

The benthos and drift fauna of a riffle in the Madison River, Yellowstone National Park
by John R Heaton

A thesis submitted to the Graduated Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Zoology
Montana State University
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Abstract:
The benthos and drift fauna of a riffle in the Madison River, Yellow-stone National Park, were sampled during June 1963 through January 1965. Sixteen collections of benthos containing 128 samples (1/4 m2) and 10 col-lections of drift containing 531 samples were taken. Benthos standing crops ranged from 455.5 organisms/m2 with a volume of 3.10 cc/m2 in Sep-tember to 2,496 organisms/m2 with a volume of 11.8l cc/m2 in April. A total of 55 different organisms was identified from the benthos samples. Bphemeroptera, Plecoptera, Coleoptera, Odonata, Diptera, Trichoptera made up 89% of the number and 93% of the volume of all benthos. Mollusca, Turbellaria and Oligochaeta contributed the remainder. Drift animals varied from 160,997 organisms with a volume of 1,460 cc/24 hours in Nov-ember to 6,219,988 organisms with a volume of 36,378 cc/24 hours in June. Aquatic invertebrates and emerged aquatic insects made up 92.1% of the total volume of drift, while fish and fish eggs contributed 4.3% and terrestrial arthropods 3.6% Immature aquatic insects dominated the drift. Most species which appeared in the benthos were taken in the drift. Most organisms had diurnal periodicity with higher drift rates at night. Highest drift rates occurred when benthos numbers were high and lowest when benthos was low, but relations between benthos and drift were not consistent. Organisms drift from unknown distances upstream making correlations of drift with benthos difficult. Drifting plant material was present throughout the year varying from 2,084.82 g(dry weight)/24 hours in October to 94,212.29 g in June.

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by

JOHN R. HEATON

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

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in

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ABSTRACT

The benthos and drift fauna of a riffle in the Madison River, Yellowstone National Park, were sampled during June 1963 through January 1965. Sixteen collections of benthos containing 128 samples (¼ m^2) and 10 collections of drift containing 531 samples were taken. Benthos standing crops ranged from 455.5 organisms/m^2 with a volume of 3.10 cc/m^2 in September to 2,496 organisms/m^2 with a volume of 11.81 cc/m^2 in April. A total of 55 different organisms was identified from the benthos samples. Ephemeroptera, Plecoptera, Coleoptera, Odonata, Diptera, Trichoptera made up 89% of the number and 93% of the volume of all benthos. Mollusca, Turbellaria and Oligochaeta contributed the remainder. Drift animals varied from 160,997 organisms with a volume of 1,460 cc/24 hours in November to 6,219,988 organisms with a volume of 36,378 cc/24 hours in June. Aquatic invertebrates and emerged aquatic insects made up 92.1% of the total volume of drift, while fish and fish eggs contributed 4.3% and terrestrial arthropods 3.6%. Immature aquatic insects dominated the drift. Most species which appeared in the benthos were taken in the drift. Most organisms had diurnal periodicity with higher drift rates at night. Highest drift rates occurred when benthos numbers were high and lowest when benthos was low, but relations between benthos and drift were not consistent. Organisms drift from unknown distances upstream making correlations of drift with benthos difficult. Drifting plant material was present throughout the year varying from 2,084.82 g (dry weight)/24 hours in October to 94,212.29 g in June.

INTRODUCTION

The benthos and the associated drift of a riffle in the upper Madison River were studied to provide information on numbers and volumes, species composition, and distribution of organisms throughout the year.

Benthos in Yellowstone National Park was investigated by Armitage (1958, 1961) on the Firehole River (a tributary of the Madison River) and four other streams and by Muttkowski (1925, 1929) and Muttkowski and Smith (1929) who reported on benthos of several other park streams. Several workers have investigated stream benthos in other areas of the Rocky Mountains. In Montana, Linduska (1942) described mayfly distribution in relation to bottom type, Brown et al. (1953) and Logan (1963) observed the effects of winter conditions on benthos and drift while Graham and Scott (1958, 1959) and Schoenthal (1963) studied the effect of DDT on benthos. In Utah, Moffett (1936) investigated the effect of flooding and measured repopulation due to drift while Gaufin (1959) studied benthos production. In Colorado, Dodds and Hisaw (1924a, 1924b, 1925a, 1925b) investigated the adaptations of stream insects to altitude and velocity while Pennak and Van Gerpen (1947) studied their relationship to the substrate. Tarzwell (1937, 1938b) observed benthos in relation to substrate and other physical conditions in several southwestern streams.

A variety of studies on benthos of coldwater streams has been made in other areas. These include: trout food relationships by Needham (1928, 1933, 1934, 1938), Moore et al. (1934), Surber (1937), Mottley et al. (1939), Allen (1940, 1942, 1951), Leonard (1941), Hess and Swartz (1941),

Smith and Moyle (1944), Horton (1961) and Tebo and Hassler (1961); relation to physical and chemical conditions by Percival and Whitehead (1929), Ide (1935, 1940), Tarzwell (1936, 1938), Sprules (1940, 1947), Briggs (1948), Jones (1948, 1951), Harker (1953), Badcock (1954a, 1954b), Needham and Usinger (1956), Scott (1958), Morgan and Egglishaw (1965); the effects of ice by O'Donnell and Churchill (1954), Maciolek and Needham (1952), and Benson (1955); colonization and repopulation from drift by Müller (1954), Kennedy (1955), and Waters (1964).

Several investigators have been concerned primarily with drift organisms originating from benthos. Needham (1928, 1933, 1938) first described the production of benthos on riffles and drift into pools. Denham (1938) found benthos organisms (benthoplankton) in the drift during normal flows with increased numbers during floods. Lennon (1941) reported increased drift with higher flows and temperatures. Dendy (1944) found that most species of benthos organisms present in a stream appeared in the drift. Müller (1954) described a "colonization cycle" which involved downstream drift of immature stages and upstream flights by adults. Waters (1961, 1962a, 1965) studied relationships of drift to benthos standing crops and made productivity estimates from drift. Tanaka (1960), Waters (1962b), Müller (1963a, 1963b, 1965), Klyuchareva (1963), and Elliot (1965) reported on diurnal periodicity of drift.

A variety of benthos studies in warm water streams has also been made. Among these are fish food relationships by Richardson (1921, 1928), Surber (1939, 1940) and Berner (1951); various physical and chemical conditions

by Gersbacher (1937), Stehr and Branson (1938), Denham (1938), Murray (1938), Shockley (1949), Slack (1955) and Minckley (1963); and pre-impoundment studies by Lyman (1942), Lyman and Dendy (1943), O'Connell and Campbell (1953).

Some investigators have studied benthos in relation to pollutants. Invertebrates as indicators of pollution have been described by Gaufin and Tarzwell (1956). Cordon and Kelly (1961) reviewed the literature concerning the effects of sediment on stream benthos.

Description of the Study Area

The present study was restricted to a riffle in the Madison River at Riverside Station (elevation 2,026.9 m) located 4 km upstream from the west boundary of Yellowstone National Park. The drainage area above the study riffle is predominantly a high forested plateau of about 121,730 hectares. Air temperature in this area ranged from 51 C below to 33 C above zero during 1963 and from 47 C below to 32 C above zero during 1964. Annual precipitation was 72.5 cm in 1963 and 72.6 cm in 1964 (48 year mean 53.9 cm) with the lowest amount during July and the highest during June (U. S. Weather Bureau 1963, 1964). Deep snow made access difficult throughout the winter and early spring months.

The study area was 70 m in length and comprised the lower portion of a riffle about 10 km in total length (Fig. 1). This area had a mean width of 54.4 m and mean depth of 29.3 cm (maximum 51.8 cm). Discharge during the study period ranged from 9.35 to 39.65 m^3/sec with the lowest flows during December and the highest following the melting snow pack in June

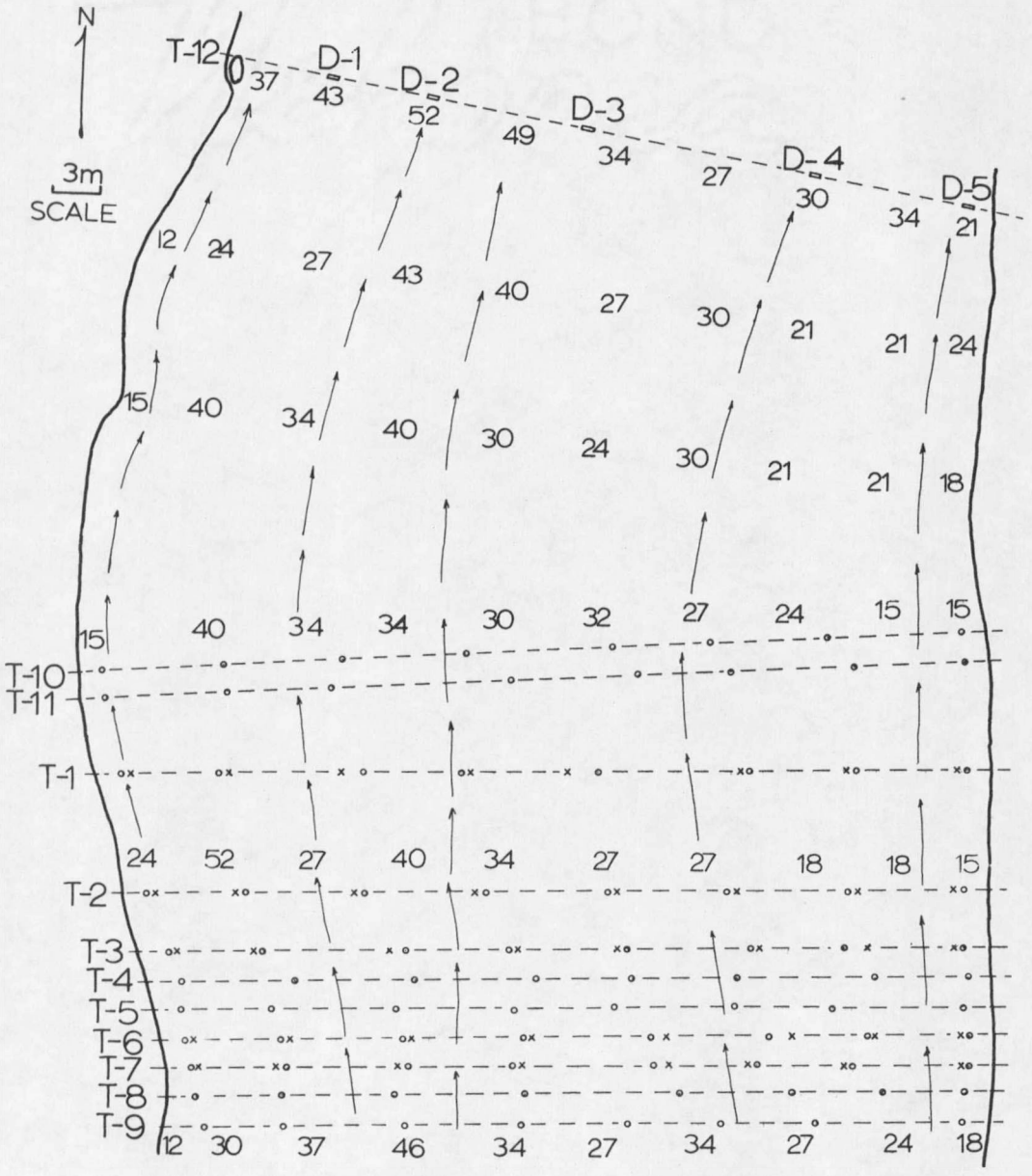


Figure 1. Study riffle on the Madison River showing: depths of the water (cm), locations of benthos transects (T-1 through T-11) and benthos samples (o=June 1963 through May 1964, x=June 1964 through January 1965), and drift stations (D-1 through D-5).

(Fig. 2). Velocities ranged from 51.8 to 134.1 cm/sec near the surface

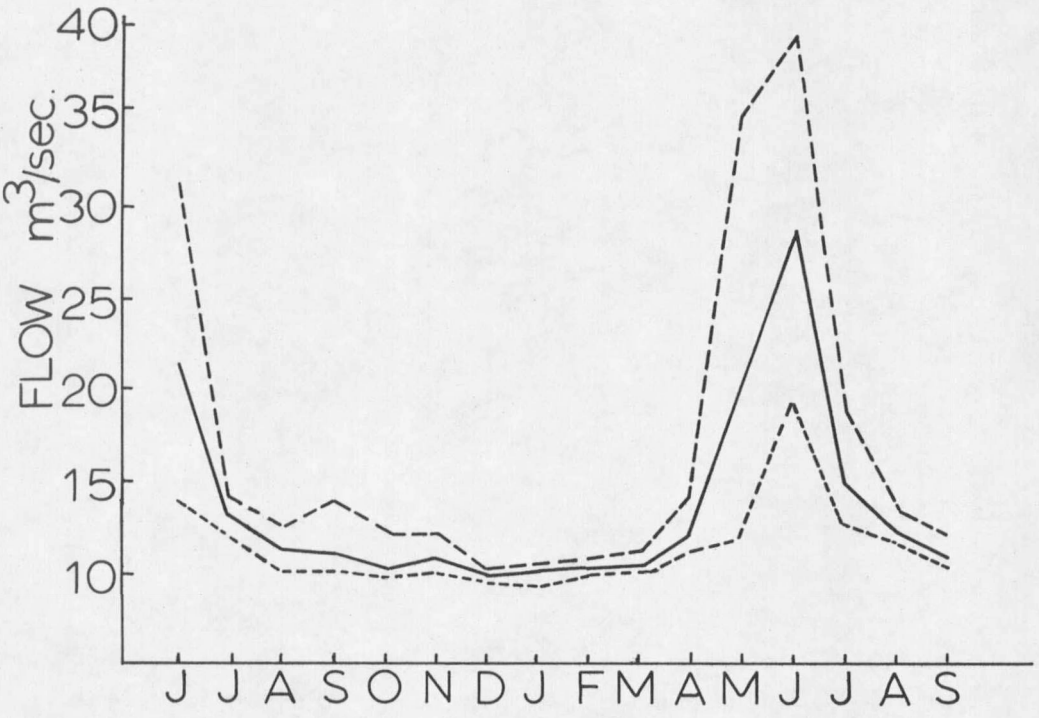


Figure 2. Monthly maximum, minimum and mean flows for the Madison River from June 1963 through September 1964.

