

Observations on the Life Histories and Biology of Ephemeroptera and Plecoptera in Northeastern Alberta

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ABSTRACT

During studies of the environmental effects of oil sands development in northeastern Alberta in 1976-1977, 36 species of Ephemeroptera and 21 of Plecoptera were collected using various techniques. Individuals of 18 mayflies and 17 stoneflies were taken in numbers sufficient to determine their basic life histories and habitat preferences. Among the mayflies, 8 (possibly 10) species exhibited fast seasonal development, 8 slow seasonal, and 2 non-seasonal. Among the Plecoptera, these patterns were exhibited by 5, 7 and 5 species, respectively. Nymphs of most fast seasonal mayflies developed in pools and silty backwaters, often in association with aquatic macrophytes. Slow seasonal mayflies and most stoneflies were found in riffles, or on bedrock and debris in the Athabasca River. The fauna included a mixture of Eastern, northern and cordilleran species. Eastern species probably reached the Athabasca River drainage via glacial Lake Agassiz.

INTRODUCTION

Prediction and assessment of the environmental effects of man's activities require a knowledge of the biology of the organisms likely to be affected. One aspect of the necessary information is the pattern of development, or life history, of the species and such data are rapidly accumulating from many areas of North America (e.g. Clifford, 1976; Coleman & Hynes, 1970; Hall et al., 1975; Lemkuhl, 1972). These studies indicate that while some species exhibit very similar life histories throughout their geographic ranges, others are capable of considerable variation in response to regional or local conditions (Hynes, 1976; Edmunds et al., 1976; Flannagan, 1979).

This paper presents observations on the life cycles of lotic Ephemeroptera and Plecoptera from northeastern Alberta. The area is of special interest because of its rather remote northern location, the occurrence of a mixture of cordilleran and plains (or eastern) species in the Athabasca River and its tributaries, and the expected rapid development of oil sands mining and related activities. This study was part of a wider investigation of aquatic resources

conducted within the Alberta Oil Sands Environmental Research Program, and is intended to describe the general life history patterns of the more common mayflies and stoneflies in the area.

THE STUDY AREA

Lotic habitats near Ft. McMurray, Alberta ($57^{\circ} 02'N$, $111^{\circ} 30'W$), range from small temporary streams which freeze completely in winter and may dry up in summer, to the Athabasca River whose discharge averages about $200 \text{ m}^3 \text{ sec}^{-1}$ in winter and often exceeds $2000 \text{ m}^3 \text{ sec}^{-1}$ in summer. The climate is subarctic; the ice-free season extends from late April to early November. Water temperatures are near 0° during winter but rise rapidly to $12^{\circ} - 16^{\circ}$ within two weeks of ice breakup and remain between 16° and 20° until late August. The underlying bedrock is principally Devonian limestone so tributary streams are generally alkaline despite the dark brown color imparted by humic and fulvic substances.

Most of the data presented here were obtained from the Muskeg and Steepbank Rivers. Ranges of selected water quality parameters in these streams in 1977 were: pH = 7.5 to 8.5; conductivity = 100 to $400 \mu\Omega \text{ cm}^{-1}$; silica = 3 to 15 mg l^{-1} , dissolved organic carbon = 10 to 30 mg l^{-1} , organic nitrogen = 0.5 to 1.8 mg l^{-1} ; total organic phosphorus = up to 0.15 mg l^{-1} . Most of the Muskeg River flows through flat, muskeg terrain (gradient = 1.1 m km^{-1}) before dropping 38 m in its last 11 km. The Steepbank River originates in muskeg but has a gradient of 2.4 m km^{-1} for most of its length, increasing to 5.7 m km^{-1} in the lower 20 km. Stream beds in muskeg reaches are mostly silty sand and mud with nearly vertical banks of sphagnum and willow roots. Where gradients are steeper, streams consist of alternating riffles and pools with substrates of glacial gravel and boulders in the upper portions of the watersheds and limestone rubble in the lower reaches. Much of the streambed in the lower 20 km of the Steepbank consists of exposed oil sand (Barton & Wallace 1979).

The dominant terrestrial vegetation is more or less discrete stands of black spruce (*Picea marina*), aspen (*Populus tremuloides*), tamarack (*Larix* sp.) and willow (*Salix* sp.) according to local differences in drainage.

