# DRIFT AND PRODUCTION OF TWO AQUATIC INSECTS IN A MOUNTAIN STREAM<sup>1</sup>

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#### Abstract

The relationships between drift rates, population density, production rates, key environmental factors, and movements of adults were studied in two populations of stream insects, the caddisfly *Oligophlebodes sigma* and the mayfly *Baetis bicaudatus*. Samples of benthic invertebrates (424 total) were collected every 28 days at four stations on Temple Fork of the Logan River, Utah, from October 1967 to September 1969. Samples of drift invertebrates (181 total) were collected every 14 days at three stations on Temple Fork during the same period. During June–September a day and a night drift sample (681 total) were collected every other day.

Drift rates of O. sigma larvae were greatest (5,987 g/year) when biomass in the benthos  $(2.56 \text{ g/m}^2)$  and production  $(4.30 \text{ g/m}^2 \text{ per year})$  were greatest. Total production (dry weight) of O. sigma larvae in the stream (bottom area = 29,487 m<sup>2</sup>) was 89.0 kg in 1968 and 80.8 kg in 1969. Total production of B. bicaudatus nymphs was 41.3 kg in 1968 and 39.8 kg in 1969. Drift rates of O. sigma larvae were related directly to biomass in the benthos over an entire year. Drift rates of O. sigma and B. bicaudatus were not related directly to density expressed as numbers/area in the benthos. Drift rates were correlated positively and significantly (r = 0.78 and 0.55 for day drift of O. sigma and B. bicaudatus, respectively) with density during the months of June–September for both O. sigma larvae and B. bicaudatus nymphs. Discharge, distance below the spring source of Temple Fork, and densities of competing aquatic insects were other factors of significance in the multiple-regression analyses of factors affecting drift rates of the two insects. The 17 or 18 independent variables used in the multiple-regression analyses accounted for 65% and 55% of the variability in day drift rates of O. sigma and B. bicaudatus, respectively.

Adult O. sigma (but not B. bicaudatus) undertook a definite upstream migration estimated at 2-3 km. This flight of adults resulted in a concentrated deposition of eggs in the upper reaches of the stream. The advantage of the upstream flight may be that it stores reproductive products in areas where they are relatively safe from effects of anchor ice during winter and of floods in late winter and early spring.

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### INTRODUCTION

Downstream drift appears to be a significant factor in the population dynamics of many lotic invertebrates. Although reports on drifting invertebrates first appeared in the 1940's (e.g., Lennon 1941, Dendy 1944), the phenomenon did not attract widespread attention among ecologists until after the publication of Müller's 1954 paper. Müller made three important contributions: (1) he documented the numerical significance of drift in relation to number of organisms in the benthos; (2) he postulated that drift resulted from conditions of crowding and competition among individuals in the benthos; and (3) he proposed the colonization cycle for invertebrates having an adult stage capable of flight. The colonization-cycle hypothesis states that the downstream drift of immatures is offset by an upstream migration of flying adults prior to oviposition.

Roos (1957) presented data which indicated that mature females of several trichopterans and a few other aquatic insects flew predominantly in an upstream direction. Elliott (1967) reported that adults of several orders of aquatic insects usually flew in the direction the wind was blowing without regard to orientation up or down the stream. He concluded that the colonization cycle was unnecessary to explain movements of immature and adult aquatic insects in a small stream in Great Britain. Waters (1968) observed the adults of a trichopteran (*Oligophlebodes sigma*) flying upstream above Temple Fork of the Logan River in Utah, and he suggested that the colonization cycle might be in operation for that species.

Waters (1961, 1962*a*, 1962*b*, 1965) followed Müller's work with several investigations and made three additional contributions:

1) he demonstrated a marked diel periodicity in the drift of several invertebrates;

2) he proposed that drift be divided into three broad and overlapping categories: (a) constant drift—due to normal accidental dislodgement; (b) behavioral drift—due to an active response by the organisms; and (c) catastrophic drift—due to floods and other unusually extreme conditions;

3) he postulated that drift is related in some way to production in excess of the carrying capacity of the streambed.

Waters (1962b) also presented a method to compute production of invertebrates under special conditions. The method involved expressing production as the net result of drift onto and off an area plus both the change in population density on the area and the emergence of adults from the area. The special conditions necessary were that no losses due to predation occurred on the area and that dead or dying organisms were swept into the drift nets and thereby accounted for. Several authors (Bailey 1966, Elliott 1967, Elliott and Minshall 1968, Hynes 1970) have expressed doubts about, or have denied, the usefulness of drift measurements in estimating production rates. These objections have been based on the authors' failure to find "correlations" between drift and density of benthos. Elliott (1967), for example, stated that drift in Walla Brook "could never be used to estimate the production rate of the benthos" because such "a small percentage of the benthos was involved in the drift at any time and because the quantity of drift was not related to the density of the benthos." A recent, comprehensive review of the drift literature was given by Waters (1969).

The objective of this study was to clarify some relationships between drift rate, population density, production rate, key environmental factors, and movements of adults within two species of drifting invertebrates. Populations of a caddisfly (*Oligophlebodes sigma* : Limnephilidae) and a mayfly (*Baetis bicaudatus* : Baetidae) in Temple Fork of the Logan River, Utah, were selected for study.

The theoretical operation of the colonization cycle would result in significant changes in the density of immature individuals in different areas along the length of a stream. Simply stated, the upstream area should lose individuals during the lifespan of the immatures while the downstream areas should gain individuals. The documentation of such a population shift required that drift and benthic density be measured along the course of a single stream.

#### STUDY AREA

Temple Fork of the Logan River is a small, clear, mountain stream located in the Bear River Range of the Wasatch Mountains in northern Utah. The stream heads at a large spring (elevation 1,988 m above sea level), flows northwest for 7.3 km, and empties into the Logan River in Logan Canyon. Four sampling stations (I-IV) were established at distances of 0.2, 1.8, 4.2, and 6.3 km below the spring source. Length, mean width, and area of streambed between stations are given in Table 1. In its first 1.2 km the stream flows northwest through a narrow, steep-sided canyon (Fig. 1). The southern exposure of this canyon supports a mountain mahogany-sagebrush (Cercocarpus ledifolius-Artemisia tridentata) community. The northern exposure of the canyon is covered by a climax forest of Douglas-fir (Pseudotsuga menziesii). The stream is heavily shaded in the canyon by Douglas-fir, aspen (Populus tremuloides), chokecherry (Prunus sp.), and willows (Salix spp.).

The stream emerges from this narrow canyon 1.3 km below its source and turns to run directly west into an open, rolling terrain covered by sagebrush and various cold-desert grasses. The stream turns to the north-northeast 2.5 km below the source Fork

TABLE 1. Dimensions of areas between stations, Temple one-half

Boundaries	Length (km)	Mean width (m)	Area (m²)
Source-I	0.20	3.05	610
I-II	1.60	3.66	5856
II-III	2.40	3.96	9504
III-IV	2.10	4.27	8967
IV-mouth	1.00	4.15	4150
Total	7.30		29,487



FIG. 1. Map of Temple Fork of the Logan River, Utah, with locations of sampling stations I-IV.

and runs between low-lying hills and out across small open flats. Willows grow intermittently along the edges of the stream in this area. At a distance of 5.8 km below the source the stream curves gently to the west again and enters a broad, open canyon before emptying into the Logan River.

Mean annual precipitation on the study area is 64 cm, two-thirds of which is received as snow. Summer showers are usually of short duration and seldom exceed 1 cm within a 24-hr period. Temple Fork receives additional water from five spring-fed tributaries (Fig. 1). Spawn Creek enters 5.6 km below the source of Temple Fork and is the largest of the tributaries with a mean annual discharge of 0.10 m<sup>3</sup>/sec. The remaining four unnamed tributaries have discharges of less than 0.03 m<sup>3</sup>/sec. Temple Fork had a mean discharge of 0.30 and 0.48 m<sup>3</sup>/sec at stations I and IV, respectively. Surface runoff contributes little water to the stream except during the spring melt and after unusually heavy thundershowers in summer.

Maximum air temperatures usually occur in July and August ( $32^{\circ}$ C in 1968 and  $35^{\circ}$ C in 1969). Minimum air temperatures usually occur in January and February ( $-21^{\circ}$ C in 1968 and  $-24^{\circ}$ C in 1969). The stream does not freeze over in winter, but anchor ice forms on the streambed in the lower one-third to one-half of the stream when the air temperature falls below -18 °C. Temple Fork has moderate populations of brown trout (*Salmo trutta*) and cutthroat trout (*S. clarki*) and is stocked two or three times each summer with catchable-sized rainbow trout (*S. gairdneri*).

### MATERIALS AND METHODS

Water temperature was recorded at stations I and III with Ryan Model-D submersible thermographs. At station II both air and water temperatures were recorded with a Foxboro two-pen recorder. Maximum and minimum water temperatures were determined at station IV with a Taylor max-min thermometer. A 12-inch mercury-glass thermometer was used for discrete measurements of both air and water temperatures. Estimates of daily maximum, mean, and minimum water temperatures were made from the thermographs at the three upper stations.

A permanent staff gage was installed in the stream at the downstream end of a large road culvert, located approximately 0.9 km below station II. Discharges from the culvert were determined at several stages of the stream, and a Gurley current meter was used to measure velocities of the water at several points across the channel. A rating curve was then established to permit the conversion of stage to discharge. Stages of the stream were recorded daily in summer and at 14-day intervals in winter.

Total alkalinity and hydrogen-ion concentrations were determined at 14-day intervals at each station. Dissolved oxygen concentrations were determined at irregular intervals throughout the study. Total alkalinity (as ppm  $CaCO_3$ ) was determined with bromcresol-green indicator by methods outlined by the American Public Health Association (1960). Hydrogen-ion concentration was determined with a Wallace and Tiernan comparator. Dissolved oxygen concentration was determined by the Thierault modification of the Winkler method.

Bottom samples were collected with a wire-mesh device similar to those described by Hess (1941) and Waters and Knapp (1961). The sampler enclosed an area of 0.093 m<sup>2</sup> (1 ft<sup>2</sup>). In use the sampler was turned securely into the stream bottom, and the stones, sand, and debris of the substrate were thoroughly stirred and scrubbed by hand. Invertebrates and organic debris were swept into a collecting net (Nitex, 471  $\mu$ ) attached to the downstream side of the sampler.

Bottom samples were collected from deep-riffle areas at each station. These areas were approximately 15 m long and were characterized by current speeds of 50–150 cm/sec, depths of 12–40 cm, and the presence of fine rubble, fine and coarse sand, and silt. An objective in sampling was to produce a set of samples from as uniform a substrate as possible. Each sample site included at least one stone exceeding 12 cm diameter in its greatest measurement. The same sample site was not utilized more than once each 3–4 months.

