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A Method to Estimate the Production Rate of a Stream Bottom Invertebrate[1]

THOMAS F. WATERS
Department of Entomology and Economic Zoology, University of Minnesota, St. Paul 1, Minnesota

ABSTRACT

An approach toward the development of a method to estimate the production rate of primary consumers in a stream was as follows: For a given unit area of stream bottom, the production rate (B) is equal to the algebraic sum of the rate of change in population density (P) and the difference between the rates of removal (R) and accrual (A):

$$B = P + (R - A).$$

Since removal and accrual both appear, for certain species, to be principally in the form of downstream drift, minimal production rates could be estimated with data on population density and total drift into and off of the unit areas of study. Population density data were obtained from periodic bottom samples, and drift nets were employed in a sampling procedure to estimate total drift rates at the various stream stations.

Production rates of a mayfly, *Baetis vagans* McDunnough, were estimated for two 24-hour periods in two riffles and two pools. The mean production rate on the riffles was 0.28 gram per square meter per day. In the pools, B was negative, indicating consumption; consumption rate in the pools was 0.45 gram per square meter per day.

INTRODUCTION

The estimation of energy flow rates within an aquatic ecosystem must include the production rates of usually three trophic levels: The primary producers (plants), primary consumers (benthic invertebrates, zooplankton), and secondary consumers (fish). Of these three groups, the development of methods for the estimation of production rates has been least advanced for the primary consumers. In the present study an approach was made toward the development of a method by which the production rate of the primary consumers of a stream could be estimated. For some species, downstream drift appears to be the major agent of removal. The proposed method was to obtain a measurement of the net rate of removal from an area of stream bottom, which is equal to a minimal estimate of production rate.

Production rates (biomass produced per unit time regardless of whether it survives to the end of that time (Clarke, 1946)) for benthic invertebrates have been computed previously from growth rate and population density. Growth rates have been determined by periodic measurement or weighing of the individuals in a recognizable age-group (Borutsky, 1939; Anderson and Hooper, 1956; Teal, 1957) or by observations of caged organisms (Odum, 1957). The estimation of population density can usually be made by bottom sampling, but the determination of growth rate *in situ* of those species where the age of an individual cannot be recognized is a major obstacle. In a stream the high rate of downstream drift of certain species (Waters, 1962) complicates the measurement of growth rate because the downstream movement results in an apparent continuous dis-

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persal of populations through a variety of stream bottom types and other environmental conditions.

A different approach to the estimation of production rate of stream invertebrates was suggested by the apparent correlation between drift rate and productive capacity of streams (Waters, 1961). Furthermore, Needham (1938) has discussed the riffles as the areas of fish-food production, and the pools, which harbor fish and receive drifting foods from upstream, as the areas of consumption. The net contribution of a riffle to an adjoining pool downstream by means of drift should therefore be a measure of the productive capacity of that riffle. The approach was based on utilizing a given area of stream bottom, such as a riffle, as the basic unit of study rather than the organism's population. For such an area, the production rate (B) is equal to the algebraic sum of the rate of change in population density (P), and difference between the rate of removal (R) and the rate of accrual (A).

$$B = P + (R - A) \tag{1}$$

The rate of change in population density is either positive or negative depending on whether it is increasing or decreasing. Removal from an area of stream bottom can be attributed to downstream drift, predation by aquatic carnivores, death and decomposition or scavenging on the area, and emergence of insects. Accrual is primarily in the form of drift from upstream.

Valley Creek, a small Minnesota stream, was appropriate for employing the above approach for several reasons: (1) Clearly distinguished riffles and pools were characteristic of the stream and available as study units. (2) Drift rates were high and easily measured. (3) Predation was low on the riffles because few fish and no carnivorous invertebrates inhabited the riffles. (4) The swift water of the riffles would probably cause dead, dying, or emerging organisms to be included in the drift.

METHODS

The study was conducted during July 1960 in Valley Creek, Washington County, Minnesota, a small trout brook which, compared to other trout streams in the state, is highly productive (Waters, 1961). The stream is characterized by clear, alkaline waters with 220 p.p.m. total alkalinity and a maximum summer temperature of about 18° C. Rubble and gravel riffles are the predominant bottom types, and a few pools occur among them. The dominant vegetation is watercress, *Nasturtium officinale*, and a benthic moss, *Fontinalis* sp. The principal invertebrates are the amphipod, *Gammarus limnaeus*; the mayfly, *Baetis vagans*; a snail, *Physa* sp.; and several caddisflies including *Glossosoma intermedium*, *Hydropsyche* sp., and several species of *Limnephilus*. Only the brook trout, *Salvelinus fontinalis*, and a sculpin, *Cottus* sp., comprise the fish species present.