MATERIAL AND METHODS

Much of the material for life history analyses was taken from random "kick" samples using a net with $500 \mu\text{m}$ mesh. The collecting effort was most intensive at sites on the lower Muskeg and Steepbank Rivers and the adjacent reaches of the Athabasca River. The tributary sites were visited approximately weekly during the open-water periods between June 1976 and November 1977. Collections were made from all accessible habitats on each visit, e.g. riffles, pools, margins, macrophyte beds, etc. Winter sampling (January 1977) was confined to holes cut through the ice near midstream in riffles. The Athabasca River was sampled at least monthly from May through October 1977 (Barton, *in press*), other sites and streams irregularly.

Large mayfly and stonefly nymphs were sorted into 70% ethanol in the field and additional bulk collections of animals and debris were stored in 10% formalin for later sorting of smaller specimens under a dissecting microscope. Mature nymphs of most species were returned to the laboratory for rearing. Adults were collected in the field by hand, sweepnet and, occasionally, light trap.

Many specimens, especially very small ones, were collected during the course of various field studies and experiments conducted during the same time period. These studies involved the use of Surber samplers, Ekman grabs, airlifts, driftnets and artificial substrates, and samples were concentrated through 100 or 200 μm mesh (Barton & Wallace, 1978).

Species determinations were based upon adults or, for certain well-known groups, mature nymphs. Total body length (exclusive of cerci) was measured to the nearest 0.5 mm under a dissecting microscope with a micrometer. Material from all sites and studies in both years was combined by week of the month. Thus the life cycles illustrated below do not represent any single population but rather the general pattern in the area. Flight periods were estimated from field collections of adults or mature nymphs with darkened wingpads.

RESULTS AND DISCUSSION

Ephemeroptera

The 36 mayflies listed in Table 1 do not constitute a complete list for the oil sands area, but probably include all of the common, and many rare, lotic genera and species. Among the genera for which no species are listed, *Baetis* and *Heptagenia* were each represented by at least 3 species but further study is needed to separate the nymphal stages. Individuals of both genera were abundant in the streams studied. It is likely that some of the local species of *Baetis* are multivoltine.

Eighteen species were collected in sufficient numbers to allow analysis of their developmental patterns or comparison with published life histories. Most would be considered fast or slow seasonal (Hynes 1979), but two, *Ephemera simulans* and *Hexagenia* sp., might be non-seasonal or semi-voltine. In southern Ontario, *E. simulans* requires 2 yr to complete development (Coleman & Hynes, 1970; Barton, 1976), while two *Hexagenia* species in Lake Winnipeg emerge 14, 22 or 24 mo. after eggs are laid (Flannagan, 1979).

Fast seasonal, or summer, species include *Anaetris eximia*, *Callibaetis coloradensis*, *Cloeon* sp., *Paraleptophlebia* sp. (fig. 1), *Tricorythodes minutus*, *Brachycercus* sp. (fig. 1), at least 2 species of *Heptagenia* and, perhaps, *Siphonurus alternatus* and *Meiretopus borealis*. They overwinter as eggs, hatch in May or early June, and then develop rapidly to emerge in July or early August. With the exception of *Anaetris*, *Paraleptophlebia* and *Heptagenia*, the preferred habitat of mature nymphs was quiet backwaters with abundant vegetation and organic debris. *Anaetris* was found only on sand in the Athabasca River and its life history there appeared to be similar to that of the

Table 1. Ephemeroptera collected from streams in the area of the Athabasca oil sands, 1976-1977. F = fast seasonal, S = slow seasonal, N = non seasonal, ? = not determined, A = Athabasca River, T = major tributary streams, B = small, cold brooks.

	Type of Development	Distribution
<i>Ameletus</i> sp.	S	T
<i>Parameletus</i> sp.	?	B
<i>Siphonurus alternatus</i> (Say)	F	T
<i>Analetris eximia</i> Edmunds	F	A
<i>Isonychia</i> sp.	?	T
<i>Metretopus borealis</i> Eaton	F	T
<i>Siphloplecton basale</i> (Walker)	S	T
<i>Ametropus neavei</i> McDunnough	S	A
<i>Baetis</i> spp.	?	A,T
<i>Callibaetis coloradensis</i> Banks	F	T
<i>Centroptilum</i> sp.	?	T
<i>Cloeon</i> sp.	F	T
<i>C. implicatum</i> McDunnough	F	A
<i>Pseudocloeon</i> sp.	?	T
<i>Epeorus</i> cf. <i>albertae</i> (McDunnough)	?	A
<i>Heptagenia</i> spp.	F,?S	A,T
<i>Rhithrogena</i> sp.	?F	A,T
<i>Stenacron interpunctatum</i> (Say)	S	T
<i>Stenonema vicarium</i> (Walker)	S	T
<i>Pseudiron</i> sp.	?	A
<i>Leptophlebia cupida</i> (Say)	S	A,T
<i>L. nebulosa</i> (Walker)	S	A,T
<i>Paraleptophlebia</i> sp.	F	A,T
<i>Ephemerella margarita</i> Needham	?	T
<i>E. simplex</i> McDunnough	?	T
<i>E. spinifera</i> Needham	S	T
<i>E. aurivilli</i> Bengtsson	?	T
<i>E. inermis</i> Eaton	S	A,T
<i>E. tibialis</i> McDunnough	?	T
<i>Tricorythodes minutus</i> Traver	F	A,T
<i>Brachycercus</i> sp.	F	T
<i>Caenis</i> spp.	?	A,T
<i>Baetisca</i> cf. <i>columbiana</i> Edmunds	?	T
<i>B. obesa</i> (Say)	?	T
<i>Ephemerella simulans</i> Walker	?N	A,T
<i>Hexagenia</i> sp.	?N	A

