Life History and Production Dynamics of *Ephoron album* Say (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba

by

Donna J. Giberson

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
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ABSTRACT

Ephoron album was the dominant summer mayfly in shallow riffles in the Valley River in west central Manitoba in 1982 and 1983. This species is univoltine with rapid nymphal development during the summer months and an obligatory embryonic diapause. Adults began emerging about half an hour after sunset during late July and early August and the adult life span was less than four hours. Hatching success of E. album eggs exposed to -2°C for varying periods of time was positively correlated with the length of the exposure period. No eggs hatched following exposure to 4° or 10°C. Production for 1982 was estimated by four methods: the instantaneous growth rate method (1.32 ± 0.44 g/m²/yr fresh dry weight); the Allen curve method (1.32 g/m²/yr); the removal-summation method (1.43 ± 0.41 g/m²/yr) and the size-frequency method (1.33 ± 0.51 g/m²/yr). Confidence intervals (95%) were calculated by the Krueger and Martin (1980) method for the size-frequency estimate of production and by bootstrapping for the removal-summation and instantaneous growth estimates.

Acknowledgements

I'd like to express my gratitude to Dr. T.D. Galloway for his support and encouragement throughout the study, and particularly for his infectious sense of wonder and excitement for all things Entomological, which helped to make everything seem worthwhile. Thanks also to Drs. S.C. Jay and A.G. Robinson and the Department of Entomology.

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I am very grateful to Dr. Ken Mount and Mr. Rick Jaworski of the Department of Statistics, University of Manitoba, for the time and energy spent in modifying the bootstrapping technique for estimating confidence intervals to production analysis. Thanks also to Dr. W.P. McCafferty of Purdue University, Lafayette, Indiana, for confirmation of the identification of Ephoron album. I would also like to thank Mr. Marc Gaboury and Mr. Colin Hughes of the Manitoba Department of Environment for permission to use the physical and chemical data on the Valley River reported in this thesis.

Finally, I'd like to express my appreciation to the supervisory committee: Dr. F. Ward, Dr. D. Rosenberg, and Dr. R. Roughley, for their time in reviewing the thesis, and for their very helpful comments.

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Chapter I

INTRODUCTION

Members of the genus Ephoron have attracted attention since the early 1800's, notably because of their spectacular mating flights. Ephoron leukon was the first mayfly to be described in the new world, by Williamson (1802, p. 72), who commented that "these flies are so numerous that they appear some evenings like thick driven snow". In the narrative of the "expedition to the source of the St. Peters River, Lake Winnipeek, Lake of the Woods, etc.", Keating (1824) reported that,

> They [Ephoron album Say] became so abundant on Rainy River toward sunset that they presented the appearance of a snow storm. They continued for some time until they were driven by the wind into a small tributary valley where they formed white clouds beautifully relieved against the dark green of the forest . . . (from Britt 1962,.pp. 45-46).

Despite this early interest in Ephoron and subsequent investigations into the life history of the two North American species (Ide 1935; Edmunds et al. 1956; Britt 1962), little is known about their ecology and energetics. Information on production dynamics is important in quantifying energy flow pathways in food webs and can provide insight into the role of insects in the functioning of aquatic ecosystems. Production analysis may also be important from a population standpoint, because in a single measurement, production com-

bines information on individual growth and population survivorship, both important ecological parameters (Benke 1984). Ephoron album occurred in high densities in shallow riffles in the Valley River in west-central Manitoba in 1982-1983. It was the purpose of this study to examine the life history and production dynamics of a population of E. album in the Valley River.

Chapter II

REVIEW OF THE PERTINENT LITERATURE

2.1 *EPHORON ALBUM*

Ephoron species are burrowing mayflies in the family Polymitarcidae. They are found in the Ethiopian, Oriental, and Holarctic regions, but only 2 species occur in North America (Edmunds *et al.* 1976). *Ephoron leukon*, described by Williamson from the Passaic River in New Jersey in 1802, was the first mayfly species to be described in the new world (Britt 1962). *Ephoron album* was described by Thomas Say from the Winnipeg River, Manitoba, 22 years later (Keating 1824, in Britt 1962). *Ephoron album* was synonymized with *E. leukon* by Hagen (1863, in Spieth 1940) and Eaton (1863, in Spieth 1940), but both species are now considered valid (McDunnough 1926; Spieth 1940; McCafferty 1975).

Ephoron album is primarily western in distribution, and *E. leukon* is eastern, though their ranges overlap in the midwestern United States (McCafferty 1975). *Ephoron album* has been reported from New Mexico (Edmunds *et al.* 1976) to the Saskatchewan River drainage of north-central Alberta and Saskatchewan (Lehmkuhl 1972; D.K. Burton, Personal Communication 1982). Life history investigations have been conducted on two populations, by Edmunds (1948; Edmunds *et al.* 1956) in Utah, and by Britt (1962) in Lake Erie. These au-

thors described all life stages and made observations on the ecology and bahaviour of the nymphs and adults. Thew (1958) investigated the mating flights of two species of mayfly in Rock Island, Illinois, one of which was Ephoron album. Koss (1968) described Ephoron album eggs and provided characters for distingishing between the eggs of the two North American species. Burks (1953) and McCafferty (1975) gave distinguishing characters for the adults and nymphs.

Ephoron album and E. leukon are found in similar habitats, but microhabitat preferences are unknown (McCafferty 1975). They are primarily detritus feeders (Britt 1962; Shapas and Hilsenhoff 1976) and are tolerant of limited amounts of organic pollution (Roback 1974; Edmunds et al. 1976). Although they frequently occur in great numbers (Edmunds et al. 1976), no estimates of their production are available.

2.2 PRODUCTION

2.2.1 Terminology

Recent developments in the understanding of ecosystem dynamics have been at least partially dependent upon progressive clarification of production terminology (Mann 1969). Early researchers often confused production with concepts such as standing stock, yield, and turnover rates (Ricker 1946), leading to difficulties in interpretation of early production data. Standard definitions for these terms were proposed in the late 1940's (Clarke 1946; Ricker 1946), and

these, with minor modifications, are now widely accepted (MacFadyen 1963; Waters 1977).

Secondary production is defined as "the living organic matter, or biomass, that is created or produced by an animal population during an interval of time" (Benke 1984, p. 289). This definition refers to net production, and to the transformation of food material into animal biomass, not to production of new material (Edmondson and Winberg 1971). Standing stock refers only to the biomass present at one point in time, yield is only that part of the production consumed by the next trophic level and turnover rate is a measure of the doubling time of the population (Waters 1977; MacFadyen 1963).

2.2.2 Methodology

Attempts at quantification of secondary production in fresh waters date from the 1930's (e.g. Slack 1934; Neill 1938; Surber 1941) but few studies exist prior to 1960. In the 1960's, the significance placed by the International Biological Program on ecosystem dynamics renewed interest in production, and led to an inventory and critical evaluation of available production methods (Edmondson and Winberg 1971). Progressive improvements in sampling methods and in the data base on taxonomy and life histories of benthic invertebrates were important in the practical application of these methods (Waters 1977, 1979). A conceptual framework for estimating benthic secondary production (in a marine

system) was developed as early as 1919 by Boysen-Jensen (in Waters 1977; Mann 1969). He concluded that what is produced by a population eventually dies or is otherwise removed, so that an estimate of the "removal" over successive time intervals equals an estimate of production. However, Boysen-Jensen's method (the removal-summation method) was overlooked for several decades, as early production work centered around the belief that standing stock, then later yeild and turnover rates, were good indicators of production (Neill 1938; Surber 1941; Slack 1934; Juday 1940; Lindeman 1941). Clarke (1946) standardized production terminology, then Ricker (1946) and Allen (1949, in Allen 1951), working with fish, demonstrated that it was possible to calculate production of a cohort algebraically if both growth and mortality were exponential (the instantaneous growth rate method). Allen (1951) later extended the algebraic method graphically, so that production was easily calculated as the area under the growth/survivorship curve for the population (Allen curve method). Problems arose however, when attempting to extend methods developed for use on fish populations to invertebrates where age classes and cohorts were often difficult to distinguish. Therefore studies on benthic invertebrate production were rare prior to 1960, and concentrated mainly on single species with relatively simple life histories (Waters 1977). In 1961, Hynes proposed a method to estimate community production that would eliminate the need for species and cohort identification. The Hynes, or

size-frequency method, was based upon a removal-summation technique, and estimated the removal of biomass between successive predetermined size classes, rather than time intervals. The method has received considerable attention (Hamilton 1969; Fager 1969; Zwick 1975; Benke 1979; Benke and Waide 1977). Although never intended to provide more than a rough estimate (Hynes 1980), the grouping of taxa of variable life history types, trophic relations, and size characteristics for whole community production led to unacceptably large errors (Hamilton 1969). Use on single species, or groups of similar species however, has resulted in estimates comparable to those obtained by more labour intensive, cohort-based methods (Waters and Crawford 1973; Resh 1975; Benke 1979; Benke and Waide 1977). Currently, the size-frequency method is widely used to estimate production of populations where cohorts are difficult or impossible to distinguish (e.g. Krueger and Waters 1983; McLure and Stewart 1976; Rodgers 1982; Fisher and Gray 1983).

Much interest has traditionally been shown in the relationship of production to standing stock, perhaps because standing stock is relatively easy to measure. Early production biologists confused the two concepts and often expressed production as the measured standing stock at one point in time, even though standing stock fluctuates and does not show a consistent relationship to production. There is however, a relationship between production and mean

biomass, both for the duration of a cohort and on an annual basis (Waters 1969, 1977). The ratio of production to mean biomass for a single cohort generally ranges from 2 to 8 with a mean of 5 (Waters 1977). Annually, the production to mean biomass ratio ($P/\bar{B}$) varies according to life history features such as voltinism and length of aquatic life (Waters 1977; Benke 1984), but for univoltine species, usually approaches the cohort $P/\bar{B}$ of around 5 (e.g. Hexagenia limbata Serville: 4.4, Horst and Marzolf 1975; Ephemerella subvaria McDunnough : 5.8, Waters and Crawford 1973; Athripsodes ancylus Vorhies : 5.8, Resh 1975). Multivoltine species with 2 or 3 generations per year have an average $P/\bar{B}$ ratio of 10 (e.g. Baetis vagans McDunnough : 9.7, Waters 1966; Baetis rhodani Pict. : 8.4; B. buceratus Etn. : 11.8, Zelinka 1977), and hemivoltine species requiring 2 years or more to complete ozne generation have $P/\bar{B}$ ratios around 2 (e.g. Hexagenia limbata and H. bilineata Say: 2.8, Hudson and Swanson 1972; Alloperla mediana Banks : 2.8, Cushman et al. 1977). The reported consistency of the $P/\bar{B}$ ratio has led to its introduction as an additional method to estimate production (e.g. Krueger and Waters 1983; Parker and Voshell 1983; Mortensen and Simonsen 1983). Use of average $P/\bar{B}$ ratios for production estimation is less reliable than previously mentioned methods, but is also less time consuming, particularly with respect to laboratory analysis (Waters 1977, 1979; Mann 1969).

Basic methodology for the estimation of secondary production in fresh waters is well established, but questions have arisen as to the validity of the production estimate (Waters 1979; Benke 1984). Errors associated with sampling benthic invertebrates, especially over successive sampling periods, may be high and are difficult to quantify (Resh 1979). A method has been proposed by Krueger and Martin (1980) to calculate 95% confidence intervals, based mainly on sample variance, for estimates of production using the size-frequency method. The procedure has become widely accepted (e.g. Rodgers 1982; MacFarlane and Waters 1982; Krueger and Waters 1983) since it provides an indication of the effect of sampling error on the production estimate. It is important to note however, that other sources of error, for example errors in determining sizes and weights of individuals, may be as large or larger than sampling error and yet be completely ignored by Krueger and Martin's (1980) procedure (Hynes 1980; Benke 1984).

2.2.3 Mayfly Production

Although mayflies are important components of freshwater ecosystems and the diets of many fish, studies of their production were rare prior to 1970 (Waters 1977; Hynes 1970). The number of studies dealing with production of mayflies since then has increased dramatically (Table 1). As may be expected, the estimates vary widely, but most fall below 1

$g/m^2/yr$ (dry weight; e.g. Horst and Marzolf 1975; Tsuda 1972; Zelinka 1980; Brooker and Morris 1978; Krueger and Waters 1983). The highest production estimates reported for stream mayflies are for two species from a desert stream in Arizona: Tricorythodes dimorphus Allen at 14.3 $g/m^2/yr$ and Baetis quilleri Dodds at 21.9 $g/m^2/yr$ (dry weight, Fisher and Gray 1983). Annual production to biomass ratios reported in Table 1 are generally consistent with those reported by Waters (1977) for benthic invertebrates. Values for most univoltine species fall between 2 and 8 (average: 5.0) and values for multivoltine species averaged 11.4, excluding the two extreme cases reported below. The importance of the length of aquatic life on the $P/\bar{B}$ ratio is illustrated by the value of 26 for Tricorythodes attratus McDunnough (Hall et al. 1980). In this case, most of the life history is spent in an embryonic, non-producing stage, resulting in a higher $P/\bar{B}$ than expected from voltinism alone (Waters 1979). The extremely high values reported by Fisher and Gray (1983) (Baetis quilleri : 64; Tricorythodes dimorphus : 75) are the result of continuous reproduction and the high number of generations per year (n = 18) for these species.

Table 1. A summary of mayfly production estimates and annual production to mean biomass ratios, based on pattern of voltinism

Species	Production ($g/m^2/yr$ dry weight)	Annual $P/\bar{B}$	Locality	Reference
I. UNIVOLTINE SPECIES				
Hexagenia limbata	0.12	4.4	Kansas reservoir	Horst & Marzolf 1975
Ephemerella strigida	0.71	2.3	Yoshino R., Japan	Tsuda 1972
Ephemerella subvaria	4.45	5.8	Luxemburg Ck., Minnesota	Waters & Crawford 1973
Rhithrogena semicolorata	2.08	8.4	trout streams Czechoslovakia	Zelinka 1977
Ecdyonuris sp.	1.41	8.4		
Ephemerella ignita	0.34	2.9	River Wye, England	Brooker & Morris 1978
Ephemerella ignita	0.09	2.5		
Rhithrogena semicolorata	0.22	3.9		
Rhithrogena semicolorata	0.35	3.4		
Ephemerella ignita	0.96	11.01	Jihlava R., Czechoslovakia	Zelinka 1980
Baetis lutheri	0.57	8.4		
Ephemerella ignita	0.72		Experimental channel, Eng.	Welton *et al.* 1982

Con't . . . .

Table 1. Con't

Species	Production	P/$\bar{B}$	Locality	Reference
Stenacron interpunctatum canadence	0.13	7.0	Redwood R., Minnesota upstream of impoundment	MacFarlane & Waters 1982
Stenonema nepotellum	0.56	5.7		
Caenis simulans	0.78	4.2		
Stenacron interpunctatum canadence	4.0	6.1	Redwood R., Minnesota downstream of impoundment	MacFarlane & Waters 1982
Caenis simulans	0.47	4.4		
Delatidium sp.	2.6		Horokiwi Stream, N.Z.	Hopkins 1976
Delatidium sp.	5.35		Hinau Stream, N.Z.	
Ephemerella sp.	0.1	5.0	Caribou R., Minnesota	Krueger & Waters 1983
Stenonema vicarium	0.6	3.7		
Paraleptophlebia	0.16	3.1		
Leptophlebia sp.	0.01	5.0		
Heptagenia hebe	0.03	4.0		

Con't . . . . .

