A COMPARISON OF RIFFLE INSECT POPULATIONS IN THE GIBBON RIVER ABOVE AND BELOW THE GEYSER BASINS, YELLOWSTONE NATIONAL PARK[1]

Ernest Richard Vincent
Zoology and Entomology Department, Montana State University, Bozeman

ABSTRACT

A study was made of the aquatic insect populations of two riffles, one above and one below the effluents of major geyser basins on the Gibbon River, Yellowstone National Park, from June through September 1963 and from October 1964 through September 1965. Eight 0.25-m^2 samples were taken from each riffle on each of the 21 collection dates. Water depths, current speeds, and bottom types were similar in both riffles. Maximum and mean temperatures were greater in the lower riffle. Alkalinity and concentrations of K^+, Na^+, Cl^-, PO_4^{3-}, and SO_4^{2-} were markedly greater in the lower riffle. There were 50 taxa in the upper riffle, 45 in the lower. The total number of individuals and biomass was slightly greater in the lower riffle. Ephemeroptera and Coleoptera occurred in greater numbers and biomass in the upper riffle, Trichoptera and Diptera occurred in greater numbers and biomass in the lower, and Plecoptera were about the same for both. Seven of the most numerous organisms in the upper riffle and two in the lower comprised about 68% of the total numbers for each. Ephemeroptera was the dominant order in the upper riffle, and Trichoptera dominated the lower. The thermal and chemical effluents entering the Gibbon River from surrounding geyser basins changed the lower riffle so that it was less diverse, contained a greater standing crop of aquatic insects, and was more favorable to Trichoptera than the upper.

INTRODUCTION

The insect populations of two riffles in the Gibbon River in the west-central part of Yellowstone National Park were studied during 1963, 1964, and 1965. The riffles were above and below the effluents of the major geyser basins. Earlier studies showed the influence of geyser water on aquatic invertebrates in Yellowstone National Park. Armitage (1958) correlated temperature and alkalinity with average annual standing crops of aquatic insects in the Firehole River, Gardiner River, and Lava Creek. Muttkowski (1929) did some descriptive work on the ecology of aquatic insects in various streams, and Brues (1924) made some general observations on aquatic organisms in various thermal areas.

Considerable work has been done on the effect of temperature on aquatic insect populations. Dodds and Hisaw (1925) attributed aquatic insect altitudinal zonation to temperature differences. Ide (1935) found that the increase in the number of mayfly species downstream was due to the higher temperatures of the lower regions of the Nottawasga River system. Sprules (1947) reported a direct correlation between the total change of species at successive stations and the average summer water temperature in a study on the Madawaska River, Ontario, Canada. Coutant (1962) stated that during the hot summer months there was a decrease in number, diversity, and total biomass of a macroinvertebrate riffle population that was in the path of a heated water effluent from a steam electric plant on the Delaware River, Pennsylvania.

The writer wishes to extend gratitude to all who helped in the course of this study. Dr. C. J. D. Brown directed the study and assisted in preparing the thesis. Dr. R. J. Graham gave valuable suggestions and field assistance as did J. Heaton, G. Algard, and A. Elser. T. Roeder did the chemical analysis of the water samples. E. Todd furnished thermograph temperature data. Sincere appreciation for the identification of the aquatic insects is extended to Dr. A. R. Gaufin (Plecoptera), O. S. Flint (Trichoptera) and S. Jensen (Ephemeroptera).

[1] Contribution from Montana State University Agricultural Experiment Station Project No. MS-844 – Paper No. 756 Journal Series.

Excellent cooperation was received from the National Park Service. This research was supported by Public Health Service Training Grant No. 5T1-WP-1 (through Dr. J. C. Wright) and Division of Water Supply and Pollution Control Research Grant No. WP-00125.

METHODS

Bottom samples were taken with a net patterned after the Surber sampler. It had a square frame enclosing an area of 0.25 m^2 and a nylon collecting net with 7.9 meshes/cm. A total of 42 collections (two on each sampling date) was taken. A collection consisted of eight 0.25-m^2 samples of bottom materials from each riffle on each sampling date. These were taken as follows: every two weeks from 26 June to 26 September 1963 and in October 1964, once a month from November 1964 to February 1965, and every two weeks in April 1965 and from 1 July to 15 September 1965. No collections were made in March 1965 because roads were impassable, or in May and June because of high water from the spring runoff. Collections were immediately preserved in 5% formalin. Aquatic organisms were sorted and preserved in 70% alcohol in the laboratory. They were classified to order and to lesser categories, including species, when practical. The number of individuals in each category was counted. Volume was determined to the nearest 0.1 ml by displacement in 70% alcohol. The term biomass is used for total volumes. The volumes in milliliters are approximately equal to grams damp weight.

Four 0.25-m^2 samples of bottom materials were collected in each riffle with a sampling net having 30 meshes/cm. Materials were dried and put through a series of Tyler soil screens to separate different sizes of material. The volume of each material size class was determined by displacement in water, and each class' per cent of the total was calculated. All material was then placed in one of three major categories that were further divided into seven minor size groups: rubble—2, gravel—2, and sand—3. Volumes of the different size classes of bottom materials from both riffles were compared statistically in a two-way analysis of variance test using the seven size groups, except for the largest (127–305 mm), which was not adequately sampled. Eight discharge measurements were computed for each riffle using average current speed, mean depth, and channel width. Current speeds were measured with a Gurley current meter. Maximum–minimum thermometers (±0.5C) were placed in each riffle and read each sampling date. Mean temperatures between sampling periods were computed to the nearest degree from these readings. A thermograph was used to check the mean temperatures. Methyl-orange alkalinities were taken on each sampling date. On two dates, *p*H values were taken.

