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Ecological Characteristics of Streams in the Barrenlands near Lac de Gras, N.W.T., Canada

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ABSTRACT. We examined spatiotemporal variation in the physical, chemical, and biological characteristics of pristine streams that represent a range of conditions near Lac de Gras in the Barrenlands region of the Northwest Territories, Canada. Principal component analysis organized streams into four groups on the basis of seven physical characteristics. Despite broad differences among groups in physical characteristics, variation in chemical and biological characteristics was generally not large, with only pH and coarse particulate organic matter differing among the four groups. Nevertheless, several chemical and biological variables were correlated with physical characteristics, particularly measures of stream size (bankfull width and depth, drainage area, and stream discharge). Annual variability in climate affected stream temperature and discharge and influenced several biotic characteristics, particularly the growth of young-of-the-year arctic grayling (*Thymallus arcticus*). Barrenland streams share basic characteristics of Alaskan tundra streams, as a result of similar climatic regimes. Key differences between the two areas, however, appear related to the lake-outlet nature of the Barrenland streams, which may contribute to higher growth of young-of-the-year arctic grayling than would be expected from regional climate.

Key words: streams, Barrenlands, tundra, reference condition, spatiotemporal variation, lake-outlet, arctic grayling, *Thymallus arcticus*, drift, Lac de Gras, Northwest Territories

RÉSUMÉ. On a étudié la variation spatio-temporelle dans les caractéristiques physiques, chimiques et biologiques de cours d'eau vierges qui témoignent d'une gamme de conditions près du lac de Gras dans la région des Barrenlands, dans les Territoires du Nord-Ouest, au Canada. L'analyse des composantes principales a divisé les cours d'eau en quatre groupes, d'après sept caractéristiques physiques. En dépit de différences marquées dans ces dernières entre les groupes, la variation dans les attributs chimiques et biologiques n'était généralement pas très grande, avec seulement le pH et les grosses particules organiques qui montraient des différences entre les quatre groupes. Plusieurs variables chimiques et biologiques étaient néanmoins corrélées avec les attributs physiques, en particulier les mesures de la taille des cours d'eau (largeur et profondeur du débordement, aire de drainage et débit). La variabilité annuelle du climat avait une incidence sur la température et le débit des cours d'eau et elle influençait plusieurs caractéristiques biotiques, en particulier la croissance des jeunes de l'année chez l'ombre arctique. Les cours d'eau des Barrenlands ont en commun les caractéristiques fondamentales des cours d'eau de la toundra alaskienne, vu qu'ils sont soumis à des régimes climatiques similaires. Les différences majeures entre les deux régions semblent cependant liées au fait que la décharge des cours d'eau des Barrenlands se fait dans un lac, ce qui pourrait contribuer à une croissance des jeunes de l'année chez l'ombre arctique plus forte que le climat régional ne le laisserait croire.

Mots clés: cours d'eau, Barrenlands, toundra, condition de référence, variation spatio-temporelle, décharge dans un lac, ombre arctique, dérive, lac de Gras, Territoires du Nord-Ouest

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INTRODUCTION

In the last 50 years, Arctic regions have experienced a steady expansion in the development of their natural resources. This growth has increased local environmental pressures and impacts, while regionally, the Arctic is being affected by depletion of ozone, climate warming, and long-distance transport of contaminants (Schindler, 2001). These increasing pressures have not been matched by increases in research directed toward assessing, predicting, or mitigating ecosystem impacts, or even defining reference conditions needed to take such actions (Reist, 1997).

For the reference-condition approach of impact assessment to succeed, we need data on physical, chemical, and biological conditions from an appropriate set of minimally affected reference sites to compare with data from potentially impaired sites (Reece et al., 2001). In many areas of North America, development has left few "pristine"

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ecosystems available for use as reference sites (e.g., Benke, 1990). This severely limits our ability to make sound management decisions or to evaluate the success of those decisions (Minns, 1996; Karr and Chu, 1999). In the Arctic, however, the problem is nearly the reverse (Oswood, 1997); there are many ecosystems still in relatively pristine condition, yet we know little about their ecological characteristics. For effective protection, management, and restoration of Arctic ecosystems, more knowledge is needed concerning the characteristics of appropriate reference sites.

