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# Drift of Oligophlebodes sigma and Baetis bicaudatus in a Mountain Stream

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# DRIFT OF *OLIGOPHLEBODES SIGMA* AND *BAETIS BICAUDATUS* IN A MOUNTAIN STREAM

by

William D. Pearson

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Fishery Biology

Approved:

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1970

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William D. Pearson

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# ABSTRACT

## Drift of *Oligophlebodes sigma* and *Baetis bicaudatus* in a Mountain Stream

by

William Dean Pearson, Doctor of Philosophy

Utah State University, 1970

Major Professor: Dr. Robert H. Kramer
Department: Wildlife Resources

The objective of this study was to clarify the relationships between drift rates, population density, production rates, key environmental factors, and movements of adults within two populations of stream insects (a caddisfly--*Oligophlebodes sigma* and a 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 summer months (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 gm/year for *O. sigma*) when density in the benthos (256 mg/0.1 $m^2$) and production (430 mg/0.1 $m^2$/year) were greatest. Drift rates were not related positively to density in the benthos over an entire year, but drift rates were correlated positively and significantly ($r = .78$ and .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. Flow, 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 independent variables in the multiple regression analyses accounted for 65 percent and 55 percent of the variability in day drift rates of *O. sigma* and *B. bicaudatus*, respectively.

The adults of *O. sigma* (but not those of *B. bicaudatus*) undertook a definite upstream migration estimated at 2-3 km. This flight of adults resulted in a concentration of eggs being laid 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 the effects of anchor-ice in the winter and floods in late winter and early spring.

(111 pages)

# INTRODUCTION

The downstream drift of individuals appears to be a significant factor in the population dynamics of many lotic invertebrates. Although reports on drifting invertebrates first appeared in the 1920-1940's (Dendy, 1944, for example) the phenomenon did not attract widespread attention among ecologists until after the publication of Müller's (1954) paper. Müller presented three important contributions: (1) he documented the numerical significance of drift with relation to the number of organisms in the benthos, (2) he postulated that drift resulted from conditions of crowding and competition between 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 the upstream migration of flying adults prior to oviposition.

Roos (1957) presented data on catches made by a bilateral trap placed over a stream which indicated that mature females of several trichopterans and a few other aquatic insects did fly predominantly in an upstream direction. Elliott (1967) reported that adults of aquatic insects in several orders 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 in explaining the movements of immatures and adults of 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 suggested that the colonization cycle might be in operation for that species.

Waters (1961, 1962a, 1962b, 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 stream bed.

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 the change in population density in the area. The special conditions necessary were that no losses due to predation or decomposition occurred on the area.

Several authors (Elliott, 1967; Elliott and Minshall, 1968; Bailey, 1966; 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 author's failure to find "correlations" between drift and density of benthos estimates. Elliott (1967), for example, states:

> Because 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, invertebrate drift in the Walla Brook could never be used to estimate the production rate of the benthos as suggested by Waters (1961, 1962). (Elliott, 1967, p. 232)

A recent comprehensive review of the drift literature is presented in Waters (1969).

The objective of this study was to clarify the 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 specific objectives of the study were:

1. To assess the role of downstream drifting in population dynamics.

2. To determine the relationship between drift and production rates in the stream.

3. To determine the effects of several key environmental factors on drift rates of immatures.

4. To determine whether upstream flight of adults occurs, and if so, the magnitude of such migration and its influence upon the distribution of immatures in the 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 1,998 m above sea level), flows northwest for 6.5 km, and empties into the Logan River in Logan Canyon. Four sampling stations (I-IV) were established at distances of 150 m, 1.9 km, 4.0 km, and 6.2 km below the spring source. The mean widths and area of streambed between stations are given in Table 1. The mouth of the stream is about 32 km northeast of the city of Logan. Two rock formations predominate in the Temple Fork area--a tan-colored limestone base and a loosely-cemented, reddish conglomerate overlayer. The conglomerate has contributed most of the gravel and cobbles found on the streambed.

Table 1. Dimensions of areas between stations, Temple Fork

| Boundaries | Length (km) | Mean width (m) | Area ($m^2$) |
|---|---|---|---|
| Source--I | 0.15 | 3.05 | 457 |
| I-II | 1.77 | 3.66 | 6,475 |
| II-III | 2.09 | 3.96 | 8,287 |
| III-IV | 2.21 | 4.27 | 9,418 |
| IV--mouth | 0.26 | 4.15 | 1,059 |
| Total | 6.48 | | 25,696 |

## Climate

Mean annual precipitation on the study area is 64 cm, two-thirds of which is received as snow (Chaudhry, 1967). Summer showers are usually of short duration and seldom exceed 1 cm within a 24-hour period. The snowpack in winter may be 60 cm on the level and drift to a depth of 1.0 m to 1.5 m at protected locations along the stream.

Maximum air temperatures usually occur in July and August (32 C in 1968 and 35 C in 1969). Minimum air temperatures usually occur in January and February (-21 C in 1968 and -24 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.

## Topography and Vegetation

Temple Fork has its beginning at a large spring which emerges at the base of a 300-meter-high ridge. In its first 1.2 km, the stream flows northwest through a narrow-steep-sided canyon (Figure 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.), willows (*Salix* spp.), and wild rose (*Rosa* sp.).

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. Bluegrass (*Poa* sp.) grows

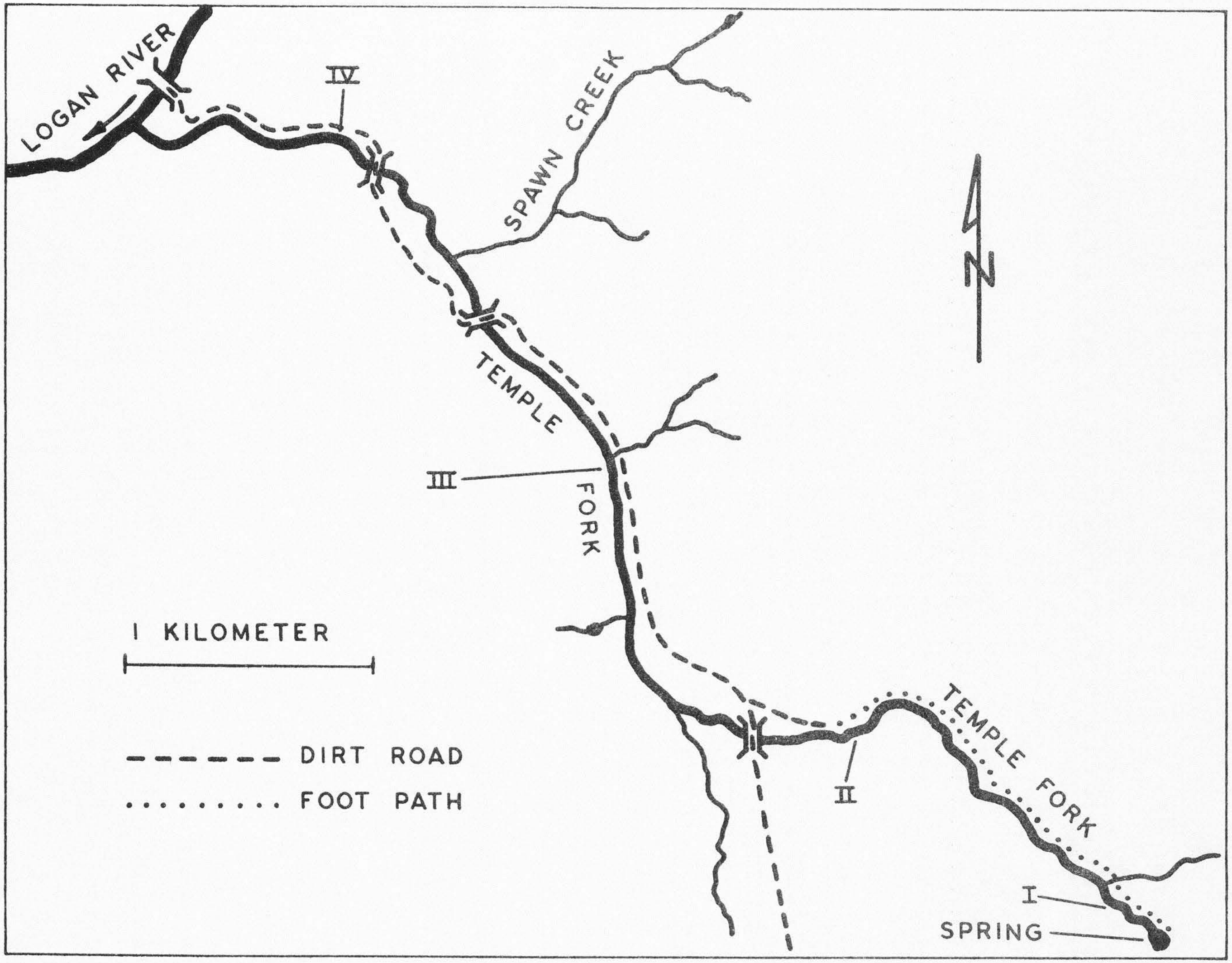

Figure 1. Map of Temple Fork with locations of sampling stations I-IV.

in a dense sward on the immediate edge of the stream. The stream turns to the north-northeast 2.5 km below the source 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 another canyon. This second canyon is not as heavily overgrown with vegetation as the upper canyon. Seven km below its source Temple Fork empties into the Logan River.

Temple Fork receives additional water from five spring-fed tributaries (Figure 1). Spawn Creek enters 5.5 km below the source of Temple Fork and is the largest of the tributaries with a mean annual flow of 0.10 $m^3$/second. The remaining four unnamed tributaries have flows of less than 0.03 $m^3$/second. Surface runoff contributes little water to the stream except during the spring melt and following unusually heavy thundershowers during the summer months. Even in spring months the increased flow is primarily a result of higher flows from the springs rather than surface runoff, as evidenced by the low turbidity of the stream (never more than 200 Jackson turbidity units and usually less than 25 JTU).

## Use-history of the Watershed

A sawmill was built 100 m below the source of Temple Fork in the late 1870's, and the Douglas-fir on the surrounding slopes was logged off. A wagon road was built along the entire length of the stream to permit the transport of lumber to Logan Canyon, and it seems likely that the stream would have been considerably disturbed in the process. The mill was abandoned before 1890, and there has been no extensive timber cutting in the area since. The watershed has been used as summer range for sheep and cattle for many years, but during this study the area was a cattle-only allotment. The cattle graze the area heavily, and the bluegrass swards near the stream are kept cropped to a lawn-like appearance. Mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) are present on the watershed and are hunted each fall. 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*). The stream receives heavy fishing pressure on the opening weekend, after which one seldom sees more than three or four anglers at one time on the stream. A dirt road parallels the lower 5.1 km of the stream, but the upper 1.9 km can only be reached by footpath.

# MATERIALS AND METHODS

## Physical and Chemical Environment

Water temperature recordings were made 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 culvert. This culvert, containing the entire flow of the stream, was located approximately 0.8 km below station II. Discharges from the culvert were determined at several stages of the stream. A Gurley current meter was used to measure velocities of the water at several points across the channel. The cross-sectional area of the channel was measured and products of the partial cross-sections and the velocities within the section were summed to obtain total discharge. A rating curve was then established to permit the conversion of stage to flow. Stages of the stream were recorded daily during the summer months and at 14-day intervals during the winter months.

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 by the methods outlined in American Public Health Association, Inc. (1960), using brom creosol green as an indicator. Hydrogen-ion concentration was determined with a Wallace and Tiernan comparator. Dissolved-oxygen concentration was determined by the Thierault modification of the Winkler method. No abrupt or severe changes in water quality (as determined by the above tests) were noticed during the study.

## Bottom Sampling

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 $m^2$ (one $ft^2$). 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 then swept into the collecting net 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 in excess of 0.5 m/second, depths in excess of 12 cm, and the presence of fine rubble, fine and coarse gravel, 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 in three or four months.

Two bottom samples were collected at each station every 14 days during June-September. Two bottom samples were collected at each station every 28 days during the remainder of each year. Entire samples were preserved in 10 percent 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 employing the sugar-flotation technique described by Anderson (1959) and by the use of a 2X macroscope. Organisms recovered from the bottom samples were stored in 80 percent ethyl alcohol.

Samples of 30-50 *Baetis bicaudatus* nymphs and *O. sigma* larvae were oven-dried at 80 C and weighed to the nearest 0.1 mg on a Voland analytical balance. A total of 424 bottom samples were collected and analyzed for this study.

The sorted organisms were identified and counted under a binocular microscope. Macroinvertebrates were identified with the aid of keys published by Edmunds (1952), Pennak (1953), Usinger (1956), and Ross (1944). Dr. Herbert H. Ross identified adult specimens of *O. sigma* and *O. minutus*.

## Drift Sampling

Invertebrates drifting in the stream were sampled with water wheel devices located at the upper three stations. The water wheel sampler has been 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 the winter months one 24-hour sample was collected at each station every 14 days. The sampling period usually began at 10-11 a.m., Mountain Standard Time, and ended between 10 a.m. and 11 a.m. on the following day. During the summer months (June-September), two samples (a day and a night sample) were collected at each station every other day. The collecting nets of the water wheels were emptied at 8-9 a.m. (2-3 hours after sunrise) and at 7:30-8:30 p.m. (30-45 minutes before sunset).

*Oligophlebodes sigma* larvae, *Baetis bicaudatus* nymphs, and the adults of *O. sigma* and *B. bicaudatus* were sorted from the drift samples under a 2X macroscope and identified and counted. *O. sigma* and *B. bicaudatus* from the 24-hour samples and from every seventh day and night sample were oven-dried and weighed. A total of 181, 24-hour samples were collected and analyzed. A total of 341 day and 340 night samples were collected and analyzed.

## Adult Flight and Oviposition

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

# PHYSICAL AND CHEMICAL ENVIRONMENT

## Water Temperature

Water temperatures at the spring source of Temple Fork ranged from 4.8 C to 6.1 C. Monthly mean temperatures ranged from a low of 5.0 in the winter months of 1968 and 1969 to means of 6.1 C in May of 1968 and 5.5 C in May of 1969 (Table 2). At station II water temperatures ranged from lows of 3.3 C in January, 1968, and 3.7 C in December, 1969, to highs of 7.6 C in July, 1968, and 7.1 C in August, 1969. At station III water temperatures ranged from lows of 2.5 C and 3.3 C in December, 1968 and 1969, respectively, to highs of 10.2 C in July, 1968, and 9.6 C in August, 1969. At station IV water temperatures ranged from 0.0 C to 17.1 C. Mean monthly temperatures were not available for station IV.

With increasing distance below the source, summer water temperatures generally increased while winter temperatures decreased under the influence of ambient air temperatures. 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 1967-1968 than in the winter months of 1968-1969. Temperatures were higher at all stations in the summer of 1968 than in the summer of 1969.

The thermograph at station I was located about 100 m above the sampling station, 50 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 interval 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.

Table 2. Mean monthly water temperatures, stations I-III, Temple Fork, 1967-1969--expressed as $^{o}C$

| Month and year | Station I | Station II | Station III |
|---|---|---|---|
| September, 1967 | 5.0 | -- | -- |
| October | 5.0 | -- | -- |
| November | 5.0 | 5.2 | 4.0 |
| December | 5.0 | 3.8 | 2.5 |
| January, 1968 | 5.0 | 3.3 | 2.9 |
| February | 5.0 | 4.0 | 4.6 |
| March | 5.1 | 4.9 | 5.0 |
| April | 5.6 | 5.4 | 5.5 |
| May | 6.1 | 6.2 | 7.2 |
| June | 5.9 | 6.8 | 8.2 |
| July | 5.7 | 7.6 | 10.2 |
| August | 5.6 | 7.4 | 9.7 |
| September | 5.2 | 6.3 | 7.7 |
| October | 5.0 | 5.3 | 6.1 |
| November | 5.0 | 4.2 | 4.4 |
| December | 5.0 | 3.7 | 3.3 |
| January, 1969 | 5.0 | 3.8 | 3.5 |
| February | 5.0 | 4.0 | 3.9 |
| March | 4.9 | 3.9 | 4.2 |
| April | 5.0 | 5.4 | 6.4 |
| May | 5.5 | 6.0 | 7.1 |
| June | 5.5 | 6.3 | 8.2 |
| July | 5.2 | 7.0 | 9.4 |
| August | 5.0 | 7.1 | 9.6 |
| September | 5.0 | 6.6 | 8.4 |

## Discharge

Mean 1967-1969 flows were 0.30, 0.34, 0.37, and 0.48 $m^3$/second at stations I-IV, respectively (Table 3). Peak discharge occurred in June, 1968 (mean flows = 0.62, 0.67, 0.74, and 0.92 $m^3$/second) and May, 1969 (mean flows = 0.94, 1.06, 1.27, and 1.49 $m^3$/second). Minimum flows occurred in January, 1968 (0.19, 0.20, 0.22, and 0.31 $m^3$/second) and February, 1969 (0.19, 0.21, 0.22, and 0.32 $m^3$/second).

Table 3. Mean monthly flow, stations I-IV, Temple Fork, 1967-1969--expressed as $m^3$/second

| | Station | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| September, 1967 | 0.30 | 0.34 | 0.38 | 0.48 |
| October | 0.25 | 0.28 | 0.30 | 0.40 |
| November | 0.24 | 0.26 | 0.27 | 0.36 |
| December | 0.23 | 0.25 | 0.27 | 0.36 |
| January, 1968 | 0.19 | 0.20 | 0.22 | 0.31 |
| February | 0.20 | 0.22 | 0.24 | 0.33 |
| March | 0.20 | 0.22 | 0.24 | 0.33 |
| April | 0.21 | 0.23 | 0.25 | 0.35 |
| May | 0.59 | 0.65 | 0.73 | 0.90 |
| June | 0.62 | 0.67 | 0.74 | 0.92 |
| July | 0.29 | 0.32 | 0.35 | 0.48 |
| August | 0.23 | 0.26 | 0.28 | 0.37 |
| September | 0.20 | 0.22 | 0.24 | 0.33 |
| October | 0.22 | 0.25 | 0.27 | 0.36 |
| November | 0.21 | 0.23 | 0.25 | 0.31 |
| December | 0.21 | 0.23 | 0.25 | 0.34 |
| January, 1969 | 0.20 | 0.22 | 0.24 | 0.34 |
| February | 0.19 | 0.21 | 0.23 | 0.32 |
| March | 0.21 | 0.23 | 0.27 | 0.36 |
| April | 0.44 | 0.49 | 0.54 | 0.65 |
| May | 0.94 | 1.06 | 1.27 | 1.49 |
| June | 0.47 | 0.51 | 0.55 | 0.68 |
| July | 0.31 | 0.34 | 0.37 | 0.45 |
| August | 0.25 | 0.28 | 0.31 | 0.40 |
| September | 0.22 | 0.25 | 0.27 | 0.36 |
| Mean | 0.30 | 0.34 | 0.37 | 0.48 |

## Water Chemistry

Total alkalinity at the four stations varied from highs of 166, 172, 173, and 187 ppm at the four stations to lows of 139, 149, 141, and

150 ppm, respectively (Table 4). Total alkalinity increased with distance below the source. Alkalinity was slightly lower in winter months and reached a peak during the increased spring flows of May-June in each year (Table 4).

