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THE POST-GLACIAL ORIGIN AND PRESENT DISTRIBUTION OF THE MAYFLIES (EPHEMEROPTERA) OF MANITOBA, CANADA

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Abstract. Twenty-nine genera, 77 species of Ephemeroptera are known from Manitoba. These include species distributed to the northwest, east, western mountains and south, as well as species that are distributed transcontinentally. Manitoba was completely covered with ice during the last ice age. As the ice retreated, western glacial waters flowed through southern Saskatchewan directly to the Missouri River system. Three major outlets from glacial Lake Agassiz were also created at various times. One flowed to the south to the Gulf of Mexico; a second flowed northwest from the Clearwater outlet to the Arctic Ocean via the Mackenzie River system, and was for a short time contemporary with the southern outlet; while the third, to the east, was present in several phases, ultimately draining via the St. Lawrence to the Atlantic. There is no longer a connection between the Churchill and Lake Winnipeg - Nelson River systems and the Mississippi-Missouri, the St. Lawrence or the Mackenzie drainage basin. Since dispersal of aquatic insects has been suggested to occur mainly by water, these post-glacial waterways are the likely migration routes for many aquatic insects present in Manitoba today. The North American distribution and probable aquatic migration routes of Manitoban mayflies are presented.

Glacial History, Lake Agassiz, Migration routes

The information presented here is an extract of a report by Flannagan and Flannagan (1982) on the Ephemeroptera, Plecoptera and Trichoptera of Manitoba. The original publication had a limited distribution, therefore, the mayfly section is reproduced here.

During the last glaciation Manitoba was completely covered with ice, eliminating the existing flora and fauna (Longwell et al. 1969, Elson 1967, Flint 1971, Pielou 1979 and others). Thus, the present aquatic insect fauna is totally composed of immigrants.

Hynes (1970) stated that no animal could occur in areas where it had not gained access for some historical reason. For aquatic insects, two types of migration are possible - by air or water. Aerial recolonization or dispersal of aquatic insect adults appears to be limited to highly developed flying species (Milne 1943, Ross 1944, Edmunds 1972, Hitchcock 1974, Cobb and Flannagan 1980, and others). These species are usually transcontinental in distribution and therefore of limited value in zoogeographic studies. Areas that are not, and were not directly connected with Manitoba's waterways, can only be recolonized by these adult stages. For the remaining species, dispersal in the immature stages (i.e. aquatic dispersal) is the most likely. Ide (1955), Ricker (1964 a, b), Ross et al. (1967), Lehmkuhl (1972, 1976a, 1980), Larson (1975), Soponis (1977), Flannagan (1978) and Scudder (1979) among others discussed the concept of aquatic dispersal of the immatures of aquatic insects, and suggested that the present day watersheds represent effective barriers to further migration of many aquatic species.

At the end of the last glacial period, population pools of aquatic animals existed in the various glacial refugia of Canada, i.e. Queen Charlotte Islands, parts of the Yukon and Alaska, Banks Island, East Baffin Island, Bylot and N.E. Ellesmere Islands, the Cypress Hills, parts of the Maritime provinces and Labrador (Matthews 1979). Another population pool existed in the unglaciated area south of the ice. The drainage patterns existing at the time the Wisconsin ice sheet was retreating provided migration routes.

This paper presents cited distributions of the mayflies (Ephemeroptera) for the province. It will also attempt to demonstrate, by examination of the continental distribution of the Manitoban species compared with the present and immediate post-glacial direct water connections between Manitoban watersheds and neighboring drainage basins (connections which do not now exist), that the extant distribution of the Ephemeroptera in Manitoba is largely a function of the direct post-glacial water connections which existed as immigration routes.

GLACIAL HISTORY

The Quaternary period began about 2×10^6 years B.P., and is divided into two epochs, the Pleistocene (up to 10^4 years B.P.) and the Holocene (10^4 years B.P. to present) (Longwell et al. 1969; Flint 1971). The Pleistocene consisted of a preglacial time followed by the "ice age", lasting about 0.5×10^6 years, in which ice masses oscillated at least four times producing 4 glacial stages each separated by an interglacial

Fig. 1. Maximum Wisconsin glaciation

stage (Pielou 1979). The last glacial stage, the Wisconsinan (Fig. 1) (called the Würm in Europe) started retreating about 12 - 15 x 10^3 B.P. As the glacier retreated various water impoundments were created, the largest of these and the most significant to Manitoba was glacial Lake Agassiz (Flint 1971).

All the stages of Lake Agassiz together are estimated to have covered a total area of 521,000 km^2, the maximum area covered by water at any one time being 208,000 km^2 (Elson 1967; Teller 1976), This area included parts of Saskatchewan, Ontario, Minnesota and the Dakotas, as well as all but the far north of Manitoba. The Lake is considered to have existed from about 15,500 - 14,000 B.P. to about 10,000 B.P. (Christiansen 1979); pre 13,500 - after 8,700 B.P. (Teller 1976); 12,500 - 7,500 B.P. (Flint 1971). The discrepancies in these and other papers concern the timing, not the basic sequence of events in Lake Agassiz. There is general agreement that, at various times in the past, Manitoba waterways, through Lake Agassiz, were directly connected to their neighboring drainage basins.