population in the Saskatchewan River described by Lehmkuhl (1976). Nymphs of *Paraleptophlebia* and *Heptagenia* were most common in stony riffles of tributary streams.

Adults of *T. minutus* (fig. 1) were collected along the Muskeg River as early as 7 July in 1976 and as late as 25 August in 1977. Nymphs of *Tricorythodes* collected from the Steepbank and Ells Rivers in both years appeared to be morphologically identical to the population in the Muskeg R. from which adult of *T. minutus* were reared. However, the sizes of nymphs from the various localities and the long flight period of the adults suggested that either more than

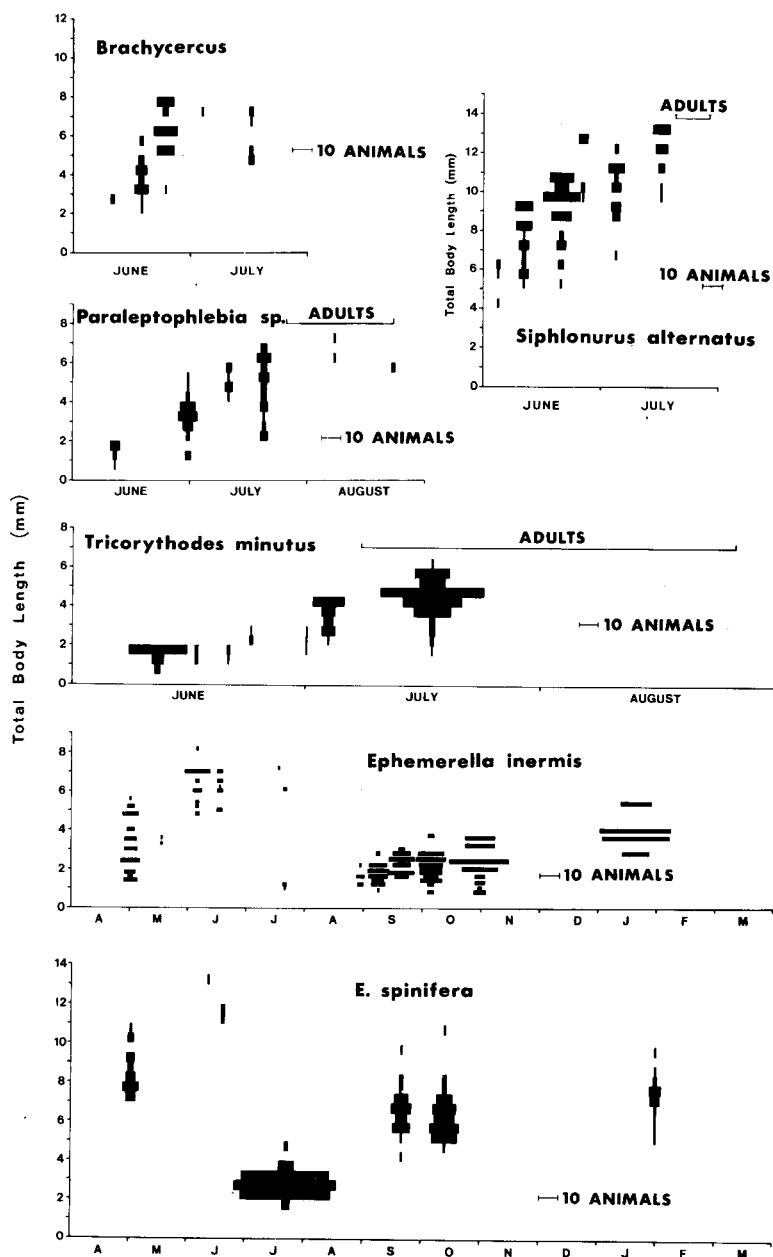


Fig. 1. Growth of *Brachycercus* sp., *Siphonurus alternatus*, *Paraleptophlebia* sp., *Tricorythodes minutus*, *Ephemerella inermis* and *E. spinifera* in the oilsand area of northeastern Alberta. No adults of *Brachycercus* sp. or *Ephemerella* spp. were collected.

one species is present in the area, or the life history of *T. minutus* varies considerably in different rivers.