DESCRIPTION OF STUDY AREA

The Gibbon River originates in Grebe Lake at an elevation of 2,447 m (8,028 ft) m.s.l. and flows 47 km in a southwesterly direction to join the Firehole River at an elevation of 2,075 m (6,806 ft). The upper riffle was approximately 7 km above and the lower was 18 km below the entrance of major geyser effluents. The river above the upper riffle drains a high mountain area with several small tributaries fed by melting snow and cold springs. Tributaries entering the river between the two riffles include those fed by melting snow and cold springs such as Solfatara Creek, Canyon Creek, and Secret Valley Creek; effluents from geyser basins at Norris, Gibbon, and Monument; and effluents from hot springs such as Sylvan, Beryl, and Iron (Fig. 1).

Physical and chemical characteristics of the riffles are shown in Table 1. Bottom materials, primarily of volcanic rhyolite, were similar at both riffles, except that more large rubble (127–305 mm) was found in the lower one. Gravel constituted the greatest fraction of total volume in both riffles. Depths and current speeds were similar in both. The stream width was about three times greater at the lower riffle. Discharge at both riffles had similar flow patterns. The high-water period started in mid-April with a rapid increase in flow due

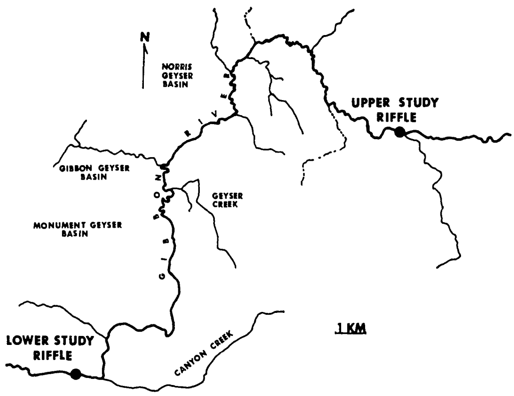

FIG. 1. Map of study area.

to melting snow runoff. Flow reached a peak by mid-June and then decreased rapidly until mid-July. During the remainder of the year, flows were low and relatively constant, except for small fluctuations in September due to heavy rains. The discharge at the lower riffle was about four times that of the upper and contained approximately 0.1 m³/sec of geyser and hot spring effluents (Allen and Day 1935). The geyser and hot spring effluents contribute about 2% of the total discharge at the lower riffle during the high-water period and 6% during low water. In both riffles, the lowest temperatures were in December, the highest in late July and early August (Fig. 2). However, the lower riffle had higher maximum and mean temperatures throughout the year. Maximum temperatures were 18C at the upper riffle, 24C at the lower. Both had a minimum temperature of 0C. The total ion concentration was two times greater in the lower riffle (Table 1) and all individual ions had greater concentrations there. Ions with marked concentration differences showed the following ratios (lower riffle : upper riffle): K^+—3 : 1, Na^+—4 : 1, Cl^-—17 : 1, PO_4^{3-}—3 : 1, and SO_4^{2-}—2 : 1. Allen and Day (1935) reported AsO_4^{3-}, $B_2O_4^{2-}$, and H_2S in Norris Geyser Basin waters. Similar *p*H values were found in both riffles. Methyl-orange alkalinity was about three times greater in the lower riffle. There was less rooted aquatic vegetation in the upper riffle and the species were not the same as those in the lower riffle. No benthic samples were taken in rooted aquatic vegetation because of these differences.

TABLE 1. *Physical and chemical factors at each riffle*

Environmental factors	Upper	Lower
Physical		
Width (m)	4.5	15.3
Depth (cm)	25–45	25–45
Current speed (m/sec)	0.73–0.90	0.67–0.90
Bottom materials (size mm)		
Rubble		
305–127	3.0*	10.6
126–76	24.5	29.4
Gravel		
75.0 –25.4	45.3	38.2
25.3 – 4.7	20.4	16.8
Sand		
4.6 – 0.58	6.3	4.5
0.57– 0.30	0.4	0.4
0.29	0.1	0.1
Discharge (m³/sec)	0.25–1.52	1.78–4.97
Temperature (C)		
Max–min	18–0	24–0
Mean	14–1	18–3
Chemical		
Ion (ppm)		
Ca^{2+}	2.81– 2.00†	3.21– 2.00
Fe^{2+}	0.27– 0.22	0.31– 0.30
K^+	4.69– 1.56	11.73– 3.91
Mg^{2+}	1.50– 0.00	1.70– 0.00
Mn^{2+}	0.28– 0.20	0.46– 0.20
Na^+	17.24– 5.06	74.72–22.99
NH_3^+	0.15–	0.25–
Cl^-	3.33– 2.00	54.96–26.00
PO_4^{3-}	0.14–Trace	0.40– 0.06
SiO_3^{2-}	69.6 –58.6	86.0 –67.6
SO_4^{2-}	6.00– 4.00	12.00–10.50
*p*H (range)	6.81– 7.45‡	7.00– 7.54
Methyl-orange alk. (ppm)	25–21	68–55

* Expressed as per cent of total volume.
† First number taken during low flow (11 Apr 1964 and 5 May 1965) and second number taken during peak flow (June 1964 and 5 Aug 1965).
‡ Taken over a 24-hr period.

RESULTS

Distribution of taxa

The majority of aquatic organisms found was aquatic insects; however, occasional nematodes, oligochaetes, *Margaritana mar-*

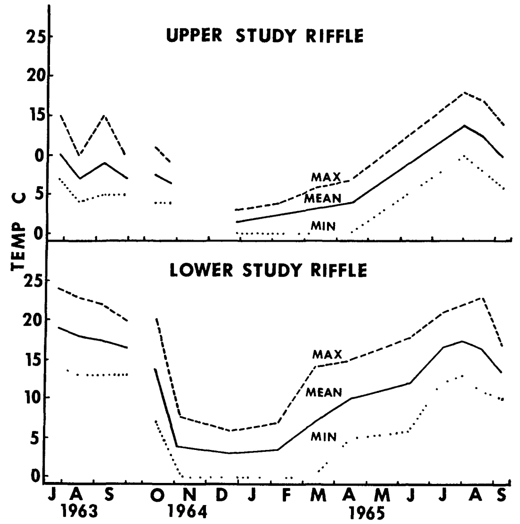

FIG. 2. Seasonal fluctuations in water temperature during the study period.

garitifera and *Pisidium* spp. were encountered. The same taxonomic distinctions were made for the organisms of each riffle.

