## Acknowledgments

I wish to thank Dr. W. R. Knight of the Department of Mathematics, University of New Brunswick, for writing computer programmes. I am also grateful to Dr. D. C. Eidt, Professor H. D. Long, and Professor N. R. Brown for their counsel. Financial assistance from the External Aid of Canada is gratefully acknowledged.


## References


Bedard, W. D. 1966. High temperature mortality of the sugar-pine cone beetle, *Conophthorus lambertianae* Hopkins (Coleoptera: Scolytidae). *Can. Ent.* **98**: 152–157.

Curtis, O. F. 1936. Leaf temperatures and cooling of leaves by radiation. *Pl. Physiol.* **11**: 343–364.

Henson, W. R. 1964. Laboratory studies on the adult behavior of *Conophthorus coniperdus* (Coleoptera: Scolytidae). IV: Response to temperature and humidity. *Ann. ent. Soc. Am.* **57**: 77–85.

Henson, W. R. and R. F. Shepherd. 1952. The effects of radiation on the habitat temperatures of the lodgepole needle miner, *Recurvaria milleri* Busck (Lepidoptera: Gelechiidae). *Can. J. Zool.* **30**: 144–153.

Schaefer, C. H. 1963. Factors affecting the distribution of the Monterey pine cone beetle (*Conophthorus radiatae* Hopkins) in Central California. *Hilgardia* **34**: 79–103.

Wellington, W. G. 1950. Effects of radiation on the temperatures of insectan habitats. *Scient. Agric.* **30**: 209–234.


(Received 16 February 1970)

# THE LIFE CYCLES OF SOME STREAM INSECTS (EPHEMEROPTERA, PLECOPTERA) IN ALBERTA[1]

D. S. RADFORD[2] and R. HARTLAND-ROWE

Department of Biology, University of Calgary, Calgary, Alberta


**Abstract** *Can. Ent.* 103: 609–617 (1971)

The life histories of *Nemoura besametsa, Epeorus deceptivus, Epeorus longimanus,* and *Ephemerella coloradensis* are described as "fast seasonal" types and *Arcynopteryx aurea, Nemoura cinctipes, Nemoura columbiana, Nemoura oregonensis, Cinygmula ramaleyi, Ephemerella doddsi,* and *Rhithrogena doddsi* as "slow seasonal" types according to Hynes' (1961) classification. All of the species are univoltine with the exception of *N. cinctipes* which may be bivoltine. There seems to be a correlation between life cycles and food availability. A means of ecological separation in the four *Nemoura* species is elucidated. Stream temperature was found to influence growth rates.


## Introduction

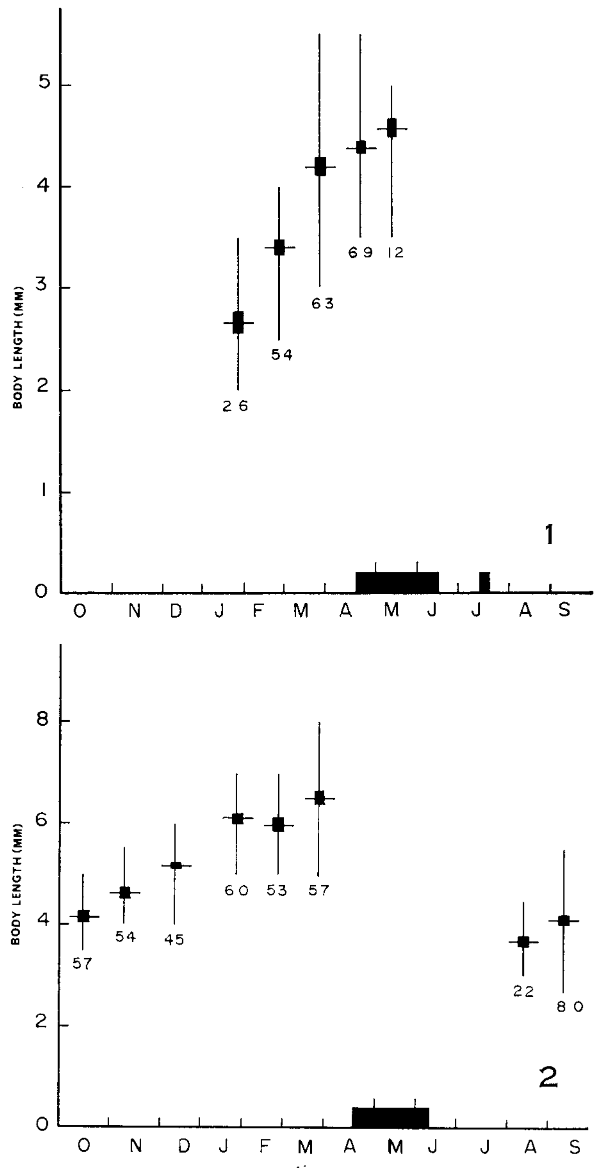
During the course of an ecological investigation of the insects in a mountain stream in Alberta the life histories of several of the most abundant species were examined. The data were obtained in order to assess the importance of these species in the benthic standing crops and in the invertebrate drift. The life cycles of some of the species were unknown, the only previous papers on Alberta species being those of Hartland-Rowe (1964) and Clifford (1969).

