Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba

D. J. GIBERSON[1] AND T. D. GALLOWAY
Department of Entomology, University of Manitoba, Winnipeg, Man., Canada R3T 2N2

Received November 8, 1984

GIBERSON, D. J., and T. D. GALLOWAY. 1985. Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba. Can. J. Zool. **63**: 1668–1674.

Ephoron album was the dominant summer mayfly in shallow riffles in the agricultural zone of the Valley River, Manitoba, in 1982 and 1983. There was one generation per year; eggs deposited in August hatched in late May of the following year and nymphs developed rapidly during the summer months. The eggs required a cold period to promote hatching and hatching success of eggs treated in the laboratory at −2°C for varying periods of time was positively correlated to the length of the exposure period. No eggs hatched following exposure to 4 or 10°C. Production for 1982 was estimated by four methods for the production interval of only 72 days: the instantaneous growth rate method (1.32 ± 0.44 g fresh dry weight $\cdot$ m^{-2} $\cdot$ year^{-1}), the Allen curve method (1.32 g $\cdot$ m^{-2} $\cdot$ year^{-1}), the removal–summation method (1.43 ± 0.41 g $\cdot$ m^{-2} $\cdot$ year^{-1}), and the size–frequency method (1.48 ± 0.51 g $\cdot$ m^{-2} $\cdot$ year^{-1}). Confidence intervals (95%) were calculated using the method of C. C. Krueger and F. B. Martin for the size–frequency estimate of production and by bootstrapping for the removal–summation and instantaneous growth estimates.

GIBERSON, D. J., et T. D. GALLOWAY. 1985. Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba. Can. J. Zool. **63**: 1668–1674.

Ephoron album s'est avéré être l'espèce dominante d'Ephéméroptère d'été dans les rapides peu profonds d'une zone agricole de la rivière Valley au Manitoba en 1982 et en 1983. L'espèce produit une génération par année: les oeufs pondus en août éclosent à la fin de mai de l'année suivante et les larves se développent rapidement au cours des mois d'été. Les oeufs de l'espèce ont besoin d'une période froide pour éclore: le succès de l'éclosion d'oeufs gardés en laboratoire à −2°C pour des périodes de durées variées était en corrélation positive avec la durée de cette période. Les oeufs n'ont pas éclos après des périodes d'exposition à 4 ou à 10°C. En 1982, la production, qui n'a duré que 72 jours, a été estimée par quatre méthodes: l'évaluation du taux instantané de croissance (1,32 ± 0,44 g $\cdot$ m^{-2} $\cdot$ an^{-1}, masse sèche de spécimens frais), la courbe d'Allen (1,32 g $\cdot$ m^{-2} $\cdot$ an^{-1}), la méthode de la somme des pertes (1,43 ± 0,41 g $\cdot$ m^{-2} $\cdot$ an^{-1}), enfin la méthode de la cohorte moyenne (1,48 ± 0,51 g $\cdot$ m^{-2} an^{-1}); dans le cas de cette méthode, les intervalles de confiance (95%) ont été calculés selon la technique de C. C. Krueger et F. B. Martin, alors qu'ils ont été déterminés par la technique du "bootstrap" lorsque la production a été estimée par la méthode de la somme des pertes ou par l'évaluation du taux instantané de croissance.

[Traduit par le journal]

Introduction

Ephoron spp. have attracted attention in North America since the early 1800's because of the conspicuous nocturnal mating flights of the adult (Williamson 1802; Keating 1824). Only two species of *Ephoron* occur in North America. *Ephoron album* (Say) is generally western in distribution and *Ephoron leukon* Williamson is eastern and the nymphs and adults of both species are easily identified (McCafferty 1975; Edmunds *et al.* 1976). *Ephoron* spp. are burrowing mayflies; nymphs are collector–gatherers in relatively large rivers and streams and in sand and gravel shoals of lakes (Edmunds *et al.* 1976; Merritt and Cummins 1978). *Ephoron album* is tolerant of a wide variety of substrate and current types, ranging from clay or sandy clay substrate in slow-moving rivers to sand and gravel substrates in riffles (Edmunds *et al.* 1976).

Ephoron album is univoltine; eggs hatch in the spring, nymphs develop during the summer months, and emergence and oviposition occur near the end of the summer. Eggs overwinter in an obligatory embryonic diapause, though diapause conditions varied in the two populations previously studied (Edmunds *et al.* 1956; Britt 1962). Although *E. album* has been recorded in very high densities (Edmunds *et al.* 1976), its production has never been assessed. Production analysis can yield important information on individual growth and population survivorship, as well as quantifying energy-flow pathways in food webs and providing insight into functional roles in ecosystems (Benke 1984). Basic methodology for assessing invertebrate production in fresh waters has been established (Edmondson and Winberg 1971), but a wide variety of factors, especially relating to life history and sampling effects, can influence the production estimate (Waters 1977, 1979; Benke 1984).

