

Spatial and temporal variation in the growth and production of *Ephoron leukon* (Ephemeroptera:Polymitarcyidae)

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Abstract. Variation in growth rates, maximum nymphal sizes, densities, and production estimates of *Ephoron leukon* (Ephemeroptera:Polymitarcyidae) were investigated at two sites over a 3-yr period on the South River, Virginia. *Ephoron leukon* is univoltine with development confined to a short (3-4 mo) period during the summer followed by a long (8-9 mo) egg diapause. The short growing season combined with a high degree of developmental synchrony makes this species ideal for comparative field studies.

Relative growth rates ranged from 0.014 to 0.028 mg/mg/day and significant differences were observed between sites and years. Spatial differences in growth rates were explained by between-site differences in thermal regime but between-year differences were not. Differences in average densities between years may have been important in explaining annual differences in growth rates.

Maximum nymphal weights averaged between 3.22 and 4.78 mg (AFDM) and were significantly higher at the downstream site for all three years. Differences were attributed to faster growth rates combined with relatively small differences in cohort production intervals.

Average densities ranged from 117 to 602 individuals/m², and significant differences were observed between sites and years, with annual differences being most pronounced. Average densities were related more to initial densities than to mortality rates and thus factors governing number of eggs laid and hatching success were responsible for annual differences in densities. The data suggest that hatching success may have been influenced by the thermal regime of the previous winter.

Annual production ranged from 398 to 2857 mg/m²/yr and differences were significant between sites and years. Much of the between-site variation in production estimates was explained by differences in maximum nymphal weight, while differences in mean densities explained much of the annual variation in production.

Key words: *Ephoron leukon*, life history variation, temperature, production, growth.

Considerable variation in the life histories of aquatic insects has been reported (Butler 1984). Even within a species, significant amounts of variation have been observed among populations for such life history parameters as voltinism (Ward and Stanford 1982), growth rates (Sweeney 1978, Humpesch 1979, Sweeney and Vannote 1981), and secondary production (Benke and Wallace 1980, Parker and Voshell 1983, Smock et al. 1985, Mackay and Waters 1986). Most attempts to explain this variation have focused on naturally occurring, geographic differences in environmental conditions such as water temperature, food quality and/or quantity, and photoperiod (Sweeney 1984), or on man-made alterations in environmental conditions such as flow regime (Boles 1981, Parker and Voshell 1983, Mackay and Waters 1986), and thermal modification (Ward and Stanford 1982, Rader and Ward 1989).

However, most quantitative studies in streams have been based on short-term data sets (Resh

and Rosenberg 1989). Therefore, much of the information regarding life histories has been little more than snapshots in time. As a result, it is impossible to determine whether estimates derived from such studies represent an average or some extreme. The importance of long-term studies has been emphasized by several investigators (e.g., Strayer 1986, Wolf et al. 1987), and the sparsity of such studies in the aquatic literature has been pointed out by McElravy et al. (1989). It is clear that to describe the life history of one or more populations, an accurate assessment of both geographic and temporal variation in the traits of interest are necessary.

Ephoron leukon is a burrowing mayfly which inhabits the riffle areas of streams in the eastern half of North America (McCafferty 1975). Previous studies suggest a long egg diapause and a short growing season confined to the summer months for both North American species of the genus (Ide 1935, Edmunds et al. 1956, Britt 1962). As a result, temporal and spatial differences in

TABLE 1. Mean (± 1 SE) values for physical and chemical variables at two sites on the South River, plus estimates of seston concentrations and algal biomass.

	Upstream	Downstream
pH ^a	7.4 (0.15)	8.0 (0.20)
Alkalinity (mg Ca CO ₃ /L) ^a	95.0 (4.8)	102.4 (3.3)
Hardness (mg Ca CO ₃ /L) ^a	152 (16)	182 (19)
Conductivity (μ Mhos/cm ²) ^a	198 (19)	285 (26)
Nitrate (mg/L) ^a	0.70 (0.04)	3.50 (0.29)
Orthophosphate (mg/L) ^a	0.05 (0.00)	0.23 (0.02)
Total phosphate (mg/L) ^a	0.07 (0.01)	0.27 (0.02)
Substrate size (cm ³) ^a	305 (9)	233 (10)
Stream flow (cm/s) ^a	80.4 (6.0)	81.3 (15.6)
Total seston (mg AFDM/L) ^b	2.40 (0.39)	2.12 (0.38)
Algal biomass (mg AFDM/cm ²) ^c	0.82 (0.27)	1.12 (0.33)
Chlorophyll- <i>a</i> (mg/cm ²) ^c	46.29 (17.96)	54.14 (27.04)

^a Monthly values averaged over 3 years (Aug 1984–Nov 1987).

