

ANNUAL PRODUCTION OF A STREAM MAYFLY POPULATION: A COMPARISON OF METHODS¹

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ABSTRACT

The annual production of the mayfly *Ephemerella subvaria* McDunnough in a small central Minnesota stream, Luxemburg Creek, was estimated by four methods: a removal-summation method, the instantaneous growth method, the Allen curve, and the Hynes method. Basic data on standing crop and growth rates were obtained from a series of bottom samples covering the life cycle of the mayfly. The life history of *E. subvaria* was clear and simple, and the data were particularly amenable to production estimation by all four methods. The first three yielded estimates of annual production that generally agreed, ranging from 26.4 to 28.9 g m⁻². The Hynes method yielded an estimate 15.2 to 26.1% higher, or 33.3 g m⁻². Cohort turnover ratios for the first three methods ranged from 4.2 to 4.6 (not calculable for the Hynes method); the annual turnover ratio for the first three methods ranged from 5.8 to 6.3 and was 7.2 for the Hynes method.

The estimation of the production rate of aquatic animal populations has been of interest for more than 50 years, but efforts to make such estimates and improve methods for doing so have increased greatly recently as a result of the emphasis placed on productivity aspects in the International Biological Program, as well as the desire to quantify function and energy flow in ecosystem studies. Knowledge of fish and fish-food production rates is of some special utility to fisheries management, in both commercial and sports fisheries.

The term "production rate" is used here in the sense of Clarke (1946), meaning that amount of tissue elaborated per unit time per unit area, regardless of its fate. The term "production" is derived from Odum (1971) for an animal population, being analogous to "net production" for plants; that is, it does not include respiratory uses of energy.

The earliest attempts to estimate production rates involved single-species populations with a simple life history, in which a series of standing crop estimates through-

out the life of a single cohort or generation was made. From such a series of samples, the mortality between successive samples, taking into account the size of organism during the period of loss, could be calculated in terms of weight or biomass. The sum of such observed mortalities over the entire life cycle was then equivalent to the total production of the cohort. If the species was univoltine, the cohort production was then equal to annual production. Estimates have been made with this method by Boysen-Jensen (1919), Anderson and Hooper (1956), Sanders (1956), and Teal (1957). Here, this method is referred to as the *removal-summation method*.

Another form of removal-summation, as a method to estimate production rate, involves independent estimates of all forms of mortality or other removal and summing of these estimates as equivalent to total production (Borutsky 1939; Odum 1957; Gerking 1962; Waters 1962), but that technique is not concerned in this study.

Ricker (1946) and Allen (1949) developed a mathematical model for estimating production rate, in which, for a given interval of time, production is the product of the instantaneous rate of growth and the mean standing crop in weight during the time interval. Here, this method is referred to as the *instantaneous growth method*.

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Later, Allen (1951) extended this mathematical method to a graphical representation constructed from a series of samples collected over the life cycle of a cohort, plotting density in numbers against mean weight; the area under the resulting curve, expressed in appropriate units, is the cohort production. This method is herein referred to as the *Allen curve method*.

The instantaneous growth and the Allen curve methods are particularly adaptable to fish populations, where age and cohort are readily discernible from scales (Chapman 1967, 1968), and have been utilized in specific studies to evaluate environmental changes (Elwood and Waters 1969; Hunt 1969, 1971). However, these two methods are basically applicable also to any organism which can be aged (Neess and Dugdale 1959; Waters 1966; Negus 1966; Mathews and Westlake 1969).

The great disadvantage of the above three methods lies in the necessity to deal with a single species of known life history and, more specifically, to be able to age a given specimen to determine growth rates or the identity of the cohort to which it belongs. In the case of lake or stream benthos, where the fauna may consist of many species, perhaps hundreds, it clearly becomes impossible to estimate the production of the entire bottom fauna with any of these three methods. Yet, in quantitative ecosystem studies, or for the resource manager desiring, for example, the production rate of the bottom fauna supplying the food source for a fish population, such total estimates of bottom fauna production rates are highly desirable.