Table 4. Total alkalinity, stations I-IV, Temple Fork, 1967-1969--expressed as ppm $CaCO_3$ (mean of two samples/month)

| Month and year | Station<br>I | <br>II | <br>III | <br>IV |
|---|---|---|---|---|
| September, 1967 | 158[a] | 172[a] | 173[a] | 187[a] |
| October | 156 | 165 | 169 | 178 |
| November | 139 | 155 | 160 | 165 |
| December | 144 | 153 | 157 | 169 |
| January, 1968 | 143 | 154 | 157 | 165 |
| February | 142[a] | 151[a] | 156 | 166 |
| March | 141 | 153 | 158 | 165 |
| April | 144 | 155 | 160 | 169 |
| May | 156 | 163 | 164 | 164 |
| June | 150 | 155 | 159 | 164 |
| July | 150 | 157 | 157 | 162 |
| August | 148 | 156 | 157 | 159 |
| September | 140 | 153 | 153 | 156 |
| October | 142[a] | 150[a] | 155[a] | 164[a] |
| November | 140 | 149 | 151 | 158 |
| December | 140 | 149 | 141 | 150 |
| January, 1969 | 138 | 149 | 142 | 152 |
| February | 138[a] | 149 | 141 | 153 |
| March | -- | -- | -- | -- |
| April | 147 | 158 | 153 | 153 |
| May | 166[a] | 166[a] | -- | 173[a] |
| June | 149[a] | 161[a] | 161[a] | 165[a] |
| July | 155 | 162 | 162 | 167 |
| August | 155 | 162 | 162 | 171 |
| September | 151 | 157 | 155 | 166 |

[a] Only one sample in these months.

Mean hydrogen-ion concentrations (pH) were 8.0, 8.2, 8.3, and 8.3 at stations I-IV, respectively. The range of pH values determined was

7.7 to 8.5

Dissolved-oxygen concentrations were usually at 80-100 percent of air saturation at each of the four stations. The range of values determined was from 8.5 ppm to 10.6 ppm.

## Physical Nature of the Substrate

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 stream was almost entirely composed of riffle and run areas, with only a few sandy-bottomed pools. The 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 each station.

## LIFE HISTORIES OF STUDY ORGANISMS

### *Oligophlebodes sigma*

*Oligophlebodes sigma* larvae hatched in October-January. The larvae constructed and lived within a round, truncated-cone case of coarse sand grains. The fifth (and final) instar larvae were typically 4-6 mm long, and they pupated within the last larval case. The mature larvae selected thin, flat stones, approximately 2 mm in diameter and 0.5 mm thick to use 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. Mature larvae selected pupation sites gregariously; that is, pupal distributions were clumped to a greater extent than larval distributions. Pupation occurred from about the first of July 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. Greatest emergences 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. A single generation was produced each year.

*Oligophlebodes sigma* adults were frequently seen drinking from the stream but were not observed feeding. Adults held in cages without water died in 1-2 days. Adults held in cages supplied with water usually lived 2-4 days with a maximum observed life of 5 days. The female adults of *O. sigma* undertook a definite upstream migration prior to depositing their eggs in the stream.

Digestive tracts of 12 *O. sigma* larvae contained green and brown algae, diatoms, and unidentifiable plant fragments. *O. sigma* larvae are day-active organisms (Waters, 1968) and were frequently observed "grazing" on the periphyton covering 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. When the boards were examined late in the afternoon, the upper surfaces of the boards were uniformly populated by many *O. sigma* larvae. When the boards were examined early in the morning, there were few larvae on the upper surfaces, while many larvae 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 generations 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. The 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.

*Baetis bicaudatus* adults were seen swarming over the stream in the early morning hours. There was no noticeable tendency for the adults to fly either upstream or downstream.

Digestive tracts of seven *B. bicaudatus* nymphs contained masses of plant debris and unidentifiable organic materials, perhaps dead leaves of terrestrial plants and small amounts of algae. *B. bicaudatus* nymphs are night-active organisms and were seldom seen on the upper surfaces of the substrate materials during daylight hours. Adult *B. bicaudatus* mouth-parts were vestigal, and the adults probably did not feed.

## DENSITY OF BENTHIC INVERTEBRATES

### *Oligophlebodes sigma*

The *O. sigma* larvae population at station I was low in numbers in both years. The population reached a maximum density of 2,000-3,000/ 0.1 $m^2$ in November and December of 1968 and 1969 (Figure 2; Appendix). From the early winter peak the population density declined rather slowly and steadily until the time of pupation in June. Apparently mortality and drift removal rates from the area were low.

The density of *O. sigma* larvae expressed as biomass at station I was also similar in the two years. In 1968, the biomass reached a maximum in March and April (58 mg/0.1 $m^2$), whereas in 1969, the maximum was not reached until May-June and was slightly higher (78 mg/0.1 $m^2$; Figure 3).

The highest densities of *O. sigma* larvae were found at stations II and III. In 1968, the density at station II reached a peak of 1,131/ 0.1 $m^2$ in February (Figure 2). From February to May the density at this station declined slowly to about 720/0.1 $m^2$. The relationship between density and time in Figure 2 shows a great deal of sampling variability as well as actual variation in density. The density at station III reached a peak of 928/0.1 $m^2$ in January of 1968 and then declined slowly to about 675/0.1 $m^2$ in March, after which it recovered to about 875/0.1 $m^2$ in May.

The densities of *O. sigma* larvae expressed as biomass at station II reached a peak of about 145 mg/0.1 $m^2$ in January, 1968, and remained at

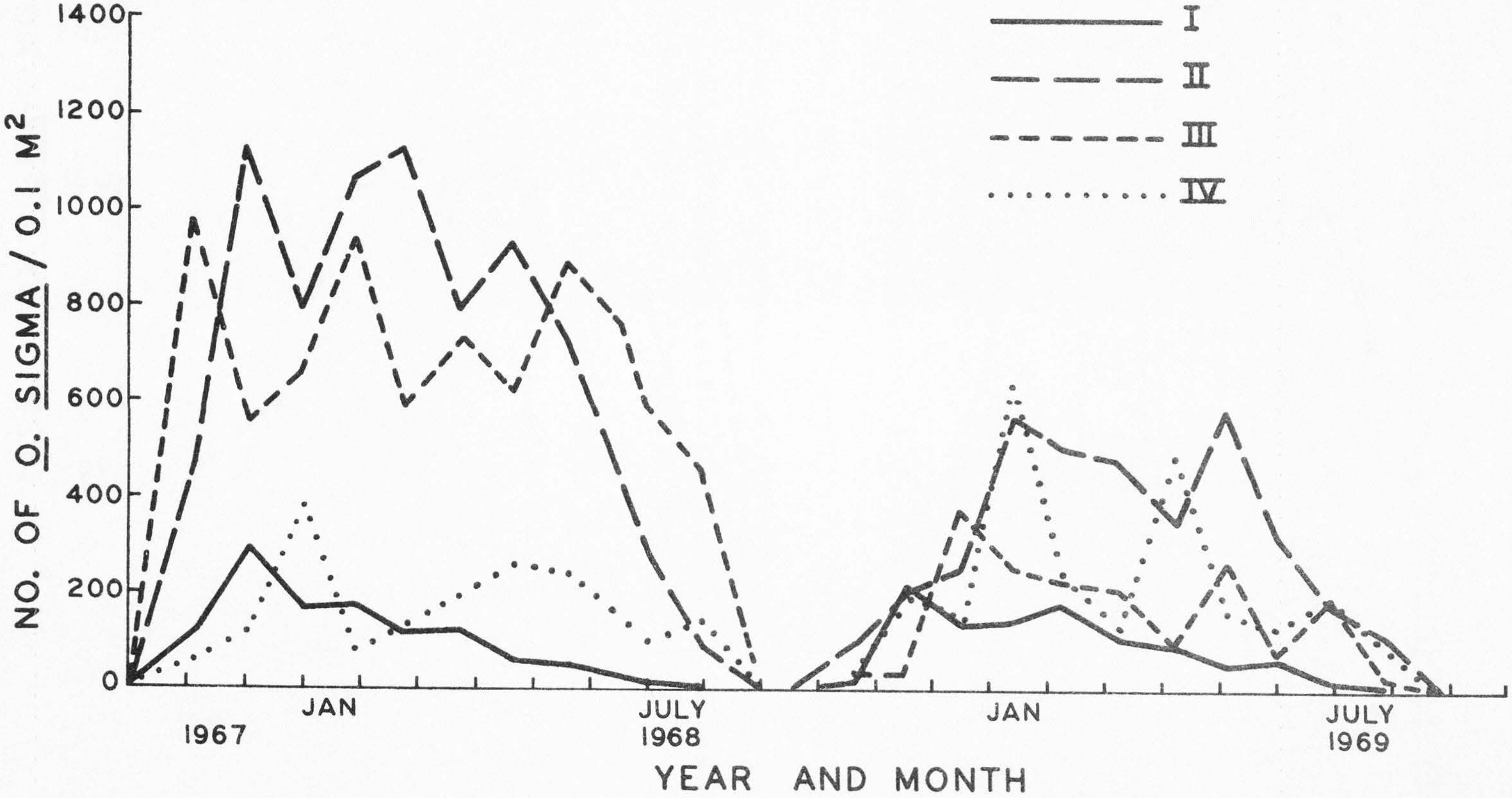

Figure 2. Density of *O. sigma* larvae on the streambed, stations I-IV, Temple Fork, 1967-1969--expressed as numbers per 0.1 m$^2$.

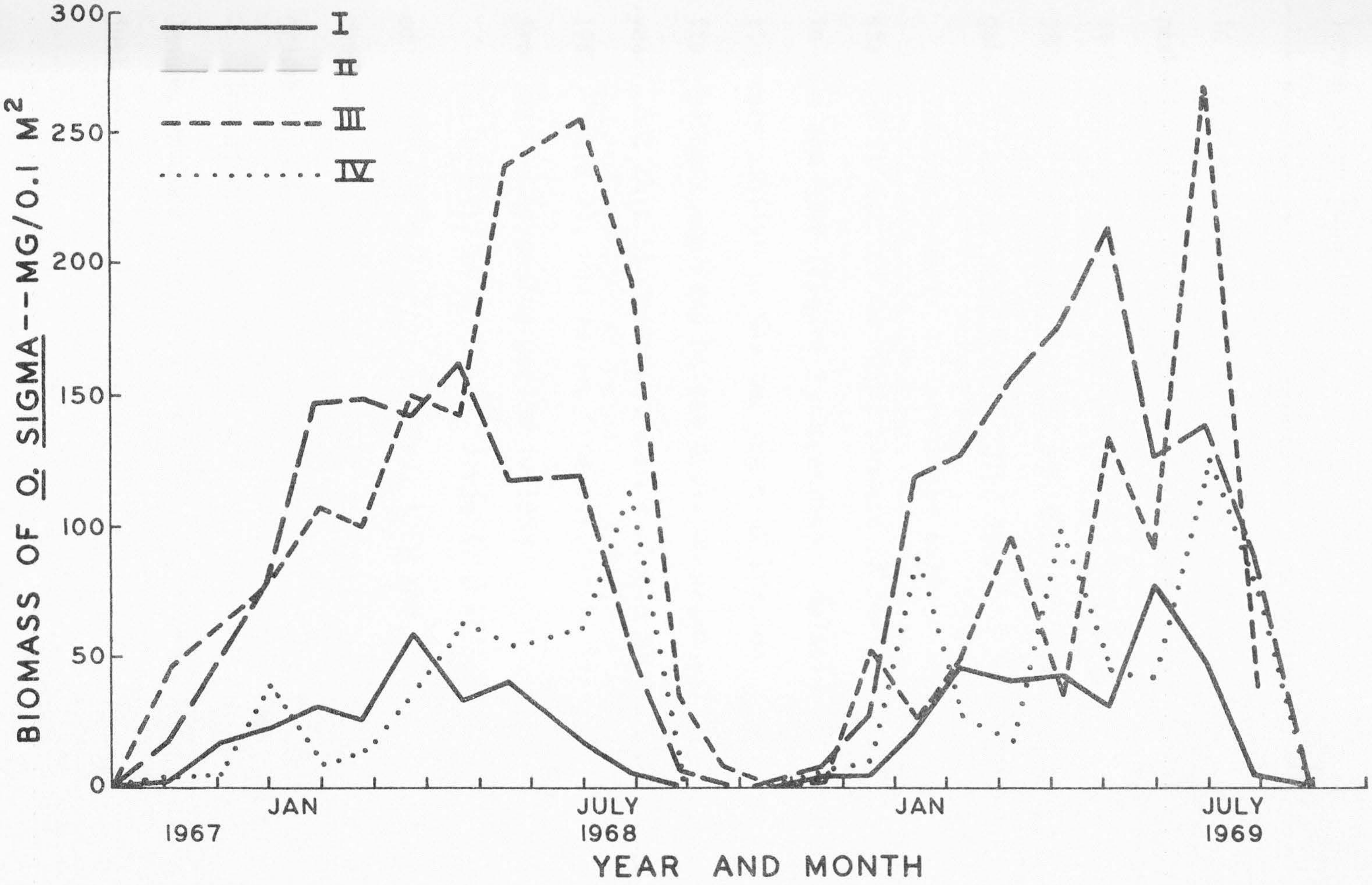

Figure 3. Biomass of *O. sigma* larvae on the streambed, stations I-IV, Temple Fork, 1967-1969--expressed as mg dry weight per 0.1 $m^2$.

that level until April, after which it declined (Figure 3; Appendix). The biomass of larvae at station III rose steadily from October, 1967, to the first of July and did not level off, or decline, until after the larvae began pupating.

Numbers of *O. sigma* larvae at stations II and III were much lower in 1969 than in 1968 (Figure 2). At station II the density of larvae peaked at 563/0.1 $m^2$ in January, declined slowly, and then peaked again at 586/0.1 $m^2$ in May. At station III the density of larvae peaked at 387/0.1 $m^2$ in December, 1968, and then declined until showing a slight gain just before pupation in July, 1969.

Although numbers of larvae per unit of area were much lower at stations II and III in 1969, biomass of larvae per unit area was similar in 1968 and 1969 (Figure 3; Appendix). Relationship between biomass and time were similar in the two years at station II. At station III the final biomass achieved before pupation began was nearly the same in both years, but this is dependent upon a single month's observation (June 29, 1969; Figure 3), and values from earlier in 1969 were lower than values from the corresponding period in 1968.

The density of *O. sigma* larvae at station IV reached peak numbers of 379 and 640/0.1 $m^2$ in January, 1968 and 1969, respectively. The density fell sharply in February and March of both years and then recovered gradually until the time of pupation.

The biomass of *O. sigma* larvae at station IV increased steadily from January to June of both years and reached peaks of 113 and 124 mg/0.1 $m^2$ just prior to the time of pupation in 1968 and 1969, respectively.

## *Baetis bicaudatus*

### Winter generation

The density of winter-generation *B. bicaudatus* nymphs was highest at stations III and I in both years (station III maximum = 809 and 434/0.1 m$^2$; station I maximum = 572 and 346/0.1 m$^2$ in 1968 and 1969, respectively; Figure 4; Appendix). Densities at II and IV were lower in both years (maximums of 152 and 153/0.1 m$^2$ at station III; 227 and 231/0.1 m$^2$ at station IV in 1968 and 1969, respectively).

Biomass of *B. bicaudatus* numphs per unit area was high at stations I, III, and IV in 1968 (maximums of 54, 52, and 77 mg/0.1 m$^2$, respectively; Figure 5; Appendix). Biomass of nymphs at station II was lower throughout the period with a maximum of 23 mg/0.1 m$^2$. In 1969, the biomass of winter-generation nymphs was high at stations III and IV (maximums of 80 and 50 mg/0.1 m$^2$). The maximum biomass at stations I and II were similar (29 and 27 mg/0.1 m$^2$, respectively) and lower than at stations III and IV.

### Summer generation

The density of summer-generation nymphs was highest at station I in both years (maximum of 1,050 and 332/0.1 m$^2$ in 1968 and 1969, respectively; Table 5). Densities at stations II and III were similar in the two years and lower in 1969 than in 1968 (maximums of 218 and 111/0.1 m$^2$ at II; 225 and 71/0.1 m$^2$ at II in 1968 and 1969, respectively). Densities of summer-generation *B. bicaudatus* nymphs were lowest at station IV in both years (maximums of 25 and 17/0.1 m$^2$ in 1968 and 1969, respectively). The relationship among stations for biomass of *B. bicaudatus* nymphs were similar to the density-as-numbers relationships in both years (Table 5).

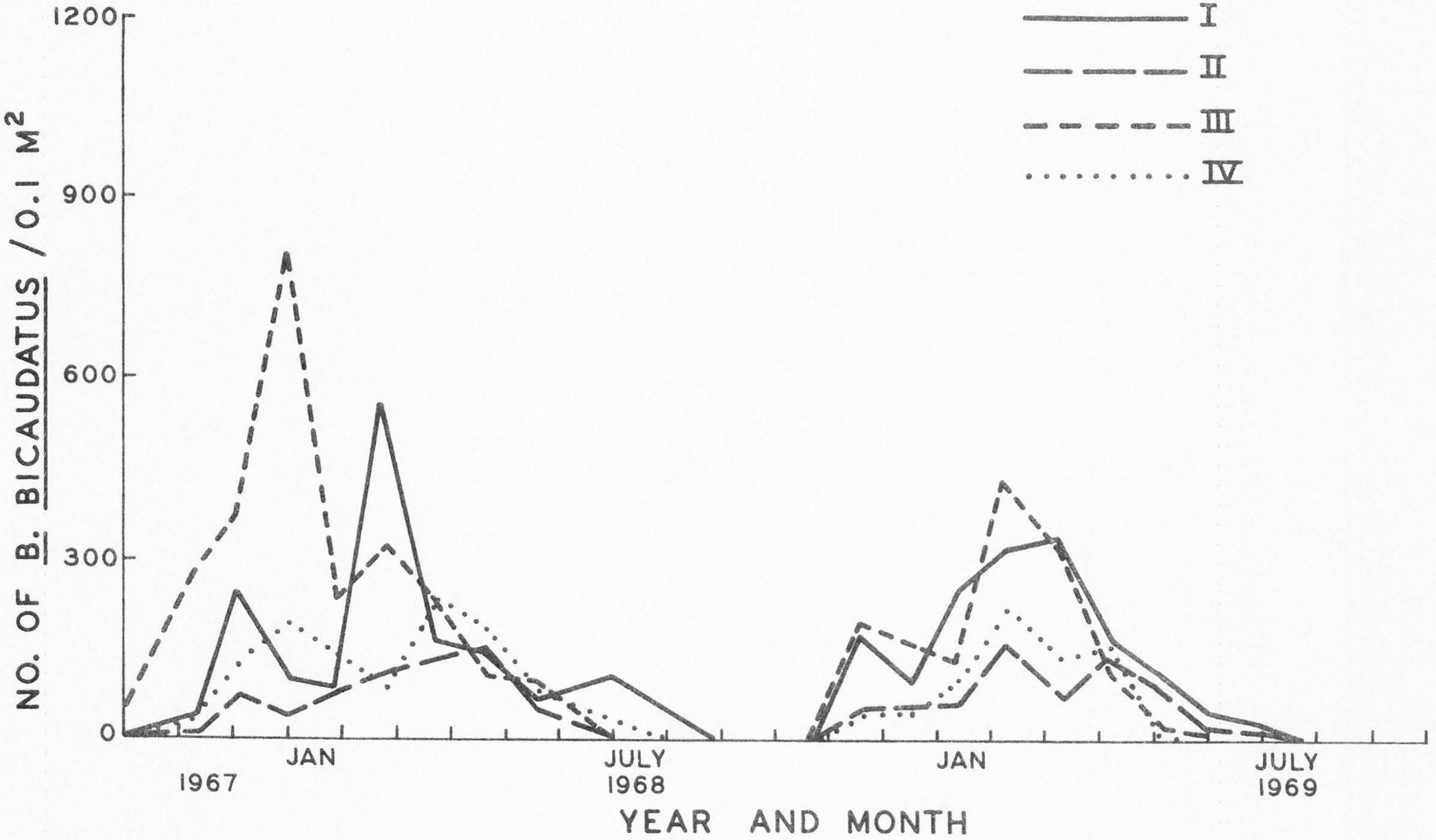

Figure 4. Density of winter generation *B. bicaudatus* nymphs on the streambed, stations I-IV, Temple Fork, 1967-1969--expressed as numbers per 0.1 $m^2$.