Two bottom samples were collected at each station every 14 days during June–September and every 28 days during the remainder of each year. Entire samples were preserved in 10% formalin and transported to the laboratory for analysis. All macroinvertebrates were sorted from one sample of each pair, but only *O. sigma* larvae were sorted from the second sample. Sorting was facilitated by using the sugarflotation technique described by Anderson (1959) and a  $2 \times$  macroscope.

A total of 424 bottom samples was collected and analyzed. Samples of 30-50 *B. bicaudatus* nymphs and *O. sigma* larvae from each bottom sample were ovendried at  $80^{\circ}$ C and weighed to the nearest 0.1 mg.

Invertebrates drifting in the stream were sampled at the upper three stations with waterwheel-driven samplers described by Pearson and Kramer (1969). The sampler at station II was installed in September 1967, and those at stations I and III in May 1968. During winter one 24-hr sample was collected at each station every 14 days. The sampling period usually began at 10–11:00 AM MST and ended at the same time the following day. During June–September two samples (a day and a night sample) were collected at each station every other day. Collecting nets on the drift samplers were emptied at 8–9 AM (2–3 hr after sunrise) and at 7:30–8:30 PM (30–45 min before sunset).

Larvae of O. sigma, B. bicaudatus nymphs, and adults of both were sorted from the drift samples under a  $2 \times$  macroscope, identified, and counted. All O. sigma and B. bicaudatus from the 24-hr samples and from every seventh day and night sample were ovendried and weighed. A total of 181 24-hr samples was collected and analyzed. In all, 341 day and 340 night samples were collected and analyzed.

Observations on the flight of adult O. sigma were made each evening while the drift samplers were being serviced. Special efforts were made to determine effects of air temperature and wind on flight behavior of adult O. sigma. In June 1969 artificial oviposition sites were placed in the stream at all four stations. These artificial sites were 33- by 19- by 4-cm pieces of unpainted pine board held vertically in the stream by a pair of supporting rods driven into the streambed. Only the lower one-third of each board was submerged in the stream. Boards were examined each evening and every other morning from July 1 to October 1, 1969, and at 1-week intervals in October 1969. Egg masses deposited on the underside of the board were counted and removed after each examination. The boards were utilized for oviposition by O. sigma, but not by B. bicaudatus.



FIG. 2. Mean monthly water temperature, stations I– III, Temple Fork, 1967–69. At station IV water temperature for this period ranged from  $0.0^{\circ}$  to  $17.1^{\circ}$ C.

## PHYSICAL AND CHEMICAL ENVIRONMENT

Water temperature at station I was nearly constant throughout the year (4.8°-6.1°C). Monthly mean temperatures ranged from a low of 5.0°C in winter to highs of 6.1°C in May 1968 and 5.5°C in May 1969 (Fig. 2). With increasing distance below the source, summer water temperatures generally increased and winter temperatures decreased under the influence of ambient air temperatures. The thermograph at station I was located about 100 m above the sampling station and 100 m below the spring source. Numerous discrete measurements of water temperature at station I indicated that on very warm summer days the stream temperature increased 0.5°-1.0°C in the 100 m between the thermograph and station I. On very cold winter days water temperatures at station I were 0.5°-1.0°C below those recorded by the thermograph. The daily range of water temperatures also increased with increasing distance below the source.

Mean monthly water temperatures were lower in the winter months of 1967–68 than in the winter months of 1968–69. Temperatures were higher at all stations in the summer of 1968 than in the summer of 1969.

Mean 1967–69 discharges were 0.30, 0.34, 0.37, and 0.48 m<sup>3</sup>/sec at stations I–IV, respectively. Peak discharge occurred in June 1968 (mean discharges  $= 0.62, 0.67, 0.74, \text{ and } 0.92 \text{ m}^3\text{/sec}$ ) and May 1969 (mean discharges  $= 0.94, 1.06, 1.27, \text{ and } 1.49 \text{ m}^3\text{/sec}$ ; Fig. 3). Minimum discharges (0.10–0.32 m<sup>3</sup>/sec) occurred in January 1968 and February 1969. The April–June peak discharges were due to increased spring flow rather than to snowmelt or rainfall.

No abrupt or severe changes in water chemistry were detected during the study. Total alkalinity at the four stations ranged from highs of 166, 172, 173, and 187 ppm at stations I–IV to lows of 139, 149, 141, 150 ppm, respectively. Alkalinity was slightly

![](_page_4_Figure_2.jpeg)

FIG. 3. Mean monthly discharge at station II, Temple Fork, 1967-69—expressed as cubic meters per second.

YEAR AND MONTH

lower in winter months and reached a peak during the increased discharge during May–June of both years. Mean annual hydrogen-ion concentrations (pH) were 8.0, 8.2, 8.3, and 8.3 at stations I–IV, respectively. The range of pH was from 7.7 to 8.5 for the entire stream. Dissolved oxygen concentrations were usually at 80–100% of air saturation at each of the four stations (8.5–10.6 ppm). Turbidity was usually less than 25 Jackson turbidity units, but never greater than 200 JTU.

The stream was almost entirely riffles or runs with only a few sandy-bottomed pools. The substrate at all stations was composed of large and small rubble, gravel, sand, and some silt. At stations I and II the bottom stones were rather loosely arranged on the streambed. At station III the bottom stones were slightly more compacted, and the stream flowed over some areas of bedrock. At station IV the substrate was noticeably more compacted than at III, and deposits of calcium carbonate were present on the stones. The stones and cobbles of the streambed were derived from a limestone base stratum and an overlying reddish conglomerate. A brown alga, Hydrurus, was common at station I, but its trailing filaments decreased in abundance with distance below the source. Aquatic mosses (Musci) grew on partially submerged stones at all stations.

# LIFE HISTORIES OF STUDY ORGANISMS

## Oligophlebodes sigma

Oligophlebodes sigma produced one generation per year and larvae hatched in October–January. They constructed and lived within a round, truncated-cone case of coarse sand grains. Fifth (and final) instar larvae were typically 4–6 mm long and pupated within the last larval case. Mature larvae selected thin flat stones, approximately 2 mm in diameter and 0.5 mm thick, as capstones on the open ends of their sand cases. The cases were securely attached to the substrate (usually on the underside of a large stone) at both ends before the capstones were secured in place. Pupal distributions were clumped to a greater extent than were larval distributions, probably because suitable pupation sites were in short supply. A prepupal stage of 1–4 weeks was evident, particularly at station I, where it appeared that the case was sealed earlier in the season and a longer time was spent in the prepupal stage. At the three lower stations the prepupal stage was usually maintained only 1–2 weeks. Pupation occurred from about July 1 through the third week of September. Adults began emerging in the first week of August in 1968 and the last week of July in 1969. Peak emergence occurred in August and September of both years, but a few adults continued to emerge as late as the first week of November in both years.

Adults of *O. sigma* were frequently seen drinking from the stream, but were not observed feeding. Adults held in cages without water died in 1-2 days, but those held in cages supplied with water usually lived 2-4 days with a maximum observed life of 5 days.

Digestive tracts of 12 O. sigma larvae examined contained green and brown algae, diatoms, and unidentifiable plant fragments. These larvae are dayactive organisms (Waters 1968) and were frequently observed "grazing" on the periphyton-detritus covering on the upper surfaces of stones in the stream. The larvae returned to the undersides of stones on the streambed each night and were apparently inactive at night. This behavior was particularly evident on the oviposition boards, which were also populated by larvae. When the boards were examined late in the afternoon, the upper surfaces of the boards were uniformly populated by many O. sigma larvae. Early in the morning few larvae were found on the upper surfaces of the boards, and most were crowded together on the edge of the board resting on the substrate.

## Baetis bicaudatus

Baetis bicaudatus had two generations per year in Temple Fork. The nymphs of the winter generation hatched over an extended period (November-February) in the late fall and winter months. The nymphs developed through an unknown number of instars (other species reportedly go through 20–30 instars, Berner 1959) before reaching maturity at a length of 5–6 mm (excluding tails) in May and June. The winter-generation adults emerged in June. Mature females returned to the stream after fertilization and deposited their eggs. Eggs of the summer generation hatched in June and July, the nymphs matured rapidly, and the adults emerged in September and October. Adults were seen swarming over the stream in bright sunlight during early morning hours.

Digestive tracts of seven *B. bicaudatus* nymphs contained masses of plant debris and unidentifiable organic materials, perhaps dead leaves of terrestrial

![](_page_5_Figure_3.jpeg)

FIG. 4. Density of *O. sigma* larvae on the streambed, stations I–IV, Temple Fork, 1967–69—expressed as numbers per  $0.1 \text{ m}^2$ .

![](_page_5_Figure_5.jpeg)

FIG. 5. Biomass of O. sigma larvae on the streambed, stations I–IV, Temple Fork, 1967–69—expressed as milligrams dry weight per  $0.1 \text{ m}^2$ .

plants and small amounts of algae. The nymphs are night-active organisms and were seldom seen on the upper surfaces of the substrate materials during daylight hours. Adults have vestigial mouth parts and probably do not feed.

## DENSITY AND BIOMASS OF BENTHIC INVERTEBRATES

## Oligophlebodes sigma

The O. sigma larva population was lowest in numbers at station I in both years. The population reached a maximum density of  $200-300/0.1 \text{ m}^2$  in November and December of 1968 and 1969 and declined slowly and steadily until the time of pupation in June (Fig. 4). Apparently mortality and driftremoval rates from the area were low.

Biomass of O. sigma larvae at station I was similarly low in the 2 years. In 1968 biomass reached a maximum in March and April (58 mg/0.1 m<sup>2</sup>), but in 1969 the maximum was not reached until May-June and was slightly higher (78 mg/0.1 m<sup>2</sup>; Fig. 5).

The highest densities of O. sigma larvae were found at stations II and III. In 1968 numbers at station II reached a peak of 1,131/0.1 m<sup>2</sup> in Feb-

ruary (Fig. 4). From February to May the density at this station declined slowly to about  $720/0.1 \text{ m}^2$ . Numbers at station III reached a peak of about 928/0.1 m<sup>2</sup> in January 1968, declined slowly into March, and recovered to about 875/0.1 m<sup>2</sup> in May 1968. The relationship between density and time in Fig. 4 suggests sampling variability as well as actual variation in density. A two-way analysis of variance was used to determine how much of the total variance in density was due to variation in month of sampling (A effect) and station (B effect) as well as sampling error and interaction between the A and B effects. Although the range between the paired benthic samples taken each month at each station was large in some cases, the analysis of variance yielded highly significant (0.01 level) F-values for month of sampling (F = 10.96; df = 25/104), station (F = 48.54; df = 3/104), and the interaction between the two main effects (F = 3.32; df = 75/ 104). The mean squares for both of the main effects were very large, indicating real and considerable effects of variation in both of these factors on the variation in density of O. sigma larvae. The mean square for the A-B interaction was much smaller and indicated that, although an interaction was present, its importance was less than that of the two main effects.

