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PRODUCTION RATE, POPULATION DENSITY, AND DRIFT OF A STREAM INVERTEBRATE[1]

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Abstract. Production rates of the stream mayfly, *Baetis vagans* McDunnough (Ephemeroptera: Baetidae), were estimated by two different methods, compared, and related to population density and drift rate. In the year of study, this mayfly had two summer generations and one winter generation. The two production rate methods yielded estimates of 9.1 and 12.6 g/m² year as the sum of the three generations, although both estimates were minimal. Production rates for the summer generations were higher than for the winter generation, although winter production was still at a significant level. The summer generations drifted in large quantities, up to about 22 g/day, but the winter generation appeared to drift little, if any, until near the end of the generation in early spring. The relation between annual production rate and mean population density, or turnover ratio, was 9.7, or 3.2 times the number of generations.

INTRODUCTION

The drift of stream invertebrates, when occurring in large numbers, is apparently of great significance in their population dynamics. For those species that exhibit a high rate of daily drift, there is often a marked diurnal periodicity with highest drift rates occurring during hours of darkness; the mayfly genus *Baetis* was represented in diurnal drift periodicities reported from such widely separated areas as Japan (Tanaka 1960), Minnesota (Waters 1962a), and Germany (Müller 1963). For some species the quantity drifting per day over or through a unit area of stream bottom is many times the standing crop found on that area (Waters 1962a, 1964).

These high drift rates are not the result of floods or mechanical disturbances (which of course may also cause high drift), but are apparently the result of some activity of the organisms. This high "behavioral" drift may be distinguished from the "catastrophic" drift caused by flood or other physical disturbance and the low levels of "constant" drift observed for all species and at all times (Waters 1965). Since stream bottom areas are not depleted by high behavioral drift (Müller 1954; Waters 1965), it would appear that drift is a mechanism of removing excess production, operating to control population density somewhat as do other density-dependent factors such as predation or disease. Müller (1954) concluded that competition among individuals for food and space was a primary cause of drift, and that the importance of drift was in "population regulation." From a comparison of drift rates in a number of streams embracing a wide range of

apparent productive capacity, I postulated (Waters 1961) that drift rate is a function of production rate. In another study, the drift of a riffle insect was observed to increase across riffles because of production where population density was high, and to decrease across pools, in which population density was low, suggesting consumption by fish or possible deposition and decomposition in the pools (Waters 1962b).

The purpose of the present study was to test the above postulate by relating the production rate, expressed as biomass produced per spatial unit and unit of time, of *Baetis vagans* McDunnough (Ephemeroptera: Baetidae) to its drift rate and population density, and also to compare the estimates of production rate obtained by two different methods.

Several methods to estimate production rate of aquatic invertebrates have been proposed in the literature, but virtually no such data obtained in small streams have appeared. Ricker (1946) and Allen (1949) presented a mathematical procedure to estimate production rate (employed on fish) involving the product of instantaneous growth rate and mean population density. Later, Allen (1951) presented a graphic modification of the method applicable to a known generation, and Neess and Dugdale (1959) proposed essentially the same graphic method for invertebrates. Anderson and Hooper (1956) estimated the production rate of a lake invertebrate by a method involving the summation of mortalities. For stream species subject to high drift rates, I suggested a method involving drift measurements (Waters 1962b). In the present study, Ricker's and Allen's growth method and the stream drift method were compared.

Life history of Baetis vagans

Various workers have studied the life history of *Baetis vagans* and related species (Murphy 1922; Ide 1935; Harker 1952; Macan 1957; Hynes 1961; Thorup 1963). In these studies several pertinent points have been elucidated. There often appear to be several generations per year, probably two or three, including a winter generation that hatches in the autumn or late summer, grows slowly through the winter, and emerges as large-sized adults in the spring, and a rapid summer generation (sometimes two) emerging in summer as small-sized adults. Some differences in life history that have been observed seem to result from different environmental conditions such as water temperature; that is, the life history, including the number of generations per year, varies from place to place and appears to be determined by the environment (Ide 1935; Macan 1957, 1961). The period of incubation may be about 1 month or less (Berner 1959; Murphy 1922), although very small nymphs of some species have been observed at all times of the year, indicating delayed or prolonged hatching (Macan 1957; Hynes 1961).