Recognizing the above difficulties in dealing with an entire bottom fauna, Hynes (1961) made a pioneer attempt to estimate the production of a stream invertebrate fauna in a Welsh stream. Although similar to a removal-summation method, Hynes's approach differed in that it was meant to sum the losses between successive size classes, essentially treating all species together, rather than between successive sample times. His early technique

contained conceptual errors, and some of these were corrected in a later paper that also enlarged on the theory and application of this new approach (Hynes and Coleman 1968). Hamilton (1969) recognized additional errors in this method and corrected these in a subsequent report, with which Hynes (1969) agreed. Simultaneously, Fager (1969) made some objections to Hamilton's ultimate technique and offered an alternate approach; however, Fager's suggested alternative was essentially a reversion to the original removal-summation method (mortality in time) as described above. The method as finally corrected and described by Hamilton (1969) is referred to here as the *Hynes method*.

A study of population dynamics and life history of a stream mayfly, *Ephemerella subvaria* McDunnough, including the estimate of annual production, was recently completed in a small central Minnesota stream, Luxemburg Creek, Stearns County, Minnesota (Crawford 1971). Although our objective was focused on the above parameters as they applied to this species (a dominant invertebrate of the bottom fauna serving as a major item of diet for the principal fish species, brown trout), the life history of *E. subvaria*, as elucidated in the results, was of such a simple and clearly discernible nature that the data appeared particularly amenable to the above-described four methods of estimating production rate. Thus, our objective here is to estimate annual production of this single species by the four methods for comparative purposes, primarily to test the validity of the Hynes method.

We are most grateful to William G. Klett for his generous cooperation in permitting us the use of his property through which the study section of Luxemburg Creek flows. We are also appreciative of the helpful suggestions of Andrew L. Hamilton who reviewed the manuscript. Assistance in identification of the mayfly was received from Edwin F. Cook.

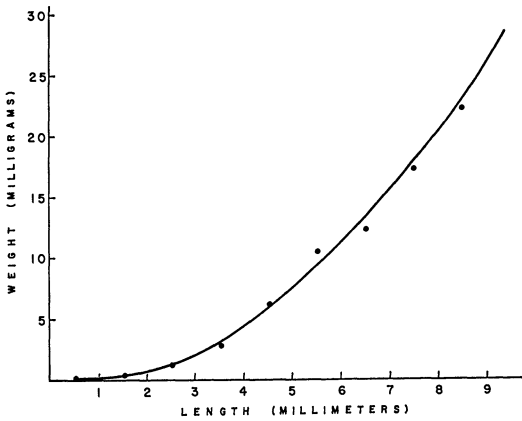


Fig. 1. Length-weight relationship for nymphs of *Ephemerella subvaria*.

LIFE HISTORY OF *EPHEMERELLA SUBVARIA*

Adults of *E. subvaria* emerged and oviposited in late spring; no nymphs remained in the stream by about 1 July. Eggs incubated through the summer months; by late August microscopic nymphs, presumably first instars, were observed. The first samples taken in which nymphs could be seen macroscopically and sorted in routine bottom sample analysis were in late September, although presumably on a somewhat earlier date they could have been sampled. Hatching period appeared relatively short, there being no small individuals present in November; this factor was one which greatly simplified and facilitated computational aspects of production estimation for several of the methods used. Growth of nymphs proceeded regularly from fall through winter and spring, leading to emergence in later spring and a succeeding generation.

METHODS

Bottom samples were collected with the stream bottom sampler described by Waters and Knapp (1961), which collected the fauna from an area of 0.1 m². Since *E. subvaria* nymphs were limited to riffles, samples were collected only from riffle areas of the stream, which constituted about 25% of the entire stream bottom in the study section, about 200 m long. Twenty sam-

