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Life History and Secondary Production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcyidae) in the Illinois River, Arkansas

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ABSTRACT: In the Ilinois River, the burrowing mayfly *Ephoron album* (Say) had a univoltine life cycle with approximately an eight month egg diapause. Nymphs were first collected on 14 April, and the adults on 23 July, with peak emergence occurring between 27 July and 9 August. Linear regression analysis showed a significant relationship between head capsule width and dry weight. Annual production estimates ranged from 5.92 to 6.70 $g/m^2/yr$ dry weight, and the cohort standing crop biomass was 8.24 g/m^2. Cohort P/B ratios ranged from 7.19 to 8.13, and annual P/B ratios from 17.26 to 19.52. The cohort production interval was estimated at 126 days, based on field observations.

Ephoron album, a burrowing mayfly, was originally described as *Baetes alba* by Say in 1824, and the nymphs were first described by Edmunds (1948) (McCafferty, 1975). The species occurs primarily in the Central and Western United States, with Arkansas being the southern limit of its distribution (McCafferty, 1975).

The life history of *Ephoron album* was investigated by Edmunds et al. (1956) in Utah, and Britt (1962) in Ohio. They found that *E. album* has a univoltine life cycle with an egg diapause, and that winter water temperature changes are the hatching stimulus. These investigators found that male subimagos molt into imagos, but that female subimagos do not and are reproductively active upon emergence.

Presently, no studies of the life history have been conducted in the southern United States. Knowledge of a species is incomplete unless we know its life history from different areas, because life cycles can vary substantially throughout the geographic range (Stewart and Stark, 1988). In addition, knowledge of the secondary production of insect species is essential to understanding both population and community dynamics in aquatic systems (Benke, 1984). Benke (1984) noted that secondary production estimates combine two characteristics of substantial ecological significance, individual growth and population survivorship, into a single measurement. No estimates of secondary production have been made for *E. album*; therefore, little is known about the contribution of this species to the benthic community of streams. The objectives of this investigation were to: 1) determine the life history of *E. album*; 2) estimate the standing stock biomass, secondary production, and calculate the production/biomass (P/B) ratio of *E. album* in the Illinois River, Arkansas.

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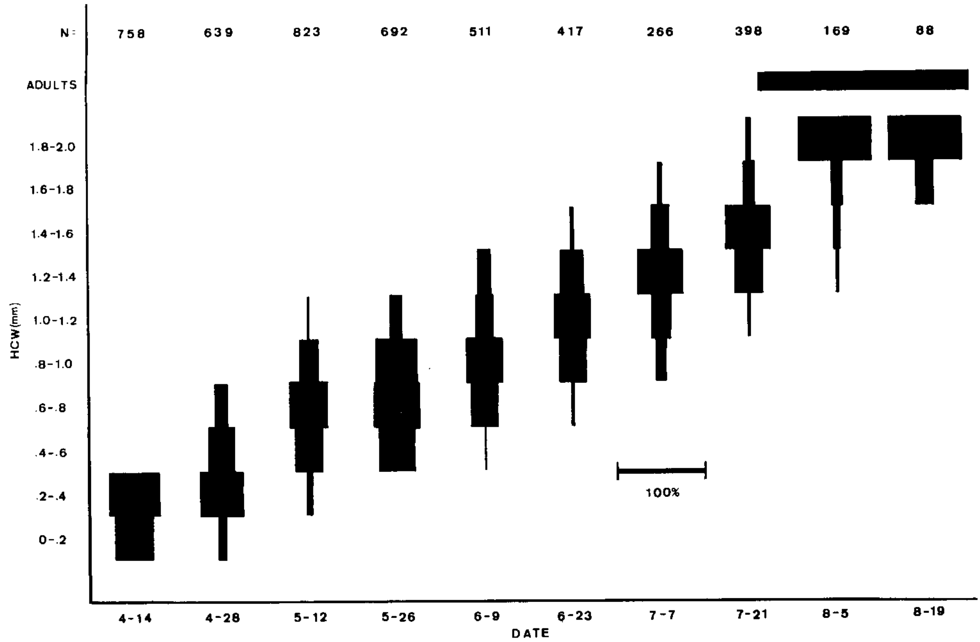

Fig. 1. Size class (HCW) frequency distribution for *Ephoron album* on each sampling date from the Illinois River, Arkansas. Width of bars indicates relative abundance of each size class on each date. Solid horizontal line designates the occurrence of adults.