(7.6 cm deep) and from 29.0 to 79.6 cm/sec near the bottom. The bottom of the study area consisted of a loose or partially-cemented surface layer resting upon a cemented base. The surface layer was composed of 84% large gravel (1.27-20.3 cm), 10% small gravel (0.24-1.27 cm), 6% sand (0.015-0.24 cm), and less than 0.05% silt (Table I). A small amount of rubble and a few boulders were also present. There was less loose or partially cemented material and a smaller proportion of small gravel, sand, and silt (less than 1.27 cm in diameter) in the area of highest velocity (approxi-

Table 1. Bottom materials in the study riffle of the Madison River as shown by eight ¼ m^2 samples.

Distance from west shore (m)	Total volume (cc)	Particle size (cm) 27-43	16.2-27	10.8-16.2	2.7-10.8	0.18-2.7	0.032-0.18	Less than 0.032
		Per cent of total volume						
1.5	2,394.2		38.6		58.3	2.7	0.4	0.02
7.61	2,992.0		36.8	20.6	37.7	4.2	0.7	0.02
15.2	6,608.6		54.5	14.6	19.9	8.2	2.8	0.01
22.9	7,461.5		53.6	12.9	21.0	8.4	3.8	0.1
30.5	8,769.5	26.7	30.7	8.6	20.0	8.8	5.2	0.02
39.6	7,048.0		28.4	16.5	36.6	11.4	7.5	0.01
45.7	6,004.0	24.4	4.2	4.6	36.1	15.5	15.4	0.08
52.1	4,999.0		43.4	8.4	28.5	12.1	7.6	0.02
Total	46,276.8	8.2	36.2	11.1	28.8	9.7	6.0	0.04

mately 1.5 m from the west shore to midstream). Submerged vegetation was abundant throughout the study riffle, and 87% of the benthos samples contained plant material. The dominant plants, in order of decreasing abundance, were an unidentified moss, Myriophyllum, Berula, Chara, Sparganium, and Potamogeton. Diatoms were the most abundant algae.

The water temperature of the Madison River is warmer than most other streams of the area because thermal water from the geyser basins enters the tributary streams (Allen and Day, 1935). The minimum temperature recorded in the study area was 1 C and the maximum 25.6 C. Temperatures from 1 to 10 C were recorded during November through February. Rapid warming occurred during early April with maximum temperatures of 18.1 C. From mid-April to late June (period of highest flow) the temperature fluctuated from 8.1 to 18.4 C. Temperatures increased in late June, as flows decreased, and were

highest during July reaching 25.6 C in 1963 and 24.4 C in 1964. There was a progressive cooling of the water after mid-August.

A chemical analysis of river water from the study area, taken in November 1964, showed the following (milligrams per liter): Na 92.0, K 9.8, Ca 2.7, Mg 0.9, HCO_3 144, Cl 73.8, SO_4 2.7, CO_2 1.5. Phosphates ranged from 0.6 mg/l during low flows in April to 0.15 mg/l during high flows in June. Nitrates were not present in measurable concentrations.

Methods

Sixteen benthos collections were made between June 1963 and January 1965 at intervals which varied from three to eight weeks (Table 2). Each collection consisted of eight ¼ m^2 samples taken along a transect across the riffle. One sample was taken approximately one meter from each shore and the remaining six at about equal intervals across the riffle (Fig. 1). This distribution was fairly representative of the various depths, velocities and bottom types. Samples were taken with a nylon net (7.9 meshes/cm) which had an opening 52 cm in width (Fig. 3). While sampling, the net was placed at the downstream edge of a metal frame which enclosed an area ¼ m^2 and all of the loose or partially-cemented material within the frame was washed by hand and the cemented base stirred so that the fine material and organisms were washed into the net by the current. Each sample was emptied into a plastic bag and preserved in 10% formaldehyde. In the laboratory the organisms were separated using a sugar flotation technique (Anderson, 1959). This was done in a transparent glass dish which was placed alternately over a black and white background during the sorting process. After separation,

Table 2. Benthos numbers and volumes per square meter for all collections (8 samples of ¼ m^2) taken in the Madison River. Volume (cc) in parentheses.

Date of collection Collection transect	6-28-63 T-1	8-1-63 T-2	8-29-63 T-3	9-17-63 T-4	10-11-63 T-5	11-9-63 T-6	1-12-64 T-7	2-29-64 T-8	4-3-64 T-9	5-2-64 T-10	5-30-64 T-11	6-26-64 T-1	7-27-64 T-2	9-1-64 T-3	10-29-64 T-6	1-16-65 T-7
Tricladida																
Planariidae		1.5 (t)	1.5 (t)		0.5 (t)	12.0 (0.05)		0.5 (t)						0.5 (t)		
Pulmonata																
Physa gyrina			1.5 (0.05)	4.5 (0.2)	2.5 (0.1)	3.0 (0.15)	0.5 (t)	1.5 (0.05)	1.5 (0.05)	1.5 (0.1)	2.0 (0.1)	1.5 (0.02)	4.0 (0.30)	2.0 (0.19)	38.5 (0.15)	2.5 (0.10)
Ctenobranchiata																
Gyraulus deflectus												0.5 (t)				
Sphaeriidae																
Pisidium casertum	24.0 (0.05)	17.5 (0.05)	13.5 (0.03)	33.5 (0.10)	231.0 (0.30)	417.0 (0.60)	75.5 (0.10)	9.0 (0.05)	83.0 (0.15)	92.0 (0.15)	127.0 (0.20)	30.0 (0.05)	26.0 (0.10)	138.5 (0.16)	185.5 (0.85)	3.0 (0.05)
Oligochaeta																
Lumbriculidae	11.5 (0.10)	13.5 (0.15)	4.5 (0.06)	6.0 (0.10)	2.0 (0.10)	8.0 (0.15)	5.5 (0.10)	6.5 (0.10)	1.0 (0.15)	8.5 (0.25)	8.0 (0.15)	15.5 (0.13)	5.5 (0.15)	8.5 (0.18)	11.0 (0.25)	5.0 (0.15)
Ephemeroptera																
Ephemerella 1/	143.5 (0.38)	23.0 (0.10)	1.5 (0.03)	5.0 (0.05)	15.0 (0.05)	37.5 (0.10)	120.0 (0.30)	241.0 (0.90)	555.5 (2.55)	472.0 (3.20)	184.5 (0.85)	85.5 (0.45)	11.5 (0.05)	0.5 (t)	51.0 (0.10)	351.5 (0.60)
Ephemerella 2/	9.5 (0.10)	0.5 (0.03)		1.0 (0.03)	7.5 (0.05)	1.0 (0.02)	3.0 (t)	2.5 (t)	26.5 (0.15)	46.5 (0.19)	32.5 (0.20)	15.5 (0.20)	0.5 (0.01)		2.5 (0.10)	2.5 (0.10)
Ephemerella heterocaudata	1.5 (t)							0.5 (t)		1.0 (0.01)	1.0 (0.03)	3.0 (0.02)				
Tricorythodes	9.5 (0.05)	1.5 (0.02)	2.5 (0.05)	0.5 (t)	3.0 (t)		2.0 (t)	2.0 (t)			1.0 (0.02)	5.5 (0.03)	6.5 (0.01)	2.0 (t)		
Baetis	28.5 (0.08)	25.0 (0.05)	14.0 (0.02)	24.5 (0.10)	28.0 (0.10)	20.0 (0.20)	34.5 (0.10)	113.5 (0.25)	339.5 (0.80)	166.0 (0.55)	62.5 (0.2)	40.5 (0.10)	21.5 (0.05)	57.0 (0.10)	16.5 (0.10)	46.5 (0.10)
Paraleptophlebia	9.0 (0.05)							3.0 (0.05)		0.5 (0.05)	0.5 (0.02)	2.0 (0.03)				0.5 (t)
Epeorus albertae	11.0 (0.08)	4.5 (0.10)	1.5 (0.05)				1.0 (0.02)			4.0 (0.05)	21.5 (0.10)	33.5 (0.13)	12.0 (0.10)	3.5 (0.05)		0.5 (t)
Rhithrogena						0.5 (0.05)			3.0 (0.10)	2.5 (0.10)	2.5 (0.05)					
Ephemera simulans		0.5 (t)														
Total Ephemeroptera	212.5 (0.74)	55.0 (0.30)	19.5 (0.15)	31.0 (0.18)	53.5 (0.20)	59.0 (0.37)	160.5 (0.42)	362.5 (1.20)	924.5 (3.60)	692.5 (4.15)	306.0 (1.47)	185.5 (0.96)	52.0 (0.22)	63.0 (0.15)	70.0 (0.30)	401.5 (0.80)

Table 2, continued.

Date of collection Collection transect	6-28-63 T-1	8-1-63 T-2	8-29-63 T-3	9-17-63 T-4	10-11-63 T-5	11-9-63 T-6	1-12-64 T-7	2-29-64 T-8	4-3-64 T-9	5-2-64 T-10	5-30-64 T-11	6-26-64 T-1	7-27-64 T-2	9-1-64 T-3	10-29-64 T-6	1-16-65 T-7
Odonata																
Ophiogomphus montanus	16.0 (0.83)	4.0 (0.45)	7.0 (0.90)	9.0 (0.40)	18.5 (0.65)	12.5 (1.10)	8.5 (0.80)	12.5 (0.70)	15.0 (0.60)	8.0 (0.40)	6.5 (0.50)	3.5 (0.15)	8.0 (0.60)	4.0 (0.19)	7.0 (0.60)	4.5 (0.30)
Argia rivida	4.0 (0.05)	1.0 (0.10)	0.5 (0.01)	1.5 (0.10)	1.5 (0.15)	0.5 (0.05)	0.5 (0.03)	0.5 (0.05)	1.0 (0.05)	4.0 (0.10)	0.5 (0.05)	9.0 (0.10)	2.0 (0.10)		0.5 (0.10)	0.5 (0.10)
Agrion aequabile									0.5 (0.05)							
Total Odonata	20.0 (0.88)	5.0 (0.55)	7.5 (0.91	10.5 (0.50)	20.0 (0.80)	13.0 (1.15)	9.0 (0.83)	13.0 (0.75)	16.5 (0.70)	12.0 (0.50)	7.0 (0.55)	12.5 (0.25)	10.0 (0.70)	4.0 (0.19)	7.5 (0.70)	5.0 (0.40)
Plecoptera																
Pteronarcys californica	9.0 (0.60)	7.5 (0.60)	11.5 (0.58)	10.5 (0.65)	12.0 (1.40)	9.0 (1.35)	8.0 (2.05)	7.0 (1.30)	5.5 (1.45)	1.5 (0.20)	5.5 (0.45)	8.0 (0.80)	13.0 (1.20)	18.5 (1.20)	14.0 (1.25)	14.0 (1.75)
Acroneuria pacifica	6.0 (1.50)	5.5 (0.10)	5.0 (0.10)	3.5 (0.10)	1.5 (0.10)	3.0 (1.50)	5.0 (0.30)	3.0 (0.30)	3.0 (1.50)	0.5 (0.10)	1.0 (0.25)	1.5 (0.30)	10.0 (0.10)	3.0 (0.05)	2.5 (0.10)	6.0 (0.20)
Claassenia sabulosa	1.5 (0.22)	5.5 (0.15)	4.5 (0.77)	4.0 (0.10)	3.0 (0.15)	4.5 (0.20)	3.0 (0.15)	2.5 (0.10)	3.0 (0.10)	4.5 (0.30)	3.0 (0.35)	2.0 (0.32)	1.5 (0.40)	1.5 (0.05)	2.0 (0.10)	4.0 (0.20)
Isoperla	1.0 (0.05)				0.5 (t)				0.5 (t)	6.0 (0.06)	11.0 (0.80)	3.5 (0.05)				
Isogenus										4.0 (0.04)						
Total Plecoptera	17.5 (2.37)	18.5 (0.85)	21.0 (1.45)	18.0 (0.85)	17.0 (1.65)	16.5 (3.05)	16.0 (2.50)	12.5 (1.70)	12.0 (3.05)	16.5 (0.70)	20.5 (1.85)	15.0 (1.47)	24.5 (1.70)	23.0 (1.30)	18.5 (1.45)	24.0 (2.15)
Coleoptera																
Elmidae	12.0 (0.02)	53.5 (0.10)	73.5 (0.10)	47.0 (0.10)	62.5 (0.10)	58.0 (0.10)	22.0 (0.03)	29.0 (0.10)	57.5 (0.10)	39.5 (0.05)	6.5 (0.05)	6.0 (0.05)	34.5 (0.10)	37.5 (0.05)	43.5 (0.10)	36.5 (0.10)
Amphizoa					0.5 (t)											
Diptera																
Chironomidae	214.0 (0.08)	111.5 (0.09)	194.5 (0.08)	97.5 (0.05)	25.5 (t)	21.5 (0.05)	43.5 (0.05)	154.5 (0.10)	485.0 (0.20)	344.5 (0.15)	321.0 (0.10)	188.0 (0.05)	162.0 (0.08)	241.0 (0.15)	22.0 (t)	114.0 (0.08)
Simulium	15.0 (0.03)	16.5 (0.05)	23.5 (0.01)	1.5 (0.02)	3.0 (0.05)	0.5 (0.02)	6.5 (0.05)	120.0 (0.25)	534.5 (0.90)	78.5 (0.20)	36.0 (0.10)	32.5 (0.05)	22.5 (0.05)	7.0 (t)	2.5 (0.05)	7.0 (0.10)

Table 2, continued.