This lack of information applies to the physical, chemical, and biological characteristics of Arctic streams and rivers (Schindler, 2001), although there are exceptions, notably from Alaska. Pioneering studies (e.g., Watson et al., 1966; Kalff, 1968) surveyed large areas, tending to collect physicochemical data, but made few comparisons in a broader context. More synthetic was Craig and McCart's (1975) classification of stream types in Beaufort Sea drainages, based mainly on physiographic characteristics. In 1983, the R4D program (Response, Resistance and Resilience to, and Recovery from, Disturbances in Arctic Ecosystems) was established, focusing efforts on the Imnavait Creek watershed in the northern foothills of the Brooks Range, Alaska (e.g., Everett et al., 1989; Kane et al., 1989; Miller and Stout, 1989; Oswood, 1989; Oswood et al., 1989; Irons and Oswood, 1992). Since 1978, research on the Kuparuk River, Alaska, has provided valuable insight into biological and chemical processes of Arctic rivers (Peterson et al., 1993; Hershey et al., 1997). More recently, Kling et al. (2000) investigated the spatial and temporal patterns of change in limnological variables of streams in the Toolik Lake District. In addition, a large body of gray literature has been generated in response to resource development; however, most of this work has focused on specific, local concerns, rarely placing them in a larger context, (e.g., to establish regional reference conditions).

In the present study, we examine the physical, chemical, and biological characteristics of streams in the Barrenlands region of the Northwest Territories, Canada. Specifically, we ask: what is the pattern of variation in the physical characteristics of Barrenland streams? Do these patterns reflect patterns in chemical and biological characteristics? How does annual variability in climate and the physicochemical characteristics of streams affect stream biota? Our intention is to use these observations to establish reference conditions for the region. To enhance our general understanding of Low Arctic rivers and streams, we also compare the largely lake-outlet Barrenland streams with other Arctic stream ecosystems.

STUDY AREA

The 4000 km^2 study area is centred on 64˚45′N, 110˚30′W (see Fig. 1), about 100 km north of the tree line within the Southern Arctic ecozone. The physiographic region, the Kazan Upland, is underlain by granite, gneiss, and schist that form broad, sloping uplands, plateaus, and lowlands. Eskers, kames, and boulder-strewn till plains cover the land. The mean annual temperature is approximately -12˚C, with a summer maximum of 27.2˚C and a winter minimum of -53.9˚C (Environment Canada, 1991). The climate is semiarid, with 200 – 300 mm of precipitation annually, 50% of which falls as snow. The permafrost layer is continuous. Thin soils in upland areas support dwarf-heath and scattered low-shrub tundra, while lowland and depressional areas near lakes and streams are characterized by sedge tussock and low-tall shrub tundra (Bliss, 1981).

The combination of relatively low topographical relief (ca. 50 m) and extensive glacial activity has moulded a landscape covered by ca. 21% water, in the form of numerous chains of lakes and connecting streams. Following spring runoff, evaporation from lakes gradually lowers lake level, stream flows diminish, and surface flow is lost from many small streams. At approximately 450 m above sea level, the streams of this area are the headwaters of the Coppermine, Back, and Burnside Rivers, which flow north to the Arctic Ocean.

METHODS

Data were collected during three summers (1998 – 2000) from streams representing a range of physical characteristics observed in the Barrenlands region. Stream selection was based mainly on proximity to base camp (within a ca. 40 km radius) and the presence of visible water in the stream channel during initial surveys in late July. Initially, nine core streams were sampled for benthic invertebrates, water chemistry, woody debris, substrate coarse particulate organic matter, epilithon, basic physical characteristics, and fish community composition. Two of these streams, Polar-Vulture and Pigeon, were subjected to intensive fisheries and invertebrate drift investigations. In 2000, an additional 11 streams were surveyed for basic physical characteristics and fish community composition.

Physicochemical Characteristics

Stream geomorphology, including length, drainage area, slope, bankfull width and depth, and substrate composition, was determined for the twenty streams both on the ground and from aerial photographs and topographic maps. Stream length was measured as the thalweg distance from the upstream lake to the downstream lake. Substrate composition was quantified along several transects perpendicular to stream flow and classified as clay and silt (< 0.0625 mm), sand (0.0625 – 2 mm), small gravel (2 – 32 mm), large gravel (32 – 64 mm), cobble (64 – 256 mm), or boulder (> 256 mm). Discharge measurements were made manually (once for each stream) in late July to mid-August, and additional data were collected by automated stage recorders.