LAKE AGASSIZ

During the late Wisconsinan, before Lake Agassiz was formed, melt-water from the Rocky Mountains was diverted from the ice-blocked channels of the Saskatchewan system south to the Missouri system (Fig. 2a) (Teller 1976; Christiansen 1979). Later, with the ice readvancing into North Dakota and Minnesota, glacial waters were impounded forming a lake which existed at a higher elevation than Lake Agassiz (Teller 1976). It was when these waters lowered to the Herman level, as the ice retreated upslope towards the Red River valley, that glacial Lake Agassiz

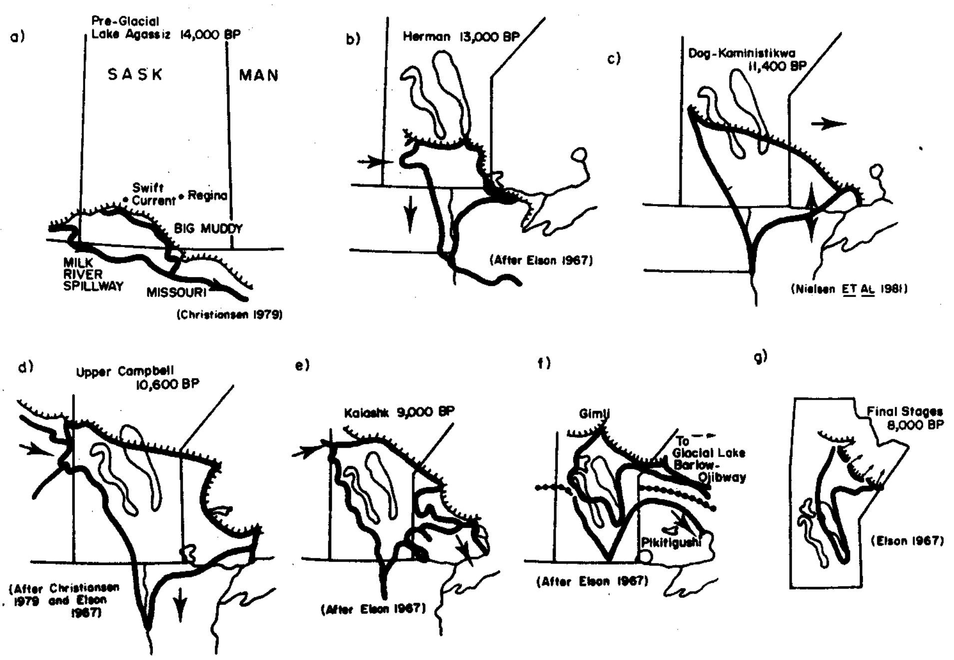

Fig. 2. Some phases of glacial Lake Agassiz

is considered, by historical precedent, to have begun (Fig. 2b) (Teller 1976). During this phase, the Herman, the Lake level was at its highest elevation and the Lake drained south into the Mississippi River system (Elson 1967). As the glacier retreated further, the Lake expanded to include melt-water from the Duck and Riding Mountains of Manitoba, drainage from the Saskatchewan system and from various ice-margin lakes via the Assiniboine spillway (Elson 1967; Christiansen 1979).

About 11,600 B.P., the ice retreated from northern Ontario and the Lake could drain out through the lower elevation outlets to the east and into Lake Superior via the Dog-Kaministikwa Spillway (Nielsen et al. 1981). This resulted in a low water period for the Lake (Fig. 2c).

At the 10,600 B.P., the Ontario ice readvanced, blocking the eastern outlets and causing water levels in Lake Agassiz to rise, stabilizing at the Upper Campbell level (Fig. 2d) and once again draining south. According to Christiansen (1979), during this second southward drainage phase, a slight readvance of the ice in Saskatchewan diverted the Athabasca River (Mackenzie River system) from glacial Lake McConnell (the precursor