Date of collection Collection transect	6-28-63 T-1	8-1-63 T-2	8-29-63 T-3	9-17-63 T-4	10-11-63 T-5	11-9-63 T-6	1-12-64 T-7	2-29-64 T-8	4-3-64 T-9	5-2-64 T-10	5-30-64 T-11	6-26-64 T-1	7-27-64 T-2	9-1-64 T-3	10-29-64 T-6	1-16-65 T-7
Diptera, continued																
Hexatoma	1.5 (0.05)	0.5 (0.50)		1.0 (0.10)		0.5 (0.10)	1.5 (0.15)	1.0 (0.05)	1.0 (0.10)		0.5 (t)	0.5 (0.03)	0.5 (0.03)	1.0 (0.20)	1.0 (0.10)	1.5 (0.15)
Antocha monticola	1.0 (0.03)						1.5 (0.05)	0.5 (0.03)	1.0 (0.05)	3.5 (0.05)	1.0 (0.05)	2.5 (0.02)	2.0 (0.05)			2.5 (0.05)
Cryptolabis	2.5 (0.03)		2.0 (0.01)	2.0 (t)	4.5 (0.05)	2.0 (0.03)	4.0 (0.03)	4.5 (0.05)	0.5 (0.05)	2.0 (0.05)	6.0 (0.05)	2.5 (0.02)				
Hemerodromiinae	6.0 (0.04)		0.5 (t)		0.5 (0.02)	0.5 (t)	2.0 (0.02)		1.0 (0.02)	2.5 (0.05)		7.5 (0.03)	0.5 (t)			0.5 (t)
Deuterophlebia nielson	3.5 (0.03)			1.0 (0.02)		7.0 (0.05)				0.5 (0.02)		3.5 (0.02)		0.5 (t)		
Atherix		0.5 (0.03)		0.5 (0.05)	0.5 (0.05)			1.0 (0.05)								3.5 (0.10)
Bezzia						0.5 (t)										
Total Diptera	243.5 (0.29)	129.0 (0.67)	220.5 (0.10)	103.5 (0.24)	34.0 (0.17)	32.5 (0.25)	59.0 (0.35)	281.5 (0.53)	1,023.0 (1.32)	431.5 (0.52)	364.5 (0.30)	237.0 (0.22)	187.5 (0.21)	249.5 (0.35)	25.5 (0.15)	129.0 (0.48)
Trichoptera																
Cheumatopsyche	13.5 (0.18)	55.0 (0.15)	68.0 (0.18)	94.0 (0.30)	163.0 (0.80)	110.5 (1.15)	118.5 (0.75)	86.5 (0.70)	152.5 (1.20)	42.5 (0.45)	28.0 (0.25)	19.5 (0.18)	62.0 (0.15)	46.5 (0.40)	212.0 (0.85)	368.0 (2.05)
Hydropsyche	71.0 (0.78)	19.0 (0.15)	50.0 (0.12)	38.5 (0.15)	136.5 (0.50)	68.0 (0.25)	93.5 (0.40)	92.0 (0.40)	122.0 (0.75)	109.5 (0.95)	94.0 (0.90)	113.5 (0.35)	55.0 (0.40)	40.5 (0.20)	78.5 (0.35)	100.5 (0.50)
Hydropsychidae pupae		4.5 (0.01)									50.5 (0.20)	8.0 (0.05)				
Brachycentrus	7.5 (0.03)	64.5 (0.10)	91.5 (0.33)	60.0 (0.30)	27.0 (0.25)	32.5 (0.20)	19.5 (0.20)	35.0 (0.45)	35.5 (0.40)	1.5 (0.05)	2.0 (0.05)	141.5 (0.10)	509.5 (0.50)	130.5 (0.39)	143.0 (0.45)	77.5 (0.55)
Micrasema							0.5 (0.02)		0.5 (0.04)	2.0 (0.05)	2.0 (0.05)	1.5 (0.01)				
Glossoma	58.0 (0.33)	69.5 (0.35)	33.5 (0.30)	1.0 (0.03)	3.0 (0.05)	17.5 (0.05)	19.5 (0.10)	22.0 (0.10)	36.5 (0.15)	30.0 (0.15)	47.5 (0.30)	86.0 (0.28)	97.5 (0.90)	38.5 (0.35)	90.0 (0.15)	227.5 (0.15)

Table 2, concluded.

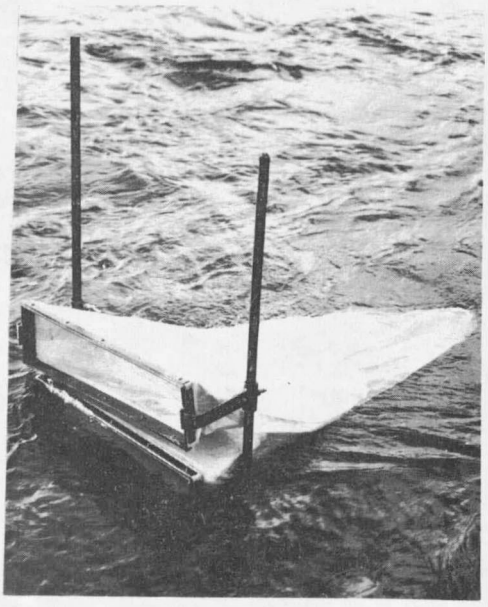
Date of collection Collection transect	6-28-63 T-1	8-1-63 T-2	8-29-63 T-3	9-17-63 T-4	10-11-63 T-5	11-9-63 T-6	1-12-64 T-7	2-29-64 T-8	4-3-64 T-9	5-2-64 T-10	5-30-64 T-11	6-26-64 T-1	7-27-64 T-2	9-1-64 T-3	10-29-64 T-6	1-16-65 T-7
Trichoptera, cont'd																
Protoptila cantha	0.5 (t)	9.5 (t)	1.5 (t)	6.0 (t)	37.0 (0.03)	50.5 (0.04)	17.0 (t)	11.0 (t)	18.5 (t)	8.0 (t)	17.0 (t)	12.0 (t)		12.5 (t)	49.5 (0.05)	32.5 (0.02)
Helicopsyche borealis	1.0 (0.02)		3.5 (0.05)		1.5 (0.05)	1.5 (0.05)	1.5 (0.03)	0.5 (0.02)	3.5 (0.05)		0.5 (0.03)	2.0 (0.02)	2.0 (0.02)		1.0 (0.05)	0.5 (0.02)
Leptocella					1.0 (0.05)	1.0 (t)	1.0 (t)	0.5 (t)								
Oecetis avara	5.0 (0.03)	1.5 (0.03)		2.0 (0.05)	1.5 (0.05)	2.0 (0.05)		1.0 (t)	5.0 (0.10)	0.5 (0.02)	3.0 (0.10)	3.5 (0.15)	2.0 (0.10)			1.0 (t)
Dolophiloides	1.5 (0.01)	1.0 (0.05)	0.5 (0.01)									0.5 (t)	0.5 (t)	2.5 (0.01)		
Lepidostoma		0.5 (0.02)	0.5 (0.03)								2.5 (0.05)	0.5 (0.03)	1.0 (0.03)			
Neophylax									0.5 (t)	0.5 (t)	0.5 (t)					
Hydroptilidae		17.5 (0.05)	1.5 (t)		5.0 (0.05)	2.0 (t)			2.5 (t)	1.0 (t)			0.5 (t)	1.5 (t)		
Total Trichoptera	158.0 (1.38)	242.5 (1.00)	250.5 (1.02)	201.5 (0.83)	375.5 (1.78)	285.5 (1.79)	270.5 (1.49)	248.5 (1.67)	377.0 (2.69)	195.5 (1.67)	247.0 (1.93)	388.5 (1.17)	730.0 (2.10)	272.5 (1.35)	574.0 (1.90)	807.5 (3.29)
Total Insecta	663.5 (5.60)	503.5 (3.47)	592.5 (3.64)	411.5 (2.60)	563.0 (4.70)	463.5 (6.71)	537.0 (5.62)	947.0 (5.95)	2,410.5 (11.46)	1,387.5 (7.59)	951.5 (6.15)	844.5 (4.17)	1,038.5 (5.03)	649.5 (3.39)	739.0 (4.60)	1,403.5 (7.22)
TOTAL BENTHOS	699.0 (5.80)	536.0 (3.67)	613.5 (3.78)	455.5 (3.10)	799.0 (5.20)	904.5 (7.61)	618.5 (5.82)	964.5 (6.15)	2,496.0 (11.81)	1,489.5 (8.09)	1,088.5 (6.60)	892.0 (4.37)	1,074.0 (5.58)	799.0 (3.92)	974.0 (5.58)	1,414.0 (7.52)

1/ Predominantly E. inermis with some E. margarita

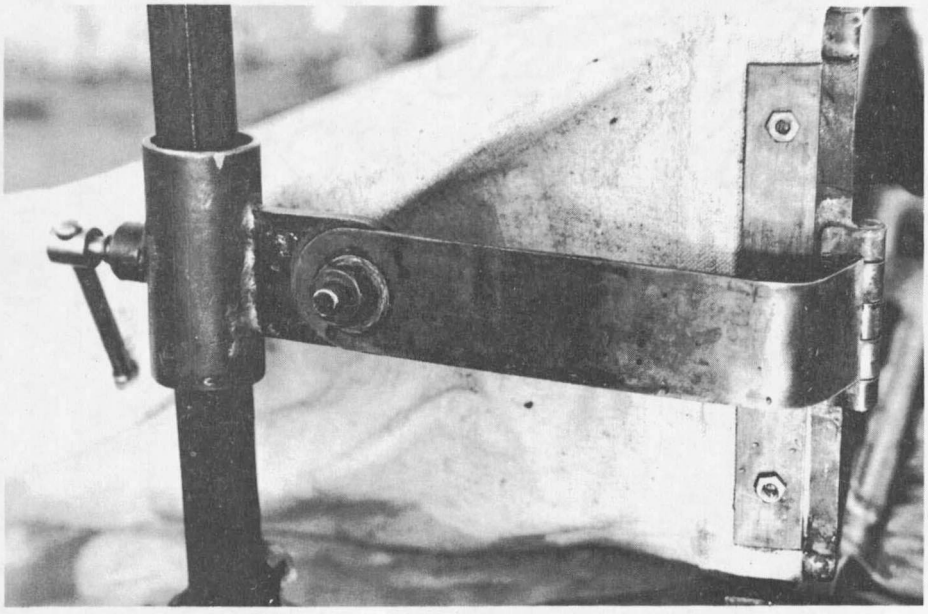
2/ Predominantly E. grandis with some E. flavilinea



A



B



C

Figure 3. Benthos and drift sampling equipment. (A) Benthos sampler showing frame (¼x¼ m) and collection net. (B) Drift nets showing position on steel rods which were driven into the streambed. (D) Detail of drift net showing hinged support arm of net and set screw device.

the organisms were preserved in 70% alcohol. Organisms were then sorted into taxonomic groups and counted. Volumes were determined by displacement in 70% alcohol after being placed on blotting paper at room temperatures for one minute.

Ten drift collections were made between August 1963 and August 1964 at intervals varying from three to nine weeks (Table 3). All were made at five fixed stations (Fig. 1) using nine drift nets along a transect (T-12) at the downstream end of the study riffle. The five stations were established to represent the various depths and velocities. One drift collection (54-72 net samples) usually consisted of samples taken six to eight different times over a 24-hour period representing various light intensities. Sampling times were reduced in January and February because of sub-zero air temperatures. No night samples were taken in January. The nine nets were set as follows: surface and bottom at two stations (D-1, D-3), surface, middle and bottom at one station (D-2), surface at D-4 and bottom at D-5. A drift sample was taken over an interval of 30 minutes except during April through June when the time was reduced to 10 minutes because of excessive plant material in the drift. During each collection velocity was determined in the opening of each net using a Gurley current meter. Drift nets had a nylon bag (7.9 meshes/cm) 1 meter in length and were attached to a brass frame with an opening of 15.2 x 60.9 cm. The frame had hinged support arms which terminated in a set screw device allowing the net to be fastened at any desired depth on two steel rods which were permanently set into the stream bed (Fig. 3). Drift samples were placed in plastic bags and preserved in 10% formaldehyde. In the labora-

Table 3. Numbers and volumes (cc) of animals and dry weights (g) of plant material for each drift collection (24 hour). Volumes in parentheses. t = trace.

Date of collection No. of sample periods	8-1,2-63 6	8-29,30-63 7	10-11,12-63 8	11-9,10-63 7	1-12-64 2 (Day only)	2-29-64 3	4-3,4-64 6	5-2,3-64 6	6-26,27-64 7	7-27,28-64 7
AQUATIC INVERTEBRATES										
Pulmonata										
Physa gyrina	124 (12.4)			154 (7.7)				346 (34.6)		171 (25.65)
Snail egg cluster		79 (2.37)						483 (32.2)		3,577 (113.24)
Ctenobranchiata										
Gyraulus deflectus	174 (18.9)							233 (0.2)		82 (16.4)
Sphaeriidae										
Pisidium casertum								8,756 (24.32)	3,012 (18.18)	
Oligochaeta										
Lumbriculidae	113 (22.6)		102 (5.1)	130 (13.0)	8,879 (591.87)	557 (55.7)	1,054 (70.3)	409 (40.9)	1,904 (11.44)	
Hirudinea (cocoon)										37 (1.1)
Ostracoda									4,402 (t)	
Amphipoda										
Gammarus									443 (22.15)	
Hydracarina						153 (t)				
Ephemeroptera										
Ephemerella [1]	26,914 (79.16)	17,724 (86.46)	4,459 (29.73)	15,852 (40.3)	46,076 (203.2)	85,094 (437.7)	1,381,222 (12,431.0)	1,268,241 (10,145.89)	210,027 (1,019.34)	14,432 (48.11)
Ephemerella [2]		382 (19.1)	474 (5.27)	130 (13.0)			6,165 (171.87)	16,496 (126.49)	11,233 (496.15)	400 (1.33)
Ephemerella heterocaudata							312 (0.31)	1,526 (4.58)	18,086 (58.53)	
Tricorythodes	4,082 (20.41)	1,014 (10.41)							777 (4.27)	5,525 (15.35)
Baetis	42,547 (64.46)	90,334 (102.96)	72,758 (156.47)	51,542 (11.65)	76,344 (175.59)	263,020 (751.47)	1,883,378 (7,535.5)	2,072,960 (6,218.88)	264,355 (658.14)	80,120 (91.72)
Paraleptophlebia	2,239 (17.22)	111 (0.85)		127 (0.38)				4,296 (35.8)	11,100 (81.4)	1,181 (14.76)
Epeorus albertae	9,471 (52.65)	870 (24.86)				262 (13.1)		1,646 (16.46)	53,126 (298.45)	13,885 (70.3)
Rhithrogena			133 (0.27)	520 (26.0)			3,281 (108.16)	8,950 (107.4)		
Ephemera simulans		71 (1.8)								

Table 3, continued.