The objectives of this study were to investigate the life history of *E. album*, the dominant summer mayfly from riffles in the agricultural zone of the Valley River, Manitoba, and to assess the production of *E. album* at one riffle site on the Valley River.

Study area

The Valley River is a fourth-order prairie river located in west-central Manitoba (Fig. 1) characterized in the study area by alternating slow deep pools and extensive low-gradient riffles. The study site riffle, located about 10 km north of the town of Dauphin, Man. (100°05′ W, 51°15′ N), measured about 70 m in length by 20 m in width (Fig. 2), except during periods of extremely high or extremely low flow, and possessed a fairly homogeneous sand–gravel–cobble substrate with few boulders. In most years, a minimum flow of 0.1–1.0 m^3 $\cdot$ s^{-1} is maintained (Surface Water Data, Manitoba, 1975–1983 (Environment Canada, Water Resources Branch, Water Survey of Canada, Ottawa)), except during spring runoff and following periods of heavy rainfall; however, in 1982, conditions were very dry and discharge fell below 0.1 m^3 $\cdot$ s^{-1} for most of July. Water temperatures at the study site rose quickly in spring to 15–20°C by the beginning of June and were generally above 20°C for July and August (see also Fig. 6).

[1]Current address: Department of Zoology, University of Toronto, Toronto, Ont., Canada M5S 1A1.

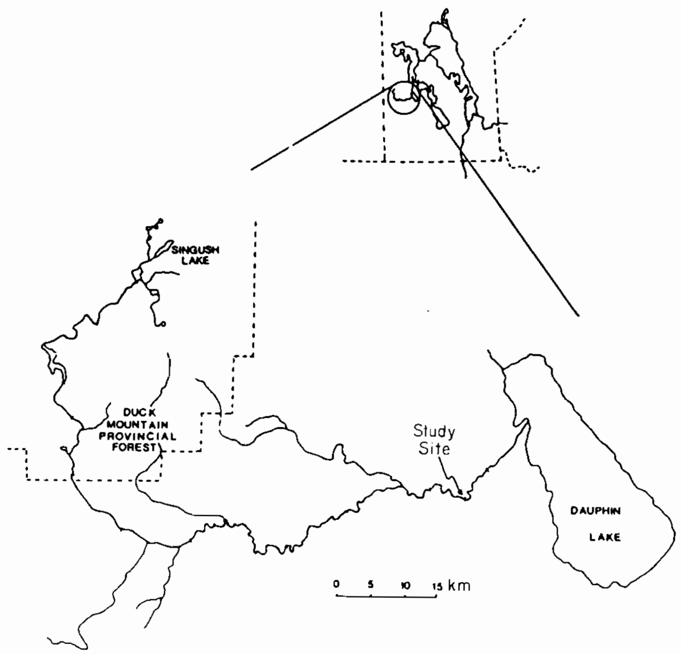

FIG. 1. The Valley River, Manitoba.

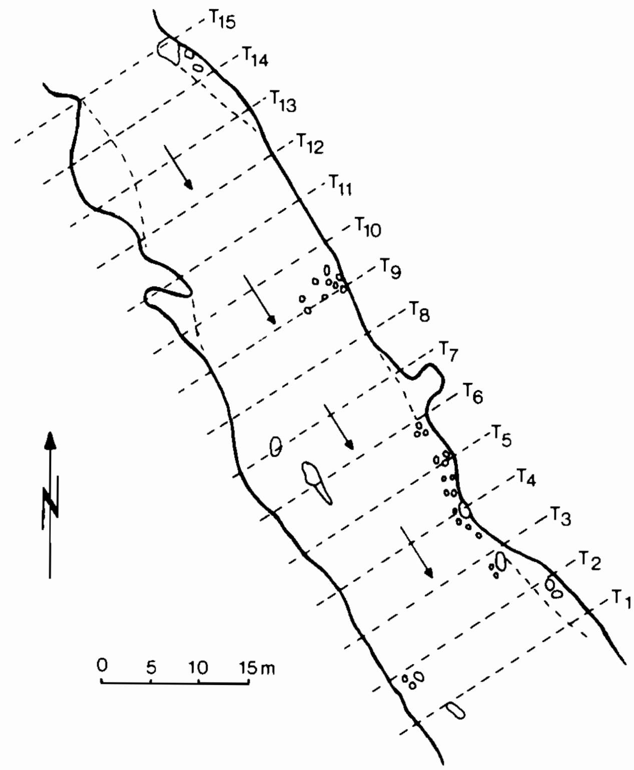

FIG. 2. Study site riffle on the Valley River, Manitoba (100°05′ W, 51°15′ N). Dashed lines refer to transects; arrows show the direction of flow.

