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Mayfly production in a Colorado mountain stream: an assessment of methods for synchronous and non-synchronous species

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Abstract

Year-round collections of mayflies (Ephemeroptera) from a Colorado mountain stream allowed critical examination of several methods of calculating production for species with different life cycles. Five of the six numerically dominant species exhibited slow seasonal, univoltine life cycles. *Baetis tricaudatus* was bivoltine. Two species demonstrated well synchronized development, three species were poorly synchronized and a sixth was intermediate. Mean density and biomass data from each sampling date were used to ascertain the goodness-of-fit of each species to the Allen curve. It is proposed that such information can provide quantitative criteria for identifying species with well synchronized development and thereby determine when it is appropriate to directly apply cohort methods while avoiding time intensive body size (e.g. head width) measurements necessary for size-frequency analyses. In addition, these data demonstrate that species specific production varies with gross changes in elevation.

Introduction

Secondary production studies may provide considerable insight into the dynamics of aquatic ecosystems (Benke, 1984). Aquatic ecologists have used production data to quantify the functional roles of both individual species and feeding guilds in ecosystem processes (Haefner & Wallace, 1981; Benke & Wallace, 1980; Hall *et al.*, 1970; Morgan *et al.*, 1980). In addition to their heuristic value, secondary production estimates provide important data for resource managers by indicating the amount of energy potentially available to higher trophic levels.

Most studies concerning secondary production have used one of the following methods: (1) Allen curve, (2) removal-summation, (3) instantaneous growth, and (4) size-frequency (Waters, 1977). The first three methods record changes in the numbers and mean individual biomass of actual cohorts from egg hatch to emergence (in the case of amphibiotic insects). These 'actual cohort' methods should only be applied to species that exhibit a high degree of developmental synchrony (distinctly separate cohorts) or to less synchronized species (i.e. for species with several size classes present simultaneously) for which cohort recognition is possible. The size-frequency method, which follows an 'average cohort', is used when individual cohorts are difficult to distinguish.

The size-frequency method of computing production requires data on the abundance of each size class represented throughout a species' life cycle. Also, cohort production methods require size measurements to determine life cycle characteristics including cohort identification and synchrony.

These data are normally based on the time consuming task of measuring the head capsule width or body length for each individual collected. This task can be avoided and actual cohort production methods applied if the plot of density versus mean individual biomass for each date closely fits the following function: $Y = Ae^{-Bx} + C$. This equation describes the Allen curve or relationship between density (Y) and mean individual biomass (x) of a population as they change through time. The graph of this function exponentially descends (B is equal to the slope) from A (the Y intercept or approximately the maximum density value in this case) to C, the smallest density value determined. To avoid fitting a curve with unrealistic negative density values, a lower limit of 1 was established for C. Therefore, the curve could not cross the x axis but would asymptotically approach 1. A similar equation describing the relationship between density and mean individual biomass was used to compute production for larval Chironomidae (Neess and Dugdale, 1959). If a species' Allen curve provides an adequate fit to this function (*D. grandis*, Fig. 1) then actual cohort techniques are reliable in estimating their production because they are represented by a single well synchronized cohort. A lack-of-fit to the Allen curve may also reflect inadequate sampling (e.g., insufficient number of samples) even when a species is well synchronized. This problem must be considered at the outset of any study designed to determine secondary production. Also, cohort production methods can be applied to species that are poorly synchronized but size measurements are required to determine the number of cohorts and their duration.

During a year-round study of the benthos of a Colorado mountain stream, 6 out 12 mayfly species, were sufficiently abundant to allow critical examination of secondary production. The objectives of this study were: (1) to develop criteria (based on goodness-of-fit to the Allen curve) to identify synchronized species and thereby determine when it is appropriate to apply actual cohort production methods without body size measurements and (2) to describe the production and life cycle characteristics of the dominant Ephemeroptera in a Rocky Mountain stream.