Biomass of O. sigma larvae at station II reached a peak of about  $145 \text{ mg}/0.1 \text{ m}^2$  in January 1968 and remained at that level until April before declining (Fig. 5). Biomass of larvae at station III rose steadily from October 1967 and did not decline until the larvae began pupating after July 1.

Numbers of *O. sigma* larvae at stations II and III were much lower in 1969 than in 1968 (Fig. 4). At station II the density of larvae peaked in January, declined slowly, and then peaked again in May. At station III the density of larvae peaked in December 1968 and then declined until showing a slight gain just before pupation in July 1969.

Although numbers of larvae per unit area were much lower at stations II and III in 1969, biomass of larvae per unit area was similar in 1968 and 1969 (Fig. 5). Relationships between biomass and time were similar in the 2 years at station II. At station III the final biomass achieved before pupation began was nearly the same in both years, though values early in 1969 were lower than those from the corresponding periods in 1968.

The density of O. sigma larvae at station IV reached peak numbers of 379 and 640/0.1 m<sup>2</sup> in January 1968 and 1969, respectively. The density fell sharply in February and March of both years and then recovered gradually until pupation. Biomass of O. sigma larvae at station IV increased steadily from January to June in both years and reached peaks just prior to pupation in both years.

## Baetis bicaudatus

Density of winter-generation *B. bicaudatus* nymphs was highest at stations I and III in both years (station I maxima = 572 and  $346/0.1 \text{ m}^2$ , station III maxima = 809 and  $434/0.1 \text{ m}^2$  in 1968 and 1969, respectively; Fig. 6). Densities at II and IV were lower in both years.

Maximum biomass of *B. bicaudatus* nymphs at stations I, II, III, and IV in 1968 was 54, 23, 52, and 77 mg/0.1 m<sup>2</sup>, respectively (Fig. 7). In 1969 the biomass of winter-generation nymphs was higher at station III and lower at stations I and II.

The density of summer-generation nymphs was highest at station I in both years (maxima of 1,050 and  $332/0.1 \text{ m}^2$  in 1968 and 1969, respectively; Table 2). Densities at stations II and III were similar in the 2 years and lower in 1969 than in 1968. Densities of summer-generation *B. bicaudatus* nymphs were lowest at station IV in both years. Biomass was highest where numbers were greatest and reflected the differences among stations described above (Table 2).

Besides O. sigma and B. bicaudatus, the 10 most abundant macroinvertebrate forms were Ephemerella

![](_page_6_Figure_7.jpeg)

FIG. 6. Density of winter-generation *B. bicaudatus* nymphs on the streambed, stations I–IV, Temple Fork, 1967-69—expressed as number per 0.1 m<sup>2</sup>.

![](_page_6_Figure_9.jpeg)

FIG. 7. Biomass of winter-generation *B. bicaudatus* nymphs on the streambed, stations I–IV, Temple Fork, 1967-69—expressed as milligrams dry weight per 0.1 m<sup>2</sup>.

sp. (coloradensis?), Rhithrogena, Cinygmula, Planariidae, Glossosoma, Tipulidae, Nemoura, Elmidae, and Psychodidae in approximate order of numerical abundance. The mean monthly numbers of all macroinvertebrates combined (including O. sigma and B. bicaudatus) were 1,065, 1,688, 1,599, and 1,211/0.1 m<sup>2</sup> at stations I–IV, respectively.

### Growth

Mean individual weights were expressed as ovendried weight (cases removed). The use of ovendried weight results in less error than the use of either live weight (when this is possible) or wet-preserved weight (Gerking 1962). Factors for converting dry to wet weights (alcohol-preserved specimens drained for 2 min on paper before weighing) were 2.57 for *O. sigma* larvae and 3.81 for *B. bicaudatus* nymphs. Growth was considered to be exponential, and daily instantaneous growth coefficients (*G*) were calculated by the method outlined by Chapman (1968):

$$G = \frac{\log_e \bar{w}_2 - \log_e \bar{w}_1}{\Delta t}$$

TABLE 2. Density (number) and biomass (milligrams dry weight/0.1 m<sup>2</sup>) of summer-generation *Baetis bicaudatus* nymphs on the streambed, stations I-IV, Temple Fork, 1968-69

		Density	(number)		Bio	mass (mg/0	.1 m²)	
Date	I	II	III	IV	I	II	III	IV
5–18–68	1.050	0	0	0	21.0	0	0	0
6-30-68	220	94	15	10	22.0	1.9	0.3	0.2
7-28-68	51	157	225	12	12.8	7.9	15.8	0.3
8-25-68	74	218	165	14	30.3	21.8	18.1	1.1
9-22-68	32		124	20	13.1		57.0	7.0
10-20-68	5	36	57	25	2.3	19.1	43.3	26.5
11-17-68	0	11	0	0	0	5.1	0	0
6–1–69	286	0	0	0	45.8	0	0	0
6-29-69	332	6	Ō	8	69.7	0.5	Ŏ	0.3
7–27–69	113	111	71	4	32.8	8.9	4.3	0.3
8-24-69	126	95	60	17	44.1	22.8	11.4	3.4
9–21–69	60	51	56	12	38.4	33.7	40.32	7.2

TABLE 3. Mean individual weight	(milligrams dry weig	ht) and daily growth rat	e (G) of O. sigma	larvae, 1968 and
1969 generations, stations I-IV,	Temple Fork			

				Sta	tion			
		I		π	III		 I	v
Generation and date	Weight (mg)	G	Weight (mg)	G	Weight (mg)	G	Weight (mg)	G
$\begin{array}{c} 1968 \; generation \\ 11-4-67 \\ 12-2-67 \\ 12-30-67 \\ 1-27-68 \\ 2-23-68 \\ 3-23-68 \\ 4-20-68 \\ 5-18-68 \\ 6-30-68 \\ 7-28-68 \\ 8-25-68 \\ 9-22-68 \\ 10-20-68 \\ 11-17-68 \end{array}$	$\begin{array}{c} 0.01 \\ 0.06 \\ 0.14 \\ 0.18 \\ 0.22 \\ 0.35 \\ 0.55 \\ 0.81 \\ 2.19 \\ 1.77 \\ 0.50 \\ 0.41 \\ \end{array}$	$\begin{array}{c}\\ 0.064\\ 0.030\\ 0.009\\ 0.007\\ 0.016\\ 0.016\\ 0.014\\ 0.023\\ -0.008\\ -0.045\\ -0.007\\\\\\\\\\\\\\\\\\\\ -$	$\begin{array}{c} 0.04 \\ 0.04 \\ 0.11 \\ 0.13 \\ 0.18 \\ 0.17 \\ 0.16 \\ 0.42 \\ 0.59 \\ 0.82 \\$	$\begin{array}{c} & & \\ & 0 \\ 0.036 \\ 0.009 \\ -0.003 \\ 0.011 \\ -0.002 \\ -0.002 \\ 0.022 \\ 0.012 \\ 0.012 \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\$	$\begin{array}{c} 0.05\\ 0.11\\ 0.12\\ 0.11\\ 0.21\\ 0.23\\ 0.27\\ 0.43\\ 0.42\\ 0.57\\ 0.52\\ 0.76\\ 0.57\\ \end{array}$	$\begin{array}{c}$	$\begin{array}{c} 0.06\\ 0.07\\ 0.11\\ 0.13\\ 0.24\\ 0.24\\ 0.34\\ 0.67\\ 0.74\\ 0.45\\ 0.40\\\\\\\\\\\\\\\\ -$	$\begin{array}{c} 0.006\\ 0.016\\ 0.016\\ -0.010\\ 0.021\\ 0\\ 0.012\\ 0.016\\ 0.004\\ -0.018\\ -0.004\\ -\end{array}$
$\begin{array}{c} 1969 \; generation \\ 10-20-68 \\ 11-17-68 \\ 12-15-68 \\ 1-12-69 \\ 2-9-69 \\ 3-9-69 \\ 4-6-69 \\ 5-4-69 \\ 6-1-69 \\ 6-1-69 \\ 6-29-69 \\ 7-27-69 \\ 8-24-69 \end{array}$	$\begin{array}{c} 0.01 \\ 0.02 \\ 0.04 \\ 0.15 \\ 0.24 \\ 0.34 \\ 0.43 \\ 0.61 \\ 1.10 \\ 1.92 \\ 1.60 \end{array}$	$\begin{array}{c}$	$\begin{array}{c} 0.02\\ 0.04\\ 0.12\\ 0.21\\ 0.25\\ 0.32\\ 0.49\\ 0.36\\ 0.39\\ 0.82\\ 0.82\\ 0.63\\ \end{array}$	$\begin{array}{c}\\ 0.025\\ 0.039\\ 0.020\\ 0.006\\ 0.009\\ 0.015\\ -0.011\\ 0.003\\ 0.027\\ 0\\ -0.009\end{array}$	$\begin{array}{c} 0.03\\ 0.07\\ 0.13\\ 0.10\\ 0.21\\ 0.45\\ 0.40\\ 0.47\\ 1.01\\ 1.75\\ 1.58\\\end{array}$	$\begin{array}{c}$	0.02 0.03 0.05 0.14 0.11 0.13 0.20 0.27 0.42 0.71 0.77	$\begin{array}{c} & & \\ 0.014 \\ 0.018 \\ 0.037 \\ -0.009 \\ 0.006 \\ 0.015 \\ 0.011 \\ 0.016 \\ 0.019 \\ 0.003 \\ \end{array}$

where  $\bar{w}_1$  and  $\bar{w}_2$  equal the mean weight of an organism at times  $t_1$  and  $t_2$ , respectively.

Larvae of O. sigma grew rapidly immediately after hatching in November (typically G = 0.006 to 0.064 mg/mg day; Table 3). Larvae grew slowly in midwinter (typically G = 0 to 0.012 mg/mg day) and then began growing rapidly again (G = 0.003 to)0.027 mg/mg day) in June. Sampling variability may be responsible for some of the negative G-values observed. Winter growth rates were slightly higher at station I, probably because of the higher water temperatures near the spring source. Larvae at station I grew to a greater final weight (range = 1.9– 2.3 mg) in both years than did larvae at the lower stations. Final larval weights were similar (0.82 mg and 0.98 mg) in both years at station II. Final larval weights at station III were 0.57-0.87 mg in 1968, but were much higher (1.51–1.75 mg) in 1969. Final larval weights were 0.74-1.37 mg in both years at station IV (Table 3).

