

Life history of the northern mayfly *Baetis bundyae* in Rankin Inlet, Nunavut, Canada, with updates to the list of mayflies of Nunavut

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Abstract—Mayflies (Ephemeroptera) were collected from 35 sites (streams and tundra ponds) across southern Nunavut in 2002–2005. Nine mayfly species were previously reported for Nunavut: *Acentrella feropagus* Alba-Tercedor and McCafferty, *Acerpenna pygmaea* (Hagen), *Baetis bundyae* Lehmkuhl, *B. flavistriga* McDunnough, *B. foemina* McDunnough, *Dipheter hageni* (Eaton) (Baetidae), *Ephemerella aurivillii* (Bengtsson) (Ephemerellidae), *Leptophlebia nebulosa* (Walker) (Leptophlebiidae), and *Metretopus borealis* (Eaton) (Metrotopidae). We add 7 species to this list, bringing the total to 16: *Ameletus inopinatus* Eaton (Ameletidae), *Acentrella lapponica* Bengtsson, *Baetis hudsonicus* Ide, *B. tricaudatus* Dodds, *Heptagenia solitaria* McDunnough (Heptageniidae), *Rhithrogena jejuna* Eaton (Heptageniidae), and *Parameletus chelififer* Bengtsson (Siphonuridae). Based on numbers collected, the dominant mayfly family was Baetidae. *Baetis bundyae* was the most common mayfly collected, particularly in coastal areas, where larvae were found in permanent and temporary streams and in small or shallow tundra ponds. Larvae hatched 2–3 weeks after ice-out and developed rapidly in 2.5–4 weeks, emerging as adults by early August. All populations containing larvae that were large enough to sex showed female-biased sex ratios, suggesting parthenogenesis. A combination of freeze-tolerant eggs, good dispersal ability, and probable parthenogenesis is probably responsible for the success of Baetidae across the Arctic.

Résumé—Nous avons récolté des éphémères (Ephemeroptera) à 35 sites (étangs et cours d'eau de la toundra) dans tout le sud du Nunavut en 2002–2005. Neuf espèces d'éphémères étaient déjà connues du Nunavut : *Acentrella feropagus* Alba-Tercedor et McCafferty, *Acerpenna pygmaea* (Hagen), *Baetis bundyae* Lehmkuhl, *B. flavistriga* McDunnough, *B. foemina* McDunnough, *Dipheter hageni* (Eaton) (Baetidae), *Ephemerella aurivillii* (Bengtsson) (Ephemerellidae), *Leptophlebia nebulosa* (Walker) (Leptophlebiidae) et *Metretopus borealis* (Eaton) (Metrotopidae). Nous en ajoutons 7 autres pour un total de 16 : *Ameletus inopinatus* Eaton (Ameletidae), *Acentrella lapponica* Bengtsson, *Baetis hudsonicus* Ide, *B. tricaudatus* Dodds, *Heptagenia solitaria* McDunnough (Heptageniidae), *Rhithrogena jejuna* Eaton (Heptageniidae) et *Parameletus chelififer* Bengtsson (Siphonuridae). D'après le nombre de spécimens récoltés, la famille dominante est celle des Baetidae. *Baetis bundyae* est l'éphémère le plus couramment récolté, particulièrement dans les régions côtières où les larves vivent dans les cours d'eau permanents et temporaires et dans les étangs petits ou peu profonds de la toundra. Les larves éclosent 2–3 semaines après la fonte des glaces et se développent rapidement en 2,5–4 semaines, alors que les adultes émergent au début d'août. Dans toutes les populations où les larves étaient assez grandes pour permettre la détermination du sexe, il y a un surplus de femelles, ce qui laisse croire à la parthénogenèse. Le succès des Baetidae dans toute la région

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arctique s'explique sans doute par la combinaison de la possession d'oeufs résistants au gel, d'un bon pouvoir de dispersion et de la présence probable de la parthénogenèse.

[Traduit par la Rédaction]

Introduction

Little is known about the insect fauna of the Canadian north, mainly because of difficulty in access and sampling in far northern Canada (Scudder 1987; Danks *et al.* 1997; Currie *et al.* 2000). This is especially true for the central and eastern portions that make up the newly formed territory of Nunavut, and for nonbiting aquatic insects such as mayflies (Ephemeroptera). Only nine mayfly species were previously reported from Nunavut: *Acentrella feropagus* Alba-Tercedor and McCafferty, *Acerpenna pygmaea* (Hagen), *Baetis bundyae* Lehmkuhl, *B. flavistriga* McDunnough, *B. foemina* McDunnough, *Dipheter hageni* (Eaton), *Ephemerella aurivillii* (Bengtsson), *Leptophlebia nebulosa* (Walker), and *Metretopus borealis* (Eaton) (reviewed by Cobb and Flannagan 1980; Harper and Harper 1981; Randolph and McCafferty 2001). Further, most previous mayfly collecting was done in coastal or near-coastal locations because of the difficulties in travelling in Nunavut, although two series of collections were made by Lawrence *et al.* (1977, cited by Cobb and Flannagan 1980) in drainage basins in the inland area south and southwest of Baker Lake. Little habitat information is available for these collection localities, making it difficult to compare mayfly distribution patterns in different areas of the Arctic. Therefore, a series of expeditions to rivers and regions of the Canadian Central Barrens to collect aquatic insects in isolated habitats in the Northwest Territories and Nunavut, and update data on species distributions for both territories, was undertaken between 2000 and 2005 (Currie *et al.* 2000; Shaverdo and Giberson 2004).

The dominant mayfly family in the Canadian tundra zone is the Baetidae, and one of the most widely distributed mayfly species across the Arctic is *Baetis bundyae* (Harper and Harper 1981). The species was described from mature larvae collected from streams and tundra ponds near Rankin Inlet, Nunavut (Lehmkuhl 1973). The adults (from the same locality) were described by Morihara and McCafferty (1979), who synonymized *Baetis bundyae* with the European *B. macani* Kimmins (described in 1957) because of

similarities in morphology and life history. The North American subspecies became known as *B. macani bundyae* Lehmkuhl. McCafferty then reinstated *B. bundyae* as a species, based on unpublished information from E. Engblom that distinctive forms of both species (*B. macani* and *B. bundyae*) coexist in northern Scandinavia (reported in McCafferty 1994). The two species differ mainly in mouthpart structure and size, and are reported to have very similar life cycles and habitats (Morihara and McCafferty 1979). Although both species occur in Europe (primarily north of the 60th parallel), only *B. bundyae* has thus far been found in North America, having been reported across the Canadian north and into Alaska (McCafferty 1994), south to Saskatchewan (Webb *et al.* 2004) and northern Minnesota (Lager *et al.* 1982), and in mountain lakes above 3000 m altitude in Wyoming (Durfee and Kondratieff 1999).