Materials and methods

Quantitative samples were collected every 2 weeks from 27 May to 2 September 1982, with a modified Neill box sampler (Neill 1938). With each sample, approximately 0.1 m^2 of stream bottom was disturbed to a depth of 10−15 cm and contents were swept into a 270-μm mesh collecting net by the current. One hundred and fifty predetermined sites were established along 15 transects, 5 m apart, along the length of the riffle (Fig. 2) and 10 sites were selected randomly (using a random number generating program on a TI55-II® pocket calculator) each sampling day. Early in the season (28 June) several samples were taken to varying substrate depths to determine the depth at which the majority of *E. album* nymphs occurred. The same area of bottom was not sampled twice on consecutive sampling days to avoid a bias in the density estimate as a result of delays in recolonizing previously sampled areas (Clifford 1982). Low water conditions prevailed during the 1st week of July 1982 and the number of predetermined sites was reduced to 90 for that sample period only.

Samples were preserved in the field in 10% Formalin, washed in the laboratory through a 250 μm brass seive, and sorted under a dissecting microscope into 70% EtOH. In 1983, nymphs were collected live from the Valley River and returned to the laboratory to determine shrinkage and weight loss following storage in preservative. All nymphs were measured and half were dried at 60°C for 24 h, transferred to a desiccator for 1 h, and individually weighed to the nearest microgram on a Cahn 25 Electrobalance® to determine the relationship between length and dry weight. The remainder were measured at weekly intervals over a 3-month period. No shrinkage in total length was noted, even after several weeks in Formalin and alcohol, but preservation procedures resulted in a weight loss of up to 50% (Fig. 3). Therefore, weights (W) used in the production calculations were estimated from a regression of length (L) on fresh dry weight (FDW) ($W = 0.002L^{3.05}$; r^2=0.89).

Production was calculated for *E. album* using the size−frequency (Hynes and Coleman 1968; Hamilton 1969; Hynes 1980), Allen curve, removal−summation, and instantaneous growth rate methods (Waters and Crawford 1973; Waters 1977). Nymphs were sorted into 1-mm size classes for the size−frequency calculations, and apparent negative production was treated arithmetically in the production summation (Hamilton 1969; Waters 1977). The cohort production interval for *E. album* in the Valley River ranged from 63 to 80 days; therefore, mean nymphal development time was assumed to be 72 days. Confidence intervals (95%) were calculated for the size−frequency method using the procedure of Krueger and Martin (1980) and for the instantaneous growth rate and removal−summation methods using a bootstrapping technique (Efron and Gong 1983) modified for production analysis by Dr. K. Mount and Mr. R. Jaworski (Department of Statistics, University of Manitoba).

Observations on emergence of adult *E. album* were conducted at the study site during July and August 1983 and fertilized eggs collected during this period were returned to the laboratory for further study. Eggs were collected by placing pans of river water near lights at the water's edge. Mated females were attracted to these lights and oviposited in the pans provided. Adults were collected at the lights and by sweeping with a net over the water surface. No adult *E. album* were captured in two floating emergence traps (0.5 × 0.5 × 0.5 m) located in the riffle during the emergence period, although large numbers were emerging all around the traps.

Eggs collected in the field on 28 July were subjected to a number of conditions to determine the optimum temperatures for egg development. Eggs were first allowed to develop at 20 ± 0.5°C (dark) in dechlorinated water in aerated pans for 60 days. Three replicates of 30 eggs each were then transferred to 12 mL glass vials for treatment at −2, 4, and 10°C for 1, 3, 7, 14, and 60 days, after which they were warmed to 20°C before assessing the percent hatch. In a second treatment, 120 days after oviposition, two out of the three vials in all initial treatments (except the 60-day treatment) were exposed to −2°C for an additional 14 days before being returned to 20°C. Three replicates of 30 eggs each were maintained at 20 ± 0.5°C for the entire experimental period.

Results

Life history

Ephoron album eggs began hatching in the Valley River in late May 1982 and nymphs first appeared in samples in early June (Fig. 4). Newly hatched *E. album* nymphs ranged from 0.8 to 0.9 mm in length and grew rapidly during the summer to reach their maximum size of about 14 mm in just 8−10