## The Study Area

The investigation was undertaken in Lusk Creek, a small tributary of the Kananaskis River, on the eastern slopes of the Rocky Mountains in southwestern Alberta. The area is approximately 70 km west of Calgary.

[1]The data was taken from a thesis submitted by D. S. Radford in partial fulfillment of the requirements for the degree of Master of Science from the University of Calgary.

[2]Present address: Department of Lands and Forests, Fish and Wildlife Division, Edmonton, Alberta.




FIGS. 1–2. Growth of *Nemoura besametsa* (Fig. 1) and of *N. columbiana* (Fig. 2) in Lusk Creek. The mean size is shown by a short horizontal line, the standard error of the mean by a black vertical rectangle, and the size range by a vertical line. The sample size is indicated for each distribution. The black rectangle on the abscissa illustrates the known emergence period; P denotes a presumed emergence period.

Lusk Creek is a small stream which varies in width from 1.5 to 4 m; depths range between 5 and 30 cm. The stream descends approximately 1000 m during its 14 km length, with a slope of roughly 70 m/km. Flows ranged between 0.2 and 0.8 $m^3$/sec with a mean discharge of 0.5 $m^3$/sec; mid-channel velocity fluctuated between 80 and 140 cm/sec. The substrate is composed of sand, gravel, and coarse rubble, with occasional large boulders. During the fall and winter, leaf litter is abundant and much of the stream is covered with a dense growth of filamentous algae.

The stream is cool and clear. The annual temperature ranged from 0° to 9.5°C; peak mean daily temperatures of 4.0°–5.0°C occurred in mid-June. The stream experiences small temperature fluctuations on a daily and seasonal basis and this is likely due to the shading effect of the dense bank vegetation, as well as the stream's brisk flow.

Lusk Creek was chosen for study because it contains a diverse bottom fauna and because it is accessible during the winter months. Ice cover does not occur during the winter and this facilitates research.

## Methods

Collections for life history analysis were taken at approximately 4-week intervals from October 1968 to September 1969. The area chosen for study was a 100 m stretch approximately 200 m from the stream's junction with the Kananaskis River. Sampling was done with a common pond net (mesh size: 1 mm) and the samples were hand-sorted in the laboratory. The specimens were preserved in 70% ethanol and measured to the nearest 0.5 mm (length from front of head to tip of abdomen).

Emergence periods were determined from weekly collections of adults obtained by sweeping the vegetation with an insect net and by aerial sampling of emerging forms (especially mayflies).

Although a considerable variety of stream insects were encountered, because of insufficient sample sizes and an inability to separate closely related larval forms, only eight of the species will be discussed in the paper.

