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FECUNDITY OF MAYFLIES (EPHEMEROPTERA), WITH SPECIAL REFERENCE TO MAYFLIES OF A BROWN-WATER STREAM OF ALBERTA, CANADA

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Abstract

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A review of studies of mayfly fecundity (number of eggs produced per life span) indicates that some of the larger mayflies, e.g. *Palingenia* and *Hexagenia*, have total potential fecundity values that are higher than found in most other insect groups. For 12 mayfly species of a brown-water stream in Alberta, Canada, fecundity of the subimagoes was generally predictable from the size of the female regardless of the particular species. An exception was *Leptophlebia cupida*, which, for a given length, had a much higher fecundity than any of the other species and a much larger increase in fecundity per unit increase in body length. *L. cupida* averaged 362 eggs/mm body length, while the other species had an average egg production of between 100 and 200 eggs/mm body length. The small species, although having a relatively low total fecundity, produced more eggs per unit volume of abdominal space than did the larger species. By combining quantitative emergence data and fecundity data, we calculated that the entire mayfly fauna produced about 300,000 eggs/m^2 per year and that it takes an average of 934 eggs to produce one subimago of the next generation.

Introduction

Fecundity, as used here, means total potential fecundity: the total number of eggs produced by the female during her lifespan regardless of the fate of the eggs. Both fecundity and fertility (or realized fecundity, i.e. the number of viable eggs laid) are important parameters in the study of population dynamics. Fecundity has not been studied extensively in the non-economically important insects. For most insect groups, it is difficult to measure accurately fecundity in the insect's natural environment because the eggs are continually maturing and being oviposited throughout the adult life span. Most insect fecundity data have been acquired from laboratory populations, and laboratory conditions may differ considerably from the insects' natural environment.

The mayflies (Ephemeroptera) are a group of insects that offer excellent material for the study of fecundity under natural conditions. The eggs develop in the large number of panoistic ovarioles of the nymphs. Ovulation apparently begins and is completed during the last nymphal instar (Smith 1935), the eggs at this time being released into the oviducts which become greatly extended, filling most of the abdomen and even extending into the thoracic segments. By the subimago stage the ovarioles have collapsed and the ovaries appear as small sac-like structures (Brinck 1957). The eggs, ranging in size from about 100 to 200 μ in diameter, are physiologically mature during the subimago stage. Several workers, e.g. Darchis (1964) and Fremling (1967), have obtained fertilized eggs and subsequent viable offspring by bringing together eggs and spermatozoa of subimagoes. Since adult mayflies usually live for only a day or two and all the eggs are produced prior to the subimago stage, total potential fecundity can be determined accurately by examining subimagoes, imagoes that have not oviposited, and even last instar nymphs.

As part of a continuing limnological study of a small brown-water stream in west-central Alberta (e.g. Clifford 1969, 1970, 1972), we examined the fecundity of the mayfly fauna. The purpose of the fecundity work was to provide a foundation for establishing yearly trends in mayfly fecundity; hence when the stream, the Bigoray River, is experimentally manipulated, mayfly fecundity can be used as one of the parameters in evaluating the subtle effects of pollutants. Since mayflies offer excellent material for the accurate determination of fecundity under natural conditions, it also seemed important to review and report on mayfly fecundity data of other studies.

Methods

All mayflies used in the study were taken from floating emergence traps of the main stream. Total number of eggs per female, either subimago or imago, was estimated using plankton counting methods. The eggs were dissected from the greatly expanded oviducts of the abdominal and thoracic body cavities in a Sedgwick-Rafter cell containing a small amount of water. For most species, the eggs, once removed from the body cavity, dispersed freely in the water; however, for a few species, e.g. *Siphloplecton*, the eggs remained clumped, and in such cases the eggs were teased apart using fine needles. The Sedgwick-Rafter cell was then completely filled with water and the coverslip rotated into place. Eggs were counted in a known volume of four or five strips across the entire cell (APHA 1971).