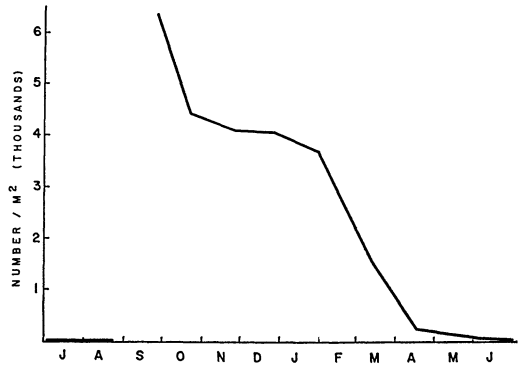


Fig. 2. Standing crop in numbers of nymphs of *Ephemerella subvaria* in Luxemburg Creek, 1968-1969.

ples were collected approximately each month from spring 1968 through summer 1969; on some sampling dates, fewer samples were taken because of weather, stream ice conditions, etc.

Nymphs of *E. subvaria* were sorted manually from the samples, separated into 1-mm size groups, and counted. All nymphs of a given size group were combined and wet-weighed, after centrifuging excess liquid, to obtain mean weights. From these data, a length-weight relationship was developed (Fig. 1), and then all standing crop data in weight were calculated from counts by size group and the length-weight relationship.

Specific methods for each of the production rate estimates, beyond those discussed above, are described below.

STANDING CROP AND GROWTH

Nymphs of *E. subvaria* appeared first in the September samples, at which time the highest number (6,350 m⁻²) was observed. Numbers declined during fall, stabilized somewhat in winter, and dropped sharply again in late winter and early spring (Fig. 2). A few individuals persisted into late spring. The basic data used in all production estimates, expressed in numbers of nymphs by size group and date, are summarized in Table 1. Standing crop data apply to the riffle sections only; standing crops in terms of the entire stream bottom

Table 1. Number of *Ephemerella subvaria* per square meter, by size group and date, 1968-1969. Samples taken 2 July, 28 July, 23 August 1968, and 1 July 1969 contained no nymphs

Size group length (mm)	26 Sep	22 Oct	27 Nov	27 Dec	30 Jan	12 Mar	17 Apr	06 Jun	Total
0-1	1,900	485	0	0	0	0	0	0	2,385
1-2	4,115	1,286	433	75	42	5	0	0	5,956
2-3	319	1,841	2,398	1,759	1,137	109	0	0	7,563
3-4	16	785	1,065	1,484	1,270	562	5	0	5,187
4-5	0	35	178	540	805	437	51	1	2,047
5-6	0	0	8	195	406	189	60	2	860
6-7	0	0	0	0	0	149	40	2	191
7-8	0	0	0	0	0	136	40	17	193
8-9	0	0	0	0	0	0	31	17	48
9-10	0	0	0	0	0	0	3	5	8
Total	6,350	4,432	4,082	4,053	3,660	1,587	230	44	24,438

would be about 0.25 times the reported values.

Standing crop in wet weight increased from September to a maximum in midwinter of over 13 g m⁻², then declined through late winter and spring (Fig. 3). The annual mean standing crop, including in the calculation those samples (11 series) in which nymphs were absent, was 4.6 g m⁻²; the cohort mean standing crop, calculated from September to June only, was 6.3 g m⁻².

The growth of the nymphs appeared to be approximately exponential from September through winter to late spring (Fig. 4). There appeared little evidence of a reduction in growth during winter, despite the fact that much of the stream was ice-covered for long periods, and water tem-

peratures were at or very near the freezing point.

Construction of size-frequency histograms assisted in elucidating the seasonal growth pattern and distribution of size groups with time (Fig. 5). From these histograms, it was obvious that the species was univoltine, simple in life history, and clearly amenable to calculation of production rate by various methods.

PRODUCTION

Calculation of production rate of *E. subvaria* by the four methods listed above was carried out using the basic data in numbers in Table 1 and the length-weight

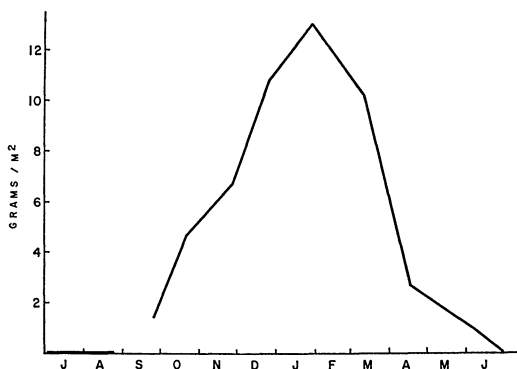


Fig. 3. Standing crop in wet weight of nymphs of *Ephemerella subvaria* in Luxemburg Creek, 1968-1969.