Despite the ubiquity of *B. bundyae* across the Canadian north, its life-cycle has not been completely described, so this is the second goal of this study. Lehmkuhl postulated a rapidly growing larval stage with a freeze-tolerant overwintering egg, based on collections of mature larvae in late July (1972 and 1973) and the absence of any larvae at the same sites in late June 1973 (Lehmkuhl 1973; Morihara and McCafferty 1979). The life cycle of *Baetis macani* is better known, with larvae hatching about 3 weeks after ice-out in northern lakes and streams in Fennoscandia, and completion of the life cycle in a few weeks (Brittain 1975). Brittain (1975) also reported the emergence of *B. macani* to be fairly prolonged, continuing throughout the open-water period into autumn, even from water at temperatures as low as 3.5 °C. Like *B. bundyae* in northern Canada, *B. macani* is believed to have eggs that are tolerant to freezing. Both *B. bundyae* and *B. macani* are unusual among Baetidae in colonizing lentic habitats as readily as streams. A freeze-tolerant egg stage, coupled with a short development cycle and rapid larval growth, contributes to the ability of these species to colonize northern or cold-water habitats where other mayflies are not able to survive.

Methods

Life history of *Baetis bundyae* at Rankin Inlet sites in 2005

Mayflies were sampled from streams and pond edges at 17 sites around Rankin Inlet, Nunavut, between 6 and 20 July 2005, using a combination of kick-netting (200 µm mesh), aerial sweeping, and hand-searching of in-stream rocks and streamside vegetation. Mayflies (all Baetidae) were found at 10 of the sites (Table 1). Baetid mayflies were found at all sampled sites with flowing water, whether temporary or permanent, in large shallow tundra ponds with boulder substrates and peaty overhangs, and in relatively deep grassy ponds. No mayflies were found in small rocky rainwater pools and obviously temporary grassy pools surrounding larger tundra pools or streams, in very large, deep tundra ponds or lakes, or in sandy pools on the top of an esker located north of Rankin Inlet. At most of the sites where baetid mayflies were found, freezing extends to the permafrost layer during winter, and many are subject to drying in summer (Table 1).

Most sites were located several kilometres from an access road, and so were sampled opportunistically during sampling trips away from our base camp, which was located north of the hamlet of Rankin Inlet and approximately 3 km from the nearest road. One site (site 1, Char River upstream of Landing Lake; Fig. 1) was beside the base camp, and so was sampled most frequently, at approximately 3 day intervals between 6 and 20 July. Two other sites (site 4, Char River at the bridge, and site 7, Meliadine River; Fig. 1) were located near an access road and were sampled until 1 August, when mayflies were emerging or were present as mature (dark wing pad) larvae. Specimens of *Baetis bundyae* were measured and size-frequency patterns were plotted in order to follow the life cycle and to compare life-cycle timing in a variety of habitats around Rankin Inlet.

Baetid larvae were sexed using the dimorphic structure of the larval compound eyes. Adult males possess turbinate compound eyes consisting of distinct upper and lower sections that begin to be expressed early in larval development. In partially grown male larvae, the upper section of the male turbinate eye is evident as a slightly different-coloured crescent-shaped faceted region above the lower portion of the eye. Females lack this eye structure, having undivided compound

eyes. When larvae reached the size and developmental stage (based on wing-pad development) where this character could be seen, those that clearly exhibited it were counted as males and those without it were counted as females. Younger larvae were not sexed.

Mayflies of Nunavut

Data for updating the list of Nunavut mayflies were obtained by comparing the results of new collecting between 2002 and 2005 (summarized in Fig. 2, Appendix A) with literature summaries by Cobb and Flannagan (1980), Harper and Harper (1981), and Randolph and McCafferty (2001). Our collecting was carried out along the Thelon River in south-central Nunavut, and near the communities of Arviat (formerly Eskimo Point), Baker Lake (Qamani'tuaq), and Rankin Inlet (Kangiqtiniq) as part of a larger project on the distribution of aquatic insects in the Canadian Central Barrens (Shaverdo and Giberson 2004). The Thelon River, its tributaries, and other streamside habitats were sampled between the confluence of Hanbury River (Northwest Territories) and the point where the Thelon River enters Beverly Lake (Nunavut) between 29 June and 12 July 2002. Habitats within several kilometres of Arviat, Baker Lake, and Rankin Inlet were sampled between 9 July and 20 July 2003 as part of the same project. Low apparent species diversity in the region closest to Hudson Bay (Arviat, Rankin Inlet) then prompted a further trip to Rankin Inlet between 6 July and 20 July 2005 to search more intensively to ensure that no available habitat was being missed. Larvae were sampled by a combination of kick-sampling (200 µm mesh) and rock searching, and adults were sampled through sweep-netting, beating, and Malaise trapping. Conditions were not dark enough to attempt black-lighting for adults during any of the northern sampling.

Results

Habitat descriptions

Most of Nunavut is tundra habitat and lies on permafrost north of treeline, with only a small section of taiga forest extending into southern Nunavut (just west of Arviat). The two regions sampled in this study differ in the severity of the climate. The coastal zone has the harsher climate and is dominated in winter by the frozen ocean of Hudson Bay; the farther north in

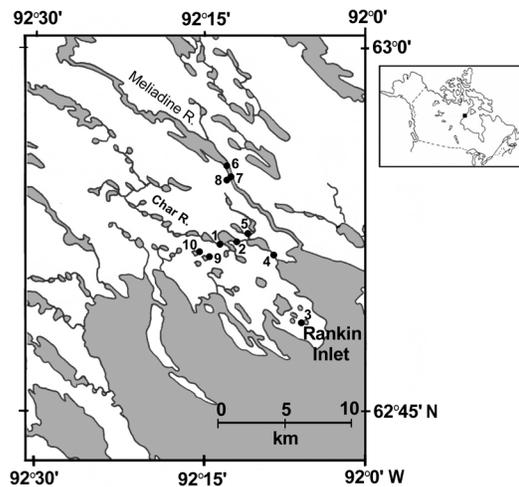
Table 1. Collection sites for *Baetis bundyae* near Rankin Inlet, Nunavut, 6–19 July 2005.