Results

Review of Mayfly Fecundity Studies

Table I lists mayfly fecundity data as gathered from the literature. Several of these values are reports by workers who, incidental to other studies, have simply commented on the fecundity of certain species. Often the averages were estimated from only a few specimens and usually without regard to size. Nevertheless, the trend is for females of the larger species to produce more eggs than those of smaller species. Fecundity values of *Palingenia*, *Hexagenia*, and *Epeorus assimilis* are greater than found in most other insect groups except the social hymenopterans (see Engelmann 1970, table 5).

If environmental conditions were to become unusually favorable for a particular species, one would expect species with high total potential fecundity to exhibit the most pronounced population increases. In fact the "mass" emergences of mayflies occurring occasionally in North America and Europe, are owing often to species of *Hexagenia* and *Palingenia* respectively.

Specific mayfly fecundity studies include those of Ide (1940), Hunt (1951), Britt (1962), Clifford (1970), and Benech (1972). Most workers studying mayfly fecundity have noted a positive correlation between body length and total number of eggs produced. For *Leptophlebia cupida*, the least square fitted regression was $\log_e Y = -6.205+3.039 \log_e X$, where Y is the egg number times 10^{-3} and X is body length in millimeters (Clifford 1970). In species with an extensive emergence period, early emerging individuals tend to be larger and hence have a higher fecundity than those emerging later. Ide (1940) found that early emerging *Paraleptophlebia mollis* averaged over 900 eggs per female, whereas females emerging 4 or 5 weeks later averaged fewer than 300 eggs. In species having two generations a year; the adults of the second generation are often smaller than those of the first generation, and hence fecundity per female would also be lower in the second generation. For example, Benech (1972) reports that some females of *Baetis rhodani*'s spring generation produced up to 4500 eggs, while females of the summer generation produced as few as 200 eggs.

Fecundity of Bigoray River Mayflies

Fecundity values were obtained for 158 specimens belonging to 12 species (Table II). Subimagoes and imagoes of the same species generally had similar fecundity values per unit size of the female. However, all *L. cupida* imagoes had oviposited at least in part. Also, some of the female imagoes of other species might possibly have deposited some eggs. For this reason and because we did not obtain imago fecundity values for *Leptophlebia nebulosa*, *Paraleptophlebia praepedita*, and *Callibaetis coloradensis*, the comparisons that follow are based entirely on data from subimagoes.

Fecundity was generally predictable from the size of the female regardless of the particular species; i.e. when fecundity was plotted against total length of females, all

Table I. Total number of eggs produced by mayflies. The stage, i.e. imago (I), subimago (SI), or last nymphal instar (LNI), is indicated when known

	Range	Av.	So.*
SIPHLONURIDAE			
Siphlonurus alternatus (SI)	884–2023	1282	1
S. lacustris	1712–2499		2
S. aestivalis	933–2678		2
Coloburiscus humeralis	3000–6000		3
Ameletus ludens (I)		670	4
Isonychia bicolor (I)		2500	4
I. bicolor	1900–2000		5
OLIGONEURIIDAE			
Oligoneuriella rhenana	1610		6
AMETROPODIDAE			
Siphloplecton basale (SI)	1009–2749	2063	1
S. interlineatum (SI)	587–1581	1083	1
HEPTAGENIIDAE			
Epeorus assimilis	9341		2
E. pleuralis (LNI)		4260	7
Ecdyonurus fluminum	1603–1994		2
E. helveticus	3973–4472		2
Heptagenia lateralis	1672–2356		2
H. maculipennis (I)		1000	4
EPHEMERELLIDAE			
Ephemerella ignita	842–1171		2
E. kreighoffi	1230–1671		2
E. belgica	1689		2
E. excrucians (I)		1950	4
CAENIDAE			
Caenis horaria	508– 607		2
C. moesta	765–1103		2
	Range	**Av.**	**So.**
BAETIDAE			
Callibaetis coloradensis (SI)	1199–1641	1343	1
C. fluctuans (I)		500	4
C. floridanus	450– 500		19
Baetis niger	592		2
B. subatrebatinus	735		2
B. pumilus	1019–1190		2
B. rhodani (I)	200–4500		9
B. tricaudatus (SI)	597–1394	1106	1
Cloeon dipterum	898– 910		2
C. simile	2378–3415		2
C. simile (SI)	2071–2533	2283	10
Centroptilum sp. (SI)	434–1063	855	1
C. lituratum	2174		2
C. luteolum	960–1513		2
C. pennulatum	1327–2410		2
EPHEMERIDAE			
Hexagenia bilineata	4252–8936	7107	11
H. limbata (SI, I)	3902–5956	4988	1
H. limbata (I)	3388–3631	3510	12
H. limbata (I)	2260–7684	4000	13
H. rigida	1800–2400		12
Ephemera simulans	3202–5879	4500	14
E. danica	2434–4600		2
E. danica	2300–3750		18
E. glaucops	2787		2