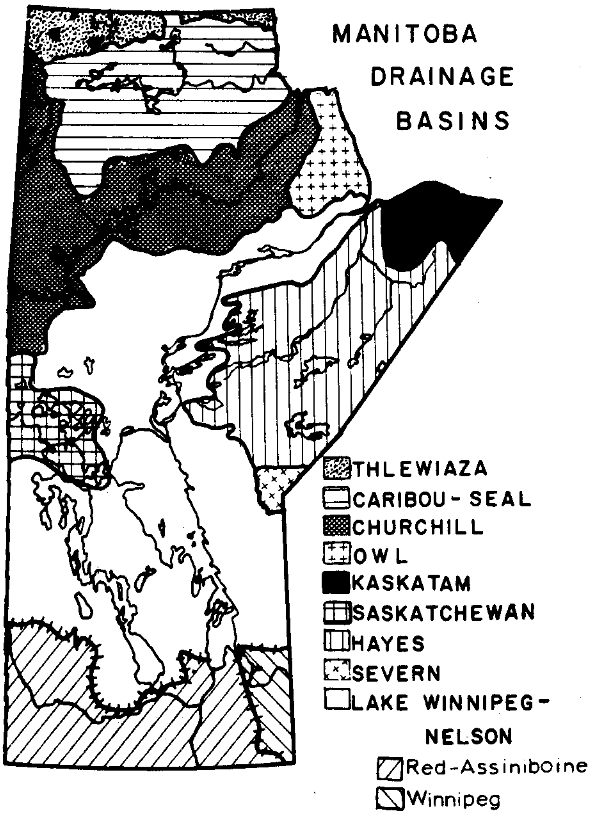

Fig. 3. Manitoba principal drainage divisions from / Manitoba Dept. Mines and Nat. Res. watershed division map, 1969.

of Athabasca, Great Slave and Great Bear Lakes) into Lake Agassiz through the Clearwater and Churchill Spillways. Elson (1967) suggested that Lake Agassiz drained, in the opposite direction, through the Clearwater outlet to the Mackenzie system at this time. For the purposes of this paper, however, the direction of the link is not important, only its existence.

A number of advances and retreats of the eastern ice followed (Elson 1967; Zoltai 1967) resulting in southward and eastward drainages. Eastward drainage during these periods included connection with Lake Superior also via Lake Nipigon (Fig. 2e), and to glacial Lake Barlow-Ojibway (Fig. 2f) via a spillway north of Lake Nipigon (Elson 1967).

About 8,000 B.P. the ice retreated even further downslope (Fig. 2g) ending with the present northeast drainage into Hudson Bay (Fig. 3). This drained the Lake except for remnants such as Lake Winnipeg, Lake Winnipegosis, Lake Manitoba and Cedar Lake. Figure 4a shows the present direction of water flow in North America.

Thus, water routes were often available as colonization routes for immature stages of aquatic insects into Manitoba, from the Mississippi-Missouri system to the South; from the Rocky Mountains to the west (still partly open via the Saskatchewan River system); from the St. Lawrence, and Northern

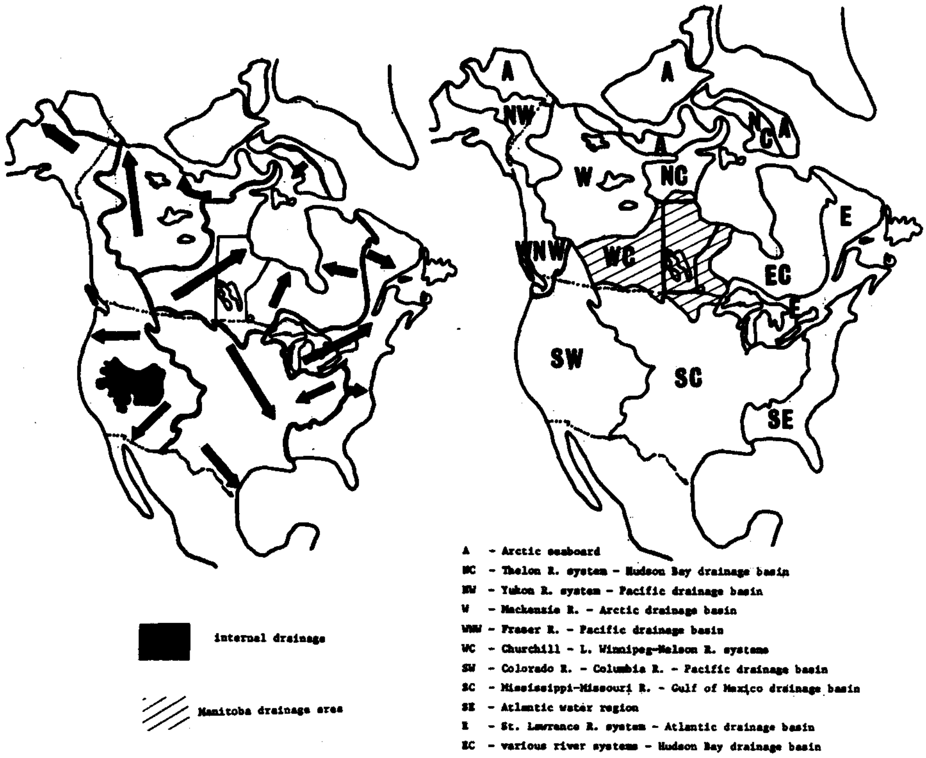

Fig. 4. Modern drainage areas of North America /from National Atlas of Canada 1974 and U.S.W.R.S. 1978/. a/ - direction of water flow. b/ - corresponding geographic subdivisions used in Table 1.