In the present study area the life history of *Baetis vagans* seems as follows: 1) An early summer generation hatches in May, grows rapidly, and emerges in early July, when adults weigh about 1 to 2 mg. 2) Hatching continues through much of the summer, and in September there is a sudden increase in size, and emergence takes place with larger adults weighing 4 to 5 mg. 3) The winter generation hatches in September and October, grows consistently through the winter until March at about which time a rapid increase in size occurs, and emergence takes place in late March and April, with large adults weighing about 5 to 6 mg. (In minor emergences taking place between the March to April, and July maxima, the adult weight is intermediate between these extremes.) It is still not clear whether those insects hatching in May all emerge in July and produce progeny that emerge in September, or whether some of those hatching in May emerge in July, and others delay until September, emerging along with those that hatched during the summer. It was considered that, in the year of the present study at least, there were two summer generations and one winter generation.

In samples from the present study, it was usually possible to distinguish the various generations. The winter generation was always distinct, because at time of hatching in September the small individuals were recognized among large, late emergents of the previous generation, and the large nymphs in March and April were easily identified among a few newly hatched individuals of the next generation. During part of the summer, however, because the adults were so much smaller and emergence appeared to occur over a longer time, it was more difficult to distinguish between generations. Therefore I have treated the summer generations together.

The life history differs in timing somewhat from year to year, apparently depending on different weather conditions, which vary widely in the continental climate of Minnesota. More recent observations in this stream (unpublished) suggest that the life history varies among different locations on the stream according to different environmental conditions, as also suggested for *Baetis* by Ide (1935). This possibility, combined with high rates of drifting from one location to another, may mean that the life history postulated above may be in part an artifact. Macan (1957) reported concentrations of *Baetis rhodani* in downstream areas and suggested either downstream movements or different life histories.

During the year of this reported study, though not in other years, possibly a fourth generation appeared, maturing very rapidly in April between the winter and summer generations and emerging in May or June as moderately large adults. The possibility that this generation was an artifact caused by drift seemed so likely that I did not include it in the annual estimates. This extra generation may be real and may occur in some years but not in others.

An additional species, *Baetis brunneicolor,* was present in the stream; the nymphs were distinguished from *B. vagans* by the uniform shading of the abdomen while *B. vagans* nymphs were banded (Burks 1953). *B. brunneicolor* apparently lived in areas upstream from the study area, where water temperatures were more constant, but drifted into the study area in spring and fall before its emergence at these two times of the year. Its complete life history in the stream is as yet unknown. It is not included in the present study, which is devoted to *B. vagans*.

METHODS

The study area was a single riffle in Valley Creek, a small trout stream in east-central Minnesota about 6 km in length. The riffle had a gradient of about 1.0 m per 100 m, a discharge of about 0.14 m³/sec (5 sec ft), and a surface current velocity of about 0.6 m/sec. The riffle was 14 m long, about 3 m wide, and 44.1 m² in area,
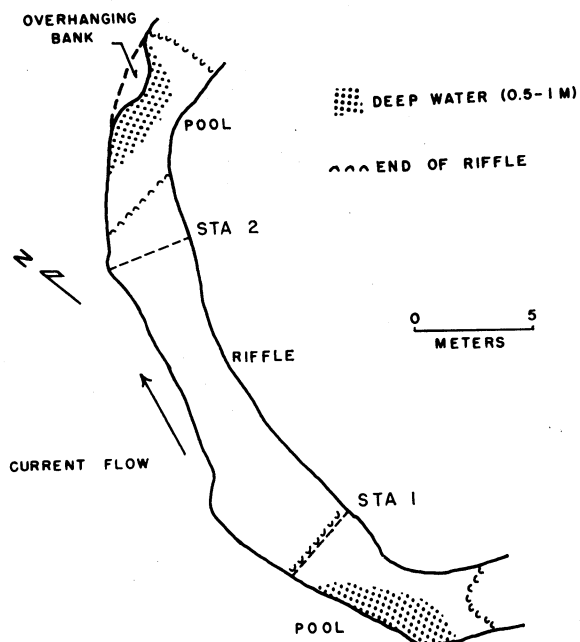
FIG. 1. Map of stream section and riffle area of study, Valley Creek, Washington County, Minnesota.