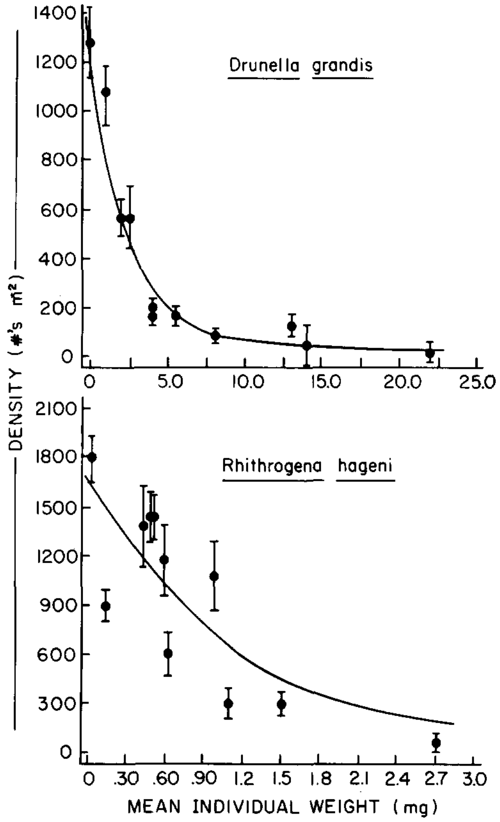

Fig. 1. Non-linear regression, based on the equation describing the Allen curve (see text), of density versus mean individual weight for *Drunella grandis* and *Rhithrogena hageni.* Note the tight fit of the observed monthly data points to the predicted curve for *D. grandis* and the poor fit for *R. hageni.* The vertical bars represented one standard error from the calculated mean density and are therefore, an estimate of sample precision.

Methods and site descriptions

Specimens were collected monthly with a Surber sampler (929 cm²; 240 μm mesh) from four stations in the Cache la Poudre River in northern Colorado (40° 40′ N; 105° 30′ W). An upper elevation site pair (2556 and 2281 m a.s.l.) and a lower elevation site pair (1850 and 1810 m a.s.l.) were sampled at locations above and below proposed reservoir sites. Three (Nov.–Feb.) or four (Mar.–Oct.) Surber samples were taken at each site for one year. Surber samples were combined for upper and lower elevation site pairs increasing the sample size to 6 or 8 Surber samples per date. Water temperature was recorded as monthly minima and maxima at each site. The upper site pair, located on a fourth order reach, was ice covered for about 4 months, remained near 0 °C for 6 months and attained an annual maximum of 20 °C. The lower site pair, located on a fifth order reach, was iced covered for about 3 months, remained near 0 °C for approximately 5 months and attained an annual maximum of 24 °C. Otherwise, all locations exhibited similar physico-chemical conditions (soft water, circumneutral pH, high gradient, rubble substrate, well-oxygenated). Life cycle characteristics were the same within the site pairs for each mayfly species, although species occurrences and abundances differed between the upper and lower site pairs. *Ephemerella infrequens* (McDunnough), *Rhithrogena hageni* (Eaton) and *Baetis tricaudatus* (Dodds) were relatively abundant at all sites and were used to compare species production between the two elevations. In order to compare production methods between well synchronized and poorly synchronized species, *Paraleptophlebia heteronea* (McDunnough), *Drunella grandis* (Eaton) and *Drunella doddsi* (Needham) were included in this analysis. Data for *P. heteronea* were collected from the lower site pair and data for *D. grandis* and *D. doddsi* were collected from the upper site pair. All together, production was calculated for 6 species of mayflies which comprised (numerically) 87% of the total Ephemeroptera.

Following identification, all nymphs were divided into 0.1 mm size classes based on head capsule width and dried at 60 °C for 48 hours. Production was recorded as grams dry weight m^{-2} $year^{-1}$, correcting for variable cohort production intervals when necessary (Benke, 1979). The standard errors for size-frequency estimates (Tables 1 & 2) were calculated using the method of Kreuger and Martin (1980). Derivative-free, non-linear regression was used to fit the exponential function describing the Allen curve to the density and mean individual biomass data from each species. Goodness-of-fit (R^2 values) were determined using BMDP (specifically BMDPAR) statistical software. Normal probability plots and plots of standardized residuals versus predicted values were used to affirm the parametric assumptions of normality and homogeneous variances.

Table 1. Mayflies from a northern Colorado stream divided into 3 groups according to their goodness-of-fit to the Allen curve (R^2 values). Production (grams dry wt m^{-2} yr^{-1}), mean standing crop (B, grams m^{-2}) and P/B ratios are estimated by 3 techniques: removal-summation (RS), instantaneous growth (IG) and size-frequency (SF). Standard errors for size-frequency estimates are in parentheses. An '*' indicates inappropriate application of method (see text). Production estimates for *D. grandis, D. doddsi, R. hageni* and *E. infrequens* are based on samples collected at the upper site location. *Baetis tricaudatus* estimates are based on data collected from the lower site location.