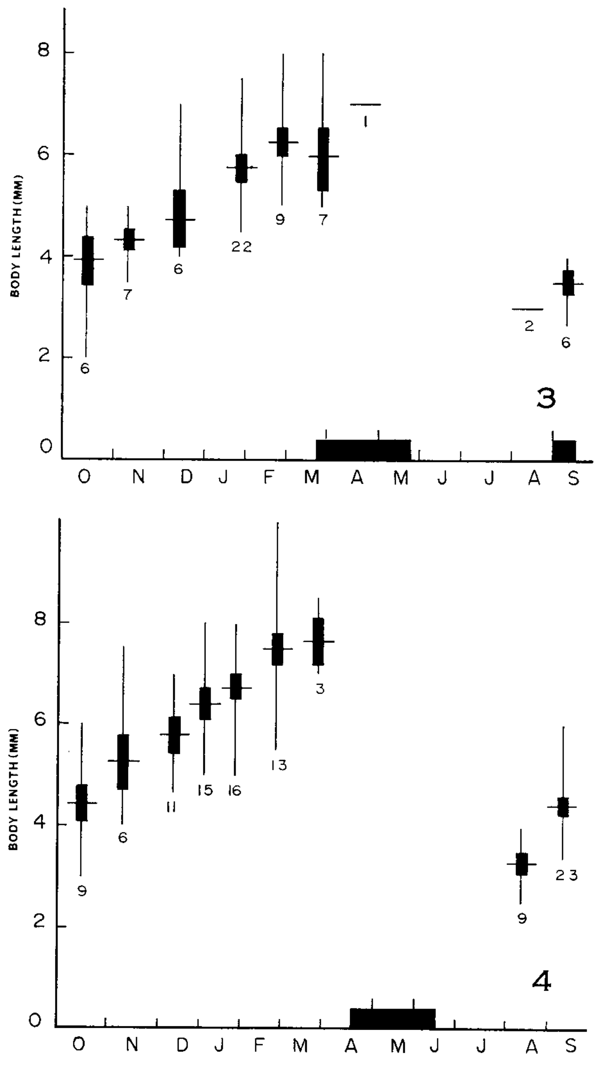
## Results

All of the species studied, except *Nemoura cinctipes,* appear to be univoltine and are separable into two categories. *N. cinctipes* probably has two generations per year judging from emergence records (Fig. 3) although this is not indicated by its size distribution.

Hynes (1961) has divided species which have a seasonal life-cycle (those in which there is a seasonally changing size distribution) into two categories, slow and fast, the former being species in which the eggs hatch soon after laying and in which larval growth is slow and steady over a long period, and the latter being species in which there is rapid growth after a long egg-diapause or an intermediate generation. Thus classified *Nemoura besametsa* would be regarded as a fast seasonal type whereas the remaining species (*Arcynopteryx aurea, Nemoura cinctipes, Nemoura columbiana, Nemoura oregonensis, Cinygmula ramaleyi, Ephemerella doddsi,* and *Rhithrogena doddsi*) would be termed slow seasonal forms (Figs. 1–8).

Although insufficient data was obtained for detailed life history analysis, it was observed that the life-cycles of *Epeorus deceptivus, Epeorus longimanus,* and *Ephemerella coloradensis* were also of the fast seasonal type.