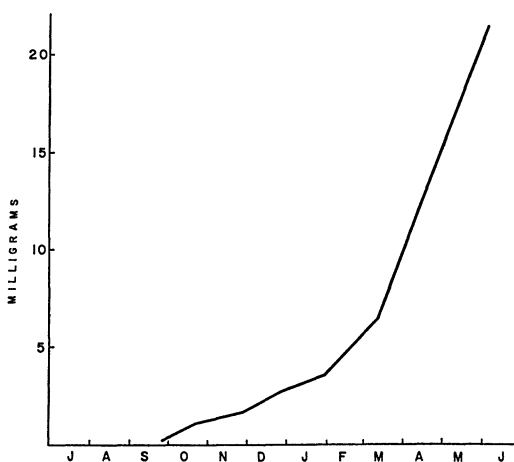


Fig. 4. Growth of *Ephemerella subvaria* as represented by mean individual weight, 1968-1969.

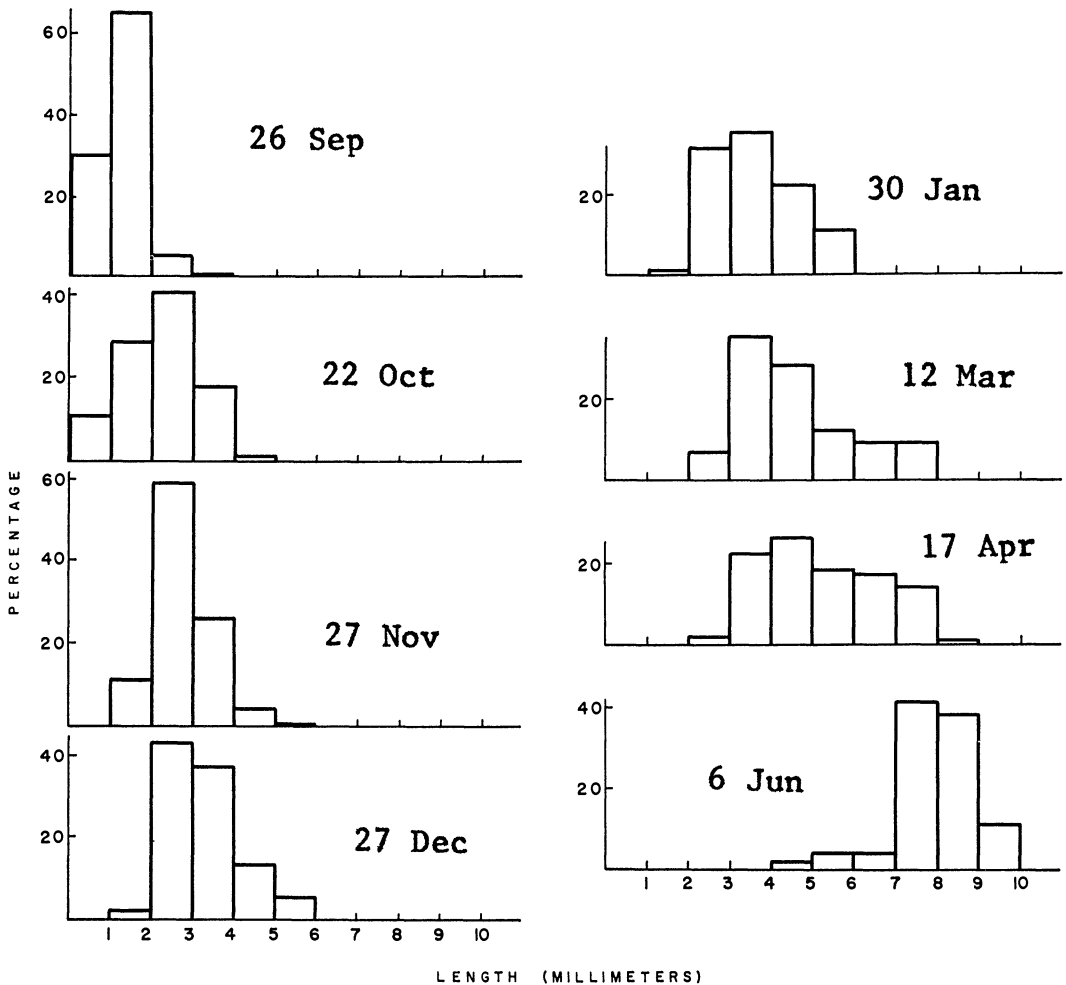


Fig. 5. Length frequencies by percentages of nymphs of *Ephemerella subvaria*, 1968-1969.

relationship in Fig. 1. Since this species was univoltine, annual production and cohort production were equivalent. In those methods where losses due to mortality or other removal were determined by a decrease in numbers, either between times or between size groups, the weight at time of loss was assumed to be the weight at the midlength point. This was considered the more valid assignment of weight loss, rather than a midweight point, as Hamilton (1969) points out. Weights at midlength points were determined with the length-weight relationship. Reported production rates apply to the riffle sections

only; in terms of the entire stream bottom, reported data would again be multiplied by about 0.25.

Removal-summation method

Production was calculated as the sum of losses, in weight, from one sampling time to the next, through the cohort life (Table 2). For example, on 26 September 6,350 individuals m^{-2} were present and on 22 October 4,432 were present, there being a loss of 1,918. The weight at loss, or midlength weight, determined from the length-weight relationship, was 0.6 mg, and the product of number loss and weight

Table 2. Calculation of production of *Ephemerella subvaria* by the removal-summation method

Date	No./m ²	Mean wt (mg)	Standing crop (g/m ²)	No. loss/m ²	Wt at loss (mg)	Wt loss (g/m ²)
26 Sep	6,350	0.23	1.46			
22 Oct	4,432	1.05	4.65	1,918	0.6	1.15
27 Nov	4,082	1.64	6.69	350	1.3	0.46