homogeneous as to bottom type which was gravel and small rubble, and bounded at both ends by pools (Fig. 1). Water temperature of springs along the stream was about 9°C; in the riffle, water temperature reached daily summer maxima of about 15 to 18°C. The riffle area developed anchor ice during extreme cold periods in the winter. Alkalinity was about 120 ppm $CaCO_3$, pH about 7.5, and the oxygen concentration was near air saturation at all times. The stream appeared highly productive of both invertebrates and fish. The species complex of both groups was relatively simple. The only fishes present were brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and the sculpin (*Cottus cognatus*). Principal invertebrate species were the mayfly, *Baetis vagans*, the subject of this report; at times also *Baetis brunneicolor*, and the crustacean *Gammarus pseudolimnaeus*. Also common were several species of Trichoptera, a snail, *Physa* sp., and the black fly genus *Simulium*. Several other species were rarely found. The stream was not subjected to severe flooding or erosion, at least during recent years, and was virtually undisturbed by angling or other activities.

All sampling equipment was constructed of Nitex with a mesh size of 0.471 mm. Wet weight was obtained by draining excess liquid by light centrifuging and weighing in a weighing bottle on a torsion balance.

Two groups of samples were required from the field: 1) bottom samples collected periodically from the riffle, and 2) drift samples at both the upstream and downstream ends of the riffle. The essential data required from the bottom samples were population density by wet weight and maximum size of the nymphs for each generation for growth rate calculations. From the drift sampling were required data to estimate the total quantity by wet weight of *Baetis vagans* drifting per day, at both ends of the riffle simultaneously, for each generation.

Sampling continued from late 1960 to mid-1963, with the first year involving development of methods. The report includes completed estimates for the summer generations of 1962 and winter generation of 1962 to 1963, covering approximately 1 complete year.

Population density

Four bottom samples of 0.1 m² each were collected at approximately 1-month intervals, using a round sampler described in a previous report (Waters and Knapp 1961). The four samples were spaced in the central area through the length of the riffle. An adjunctive study indicated that *Baetis* quickly recolonized those areas denuded by previous bottom samples (Waters 1964). Each sample was sorted by hand for all *Baetis vagans* present, and where it was possible to distinguish two generations, these were separated and counted into two groups. Maximum weight was determined on each date by weighing separately a few of the largest nymphs, but where more than one generation was present, the mean size of the smaller (younger) generation (usually present in small numbers) was taken as the maximum size of that generation.

Production rate

Growth method

For each approximately 1-month period, production rate was computed for each generation as follows, using relationships proposed by Ricker (1946) and Allen (1949):

$$B = k\,\overline{P}$$

where B = production rate in g per m² day, k = instantaneous rate of growth in g per g day, and $\overline{P}$ = mean population density in g per m². Instantaneous growth rate for the 1-month period was calculated as the natural logarithm of the ratio of the maximum size at the end of the period to the maximum size at the beginning of the period; the result was divided by the number

of days in the period to obtain k for one day. Maximum sizes were used rather than mean sizes because, as Macan (1957) has pointed out, delayed, continuous hatching causes an underestimate of growth rate when mean size data are used for growth calculation; the continuous recruitment of small nymphs to the samples would result in low calculated mean sizes. In an attempt to eliminate or reduce this error in the present study, maximum size of the generation was used for growth rate calculation, because successive measurements of the same cohort would then be obtained. $\overline{P}$ was the arithmetic mean of population densities at the beginning and end of the period. Production of an approximate 1-month period was computed as the product of B and the number of days in the period.

Drift method

The procedure employed was essentially the same as that detailed in a previous report (Waters 1962b). The principal elements of the method were 1) the measurement of daily drift simultaneously off and into the riffle area, obtaining most often a net increase in drift across the riffle, 2) the algebraic addition of the daily change in population density to the above drift difference, and 3) the addition (if known) of other removal from the riffle, such as emergence. The following formula was used in computation:

$$B = \Delta P + (D_o - D_i) + E$$

where B = production rate; ΔP = rate of change in population density; $(D_o - D_i)$ = net increase in drift across the riffle, D_o and D_i being the total drift in g per day off and into the riffle area at stations 2 and 1 respectively (Fig. 1); and E = daily emergence; all in units of g per m² day.