Site No.	Site location	No. of <i>B. bundyae</i> collected	Coordinates	Description
1	Char River	457	62°51'45.1"N, 92°13'04.6"W	Fast-flowing rocky tundra stream (≈7 m wide), inflow to upper Landing Lake; mostly low vegetation but with a few low arctic willows; freezes in winter, may dry in summer
2	Char River	13	62°51'56.0"N, 92°11'30.5"W	Outlet to upper Landing Lake; rapid rocky stream (≈7 m wide) with arctic willow along edges; freezes in winter, may dry in summer
3	Un-named grassy pools	28	62°48'41.2"N, 92°05'37.6"W	Small shallow grassy pools alongside Williamson Lake in town of Rankin Inlet; freeze solid in winter
4	Char River	167	62°51'34.2"N, 92°08'39.2"W	Large (≈10 m wide) stony stream upstream and downstream of bridge on the Meliadine River road north of Rankin Inlet; freezes in winter, may dry in summer
5	Un-named seep between ponds	15	62°52'15.1"N, 92°10'37.3"W	Small seep (<1 m wide) flowing between two tundra ponds; freezes in winter, may dry in summer
6	Meliadine River	16	62°54'51.1"N, 92°12'39.3"W	Large, fast, permanent tundra river (>30 m wide) with boulders and large cobble, right at outlet to small lake
7	Meliadine River	33	62°54'31.0"N, 92°12'23.5"W	Large, fast, permanent tundra river (>30 m wide) with boulders and large cobble, about 200 m downstream of site 6
8	Un-named pool and seep beside river	17	62°54'31.0"N, 92°12'23.5"W	Shallow grassy tundra pool located beside the Meliadine River, with short stony outflow (<1 m wide) draining to the Meliadine River; sample collected in the pool and the stream
9	Un-named tundra pond	5	62°51'30.6"N, 92°12'49.3"W	Large shallow tundra pond, not part of the Char River system, with overhanging peaty banks and large-boulder substrate
10	Un-named tundra pond	55	62°51'26.9"N, 92°12'41.5"W	Large shallow tundra pond, not part of the Char River system, with overhanging peaty banks and large-boulder substrate

Nunavut, the greater the influence of the frozen ocean on the climate becomes. Inland, the climate is not as harsh, and rivers may thaw several weeks earlier than on the coast. For example, the tundra vegetation along the Nunavut portion of the Thelon River (the only inland river sampled for this survey) was characterized by scattered occasional spruce trees (*Picea* A. Dietr. (Pinaceae)) and clumps of willow (*Salix* L. (Salicaceae)) that reached 2 m in height, as well as low shrubs and wildflowers.

Much of the sampled part of the Thelon River was part of ancient Glacial Lake Thelon, and had a low gradient with sand, gravel, and cobble substrate. Substrates were similar in the tributaries, which consisted mainly of bog or tundra pond outflows. Tundra ponds and pools were also common, and were surrounded by dense willow riparian zones. In contrast, the coastal tundra zone (including the Baker Lake region) was dominated by the Canadian Shield, with rocky outcrops and no tall trees or shrubs.

Fig. 1. *Baetis bundyae* collection sites near Rankin Inlet, Nunavut, from 6 July to 1 August 2005.



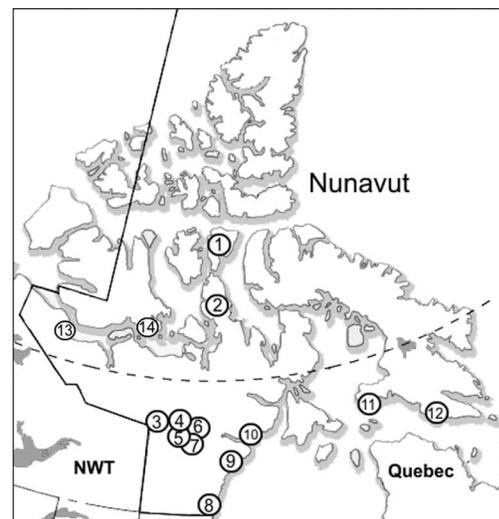
Streams and ponds were also rocky, and were characterized by boulders and large cobble. Vegetation in the coastal zone was sparse and dwarf in character.

Rankin Inlet, 2003–2005: mayfly diversity and life history of *Baetis bundyae*

A total of 942 mayflies were collected from the Rankin Inlet area in 2003 and 2005. They all belonged to the Baetidae, though local fly-fishers reported the emergence of a large olive dun (subimago) from the Meliadine River just after the river opened in late June. This matched the description of *Ephemera aurivillii*, which we collected from a similar large river near Arviat in early July 2003. The dominant species in the Rankin area was *Baetis bundyae*, which made up nearly 97% of the mayflies collected, and occurred in a large variety of lentic and lotic habitats (Table 1). Four other species of Baetidae were found, but none was common. *Acentrella feropagus* occurred at Char River sites 1 and 4 in 2005 (1.6% of the total collected), *A. lapponica* Bengtsson occurred at Char River site 4 in 2003 (1.7% of the total), and a single specimen of *B. flavistriga* occurred at Char River site 1 during 2005 (0.1% of the total). A single specimen of *B. hudsonicus* Ide was found in a tundra pond on the Tudlik peninsula west of Rankin Inlet during 2003 (Appendix A).

Most of the study sites in the Rankin Inlet area were clear, circumneutral, low-conductivity water bodies with little vegetation and temperature patterns that tracked those of the ambient air.

Fig. 2. Reported collection localities for mayflies in Nunavut (a, b, and c denote references included in the list of species in the following section, "Mayflies of Nunavut"): 1, Sanagak Lake drainage system, Boothia Peninsula (Cobb and Flannagan 1980); 2, Murchison Lake drainage system (Cobb and Flannagan 1980); 3, Middle Thelon River, between Hanbury River and Beverly Lake (this study); 4, Lower Thelon River, upstream of Baker Lake (this study); 5, Pitz Lake drainage system Cobb and Flannagan 1980); 6, Baker Lake and environs, including Prince River (a, Harper and Harper 1981; b, this study); 7, Thirty Mile Lake drainage (on the Kazan River system) (Cobb and Flannagan 1980); 8, Arviat area (formerly Eskimo Point), including the Maguse River system and sites slightly inland and north or south (Padlei), Geillini Lake (southwest of Arviat on Thelwiza River), McConnell River (south of Arviat) (a, Cobb and Flannagan 1980; b, Harper and Harper 1981; c, this study); 9, Rankin Inlet area, including the Meliadine River, Char River, and Diane River drainages (a, Cobb and Flannagan 1980; b, this study); 10, Saqvaquac River (Cobb and Flannagan 1980); 11, Cape Dorset (Harper and Harper 1981); 12, Kimmirut (formerly Lake Harbour) (Cobb and Flannagan 1980); 13, Kugluktuk (formerly Coppermine) (Harper and Harper 1981); 14, Cambridge Bay (Harper and Harper 1981).



Virtually all surface waters of this region are potable without treatment or filtration, and local families collect drinking water from many of the sites we sampled. Streams generally had cobble/boulder substrates, and most of the tundra ponds were characterized by shallow water, overhanging peaty vegetation, and large boulder substrate. Most sites had pH and conductivity values ranging from 6.8 to 7.2 and from 50 to 150 $\mu\text{S}/\text{cm}$, respectively, and water temperatures ranging from

12 to 23 °C depending on air temperature (which ranged from 8 to 27 °C during the sampling period). Two sites differed somewhat from the other sites. Site 3 was a series of grassy pools along a path within the hamlet of Rankin Inlet that had higher pH, conductivity, and temperature values than the other sites (pH 8.2, conductivity 430 µS/cm, and temperature usually 3–4 °C higher than at open tundra sites). The Meliadine River (sites 6 and 7) is a large permanent river with relatively low pH and conductivity values (pH 6.6 and 30 µS/cm, respectively), and the temperature was fairly constant at ~13 °C during the study period regardless of air temperature.