^b Monthly values averaged over 2 years (Aug 1985–Mar 1987).

^c Monthly values averaged over four months (May–Aug 1984).

environmental conditions would have less time to affect the magnitude of many life history parameters such as growth rates, maximum sizes, and production rates. Therefore, a minimum amount of variation may be expected relative to other species of aquatic insects with longer life cycles. The specific objectives of our study were to 1) describe the life history and estimate the secondary production of *Ephoron leukon* on the South River, Virginia; 2) determine the spatial (two sites) and temporal (three years) variation in both life history and production estimates; and 3) examine the extent to which temperature explained the observed variation.

Study Sites

The South River is a fourth-order tributary of the South Fork of the Shenandoah River in north-central Virginia. The drainage basin of the South River is primarily limestone and shale with a diverse riparian forest. The rural area along the river is used extensively for crops and livestock.

Two sites were chosen on the basis of ecological similarity. One site (38°2'N, 78°55'W) was about 2.5 km upstream of Waynesboro, Virginia, and the other (38°9'N, 78°55'W) was about 15 km downstream of Waynesboro. The two sites will be referred to as upstream and downstream sites respectively in the text. A complete list of physical and chemical measurements taken from both sites is shown in Table 1. The

two sites were similar in all variables except summer water temperatures (Fig. 1) and nutrients, both of which were higher at the downstream site. However, estimates of algal biomass and seston concentrations were not significantly different at the two sites (Table 1) and therefore it is not clear whether food supplies were actually higher downstream. Higher nutrient concentrations at the downstream site were due to effluent from the Waynesboro sewage treatment plant.

Methods

Sampling and laboratory procedures

To obtain quantitative estimates of densities and relative abundances of the various size classes, six Hess samples were taken at random towards the end of each month during the study period (August 1984 through October 1987). Since growth of *E. leukon* was rapid and confined to summer, an extra set of samples ($n = 3$) was taken near the middle of each month during the summers of 1986 and 1987. All benthic material located within the frame of the sampler (0.1 m²) down to bedrock or a depth of fifteen centimeters was washed into the collecting net (mesh = 243 μ m) and preserved with 10% formalin. Width of head capsules was measured to the nearest 0.01 mm using an ocular micrometer, and ten 0.2-mm size classes were established ranging from 0.5 to 2.5 mm. Num-

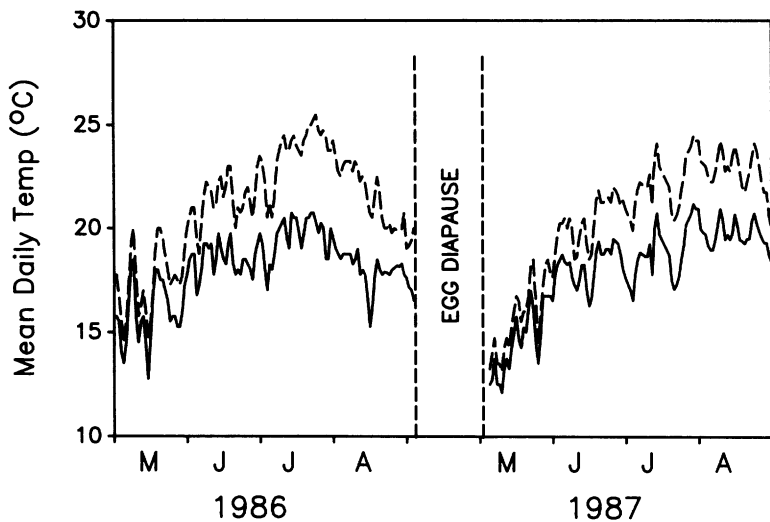


FIG. 1. Mean daily water temperature at upstream (solid lines) and downstream sites (dashed lines) for summers of 1986 and 1987.

bers of nymphs per size class and the proportion of each size class per collection date were calculated for each site.

Monthly estimates of ash-free dry mass (AFDM) for each size class were based upon the weights of several (3–35) unpreserved individuals of each size collected separately with a kick net. Nymphs used in weighings were placed in a drying oven (55°C) for 24 h and then transferred to a desiccator for an additional 24 h. Oven-dried specimens were weighed on a Cahn 28 electrobalance to the nearest μg to obtain dry mass and then ashed in a muffle furnace (500°C) for 1 h and reweighed to obtain AFDM. Variation in weight within a size class never exceeded 30% of the mean. Average weight of a particular size class was then multiplied by the relative abundance of that size class for that sampling date. These values were summed to obtain the weight of an average individual in the population for each sampling date.