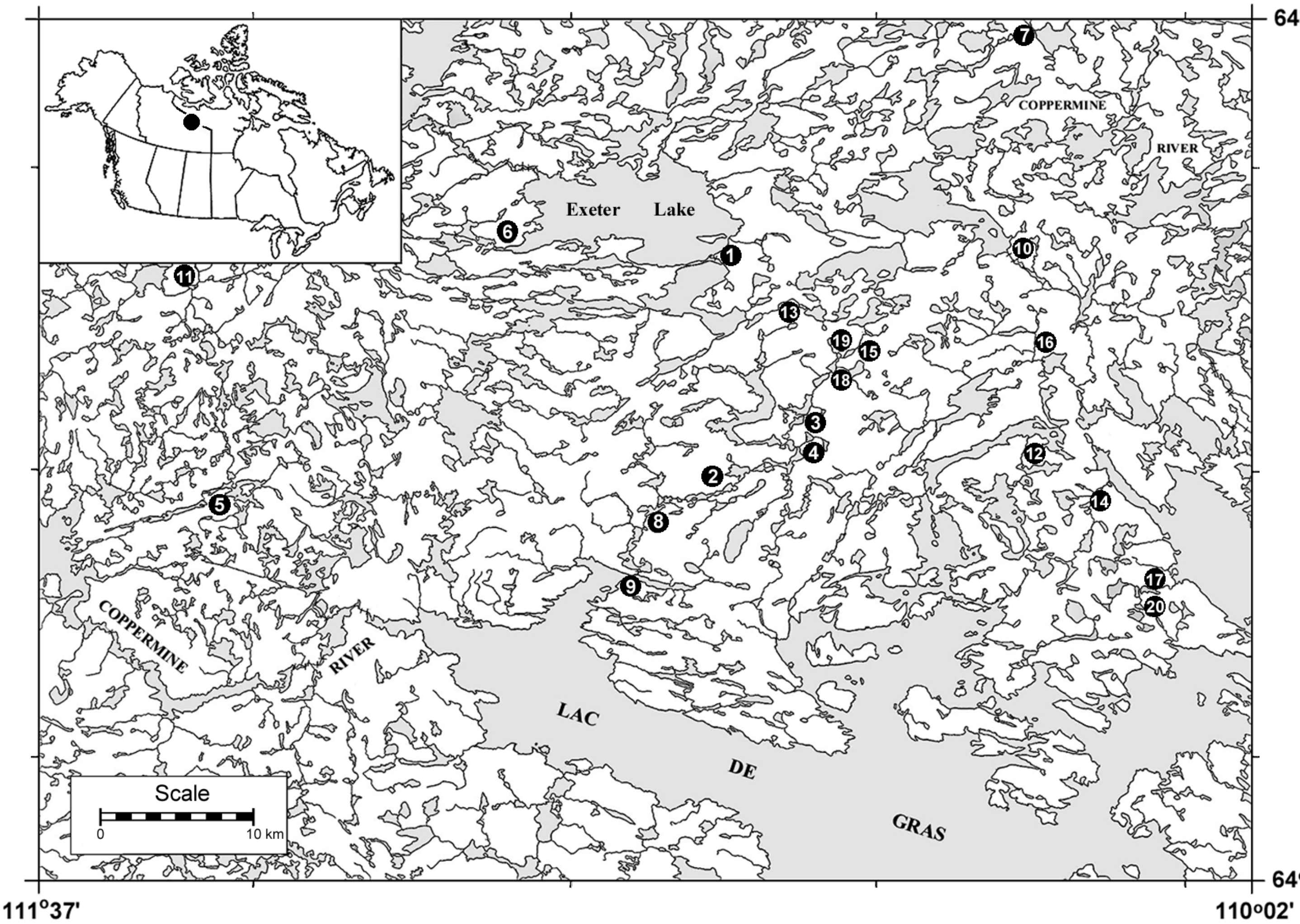

FIG. 1. Map showing the Lac de Gras study area, with study stream locations indicated by black dots (●). Numbers within dots correspond to streams listed in Table 1. Insert: Location of study area in the Northwest Territories, Canada.

Weather data were collected during the ice-free season from a meteorological station situated in a central location on the study area. Rain was measured daily with an automatic tipping bucket. Air temperature (± 0.5˚C) was measured automatically every hour at a height of 1.9 m above ground level. Hobo temperature loggers recorded stream water temperature (± 0.1˚C) in Polar-Vulture and Pigeon streams every four hours.