The open-water growth season is very short in all the habitats examined. Ice was seen around the edges of the large Meliadine River well into July 2005. The small streams and small tundra ponds usually begin to break up in early to mid-June, but the larger lakes (such as Meliadine Lake) may have ice until mid-July. Most of the smaller streams slow to a trickle by early August, and in some years may dry to a series of unconnected puddles. Ice can return to these sites as early as September, and no hyporheic refuge zone exists at the aestival stream and shallow pond sites, since they freeze to the permafrost layer in winter.

The life cycle of *Baetis bundyae* showed adaptations for the short open-water period and the generally harsh northern conditions. Larval development was rapid in the ponds and streams in the Rankin Inlet area, occurring over 2.5–4 weeks. Tiny larvae (<1 mm in length) were first seen in the upper Char River on 6 July, but were not seen on 4 or 5 July despite intensive searching. Mature larvae (those with well-developed and darkened wing pads) were seen by 20 July (Fig. 3). Hatching time varied among habitats, though, resulting in variation in the timing of specific stages at the different sites (Fig. 4). For example, larvae were not found in the colder Meliadine River until 13 July (they were not present on 12 July). However, emergence was seen by 1 August at all sites investigated, including the Meliadine River, indicating that larval development could take as little as 2.5 weeks. Larval sex ratios indicated a female bias, on at least some sampling dates, at all sites where larvae were large enough to sex (Table 2). On some dates and sites (9 July, site 1; 13 July, site 14; 18 July, site 10), only females were observed.

In addition to variation in larval timing, larval size distributions for similar-aged larvae (based on wing-pad development) differed

between the pools in Rankin Inlet and the remaining sites (Fig. 4). Mature larvae (those with well-developed and (or) dark wing pads) ranged from about 5 to 6.5 mm in length at the Char River, Meliadine River, and tundra pond sites, but larvae at equivalent wing-pad stages were much larger in the grassy pools in Rankin Inlet (site 3; Figs. 1 and 4), and even partially grown larvae reached 6.5–7.5 mm in length.

We also noted some distinct differences in larval morphology, which we refer to here as “wide” or “narrow” body forms (Table 2). Wide forms were noted at site 1 on 9 July (72 individuals, all female) and site 18 on 17 July (23 individuals, all female). Narrow forms were observed (a mix of males and females) at site 1 on 9 July (1 individual) and site 10 on 17 July (32 individuals). The difference between the forms relates to the width across the thorax and anterior abdomen. Wide larvae appear initially to be dorsally compressed, but are actually more rotund, whereas narrow forms have a more cylindrical thorax and no distinctive difference in width where the thorax joins the abdomen. Most other *B. bundyae* larvae fell between these two body-form extremes.

Mayflies of Nunavut

Only nine species of mayflies were recorded previously from Nunavut (*Acentrella feropagus*, *Acerpenna pygmaea*, *Baetis bundyae*, *B. flavistriga*, *B. foemina*, *Dipheter hageni*, *Ephemera aurivillii*, *Leptophlebia nebulosa*, and *Metrotopus borealis*). The following is a list of the families and species now known to occur in Nunavut (an asterisk indicates a new Nunavut record from this study; the numbers in parentheses indicate the location and references from Figure 2):

Ameletidae

**Ameletus inopinatus* (3, 4, 8c)

“*Ameletus* gr. *velox*” (8b; damaged specimen from Padlei)

Baetidae

Acentrella feropagus (1, 2, 3, 9b) (specimens from sites 1 and 2 verified by Alba-Tercedor and McCafferty 2000)

**Acentrella lapponica* (4, 8, 9b); specimens identified as *Baetis lapponicus* by Cobb and Flannagan (1980) but not checked to confirm identity (5, 7, 11, 12)

Acerpenna pygmaea (8a)

Baetis bundyae (2, 4, 5, 6a, 6b, 7, 8b (specimen from Geillini Lake), 8c, 9a, 9b, 10, 11, 14)

Baetis flavistriga (2, 5, 7, 8c, 9b)

Baetis foemina (12)

**Baetis hudsonicus* (9b)

**Baetis tricaudatus* (3)

Baetis sp. (6b, 8b, "Chesterfield" (Harper and Harper 1981))

Diphetero hageni (2, 8b) (as *B. parvus* Dodds at site 2)

Ephemerellidae

Ephemerella aurivillii (3, 8b (record from Padlei), 8c, probably also from 9b, based on conversation with local fly-fisher)

Ephemerella sp. (5, 7)

Ephemerellidae (13)

Heptageniidae

**Heptagenia solitaria* (3, 8c)

Heptagenia sp. (7)

**Rhithrogena jejuna* (3)

Leptophlebiidae

Leptophlebia nebulosa (4, 8b (record from Geillini Lake))

Leptophlebia sp. (8a, 8b (records from both Geillini Lake and Padlei))

Metretopodidae

Metretopus borealis (5, 7)

Siphonuridae

**Parametopus chelififer* (3, 4, 8c)

During the summers of 2002–2005, 1417 additional mayfly specimens were collected in southern Nunavut, resulting in the addition of 7 species to the list, for a total of 16 species in seven families (see the list above). The additional records for Nunavut are *Ameletus inopinatus* Eaton, *Acentrella lapponica*, *Baetis hudsonicus*, *B. tricaudatus* Dodds, *Heptagenia solitaria* McDunnough, *Rhithrogena jejuna* Eaton, and *Parametopus chelififer* Bengtsson (see the list above). In addition, several species are now known to extend farther inland in Nunavut than was previously reported. Of the species we collected, several (the heptageniids, *E. aurivillii*, *Ameletus inopinatus*, *B. tricaudatus*, *Metretopus borealis*, and *P. chelififer*) were found almost exclusively in large permanent water bodies that did not freeze solid during winter.

Overall regional diversity did not differ between northern Hudson Bay coastal sites and inland sites (11 and 12 species, respectively; see the list above and Fig. 5), but there were some distinct diversity patterns for each area. The highest mayfly diversity at any one location in the 2002–2005 survey occurred at sites along the Thelon River (up to 6 species at individual sites along the Thelon River compared with a maximum of 3 species in coastal areas; see Appendix A). Seven mayfly families are represented in Nunavut, but

most have only 1 or 2 species, and 9 of the 16 species belong to the Baetidae. Only 4 species, all Baetidae (*Acentrella feropagus*, *Baetis bundyae*, *B. flavistriga*, and *B. foemina*), are reported from the most northerly sites (see the list above and Fig. 5), although unidentified specimens of Ephemerellidae have been collected at Kugluktuk (Coppermine (site 13 in Fig. 2); Harper and Harper 1981). *Baetis bundyae* was the most abundant and widespread mayfly across Nunavut (making up >80% of the mayflies in the present survey and appearing at most collecting locales), followed by *Acentrella feropagus* and *Acentrella lapponica* (Fig. 5, Appendix A).