Rate of change in population density (ΔP) was obtained with the bottom samples described in the previous section, taken approximately 2 weeks before and 2 weeks after the drift measurements. The change in population density in wet weight for the period was divided by the number of days in the period to obtain ΔP in g per m² day. D_o and D_i were estimated using three sample drift nets at each of the upstream and downstream ends of the riffle (Fig. 2), sampled in time over a 24-hr period, combining sample results with previously determined horizontal distributions along the width transects to obtain total estimates (Waters 1962b); the increase in drift across the riffle was divided by the area of the riffle in m² to obtain $(D_o - D_i)$ in g per m² day. Emergence, when occurring, was estimated from adults present in the drift samples, computing the difference be-
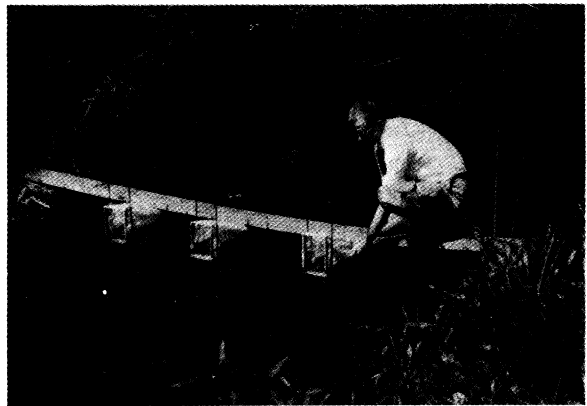

FIG. 2. Sample drift nets in place at station 2, the downstream end of the riffle.

tween the quantities of adults at the downstream and upstream stations and dividing by the riffle area, to obtain E in g per m² day.

These daily production rate estimates were made at approximately 1-month intervals, midway between bottom samples. They were plotted, connected by a curve, and the area under the curve determined planimetrically to obtain the production of each generation. Drift rates referred to in this paper were those estimated at the downstream end of the riffle, or station 2, i.e., D_o in g per day.

RESULTS

Population density

Beginning with the early summer generation in 1962, hatching apparently occurred mostly in May, with greatest numbers appearing in the bottom samples in June (Fig. 3). Numbers declined through the summer to the end of the summer generations in early autumn. Population
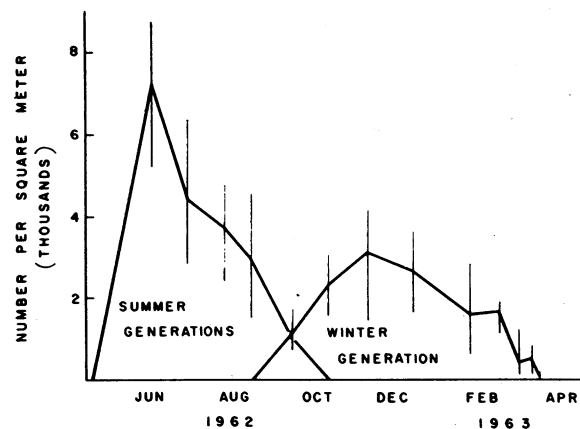

FIG. 3. Population density of *Baetis vagans* on riffle, in numbers, mean of four samples. Vertical lines represent range.
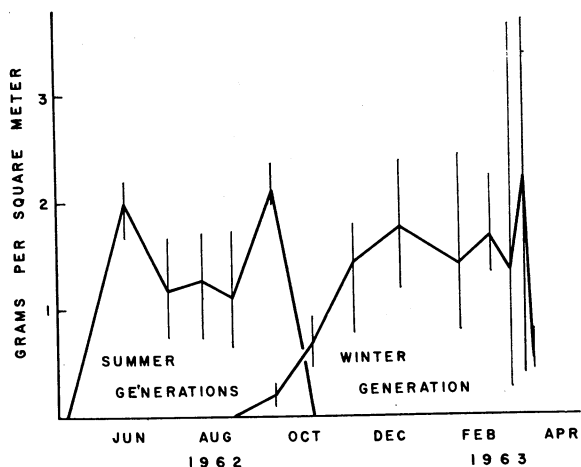
FIG. 4. Population density of *Baetis vagans* on riffle, in wet weight, mean of four samples. Vertical lines represent range.

FIG. 5. Maximum weight of *Baetis vagans,* from which growth rates were computed.

density, in weight, also reached a peak in June for the summer generations, but a second peak occurred in September due to a much-increased size of the nymphs at that time (Fig. 4). Similar patterns with respect to both numbers and weight were observed in the case of the winter generation, with larger sized nymphs again being present just before emergence. The mean annual population density, determined by measuring planimetrically the area under the curves in Figure 4 and dividing by the abscissal scale, was 1.3 g/m². This mean is somewhat less than would be observed in a periodical bottom sampling program where generations were not separated, because there were actually present individuals, not considered here from overlapping generations at both ends of the abscissal scale. However, the ratio of production rate to mean population density (turnover ratio), to be discussed later, was based on the specific generations under consideration. The ranges of the groups of four samples, indicated by vertical lines in Figures 3 and 4, reflect variation in the bottom samples, which in the present case was usually low, because the riffle bottom was fairly homogeneous.