Date of collection Collection transect	6-28-63 T-1	8-1-63 T-2	8-29-63 T-3	9-17-63 T-4	10-11-63 T-5	11-9-63 T-6	1-12-64 T-7	2-29-64 T-8	4-3-64 T-9	5-2-64 T-10	5-30-64 T-11	6-26-64 T-1	7-27-64 T-2	9-1-64 T-3	10-29-64 T-6	1-16-65 T-7
Odonata																
Ophiogomphus montanus	16.0 (0.83)	4.0 (0.45)	7.0 (0.90)	9.0 (0.40)	18.5 (0.65)	12.5 (1.10)	8.5 (0.80)	12.5 (0.70)	15.0 (0.60)	8.0 (0.40)	6.5 (0.50)	3.5 (0.15)	8.0 (0.60)	4.0 (0.19)	7.0 (0.60)	4.5 (0.30)
Argia rivida	4.0 (0.05)	1.0 (0.10)	0.5 (0.01)	1.5 (0.10)	1.5 (0.15)	0.5 (0.05)	0.5 (0.03)	0.5 (0.05)	1.0 (0.05)	4.0 (0.10)	0.5 (0.05)	9.0 (0.10)	2.0 (0.10)		0.5 (0.10)	0.5 (0.10)
Agrion aequabile									0.5 (0.05)							
Total Odonata	20.0 (0.88)	5.0 (0.55)	7.5 (0.91	10.5 (0.50)	20.0 (0.80)	13.0 (1.15)	9.0 (0.83)	13.0 (0.75)	16.5 (0.70)	12.0 (0.50)	7.0 (0.55)	12.5 (0.25)	10.0 (0.70)	4.0 (0.19)	7.5 (0.70)	5.0 (0.40)
Plecoptera																
Pteronarcys californica	9.0 (0.60)	7.5 (0.60)	11.5 (0.58)	10.5 (0.65)	12.0 (1.40)	9.0 (1.35)	8.0 (2.05)	7.0 (1.30)	5.5 (1.45)	1.5 (0.20)	5.5 (0.45)	8.0 (0.80)	13.0 (1.20)	18.5 (1.20)	14.0 (1.25)	14.0 (1.75)
Acroneuria pacifica	6.0 (1.50)	5.5 (0.10)	5.0 (0.10)	3.5 (0.10)	1.5 (0.10)	3.0 (1.50)	5.0 (0.30)	3.0 (0.30)	3.0 (1.50)	0.5 (0.10)	1.0 (0.25)	1.5 (0.30)	10.0 (0.10)	3.0 (0.05)	2.5 (0.10)	6.0 (0.20)
Claassenia sabulosa	1.5 (0.22)	5.5 (0.15)	4.5 (0.77)	4.0 (0.10)	3.0 (0.15)	4.5 (0.20)	3.0 (0.15)	2.5 (0.10)	3.0 (0.10)	4.5 (0.30)	3.0 (0.35)	2.0 (0.32)	1.5 (0.40)	1.5 (0.05)	2.0 (0.10)	4.0 (0.20)
Isoperla	1.0 (0.05)				0.5 (t)				0.5 (t)	6.0 (0.06)	11.0 (0.80)	3.5 (0.05)				
Isogenus										4.0 (0.04)						
Total Plecoptera	17.5 (2.37)	18.5 (0.85)	21.0 (1.45)	18.0 (0.85)	17.0 (1.65)	16.5 (3.05)	16.0 (2.50)	12.5 (1.70)	12.0 (3.05)	16.5 (0.70)	20.5 (1.85)	15.0 (1.47)	24.5 (1.70)	23.0 (1.30)	18.5 (1.45)	24.0 (2.15)
Coleoptera																
Elmidae	12.0 (0.02)	53.5 (0.10)	73.5 (0.10)	47.0 (0.10)	62.5 (0.10)	58.0 (0.10)	22.0 (0.03)	29.0 (0.10)	57.5 (0.10)	39.5 (0.05)	6.5 (0.05)	6.0 (0.05)	34.5 (0.10)	37.5 (0.05)	43.5 (0.10)	36.5 (0.10)
Amphizoa					0.5 (t)											
Diptera																
Chironomidae	214.0 (0.08)	111.5 (0.09)	194.5 (0.08)	97.5 (0.05)	25.5 (t)	21.5 (0.05)	43.5 (0.05)	154.5 (0.10)	485.0 (0.20)	344.5 (0.15)	321.0 (0.10)	188.0 (0.05)	162.0 (0.08)	241.0 (0.15)	22.0 (t)	114.0 (0.08)
Simulium	15.0 (0.03)	16.5 (0.05)	23.5 (0.01)	1.5 (0.02)	3.0 (0.05)	0.5 (0.02)	6.5 (0.05)	120.0 (0.25)	534.5 (0.90)	78.5 (0.20)	36.0 (0.10)	32.5 (0.05)	22.5 (0.05)	7.0 (t)	2.5 (0.05)	7.0 (0.10)

Table 3, continued.

Date of collection No. of sample periods	8-1,2-63 6	8-29,30-63 7	10-11,12-63 8	11-9,10-63 7	1-12-64 2 (Day only)	2-29-64 3	4-3,4-64 6	5-2,3-64 6	6-26,27-64 7	7-27,28-64 7
Simulium	1,947 (14.98)	1,726 (10.79)	338 (3.07)	215 (2.15)	6,178 (13.68)	274,599 (607.96)	303,672 (731.2)	33,227 (118.65)	9,674 (50.92)	2,832 (8.33)
Hexatoma	196 (39.2)					417 (83.4)				
Antocha monticola	198 (2.18)				311 (2.83)	153 (1.53)	1,963 (19.62)	1,226 (12.26)	591 (5.91)	88 (1.32)
Cryptolabis			91 (t)							
Hemerodromiinae	771 (19.28)	237 (2.63)								37 (t)
Atherix			30 (3.0)	87 (26.1)			416 (26.8)		10,911 (727.33)	
Total Diptera	53,939 (196.64)	60,379 (134.36)	2,978 (8.3)	7,504 (45.4)	18,790 (43.57)	283,110 (716.95)	344,474 (806.02)	121,861 (175.05)	110,101 (833.83)	50,799 (36.37)
Trichoptera										
Cheumatopsyche	1,802 (24.03)	2,985 (17.56)	4,612 (30.75)	4,816 (48.16)	2,283 (32.61)	4,745 (129.41)	2,971 (74.3)	3,688 (69.15)	10,130 (135.06)	2,582 (30.98)
Hydropsyche	3,694 (44.78)	5,498 (33.66)	5,953 (43.56)	5,780 (47.18)	16,860 (102.02)	5,332 (66.65)	20,589 (147.6)	23,932 (258.73)	138,541 (1,316.44)	29,515 (272.74)
Brachycentrus	22,453 (49.35)	7,774 (34.1)	16,672 (87.75)	5,091 (50.37)	1,940 (57.91)	2,704 (54.08)	8,546 (213.7)	1,474 (24.47)	715,877 (375.84)	88,922 (197.6)
Micrasema							78,929 (197.3)	439,021 (1,756.1)	16,470 (94.11)	
Glossoma	3,406 (30.96)	2,383 (25.08)		94 (t)	2,466 (12.82)	1,604 (14.43)	62 (0.62)	1,412 (28.24)	2,767 (92.23)	2,350 (36.15)
Protoptila cantha			288 (t)				109 (t)	1,218 (0.4)		
Helicopsyche borealis	204 (0.51)								530 (13.25)	
Leptocella		125 (1.0)	412 (10.3)	31 (1.55)		152 (7.6)			148 (0.8)	
Oecetis avara	122 (4.44)	228 (7.59)			44 (t)		1,401 (105.1)		987 (13.25)	119 (2.38)
Dolophiloides		640 (1.92)	368 (1.1)				33 (0.3)			
Lepidostoma	82 (4.1)									
Hydroptilidae	232 (t)	57 (t)		34 (t)						
Rhyacophila							133 (0.66)			
Total Trichoptera	31,995 (158.17)	19,690 (120.91)	28,305 (173.46)	15,846 (147.26)	23,593 (205.36)	14,537 (272.17)	112,773 (739.58)	470,745 (2,137.09)	885,541 (2,040.98)	123,488 (548.95)

Table 3, continued.

Date of collection No. of sample periods	8-1,2-63 6	8-29,30-63 7	10-11,12-63 8	11-9,10-63 7	1-12-64 2 (Day only)	2-29-64 3	4-3,4-64 6	5-2,3-64 6	6-26,27-64 7	7-27,28-64 7
Lepidoptera										
Elophila								842 (2.53)		
Total Insecta	181,555 (746.37)	199,112 (867.89)	112,015 (583.18)	97,224 (761.54)	168,081 (870.44)	650,304 (2,516.59)	3,737,511 (22,146.28)	4,078,821 (20,097.16)	1,860,798 (10,771.53)	304,178 (1,099.93)
Total Aquatic Invertebrates	181,966 (800.27)	199,191 (870.26)	112,117 (588.28)	97,508 (782.24)	176.960 (1,462.31)	651,014 (2,572.29)	3,738,565 (22,216.58)	4,089,048 (20,229.38)	1,870,559 (10,823.30)	308,045 (1,256.32)
EMERGING AND ADULT AQUATIC INSECTS										
Ephemeroptera	83,476 (419.22)	73,852 (348.14)	166,841 (392.41)	39,649 (248.56)		343 (1.97)	657 (3.60)	281,131 (1,127.27)	3,300,140 (22,496.33)	251,481 (446.95)
Plecoptera										
Claassenia sabulosa										80 (32.0)
Alloperla pallidula	145 (1.90)									
Isoperla	3,087 (41.53)								494 (13.83)	825 (17.33)
Isogenus tostonus									247 (6.91)	
Total Plecoptera	3,232 (43.43)								741 (20.74)	905 (49.33)
Diptera	62,625 (31.02)	102,237 (207.13)	281,193 (249.13)	5,571 (17.66)	12,300 (52.7)	128,148 (198.37)	889,443 (1,206.97)	802,636 (665.39)	316,105 (341.39)	38,335 (41.4)
Chironomidae										
Simulium	704 (11.73)	1,726 (17.26)	1,394 (12.57)	1,990 (19.9)		1,080 (6.69)	18,442 (65.83)	258,563 (923.33)	105,101 (238.39)	2,940 (20.9)
Tipulidae	10,761 (43.04)	1,495 (23.6)	16,412 (51.29)						16,877 (76.62)	5,447 (35.8)
Duterophlebia nielson	163 (0.33)	1,463 (2.93)	1,480 (2.96)	977 (1.95)					277,131 (554.26)	4,287 (8.57)
Hemerodromia	564 (3.63)	705 (4.53)							577 (3.7)	4,534 (29.75)
Aedes fitchii	70 (0.14)		140 (0.28)							
Total Diptera	74,887 (89.89)	107,626 (255.45)	300,619 (316.23)	8,538 (39.51)	12,300 (52.7)	129,228 (205.06)	907,885 (1,272.8)	1,061,199 (1,588.72)	715,791 (1,214.36)	55,543 (136.42)
Trichoptera	35,015 (384.46)	7,418 (37.09)	4,088 (22.71)	1,356 (1.29)		567 (0.6)	2,631 (7.89)	3,694 (23.64)	176,104 (1,148.2)	90,157 (587.82)
Total emerging and adult aquatic insects	196,610 (937.07)	188,896 (640.68)	471,548 (731.35)	49,543 (289.36)	12,300 (52.7)	130,138 (207.63)	911,173 (1,284.29)	1,346,024 (2,739.63	4,192,776 (24,879.63)	398,086 (1,220.52)

Table 3, continued.

Date of collection No. of sample periods	8-1,2-63 6	8-29,30-63 7	10-11,12-63 8	11-9,10-63 7	1-12-64 2 (Day only)	2-29-64 3	4-3,4-64 6	5-2,3-64 6	6-26,27-64 7	7-27,28-64 7
FISH AND FISH EGGS										
Salmo trutta (young)							4,535 (425.16)	5,152 (1,002.24)		
Salmo gairdneri (young)			102 (224.4)							80 (16.0)
Prosopium williamsoni (eggs)			284 (5.1)	12,882 (231.88)	2,182 (54.31)	7,211 (179.75)				
Prosopium williamsoni (young)					1,093 (27.23)	21,632 (539.25)	1,865 (30.77)			
Rhinichthys cataractae (young)	13,531 (254.4)	421 (34.52)		381 (139.83)					14,071 (49.11)	9,623 (40.32)
Rhinichthys cataractae (adult)	347 (954.3)	57 (159.6)								80 (44.0)
Cottus bairdi (young)									122 (0.6)	
Unidentified fish eggs	730 (0.4)									
Total fish and fish eggs	14,608 (1,209.1)	478 (194.12)	386 (229.5)	13,263 (371.71)	3,275 (81.54)	28,843 (719.0)	6,400 (455.93)	5,152 (1,002.24)	14,193 (49.71)	9,783 (100.32)
TERRESTRIAL ARTHROPODS										
Hemiptera	1,022 (8.48)	30,961 (29.47)	1,174 (23.48)						3,237 (92.48)	10,711 (50.04)
Homoptera	23,629 (64.47)	86,497 (146.08)	224,499 (322.03)						7,890 (19.64)	39,674 (84.06)
Neuroptera	277 (2.83)	692 (7.07)	424 (4.33)							14,552 (148.59)
Coleoptera	3,235 (84.37)	2,347 (46.94)	1,679 (55.97)	170 (8.5)					49,482 (195.95)	15,040 (270.37)
Diptera	12,385 (95.51)	9,809 (73.98)	12,564 (77.59)	513 (8.55)					47,355 (189.23)	103,060 (277.57)
Lepidoptera	195 (29.25)									178 (35.6)
Hymenoptera	13,798 (38.77)	114,144 (410.69)	2,884 (21.36)				254 (2.54)	200 (0.2)	30,466 (327.05)	24,489 (237.68)
Arachnida	1,163 (33.23)	88 (8.8)	76 (0.8)						4,030 (161.2)	3,921 (41.27)
Total terrestrial arthropods	55,704 (356.91)	244,538 (723.03)	243,300 (505.56)	683 (17.05)			254 (2.54)	200 (0.2)	142,460 (985.55)	211,625 (1,145.18)

Table 3, concluded.