Materials and Methods

Benthic collections were made from riffle areas of third and fourth order reaches of the Illinois River (Washington County, Arkansas) from 24 March through 19 August 1992. Random benthic samples were collected weekly beginning in late March to determine when hatching occurred, then twice monthly after hatching. Collections were made from five different riffle areas using a Surber sampler (243 μm mesh), after the suggestion of Bowles (1990) for multiple riffle sampling. Twenty samples were collected from each site during each sampling period. Samples were preserved in 10% formalin, and were sorted in the laboratory using a dissecting microscope. The *E. album* nymphs were separated from the samples and counted. The head capsule widths (HCW) were measured just behind the eyes, to the nearest 0.1 mm using an ocular micrometer. Specimens were then grouped by size class for each sampling period, and dried at 55°C for 24 hours, and later weighed. Adults were sampled every other night from mid July through mid August using light trapping and sweep netting. Although there is no method to quantify these data, relative abundances were calculated to roughly determine periods of greatest emergence.

Head capsule width and weight data were transformed using the ln, and linear regression analysis of weight on head capsule width was conducted. Mean weights for each size class were then calculated from the linear regression growth equation. Because *E. album* has a relatively tightly synchronous development, secondary production was estimated using the removal-summation, increment summation, and instantaneous growth methods (Waters and Crawford, 1973; Benke, 1984).

Table 1. Production calculations for *Ephoron album* in the Illinois River Arkansas. The summation of column F is the removal-summation production estimate. The summation of column I is the increment-summation production estimate, and the summation of column L is the instantaneous growth production estimate. All weights are grams.

Date	A Number/m^2	B Mean wt.	C Standing crop	D Number lost/m^2	E Wt. at loss	F Wt. loss g/m^2 D × E	G Mean number/m^2	H Change in wt.	I P g/m^2 G × H	J G	K (B)	L P g/m^2 J × K
4/14	908	0.00001	0.011									
4/28	732	0.00010	0.075	170	0.00052	0.088	817	0.00009	0.074	2.163	0.043	0.093
5/12	622	0.00042	0.261	110	0.00026	0.029	677	0.00032	0.215	1.408	0.168	0.237
5/26	456	0.00102	0.467	166	0.00072	0.120	539	0.00060	0.326	0.892	0.364	0.325
6/9	378	0.00146	0.554	78	0.00124	0.097	417	0.00044	0.184	0.358	0.510	0.183
6/23	321	0.00322	1.032	57	0.00234	0.133	350	0.00175	0.613	0.787	0.793	0.624
7/7	212	0.00624	1.323	109	0.00473	0.515	266	0.00302	0.804	0.663	1.178	0.780
7/21	151	0.01072	1.618	61	0.01171	0.714	182	0.00448	0.815	0.541	1.471	0.795
8/5	53	0.03459	1.833	98	0.02265	2.220	102	0.02387	2.435	1.172	1.726	2.022
8/19	15	0.07083	1.062	38	0.05271	2.003	34	0.03624	1.232	0.717	1.448	1.038
						5.919			6.698			6.097

All secondary production estimates were calculated using the combined data from all five riffle areas. Standing stock biomass was measured, and P/B ratios were calculated using all three production estimate methods.

Results

Nymphs in the 0–0.2 and 0.2–0.4 HCW size class were first collected on 14 April, indicating that hatching began between 7 and 14 April. Nymphs were last collected on 19 August. Nymphal growth was very rapid after hatching, and the duration from hatching to emergence was less than 18 weeks. First instar nymphs were easy to distinguish, because they lack gill filaments, and were collected only during the 14 April sampling period, indicating relatively synchronous hatching. Size frequency distribution of nymphs also showed a synchronous growth period after hatching (Fig. 1). Adults were first collected in low densities on 23 July, and emergence reached peak densities between 27 July and 9 August. Adults continued to be collected in diminishing numbers until 21 August. Emergence began just after sunset and usually continued for approximately 1.5 hours. These data indicate that *E. album* has a univoltine life cycle in the Illinois River. The life cycle includes approximately an eight month egg diapause followed by hatching in early April, rapid growth through nymphal stages, and emergence and oviposition in late July through mid August.