Ontario, Hudson Bay drainage systems to the East and Northeast, and from the Mackenzie basin to the Northwest.

PRESENT NORTH AMERICAN DISTRIBUTION AND MIGRATION PATTERNS

In addition to compiling cited distributions of mayflies, some specimens from the authors' collections at the Freshwater Institute and the Provincial Fisheries Branch were identified and incorporated into Table 1. Geographic divisions corresponding to appropriate North American major drainage basins (Fig. 4b) were used in the tables. For the purposes of this paper, aquatic insects distributed within Manitoba and "SC" are considered southern; "W" abd "NW" as northwestern; "SW" and "WNW" as western montane; "E", "EC" and "SE" as eastern and "A" and "NC" as northern.

Table 1 lists the 29 genera and 77 separate species of mayfly recorded from Manitoba and their North American distri-

Table 1. The Ephemeroptera of Manitoba

Species list	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	Manitoban Distribution
	North American Distribution											
F. Siphlonuridae												
Isonychia Eaton												
I. cf bicolor /Walker/	-	-	-	-	-	-	X	-	X	X	X	Roseau R. /13/
I. harperi Traver	-	-	-	-	-	-	-	-	-	X	X	Roseau R. /13/
I. rufa McDunnough	-	-	-	-	-	-	X	-	-	-	X	Roseau R. /13/
I. sicca Walsh	-	-	-	-	X	X	X	-	-	X	?	Aweme, Treesbank /6/
Parameletus Bengtsson												
P. midas McDunnough	-	-	-	-	-	-	-	-	-	X	-	Churchill /15/
Siphlonurus Eaton												
S. alternatus /Say/	-	-	-	X	-	X	X	-	X	X	X	Pigeon R. /28/; Snow L./30/
S. phyllis McDunnough	-	-	-	X	-	X	-	-	-	X	-	Douglas /6/
F. Metretopodidae												
Metretopus Eaton												
M. borealis Eaton	-	-	X	X	-	X	?	X	X	X	X	Churchill /8/
Siphloplecton Clemens												
S. basale /Walker/	-	-	-	X	-	-	X	-	X	X	X	Lockport, Manigotogan R., Pigeon R., L. Winnipeg /28/
S. interlineatum /Walsh/	-	-	-	X	-	X	X	-	-	-	-	Aweme /23/, Assiniboine R. 1 mi. upstream from Winnipeg /3/
F. Baetidae												
Baetis Leach												
B. brunneicolor McDunnough	-	-	-	-	-	-	X	-	X	X	X	Churchill /15, 27/
B. dardanus McDunnough	-	-	-	-	-	-	-	-	-	X	-	Aweme /22/

	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	
B. flavistriga McDunnough	X	-	-	-	-	-	X	X	X	X	X	Churchill /27/; Clear L. /20/; as B. cingulatus and B. phoebus in Scott Ck., McKinnon Ck. /8/
B. hageni Eaton	X	-	-	-	X	X	X	X	-	X	-	Rat R. /14/
B. harti McDunnough	-	-	-	-	-	-	X	-	-	-	-	Roseau R. /13/
B. hudsonicus Ide	-	-	-	-	-	-	-	-	-	-	-	Churchill /27/
B. intercalaris McDunnough	-	-	-	-	-	-	X	-	-	X	X	Aweme /6, 27/; Rat R. /14/; Roseau R. /13/
B. macani bundyae Lehmkuhl	-	-	-	X	-	-	-	X	X	X	-	Churchill /15/
B. propinquus /Walsh/	-	-	X	-	-	-	X	-	X	X	X	Aweme, Darlingford /24/; Roseau R. /13/ as B. spin-osus
B. pygmaeus /Hagen/	-	-	-	-	-	-	X	X	X	X	X	Churchill /15/; Roseau R. /13/
B. tricaudatus Dodds	-	-	X	X	X	X	X	-	X	X	X	McKinnon Ck., Scott Ck. /9/ as B. vagans
Callibaetis Eaton												
C. americanus Banks	-	-	-	-	X	-	X	-	-	X	X	Aweme /6/
C. ferrugineus /Walsh/	-	-	-	-	-	-	X	-	X	X	X	Husavick, Pigeon R., Red R., Riverton /28/
C. pallidus Banks	-	-	-	-	-	X	X	-	-	-	-	Aweme /6/
C. semicostatus Banks	-	-	-	-	-	-	X	-	-	-	-	Stoney Mt., Teulon /6/
Centroptilum Eaton												
C. infrequens McDunnough	-	-	-	-	-	X	-	-	-	-	-	Winnipeg /6/; Winnipeg Beach /23/
C. quaesitum McDunnough	-	-	-	-	-	X	X	-	-	-	-	Gull Bay, Warren's Landing /28/
C. rufostrigatum McDunnough	-	-	-	-	-	-	X	-	X	X	?	Aweme /6, 23/; Darlingford /6/; Roseau R. /13/; Treesbank /23/
Cloeon Leach												
C. inanum McDunnough	-	-	-	-	-	-	X	-	-	-	-	Churchill /15/