27 Dec	4,053	2.67	10.82	29	2.1	0.06
30 Jan	3,660	3.56	13.03	393	3.1	1.22
12 Mar	1,587	6.38	10.13	2,073	4.8	9.94
17 Apr	230	11.61	2.67	1,357	8.8	11.94
06 Jun	44	21.59	0.95	186	16.3	3.03
				44	25.0*	1.10
Production = Total losses =						28.90

*Weight at loss between 21.59 mg on 06 Jun and observed maximum of 29.00 mg.

at loss (1,918 m⁻² × 0.6 mg) was 1.15 g m⁻². The sum of all such losses through the cohort life was 28.90 g m⁻², the estimate of annual and cohort production.

Instantaneous growth method

Production by this method was calculated with the formula,

$$P = G\langle B \rangle$$

where, *P* = production in g m⁻² for the given interval of time, *G* = instantaneous rate of growth during this time, and $\langle B \rangle$ = mean standing crop in g m⁻² during the time interval (Ricker 1946; Allen 1949). Chapman (1967, 1968) discusses the details and application of the method. Our calculations were made separately for each interval between sampling dates from September to June (when nymphs were present) and summed for the total annual or cohort production (Table 3). *G*, instantaneous rate of growth, was computed as the natural logarithm of the ratio of the mean weight at the end of the interval to the mean weight at the beginning of the interval; $\langle B \rangle$, mean standing crop, was computed as the average of the standing crops at the beginning and end of the interval.

For example, for the interval from 26 September to 22 October, $G = \ln(1.05/0.23) = 1.52$, and $\langle B \rangle = (4.65 + 1.46)/2 = 3.06$. $P = G\langle B \rangle = 1.52 \times 3.06 = 4.65$ g m⁻². The sum of production for all intervals was 26.71 g m⁻², the annual and cohort production.