Only the data for the mayfly, *Baetis vagans* McDunnough, are included in this report, since it was the only riffle species which was sufficiently abundant in the drift at this time of year.

Production rates were computed as equal to the change in population density, plus the difference between the drift off the unit area (riffle or pool) and the drift into the area, according to formula (1) modified as follows:

$$B = P + (D_0 - D_1) \tag{2}$$

where D_0 = drift rate off the area, the principal form of removal, and
D_1 = drift rate into the area, or accrual.

Population densities were not obtained from the riffles on which the drift was measured, but, rather, from a similar riffle about 150 meters downstream. The estimates of production rate were minimal because removal due to predation, decomposition, and emergence was not measured. These losses were probably small. The drift sampling included the measurement, for two 24-hour periods, of drift rates at points above, between, and below two pools and two riffles. Negative values of B occurring in pools were termed "consumption rates." These too were minimal because the extent of production in the pools was unknown; however, it is probably safe to assume on the basis of this insect's known preference for swift-water riffles that production in the pools was negligible.

Two pools and two riffles were selected where the two types of habitat were contiguous and clearly distinct from each other (Fig-

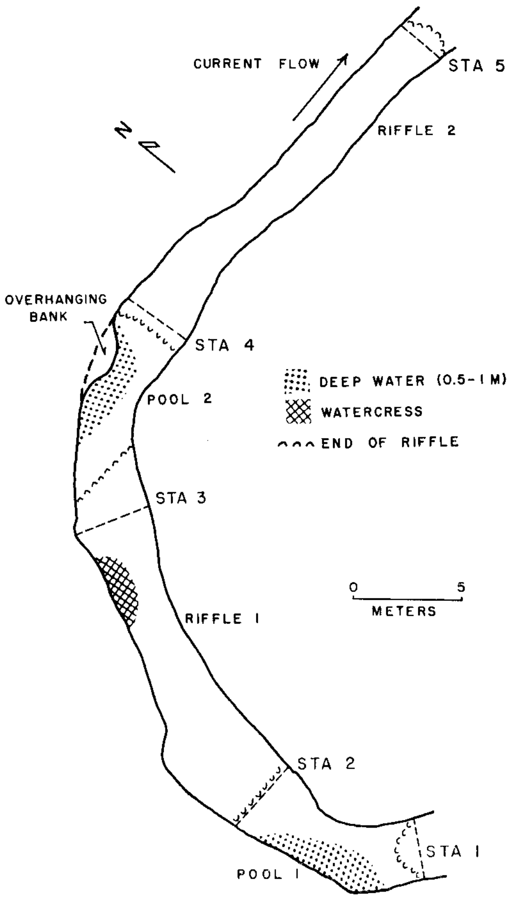

FIGURE 1.—Map of study section on Valley Creek, T28N, R20W, Section 16, Washington County, Minnesota. Map drawn August 1, 1960.

ure 1). Sampling stations were established where the downstream drift was to be measured. At each station a narrow board was anchored flush into the stream bottom. Holes were drilled along the board at appropriate intervals to receive iron rods which held the drift nets in place. The drift nets (Waters, 1962), 0.3 meter wide, could be set along the board at numbered, fixed locations.

Concurrent estimates of the daily total drift from bank to bank at all five stations were required. Complete bank-to-bank sampling would, however, decrease the drift at a downstream station, as well as influence the productive processes on the area between stations. Therefore, two chronologically separated procedures were followed to obtain an estimate of total drift at a station without removing an unnecessarily large number of organisms: (1) A prior determination of the horizontal distribution of the drift rate was made along the width of each station. (2) The drift was sampled at each station.

The horizontal distribution at each station was determined 1 or 2 days prior to sampling by measuring the drift rate at all locations along the station's width with a number of nets set side by side from bank to bank (Figure 2). This measurement was made in late evening when the drift rate was high. At each station a sampling location was selected near the point of maximum drift near midstream (Figure 3). From each distribution a ratio of total drift to drift at the selected sampling location was computed.