The mean individual weights (and the negative G-values) of larvae toward the end of each generation (Table 3) may be misleading, because they were influenced by the increasing percentage of slowgrowing individuals (remaining after the rapid-growing individuals pupated). Therefore, the weight of

TABLE 4. Mean individual weight (milligrams) and density (number) of *O. sigma* pupae, and mean monthly density of *O. sigma* larvae (April–June), stations I– IV, Temple Fork, 1968–69

		Sta	tion	
Item and year	I	II	III	IV
Mean individual dry weight of immature pupae (mg)				
1968	2.33	0.94	0.87	1.02
1969	2.20	0.98	1.51	1.37
Mean density (number) of pupae on the streambed				
(Julie-Sept.)/0.1 III-	10	50	40	50
1908	10	50	42	52
1969	7	54	72	13
Mean density (number) of larvae on the streambed				
(April-June)/0.1 m <sup>2</sup>				
1968	39	686	697	166
1969	72	422	148	247
	. –		2.0	

immature pupae provides a better measure of the final larval weight obtained at each station. Mean pupal weight (without cases) was 2.33 mg and 2.20 mg in 1968 and 1969 at station I (Table 4). Pupae were smaller at the three lower stations (0.87-1.51 mg). Mean monthly pupal densities (number)

TABLE 5.	Mean	individual	weight	(milligrams	dry	weight)	and	daily	growth	rate	(G)	of I	B. bicaua	atus 1	nymphs,
1968 a	nd 196	9 winter	and sum	nmer genera	tions	, stations	s I–IV	/, Ten	nple For	·k					

				Sta	tion			
	]			II	II	I	Г	V
Generation and date	Weight (mg)	G	Weight (mg)	G	Weight (mg)	G	Weight (mg)	G
1968 winter genera	tion				0.02			
$10-1-67 \\ 11-4-67 \\ 12-2-67 \\ 12-30-67 \\ 1-27-68 \\ 2-23-68 \\ 3-23-68 \\ 4-20-68 \\ 5-18-68 \\ 6-30-68 \\ 7-28-68 \\ \end{array}$	$\begin{matrix}$	$\begin{array}{c}$	$\begin{array}{c} 0.02\\ 0.06\\ 0.04\\ 0.05\\ 0.04\\ 0.06\\ 0.11\\ 0.15\\ 0.40\\ 0.45\\ \end{array}$	$\begin{matrix} -0.033 \\ -0.014 \\ 0.008 \\ -0.008 \\ 0.014 \\ 0.022 \\ 0.011 \\ 0.035 \\ 0.003 \\ - \end{matrix}$	$\begin{array}{c} 0.03 \\ 0.03 \\ 0.04 \\ 0.08 \\ 0.10 \\ 0.14 \\ 0.23 \\ 0.16 \\ 0.19 \\ 0.55 \end{array}$	$\begin{array}{c}$	0.06 0.06 0.07 0.09 0.15 0.34 0.27 0.19 0.22	$\begin{array}{c}$
1968 summer gener 6-30-58 7-28-68 8-25-68 9-22-68 10-20-68	ration 0.10 0.25 0.41 0.41 0.45	0.033 0.018 0 0.003	$\begin{array}{c} 0.02 \\ 0.05 \\ 0.10 \\ 0.31 \\ 0.53 \end{array}$	0.033 0.025 0.040 0.019	$\begin{array}{c} 0.02 \\ 0.07 \\ 0.11 \\ 0.46 \\ 0.76 \end{array}$	0.045 0.016 0.051 0.018	$\begin{array}{c} 0.02 \\ 0.06 \\ 0.08 \\ 0.35 \\ 1.06 \end{array}$	0.039 0.006 0.053 0.040
1969 winter genera 10-20-68 11-17-68 12-15-68 1-12-69 2-9-69 3-9-69 4-6-69 5-4-69 6-1-69 6-29-69	tion 0.02 0.03 0.04 0.04 0.04 0.07 0.07 0.23 0.61 0.97	$\begin{array}{c}$	0.03 0.06 0.09 0.05 0.11 0.19 0.30 0.57		$\begin{array}{c} 0.03 \\ 0.07 \\ 0.07 \\ 0.12 \\ 0.25 \\ 0.40 \\ 0.42 \\ 0.50 \\ \end{array}$	 0.030 0 0.019 0.026 0.017 0.002 0.006 	0.07 0.05 0.07 0.08 0.12 0.18 0.32 0.72	$\begin{array}{c} -0.012\\ 0.012\\ 0.005\\ 0.014\\ 0.014\\ 0.021\\ 0.029\\\\\\\\\\\\\\\\ -$
1969 summer gener 5-4-69 6-1-69 6-29-69 7-27-69 8-24-69 9-21-69	0.16 0.21 0.29 0.35 0.37	0.010 0.012 0.007 0.002	0.09 0.08 0.24 0.66	-0.004 0.039 0.036	0.06 0.07 0.11 0.19 0.72	 0.006 0.016 0.055 0.048	$\begin{array}{c} 0.04 \\ 0.04 \\ 0.08 \\ 0.07 \\ 0.20 \\ 0.60 \end{array}$	$\begin{array}{c} & & \\ & 0 \\ 0.025 \\ -0.005 \\ 0.038 \\ 0.039 \end{array}$

were lowest at station I (10 and 7/0.1 m<sup>2</sup>) in 1968 and 1969 and higher at the three lower stations (13–72/0.1 m<sup>2</sup>; Table 4).

The final weight of immature pupae attained was probably a function of nutrition and crowding of larvae. The relationships between pupal weights and larval densities during the rapid-growth months of April, May, and June at each of the four stations are shown in Fig. 8. The mean weight of pupae decreased as larval density increased. Many insects are known to attain a smaller adult size under conditions of crowding or lack of food, or both (e.g., Ullyett 1950).

Nymphs of *B. bicaudatus* also grew slowly during the winter months at all stations, including station I (Table 5). The prolonged hatching period of *B. bicaudatus* eggs resulted in the presence of nymphs of many sizes at all times of the year. Therefore, the mean nymphal weights of 0.45-1.06 mg shown in Table 5 do not accurately reveal the final size (1.2-1.8 mg) of winter-generation nymphs. Nymphs of *B. bicaudatus* grew to approximately the same size at each station (Table 5).

### PRODUCTION

Annual production of O. sigma larvae and B. bicaudatus nymphs at each station was computed by Allen's (1951) graphical method. Number of individuals per 0.1 m<sup>2</sup> of streambed was plotted against mean dry weight, and the area under the resultant curve provided an estimate of the total production of tissue for the time period involved. The actual coordinates of density and individual weight used for the Allen curves were taken from smoothed curves fitted to original scatter diagrams of the density and individual weight data, as suggested by Chapman (1968). The Allen curve for production of the 1968 generation of O. sigma larvae at station II is shown in Fig. 9. Production estimates were not made according to Waters' (1962b) method because (1) the distance between stations was too great to assume uniform populations and (2) rates of emergence, predation, and decomposition in the areas could not be measured and were known to be of importance.

The relatively long hatching period (for both spe-

![](_page_9_Figure_5.jpeg)

FIG. 8. Mean density of *O. sigma* larvae during the rapid-growth months of April–June and mean individual dry weight of *O. sigma* pupae, stations I–IV, Temple Fork, 1968–69. Solid circle, 1968 data; open circle, 1969 data.

![](_page_9_Figure_7.jpeg)

FIG. 9. Allen curve to compute production of O. sigma larvae per 0.1 m<sup>2</sup>, station II, Temple Fork, 1968. Area under curve = 384.8 mg dry weight per 0.1 m<sup>2</sup>.

TABLE 6. Production of O. sigma larvae and B. bicaudatus nymphs, 1968 and 1969 generations, stations I-IV, Temple Fork—expressed as milligrams dry weight per  $0.1 \text{ m}^2$  of streambed unless otherwise stated

		B. bicc	udatus
Generation and station	O. sigma	Winter generation	Summer generation
1968	··		
I	128	84	112
ĪI	385	55	63
ĪĪI	430	114	99
ĪV	175	44	21
Mean value for			
entire stream	301 7	72 8	67.2
Total production (kg)	501.7	12.0	07.2
for entire stream	88 0	21 5	19.8
for entire stream	00.7	21.5	17.0
1969			
I I	129	93	102
ÎT	347	51	56
ÎII	331	131	45
ÎV	220	89	ğ
11	220	0,	,
Mean value for			
entire stream	273 9	91.4	43.6
Total production (kg)			
for entire stream	80.8	27.0	12.8
io. onure ou cum	00.0	2	

cies) meant that Allen's method would underestimate production by the weight of all immatures dying during the hatching period (assuming constant rates of hatching and mortality). This quantity, therefore, was estimated by determining the mortality rate for immatures in the month after hatching ceased (January for *O. sigma*) and applying this rate to larvae present during the hatching period. This method probably underestimated the actual mortality loss within the hatching period, because the mortality rate applied (obtained from older larvae) was probably lower than the actual mortality rate. Production of winter and summer generations of *B. bicaudatus* were computed separately.

Production of *O. sigma* larvae was lowest at station I in both years (128 and 129 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively; Table 6). Production at station II was 385 and 347 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively. The highest production of *O. sigma* larvae was at station III in 1968 (430 mg/0.1 m<sup>2</sup>). In 1969 production at station III was 331 mg/0.1 m<sup>2</sup>, slightly below that at station II in the same year. Production at station IV was above that at station I, but below that at II and III in both years (175 and 220 mg/0.1 m<sup>2</sup>).

The year-to-year variation within stations was relatively small compared to the between-station variability, with the exception of station III where production of *O. sigma* larvae dropped from 430 in 1968 to 331 mg/0.1 m<sup>2</sup> in 1969 (Table 6). The production at station I was approximately one-third that at station III in both years, although the density

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of larvae at station I was only about one-sixth that at station II. The higher final weight achieved and the lower mortality rates at station I accounted for these different ratios in production and density. The production estimates made at the upper and lower boundaries of each interstation area were averaged, multiplied by the area of the streambed  $(29,487 \text{ m}^2)$ , and then summed to yield estimates of the total production for the stream. Total production for each generation was 89.0 kg (196.2 lb.) in 1968 and 80.8 kg (178.1 lb.) in 1969 (Table 6).

Production of winter-generation *B. bicaudatus* nymphs was highest at station III (114 and 131 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively; Table 6). The production of winter-generation nymphs was lowest at stations II and IV (55 and 51 mg/0.1 m<sup>2</sup> at station II; 44 and 89 mg/0.1 m<sup>2</sup> at station IV).

