e).

Stations in clusters a, b, c and e were located in close proximity to one another along the river, a factor which may contribute to their high degree of correlation. Stations 14 and 15 of cluster a had relatively similar physical and chemical characteristics although the bottom types were different; station 14 had small cobble while station 15 had large cobble. Stations 8 and 11 of

cluster b differ on the same basis. Stations 6 and 7 of cluster c were small cobble riffles while station 12 was a gravel riffle. Station 13 of this cluster was a boulder riffle and represented a more varied habitat. Stations 27 and 28 of cluster e were both slackwater stations with about the same physical and chemical characteristics. It should be noted that insect drift is a common phenomenon in streams (Waters, 1966) causing transient populations to sometimes occur in habitats which may not be optimal. It is conceivable that this condition could change or affect the station correlations.

Stations 2, 3 and 25 (cluster d) were also highly correlated, however, relative location, bottom types and current speeds were noticeably different. The high correlations of stations 2 and 3, a small cobble riffle and silt-gravel pool respectively, may be explained by their close proximity (200 yds.) to one another. The correlation of station 25, a boulder riffle, with stations 2 and 3 appears unique. The correlation of these three stations demonstrated that grossly different appearing habitats may through subtle means provide many of the same or similar microhabitat requirements as to support similar populations of mayflies and algae.

A few stations showed little correlation with other stations, e.g. station 1, a pebble-gravel riffle represented the most uncorrelated of all 28 stations having a similarity value of .727. This station was somewhat isolated from the other stations, being located approximately four miles upstream from station 2. The

remoteness of the station and the fact that it is unique in being a headwaters station on the West Fork may in part explain its dissimilarity with other stations. Station 17 also had a lower correlation value (.772) than most stations. This station was a small cobble riffle located on Merry Creek, a tributary of the St. Maries River. Its physical characters were quite similar to several riffle stations on the St. Maries River, as 2, 6, 7, 8, 14 and 18. Station 17 apparently possessed subtle biotic, physical or chemical differences from other stations. Station 23, a large cobble riffle with moderate siltation, also had a low correlation value (.757) with other stations. Station 23 was located adjacent to a sawmill which may have altered the water chemistry sufficiently so as to change the population composition of mayflies and algae. In similar manner, station 4, a lightly-silted, small-cobble riffle, was not highly correlated with other riffles as would be expected based upon general appearance. This station contained the most homogenous bottom type of all the stations. The bottom was uniformly small cobble with sizes ranging from 2 1/2-5"; no large cobble or boulders were present as in many other riffles. This may have been a contributing factor to its low correlation; other factors as water chemistry, siltation and current speed were similar to several other stations.

The dendrogram provided a useful tool in comparing station habitats on the St. Maries River. It demonstrates that many habitats which are morphometrically dissimilar in respect to bottom

type, current speed, water depths, temperature, etc., may in reality manifest many similar microhabitats responsible for the presence or absence of species. In the future, it is believed that by comparing habitats through numerical analysis of biotic and abiotic factors at the microhabitat level, a more definitive understanding of the relationships of aquatic insects with their environment will be obtained.

#### D. Water Chemistry

Total hardness (ppm  $\text{CaCO}_3$ ) 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  $\text{CaCO}_3$ . Dissolved oxygen ranged from 8 to 11 ppm throughout the river. Hydrogen ion concentration (pH) in the river was relatively consistent for samples taken during April and August; June samples 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.

The water chemistry of the St. Maries River was relatively consistent throughout the river. It is believed that differences in the four chemical characters of the water were not sufficiently significant 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. Age-class two and three nymphs usually had similar feeding habits.

The distribution of mayfly nymphs of the St. Maries River was varied. Species as Cinygmula and Ephemerella tibialis had a wide distribution, adapting to a variety of habitats; other species as Epeorus grandis, Centroptilum and Heptagenia solitaria had limited distribution. The microhabitats largely determined mayfly distribution.

Different mayfly species generally had different environmental requirements. Nymphs as Paraleptophlebia bicornuta, P. heteronea and P. memorialis had strong affinities to detritus, while nymphs as Epeorus grandis and Ephemerella edmundsi were found in more detrital-free habitats.

In addition to biotic factors, several physical factors of the environment influenced mayfly distribution on the St. Maries River, most important of which are believed to be bottom type and current speed.

Moderately-flowing, lightly-silted, cobble riffles supported the largest populations of mayfly nymphs.

The dendrogram was used to correlate station similarities biotically; several diverse habitats supported the same species.



