LIFE CYCLE PATTERNS OF MAYFLIES (EPHEMEROPTERA) FROM SOME STREAMS OF ALBERTA, CANADA

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INTRODUCTION

Taxonomically, the mayfly fauna of the Province of Alberta, Canada is poorly known. Following the classification system of EDMUNDS (1962), representatives of all five super-families are known to occur in Alberta. Of the 15 families of North American mayflies, at least 11 are found in Alberta. Behningiidae most likely does not occur in the province, and I know of no reports of Potamanthidae, Neoephemeridae and Oligoneuriidae from Alberta, although an oligoneuriid, *Lachlania,* is found in adjoining Saskatchewan.

Although our faunistic list is incomplete, considerable life history information for certain Alberta mayfly species has started to accumulate. HARTLAND-ROWE (1964) described the life histories of four mayfly species from a stream on the eastern slopes of the Canadian Rockies. Starting in 1965, University of Alberta personnel have been carrying out long range limnological programs on three Alberta streams, and in the process gathering life history information of the more abundant aquatic invertebrates, including the mayflies. This report is a synopsis of our mayfly life histories to date, including a discussion of mayfly life history patterns in Alberta, a region lying between the warmer temperate regions to the south and the arctic region to the north.

STUDY AREAS AND METHODS

Although Alberta remained as an ice-free corridor for most of the Ice Age, about 35,000 years ago Wisconsin ice sheets from the north and east converged with an ice sheet flowing out of the Rocky Mountains and eventually covered all of Alberta, except for a small area in southeastern Alberta and possibly some of the high mountain peaks. The last retreat of ice began about 12,000 years ago; the streams of the study areas probably attained their present drainage patterns about 11,500 years ago.

Wampus Creek, Bigoray River and La Biche River are located in about the middle of the province; from west to east they represent respectively, and are hereafter referred to as ,a small foothills stream of the Canadian Rockies, a small brown-water, or muskeg, stream of the boreal forest, and a large boreal forest river, originating from an oligotrophic lake (Fig. 1). Physical and chemical features of the foothills stream, the brown-water stream, and the boreal forest river have been reported by ZELT (1970), CLIFFORD (1969), and ROBERTSON (1967) respectively. All three streams are completely ice-covered for about six months of the year. The fourth stream for which mayfly life histories are available is Gorge Creek; this stream is similar to the above mentioned foothills stream (Wampus Creek) and was studied by HARTLAND-ROWE (1964).

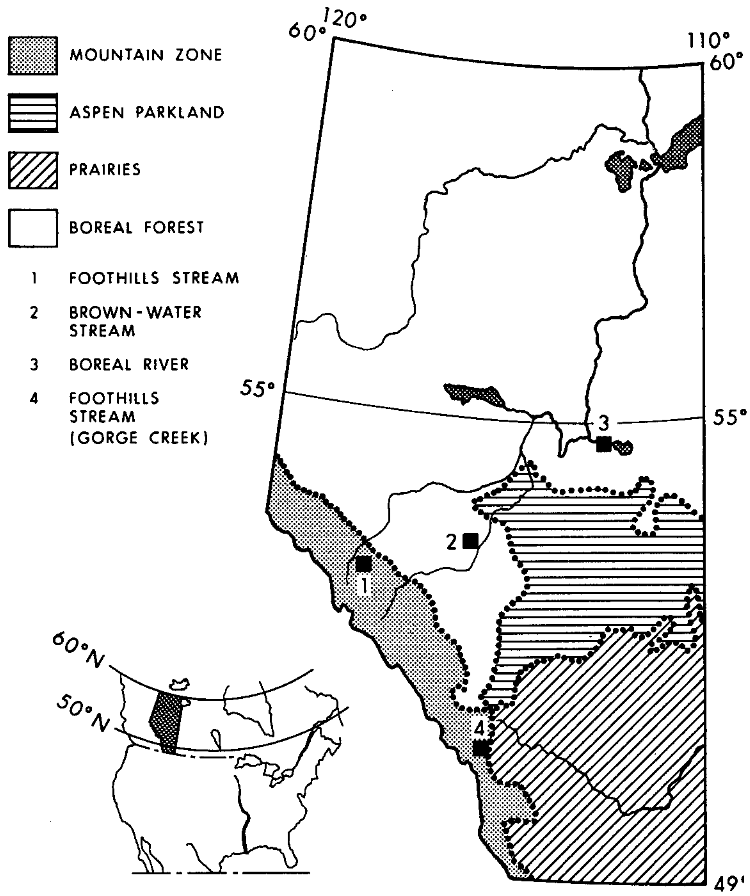

FIGURE 1. Map of Alberta, showing major topographic regions and the location of the four streams from which mayfly life cycles are known.