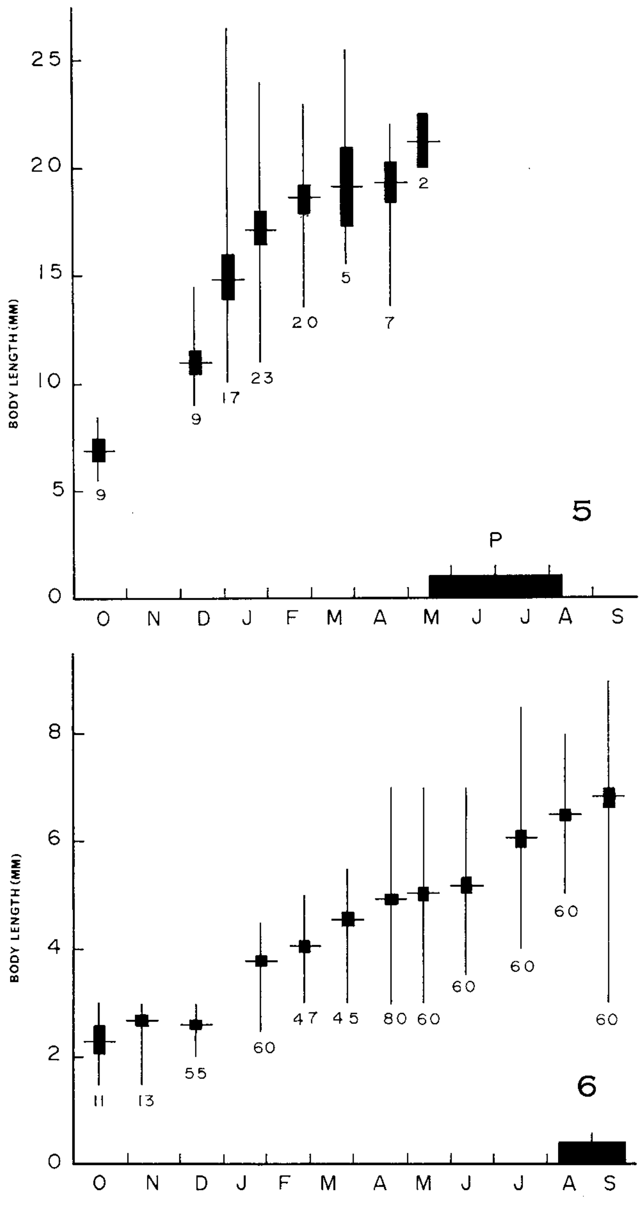
The eggs of *N. besametsa* are laid in the spring and early summer; however, it is not until 7 or 8 months later that nymphs about 2 mm in length appear. A




FIGS. 3–4. Growth of *Nemoura cinctipes* (Fig. 3) and of *N. oregonensis* (Fig. 4) in Lusk Creek. For explanation see caption Figs. 1–2.

diapause is likely responsible. These nymphs grow rapidly to complete their development by April or May.

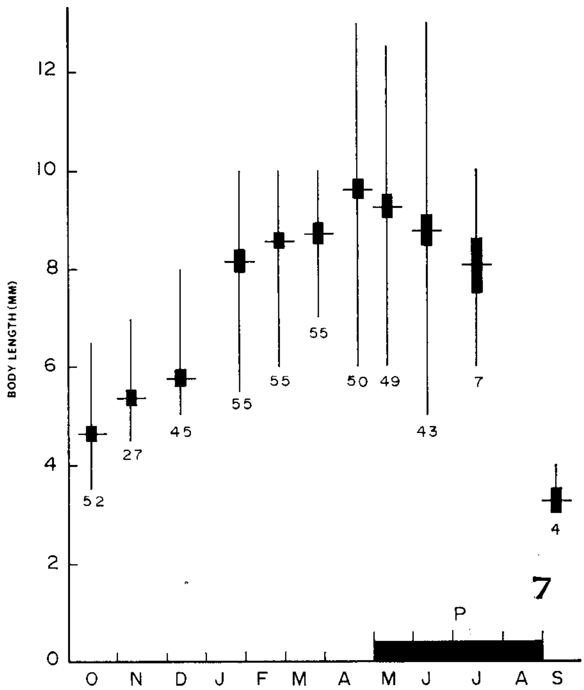
The eggs of the remaining species of *Nemoura* are deposited in the spring (late March to early June) and hatch soon after. The growth rate is uniform, and the nymphs grow throughout the summer, fall, and winter. The absence of small nymphs (less than 2 mm) in early summer is probably an artifact as these would pass through the coarse collecting net. An analogous life-cycle is evident for *A. aurea* except that emergence is probably somewhat later. Also, the growth of nymphs of this species is much faster than for any other type studied. It is notable that *A. aurea* is univoltine in Lusk Creek since most large plecopterans require 2 or 3 years to mature.