For the early summer generation, maximum weights of nymphs indicated growth from hatching in May to a size of about 1 mg in June and 1.5 mg for the remainder of the summer; a sharp increase to near 4 mg occurred in September (Fig. 5). Because the maximum size remained fairly constant through the summer, probably owing to delayed hatching and extended emergence at a small size, the increase in maximimum size from May 4 to June 15 was used for production rate calculations for all periods through August. The
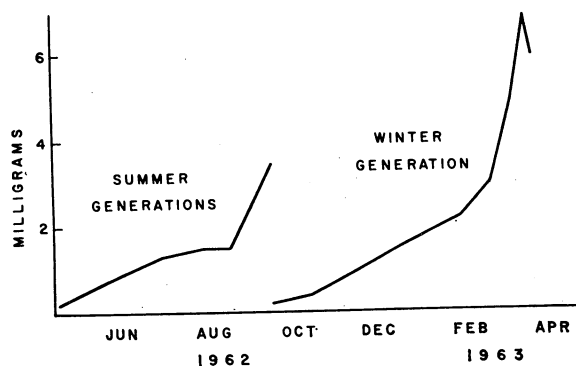
maximum size of the winter generation increased through the winter months to above 6 mg just before emergence in March and April.

Production rate

Growth method

For the summer generations, appearing first in significant quantities in May and June, production rates were about 0.04 g/m² day during most of the summer, then dropped sharply with emergence in the autumn (Table I). The daily instantaneous rate of growth for the May 4 to June 15 period, 0.0358, was used for most of the summer periods, as described above, in order to avoid as much as possible an underestimate owing to delayed hatching and emergence at a small size. The daily instantaneous rate of growth, e.g., 0.0358, means that for each 1 g present on the unit area, there is 0.0358 g produced by the organisms on that area per day. The instantaneous rate computed for the August 31 to September 29 period, 0.0292, was also used for the succeeding period, because emergence was occurring in the latter period and no growth rates could be determined, and the growth of all pre-emergents at this time was probably similar.

For the winter generation, it was possible to determine growth rates with more precision because extended hatching and early emergence did not occur. Starting about September 1, production rates reached approximately 0.03 g/m² day in November, decreased through much of the winter, and increased in March to about 0.08 g/m² day just before emergence (Table I).

The total estimates of production were about 7.6 and 5.0 g/m² for the summer and winter generations respectively, with an annual sum of 12.6 g/m² (112 lb/acre).

TABLE I. Production rate of *Baetis vagans* by the growth method

Period	Days	k g/g day	$\bar{P}$ g/m²	Production rate—B for day g/m² day	Production rate—B for period g/m²
Summer generations					
May 4-Jun. 15......	42	.0358	1.09	.039	1.640
Jun. 15-Jul. 16.....	31	.0358	1.59	.057	1.770
Jul. 16-Aug. 10.....	25	.0358	1.21	.043	1.085
Aug. 10-Aug. 31....	21	.0358	1.18	.042	0.886
Aug. 31-Sep. 29.....	29	.0292	1.61	.047	1.360
Sep. 29-Oct. 27.....	28	.0292	1.06	.031	0.867
Total summer......					7.608
Winter generation					
Aug. 31-Sep. 29.....	29	.0248	0.10	.003	0.072
Sep. 29-Oct. 27.....	28	.0248	0.45	.011	0.314
Oct. 27-Nov. 25.....	29	.0280	1.06	.030	0.861
Nov. 25-Dec. 27....	32	.0161	1.59	.026	0.820
Dec. 27-Feb. 7......	42	.0092	1.58	.015	0.610
Feb. 7-Mar. 2.......	23	.0134	1.53	.020	0.466
Mar. 2-Mar. 16.....	14	.0336	1.51	.051	0.710
Mar. 16-Mar. 26....	10	.0457	1.79	.082	0.819
Mar. 26-Mar. 31....	5	.0457	1.39	.064	0.318
Total winter........					4.990
Total annual production.......					12.598 (=112 lb/acre)