Procedures for collecting and treating the mayfly samples varied slightly from stream to stream, depending on the purpose of the study [1]; but generally all streams were sampled at less

[1] The foothills stream is being studied to provide a foundation for assessing the effects of "clear-cutting" (for pulpwood extraction) on the streams of a small watershed. After accumulating basic limnological data for the brown-water stream, it is to be experimentally manipulated to assess the effects of pollutants on this type stream. The boreal forest river is being studied to determine how northern oligotrophic and eutrophic lakes influence their associated streams.

than monthly intervals during the ice-free season, and at least every other month in the winter. Mayfly nymphs were collected with dip nets. Both regular mesh nets (apertures of 0.73 mm) and fine mesh nets (apertures of 0.32 mm) were used in the foothills and brown-water streams; only regular mesh nets were used in the boreal forest river. Because of the remoteness of the sampling sites, it was not possible to obtain complete emergence and flight records; however, a considerable number of adults was collected. Also the presence of the darkened wing pads of nymphs, which were recorded if present, indicated impending emergence.

The mayfly life histories reported here are based on changes of sizeclass (total length) distributions throughout the year. We are aware that one must use caution when interpreting life history phenomena from changes in body size. Several workers, e.g. PLESKOT (1962), and LEVANIDOVA and RUBANENKOVA (1965), have pointed out some of the difficulties that can arise in this respect. It is important to distinguish between growth (increase in body size, usually total length) and postembryonic development (maturing in the sense of physiological aging). Only the former can be strictly inferred from changes in size-class distributions; and, because of delayed hatching, this is not always possible. Also the choice of the linear measurement used to construct the size-class distribution can be important (CLIFFORD, 1970a). Nevertheless with proper precautions, useful life history information can be obtained for most species from body size analysis, especially if the sampling is done over short intervals and a fine mesh net is used.

RESULTS

Mayfly species made up a considerable part of the total fauna of each of the three Alberta streams. Comparable faunistic information is also available for Plecoptera and Trichoptera. The relative composition in terms of species for the three orders in each of the three streams is as follows : foothills stream — Ephemeroptera 28 %, Plecoptera 48 %, Trichoptera 24 %, (total number of species, 61); brown-water stream — Ephemeroptera 45 %, Plecoptera 10 %, Trichoptera 45 %, (total number of species, 33); and boreal forest river — Ephemeroptera 43 %, Plecoptera 14 %, Trichoptera 43 %, (total number of species, 23). Obviously when compared to North American streams of more moderate latitudes, the mayfly fauna of these three Alberta streams would be considered poor in number of species. In terms of standing crop (biomass) throughout the year and considering all aquatic taxa, the mayflies made up the largest standing crops in the brown-water and foothills streams, and Trichoptera was most important in the boreal forest river, a river originating from a lake.

Table 1 is a synopsis of the life cycles of 17 mayfly species from Alberta streams. The life cycles are grouped according to LANDA's (1968) classification, which is abridged as follows :

A. One generation in a year. A1 (winter species) : Nymphs hatch in summer and autumn, continue to grow throughout the winter, and emerge the following spring or summer. A2 (summer species) : Nymphs hatch, grow and emerge during a short period of summer, the eggs being in a supposedly diapause state for most of the year. A3 (winter species) : Nymphs hatch and grow in summer and autumn, but not in winter, growth resuming in the following spring. B. Two or more generations in a year. C. One generation in two or more years. D. Others (LANDA further subdivides Groups, B, C, and D).

Figure 2 illustrates a typical A2 and an A3 cycle, the latter being inferred from both regular and fine mesh net samples. Although the life cycle of *Ephemerella doddsi* is as accurately deduced from the regular mesh samples as from the fine mesh samples, this was not the case for all the mayflies of the foothills stream; for a few species that hatched and then grew very slowly for a considerable period of time, the regular mesh samples gave an erroneous picture of the species phenology (ZELT and CLIFFORD, in preparation). All life cycles of Table 1 were inferred from histograms similar to those of Figure 1, and for the foothills stream are reported in full by ZELT (1970), for the brown-water stream by CLIFFORD (1969 and 1970b), and for the boreal forest river by ROBERTSON (1967).