Table 1. Con't

Species	Production	P/B	Locality	Reference
Ephemerella sp.	0.08	4.0	Blackhoof R., Minnesota	Krueger & Waters 1983
Stenonema sp.	0.02	3.7		
Paraleptophlebia sp.	0.05	3.5		
Stenacron sp.	0.002	5.0	North Branch Cr., Minnesota	Krueger & Waters 1983
Stenonema vicarium	0.03	3.7		
Leptophlebia sp.	0.002	5.0		
Pseudocloeon sp.	0.016	5.0		
Ephemerella sp.	1.42	5.9		
II MULTIVOLTINE SPECIES				
Baetis bicaudatus	1.37		Logon River, Utah	Pearson & Kramer 1972
Choroterpes mexicana	0.25	15.4	Brazos R., Texas	McLure & Stewart 1976
Baetis vagans	2.1	9.7	Valley Ck., Minnesota	Waters 1966

Con't . . . . .

Table 1. Con't

Species	Production	$P/\bar{B}$	Locality	Reference
Delatidium sp.	4.23	3.5	Selwyn R., N.Z.	Winterbourn 1974
Baetis rhodani	0.89	8.4	trout streams, Czech.	Zelinka 1977
Tricorythodes atratus	8.56	26	Mississippi headwaters	Hall *et al.* 1980
Caenis ?amica	0.67	12.7	artificial channel, Tenn.	Rodgers 1982
Baetis buceratus	1.11	11.8	Jihlava R., Czechoslovakia	Zelinka 1980
Ecdyonuris venosus	0.48	9.4		
Potomanthus luteus	0.48	7.5		
Baetis fuscatus	0.27	11.2		
Caenis macrura	0.20	13.0		
Cloeon dipterum	0.07	11.2		
Baetis rhodani	0.93		experimental channel, Eng.	Welton *et al.* 1982
Baetis sp.	0.07	8.7	Caribou R., Minnesota	
Baetis sp.	0.67	12.4	Blackhoof R., Minnesota	Krueger & Waters 1983
Baetis sp.	0.78	10.4	North Branch Ck., Minn.	

Con't . . . . .

Table 1. Con't

Species	Production	P/$\bar{B}$	Locality	Reference
Baetis quilleri	21.9	64	Sycamore Ck., Arizona	Fisher & Gray 1983
Tricorythodes dimorphus	14.3	75		
III. HEMIVOLTINE SPECIES				
Hexagenia bilineata & H. limbata	1.5	2.8	Lewis & Clarke Lake, Neb.	Hudson & Swanson 1972
Hexagenia limbata	0.8	2.1	Savanne Lake, Ontario	Ricklik & Momot 1982

Chapter III

MATERIALS AND METHODS

3.1 THE STUDY SITE

3.1.1 The Valley River

The Valley River (Fig. 1) originates in open boggy terrain north of Singush Lake in Duck Mountain Provincial Park, Manitoba (Fig. 2), and as a small, heavily shaded woodland stream, cuts down through the Manitoba escarpment in the Duck Mountain Provincial Forest (Fig. 3). In the open terrain of the agricultural zone, it widens to a larger meandering prairie river, characterized by alternating large deep pools and extensive low-gradient riffles, its banks shaded by dense vegetation (Fig. 4). The riffles are generally shallow, ranging from a few cm to 30 or 40 cm deep except during spring runoff or periods of heavy rainfall, and large portions of the riffles can be expected to freeze to the bottom each winter. Substrate in the riffles consists of sand, gravel, and cobble with some boulders in the agricultural zone, and large cobble and boulder in the headwater zone. Pools can be 2 or more metres deep and have a sandy-clay substrate. Stream widths range from 1 - 2 metres in the headwater zone, 5 - 6 metres at the beginning of the agricultural zone and 25 - 35 metres near the mouth. In most

Fig. 1. The Valley River drainage, Manitoba.

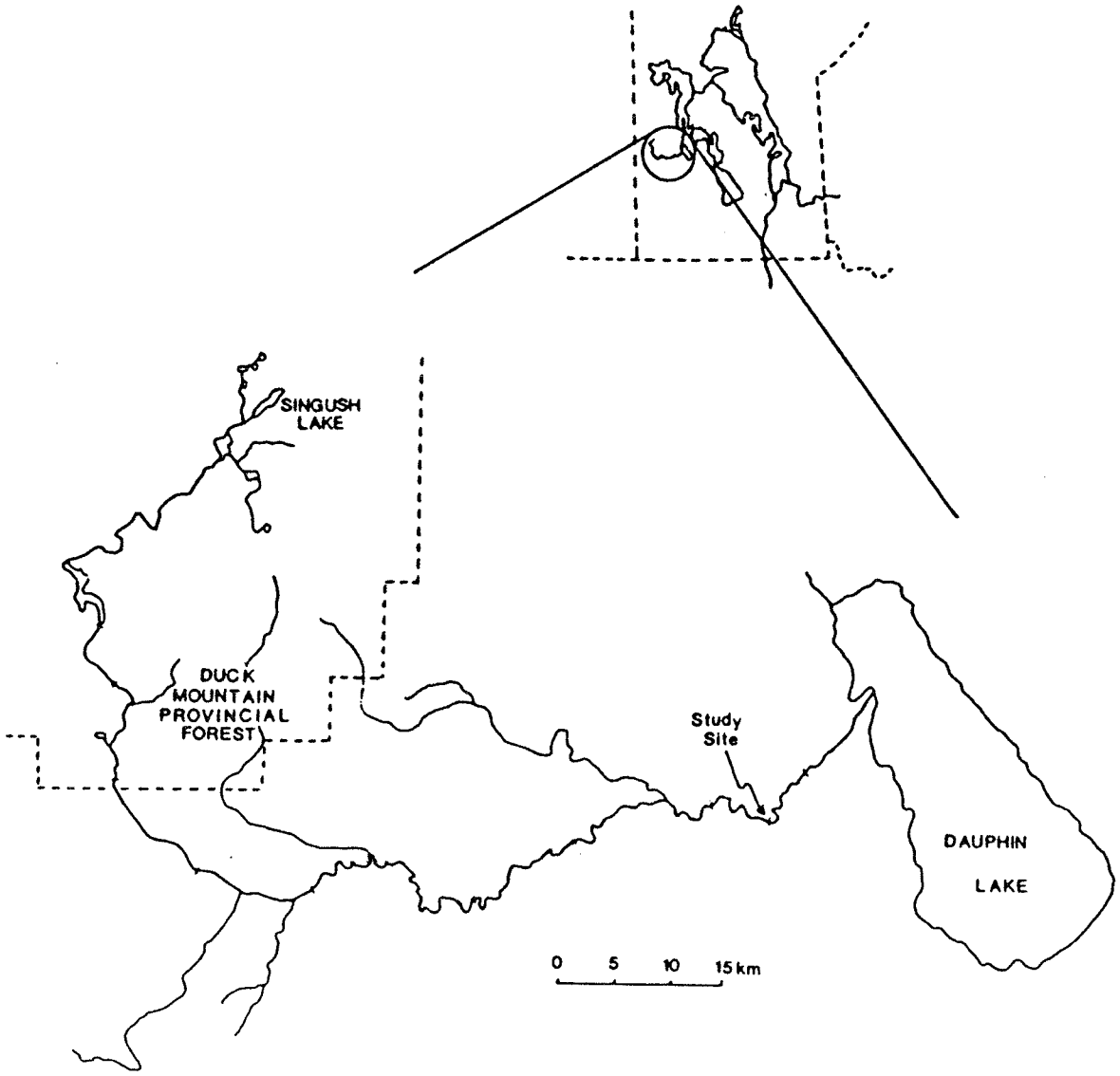

SINGUSH
LAKE
DUCK
MOUNTAIN
PROVINCIAL
FOREST
Study
Site
DAUPHIN
LAKE
0 5 10 15 km

Fig. 2. The Valley River near its source, north of Singush Lake, Manitoba, 27 June 1983.

Fig. 3. The Valley River, at the southern boundary of the Duck Mountain Provincial Forest, Manitoba, 23 June 1983.

Fig. 4. The Valley River, Manitoba, near the study site (100°05'W, 51°15'N), 27 May 1982.

years, a minimum flow of 0.1 to 1.0 m^3/sec is maintained except during spring runoff and periods of heavy rainfall. In 1983, water levels were unusually high and discharge exceeded 10 m^3/sec for most of the summer (Fig. 5; Environment Canada 1982). Water temperatures are at or near zero during the winter but rise quickly in spring and remain above 20°C for most of the summer (Fig. 6; M. Gaboury, Manitoba Dept. of Environment, personal communication). Water chemistry data for 1982 for a site in the forested headwater zone, and one in the agricultural zone just downstream of the study site riffle, are shown in Fig. 7 (C. Hughes, Manitoba Department of Environment and Workplace Safety and Health, Environmental Management Division, Water Standards and Studies Section, personal communication). Conductivity, hardness, pH, coliform counts, and nitrogen levels were generally higher in the agricultural zone than in the forested location.

3.1.2 The Study Site Riffle

The Valley River at the study site location (L.S.D. 9, Sect. 9, Tp 26, R 19, W 1) drains 1,720 km^2, much of that agricultural land. The study site riffle was approximately 70 m long and 20 m wide, except during the early summer of 1983 when the river repeatedly overflowed its banks. The bottom was fairly uniform gravel and cobble (Fig. 8) with few boulders (Fig. 9). Riparian vegetation consisted mainly

Fig. 5. Discharge for the Valley River, Manitoba, at a site 200 m downstream of the study site, 1982 and 1983 (Environment Canada 1982;1983)

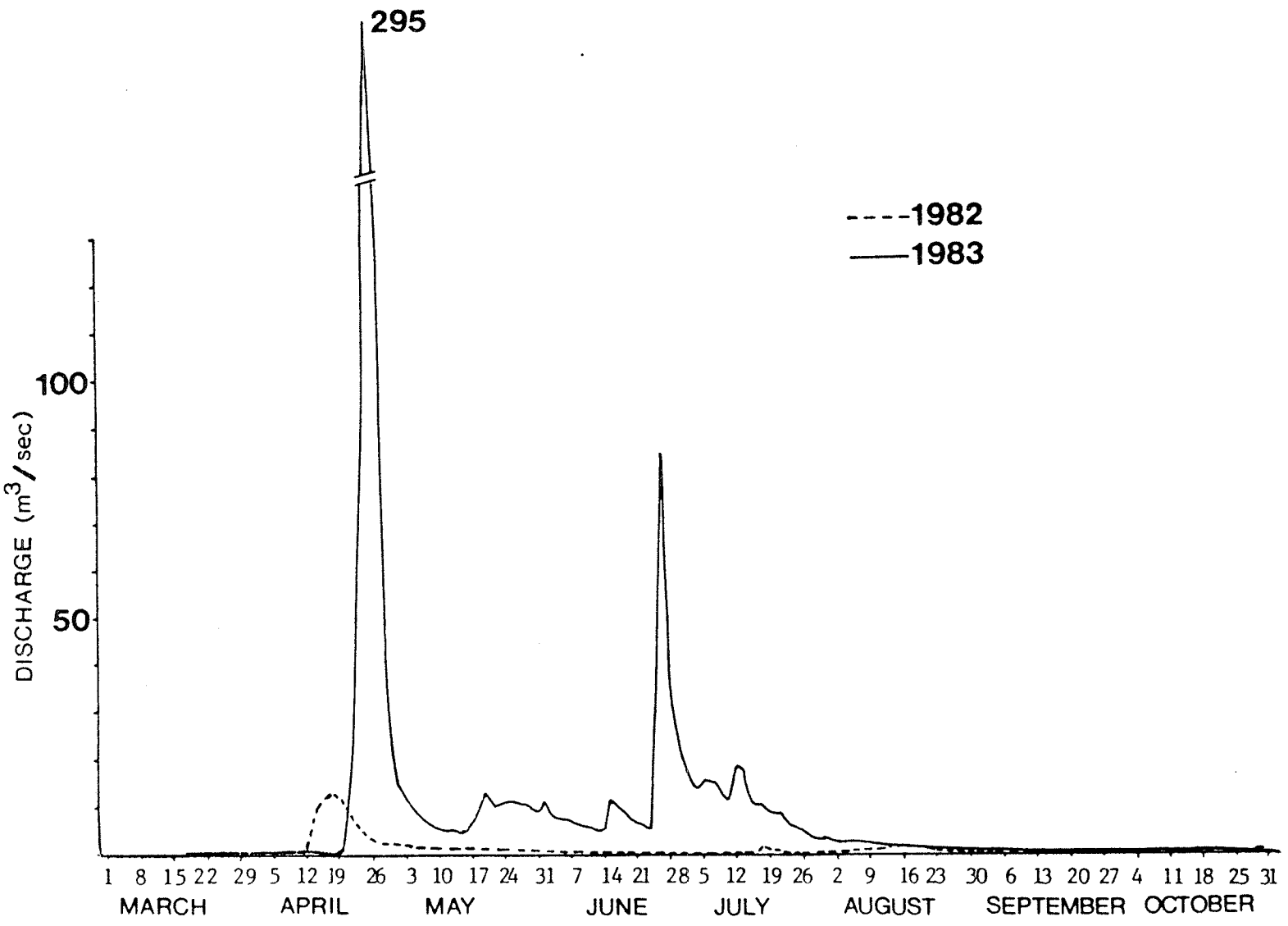

295
----1982
——1983
100
50
DISCHARGE (m^3/sec)
1 8 15 22 29 5 12 19 26 3 10 17 24 31 7 14 21 28 5 12 19 26 2 9 16 23 30 6 13 20 27 4 11 18 25 31
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

Fig. 6. Minimum daily water temperatures at the study site on the Valley River, Manitoba, 16 April to 28 August, 1982 and 1983 (M. Gaboury, Manitoba Dept. of Environment, personal communication)