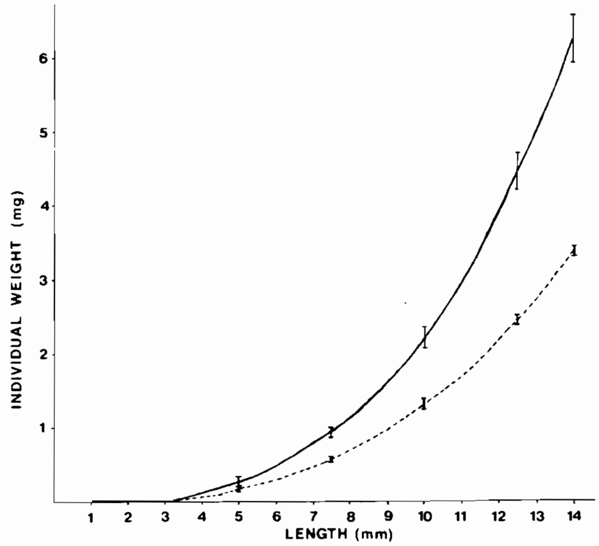

FIG. 3. Relationship between length and dry weight of preserved (---; $W = 0.002\,L^{2.81}$) and freshly killed (—; $W = 0.002L^{3.05}$) *Ephoron album* nymphs from the Valley River, Manitoba. Vertical bars represent ± 1 SE.

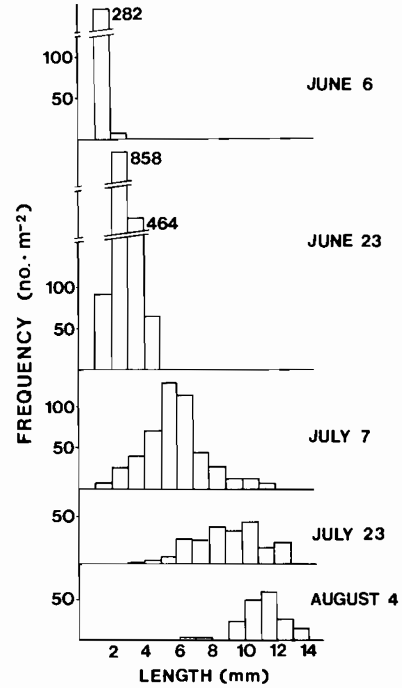

FIG. 4. Length–frequency distribution of *Ephoron album* nymphs in the Valley River, Manitoba, 1982.

weeks. Males could be distinguished by the presence of the rudiments of the penes and forceps after they reached 5 mm in length. In nymphs >5 mm in length, differences in body size (females were generally larger than males) and in eye size (eyes of males were larger than those of females) were also detectable. The average sex ratio (males : females) for nymphs >5 mm in size was 1 : 1.12.

Emergence began in late July and ended by mid-August. Male subimagos began rising out of the water about 0.5 h after sunset (2130) and flew immediately to rocks and vegetation near shore to moult. By 2200 each evening, large numbers of *E. album* males were seen flying rapidly back and forth along the length of the riffle to a height of about 1.5 m above the water surface. Females were first noticed about 0.75 h after sunset; they did not moult to the imago stage, but emerged into the male swarm and began mating and ovipositing immediately. *Ephoron album* females oviposit by flying to the water surface and expelling their eggs, which disperse upon contact with water. Each female produced about 700 eggs and although mean adult size and fecundity decreased slightly over the 3-week emergence period, no significant differences ($P < 0.05$) were noted. Within 5 min of the first appearance of females each evening, spent and dead females could be seen on the water surface. After 2.5 h all swarming had ceased at the riffle site, but females were still being collected at a light 200 m downstream of the riffle at 0100, 3.5 h after the start of emergence. After 0100 no more females were seen and next morning virtually no sign of the previous evening's emergence remained.

Ephoron album eggs were opaque white when deposited, with a posterior adhesive polar cap which served to attach the egg to substrate materials immediately after oviposition (Fig. 5*a*). The developing embryo could be clearly seen through the chorion (Fig. 5*b*), though after 21–28 days no further development was detected and no hatching occurred until the eggs were subjected to a period of cold temperatures. Hatching success of eggs treated at −2°C was positively correlated to the duration of the exposure period (Table 1). Eggs treated at 4 and 10°C did not hatch until exposed in a secondary treatment to −2°C for an additional 14 days (Table 1); however, hatching success in the secondary treatment was lower and more variable than that noted in the initial 14-day treatment at −2°C (Table 1). The eggs began to hatch 103–104 days after oviposition, except where the treatment period extended beyond this time. In all cases where the treatment period extended beyond 104 days after oviposition (e.g., the 60-day treatment and the secondary treatments), hatching began within 3 days of warming the eggs to 20°C. The period of time over which hatching occurred ranged from 3 to 7 days and was not correlated to treatment.