Water temperatures were recorded continuously at both sites using submersible thermographs. Accumulated degree-days above specific thresholds were calculated by integrating thermograph tapes with a digital planimeter.

Growth

The cohort production interval of *E. leukon* is very short, thus errors resulting from differing

dates of birth make comparisons of growth rates between cohorts tenuous (Hawkins 1986). To correct for differing dates of birth, weight data were log transformed and a regression line was fitted to the straight-line portion of the respective growth curves. The regression equation was used to predict the date on which 100% of the individuals were the weight of size class one. Relative growth rates were then calculated from the corrected (i.e., days from hatching) growth curves. Statistical comparisons of growth rates between sites and years were made using the *t*-test for parallelism (Kleinbaum and Kupper 1978).

As with hatching dates, reasonable estimates for emergence periods were necessary in order to describe the cohort production interval (CPI) for each cohort and to minimize the error associated with estimates of mean standing stocks and turnover ratios. When mortality was >75% between two successive sampling intervals during the last half of the growing season, we assumed peak emergence occurred sometime between those dates. We define peak emergence to be the date in which most emergence takes place (i.e., the mode of the distribution).

Log of mean individual weight for each cohort was regressed against degree-day accumulation above 13°C to determine the relationship between growth and temperature. If differences in growth rates between cohorts are

primarily the result of differences in temperature, all cohorts would show the same relationship (i.e., slopes would not be significantly different from each other). This hypothesis was also tested using the *t*-test. A threshold of 13°C was chosen because it was found to be the physiological lower limit of growth and development in the closely-related *E. album* (D. J. Giberson, Freshwater Institute, Winnipeg, personal communication). As water temperatures near predicted hatching dates were between 14.2 and 16.3°C, the same analysis was also carried out using a 15°C threshold. No significant differences in patterns were observed and therefore only the 13°C analysis is reported.

Survivorship

Shapes of the survivorship curves varied and therefore no single transformation linearized the data for all cohorts. As a result, comparison of mortality rates between cohorts was impossible. Also, densities observed for a particular sample date could not be compared between cohorts because each date corresponded to a different point in each population's development, owing to differing dates of birth.

However, average densities could be calculated for each cohort by integrating the area under the survivorship curves and dividing by the CPI. Confidence limits (95%) could then be calculated by the boot-strap method (Efron and Gong 1983) thus enabling us to compare densities between cohorts. See Gilinsky and Bambach (1986) for a simplified explanation of the boot-strap method. Area under the survivorship curves was calculated algebraically using the increment-summation method.

Production

Production was calculated for all cohorts using the increment-summation method (Benke 1984). Data and calculations of production for all cohorts will be made available upon request. Production of each cohort was the sum of the weight-lost column plus the initial biomass, and thus avoided underestimation of production (see Morin et al. 1987). Confidence limits (95%) were generated for production estimates using the boot-strap method. Statistical differences in production and density estimates between sites and years were inferred according to overlaps

in 95% confidence limits estimated for one site or year and the mean of the other, and vice versa.

Results

Temperature

Summer water temperatures were warmer at the downstream site in both years. This pattern was most pronounced in 1986 when the maximum average daily temperature was >4°C warmer at the downstream site (Fig. 1). Consequently, the downstream site accumulated nearly 400 more degree-days above zero than the upstream site between 1 May and 21 August 1986. Patterns were similar, although between-site differences were less pronounced, in 1987.

Both sites warmed faster in 1986 than in 1987 with mean daily temperatures being one or two degrees higher throughout the spring and early summer (Fig. 1). Thermal maxima at both sites in 1986 were distinct peaks, whereas in 1987 thermal maxima were represented by a series of peaks which formed more of a plateau. Also, the cooling period following thermal maxima was more gradual in 1987.

Although temperature data for the summer of 1985 were incomplete, we noted that stream temperatures began to rise at about the same time as they did in 1986, and that the downstream site reached its thermal maximum on 10 August in 1985 at 20.0°C, indicating that stream temperatures warmed more gradually in 1985 than they did in 1986. Thus, the temperature regime in 1985 was more like that observed in 1987 except thermal maxima were considerably lower.