The sampling at a given station was done by measuring the drift rate with a single net at the selected location for 15 or 30 minutes, after which another station was sampled. The work was done from a small bridge to avoid stepping on the stream bottom and disturbing the fauna (Figure 4). No two stations were sampled simultaneously. Each station was sampled about once each 1.5 or 3 hours, depending on the time of day. Less than 5 percent of the drifting invertebrates were removed for sampling by this procedure. As an additional precaution against the effects of removing the organisms, sampling proceeded from the downstream station toward the upstream station so that each station was sampled the maximum time after the immediate upstream station had been sampled. Sampling in this fashion was continued for two 24-hour periods, July 18–19 and July 19–20, 1960.

All drift samples were treated as follows: The drift net was removed from its location on the board, and its contents were rinsed out with a wash bottle. The organisms were sorted out of the debris, separated into taxonomic groups, and measured volumetrically by a liquid-displacement technique. Conversion to wet-weight units was made with an empirically determined density factor. The drift rate was then expressed in grams per hour. There were few dead organisms present in the drift, and these were included with the live ones.

The population density data from a nearby

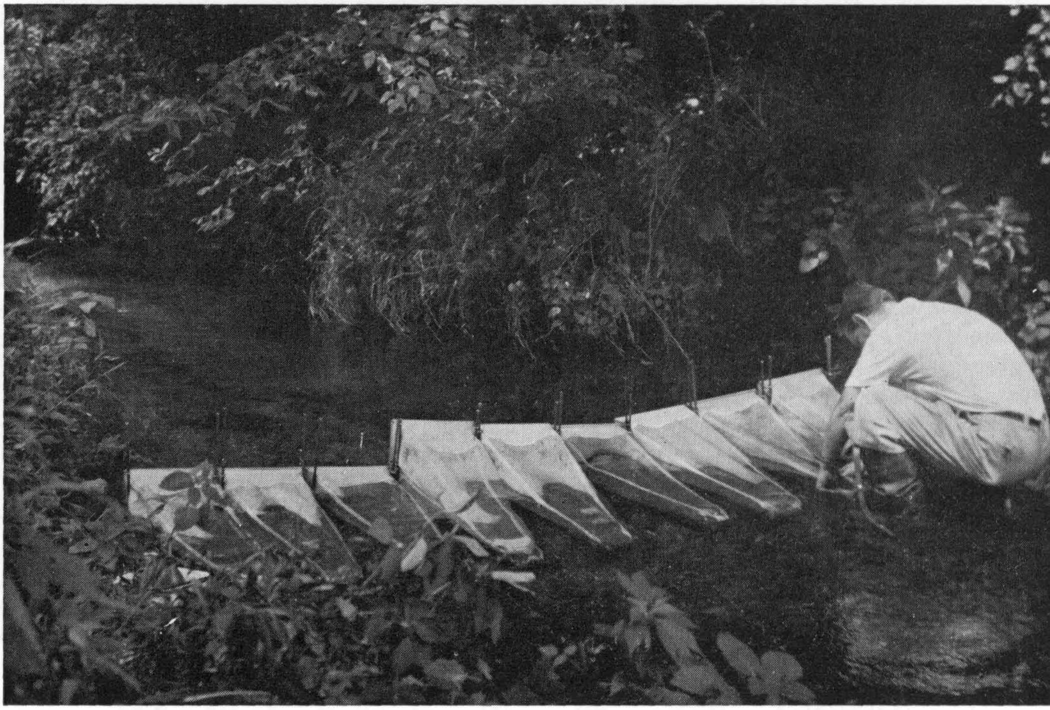

FIGURE 2.—Drift nets set in place along Station 4 to determine the horizontal distribution of drift rates.

riffle were obtained with a bottom sampler described in an earlier report (Waters and Knapp, 1961). Four samples were collected from the riffle at approximately 2-week intervals for 2 years, including the dates of the drift sampling. As in the case of the drift sampling, population density data for only the mayfly *Baetis* are included here.

Computation of total 24-hour drift at each station was made in the following manner: (1) Each sample drift rate obtained at a given station and time was multiplied by the appropriate ratio of total drift to sample obtained from the horizontal distribution; the product was an estimate of the total or bank-to-bank drift rate at that time and station. (2) The total drift rates were plotted as curves for the two 24-hour periods for each of the five stations. The area under each curve was equal to the 24-hour drift in grams. These areas were measured with a polar planimeter.