	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	
C. ingens McDunnough	–	–	–	–	or ? SC	X	–	–	–	X	X	Douglas /6/
C. rubropictum McDunnough	–	–	–	–	–	–	X	–	X	X	–	Roseau R. /13/
Pseudocloeon Klapalek												
P. dubium /Walsh/	–	–	–	–	–	–	X	–	–	X	X	Aweme /6/; Roseau R. /13/
P. cf dubium												Churchill /15/
P. myrsum /Burks/	–	–	–	–	–	–	X	–	–	–	–	Rat R. /14/; Scott Ck. /9/
P. parvulum /McDunnough/	–	–	–	?	or	?	X	–	X	X	X	McKinnon Ck. /9/
P. punctiventris McDunnough	–	–	–	–	–	–	X	–	–	X	X	Roseau R. /13/
F. Heptageniidae												
Epeorus Eaton												
E. /Iron/ vitreus /Walker/	–	–	–	–	–	–	X	–	X	X	?	Roseau R. /13/
Heptagenia Walsh												
H. aphrodite McDunnough	–	–	–	–	–	–	X	–	–	X	X	Scott Ck. /9/
H. cruentata Walsh	–	–	–	–	–	–	X	–	–	?	–	Aweme /6, 23/ as H. rever-salis
H. elegantula /Eaton/	–	–	–	–	X	X	X	–	–	–	–	Aweme, Treesbank /6/; Winnipeg /7/
H. flavescens /Walsh/	–	–	–	X	– or	? NC	X	–	–	–	X	Aweme /6/; Roseau R. /13/
H. hebe McDunnough	–	–	–	X	–	?	X	–	X	X	X	Aweme /6/, Husavick /6,28/; Gimli /28/, Roseau R./13/
H. inconspicua McDunnough	–	–	–	–	–	–	X	–	–	–	–	Aweme, Treesbank, Wawanesa /6/
H. jewetti Allen	–	–	–	–	X	–	–	–	–	–	–	Roseau R. /13/
H. maculipennis Walsh	–	–	–	X	–	–	X	–	–	X	X	Aweme /6, 23/; Rat R. /14/; Treesbank /6/
H. pulla /Clemens/	–	–	–	X	–	?	–	–	X	X	X	Pigeon R., L. Winnipeg /28/
H. umbratica McDunnough	–	–	–	–	–	–	X	–	–	X	–	McKinnon Ck., Scott Ck. /9/
Pseudiron McDunnough												
P. centralis McDunnough	–	–	–	–	–	X	X	–	–	–	X	Aweme /25/
Rhithrogena Eaton												
R. pellucida Daggy	–	–	–	–	–	–	X	–	–	X	X	Roseau R. /13/

	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	
Stenacron Jensen												
S. interpunctatum /Say/	-	-	-	X	-	X	X	-	X	X	X	Aweme /6/; Clear L. /20/; Heming L. /12/;Pigeon R. /28/; Rat R. /14/; Roseau R. /13/; Willow Ck - 64 km. N. of Wpg. /21/; L. Winnipeg /28/
Stenonema Traver												
S. femoratum /Say/	-	-	-	X	-	X	X	-	X	X	X	Clear L., Katherine L, Moon L. /20/, Red R. /28/; Scott Ck. /9/; L. Winnipeg /21, 28/ all as S. tripunctatum
S. cf integrum /McDunnough/	-	-	-	-	-	-	X	-	-	X	X	Roseau R. /13/
S. mediopunctatum McDunnough	-	-	-	-	-	-	X	-	-	X	X	Rat R. /14/; Roseau R. /13/, both as S. nepotellum
S. terminatum /Walsh/	-	-	-	-	X	X	X	-	-	X	X	Aweme /2, 6/; Gimli /28/; Roseau R. /13/; as S. bipunctatum-Aweme /2, 6/; Assiniboine R. /21/; George I. - L. Wpg. /28/; Gimli /28, 29/; Grindstone Pt. /28/; Roseau R. /13/
S. vicarium /Walker/	-	-	-	X	-	X	X	-	X	X	X	Churchill /2/; Scott Ck. as S. fuscum /9/
F. Leptophlebiidae												
Leptophlebia Westwood												
L. cupida /Say/	-	-	-	X	-	X	X	-	X	X	X	Aweme /6/; Manigotagan R. /28/; Winnipeg Beach, Winnipeg to mouth of Red R. /28/ - as Blasturus
L. nebulosa /Walker/	-	-	X	X	X	X	X	X	X	-	X	L. Athapapuskow /32/; George I., Grindstone Pt.-L. Wpg. /28/