For the nine core streams, we measured limnological parameters in the field. Dissolved oxygen concentrations (± 0.01 mg/L) were determined with a WTW Multiline P4 portable meter fitted with a CellOx 325 probe. Conductivity (± 1 μS/cm) and pH (± 0.01 pH unit) were measured with the same meter fitted with a TetraCon 325 and SenTix 41 probe, respectively. Turbidity (± 0.1 nephelometric turbidity units) was measured using a Global Water turbidity meter. Stream water samples (three from each stream) were collected in late July and stored in a cold, light-free environment for later laboratory analysis.

In the laboratory, total nitrogen was analyzed using the persulfate digestion method and determined on a Technicon Autoanalyzer. Total organic carbon (TOC) in 1999 and dissolved organic carbon (DOC) in 2000 were determined using a Shimadzu total organic carbon analyzer (Model TOC5000A) fitted with an ASI–5000A autosampler. DOC samples were filtered (0.5 μm) prior to measurement. Total phosphorus (±1 μg/L) was determined spectroscopically, using persulfate-oxidized samples, by molybdate blue absorption. Total suspended solids were determined gravimetrically from total residue retained by a standard glass fibre filter (0.45 μm), dried to a constant weight at 105˚C.

Biological Characteristics

All pieces of woody debris longer than 10 cm were counted along 40 to 150 m lengths of stream channels for the nine streams. We measured the length of each piece, determined the mean diameter by averaging the diameters at each end, and converted these dimensions to volume estimates. Woody debris volume was standardized as $cm^3/100\ m^2$ by multiplying the transect length by

TABLE 1. Physical characteristics of the 20 study streams from the Lac de Gras region of the Barrenlands, N.W.T., Canada, that were used in the principal component analysis of Figure 2. Fine substrates include clay, silt, and sand, and coarse substrates include cobble and boulder. Roman numerals refer to the four groups of streams from Figure 2. A single asterisk indicates streams sampled for benthic invertebrates, water chemistry, woody debris, organic matter, and epilithon. A double asterisk indicates streams intensively sampled for fish and drifting invertebrates. The remaining 11 streams were surveyed for physical characteristics and fish community composition.

No.	Group	Stream	Drainage area (km^2)	Length (m)	% Slope	Bankfull width (m)	Bankfull depth (m)	Depth:Width	% Fine	% Coarse
1*	I	Norm's Camp	223	600	2.0	35.0	0.89	0.025	5	73
2	I	Nema Martine	114	120	0.2	41.1	0.49	0.012	0	95
3	I	Kodiak-Little	36	80	0.1	43.6	0.50	0.011	0	95
4	I	Moose Nero	87	90	0.1	48.3	0.50	0.010	0	100
5	II	Bedrock	46	520	2.5	14.9	0.49	0.033	10	75
6	II	Sandy	55	350	2.9	9.0	0.45	0.050	8	78
7	II	Nanuq	14	425	0.9	14.7	0.31	0.021	5	75
8*	II	Slipper Rene	176	410	1.2	17.5	0.39	0.022	2	93
9*	II	Slipper Lac de Gras	185	280	2.9	20.0	0.29	0.015	5	80
10*	II	Ursula	86	250	8.0	15.5	0.47	0.031	4	85
11	II	Snow	87	225	8.9	6.2	0.42	0.067	0	95
12	III	Willow	29	2020	1.5	5.1	0.73	0.143	75	20
13**	III	Pigeon	9	2900	0.5	2.4	0.46	0.192	30	58
14*	III	Counts	4	1200	0.6	3.7	0.31	0.083	48	33
15**	III	Polar-Vulture	7	700	1.4	2.7	0.44	0.163	20	55
16*	III	Pikejaw	39	1710	1.8	3.9	0.52	0.135	10	76
17	III	Christine	15	2050	1.2	4.9	0.50	0.102	5	85
18*	IV	Grizzly	7	180	0.4	2.9	0.25	0.087	18	67
19	IV	Polar Panda	9	230	3.0	3.5	0.43	0.123	10	75
20	IV	Cujo	2	150	1.7	2.8	0.21	0.077	20	70
		Median		380	1.5	7.6	0.45	0.058	6	76
		SD		810	2.4	15.1	0.15	0.057	19	20

the mean stream width measured at four locations along the transect.