Table 3. Calculation of production of *Ephemerella subvaria* by the instantaneous growth method. *G* = instantaneous rate of growth, $\langle B \rangle$ = mean standing crop, *P* = production, for interval between successive dates

Date	Standing crop-B (g/m ²)	Mean wt (mg)	<i>G</i>	$\langle B \rangle$ (g/m ²)	<i>P</i> (g/m ²)
26 Sep	1.46	0.23			
22 Oct	4.65	1.05	1.52	3.06	4.65
27 Nov	6.69	1.64	0.44	5.67	2.49
27 Dec	10.82	2.67	0.49	8.76	4.29
30 Jan	13.03	3.56	0.29	11.93	3.46
12 Mar	10.13	6.38	0.58	11.58	6.72
17 Apr	2.67	11.61	0.60	6.40	3.84
06 Jun	0.95	21.59	0.62	1.81	1.12
			0.30*	0.48	0.14
Total production =					26.71

*Calculated as growth from 21.59 mg on 06 Jun to observed maximum of 29.00, assumed as of 01 Jul.

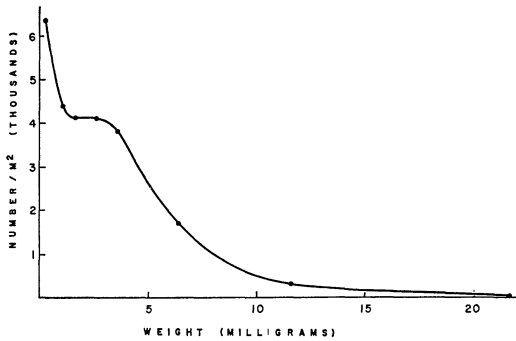


Fig. 6. Allen curve used for annual production estimate of *Ephemerella subvaria*.

Allen curve method

The growth-survivorship curve, or Allen curve, for *E. subvaria* was constructed by plotting No. m^{-2} on the ordinate and mean individual weight on the abscissa for each sampling date from September to June; the area under the curve, or production in terms of $g\ m^{-2}$, was 26.4 (Fig. 6). It is clear that this is somewhat of an underestimate, since at the time of the first sample from which nymphs were sorted (26 Sep-

tember), some growth and mortality had already occurred, and the first point should be higher and closer to the ordinate. However, the relative error in area so lost appeared to be small, particularly since part of this area was assignable to the previous generation in the form of the weight of eggs or newly hatched first instars, rather than to the subject cohort. The irregularity in the curve was due to low mortality, but continued growth, during winter.

Hynes method

Production calculated by the Hynes method involved the summing of losses from one size group to the next, assigning the weight at loss to the midlength point, as described above (Table 4). The table was constructed according to the form used by Hamilton (1969, his table 2), except that we used weight units directly. In some instances, negative results were obtained, and these were included in making the algebraic sum in the last column, as pointed out as essential in the method by Hamilton. The weight loss (column 7) was multiplied by the number of size groups,

Table 4. Calculation of production of *Ephemerella subvaria* by the Hynes method. Annual production based on 11 sets of samples, including those with no nymphs

Size group length (mm)	No./ m^2	Mean wt (mg)	Standing crop (g/m^2)	No. loss/ m^2	Wt at loss (mg)	Wt loss (g/m^2)	X 10 Production (g/m^2)
0-1	217	0.06	0.01				
1-2	541	0.24	0.13	-324	0.1	-0.03	-0.3
2-3	688	1.0	0.69	-147	0.6	-0.09	-0.9
3-4	472	2.9	1.37	216	1.9	0.41	4.1
4-5	186	5.6	1.04	286	4.2	1.20	12.0
5-6	78	9.1	0.71	108	7.4	0.80	8.0
6-7	17	13.1	0.22	61	11.0	0.67	6.7
7-8	18	17.6	0.32	-1	15.4	-0.02	-0.2
8-9	4	22.5	0.09	14	20.0	0.28	2.8
9-10	1	29.0	0.03	3	25.5	0.08	0.8
				1	29.0	0.03	0.3
					Total production =		33.3