Table I. *(Concluded)*

	Range	Av.	So.*		Range	Av.	So.
TRICORYTHIDAE				POLYMITARCIDAE			
Tricorythodes allectus (I)		750	4	*Ephoron album*	593–1672	908	14
LEPTOPHLEBIIDAE				*Povilla adusta*	900–2500		15
Leptophlebia vespertina	1016–1612		2				
L. cupida (SI)	1772–6166	4081	1				
L. cupida (I)		3700	4	PALINGENIIDAE			
Paraleptophlebia debilis (SI)	595–1522	1013	1	*Palingenia sublongicauda*	12000		16
P. praepedita (SI)	432– 442	438	1				
P. mollis (SI)		504	8				
P. adoptiva (SI)		1160	8	BAETISCIDAE			
P. volitans (SI)		264	8	*Baetisca rogersi*	1500–2650	2168	17
Habrophlebia auberti	1412–1685		2				
H. lauta	450– 790		2				
H. modesta	932–2324		2				
Choroterpes picteti	724		2	PROSOPISTOMATIDAE			
Thraulus bellus	1371		2	*Prosopistoma* sp.	174		2

*Source: 1, Present study; 2, Degrange (1960); 3, Wisely (1961); 4, Morgan (1913); 5, Clemens (1917); 6, Grandi (1947); 7, Minshall (1967); 8, Ide (1940); 9, Benech (1972); 10, Davidson (1956); 11, Fremling (1960); 12, Neave (1932); 13, Hunt (1951); 14, Britt (1962); 15, Hartland-Rowe (1958); 16, Kosova (1967); 17, Pescador and Peters (1974); 18, Rousseau (1921); 19, Trost and Berner (1963).

Table II. Total number, average total length, and average fecundity of subimagoes (SI) and imagoes (I) of the brown-water stream

	No. of specimens		Av. size (mm)		Av. no. of eggs	
	SI	I	SI	I	SI	I
Siphlonurus alternatus	12	6	13.8	13.1	1282	1211
Siphloplecton basale	28	9	15.5	15.0	2063	2288
S. interlineatum	6	6	9.9	9.7	1083	1285
*Leptophlebia cupida**	17	-	11.3	-	4081	-
L. nebulosa	3	0	9.5	-	2023	-
Paraleptophlebia debilis	16	9	7.6	7.9	1013	867
P. praepedita	2	0	6.5	-	438	-
Callibaetis coloradensis	7	0	10.7	-	1343	-
Baetis tricaudatus	12	11	6.0	6.3	1106	1304
Centroptilum sp. A	5	5	6.1	5.0	855	758
Hexagenia limbata	1	3	25.0	24.3	5959	4664

*Several *L. cupida* imagoes were examined; all had fewer than 100 eggs.

points except those for the two *Leptophlebia* species fell along a single line (Fig. 1). For a given length, *L. cupida* and *L. nebulosa* had much higher fecundity and much larger increases in egg production per unit increase of body length than any of the other species. Hunt (1951) for *Hexagenia limbata* and Britt (1962) for *Ephemera simulans* also give body length data along with total egg production; if their data were plotted on Fig. 1, the points for both species would fall, within limits, along the lower line.