Production

Production calculated over the entire riffle ranged from 1.32 to 1.48 g FDW · m^{-2} · $year^{-1}$, depending upon the method of calculation used (Table 2; data in Giberson 1984). Habitat stratification (Benke 1984) was not attempted because the riffle was generally homogeneous and no correlations were found between mayfly density and such parameters as substrate particle size, substrate organic content, water depth, or current. For calculation of production by the size–frequency method, use of a geometric mean (Krueger and Martin 1980) to obtain mean biomass between size classes resulted in an estimate of 1.36 g FDW · m^{-2} · $year^{-1}$, compared with 1.48 g FDW · m^{-2} · $year^{-1}$ using an arithmetic mean. The estimate of 1.48 g FDW · m^{-2} · $year^{-1}$ for the size–frequency method was based upon an average cohort production interval of 72 days, but the true value may lie anywhere between 63 and 80 days, resulting in a possible range for the production estimate of 1.68–1.33 g FDW · m^{-2} · $year^{-1}$. Ignoring apparent negative production in the production summation (Benke 1984) for the size–frequency method resulted in an estimate of 1.52 g FDW · m^{-2} · $year^{-1}$. Production estimates were calculated separately for male and female nymphs, but there was little difference between total production calculated as the sum of the production for the males and females (Table 3) and that calculated

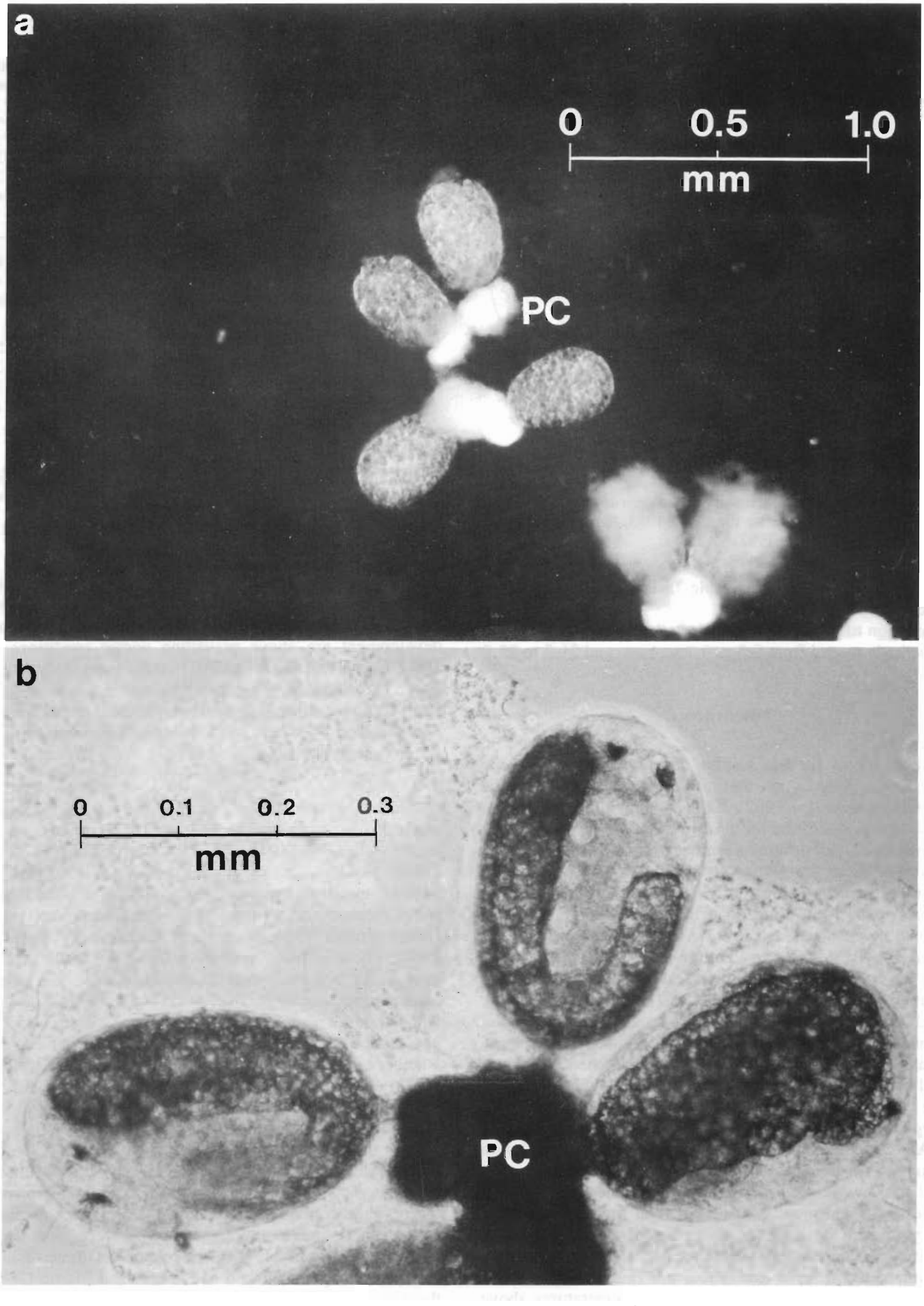

FIG. 5. Eggs of *Ephoron album*. (*a*) Newly deposited eggs. (*b*) Four weeks after oviposition. PC, polar cap.