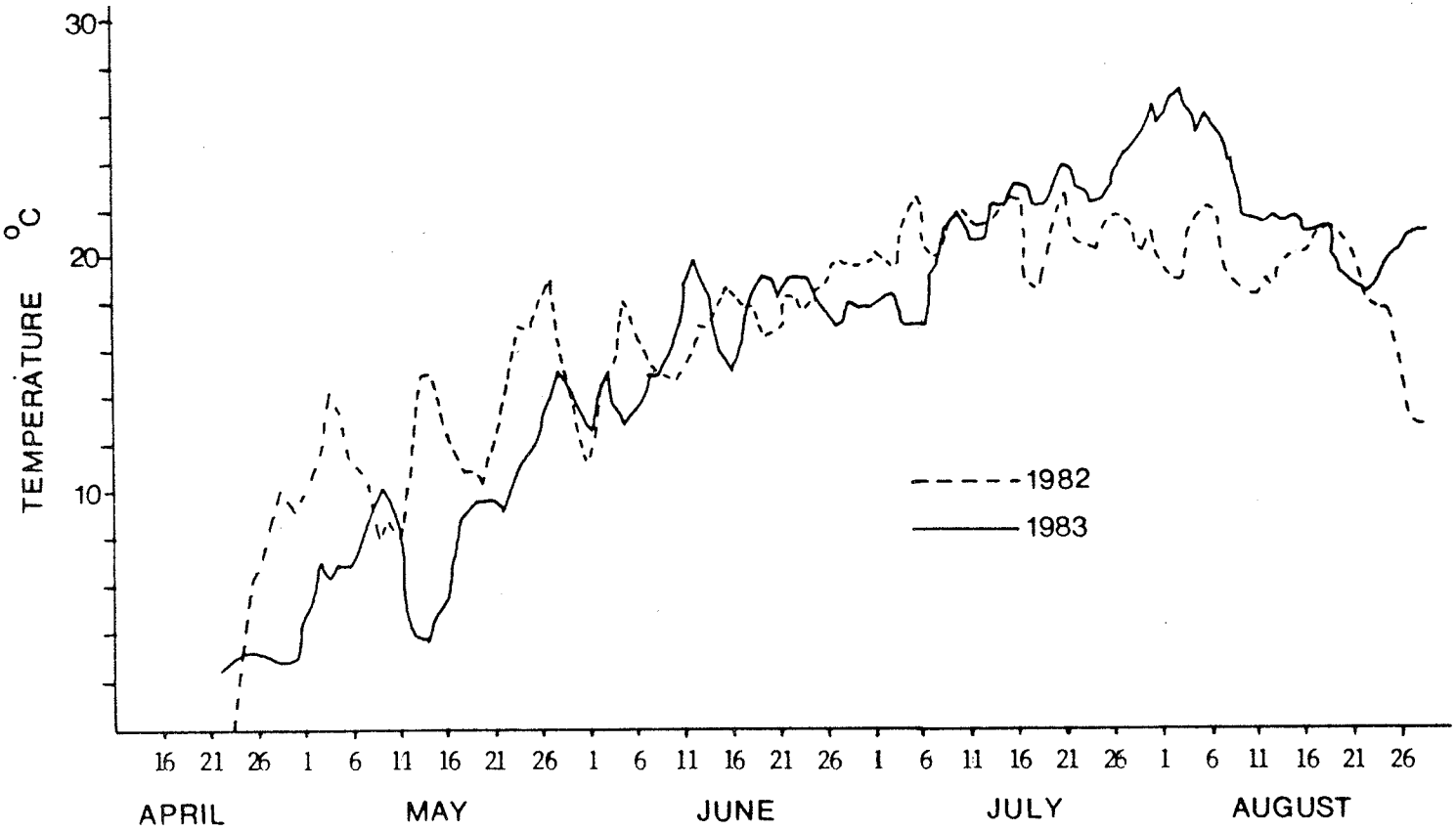

TEMPERATURE °C
30
20
10
16 21 26 1 6 11 16 21 26 1 6 11 16 21 26 1 6 11 16 21 26 1 6 11 16 21 26
APRIL
MAY
JUNE
JULY
AUGUST
1982
1983

Fig. 7. Water Chemistry data for two sites on the Valley River, Manitoba, 1982 (C. Hughes, Manitoba Dept. of Environment, personal communication).

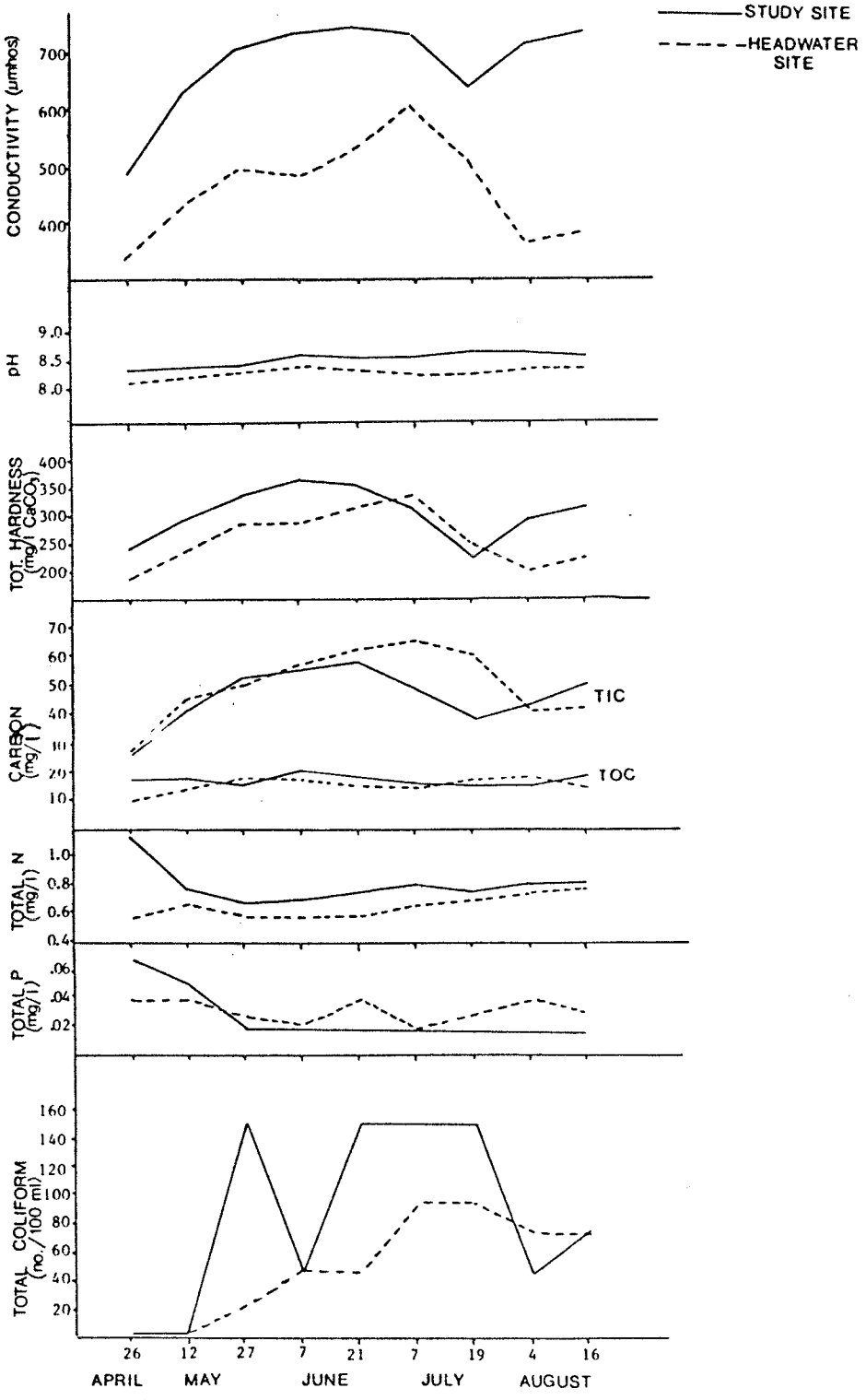

STUDY SITE
HEADWATER SITE
CONDUCTIVITY (µmhos)
700
600
500
400
pH
9.0
8.5
8.0
TOT. HARDNESS (mg/l CaCO3)
400
350
300
250
200
CARBON (mg/l)
70
60
50
40
30
20
10
TIC
TOC
TOTAL N (mg/l)
1.0
0.8
0.6
0.4
TOTAL P (mg/l)
.06
.04
.02
TOTAL COLIFORM (no./100 ml)
160
140
120
100
80
60
40
20
26
12
27
7
21
7
19
4
16
APRIL
MAY
JUNE
JULY
AUGUST

Fig. 8. Representative substrate found over most of the study site riffle on the Valley River, Manitoba (coin in upper left quadrant is a Canadian 25¢ piece).

Fig. 9. View of the study site riffle on the Valley River, Manitoba, 23 June 1983.

of poplar, elm, scrub willow, and grasses. Little macrophyte growth was noted within the river, and examination of river water and rock scrapings revealed few algal cells.

3.2 MATERIALS AND METHODS

3.2.1 Sampling

Quantitative samples were taken every two weeks during the summer of 1982 with a modified Neill sampler (Neill 1938; Fig. 10). With each sample, approximately 0.1 m^2 of bottom was removed to a depth of 10 to 15 cm. This sampler was chosen over the more conventional Surber sampler (Surber 1941) to eliminate problems of backwash and nymphs escaping from the open enclosure of the Surber (Cummins 1962; Edmondson and Winberg 1971; Hynes 1970). One hundred and fifty predetermined sites were established along 15 transects, 5 m apart, along the length of the riffle (Fig. 11), and 10 sites were selected randomly each sampling day by means of a random number program on a TI55-II® pocket calculator. Early in the season (28 June) several samples were taken to varying substrate depths to determine the depth to which *E. album* occurred. Care was taken not to sample the same area of bottom twice on consecutive sampling days, to avoid a bias in the density estimates due to delays in recolonizing previously sampled areas (Clifford 1982). Low water conditions prevailed during the first week of July 1982, and the number of predetermined sites on 8 July was reduced to 90 for that

Fig. 10. Modified Neill sampler used to sample Ephoron album in the Valley River, Manitoba, 1982 and 1983.

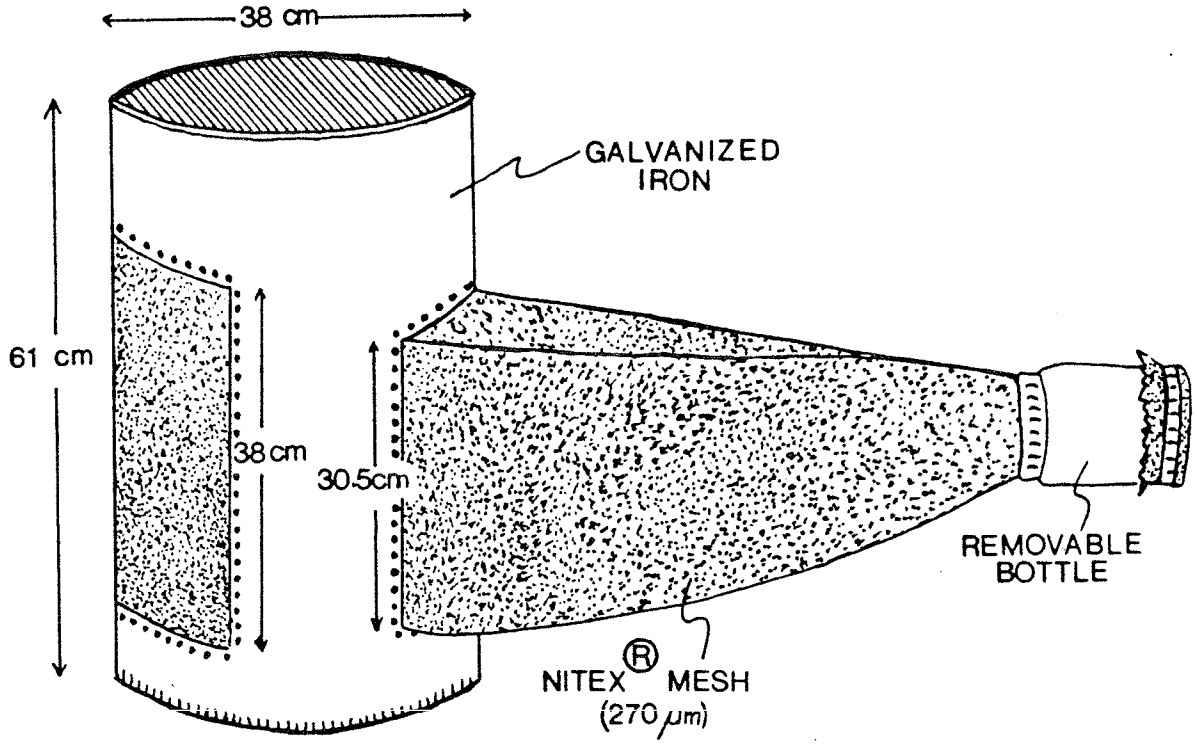
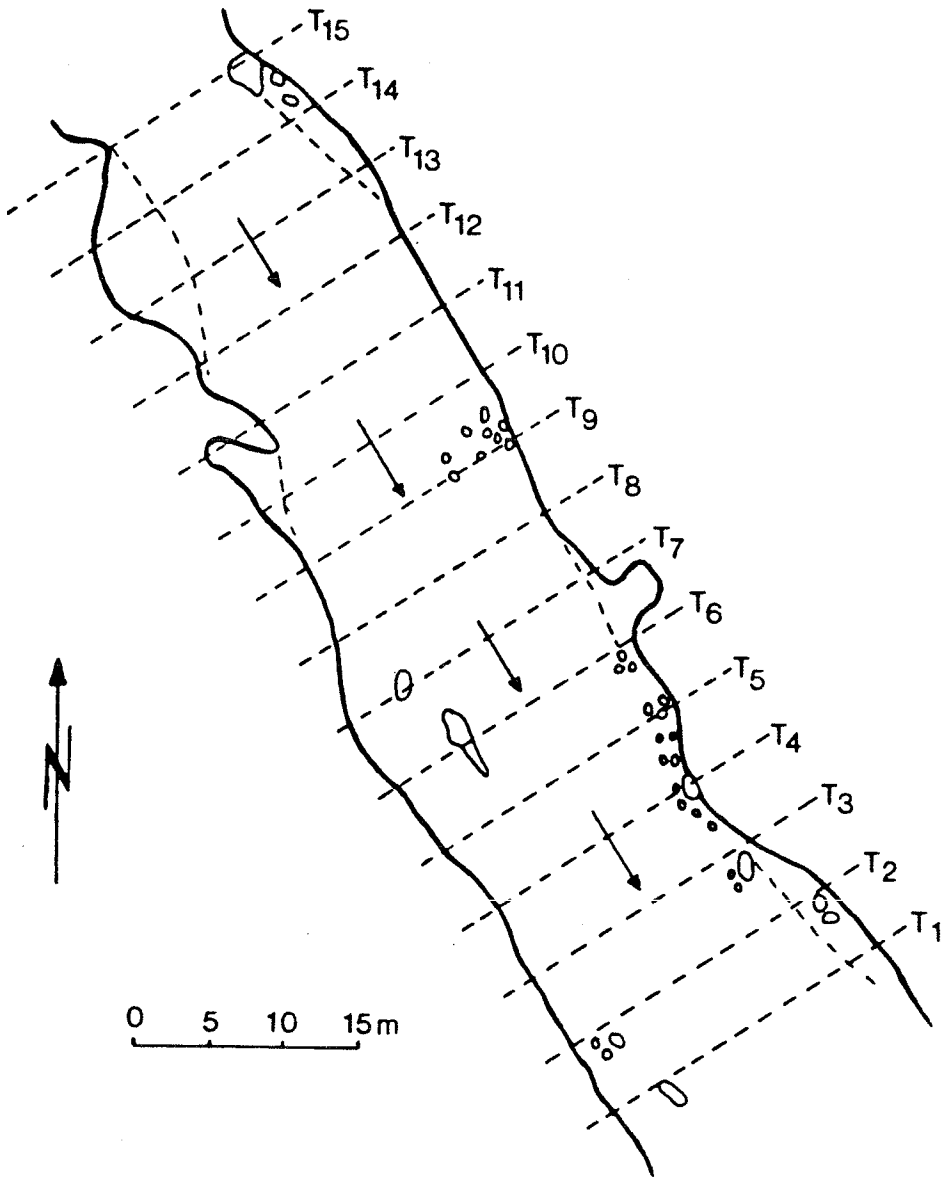

38 cm
GALVANIZED IRON
61 cm
38 cm
30.5cm
REMOVABLE BOTTLE
NITEX® MESH
(270 μm)

Fig. 11. Study site riffle on the Valley River, Manitoba (L.S.D. 9, Sect. 9, Tp 26, R 19, W 1). Dashed lines refer to transects; arrows refer to direction of flow.