Date of collection	8-1,2-63	8-29,30-63	10-11,12-63	11-9,10-63	1-12-64	2-29-64	4-3,4-64	5-2,3-64	6-26,27-64	7-27,28-64
	6	7	8	7	2 (Day only)	3	6	6	7	7
TOTAL ANIMAL DRIFT	448,888 (3,303.35)	633,103 (2,428.09)	827,351 (2,054.69	160,997 (1,460.36	192,535 (1,596.55)	809,995 (3,498.92)	4,656,392 (23,959.34)	5,440,424 (23,971.45)	6,219,988 (36,738.19)	927,539 (3,722.34)
Number/1,000 m^3 Volume/1,000 m^3	433.70 (3.19)	706.95 (2.71)	941.86 (2.34)	166.16 (1.51)	224.82 (1.86)	922.106 (3.98)	4,604.54 (23.69)	4,319.55 (19.03)	3,234.15 (19.10)	563.67 (3.34)
TOTAL PLANT DRIFT (dry weight/24 hours)		10,557.22	2,084.82	6,441.12	21,323.0	42,912.81	61,222.0	52,581.30	94,212.29	8,728.99

1/ Predominantly E. inermis with some E. margarita

2/ Predominantly E. grandis with some E. flavilina

tory the same techniques were used for drift as for benthos. The number of organisms in each net sample was calculated for 1000 m^3 of discharge. The data from all nine nets were expanded to provide an estimate of the drift for the total flow of the river during a sample period. The mean number of organisms per unit of time was then calculated for the daylight period (sunrise to sunset) and for the dark period (sunset to sunrise). An estimate of the total number of drift organisms passing the drift transect during a 24-hour period was calculated from these means.

DATA AND RESULTS

Benthos

The macroinvertebrate benthos population of the study riffle was estimated from 16 collections containing 128 samples taken in an area of 1,425 m^2. Each collection was limited to eight samples because a larger number could not be sorted in a reasonable length of time. Sorting was difficult because large amounts of plant material were present. One collection, consisting of 32 samples, was taken on one date in an attempt to test sampling efficiency. Estimates of total numbers were made for 8, 16 and 32 samples. There was no significant difference in estimates for these three lots except for species which appeared in low numbers. The lot with 32 samples contained 37 taxonomic groups while that of eight samples contained only 33 of these.

Standing Crop

The number and volume of each taxonomic group per m^2 and the percentage that each order contributed to the total volume of each collection is shown in Table 2. During one annual cycle the total benthos was lowest in

numbers and volume during September and highest during April (Fig. 4). Total numbers and volumes of benthos taken in the collections generally increased during the period of October through March as the organisms increased in size. The rapid decrease in total numbers and volumes during April through June was due to the emergence of adults. The major fluctuations resulted from changes in the numbers and sizes of aquatic insects, particularly Ephemeroptera, Trichoptera and Diptera. Sampling was inadequate for taxa with high concentrations in restricted portions of the riffle and for those with low numbers. Needham and Usinger (1952) have discussed the variability in distribution of benthos in a riffle and the large number of samples needed to adequately sample all taxa in a riffle.

Standing crop estimates for all benthos varied from a minimum number of 455.5/m^2 with a volume of 3.10 cc/m^2 in September 1963 to a maximum of 2,496.0/m^2 with a volume of 11.81 cc/m^2 in April 1964. The average standing crop of 1,075.5 organisms/m^2 with a volume of 6.44 cc/m^2 was computed from 10 collections taken from September 1963 through August 1964 representing a one-year cycle. Total numbers and volumes of benthos were greater in collections made during 1964-65 than those taken at comparable times during 1963-64. The September 1964 collection contained a 77% greater number and a 20% greater volume than the September 1963 collection while the January 1965 collection was 129% greater in number and 29% greater in volume than the January 1964 collection. These increases were primarily due to increased numbers of Ephemeroptera and Trichoptera. Winter conditions were probably involved in this change for there was much anchor ice in the stream during the winter of 1962-63 and a large

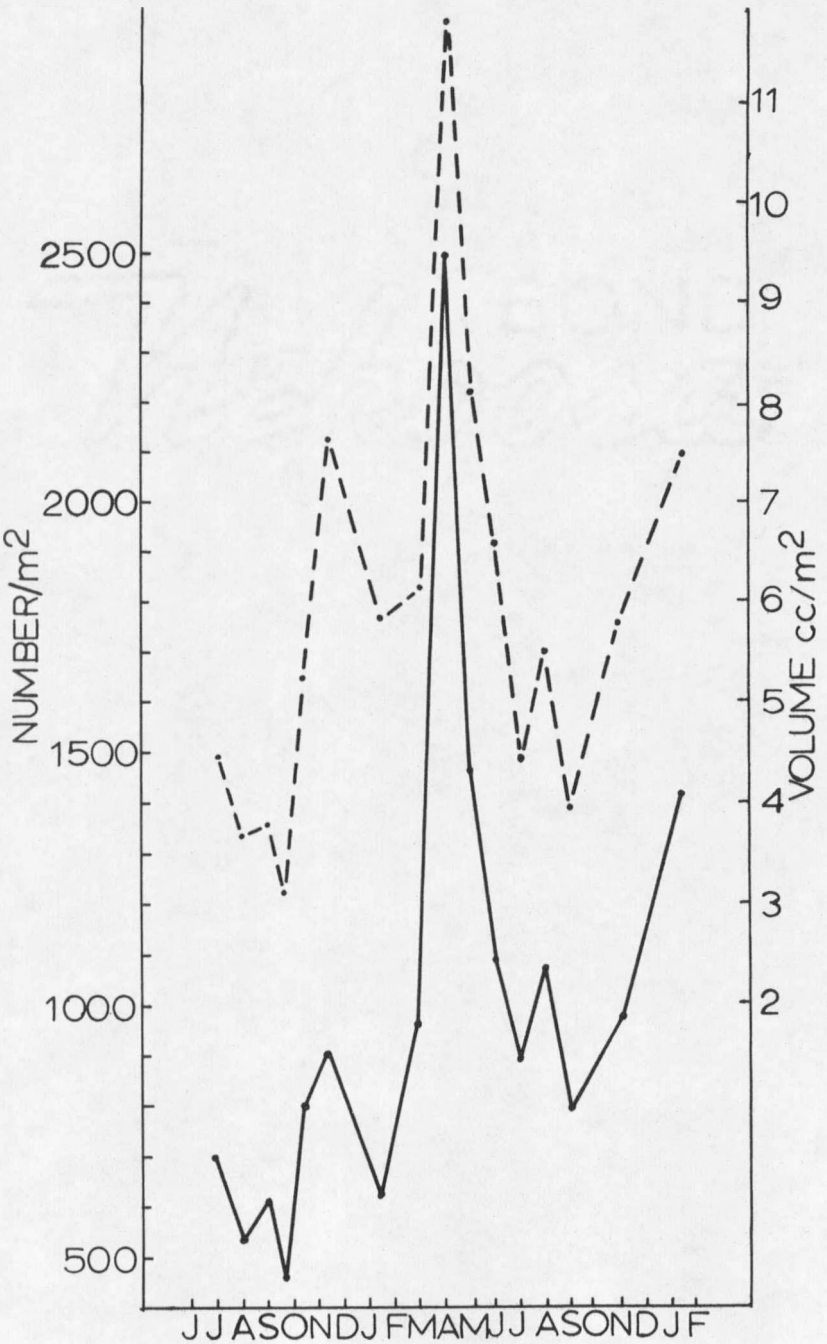


Figure 4. Total numbers and volumes of benthos for all collections (June 1963-January 1965).

ice jam covered the study riffle and extended for some distance upstream while there was no ice formed in the river in the milder winters of 1963-64 and 1964-65. Standing crop estimates by various workers for several Rocky Mountain streams are given in Table 4. Total numbers and volumes of benthos in the present study were less than those reported for an area of the lower Madison River, about equal to those of the lower Firehole River and generally lower than those reported for other streams in the Rocky Mountain area.

The benthos fauna of the study riffle in the Madison River is typical of unpolluted waters as described by Gaufin and Tarzwell (1965). There were 55 taxa identified with several of these identified only to family or genus. Aquatic insects of six orders were the dominant organisms and representatives of Gastropoda, Pelecypoda, Oligochaeta, Turbellaria and Arachnida also taken (Table 2). The contributions of each taxon is discussed in the next section.

Benthos organisms had definite distribution patterns in relation to the velocity and/or substrate of the riffle. Macan (1963) discussed current and substrate and concluded that the current determines the substrate and vegetation and these in turn greatly influence the composition of the fauna. In the Madison River Ephemerella, Baetis, Epeorus, Rhithrogena, Hydropsyche, Cheumatopsyche and Glossoma were most abundant in areas with high velocities and where cemented large gravel predominated. Chironomidae was abundant throughout the riffle. Simulium was slightly more abundant in areas with less current while Physa, Pisidium, Lumbriculidae, Ophiogomphys, Argia, Acroneuria, Helicopsyche and Brachycentrus were

Table 4. Benthos standing crop estimates for some Rocky Mountain streams.

Name of stream	Location	Number/m^2	Volume or weight/m^2	Reference
Madison River	Yellowstone National Park	1,075.5	6.44 cc	Heaton
Madison River (lower)	Montana	820.0[1/]	15.82 cc	Graham and Scott (1959)
Ruby River	Montana	1,207.0[1/]	38.50 cc	Graham and Scott (1959)
Firehole River	Yellowstone National Park	1,214.0	9,895.00 mg	Armitage (1958)
Gardiner River	Yellowstone National Park	3,261.9	32,085.40 mg	Armitage (1958)
Willow Creek	Utah	8,640.0	19.26 cc	Moffett (1936)
Provo River	Utah	2,076.0	28.84 cc	Gaufin (1958)
Horton Creek	Arizona	17,721.0	34.75 cc	Tarzwell (1937)
St. Vrain Creek	Colorado	610.0	2.50 cc	Pennak and Van Gerpen (1947)

[1/] Samples from June and July only

more abundant near shore where there was low velocity and uncemented sand and small gravel. Distribution of most taxa in the study riffle was similar to those found in other streams (Percival and Whitehead, 1929; Linduska, 1942; Pennak and Van Gerpen, 1947; Scott, 1958).

BENTHOS INVERTEBRATES

Turbellaria

The number of Planariidae taken was not representative of the population since many of these undoubtedly passed through the net.

Mollusca

Physa gyrina and Gyraulus deflectus were present but only Physa gyrina was of importance to the standing crop. This species made up 0.4% of the number and 1.7% of the volume of all benthos. No seasonal trends in abundance were apparent. It was found only in areas with low velocity and about 88% were in samples taken adjacent to the west shore. Pisidium casertum was the only Pelecypod taken. It comprised 9.5% of the number and 3.0% of the volume of all benthos and was present in all collections with great variations in numbers. The largest numbers were taken during September through November. Eighty-eight percent were found in samples taken adjacent to the west shore.

Oligochaeta

Lumbriculidae was the only family taken and it comprised 0.8% of the number and 2.4% of the volume of all benthos. It was present in all collections with the greatest number in June when most individuals were small and immature. These worms were dispersed throughout the riffle in the sand and silt accumulated by vegetation and in clumps of moss. The largest number was taken 1 m from the west shore.

Insecta

Aquatic insects were the most abundant organisms and contributed the largest volume in each collection. There were seven orders comprising 89% of the number and 93% of the volume of all benthos. The largest number and volume were taken in April and the lowest in September.

Ephemeroptera. Seven genera of this order were taken and these comprised 22.5% of the number and 16.3% of the volume of all benthos. Ephe-

merella was the most abundant genus and made up 69.3% of the number and 72.2% of the volume of all Ephemeroptera while Ephemerella inermis was the most abundant species. One group of Ephemerella was predominantly E. inermis with some E. margarita identified from the July collection. This group comprised 65.8% of the number and 63.8% of the volume of all Ephemeroptera. Highest numbers and volumes were in the April and May collections and the lowest in August and September. Numbers were greater in October 1964 and January 1965 than in collections taken at comparable times in 1963-64. They were numerous throughout the riffle but were most abundant in areas with high velocity. The largest emergence occurred during May and June but extended from April through August. A second group of Ephemerella was predominantly E. grandis with some E. flavilinea identified from a collection containing late instars. This group made up 4.3% of the number and 7.8% of the volume of all Ephemeroptera and was most abundant in the May collection. Emergence occurred during June. Ephemerella heterocaudata heterocaudata contributed less than 0.5% of the number and volume of Ephemeroptera.

Baetis was the second most abundant genus. It constituted 29.3% of the number and 19.1% of the volume of all Ephemeroptera. The largest number was present in April and the smallest during July through November. Baetis was distributed throughout the riffle with the largest number occurring in areas with highest velocity. Emergence was observed from late February through November with the greatest numbers during April through June.

The remaining five genera of Ephemeroptera were relatively low in

abundance. Epeorus albertae made up 2.6% of the number and 4.5% of the volume of all Ephemeroptera, Tricorythodes 1.0% of the number and volume and Rhithrogena, Paraleptophlebia, Ephemera simulans together constituted about 0.6% of the number and 3.0% of the volume.

Odonata. Three species of this order were taken and these contributed 1.0% of the number and 10.9% of the volume of all benthos. The number in each collection was low and varied little during the year. Individuals varied greatly in size. Ophiogomphus montanus was the most abundant species and made up 83.8% of the number and 88.5% of the volume of Odonata. It was taken throughout the riffle but about 70% were in samples 1 m from the west shore. Argia rivida comprised 16.2% of the number and 11.5% of the volume of Odonata. Practically all were taken adjacent to the west shore. One Agrion aquasable was taken. O. montanus and Argia rivida were observed emerging in early July 1964.

Plecoptera. Five genera of this order were taken and these contributed 1.8% of the number and 28.6% of the volume of all benthos. Numbers and volumes in the collections remained relatively constant throughout the study period. Pteronarcys californica was the most abundant species and made up 53.5% of the number and 59.9% of the volume of all Plecoptera. It was found throughout the riffle in association with unconsolidated large gravel and rubble. The emergence period was from early June into early July with the largest number in late June 1964.