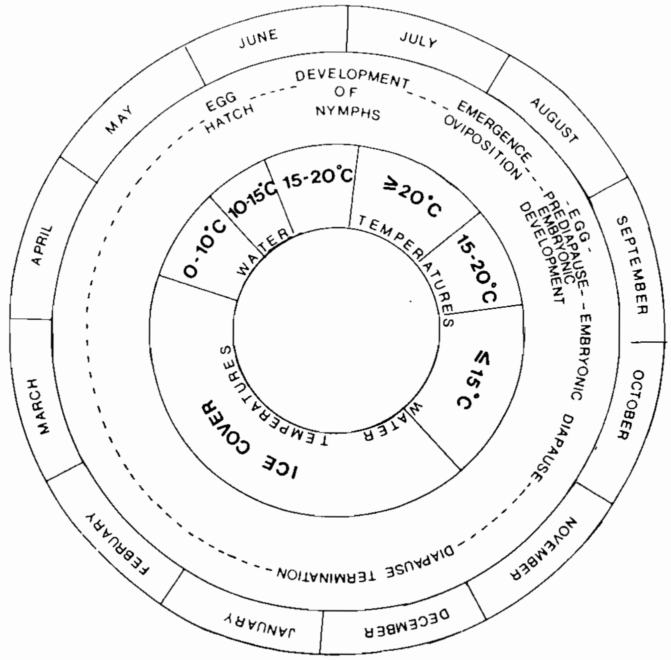

FIG. 6. Summary of the life history of *Ephoron album* in the Valley River, Manitoba (based on data for 1982–1983; temperatures based on 20-year average, 1962–1982).

TABLE 1. Effect of temperature on hatching success of *Ephoron album* eggs collected 28 July 1983 from the Valley River, Manitoba

Treatment temperature (°C)	Initial exposure time (days)	Initial treatment (mean % hatch)[b]	Secondary treatment[a] (mean % hatch)[c]
−2	1	5.5±2.9	35.0±15.0
	3	4.4±1.1	10.0±2.0
	7	24.4±4.8	13.3±2.0
	14	59.8±8.0	6.6±4.7
	60	84.4±2.9	
4	1	0	15.0±7.1
	3	0	25.0±8.3
	7	0	28.3±1.6
	14	0	31.7±8.4
	60	0	
10	1	0	45.0±5.0
	3	0	20.0±3.3
	7	0	25.0±1.7
	14	0	25.0±1.0
	60	0	
20	130	0	

[a]Two of the three replicates taken from initial treatment were exposed to −2°C for an additional 14 days; hatch was then recorded after warming to 20°C. No eggs hatched in single replicate held as control.
[b]Mean (±SE) percent hatch in three replicates of 30 eggs each (after warming to 20°C).
[c]Calculated as percent of total eggs.

for the population as a whole (Table 2). Production by females formed 55% of total production.

Production to mean biomass ratios ($P:\bar{B}$) calculated for the four methods ranged from 5.3 to 5.7 (cohort) and 21.2 to 22.8 (annual).

Discussion

Life history

A summary of the life history of *Ephoron album* in the Valley River, based upon data for 1982–1983 and average water temperatures for 1962–1982, is shown in Fig. 6. Previous investigators of the life history of *E. album* (Britt 1962; Edmunds *et al.* 1956) found a similar pattern of development, but nymphs from the Valley River completed development faster (8–10 weeks compared with 12–17 weeks) and were smaller at maturity (14 mm in length compared with 17–20 mm) than nymphs reported from Utah (Edmunds *et al.* 1956) or Lake Erie (Britt 1962). In addition, adults collected from the Valley River were smaller and less fecund than those reported by Edmunds *et al.* (1956) or Britt (1962). The Valley River is located near the northern limit of the range of *E. album* and differences in size and fecundity may reflect suboptimal developmental conditions in the Valley River, compared with more central portions of the range (Sweeney and Vannote 1978).

The critical temperature for diapause development in *E. album* eggs in the Valley River appears to lie between −2 and 4°C. At −2°C, hatching success was generally correlated with the duration of the exposure period (Table 1), although eggs treated for 2 weeks in a second experiment later in the year showed lower and more variable hatching success than those initially treated for 2 weeks. High temperatures during the diapause period are reported to reduce postdiapause survival by depleting metabolic reserves (Tauber and Tauber 1976), so that continued exposure of *E. album* eggs to temperatures above optimum for diapause development may have been responsible for the lower hatching success. Diapause termination in insects generally consists of a gradual transition from a diapause to a postdiapause state. Many northern species end diapause in midwinter, but do not hatch, since thresholds for postdiapause development are above prevailing winter conditions (Beck 1980; Tauber and Tauber 1976). In the present study, eggs held at −2°C for 60 days began hatching within 3 days of warming to 20°C; diapause was apparently terminated during the 60-day period and required only an increase in temperature to complete development and hatch.