Production of the summer generations was highest at station I in both years. Production of the summer generations was somewhat less at stations II and III and was lowest at station IV in both years. Mortality rates and final weights obtained appeared to have less between-station variability for *B. bicaudatus* nymphs than for *O. sigma* larvae (Table 6). Therefore, density and production ratios were not as variable for *B. bicaudatus*. Total production of nymphs for the entire stream in 1968 was estimated to be 21.5 kg for the winter generation and 19.8 kg for the summer generation. In 1969 total production was 27.0 kg for the winter generation and 12.8 kg for the summer generation (Table 6).

#### DRIFT

Total number and biomass of each organism passing the upper three stations were calculated by multiplying the drift-sampler-catches/volume-water-sampled by the daily flow of the stream. Daily totals were then multiplied by the number of days between the winter (14 days) and summer (7 days) samples and summed over the entire generation. All references

![](_page_10_Figure_7.jpeg)

FIG. 10. Total number of *O. sigma* larvae drifting past stations I-III, Temple Fork, 1967-69—expressed as grams dry weight per 24 hr.

![](_page_10_Figure_9.jpeg)

FIG. 11. Biomass of *O. sigma* larvae drifting past stations I-III, Temple Fork, 1967–69—expressed as grams dry weight per 24 hr.

to "1968" and "1969" refer to the drift of the 1968 and 1969 generations. Therefore, the figures representing the total drift of *O. sigma* larvae past a given station for 1968, for example, actually refer to individuals drifting past from October 1967 to September 1968, the period of larval existence for the 1968 generation, and not to individuals drifting past within the calendar year of 1968.

Drift rates of *O. sigma* larvae were low at all stations from September through March of both years (Fig. 10 and 11). Drift rates (expressed as both numbers and biomass per 24 hr) began increasing in April and reached maxima in June and July. A slight increase in the winter rates was apparent at stations II and III in January 1969 and at station III in January 1968 (Fig. 10 and 11).

Both total number and biomass of O. sigma larvae drifting past station I were very low in both years. In 1968 minimal figures of  $6 \times 10^4$  individuals and 30 g dry weight were calculated as the total number and biomass of larvae drifting past station I (Table 7). In 1969 an estimated  $27 \times 10^4$  larvae weighing a total of 134 g drifted past station I. About 90% of this total drift occurred in May and June 1969. It was assumed that no larvae were present in the water issuing from the spring source of Temple Fork, and, therefore, the net differences between biomass drifting on and off the area between the source and station I were -30 g and -134 g in 1968 and 1969, respectively (Table 7). The net differences in the area above station I were -4.9 and -22.0 mg/0.1 m<sup>2</sup> of streambed in 1968 and 1969, respectively (Table 7).

In 1968 an estimated  $888 \times 10^4$  larvae weighing 2,567 g drifted past station II. In 1969 fewer larvae drifted past station II ( $517 \times 10^4$ ), but they were larger and a greater proportion of them drifted past later in the summer. Therefore, the biomass drifting past (2,318 g) was only slightly less than that of 1968 (Table 7). The net differences between drift

		O. sigma		В	. bicaudatus	
Item and generation	I	II	III	I	II	III
Number drifting by (× 104) 1968 generation 1969 generation	6ª 27	888 517	1,559ª 266	303ª 770	1,065 873	652ª 1,397
Biomass drifting by (g dry weight) 1968 generation 1969 generation	30ª 134	2,567 2,318	5,987ª 1,335	1,342ª 1,990	2,137 2,621	1,085 4,381
Net gain or loss (biomass drifting on minus biomass drifting off (g dry weight)) 1968 generation 1969 generation		-2,537 -2,184	-3,420ª +983	1,342ª 1,990	<b>79</b> 5 631	+1,052ª -1,761
Net gain or loss (mg/0.1 m <sup>2</sup> of streambed) 1968 generation 1969 generation	0-I -4.9 <sup>a</sup> -22.0	I-II -43.3 -37.3		0-I - 220.0ª - 326.2	I–II – 13.6 – 10.8	II–III +11.1ª -18.5

TABLE 7. Total numbers and biomass of O. sigma larvae and B. bicaudatus nymphs drifting past stations I-III and the net gain or loss between stations, Temple Fork, 1968-69 generations

<sup>a</sup>Minimal estimates because samples were not collected at stations I and III until May 1968; hence these figures omit winter and spring drift for the 1968 generations.

on and off the total streambed area between stations I and II were -2,537 g in 1968 and -2,184 g in 1969. The net differences expressed on an areal basis were -43.3 and -37.3 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively.

The highest drift rates of O. sigma larvae occurred at station III during the 1968 generation. A minimum of  $1.559 \times 10^4$  larvae weighing 5,987 g drifted past station III in 1968. These figures are minimal because drift sampling at station III did not begin until May 3, 1968. The total drift past station III in 1969 was much less than in 1968 and was also less than the drift at station II in either year. Only  $266 \times 10^4$ larvae weighing 1,335 g drifted past station III in 1969. The net differences in biomass drifting on and off the area between stations II and III were -3,420g and +983 g in 1968 and 1969, respectively. The positive value of 983 g for 1969 represents the only instance in which drift of O. sigma larvae onto an area exceeded drift off the area in this study. The net differences expressed on an areal basis were -36.0 and +10.3 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively.

Total annual drift and annual production of O. sigma larvae appeared to be positively related (Fig. 12). Both quantities were greatest at station III in 1968 and least at station I in 1968.

Drift rates of *B. bicaudatus* nymphs were also low in winter months, but they were not as low with respect to the summer peaks as were the winter drift rates of *O. sigma* larvae. Drift of *B. bicaudatus* nymphs showed two peaks each year corresponding to the time of maturity of the winter (April–June) and summer (August–September) generations (Fig.

![](_page_11_Figure_9.jpeg)

FIG. 12. Relationship between total annual production and total annual drift, stations I–III, Temple Fork. Open circles, *B. bicaudatus;* solid circles, *O. sigma*.

13 and 14). The peak periods of drift for the winter generations were in March and April of both years at station III, whereas at stations I and II the peak periods were late in May. The peak emergence of adults occurred in June and September of each year, so the peak drift rates of nymphs were not associated with emergence.

Total numbers of nymphs drifting past station I were  $303 \times 10^4$  and  $770 \times 10^4$  in 1968 and 1969, respectively, but the 1968 figure is a minimal estimate. Biomass of nymphs drifting past station I was 1,342 g in 1968 and 1,990 g in 1969. Estimates of biomass show a greater similarity in the 2 years than do those for total numbers because the nymphs were small in the omitted portion (because of the late

1

]

![](_page_12_Figure_2.jpeg)

FIG. 13. Total number of *B. bicaudatus* nymphs drifting past stations I-III, Temple Fork, 1967–69—expressed as numbers per 24 hr.

![](_page_12_Figure_4.jpeg)

FIG. 14. Biomass of *B. bicaudatus* nymphs drifting past stations I–III, Temple Fork, 1967–69—expressed as grams dry weight per 24 hr.

drift-sampler installation) of the 1968 generation. The net differences between drift on and off the area between the source and station I were -220.0 and -326.2 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively.

The total numbers of nymphs drifting past station II were  $1,065 \times 10^4$  and  $873 \times 10^4$  in 1968 and 1969, respectively. Total weight of nymphs drifting past was 2,137 g in 1968 and 2,621 g in 1969. Net differences between biomass drifting on and off the area between stations I and II were -795 g and -631 g in 1968 and 1969, respectively. The net differences expressed on an areal basis were -13.6 and -10.8 mg/0.1 m<sup>2</sup>.

The highest drift rates of *B. bicaudatus* nymphs occurred at station III during the 1969 generation. An estimated  $1,397 \times 10^4$  nymphs weighing 4,381 g drifted past this station in 1969. In 1968 the total drift past station III was  $652 \times 10^4$  nymphs weighing 1,085 g. The net differences between drift on and off the area between stations II and III were +1,052 g in 1968 and -1,761 g in 1969. These differences expressed on an areal basis were +11.1 and -18.5 mg/0.1 m<sup>2</sup> in 1968 and 1969, respectively (Table 7). No definite relationship between annual drift and annual production of *B. bicaudatus* nymphs was TABLE 8. Simple correlation coefficients (r) indicating the degree of association between drift and benthos when both are expressed as biomass and density (number), stations I-III, Temple Fork, 1968-69

Factors compared and species	<i>r</i> -va	lues		
Annual comparisons (samples every 14 days, station II only)				
<i>O. sigma</i> Drift density vs. benthos density Drift biomass vs. benthos biomass <i>B. biograduum</i>	0. 0.	14 45*		
Drift density vs. benthos density Drift biomass vs. benthos biomass	0.27 0.11			
une-October comparisons (daily samples, stations I-III combined)	Davi	Nicolad		
0 sigma	Day	Night		
Drift density vs. benthos density Drift density vs. benthos biomass Drift biomass vs. benthos density	0.81* 0.68* 0.78*	0.82* 0.68* 0.77*		
Drift biomass vs. benthos biomass B. bicaudatus	0.67*	0.67*		
Drift biomass vs. benthos density	0.55*	0.43*		

\*Significantly different from r = 0 at the 0.01 level.

evident. The points plotted for *B. bicaudatus* in Fig. 12 were widely scattered.

# ANALYSIS OF FACTORS AFFECTING DRIFT RATES

Correlation coefficients were calculated for two sets of data: (1) the total number and biomass of organisms drifting past station II vs. the density and biomass of those organisms in the benthos at station II every 14th day from October 25, 1967, to September 19, 1969; and (2) the total number and biomass of organisms drifting past stations I–III vs. the density and biomass in the benthos of those organisms for each day and night sample taken at each station in the summers of 1968 and 1969 (Table 8).

The highest correlations for O. sigma were obtained in the summer analyses (r = 0.67-0.82). There were virtually no differences between the day and night correlation coefficients obtained from the analyses of O. sigma larvae. The correlation coefficients for the O. sigma analyses were highest (r = 0.77-0.82) when the benthic component was entered as number/area (density) rather than as biomass/area. This should, perhaps, be expected since the biomass estimate was derived by multiplying the density estimate by the estimate of mean individual weight, which adds another source of error.