The other summer species were also collected only in small numbers, usually in weedy areas with little current. Clifford (1969) described *Callibaetis coloradensis* and *Cloeon* sp. as fast seasonal in the Bigorary River and the sizes and timing of the few specimens I collected agreed with his observations.

The life history of *Metretopus borealis* remains in doubt: nymphs 7 mm in length were collected in early June and development was rapid through mid-July. Since the smallest specimens collected were already half-grown (in length), early development seems to take place in inaccessible parts of the stream, perhaps in the hyporrheic, more likely in the deepest pools. Whether growth is slow throughout the winter or very rapid in spring remains to be determined. Mature female nymphs (13 mm long) were 1 - 1.5 mm longer than males. Development of a population in a small cold brook appeared to be about 2 weeks behind that in the warmer Muskeg River. The observed development of *S. alternatus* (fig. 1) was very similar and open to the same alternative interpretations.

The eggs of slow seasonal mayflies hatch shortly after being laid (Hynes, 1970) and the nymphs grow steadily until water temperatures reach low levels in autumn. They grow slowly in winter, then rapidly complete development and emerge in spring. This pattern applies to at least 8 species in the study area: *Ameletus* sp., *Ametropus neavei*, *Leptophlebia cupida*, *Ephemerella inermis*, *E. spinifera*, *Siphloplecton basale*, *Stenacron interpunctatum* and *Stenonema vicarium*.

Detailed study of *Ametropus neavei* (Clifford & Barton, 1979), which was found only in the Athabasca River, indicated that it is a small-particle detritivore with slow seasonal development and an extended emergence period. The life history of *Leptophlebia cupida* in the Muskeg River followed the pattern described by Clifford (1969), including migration into small tributaries as the ice goes out in April (Hayden & Clifford, 1974). Migrating nymphs transferred to the laboratory emerged as typical adults of *L. cupida* as well as a few *L. nebulosa*, thus supporting the suggestion by Clifford et al. (1979) that these may be color variants of the same species.

With the possible exception of *Baetis*, the most abundant mayfly in riffles of the lower Muskeg River and on bedrock in the Athabasca was *Ephemerella inermis*. Although this species is tolerant of silty water (Allen & Edmunds, 1965), it was abundant only in non-depositional areas. *E. inermis* has been reported to be multivoltine in some localities (Allen & Edmunds, 1965) but is univoltine and slow seasonal in southwestern (Hartland-Rowe, 1964) and northeastern Alberta (fig. 1). Adults emerge from early June through late July and there is an extended hatching period from July through October. Growth is slow through autumn and winter, and rapid in May.

Ephemerella spinifera was rarely collected in the Muskeg River but was abundant on moss covered stones in riffles and rapids of the Steepbank. No adults were collected. Emergence probably occurs in June when mature nymphs were taken whose size corresponded to measurements given by Allen &

Edmunds (1962a). Young nymphs were abundant in mid-July and were half-grown by mid-October (fig. 1). There appeared to be little growth in winter.

Several slow seasonal mayflies were found only in small numbers. Young and half-grown nymphs of *Ameletus* sp. were collected in October. Mature female nymphs in very early May were 1.3 mm longer than males. Previously published life histories suggest that other slow seasonal mayflies in the study area include *Siphloplecton basale* (Clifford, 1976), *Stenacron interpunctatum* and *Stenonema vicarium* (Coleman & Hynes, 1970). Nymphs of *S. vicarium* were found only in tributary streams, most often on sticks and logs. The wide range of sizes present in most collections agrees with Coleman & Hynes' (1970) description of a long flight period, short egg incubation and steady growth of the nymphs.