Discussion

The mayfly fauna of northern Canada is relatively rich, consisting of at least 82 species from the northern tundra and open boreal forest north of the permafrost line (Cobb and Flannagan 1980; Harper and Harper 1981). However, the number of species drops dramatically north of the treeline, with only 17 species reported, 6 of which have been reported only from Churchill, Manitoba, where both tundra and taiga habitats occur. Eleven of the 17 north-of-treeline species in North America (based on Harper and Harper 1981) are now known from Nunavut, and we add 5 species to this list: *Ameletus inopinatus*, *Acentrella feropagus*, *Baetis tricaudatus*, *Heptagenia solitaria*, and *Rhithrogena jejuna*. We expected that most of the additions to the list of mayflies of Nunavut would result from inland sampling, because the inland region has greater habitat and vegetation diversity than the coastal zone (suggesting a less severe climate), and because most of the previous collecting had been carried out in coastal regions of Nunavut. However, only 3 species appeared to be restricted to the inland river sites (*B. tricaudatus*, *R. jejuna*, and *M. borealis*; Cobb and Flannagan 1980; this study), with *B. tricaudatus* and *R. jejuna* constituting additional Nunavut records. The species that were associated with large river systems (the heptageniids, *E. aurivillii*, *A. inopinatus*, *B. tricaudatus*, *M. borealis*, and *P. chelififer*) were found primarily in the inland areas, but extended to the coast in the large river systems such as the Maguse River (near Arviat) or Meliadine River (near Rankin Inlet).

Previous study (Cobb and Flannagan 1980; Harper and Harper 1981) reported only 6 exclusively tundra species in the Canadian north,

Fig. 3. Size-frequency patterns of *Baetis bundyae* at all three sites (corresponding (from left to right) to sites 1, 4, and 6 in Table 1) near Rankin Inlet, Nunavut, from 6 July to 1 August 2005. The oval on the graphs for 1 August indicates sizes of adults.

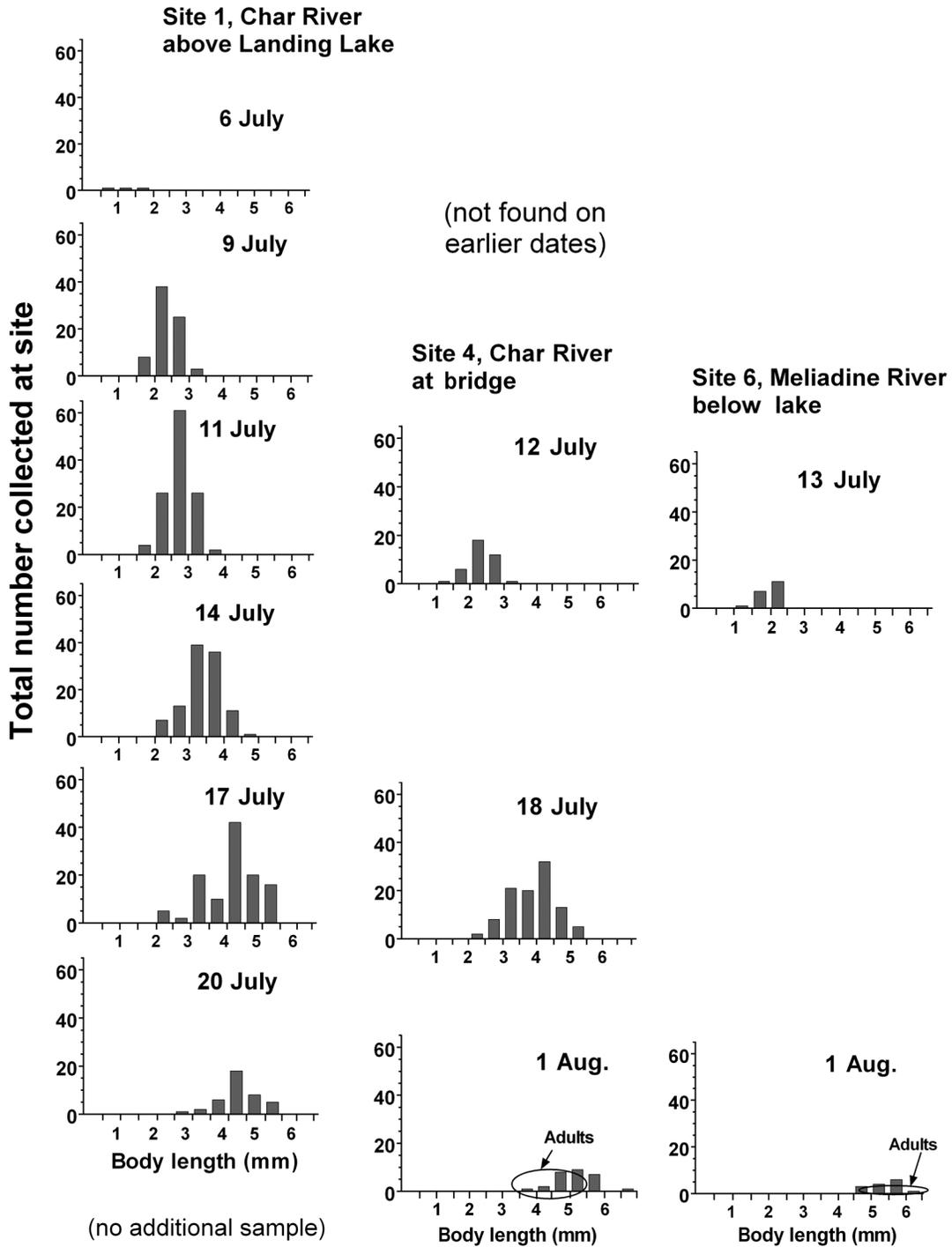
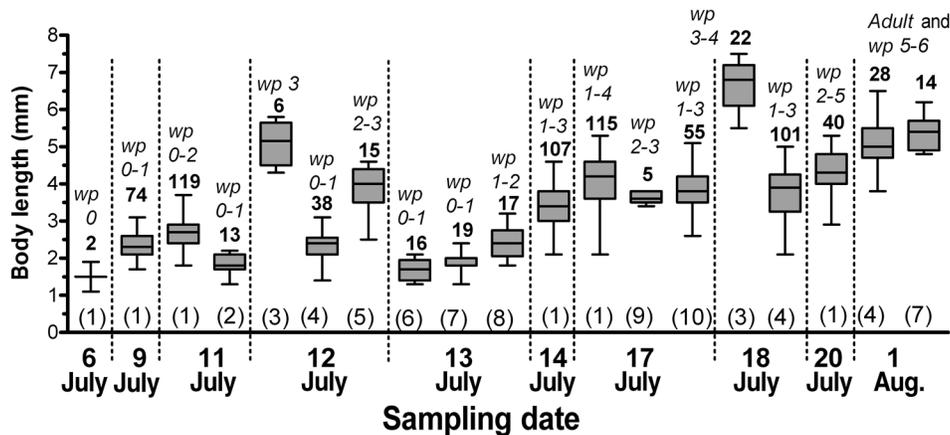