Life history patterns

Ephoron leukon was found to be univoltine in the South River, with the entire growing season restricted to the period between mid-May and late August (Fig. 2). The remainder of the year was apparently spent in egg diapause. This general pattern was consistent at both sites for all three years.

Estimates of the onset of hatching for all six cohorts fell within an 11-d period in the middle of May (Table 2). However, in 1987 densities at both sites increased throughout much of the growing season (Fig. 4), suggesting there was

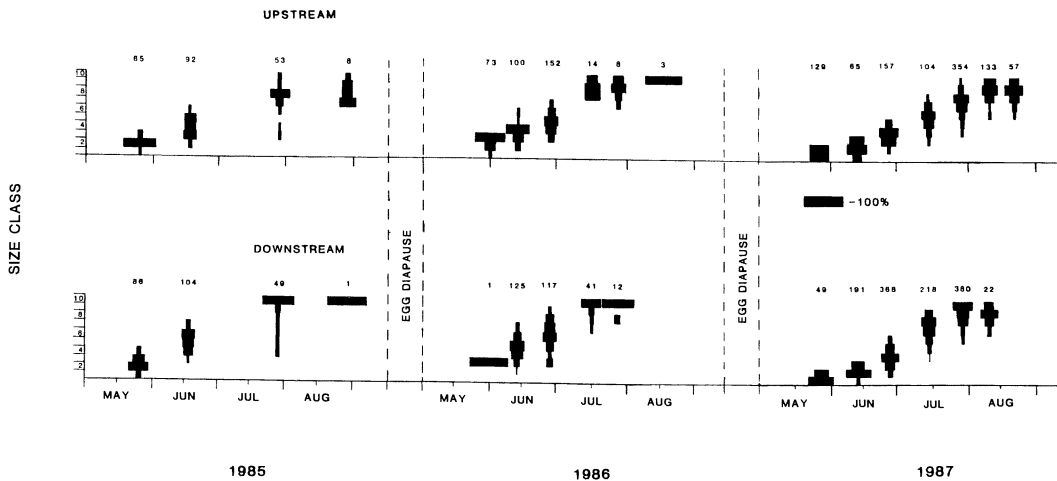


FIG. 2. Size-frequency histograms for *Ephoron leukon* at two sites on the South River for three consecutive years. The number of nymphs per collection is shown above each histogram; the width of each bar indicates the relative proportions of size classes.

either an extended hatching period or a significant amount of migration onto the study riffles relative to the two previous years. Development was reasonably synchronous at both sites for all three years, although faster at the downstream site, and somewhat less synchronous in 1987 compared with the previous two years (Fig. 2). In addition, the downstream site accumulated more degree-days $> 13^{\circ}\text{C}$ than the upstream site during the developmental period (Table 2).

Estimated dates of peak emergence were later at the upstream site in 1986 and 1987 (Table 2). Identical emergence ranges were reported for 1985; however, this was likely the result of small number of sample dates ($n = 4$). Between-site differences in survival between the final two sampling dates in 1985 (downstream = 2.0%;

upstream = 15.5%) suggest that emergence was later at the upstream site in 1985 as well. Date of peak emergence was earlier in 1986 than in the other two years at both sites.

We were fortunate in observing an emergence at the downstream site in 1986 on 23 July, which fell within the range estimated. Emergence and ovipositioning behavior was similar to that reported for *E. album* (Giberson and Galloway 1985). Swarming lasted 2-3 h and was extremely dense over the study riffle. By the end of the emergence period, the water and surrounding banks were literally covered with spent adults (almost exclusively males on the banks). The next morning no evidence of the previous evening's emergence remained, and repeated kick samples revealed very low

TABLE 2. Estimates of hatching date, emergence period, cohort production intervals, and accumulated degree-days $> 13^{\circ}\text{C}$ for all six cohorts of *E. leukon*. See text for explanation of methods for determining these estimates.

Site/year	Predicted hatching date	Emergence period	Cohort production interval	Accum. deg-days
Up/1985	18 May	21 Jul-28 Aug	78	ND ^a
Down/1985	18 May	21 Jul-28 Aug	78	ND ^a
Up/1986	27 May	29 Jul-19 Aug	74	432
Down/1986	23 May	17 Jul-29 Aug	61	543
Up/1987	16 May	12 Aug-19 Aug	92	508
Down/1987	20 May	28 Jul-12 Aug	76	629

^a ND = No data. Temperature data were incomplete for 1985.