Differences were observed in the distribution of 13 of the 54 taxa encountered. Nine of these were found only in the upper riffle and four only in the lower (Table 2). Taxa found less than four times were not used in the comparisons. Those occurring rarely were: *Hydroptila* spp., *Neophylax* spp., and *Helicopsyche* spp. (Trichoptera), *Bezzia* spp. (Diptera), Nematoda, Oligochaeta, *Margaritana margaritifera*, and *Pisidium* spp. (Pelecypoda) all found in both riffles; *Ephemerella coloradensis* (Ephemeroptera) and *Pericoma* spp. (Diptera), found only in the upper; and *Protophila* spp. (Trichoptera), found only in the lower.

Comparison of numbers and biomass of aquatic insects

Comparisons were limited to aquatic insects. Both riffles had the same general seasonal trends in total numbers and biomass. Maximal numbers occurred during September in the lower riffle and during November in the upper, with minima in July. The greatest biomass was in April and the least in July. Total numbers and biomass were greater in the lower riffle for most of the sampling period (Table 2). The ratio of total numbers for the upper and lower riffles was about 1:2 in June and 2:1 in August 1963, with an average annual ratio of 5:6. The ratio of total biomass for the upper and lower riffle varied from about 3:4 in August 1963 to 2:1 in December 1964 with an average annual ratio of 3.4:3.9.

Five orders of aquatic insects were encountered in each riffle. Numbers and biomass varied within the orders in both riffles.

Ephemeroptera. Annual fluctuations in total numbers and biomass of this order were similar in both riffles. Maximal numbers and biomass occurred in April. Minimal numbers were in September in the lower riffle and December for the upper, while the minimal biomass was in September in both. Total numbers varied from 17 times greater for the upper riffle in September 1963 to approximately two times greater in April 1965; the annual average was four times greater. Biomass ranged from eight times greater for the upper riffle in January 1965 to about two times greater in June 1963; the yearly average was four times greater. Of the 14 taxa of Ephemeroptera encountered, 13 were found in the upper riffle and 12 in the lower. *Baetis* spp. and *Ephemerella inermis* were the most numerous organisms in the lower riffle and comprised 75% of the number and 72% of the biomass. These were also numerous in the upper riffle along with *E. doddsi*, *E. hystrix*, *Iron longimanus*, *Rhithrogenia hageni*, and *Cinygmula* sp. These seven organisms made up 92% of the numbers and 91% of the biomass. All of the abundant organisms occurred in greater numbers and biomass in the upper riffle. *Ephemerella flavilinea* and *E. grandis ingens* were the only organisms found in both riffles that were also more abundant in the lower (Table 2).

Plecoptera. Annual fluctuations in total numbers and biomass were similar in both riffles. Maximum numbers occurred in December 1964 in the upper riffle and in February 1965 in the lower, while minima

TABLE 2. *Total numbers/m² and volumes (ml) of aquatic insects in the upper (U) and lower (L) riffles for each sampling period (volumes in parentheses)*