Acroneuria pacifica made up 20.8% of the number and 23.5% of the volume of Plecoptera and was present in all collections. This species was found throughout the riffle but was most abundant adjacent to each

shore. The emergence period extended from late June through July.

Claassenia sabulosa contributed 17.3% of the number and 13.0% of the volume of Plecoptera and was present in all collections. It was found throughout the riffle. Emergence was from late June through July.

Isoperla made up about 8% of the number and 3.5% of the volume of all Plecoptera. This group was sorted only to genus but subsequent identification showed that Isoperla pinta was the most abundant species with I. fulva also present. Isoperla was collected mainly from April through June. Emergence was observed during June and July. A small number of Isogenus was taken in the May collection.

Coleoptera. Elmidae constituted 3.9% of the number and 1.3% of the volume of all benthos. Adults and larvae were present in all collections with the lowest number in May and June. They were distributed about equally throughout the riffle. I identified this group to family but Zaitzevia parvula and Optioservus castanipennis were subsequently identified by a specialist. A single Amphizoa was taken.

Diptera. Seven families of this order were taken and constituted 23.8% of the number and 6.5% of the volume of all benthos. The largest number and volume occurred in April and the smallest in September, October and November. Chironomidae were identified only to family. Simuliidae, Rhagionidae, Empididae, Ceratopogonidae and Duterophlebiidae had one genus each and Tipulidae contained three genera. Chironomidae made up 73.0% of the number and 21.3% of the volume of all Diptera. Numbers and volumes of this family were probably underestimated in most collections since many were small enough to pass through the net. The

largest number and volume were found in the April collection and the smallest during October and November. Chironomidae was found in large numbers at all sample stations. Emerging adults were observed throughout the year with the largest number occurring during April through June.

Simuliidae (Simulium) contributed 24.2% of the number and 31.4% of the volume of all Diptera. The largest number was present in April and the smallest during the period from September through January. Simulium was found in all sample areas but was slightly more abundant where velocities were low. Emergence was greatest during April and May but continued into October. I was unable to separate the species from collections but Simulium arcticum and Simulium tuberosum were subsequently identified by a specialist.

Tipulidae made up 1.6% of the number of all Diptera. Of these Hexatoma constituted 17.9% of the volume while Cryptolabis and Antocha monticola each contributed about 6%.

Atherix (Rhagionidae), Hemerodromiinae (Empididae), Bezzia (Ceratopogonidae), and Dûterophlebia nielson (Duterophlebiidae) were collected but contributed little to the standing crop. All except Atherix were small and many probably escaped through the net.

Trichoptera. Fifteen genera of this order were found and constituted 35.4% of the number and 28.5% of the volume of all benthos. Trichoptera were abundant in all collections and made their greatest contribution to the standing crop in the September-October 1964 and January 1965 collections. Two genera of Hydropsychidae were abundant in most collections. Cheumatopsyche contributed 29.3% of the number and 36.0% of the volume of

all Trichoptera. It was most abundant during October through April and least in June. Numbers were greater in the October 1964 and January 1965 collections than in those taken a year earlier. The largest volumes were taken in April 1964 and January 1965 collections. Hydropsyche made up 22.8% of the number and 26.4% of the volume of all Trichoptera with the largest volume in May. The largest number was taken in October and the smallest in August. These two genera were distributed throughout the riffle but were most numerous in areas of high velocity. Emergence occurred from April through October with the largest number of Cheumatopsyche emerging in April and those of Hydropsyche in July.

Brachycentrus and Micrasema were the only genera of Brachycentridae taken. Brachycentrus contributed 24.6% of the number and 15.9% of the volume of all Trichoptera. It was most numerous during August 1963 and July 1964 and least during May and was more abundant in the 1964-65 collections than in those from comparable times in 1963-64. The largest volume was found in February 1964 and January 1965. It was distributed throughout the riffle but was most abundant adjacent to each shore. It was found in both high and low velocities. Emergence occurred in April and May. These were sorted only to genus but Brachycentrus occidentalis (the most abundant species) and B. americanus were subsequently identified by a specialist. Micrasema contributed 0.1% of the number of all Trichoptera and was found during January through June.

In the Glossosomatidae, Glossoma contributed 15.7% of the number and 13.8% of the volume of all Trichoptera. The largest numbers were found in August 1963, July 1964 and January 1965 collections. It was more

abundant in 1964-65 collections than in those made on comparable dates in 1963-64. Glossoma was found throughout the riffle with the largest numbers in areas of high velocity. Pupae were taken in all collections with emergence starting in April and continuing into October. Protoptila cantha was present in most collections and made up 5.1% of the total number of all Trichoptera but was of insignificant volume. Many undoubtedly passed through the net so the standing crop was probably underestimated. June was the only month when emergence was observed.

Hydroptilidae was found in some collections making up only 0.6% of the total number and an insignificant volume of all Trichoptera. Many probably passed through the net. These were sorted only to family but Hydroptila hemata, Hydroptila consimilis, Neotrichia and Leucotrichia were subsequently identified by a specialist. Helicopsyche borealis was present in most collections but in low numbers. It made up about 1% of the volume of Trichoptera and occurred adjacent to the shore. Of the Leptoceridae, Oecetis avara was taken in most collections and made up 2.5% of the volume of all Trichoptera. A few Leptocella were also found. Dolophiloides (Philopotamidae), Lepidostoma (Lepidostomatidae) and Neophylax (Limnephilidae) occurred occasionally in the collections.

Drift

Drift-Standing Crop

Estimates of standing crop of macroscopic drift animals and plants were made for each of 10 collections taken at intervals during one year. Drift animals consisted primarily of aquatic invertebrates, however, fish, fish eggs and terrestrial arthropods were abundant in some collections.

Drift animals were classified into the following categories: aquatic invertebrates, including all immature and adults normally found in the benthos and nekton; emerging and adult aquatic insects, including pupae and sub-imago stages; fish and fish eggs; terrestrial arthropods.

Number and volume estimates of animals and dry weight of plants in the drift for each collection (24 hours) are shown in Table 3. Drift organisms were present in the Madison River throughout the year and at all times of the day and night and the mean for all collections was 203,172 organisms and the volume was 10,273.33 cc/24 hours. Animal drift was greatest in the June collection when there were 6,219,988 organisms with a total volume of 36,738.19 cc/24 hours and least in November when there were 160,997 organisms with a volume of 1,460.36 cc. Aquatic invertebrates and emerging or adult aquatic insects made up 92.1% of the total volume of drift while fish and fish eggs contributed 4.3% and terrestrial arthropods 3.6%. The volume of each of the categories of drift varied during the year as did the proportion each contributed to the total drift but aquatic invertebrates usually made up the largest proportion of the drift (Fig. 5). The drift contained a wide variety of organisms with 60 taxa identified from among the aquatic invertebrates, 41 taxa from the emerging and adult aquatic insects, five species of fish and seven orders of terrestrial insects.

Drift of this magnitude involving practically all aquatic species is obviously an important aspect in the ecology of the Madison River as has been reported for other streams (Müller, 1954; Waters, 1961, 1962, 1965). Aquatic organisms constitute a greater proportion of the drift in the

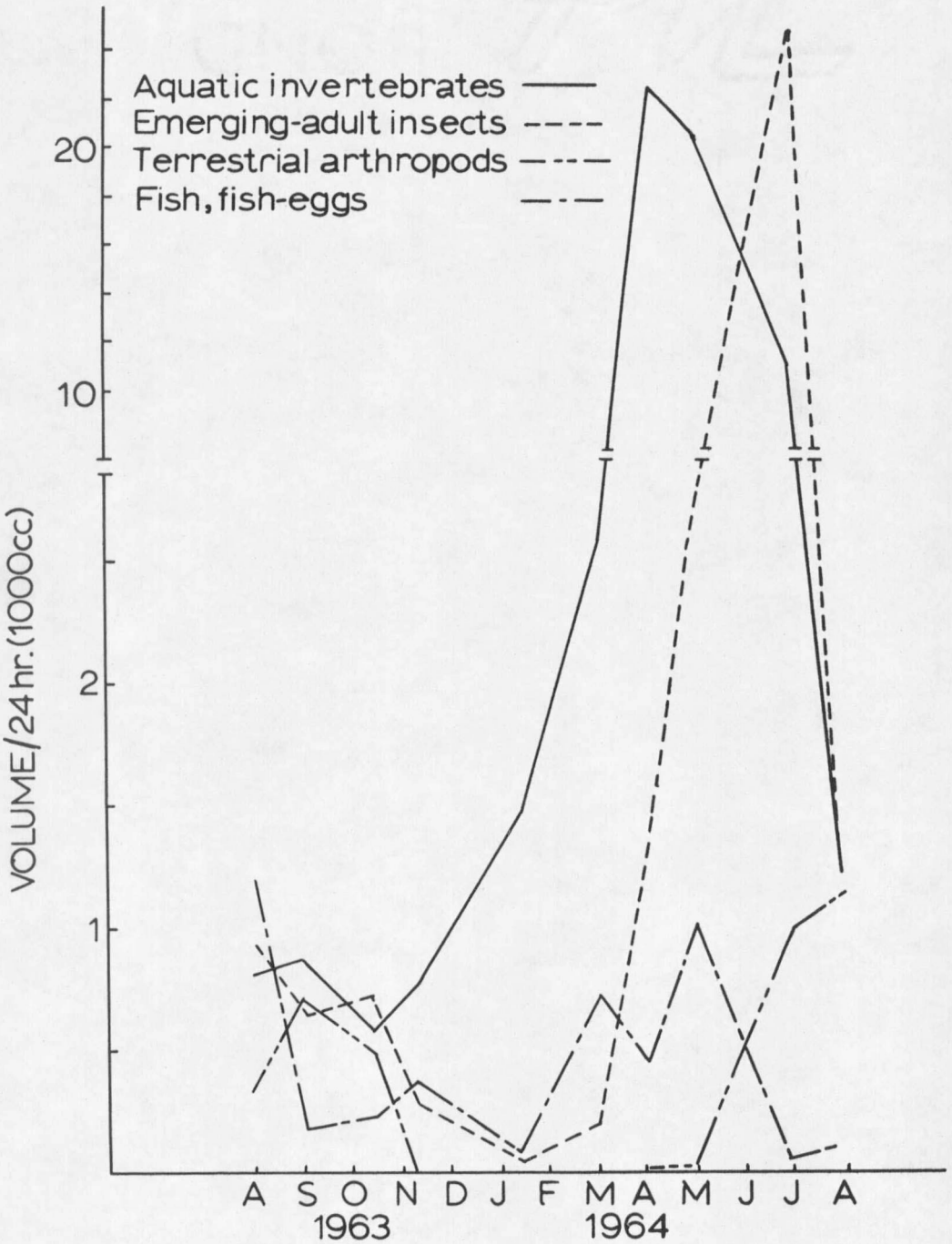


Figure 5. Volumes of the major groups of organisms in the drift for each collection (24 hours).

Madison River with terrestrial arthropods less important than reported by Needham (1928, 1938).

No published estimates of drift for a large coldwater stream comparable to the Madison River have been found. In a small Swedish stream (5 m wide) Müller (1954) reported summer drift collections containing as high as 192,000 benthos organisms with a weight of 288 g/24 hours. Lennon (1941) measured total drift in a New Hampshire stream (18-20 ft wide) during July and August and found a maximum of 45.21 g/24 hours. Waters (1964) reported total drift of Baetis from 0.04 to about 1 g/day and Gammarus total drift of from 0.5 to 6.7 g/day for a small Minnesota stream. Horton (1961) estimated drift of 15,000 organisms with a weight of 70.3 g/24 hours in January and 3,690 organisms weighing 1.78 g in April in an English stream. In a warmwater stream Denham (1938) reported the drift of benthos (benthoplankton) was as high as 6.81 organisms/m^3 of flow but the estimate was probably low since he sampled only during daylight. Berner (1951) estimated the total drift of the Missouri River was 64,000,000 organisms weighing 450 pounds in one 24-hour period which amounted to about 10% of his estimate for the benthos standing crop.

Plant drift was found throughout the year with a mean dry weight of 30,006.36 g/24 hours. Total weight of plant drift was highest in June when the dry weight was 94,212.29 g/24 hours and lowest in October when it was 2,084.82 g/24 hours. The volume of plant drift increased during November through early April, although the flow remained about constant, as senescent and dead plant fragments were washed downstream. Increased flows of late April through June completed the removal of this plant

material. Some benthos organisms entered the drift samples by clinging to plant fragments but this was not true for most species since individual drift samples which contained no plant fragments had about equal numbers of benthos organisms.

AQUATIC INVERTEBRATES

Aquatic invertebrates made up 56.2% of the total number and 60.0% of the volume of all drift animals. The largest numbers and volumes were found in the April and May collections and the smallest in October and November. This group contributed the largest volumes in all but the June, August and October collections.

Mollusca

Physa gyrina, Gyraulus deflectus and unidentified snail egg clusters together contributed 0.1% of the number and 0.3% of the volume of aquatic invertebrates. Pisidium casertum was taken only in May and June when discharge was greatest. It comprised 0.1% of the number and 0.1% of the volume of aquatic invertebrates.

Annelida

Representatives of Lumbriculidae (Oligochaeta) were taken throughout the year and contributed 0.1% of the number and 1.3% of the volume of aquatic invertebrates. They were most abundant in the January collection when several individuals were found in a clump of moss. One Hirudinea cocoon, containing well developed young, was taken in July.

Crustacea

Ostracoda and Amphipoda (Gammarus) were taken in June and were less

than 0.05% of the number and volume of aquatic invertebrates.

Arachnida

Only a few Hydracarina were taken, but others probably passed through the nets.

Insecta

Aquatic insects, of eight orders, contributed 99.7% of the number and 98.1% of the volume of aquatic invertebrates with the largest numbers and volumes in April and May and the smallest in October and November.