Table 1

Life cycle patterns of 17 species of mayflies from Alberta. The cycles are classified according to LANDA (1968); *see text for further explanation of cycles.*

Species	*Emergence*	*Percent of Final Size During Winter* [1]	*Stream*
A2			
Siphlonurus alternatus (SAY)	July	0	Brown-water
Cloeon sp.	July-Aug.	0	Brown-water
Paraleptophlebia debilis (WALKER)	Aug.	0	Brown-water
Tricorythodes minutus TRAVER	Aug.	0	Boreal river
Ephemerella tibialis McDUNN.	Aug.	0	Foothills
Ephemerella lapidula McDUNN.	Aug.	0	Foothills [2]
A3			
Ephemerella coloradensis DODDS	Aug.	15	Foothills
Epeorus longimanus (EATON)	Aug.-Sept.	15	Foothills
Ephemerella inermis EATON	July	40	Foothills
Caenis simulans McDUNN.	June-July	40	Boreal river
Cinygmula ramaleyi (DODDS)	June-Sept.	40	Foothills [2]
Ephemerella doddsi NEEDHAM	July-Aug.	45	Foothills
Ephemerella grandis ingens McDUNN.	July	50	Foothills
Leptophlebia cupida (SAY)	May-July	60	Brown-water
Rhithrogena virilis McDUNN.	July	60	Foothills
Callibaetis coloradensis BANKS	May	100	Brown-water
Combination A2 and A3			
Baetis tricaudatus DODDS (A2)	Aug.-Sept.	0	Brown-water
(A3)	June-July	40	

[1] Mean size of nymphs in winter divided by mean size of nymphs with darkened wing pads.
[2] From HARTLAND-ROWE (1964).

Winter species without growth in the winter (A3) predominate in the Alberta fauna studied so far, but there is, when compared to other regions, a relatively large number of summer species. Two of the A3 species, *Epeorus longimanus* and *Ephemerella coloradensis*, over-winter as small nymphs having an average size of about 1.5 mm. In a sense they might be considered summer species, since almost all the growth takes place during a short period in the summer. But the nymphs are probably not in an obligate diapause state in the winter; it is more likely a quiescent period controlled by low temperatures. LEHMKUHL (1968) reports large *E. longimanus* nymphs during the winter in a stream of western Oregon. In contrast to *E. longimanus* and

E. coloradensis, *Callibaetis coloradensis* over-winters as very large (ultimate nymphal instar size) non-growing nymphs.