	1963								1964						1965											
	June		July		Aug		Sept		Oct		Nov		Dec		Jan		Feb		Apr		July		Aug		Sept	
	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L
Ephemeroptera	384.0 (1.6)	77.0 (0.8)	294.9 (1.2)	45.0 (0.3)	259.2 (0.8)	17.8 (0.1)	291.6 (0.4)	16.9 (T)*	241.1 (0.7)	43.3 (0.1)	303.0 (0.7)	55.0 (0.1)	220.5 (0.8)	57.0 (0.2)	401.0 (1.7)	77.5 (0.2)	427.0 (2.0)	228.0 (0.7)	459.1 (2.9)	259.6 (0.9)	172.4 (1.1)	38.7 (0.3)	174.2 (0.8)	20.9 (0.1)	392.8 (0.8)	27.5 (0.1)
Ephemerella aurivilli	12.0 (T)	9.0 (T)	42.7 (0.1)	7.8 (0.1)	23.4 (0.2)	2.5 (T)															10.0 (T)	2.6 (T)	12.0 (0.1)	1.0 (T)		
E. doddsi	3.0 (0.2)		0.3 (0.1)		55.5 (T)		107.6 (0.1)	0.3 (T)	28.3 (0.2)	1.8 (T)	34.0 (0.1)		26.5 (0.3)		36.0 (0.3)		38.0 (0.3)		35.0 (0.7)		2.3 (0.2)		15.0 (T)		46.5 (0.1)	
E. flavilinea	7.0 (T)	20.0 (0.3)	7.2 (0.1)	4.3 (0.1)	0.6 (T)	0.2 (T)											0.5 (T)	12.0 (T)	17.5 (T)	68.5 (0.2)	6.8 (0.1)	6.8 (T)	0.3 (T)	0.5 (T)		
E. grandis ingens								0.6 (T)		0.8 (T)		0.5 (T)		0.5 (T)					0.3 (T)	0.3 (T)	0.3 (T)	0.3 (T)				
E. heterocaudata		3.0 (T)		0.8 (T)												4.0 (T)		6.0 (T)		21.0 (T)		1.6 (0.1)		1.8 (T)		
E. hystrix			0.3 (T)		5.7 (T)		4.3 (T)		59.5 (0.1)	0.8 (T)	59.0 (0.1)	1.0 (T)	28.0 (T)		154.0 (0.5)	2.0 (T)	184.5 (0.6)		118.3 (0.7)		2.8 (T)	0.3 (T)	2.5 (T)		21.0 (0.1)	
E. inermis	2.0 (T)	4.0 (T)	0.3 (T)	0.8 (T)	10.2 (T)	2.2 (T)	49.4 (T)	2.5 (T)	41.5 (0.1)	6.5 (T)	76.0 (0.2)	31.0 (T)	42.5 (0.1)	43.5 (0.2)	46.0 (0.1)	52.0 (0.2)	38.5 (0.1)	117.0 (0.5)	59.8 (0.4)	59.5 (0.3)	0.3 (T)	0.8 (T)	0.3 (T)	1.3 (T)	10.5 (T)	0.5 (T)
E. spinifera	1.0 (T)		0.3 (T)		10.5 (T)	1.3 (T)	30.5 (T)		11.0 (T)		26.5 (T)		8.5 (T)		10.5 (T)		14.5 (T)		10.3 (0.1)				0.5 (T)	2.5 (T)	2.0 (T)	6.5 (T)
Baetis spp.	66.0 (0.3)	18.0 (0.3)	64.5 (0.3)	26.8 (0.1)	41.0 (0.1)	10.5 (0.1)	27.0 (0.1)	13.5 (T)	9.8 (T)	32.8 (0.1)	6.5 (T)	22.0 (0.1)	13.5 (T)	13.0 (T)	21.5 (0.1)	19.5 (T)	4.0 (T)	92.0 (0.2)	51.3 (0.1)	91.3 (0.3)	31.3 (0.1)	20.2 (0.2)	26.5 (0.1)	12.8 (0.1)	79.5 (0.2)	20.0 (0.1)
Cinygmula sp.	114.0 (0.3)		86.5 (0.2)		64.0 (0.3)		29.6 (0.1)		4.7 (T)		32.5 (0.1)		28.0 (0.1)		26.5 (0.2)		43.5 (0.5)		55.5 (0.4)		55.3 (0.2)		34.0 (0.2)		5.0 (T)	
Paraleptophlebia sp.	5.0 (0.1)	1.0 (T)	0.8 (T)	0.3 (T)	0.5 (T)	0.3 (T)	2.6 (T)		4.5 (T)		1.0 (T)				0.5 (T)				0.3 (T)			0.3 (T)			1.8 (T)	
Iron longimanus	158.0 (0.4)	21.0 (0.2)	90.0 (0.3)	3.9 (T)	26.6 (0.1)	0.8 (T)	19.0 (T)		8.0 (T)	0.3 (T)	10.0 (T)		2.0 (T)		1.5 (T)		1.0 (T)		22.0 (T)	18.5 (0.1)	53.5 (0.3)	5.8 (T)	46.5 (0.3)	1.0 (T)	19.5 (0.1)	
Ironopsis grandis					1.2 (T)				1.5 (T)		5.5 (T)				14.0 (0.1)		6.0 (0.1)		4.0 (T)				4.3 (T)		10.0 (T)	
Rhithrogenia hageni	16.0 (0.3)	1.0 (T)	2.0 (0.1)	0.3 (T)	20.0 (0.1)		21.6 (0.1)		72.3 (0.3)	0.3 (T)	52.0 (0.2)	0.5 (T)	71.5 (0.3)		90.5 (0.4)		96.5 (0.4)	0.5 (T)	81.8 (0.5)	0.5 (T)	9.8 (0.2)		32.3 (0.1)		197.0 (0.3)	0.5 (T)
Plecoptera	13.0 (0.3)	17.0 (2.3)	15.5 (0.7)	8.7 (1.0)	30.5 (1.3)	25.9 (1.7)	33.6 (0.5)	22.9 (0.9)	22.5 (1.6)	18.0 (1.5)	25.5 (0.9)	16.5 (0.9)	73.5 (0.2)	16.0 (0.7)	49.0 (1.9)	20.5 (1.9)	18.5 (0.2)	48.5 (1.2)	33.8 (0.5)	24.0 (1.5)	12.9 (0.3)	6.1 (0.8)	11.9 (0.5)	8.5 (1.0)	25.5 (1.1)	30.0 (1.5)
Nemoura spp.	1.0 (T)		0.8 (T)		3.2 (T)		1.1 (T)		5.5 (T)		9.0 (T)		11.0 (T)		5.0 (T)		3.0 (T)		4.8 (T)		0.3 (T)		0.8 (T)		4.5 (T)	
Leutra sp.	1.0 (T)				0.8 (T)		5.4 (T)		0.8 (T)		3.0 (T)		20.5 (T)		16.0 (T)		4.0 (T)		5.3 (T)						2.0 (T)	
Brachyptera sp.													2.5 (T)		6.0 (T)		0.5 (T)		9.3 (0.1)							
Pteronarcys californica		3.0 (0.9)		0.5 (0.4)	0.7 (0.4)	0.5 (0.5)		1.1 (T)	2.3 (0.7)	1.5 (0.5)	1.0 (0.3)	2.0 (0.1)		0.5 (T)	0.5 (0.4)			2.0 (0.1)	0.3 (T)	1.8 (0.2)		1.4 (0.3)		1.0 (0.3)	1.0 (0.4)	2.5 (0.6)
Arcynopteryx spp.					5.3 (T)	1.5 (T)	13.0 (0.1)	0.5 (0.3)	1.0 (T)		4.5 (0.1)		1.0 (T)				1.5 (0.1)		0.5 (0.1)	0.3 (T)			1.0 (T)		4.0 (T)	2.5 (T)
Isogenus spp.	6.0 (0.1)		3.2 (T)		1.0 (T)		0.3 (T)						16.5 (0.1)		2.5 (T)		1.0 (T)		1.5 (T)		2.5 (0.1)		0.8 (0.1)		0.5 (T)	
Isoperla spp.								0.6 (T)		0.5 (T)	(T)	0.5		6.0 (T)		7.5 (T)		31.0 (0.4)		9.3 (0.1)		0.2 (T)				