Five replicate samples of substrate coarse particulate organic matter (CPOM), epilithon, and benthic invertebrates were collected from the nine core streams in late July, in both riffles (mean depth and velocity, 0.24 m and 0.25 m/s; n = 9) and pools (mean depth and velocity, 0.34 m and 0.08 m/s; n = 8). CPOM samples were from substrate cores, 90 mm deep by 80 mm diameter. Within 48 hours, we washed the samples, removing inorganic material and invertebrate cases and exuviae, and sieved them through 1 mm mesh. Filtered organics on the screen were dried to constant mass at 40˚C (± 0.1 mg). Epilithon samples were scraped from the upper surfaces (4.9 or 9.6 cm^2) of randomly selected stones. Invertebrates visible without the aid of magnification were removed from scrapings. Samples were stored frozen in the dark for two to four weeks before being dried at 40˚C, weighed, ashed at 550˚C, and reweighed for ash-free dry mass determination (± 0.1 mg). Benthic invertebrate samples were collected using a 0.093 m^2 (1 sq. ft.) Surber sampler with 0.25 mm mesh. All samples were preserved with 70% ethanol in the field. Invertebrates were identified to genus or species, with the exception of Nematoda, Turbellaria, and terrestrial invertebrates, which were typically identified only to Family or Order. Following enumeration, samples were dried to constant mass at 40˚C (± 0.1 mg).

Invertebrate drift was sampled in July-August from Polar-Vulture in 1999 and from Polar-Vulture and Pigeon streams in 2000 with two Field-Dodgson tri-net drift samplers (0.25 mm mesh). Samples were collected during summer, three times in 1999 and four times in 2000. During each period, samples were collected at dawn, noon, and dusk. Drift samples were preserved in 70% ethanol and later counted and identified as described for benthos.

Eighteen streams were electrofished at least once over the course of the study to determine fish community composition and catch-per-unit-effort (fish per minute). To assess their first summer's growth, we collected young-of-the-year (YOY) arctic grayling (*Thymallus arcticus*) in late summer, just before the out-migration, from one stream in 1998, two streams in 1999, and 10 streams in 2000. For both types of sampling, captured fish were identified, enumerated, weighed (± 0.01 g), and measured (fork length ±1 mm).

Statistical Analyses

We applied principal component analysis, using the correlation matrix, to summarize the pattern of variation among all 20 streams on the basis of seven physical characteristics (see Table 1). We used analysis of variance (ANOVA) to compare chemical and biological variables among the resulting groups of streams. Linear regression was used to examine relationships of the chemical and biological variables to the physical characteristics. Logistic regression was used to examine the presence of pike in relation to physical characteristics. ANOVAs were also used to examine among-year variability in biotic characteristics; significant ANOVAs were followed by Tukey multiple comparison tests. Lastly, paired t-tests were used to determine whether densities or biomass of coarse particulate organic matter, epilithon, and benthic invertebrates differed between riffles and pools. We used the Kolmogorov-Smirnov test to examine data for normality and the Levene median test for homogeneity of variances. For all statistical tests, we used $\alpha = 0.05$ as a critical level of significance (after performing the Bonferroni adjustment, when that was required, to reduce the experimentwise error rate).

RESULTS

Physicochemical Characteristics

Although physical characteristics varied among the 20 study streams, virtually all Barrenland streams are lake-outlet systems of moderate length (Fig. 1, Table 1). Streams flow over folded rock and glacial features, creating highly irregular drainage patterns, but occasionally follow trellis and dendritic configurations for short distances. They typically have a low sinuosity, are “braided” (or, more appropriately, multi-channelled), with up to seven channels, and are dominated (> 50%) by large boulders. Stream channel slopes ranged from 0.1% to 8.9%, but most were less than 3%.

Principal component analysis organized the 20 streams into four groups on the basis of seven physical characteristics (Fig. 2, Table 1). Axis 1 explained 67% of the total variance, and Axis 2 explained 27%. Drainage area was not included in the analysis because it was highly correlated with bankfull width (r = 0.55). The four Group I streams are short, wide, and boulder-dominated. They generally follow weak hydraulic gradients through unconfined channels. Although these streams are moderately deep, their depth-to-width ratios are low. The seven streams in Group II are of medium length and contain a moderate diversity of substrate sizes, with water flowing through unconfined, braided channels of moderate widths with moderate-to-high gradients. The six streams in Group III comprise some of the longest and narrowest streams of the region, which generally follow one or two confined channels. This group also has the greatest depth-to-width ratios: some sections of stream are deeper than they are wide. The streams in this group have low-to-moderate stream gradients and a moderate-to-high proportion of fine substrates. The three Group IV streams are braided, short, and narrow, with moderate gradients and depth-to-width ratios, and contain a mixture of substrate sizes.