RESULTS

The drift rates showed a marked diurnal periodicity (Figure 5), a phenomenon which has been discussed earlier (Waters, 1962). The weight of organisms drifting past each station during each 24-hour period was computed as the area under the appropriate curve in Figure 5 (Table 1). The drift of *Baetis* decreased through the pools and increased across the riffles for each 24-hour period. Production, an increase in drift, is indicated as positive; and consumption, a decrease, is indicated as negative, for the pool or riffle between pairs of successive stations. These quantities, divided by the area of stream bottom in the pool or riffle, were expressed as rates of production or consumption in grams per square meter per day. The mean daily production rate on both riffles was 23.5 grams, or 0.28 gram per square meter, and the mean daily consumption rate in the pools was 23 grams, or 0.45 gram per square meter.

The population density data obtained from the nearby riffle (Figure 6) indicate peaks in late winter or early spring and again in early summer; these times correspond roughly to just before the major periods of emergence

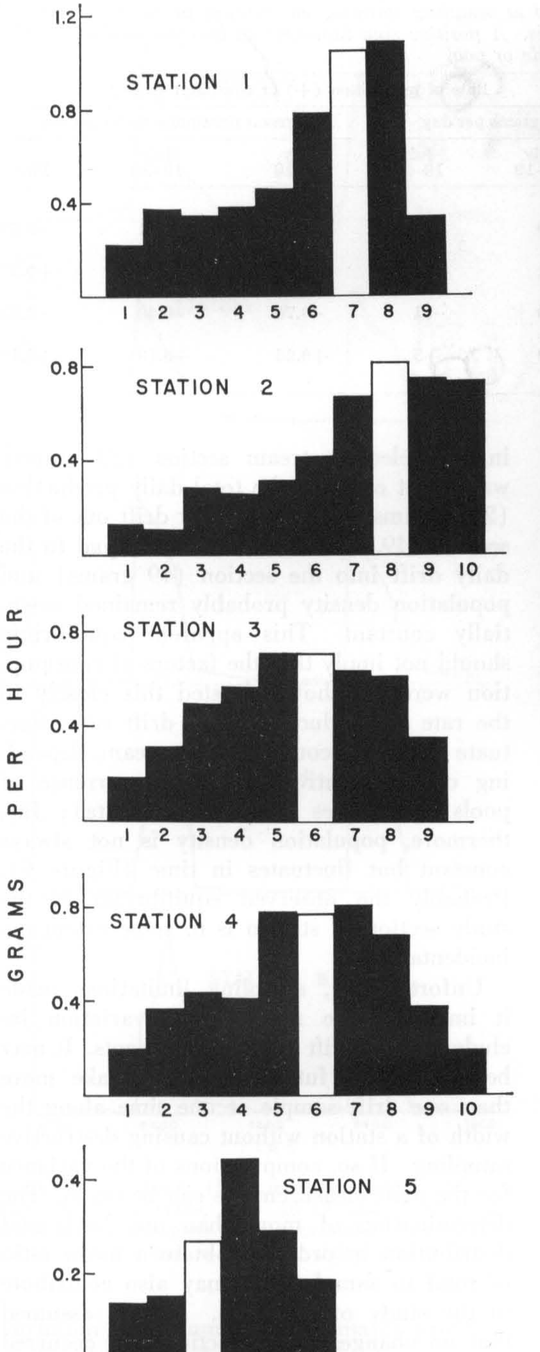

FIGURE 3.—Horizontal distributions of drift rates of *Baetis vagans*. Each numbered location was 0.3 meter wide, in order from south to north banks. White bar represents selected sampling location.

FIGURE 4.—Sampling drift net being set in place at Station 3, with operator working from a small bridge to avoid disturbing the bottom fauna downstream from the station.

for *Baetis* in this stream. Between the two bottom sampling dates (July 15 and 29, 1960) which embraced the dates of drift sampling, the population density change was not statistically significant, and therefore the population of *Baetis* was considered to be in a steady state for the purpose of computing the production rates. If the mean population density changes between these two dates were taken into account, even though they were not statistically significant, the mean production rate for *Baetis* would be decreased a small amount, 0.02 gram per square meter per day, or about 7 percent.