TABLE 2. *(Continued)*

Acroneuria theodora			5.0 (0.5)		5.7 (0.5)		2.2 (0.2)		6.8 (0.7)		5.0 (0.4)		7.0 (0.1)		12.0 (1.5)		6.0 (0.1)		3.5 (0.1)		4.3 (0.2)		6.3 (0.4)		5.5 (0.5)	
A. pacifica	1.0 (0.2)	2.0 (T)	1.4 (0.2)	5.0 (0.3)	3.0 (0.2)	4.7 (0.3)	1.1 (0.1)	6.5 (0.3)	4.3 (0.2)	5.5 (0.5)	1.0 (0.1)	2.0 (0.3)	0.5 (T)	4.5 (0.6)	0.5 (T)	4.5 (1.4)	1.0 (T)	2.5 (0.2)	1.3 (0.1)	2.8 (0.7)	1.5 (T)	1.1 (0.1)	0.5 (T)	2.2 (0.1)	5.0 (0.2)	6.0 (0.2)
Claassenia sabulosa		12.0 (1.4)		2.7 (0.3)	0.2 (0.1)	17.2 (0.9)		11.5 (0.3)		8.5 (0.5)		10.5 (0.5)		4.0 (0.1)		6.0 (0.5)		10.0 (0.5)		9.3 (0.5)		3.4 (0.4)		4.8 (0.6)		15.0 (0.7)
Coleoptera Elmidae	174.0 (0.3)	46.0 (0.1)	161.0 (0.2)	30.8 (T)	212.8 (0.2)	54.2 (0.1)	138.5 (0.1)	60.5 (0.1)	92.0 (0.1)	47.3 (0.1)	117.0 (0.1)	20.0 (T)	94.0 (0.1)	42.5 (0.1)	98.5 (0.1)	51.0 (0.1)	40.5 (0.1)	30.5 (0.1)	44.8 (0.1)	52.3 (0.1)	33.5 (0.1)	23.2 (T)	53.3 (0.1)	24.3 (T)	49.0 (0.1)	128.5 (0.1)
Trichoptera	56.0 (0.8)	103.0 (1.1)	45.6 (0.6)	91.8 (0.5)	234.4 (1.0)	616.8 (0.6)	149.9 (0.8)	1,099.5 (3.4)	373.4 (1.2)	994.8 (1.6)	371.0 (1.3)	873.5 (1.5)	148.0 (0.7)	646.5 (1.9)	133.5 (0.8)	772.0 (2.1)	150.5 (0.9)	432.5 (1.2)	105.6 (0.9)	576.8 (1.8)	33.6 (0.4)	115.1 (0.6)	178.6 (1.1)	417.1 (0.6)	265.5 (2.2)	275.2 (1.5)
Rhyacophila acropedes	2.0 (T)	6.0 (0.4)	3.3 (T)	1.7 (0.1)	9.0 (0.1)	0.2 (T)	7.0 (0.1)	2.6 (T)	13.0 (0.2)	1.7 (T)	17.5 (0.2)	1.5 (T)	13.5 (0.2)	4.0 (T)	15.0 (0.3)	6.5 (T)	8.0 (0.1)	3.0 (T)	12.8 (0.3)	4.3 (0.1)	0.8 (T)	0.8 (T)	5.5 (0.1)	0.3 (T)	14.5 (0.1)	0.5 (T)
Rhyacophila spp.	20.0 (0.7)		8.6 (0.6)		8.1 (0.1)		11.6 (0.1)	0.3 (T)	11.5 (0.1)		29.0 (0.2)	0.5 (T)	27.5 (0.2)		27.5 (0.2)	0.5 (T)	14.5 (0.2)	1.0 (T)	20.8 (0.2)	1.3 (T)	13.0 (0.4)	0.5 (T)	3.0 (0.1)		6.0 (T)	0.5 (T)
Glossosoma sp.	5.0 (T)	83.0 (0.4)	24.4 (T)	61.3 (0.3)	147.4 (0.3)	505.7 (0.2)	85.1 (0.2)	587.3 (0.2)	274.0 (0.3)	660.3 (0.3)	238.5 (0.2)	669.0 (0.4)	90.0 (0.1)	300.0 (0.2)	70.5 (0.1)	428.0 (0.2)	98.5 (0.2)	217.0 (0.2)	60.5 (0.2)	364.3 (0.3)	15.0 (T)	66.8 (0.2)	122.0 (0.3)	350.0 (0.1)	131.5 (0.3)	114.5 (0.1)
Dolophilodes sp.				1.0 (T)	0.3 (T)	1.7 (T)	0.3 (T)		0.5 (T)		0.5 (T)		0.5 (T)		1.0 (T)								6.0 (0.1)	1.0 (T)	9.0 (0.3)	
Arctopsyche grandis			0.3 (T)	4.0 (T)	60.7 (0.5)	3.0 (0.1)	35.4 (0.4)	4.5 (0.3)	54.7 (0.6)	5.0 (0.1)	70.5 (0.7)	3.0 (0.2)	13.5 (0.2)	4.0 (0.4)	10.5 (0.1)	2.0 (0.1)	20.5 (0.3)	2.0 (0.1)	5.0 (0.2)	1.3 (0.1)	0.8 (T)	1.7 (T)	32.3 (0.4)	5.5 (0.2)	91.0 (1.3)	4.0 (0.4)
Hydropsyche sp.		10.0 (0.3)		9.8 (0.1)	0.4 (T)	95.3 (0.2)	2.9 (T)	456.7 (2.6)		304.5 (1.1)		175.5 (0.8)		318.5 (1.2)		304.5 (1.6)		166.5 (0.7)	0.5 (T)	164.5 (1.2)		24.7 (0.3)	0.3 (T)	49.0 (0.3)		125.5 (0.9)
Leptosoma sp.			0.5 (T)		0.8 (T)	0.3 (T)				4.0 (T)	1.0 (T)	17.0 (T)		3.5 (T)	0.5 (T)	2.0 (T)		16.0 (T)		3.3 (T)		0.3 (T)			0.5 (T)	2.7 (T)