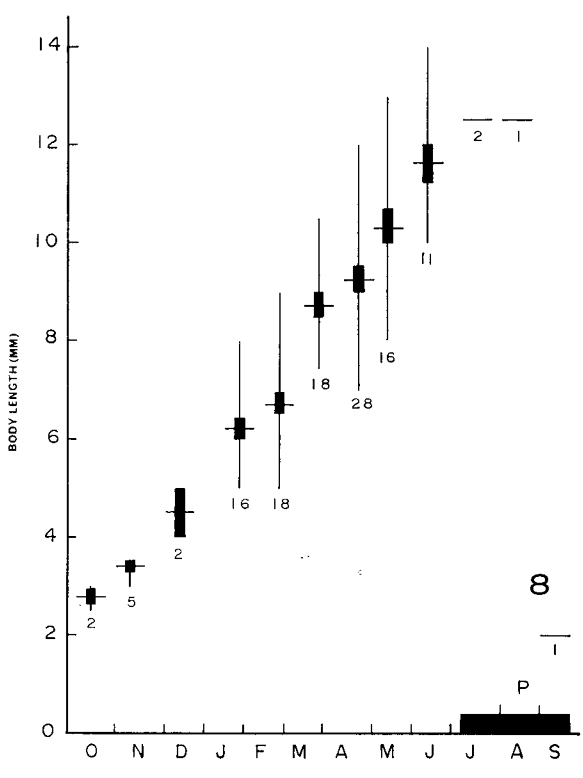

FIGS. 5–6. Growth of *Arcynopteryx aurea* (Fig. 5) and of *Cinygmula ramaleyi* (Fig. 6) in Lusk Creek. For explanation see caption Figs. 1–2.

The life cycles of *N. cinctipes* and *N. columbiana* are of the same type as described for the former in the Bigoray River, Alta. (Clifford 1969) and the latter in Gorge Creek, Alta. (Hartland-Rowe 1964). However, in Lusk Creek a small proportion of the population of *N. cinctipes* completes a second generation between April and September.

Although the ephemeropteran species are of the same "slow seasonal" type as the plecopterans studied, the former lay their eggs throughout the summer until