Ephemeroptera. Eight genera of Ephemeroptera were found and contributed 71.3% of the number and 68.4% of the volume of all aquatic invertebrates. The genus Ephemerella made up 38.4% of the number and 60.4% of the volume of all Ephemeroptera. E. inermis was the most numerous species. One group of Ephemerella, composed predominantly of E. inermis but with E. margarita and possibly other species, comprised 37.7% of the number and 58.2% of the volume of Ephemeroptera. The largest number and volume were in April and the smallest in October. A second group of Ephemerella (predominantly E. grandis with some E. flavilina) contributed 0.4% of the number and 2.0% of the volume of Ephemeroptera and was most abundant during May and June. Ephemerella heterocaudata heterocaudata contributed only 0.2% of the number and 37.5% of the volume of Ephemeroptera. Baetis was abundant in all collections with the largest numbers and volumes in April and May and the smallest in November. A few Centroptilum were identified from the April collection only and are included in the estimates for Baetis. Epeorus albertae made up 1.0% of the number and 1.1% of the volume of Ephemeroptera. It was most numerous in

June and was absent during October through January. Tricorythodes contributed 0.1% of the number and volume of Ephemeroptera. Paraleptophlebia, Rhithrogena and Ephemera simulans together made up 0.4% of the number and 1.0% of the volume of Ephemeroptera. Paraleptophlebia was most abundant in June, Rhithrogena in May and Ephemera simulans was found only during August.

Odonata. Odonata constituted 0.1% of the number and 3.1% of the volume of aquatic invertebrates. Ophiogomphus montanus was present in all collections contributing 84.0% of the number and 81.4% of the volume of Odonata. It was most numerous in February but contributed the greatest volume in November. Argia rivida contributed 16.0% of the number and 18.6% of the volume. It was present in only four collections and made the largest contribution in May.

Plecoptera. Five genera were taken and these made up 3.1% of the number and 9.6% of the volume of aquatic invertebrates. This order made the largest contribution to numbers and volumes of drift in June and the smallest in January. Isoperla comprised 82.2% of the number and 54.3% of the volume of Plecoptera. It was most abundant in June and was absent during September and October. Although Isoperla was not sorted to species in this study I. pinta and I. fulva were later identified. The former was the most abundant species. Isogenus made up 12.2% of the number and 8.2% of the volume of Plecoptera and were taken only in April, May and June collections. Pteronarcys californica constituted 2.4% of the number and 25.9% of the volume of Plecoptera and was taken in most collections during the year. The largest number and volume occurred in June. Acro-

neuria pacifica made up 1.6% of the number and 14.0% of the volume of Plecoptera. It was most abundant in June and was absent in January and February. Claassenia sabulosa contributed 1.6% of the number and 3.2% of the volume of all Plecoptera and occurred in five collections.

Hemiptera. Four genera of Hemiptera contributed 0.04% of the number 0.5% of the volume of aquatic invertebrates. Corixidae, Cenocorixa bifida and Sigara washingtonensis, made up 85.2% of the number and 88.5% of the volume of Hemiptera. Gerris remigis and Rhagovolia distincta each occurred in a single collection.

Coleoptera. Three families of Coleoptera contributed 0.8% of the number and 1.1% of the volume of aquatic invertebrates. Elmidae, adults and/or larvae, were present in all collections and made up 97.0% of the number and 39.1% of the volume of all Coleoptera. They were most abundant in the May collection and least in October. This group was sorted only to family but a specialist identified Optioservus castanipennis and Zaitzevia parvula from the collections. Gyrinidae (Gyrinus maculiventris) occurred in four collections and Dytiscidae (Colymbetes sculptilis) in one and together made up 2.6% of the number and 60.9% of the volume of Coleoptera.

Diptera. Diptera, of five families, made up 9.2% of the number and 4.8% of the volume of all aquatic invertebrates. Diptera were most abundant in April and contributed the largest volume during June and the lowest number and volume in October. Simulium made up 60.2% of the number and 52.1% of the volume of Diptera. It contributed the largest number and volume in April and the least in November. This genus was not sorted to species but a specialist identified Simulium arcticum and Simulium

montanus from the collections. Chironomidae made up 38.1% of the number and 15.4% of the volume of all Diptera. It was taken in greatest numbers and volumes in June and least in October. During most of the year the numbers and volumes were probably underestimated since these organisms were small enough to pass through the nets. Atherix (Rhagionidae) occurred in four collections and made up 1.1% of the number and 26.1% of the volume of all Diptera. Three genera of Tipulidae were taken with Hexatoma contributing 0.1% of the number and 4.1% of the volume of all Diptera while Antocha monticola contributed 0.4% of the number and 1.5% of the volume and Cryptolabis contributed a trace. Hemerodromiinae (Empididae) contributed less than 0.5% of all Diptera.

Trichoptera. Trichoptera made up 15.1% of the number and 10.6% of the volume of aquatic invertebrates. Fifteen genera were identified from the samples. They were most abundant in June and least in February and contributed the largest volume in May and the smallest in the August 29 collection. Brachycentrus made up 50.5% of the number and 17.5% of the volume of Trichoptera. The largest number and volume occurred in June and the lowest number in November with the lowest volume in August. Micrasema made up 31.0% of the number and 31.3% of the volume of Trichoptera although it occurred only in the April, May and June collections. Two genera of Hydropsychidae were taken in all collections. Hydropsyche constituted 14.8% of the number and 35.7% of the volume of all Trichoptera. It made the largest contribution to the standing crop in June and the least in August. Cheumatopsyche made up 2.4% of the number and 9.0% of the volume of Trichoptera with the largest number and volume occurring in the

June collection and the smallest in August. Two genera of Glossosomatidae were taken. Glossoma contributed 1.0% of the number and 3.7% of the volume of Trichoptera. It contributed the largest number in August and volume in June and was absent in October. Protoptila cantha occurred in three collections and contributed 0.1% of the number and had no significant volume. Most of them probably passed through the nets. Leptocella and Oecetis avara (Leptoceridae) were taken in about half of the collections constituting 0.3% of the number and 2.3% of the volume of Trichoptera. Oecetis avara had a heavy sand case and probably was clinging to vegetation in the drift. Helicopsyche borealis (Helicopsychidae), Dolophiloides (Philopotamidae), Lepidostoma (Lepidostomatidae), Neotrichia, Hydroptila hemata, Hydroptila consimilis (Hydroptilidae) and Rhyacophila (Rhyacophilidae) together made up 0.4% of the volume of Trichoptera.

Lepidoptera. Elophila was taken in May but contributed little to the standing crop.

EMERGING AND ADULT AQUATIC INSECTS

Emerging and adult insects of four orders were taken and these constituted 38.9% of the total number and 32.1% of the volume of all drift animals. Numbers and volumes were greatest in May and June and least in January.

Ephemeroptera. Sub-imagos and adults constituted 63.2% of the number and 53.2% of the volume of emerging and adult aquatic insects. These were most abundant in June and were absent in January. Adult Ephemeroptera of the following taxa were identified from the drift: Ephemerella inermis,

E. grandis ingens, E. flavilina, E. heterocaudata heterocaudata, E. in frequens, Tricorythodes, Epeorus albertae, Rhithrogena, Baetis tricaudatus, Siphlonurus occidentalis.

Plecoptera. Adult Plecoptera were taken only in June, July and August and made up 0.1% of the number and 0.3% of the volume of emerging and adult aquatic insects. Isoperla was encountered in June, July and August and made up 90.3% of the number and 64.0% of the volume of Plecoptera. Claassenia sabulosa was taken in July and made up 1.1% of the number and 28.2% of the volume of Plecoptera. Isogenus tostonus occurred in June only and Alloperla pallidula in August.

Diptera. Diptera constituted 42.7% of the number and 15.7% of the volume of emerging and adult aquatic insects. The largest number and volume were taken in June and the smallest in November. It was the only order present in January. Chironomidae was present in all collections and made up 78.2% of the number and 58.2% of the volume of Diptera. It was most abundant and contributed the largest volume in April and the least in November. Simulium was taken in all collections except January and contributed 11.6% of the number and 25.5% of the volume of Diptera. The largest number and volume occurred in May. Simulium arcticum and S. montanus were identified from the collections. Tipulidae made up 1.5% of the number and 4.5% of the volume of Diptera and was present in June through October collections. The largest number and volume were in June. This group was identified only to family but a specialist identified the following genera and species: Antocha monticola, Cryptolabis, Tipula albocaudata from my collections. Emerging and adult Duterophlebia

nielson (Duterophlebiidae) contributed 8.5% of the number and 11.0% of the volume of Diptera. It was abundant in June with comparatively low numbers in July through November. Hemerodromia (Empididae) constituted 0.2% of the number and 0.8% of the volume of Diptera and occurred in June, July and August collections. Aedes fitchii (Culicidae) made up less than 0.05% of the number and volume of Diptera.

Trichoptera. Adult Trichoptera constituted 4.1% of the number and 6.7% of the volume of emerging and adult insects. These occurred in all collections except January, with the largest number and volume in June. I was unable to sort the adults to genera but subsequent identification showed the following genera and species: Hydropsychidae, Hydropsyche occidentalis, Cheumatopsyche campyla; Brachycentridae, Brachycentrus occidentalis, Brachycentrus americanus, Micrasema; Glossosomatidae, Glossoma velona, G. montana, Protoptila cantha; Helicopsychidae, Helicopsyche borealis; Leptoceridae, Leptocella albida, Oecetis avara; Philopotamidae, Dolophiloides; Lepidostomatidae, Lepidostoma knulli; Hydroptilidae, Hydroptila hemata, Hydroptila consimilis, Agraylea, Oxyethira.

TERRESTRIAL ARTHROPODS

Terrestrial insects or arachnids were taken in all collections except January and February and constituted 4.4% of the number and 3.6% of the volume of all animal drift. Their greatest numbers were in August and October and the greatest volumes in June and July. Insecta made up 99.0% of the total number and 93.2% of the volume. The contributions of

each order of Insecta to the total volume of terrestrial arthropods were as follows: Hymenoptera 27.8%, Diptera 19.3%, Coleoptera 17.7%, Homoptera 17.0%, Hemiptera 5.4%, Neuroptera 4.4%, Lepidoptera 1.7%.

FISH AND FISH EGGS

Fish and/or fish eggs were taken in all collections and made up 0.5% of the number and 4.3% of the volume of all drift animals. Although they were relatively unimportant in the total volume of drift they constituted 36.6% of the volume in one August collection. Except for the Longnose dace all fish captured were fry and fingerlings. Salmo trutta fingerlings were taken in April and May and constituted 32.3% of the volume of fish and fish eggs. Salmo gairdneri occurred in October and July and made up 5.4% of the volume. Prosopium williamsoni eggs were collected in October and November with eggs and yolk sac fry in January and February and fry in April. These constituted 24.2% of the volume of fish and fish eggs. Rhinichthys cataractae fry were taken in June, July, August and October collections and made up 11.7% of the volume of all fish and fish eggs. Adults of this species were taken in June and August and made up 26.3% of all fish and fish eggs. Fish eggs thought to be this species, were taken in one August collection. Cottus bairdi were taken in June and constituted 0.6% of the volume of fish.

VEGETATION

Plant material was present in the drift throughout the year with the largest volume occurring in June and the smallest in October. The volume of plant drift increased from early October through June. The stream

flow was relatively constant for most of this period so the increase appeared to result from fragmentation of senescent aquatic vegetation. The increased flows during late April through June completely removed this material. Plant drift was predominantly fragments of higher aquatic plants with some filamentous algae, blue green algae and needles and buds from lodgepole pine and Douglas fir.

Drift-Variations

VERTICAL DISTRIBUTION

There were no consistent differences in the drift rates of benthos organisms in samples taken from surface, mid-depth or near the bottom. Denham (1938) and Waters (1965) found that benthos organisms drift about equally at all depths. Although the drift rates at various depths in the Madison River were about equal the surface samples usually contained the largest number of organisms because a larger quantity of water passed through the surface nets in a given length of time. Terrestrial insects and emerged aquatic insects had higher drift rates at the surface although some were taken at all depths.

DIURNAL CHANGES IN DRIFT RATE

Most drift organisms showed consistent diurnal periodicity. Mean drift rates were calculated for day samples (sunrise to sunset) and night samples (sunset to sunrise) in each collection and the ratios of the night-drift-rate to day-drift-rate were determined. All drift rates are expressed as the number of organisms/1,000m^3.

Most organisms had consistently higher drift rates at night includ-

ing representatives of Lumbriculidae, Ephemeroptera, Odonata, Plecoptera, Coleoptera, Diptera, Trichoptera, terrestrial Neuroptera and fish (Table 5). A few organisms were taken only in night samples but most occurred throughout the day and night with the mean night drift rates varying from 3 to 209 times greater than the day rates for individual taxa.