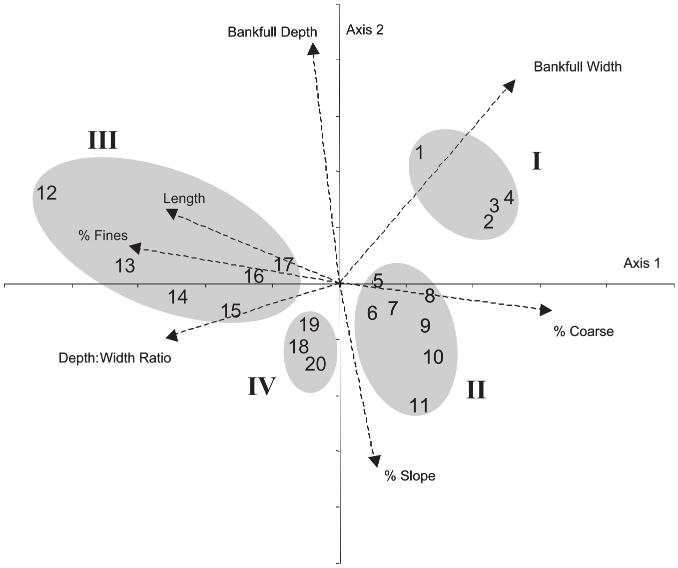

FIG. 2. Principal component analysis ordination of the 20 study streams (numbered as in Table 1), based on seven physical variables. Vectors (arrows) point in the direction of increasing values for the respective variables, with vector length reflecting the strength of the relationship. Shaded ellipses highlight four groups of physically similar streams (see text for details).

Hydrothermal Regime: Climate governs surface hydrological processes of this area. Streams are frozen solid from approximately late September to late May. The snow pack melts rapidly during freshet, creating a large peak in discharge. Stream hydrographs (BHP Billiton Diamonds Inc., unpubl. data) indicate that seasonal variation in mean daily discharge is moderately high, ranging from 15 to 100-fold of minimum summer flows in Polar-Vulture Creek. Over the summer, water levels fall slowly, substantially reducing flows to side channels or leaving them hydraulically isolated, especially in highly braided streams. In autumn, precipitation increases stream discharges to ca. five times the minimum summer flows, reconnecting stream channels. Though not measured, groundwater movement is probably limited in this region by a shallow active layer, relatively low relief, and mud/clay soils that typically have a low hydraulic conductivity.

Among the three study years, 1998 was relatively dry and hot, 1999 was moderately wet and cool, and 2000 was intermediate. Correspondingly, the initiation date of freshet varied by 17 days among years (Table 2). Mean daily discharge also varied by a factor of four among years, being lowest in 1998 and highest in 1999 (Table 2). Stream water temperatures often reached 21˚C, but daily averages during the summer typically ranged between 12˚ and 15˚C. Diel fluctuations in temperature averaged 3˚C and rarely exceeded 6˚C. From 1 June to 1 September, streams accumulated 960–1226 degree-days; we estimate that from ice-out to ice-on, streams would have accumulated an additional 100–200 degree-days.

Water Chemistry: Barrenland stream water is circumneutral and low in total phosphorus and total nitrogen (Table 3). Levels of turbidity, DOC, and suspended solids are highest in the spring and fall, coinciding with higher flows. Overall, water chemistry varied little among the core streams (Table 3). Only pH varied among the four groups of streams ($F_{3,5} = 36.6$, $p = 0.002$, group I > II > III = IV) and was positively correlated with bankfull width (r = 0.94, n = 9, $p < 0.001$). There was also a positive correlation between TOC and drainage area (r = 0.72, n = 5, $p = 0.032$).

TABLE 2. Annual variation (1998–2000) in accumulated mean monthly air temperature and precipitation, accumulated mean daily degree-days and mean daily discharge from 1 June to 1 September, and date of freshet initiation for the study area and streams in the Barrenlands, NWT, in relation to several biotic characteristics of the streams. Numbers in parentheses are standard errors among streams for Polar-Vulture, Pikejaw, and Slipper-Lac de Gras (except those for drift density and YOY length and mass, which are from Polar-Vulture Creek). ANOVAs and multiple comparisons were used to determine significant differences among years.