Production

Production estimates obtained using any of the available methods of calculation can be expected to be in close agreement (Waters and Crawford 1973; Cushman *et al.* 1978; Benke 1984). However, attempts to improve the accuracy of one method, the size–frequency method, have resulted in a number of recent modifications to the original method proposed by Hynes (Hynes 1961; Hynes and Coleman 1968; Hamilton 1969). These include a correction factor for cohort production interval for organisms that do not spend exactly a year in an aquatic producing stage (Benke and Waide 1977; Benke 1979), whether or not mean biomass between size classes is calculated geometrically or arithmetically (Krueger and Martin 1980) and whether or not the apparent negative production is included in the production summation (Benke and Wallace 1980). In the present study, production estimates calculated by the size–frequency method, taking the above factors into account, ranged from 1.33 to 1.68 g FDW · m^{-2} · $year^{-1}$, compared with a value of about 1.4 g FDW · m^{-2} · $year^{-1}$ obtained from cohort-based methods. However, all of these approaches require a number of assumptions about life history and sampling, so it is impossible to say which method is the more accurate.

Confidence intervals were calculated for three of the four estimates using the method of Krueger and Martin (1980) for the size–frequency estimate and a bootstrapping procedure (Efron and Gong 1983) for the instantaneous growth and removal–summation methods. Bootstrapping is a computer-

TABLE 2. Production and production to mean biomass ratios for *Ephoron album* in the Valley River, Manitoba, 1982.

Method of calculation	Annual production (g FDW · m^{-2} · $year^{-1}$)	$P:\bar{B}$ Cohort	Annual
Removal−summation	1.43±0.41[a]	5.7	22.8
Instantaneous growth rate	1.32±0.44[a]	5.3	21.2
Allen curve	1.32	5.3	21.2
Size−frequency	1.48±0.51[b]	5.4	21.3

[a]Mean ± 95% confidence interval calculated by bootstrap method (Efron and Gong 1983).
[b]Mean ± 95% confidence interval calculated by Krueger and Martin (1980) method.

TABLE 3. Production of male and female *Ephoron album* nymphs in the Valley River, Manitoba, 1982

Method of calculation	Annual production (g FDW · m^{-2} · $year^{-1}$) Females	Males	Total
Removal−summation	0.764	0.656	1.42
Instantaneous growth rate	0.707	0.613	1.32
Allen curve	0.711	0.613	1.32
Size-frequency	0.774	0.666	1.44

intensive procedure that consists of duplicating a data set an unlimited number of times and then drawing data points at random from the much larger data set; essentially calculating a range of possible production estimates from which a 95% confidence interval can be derived. In the present study, the bootstrapping procedure produced a comparable 95% confidence interval for cohort-based methods to the Krueger and Martin (1980) method for size−frequency calculations. It is important to realize, however, that both methods are based primarily on sample variance and do not address the problem of errors such as the failure to adequately sample the habitat, the use of an inappropriate net mesh size, or the failure to account for losses as a result of the preservative. For example, failure to account for preservative effects in the present study would have resulted in an underestimate of nearly 40%, a factor at least as great as the calculated confidence intervals. Since systematic errors of this type are largely unmeasurable, attempts should be made to account for and eliminate them in the original experimental design (Waters 1979).

Few data are available on insect production dynamics from prairie rivers such as the Valley River. MacFarlane and Waters (1982) suggested that the overall productivity of prairie streams and rivers is higher than that of the small, low-order streams frequently studied, mainly because of high organic seston loads from croplands. Without data on whole-community and functional-group production in the present study, it is difficult to say whether the Valley River data support this hypothesis. The production estimate of 1.4 g FDW · m^{-2} · $year^{-1}$ for *E. album* in the Valley River does not appear abnormally high when compared with estimates for other univoltine mayflies (e.g., Waters and Crawford 1973; MacFarlane and Waters 1982). However, the cohort production interval for *E. album* is very short, only about 72 days, so that the annual production value represents rapid growth and a high production rate for a brief period, rather than steady accumulation over the entire year. The rapid growth and high production rate of *E. album*, the dominant summer mayfly in shallow riffles in the agricultural zone of the Valley River, is consistent with the findings of MacFarlane and Waters (1982) for a prairie river.

Acknowledgements

A grant from Agriculture Canada and a Professional Fellowship from the Canadian University Women's Federation provided necessary support for the project, and a travel award from the Great Plains Research Center enabled completion of the 1983 field season. Daryl Wright helped sort samples and Dr. Ken Mount and Mr. Rick Jaworski set up the bootstrapping program for the calculation of confidence limits. Dr. W. P. McCafferty verified the identification of *E. album*. Thanks are also owed to Dr. D. M. Rosenberg, Dr. R. J. MacKay, and J. Flannagan for their helpful comments on the manuscript.