Fig. 4. Comparison of sizes of *Baetis bundyae* specimens collected at various sites around Rankin Inlet in summer 2005. The numbers in parentheses correspond to site numbers in Figure 1; the boldface number above each box indicates the number of larvae collected on that site and date; *wp* refers to the wing-pad stages of collected larvae (0 = no wing pads; 1 = front wing pads tiny, but no hind wing pads; 2 = front wing pads do not extend beyond the end of the metathorax and hind pads are visible; 3 = front wing pads extend to somewhere on abdominal segment 1; 4 = front wing pads extend to somewhere on abdominal segment 2; 5 = front wing pads fall beyond the tip of abdominal segment 2, but are not dark; 6 = front wing pads fall beyond the tip of abdominal segment 2 and are dark).



dominated by species in the Baetidae: *A. lapponica*, *A. feropagus*, *B. bundyae*, *B. foemina*, *B. hudsonicus*, and *P. chelififer*. The remaining 10 species in Nunavut represent elements of the northern transcontinental group of Harper and Harper (1981) (*M. borealis*, *L. nebulosa*, *B. flavistriga*, *B. tricaudatus*, *D. hageni*, *E. aurivillii*), 1 species with western montane affinities (*H. solitaria*), and 1 species with central and northeastern North American affinities (*R. jejuna*). Six of the 16 species, *Ameletus inopinatus*, *Acentrella lapponica*, *B. bundyae*, *E. aurivillii*, *M. borealis*, and *P. chelififer*, are Holarctic. *Acerpenna pygmaea* is widely distributed, but is not a high-latitude specialist; since it is generally considered to be limited by treeline, its presence near Arviat was somewhat surprising.

The domination of the above-treeline fauna by baetids, especially *Baetis bundyae*, probably relates to adaptations that allow these species to complete their development within the short arctic summer. *Baetis bundyae* was common in habitats around Arviat, Baker Lake, and Rankin Inlet, often in association with *A. lapponica* and *A. feropagus* at stream sites and *B. hudsonicus* in a tundra pond. Many of these habitats are aestival (Johansson and Nilsson 1994), freezing to the permafrost layer in winter and drying up in late summer. Unlike southern habitats, unfrozen hyporheic refuge zones exist only in places where deep or running water is maintained under the ice, so species that overwinter

as active larvae are excluded from these small temporary habitats.

The rapid development of *Baetis bundyae* allows the species to complete its life cycle in the very short window of time available at the northern sites. *Baetis bundyae* also grows rapidly in northern Sweden (Johansson and Nilsson 1994), where it also inhabits aestival streams that dry in summer and freeze solid in winter. Similarly, the close European relative, *B. macani*, also showed rapid development in streams in Norway (Brittain 1975). The close association of three other baetid species with *B. bundyae* in aestival streams and ponds suggests that they may have similar life histories. However, their extremely low abundance in these habitats relative to that of *B. bundyae* might indicate that they are not as tolerant of freezing or drying, and are maintained only in certain refuges at the sites. Johansson and Nilsson (1994) also hypothesized that although their streams in northern Sweden froze solid in winter, certain unfrozen refuges might occur in some years in short stream sections with deep water.

Baetid mayflies may also have an advantage at high latitudes because of a good dispersal ability. The dispersal ability of mayflies is related to the relationship between wing length and body size, and small mayflies such as baetids are considered to be good dispersers (Corkum 1987).

Another factor that may facilitate colonization of unstable or extreme arctic habitats is parthenogenesis,

Table 2. Sex ratios and morphological patterns of mayflies (collected in 2005) examined from sites in the Rankin Inlet area.

Site No.	Date	Species	No. in sample	No. of ♂	No. of ♀	♂:♀ ratio
1	6 July	<i>Baetis bundyae</i>	2*			
	9 July	<i>B. bundyae</i> (wide)	1		1	
		<i>B. bundyae</i> (narrow)	72		72	
	11 July	<i>B. bundyae</i>	119*			
	14 July	<i>B. bundyae</i>	104	40	64	1:1.60
		<i>B. flavistriga</i>	1*			
	17 July	<i>Acentrella ferropagus</i>	1		1	
		<i>B. bundyae</i>	91	38	53	1:1.39
		<i>B. flavistriga</i>	9	1	8	1:800
	20 July	<i>B. bundyae</i>	18	9	9	1:100
<i>B. flavistriga</i>		5	2	3	1:1.50	
2	11 July	<i>B. bundyae</i>	13*			
3	12 July	<i>B. bundyae</i>	7	5	2	2.50:1
	18 July	<i>B. bundyae</i>	17	4	13	1:3.50
4	12 July	<i>B. bundyae</i>	38	1	37	1:370
		<i>A. ferropagus</i>	2*			
	18 July	<i>B. bundyae</i>	80	16	64	1:4.00
		<i>A. ferropagus</i>	7	4	3	1.30:1
		<i>B. bundyae</i> (adults)	14	6	8	1:1.33
1 Aug.	<i>B. bundyae</i>	4		4		
	<i>A. ferropagus</i> (adults)	3		3		
	<i>B. bundyae</i> (adults)	14	1	13	1:13.0	
5	12 July	<i>B. bundyae</i>	14	1	13	1:13.0
6	13 July	<i>B. bundyae</i>	15*			
7	13 July	<i>B. bundyae</i>	17*			
	1 Aug.	<i>B. bundyae</i> (adults)	7	4	3	1.33:1
8	13 July	<i>B. bundyae</i>	13		13	
9	17 July	<i>B. bundyae</i>	4	1	3	1:3.00
10	17 July	<i>B. bundyae</i> (wide)	23	9	14	1:1.50
		<i>B. bundyae</i> (narrow)	32	9	23	1:2.50