("times loss" factor) or 10 in this case, as discussed by Hamilton, one of the corrections he made of Hynes and Coleman's (1968) treatment. For example, between the 2-3-mm size group and the 3-4-mm size group, there was a loss of 216 individuals m^{-2} . Weight at loss, or weight at mid-length, was 1.9 mg. The product of $216 \times 1.9 \times 10$ is a positive $4.1 \text{ g } m^{-2}$, appearing in column 8. On the other hand, between the 0-1-mm size group and the 1-2-mm size group, there was an increase (or negative loss) of 324 individuals m^{-2} . The product, $324 \times 0.1 \times 10$, is a negative $0.3 \text{ g } m^{-2}$ in column 8. The algebraic sum of the products in column 8, or annual production, was $33.3 \text{ g } m^{-2}$.

The mean No. m^{-2} in column 2 was calculated for each size group using the complete annual set of samples (11), rather than only those sets that contained nymphs (8), to estimate annual production. Computing cohort production by using only the 8 sets of samples would result in higher numbers in column 2 and a higher estimate of production, which would be an obvious error. For the same reason, only annual mean standing crop could be calculated. Hamilton (1969) emphasizes that the products in the last column are usually not accurate for a particular size group, but rather it is the total of this column that is the relevant datum. The sum of the standing crops for the size groups in column 4, totaling $4.6 \text{ g } m^{-2}$, constituted the mean annual standing crop.

TURNOVER RATIO

The production estimates are summarized in Table 5 as are turnover ratios. Although annual and cohort production are the same for this univoltine species, the turnover ratios are different. Annual turnover ratio is defined as the annual production divided by the annual mean standing crop; cohort turnover ratio is the cohort production (equal to annual production in the present case) divided by the mean cohort standing crop. The annual turnover ratio is the larger because the mean annual standing crop is the smaller, being

Table 5. Summary of annual production and turnover ratios estimated for *Ephemera subvaria* by the four methods

Method	Annual production (g/m^2)	Cohort turnover ratio	Annual turnover ratio
Removal-summation	28.9	4.6	6.3
Instantaneous growth	26.7	4.2	5.8
Allen curve	26.4	4.2	5.7
Hynes	33.3	---	7.2

calculated over the full year and including the 11 series of samples, some empty of nymphs (Waters 1969). Cohort turnover ratio, on the other hand, is smaller because the mean cohort standing crop is higher, being calculated only for that portion of the year in which the cohort exists in the nymphal form. Cohort turnover ratio cannot be computed in the Hynes method when the length of nymphal life, or cohort life, is less than a full year.

DISCUSSION

The most obvious generalization that emerges from comparison of the results from the four methods is that, while the production estimates from the removal-summation, instantaneous growth, and Allen curve methods generally agree (about $28 \text{ g } m^{-2}$), the estimate by the Hynes method appears substantially higher ($33.3 \text{ g } m^{-2}$)—15.2 to 26.1% higher. The Hynes method may be therefore suspect as resulting in an overestimate, although caution naturally should be exercised in making such a conclusion.

Two possibilities are suggested to account for an overestimate in the Hynes method.

One is that, for *E. subvaria*, there may be a size differential between sexes, with the female of the last instar being the larger; Jennings (1935) indicates such a differential in the adults of *E. invaria*, a closely related species. This possibility, if true, would invalidate one of the principal assumptions in the method, namely, that all "species" must have the capability of growing to the same maximum size (Hamilton 1969). In this case, the "times loss"

correction factor of 10 is applied to the males as well as to the females, with the result being an overestimate when the sexes are not differentiated. A correction could be made, of course, by making separate calculations by sex, if possible. Even so, this factor alone would not appear to be able to account for the entire difference or even a major part of it.