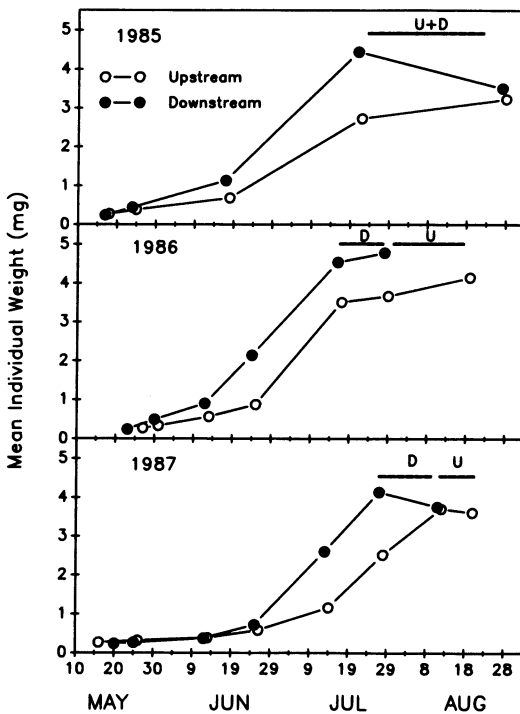


FIG. 3. Growth curves for all six cohorts of *Ephoron leukon* on the South River. The horizontal bars above the curves represent the estimated ranges for peak emergence (U = upstream, D = downstream).

nymphal densities, suggesting that most emergence probably took place on that single evening.

Growth was exponential throughout most of the growing season for all cohorts ($r^2 > 0.95$) (Fig. 3). The overall average growth rate (taken over both sites for all three years) was 0.0193 mg/mg/day with a coefficient of variation of 26.4%. Growth rates ranged from 0.0145 to 0.0284 mg/mg/day (Table 3), and were significantly higher at the downstream site within each year ($p < 0.01$).

Relative growth rates corrected for temperature differences (i.e., the slope of the line generated by regressing log mean individual weight by accumulated degree-days [DD] above 13°C) ranged from 0.00238 to 0.00367 mg/mg/DD among cohorts (Table 3). No significant between-site differences were observed ($p > 0.10$). Since between-site differences were not significant, the data for both sites were pooled for the between-year comparison (Table 3). Relative growth rate corrected for temperature was

significantly higher in 1986 than in 1987 ($p < 0.001$).

The average maximum size attained by nymphs (taken from both sites for all three years) was 4.10 mg AFDM, and the coefficient of variation was 13.5%. Some individuals of all six cohorts reached the largest size class (head width = 2.3–2.5 mm) which had an average weight of 4.89 mg. However, the maximum size of an average individual was higher at the downstream site for all three years (Table 4). Also, the maximum average size in 1985 at the upstream site was significantly lower than at the upstream site in 1986 and 1987. However, this may be due to the length of time between sampling intervals in 1985 (i.e., growth may have continued between the last two sampling intervals). No other between-year differences were significant.

Within each year, shapes of survivorship curves were similar between sites although average densities were higher at the downstream site in 1987 (Fig. 4). The survivorship pattern in 1987 was clearly different from the previous two years, with densities increasing well into the summer.

Average densities ranged from 117 to 602 individuals/m² (Table 4) with an overall average of 268 and a coefficient of variation of 72%. Between-site differences were significant only in 1987. However, within each site, year-to-year differences were significant, with highest densities recorded in 1987, followed by 1986 and 1985.

Production

Production estimates ranged from 398 to 2857 mg/m²/yr (Table 4) with an overall average of 1224 and a coefficient of variation of 76%. Within each year, annual production was between 1.5 (1986) and 1.6 (1985 and 1987) times higher at the downstream site. Between-site differences were significant in 1985 and 1987 but not in 1986 owing to high sample variance (Table 4). Relative differences in mean standing stock between sites closely approximated observed differences in production in 1985 and 1987. However, in 1986 the mean annual biomass was >167% higher at the downstream site while production was only 48% higher.

Within each site, annual production was higher in 1986 than in 1985 (upstream = 1.7×,

TABLE 3. Regression equations for growth models. Log mean individual weight by days from hatching (DFH) and by accumulated degree-days >13°C. Equations are in the form, $y = ax + b$ where, a = relative growth rate (slope) and b = log weight at hatching (y intercept).