Species	Production					Annual P/B Ratios		
	R^2	B	RS	IG	SF	RS	IG	SF
Group 1								
D. grandis	0.98	0.81	4.05	4.05	3.95 (0.26)	5.0	5.0	4.9
D. doddsi	0.91	0.48	2.14	2.30	2.56 (0.31)	4.4	4.6	5.2
Group 2								
P. heteronea	0.81	0.21	0.57*	0.72*	0.85 (0.24)	2.7*	3.4*	4.1
Group 3								
R. hageni	0.52	0.44	0.91*	1.30*	2.20 (0.52)	2.0*	2.8*	5.0
E. infrequens	0.61	0.24	0.95*	0.87*	1.10 (0.29)	3.9*	3.6*	4.6
B. tricaudatus	0.67	0.20	0.59*	0.99*	3.15 (0.47)	3.0*	4.9*	15.8

Table 2. Production (grams dry wt m^{-2} yr^{-1}), mean standing crop (B, grams m^{-2}) and annual P/B ratios for mayflies from two reaches of a northern Colorado River. Standard errors for size-frequency estimates are in parentheses.

Species	Upper Reach[a]			Lower Reach[b]		
	SF	B	P/B	SF	B	P/B
R. hageni	2.2 (0.52)	0.44	5.0	0.72 (0.28)	0.13	5.5
E. infrequens	1.1 (0.29)	0.24	4.6	1.63 (0.83)	0.27	6.0
B. tricaudatus	0.64 (0.38)	0.10	6.3	3.15 (0.47)	0.20	15.8

[a] 2500 m a.s.l.; [b] 1800 m a.s.l.

Results and discussion

Life cycle descriptions and elevational distributions

Rhithrogena hageni demonstrated a relatively unsynchronized, univoltine, slow seasonal life cycle with more than one cohort per generation. At the upper site locations emergence extended from approximately mid-June through August. Large numbers of early instars appeared in July. At the lower site locations emergence began earlier (mid-March) and extended through July with large numbers of early instars appearing in August. This species elevational distribution extends from approximately 2800 m a.s.l. to the plains (approx. 1550 m a.s.l.) (Ward, 1986). Therefore, all sites sampled during the present study were well within the elevational distribution of this species.

Ephemerella infrequens also demonstrated a relatively unsynchronized, univoltine, slow seasonal life cycle with more than one cohort per generation. At the upper site locations emergence occurred in July and August. There was a pulse of early instars in September. At the lower site locations emergence began earlier (June) and extended through July with a large pulse of early instars in August. This species elevational distribution extends from approximately 2650 m a.s.l. to the plains (Ward, 1986). Therefore, the upper site locations are very near the upper extent of this species elevational distribution.

Baetis tricaudatus appeared to demonstrate a bivoltine cycle. Some nymphs over-wintered in the nymphal stage and there was an abundance of early instars in September and April. Adults were identified from both summer and winter collections. Based on these data, determination of cohorts and egg dormancy were not possible. The average larval development time, which is the same as CPI values in univoltine populations (Benke, 1979), appeared to be approximately 4 months. Therefore, production estimates, based on the size-frequency method, were multiplied by 12/4 in order to calculate annual production. The elevation range of this species extends from 3100 m a.s.l. to the plains (Ward, 1986). Therefore, all sites sampled in the present study were well within the elevational limits for this species.

Paraleptophlebia heteronea demonstrated a univoltine, slow seasonal life cycle. Emergence occurred in June and July and there was a large pulse of early instars in September. This species was abundant only at the lower site pair.

Drunella grandis demonstrated a univoltine, slow seasonal life cycle where a generation was represented by a single well synchronized cohort. Emergence occurred from late June to early July and early instars were abundant in August. *D. doddsi* also demonstrated a univoltine, slow seasonal life cycle where a generation was represented by a single well synchronized cohort. However, emergence occurred in early June and early instars were abundant in July. Although both species were present at the lower site pair, they were abundant only at the upper location.

Production estimates

As expected, the exponential power function (Allen curve) was best fit by univoltine species which demonstrate a single well synchronized cohort per generation (see *D. grandis* and *D. doddsi* R^2 values, Table 1). Size-frequency measurements would not be necessary for these species. Their tight fit ($R^2 > 0.90$) to the Allen curve demonstrated sufficient cohort synchronization to warrent direct application of actual cohort techniques. Data from Waters and Crawford (1973) for the stream mayfly *Ephemerella subvaria* have been used to illustrate the practice of cohort production estimates (Benke, 1984). Like the synchronized species of the present study, *E. subvaria* exhibits a tight fit ($R^2 = 0.97$) to the Allen curve. When compared to cohort techniques, the size-frequency method provided a reliable estimate of production (Table 1). It is interesting to note that the species attaining the largest mean individual biomass (*D. grandis*) had the largest production. It was greater than the small but abundant bivoltine species, *B. tricaudatus* (Table 1).