BODY LENGTH (MM)
12
10
8
6
4
2
0
52
27
45
55
55
55
50
49
43
7
4
P
O N D J F M A M J J A S

7


BODY LENGTH (MM)
14
12
10
8
6
4
2
0
2
5
2
16
18
18
28
16
11
2
1
1
P
O N D J F M A M J J A S
MONTHS OF YEAR

8

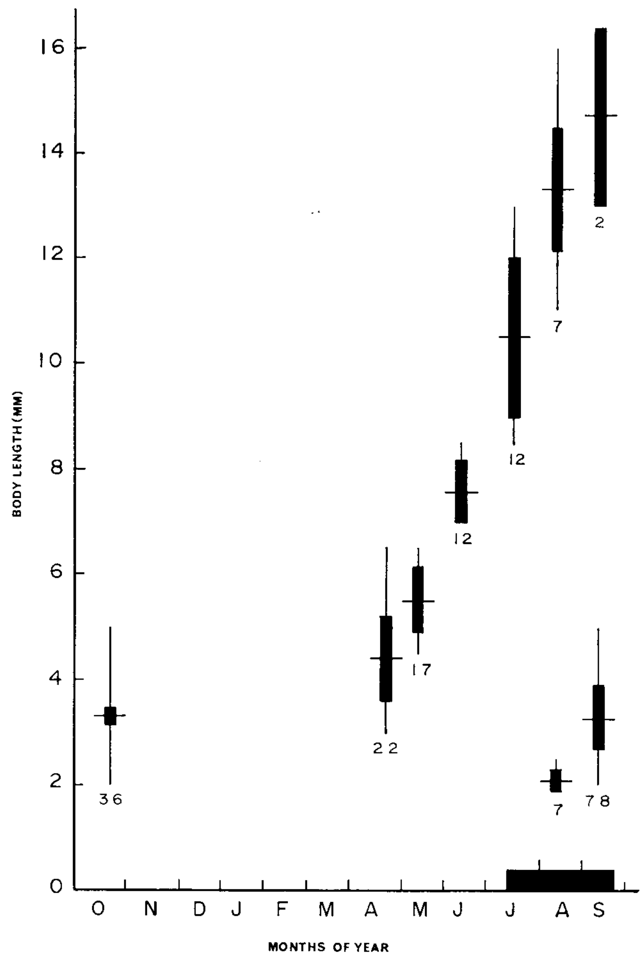



FIG. 9. Growth of *Ephemerella doddsi* in the Kananaskis River. For explanation see caption Figs. 1–2.

early fall, in contrast to the spring oviposition of the stoneflies. Winter growth does not appear to be retarded in either *E. doddsi* or *R. doddsi* in Lusk Creek although it seems to slow down in *C. ramaleyi,* as was observed by Hartland-Rowe (1964).

Some stream insects were obtained from the Kananaskis River from April to September 1969, and a single collection was made in October 1968. From this material the life history of *E. doddsi* was determined for the river (Fig. 9).

Comparison of the data for this species in Lusk Creek and the Kananaskis River (Figs. 8, 9) reveals that the mean size is consistently smaller in the river from April until August, after which time the sizes are similar. The emergence period is similar for the two locations and the differences in mean sizes are due to a marked difference between the growth rates of the two populations. Although winter

---

FIGS. 7–8. Growth of *Rhithrogena doddsi* (Fig. 7) and of *Ephemerella doddsi* (Fig. 8) in Lusk Creek. For explanation see caption Figs. 1–2.

Table 1. Mean monthly size (mm) of *Nemoura* spp. in Lusk Creek, 1968–69

| | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | June–Jul. | Aug. | Sep. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *N. besametsa* | | | | 2.7 | 3.4 | 4.2 | 4.4 | 4.6 | | | |
| *N. cinctipes* | 3.9 | 4.4 | 4.8 | 5.8 | 6.2 | 6.0 | 7.0 | | | 3.0 | 3.5 |
| *N. columbiana* | 4.2 | 4.6 | 5.2 | 6.1 | 6.0 | 6.5 | | | | 3.7 | 4.1 |
| *N. oregonensis* | 4.4 | 5.3 | 5.8 | 6.4 | 6.7 | 7.5 | 7.7 | | | 3.3 | 4.4 |

growth is continual in Lusk Creek there is a virtual cessation in the Kananaskis River (which is covered by ice at this time); the length increase from October to April in each stream is about 6.0 and 0.8 mm, respectively.

The difference in growth rates prior to emergence is probably due to the amount of heat available during the 20-week period from May until mid-September. Lusk Creek accumulated only 11477 degree-hours over this period, whereas the comparable total for the Kananaskis River was 19168 degree-hours. This is interesting because it illustrates that caution must be used in generalizing about life cycles. These are directly influenced by the local environment and may change with geography. For instance, we have found maturing nymphs of *A. aurea* right into July in some streams at higher altitudes in this area.

An interesting situation is apparent in the genus *Nemoura*. In all instances *N. besametsa* has the smallest mean size, and almost without exception *N. cinctipes* is the next smallest, *N. oregonensis* the largest, with *N. columbiana* occupying an intermediate position (Table I). The mean sizes of the latter three species are seldom widely separated (usually less than 1 mm difference between the largest and the smallest) and this pattern is consistent. *N. columbiana* and *N. besametsa* occurred in the greatest numbers with relatively few specimens of *N. cinctipes* and *N. oregonensis* present.