Site/date	n	Days from hatching				Degree-days >13°C			
		Slope (mg/mg/ day)	Y intercept			Slope (mg/mg/ deg-day)	Y intercept		
			(mg)	r^2	p		(mg)	r^2	p
Up/1985	16	0.0149	-0.585	0.96	<0.0001	ND ^a	ND	ND	ND
Down/1985	19	0.0178	-0.506	0.98	<0.0001	ND	ND	ND	ND
Up/1986	17	0.0145	-0.602	0.97	<0.0001	0.00367	-0.577	0.98	<0.0001
Down/1986	10	0.0195	-0.588	0.97	<0.0001	0.00356	-0.539	0.97	<0.0001
Up/1987	26	0.0210	-0.734	0.95	<0.0001	0.00256	-0.648	0.97	<0.0001
Down/1987	24	0.0284	-0.740	0.96	<0.0001	0.00238	-0.662	0.98	<0.0001
Both/1986	27	NA ^b	NA	NA	NA	0.00365	-0.567	0.98	<0.0001
Both/1987	50	NA	NA	NA	NA	0.00244	-0.646	0.97	<0.0001

^a ND = No data. Temperature data were incomplete in 1985.

^b NA = Not appropriate. Since between-site differences in growth rates were significant on a DFH basis for both years, data could not be pooled.

downstream = 1.6 \times), and higher in 1987 than in 1986 (upstream = 2.6 \times , downstream = 2.8 \times). Differences in production were significant for all comparisons except for the upstream site between 1985 and 1986 (Table 4).

Between-site differences in production were primarily due to larger maximum sizes of nymphs from the downstream site although densities were important in 1987. Between-year differences in production were mostly due to higher average densities in consecutive years. Differences in growth rates were small relative to differences in production between sites and years.

Discussion

Life history patterns

The life history of this genus is consistent across a wide range of habitats (Ide 1935, Edmunds et al. 1956, Britt 1962, Giberson and Galloway 1985). However, within this general framework significant differences in growth rates, maximum nymphal sizes, average densities, and production were observed between sites and years on the South River.

Between-site differences in summer water temperatures were sufficient to explain spatial differences in growth rates, at least in 1986 and 1987 when temperature data were complete. This is consistent with other studies where temperature has been shown to be important in reg-

ulating growth rates of aquatic insects (e.g., Lutz 1974, Brittain 1976, Markarian 1980, Vannote and Sweeney 1980, Ward and Stanford 1982). Food availability was not measured over the entire length of this study, so direct comparisons of growth with food were impossible. Although nutrient concentrations were higher at the downstream site, no significant differences in algal biomass or seston concentrations were observed. This, combined with the strong relationship observed between growth and temperature, suggests temperature was probably more important than food in explaining spatial differences in growth rates.

Annual differences in growth rates were not explained by differences in water temperature. That is, after correcting for temperature, significant between-year variation in growth rates remained. Densities may have been important in explaining annual differences in individual growth rates. If food resources remain relatively stable among years, then as densities increase, the per capita food availability decreases, which could lead to lower individual growth rates. In 1987, when densities were highest, temperature-corrected individual growth rates were lowest. Although temperature data were incomplete in 1985, the thermal regime appeared to be coolest that year, whereas growth rates appeared only marginally lower than in 1986 and virtually identical to 1987. Therefore, it is likely that both sites in 1985 had the highest temper-

TABLE 4. Average biomass, maximum weight, density, annual production, and P/B ratios for each cohort of *E. leukon*. Production was calculated using the Increment-Summation Method.

Site/year	Mean maximum weight (95% CL)	Mean density (95% CL)	Production mean (95% CL) (mg/m ² /yr)	Average biomass (mg/m ²)		Cohort P/B	Annual P/B
				Cohort	Annual		
Up/1985	3.22 (2.15-4.32)	117 (79-157)	398 (270-576)	99	26	4.0	15.3
Down/1985	4.44 (4.05-4.82)	125 (98-156)	638 (468-844)	146	38	4.4	16.8
Up/1986	4.14 (3.47-4.81)	152 (96-221)	684 (452-925)	109	24	6.2	28.5
Down/1986	4.78 (4.50-5.06)	221 (106-355)	1011 (487-1630)	292	64	3.5	15.8
Up/1987	3.71 (3.52-3.90)	390 (319-470)	1753 (1437-2202)	608	142	2.9	12.3
Down/1987	4.14 (3.95-4.33)	602 (500-697)	2857 (2313-3519)	911	212	3.1	13.5

ature-corrected growth rates of all three years. In addition, densities were significantly lower in 1985 than the other two years. These data suggest an inverse relationship between growth and abundance.