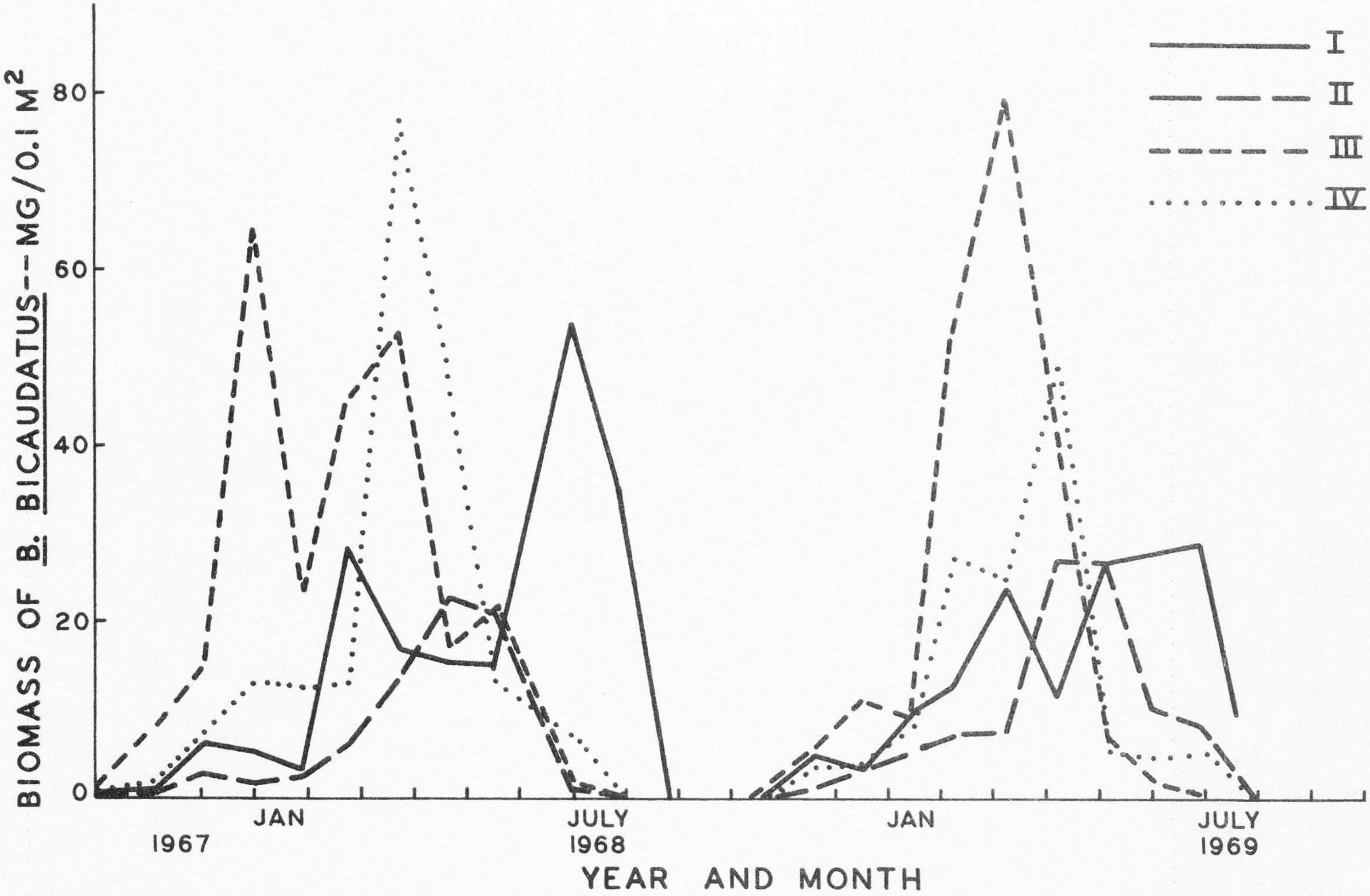

Figure 5. Biomass of winter generation *B. bicaudatus* nymphs on the streambed, stations I-IV, Temple Fork, 1967-1969--expressed as mg dry weight per 0.1 $m^2$.

Table 5. Density of summer-generation *Baetis bicaudatus* nymphs on the streambed, Temple Fork, 1967-1969--expressed as numbers and biomass dry-weight per 0.1 $m^2$

| Date | Numbers station | | | | Dry weight (mg) station | | | |
|---|---|---|---|---|---|---|---|---|
| | 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 |
| 6-01-69 | 286 | 0 | 0 | 0 | 45.8 | 0 | 0 | 0 |
| 6-29-69 | 332 | 6 | 0 | 8 | 69.7 | 0.5 | 0 | 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 | 40.3 | 7.2 |

## Other Macroinvertebrates

Numbers of all other macroinvertebrates from the bottom samples are given in the Appendix. The most abundant macroinvertebrate forms (besides *O. sigma* and *B. bicaudatus*) were: *Ephemerella* sp. (*coloradensis*?), *Rhithrogena*, *Cinygmula*, Chironomidae, Tricladida, *Glossosoma*, Tipulidae, *Nemoura*, Elmidae, and Psychodidae in approximate order of abundance. The mean monthly numbers of all macroinvertebrates were 1,065, 1,688, 1,599, and 1,211/0.1 $m^2$ at stations I-IV, respectively (Appendix).

## GROWTH OF *OLIGOPHLEBODES SIGMA* AND *BAETIS BICAUDATUS*

Mean individual weights were expressed as oven-dried weight (cases removed). The use of oven-dried 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 two minutes 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).

### *Oligophlebodes sigma*

*Oligophlebodes sigma* larvae grew rapidly immediately after hatching in November and December of each year (G typically = .018 to .064 mg/mg day; Table 6). Larvae grew slowly in mid-winter (G typically = 0 to .012 mg/mg day) and then began growing rapidly again (G = .019 to .027 mg/mg day) in June of each year. Sampling variability was great and may have accounted for some of the negative G values. 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 (1.9-2.3 mg) in both years than did larvae at the lower stations. Final larval weights were similar (.82 mg and .98 mg) in both years at station II. Final larval weights at station III were .57-.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 6).

Table 6. Mean individual weight and daily growth rate of *O. sigma* larvae, stations I-IV, Temple Fork, 1967-1969--expressed as mg dry weight

| | Station | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | I | | II | | III | | IV | |
| Date | Mean weight | G | Mean weight | G | Mean weight | G | Mean weight | G |
| | | | | 1968 generation | | | | |
| 11-04-67 | .01 | -- | .04 | -- | .05 | -- | .06 | -- |
| 12-02-67 | .06 | .064 | .04 | 0 | .11 | .028 | .07 | .006 |
| 12-30-67 | .14 | .030 | .11 | .036 | .12 | .003 | .11 | .016 |
| 1-27-68 | .18 | .009 | .14 | .009 | .11 | -.003 | .17 | .016 |
| 2-23-68 | .22 | .007 | .13 | -.003 | .17 | .016 | .13 | -.010 |
| 3-23-68 | .35 | .016 | .18 | .011 | .21 | .007 | .24 | .021 |
| 4-20-68 | .55 | .016 | .17 | -.002 | .23 | .003 | .24 | 0 |
| 5-18-68 | .81 | .014 | .16 | -.002 | .27 | .006 | .34 | .012 |
| 6-30-68 | 2.19 | .023 | .42 | .022 | .43 | .011 | .67 | .016 |
| 7-28-68 | 1.77 | -.008 | .59 | .012 | .42 | -.001 | .74 | .004 |
| 8-25-68 | .50 | -.045 | .82 | .012 | .57 | .011 | .45 | -.018 |
| 9-22-68 | .41 | -.007 | -- | -- | .52 | -.003 | .40 | -.004 |
| 10-20-68 | -- | -- | -- | -- | .76 | .014 | -- | -- |
| 11-17-68 | -- | -- | -- | -- | .57 | -.010 | -- | -- |
| | | | | 1969 generation | | | | |
| 10-20-68 | .01 | -- | .02 | -- | .03 | -- | .02 | -- |
| 11-17-68 | .02 | .025 | .04 | .025 | .07 | .030 | .03 | .014 |
| 12-15-68 | .04 | .025 | .12 | .039 | .13 | .022 | .05 | .018 |
| 1-12-69 | .15 | .047 | .21 | .020 | .10 | .009 | .14 | .037 |
| 2-09-69 | .24 | .019 | .25 | .006 | .21 | .027 | .11 | -.009 |
| 3-09-69 | .34 | .012 | .32 | .009 | .45 | .027 | .13 | .006 |
| 4-06-69 | .43 | .008 | .49 | .015 | .40 | -.004 | .20 | .015 |
| 5-04-69 | .61 | .013 | .36 | -.011 | .47 | .006 | .27 | .011 |
| 6-01-69 | 1.10 | .021 | .39 | .003 | 1.01 | .027 | .42 | .016 |
| 6-29-69 | 1.92 | .020 | .82 | .027 | 1.75 | .020 | .71 | .019 |
| 7-27-69 | 1.60 | -.007 | .82 | 0 | 1.58 | -.004 | .77 | .003 |
| 8-24-69 | -- | -- | .63 | -.009 | -- | -- | -- | -- |

The mean individual weights (and the negative G values) of larvae in Table 6 may be misleading, because towards the end of each generation, they were influenced by the increasing percentage of slow-growing individuals (left when the rapid growing individuals pupated). Therefore, the weight of immature pupae may provide a better measure of the final larval weight obtained at each station. Mean pupal weight (without cases) were 2.33 mg and 2.20 mg in 1968 and 1969 at station I (Table 7). Pupae were lighter at the three lower stations (0.87-1.37 mg). Mean monthly pupal densities were low at station I (10 and 7/0.1 $m^2$) in 1968 and 1969 and higher at the three lower stations (13-54/0.1 $m^2$; Table 7).

Table 7. Mean individual weight and density of *O. sigma* pupae, and mean monthly density of *O. sigma* larvae (April-June), stations I-IV, Temple Fork, 1968-1969

| Item | Station | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Mean individual dry weight of immature pupae (mg) | | | | |
| 1968 | 2.33 | .94 | .87 | 1.02 |
| 1969 | 2.20 | .98 | 1.51 | 1.37 |
| Mean density of pupae on the streambed (June-Sept.)/0.1 $m^2$ | | | | |
| 1968 | 10 | 50 | 42 | 52 |
| 1969 | 7 | 54 | 72 | 13 |
| Mean density of larvae on the streambed (April-May)/0.1 $m^2$ | | | | |
| 1968 | 39 | 686 | 697 | 166 |
| 1969 | 72 | 422 | 148 | 247 |

The final weight (of immature pupae) attained was probably a function of nutrition and crowding of larvae. Many insects are known to attain a smaller adult size under conditions of crowding and/or lack of food

(Ullyett, 1950). 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 Figure 6. The mean weight of pupae decreased as larval density increased.

### *Baetis bicaudatus*

*Baetis bicaudatus* nymphs also grew slowly during the winter months at each station, including station I (Table 8). 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 8 do not accurately reveal the final size (1.2-1.8 mg) of winter-generation nymphs. *Baetis bicaudatus* nymphs grew to approximately the same size at each of the four stations (Table 8).

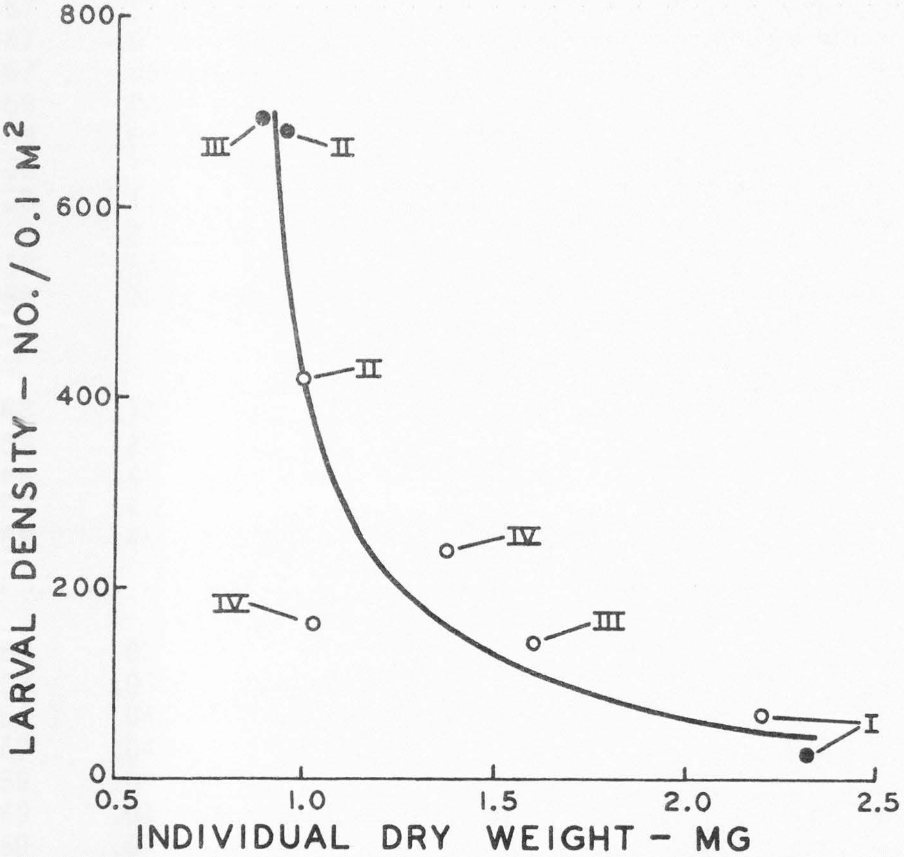

Figure 6. Mean density of *O. sigma* larvae during the rapid-growth months of April-June and mean individual dry weight of *O. sigma* pupae, stations I-IV, Temple Fork, 1968-1969--solid circle = 1968 data, open circle = 1969 data.

Table 8. Mean individual weight and daily growth rate of *B. bicaudatus* nymphs, stations I-IV, Temple Fork, 1967-1969--expressed as mg dry weight

| | Station | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | I | | II | | III | | IV | |
| Date | Mean weight | G | Mean weight | G | Mean weight | G | Mean weight | G |
| | <u>1968 winter generation</u> | | | | | | | |
| 10-01-67 | -- | -- | .02 | -- | .03 | -- | -- | -- |
| 11-04-67 | .02 | -- | .06 | .033 | .03 | 0 | .06 | -- |
| 12-02-67 | .03 | .014 | .04 | -.014 | .04 | .010 | .06 | 0 |
| 12-30-67 | .05 | .018 | .05 | .008 | .08 | .025 | .07 | .006 |
| 1-27-68 | .04 | -.008 | .04 | -.008 | .10 | .008 | .09 | .009 |
| 2-23-68 | .05 | .008 | .06 | .014 | .14 | .012 | .15 | .018 |
| 3-23-68 | .11 | .028 | .11 | .022 | .23 | .018 | .34 | .029 |
| 4-20-68 | .11 | 0 | .15 | .011 | .16 | -.013 | .27 | -.008 |
| 5-18-68 | .23 | .026 | .40 | .035 | .19 | .006 | .19 | -.013 |
| 6-30-68 | .54 | .020 | .45 | .003 | .55 | .025 | .22 | .003 |
| 7-28-68 | .70 | .009 | -- | -- | -- | -- | -- | -- |
| | <u>1968 summer generation</u> | | | | | | | |
| 6-30-68 | .10 | -- | .02 | -- | .02 | -- | .02 | -- |
| 7-28-68 | .25 | .033 | .05 | .033 | .07 | .045 | .06 | .039 |
| 8-25-68 | .41 | .018 | .10 | .025 | .11 | .016 | .08 | .006 |
| 9-22-68 | .41 | 0 | .31 | .040 | .46 | .051 | .35 | .053 |
| 10-20-68 | .45 | .003 | .53 | .019 | .76 | .018 | 1.06 | .040 |
| | <u>1969 winter generation</u> | | | | | | | |
| 10-20-68 | .02 | -- | -- | -- | .03 | -- | .07 | -- |
| 11-17-68 | .03 | .014 | .03 | -- | .03 | -- | .05 | -.012 |
| 12-15-68 | .04 | .010 | .06 | .025 | .07 | .030 | .07 | .012 |
| 1-12-69 | .04 | 0 | .09 | .014 | .07 | 0 | .08 | .005 |
| 2-09-69 | .04 | 0 | .05 | -.021 | .12 | .019 | .12 | .014 |
| 3-09-69 | .07 | .020 | .11 | .028 | .25 | .026 | .18 | .014 |
| 4-06-69 | .07 | 0 | .19 | .020 | .40 | .017 | .32 | .021 |
| 5-04-69 | .23 | .043 | .30 | .016 | .42 | .002 | .72 | .029 |
| 6-01-69 | .61 | .035 | .57 | .023 | .50 | .006 | -- | -- |
| 6-29-69 | .97 | .017 | -- | -- | -- | -- | -- | -- |
| | <u>1969 summer generation</u> | | | | | | | |
| 5-04-69 | -- | -- | -- | -- | -- | -- | .04 | -- |
| 6-01-69 | .16 | -- | -- | -- | .06 | -- | .04 | 0 |
| 6-29-69 | .21 | .010 | .09 | -- | .07 | .006 | .08 | .025 |
| 7-27-69 | .29 | .012 | .08 | -.004 | .11 | .016 | .07 | -.005 |
| 8-24-69 | .35 | .007 | .24 | .039 | .19 | .055 | .20 | .038 |
| 9-21-69 | .37 | .002 | .66 | .036 | .72 | .048 | .60 | .039 |

# PRODUCTION COMPUTATIONS

Annual production of *O. sigma* larvae and *B. bicaudatus* nymphs at each of the four stations was computed by Allen's (1951) graphical method. The number of individuals per 0.1 $m^2$ of streambed was plotted against the mean dry weight of individuals in each sample. 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 for plotting the Allen curves were taken from smoothed curves drawn through the 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 Figure 7. Production estimates could not be made using Water's (1962) 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 species, meant that the Allen 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

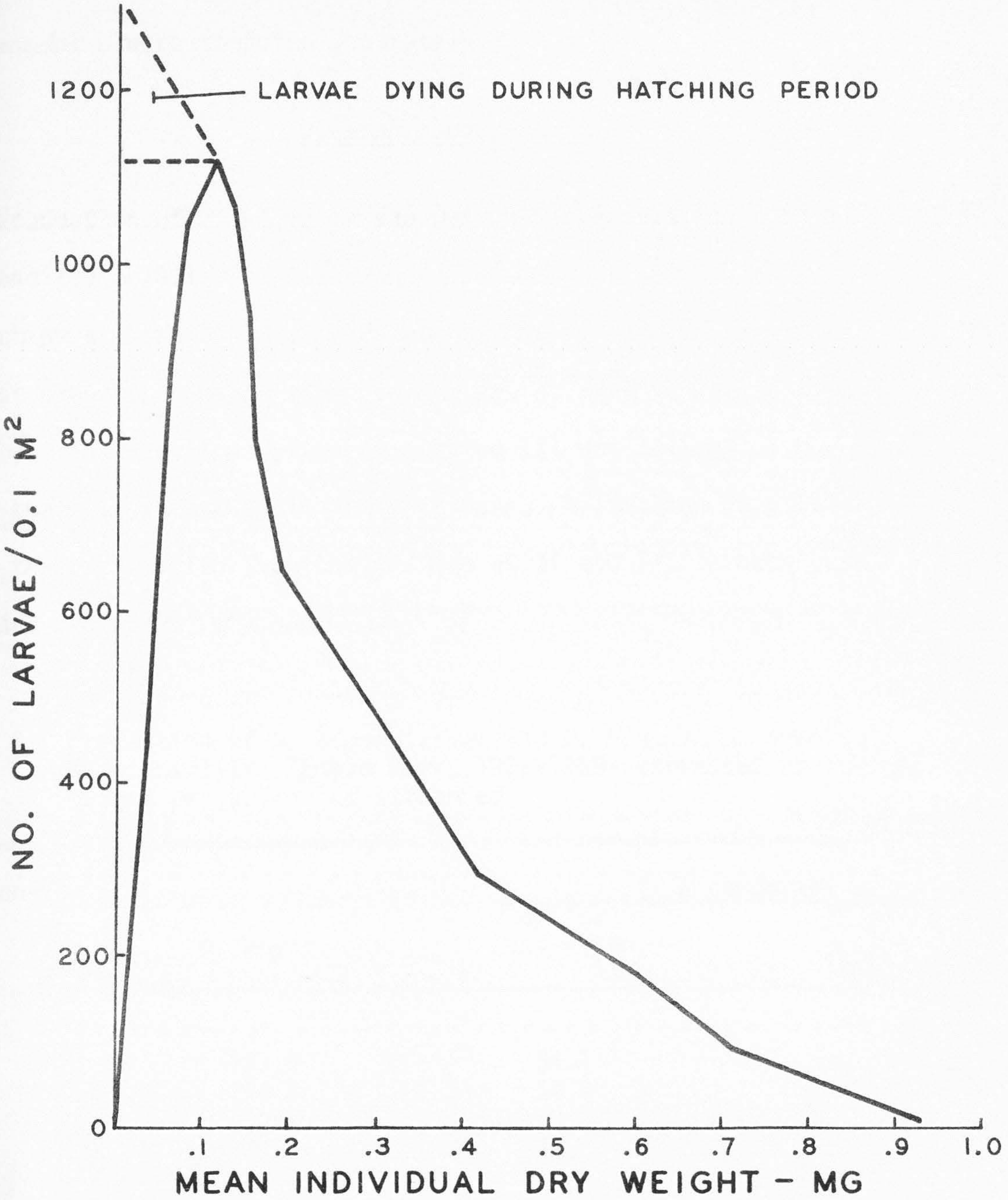

Figure 7. Allen curve to compute production of *O. sigma* larvae per 0.1 $m^2$, station II, Temple Fork, 1968, area under curve = 384.8 mg dry weight per 0.1 $m^2$.

actual mortality rate. Production of winter and summer generations of *B. bicaudatus* were computed separately.