Because fecundity varied with the average size of the species (Table II; Fig. 2A), a more meaningful calculation for making comparisons between species would be egg production per unit body size. For the Bigoray River mayflies, average number of eggs per millimeter of total length ranged from about 100 to 200, with the exception of *L. cupida*, whose fecundity per unit length was twice as great as any of the other species (Fig. 2B). Data of Hunt (1951) for *H. limbata* (Pine Creek population) and of Britt (1962) for *E. simulans* would calculate to 137 eggs/mm and 222 eggs/mm respectively.

The female shape, especially the width and depth of the abdomen, is important in determining the number of eggs produced by each species. We assumed that the abdomen was in the shape of a cylinder and that the circumference of the third abdominal segment (measuring the tergitum and sternum under a microscope) represented the circumference of the cylinder. Hence the volume (by knowing abdominal length) of the abdomen could be estimated roughly, and the number of eggs per cubic millimeter of abdomen volume could be calculated. When this parameter is plotted against average total length of each species, it is evident that the smaller species produce more eggs per unit of abdomen volume than the larger species, although *L. cupida*'s fecundity volume is high relative to that of the other large species (Fig. 2C). Although fecundity per unit abdomen volume is probably the most informative calculation when comparing species, the values for the Bigoray River females are only rough approximations, since the abdomen is not a true cylinder for any of the species, the shape of the abdomen varying from species to species. Also, in most species some eggs extended into the metathorax and even the mesothorax; and in *Baetis tricaudatus* and *Centroptilum* sp. A, eggs were found as far forward as the prothorax.

Discussion

In a related study, Boerger and Clifford (in preparation) quantitatively studied the emergence of mayflies from the brown-water stream throughout the entire emergence period. By combining fecundity data with females emergence data, we calculated the total number of eggs produced by each species per square meter of stream per year (Table III, cols. A, B, and C). We did not have fecundity values for *Ameletus oregonensis* and *Centroptilum* sp. B; by knowing the average sizes of these two species, we extrapolated fecundity values from the lower line of Fig. 1. For the entire mayfly fauna of the brown-water stream, about 300,000 eggs are produced/m^2 per year.

By knowing the number of eggs produced in a given area and then the number of males and females emerging from the same area at the next emergence period (1 year later in the case of univoltine species), one can obtain some idea of mortality from unfertilized egg to subimago stage. Since our emergence data covered only one emergence season, we assumed that the total number of males and females of each species emerging per square meter (Table III, col. D) approximated the total number that would emerge at the next emergence period (1 year later since our species, with the possible exception of *Centroptilum* sp. A and *H. limbata*, were all univoltine species). As one might expect, mortality from egg to the subimago stage based on total potential fecundity was very high, averaging 99.8% for the entire fauna. Using a similar technique, Ide (1940) calculated mortality from unfertilized egg to imago stage to be 99.8%, 99.6%, and 99.8% for *Paraleptophlebia adoptiva*, *P. mollis*, and *P. volitans* respectively.