	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	
Paraleptophlebia Lestage												
P. debilis /Walker/	–	–	–	X	X	?	?	–	X	X	X	Aweme /6/
P. mollis /Eaton/	–	–	–	–	–	–	X	–	X	X	X	Roseau R. /13/
P. praepidita /Eaton/	–	–	–	or ? WC	–	–	X	–	–	X	X	Churchill /15/; Gimli /24/; Rat R. /14/
F. Ephemerellidae												
Dannella Edmunds												
D. simplex /McDunnough/	–	–	–	X	–	?	X	–	–	X	X	Churchill /1/
Ephemerella Walsh												
E. invaria /Walsh/	–	–	–	X	–	–	X	–	X	X	X	McKinnon Ck., Scott Ck./9/
Eurylophella Tiensuu												
E. bicolor /Clemens/	–	–	–	–	–	–	–	–	–	X	–	Pigeon R. /28/ as Ephemerella
E. temporalis /McDunnough/	–	–	–	?	–	–	X	–	X	X	X	Heming L. /12/; McKinnon Ck. /9/; Winnipeg R. /19/ – all as Ephemerella
F. Tricorythidae												
Tricorythodes Ulmer												
T. nr allectus Needham	–	–	–	–	–	–	X	–	–	X	X	Roseau R. /13/
F. Caenidae												
Caenis Stephens												
C. forcipata McDunnough	–	–	–	–	–	–	X	–	X	X	X	Clear L. /20/; File L. /16/; Heming L. /12/; Roseau R. /13/; Victoria Beach – L. Wpg. /25, 28/; Gimli, Gull Bay, Riverton /28/
C. simulans McDunnough	–	–	–	–	X	X	X	–	X	X	X	Aweme /25/; Winnipeg R./19/
C. tardata McDunnough	–	–	–	?	–	X	X	–	–	–	–	Roseau R. /13/

	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	
F. Baetiscidae												
Baetisca Walsh												
B. bajkovi Neave	-	-	-	-	-	X	X	-	-	-	-	Headingley /28/; McKinnon Ck. /9/; Pigeon R., Sturgeon Falls /28/
B. lacustris McDunnough	-	-	-	-	-	X	-	-	-	X	-	Aweme, Treesbank /6/; Winnipeg R. /19/
B. obesa /Say/	-	-	-	X	-	X	X	-	-	X	X	Manitoba /4/
F. Potamanthidae												
Potamanthus Pictet												
P. nr myops /Walsh/	-	-	-	-	-	-	X	-	-	X	X	Roseau R. /13/
F. Ephemeridae												
Ephemera Linnaeus												
E. simulans Walker	-	-	-	X	X	X	X	-	X	X	X	L. Athapapuskow /32/; Aweme /6/; L. Dauphin /31/; Heming L. /12/; L. Winnipeg /10, 28/; Winnipeg R. /19/; Winnipeg /28/
Hexagenia Walsh												
H. limbata Serville	-	-	-	X	X	X	X	-	X	X	X	Assiniboine R. /33/; Aweme /33/; Berens R. /33/; L. Dauphin /31/; Grand Beach /33/; Heming L. /12/; Icelandic R. /28/; Lander, Melita, Pigeon R., Red R. /28/; Roseau R. /13/; Snow L. /30/; Victoria Beach - L. Wpg. /33/; White L. /5/; L. Winnipeg /10, 28/; Winnipeg R. /19/; Winnipeg /33/

	A	WNW	NW	W	SW	WC*	SC	NC	EC	E	SE	
H. rigida McDunnough	-	-	-	-	-	-	X	-	X	X	X	Assiniboine R. /11/; Red R., L. Winnipeg /10, 28/; Winnipeg R. /19/; Winnipeg /6/
Pentagenia Walsh												
P. vittigera /Walsh/	-	-	-	-	-	-	X	-	-	X	X	Assiniboine R. /18/; Aweme /6/; Red R. /18/
F. Polymitarcidae												
Ephoron Williamson												
E. album /Say/	-	-	-	-	X	X	X	-	-	X	-	Rat R. /14/; Roseau R. /13/; Winnipeg R. /19/; as Polymitarcys albus - Aweme, L. Winnipeg /6/
Tortopus Needham and Murphy												
T. primus /McDunnough/	-	-	- or ?WC		-	-	X	- or ?E		-	-	Assiniboine R. at Cartier; Red R. - as Campsurus manitobensis /17/

* This division is contained within the Manitoba drainage area.