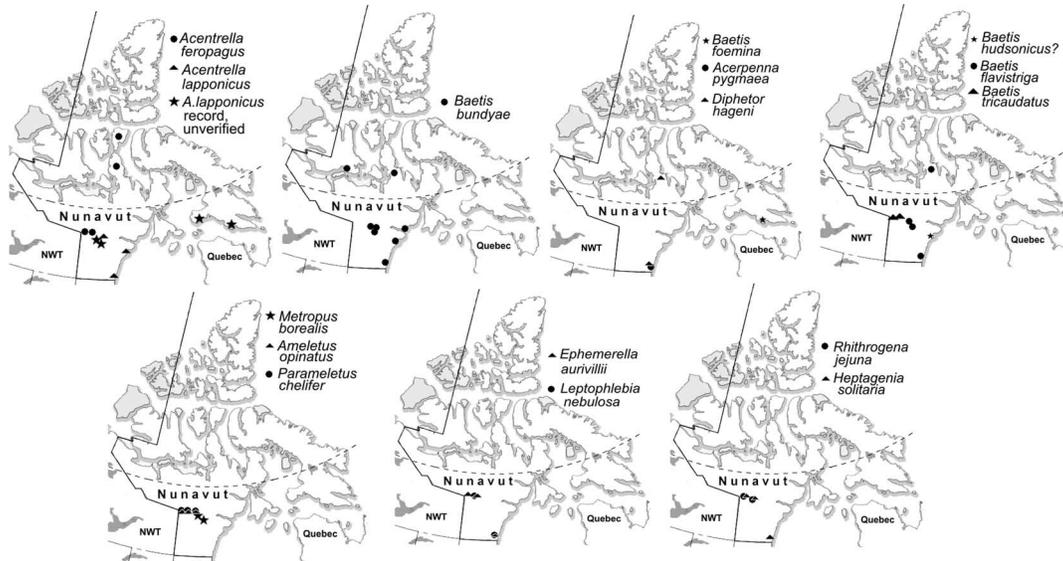
Note: Counts are for larvae except where noted. Specimens with a distinctive "wide" or "narrow" body form are indicated. An asterisk denotes individuals that were too small to sex reliably. Site numbers correspond to those in Figure 1.

which has been reported for several species of North American and European mayflies. It may be an important life-history strategy, but the details of this mode of reproduction have only recently begun to be investigated (Ball 2001; Funk *et al.* 2006). The occurrence of female-biased sex ratios is thought by many (*e.g.*, Sweeney and Vannote 1987; Gibbs and Siebenman 1996; Ball 2001) to indicate parthenogenesis. This type of life-history pattern (even with low hatching success probable in unfertilized eggs) may allow colonization of transient habitats during short summers with uncertain weather. Not only is the larval-development window very short at these high latitudes, but conditions conducive to swarming (warm, calm days or evenings, which are relatively common at lower latitudes) are short-lived and unpredictable, making

successful mating problematic. Currently, at least two species of arctic mayflies (*B. foemina* and *B. hudsonicus*) are suspected to be entirely parthenogenetic (McDunnough 1936; Ide 1937) because males have yet to be found. It is not yet possible to confirm or refute this suggestion because no detailed studies of these taxa have been made.

However, female-biased sex ratios may not always represent parthenogenesis. In a recent study, Funk *et al.* (2006) explored the genetic structure of what was believed to be a single baetid species with parthenogenetic, female-skewed sex ratios (*Centroptilum triangulifer* (McDunnough)), showing instead that two coexisting baetid species (*C. triangulifer* and *C. alamanca* (Traver)) were present. The two species were similar morphologically, but one was exclusively female and

Fig. 5. Distributions of mayfly species in Nunavut. For details of collection sites see Figure 2.



parthenogenetic, whereas the other possessed a normal life cycle with sexual reproduction. However, data collected here on *Baetis bundyae* point more towards a primarily sexually reproducing species with occasional parthenogenetic reproduction, as documented by Ball (2001) for *Stenonema femoratum* (Say) (Heptageniidae).

The *B. bundyae* specimens were similar in size and shape at given developmental stages in most of the habitats around Rankin Inlet, but some differences were seen. The larvae at site 3, for example, were much larger at given developmental stages than those at other sites. Site 3 consisted of a series of grassy ponds within the town limits that had much higher specific conductance and pH levels than ponds or streams on the tundra, which were consistently warmer than the open-tundra sites, and showed visible accumulations of filamentous algae. The larger size of these larvae may have been due to greater food availability than in other habitats, a pattern that has been reported for many mayfly species (e.g., Hinterleitner-Anderson *et al.* 1992). Both the high conductivity levels and the presence of visible filamentous algae (absent at tundra sites) point to nutrient enrichment at this site, probably because of the proximity to human habitats and nutrient sources (dogs, domestic sewage) relative to tundra sites. Some site-specific morphological differences were also seen (either a wide or a narrow body form relative to other larvae) in larvae collected on 9 July at site 1 and 17 July at site 10. The significance of these apparent

differences is not immediately obvious, since we did not collect these body forms at any of the other sites or times. They may simply be phenotypic variants resulting from some local conditions.

Information about the life history of arctic-tundra species is difficult to obtain, mainly because of the inaccessibility of the habitats. Most studies on the distribution of arctic insect species involve brief sampling trips that do not allow life cycles or overall sex ratios to be assessed or year-round information on habitat to be obtained. In this study, many sites that appeared in midsummer to be permanent and suitable for mayflies were checked, but had few or no mayflies. Information on annual ice and flow conditions was critical in interpreting species patterns. Parthenogenesis probably plays a role in new populations, and coupled with rapid development, freeze-tolerant eggs, and superior dispersal ability aided by wind, helps to explain the success of *Baetis bundyae* as well as other species in this group across arctic habitats.

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Appendix A

Appendix appears on the following pages.

Table A1. Collection sites used for the Nunavut mayfly project, 2000–2005.