Plecoptera

The 21 species of stoneflies found in the study area (Table 2) also included fast, slow and non-seasonal species. Fast seasonal development in Plecoptera differs from that in Ephemeroptera in that growth occurs mainly in winter or very early spring, most of the summer being spent in diapause at the egg or larval stage (Hynes, 1976). An exception is *Amphinemura linda* which overwinters as diapausing eggs (Harper, 1973). In the oil sands area, adults emerged in mid to late August from small brooks which froze completely in winter. Fast seasonal, winter species include *Oemopteryx fosketti*, *Taeniopteryx nivalis*, *T. parvula*, and *Shipsa rotunda*.

Table 2. Plecoptera collected from streams in the area of the Athabasca oil sands, 1976-1977. Symbols as in Table 1.

	Type of Development	Distribution
<i>Amphinemura linda</i> (Ricker)	F	B
<i>Nemoura arctica</i> Esben-Petersen	F	T
<i>Shipsa rotunda</i> (Claassen)	F	A,T
<i>Zapada cinctipes</i> (Banks)	?	T
<i>Paraleuctra</i> cf. <i>sara</i> Claassen	?	T
<i>Capnia</i> spp.	F	A,T
<i>Oemopteryx fosketti</i> (Ricker)	F	A
<i>Taeniopteryx nivalis</i> (Fitch)	F	T
<i>T. parvula</i> Banks	F	T
<i>Pteronarcella regularis</i> (Hagen)	N	A,T
<i>Pteronarcys dorsata</i> (Say)	N	A,T
<i>Arcynopteryx</i> sp.	S	T
<i>Isogenoides colubrinus</i> (Hagen)	S	A
<i>Isoperla fulva</i> Claassen	?	T
<i>I. fusca</i> Needham & Claassen	S	T
<i>I. longiseta</i> Banks	S	A
<i>I. sordida</i> (Banks)	?	A
<i>Hastaperla brevis</i> (Banks)	S	A,T
<i>Acroneuria abnormis</i> (Newman)	N	A
<i>A. lycorias</i> (Newman)	N	T
<i>Claassenia sabulosa</i> (Banks)	N	T

The pattern of growth of *T. nivalis* (fig. 2) seems to be typical for the genus, differing from that reported from more southerly locations (Harper & Magnin, 1969; Harper & Hynes, 1972) only in that larval diapause is broken about a month earlier and emergence is slightly later. Development of *S. rotunda* also is prolonged over that in southern Ontario (Harper, 1973). There seemed to be fairly rapid growth beginning in August, little in winter and rapid development in very early spring (fig. 2). This species was most common in larger tributary streams such as the Muskeg and Steepbank.

N. arctica was seldom collected, being largely restricted to the smaller, cooler streams draining the Birch Mountains to the northwest. The development of this species is probably slow-seasonal and its peak of emergence appeared to be about two weeks later (20 May - 17 June) than for *S. rotunda*.

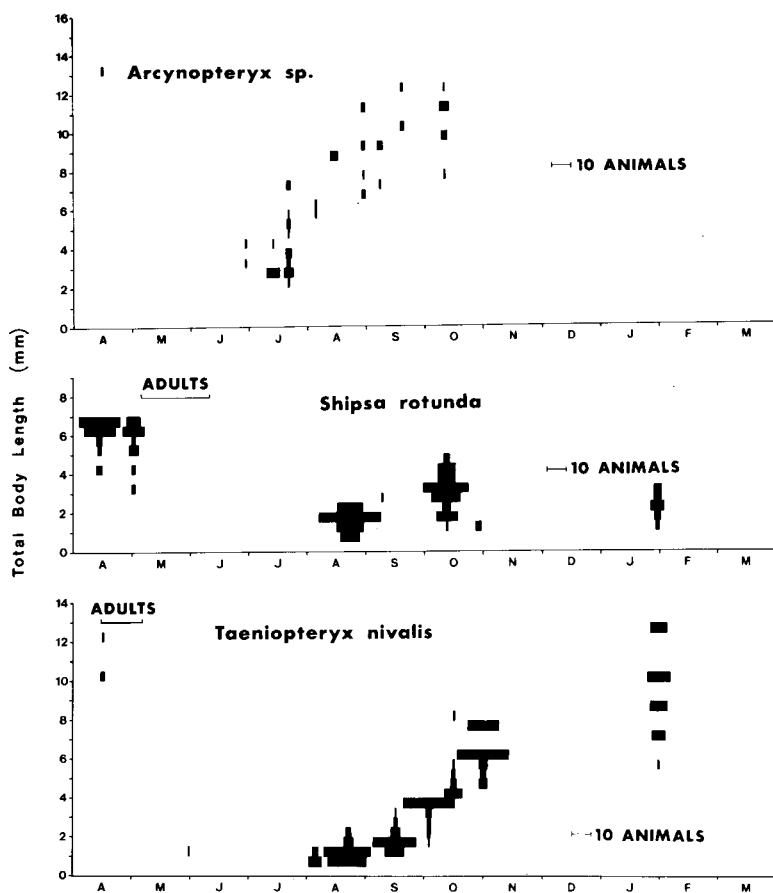


Fig. 2. Growth of *Arcynopteryx* sp., *Shipsa rotunda* and *Taeniopteryx nivalis* in the oilsands area of northeastern Alberta. No adults of *Arcynopteryx* were collected.