BECK, S. D. 1980. Insect photoperiodism. 2nd ed. Academic Press, New York.

BENKE, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. **24**: 168−171.

BENKE, A. C. 1984. Secondary production of aquatic insects. *In* The ecology of aquatic insects. Chap. 10. *Edited by* V. H. Resh and D. M. Rosenberg. Frederick A. Praeger Inc., New York.

BENKE, A. C., and J. B. WAIDE. 1977. In defence of average cohorts. Freshwater Biol. **7**: 61−63.

BENKE, A. C., and J. B. WALLACE. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology, **61**: 108−118.

BRITT, N. W. 1962. Biology of two species of Lake Erie mayflies: *Ephoron album* and *Ephemera simulans*. Bull. Ohio Biol. Surv. **1**: 1−70.

CLIFFORD, H. F. 1982. Effects of periodically disturbing a small area of substratum in a brown water stream of Alberta, Canada. Freshwater Invertebr. Biol. **1**: 39−47.

CUSHMAN, R. M., H. H. SHUGART, JR., S. G. HILDEBRAND, and J. W. ELWOOD. 1978. The effect of growth curve and sampling regime on instantaneous growth, removal summation, and Hynes/Hamilton estimates of aquatic insect production: a computer simulation. Limnol. Oceanogr. **23**: 184−189.

EDMONDSON, W. T., and G. G. WINBERG. 1971. A manual of methods for the assessment of secondary productivity in freshwaters. Int. Biol. Programme Handb. No. 17.

EDMUNDS, G. F., S. L. JENSEN, and L. BERNER. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis, MN.

EDMUNDS, G. F., JR., L. T. NIELSON, and J. R. LARSEN. 1956. The life history of *Ephoron album* (Ephemeroptera: Polymitarcidae). Wasmann J. Biol. **14**: 145−153.

EFRON, B., and G. GONG. 1983. A leisurely look at the bootstrap, the jackknife, and cross validation. Am. Stat. **37**: 36−45.

GIBERSON, D. J. 1984. Life history and production dynamics of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba. M.Sc. thesis, University of Manitoba, Winnipeg, Man.

HAMILTON, A. L. 1969. On estimating annual production. Limnol. Oceanogr. **14**: 771−782.

HYNES, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. **57**: 344−388.

——— 1980. A name change in the secondary production business. Limnol. Oceanogr. **25**: 778.

HYNES, H. B. N., and M. J. COLEMAN. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. **13**: 569–573.

KEATING, W. M. 1824. Narrative on an expedition to the source of the St. Peters River, Lake Winnipeek, Lake of the Woods, etc. Performed in the year 1823 by order of the Hon. J. C. Calhoun, Secretary of War, under the command of Stephan H. Long, Major U.S.T.E. Philadelphia, compiled from the notes of Major Long and Messrs. Say, Keating, and Calhoun. Reprinted in 1959 by Ross and Haines, Inc., Minneapolis, MN.

KRUEGER, C. C., and F. B. MARTIN. 1980. Computation of confidence intervals for the size–frequency (Hynes) method of estimating secondary production. Limnol. Oceanogr. **25**: 773–777.

MACFARLANE, M. B., and T. F. WATERS. 1982. Annual production by caddisflies and mayflies in a western Minnesota plains stream. Can. J. Fish. Aquat. Sci. **39**: 1628–1635.

MCCAFFERTY, W. P. 1975. The burrowing mayflies of the United States. (Ephemeroptera: Ephemeroidea). Trans. Am. Entomol. Soc. **101**: 447–504.

MERRITT, R. W., and K. W. CUMMINS. (*Editors*). 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co., Dubuque, IA.

NEILL, R. M. 1938. The food and feeding of the brown trout (*Salmo trutta* L.) in relation to the organic environment. Trans. R. Soc. Edinburgh, **59**: 481–520.

SWEENEY, B. W., and R. L. VANNOTE. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. Science (Washington, D.C., 1883–), **200**: 444–446.

TAUBER, J. J., and C. A. TAUBER. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Annu. Rev. Entomol. **17**: 81–107.

WATERS, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. **10**: 91–164.

——— 1979. Influence of benthos life history upon the estimation of secondary production. Can. J. Fish. Aquat. Sci. **36**: 1425–1430.

WATERS, T. F., and G. W. CRAWFORD. 1973. Annual production of a stream mayfly population: a comparison of methods. Limnol. Oceanogr. **18**: 286–296.

WILLIAMSON, H. 1802. On the *Ephoron leukon*, usually called white-fly, of the Passaick River. Trans. Am. Philos. Soc. **5**: 71–73.