TABLE II. Production rate of *Baetis vagans* by the drift method (all data in g/m² day)

Period	ΔP	D_o-D_i	E	Production rate—B
Summer generations				
May 31-Jun. 1...............	+.001	+.004	0	.005
Jul. 3-4....................	−.027	+.053	+.010	.036
Jul. 31-Aug. 1...............	+.004	+.005	0	.009
Aug. 21-22.................	−.007	+.053	0	.046
Sep. 11-12.................	+.035	+.112	0	.147
Winter generation				
Sep. 11-12.................	+.007	0	0	.007
Oct. 12-13.................	+.018	0	0	.018
Nov. 8-9...................	+.026	0	0	.026
Dec. 8-9...................	+.010	+.003	0	.013
Jan. 17-18.................	−.008	0	0	0
Feb. 21-22.................	+.012	0	0	.012
Mar. 22....................	——High water——			

Total summer (planimetrically from seasonal curve)=6.7 g/m²
Total winter (planimetrically from seasonal curve)=2.4 g/m²
Total annual production=9.1 g/m² (=81 lb/acre)

Drift method

Production rates estimated with the drift method fluctuated around 0.020 g/m² day for much of the summer and increased sharply with the September estimate of 0.147 g/m² day (Table II). For the winter generation, production rates increased after hatching during the autumn to a maximum in November of 0.026 g/m² day and decreased during much of the winter. Probably an increase occurred again in March, but the drift sampling at this time was interrupted by high waters; for this reason the estimates for the winter

generation by the drift method was probably low. In both summer and winter, underestimates were probably obtained when the major emergences, an essential element in the estimate, were missed. At no time during the present study did production rate estimates by the drift method reach levels of 0.48 and 0.27 g/m² day that were estimated on the same riffle by a similar method 2 years previously (Waters 1962b), which may reflect large annual variations. Estimates by the drift method included considerably more seasonal variation than the growth method and were therefore probably less reliable.

The total estimates of production by the drift method were 6.7 and 2.4 g/m² for the summer and winter generations respectively, with an annual total of 9.1 g/m² (81 lb/acre).

Drift

Drift rates differed markedly between the summer and winter generations. Drift of the summer generations varied around 20 g/day for most of the summer, with a maximum of about 22 g/day, whereas the drift of the winter generation was comparatively slight except in late winter and early spring (Fig. 6). The simple point of high
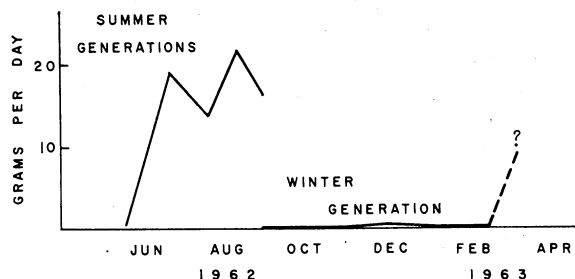

FIG. 6. Drift of *Baetis vagans* at station 2. The datum shown for March 1963 by dashed line was taken from other years.

drift for the winter generation in March, indicated with a question mark in the figure, is an assumed point that is approximately the drift rate found in other years in March (unpublished); the March drift sampling in the present study was interrupted by high water.

DISCUSSION OF PRODUCTION RATES

One of the purposes of this study was to evaluate the possibility of a relationship between production rate and drift rate. I had suggested in an earlier report that the drift mechanism acted as a density-related removal factor such that high production rates tended to increase drift rates in order to remove the organisms from areas where

they were being produced; drift rates might therefore be employed as a relative measure, or index, to production rates. In the present study, both drift and production rates were higher in the summer than in the winter; however, the relationship was clearly not a linear one, since production rates were not nearly so disparate as drift rates between summer and winter.

Several reasons may be postulated to explain this nonlinearity. The relationship between rates of production and drift may change as a function of the phenology of the species, or it may change with seasonal differences in the environment such as water temperature. Furthermore, there is the suggestion among the present data for both the late summer and winter generations that drift rates near the end of the generation are influenced by some preemergence activity of the mature nymphs, an influence that may be entirely independent of production rate.