Slow seasonal development was also observed in *Capnia* spp., *Arcynopteryx* sp. (fig. 2). *Isogenoides colubrinus*, *Hastaperla brevis*, *Isoperla fusca* and *I. longiseta*.

Both emergence of adults and hatching of eggs were prolonged over several months in *Hastaperla brevis* (fig. 4). Growth was slow through the autumn and winter, and rapid in spring. This represents a substantial departure from the restricted emergence period in late May reported by Harper & Magnin (1969) in Quebec and Neves (1978) in Massachusetts. Harper & Pilon (1970) reported emergence from a Quebec stream only in June and in both Quebec studies young of the next generation were not found until October. The nonsynchronous growth of nymphs in Quebec and in northeastern Alberta were similar. This species was very abundant in riffles of tributary streams and on bedrock in the Athabasca, migrating onto gravel and coarse sand as discharge declined in autumn (Barton, *in press*).

The two abundant species of *Isoperla*, *I. fusca* and *I. longiseta*, were restricted to tributary streams and the Athabasca River respectively, and differed somewhat in their life histories. Adults of *I. fusca* were collected from late May to late June and young nymphs appeared in July (fig. 3). Growth was slow through the following April and rapid in May. The lack of winter collections from the Athabasca hinders the interpretation of the life history of *I. longiseta* but it appeared that eggs hatched either in August, followed by steady growth through the winter, or in late winter and early spring, followed by rapid growth through June and July (fig. 3). Maximum emergence was observed in early June and adults were taken through late August. No change in the size of adults was detected as the summer progressed. The preferred habitat of both species was similar to that of *H. brevis* but mature *I. longiseta* were especially abundant in accumulations of leafy and woody debris in the main current during July. At least some individuals may reach sites for emergence by drifting or swimming rather than by walking across the riverbed. On 21 June 1977, large numbers of mature nymphs were observed walking along the underside of the surface film in the middle of the river. These immediately seized any solid object encountered (floating debris, boats, etc.) and crawled out of the water.

At least four non-seasonal species required three or more years to complete their development: *Pteronarcys dorsata*, *Claassenia sabulosa*, *Acroneuria abnormis* and *A. lycorias*. A fifth species, *Pteronarcella regularis*, probably has a two year life cycle (Gaufin et al., 1972) and was found in small numbers on debris in the Athabasca and beneath undercut banks in the Steepbank. *A. lycorias* was found in riffles and rapids in tributary streams. Adults were reared and collected in the field in mid-June. *A. abnormis* was found on bedrock and debris in the Athabasca River. Both species were collected only in small numbers but their life histories are probably as described elsewhere (Gaufin et al., 1972; Hitchcock, 1974; Flannagan, 1977).

My observations indicated that *P. dorsata* has an egg diapause of 10 to 11 months and a total of three, or in some individuals four, years are required to complete the life cycle (fig. 4), a pattern similar to that described for *A. proteus* (Newman) (Holdsworth, 1941). Adults emerged over a very short period in the