T15
T14
T13
T12
T11
T10
T9
T8
T7
T6
T5
T4
T3
T2
T1
N
0 5 10 15m

sample period only. Conditions returned to normal on subsequent sample dates.

For each sample, all rocks enclosed by the sampler were scrubbed clean and the substrate disturbed to a depth of 10 to 15 cm. The animals thus released were swept by the current into the sample net. These were preserved in the field in 10% formalin for later sorting in the lab. Water velocity, water depth, and substrate particle size were recorded for each sample location, and an analysis of organic content was made for each sample based on a subjective scale of 1 to 5.

In 1983, collection of quantitative samples was impossible until late July, due to extremely high water conditions, so only qualitative sampling was carried out. Samples were immediately taken back to the laboratory for live sorting. Shrinkage and weight loss following preservation and storage in formalin and alcohol were determined using live Ephoron nymphs collected during this period.

Observations on emergence of adult E. album were conducted in the field in late July and August, 1983. Fertilized eggs were collected and returned to the laboratory for later 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 both at the lights, and by sweeping with a net over the water surface. Two floating emergence traps (measuring 0.5 m X 0.5 m X 0.5 m) were located in the

riffle and monitored at 30 minute intervals during the emergence periods on 28 July, 4 August, and 7 August.

3.2.2 Hatching Stimulus for E. album eggs

Eggs collected in the field on 28 July, 1983, were subjected to a number of conditions to determine the optimum temperatures for egg development. Eggs were maintained at 20°C in dechlorinated water in aerated pans for 60 days, then transferred to 12 ml glass vials for treatment. Each treatment consisted of 3 replicates of 30 eggs each, held at -2°,4°, or 10°C in complete darkness for 1, 3, 7, 14, and 60 days, then incubated at 20°C (dark) until hatching was complete. Three additional vials of 30 eggs each (60 days after oviposition) were incubated at 13°C after treatment at each temperature for 3 days. Eight weeks after initiation of the experiment, two out of the three vials in all treatments (except the 60 day treatment) were subjected to -2°C for an additional 14 days.

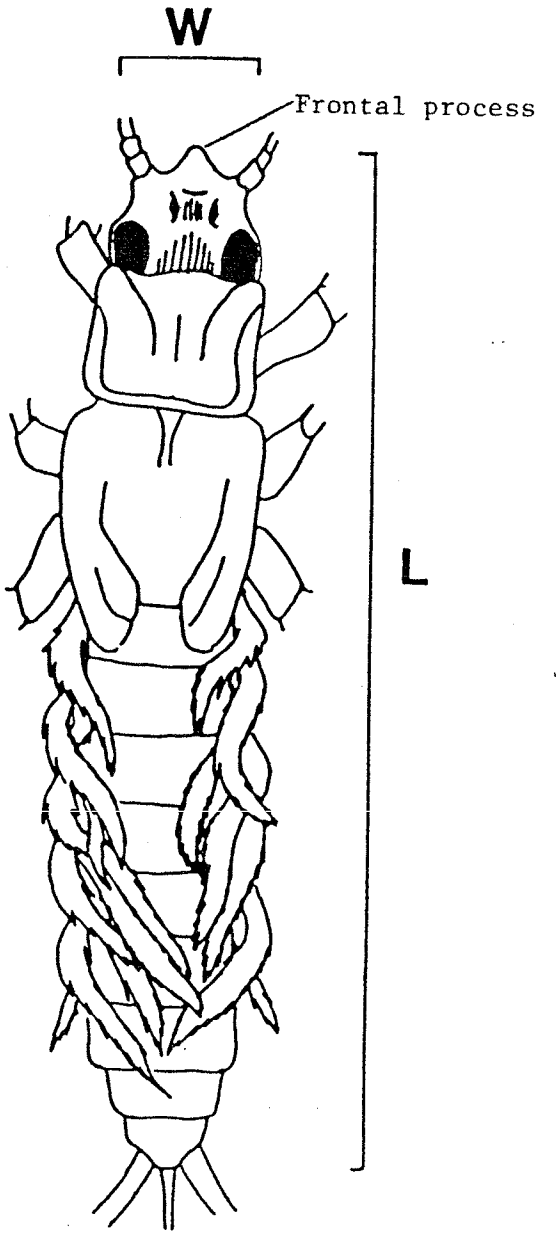
3.2.3 Biomass Determination

All samples were washed through a 250 micron brass seive, and Ephoron nymphs sorted into 70% ethyl alcohol using an Olympus dissecting microscope. Nymphs were identified using the keys of Burks (1953) and McCafferty (1975). Ephoron album was the only burrowing mayfly in the study riffle, facilitating identification of even the smallest stages.

Lengths and head capsule widths of all nymphs were measured using a measuring ocular in an Olympus dissecting microscope. Length was measured from the tip of the frontal process to the distal end of the abdomen (excluding the caudal filaments). Head capsules were measured just anterior to the eyes (Fig. 12). Six hundred nymphs, ranging in size from 1 mm to 14.2 mm, were measured, then dried at 60°C for 24 hours and cooled in a desiccator for one hour, before weighing to the nearest microgram on a Cahn 25® electrobalance (Ventron Corp., Cerritos, California). Preserved dry weights of remaining nymphs were estimated from a regression of length to dry weight ($W = 0.002\ L^{2.814}$, $r^2 = 0.97$; see Fig. 20).

The effects of preservation on length and weight were also examined. In 1983, 150 nymphs of varying sizes were killed by exposure to heat, then measured and dried as above, without prior exposure to formalin or alcohol. In addition, 70 nymphs were killed as above, and measured at intervals during exposure to preservative. These were first placed into 10% formalin for 2 weeks, and measured at 1, 3, 7, and 14 days; then nymphs were washed and transferred to 70% ethyl alcohol and again measured at 1, 3, 7, 14, and 30 days. No shrinkage in total length was noted, but preservation procedures were responsible for a weight loss of up to 50% (Fig. 21). Therefore weights used in the production calculations were estimated from a regression of live length on fresh dry weight (FDW) ($W = 0.002\ L^{3.05}$, $r^2 = 0.89$).

Fig. 12. Dorsal view of Ephoron album nymph with legs and mandibular tusks removed. L = measured length from tip of frontal process to posterior tip of abdomen. W = head capsule width, measured just anterior to eyes.


W
Frontal process
L

3.2.4 Production Calculations

Production was calculated by four methods: the instantaneous growth rate method (Ricker 1946), the Allen curve method (Allen 1951), the removal-summation method (Boysen-Jensen 1919, in Waters 1977), and the size-frequency method (Hynes 1961; Hynes and Coleman 1968; Hamilton 1969). Nymphs were sorted into 13 - 1 mm size classes for calculation of production by the size-frequency method, and apparent negative production between size classes was treated arithmetically in the production summation (Hamilton 1969; see Appendix Table I-c). The cohort production interval (C.P.I.) for Ephoron album in the Valley River for 1982 was 80 days, so the estimate obtained by the size-frequency method was multiplied by a C.P.I. correction of 365/80 (Benke 1979). Confidence intervals (95%) were calculated for the size-frequency method using the technique of Krueger and Martin (1980), and for the instantaneous growth and removal-summation methods by a bootstrapping procedure (Efron and Gong 1983) modified for production analysis by Dr. K. Mount, Dept. of Statistics, University of Manitoba.

Chapter IV

RESULTS

4.1 LIFE HISTORY OF EPHORON ALBUM

4.1.1 Distribution

Ephoron album nymphs were restricted in the Valley River to the agricultural zone (Fig. 13), where they were found only in open, low-grade riffles characterized by sand-gravel-cobble substrates. Riffle areas in the head-water zone were generally smaller and steeper with boulder-cobble substrates apparently unsuitable for E. album.

Within the study site riffle, E. album distribution was not consistently related to substrate particle size, organic content of the substrate, water velocity or water depth. However there was a significant correlation between density and substrate particle size ($P<0.05$), and density and organic content ($P<0.05$) on 6 June only (Table 2).

4.1.2 The Egg

Ephoron album eggs were opaque white when deposited and averaged 0.33 ± 0.03 by 0.15 ± 0.02 mm ($\pm$S.E., n = 20) in size. An adhesive polar cap present at the posterior end of each egg served to attach the egg to substrate materials immediately after oviposition (Fig. 14). The developing embryo was clearly visible through the chorion (Fig. 14b), but af-

Fig. 13. Riffle sites sampled for *Ephoron album* in the Valley River, Manitoba, during 1983.

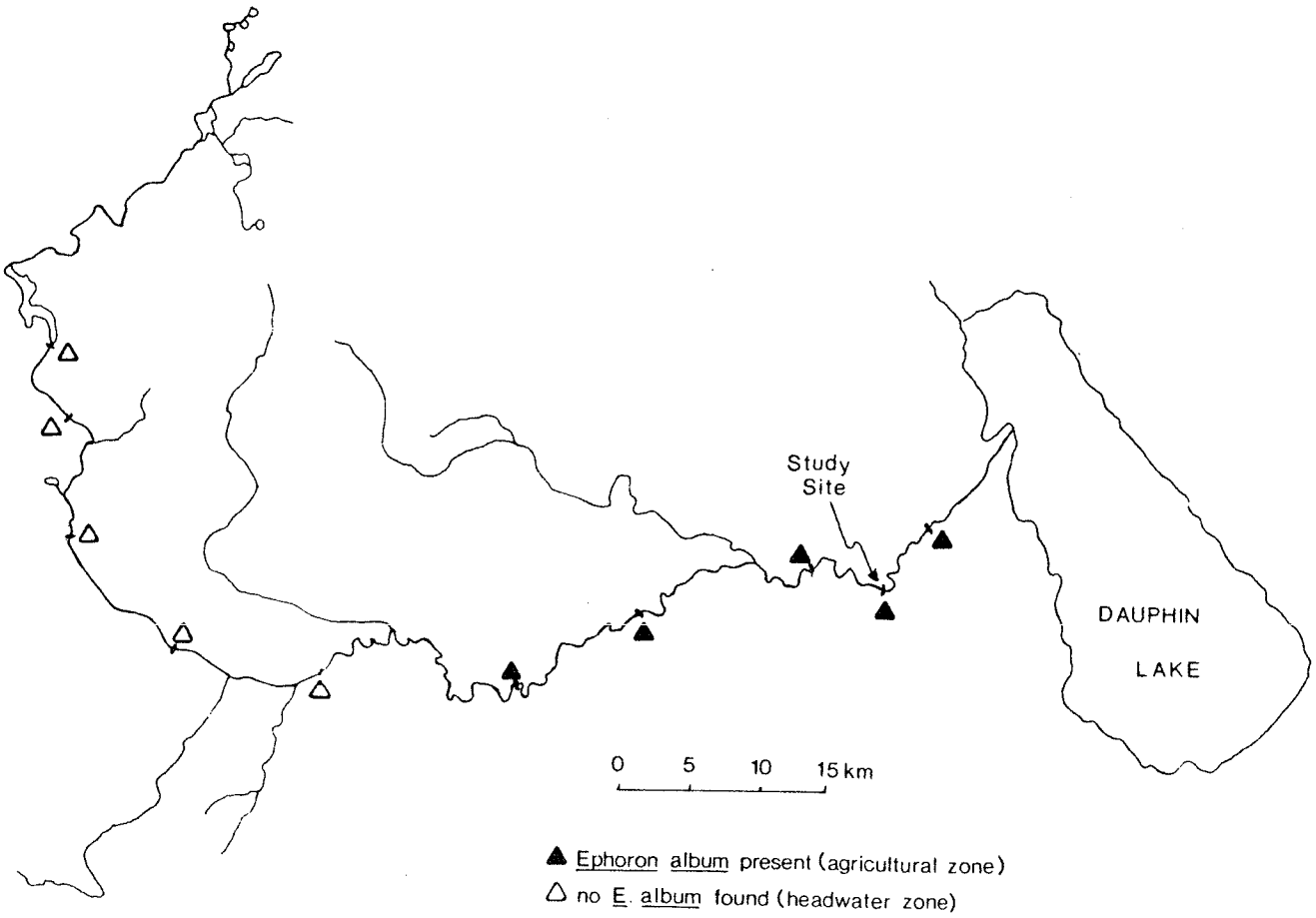

Study
Site
DAUPHIN
LAKE
0 5 10 15 km
▲ Ephoron album present (agricultural zone)
△ no E. album found (headwater zone)

Table 2. Correlation coefficients (r) for regression of sample density on amount of organic material, substrate particle size, water velocity, and water depth, on five sample dates, 1982 (samples from 19 August contained too few nymphs to analyze), in the Valley River, Manitoba.

Date	Variable			
	Organic Matter	Substrate Particle Size	Column Water Velocity	Water Depth
6 June[a]	0.39[b]	-0.62[c]	-0.48	0.20
23 June[d]	0.14	-0.32	-0.37	-0.29
7 July[d]	0.30	-0.51	-0.25	-0.39
23 July[d]	-0.57	-0.26	-0.18	0.17
4 Aug.[d]	-0.51	-0.04	-0.14	0.02