Area	Locality No.*	Coordinates	Habitat description	Date	Species
Thelon River	3	64°15.215'N, 102°00.300'W	Large river, slow current	7 July 2002	<i>B. tricaudatus</i> , <i>Am. inopinatus</i>
	3	64°15.215'N, 102°00.300'W	Small tributary, moderate current	7 July 2002	<i>A. feropagus</i> , <i>B. tricaudatus</i> , <i>Baetis</i> sp. 1 and 2, <i>P. chelififer</i> , <i>Am. inopinatus</i>
	3	64°19.220'N, 101°50.185'W	Small tributary, moderate current	8 July 2002	<i>P. chelififer</i> , <i>Am. inopinatus</i>
	3	64° 9.220'N, 101°50.185'W	Small tundra pools	8 July 2002	<i>P. chelififer</i>
	3	64°19.687'N, 101°50.313'W	Large river	8 July 2002	<i>B. tricaudatus</i> , <i>P. chelififer</i>
	3	64°21.423'N, 101°48.815'W	Small brown-water tributary	9 July 2002	<i>P. chelififer</i> , <i>L. nebulosa</i>
	3	64°26.250'N, 101°43.918'W	Large tundra pond	9 July 2002	<i>B. tricaudatus</i> , <i>P. chelififer</i> , <i>Am. inopinatus</i> , <i>E. aurivillii</i> , <i>L. nebulosa</i>
	3	64°30.657'N, 101°29.605'W	Large river, slow current, sandy	9 July 2000	<i>L. nebulosa</i>
	3	64°32.420'N, 101°24.815'W	Small tributary, moderate current	10 July 2002	<i>P. chelififer</i> , <i>L. nebulosa</i>
	3	64°31.598'N, 101°16.605'W	Small tributary, moderate current	11 July 2002	<i>A. feropagus</i> , <i>Am. inopinatus</i> , <i>E. aurivillii</i> , <i>H. solitaria</i> , <i>R. jejuana</i>
Arviat	3	64°31.443'N, 101°16.263'W	Large river, fast current	11 July 2002	<i>B. tricaudatus</i> , <i>Am. inopinatus</i> , <i>E. aurivillii</i> , <i>H. solitaria</i>
	8	61°13.026'N, 94°06.482'W	Large stony stream, fast current	9 July 2004	<i>B. bundyae</i> , <i>A. lapponicus</i>
	8	61°12.801'N, 94°06.469'W	Small stony stream, fast current	9 July 2004	<i>B. bundyae</i> , <i>A. lapponicus</i>
	8	61°12.801'N, 94°06.482'W	Tundra pond seeping outflow	9 July 2004	<i>B. bundyae</i>
	8	61°09.339'N, 94°03.335'W	Large stream, pond outflow	9 July 2004	<i>B. bundyae</i>
	8	61°17.993'N, 94°04.811'W	Maguse River; large river, fast current	10 July 2004	<i>P. chelififer</i> , <i>E. aurivillii</i> , <i>H. solitaria</i>
	8	61°17.940'N, 94°05.116'W	Small tributary, slow current	10 July 2004	<i>P. chelififer</i> , <i>Am. inopinatus</i>
	8	61°15.053'N, 94°08.274'W	Small tundra pond on esker	12 July 2004	<i>B. bundyae</i>
	8	61°15.859'N, 94°13.899'W	Slow pond outflow	12 July 2004	<i>B. flavistriga</i> , <i>B. bundyae</i> , <i>Baetis</i> sp.
	8	61°13.026'N, 94°06.482'W	Stony seep from bog	12 July 2004	<i>B. bundyae</i> , <i>A. lapponicus</i>
Baker Lake	8	61°06.400'N, 94°06.200'W	Shallow grassy pond in town	13 July 2004	<i>B. bundyae</i>
	8	61°06.400'N, 94°06.200'W	Large tundra pond in town	13 July 2004	<i>B. bundyae</i>
	8	61°06.400'N, 94°06.200'W	Small pond outflow in town	13 July 20024	<i>Baetis flavistriga</i> , <i>B. bundyae</i>
	8	61°03.845'N, 94°08.621'W	Wolf Creek, braided stream	13 July 2004	<i>B. bundyae</i> , <i>A. lapponicus</i>
	6	64°19.385'N, 96°00.650'W	Tiny, stony tundra stream	14 July 2004	<i>B. bundyae</i>

Table A1 (continued).

Area	Locality No.*	Coordinates	Habitat description	Date	Species
	6	64°18.937'N, 96°03.238'W	Small, deep, grassy pond at campground	14 July 2004	<i>P. chelififer</i>
	6	64°19.139'N, 96°02.866'W	Small, stony tundra stream	14 July 2004	<i>B. bundyae</i> , <i>A. lapponicus</i>
	6	64°19.200'N, 96°02.700'W	Small, fast, stony tundra stream	14 July 2004	<i>B. bundyae</i> , <i>A. lapponicus</i>
	6	64°19.268'N, 96°02.511'W	Grassy, ditch-like stream	14 July 2004	<i>B. bundyae</i>
	6	64°22.516'N, 95°52.825'W	Prince River; large, fast river	15 July 2004	<i>Baetis</i> sp. (too small to identify)
	6	64°19.249'N, 95°58.508'W	Grassy, ditch-like stream, very fast current, inlet to Airplane Lake	15 July 2003	<i>B. bundyae</i>
	4	64°19.801'N, 96°17.691'W	Large clear stream, fast current, tributary of the Thelon River	16 July 2003	<i>B. bundyae</i>
	4	64°20.730'N, 96°19.064'W	Small, fast boulder stream, tributary of the Thelon River	16 July 2003	<i>P. chelififer</i> , <i>Am. inopinatus</i>
	4	64°23.618'N, 96°24.278'W	Small, fast boulder stream, tributary of the Thelon River	16 July 2003	<i>B. bundyae</i> , <i>P. chelififer</i>
	4	64°29.304'N, 96°28.862'W	Small fast boulder stream, tributary of the Thelon River	16 July 2003	<i>B. bundyae</i> , <i>A. lapponicus</i>
Rankin Inlet	9	62°50.600'N, 96°08.100'W	Small grassy pools in town	18 July 2003	<i>B. bundyae</i>
	9	62°48.302'N, 96°06.974'W	Hillside seep above town	18 July 2003	<i>B. bundyae</i>
	9	62°54.849'N, 92°12.652'W	Meliadine River; large river, lake outflow	19 July 2003	<i>B. bundyae</i>
	9	62°54.849'N, 92°12.652'W	Meliadine River; large river, 100 m below lake outflow	19 July 2003	<i>B. bundyae</i>
	9	62°51.532'N, 92°08.503'W	Char River, large stream, fast current	19 July 2003	<i>B. bundyae</i> , <i>A. lapponicus</i>
	9	62°49.152'N, 92°11.931'W	Tundra pond, overhanging peat, boulder substrate	20 July 2003	<i>B. bundyae</i> , <i>B. hudsonicus</i>
	9	62°51.752'N, 92°13.077'W	Char River above Landing Lake; large stream, fast current	6–20 July 2005	<i>B. bundyae</i> , <i>B. flavistriga</i> , <i>A. ferropagus</i>
	9	62°51.933'N, 92°11.508'W	Large stream, fast current, Landing Lake outlet	11–19 July 2005	<i>B. bundyae</i>

Table A1 (concluded).

Area	Locality No.*	Coordinates	Habitat description	Date	Species
	9	62°48.687'N, 92°05.627'W	Grassy pools in town	12–18 July 2005	<i>B. bundyae</i>
	9	62°51.570'N, 92°08.653'W	Char River at bridge; large stream, fast current	12–18 July 2005	<i>B. bundyae</i> , <i>A. feropagus</i>
	9	62°52.252'N, 92°10.622'W	Small stream, pond outlet	12 July 2005	<i>B. bundyae</i>
	9	62°54.852'N, 92°12.655'W	Meliadine River; large river, lake outflow	12 July 2005	<i>B. bundyae</i>
	9	62°54.517'N, 92°12.392'W	Meliadine River; large river, 200 m below lake outflow	13 July 2005	<i>B. bundyae</i>
	9	62°54.517'N, 92°12.392'W	Tundra pond	13 July 2005	<i>B. bundyae</i>
	9	62°51.448'N, 92°12.692'W	Tundra pond	17 July 2005	<i>B. bundyae</i>
	9	62°51.510'N, 92°12.822'W	Tundra pond	17 July 2005	<i>B. bundyae</i>

*Locality numbers correspond to those in Figure 2.