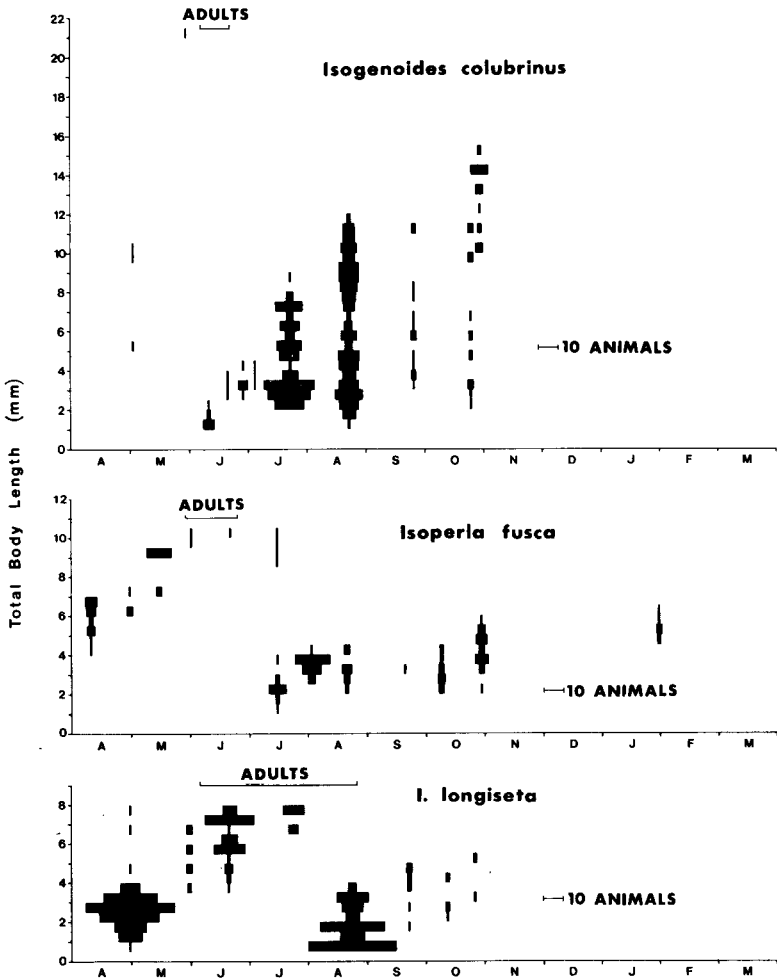


Fig. 3. Growth of *Isogenoides colubrinus*, *Isoperla fusca* and *I. longiseta* in the oil sands area of north-eastern Alberta.

second half of May and young nymphs first appeared in the following April. Growth was fairly uniform and rapid through the second summer but erratic in the third, some nymphs reaching full size 28 months after the eggs were laid, others apparently needing another summer to complete their development. There was little or no growth in winter. Nymphs were most abundant among accumulations of debris (sticks, leaves, etc.) during the summer months and probably play a major role in the secondary processing of allochthonous organic matter (Short & Maslin, 1977). In late summer and early autumn, the

nymphs migrated to the deepest part of riffles and rapids where they remained under large stones throughout the winter.

In all of the above mentioned species there was good agreement among observations made in both 1976 and 1977. This was not the case, however, for *Claassenia sabulosa*. This stonefly was very abundant in riffles in the Muskeg and Steepbank Rivers in 1976 but was virtually absent in 1977. The reason for