[a] n = 15

[b] significantly correlated at $P < 0.01$

[c] significantly correlated at $P < 0.05$

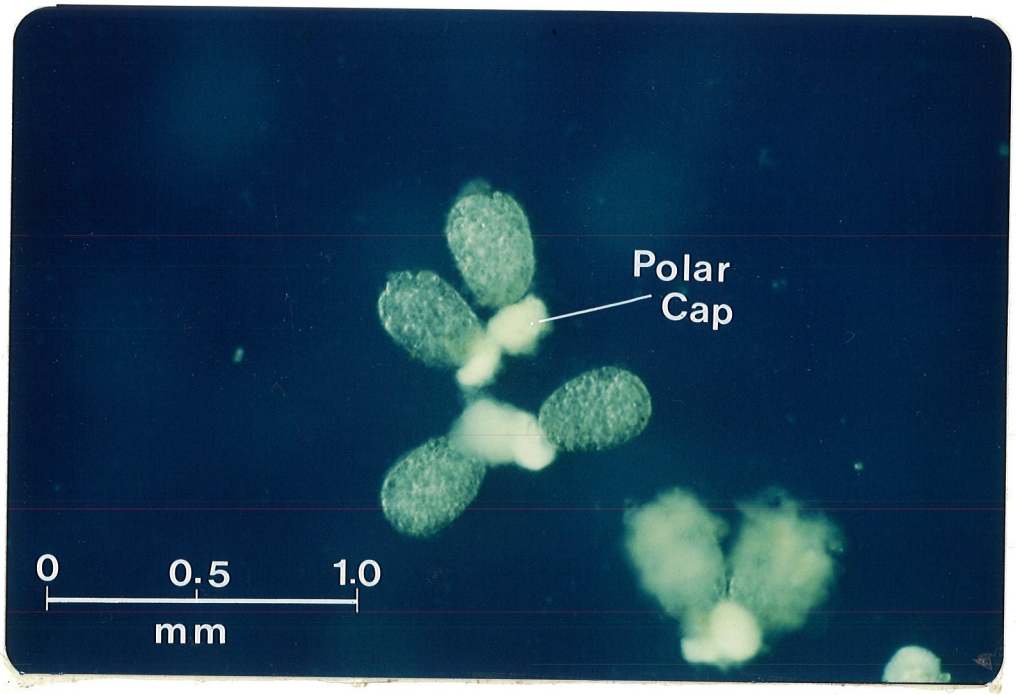
[d] n = 10

Fig. 14. Eggs of Ephoron album

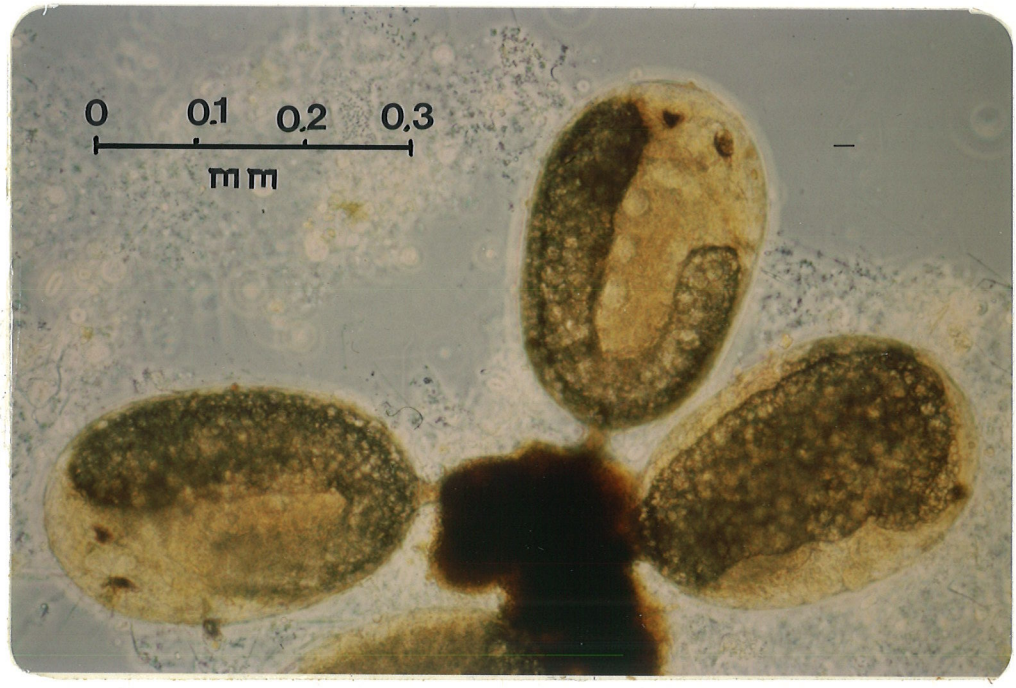
a. undifferentiated newly deposited eggs.

b. four weeks after oviposition.

a.



b.



ter 21 to 28 days, no further development was observed and no hatching occurred until eggs had been subjected to a period of cold temperatures. Eggs treated at 4° and 10°C did not hatch, but hatching success of eggs treated at -2°C was positively correlated with duration of exposure (Table 3). When eggs initially exposed to 4° and 10°C for up to 60 days were exposed to -2°C for an additional 14 days, a large percentage of the eggs hatched (Table 3). However, hatching success in the secondary treatment was lower and more variable than when eggs were treated initially for 14 days at -2°C (Table 3). The amount of time required for hatching after the initial exposure to -2°C was also variable, ranging from 3 to 41 days (Table 4). However, total amount of time from onset of treatment to the start of the hatch was consistently 42 to 43 days (103 to 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, hatching began within three days of warming the eggs to 20°C (± 0.5°C).

4.1.3 The Nymph

Newly hatched Ephoron album nymphs ranged from 0.79 to 0.87 mm in length and averaged 0.003 mg (FDW, n = 20). First instar nymphs possessed neither the mandibular tusks nor the abdominal gills (Fig. 15) present in later stage nymphs (Fig. 16). The maximum size of a mature nymph was

Table 3. Effect of temperature on hatching success of Ephoron album eggs collected 28 July 1983, from the Valley River, Manitoba.

Initial Treatment				Subsequent[b] treatment
Treatment temp. (°C)	Exposure time (days)	Post-treatment temp. (°C)	Mean[a] % hatch	Mean[c,d] % hatch
-2	1	20	5.5 ± 2.9	35.0 ± 15.0
	3 [d]	13	1.7 ± 1.0	7.1 ± 2.0
	3	20	4.4 ± 1.1	10.0 ± 2.0
	7	20	24.4 ± 4.8	13.3 ± 2.0
	14	20	59.8 ± 8.0	6.6 ± 4.7
	60	20	84.4 ± 2.9	
4	1	20	0	15.0 ± 7.1
	3	13	0	26.7 ± 3.4
	3	20	0	25.0 ± 8.3
	7	20	0	28.3 ± 1.6
	14	20	0	31.7 ± 8.4
	60	20	0	
10	1	20	0	45.0 ± 5.0
	3	13	0	16.7 ± 3.4
	3	20	0	20.0 ± 3.3
	7	20	0	25.0 ± 1.7
	14	20	0	25.0 ± 5.0
	60	20	0	
20	130	20	0	

[a] mean % hatch in 3 replicates of 30 eggs each, ± S.E.

[b] Two out of 3 replicates taken from initial treatment were further exposed to -2°C for 14 days, then warmed to 20°C to record hatch (no additional eggs hatched in single replicate kept as control).

[c] calculated as per cent of total eggs.

[d] 2 replicates of 30 eggs each, ± S.E.

Table 4. Time required for hatching of Ephoron album eggs held at -2°C for varying time periods (Eggs collected 28 July, 1983; treatments began 28 September, 1983).

Exposure period (days)	Total days to first hatch after onset of treatment
1	42
3	43
7	42
14	42
60	63

Fig. 15. Newly hatched Ephoron album nymph.

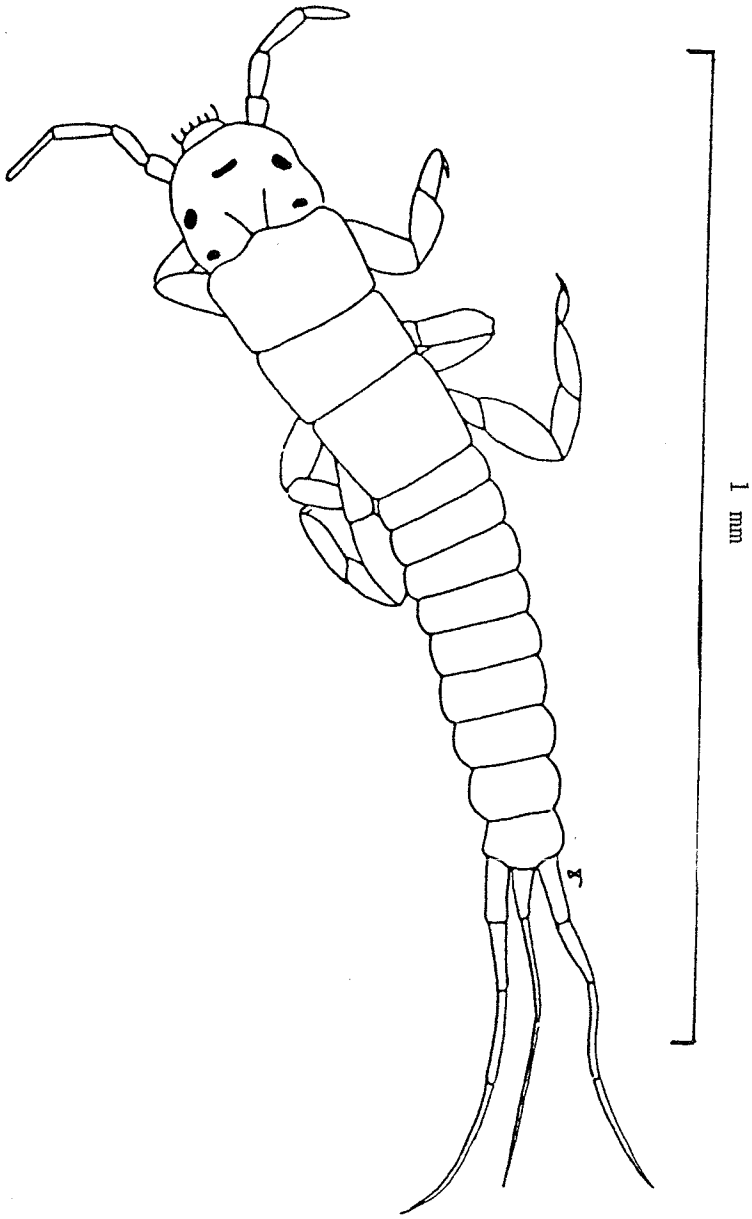
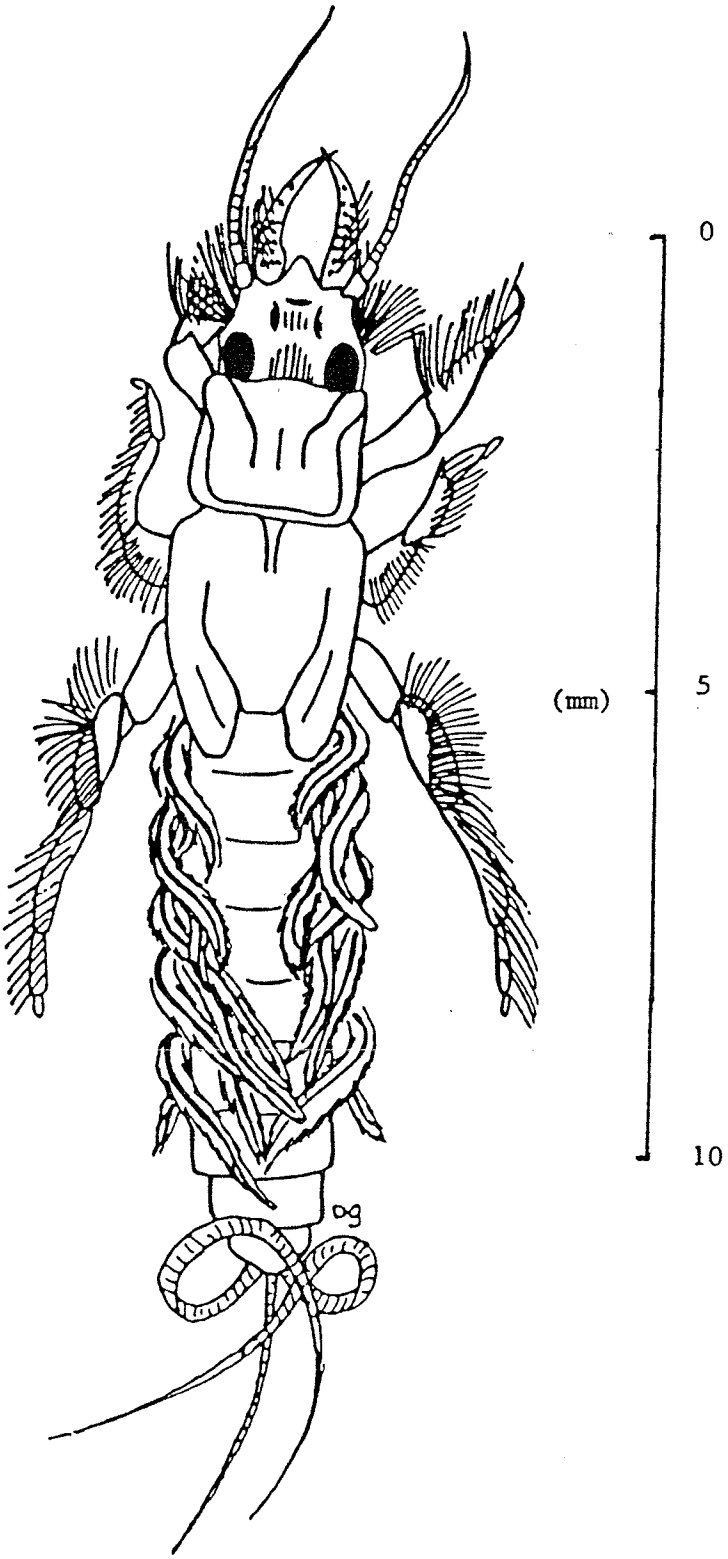

1 mm

Fig. 16. Nearly mature Ephoron album nymph (female).


0
5
(mm)
10
og

14.2 mm in length and females were generally larger than males. The rudiments of the male penes and forceps (Fig. 17) were detectable when nymphs were 5 mm in length. The average sex ratio for nymphs greater than 5 mm in length was 1♂ : 1.12♀ . There was no difference between male and female body weight until nymphs reached 9 mm in length (Table 5). In 1982, nymphs hatched in the Valley River in late May and first appeared in samples on 6 June (Fig. 18). Minimum daily water temperatures at this time ranged from 12° to 18°C (Fig. 6). Time of hatch in the field in 1983 could not be determined due to flooding (Fig.5), but water temperatures in late May and early June 1983 were similar to the same period in 1982 (Fig. 6), and eggs presumably hatched about the same time. Length-frequency histograms for E. album nymphs in late July and August 1983 were also similar to those for the same period in 1982 (Fig. 19). Nymphal development in both years was rapid and nymphs reached their mature size of about 14 mm in length in 8 to 10 weeks.

4.1.4 The Adult

Ephoron album adults are snow white with purplish-brown markings on the wings and thorax. The meso- and metathoracic legs of the males and all legs of the females are reduced and non-functional, and mating occurs on the wing. Adults measured 9.8 ± 1.2 mm in length and had a wingspan of 21.2 ± 0.4 mm (± S.E., n=20). Each female produced about 700

Fig. 17. Terminal segments of male and female Ephoron album nymphs.

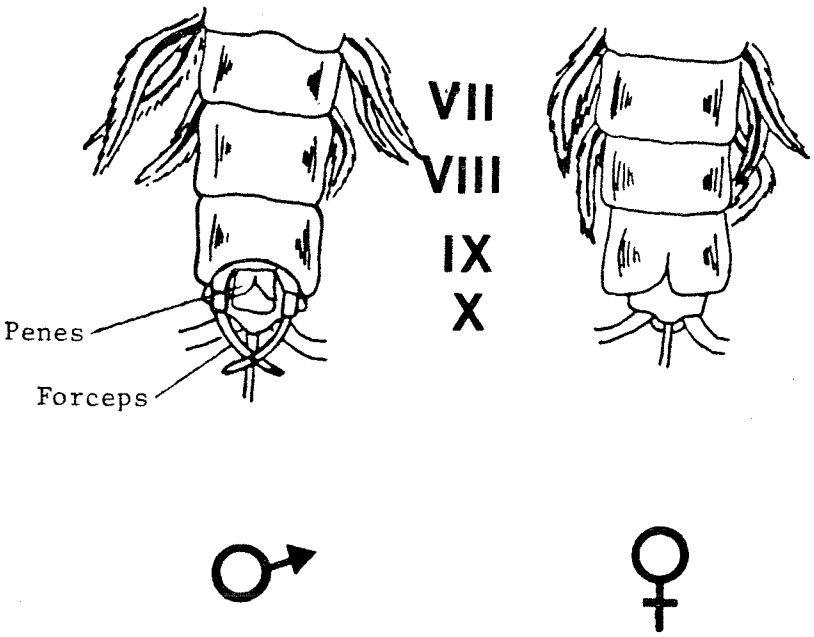

VII
VIII
IX
X
Penes
Forceps

Table 5. Fresh dry weights of male and female Ephoron album nymphs from the Valley River, Manitoba (beginning at size where sexes could be determined).