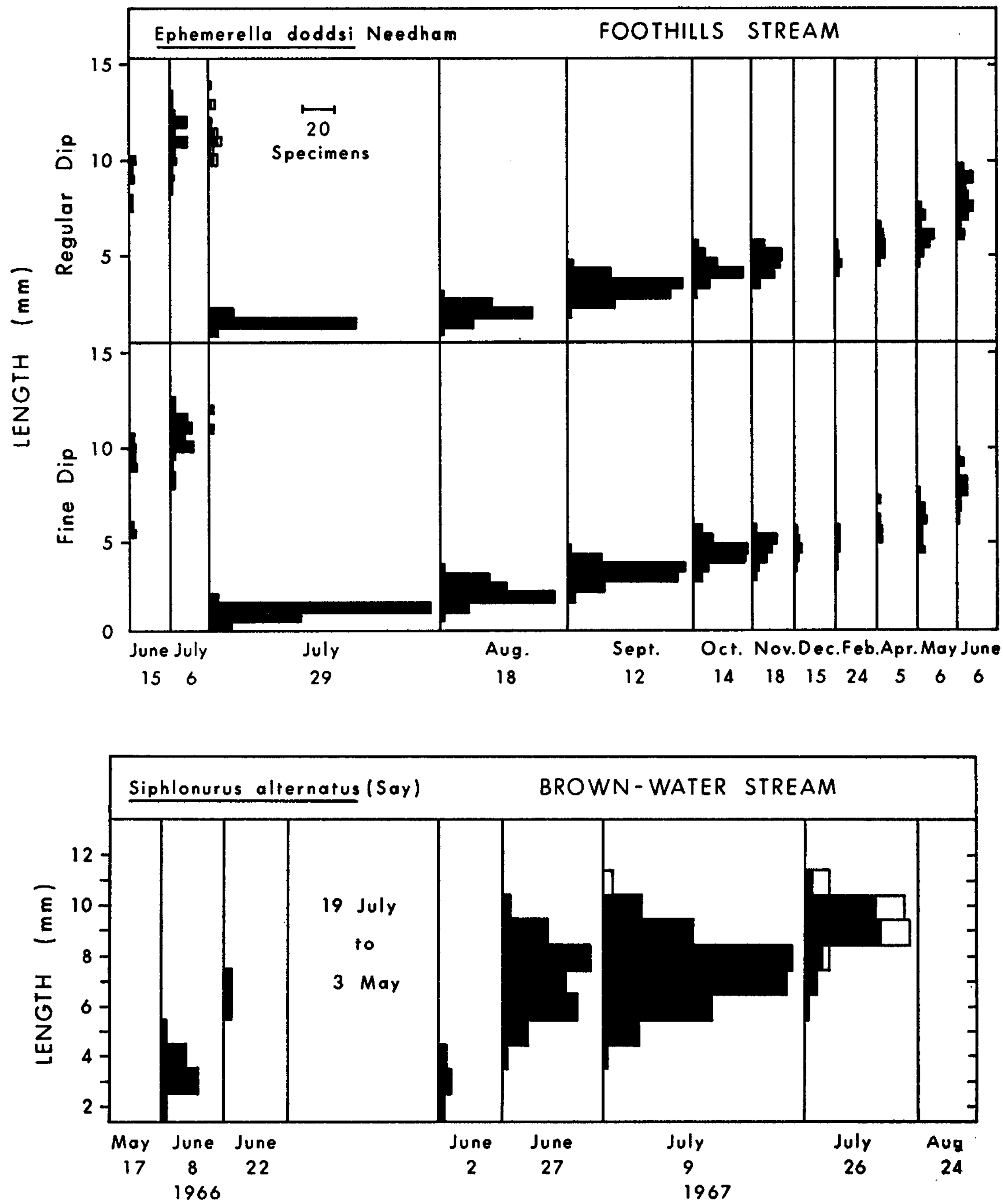

FIGURE 2. Length-frequence histograms of *Ephemerella doddsi* and *Siphlonurus alternatus*, illustrating a winter species without growth in the winter and a summer species respectively. Unshaded bars represent nymphs with darkened wing pads.

The *Baetis tricaduatus* "complex" (along with a few other baetid species) occurs in all three streams, and the life cycle pattern is similar for the three streams. But the cycle is perplexing and it is the one cycle of Table 1 that is subject to some speculation. The nymphs of one population hatch and grow in the autumn, but very little if at all in the winter; they complete growth and emerge in the summer (an A3 cycle); by the time of emergence of the A3 population, the eggs of a second population have already hatched. The nymphs of the second population grow rapidly and emerge in late summer, but their eggs lie dormant until the following summer (an A2 cycle). Although there are possibly two species, we have been unable to separate the nymphs and adults of these two populations on the basis of morphological criteria. Given the right environmental conditions, it is possible that the adult stages of the two populations might overlap, with subsequent interbreeding of the two populations.

When compared with mayfly life cycle patterns of other regions, the generalized patterns of the Alberta species are more or less in tune with and reflect the short open-season characteristic of Alberta's cold temperate to subartic climate (Table 2). The Alberta fauna is characterized by winter species without winter growth, a relatively large number of summer species, and a lack of species with multivoltine cycles and winter species growing throughout the winter (in contrast, several of the stoneflies from the streams in question did grow throughout the winter).

Table 2

Comparison of mayfly cycles of some streams in Alberta with those of the Lake District, England (MACAN 1957), *central Europa* (LANDA 1968) *and Swedish Lapland* (ULFSTRAND 1968). *See text for explanation of life cycle types.*

Type Cycle [1]	*Percent of total species reported*			
	Lake District, England	*Central Europe*	*Lapland, Sweden*	*Alberta, Canada*
A1	43	32	10	0
A2	14	31	50	39
A3	14	5	30	61
B	29	28	0	0
C	0	4	10	0
D	0	0	0	0
Total number of species	7	75	10 [2]	17 [3]

[1] The grouping of MACAN's and ULFSTRAND's species into the LANDA classification is my interpretation of their life history information.

[2] Including one species having both an A3 population and a C population.

[3] Including one species having both an A2 population and an A3 population.