Variable	1998 A	1999 B	2000 C	*p* value	Post hoc testing
Air temperature (˚C)	37	28	34		
Rainfall (mm)	88	180	118		
Degree-days (˚C)	1226	930	1079		
Discharge (m^3/s)	2.9	12.8	11.8		
Initiation of freshet	May 14	May 31	May 24		
Epilithon (mg/cm^2)	1.7 (0.7)	2.0 (0.6)	1.9 (0.4)	0.941	
Benthic density (individuals/m^2)	31 484 (7541)	3423 (565)	13 720 (1891)	0.046	A B AB
Benthic biomass (g/m^2)	13.7 (4.7)	0.5 (0.1)	1.2 (0.3)	0.023	A B B
Drift density (individuals/100 m^3)		4400 (3235)	14 425 (5686)	0.225	
YOY length (mm)	77	56.7 (0.5)	63.9 (0.9)	< 0.01	A B C
YOY mass (g)	3.8	1.78 (0.05)	2.55 (0.12)	< 0.01	A B C

TABLE 3. Physical and chemical properties of water from Barrenland streams in late July, 1998–2000. Ranges from Alaskan tundra streams are provided for comparison (see text). SE is standard error and n is the number of streams sampled.

Variable	Mean	SE	n	Min–Max	Alaska[1]
Dissolved oxygen (mg/L)	9.8	0.2	9	8.2 – 12.0	9.9 – 12.6
% Saturation	95.3	2.8	9	81.0 – 121.9	75 – 100
Conductivity (μS/cm)	14.3	1.1	9	8.0 – 19.2	21 – 125
pH	6.78	0.14	9	5.87 – 7.52	5.3 – 8.2
Turbidity (NTU)	0.4	0.04	8	0.2 – 0.5	0.9 – 1.8
Total suspended solids (mg/L)	1.78	0.28	8	1.5 – 3.7	5.4 – 6.1
Total phosphorus (μg/L)	6.92	0.72	9	4.00 – 10.20	< 10 – 21
Total nitrogen (μg/L)	167.2	8.9	9	143.3 – 202.1	~300
Dissolved organic carbon (mg/L)	3.06	0.12	5	2.56 – 3.48	2.3 – 9.6
Total organic carbon (mg/L)	5.25	0.19	6	4.67 – 5.83	6.8 – 9.9

[1] Data from Watson et al. (1966), Craig and McCart (1975), Oswood et al. (1989), Peterson et al. (1992), and Hershey et al. (1997).

Biological Characteristics

Organic Matter: Many streams pass through thick growths of dwarf birch and willow, producing considerable quantities of coarse particulate organic matter (CPOM, Table 4) and relatively small pieces of woody debris (mean length, 370 mm; mean diameter, 5 mm). Woody debris volumes were 917 ± 350 $cm^3/100\ m^2$ of stream (mean ± SE). Barrenland caribou (*Rangifer tarandus*) also add sizeable amounts of woody debris when migrating across the streams by trampling the riparian shrubs and kicking pieces into the stream (N. Jones, pers. obs.).

The quantity of epilithon ($F_{3,5} = 0.05$, $p = 0.832$) and woody debris ($F_{3,5} = 1.94$, $p = 0.222$) did not differ among the four groups of streams. There were no correlations between individual physical stream characteristics and epilithon and woody debris. CPOM, however, differed among stream groups ($F_{3,5} = 8.43$, $p = 0.034$, group II > III, I = IV). CPOM was also correlated with substrate type, increasing as the percentage of coarse ($r = 0.77$, $p = 0.016$) and fine ($r = 0.72$, $p = 0.028$) substrates increased. Pools generally contained larger amounts of CPOM (paired $t = 2.7$, $p = 0.015$) and epilithon (paired $t = 4.1$, $p = 0.001$) than did riffles (Table 4). By mid-July, most pools contain an abundance of aquatic plants (e.g., bur-reed, *Sparganium hyperboreum*, and mare's tail, *Hippuris vulgaris*). Riffles contain few instream plants, aside from filamentous algae (*Zygnema* spp.), which grow profusely in some areas, covering up to 30% of the stream bed by mid-August.