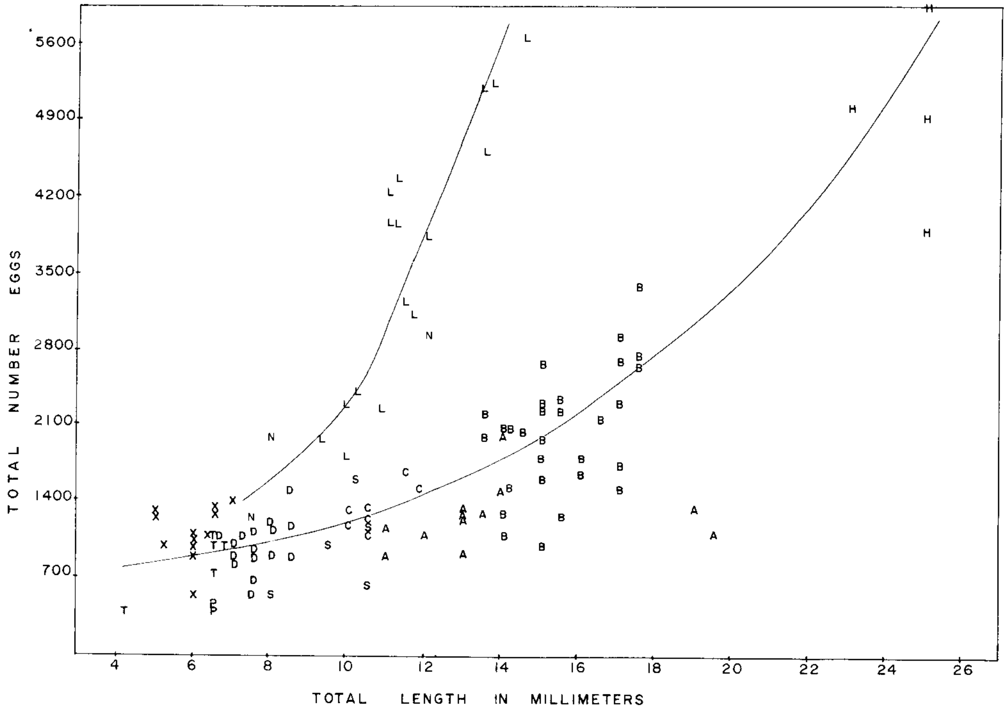

FIG. 1. Total length and total number of eggs of individual females. All values are from subimagoes except *H. limbata*, which include also imago values. The two lines were fitted by eye. A, *Siphlonurus alternatus* (Say); B, *Siphloplecton basale* (Walker); C, *Callibaetis coloradensis* Banks; D, *Paraleptophlebia debilis* (Walker); H, *Hexagenia limbata* (Serville); L, *Leptophlebia cupida* (Say); N, *Leptophlebia nebulosa* (Walker); P, *Paraleptophlebia praepedita* (Eaton); S, *Siphloplecton interlineatum* (Walsh); T, *Centroptilum* sp. A; X, *Baetis tricaudatus* Dodds.

Another expression of mortality, based on total egg production, is the number of eggs necessary to produce one adult (Table III, col. E, which is the ratio of columns C to D). For the entire stream mayfly fauna, it takes an average of about 900 eggs to produce one adult. For every 1000 eggs found in last instar nymphs of *Baetis rhodani*, Benech (1972) estimated that 277 eggs are eventually oviposited; and from the 277 oviposited eggs, one nymph will survive to the last nymphal instar. For individual species of our study, there was a wide range in column E values; and one can suggest these values, within limits, express the total environmental stress encountered by each species in the brown-water stream. For example, subimagoes of *L. cupida* and *Siphloplecton interlineatum* are found in about equal numbers, but it takes about 4 times as many eggs to maintain the *L.cupida* population as it does the *S. interlineatum* population; likewise *P. praepedita* and *H. limbata* have similar subimago densities, but it takes about 30 times as many eggs to maintain the *H. limbata* population. Although these values are only rough approximations, they would seem to indicate that the total environment of the brown-water stream is more favorable to