Length (mm)	Average fresh dry weight (mg ± S.E.)	
	Females	Males
5 - 6	0.32 ± 0.01	0.33 ± 0.01
6 - 7	0.56 ± 0.01	0.55 ± 0.01
7 - 8	0.88 ± 0.01	0.85 ± 0.02
8 - 9	1.27 ± 0.02	1.29 ± 0.03
9 - 10	1.98 ± 0.03	1.89 ± 0.03
10 - 11	2.71 ± 0.03	2.60 ± 0.03
11 - 12	3.65 ± 0.03	3.37 ± 0.04
12 - 13	4.64 ± 0.06	4.35 ± 0.06
13 - 14	5.93 ± 0.11	5.42 ± 0.03

Fig. 18. Length-frequency distribution of Ephoron album in the Valley River, Manitoba, 1982 (19 Aug. sample contained too few nymphs to analyze).

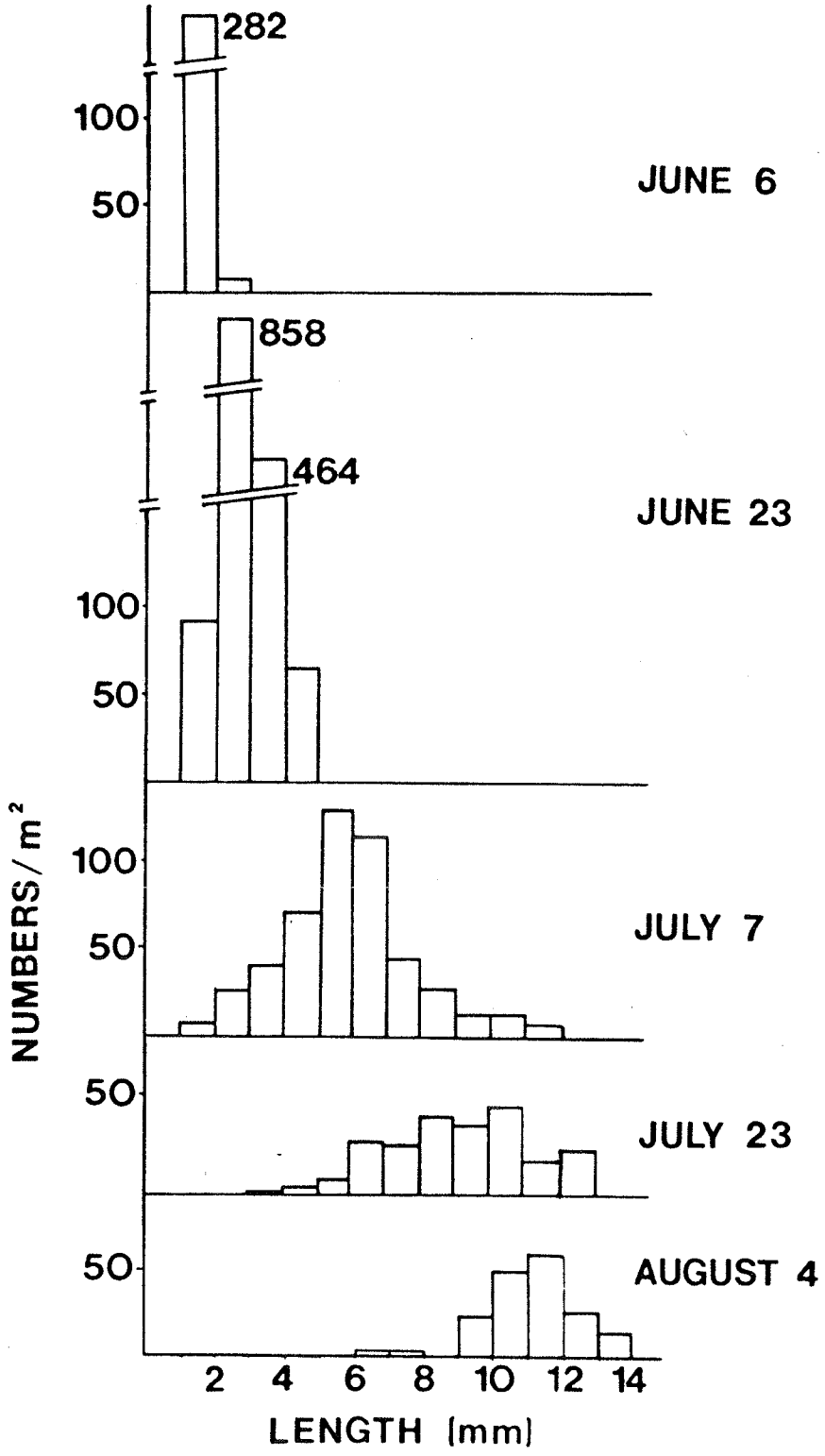
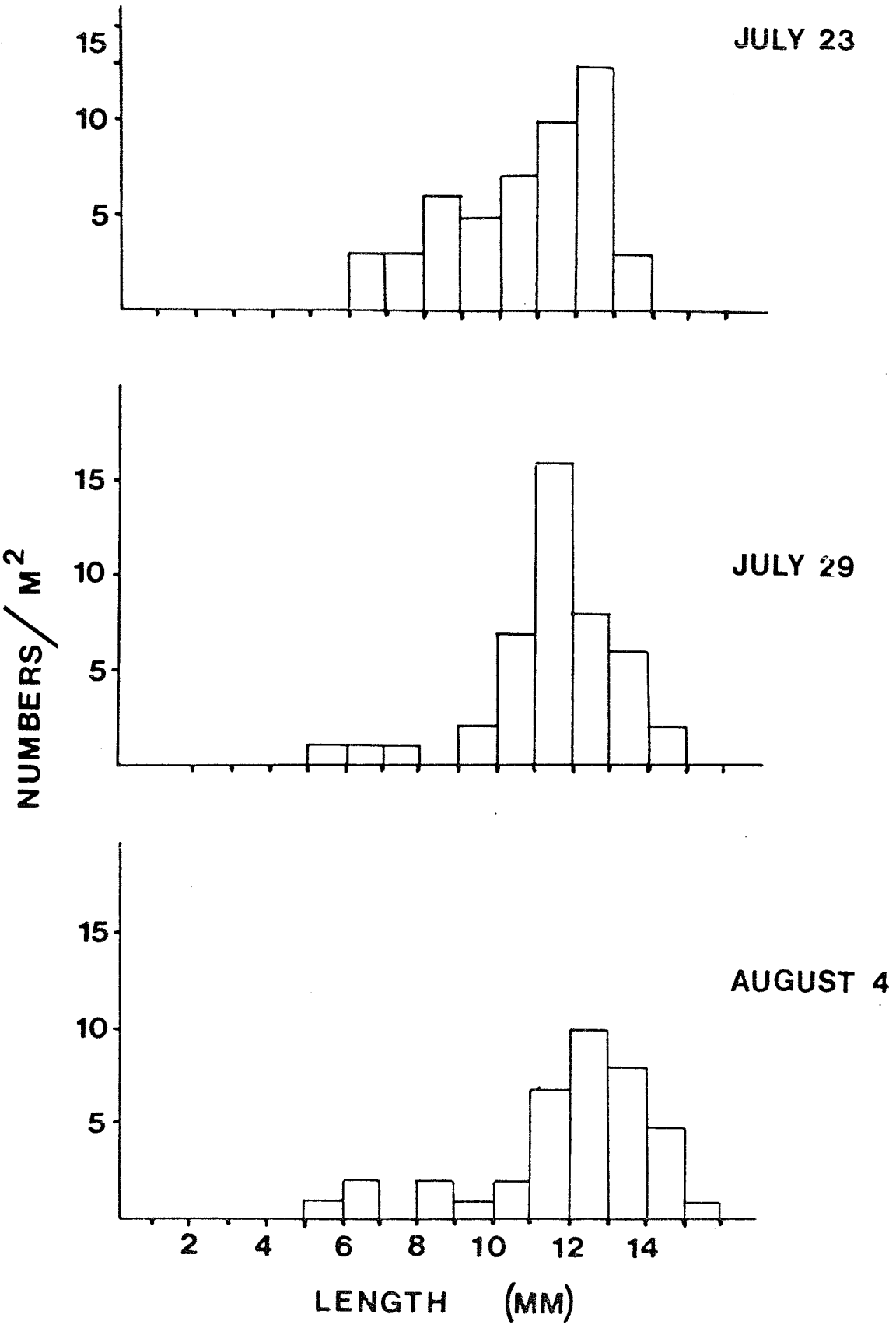

282
100
50
JUNE 6
858
464
JUNE 23
100
50
100
50
JULY 7
50
JULY 23
50
AUGUST 4
NUMBERS/ m²
2
4
6
8
10
12
14
LENGTH (mm)

Fig. 19. Length-frequency distribution of Ephoron album in the Valley River, Manitoba, 23 July to 4 August 1983.


JULY 23
JULY 29
AUGUST 4
NUMBERS / M2
15
10
5
2
4
6
8
10
12
14
LENGTH (MM)

eggs and showed no significant difference ($P<0.01$) in size or fecundity throughout the 3 week emergence period extending from 27 July to 15 August 1983 (Table 6).

Emergence and mating were nocturnal and the total adult life span was less than 4 hours. Air temperatures during the 1983 emergence period generally ranged from about 30°C at sunset (2100h) to 20° - 23°C three hours later. Water temperatures varied between 22° and 28°C during the three week period. The males were the first to emerge each evening, beginning about 30 minutes after sunset (2130 to 2145h), followed by the first females 15 to 20 minutes later. After emergence, male subimagos flew immediately to rocks and bushes near shore to moult. The moult was rapid, requiring only 45 to 65 seconds, and many males flew off with the subimaginal skin still attached. By 2200h each evening, large numbers of Ephoron 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 did not moult, but emerged into the male swarm and mated immediately. They then flew to the water surface, expelled their eggs, and died. Within a few minutes of noticing the first females each evening, many spent females (females which had oviposited and were dead) were observed drifting by on the water surface. Concurrently, females began collecting at a light at the water's edge, and would oviposit in pans of water placed near the light. Peak numbers of fe-

Table 6. Average weight and fecundity of female Ephoron album adults throughout emergence period, 1983 (based on 10 females captured each sample date).

Date	Number of eggs per female	Mean weight of each female (mg dry wt. ± S.E.)
28 July	733 ± 88	2.50 ± 0.16
4 August	706 ± 106	2.38 ± 0.31
11 August	670 ± 101	2.31 ± 0.35

males at the light occurred 60 to 70 minutes after the start of emergence. No males were collected at the light. After 2.5 hours, no adults were seen at the riffle, but a light source about 200 m downstream of the riffle still attracted gravid females at 0100h, 3.5 hours after the start of emergence. After 0100h, no more were seen, and next morning, virtually all sign of the previous night's emergence had disappeared. No Ephoron album adults were collected from floating emergence traps placed in the riffle, though large numbers of E. album were emerging all around the traps.

4.2 PRODUCTION

Densities and mean individual weights (± S.E.) for each sample period are given in Table 7. Maximum densities were recorded on 23 June and approached 3,000/m² in some samples. No E. album nymphs were found in bottom samples on 27 May and 25 August 1982, or in pools immediately upstream and downstream of the riffle at any time.

Weights of individuals were determined from a regression of length on fresh dry weight for E. album nymphs (Fig. 20). Body length was used in the regression because it showed a more consistent relationship to weight than did head capsule width. Fresh dry weights were used in the production calculations after it was shown that preserved specimens of E. album weighed up to 50% less than freshly killed ones (Figs. 20 and 21). Stratification of production according to habi-

Table 7. Densities and mean individual weights of Ephoron album nymphs in the Valley River Manitoba, 1982.

Date	Density (Number/m^2)	Mean individual weight (mg) (± S.E.)
7 June	1568[a]	0.008 ± 0.0002
23 June	1480.2 ± 221.9	0.046 ± 0.0008
8 July	497.2 ± 135.9	0.460 ± 0.0186
23 July	263.9 ± 79.1	2.269 ± 0.0996
4 August	170.1 ± 40.0	3.304 ± 0.1156
19 August	7.0 ± 3.0	3.537 ± 0.4900

[a] density extrapolated from Allen curve (Appendix Fig. I-a) due to underestimate of density on first sample date (from use of too coarse of net mesh size).

Fig. 20. Relationship between length and dry weight of preserved and freshly killed Ephoron album nymphs from the Valley River Manitoba (± S.E.)