LITERATURE CITED

- Allen R. K. and G. F. Edmunds, Jr. 1961. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). III. The subgenus Attenuatella. J. Kans. Entomol. Soc., 34:161-73.
- \_\_\_\_\_. 1962. A revision of the genus Ephemerella (Ephemeroptera: Ephemerellidae). V. The subgenus Drunella in North America. Misc. Publ. Entomol. Soc. Amer., 3:145-79.
- Berner, L. 1950. The mayflies of Florida. Univ. Fla. Studies, Biol. Sci. Ser., 4(4):1-267.
- \_\_\_\_\_. 1959. A tabular summary of the biology of North American mayfly nymphs (Ephemeroptera). Bull. Fla. State Mus., 4(1):1-58.
- Chapman, D. W. and R. L. Demory. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. Ecology 44(1):140-46.
- Clemens, W. A. 1913. New species and life histories of Ephemeridae or mayflies. Can. Entomol., 45:246-62.
- \_\_\_\_\_. 1915. Mayflies of the Siphonurus group. Can. Entomol., 47:245-60.
- \_\_\_\_\_. 1917. An ecological study of the mayfly Chironetes. Univ. Toronto Studies, Biol. Ser. No. 17, 43 pp.
- Daubenmire, R. F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr., 22:301-30.
- Day, W. C. 1963. Ephemeroptera, pp. 79-105. In: Aquatic Insects of California, R. L. Usinger (editor). Univ. of Calif. Press, Berkeley and Los Angeles, 508 pp.
- Dodds, G. S. and F. L. Hisaw. 1924. Ecological studies of aquatic insects. I. Adaptation of mayfly nymphs to swift streams. Ecology, 5:137-48.
- Edmunds, G. F., Jr. 1952. Studies on the Ephemeroptera. Part II. The taxonomy and biology of the mayflies of Utah. Unpubl. Ph.D. Thesis, Univ. of Mass., 399 pp.

- \_\_\_\_\_. 1954. The mayflies of Utah. Proc. Utah Acad. Sci., Arts and Letters, 31:64-66.
- \_\_\_\_\_. 1957. On the life history of Parameletus columbiae McDunnough (Ephemeroptera). Proc. Utah Acad. Sci., Arts and Letters, 34:25-26.
- \_\_\_\_\_. 1960. The food habits of the nymphs of the mayfly Siphonurus occidentalis. Proc. Utah Acad. Sci., Arts and Letters, 37:73-74.
- Edmunds, G. F., Jr. and R. K. Allen. 1957. The Rocky Mountain species of Epeorus (Iron) Eaton (Ephemeroptera: Heptageniidae). J. Kans. Entomol. Soc., 37:275-88.
- \_\_\_\_\_. 1966. The significance of nymphal stage in the study of Ephemeroptera. Ann. Entomol. Soc. Amer., 59(2):300-303.
- Edmunds, G. F., Jr., R. K. Allen and W. L. Peters. 1963. An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). Univ. Utah Biol. Ser., 13:1-49.
- Flowers, S. Undated. The algae of Utah. Unpublished pamphlet. Dept. of Botany, Univ. of Utah, 70 pp.
- Fremling, C. R. 1960. Biology of a large mayfly, Hexagenia bilineata (Say) of the Upper Mississippi Rivers. Ag. and Home Econ. Exp. Sta., Iowa State Univ. Res. Bull., 482:842-51.
- \_\_\_\_\_. 1964. Mayfly distribution indicates water quality on the Upper Mississippi River. Science, 146(3648):1164-166.
- Gaufin, A. R. and C. M. Tarzwell. 1965. Aquatic invertebrates as indicators of stream pollution, pp. 57-64. In: Biological problems in water pollution, Robert A. Taft Sanitary Engineering Cen., 3rd Seminar, 1962. Pub. Health Ser. Publ. 999-WP-25, 424 pp.
- Gilpin, B. R., M. A. Brusven and J. L. McMullen. 1969. Algae of the St. Maries River in Idaho. Northwest Sci. (in press).
- Harberd, D. J. 1960. Association-analysis in plant communities. Nature, 185:53-54.
- Hora, S. L. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. Phil. Trans. Roy. Soc. London, Section B., 218:171-282.