Brachycentrus occidentalis	27.0 (0.1)	3.0 (T)	4.0 (T)	11.8 (T)	2.4 (T)	10.2 (0.1)	6.1 (T)	43.4 (0.3)	5.7 (T)	16.3 (0.1)	3.5 (T)	5.5 (0.1)	1.5 (T)	13.0 (0.1)	4.5 (0.1)	19.0 (0.2)	6.5 (0.1)	19.5 (0.2)	4.0 (T)	11.0 (0.1)	2.3 (T)	17.0 (0.1)	7.8 (0.1)	10.5 (T)	12.5 (0.2)	20.0 (0.1)
Micrasema sp.	2.0 (T)	1.0 (T)	4.5 (T)	2.2 (T)	5.3 (T)	0.3 (T)	1.5 (T)	4.8 (T)	14.0 (T)	3.0 (T)	10.5 (T)	1.5 (T)	1.5 (T)	2.5 (T)	4.0 (T)	9.5 (T)	2.5 (T)	7.5 (T)	2.0 (T)	26.8 (T)	1.7 (T)	3.3 (T)	1.7 (T)	0.8 (T)	0.5 (T)	7.5 (T)
Diptera	7.0 (0.3)	28.3 (0.2)	18.3 (0.2)	55.4 (0.5)	26.3 (0.5)	74.8 (0.4)	4.4 (0.7)	55.3 (0.6)	3.1 (0.2)	45.9 (0.8)	9.0 (0.2)	44.5 (0.4)	10.0 (0.3)	119.5 (1.5)	19.0 (0.1)	126.5 (1.3)	20.0 (0.1)	124.5 (1.7)	17.0 (0.3)	122.4 (2.0)	5.9 (0.1)	23.7 (0.2)	17.4 (0.1)	28.9 (0.4)	8.5 (0.5)	17.8 (0.3)
Antocha spp.		17.0 (T)		12.8 (0.1)		5.2 (T)	0.3 (T)	6.4 (T)		12.5 (T)	0.5 (T)	8.5 (0.1)	1.0 (T)	39.5 (0.1)	1.0 (T)	32.0 (0.1)		23.5 (0.1)		26.0 (0.1)	0.3 (T)	7.5 (0.1)		2.5 (T)		3.5 (T)
Cryptolabis spp.		4.3 (T)		0.3 (T)				5.9 (T)		4.3 (T)		3.0 (T)		8.0 (0.1)		7.0 (0.1)		8.0 (0.1)		8.3 (0.1)		0.5 (T)				0.3 (T)
Hexatoma spp.	5.0 (0.3)	3.0 (0.2)	3.3 (0.2)	4.2 (0.2)	2.5 (0.5)	4.2 (0.3)	3.4 (0.7)	5.3 (0.4)	1.3 (0.2)	5.8 (0.5)	2.5 (0.2)	0.5 (0.1)	1.0 (0.3)	10.0 (0.8)	2.5 (0.1)	4.5 (0.2)	2.0 (0.1)	5.0 (0.5)	2.0 (0.2)	2.3 (0.4)	1.3 (0.1)	1.1 (0.1)	1.3 (0.1)	2.5 (0.2)	2.0 (0.5)	1.0 (0.2)
Tendipedidae	1.0 (T)	1.0 (T)	7.2 (T)	18.5 (T)	21.2 (T)	58.8 (0.1)	0.5 (T)	25.2 (T)	1.0 (T)	7.7 (T)	4.5 (T)	8.0 (T)	4.5 (T)	5.0 (T)	5.0 (T)	11.5 (T)	2.0 (T)	5.5 (T)	4.5 (T)	18.0 (T)	0.5 (T)	4.4 (T)	5.8 (T)	11.5 (T)	4.0 (T)	7.5 (T)
Simulium spp.	1.0 (T)	2.0 (T)	7.3 (T)	11.2 (0.1)	2.1 (T)	2.5 (T)		0.9 (T)	0.8 (T)	0.5 (T)	1.5 (T)	1.5 (T)	2.5 (T)	30.0 (0.1)	1.5 (T)	36.5 (0.1)	2.0 (T)	53.0 (0.2)	2.0 (T)	41.8 (0.2)	3.8 (T)	2.5 (T)	10.3 (T)	3.3 (T)	2.0 (T)	1.5 (T)
Blephariceridae				0.3 (T)		0.5 (T)		6.7 (T)		9.8 (T)		18.5 (0.1)		18.0 (0.1)	8.5 (T)	17.5 (0.1)	14.0 (T)	19.0 (0.3)	7.5 (0.1)	11.5 (0.3)		0.3 (T)		1.5 (T)		1.0 (T)
Deuterophebia sp.		1.0 (T)		2.1 (T)		0.3 (T)		0.3 (T)													0.3 (T)	5.2 (T)		0.8 (T)		1.5 (T)
Atherix spp.			0.5 (T)	6.0 (0.1)	0.5 (T)	3.3 (T)	0.2 (T)	4.6 (0.2)		5.3 (0.3)		4.5 (0.1)	1.0 (T)	9.0 (0.3)	0.5 (T)	17.5 (0.7)		10.5 (0.5)	1.0 (T)	14.5 (0.9)		2.2 (T)		6.8 (0.2)	0.5 (T)	1.5 (0.1)
Totals	634.0 (3.3)	271.3 (4.3)	535.3 (2.9)	231.7 (2.3)	763.2 (3.8)	789.5 (2.9)	618.0 (2.5)	1,255.1 (5.0)	732.1 (3.8)	1,149.3 (4.1)	825.5 (3.2)	1,009.5 (2.9)	546.0 (2.1)	880.5 (4.4)	701.0 (4.6)	1,047.5 (5.6)	656.5 (3.3)	864.0 (4.9)	660.3 (4.7)	1,035.1 (6.3)	258.3 (2.0)	206.8 (1.9)	435.4 (2.6)	499.7 (2.1)	741.3 (4.7)	479.0 (3.5)
Alloperla spp.	4.0 (T)		5.1 (T)	0.5 (T)	10.6 (0.1)	2.0 (T)	10.5 (0.1)	2.7 (T)	1.8 (T)	2.0 (T)	2.0 (T)	1.5 (T)	14.5 (T)	1.0 (T)	6.5 (T)	2.5 (T)	1.5 (T)	3.0 (T)	6.0 (0.1)	0.5 (T)	4.3 (T)		2.5 (T)	0.5 (T)	3.0 (T)	4.0 (T)