## *Oligophlebodes sigma*

Production of *O. sigma* larvae was lowest at station I in both years (128 and 129 mg/0.1 $m^2$ in 1968 and 1969, respectively; Table 9). Production at station II was 385 and 347 mg/0.1 $m^2$ in 1968 and 1969. The highest production of *O. sigma* larvae was at station III in 1968 (430 mg/0.1 $m^2$). In 1969, production at station III was 331 mg/0.1 $m^2$, 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 $m^2$).

Table 9. Production of *O. sigma* larvae and *B. bicaudatus* nymphs, stations I-IV, Temple Fork, 1968-1969--expressed as mg dry weight per 0.1 $m^2$ of streambed

| Station and year | *O. sigma* | *B. bicaudatus* | |
|---|---|---|---|
| | | Winter generation | Summer generation |
| 1968 | | | |
| I | 127.5 | 84.1 | 111.6 |
| II | 384.8 | 54.8 | 63.2 |
| III | 430.4 | 113.8 | 99.3 |
| IV | 174.7 | 43.6 | 21.2 |
| 1969 | | | |
| I | 128.6 | 92.6 | 102.0 |
| II | 347.0 | 50.8 | 55.6 |
| III | 331.2 | 131.1 | 45.1 |
| IV | 219.8 | 88.8 | 9.3 |

The year-to-year variation within stations was relatively small compared to the among-stations variability, with the exception of station III where production dropped from 420 in 1968 to 331 mg/0.1 $m^2$ in 1969 (Table 9). The production at station I was approximately one-third that at station II in both years, in spite of the fact that the density 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.

### *Baetis bicaudatus*

Production of winter-generation *B. bicaudatus* nymphs was highest at station III (114 and 131 mg/0.1 $m^2$ in 1968 and 1969, respectively) in both years (Table 9). The production of winter-generation nymphs was smaller in both years at station I (84 and 93 mg/0.1 $m^2$). Production of the winter generation was least at stations II and IV (55 and 51 mg/0.1 $m^2$ at station II; 44 and 89 mg/0.1 $m^2$ at station IV).

Production of the summer generations was highest at station I (112 and 102 mg/0.1 $m^2$) in both years. Production of the summer generations was somewhat less at stations II and III (63 and 56 mg/0.1 $m^2$ at station II; 99 and 45 mg/0.1 $m^2$ at station III). Production of the summer generations was very low at station IV in both years (21 and 9 mg/0.1 $m^2$). Mortality rates and final weights obtained appeared to have less among-station variability for *B. bicaudatus* nymphs than for *O. sigma* larvae (Table 9). Therefore, density and production ratios were not as variable for *B. bicaudatus*.

# DRIFT OF *OLIGOPHLEBODES SIGMA* AND *BAETIS BICAUDATUS*

The drift densities of *O. sigma* larvae and *B. bicaudatus* nymphs were determined from the water wheel catches. Total number and biomass of each organism passing the upper three stations were calculated by multiplying the densities 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 to the years 1968 and 1969 refer to the drift of immatures of the two generations previously referred to as the 1968 and 1969 generations. Therefore, the figures representing the total drift of *O. sigma* larvae past a given station in 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.

## *Oligophlebodes sigma*

Drift rates of *O. sigma* larvae were low at all stations from September through March of both years (Figures 8 and 9). Drift rates (expressed as both numbers and biomass/24 hours) began increasing in April and reached maximums 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 (Figures 8 and 9).

Both the total number and the 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 gm dry weight were calculated as the total

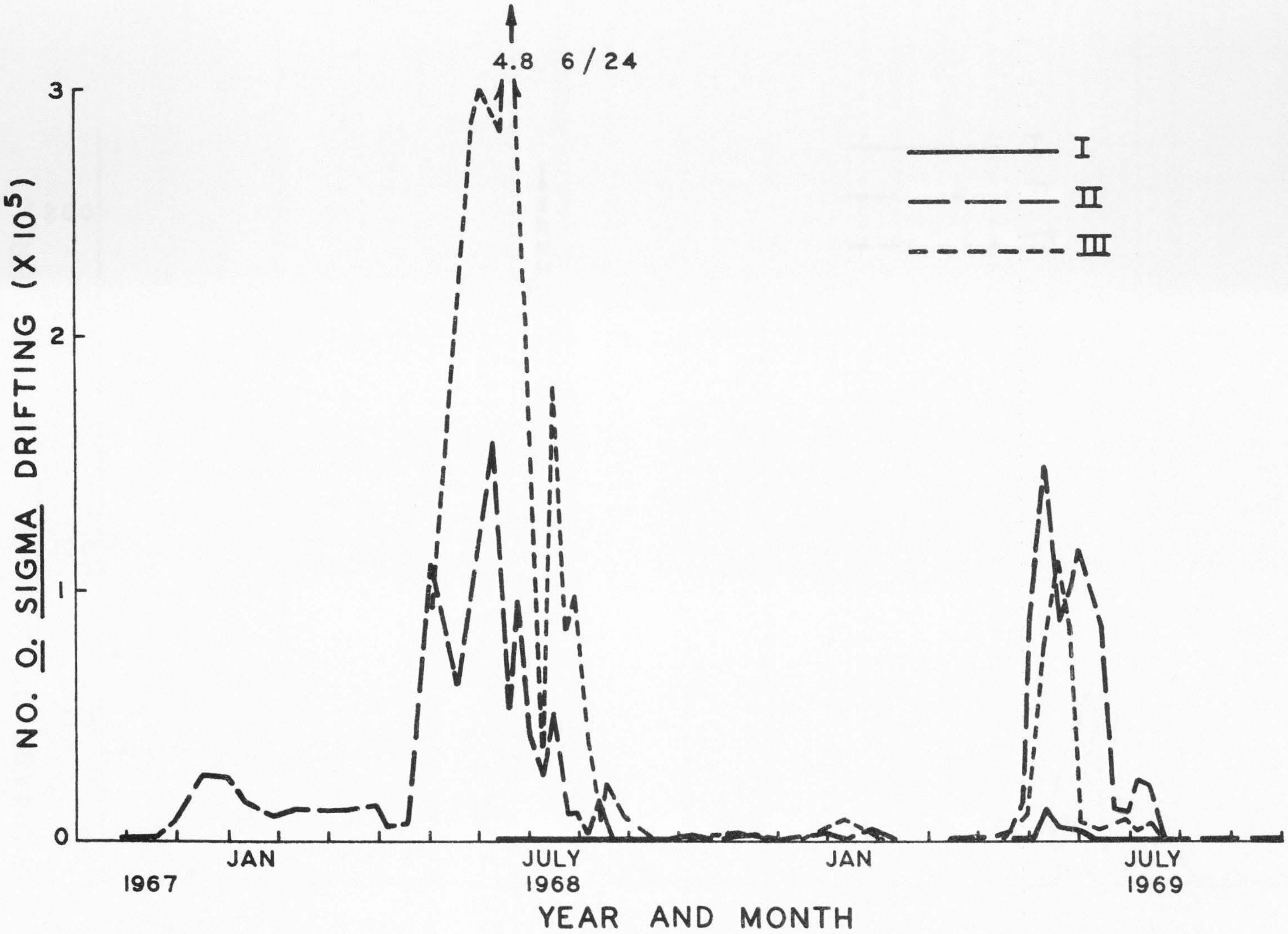

Figure 8. Total number of O. *sigma* larvae drifting past stations I-III, Temple Fork, 1967-1969--expressed as numbers per 24 hours.

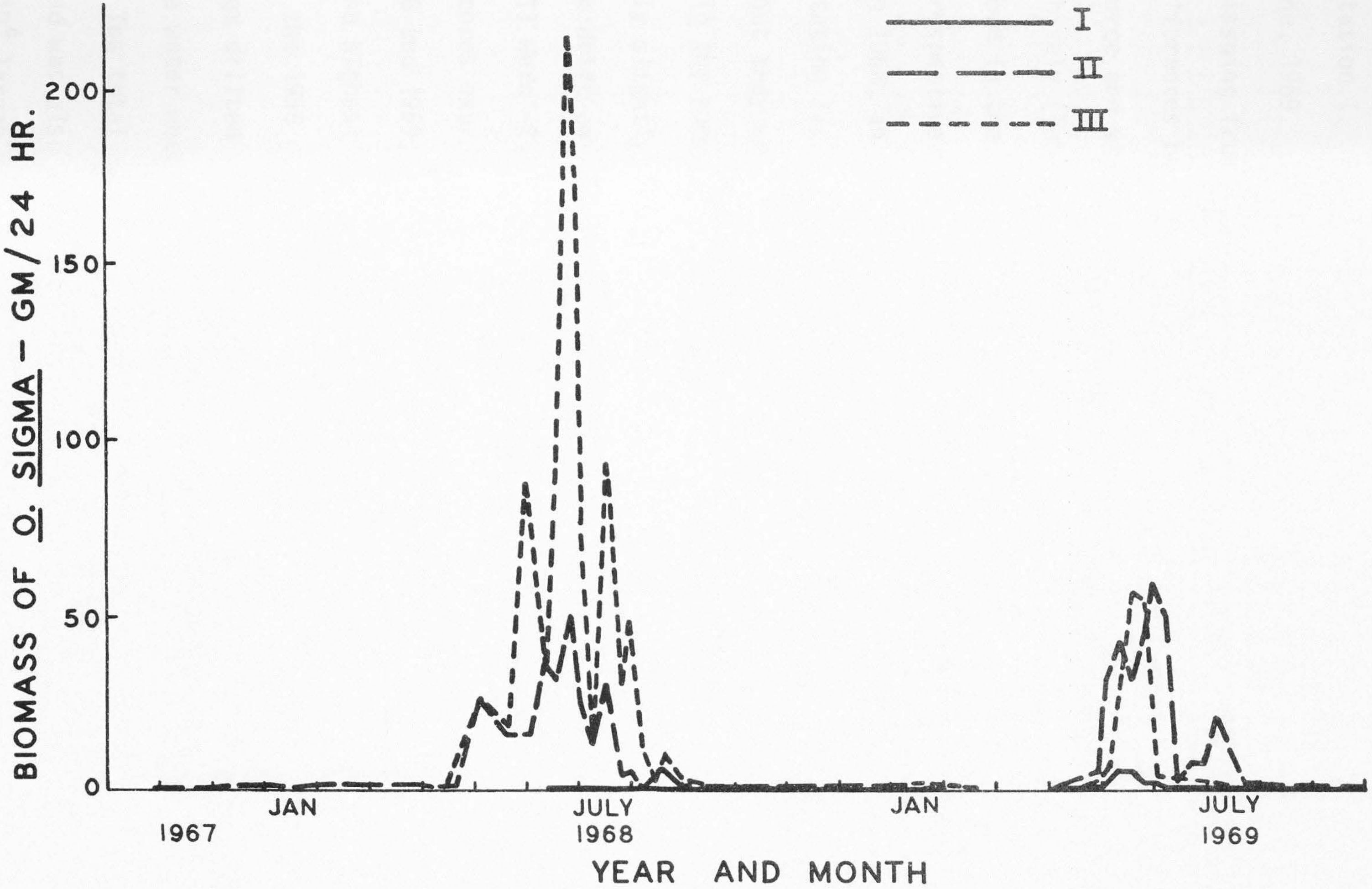

Figure 9. Biomass of *O. sigma* larvae drifting past stations I-III, Temple Fork, 1967-1969--expressed as gm dry weight per 24 hours.

number and biomass of larvae drifting past station I (Table 10). In 1969, an estimated 27 X $10^4$ larvae weighing a total of 134 gm drifted past station I. About 90 percent 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 of the area between the source and station I were -30 gm and -134 gm in 1968 and 1969, respectively (Table 10). The net differences expressed as mg/0.1 $m^2$ of streambed in the area above station I were -6.6 and -29.3 in 1968 and 1969, respectively (Table 10).

In 1968, an estimated 888 X $10^4$ larvae weighing 2,567 gm drifted past station II. In 1969, fewer larvae drifted past station II (517 X $10^4$), but they were larger and a greater proportion of them drifted past later in the summer. Therefore, the biomass drifting past (2,318 gm) was only slightly less than that of 1968 (Table 10). The net differences between drift on and off of the total stream bottom area between stations I and II were -2,537 gm in 1968 and -2,189 gm in 1969. The net differences expressed on an areal basis were -39.2 and -33.7 mg/0.1 $m^2$ 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 X $10^4$ larvae weighing 5,987 gm drifted past station III in 1968. These figures are minimal because water wheel 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 X $10^4$ larvae weighing 1,335 gm drifted past station III in 1969. The net differences in biomass drifting on and off of the area between

Table 10. Total numbers and biomass of *O. sigma* larvae and *B. bicaudatus* nymphs drifting past three stations and the net gain-loss between stations, Temple Fork, 1968-1969 generations

| Item and year | *O. sigma* station |  |  | *B. bicaudatus* station |  |  |
|---|---|---|---|---|---|---|
|  | I | II | III | I | II | III |
| Number drifting by ($X\ 10^4$) |  |  |  |  |  |  |
| 1968 generation | 6[a] | 888 | 1,559[a] | 303[a] | 1,065 | 652[a] |
| 1969 generation | 27 | 517 | 266 | 770 | 873 | 1,397 |
| Biomass drifting by (gm dry weight) |  |  |  |  |  |  |
| 1968 generation | 30[a] | 2,567 | 5,987[a] | 1,342[a] | 2,137 | 1,085[a] |
| 1969 generation | 134 | 2,318 | 1,335 | 1,990 | 2,621 | 4,381 |
| Net difference (biomass drifting on - biomass drifting off--gm) |  |  |  |  |  |  |
| 1968 generation | -30[a] | -2,537 | -3,420[a] | -1,342[a] | -795 | +1,052[a] |
| 1969 generation | -134 | -2,184 | +983 | -1,990 | -631 | -1,761 |
| Net difference expressed as mg/0.1 $m^2$ of streambed |  |  |  |  |  |  |
| 1968 generation | -6.6[a] | -39.2 | -41.3[a] | -271.6[a] | -12.3 | +12.7[a] |
| 1969 generation | -29.3 | -33.7 | +11.9 | -435.1 | -9.8 | -21.3 |

[a] Minimal estimates because water wheel samples were not collected at stations I and III until May, 1968, hence these figures omit winter and spring drift for the 1968 generations.

stations II and III were -3,420 gm and +983 gm in 1968 and 1969, respectively. The positive value of 983 gm for 1969 represents the only instance in which drift of *O. sigma* larvae onto an area exceeded drift off of the area in this study. The net differences expressed on an areal basis were -41.3 and +11.9 mg/0.1 $m^2$ in 1968 and 1969, respectively.

### *Baetis bicaudatus*

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 the winter drift rates of *O. sigma* larvae were. The 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 (Figures 10 and 11). The peak periods of drift for the winter generations were in March and April of both years at station III, while at stations I and II the peak periods were late in May.

The total numbers of nymphs drifting past station I were 303 X $10^4$ and 770 X $10^4$ in 1968 and 1969, respectively, but the 1968 figure is minimal. The weights of nymphs drifting past station I were 1,342 gm and 1,990 gm in 1968 and 1969. The figures for biomass show a greater similarity in the two years than the figures for total numbers, because the nymphs were small in the omitted portion (because of the late water wheel installation) of the 1968 generation. The net differences between drift on and off of the area between the source and station I expressed as mg/0.1 $m^2$ were very high in both years (-271.6 and -435.1 mg/0.1 $m^2$ in 1968 and 1969, respectively).

The total numbers of nymphs drifting past station II were 1,065 X $10^4$ and 873 X $10^4$ in 1968 and 1969, respectively. Total weight of

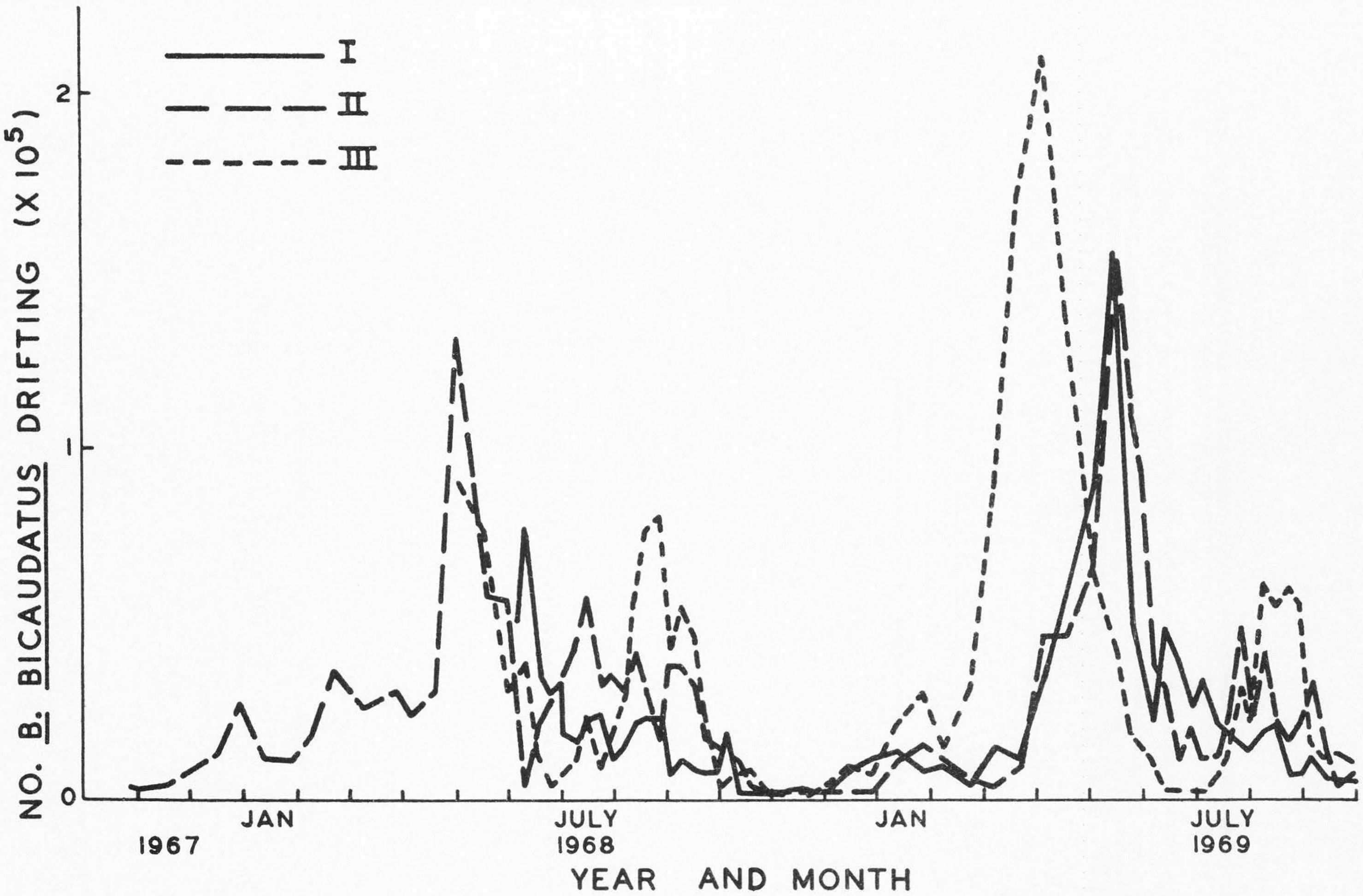

Figure 10. Total number of *B. bicaudatus* nymphs drifting past stations I-III, Temple Fork, 1967-1969--expressed as gm dry weight per 24 hours.