/1/ Allen and Edmunds 1962; /2/ Bednarik and McCafferty 1979; /3/ Berner 1978; /4/ Berner and Pescador 1980; /5/ Blunt 1975; /6/ Criddle 1925; /7/ Daggy 1945; /8/ Edmunds 1957; /9/ Flannagan 1972; /10/ Flannagan 1979; /11/ Flannagan unpublished data; /12/ Flannagan and Lawler 1972; /13/ Friesen et al. 1980; /14/ Gyselman 1980; /15/ Harper and Harper 1981; /16/ Hughes 1976; /17/ Ide 1941; /18/ Ide 1955; /19/ Ireland 1968; /20/ Kooyman and Hutchinson 1979; Kooyman 1980a, b; and Saunders 1979; /21/ Lewis 1974; /22/ McDunnough 1923; /23/ McDunnough 1924b; /24/ McDunnough 1925a; /25/ McDunnough 1931c; /26/ McDunnough 1932; /27/ Morihara and McCafferty 1979; /28/ Neave 1934; /29/ Needham et al. 1935; /30/ Stewart - Hay 1951a; /31/ Stewart - Hay 1951b; /32/ Stewart - Hay 1953; /33/ Spieth 1941

North American distributions are also compiled from:
Allen 1966; Allen and Edmunds 1961; Banks 1900, 1924; Berner 1977; Burks 1953; Cobb and Flannagan 1980; Dobbs and Hisaw 1925; Edmunds et al. 1976; Flowers and Hilsenhoff 1975; Lehmkuhl 1976b; McCafferty 1975; McCafferty and Provansha 1978; McDunnough 1924a, 1925b, 1926, 1930, 1931a, b; Rawson 1928; Ricker 1932; Sprules 1947; Wiens et al. 1975.

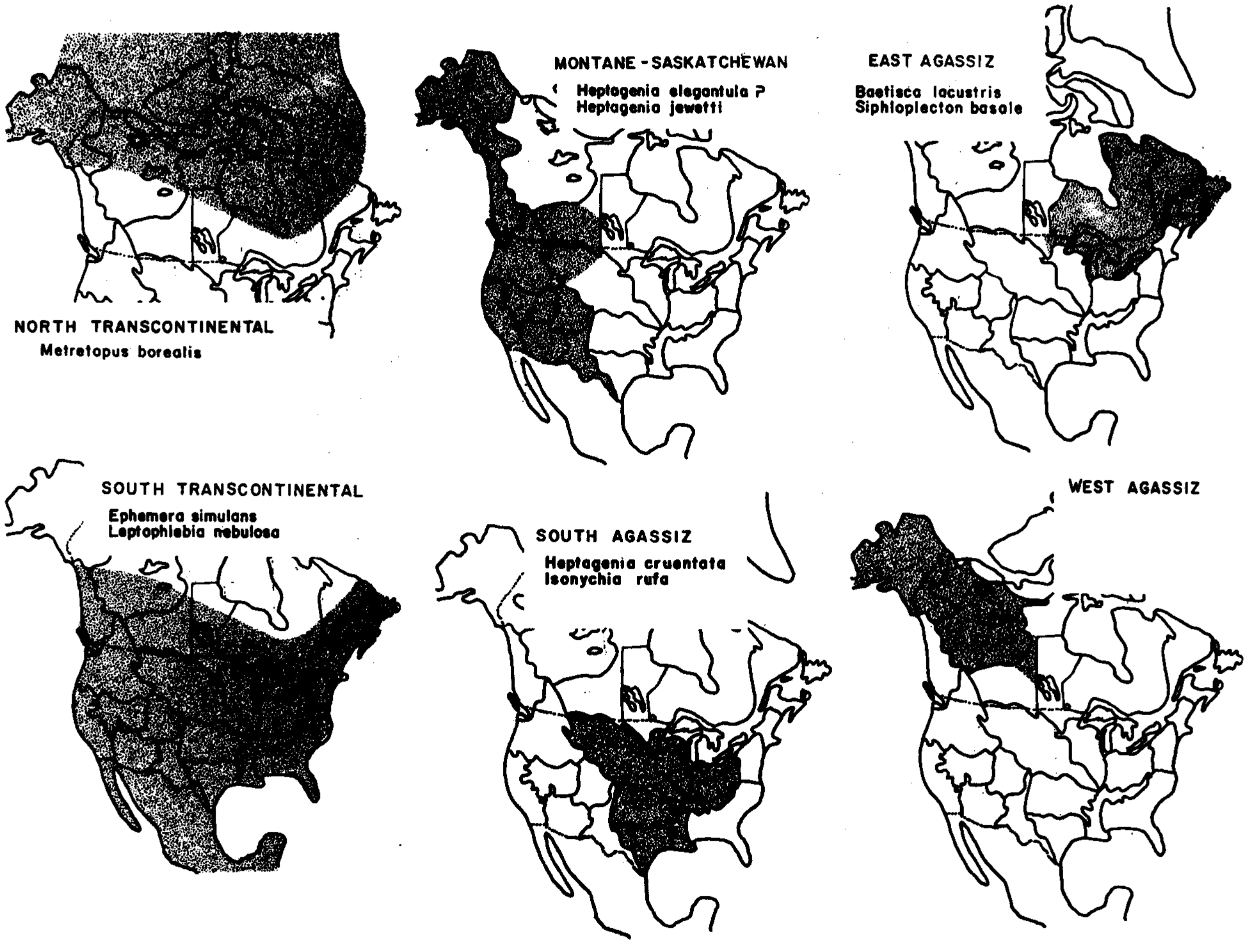

Fig. 5: Migration routes of Manitoba Ephemeroptera.

bution.