Drift rate did not appear to be a linear function of population density (Fig. 4 and 6). It may be thus hypothesized that, at the beginning of a generation when the capacity of the stream bottom is short of being filled, production may proceed and population density increase without causing undue competition, similar to conditions in the exponential stage of a population development curve. When the population density approaches carrying capacity, increasing competition results in increased drift as a means of removal and population control. Drift, then, rather than being a linear function of either production rate or population density, may be a function of production rate at or above the point at which the carrying capacity is reached, or in other words, a function of the degree to which the carrying capacity tends to be exceeded.

A more illuminating test of the hypothesis would be a comparison, at the same time of year, of rates of production and drift among several streams containing the same species. For this purpose, drift rates would have to be based on some unit of stream size, such as discharge, to be comparable among the several streams in the same sense that production rate is based on a unit of area.

Another purpose of this study was to examine the relationship between population density and production rate. This is a subject that has received the attention of many biologists, because prior to more recent and better understanding of the dynamic character of populations, population density, or standing crop, was often assumed to be a measure of productivity. By definition in Ricker's and Allen's formulations, the relationship between population density and production rate is a function of the growth rate of the individuals. This relationship was apparent in the results of both the drift and growth methods of estimating production rates: although population densities were approximately the same in summer and winter (Fig. 4), production rates were higher in summer (Tables I and II) as were also instantaneous growth rates (Table I).

Although production rates were higher in summer than in winter, it is interesting to note that production proceeded in the winter at levels that made significant contributions to the annual production. This is in contradiction to popular concepts that winter is a time of almost complete cessation of biological processes (Adelman, Bingham and Maatch 1955), concepts perhaps strengthened by early knowledge that fish growth essentially ceases during winter in temperate regions. Gerking (1962) considers the winter a "catch-up" period when populations of invertebrates, freed of fish predation, are able to return to high levels because of production.

Comparing the two methods of estimating production rate, it would seem that greater confidence could be placed in the growth method, because of the greater fluctuations in the drift method estimates (Table II). These fluctuations were probably the result of variation in one of the method's major elements $(D_o - D_i)$, which usually was a small difference between two relatively large quantities, both of which were subject to sampling error. The results obtained by the two methods were similar and should lend some confidence to the estimates; but because of the observed fluctuations in the drift method, the annual estimate of 12.6 g/m^2 obtained by the growth method would appear the more acceptable.

Sources of error

Various systematic errors were possible in both the growth and drift methods of estimating production rate. In the drift method, the estimate was probably low because other forms of removal from the riffle, such as decomposition and predation, were not estimated. However, predation must have been low because few fish and no carnivorous invertebrates were present on the riffle, and it was possible that most of those organisms dying on the riffle from injury, disease, etc., drifted off the riffle before decomposing and thus were included in the drift samples. Emergence, another possible form of removal from the riffle, was estimated from the drift samples; how-

ever, it was obvious that some major emergences were missed by the sampling schedule, resulting in a significant source of error. Those emerging adults leaving the water in the area of the riffle were not estimated in the drift samples and thus comprised another source of underestimate, although probably small; many individuals reaching the surface in the riffle area would have drifted off the riffle before leaving the water surface.

The estimate of production rate for the winter generation, as determined by the drift method, apparently was low because significant removal occurred other than drift, as evidenced by the decrease in numbers (Fig. 3) despite the very low drift rates observed (Fig. 6). The loss of the March drift method estimate, referred to above, undoubtedly also caused an underestimate of production rate for the winter generation, since this was a time of rapid growth and probably high drift rates.

A possible source of error in both methods was the use of screening material in the bottom sampler and drift nets of a size that probably permitted the smallest individuals to escape. The size of the mesh opening was 0.471 mm (39 meshes/in.); Macan (1957) found that by reducing the mesh size in his nets from 20 to 160 threads/in. the size of the samples of *Baetis rhodani* increased greatly because of the inclusion of many very small individuals. This factor in the present study was of greatest significance during the summer when hatching was continuous, and possibly resulted in a serious underestimate in the summer generations, but could not have been serious in the winter generation.

Finally, another source of error may be suspected in the rapid acceleration in growth observed near the end of both the summer and winter generations, which occurred at times when the drift rate usually increased. If this observed increase in growth was due to larger individuals drifted down from upstream areas—where larger individuals may have been present in a different life cycle—then the observed increased growth was an artifact. This source of error would thus have caused an overestimate.