Hawkins (1986) found little variation in individual growth rates of ephemereid mayflies even when significant variation in densities was observed, and suggested that individual fitness (i.e., growth rate) was maintained by migration from resource-poor to resource-rich patches by drift. That is, constant per capita food availability was maintained by changing densities. In that study, only one species was never found in drift samples, and it was also the only species to show significant variation in individual growth rates. Therefore, those species that do not have good dispersal mechanisms as nymphs may be unable to maintain optimum growth rates. In the only report of *Ephoron* sp. in drift samples, Morris et al. (1968) found *Ephoron* nymphs only in drift samples collected from severely channelized portions of the river. At undisturbed sites, *Ephoron* nymphs were never found in drift samples.

Larger average maximum sizes of nymphs at the downstream site were the result of both higher growth rates and relatively small differences in CPI. Higher individual growth rates of nymphs from the downstream site resulted in a larger average body size throughout the growing season, and although the CPI was longer at the upstream site, it was not sufficient to make up the size differential that existed prior to emergence. Longer growing seasons (CPI) at the upstream site were related to later dates of peak emergence. However, while peak emer-

gence occurred later at the upstream site, growth patterns suggest that the onset of emergence at both sites may have occurred on or near the same date in 1985 and 1986. Growth at both sites began to level off at approximately the same time (Fig. 3) indicating that either nymphs at the upstream site began to grow more slowly, or, more likely, heavier nymphs from both sites were emerging. In 1987 growth continued at the upstream site for nearly two weeks after growth leveled off at the downstream site. However, when mean individual weight of nymphs at the downstream site had peaked and begun to decline, nymphs at the upstream site were substantially smaller (<2.5 mm) and weight was still increasing exponentially (Fig. 3). Therefore, unlike the previous year, the onset of emergence as well as peak emergence was delayed in 1987 at the upstream site.

Developmental temperature requirements were greater in the downstream site (i.e., development slightly longer than would be predicted from thermal accumulation alone). This suggests that actual emergence timing may be related to some environmental cue (e.g., photoperiod, thermal threshold, etc.). If we assume that the flattening out of growth curves is indicative of the onset of emergence, then our data suggest a model where the environmental cue for emergence occurs at about the same date for both sites but that only those individuals of threshold size emerge while the rest of the population continues to grow (i.e., maturation is size dependent). Thus, in 1986, nymphs at both sites emerged at the same time because at both sites they were above some critical size threshold. Conversely, in 1987, nymphs from the up-

stream site began emerging later because most nymphs at the upstream site were below the critical size threshold and therefore continued to grow until the threshold was reached. Data from the upstream site in 1987 suggest a critical size threshold of about 3.5 mg (Fig. 3). Because of the low frequency of sampling in 1985, there is no way to be sure that upstream nymphs did not continue to grow between the third and fourth sampling period. In fact, it is likely that mean individual weight of nymphs from the upstream site did continue to increase to the critical threshold (about 3.5 mg). Thus, larger maximum sizes observed at the downstream site were due to more growth being achieved prior to receipt of the cue for emergence.

We were unable to determine experimentally the importance of various environmental variables in cueing emergence because *E. leukon* cannot be kept alive in the laboratory for more than a few days (W. P. McCafferty, Purdue University, personal communication). However, rough correlations of the estimated date for the onset of emergence (hypothesized to be the date at which growth curves leveled off) with environmental variables suggested that photoperiod, specific temperature thresholds, and diurnal variation were all unimportant. Conversely, the onset of emergence of *E. leukon* appeared to correlate well with declining stream temperature following the thermal maximum (Table 2 and Fig. 1). Similar cues for emergence have been reported for other burrowing mayflies. For example, Peters et al. (1987) found that emergence of *Dolania americana* nymphs was cued by a shift from a declining to rising thermograph at dawn the previous morning, and not a simple degree-day relationship. Temperature trends appear to explain emergence patterns in the closely related *Ephoron album*, as well (Britt 1962).