DISCUSSION

The production rates computed for the riffles are minimal because the rates of removal from the riffles by means other than drift were not measured, although these sources of removal were probably small. Other possible forms of removal were predation by aquatic carnivores, decomposition, and emergence.

TABLE 1.—*Total drift rates of* Baetis vagans *estimated at sampling stations, and rates of production (+) and consumption (–) computed for the riffles and pools. A positive sign indicates an increase and a negative sign indicates a decrease in the drift across the riffle or pool*

Location	Total drift rate in grams per day		Area in square meters	Rate of production (+) or consumption (–)				
				In grams per day		In grams per square meter per day		
	July 18–19	July 19–20		July 18–19	July 19–20	July 18–19	July 19–20	Mean
Station 1	48	50						
Pool 1			22.6	–9	–7	–0.40	–0.31	–0.35
Station 2	39	43						
Riffle 1			44.1	+21	+12	+0.48	+0.27	+0.37
Station 3	60	55						
Pool 2			27.2	–19	–11	–0.70	–0.40	–0.55
Station 4	41	44						
Riffle 2			38.6	+9	+5	+0.23	+0.13	+0.18
Station 5	50	49						

Of these three factors, least was known about possible decomposition on the area. It seems reasonable to assume that relatively little animal material decomposes where the water is swift, and that dead or dying organisms are probably swept away to undergo decay in a quiet-water area downstream. Emergence would have had a significant effect on the production computation for *Baetis*, but the study was not conducted during a major emergence period. Possibly the factor having the most significant effect was predation by the brook trout, since there were a few present on the riffles.

Production rates are probably of greatest ecological interest in stream community studies, and it appears that in the case of *Baetis vagans*, production is limited to the riffles. It may be of some ecological interest to study consumption as well, particularly in the pools where its effect is greatest. In a stream where the production of invertebrates is not being exploited efficiently by the fish population—*i.e.*, where the fish production is not limited by the food supply, such as appears to be the case with Valley Creek—consumption may be also a function of other factors, such as the size and extent of the pools, which affect the degree of settling and decomposition, opportunity for emergence, etc. Thus the consumption rates have been presented on a per-unit-area-of-pool basis as being of some ecological significance. In this case, consumption per unit area of pool (0.45 gram per square meter per day) was higher than production per unit area of riffle (0.28 gram per square meter per day). The total daily consumption in the selected stream section (23 grams) was about equal to the total daily production (23.5 grams), since the daily drift out of the section (49.5 grams) was about equal to the daily drift into the section (49 grams) and population density probably remained essentially constant. This apparent equilibrium should not imply that the factors of consumption were somehow adjusted this closely to the rate of production. The drift rates fluctuate along the course of the stream, depending on the relative size and occurrence of pools and riffles (unpublished data); furthermore, population density is not always constant but fluctuates in time (Figure 6). Probably the observed equilibrium in the study section of stream is to some extent coincidental.

Unfortunately, sampling limitations made it impossible to measure the variation included in the drift rate measurements. It may be possible in future studies to take more than one drift sample at one time along the width of a station without causing destructive sampling. If so, computations of the variance for the drift measurements can be made. The determination of more than one horizontal distribution in order to obtain a mean ratio of total to sample drift may also contribute to the study of variation. If it is assumed that no changes in production rate occurred in these two days attributable to daily or seasonal effect, then the differences between the two 24-hour periods may be taken as indicative of sampling variation. Encouragingly, these differences were never as large as 50 percent of the greater value. If a high