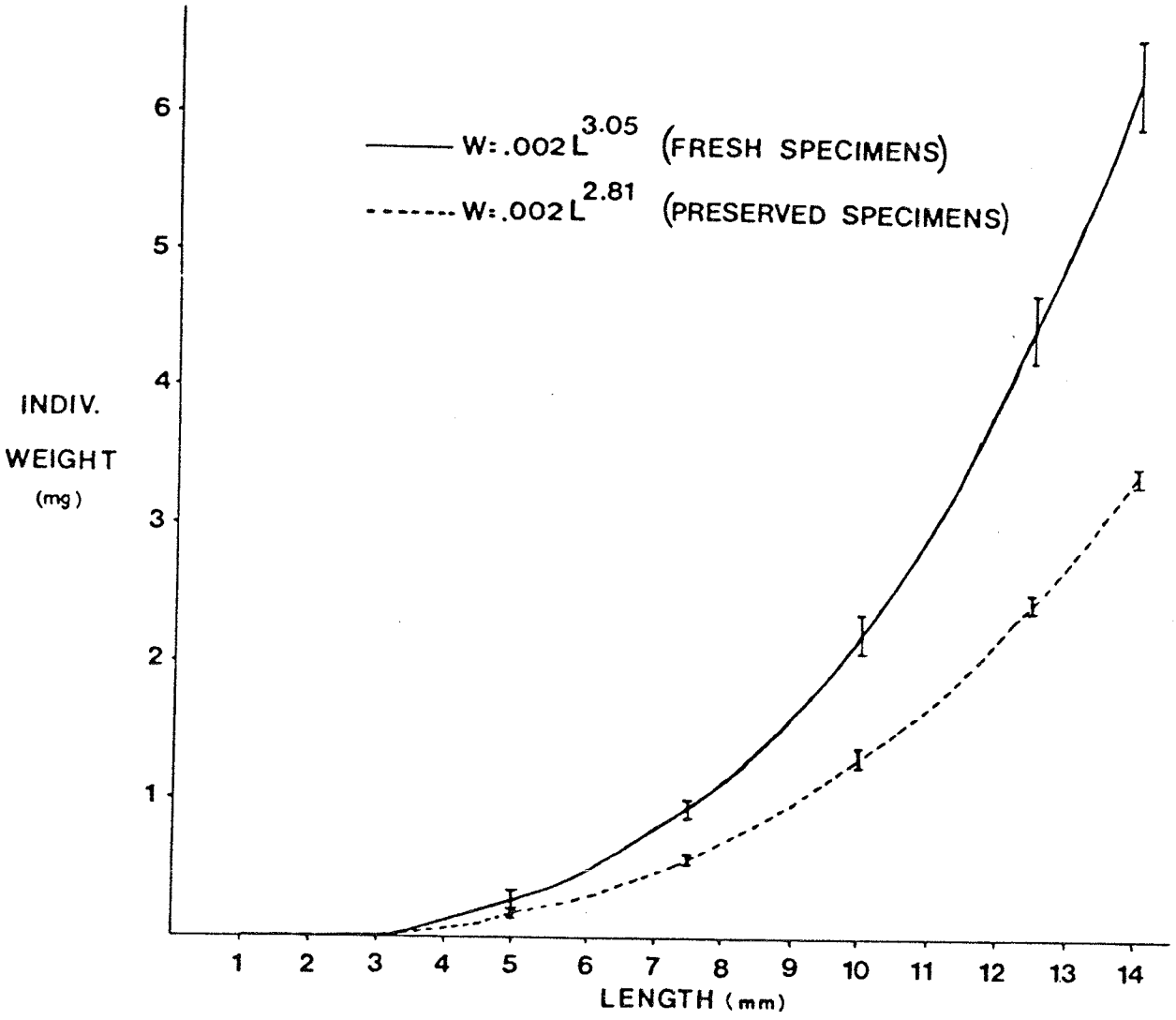
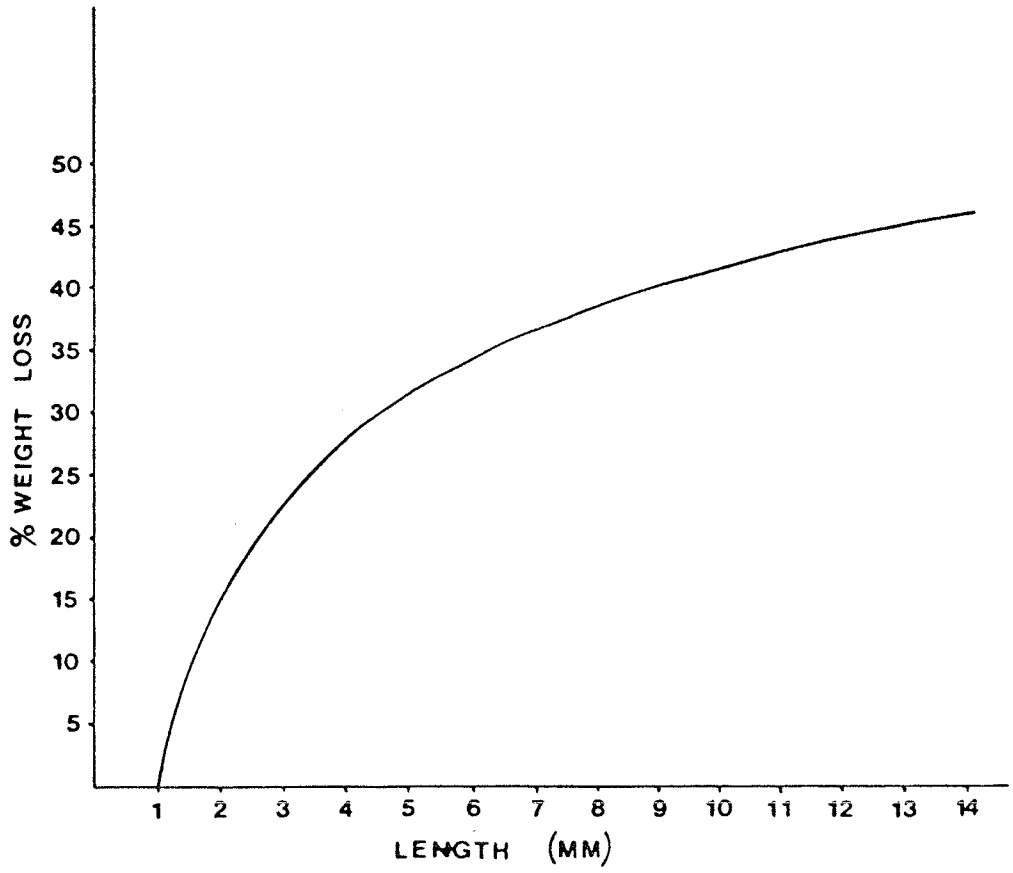

W=.002L^3.05 (FRESH SPECIMENS)
W=.002L^2.81 (PRESERVED SPECIMENS)
INDIV. WEIGHT (mg)
1
2
3
4
5
6
1 2 3 4 5 6 7 8 9 10 11 12 13 14
LENGTH (mm)

Fig. 21. Average per cent weight loss by body length of Ephoron album nymphs after 3 months in preservative.


% WEIGHT LOSS
50
45
40
35
30
25
20
15
10
5
1
2
3
4
5
6
7
8
9
10
11
12
13
14
LENGTH (MM)

tat (Benke 1984) was not attempted because the riffle was fairly homogeneous and no consistent correlation was found between density and water velocity, water depth, substrate particle size, or substrate organic content.

A production estimate of about 1.4 ± 0.4 g/m²/yr (FDW) was obtained by the four methods used (Table 8; calculations are shown in Appendix I). Separation of E. album nymphs into 7 size classes of 2 mm each for the size frequency method resulted in a production estimate of 1.38 g/m²/yr, compared to 1.33 g/m²/yr using 13 size classes. Ignoring apparent negative production in the production summation for the size-frequency method (Table I-c) resulted in an estimate of 1.64 g/m²/yr. 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 and that calculated for the population as a whole (Table 9). Production of females comprised 55% of the total production (Table 9).

Cohort production to mean biomass ratios calculated by the four methods ranged from 5.3 to 5.7. Annual $P/\bar{B}$ ratios for E. album in the Valley River were 21 to 23 (Table 8).

Table 8. Production and production to mean biomass ratios for Ephoron album in the Valley River, Manitoba, 1982.

Method of Calculation	Annual Production ($g/m^2/yr$ fresh dry wt.)	$P/\bar{B}$	
		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	1.33 ± 0.51[b]	5.4	21.3

[a] 95% confidence interval calculated by bootstrap method (Efron and Gong 1983).

[b] 95% confidence interval calculated by Krueger & Martin (1980) method.

Table 9. Production of male and female Ephoron album nymphs in the Valley River, Manitoba, 1982.

Method of calculation	Annual Production ($g/m^2/yr$ FDW)		
	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	1.33
Size-frequency	0.697	0.599	1.30

Chapter V

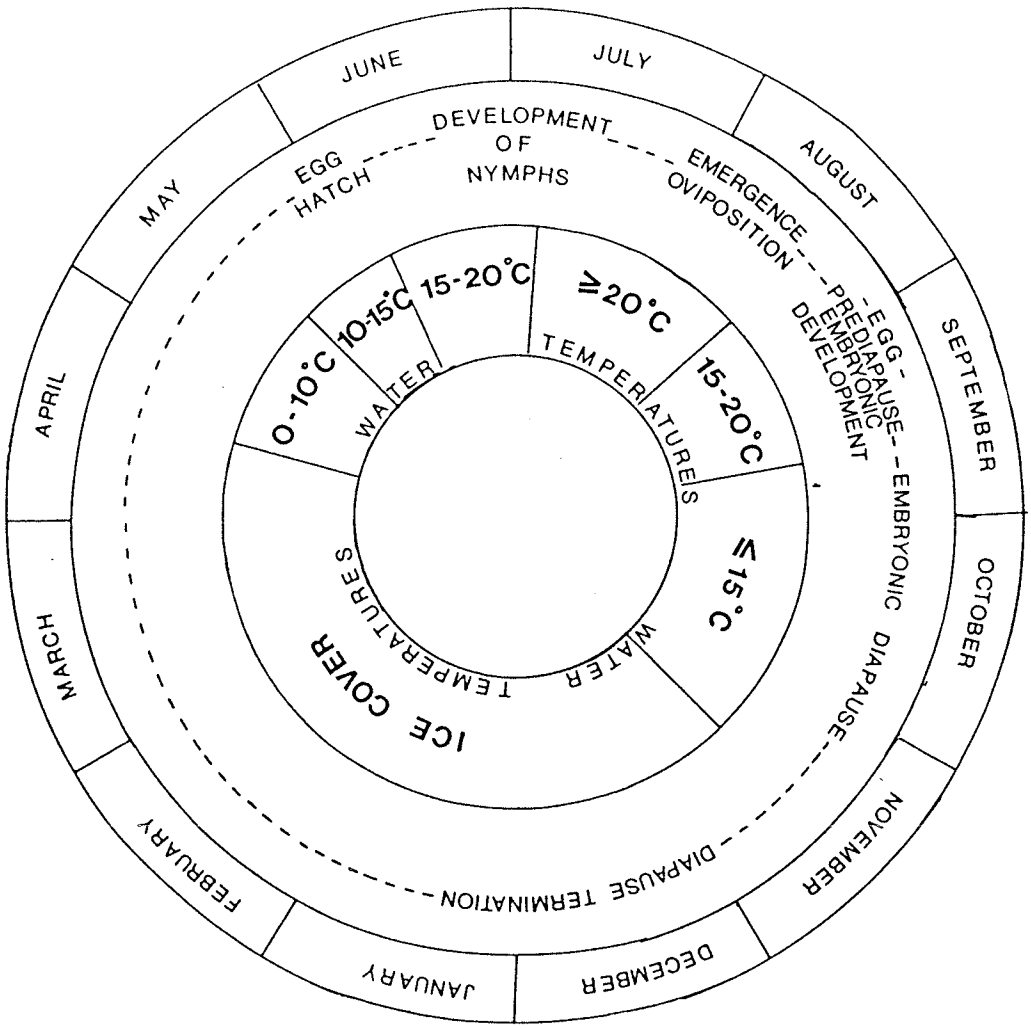
DISCUSSION

5.1 LIFE HISTORY OF EPHORON ALBUM

The life history of Ephoron album in the Valley River, Manitoba, is summarized in Fig. 22. Previous investigations into the life history of Ephoron album have been conducted by Edmunds et al. (1956) and Britt (1962). Nymphal development time reported in the two studies varied from 14 to 17 weeks in Utah (Edmunds et al. 1956) to 12 to 15 weeks in Lake Erie (Britt 1962), though nymphs grew to the same maximum length of about 17 mm. In the present study, nymphs developed in 8 to 10 weeks and attained a maximum size of just over 14 mm in length.

Ephoron album eggs from the Valley River developed for about four weeks after oviposition, then entered a state of diapause, hatching only after exposure to a period of cold temperatures. Eggs collected from the Valley River (present study) and Lake Erie (Britt 1962) populations did not hatch until exposure to freezing or near freezing temperatures, though exposure to 11°C was sufficient to promote hatching in eggs collected in Utah (Edmunds et al. 1956). Hatching success of E. album eggs exposed to -2°C two months after oviposition was positively correlated to the duration of the cold period, although those exposed to -2°C for 14 days lat-

Fig. 22. A summary of the life history of Ephoron album in the Valley River, Manitoba, based on 1982 and 1983 sampling and upon average water temperatures from 1962 - 1982.


JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
MAY
DEVELOPMENT OF NYMPHS
EGG HATCH
EMERGENCE OVIPOSITION
EGG - PREDIAPAUSE EMBRYONIC DEVELOPMENT - EMBRYONIC DIAPAUSE
DIAPAUSE TERMINATION
0-10°C
10-15°C
15-20°C
≥20°C
WATER TEMPERATURES
15-20°C
≤15°C
WATER TEMPERATURES
ICE COVER

er in the experimental period (after vaying periods at 4°, 10° and 20°C) showed lower and more variable hatching success than in the initial 14 day trial (Table 3). Similarly, Britt (1962), reported greater hatching success in eggs treated at -7°C early in the experimental period than in those treated several weeks later. High temperatures during the diapause period can reduce post-diapause survival, by depleting metabolic reserves (Tauber and Tauber 1976). Continued exposure of E. album eggs to temperatures above optimum for diapause development may have been responsible for the lower hatching success in the secondary treatment. Diapause termination in insects generally consiss of a gradual transition from a diapause to a post-diapause state, and many northern species end diapause in midwinter. Since temperature thresholds for post-diapause development may be substantially above prevailing winter conditions, no development occurs until warmer temperatures prevail (Beck 1980; Tauber and Tauber 1976). In the present study, eggs exposed to -2°C for periods of 14 days or less in the laboratory not begin hatching until 42 to 43 days after the onset of treatment. Since eggs held at -2°C sfor 60 days hatched within 3 days of warming to 20°C, diapause was apparently terminated during the 60 day period and eggs required only an increase in temperature to complete development and hatch.

Emergence of E. album adults began in late July to early August in all three locations, but the duration of the emer-

gence period was 7 to 8 weeks in Utah and Lake Erie and only 3 weeks in the Valley River. Swarming and mating behaviour were similar in all cases. In the present study however, adult females were about twice as long lived as previously reported (Britt 1962, Edmunds et al. 1956; Edmunds et al. 1976). Adults collected from the Valley River were smaller than those from Utah and Lake Erie, and females produced correspondingly fewer eggs (average of 703 eggs per female, compared to 908 eggs per female in Lake Erie).

The Valley River population represents a population of E. album very near its extreme northern limit. E. album has been reported in western North America from about 36° N latitude (McCafferty 1975; Edmunds et al. 1976) to 54° N latitude (Lehmkuhl 1972; D.K. Burton, personal communication, 1982). According to Sweeney and Vannote (1978), adult size and fecundity of many hemimetabolous aquatic insects are reduced in populations found at the extreme northern limits of their ranges. Differences in size and fecundity between specimens collected in the Valley River and those reported from the more central portions of the range may reflect suboptimal temperature conditions at the northern limit. Unfortunately, there are no published data for populations of E. album found at the southern extent of the range. The northern limit of E. album depends upon the presence of high summer temperatures (20°C or greater for most of the 8 to 10 week period of nymphal development) and temperatures of 15°

to 20°C for an additional four weeks for pre-diapause embryonic development. The southern limit would depend primarily upon the occurrence of winter temperatures cool enough or for a sufficiently long period of time for successful diapause termination, though presumably, temperatures during nymphal development would also be important.

It is interesting to note that in all cases where E. album has been studied in detail, harsh winter conditions prevail, preventing establishment of stable, year-round invertebrate communities. In the Valley River, E. album occurred in shallow riffles subject to freezing in the winter; in Lake Erie, in areas frequently exposed to both freezing and drying conditions (Britt 1962), and in Utah, in a canal that was allowed to dry during the winter months(Edmunds et al. 1956). The nymphs are also reported to be tolerant of a limited amount of organic pollution (Edmunds et al. 1976; Roback 1974) and in Manitoba are found in highest numbers in prairie rivers located in regions of intensive agriculture. The dominance of E. album in shallow riffles in the agricultural zone of the Valley River reflects a successful adaptation to harsh winter conditions and an ability to develop rapidly, even in the presence of organic pollution.

5.2 PRODUCTION

The annual production for E. album in the Valley River in 1982 (1.4 g/m²/yr FDW) falls within the range of estimates reported in the literature for mayflies (Table 1). It should be noted though, that E. album spends most of the year in the egg stage, so that the total production represents rapid growth and a high production rate during a few weeks in summer, rather than steady growth throughout the year. The cohort production to mean biomass ratio was consistent (5.2 - 5.7) with that reported by Waters (1969). The annual $P/\bar{B}$ ratio however, was more than four times higher than that predicted for most univoltine species, largely an effect of the brief period of aquatic life on the annual $P/\bar{B}$ (Benke 1979; Waters 1979).