Consecutive increases in densities during the three years of the study may indicate that these populations were recovering from some earlier perturbation that substantially reduced population numbers below carrying capacity. A major spate occurred in November of 1985 when the 1986 cohorts were in egg diapause. The discharge on that single day represented nearly 25% of the total discharge for that water year, and the discharge for the month of November represented 54% of the total annual discharge (U. S. Geological Survey hydrologic data,

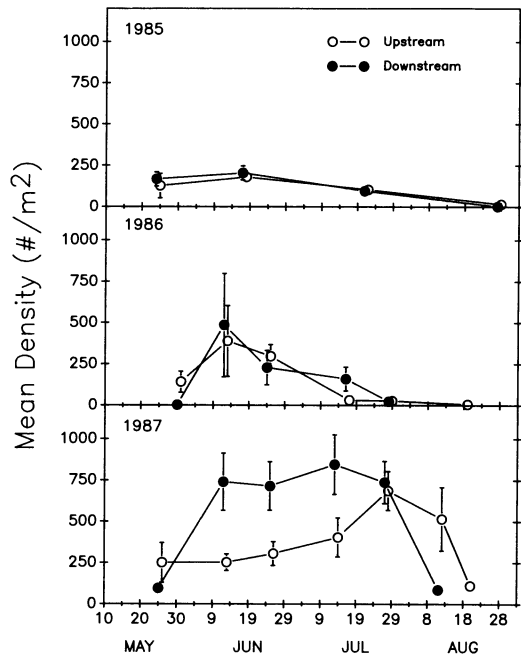


FIG. 4. Survivorship curves of all six cohorts of *E. leukon*. Means \pm 1 SE.

Waynesboro gauging station, for the 1985 water year). As a result, we predicted a reduction in densities and thus lower production of *E. leukon* in 1986 as compared with 1985. However, this was not the case as both densities and production were significantly higher in 1986. Clearly the egg stage is extremely durable and resistant to scouring.

A more plausible explanation for the observed between-year differences in densities concerns the relationship between winter temperatures and the hatching success of eggs. Annual differences in densities were associated with the early stages of the growing season except in 1987, when densities were higher throughout the growing season. Therefore, factors governing the number of eggs being laid or the hatching success of eggs seem to be most important in explaining annual differences in density.

Giberson and Galloway (1985) found that *Ephoron album* eggs required below-zero temperatures for successful hatching and that the relative success of hatching was positively correlated to the duration of exposure to freezing temperatures. *Ephoron leukon* clearly does not require below-zero temperatures for hatching

because in 1986 there were no days where water temperature averaged less than zero. However, both species rely on a long egg diapause during the winter, which ensures eclosion will occur during optimum growing temperatures. Therefore, it is likely that there is some thermal threshold during winter for *E. leukon*, above which hatching success will be compromised. Densities were higher in 1987 than in 1986, and the winter of 1986–1987 was colder than 1985–1986 with twice as many days $<5^{\circ}\text{C}$. These field data are in accord with the experimental results of Giberson and Galloway (1985) which suggest an inverse relationship between density and temperatures during diapause.

Secondary production

The magnitude of production of *E. leukon* was surprisingly high given the short growing season, and as such, *E. leukon* represents a significant carbon source for other trophic levels during the summer. Production of *E. album* in the Valley River in Canada (Giberson and Galloway 1985) was about 1300 mg AFDW/m²/yr (units transformed to AFDM using correction factor from Waters [1977]). This falls within the range reported for *E. leukon* in our study. Based on the length-weight relationship (Giberson and Galloway fig. 3) and size-frequency distribution (Giberson and Galloway fig. 4), we estimated that the maximum weight of an average individual in their study was approximately 3.2 mg AFDM (transformed units), which falls within the low end of the range observed for *E. leukon*.

Between-site differences in production resulted primarily from differences in maximum weights observed at the downstream site. Therefore, since temperature was shown to indirectly affect maximum sizes by regulating growth rates, it is likely that temperature has a positive effect on production. Annual differences in production were due primarily to differences in densities. Differences in winter temperatures may have been important in determining hatching success of eggs, which may partially explain observed differences in densities. Therefore, water temperature may have been responsible for annual differences in production.

In conclusion, significant differences between sites and years were observed for all life history parameters measured including second-

ary production. Coefficients of variation ranged from 17% for growth rates to $>76\%$ for production. Temperature was important in explaining spatial differences in individual growth rates and maximum sizes, and may have been important in determining hatching success, and thus densities. Too often, models of population dynamics and food webs are based on short-term data sets which lack estimates of spatial and temporal variation. Consequently, predictions obtained from such models are unreliable. Our results further stress the need for multiyear studies when evaluating life history parameters.

Acknowledgements

We thank L. Western for allowing us to use his periphyton data and A. Morin for help in calculating confidence limits. We would also like to thank J. R. Webster, A. C. Benke, R. J. Mackay, B. W. Sweeney, B. M. Stout III, and two anonymous reviewers for editorial comments on an earlier version of this paper. Research leading to this report was supported by the E. I. Dupont Co. of Waynesboro, Virginia.

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Received: 10 April 1990

Accepted: 26 November 1990