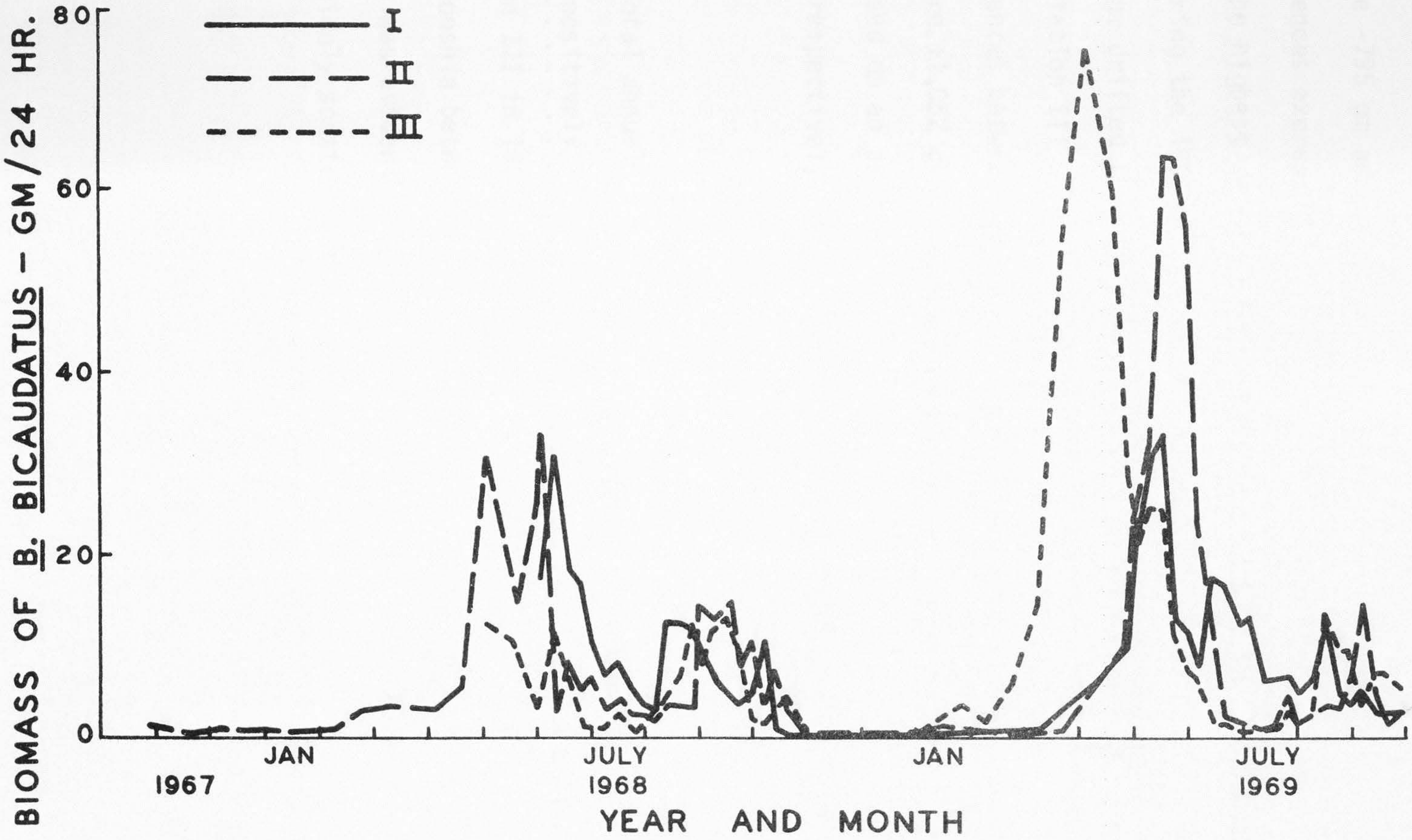

Figure 11. Biomass of *B. bicaudatus* nymphs drifting past stations I-III, Temple Fork, 1967-1969--expressed as gm dry weight per 24 hours.

nymphs drifting past were 2,137 gm in 1968 and 2,621 gm in 1969. Net differences between drift on and off the area between stations I and II were -795 gm and -631 gm in 1968 and 1969, respectively. The net differences expressed on an areal basis were -12.3 and -9.8 mg/0.1 $m^2$.

The highest drift rates of *B. bicaudatus* nymphs occurred at station III during the 1969 generation. An estimated 1,397 X $10^4$ nymphs weighing 4,381 gm drifted past this station in 1969. In 1968, the total drift past station III was 652 X $10^4$ nymphs weighing 1,085 gm. The net differences between drift on and off the area between stations II and III were +1,052 gm in 1968 and -1,761 gm in 1969. These differences expressed on an areal basis were +12.7 and -21.3 mg/0.1 $m^2$ in 1968 and 1969, respectively (Table 10).

## Drift-production Relationships

Total annual drift and annual production of *O. sigma* larvae appeared to be positively related (Figure 12). Both quantities were greatest at station III in 1968 and least at station I in 1968. No definite relationship between annual drift and annual production of *B. bicaudatus* nymphs was evident. The points plotted for *B. bicaudatus* in Figure 12 were widely scattered.

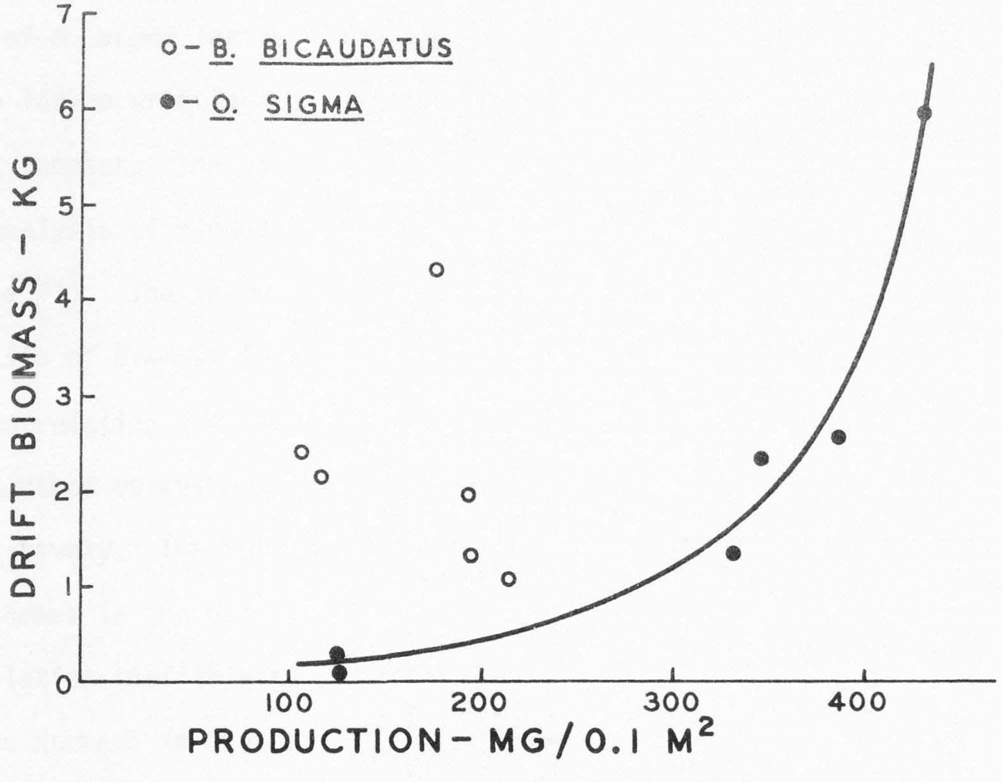

Figure 12. Relationship between total annual production and total annual drift, stations I-III, Temple Fork--open circles = *B. bicaudatus*, solid circles = *O. sigma*.

## MULTIPLE REGRESSION ANALYSES OF FACTORS AFFECTING DRIFT RATES

A pair of water wheel samples (one day and one night sample) was collected at each of the three upper stations every other day from June 1 to October 1 in 1968 and 1969. The day and night samples were analyzed separately.

Correlation coefficients between density (as numbers/area) and biomass of *O. sigma* larvae in the benthos and density and biomass of *O. sigma* larvae drifting past each station were calculated for the day and night samples. The highest correlation (r = .81) was obtained in the day analysis of numbers in the benthos versus numbers in the drift (Table 11). The second highest correlation was obtained in the day analysis of biomass in the drift versus numbers in the benthos (r = .78). The correlation coefficients obtained in the day analyses of biomass in the benthos versus numbers and biomass in the drift were .69 and .67, respectively. The correlation coefficient obtained in the night analysis of biomass in the drift versus numbers in the benthos was .77. Correlation coefficients obtained in the analyses of biomass in the drift versus numbers in the benthos for *B. bicaudatus* nymphs were lower (r = .55 and .43 for the day and night analyses, respectively; all r values significant at the .01 level).

The unique contributions of 17 independent factors to the variability of drift rates of *O. sigma* and *B. bicaudatus* were determined through multiple regression analysis. Dependent variables (nos. 18-21, Table 12) 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*

Table 11. Simple correlation coefficients (r) indicating the degree of association between drift and density, stations I-III, Temple Fork, June-October, 1968-1969

| Factors | r values |
|---|---|
| Day drift of *O. sigma* | |
| Nos. in drift vs. nos. in benthos | .81 |
| Nos. in drift vs. biomass in benthos | .69 |
| Biomass in drift vs. nos. in benthos | .78 |
| Biomass in drift vs. biomass in benthos | .67 |
| Night drift of *O. sigma* | |
| Biomass in drift vs. nos. in benthos | .77 |
| Day drift of *B. bicaudatus* | |
| Biomass in drift vs. nos. in benthos | .55 |
| Night drift of *B. bicaudatus* | |
| Biomass in drift vs. nos. in benthos | .43 |

Table 12. Variables entered in the multiple regression analyses with identifying numbers and units of measurement

| Identification number | Variable | Unit of measurement |
|---|---|---|
| Independent variables | | |
| 1 | Distance below the source | km |
| 2 | Flow | cms |
| 3 | Maximum water temperature | $^{o}$C |
| 4 | Minimum water temperature | $^{o}$C |
| 5 | Mean water temperature | $^{o}$C |
| 6 | Solar radiation (at Logan, Utah) | Langleys |
| 7 | Length of sampling period | hr |
| 8 | Daily growth rate of *O. sigma* | mg/mg day |
| 9 | Daily production rate of *O. sigma* | mg/day |
| 10 | Density of *O. sigma* | no./.09 m$^2$ |
| 11 | Density of *B. bicaudatus* | " |
| 12 | Density of *Ephemerella* sp. | " |
| 13 | Density of *Ephemerella doddsi* | " |
| 14 | Density of *Cinygmula* and *Rhithrogena* | " |
| 15 | Density of *Glossosoma* | " |
| 16 | Density of *Rhyacophila* | " |
| 17 | Density of Chironomidae | " |
| Dependent variables | | |
| 18 | Biomass of *O. sigma* drifting/period | mg/period |
| 19 | Biomass of *B. bicaudatus* drifting/period | mg/period |
| 20 | Number of *O. sigma* drifting/period | no./period |
| 21 | Number of *B. bicaudatus* drifting/period | no./period |

and *B. bicaudatus* drifting past each station during the sampling period. The independent variables and their units of measure are given in Table 12. Distance below the source and flow at the sampling station are self-explanatory. The water temperature extremes and means refer to values recorded during the combined 24-hour period and not to values within a single day or night sampling period. The minimum temperature, for example, might occur at 2 a.m. 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 hours. 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 two-week intervals, interpolating to seven-day intervals, and then dividing by seven to obtain the daily rates. Densities of all organisms were determined at 14-day intervals from the bottom samples, and these values used for all sampling dates within the two-week 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 these genera could not be distinguished in early instars.

After the initial four regression analyses (biomass and numbers of *O. sigma* and *B. bicaudatus* versus 17 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 step-wise fashion until only one independent variable remained. The $R^2$ values (representing that portion of the total variability in the dependent variable accounted for by the independent variables) were then accumulated and entered in Tables 13 and 14.

## *Oligophlebodes sigma*

Four variables were significant (at the .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, flow, density of *Glossosoma* on the bottom, and distance below the source. Flow and density of *Glossosoma* had negative coefficients, density of *O. sigma* and distance below the source had positive coefficients (Table 15). The $R^2$ values indicated that 65 percent of the variability in the biomass of *O. sigma* drifting during the day was accounted for by the 17 independent variables.

Only two variables had significant mean squares in the analysis of biomass of *O. sigma* drifting during the night: (1) density of *O. sigma* larvae (coefficient +), and (2) density of *Glossosoma* (coefficient +, Table 16). The $R^2$ value indicated that 62 percent of the variability in drift of *O. sigma* biomass at night was accounted for by the 17 independent variables.

The order of rejection of independent variables (based on successive minimum mean squares) for the step-wise regression analysis of *O. sigma* biomass is given in Table 13). The outstanding feature of both the day and night analyses was the importance of *O. sigma* density on the bottom in explaining the variability of the biomass of *O. sigma* drifting by

Table 13. Order of rejection of independent variables and resultant $R^2$ values for multiple regression analyses of biomass and numbers of *O. sigma* and *B. bicaudatus* immatures drifting past three stations, Temple Fork, 1968-1969 - stepped on minimum mean squares in the analyses of *O. sigma* biomass

| Variable rejected | Dependent variable analyzed | | | |
|---|---|---|---|---|
| | #18 | #19 | #20 | #21 |
| **Day analyses** | | | | |
| - | .65 | .55 | .71 | .43 |
| # 5--Mean temperature | .65 | .55 | .71 | .42 |
| #14--Density of *Cinygmula* | .65 | .53 | .71 | .42 |
| #12--Density of *Ephemerella* sp. | .65 | .52 | .71 | .42 |
| #13--Density of *Ephemerella doddsi* | .65 | .52 | .71 | .42 |
| # 7--Length of period | .65 | .51 | .70 | .41 |
| #17--Density of Chironomidae | .65 | .51 | .70 | .41 |
| # 9--P/day of *O. sigma* | .65 | .50 | .70 | .41 |
| # 8--G/day of *O. sigma* | .65 | .50 | .70 | .41 |
| # 3--Maximum temperature | .65 | .49 | .70 | .37 |
| # 6--Radiation | .65 | .48 | .70 | .37 |
| #16--Density of *Rhyacophila* | .64 | .48 | .68 | .22 |
| #15--Density of *Glossosoma* | .63 | .48 | .68 | .22 |
| #11--Density of *B. bicaudatus* | .63 | .37 | .67 | .16 |
| # 1--Distance below source | .62 | .34 | .67 | .16 |
| # 2--Flow | .62 | .01 | .66 | .11 |
| # 4--Minimum temperature | .60 | .00 | .66 | .01 |
| #10--Density of *O. sigma* | | | | |
| **Night analyses** | | | | |
| - | .62 | .55 | .70 | .52 |
| # 6--Radiation | .62 | .54 | .70 | .52 |
| # 8--G/day of *O. sigma* | .62 | .54 | .70 | .52 |
| #14--Density of *Cinygmula* | .62 | .54 | .70 | .51 |
| #11--Density of *B. bicaudatus* | .62 | .53 | .70 | .50 |
| # 5--Mean temperature | .62 | .52 | .70 | .46 |
| #17--Density of Chironomidae | .62 | .51 | .70 | .46 |
| # 7--Length of period | .62 | .50 | .69 | .46 |
| # 2--Flow | .62 | .40 | .69 | .41 |
| # 3--Maximum temperature | .62 | .40 | .69 | .41 |
| #12--Density of *Ephemerella* sp. | .61 | .39 | .69 | .40 |
| #13--Density of *Ephemerella doddsi* | .61 | .34 | .69 | .40 |
| # 1--Distance below source | .61 | .32 | .68 | .40 |
| #16--Density of *Rhyacophila* | .61 | .16 | .68 | .37 |
| #15--Density of *Glossosoma* | .61 | .07 | .68 | .08 |
| # 9--P/day of *O. sigma* | .60 | .07 | .67 | .08 |
| # 4--Minimum temperature | .59 | .04 | .67 | .02 |
| #10--Density of *O. sigma* | | | | |

Table 14. Order of rejection of independent variables and resultant $R^2$ values for multiple regression analyses of biomass and numbers of *O. sigma* and *B. bicaudatus* immatures drifting past three stations, Temple Fork, 1968-1969 - stepped on minimum mean squares in the analyses of *B. bicaudatus* biomass

| Variable rejected | Dependent variable analyzed #18 | #19 | #20 | #21 |
|---|---|---|---|---|
| Day analyses | | | | |
| - | .65 | .55 | .71 | .43 |
| # 7--Length of period | .65 | .55 | .70 | .42 |
| # 5--Mean temperature | .65 | .55 | .70 | .42 |
| #15--Density of *Glossosoma* | .64 | .54 | .69 | .34 |
| # 4--Minimum temperature | .63 | .54 | .69 | .34 |
| #16--Density of *Rhyacophila* | .63 | .54 | .69 | .33 |
| # 3--Maximum temperature | .62 | .54 | .68 | .25 |
| # 1--Distance below source | .61 | .54 | .67 | .20 |
| # 8--G/day of *O. sigma* | .61 | .53 | .67 | .19 |
| # 9--P/day of *O. sigma* | .61 | .53 | .66 | .19 |
| # 6--Radiation | .61 | .52 | .66 | .19 |
| #17--Density of Chironomidae | .61 | .51 | .66 | .15 |
| #12--Density of *Ephemerella* sp. | .61 | .50 | .66 | .12 |
| #14--Density of *Cinygmula* | .61 | .49 | .66 | .11 |
| #13--Density of *Ephemerella doddsi* | .61 | .48 | .66 | .10 |
| #10--Density of *O. sigma* | .21 | .45 | .23 | .09 |
| # 2--Flow | .03 | .31 | .02 | .07 |
| #11--Density of *B. bicaudatus* | | | | |
| Night analyses | | | | |
| - | .62 | .55 | .70 | .52 |
| # 4--Minimum temperature | .62 | .55 | .70 | .52 |
| #13--Density of *Ephemerella doddsi* | .62 | .55 | .69 | .52 |
| #14--Density of *Cinygmula* | .62 | .55 | .69 | .52 |
| # 1--Distance below source | .61 | .54 | .69 | .51 |
| # 6--Radiation | .61 | .54 | .69 | .51 |
| # 9--P/day of *O. sigma* | .61 | .54 | .69 | .51 |
| #17--Density of Chironomidae | .61 | .54 | .69 | .51 |
| #15--Density of *Glossosoma* | .61 | .54 | .69 | .39 |
| #11--Density of *B. bicaudatus* | .61 | .53 | .69 | .39 |
| # 3--Maximum temperature | .61 | .52 | .69 | .34 |
| # 8--G/day of *O. sigma* | .60 | .50 | .68 | .30 |
| # 7--Length of period | .60 | .48 | .68 | .30 |
| # 5--Mean temperature | .60 | .41 | .67 | .29 |
| #12--Density of *Ephemerella* sp. | .60 | .32 | .67 | .28 |
| # 2--Flow | .60 | .19 | .67 | .27 |
| #10--Density of *O. sigma* | .02 | .11 | .04 | .21 |
| #16--Density of *Rhyacophila* | | | | |