The production values obtained by the four methods were in close agreement, as expected according to Waters and Crawford (1973), Cushman et al. (1978), and Benke (1984), though the removal-summation method resulted in a slightly higher value than the others (Table 8). Part of the excess is due to the incorporation of the initial standing stock (weight at hatch) into the production estimate for removal-summation. The initial biomass of E. album may be considered as part of the production of the preceeding generation, so should not be included in the production estimate. However, the amount involved is small (<1% of total production) and should not radically affect the production estimate. Other researchers (e.g. Waters and Crawford 1973;

Lapchin and Neveu 1980; Resh 1975; Cudney and Wallace 1980) have reported that the size-frequency method of calculation results in higher estimates than other methods, but this effect was not noted in the present study. Attempts to improve the accuracy of the size-frequency method have resulted in a number of modifications to the original method proposed by Hynes in 1961 (Hynes and Coleman 1968; Hamilton 1969; Benke 1979; Benke and Wallace 1980; Waters 1979), making it difficult to compare estimates obtained taking different factors into account (e.g. Waters and Crawford 1973 vs. Benke and Wallace 1980). In the present study, estimates varied from 1.3 to 1.64 $g/m^2/yr$ depending upon the number of size classes used, whether or not the sexes were separated, and whether or not apparent negative production was included in the production summation. Therefore, the reported differences are probably not biologically significant, given the range of factors that can affect the size-frequency estimate.

Since the development of a method to estimate confidence intervals for a production estimate obtained using the size-frequency method (Krueger and Martin 1980), several researchers have used the technique to obtain a measure of the precision of their production estimate (e.g. Krueger and Waters 1983; MacFarlane and Waters 1982; Georgian and Wallace 1983; Rodgers 1982). The resultant 95% confidence intervals have proven to be about as variable as the production esti-

mates themselves, ranging from less than 4% of production (e.g. Caenis simulans McDunnough : 4.7 ± 0.08 g/m²/yr (wet), MacFarlane and Waters 1982) to greater than 100% of production (e.g. Goera fuscula Banks : 9.48 ± 5.6 mg/m²/yr (dry), Georgian and Wallace 1983). In the present study, confidence intervals calculated by the Krueger and Martin method (1980) were about 20% larger than those obtained by bootstrapping (± 10% of the mean), but at present, it is impossible to say whether one method is more suitable than the other for production calculations.

It is important to realize that both methods (the Krueger and Martin 1980 method and the bootstrap technique) are based mainly on sample variance and can not address the problem of systematic errors included in production estimation. Common errors of this type include failure to adequately sample the habitat, use of inappropriate net-mesh size, or failure to account for weight loss due to preservative effects. Since these systematic errors are largely unmeasurable, attempts should be made to account for and eliminate them whenever possible in the original experimental design (Waters 1979). In the present study, very small nymphs were probably under-represented on the first sample date, introducing an underestimate of about 1 or 2% of final production. An enclosed box-type sampler was used to eliminate the problems of backwash and escape of nymphs from an open sampler (Hynes 1970; Edmondson and Winberg 1971) and an

appropriate substrate depth to adequately sample for E. album was determined from preliminary studies. Finally, after noting an important preservative effect on the estimation of mean individual weights of E. album, only fresh weights were used in the production calculations. Considerable controversy exists with respect to the importance of considering the effect of preservative on invertebrate biomass estimation (Donald and Patterson 1977; Howmiller 1972; Stanford 1973; Benke and Wallace 1980; Iverson 1980). In the present study, failure to take the preservative effect into account would have produced an underestimate in production of approximately 40%, a factor at least as great as the calculated 95% confidence intervals.

Little data is available on 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 traditionally studied, due mainly to high organic seston loads derived from erosion and runoff from croplands. Without data on whole community and functional group production for the present study, it is difficult to speculate whether the Valley River data support this hypothesis. However, the rapid growth and high production rate of Ephoron album, the dominant summer mayfly in the Valley River, is consistent with the findings of MacFarlane and Waters (1982) for a prairie river.

Chapter VI

CONCLUSIONS

Ephoron album is a univoltine species which undergoes rapid nymphal development during the warm summer months and has an obligatory embryonic diapause. The adult life span is very short, only a few hours at most. Eggs require a period of cool temperatures to promote hatching, but the extent and duration of this period appears to vary with latitude and the mechanisms of diapause development and termination are not known. Experimental manipulation of hatching conditions for E. album eggs, particularly with respect to latitudinal differences in photoperiod and temperature throughout its range, would be necessary to gain some understanding of the factors affecting diapause.

The small size and reduced fecundity of E. album adults from the Valley River, relative to those reported from more central portions of their range (Britt 1962), support the thermal equilibrium hypothesis of Sweeney and Vannote (1978). These authors suggested that suboptimal temperature conditions at the northern and southern limits of the geographic range of many hemimetabolous aquatic insects result in reduced adult body size and fecundity. Data on populations found at the southern extent of the range are also

needed to test the thermal equilibrium hypothesis for E. album.

Production estimates obtained using four different methods of production calculation were in close agreement. The cohort production interval for E. album was very short (80 days in the Valley River in 1982) so the total annual production of 1.3 to 1.4 $g/m^2/yr$ (FDW) is the result of rapid growth and a high rate of production during the brief summer growth period. Seemingly high production rates reported for species found in large prairie rivers, compared to those from small woodland streams, are probably related to high summer temperatures and high organic seston loads, especially in areas of intensive agriculture.

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Chapter VII

APPENDICES

7.1 APPENDIX I CALCULATION OF PRODUCTION IN THE VALLEY RIVER, MANITOBA, 1982.

7.1.1 Removal-summation Method

The removal-summation method is based upon the assumption that what is produced by a population eventually dies or is otherwise removed, so that an estimate of the "removal" over successive time intervals equals an estimate of production (Boysen-Jensen 1919, in Waters 1977). The cohort production estimate is obtained by estimating the biomass removed between sampling intervals and summing it over the life of the cohort (Table I-a).

7.1.2 Instantaneous Growth Rate Method

With this method, one assumes exponential growth and mortality. Production for a time interval is calculated as the product of the rate of growth during that interval (G) and the average biomass for the interval ($\bar{B}$) (Ricker 1946) and cohort production equals the sum of the interval production estimates for the duration of the cohort. G is calculated as the natural log of the mean weight at the end of the interval divided by the mean weight at the beginning of the interval (Table I-b).

7.1.3 Allen Curve Method

The Allen curve is graphic representation of the instantaneous growth rate method (Allen 1951). Cohort production is obtained by calculating the area under the growth-survivorship curve (a plot of density in numbers/m^2 vs. mean individual weight) for the population (Fig. I-a).

7.1.4 Size-frequency Method

The size-frequency method (Hynes 1961) is the only one of the four discussed which can be used to calculate production where cohorts can not be distinguished, though it also yields results consistent with the above methods for populations where cohorts are easily identified. The size-frequency method is based upon the assumption that an average size frequency distribution calculated from samples taken over the period of a year will approach the average survivorship of a hypothetical average cohort. The calculations are similar to the removal-summation method except that the estimate of biomass removal is made between successive size classes rather than time intervals. However, the average cohort does not represent actual density, and certain assumptions must be made to approximate actual numbers reaching a given size class over the period of a year. Assuming linear growth, the insect will remain in each of N size classes only 1/N part of the year, so the estimate of "average" biomass removal for each size class must be multiplied

by N to estimate the actual biomass removal for the size class (Benke 1984). An additional assumption in the size frequency method is that larval development takes a full year. In situations where larval development requires less than or more than a year, the C.P.I., or Cohort Production Interval, must be taken into account. In the present study, Ephoron album nymphs were present in the Valley River from 3 June to 21 August, 1982, or for a total C.P.I. of 80 days. the annual production must therefore be multiplied by a correction factor of 365/80 days (Benke 1979). Variance of the production estimate was calculated according to Krueger and Martin (1980). An example of calculation of production by the size frequency method, and variances for each size class are given in Table I-c.

Appendix
Table I-a Calculation of production (P) in the Valley River, Manitoba, by the removal-summation method, 1982.

Sample date	#/m^2	mean indiv. weight (mg)	numbers lost per m^2	weight at loss (mg)	weight loss (g)
7 June	1568.4[a]	0.0085			
			88.2	0.0271	0.0024
23 June	1480.2	0.0457			
			983.0	0.2529	0.2486
8 July	497.2	0.4601			
			233.3	1.364	0.3183
23 July	263.9	2.269			
			93.8	2.786	0.2613
4 Aug.	170.1	3.304			
			163.1	3.420	0.5578
19 Aug.	7.0	3.537			
			7.0	5.675	0.0400
		7.813[b]			
				P =	1.428

[a] density extrapolated from Allen curve (Appendix Fig. I-a; observed density for 7 June was 290.0 nymphs/m^2).

[b] maximum observed weight.

Table I-b Calculation of production (P) in the Valley River, Manitoba, by the instantaneous growth rate method, 1982.

Sample date	Standing Crop (g)[a]	Mean indiv. wt. (mg)	G[b]	$\bar{B}$ (g/m^2)[c]	P (g/m^2)[d]
7 June	0.0133	0.0085			
			1.683	0.040	0.067
23 June	0.6760	0.0457			
			2.310	0.148	0.342
8 July	0.2288	0.4601			
			1.596	0.414	0.661
23 July	0.5987	2.269			
			0.376	0.580	0.218
4 Aug.	0.5620	3.304			
			0.068	0.293	0.020
19 Aug.	0.0248	3.537			
			0.793	0.012	0.010
		7.813[e]			
				P =	1.318

[a] Standing Crop = $\#/m^2$ X mean individual weight (g)

[b] $G = \ln \left(\frac{\text{mean wt. at end of interval}}{\text{mean wt. at start of interval}} \right)$

[c] $\bar{B}$ = average of standing crops for successive intervals

[d] $P = G \cdot \bar{B}$

[e] maximum observed weight.

Fig. I-a. Allen curve for Ephoron album in the Valley River, Manitoba, 198 (Production is equal to the area under the curve).

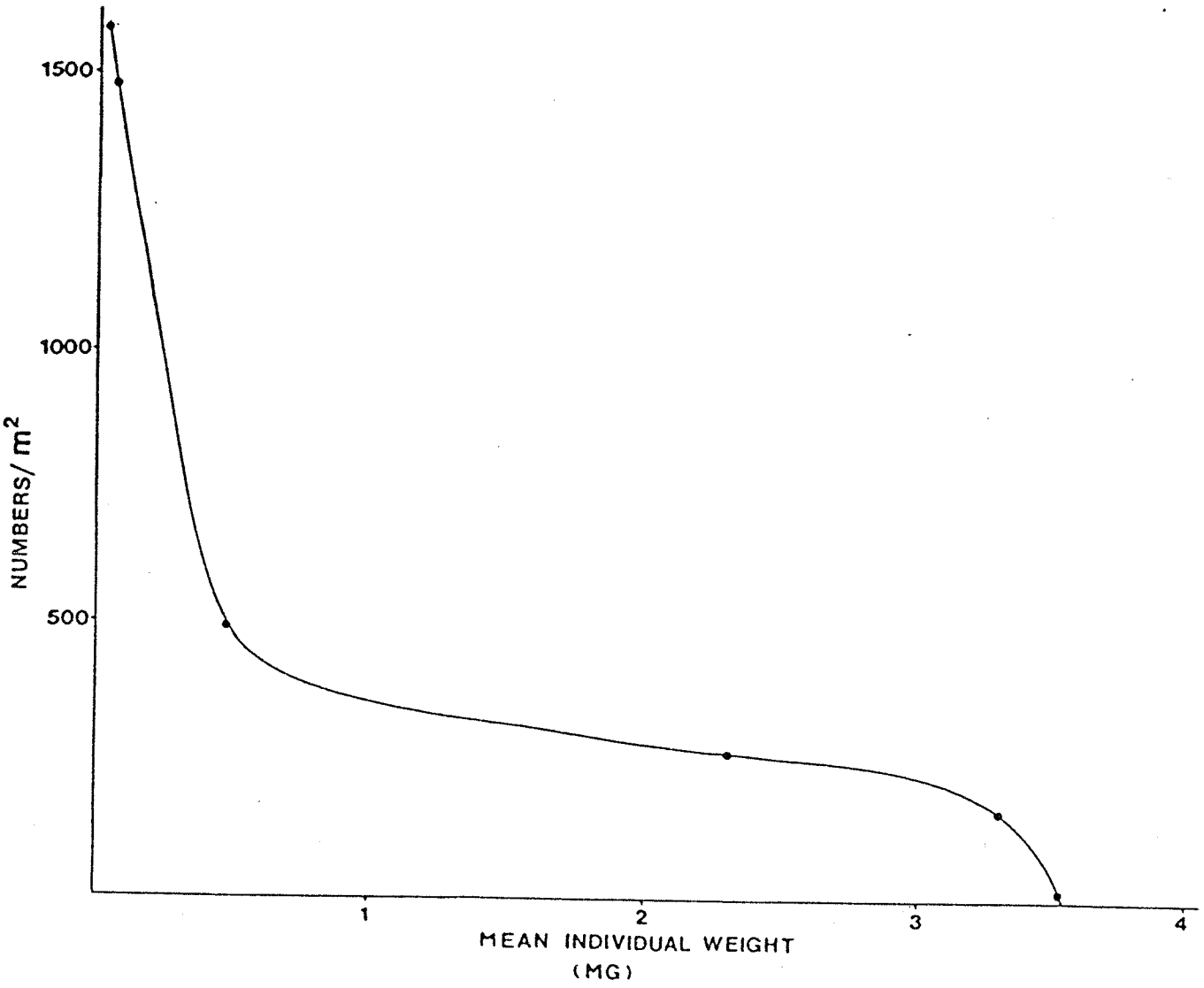
1500
1000
500
NUMBERS/ m²
1
2
3
4
MEAN INDIVIDUAL WEIGHT
(MG)

Table I-c. Calculation of production (P) in the Valley River, Manitoba by the size-frequency method, 1982.

Size class	#/m^2	v(#/m^2)[a]	#lost per m^2	Mean indiv. wt. (mg)	wt. at loss (mg)[b]	wt. loss	X N[c] Production
1-2	16.5	79.9		0.0083			
			-18.8		0.158	-0.0003	-0.0039
2-3	35.3	684.9		0.0301			
			13.5		0.0486	0.0007	0.0085
3-4	21.8	117.5		0.0785			
			15.9		0.1147	0.0018	0.0237
4-5	5.9	15.1		0.1675			
			0.2		0.2373	0.0001	0.0006
5-6	5.7	30.7		0.3362			
			-0.6		0.4355	-0.0003	-0.0034
6-7	6.3	23.2		0.5640			
			3.1		0.7013	0.0022	0.0283
7-8	3.2	1.2		0.8721			
			0.2		1.085	0.0002	0.0028
8-9	3.0	3.9		1.351			
			-0.4		1.657	-0.0007	-0.0086
9-10	3.4	4.8		2.033			
			-1.8		2.365	-0.0043	-0.0553
10-11	5.2	4.0		2.752			
			1.3		3.162	0.0041	0.0534
11-12	3.9	3.2		3.632			
			1.7		4.076	0.0069	0.0901
12-13	2.2	2.8		4.575			
			1.7		5.209	0.0089	0.1151
13-14	0.5	0.3		5.930			
			0.5		5.930	0.0030	0.0385
							P = 0.2898

C.P.I. = 80 days

Annual Production = P X 365/C.P.I.
= 0.2898 X 365/80
= 1.32

v(P) = 0.065

95% confidence interval = 2 $(0.065)^{0.5}$ = 0.51

[a] variance for each size class, after Krueger & Martin (1980)

[b] geometric mean of weights for successive size classes.

[c] N = 13 size classes.