Linear regression analysis showed a strong significant relationship between ln HCW and ln dry weight (W) ($F = 606.58$, $P = 0.0001$, $R^2 = 0.989$). The linear relationship between HCW and dry weight can be explained by the equation: $\ln W = -4.741 + 4.469(\ln HCW)$. The standard error for the Y intercept and the slope were 0.105 and 0.181, respectively.

Annual production estimates ranged from 5.92 to 6.70 $g/m^2/yr$ dry weight (Table 1). The cohort yearly standing crop biomass was 8.24 g/m^2 (summation of column C, Table 1), and the mean cohort standing stock was 0.82 g/m^2. The annual mean standing crop biomass was 0.34 g/m^2. The cohort P/B ratios were 7.19 using the removal-summation production estimate, 8.13 using the increment-summation method, and 7.40 using the instantaneous growth method. The annual P/B ratios were 17.26 using the removal-summation production estimate, 19.52 using the increment-summation estimate, and 17.77 using the instantaneous growth production estimate. The cohort production interval (CPI) was estimated at 126 days based on field observations. The actual CPI was probably slightly less than 126 days, but attempts to rear *E. album* in the laboratory were unsuccessful, precluding precise CPI estimates.

Discussion

Our findings of a univoltine life cycle with egg diapause for *E. album* concur with the two previous life history investigations from other regions of the United States (Edmunds et al., 1956; Britt, 1962). Development from first instar nymphs to subimagos and/or imagos took approximately the same length of time in the Illinois River, Arkansas as it did in Utah (Edmunds et al., 1956), and Lake Erie (Britt, 1962). The development time for the Lake Erie population may have been slightly shorter. Egg hatching began earlier in Arkansas than it did in either Utah or Lake Erie. We first collected nymphs in April compared with early May for the two previous investigations. Egg hatching is induced by freezing temperatures followed by warming waters (Edmunds et al., 1956; Britt, 1962). The water probably warmed to the appropriate temperature earlier in the spring in Arkansas than in either Utah or Lake Erie. Because hatching occurred earlier and development took about the same length of time, emergence of *E. album* occurred earlier in Arkansas. Emergence began in late July, compared to early and late August in Ohio and Utah, respectively (Edmunds et al., 1956; Britt, 1962). A Michigan population of *E. album* began emergence during mid August (Kraft et al., 1978). The time of emergence of *E. album* in Northwest Arkansas agrees with the observations of Peters and Warren (1966), although we found the emergence period to begin earlier, and last longer.

No secondary production or standing stock biomass estimates have been made for *E. album.* Production for other species of burrowing mayflies, however, have shown varying results. Horst and Marzolf (1975) found the production of *Hexagenia limbata* (Serville) to be 1.2 kg/ha/yr in a Kansas reservoir. Waters (1977) reported the production of *H. limbata* and *Hexagenia bilineata* (Say) to be 15.0 kg/ha/yr in Lewis and Clark Lake, South Dakota and Nebraska.

Cohort P/B ratios varied from 7.19 and 8.13 and were high when compared with the usual range of 2–5 for aquatic insects that emerge as adults from aquatic habitats (Waters, 1987). One of the factors that may have contributed to the high cohort P/B ratio is the high nymphal mortality rate (94.1%). Waters (1969) proposed that the ratio of final to initial density (survival) had the greatest effect on cohort P/B, and he suggested that survival for emerging aquatic insects may be approximately 10%. Our findings for *E. album* showed that the ratio of final to initial density was 5.9%, which is a little more than half the ratio proposed by Waters (1969).

Cohort P/B is calculated by dividing the production estimate by the mean biomass for the length of time it takes for the cohort to develop; whereas, annual P/B is the production estimate divided by the yearly mean biomass (Benke, 1984). We found a large difference between cohort P/B ratios and annual P/B ratios, which is usually not the case with univoltine species. Waters (1977) predicted that for univoltine species annual and cohort production ratios will be very similar, and that bivoltine species will have an annual P/B ratio that is approximately twice that of the cohort P/B ratio. We found annual P/B to be a little over twice that of cohort P/B even though *E. album* was univoltine. This can be explained by *E. album* spending the majority of its yearly life cycle in an egg diapause, which is not accounted for in either production estimates, or P/B ratios.

Instantaneous growth estimates for *E. album* showed that the greatest periods of growth occurred during the first two weeks after hatching. Growth rate then slowed somewhat until the period just before emergence when it again increased substantially (Table 1). The greatest production occurred during the final two weeks before emergence.

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