- Hughes, D. A. 1966a. On the dorsal light response in a mayfly nymph. *Anim. Behav.*, 14(1):13-16.
- \_\_\_\_\_. 1966b. The role of responses to light in the selection and maintenance of microhabitats by nymphs of two species of mayfly. *Anim. Behav.*, 14(1):17-33.
- Ide, F. P. 1935. The effects of temperature on the distribution of the mayfly fauna of a stream. *Univ. of Toronto Studies, Biol. Ser.* 39, *Pub. Ont. Fish. Res. Lab.*, 50:9-76.
- Jensen, S. L. 1966. The mayflies of Idaho. Unpubl. Masters Thesis, Univ. of Utah, 367 pp.
- Jones, J. R. E. 1949. A further ecological study of calcerous streams in the "black mountain" district of South Wales. *J. Anim. Ecol.*, 18:142-59.
- Leonard, J. W. 1965. Environmental requirements of Ephemeroptera, pp. 110-17. In: *Biological Problems in water pollution*, Robert A. Taft Sanitary Engineering Cen., 3rd Seminar, 1962. *Pub. Health Ser. Publ.* 999-WP-25, 424 pp.
- Leonard, J. W. and F. A. Leonard. 1962. Mayflies of Michigan trout streams. *Cranbrook Inst. Sci. Bull.*, 43:1-139.
- Linduska, J. P. 1942. Bottom type as a factor influencing the local distribution of mayfly nymphs. *Can. Entomol.*, 74: 26-30.
- Lyman, F. E. 1956. Environmental factors affecting distribution of mayfly nymphs in Douglas Lake, Michigan. *Ecology*, 37(3): 568-76.
- Morgan, A. H. 1913. A contribution to the biology of mayflies. *Ann. Entomol. Soc. Amer.*, 6:371-413.
- Neave, F. 1930. Migratory habits of the mayfly, Blasturus cupidus Say. *Ecology*, 11:568-76.
- Needham, J. G. 1920. The life history and habits of a mayfly from Utah. *Can. Entomol.*, 59:133-36.
- Needham, J. G., J. R. Traver and Yin Chi Hsu. 1935. The biology of mayflies. *Comstock Pub. Co.*, Ithaca, N. Y., 759 pp.
- Nielsen, A. 1950. The torrential invertebrate fauna. *Oikos*, 2: 176-96.

- Orloci, L. 1967. An agglomerative method for classification of plant communities. *J. Ecol.*, 55(1):193-206.
- Prescott, G. W. 1951. Algae of the Western Great Lakes area. Cranbrook Inst. of Sci., Boomfield Hills, Mich., 946 pp.
- Ross, C. P. and J. D. Forrester. 1959. Geologic map of Idaho (Prepared in cooperation with U. S. Geological Survey).
- Smith, G. M. 1950. The freshwater algae of the United States. 2nd ed., McGraw Hill Book Co., Inc., N. Y., 719 pp.
- Sokal, R. R. and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, 359 pp.
- Swanson, G. A. 1967. Factors influencing the distribution and abundance of Hexagenia nymphs (Ephemeroptera) in a Missouri river reservoir. *Ecology*, 48(2):216-25.
- Travis, W. I., H. A. Wright and J. F. Santos. 1964. Water resources. Published by Mineral and Water Resources of Idaho, Special Rep. No. 1., pp. 255-78.
- Waters, T. F. 1966. Production rate, population density and drift of a stream invertebrate. *Ecology*, 47(4):595-604.
- Webb, L. J., J. G. Tracey, W. T. Williams and G. N. Lance. 1967. Studies in the numerical analysis of complex rain-forest communities. II. The problem of species sampling. *J. Ecol.*, 55(2):525-38.
- Welch, P. S. 1948. Limnological methods. The Blakiston Co., Philadelphia, 381 pp.
- Williams, W. T. and J. M. Lambert. 1959. Multivariate methods in plant ecology. I. Association-analysis in plant communities. *J. Ecol.*, 47:83-101.

APPENDIX

Table 6. Check list of the mayfly species of the St. Maries River

## Family SIPHLONURIDAE

Ameletus Eaton  
Parameletus columbiae McDunnough  
Siphonurus occidentalis Eaton

## Family BAETIDAE

Baetis bicaudatus Dodds  
Baetis parvus Dodds  
Baetis tricaudatus Dodds  
Centroptilum Eaton

## Family HEPTAGENIIDAE

Cinygmula McDunnough  
Epeorus (Iron) albertae (McDunnough)  
Epeorus (Iron) longimanus (Eaton)  
Epeorus (Ironopsis) grandis (McDunnough)  
Heptagenia criddlei McDunnough  
Heptagenia solitaria McDunnough  
Rhithrogena hageni Eaton  
Rhithrogena robusta Dodds

## Family LEPTOPHLEBIIDAE

Paraleptophlebia bicornuta (McDunnough)  
Paraleptophlebia debilis (Walker)  
Paraleptophlebia heteronea (McDunnough)  
 and P. memorialis (Eaton)

## Family EPHEMERELLIDAE

Ephemerella (Attenuatella) margarita Needham  
Ephemerella (Caudatella) edmundsi Allen  
Ephemerella (Caudatella) hystrix Traver  
Ephemerella (Drunella) coloradensis Dodds  
Ephemerella (Drunella) doddsi Needham  
Ephemerella (Drunella) flavilinea McDunnough  
Ephemerella (Drunella) grandis Eaton  
Ephemerella (Drunella) spinifera Needham  
Ephemerella (Ephemerella) inermis Eaton  
 and E. infrequens McDunnough  
Ephemerella (Serratella) teresa Traver  
Ephemerella (Serratella) tibialis McDunnough  
Ephemerella (Timpanoga) hecuba Eaton

## Family TRICORYTHIDAE

Tricorythodes minutus Traver