The second possibility that may account for a high estimate by the Hynes method is, admittedly, highly subjective. This has to do with the presence of only a very low number of individuals in the largest size groups, a mean of only 1 m^{-2} in the 10th group here. [This was also true for several species in Hynes' (1961) original data, upon which the method was developed.] This result may lead to some skepticism, when such relatively few individuals result in a much larger effect on the total estimate; 10 size groups, for example, make the estimate more than 10% higher than if 9 groups were used as the "times loss" factor. The presence of few individuals in the largest size groups might merely be the result of technician error, body length extension in the preservative used, etc., resulting in a larger number of recorded size groups than actually exists.

The arbitrary selection of a "times loss" factor one or two size groups lower than observed or a correction factor of about 0.85 or 0.90, especially when very low numbers appear in the largest size groups, may be further corrections in the method. Yet this type of correction has no mathematical justification, and it should be considered seriously only after further empirical studies with similar results.

It is not our intention to discourage or reject the Hynes method on the basis of these results. To the contrary, it is obviously of great advantage to have this method available as a working tool if it can be used to obtain even approximately valid results for an entire bottom fauna. Hynes and Coleman (1968) emphasized that it was intended to obtain approximations that may be crude but have the merit of simplicity and applicability to an entire

fauna. The utility of such information to resource managers is, of course, very great, and it cannot be obtained by the other three methods.

An examination of the numbers appearing in column 2 of Table 4 (No. m^{-2} by size groups) leads to the obvious conclusion that many small individuals were missed in the sampling, because they passed through the mesh in the sampler, were missed in the sample analysis, or grew through a size group or two between sample dates. Whatever the reason, such failure to sample these small individuals adequately must result in an underestimate of production by all methods. The degree of error is not determinable with precision. However, extrapolation of a "catch curve," constructed on semilog paper with the data in column 2, to provide possible corrections in numbers within the smallest size groups, permitted some recalculations, albeit rather rough, of production by all four methods. These "corrections" suggested an underestimate on the order of 10 to 20%.

The turnover ratios ($P:B$ of some authors) are of some special interest, as they also allow a comparison among methods (Table 5), as well as with other empirical and theoretical turnover ratios. In a previous report (Waters 1969), it was pointed out that the cohort turnover ratio obtained by various authors was fairly constant, usually about 2.5 to 5. A consideration of cohort turnover ratios in the same paper, based on several series of theoretical Allen curves, suggested a relatively constant cohort turnover ratio of about 3.5. The present results suggest a slightly higher ratio of about 4 to 4.5 (Table 5). The reason is that the numbers do not decrease sharply with emergence, postulated as being the usual case (final population 10% of initial) in the previous paper (Waters 1969). With a final population of 1% and logarithmic growth (Type III), the theoretical cohort turnover ratio of 4.6 (figure 6 and table 4: Waters 1969) fits well with the cohort turnover ratios obtained in the present empirical results.

The life-cycle instantaneous growth rate should be similar to the cohort turnover ratio, although it was usually about one unit higher, as calculated for several species of aquatic invertebrates (table 5: Waters 1969). In the present case, life-cycle instantaneous growth rate is calculated as $\ln(29/0.06) = 6.2$, or 1.6 to 2 units higher than the calculated cohort turnover ratios.

It is, of course, the annual turnover ratio which is of greatest practical use. This cannot be expected to be constant, since it is dependent on the voltinism and, even for a univoltine species, on the proportion of the year the species is present in the aquatic, immature form. It will be higher than the cohort turnover ratio for multivoltine species and lower for hemivoltine species. It will also be higher even for univoltine species, because the organisms will be in the egg, pupal, or adult stage for part of the year (Waters 1969). The annual turnover ratio in this study, about 6, is of course higher than the cohort turnover ratio, 4 to 4.5. The annual turnover ratio of 7.2 obtained with the Hynes method is the result of the higher production estimated and may be in error for the same reason as for the production estimate.

It is obvious that more empirical results are desirable. The development of a reliable and simple method, even though approximate, to estimate annual production of an entire bottom fauna or of separate fractions of a fauna would be of much value to resource managers. The Hynes method, with the possible limitation that it may produce an overestimate, shows promise in being capable of accomplishing this objective.

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