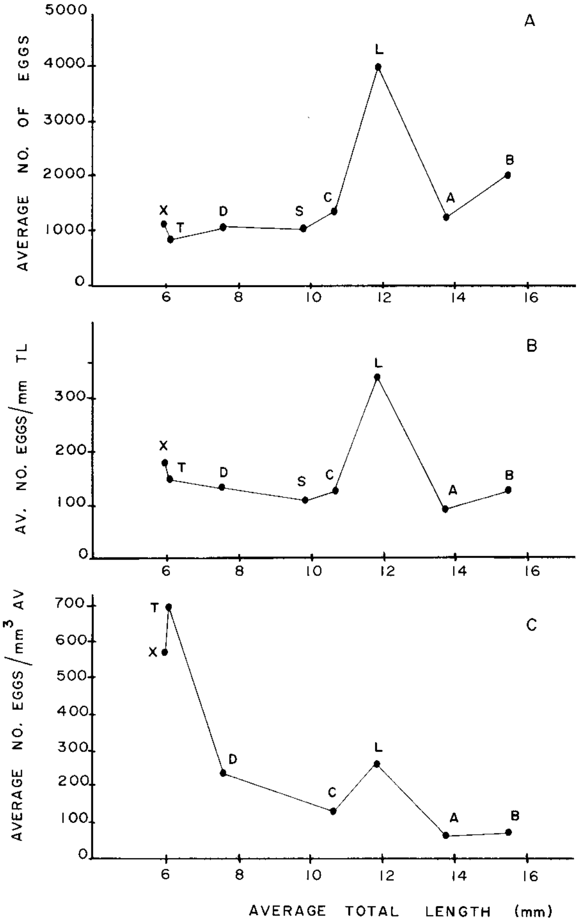

FIG. 2. Average total length of each species (female subimagoes) plotted against (A) average number of eggs, (B) average number of eggs/mm of total length, and (C) average number of eggs/mm^3 of abdomen volume. See Fig. 1 for species symbols.

Table III. Total number of males and females emerging per m² per year and total number of eggs produced by each species per m² per year. See text for further explanation

	(A) Av. no. eggs per female	(B) Total no. females emerging/ m²/year	(C) Total no. eggs/ m²/year	(D) Total no. females and males emerging/ m²/year	(E) Ratio C/D
Siphlonurus alternatus	1282	35.3	45255	68.3	663
Siphloplecton basale	2063	25.9	53432	44.5	1201
S. interlineatum	1083	13.2	14296	22.4	638
Leptophlebia cupida	4081	14.9	60807	24.1	2523
L. nebulosa	2023	1.4	2832	4.4	644
Paraleptophlebia debilis	1013	30.7	31099	41.3	753
P. praepedita	438	2.0	876	4.6	190
Callibaetis coloradensis	1343	2.5	3358	12.4	271
Baetis tricaudatus	1106	50.7	56074	73.4	764
Centroptilum sp. A	855	15.5	13253	33.5	396
Hexagenia limbata	5959	2.8	16685	5.2	3209
Ameletus oregonensis	1300	0.8	1040	1.6	650
Centroptilum sp. B	800	3.5	2800	11.4	246
Totals and C/D average		199.2	301807	347.1	934

species such as *P. praepedita*, *C. coloradensis*, and *Centroptilum* sp. B than to species such as *H. limbata*, *L. cupida*, and *Siphloplecton basale*.

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References

American Public Health Association *et al.* 1971. Standard methods for the examination of water and wastewater. 13th ed. Am. Public Health Assoc., New York. 874 pp.

Benech, V. 1972. La fecondité de *Baetis rhodani* Pictet. *Freshwat. Biol.* **2**: 337–354.

Brinck, P. 1957. Reproductive system and mating in Ephemeroptera. *Opusc. ent.* **22**: 1–37.

Britt, N. W. 1962. Biology of two species of Lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. *Bull. Ohio biol. Surv.*, No. 1. 70 pp.

Clemens, W. A. 1917. An ecological study of the mayfly *Chirotenetes*. *Univ. Toronto Stud. biol. Ser.* **17**: 3–43.

Clifford, H. F. 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. *Am. Midl. Nat.* **82**: 578–597.