Diurnal changes in drift rates for some Ephemeroptera, Trichoptera and Plecoptera are shown in Figs. 6 and 7. Most of these had highest

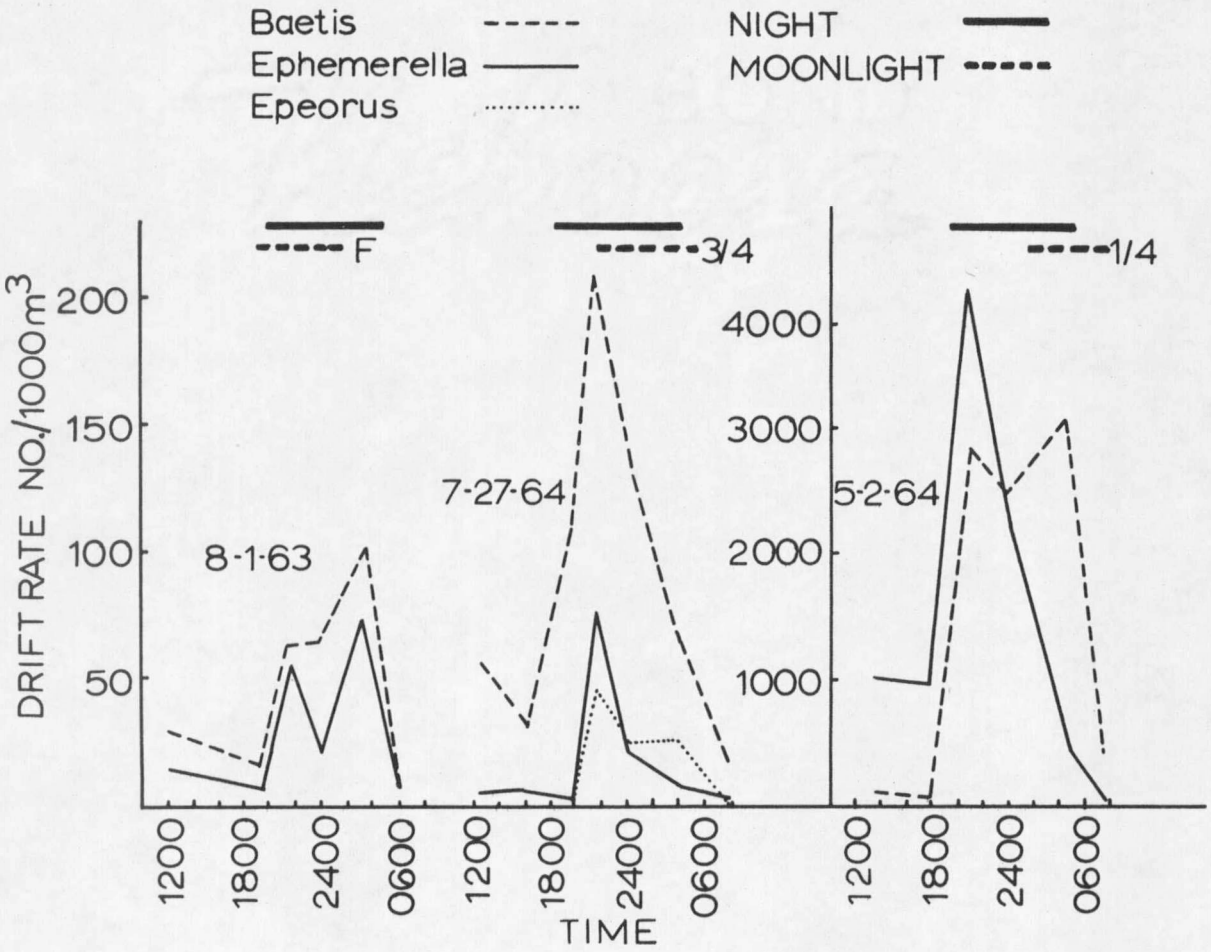


Figure 6. Diurnal drift rates for Baetis, Ephemerella inermis and Epeorus albertae during collections with bright moonlight (F=Full moon) and dark nights (¼=one quarter moon).

Table 5. Drift rates and ratios of mean night and day drift rates for organisms with higher night drift rates.

	Ratios of Night/ Day Mean Drift Rates (all collections)	Drift Rates No./ 1000m^3 for the collection with the maximum rate		
		Night	Day	Month
OLIGOCHAETA				
Lumbriculidae	4:1	2.28	0	May
EPHEMEROPTERA				
Baetis	5:1	2,790.72	811.94	April
Ephemerella (predominantly E. inermis)	25:1	2,817.19	88.44	April
Ephemerella (predominantly E. grandis)	4:1	20.93	8.08	May
Ephemerella heterocaudata	9:1	22.53	2.28	June
Tricorythodes	12:1	12.75	0.19	July
Paraleptophlebia	8:1	36.38	1.07	June
Epeorus albertae	60:1	77.22	0.91	June
Rhithrogena	16:1	16.43	0.56	May
ODONATA				
Ophiogomphus montanus	4:1	2.89	0	Nov.
Argia rivida	All night	1.18	0	June
PLECOPTERA				
Isoperla	209:1	401.02	1.26	June
Acroneuria pacifica	34:1	4.06	0	June
Claassenia sabulosa	5:1	4.14	0.32	Aug.
Pteronarcys californica	22:1	6.93	0.27	June
COLEOPTERA				
Elmidae	3:1	49.04	30.1	May
DIPTERA				
Tipulidae (adults)	6:1	31.82	3.68	Oct.
Empididae (adults)	14:1	11.06	0.31	July
Atherix	All night	15.32	0	June
TRICHOPTERA				
Cheumatopsyche	4:1	74.44	2.5	July
Hydropsyche	10:1	814.19	51.06	July
Brachycentrus	6:1	906.96	84.24	June
Micrasema	45:1	827.26	12.7	May
FISH				
Salmo trutta	All night	9.9	0	May
Salmo gairdneri	All night	1.47	0	July
Prosopium williamsoni eggs	17:1	21.65	1.29	Nov.
Rhinichthys cataractae	19:1	178.14	7.01	June

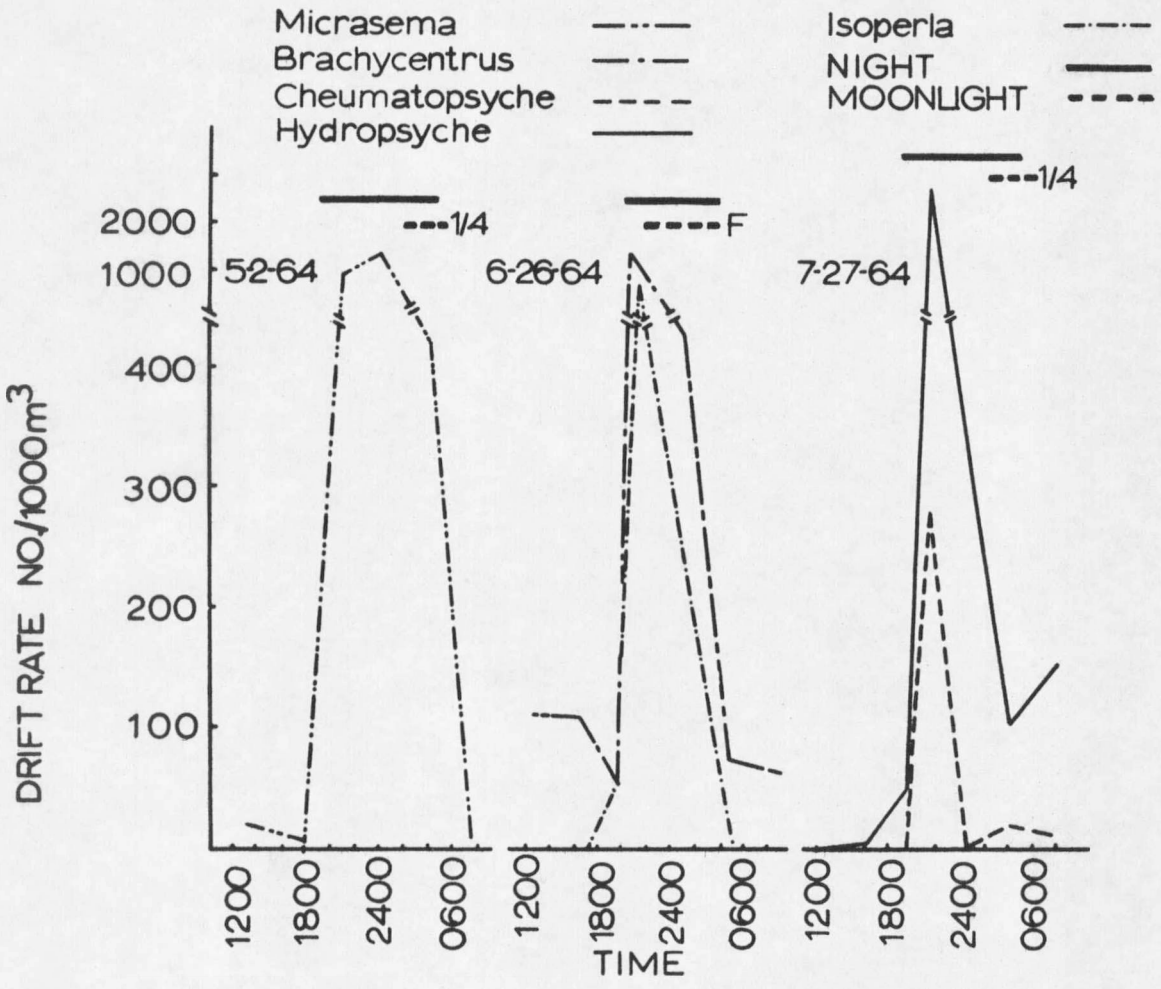


Figure 7. Diurnal drift rates for Micrasema, Brachycentrus, Hydropsyche, Cheumatopsyche and Isoperla.

drift rates soon after sunset with lower rates in successive samples during the night. Included in this group were Ephemerella, Epeorus, Hydropsyche, Cheumatopsyche, Brachycentrus and Isoperla. Baetis usually had highest drift rates soon after sunset and again just before sunrise as is

shown for May 1964. Micrasema had highest drift rates in the middle of the night. Bright moonlight inhibited drift as indicated by the drift rates of Baetis and Ephemerella (Fig. 6). Higher day drift rates were found for Duterophlebia nielson adults and for terrestrial Coleoptera, Hemiptera and Hymenoptera. The mean drift rates of Duterophlebia were 219.99 during the day and 2.57 at night during June when drift was highest. Most of the drift occurred between 0800 and 1200 hours with practically none taken in the remainder of the day and night. Some organisms showed no consistent higher drift rates during the day or night. These include adult Baetis, certain Trichoptera, aquatic and terrestrial Diptera and Homoptera. Adult Baetis, larvae of Glossoma and Oecetis avara and larvae and adults of Simulium and Chironomidae had higher night drift rates in about half of the collections and day rates in the other half.

Light intensity has been suggested as a cause of diurnal periodicity in stream drift (Tanaka, 1960; Müller, 1963; Waters, 1965; Elliot, 1965). Moon (1940) showed that recolonization of stream bottoms was more rapid at night than during the day although a few species moved more during the day. Tanaka (1960) found several species of Ephemeroptera, Plecoptera and Trichoptera had higher drift rates at night while Chironomidae and Simulium tended to drift more at twilight or during the day. Waters (1962a) reported increased drift rates at night for Baetis vagans, Gammarus, Glossoma, Dixia and Hesperocorixa and no change between night and day for Simulium. Müller (1963a, b) found higher night drift rates for Baetis and Gammarus while Elliot (1965) reported increased night drift rates for Baetis, Simulium and Helmis. Hartman et al. (1962) ob-

served active downstream migration of salmon fry during the night.

DISCUSSION

Practically all macro-invertebrate taxa taken in the study riffle were found in both benthos and drift samples. A few taxa occurred only in the benthos or drift but these were present at infrequent intervals and in low numbers. Dendy (1944) reported that almost all benthos animals appeared in the drift in Michigan streams. Although most aquatic invertebrates appeared to enter the drift in the Madison River it was difficult to determine the relationship between numbers and volumes of benthos and numbers and volumes of drift. The high reproductive rate of most organisms is undoubtedly involved in the benthos-drift relationship. Allee et al. (1949) list three factors which affect the population growth form: natality, mortality and dispersion. A normal population has a natality rate in excess of the carrying capacity of the environment and is adjusted to the proper level by mortality and dispersion. In a stream, dispersion is accomplished most rapidly by downstream movement with the current. Upstream movement against the current is relatively slow but has been reported by several workers (Neave, 1930; Stehr and Branson, 1938; Minckley, 1964; Ball et al., 1963). Müller (1954) proposed that drift and upstream flights by adult insects were parts of a "colonization cycle" which serve as a method of population control. Upstream flights of adult aquatic insects were found by Roos (1957). Waters (1961) proposed that drift is density dependent and removes only the excess benthos production since there is no upstream depletion of the population. In a subsequent study

Waters (1965) discussed behavioral responses, such as those causing diurnal periodicity, which modify drift rates.

Correlation of drift numbers and volumes with benthos numbers and volumes are dependent upon the origin of the various taxa in the drift and such information is not available at this time. In the Madison River the lowest total drift for any collection occurred when the benthos was low and the highest when the benthos was high. However there was considerable variation in this relationship between the various samples. Comparisons of drift and benthos for individual taxa showed even greater inconsistencies than total drift and benthos. Some taxa were present in low numbers in the benthos but had high drift rates which suggests that they originated from an upstream area with greater population density. Micrasema had a maximum density of $2/m^2$ in the benthos at a time when there were 439,021/24 hours in the drift. This amount of drift would have depopulated 119,510 square meters of stream bottom or about 4,000 meters of the stream if it had the same population density as the study area. Isoperla was also present in low numbers in the benthos and had high drift rates. The distance various taxa will drift is not known but Denham (1938) found species in the drift which were not present in the benthos of the immediate area and Waters (1965) estimated Baetis and Gammarus drifted more than 38 meters. Repopulation of areas denuded by floods as reported by Moffett (1936) suggest that some organisms may drift for considerable distances. In the Madison River some taxa had highest drift rates when benthos numbers were high. These include: Ephemerella, Baetis, Epeorus, Rhithrogena, Simulium and Chironomidae.

Others, such as Brachycentrus and Micrasema had highest drift rates when benthos numbers were at intermediate levels. Increased benthos numbers in the subsequent collection may have been caused by colonization from the drift. Cheumatopsyche and Hydropsyche had highest drift rates in July although several other collections had higher numbers of benthos. Although these two genera occurred in the same samples Cheumatopsyche was more abundant in the benthos and Hydropsyche numerically greater in the drift.

The total number and volume of organisms drifting over a unit area of bottom during a 24-hour period was always greater than the benthos standing crop. This has been reported for other streams (Berner, 1951; Horton, 1961; Waters, 1962b, 1965). A comparison between benthos and drift passing over a unit area of bottom of the Madison River was made by dividing the total drift of benthos organisms per 24 hours by the width of the riffle. It was assumed that the organisms drifted at least one meter. In individual collections the number of organisms in the drift which passed over a m^2 of bottom varied from about 2 to 51 times greater than the benthos while volume was from 2 to 40 times greater. Drift of this magnitude is obviously of ecological significance. Drift is readily available for feeding fish and investigation of the relationship between drift and fish food habits is needed.

In the Madison River there were behavioral responses which caused benthos organisms to enter the drift since drift was present even when the total population was lowest and presumably competition was at a minimum. Diurnal periodicity in the drift is another behavioral response.

Drifting of benthos animals was not caused by the accidental washing away of a few individuals by the current for even at lowest drift rates there was diurnal periodicity in the drift. It appears that such behavioral responses would give a species a survival advantage in a genetic sense in that it facilitates dispersal of the species. It is suggested that behavioral responses cause drift at all population levels with density dependent factors becoming more important as the population increases.

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