The correlation coefficients obtained in the annual comparisons were much lower (r = 0.14-0.45) for O. sigma than those of the daily comparisons. When both the drift and benthic components were expressed as biomass, the correlation coefficient obtained (r = 0.45) was significantly different from zero at the 0.01 level. When both were expressed as TABLE 9. Variables used in multiple-regression analyses to determine unique contributions of each to variability of summer drift rates of *O. sigma* and *B. bicaudatus* 

Variable and identification number	Unit
Independent variables	
1 Distance below the source	km
2 Discharge	m <sup>3</sup> /sec
3 Maximum water temperature	
4 Minimum water temperature	°Č
5 Mean water temperature	°Č °
6 Solar radiation (at Logan Utah)	Langlevs
7 Length of sampling period	br
8 Daily growth rate of <i>O</i> sigma	ma dry wt/day
9 Daily production rate of <i>O</i> signa	mg dry wt/day
10 Density of <i>O</i> sigma	number/0 00 $m^2$
11 Density of <i>B</i> bicaudatus	""""""""""""""""""""""""""""""""""""""
12 Density of Enhamaralla sp	"
13 Density of Ephemerella doddsi	"
14 Density of <i>Cinvamula</i> and	
Rhithrogana	"
15 Density of Glassosoma	"
16 Density of <i>Rhyacophila</i>	"
17 Density of Chironomidaa	"
18 Biomass of <i>O</i> sigma (bonthos)	$m_{\alpha} dm_{\gamma} wt /0.00 m^{2}$
18 Diomass of O. sigma (benthos)	mg my wt/0.09 m <sup>2</sup>
Dependent variables	
19 Biomass of O. sigma drifting/	
period	mg dry wt/period
20 Biomass of <i>B. bicaudatus</i> drifting/	/1
period	mg dry wt/period
21 Number of O. sigma drifting/	
period	number/period
22 Number of <i>B. bicaudatus</i> drifting/	
period	number/period

numbers, the correlation was not significantly different from zero at the 0.01 level (r = 0.14).

The highest correlations for *B. bicaudatus* were obtained in the summer analyses (day analysis: r = 0.55; night analysis: r = 0.43; significantly different from zero at the 0.01 level). The correlations obtained in the annual comparisons for *B. bicaudatus* were lower than those for *O. sigma* (r = 0.27 and 0.11 for density and biomass comparisons respectively; not significantly different from zero at the 0.01 level).

The unique contributions of 17 or 18 independent factors to the variability of summer drift rates of O. sigma and B. bicaudatus, respectively, were determined through multiple-regression analysis. Biomass of O. sigma larvae in the benthos (variable 18) was not included in the analyses of B. bicaudatus drift. Dependent variables (numbers 19–22, Table 9) were (1) total biomass of O. sigma and B. bicaudatus drifting past each station during the sampling period, and (2) total numbers of O. sigma and B. bicaudatus drifting past each station during the sampling period. The independent variables and their units of measure are given in Table 9. Distance below the source and discharge at the sampling station are selfexplanatory. Water-temperature extremes and means refer to values recorded during the combined 24-hr period and not to values within a single day or night

TABLE 10. Order of rejection of independent variables and resultant  $R^2$  values for multiple-regression analyses of biomass and numbers of *O. sigma* larvae drifting past stations I-III, Temple Fork, 1968-69—rejected in stepwise fashion on minimum mean squares in the analyses of *O. sigma* biomass

	Dependent variable analyzed		
Variable and identification number	Biomass drifting/ period (No. 19)	Numbers drifting/ period (No. 21)	
Day analyses			
<ul> <li>Intact analysis</li> </ul>	0.65	0.71	
14 Density of Cinygmula	0.65	0.71	
5 Mean water temperature	0.65	0.71	
12 Density of Ephemerella sp.	0.65	0.71	
13 Density of Ephemerella doddsi	0.65	0.71	
17 Density of Chironomidae	0.65	0.71	
7 Length of sampling period	0.65	0.71	
8 Daily growth rate of O. sigma	0.65	0.71	
9 Daily production rate of O. sigma	0.65	0.71	
16 Density of Rhyacophila	0.65	0.71	
4 Minimum water temperature	0.65	0.71	
6 Solar radiation	0.64	0.70	
18 Biomass of O. sigma (benthos)	0.63	0.69	
11 Density of B. bicaudatus	0.63	0.67	
1 Distance below the source	0.62	0.67	
3 Maximum water temperature	0.62	0.67	
2 Discharge	0.61	0.66	
15 Density of Glossosoma 10 Density of O. sigma	0.60	0.65	
Night analyses			
<ul> <li>Intact analysis</li> </ul>	0.62	0.70	
6 Solar radiation	0.62	0.70	
8 Daily growth rate of O. sigma	0.62	0.70	
7 Length of sampling period	0.62	0.70	
14 Density of Cinygmula	0.62	0.70	
11 Density of B. bicaudatus	0.62	0,70	
5 Mean water temperature	0.62	0.70	
17 Density of Chironomidae	0.62	0.70	
2 Discharge	0.62	0.70	
3 Maximum water temperature	0.62	0.70	
1 Distance below the source	0.62	0.69	
12 Density of Ephemerella sp.	0.62	0.69	
13 Density of Ephmerella doddsi	0.62	0.69	
18 Biomass of O. sigma (benthos)	0.61	0.68	
16 Density of Rhyacophila	0.61	0.68	
15 Density of Glossosoma	0.61	0.68	
9 Daily production rate of O. sigma	0.60	0.67	
4 Minimum water temperature	0.59	0.67	
10 Density of O. sigma			

sampling period. The minimum temperature, for example, might occur at 2:00 AM during the course of a night sample, but it would be entered as a variable for both that night sample and the following day sample. Radiation refers to the global radiation recorded at Logan, Utah (32 km southwest of the study area), in 24 hr. Length of sampling period refers to the total length of the day and night periods. Daily growth and production rates of *O. sigma* larvae were calculated by determining *G* and *P* at 2-week intervals, interpolating to 7-day intervals, and then dividing by 7 to obtain the daily rates. Densities of all organisms were determined at 14-day intervals from the bottom samples, and these values were used for all sampling dates within the 2-week TABLE 11. Order of rejection of independent variables and resultant  $R^2$  values for multiple-regression analyses of biomass and numbers of *B. bicaudatus* nymphs drifting past stations I-III, Temple Fork, 1968-69stepped on minimum mean squares in the analyses of *B. bicaudatus* biomass

	Dependent variable analyzed		
Variable rejected	Biomass drifting/ period (20)	Numbers drifting/ period (22)	
Day analyses			
- Intact analysis	0.55	0.43	
7 Length of period	0.55	0.42	
5 Mean temperature	0.55	0.42	
15 Density of Glossosoma	0.54	0.34	
4 Minimum temperature	0.54	0.34	
16 Density of Rhyacophila	0.54	0.33	
3 Maximum temperature	0.54	0.25	
1 Distance below source	0.54	0.20	
8 G/day of O. sigma	0.53	0.19	
9 P/day of O. sigma	0.53	0.19	
6 Radiation	0.52	0.19	
17 Density of Chironomidae	0.51	0.15	
12 " " Ephemerella sp.	0.50	0.12	
14 " " Cinygmula	0.49	0.11	
13 " " Ephemerella doddsi	0.48	0.10	
10 " " O. sigma	0.45	0.09	
2 Discharge	0.31	0.07	
11 Density of B. bicaudatus			
Night analyses			
<ul> <li>Intact analysis</li> </ul>	0.55	0.52	
4 Minimum temperature	0.55	0.52	
13 Density of Ephmerella doddsi	0.55	0.52	
14 Density of Cinygmula	0.55	0.52	
1 Distance below source	0.54	0.51	
6 Radiation	0.54	0.51	
9 P/day of O. sigma	0.54	0.51	
17 Density of Chironomidae	0.54	0.51	
15 " " Glossosoma	0.54	0.39	
11 " " B. bicaudatus	0.53	0.39	
3 Maximum temperature	0.52	0.34	
8 G/day of O. sigma	0.50	0.30	
7 Length of period	0.48	0.30	
5 Mean temperature	0.41	0.29	
12 Density of Ephemerella sp.	0.32	0.28	
2 Discharge	0.19	0.27	
10 Density of O. sigma	0.11	0.21	
16 Density of Rhyacophila			

period. Densities of six most abundant forms (other than *O. sigma* and *B. bicaudatus*) were selected for the regression analyses. Values for *Cinygmula* and *Rhithrogena* were combined because individuals of these genera could not be distinguished in early instars.

After the initial four regression analyses (biomass and numbers of *O. sigma* and *B. bicaudatus* vs. independent factors) were complete, the independent variables having the smallest mean square in the analyses for *O. sigma* and *B. bicaudatus* biomasses were dropped and a second level of regressions was run. This procedure of rejecting the variable with the smallest mean square was repeated in stepwise fashion until only one independent variable remained. The  $R^2$  values (representing that portion of the total variability in the dependent variable accounted for TABLE 12. Abbreviated regression analysis of factors affecting biomass of *O. sigma*, day drift, Temple Fork, 1968–69

Source of variation	Degrees of freedom	Mean square	Coefficient
Total	342	0.641 X 10 <sup>13</sup>	-0.366 X 10 <sup>6</sup>
Distance below source	1	0.265 X 1014*	0.869 X 10 <sup>5</sup>
Discharge	1	0.436 X 1014*	-0.536 X 10 <sup>5</sup>
Maximum temperature	1	0.784 X 10 <sup>12</sup>	-0.137 X 10 <sup>5</sup>
Minimum temperature	1	0.245 X 10 <sup>13</sup>	-0.297 X 10 <sup>5</sup>
Mean temperature	1	0.189 X 10 <sup>12</sup>	-0.129 X 10 <sup>5</sup>
Radiation	1	0.560 X 10 <sup>13</sup>	0.128 X 10 <sup>4</sup>
Length of period	1	0.329 X 10 <sup>13</sup>	0.245 X 10 <sup>5</sup>
G/day of O. sigma	1	0.292 X 10 <sup>13</sup>	-0.296 X 10 <sup>5</sup>
P/day of O. sigma	1	0.414 X 10 <sup>13</sup>	0.364 X 104
Density of O. sigma	1	0.258 X 10 <sup>15</sup> *	0.139 X 10 <sup>5</sup>
B. bicaudatus	1	0.715 X 10 <sup>13</sup>	0.286 X 104
Ephemerella sp.	1	0.723 X 10 <sup>12</sup>	-0.598 X 10 <sup>3</sup>
Ephemerella			
doddsi	1	0.980 X 10 <sup>12</sup>	0.540 X 104
Cinygmula	1	0.317 X 10 <sup>11</sup>	-0.153 X 10 <sup>3</sup>
Glossosoma	1	0.288 X 10 <sup>14</sup> *	-0.131 X 10 <sup>5</sup>
Rhyacophila	1	0.540 X 10 <sup>13</sup>	0.249 X 10 <sup>5</sup>
Chironomidae	1	0.102 X 10 <sup>13</sup>	-0.779 X 10 <sup>3</sup>
Biomass of O. sigma	1	0.141 X 10 <sup>14</sup> *	-0.990 X 104
Model	18	0.797 X 10 <sup>14</sup>	
Error	324	0.234 X 10 <sup>13</sup>	$R^2 = 0.65$

\*Significant at the 0.05 level.

by the independent variables) were then accumulated and entered in Tables 10 and 11.