Considering all sources of error for the two methods, it would appear that the annual production rate of 12.6 g/m² year, as obtained by the growth method, would be a reasonable, if somewhat minimal, estimate. It should not be inferred that this estimate represents the production rate of the entire bottom fauna. Though often the most numerous macroinvertebrate in the stream,

Baetis vagans was far below the population density in biomass of *Gammarus pseudolimnaeus*, which was always the major component of the bottom fauna. Population density in biomass of *Gammarus* was usually 10 to 100 times that of *Baetis*, even when the latter was abundant; consequently the production rate of the entire bottom fauna was undoubtedly dominated by the contribution of *Gammarus* and was much higher than that reported here for *Baetis vagans* alone.

TURNOVER RATIO

Some published studies of invertebrate production rates have also included the calculation of the turnover ratio, defined as the ratio of annual production rate to mean annual population density. As so defined, the turnover ratio may be taken as an indication of how rapidly, or how many times, the population replaces itself in one year.

Using 12.6 g/m² year as the best estimate of production rate, the annual turnover ratio was calculated for *Baetis vagans* as 12.6/1.3 = 9.7, or, assuming three generations (two summer, one winter), 3.2 times the number of generations.

There is some evidence that the turnover ratio may be approximately constant for a given species, trophic status, or number of generations per year. If so, the ratio has a potential value in energy flow methodology. Lindeman (1941) essentially assumed the turnover ratio per generation to be unity, and multiplied the mean annual population density by the number of generations to obtain production rate. This procedure appears logical at first glance but, as Allen (1951) has pointed out, takes into account neither mortality that took place before measurement of population density nor potential growth after such measurement, and it thus results in a serious underestimate. A ratio of 1 would result when the population density was measured only on the final standing crop and if no mortality had previously occurred, obviously an impossibility with populations in nature. A ratio greater than 1 times the number of generations would seem appropriate, and where studies have been reported based on aquatic insect species of known life history, mostly Chironomidae, the ratio was often about two to four times the number of generations per year (Table III). Annual ratios for crustaceans appear higher, with presumably several generations per year.

In studies where production rate of fish and knowledge of fish predation rates have been employed to estimate invertebrate production rates, turnover ratios were reported larger than by direct methods (Allen 1951; Hayne and Ball 1956;

TABLE III. Turnover ratio of *Baetis vagans* compared with ratios obtained elsewhere

Organism	Turnover ratio	Number of generations	Location, remarks	Authority
Insects				
Baetis vagans	9.7	3	Valley Creek	
Chironomidae	8–9	1–2	Littoral	Miller 1941
Chironomidae	2–3	½–1	Profundal	Miller 1941
Tanytarsus jucundus	3.4[1]	1	Lake	Anderson and Hooper 1956
Calopsectra dives	3.5[1]	1	Cold spring, summer only	Teal 1957
Anatopynia dyari	2.7[1]	1	Cold spring, entire year	Teal 1957
Corixa germari	2.5[1]	1	Reservoir	Crisp 1962
Crustaceans				
Asellus	14[1]	?	Cold spring	Teal 1957
Planktonic	10.0	?	Lime-treated lake	Stross, Neess, and Hasler 1961
Planktonic	4.8	?	Untreated lake	Stross et al. 1961

[1] Computed from author's data

Gerking 1962); in these cases however the entire bottom fauna as a whole was under study and the number of generations was not considered. Probably the fauna included some multivoltine or continuously breeding species. The extremely high ratios reported by Allen (1951) appear to be in error, as discussed by Gerking (1962). Gerking also pointed out that production rates determined by predation methods tended to be larger than by the direct method, despite the probability that they were minimal because forms of removal other than by fish predation were usually not included in the computations. Perhaps supplementary foods, such as microscopic organisms, dissolved organic matter, or amorphous debris, are utilized by the fish but not recognized in the usual stomach-content analysis; this leads to an overestimate of the contribution of bottom fauna foods to the fish diet. Direct methods, however, may lead to an underestimate for reasons suggested in the present study.

Turnover ratios should prove illuminating in energy flow studies when more data are obtained for different taxonomic groups and in different environmental conditions. The ratio is a function of the ability of a unit of biomass to reproduce itself. One would expect this ability to vary with taxonomic group, water temperature, food supply, lentic vs. lotic conditions, and perhaps other factors. But within an ecological group (e.g., aquatic insects), narrow range of water temperature (e.g., trout stream, warm stream, or temperate lake), a probably ample food supply, and in either still or flowing waters, the ratio might be found to vary within relatively narrow limits.

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