———. 1970. Analysis of a northern mayfly (Ephemeroptera) population, with special reference to allometry of size. *Can. J. Zool.* **48**: 305–316.

——— 1972. A year's study of the drifting organisms in a brown-water stream of Alberta, Canada. *Can. J. Zool.* **50**: 975–983.

Darchis, A. 1964. Essais de réalisation de la fécondation artificielle chez *Ephemera vulgata* (Linné). *Archs Zool. exp. gén.* **104**: 135–139.

Davidson, A. 1956. A method of counting ephemeropteran eggs. *Entomologist's mon. Mag.* **92**: 109.

Degrange, C. 1960. Recherches sur la production des Ephémeroptères. *Trav. Lab. Hydrobiol. Piscicult. Univ. Grenoble* **50/51**: 7–193.

Engelmann, F. 1970. The physiology of insect reproduction. Pergamon Press. 377 pp.

Fremling, C. R. 1960. Biology of a large mayfly, *Hexagenia bilineata* (Say), of the Upper Mississippi River. *Iowa St. Univ. Agric. Home Econ. exp. Stn Res. Bull.* 482, pp. 841–852.

——— 1967. Methods for mass-rearing *Hexagenia* (Ephemeroptera: Ephemeridae). *Trans. Am. Fish. Soc.* **96**: 407–410.

Grandi, M. 1947. Contributi allo studio degli Efemeroidei italiani. IX. *Oligoneuriella rhenana* Imh. *Boll. Ist. Ent. Univ. Bologna* **16**: 176–218.

Hartland-Rowe, R. 1958. The biology of a tropical mayfly *Povilla adusta* Navas (Ephemeroptera, Polymitarcidae) with special reference to the lunar rhythm of emergence. *Revue Zool. Bot. afr.* **58**: 185–202.

Hunt, B. P. 1951. Reproduction of the burrowing mayfly, *Hexagenia limbata* (Serville), in Michigan. *Fla Ent.* **34**: 59–70.

Ide, F. P. 1940. Quantitative determination of the insect fauna of rapid water. *Univ. Toronto Stud. Fish. Res. Lab.* **59**: 1–20.

Kosova, A. A. 1967. A contribution to the ecology of the mayfly *Palingenia sublongicauda* Tshern. in the Volga Delta. (In Russian, English summary.) *Zool. Zh.* **46**: 1856–1859.

Minshall, J. D. 1967. Life history and ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae). *Am. Midl. Nat.* **78**: 369–388.

Morgan, A. H. 1913. A contribution to the biology of mayflies. *Ann. ent. Soc. Am.* **6**: 371–413.

Neave, F. 1932. A study of the May flies (*Hexagenia*) of Lake Winnipeg. *Contr. Can. Biol. Fish.* **7**: 179–201.

Pescador, M. L. and W. L. Peters. 1974. The life history and ecology of *Baetisca rogersi* (Ephemeroptera: Baetiscidae). *Bull. Fla St. Mus. biol. Sci.* **17**: 151–209.

*Rousseau, E. 1921. Les larves and nymphes aquatiques des insectes d'Europe, I. Office de Publicité, Brussels. 967 pp.

Smith, O. R. 1935. The eggs and egg-laying habits of North America mayflies, pp. 67–89. *In* J. G. Needham, J. R. Traver, and Yin-Chi Hsu, The biology of mayflies with a systematic account of North American species. Comstock, Ithaca. 793 pp.

Trost, L. M. W. and L. Berner. 1963. The biology of *Callibaetis floridanus* Banks (Ephemeroptera: Baetidae). *Fla Ent.* **46**: 285–299.

Wisely, B. 1961. Studies on Ephemeroptera. I. *Coloburiscus humeralis* (Walker); early life history and nymph. *Trans. R. Soc. N.Z. (Zool.)* **1**: 249–257.

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*Reference not seen in the original.

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