DISCUSSION

In regards to different latitudes (or the comparable climatological regions), there are several ways that one might expect mayfly life cycle patterns to change. It is of course necessary to keep in mind that variability will occur, even within the same biotope, and the immediate environment can differ widely from the general environment. In the rainy tropical regions (away from the mountains), where temperatures are constant and photoperiods are unform, generally the species will have multivoltine cycles with overlapping generations and continuous emergence. Few species with temporary (summer) cycles have been reported from the tropics. When emergence is cyclic, it is due to factors other than seasonally varying temperatures and photoperiods, e.g. the lunar emergence rhythms of *Povilla adusta* NAVÁS (HARTLAND-ROWE 1958). Even in the subtropical and warm temperate regions of Florida, BERNER (1950) found few seasonal species. In short, there is probably a predominance of species with multivoltine cycles (B species, according to LANDA's classification) in the tropics.

In the moderate temperate regions (e.g. in North America to about latitude 42°, the northern limit of the Austral Region), seasonally varying temperatures and photoperiods influence life cycle patterns. The mayflies usually have only one generation in a year, and generally the pattern is one of winter species with some growth in winter. Summer species also become numerically more important. For central Europe, LANDA (1968) reports 23 summer species, which comprise 31 % of the total central European mayfly fauna. Although not nearly as many summer species are as yet known for a comparable region of North America, most of those that have been reported are species living in streams periodically subjected to drought, e.g. *Ameletus ludens* NEEDHAM (CLEMENS 1922) and a species of *Heptagenia* (CLIFFORD 1966). EDMUNDS (1957) reports *Parameletus columbiae* MCDUNNOUGH to have a summer cycle in a high elevation lake of Utah, but this region would have a subarctic-like climate. For the marine mesothermal climates of England and the western side of the Cordillera of North America, there are few summer species (MACAN 1957, LEHMKUHL 1969). In short, for the moderate temperate regions, mayfly life cycles are seasonally modified from those of the tropics, and the fauna can be characterized as having mainly non-overlapping generations consisting of winter species with growth in the winter; and, in contrast to the tropics and the humid maritime climates, summer species are more abundant.

In the cold temperature and subarctic regions of North America, lying on the continental side of the Cordillera (e.g. above latitude 42° and to the tree line) and in which the mayfly fauna of Alberta belongs, there is a tendency for the winter species with growth in the winter to give way to winter species without growth in the winter. There are fewer species with multivoltine life cycles, but species with summer cycles become increasingly more numerous. Farther north above the tree line in the low and high arctic, the mayfly fauna, as is true of almost all groups of insects, is poorly represented. Two of the most northerly species of mayflies of continental North America are *Baetis foemina* MCDUNNOUGH and *B. lapponica* BENGTSSON, both occurring above the tree line in the low arctic. Little is known of their life cycles in North America. Photoperiodic control of the seasonal cycles might be lacking, since by the time of snowmelt and break-up of ice, the sun is or will be shortly continuously above the horizon (DOWNES 1964). *B. foemina* is believed to be parthenogenetic, no males having been found (MCDUNNOUGH 1936). *B. lapponica* is circumpolar and ULFSTRAND (1968) reports it to be a summer species in Swedish Lapland.

What is the nature of summer cycles in the cold-temperate and subarctic regions of Alberta? Casually at least, these cycles can be related to temperature. In the foothills stream, *Epeorus longimanus* and *Ephemerella coloradensis*, although considered winter species with no growth in winter, over-winter as fairly small nymphs. These two species emerge later than any of the other A3 species (Table 1). The summer species, with the exception of *Siphlonurus alternatus*, generally emerge later than the winter species. A slight change in the mean water temperature during the short open-season would probably alter these life cycle patterns. For example a slightly lower mean water temperature in the latter part of the open season, as would occur farther north, could conceivably push *E. longimanus* and *E. coloradensis* into summer cycles. Alternately, higher water temperatures in the latter part of the open season might allow the eggs of some of the summer species to hatch and the nymphs to grow to a size where they would be considered winter species. It is likely that many of the summer species of the Alberta region are faculative summer species, originating from winter species without growth in the winter, their summer cycle being an adaptation to the long winter and consequently short growing season.

The reasons for a particular life cycle pattern are complex, and one must use the utmost caution in relating a few enrivonmental factors to life cycle modifications. However it does seem that, speaking in broad general terms, temperature, independently or along with photoperiod, has influenced mayfly life cycle patterns in a predictable way. Going from the equator to the arctic we have a mayfly fauna changing along the following lines in regards to life cycle patterns : species with multivoltine cycles (tropics), to species having one-year cycles with growth during most of the year (moderate-temperate regions), to species having one-year cycles with most of the growth restricted to a short period of the year (cold temperate and subarctic regions), and finally to one-year cycles with hatching, growth, and emergence restricted to a very short part of the year (arctic). Possibly when more information is available for the few arctic mayfly species two-year cycles will be of importance.