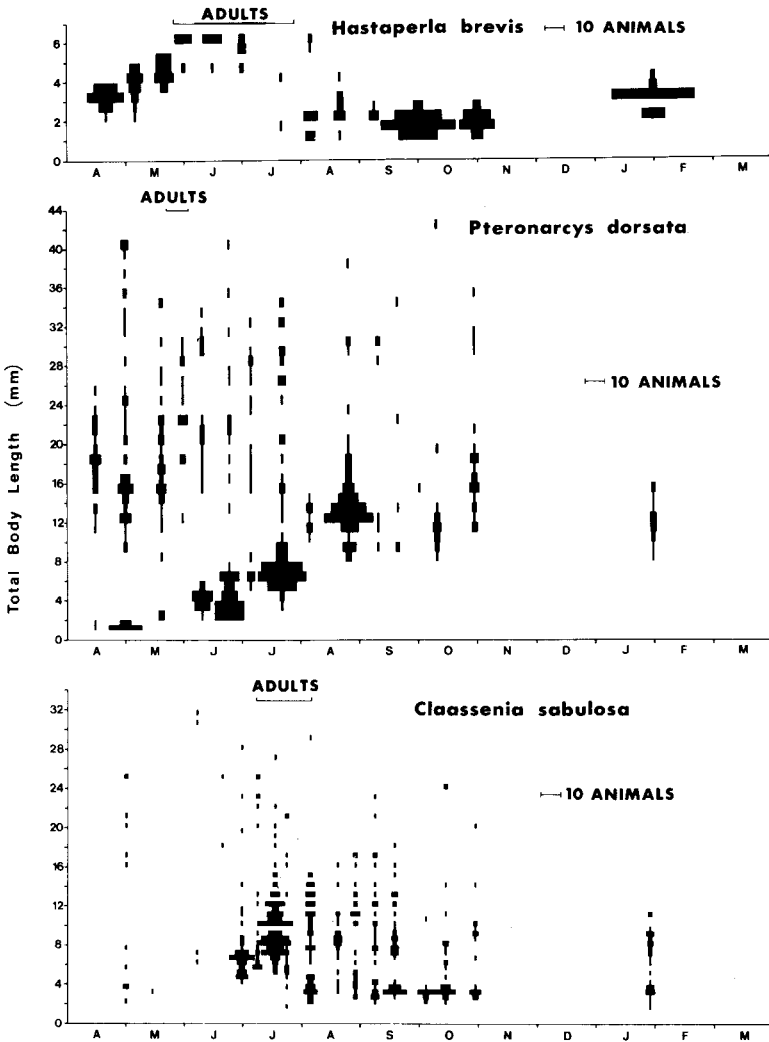


Fig. 4. Growth of *Hastaperla brevis*, *Pteronarcys dorsata* and *Claassenia sabulosa* in the oil sands area of northeastern Alberta.

this disappearance remains a complete mystery. Collections from 1976 (all of the specimens for the period late-June through October) suggested at least a three year life cycle with emergence in June and July (fig. 4). Adults were found under stones within a few metres of the water's edge. Eggs appeared to hatch throughout the year.

The life history of *Isogenoides colubrinus* could not be determined on the basis of the collections summarized in Figure 3. Most emergence probably occurred in May but only 2 adults were caught, on 7 and 21 June 1977. Very young nymphs were collected in June and August and growth seemed to be rapid throughout the year. Flannagan (1977) concluded that this species has a one year life cycle in the Athabasca River upstream of Ft. McMurray, but the bimodality of sizes present in most of my collections and the presence of small nymphs in early May (fig. 3) suggest the possibility of semivoltinism. However, very rapid growth rates have been reported for several large perlodid species (Hynes, 1941; Schwarz, 1970), so the possibility of a 1 yr cycle, with the very wide range of sizes serving to minimize intraspecific competition, cannot be discounted. It is interesting to note that Minshall and Minshall (1966) reported a univoltine cycle for *Cultus decisus* (Walker) in a Kentucky stream and collected nymphs ranging from 3 to 18 mm in length just prior to the onset of adult emergence.

Biogeographical considerations

The Ephemeroptera and Plecoptera of the oil sands area include species whose principal distributions are eastern, western and northern. Among the stoneflies, the first group includes *Capnia vernalis* Newport, *T. nivalis*, *T. parvula* and both species of *Acroneuria* (Hitchcock, 1974; Ricker, 1946; Harper & Hynes, 1971 b, c). Western species include *I. fulva*, *I. fusca*, *I. sordida*, *P. regularis* and *C. sabulosa* (Gaufin et al., 1972; Jewett, 1959). Widespread, essentially northern species include *S. rotunda*, *N. arctica*, *P. sara*, *P. dorsata*, *I. colubrinus*, *I. longiseta* and *H. brevis* (Hitchcock, 1974; Harper & Hynes, 1971a; Jewett, 1959; Gaufin et al., 1972; Ricker, 1946; Ricker & Scudder, 1975; Wiens et al., 1975).

Among the mayflies, most genera and many of the species are known to be distributed throughout northern North America (Edmunds et al., 1976); however a few species are worthy of special mention. Both *E. inermis* and *E. spinifera* are principally western in their distributions (Allen & Edmunds, 1962b, 1965). Among the other species found in the study area, *E. simplex* has previously been reported only as far west as Manitoba, *E. tibialis* is a western species, and disjunct eastern and western populations of *E. aurivilli* and *E. margarita* have been reported (Allen & Edmunds, 1961, 1962a, 1963, 1965).

The genera *Baetisca*, *Stenacron* and *Stenonema* occur mostly in eastern North America. One species, *B. columbiana*, found in the Steepbank and Muskeg Rivers, has previously been recorded only as a single type specimen from the Columbia River, Washington, U.S.A. (Edmunds, 1969). *B. obesa* seems to be widespread in the Mackenzie River drainage (D.M. Rosenberg, pers. comm.). Only one (undescribed) species of *Stenonema* has been recorded west of Ontario (Edmunds et al., 1976).

Since the Athabasca River arises in the Rocky Mountains, it is not surprising that a large number of cordilleran species occur in the oil sands area. Nymphs of principally eastern species, including *A. lycorias*, *E. simplex*, *S. interpunctatum*, *S. vicarium* and *B. obesa*, are known to inhabit both rivers and the wave-washed shores of large lakes (McDunnough, 1933; Edmunds et al., 1976; Barton & Hynes, 1978). Thus it is probable that postglacial dispersal from the Mississippi basin through the Laurentian Great Lakes into Lake Agassiz (Elson, 1967; Lehmkuhl, 1972) enabled these species to reach the Athabasca River.

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