This phenomenon appears fairly common in aquatic habitats (Hynes 1961; Hartland-Rowe 1964) and may be a way of reducing interspecific competition. The size distribution may lessen the interaction for resources since the species probably have similar food requirements. It could be significant that the size range of *N. cinctipes* and *N. oregonensis* usually averages 3 mm whereas the range of *N. columbiana* consistently approximates 2 mm. It is conceivable that a larger size range would provide a means of increasing the efficiency of utilizing a resource; since the mean sizes of the three species do not differ markedly, this may be the only possible method of lessening the competitive effect of *N. columbiana*. *N. besametsa* avoids the problem by remaining much smaller than any of the species.

## Conclusions

As was observed by Ulfstrand (1967), there is a correlation between life cycles and food availability. Leaf consumers (*Nemoura* spp.) grow intensely during the fall and winter, and populations are high, whereas their biomass is low during the summer when allochthonous matter is rare. Algal grazers (*Cinygmula ramaleyi, Epeorus* spp., and *Rhithrogena doddsi*) have their most intense growth periods in the spring and early summer (the season with the most light and photosynthesis) with coincident high standing crops.

It has been found that the life history of stream insects is influenced by water temperatures, some species showing cessation of growth at 0°C (Hartland-Rowe 1964; Svensson 1966; Ulfstrand 1968). This was further substantiated in the Kananaskis River for the life cycle of *E. doddsi,* when the river was covered by ice during the winter. It was unfortunately not possible to record winter water temperatures, but it may be assumed that the temperature was close to 0°C. The fact that the growth of this and other species did not stop during the winter in Lusk Creek indicates that the potential for growth is present; if temperatures are not limiting, growth will continue.

## Acknowledgments

This work was supported by a grant to the junior author from the National Research Council of Canada. Thanks are due to Mr. R. J. Paterson of the Fish and Wildlife Division, Alberta Department of Lands and Forests, for arranging summer financial support for the senior author, and for his continued interest in the study.

## References

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**(2): 578–597.

Hartland-Rowe, R. 1964. Factors influencing the life-histories of some stream insects in Alberta. *Verh. int. Verein. Theor. angew. Limnol.* **XV**: 917–925.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* **57**: 344–488.

Svensson, P. O. 1966. Growth of nymphs of stream living stoneflies (Plecoptera) in northern Sweden. *Oikos* **17**: 197–206.

Ulfstrand, S. 1967. Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams. *Oikos* **18**: 293–310.

——— 1968. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae). *Oikos* **19**: 167–190.

(Received 13 August 1970)

# RELATIONSHIP BETWEEN CONE CROP SIZE AND CONE DAMAGE BY INSECTS IN RED PINE SEED-PRODUCTION AREAS

WILLIAM J. MATTSON JR.

North Central Forest Experiment Station,[1]
Forest Service, U.S. Department of Agriculture, St. Paul, Minnesota

**Abstract** *Can. Ent.* 103: 617–621 (1971)

Annual cone abundance and insect damage to cones are highly variable in red pine seed-production areas. Cone crop size fluctuates almost unpredictably from year to year, but the number of insect-attacked cones tends to increase annually unless limited by cone abundance. Sixty-six per cent of the variation in cone damage can be associated with variations in cone abundance. This information, coupled with the fact that red pine cone insects are almost entirely dependent on red pine cones for food, implies that crop size is highly important in regulating populations of cone insects. Insects will be most devastating in areas where crop size varies little from year to year.

Several authors have stated that amount of insect damage to cone crops tends to be related to crop size. Generally, insect-caused damage has been less in years immediately following small cone crops than in years after moderate to large crops (Lyons 1957; Hedlin 1964; Lester 1963; Graham and Knight 1965). However, the relationship of cone crop size to cone damage has seldom been evaluated quantitatively. This paper reports an investigation into this relationship.

[1]Maintained in cooperation with the University of Minnesota.