Table 15. Abbreviated regression analysis of factors affecting drift-biomass of *O. sigma*, day samples, Temple Fork, 1968-1969

| Source | Degrees freedom | Mean square | Coefficient |
|---|---|---|---|
| Total | 343 | $.640 \times 10^{13}$ | $.408 \times 10^{7}$ |
| Distance below source | 1 | $.143 \times 10^{14}$* | $.569 \times 10^{5}$ |
| Flow | 1 | $.364 \times 10^{14}$* | $-.485 \times 10^{5}$ |
| Maximum temperature | 1 | $.930 \times 10^{12}$ | $-.150 \times 10^{5}$ |
| Minimum temperature | 1 | $.687 \times 10^{13}$ | $-.504 \times 10^{5}$ |
| Mean temperature | 1 | $.301 \times 10^{11}$ | $.521 \times 10^{4}$ |
| Radiation | 1 | $.461 \times 10^{13}$ | $.117 \times 10^{4}$ |
| Length of period | 1 | $.274 \times 10^{12}$ | $-.620 \times 10^{4}$ |
| G/day of *O. sigma* | 1 | $.126 \times 10^{13}$ | $-.195 \times 10^{5}$ |
| P/day of *O. sigma* | 1 | $.936 \times 10^{12}$ | $.169 \times 10^{4}$ |
| Density-*O. sigma* | 1 | $.334 \times 10^{15}$* | $.118 \times 10^{5}$ |
| " -*B. bicaudatus* | 1 | $.725 \times 10^{13}$ | $.287 \times 10^{4}$ |
| " -*Ephemerella* sp. | 1 | $.300 \times 10^{12}$ | $.366 \times 10^{3}$ |
| " -*Ephemerella doddsi* | 1 | $.318 \times 10^{12}$ | $-.291 \times 10^{4}$ |
| " -*Cinygmula* | 1 | $.846 \times 10^{11}$ | $-.241 \times 10^{3}$ |
| " -*Glossosoma* | 1 | $.181 \times 10^{14}$* | $-.958 \times 10^{4}$ |
| " -*Rhyacophila* | 1 | $.295 \times 10^{13}$ | $.182 \times 10^{5}$ |
| " -Chironomidae | 1 | $.623 \times 10^{12}$ | $-.609 \times 10^{3}$ |
| Model | 17 | $.838 \times 10^{14}$ | |
| Error | 326 | $.236 \times 10^{13}$ | $R^2 = .65$ |

*Significant at the .05 level.

Table 16. Abbreviated regression analysis of factors affecting drift-biomass of *O. sigma*, night samples, Temple Fork, 1968-1969

| Source | Degrees freedom | Mean square | Coefficient |
|---|---|---|---|
| Total | 336 | $.225 \times 10^{11}$ | $.380 \times 10^{5}$ |
| Distance below source | 1 | $.178 \times 10^{11}$ | $-.201 \times 10^{4}$ |
| Flow | 1 | $.601 \times 10^{10}$ | $.643 \times 10^{3}$ |
| Maximum temperature | 1 | $.648 \times 10^{10}$ | $.111 \times 10^{4}$ |
| Minimum temperature | 1 | $.877 \times 10^{10}$ | $-.196 \times 10^{4}$ |
| Mean temperature | 1 | $.150 \times 10^{10}$ | $-.104 \times 10^{4}$ |
| Radiation | 1 | $.708 \times 10^{7}$ | $.164 \times 10^{1}$ |
| Length of period | 1 | $.346 \times 10^{10}$ | $.695 \times 10^{3}$ |
| G/day of *O. sigma* | 1 | $.366 \times 10^{9}$ | $.327 \times 10^{3}$ |
| P/day of *O. sigma* | 1 | $.300 \times 10^{10}$ | $.949 \times 10^{2}$ |
| Density-*O. sigma* | 1 | $.878 \times 10^{12}$* | $.610 \times 10^{3}$ |
| " -*B. bicaudatus* | 1 | $.137 \times 10^{10}$ | $-.400 \times 10^{2}$ |
| " -*Ephemerella* sp. | 1 | $.145 \times 10^{11}$ | $.817 \times 10^{2}$ |
| " -*Ephemerella doddsi* | 1 | $.157 \times 10^{11}$ | $-.663 \times 10^{3}$ |
| " -*Cinygmula* | 1 | $.757 \times 10^{9}$ | $-.240 \times 10^{2}$ |
| " -*Glossosoma* | 1 | $.460 \times 10^{11}$* | $.492 \times 10^{3}$ |
| " -*Rhyacophila* | 1 | $.167 \times 10^{11}$ | $-.135 \times 10^{4}$ |
| " -Chironomidae | 1 | $.356 \times 10^{10}$ | $.461 \times 10^{2}$ |
| Model | 17 | $.275 \times 10^{12}$ | |
| Error | 319 | $.903 \times 10^{10}$ | $R^2 = .62$ |

*Significant at the .05 level.

each station. When every independent variable was eliminated from the analyses except density of *O. sigma*, the $R^2$ values were only reduced from .65 to .60 for the day analysis and from .62 to .59 in the night analysis (Table 13). The other 16 independent variables had so little effect on the $R^2$ values that their 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 .02 and .01 in the $R^2$ values (Table 13).

The $R^2$ values for the analyses of number of *O. sigma* larvae drifting past the three stations (dependent variable no. 20) were only reduced from .71 to .66 for the day samples and from .70 to .67 for the night samples after the elimination of all independent variables except density of *O. sigma*.

## *Baetis bicaudatus*

Twelve of the 17 independent variables had significant (at the .05 level) mean squares in the analysis of biomass of *B. bicaudatus* drifting during the day (Table 17). In order of decreasing size of mean square, they were: flow, 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 percent of the variability in drift of *B. bicaudatus* during the day was accounted for by the 17 independent variables.

Table 17. Abbreviated regression analysis of factors affecting drift-biomass of *B. bicaudatus*, day samples, Temple Fork, 1968-1969

| Source | Degrees freedom | Mean square | Coefficient |
|---|---|---|---|
| Total | 343 | $.740 \times 10^{11}$ | $-.171 \times 10^{6}$ |
| Distance below source | 1 | $.147 \times 10^{12}$* | $-.578 \times 10^{4}$ |
| Flow | 1 | $.258 \times 10^{13}$* | $.129 \times 10^{5}$ |
| Maximum temperature | 1 | $.110 \times 10^{12}$ | $.518 \times 10^{4}$ |
| Minimum temperature | 1 | $.149 \times 10^{11}$ | $-.235 \times 10^{4}$ |
| Mean temperature | 1 | $.831 \times 10^{10}$ | $-.274 \times 10^{4}$ |
| Radiation | 1 | $.214 \times 10^{12}$* | $-.252 \times 10^{3}$ |
| Length of period | 1 | $.668 \times 10^{10}$ | $.968 \times 10^{3}$ |
| G/day of *O. sigma* | 1 | $.145 \times 10^{12}$* | $-.660 \times 10^{4}$ |
| P/day of *O. sigma* | 1 | $.230 \times 10^{12}$* | $.840 \times 10^{3}$ |
| Density-*O. sigma* | 1 | $.618 \times 10^{12}$* | $-.507 \times 10^{3}$ |
| " -*B. bicaudatus* | 1 | $.107 \times 10^{13}$* | $.110 \times 10^{4}$ |
| " -*Ephemerella* sp. | 1 | $.218 \times 10^{12}$* | $-.312 \times 10^{3}$ |
| " -*Ephemerella doddsi* | 1 | $.395 \times 10^{12}$* | $.324 \times 10^{4}$ |
| " -*Cinygmula* | 1 | $.365 \times 10^{12}$* | $-.501 \times 10^{3}$ |
| " -*Glossosoma* | 1 | $.585 \times 10^{11}$ | $-.544 \times 10^{3}$ |
| " -*Rhyacophila* | 1 | $.154 \times 10^{12}$* | $.415 \times 10^{4}$ |
| " -Chironomidae | 1 | $.324 \times 10^{12}$* | $-.439 \times 10^{3}$ |
| Model | 17 | $.817 \times 10^{12}$ | |
| Error | 326 | $.352 \times 10^{11}$ | $R^2 = .55$ |

*Significant at the .05 level.

Five variables had significant mean squares in the analysis of biomass of *B. bicaudatus* drifting during the night: flow, length of period, density of *Rhyacophila*, mean temperature, and G/day of *O. sigma*. The $R^2$ value indicated that 55 percent of the variability in drift of *B. bicaudatus* biomass during the night was accounted for by the 17 independent variables (Table 18).

The order of rejection of independent variables in the step-wise regression analysis of *B. bicaudatus* biomass is given in Table 14. 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 no. 19 (biomass of *B. bicaudatus* drifting during the day) was only reduced from .55 to .48 with density of *O. sigma*, density of *B. bicaudatus*, and flow remaining in the analysis. With only density of *B. bicaudatus* remaining, the $R^2$ fell to .31 (Table 14).

Table 18. Abbreviated analysis of factors affecting drift-biomass of *B. bicaudatus*, night samples, Temple Fork, 1968-1969

| Source | Degrees freedom | Mean square | Coefficient |
|---|---|---|---|
| Total | 336 | .120 X $10^{12}$ | -.977 X $10^{6}$ |
| Distance below source | 1 | .441 X $10^{11}$ | .316 X $10^{4}$ |
| Flow | 1 | .248 X $10^{13}$* | .131 X $10^{5}$ |
| Maximum temperature | 1 | .136 X $10^{12}$ | .506 X $10^{4}$ |
| Minimum temperature | 1 | .209 X $10^{10}$ | -.957 X $10^{3}$ |
| Mean temperature | 1 | .305 X $10^{12}$* | -.148 X $10^{5}$ |
| Radiation | 1 | .410 X $10^{11}$ | .125 X $10^{3}$ |
| Length of period | 1 | .104 X $10^{13}$* | .120 X $10^{5}$ |
| G/day of *O. sigma* | 1 | .261 X $10^{12}$* | .873 X $10^{4}$ |
| P/day of *O. sigma* | 1 | .640 X $10^{11}$ | -.438 X $10^{3}$ |
| Density-*O. sigma* | 1 | .188 X $10^{12}$ | -.282 X $10^{3}$ |
| " -*B. bicaudatus* | 1 | .109 X $10^{12}$ | .356 X $10^{3}$ |
| " -*Ephemerella* sp. | 1 | .588 X $10^{11}$ | .164 X $10^{3}$ |
| " -*Ephemerella doddsi* | 1 | .367 X $10^{10}$ | .320 X $10^{3}$ |
| " -*Cinygmula* | 1 | .196 X $10^{11}$ | .122 X $10^{3}$ |
| " -*Glossosoma* | 1 | .863 X $10^{11}$ | .673 X $10^{3}$ |
| " -*Rhyacophila* | 1 | .437 X $10^{12}$* | .688 X $10^{4}$ |
| " -Chironomidae | 1 | .642 X $10^{11}$ | .196 X $10^{3}$ |
| Model | 17 | .129 X $10^{13}$ | |
| Error | 319 | .572 X $10^{11}$ | $R^2$ = .55 |

*Significant at the .05 level.

The $R^2$ values in the step-wise regression analysis of biomass of *B. bicaudatus* drifting during the night were reduced from .55 to .19 with flow, and densities of *O. sigma* and *Rhyacophila* remaining in the analysis (Table 14). With only the density of *Rhyacophila* remaining, the $R^2$ value fell to .11. The density of *B. bicaudatus* was the ninth variable to be eliminated in the step-wise process.

## UPSTREAM FLIGHT AND OVIPOSITION OF *O. SIGMA*

Waters (1968) observed the upstream flight of *O. sigma* adults over Temple Fork in August, 1966. In 1968, adult *O. sigma* were observed over the stream between August 3 and November 8. In 1969, adults were seen between July 25 and October 28. The largest swarms of adults were seen in late August and early September of both years.

Adult *O. sigma* rested quietly on streamside vegetation during most of the night, morning, and early afternoon hours. At approximately 2-4 hours before sunset the adults 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 tree top to another. Mating was frequently observed in the midst of this swarming behavior.

### Upstream Flight

In the early evening hours (30-120 minutes before sunset) groups of adults would begin to leave the mating swarm and fly in an upstream direction. A given bush or shrub was usually vacated entirely within 60 seconds, and the flight of the first few adults seemed to trigger the flight of those remaining. This evening flight usually lasted 20-50 minutes ending near 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 altitudes of 1-4 m, but a few flew as high as 10-12 m. At times the flight would leave the stream to detour around a patch of dense shrubbery, and at times, the flight would temporarily fly along above the dirt road which paralleled the stream.

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

The life span of *O. sigma* adults is probably five days. It is not known if each individual participates in the flight each evening of its life, or even if it flies for the entire period each evening. The above observations seem to indicate that the average adult flies upstream a distance of 0.3-6.0 km, with the most likely distance being 2-3 km.

Observations on the adult flight were made each evening during August and September in both years. Early in the investigation it became apparent that air temperature had an important influence on the initiation and cessation of the evening flight. 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. The time of flight appeared to be legislated to the period of 2.5-3.0 hours before sunset and one-half hour after sunset. Within this period the flight appeared to be governed by the upper and lower air temperature thresholds. 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 one-half hour of darkness. However, on most evenings, at the altitude of Temple Fork, the air temperature fell rather swiftly and steadily, and the governed flight period lasted only 30-50 minutes.

On several occasions, winds of more than 2-3 km/hour from an upstream direction, or greater than 4-5 km/hour 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 left the mouth of 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 instead of northwest (Figure 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 minutes before sunset, while the area between stations I and II was heavily shaded, both by the ridge to the southwest and by the dense growth of vegetation within the canyon, from 2.5 hours to 3.5 hours 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 important, though imperfect, barrier to upstream flight at the mouth of the canyon immediately above station II.

## Sex Ratio

Random samples of adults (348 total) were selected and sexed from catches made by the water wheels at the three upper stations and from collections of adults swept from shore vegetation or from the evening upstream flight with an aerial net. These collections were made in August and September of both years.

Collections from streamside vegetation contained 5.5 males per female (Table 19). The ovaries of 61 percent of the females swept from streamside vegetation were in an immature condition (the remaining 39 percent being 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 these females were all mature (Table 19).

Table 19. Sex ratios of *O. sigma* adults from water wheels, shore vegetation, and upstream migration flight, Temple Fork, 1968-1969

| Type of collection | Males | Females | Ratio |
|---|---|---|---|
| Water wheel | 107 | 99[a] | 1.1:1 |
| From streamside vegetation | 238 | 43[b] | 5.5:1 |
| Flying upstream | 18 | 43[c] | 0.4:1 |

[a] Condition of ovaries: 26 percent immature, 40 percent mature, 34 percent spent.

[b] Condition of ovaries: 61 percent immature, 39 percent mature.

[c] Condition of ovaries: 100 percent mature.

Collections of adults captured in the water wheels contained 1.1 males for every female. Of the females from the water wheel samples, 26 percent had ovaries in an immature condition, 40 percent had mature ovaries, and 34 percent had spent ovaries.

Apparently the initial *O. sigma* adult population had a male to female ratio of 5.5:1 (although it is possible that behavioral differences between the sexes may have made males more vulnerable to the aerial 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 small--61 individuals). The water wheel catches were apparently made up of emerging adults and pupae, mature adults returning to the stream to drink or oviposit, and dying, post-oviposition females.

## Oviposition

In the fall of 1968, two bilateral traps similar to that described by Gressitt and Gressitt (1962) were used to capture *O. sigma* adults flying upstream. Adults were rarely captured in the traps because they almost invariably detected the traps at a distance of 1-2 m and either flew around or over the traps. Therefore, the bilateral traps were abandoned and oviposition boards were installed in the stream in June, 1969. Boards 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 deposited their egg masses 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 and not scattered about over the entire available surface.

Six egg masses were deposited on the board at station I (Table 20). The board at station II received the greatest number of egg masses deposited (6,103). The numbers of egg masses deposited at stations III and IV (524 and 330, respectively) were less than one-tenth that at station II but were much higher than that at station I (Table 20). The maximum number of masses deposited on a 19 cm X 4 cm area within a 24-hour period was 239 at station II on August 25-26, 1969.

Table 20. Egg masses of *O. sigma* on oviposition boards placed in stream at stations I-IV, Temple Fork, 1969--expressed as total number per month, on 19 cm X 4 cm area

| Month | Station | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| June | 0 | 0 | 0 | 0 |
| July | 0 | 6 | 0 | 0 |
| August | 1 | 2,747 | 366 | 120 |
| September | 5 | 3,311 | 150 | 204 |
| October | 0 | 39 | 8 | 6 |
| Total | 6 | 6,103 | 524 | 330 |

# DISCUSSION

Drift has been associated with production in excess of the carrying capacity of the streambed (Waters, 1966), illumination (Waters, 1962a; 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/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 one to several short-lived summer generations. Many of these insects (including *O. sigma* and *B. bicaudatus*) have major emergences in the fall months and over winter 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). Obviously, many factors in the environment and many population parameters are correlated with the change in season from winter through spring to summer. Water temperature, flow, growth rates, production rates, day-length, primary production rates, age-associated changes in behavioral patterns, mortality rates, metabolic rates, and a host of others may increase with the onset of spring and summer, and so do drift rates. The assignation of a cause-and-effect 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 percent of the total numbers and biomass of *O. sigma* larvae drifting past each station did so in May, June, and July of each year. 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 a single year density did not appear to correlate positively with drift.

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 (the simple, one-to-one correlation coefficients for the day and night analyses were .78 and .77, respectively; but of even more importance, the $R^2$ values from the multiple regression analyses indicated that 60 percent and 59 percent of the total variability in biomass drifting during the day and night, respectively, was accounted for by density (number) alone). It would also seem reasonable to assume that given a sufficient number of years of data, one would be able to show a positive correlation between annual mean 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 (as 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 (correlation coefficients for day and night analyses of drift and density were .55 and .43), but they were positive and significant at the .05 level.

The regression analyses indicated that 31 percent of the variability in day drift of *B. bicaudatus* was accounted for by density of *B. bicaudatus* alone. *Baetis bicaudatus* density was rejected early in the step-wise process during the analysis of night drift. This is difficult to understand, but perhaps there was a significant interaction 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-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 states 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 presented is 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 is provided at densities between 0 and 400-500 insects/0.9 $m^2$. The data presented merely show the variability in drift which one encounters at densities of 400-500 insects/0.9 $m^2$.