Species that were poorly synchronized (group 3, Table 1) demonstrated a lack of developmental synchronization and therefore poorly fit ($R^2 < 0.67$) the Allen curve. Size-frequency data were necessary to estimate production. Cohorts were difficult to distinguish; therefore, the application of cohort methods was inappropriate for these species. The application of cohort production methods to unsynchronized species, when cohorts are difficult to distinguish, produces inaccurate estimates (see group 3, Table 1).

The previous species either provided a very good or very poor fit to the Allen curve. In order to establish a criterion based on a goodness-of-fit analysis, it was necessary to analyze intermediate conditions. *Paraleptophlebia heteronea* provided a reasonably tight fit to the Allen curve ($R^2 = 0.81$). However, a size-frequency analysis of *P. heteronea* indicated that it was less synchronized than either *D. grandis* or *D. doddsi* (Fig. 2 and Table 1). In addition, cohort production estimates were considerably lower than the size-frequency estimate of production (Table 1). These results suggest that moderately synchronized species can provide a reasonably tight fit to the Allen curve but that application of cohort methods without body size measurements (e.g. head width) would be unwarranted.

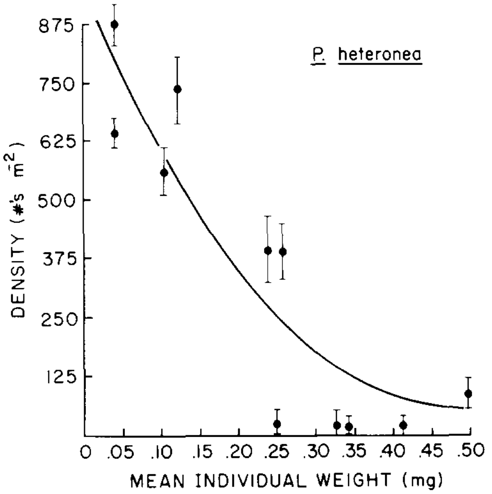

Fig. 2. Non-linear regression, based on the equation describing the Allen curve (see text), of density versus mean individual weight for *Paraleptophlebia heteronea*. The vertical bars represent one standard error from the calculated mean density.

Species specific relationships between production and elevation are worth noting even though there are only two locations. The elevational range of each species has been determined for a nearby drainage basin (Ward, 1986). Both the upper and lower site pairs were well within the elevational range of *R. hageni*. However, its production at the upper site pair was 305% greater than at the lower site pair (Table 2). *Ephemeralla infrequens* production was 148% greater at the lower sites (Table 2). The location of the upper site pair is very close to the elevational upper limit for this species (Ward, 1986). In addition, production was 492% greater at the lower sites for *B. tricaudatus* (Table 2) even though both upper and lower site pairs were within its elevational range (Ward, 1986). The thermal equilibrium hypothesis (Vannote and Sweeney, 1980) suggests that adult body size and fecundity of hemimetabolous aquatic insects are maximized where the temperature regime provides optimal thermal conditions for nymphal growth and development. A temperature regime that deviates from the optimum may result in smaller, less fecund adults. Data from the present study show that production may vary considerably as a function of elevation. Although many factors influence production, it may be, based on Vannote and Sweeney's hypothesis, that *R. hageni* is closer to its optimum temperature regime at the upper site pair where production was 305% greater than at the lower site. Whereas, the opposite appears to be the case for *E. infrequens* and *B. tricaudatus*.

Summary

All mayfly species, except *B. tricaudatus*, used for this analysis demonstrated a univoltine, slow seasonal life cycle. These species were separated into three groups according to their degree of developmental synchrony. These data suggest that species that fit the Allen curve with an R^2 value of 0.90 or greater adequately meet the assumptions required to use actual cohort production estimates. This technique is an easy method of identifying well synchronized species. In such cases, size-frequency data based on head capsule width measurements are not necessary. Application of cohort methods to species that demonstrate poor developmental synchrony, where cohorts are difficult to distinguish, produces inaccurate results. In addition, these data demonstrate that single species production varies considerably with gross changes in elevation.

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