* T = trace.

were in August 1965 in both. Maximum biomass was in January 1965 in the upper riffle and in June 1963 in the lower, while minima occurred in December 1964 in both. The ratio of total numbers in the upper and lower riffles varied from 5:1 in December 1964 to 1:2 in February 1965 with an annual average of 7:5. The ratio of biomass in the upper and lower riffles varied from 1.6:1.5 in October 1964 to 1:8 in June 1963; the yearly average was 2:3. Eleven Plecoptera taxa were encountered (10 in the upper and six in the lower riffle). In the upper riffle, *Nemoura* spp., *Leutra* sp., *Alloperla* spp., and *Acroneuria theodora* were the most numerous organisms, comprising 68% of the numbers. In the lower riffle, *Isoperla* spp., *Acroneuria pacifica,* and *Claassenia sabulosa* constituted 85% of the numbers. *Acroneuria theodora, Pteronarcys californica,* and *Acroneuria pacifica* made up 84% of the biomass in the upper riffle, while the latter two plus *Claassenia sabulosa* comprised 95% of the biomass in the lower. Of the five Plecoptera found in both riffles, only *Acrynopteryx* spp. and *Alloperla* spp. occurred in greater numbers and biomass in the upper (Table 2).

Coleoptera. Both adult and larval forms were found in each riffle. The adult and larva total numbers and biomass were combined in each riffle for each month (Table 2). Seasonal trends of this order show irregular monthly fluctuations in total numbers for both riffles, while the biomass was more constant throughout the sampling period. The ratio of the total yearly numbers and biomass in the upper and lower riffle were 2:1 and 1:1.

Trichoptera. Both study riffles had the same general seasonal trends in numbers and biomass. Maximal numbers occurred during the September–November period with the minimum in July. Maximal biomass was in September and minimum in July. The ratio of total numbers in the upper and lower riffle varied from 1:7 in September 1963 to 1:1 in September 1965; the yearly average was 1:3. The ratio of biomass in the upper and lower riffle varied from 5:3 in August 1963 to 1:4 in September 1963; the yearly average was 5:7. Of the 14 Trichoptera taxa encountered, 13 were found in the upper riffle and 14 in the lower. The most numerous Trichoptera in the upper riffle were *Rhyacophila* spp., *Arctopsyche grandis,* and *Glossosoma* sp.; these three comprised 90% of the total numbers. The same three organisms with *Rhyacophila acropedes* constituted 90% of the biomass. In the lower riffle, *Glossosoma* sp. and *Hydropsyche* sp. made up 94% of the numbers and 79% of the biomass. *Rhyacophila acropedes, Rhyacophila* spp., *Dolophilodes* sp., and *Arctopsyche grandis* were the only Trichoptera present in both riffles that were also most abundant in the upper riffle (Table 2).

Diptera. In the upper riffle, maximum numbers occurred in August and minima in October. In the lower riffle, maximum numbers were in January and minima in September. Maximum biomass occurred in September and minima during midwinter (January–February) in the upper riffle. Maximum biomass in the lower riffle occurred in January and minima in July. Nine taxa of Diptera were encountered—eight in each riffle. The ratio of total numbers in the upper and lower riffles varied from 1:2 in August 1965 to 1:17 in October 1964; the yearly average was 1:5. The ratio of biomass in the upper and lower riffles varied from 3:2 in June 1963 to 1:17 in February 1965; the annual average was 3:8. In the upper riffle, *Hexatoma* spp., Tendipedidae, *Simulium* spp., and Blephariceridae were the most numerous organisms and comprised 94% of the total numbers. In the lower riffle, *Antocha* spp., Tendipedidae, *Simulium* spp., Blephariceridae, and *Atherix* spp. comprised 87% of the total numbers. *Hexatoma* spp. constituted 90% of the biomass in the upper riffle, while these with *Atherix* spp. made up 72% of the biomass in the lower. All Diptera present in both riffles were more numerous in the lower (Table 2).

The seven most numerous organisms in the upper riffle in order of abundance were *Glossosoma* sp., Elmidae, *Rhithrogenia hageni, Ephemerella hystrix, Cinygmula* sp.,

TABLE 3. *Relative abundance (upper row) and relative biomass (lower row) for each aquatic insect order, expressed as per cent of total number and biomass*

Aquatic insect orders	Upper riffle		Lower riffle	
	Range	Average	Range	Average
Ephemeroptera	32.5–69.5	49.2	1.4–28.4	9.8
	16.0–61.7	35.3	0.5–15.9	7.7
Plecoptera	2.1–13.4	4.5	1.6– 6.1	2.6
	6.1–41.3	23.5	15.9–58.6	33.3
Coleoptera	6.2–27.5	16.1	2.0–16.8	6.3
	2.1– 9.1	2.9	0.5– 3.4	2.6
Trichoptera	8.6–51.2	26.9	38.0–87.5	72.2
	17.4–46.8	29.4	20.7–68.0	35.9
Diptera	0.4– 3.9	2.1	3.7–24.0	8.9
	2.2–28.0	8.8	4.5–34.1	20.5

Iron longimanus, and *Baetis* spp. In the lower riffle, the two most numerous aquatic insects were *Glossosoma* sp. and *Hydropsyche* sp. These organisms comprised 68% of the total numbers in each riffle. The seven organisms that constituted most of the biomass in the upper riffle were *Acroneuria theodora, Arctopsyche grandis, Hexatoma* spp., *Rhyacophila* spp., *Rhithrogenia hageni, Ephemerella doddsi,* and *Cinygmula* sp. In the lower riffle, the four organisms comprising most of the biomass were *Hydropsyche* sp., *Claassenia sabulosa, Acroneuria pacifica,* and *Hexatoma* spp. These organisms constituted 54% of the biomass in the upper riffle and 56% in the lower.

The index of diversity (d) was derived from the linear relationship between the number of species (m) and the logarithm of total individuals (N). They were calculated using the following equation (Margalef 1951):

$$d = \frac{m-1}{\ln N}.$$

The average yearly index of diversity in the upper riffle was 11.19, and in the lower it was 9.67.