## Oligophlebodes sigma

The  $R^2$  values indicated that 65% of the variability in the biomass of *O. sigma* drifting during the day was accounted for by the 18 independent variables. Five variables were significant (at the 0.05 level) in the analysis of day-drifting *O. sigma* biomass. In decreasing order of mean square size they were: density of *O. sigma* on the bottom, discharge, density of *Glossosoma* on the bottom, discharge, density of *Glossosoma* on the bottom, distance below the source, and biomass of *O. sigma* in the benthos. Discharge and density of *Glossosoma* had negative coefficients; density of *O. sigma*, distance below the source, and biomass of *O. sigma* had positive coefficients (Table 12; Note: Only the analysis of independent variable 19 is given; other regression analyses are available from the authors upon request).

The  $R^2$  value indicated that 62% of the variability in drift of *O. sigma* biomass at night was accounted for by the 18 independent variables. Only one variable, however, had a significant mean square in the analysis of biomass of *O. sigma* drifting during the night: density of *O. sigma* larvae (coefficient positive).

The order of rejection of independent variables (based on successive minimum mean squares) for the stepwise regression analysis of O. sigma biomass is given in Table 10. The outstanding feature of both the day and night analyses was the importance of O. sigma density (numbers) on the bottom in explaining the variability of the biomass of O. sigma

drifting by each station. When every independent variable was eliminated from the analyses except density of O. sigma, the  $R^2$  values were only reduced from 0.65 to 0.60 for the day analysis and from 0.62 to 0.59 in the night analysis (Table 10). The other 17 independent variables had so little effect on the  $R^2$  values that the order of rejection probably does not have much significance in the estimation of their relative order of importance in affecting drift rates of O. sigma. Minimum temperature was the next-to-the-last variable to be rejected in both day and night analyses, but its rejection resulted in decreases of only 0.02 and 0.01 in the  $R^2$  values (Table 10).

The  $R^2$  values for the analyses of number of *O*. sigma larvae drifting past the three stations (dependent variable 21) were only reduced from 0.71 to 0.65 for the day samples, and from 0.70 to 0.67 for the night samples after the elimination of all independent variables except density of *O*. sigma.

## Baetis bicaudatus

The  $R^2$  value indicated that 55% of the variability in drift of *B. bicaudatus* during the day was accounted for by the 17 independent variables. Twelve of the 17 independent variables had significant (0.05 level) mean squares in the analysis of biomass of *B. bicaudatus* drifting during the day. In order of decreasing size of mean square they were: discharge, density of *B. bicaudatus*, density of *O. sigma*, density of *Ephemerella doddsi*, density of *Cinygmula*, density of Chironomidae, *P*/day of *O. sigma*, density of *Ephemerella* sp., radiation, density of *Rhyacophila*, distance below source, and *G*/day of *O. sigma*.

The  $R^2$  value indicated that 55% of the variability in drift of *B. bicaudatus* biomass during the night was accounted for by the 17 independent variables. Five variables had significant mean squares in the analysis of biomass of *B. bicaudatus* drifting during the night: discharge, length of period, density of *Rhyacophila*, mean temperature, and *G*/day of *O. sigma*.

The order of rejection of independent variables in the stepwise regression analysis of *B. bicaudatus* biomass is given in Table 12. The reduction in the  $R^2$  values with the deletion of variables was much more gradual for *B. bicaudatus* than for *O. sigma*. This was to be expected since more variables were significant in the analyses for *B. bicaudatus*. The  $R^2$ values for the regression on variable 19 (biomass of *B. bicaudatus* drifting during the day) was only reduced from 0.55 to 0.48 with density of *O. sigma*, density of *B. bicaudatus*, and flow remaining in the analysis. With only density of *B. bicaudatus* remaining, the  $R^2$  was reduced to 0.31 (Table 11).

The  $R^2$  values in the stepwise regression analysis of biomass of *B. bicaudatus* drifting during the night were reduced from 0.55 to 0.19 with discharge and densities O. sigma and Rhyacophila remaining in the analysis (Table 12). With only the density of Rhyacophila remaining, the  $R^2$  value fell to 0.11. The density of B. bicaudatus was the ninth variable to be eliminated in the stepwise process.

# UPSTREAM FLIGHT AND OVIPOSITION OF Oligophlebodes sigma

Waters (1968) observed the upstream flight of O. sigma adults over Temple Fork in August 1966. During the present study observations on the adult flight were made each evening during August and September. In 1968 O. sigma adults were observed over the stream between August 3 and November 8. In 1969 adults were observed between July 25 and October 28. The largest swarms of adults were seen in late August and early September of both years.

Adults of *O. sigma* rested quietly on streamside vegetation during most of the night, morning, and early afternoon. Approximately 2–4 hr before sunset they began swarming at the upper branches of willows and other shrubs growing along the stream. This swarming behavior consisted of rapid running up and down the twigs, and short flights from one branch to another. Mating was frequently observed in the midst of this swarming behavior.

In the early evening (30-120 min before sunset) groups of adults began to leave the mating swarm and flew in an upstream direction. Each bush or shrub was usually vacated entirely within 60 sec, and the flight of the first few adults seemed to trigger the flight of those remaining. This evening flight usually lasted 20-50 min, ending about sunset. The adults flew slowly and steadily up the stream, with each individual maintaining about the same speed. Most adults flew directly over the stream at heights of 1-4 m, but a few flew as high as 10-12 m. At times the flight left the stream to detour around a patch of dense shrubbery, and at times the flight temporarily followed the dirt road paralleling the stream. During the flight individuals were uniformly spaced above the stream, and there was no noticeable tendency to form groups or swarms as do many mayflies in the courtship flight. In a sense, the flight resembled a slow, stately, upstream parade, although an occasional individual flew across the stream or downstream briefly.

The speed of flight of *O. sigma* adults was measured on several occasions by walking beside an individual on evenings when relatively few adults were flying, and timing its progress over a measured course of 30 m. The mean speed in calm air was 3.1 km/hr. The maximum speed observed was 4.3 km/hr; the minimum was 2.3 km/hr. Many attempts were made to follow single individuals throughut the flight period, but this was difficult because invariably the adult being followed would be lost from sight or confused with another individual. However, one individual flew 213 m upstream in 3 min before being lost to view.

The life span of O. sigma adults was probably 5 days. It is not known if each individual participated in the flight each evening of its life, or if it flew for the entire period each evening. The above observations indicated that the average adult flew upstream a distance of 0.3-6.0 km, with the most likely distance being 2-3 km.

The time of flight was confined to a period from 2.5-3.0 hr before sunset to 0.5 hr after sunset. Within this period the flight appeared to be governed by upper and lower air-temperature thresholds. The flight began each evening only after the air temperature fell below 17°-18°C, and the flight ended when the air temperature fell below 12°-13°C. On days when the air temperature did not exceed 12°-13°C there were no flights. On cool days, when the air temperature hovered within the legislated period, the evening flight began early. On very warm days the flight began late and sometimes continued into the first 0.5 hr of darkness. However, on most evenings the air temperature fell rather swiftly and steadily, and the governed flight period lasted only 30-50 min.

On several occasions winds of more than 2-3 km/hr from an upstream direction, or greater than 4-5 km/hr from a downstream direction interrupted or prevented the evening flight. A steady rainfall also interrupted or prevented the flight on several occasions.

The topography of the study area had an important influence on air temperatures at different points along the stream. For example, at station II the stream emerged from a rather narrow, deep, and heavily overgrown canyon and flowed out upon an area of low, rolling hills. At the same point it turned and flowed directly west (Fig. 1). In late summer and early fall this part of the stream (between stations II and III) received the direct rays of the sun until 20-30 min before sunset, whereas the area between stations I and II was heavily shaded, both by the ridge to the southwest and by the dense growth of trees within the canyon, from 2.5 to 3.5 hr before sunset. Consequently, on most evenings the air temperature in the canyon area between stations I and II fell below the upper threshold for flight much earlier than it did in the area below station II. Also, on most evenings by the time the air temperature below station II had fallen to the upper threshold for flight the air temperature in the canyon above station II was already approaching the lower threshold for flight. The result was an effective, though imperfect, barrier to upstream flight at the mouth of the canyon immediately above station II.

In the fall of 1968 two bilateral traps similar to that described by Gressitt and Gressitt (1962) were

TABLE 13. Sex ratios of O. sigma adults from drift samples, shore vegetation, and upstream migration flight, Temple Fork, 1968–69

Type of collection	Males	Females	Ratio
Drift samples	107	99ª	1.1:1
From streamside vegetation	238	43 <sup>b</sup>	5.5:1
Flying upstream	18	43°	0.4:1

Condition of ovaries: 26% immature, 40% mature, 34% spent.
 Condition of ovaries: 61% immature, 39% mature.
 Condition of ovaries: 100% mature.

used in an attempt to capture O. sigma adults flying upstream. Adults were rarely captured in the traps because they easily detected the traps at a distance of 1-2 m and either flew around or over them. Therefore the bilateral traps were abandoned, and adults were collected by the drift samplers and with sweepnets. A total of 348 adults was taken in August and September of both years combined.

Collections of adults swept from streamside vegetation contained 5.5 males per female (Table 13). The ovaries of 61% of the females swept from streamside vegetation were immature; the remaining 39% were mature. Collections of adults swept from the evening upstream flight (between stations II and III) contained 0.4 males for every female, and the ovaries of all females were mature (Table 13).

Collections of adults captured in the drift samplers contained 1.1 males per female. Twenty-six per cent of the females from the drift samples were immature, 40% mature, and 34% were spent.

Apparently the initial O. sigma adult population had a male: female ratio of 5.5:1 (although it is possible that behavioral differences between the sexes may have made males more vulnerable to the sweep-net while on vegetation). Either a higher percentage of females migrated upstream than did males, or females flew a greater distance than did males (although the sample size here was only 51 individuals). The drift-sampler catches were apparently made up of emerging adults, mature adults returning to the stream to drink or oviposit, and postoviposition females.

Oviposition boards were installed in the stream in June 1969, and they were examined for O. sigma egg masses every evening and every other morning. Mature O. sigma females flew to the boards in the afternoon, crawled beneath the water, and oviposited on the bottom edge of the board, next to the streambed. Each egg mass contained 80-120 eggs (mean = 97). The egg masses were deposited in large aggregates or clumps rather than scattered about over the entire available surface.

Six egg masses were deposited on the board at station I (Table 14). The board at station II received the greatest number of egg masses; the total number

TABLE 14. Egg masses of *O. sigma* on ovoposition boards placed in stream at stations I–IV, Temple Fork, 1969—expressed as total number per month on 19- by 4-cm area

	Station				
Month	I	II	III	IV	Total
June July August September October	$     \begin{array}{c}       0 \\       0 \\       1 \\       5 \\       0     \end{array} $	0 6 2,747 3,311 39	0 0 366 150 8	0 0 120 204 6	0 6 3,234 3,670 53
Total	6	6,103	524	330	6,963

deposited was 6,103. The numbers of egg masses deposited at stations III and IV were 524 and 330, respectively. Greatest numbers of egg masses were laid in August and September. The maximum number of masses deposited on the 19- by 4-cm edge of the board within a 24-hr period was 239 at station II on August 25-26, 1969.