A numerical comparison of the Manitoban with Canadian fauna, indicates that the known mayfly species of Manitoba are only 25% of the Canadian total of 47 genera, 301 spp (Lehmkuhl 1979).

Three general migration groups are evident from the distribution data;

1) A simple, distinct set of patterns that show migration into, but not out of Manitoba. For example, species that occur in Manitoba and are distributed only to the south such as Tortopus primus McD., Heptagenia inconspicua McD. and Callibaetis pallidus Banks.

2) A more complex pattern apparently showing migration through Manitoba, and including transcontinental species and species distributed, for example, only to the east, northwest and in Manitoba - Metrotopus borealis Eaton and Siphloplecton basale Clemens.

3) A heterogeneous group showing patterns such as the common south + eastern distribution, in which animals may have migrated using either of the above pathways.

Groups 2 and 3 contain the most common distribution patterns found in Manitoba mayflies. The south + eastern and (south, east + northwestern) patterns are dominant.

MIGRATION ROUTES

Using Table 1, as well as the post-glacial history of the province, one can delineate six basic distributional routes in Manitoba:

a) North Transcontinental (Fig. 5)

Species within this group are Nearctic or Holarctic and have probably migrated from the northern refugia mentioned earlier to the south, west or east. The group is probably cold stenothermic and now restricted to their present distribution by temperature.

b) South Transcontinental (Fig. 5)

This group is likely composed of species which preceded the glacier southwards and followed it north as the ice retreated (Ricker 1964b). Its east-west dispersal was probably along ice-margin lakes and spillways (Ross 1958; Nimmo 1971). Since these species have not invaded the north, even where present day drainages would allow it, it is likely that they are warm stenotherms, restricted by low temperature.

c) South Agassiz (Fig. 5)

This group is restricted to the Gulf of Mexico watershed dominated by the Mississippi-Missouri River system, and Manitoba, and can be expected to have migrated into Manitoba during the times when Lake Agassiz drained southwards. Present day watershed barriers probably limit their further dispersal.

d) East Agassiz (Fig. 5)

This group is confined to Manitoba and the eastern Hudson Bay and St. Lawrence drainage systems. The animals in this group can be expected to have migrated into Manitoba during the eastern and northeastern drainage periods of Lake Agassiz. Further distribution is likely limited, as above, by present watershed barriers.

e) West Agassiz (Fig. 5)

This route was opened when the Mackenzie River system drained south-east into Lake Agassiz or vice versa. Presently, we have no Manitoba mayfly examples, although stoneflies and caddisflies have used this route. It seems to be a major conduit (see Barton 1980) for eastern species spreading northwest. As before, further distribution is probably limited by present watershed barriers.

f) Montane-Saskatchewan (Fig. 5)

This final route is a combination of two routes, a southwestern route using the Missouri River system during early pre-Lake Agassiz time (Fig. 2a), and the still open Saskatchewan River system in the Hudson Bay drainage basin. Lehmkuhl (1980) notes the special faunal relationships of the Cypress Hills, Sask. fauna with Colorado species. Indeed, the Missouri River used to drain to Hudson Bay before the "ice age" (McPahil and Lindsey 1970). Present distributions within the area are limited by the continental divide and the watershed barriers. The restrictive ecological needs of the montane species probably also limit their ability to establish new populations.

The North American distributions of the Manitoban species can be explained by the above six patterns, or more commonly a combination of the above. The various advances and retreats of the ice sheets described earlier, e.g. the Dog-Kaministikwa event and other glacial events in other areas of North America, e.g. the redirection of Peel River waters from the Mackenzie to Yukon River drainage systems and back again (Bodaly and Lindsey 1977), allowed multiple basin interchanges.

It seems likely that, since only a few areas of Manitoba have been intensively collected and the collections accurately identified to species (e.g. Lake Winnipeg, Duck Mountains, Roseau River, Aweme, Churchill) further studies will add many species to the records given in Table 1. This, and more intensive research into the migration roles of adults vs immatures in colonization should provide insights into some of the other reasons for the quite limited representation of the North American fauna in Manitoba and Canada as a whole. It is also interesting to note that Baetis hudsonicus Ide, is apparently endemic to Manitoba.

Of perhaps more interest is almost the opposite problem - why have some species, which have had the opportunity to move into Manitoba not done so? Undoubtedly, further collections will add more species to the Manitoba list, but some very large and obvious species should have been found if they occur here. E.g., Hexagenia bilineata, a very large and almost a pest mayfly species (because of its mass emergence) in the Mississippi-Missouri system is not found here while two other species of the genus which occur to the South are. All three species have similar macro-ecological requirements (Edmunds et al. 1976) and all had the opportunity, during the south-flowing phases of Lake Agassiz, to migrate here. Further research into the micro-ecological requirements of this and other species which have not colonized this area, but which have had the opportunity, may provide answers to some puzzling questions.

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