Comparison of aquatic insect orders

In the upper riffle, Ephemeroptera was the most abundant order during most of the sampling period, except in August 1963 and October and November 1964, when Trichoptera was the most numerous (Table 3). During the remainder of the sampling period, Trichoptera was second and Coleoptera third. Diptera was the least abundant. Ephemeroptera had the greatest biomass, Trichoptera was second, and Plecoptera third. In the lower riffle, Trichoptera was the most abundant order during the entire sampling period with Ephemeroptera second and Diptera third. Plecoptera was the least abundant. Trichoptera had the greatest biomass, Plecoptera was second, and Diptera third.

DISCUSSION

The upper riffle had the largest number of taxa, while the lower had the largest number of individuals and biomass. Ephemeroptera was the dominant order in total numbers and biomass in the upper riffle; Trichoptera dominated the lower. Most of the taxa were common to both riffles, but the number of individuals in each taxa varied. Water temperature and water chemistry probably account for most of the differences in the taxa present, number of individuals, and total biomass in the two riffles.

Temperature is important in determining the distribution of many aquatic insects. As the mean and minimum temperatures increase from the upper to the lower riffle, some of the cold-water forms are probably eliminated or reduced in abundance, while warmer-water forms appear. Dodds and Hisaw (1925) found a definite altitudinal zonation of 100 species of aquatic insects that was due mainly to temperature changes. The range in temperature also influences the number of taxa present. As the range increases, the number of taxa should increase. The lower riffle had a wider range in temperature and fewer taxa than the upper. The number of Ephemeroptera and Plecoptera taxa decreased from the upper to the lower riffle, while the number of Trichoptera increased. In contrast, Ide (1935) found an increase in the number of Ephemeroptera species downstream from its source where the greater temperature fluctuations occurred. Sprules (1947) stated that as the average summer temperature increased, the number of Ephemeroptera and Trichoptera species increased, while Plecoptera decreased. The formation of anchor ice in the upper riffle may have eliminated or limited certain taxa. Armitage (1961) listed certain aquatic insects as cold-water forms, warm-water forms, and forms with no temperature preference. Three of the cold-water forms and three of the no-temperature-preference forms were more abundant in the lower riffle, suggesting that additional factors probably influence their distribution in the Gibbon River. The high concentrations of K^+, Na^+, Cl^-, PO_4^{3-} and SO_4^{2-} in the lower riffle may have eliminated or limited certain organisms or have been favorable to other organisms.

Differences observed in the standing crop in the upper and lower riffles probably were the result of water temperature and chemistry differences. As mean and maximum temperatures increase from the upper to the lower riffle, the standing crop should increase. Warm water is usually more productive than cold water, other factors being favorable. No appreciable amount of surface ice formed on either riffle, but anchor ice appeared in the upper riffle during December 1964. No anchor ice was observed in the lower riffle. A noticeable decline in total numbers and biomass, especially of *Arctopsyche grandis,* occurred at this time in the upper riffle but not in the lower. Another net-building Trichoptera (*Hydropsyche*), comprising about 22% of the total biomass in the lower riffle, was rare in the upper. Benson (1955) collected species of *Ephemerella, Glossosoma, Hydropsyche, Simulium,* and *Elmis* from floating anchor ice. Brown, Clothier, and Alvord (1953) found no appreciable change in the number of organisms where anchor ice had occurred, but they stated that bottom organisms could be dislodged and carried away. The greater ion concentrations and alkalinity in the lower riffle probably accounted for the larger numbers and biomass there. Armitage (1958) concluded that bicarbonates appeared to be the main factor determining the total number of organisms, but other factors such as temperature and bottom type modify the influence of bicarbonates.

The index of diversity is used to relate total numbers of individuals with the number of taxa present. The thermal and chemical effluents entering the Gibbon River between the two riffles may have reduced the index of diversity in the lower one. The higher water temperatures and dissolved solids in the lower riffle are apparently more favorable for production of Trichoptera than Ephemeroptera.

REFERENCES

ALLEN, E. T., AND A. L. DAY. 1935. Hot springs of Yellowstone National Park. Carnegie Institute of Washington. 525 p.

ARMITAGE, K. B. 1958. Ecology of the riffle insects of the Firehole River, Wyoming. Ecology, **39**: 571–580.

———. 1961. Distribution of riffle insects of the Firehole River, Wyoming. Hydrobiologia, **17**: 152–174.

BENSON, N. G. 1955. Observations of anchor ice in a Michigan trout stream. Ecology, **36**: 529–530.

BROWN, C. J. D., W. D. CLOTHIER, AND W. ALVORD. 1953. Observations on ice conditions in the West Gallatin River, Montana. Proc. Montana Acad. Sci., **13**: 21–27.

BRUES, C. T. 1924. Observations on animal life in the thermal waters of Yellowstone Park, with a consideration of the thermal environment. Proc. Am. Acad. Arts Sci., **59**: 371–487.

COUTANT, C. C. 1962. The effect of a heated water effluent upon the macroinvertebrate riffle fauna of the Delaware River. Proc. Penn. Acad. Sci., **36**: 58–71.

DODDS, G. S., AND F. L. HISAW. 1925. Ecological studies on aquatic insects IV. Altitudinal range and zonation of mayflies, stoneflies and caddiceflies in the Colorado Rockies. Ecology, **6**: 380–390.

IDE, F. P. 1935. The effect of temperature on the distribution of the mayfly fauna of a stream. Univ. Toronto Studies, **39**: 1–76.

MARGALEF, R. 1951. Diversidad de especies en las comunidades naturales. Publ. Inst. Biol. Apl. (Barcelona), **9**: 5–27.

MUTTKOWSKI, R. A. 1929. The ecology of trout streams in Yellowstone National Park. Roosevelt Wildlife Ann., **2**: 155–240.

SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ont. Univ. Toronto Studies, **56**: 1–81.