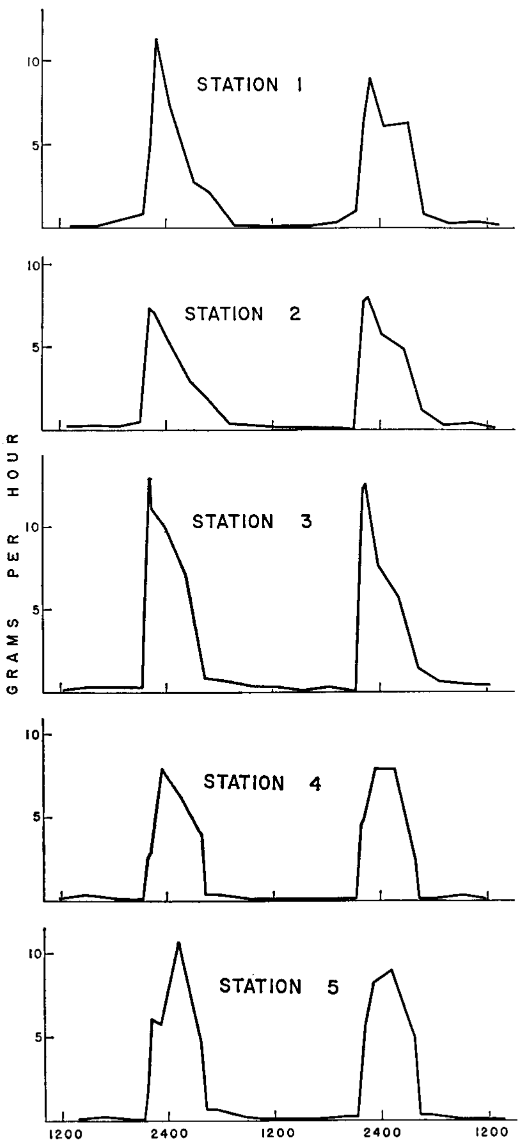

FIGURE 5.—Total (bank-to-bank) drift rates for two 24-hour periods, July 18–19 and July 19–20, 1960, of *Baetis vagans*. The area under each 24-hour curve is equivalent to the total daily drift rate.

variation were found to be a major problem, the method may be limited to those stream circumstances where high drift rates, resulting from high production rates, were found.

The crustacean, *Gammarus limnaeus* Smith, was even more abundant than *Baetis*, but computations of production rates were not consistent. This species is not restricted to the riffles and, in fact, is present in larger numbers in sand, silt, and watercress beds. Since the method employed involved a riffle as the study unit and depended on a measurable difference in the drift rates into and out of the area, it is not surprising that the method was not successful for *Gammarus*. The method may thus be limited not only to those species which are highly susceptible to drift, but also to those which inhabit a distinct habitat type.

The incorporation of satisfactory population density data in the computations of production rate remains a difficult problem. If bottom samples are collected from the areas employed in the drift studies, destructive sampling may be prohibitive, particularly if the area is small. The use of data from another similar area, such as was done in the present study, has the obvious disadvantage of a possible dissimilarity in the populations. An alternative may be to collect bottom samples from the study area only after the drift sampling is finished and to repeat both operations periodically. In this case, the interval between sampling times must be at least as long as the time necessary for denuded areas to become recolonized. Another alternative is to make the assumption that population density is relatively constant, unless there is evidence to the contrary. Seasonal changes in drift rate (probably reflecting changes in production rate) were large (Waters, 1962), whereas seasonal changes in standing crop could be relatively small. Thus the errors caused by neglecting population density changes entirely would probably be small, at least during those times when drift rates, and also production rates, were high. These last considerations do not lend precision to the method, and may be entirely misleading in streams with widely fluctuating populations due to floods, droughts, or other catastrophic factors; but in relatively stable populations they may at least lead to useful approximations.

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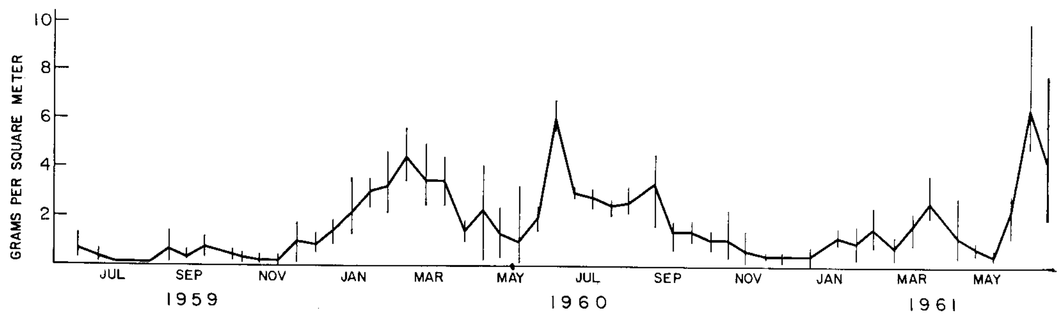

FIGURE 6.—Population density of *Baetis vagans* on a riffle about 150 meters downstream from the production study area; mean of four samples per date. Vertical lines represent ranges.

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