The production of *B. bicaudatus* nymphs showed less among station variability than did production of *O. sigma* larvae. Annual production of *B. bicaudatus* nymphs was about the same (range: 176.2 - 213.1 mg/0.1 $m^2$) at stations I and III in both years. Production was less at stations I and IV (range: 117 - 64 mg/0.1 $m^2$). 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. While the production calculated by Allen's (1951) method was only 194.6 mg/0.1 $m^2$ for the area above station I, the total drift from the area was estimated at 435.1 mg/0.1 $m^2$. 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. Other key factors which seemed to influence drift rates of *O. sigma* or *B. bicaudatus* were: flow, distance below the source, density of *Glossosoma*, and density of *Rhyacophila*.

Flow 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 flow would increase the number of organisms being swept away (constant and catastrophic drift). The spring increase in flow 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.) correlate with distance below the source and it is difficult to explain this contribution. The density 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 (150 m 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. Drift of *O. sigma* larvae at station I was higher during daylight hours. This 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 other 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 $m^2$). The density of pupae at stations I and IV was lower (7 and 13/0.1 $m^2$). 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. The 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 no. 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 -20 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 the flooding, reduced 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 only because the larvae over-winter 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.

# CONCLUSIONS

Downstream drift of immatures was an important factor in the population dynamics of *O. sigma*, and to a lesser extent, in the population dynamics of *B. bicaudatus*. Drift removal was low in areas where population density was low. Drift removals from areas of high population density were high and increased the density in areas downstream. The presence of small pupae (of *O. sigma*) at stations where densities were high indicates that intraspecific competition existed and supports the hypothesis that high drift rates are in part the result of overcrowding.

Both drift and production were highest at station III in 1968 and lowest at station I in 1968. Drift may be related to production in "excess" of the carrying capacity of the streambed, but this hypothesis could not be tested directly because of the difficulties in determining what portion of the total annual production should be considered as "excess."

Density (as either biomass or numbers/area) did not appear to be directly related to drift rates when considered over an entire year, but density was the single most important factor contributing to the variability of day and night drift of *O. sigma* larvae during the months of June-September. Density (as numbers) was also the single most important contributor to variability in day drift of *B. bicaudatus* nymphs. Flow, distance below the spring source of Temple Fork, and density of *Glossosoma* larvae were other factors of significance in the regression analyses of drifting *O. sigma* larvae. Flow, distance below the source, and density of *Rhyacophila* larvae were among the significant variables in the regression analyses of drifting *B. bicaudatus* nymphs.

The upstream flight of *O. sigma* adults appeared to be important in determining the distribution of eggs in the stream. The flight of adults was governed by time of day and air temperature. Females probably flew 2-3 km upstream before depositing their eggs. The evolutionary advantage of the upstream flight may be that it concentrates reproductive products in upstream areas where they are relatively safe from the effects of anchor-ice in winter and floods in late winter and early spring.

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# APPENDIX

Table 21. Abundance of benthic invertebrates at station I, Temple Fork, 1967-1968--expressed as mean number per 0.1 $m^2$

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 25 | Sept. 22 |
| Tricladida | 0 | 29 | 88 | 13 | 1 | 22 | 10 | 10 | 55 | 28 | 1 | 8 | 69 |
| Oligochaeta | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Hydracarina | 0 | 0 | 10 | 0 | 0 | 20 | 1 | 1 | 5 | 0 | 1 | 0 | 3 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 48 | 58 | 134 | 44 | 16 | 76 | 72 | 25 | 130 | 48 | 88 | 34 | 81 |
| *Capnia* | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachyptera* | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arcynopteryx* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Alloperla* | 8 | 45 | 43 | 13 | 11 | 20 | 63 | 1 | 18 | 20 | 29 | 12 | 79 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 29 | 83 | 99 | 153 | 156 | 21 | 91 | 16 | 4 | 3 | 46 | 31 | 360 |
| *Cinygmula* | 17 | 133 | 114 | 33 | 54 | 267 | 239 | 53 | 80 | 46 | 319 | 53 | 74 |
| *Baetis bicaudatus* | 6 | 47 | 212 | 117 | 82 | 572 | 154 | 141 | 1,117 | 320 | 101 | 74 | 32 |
| *Baetis* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Ephemerella doddsi* | 11 | 6 | 26 | 32 | 27 | 17 | 20 | 17 | 7 | 0 | 2 | 54 | 113 |
| *Ephemerella* sp. | 35 | 100 | 169 | 57 | 113 | 302 | 205 | 33 | 55 | 25 | 53 | 46 | 454 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 11 | 2 | 33 | 6 | 11 | 20 | 20 | 13 | 54 | 18 | 12 | 6 | 14 |
| *Glossosoma* larvae | 0 | 0 | 1 | 2 | 0 | 1 | 3 | 4 | 6 | 0 | 5 | 9 | 3 |
| *Glossosoma* pupae | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Parapsyche* | 1 | 10 | 56 | 23 | 5 | 6 | 15 | 6 | 11 | 2 | 15 | 3 | 4 |
| *Oligophlebodes sigma* | 0 | 117 | 292 | 163 | 179 | 117 | 165 | 60 | 49 | 8 | 3 | 2 | 0 |
| *O. sigma* pupae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 11 | 29 | 0 |
| *Micrasema* | 0 | 1 | 5 | 9 | 0 | 20 | 11 | 0 | 0 | 0 | 0 | 2 | 1 |
| *Brachycentrus* | 2 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 3 | 0 | 0 | 0 | 0 |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 |

Table 21. Continued

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 25 | Sept. 22 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 2 | 0 | 0 |
| Simuliidae | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| Chironomidae | 83 | 136 | 165 | 46 | 11 | 124 | 63 | 82 | 199 | 589 | 15 | 33 | 377 |
| Rhagionidae | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 1 | 1 | 8 |
| pupae (unidentified) | 4 | 0 | 3 | 1 | 0 | 1 | 0 | 1 | 11 | 11 | 1 | 2 | 42 |
| Total | 258 | 768 | 1,452 | 717 | 678 | 1,610 | 1,141 | 464 | 1,812 | 1,123 | 705 | 399 | 1,718 |

Table 22. Abundance of benthic invertebrates at station II, Temple Fork, 1967-1968--expressed as mean number per 0.1 m$^2$

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 25 | Sept. 22 |
| Tricladida | 1 | 146 | 83 | 31 | 71 | 38 | 34 | 77 | 63 | 55 | 32 | 85 | -- |
| Oligochaeta | 1 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| Hydracarina | 5 | 4 | 14 | 9 | 5 | 9 | 0 | 2 | 0 | 0 | 0 | 0 | -- |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 14 | 85 | 39 | 5 | 32 | 30 | 5 | 27 | 16 | 20 | 5 | 34 | -- |
| *Capnia* | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| *Brachyptera* | 0 | 0 | 0 | 1 | 3 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | -- |
| *Alloperla* | 35 | 52 | 56 | 28 | 36 | 17 | 12 | 39 | 28 | 7 | 27 | 46 | -- |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 18 | 65 | 99 | 267 | 55 | 26 | 80 | 38 | 26 | 7 | 47 | 33 | -- |
| *Cinygmula* | 131 | 332 | 704 | 70 | 366 | 172 | 169 | 264 | 298 | 180 | 173 | 117 | -- |
| *Baetis bicaudatus* | 114 | 70 | 74 | 34 | 73 | 108 | 132 | 155 | 52 | 94 | 157 | 218 | -- |
| *Ephemerella doddsi* | 38 | 53 | 58 | 34 | 35 | 10 | 30 | 9 | 1 | 0 | 0 | 169 | -- |
| *Ephemerella* sp. | 318 | 414 | 1,255 | 410 | 325 | 162 | 70 | 114 | 45 | 18 | 111 | 1,555 | -- |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 11 | 17 | 32 | 11 | 26 | 20 | 17 | 25 | 38 | 4 | 26 | 19 | -- |
| *Glossosoma* larvae | 12 | 12 | 13 | 26 | 7 | 9 | 4 | 5 | 61 | 61 | 194 | 90 | -- |
| *Glossosoma* pupae | 3 | 3 | 0 | 17 | 6 | 4 | 0 | 2 | 0 | 6 | 13 | 0 | -- |
| *Parapsyche* | 4 | 32 | 11 | 3 | 43 | 15 | 14 | 11 | 6 | 15 | 2 | 5 | -- |
| *Dolophilodes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | -- |
| *Oligophlebodes sigma* | 0 | 452 | 1,123 | 788 | 1,074 | 1,131 | 791 | 928 | 726 | 404 | 88 | 18 | 1 |
| *O. sigma* pupae | 11 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 33 | 116 | -- |
| *Lepidostroma* larvae | 1 | 27 | 0 | 3 | 11 | 6 | 4 | 12 | 2 | 5 | 0 | 24 | -- |
| *Lepidostoma* pupae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| *Micrasema* | 0 | 0 | 3 | 1 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| *Brachycentrus* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 2 | 9 | 12 | 1 | 1 | 0 | 0 | 0 | -- |

Table 22. Continued

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 25 | Sept. 22 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 28 | 14 | 51 | 19 | 8 | 0 | 1 | 4 | 18 | 2 | 16 | 28 | -- |
| Elmidae adult | 1 | 1 | 3 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | -- |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 1 | 0 | 6 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 6 | 0 | -- |
| Psychodidae | 19 | 4 | 14 | 2 | 8 | 4 | 3 | 3 | 4 | 0 | 0 | 0 | -- |
| Simuliidae | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| Chironomidae | 82 | 392 | 137 | 11 | 32 | 86 | 18 | 61 | 47 | 25 | 21 | 102 | -- |
| Stratiomyiidae | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | -- |
| Rhagionidae | 9 | 3 | 10 | 5 | 1 | 0 | 1 | 5 | 5 | 0 | 1 | 0 | -- |
| pupae (unidentified) | 0 | 34 | 17 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | -- |
| Total | 858 | 2,224 | 3,803 | 1,792 | 2,224 | 1,863 | 1,402 | 1,791 | 1,440 | 904 | 954 | 2,660 | 1 |

Table 23. Abundance of benthic invertebrates at station III, Temple Fork, 1967-1968--expressed as mean number per 0.1 $m^2$

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 28 | Sept. 22 |
| Tricladida | 0 | 83 | 102 | 112 | 101 | 54 | 77 | 144 | 215 | 38 | 154 | 55 | 114 |
| Oligochaeta | 3 | 3 | 4 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| Hydracarina | 2 | 4 | 2 | 4 | 6 | 1 | 2 | 1 | 1 | 4 | 4 | 2 | 2 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 32 | 134 | 201 | 48 | 75 | 26 | 32 | 53 | 80 | 14 | 0 | 5 | 8 |
| *Capnia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 0 | 0 |
| *Brachyptera* | 0 | 0 | 10 | 0 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| *Isoperla* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arcynopteryx* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Alloperla* | 3 | 29 | 21 | 5 | 27 | 12 | 16 | 3 | 1 | 1 | 0 | 15 | 11 |
| *Acroneuria* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 14 | 38 | 38 | 37 | 45 | 62 | 58 | 4 | 7 | 4 | 0 | 10 | 60 |
| *Cinygmula* | 30 | 128 | 98 | 101 | 245 | 168 | 159 | 66 | 111 | 48 | 153 | 47 | 2 |
| *Baetis bicaudatus* | 60 | 273 | 364 | 809 | 232 | 324 | 228 | 102 | 113 | 19 | 225 | 165 | 124 |
| *Baetis* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Ephemerella doddsi* | 3 | 14 | 7 | 7 | 30 | 30 | 16 | 11 | 10 | 1 | 1 | 12 | 46 |
| *Ephemerella* sp. | 190 | 724 | 653 | 699 | 771 | 691 | 549 | 259 | 158 | 35 | 63 | 142 | 337 |
| *Paraleptophlebia* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 6 | 32 | 37 | 35 | 31 | 48 | 48 | 39 | 43 | 18 | 62 | 54 | 46 |
| *Glossosoma* larvae | 14 | 6 | 12 | 27 | 12 | 10 | 7 | 17 | 17 | 71 | 240 | 262 | 108 |
| *Glossosoma* pupae | 4 | 4 | 1 | 6 | 12 | 4 | 0 | 9 | 0 | 0 | 1 | 0 | 0 |
| *Parapsyche* | 14 | 28 | 35 | 44 | 30 | 20 | 61 | 66 | 24 | 4 | 13 | 18 | 28 |
| *Oligophlebodes sigma* | 58 | 981 | 556 | 661 | 928 | 587 | 733 | 616 | 884 | 590 | 467 | 61 | 14 |
| *O. sigma* pupae | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 46 | 87 | 36 |
| *Micrasema* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 23. Continued

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 28 | Sept. 22 |
| *Brachycentrus* | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 5 | 0 | 0 | 2 | 0 | 0 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 11 | 18 | 12 | 1 | 11 | 0 | 1 | 1 | 30 | 5 | 24 | 18 | 20 |
| Elmidae adult | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 3 | 8 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 2 | 7 | 6 | 7 | 8 | 5 | 3 | 10 | 46 | 8 | 0 | 5 | 3 |
| Psychodidae | 41 | 47 | 28 | 42 | 33 | 6 | 9 | 5 | 41 | 0 | 0 | 3 | 17 |
| Simuliidae | 0 | 16 | 22 | 4 | 1 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Chironomidae | 85 | 188 | 169 | 159 | 74 | 74 | 37 | 2 | 14 | 3 | 42 | 52 | 51 |
| Ceratopogonidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Stratiomyiidae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rhagionidae | 4 | 1 | 5 | 4 | 4 | 4 | 2 | 1 | 14 | 5 | 0 | 9 | 13 |
| pupae (unidentified) | 6 | 12 | 14 | 15 | 3 | 7 | 9 | 5 | 0 | 1 | 7 | 31 | 9 |
| Total | 583 | 2,772 | 2,398 | 2,828 | 2,686 | 2,148 | 2,054 | 1,424 | 1,813 | 870 | 1,536 | 1,056 | 1,067 |

Table 24. Abundance of benthic invertebrates at station IV, Temple Fork, 1967-1968--expressed as mean number per 0.1 m$^2$

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 25 | Sept. 22 |
| Tricladida | 0 | 42 | 65 | 49 | 73 | 27 | 68 | 68 | 20 | 19 | 69 | 63 | 150 |
| Oligochaeta | 2 | 1 | 0 | 1 | 1 | 1 | 6 | 4 | 0 | 0 | 0 | 1 | 5 |
| Hydracarina | 0 | 2 | 2 | 3 | 0 | 0 | 1 | 4 | 0 | 0 | 1 | 7 | 6 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 0 | 10 | 13 | 7 | 3 | 2 | 3 | 4 | 0 | 0 | 0 | 0 | 28 |
| *Capnia* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachyptera* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 |
| *Arcynopteryx* | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Alloperla* | 7 | 0 | 19 | 1 | 3 | 7 | 0 | 0 | 0 | 3 | 6 | 1 | 16 |
| *Acroneuria* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 97 | 87 | 125 | 87 | 55 | 48 | 9 | 13 | 28 | 21 | 0 | 5 | 124 |
| *Cinygmula* | 7 | 6 | 61 | 10 | 18 | 4 | 13 | 31 | 33 | 60 | 34 | 42 | 29 |
| *Baetis bicaudatus* | 6 | 31 | 127 | 193 | 134 | 88 | 227 | 181 | 70 | 43 | 4 | 14 | 20 |
| *Ephemerella doddsi* | 2 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 30 | 20 |
| *Ephemerella* sp. | 102 | 230 | 536 | 239 | 294 | 154 | 238 | 259 | 75 | 34 | 39 | 87 | 664 |
| *Paraleptophlebia* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 5 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 11 | 11 | 7 | 12 | 7 | 12 | 31 | 18 | 6 | 7 | 19 | 24 | 22 |
| *Glossosoma* larvae | 95 | 110 | 240 | 102 | 317 | 92 | 68 | 239 | 174 | 56 | 219 | 249 | 520 |
| *Glossosoma* pupae | 42 | 5 | 4 | 5 | 9 | 0 | 21 | 3 | 4 | 12 | 35 | 16 | 4 |
| *Sortosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Parapsyche* | 0 | 6 | 3 | 4 | 1 | 6 | 10 | 4 | 0 | 0 | 6 | 0 | 1 |
| *Oligophlebodes sigma* | 9 | 55 | 119 | 379 | 71 | 132 | 190 | 255 | 241 | 91 | 152 | 5 | 5 |
| *Oligophlebodes* pupae | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 137 | 66 | 4 |
| *Lepidostoma* larvae | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

Table 24. Continued

| | 1967 | | | | 1968 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 1 | Nov. 4 | Dec. 2 | Dec. 30 | Jan. 27 | Feb. 23 | Mar. 23 | Apr. 20 | May 18 | June 30 | July 28 | Aug. 25 | Sept. 22 |
| *Micrasema* | 0 | 0 | 0 | 2 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachycentrus* | 0 | 0 | 10 | 2 | 0 | 0 | 1 | 4 | 0 | 2 | 13 | 1 | 8 |
| *Oligophlebodes minutus* | 0 | 11 | 8 | 8 | 3 | 9 | 10 | 5 | 3 | 1 | 0 | 2 | 1 |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 1 | 5 | 6 | 0 | 0 | 0 | 16 | 1 | 0 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 10 | 18 | 26 | 29 | 43 | 6 | 21 | 34 | 23 | 13 | 46 | 38 | 60 |
| Elmidae adult | 3 | 5 | 5 | 4 | 0 | 1 | 5 | 2 | 4 | 0 | 1 | 20 | 21 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 25 | 19 | 17 | 35 | 5 | 13 | 45 | 18 | 32 | 1 | 5 | 19 | 16 |
| Psychodidae | 9 | 18 | 60 | 55 | 53 | 0 | 48 | 31 | 5 | 0 | 0 | 1 | 44 |
| Simuliidae | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Chironomidae | 44 | 44 | 59 | 42 | 13 | 10 | 17 | 32 | 9 | 4 | 115 | 66 | 114 |
| Ceratopogonidae | 0 | 0 | 0 | 0 | 1 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Stratiomyiidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Rhagionidae | 2 | 2 | 3 | 6 | 2 | 0 | 2 | 7 | 2 | 0 | 1 | 2 | 0 |
| pupae (unidentified) | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 0 | 0 | 1 | 18 | 13 |
| Total | 475 | 727 | 1,513 | 1,277 | 1,109 | 637 | 1,055 | 1,222 | 731 | 368 | 920 | 783 | 1,909 |

Table 25. Abundance of benthic invertebrates at station I, Temple Fork, 1968-1969--expressed as mean number per 0.1 $m^2$

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 20 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| Tricladida | 22 | 20 | 4 | 19 | 24 | 25 | 20 | 17 | 73 | 49 | 8 | 65 | 16 |
| Oligochaeta | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 |
| Hydracarina | 5 | 10 | 0 | 2 | 4 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 22 | 82 | 19 | 47 | 84 | 43 | 79 | 17 | 96 | 102 | 58 | 136 | 122 |
| *Capnia* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Brachyptera* | 0 | 3 | 1 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arcynopteryx* | 9 | 8 | 4 | 0 | 2 | 2 | 5 | 12 | 0 | 0 | 0 | 5 | 4 |
| *Alloperla* | 43 | 67 | 113 | 19 | 24 | 24 | 38 | 32 | 61 | 40 | 9 | 32 | 19 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 127 | 438 | 636 | 444 | 381 | 194 | 510 | 298 | 403 | 2 | 8 | 11 | 11 |
| *Cinygmula* | 32 | 49 | 0 | 12 | 9 | 0 | 6 | 0 | 0 | 343 | 232 | 178 | 20 |
| *Baetis bicaudatus* | 5 | 178 | 91 | 250 | 324 | 346 | 168 | 117 | 332 | 362 | 113 | 126 | 60 |
| *Baetis* sp. | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Ephemerella doddsi* | 51 | 144 | 41 | 174 | 84 | 22 | 19 | 38 | 2 | 3 | 4 | 12 | 28 |
| *Ephemerella* sp. | 492 | 545 | 145 | 438 | 159 | 125 | 161 | 39 | 75 | 72 | 23 | 34 | 67 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 6 | 17 | 6 | 16 | 16 | 14 | 22 | 16 | 29 | 25 | 10 | 18 | 17 |
| *Glossosoma* larvae | 2 | 2 | 1 | 14 | 4 | 4 | 5 | 0 | 32 | 2 | 9 | 3 | 2 |
| *Glossosoma* pupae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| *Parapsyche* | 1 | 19 | 0 | 18 | 18 | 13 | 5 | 0 | 29 | 36 | 6 | 24 | 6 |
| *Oligophlebodes sigma* | 21 | 224 | 133 | 151 | 187 | 111 | 96 | 50 | 71 | 24 | 3 | 0 | 0 |
| *O. sigma* pupae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 13 | 9 |
| *Micrasema* | 32 | 22 | 6 | 5 | 23 | 14 | 1 | 0 | 4 | 1 | 0 | 2 | 0 |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |

Table 25. Continued

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 20 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 92 | 253 | 108 | 46 | 44 | 100 | 48 | 45 | 124 | 278 | 23 | 50 | 150 |
| Rhagionidae | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1 |
| Psychodidae | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| pupae (unidentified) | 22 | 10 | 2 | 2 | 0 | 0 | 1 | 2 | 4 | 16 | 2 | 2 | 9 |
| Pelecypoda | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 991 | 2,096 | 1,315 | 1,660 | 1,390 | 1,039 | 1,190 | 687 | 1,341 | 1,360 | 512 | 714 | 544 |

Table 26. Abundance of benthic invertebrates at station II, Temple Fork, 1968-1969--expressed as mean number per 0.1 $m^2$

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 17 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| Tricladida | 161 | 118 | 145 | 118 | 93 | 74 | 55 | 91 | 196 | 65 | 30 | 25 | 73 |
| Oligochaeta | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| Hydracarina | 8 | 9 | 1 | 2 | 10 | 1 | 1 | 2 | 3 | 0 | 0 | 0 | 0 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 82 | 37 | 22 | 37 | 13 | 5 | 5 | 15 | 28 | 10 | 4 | 8 | 6 |
| *Capnia* | 0 | 0 | 4 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 4 |
| *Brachyptera* | 1 | 4 | 4 | 5 | 1 | 1 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arcynopteryx* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Alloperla* | 64 | 48 | 52 | 22 | 30 | 62 | 10 | 15 | 15 | 17 | 5 | 3 | 41 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 562 | 1 | 377 | 298 | 332 | 339 | 124 | 157 | 184 | 10 | 0 | 10 | 75 |
| *Cinygmula* | 17 | 654 | 0 | 5 | 33 | 0 | 0 | 0 | 0 | 164 | 99 | 90 | 105 |
| *Baetis bicaudatus* | 36 | 61 | 56 | 60 | 153 | 71 | 144 | 91 | 18 | 19 | 111 | 95 | 51 |
| *Baetis* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Ephemerella doddsi* | 324 | 173 | 126 | -- | 18 | 13 | 10 | 3 | 3 | 0 | 2 | 17 | 53 |
| *Ephemerella* sp. | 1,535 | 1,662 | 1,169 | -- | 649 | 398 | 308 | 161 | 89 | 22 | 14 | 20 | 392 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 14 | 8 | 12 | 24 | 4 | 6 | 13 | 37 | 16 | 1 | 10 | 12 | 6 |
| *Glossosoma* larvae | 73 | 65 | 92 | 10 | 26 | 15 | 10 | 13 | 22 | 42 | 27 | 112 | 52 |
| *Glossosoma* pupae | 2 | 2 | 3 | 4 | 4 | 0 | 3 | 0 | 0 | 5 | 8 | 4 | 4 |
| *Parapsyche* | 81 | 8 | 18 | 35 | 4 | 4 | 12 | 36 | 27 | 1 | 15 | 4 | 0 |
| *Oligophlebodes sigma* | 102 | 201 | 253 | 563 | 505 | 480 | 359 | 586 | 322 | 174 | 109 | 3 | 0 |
| *O. sigma* pupae | 3 | 9 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 90 | 92 | 31 |
| *Lepidostoma* | 44 | 28 | 20 | 8 | 17 | 9 | 4 | 12 | 22 | 6 | 5 | 5 | 14 |
| *Micrasema* | 0 | 3 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 26. Continued

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 17 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 17 | 29 | 11 | 2 | 13 | 9 | 0 | 6 | 11 | 0 | 3 | 6 | 12 |
| Elmidae adult | 3 | 1 | 1 | 1 | 3 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Psychodidae | 17 | 17 | 27 | 0 | 12 | 5 | 2 | 9 | 2 | 0 | 0 | 0 | 1 |
| Simuliidae | 1 | 0 | 4 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 62 | 415 | 72 | 103 | 89 | 48 | 24 | 151 | 36 | 12 | 11 | 6 | 29 |
| Ceratopogonidae | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rhagionidae | 14 | 15 | 4 | 3 | 3 | 6 | 1 | 6 | 3 | 0 | 0 | 0 | 2 |
| pupae (unidentified) | 6 | 31 | 0 | 8 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 4 | 9 |
| Total | 3,230 | 3,599 | 2,490 | 1,317 | 2,018 | 1,548 | 1,097 | 1,400 | 1,000 | 553 | 543 | 523 | 961 |

Table 27. Abundance of benthic invertebrates at station III, Temple Fork, 1968-1969--expressed as mean number per 0.1 $m^2$

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 17 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| Tricladida | 86 | 248 | 132 | 79 | 98 | 177 | 57 | 113 | 24 | 60 | 109 | 96 | 60 |
| Oligochaeta | 0 | 0 | 0 | 2 | 1 | 0 | 10 | 9 | 1 | 1 | 1 | 0 | 0 |
| Hydracarina | 0 | 0 | 1 | 4 | 5 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 34 | 126 | 67 | 59 | 23 | 49 | 16 | 5 | 1 | 8 | 4 | 14 | 11 |
| *Capnia* | 0 | 0 | 3 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Brachyptera* | 3 | 8 | 5 | 1 | 6 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Isoperla* | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Alloperla* | 9 | 9 | 9 | 12 | 3 | 2 | 3 | 4 | 0 | 2 | 5 | 5 | 1 |
| *Acroneuria* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 1 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 152 | 74 | 343 | 125 | 159 | 116 | 104 | 52 | 6 | 0 | 0 | 4 | 8 |
| *Cinygmula* | 2 | 1 | 15 | 3 | 12 | 0 | 0 | 0 | 0 | 20 | 83 | 48 | 15 |
| *Baetis bicaudatus* | 57 | 186 | 157 | 130 | 434 | 318 | 100 | 17 | 4 | 1 | 71 | 60 | 56 |
| *Baetis* sp. | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ephemerella doddsi* | 25 | 47 | 24 | 5 | 18 | 51 | 6 | 5 | 1 | 5 | 0 | 2 | 12 |
| *Ephemerella* sp. | 498 | 1,059 | 997 | 1,419 | 1,090 | 823 | 530 | 535 | 57 | 121 | 133 | 86 | 351 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 26 | 65 | 25 | 16 | 24 | 52 | 9 | 15 | 1 | 16 | 20 | 13 | 27 |
| *Glossosoma* larvae | 76 | 30 | 24 | 9 | 10 | 18 | 2 | 65 | 13 | 19 | 138 | 86 | 86 |
| *Glossosoma* pupae | 11 | 6 | 0 | 1 | 5 | 10 | 1 | 14 | 0 | 4 | 3 | 6 | 22 |
| *Parapsyche* | 46 | 99 | 34 | 27 | 15 | 65 | 12 | 20 | 0 | 22 | 20 | 20 | 10 |
| *Oligophlebodes sigma* | 28 | 35 | 387 | 251 | 233 | 208 | 89 | 279 | 76 | 198 | 25 | 1 | 0 |
| *O. sigma* pupae | 5 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 10 | 254 | 22 | 2 |
| *Lepidostoma* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| pupae (unidentified) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 0 | 0 | 0 |

Table 27. Continued

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June | June | July | Aug. | Sept. |
| | 20 | 17 | 15 | 12 | 9 | 9 | 6 | 4 | 1 | 29 | 27 | 24 | 21 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 10 | 34 | 4 | 36 | 12 | 8 | 9 | 20 | 4 | 2 | 18 | 5 | 22 |
| Elmidae adult | 1 | 0 | 9 | 3 | 6 | 2 | 0 | 0 | 0 | 0 | 1 | 3 | 0 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 6 | 24 | 0 | 6 | 8 | 0 | 3 | 16 | 0 | 1 | 0 | 0 | 8 |
| Psychodidae | 10 | 42 | 2 | 51 | 3 | 16 | 41 | 13 | 0 | 0 | 0 | 3 | 10 |
| Simuliidae | 0 | 5 | 0 | 1 | 3 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 2 | 144 | 185 | 163 | 298 | 562 | 30 | 11 | 5 | 2 | 26 | 11 | 23 |
| Ceratopogonidae | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Stratiomyiidae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rhagionidae | 5 | 19 | 3 | 18 | 5 | 3 | 13 | 10 | 2 | 1 | 1 | 2 | 2 |
| pupae (unidentified) | 3 | 3 | 5 | 27 | 9 | 15 | 6 | 2 | 0 | 0 | 2 | 5 | 4 |
| Pelecypoda | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| Total | 1,096 | 2,266 | 2,431 | 2,451 | 2,487 | 2,519 | 1,046 | 1,212 | 195 | 494 | 918 | 496 | 731 |

Table 28. Abundance of benthic invertebrates at station IV, Temple Fork, 1968-1969--expressed as mean number per 0.1 $m^2$

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 17 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| Tricladida | 62 | 242 | 70 | 156 | 132 | 155 | 145 | 4 | -- | 140 | 17 | 30 | 96 |
| Oligochaeta | 1 | 10 | 3 | 2 | 2 | 9 | 16 | 0 | -- | 3 | 1 | 0 | 3 |
| Hirudinia | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | -- | 0 | 0 | 0 | 0 |
| Hydracarina | 1 | 1 | 0 | 3 | 6 | 3 | 3 | 0 | -- | 2 | 0 | 0 | 0 |
| Plecoptera | | | | | | | | | | | | | |
| *Nemoura* | 12 | 19 | 5 | 8 | 9 | 5 | 13 | 0 | -- | 1 | 0 | 5 | 2 |
| *Capnia* | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | -- | 0 | 0 | 0 | 0 |
| *Brachyptera* | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | -- | 0 | 0 | 0 | 0 |
| *Alloperla* | 8 | 9 | 3 | 16 | 2 | 4 | 0 | 0 | -- | 9 | 0 | 5 | 1 |
| *Isoperla* | 0 | 3 | 0 | 3 | 0 | 3 | 2 | 0 | -- | 0 | 0 | 0 | 0 |
| *Acroneuria* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | -- | 0 | 0 | 0 | 1 |
| Ephemeroptera | | | | | | | | | | | | | |
| *Rhithrogena* | 278 | 48 | 201 | 90 | 162 | 287 | 119 | 34 | -- | 1 | 0 | 9 | 4 |
| *Cinygmula* | 2 | 6 | 1 | 0 | 0 | 0 | 0 | 0 | -- | 85 | 33 | 44 | 15 |
| *Baetis bicaudatus* | 25 | 57 | 49 | 101 | 231 | 137 | 156 | 8 | -- | 16 | 4 | 17 | 12 |
| *Ephemerella doddsi* | 13 | 4 | 11 | 2 | 9 | 13 | 9 | 0 | -- | 1 | 0 | 2 | 0 |
| *Ephemerella* sp. | 232 | 1,003 | 555 | 801 | 791 | 920 | 777 | 40 | -- | 131 | 28 | 29 | 123 |
| *Paraleptophlebia* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | -- | 0 | 2 | 0 | 1 |
| Trichoptera | | | | | | | | | | | | | |
| *Rhyacophila* | 16 | 13 | 5 | 9 | 29 | 38 | 27 | 8 | -- | 7 | 3 | 2 | 11 |
| *Glossosoma* larvae | 316 | 464 | 306 | 290 | 525 | 605 | 316 | 54 | -- | 28 | 24 | 73 | 278 |
| *Glossosoma* pupae | 13 | 4 | 3 | 2 | 9 | 25 | 0 | 2 | -- | 1 | 5 | 0 | 5 |
| *Agraylea* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | -- | 0 | 0 | 0 | 1 |
| *Parapsyche* | 3 | 0 | 2 | 0 | 3 | 12 | 4 | 1 | -- | 0 | 0 | 0 | 0 |
| *Oligophlebodes sigma* | 45 | 199 | 142 | 640 | 240 | 124 | 490 | 162 | 91 | 176 | 96 | 1 | 0 |
| *O. sigma* pupae | 2 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | -- | 1 | 4 | 22 | 27 |

Table 28. Continued

| | 1968 | | | 1969 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Oct. 20 | Nov. 17 | Dec. 15 | Jan. 12 | Feb. 9 | Mar. 9 | Apr. 6 | May 4 | June 1 | June 29 | July 27 | Aug. 24 | Sept. 21 |
| *Micrasema* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | -- | 0 | 0 | 0 | 0 |
| *Brachycentrus* | 6 | 14 | 3 | 1 | 10 | 11 | 1 | 1 | -- | 46 | 10 | 10 | 3 |
| pupae (unidentified) | 0 | 19 | 0 | 1 | 0 | 8 | 9 | 0 | -- | 1 | 1 | 6 | 0 |
| *Oligophlebodes minutus* | 2 | 10 | 9 | 13 | 8 | 6 | 7 | 6 | 2 | 3 | 1 | 0 | 0 |
| Coleoptera | | | | | | | | | | | | | |
| Elmidae larvae | 23 | 113 | 44 | 54 | 35 | 23 | 34 | 9 | -- | 87 | 6 | 4 | 100 |
| Elmidae adult | 36 | 0 | 9 | 13 | 22 | 14 | 16 | 1 | -- | 1 | 1 | 0 | 11 |
| Diptera | | | | | | | | | | | | | |
| Tipulidae | 15 | 55 | 51 | 22 | 131 | 43 | 31 | 6 | -- | 12 | 2 | 0 | 14 |
| Psychodidae | 65 | 114 | 59 | 37 | 73 | 87 | 148 | 4 | -- | 0 | 0 | 0 | 71 |
| Simuliidae | 2 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | -- | 0 | 0 | 0 | 0 |
| Chironomidae | 24 | 74 | 38 | 36 | 132 | 92 | 24 | 4 | -- | 0 | 5 | 5 | 18 |
| Ceratopogonidae | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | -- | 0 | 0 | 0 | 0 |
| Stratiomyiidae | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | -- | 0 | 0 | 0 | 0 |
| Rhagionidae | 1 | 0 | 2 | 2 | 0 | 4 | 3 | 1 | -- | 3 | 0 | 0 | 1 |
| Total | 1,206 | 2,485 | 1,574 | 2,312 | 2,567 | 2,634 | 2,355 | 345 | 91 | 755 | 243 | 264 | 798 |

Table 29. Biomass of *O. sigma* larvae in the benthos, stations I-IV, Temple Fork, 1968-1969--expressed as mg dry weight per 0.1 m$^2$ of streambed

| Date | Station | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| | | 1968 generation | | |
| 10-01-67 | 0 | 0 | 2.67 | .31 |
| 11-04-67 | 1.56 | 18.08 | 45.13 | 1.87 |
| 12-02-67 | 16.94 | 49.41 | 63.38 | 5.00 |
| 12-30-67 | 23.15 | 88.26 | 76.68 | 36.76 |
| 1-27-68 | 31.50 | 145.93 | 105.79 | 8.02 |
| 2-23-68 | 25.97 | 149.16 | 99.79 | 13.20 |
| 3-23-68 | 58.41 | 140.80 | 151.00 | 30.97 |
| 4-20-68 | 33.24 | 161.64 | 141.68 | 67.07 |
| 5-18-68 | 39.98 | 114.71 | 235.14 | 53.78 |
| 6-30-68 | 17.49 | 118.71 | 256.06 | 61.52 |
| 7-28-68 | 5.30 | 52.18 | 197.07 | 113.09 |
| 8-25-68 | .50 | 6.56 | 35.01 | 2.25 |
| 9-22-68 | 0 | .82 | 7.24 | 2.25 |
| 10-20-68 | 0 | 1.64 | .76 | 0 |
| 11-17-68 | 0 | 0 | .57 | 0 |
| 12-15-68 | 0 | 0 | .60 | 0 |
| | | 1969 generation | | |
| 10-20-68 | .19 | 1.70 | .81 | .95 |
| 11-17-68 | 5.38 | 7.64 | 2.26 | 5.97 |
| 12-15-68 | 5.45 | 29.10 | 51.47 | 7.53 |
| 1-12-69 | 22.95 | 117.66 | 25.60 | 89.60 |
| 2-09-69 | 45.25 | 127.26 | 48.23 | 26.88 |
| 3-09-69 | 38.18 | 155.52 | 92.98 | 16.12 |
| 4-06-69 | 41.66 | 176.99 | 35.60 | 96.04 |
| 5-04-69 | 30.70 | 213.30 | 131.97 | 43.25 |
| 6-01-69 | 78.38 | 126.87 | 93.56 | 37.86 |
| 6-29-69 | 46.10 | 142.33 | 347.29 | 125.14 |
| 7-27-69 | 4.80 | 89.60 | 39.38 | 74.30 |
| 8-24-69 | 0 | 1.88 | 1.75 | 1.70 |
| 9-21-69 | 0 | 0 | 0 | 0 |

Table 30. Biomass of winter generation *B. bicaudatus* nymphs in the benthos, stations I-IV, Temple Fork, 1967-1969--expressed as mg dry weight per 0.1 $m^2$ of streambed

| Date | Station I | II | III | IV |
|---|---|---|---|---|
| | **1968 winter generation** | | | |
| 10-01-67 | .12 | 0 | 1.80 | .36 |
| 11-04-67 | .94 | .60 | 8.31 | 1.86 |
| 12-02-67 | 6.36 | 2.96 | 14.96 | 7.62 |
| 12-30-67 | 5.60 | 1.70 | 64.72 | 13.51 |
| 1-27-68 | 3.28 | 3.00 | 23.10 | 12.15 |
| 2-23-68 | 28.60 | 6.48 | 45.36 | 13.20 |
| 3-23-68 | 16.94 | 14.52 | 52.44 | 77.18 |
| 4-20-68 | 15.51 | 22.80 | 16.32 | 48.87 |
| 5-18-68 | 15.41 | 20.80 | 21.47 | 13.30 |
| 6-30-68 | 54.00 | .90 | 1.65 | 7.26 |
| 7-28-68 | 35.00 | 0 | 0 | 0 |
| | **1969 winter generation** | | | |
| 11-17-68 | 5.34 | 1.50 | 5.58 | 3.99 |
| 12-15-68 | 3.64 | 3.36 | 10.99 | 3.43 |
| 1-12-69 | 10.00 | 5.40 | 9.10 | 8.08 |
| 2-09-69 | 12.96 | 7.65 | 52.08 | 27.72 |
| 3-09-69 | 24.22 | 7.81 | 79.50 | 24.66 |
| 4-06-69 | 11.76 | 27.36 | 40.00 | 49.92 |
| 5-04-69 | 26.91 | 27.30 | 7.14 | 5.76 |
| 6-01-69 | 28.06 | 10.26 | 2.00 | 5.04 |
| 6-29-69 | 29.10 | 7.41 | .50 | 5.76 |
| 7-27-69 | 0 | 0 | 0 | 0 |

# VITA

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Doctor of Philosophy

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