This does not mean that the basic, or original, mayfly life cycle pattern was one of multiple generations in a year. ILLIES (1968) hypothesized that the Ephemeroptera, like the Plecoptera, originated as cold-stenothermal animals in the Amphinotic region and crossed the equator at a climatologically favorable time, e.g. a Permian glacial period. If we assume that the Ephemeroptera at least originated in the Southern Hemisphere, then a one-year cycle, possibly similar to winter species with growth throughout the year, would seem to be closer to the basic pattern. Also it was the events of the Pleistocene Ice Age that have influenced the life cycle patterns of most of the extant species. Visualizing then the winter species with growth throughout the year as a central sphere, on the one side there would be a branch culminating in the multivoltine patterns to the south, and on the other side a branch ending in the summer cycles to the north.

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RÉSUMÉ

Les cycles de vie des Éphéméroptères de quelques rivières de l'Alberta, Canada

Les 16 espèces d'éphémères de certaines rivières de l'Alberta ne présentent qu'une génération par an (Tableau 1). Dix d'entre elles sont des espèces d'hiver mais sans croissance en hiver (A3) et six sont des espèces d'été, leur éclosion, leur croissance et leur émergence se faisant pendant une période relativement courte au cours de la saison sans gel (A2). Un type

de cycle possible pour une 17e espèce est également décrit (A2 et A3). Dans la région étudiée il n'a pas été trouvé d'espèces d'hiver avec croissance en hiver ni d'espèces à générations multiples. Les différents cycles de vie sont comparés avec ceux des éphémères d'autres régions (Tableau 2) et les cycles de vie typiques de diverses régions climatiques sont discutés. Il y a un nombre relativement grand d'espèces d'été dans la faune de l'Alberta et cela semble indiquer que beaucoup d'entre elles sont des espèces d'été facultatives s'adaptant ainsi à la courte saison sans gel.

Zusammenfassung

Lebenskreisläufe der Eintagsfliegen (Ephemeroptera) in einigen Strömen von Alberta, Kanada

Von 16 Eintagsfliegenarten der Flüsse von Alberta hatten alle eine Generation pro Jahr (Tabelle 1). Zehn Arten waren Winterarten aber ohne Wachstum im Winter (A3), sechs waren Sommerarten, welche während einer verhältnismässig kurzen Zeit in der eisfreien Saison ausgebrütet, gewachsen und ausgeschlüpft sind (A2). Der mögliche Lebenskreislauf einer siebzehnten Art ist auch diskutiert (A2 & A3). Es waren weder Winterarten mit Wachstum während des Winters noch multivoltine Arten in der beobachteten Grundfläche. Die Lebenskreisläufe sind mit Eintagsfliegen von anderen Regionen verglichen (Tabelle 2), und allgemeine Lebensläufe von verschiedenen klimatischen Gegenden sind besprochen. Es gibt eine verhältnismässig grosse Anzahl von Sommerarten in der Fauna von Alberta, und es ist vorgeschlagen, dass viele von diesen fakultative Sommerarten sind, welche sich auf diese Weise an die kurze eisfreie Zeit anpassen.

Discussion

K. Wood : Those of us who must work in polluted streams might wonder why you want to pour oil on one of your fine habitats. I think it seems obvious that this would kill the fauna. Why would you want to do this to one of your very fine Alberta streams ?

H. Clifford : We have, as I mentioned, thousands of this type stream in Alberta and other parts of northern Canada, and we want to find out what happens when oil enters the stream. As you are aware, there is the possibility of a large pipe line extending from Alaska through Alberta into the United States, and we would like to know what is going to happen if we have a large oil spill. This is the most logical way to go about this — rather than waiting until the oil is accidentally introduced into the streams. We want preliminary information.

J. Leonard : I am very interested in the fact that you only have single year cycles. Have you had the opportunity to look at some of the other orders ? How about some of the dragonflies — those that often live three or four years in the nymphal stage in the north ?

H. Clifford : I can't tell you about the dragonflies. For stoneflies we have three or four species with two-year or perhaps three-year cycles.

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