#### DISCUSSION

Drift has been associated with production in excess of the carrying capacity of the streambed (Waters 1966), illumination (Waters 1962*a*, Holt and Waters 1967), periods of rapid growth (Elliott 1967), water temperature (Müller 1966, Pearson and Franklin 1968), flow (Minshall and Winger 1968), age of immatures (Müller 1966), and population density expressed as numbers per area (Pearson and Franklin 1968).

The subject species of many drift studies have been aquatic insects with either one generation per year or with a long-lived winter generation and oneto-several short-lived summer generations. Many of these insects (including O. sigma and B. bicaudatus) have major emergences in the fall months and overwinter as small, slow-growing immatures. The immatures begin growing rapidly in spring and early summer. Drift rates are usually highest in spring and early summer and lowest in winter months (Waters 1969). Many factors in the environment and many population parameters are correlated with the change in season from winter through spring to summer. Water temperature, discharge, growth rates, production rates, day length, primary production rates, ageassociated changes in behavioral patterns, mortality rates, metabolic rates, and a host of other factors may increase with the onset of spring and summer, and so do drift rates. The assignation of a cause-andeffect relationship to any of these factors and drift rates should not be made without considering the existence of hidden correlations between the "cause" and other factors in the environment.

#### Density-drift relationships

The relationship between drift and density may be considered over an entire year or over that period when most of the drift occurred. About 90% of the total annual numbers and biomass of O. sigma larvae drifted past each station in May, June, and July. At station II, for example, the highest density expressed as number/area occurred in the winter months when drift was very low. In the spring and early summer density declined while drift increased. Over the entire year density and biomass did not appear to correlate positively with drift (with the exception of drift biomass of O. sigma vs. biomass in the benthos). The correlation coefficient between the two variables was low (r = 0.45) but significantly different from zero when computed over the entire study period at station II.

However, when drift and density measurements were compared over a short interval of time (as they were in the regression analyses), drift biomass correlated positively with density as numbers. Given a sufficient number of years of data, one would probably be able to show a positive correlation between annual drift and annual mean density for each generation.

The final size attained by *O. sigma* larvae (as indicated by pupal weight) was inversely related to density (number) during April–June. Pupae were small at station III in 1968 and station II in 1968 and 1969. Densities and drift were highest at these same locations and in the same years. Apparently intraspecific competition (probably for food, but perhaps for space as well) was severe at these locations and times. The highest drift rates may have occurred as individuals were forced to expend more time searching for food in exposed locations.

The above remarks concerning the relationship between density and drift over a year and over the summer apply to the results for *B. bicaudatus* as well. The summer drift-density relationship was not as definite for *B. bicaudatus* nymphs as it was for *O. sigma* larvae, but the correlation coefficients were positive and significant at the 0.05 level.

Regression analyses indicated that 31% of the variability in day drift of *B. bicaudatus* was accounted for by density of *B. bicaudatus* alone. Density of *B. bicaudatus* was rejected early in the stepwise process during the analysis of night drift. This is difficult to understand, but perhaps the interaction was significant between density of *B. bicaudatus* and density of *Rhyacophila* (density of *Rhyacophila* was the last variable to be rejected in the analysis).

# **Production** relationships

Production of *O. sigma* larvae was high at station III in 1968 and at station II in both years, as were density and drift.

Waters (1966) proposed that behavioral drift may represent production in excess of the carrying capacity of the streambed. To test this hypothesis it would be necessary to determine total production and determine what portion of the total was "excess." The net gain or loss between stations presented in Table 10 may represent this excess (if mortality and decomposition on the area are not regarded as excess), or it may simply be operationally defined as the excess. Such an operational definition may be necessary because of the difficulties in measuring carrying capacity directly. Carrying capacity will fluctuate widely with variations in food availability, metabolic rates, behavioral patterns of the larvae, water temperature, and many other factors. In addition, carrying capacity is probably not a definite threshold figure even at a given instant in time. It is probably best represented by a noticeable inflection in a curve. Dimond (1967) presented a plot of density (rather than production) versus drift which showed a sharp inflection at a density of about 450 insects/0.9  $m^2$ . Dimond stated that his data might best be fitted with two straight lines converging at the inflection point. Two criticisms may be made of this plot: (1) the data present the sum of all aquatic insects in the several streams examined, and this in itself is objectionable because not all insects drift, and overlapping chronologies of appearance of different species would destroy precision; and (2) no data are provided at densities between zero and 400-500 insects/0.9 m<sup>2</sup>. The data presented merely show the variability in drift which one encounters at densities of 400–500/0.9 m<sup>2</sup>.

The production of *B. bicaudatus* nymphs showed less between-station variability than did production of *O. sigma* larvae. Annual production of *B. bicaudatus* nymphs was about the same at stations I and III and somewhat less at stations II and IV in both years. Annual drift rates did not correspond to production rates for *B. bicaudatus* as they did for *O. sigma*. Although drift was highest at station III in 1969, production was highest at station III in 1968.

An important contradiction appeared in the data at station I in 1969. The production calculated by Allen's method was only 195.7 mg/0.1 m<sup>2</sup> (summer and winter generation; Table 7) for the area above station I, but the total drift from the area was estimated at 326.2 mg/0.1 m<sup>2</sup> (Table 8). Obviously more could not drift from the area than was produced. The source of the error leading to this contradiction is unknown, but one possibility is that more than two generations of *B. bicaudatus* may have been produced each year, and the overlap in generations went unnoticed.

# Key factors affecting drift rates

Density was the single most important factor in

the regression analyses of both day and night drift of *O. sigma* larvae. Density was also the most important factor in the regression analysis of day-drifting *B. bicaudatus* nymphs.

Discharge contributed significantly to the variability in day and night drift of B. bicaudatus and to day drift of O. sigma. The regression coefficients for the Baetis analyses were positive; that for the O. sigma analysis was negative. Again, because such large percentages of the total variability in drift of O. sigma larvae were accounted for by a single independent variable (density), the order of rejection of the remaining variables is probably of little significance. One would expect that any increase in discharge would increase the number of organisms being swept away (constant and catastrophic drift). The spring increase in discharge eroded and redistributed bottom materials at all stations, and this mechanical action may have accounted for most of the drift at station I and smaller percentages of the drift at the lower stations.

Distance below the source contributed significantly to variability in the day drift of both *O. sigma* and *B. bicaudatus*. Many factors (total alkalinity, compaction of the substrate, temperature, etc.) are correlated with distance below the source, and it is difficult to explain this contribution. The densities of other invertebrates (*Glossosoma* and *Rhyacophila* particularly) were significant independent variables in the multiple-regression analyses, particularly those for *B. bicaudatus*. It is possible that interspecific competition might induce behavior that would result in drift, much as intraspecific competition is thought to do.

Müller (1966) presented data showing that drift of some species of aquatic insects increased with a rise in water temperature, while that of other species decreased. Waters (1968) reported a close positive relationship between drift of O. sigma larvae in Temple Fork and water temperature. The temperature of water issuing from the spring source of Temple Fork was about 5.0°C in winter months and 5.5°-6.0°C in summer months. The daily temperature fluctuation at the spring was near zero, but at station I (0.2 km below the source) the water temperature typically rose 1°C on warm summer days and fell 1°C on winter days. Still, this meant that station I approached the condition of a constant-temperature environment. The higher drift of O. sigma larvae at station I during daylight hours may indicate that the diel periodicity of O. sigma drift is set by light or some other diurnal clue rather than temperature, but temperature cannot definitely be ruled out as a mechanism.

Although the water temperature during the winter was highest at station I, winter growth rates of O. sigma larvae at station I were only slightly higher than rates at the lower stations. This may mean that

day length or some seasonal variable associated with food supply and feeding rather than water temperature determined the period of rapid growth.

# Significance of the upstream flight of adults

In 1969 the mean monthly density of *O. sigma* pupae on the streambed was similar at stations II and III (54 and 72/0.1 m<sup>2</sup>). The density of pupae at stations I and IV was lower (7 and  $13/0.1 \text{ m}^2$ ). The distribution of egg masses on the oviposition boards was quite different. The number of egg masses laid on the board at station II was about 10 times that at station III and about 18 times that at station IV. Apparently the upstream flight of adults was extensive, and the mature adult females were concentrated at station II. Adults were prevented from flying above station II by the topography-induced air temperature barrier in the canyon between stations I and II.

The evolution of the colonization cycle, as proposed by Müller, might be interpreted in two ways: (1) adults fly upstream because it is advantageous for the species to recolonize an area depleted by drift, or (2) adults fly upstream because it is advantageous for the species that the eggs be concentrated in the upstream area.

Drift did not result in the complete removal of either O. sigma or B. bicaudatus populations at either station I or II. Waters (1968) has also reported that upstream populations of *Baetis vagans* in Valley Creek, Minnesota, are not depleted by drift removal. Interpretation 1 above is not valid for these populations in Temple Fork or Valley Creek. The density of O. sigma larvae in the benthos dropped sharply at station IV in January of each year. This drop occurred after the formation of anchor ice on the streambed below station III. The anchor ice formed during nights when air temperatures fell below -18 °C. When the stream began to warm the following morning, the anchor ice detached from the bottom and formed ice dams across the stream. The resulting impoundments and the ultimate washing away of the ice dams resulted in minor floods. The direct action of the ice, combined with flooding, apparently reduced the invertebrate populations in the area. Benson (1955) reported reductions of insect populations in a Michigan stream following severe anchor-ice conditions. Mecom (1970) also reported the reduction of larval populations of two caddisflies (Brachycentrus americanus and Ecclisomyia maculosa) following anchor-ice conditions and suggested that the population of a third caddisfly (Hydropsyche occidentalis) was not affected because the larvae overwintered in a stone-cased hibernaculum.

Most drift investigations have been conducted in northern climates and in small streams subject to either anchor ice or spring floods. The upper reaches of many small streams are spring fed and do not freeze during winter months. In other streams the upper reaches do not receive excessive amounts of runoff and are not, therefore, subject to severe flooding in late winter and early spring. The evolutionary advantage of the colonization cycle, for those species exhibiting it, may be that it concentrates the eggs (and thereafter the young larvae) in upstream areas where they are protected from extremes of temperature and flow. In late spring and early summer, when these extreme conditions are past, the immatures may disperse throughout the stream as drift organisms.

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