Benthic Invertebrates: Dipterans were well represented in all streams, contributing about 43% of all individuals and consisting of 10 families. Chironomidae were numerically dominant (Table 5) and comprised 29 genera. Similarly, most benthic biomass (42%) was contributed by Dipterans, 19% of which were chironomids. Dominant members of the poorly represented Ephemeroptera, Trichoptera, Plecoptera (ETP) group included *Baetis tricaudatus*, *Brachycentrus* spp., and *Nemoura* spp. Mean density and biomass of benthic invertebrates varied considerably among years (Table 2) and streams (Table 4), but density did not differ among the four groups of streams ($F_{3,5} = 4.52$, $p = 0.087$). Density increased, however, with bankfull depth ($r = 0.84$, $p = 0.005$). Although riffles and pools differed in their organic matter content (CPOM, epilithon), they contained similar numbers of invertebrates (paired $t = 1.4$, $p = 0.170$, Table 4).

Invertebrate Drift: Drift was composed mainly of microcrustaceans, including cladocerans, copepods, and ostracods (Table 5). The remaining organisms consisted primarily of dipterans and mites. Drift density differed

TABLE 4. Characteristics of coarse particulate organic matter (CPOM), and biota from study streams in the Barrenlands, NWT. Data are from late July 1998–2000 except those for fork length and mass of young-of-the-year (YOY) arctic grayling, which are from late August. CPOM, epilithon, and benthic density and biomass are subdivided into riffles and pools, all of which were significantly different except for benthic densities. SE is standard error and n is the number of streams sampled. Min and max represent the minimum and maximum values from all samples.

Variable		Mean	SE	n	Min – Max
CPOM (g/m^2)	Riffles	72.2	10.8	9	9.5 – 148.5
	Pools	92.3	7.4	8	15.3 – 218.8
Epilithon (mg/cm^2)	Riffles	1.7	0.4	9	0.64 – 4.2
	Pools	2.8	0.4	8	0.9 – 7.26
Benthic biomass (g/m^2)	Riffles	9.2	3.7	9	0.26 – 28.9
	Pools	5.2	1.9	8	0.25 – 18.3
Benthic density (individuals/m^2)	Riffles	24 037	6139	9	1620 – 90 380
	Pools	15 934	3236	8	2483 – 41 477
Drift density (individuals/100 m^3)		12 055	2642	2	152 – 188 690
Drift biomass (mg/100 m^3)		156.9	42.4	2	10.9 – 936.7
YOY length (mm)		68.4	4.8	10	42 – 89
YOY mass (g)		3.0	0.5	10	0.78 – 6.29

little between the two streams sampled in 2000 (Table 4), but varied greatly between years in Polar-Vulture (Table 2). Catastrophic drift was associated with the seasonal caribou migration. For example, on 12 July 1999, a drift sample was collected 50 m downstream from where ca. 100 caribou had crossed the Polar-Vulture stream 30 minutes earlier. This sample contained eight times the drift biomass of a sample measured three days later (Fig. 3). Most of the difference was due to larger non-microcrustaceans, the July 12 sample contained 50 times as many as the July 15 sample. The microcrustacean fraction, in contrast, was similar in the two samples.

Fish: Nine species of fish were found in the study streams (Table 6). All streams contained at least one species (max. = 6), but modal richness was only three species, typically arctic grayling, burbot (*Lota lota*), and slimy sculpin (*Cottus cognatus*). Arctic grayling were numerically dominant in most streams (Table 6). Species richness was strongly and positively related to minimum summer discharge (r = 0.88, p = 0.001, Fig. 4), as well as to basin area (r = 0.72, p = 0.001), and negatively related to the distance to source populations (r = 0.41, p = 0.08), e.g., the Coppermine River. The presence of pike was marginally related to the difficulty of colonizing a stream, determined by the stream's slope (rise: run), i.e., its elevation above and distance from source pike populations (r = 0.45, p = 0.075). Catch-per-unit-effort (CPUE) of all fish did not differ among the four stream groups ($F_{3,5} = 1.11$, $p = 0.377$), nor was total CPUE related to any single physical variable.

Adult grayling began their spawning migration from lakes as soon as water began to flow in stream channels. The peak of migration coincided with decreasing discharge after the main freshet, when water temperatures hovered around 0˚C. Adult migration was followed by migrations of juvenile grayling and, where they occurred, lake trout and burbot. Once in the streams, male grayling quickly established and defended territories. Spawning activity peaked when water temperatures reached 5˚C and was concentrated in moderately fast-flowing, turbulent, and gravelly areas. Fish activity, including migration, aggressive behaviour, spawning, and feeding, generally increased over the course of a day as water temperatures increased. After spawning, adult grayling normally spent several days feeding, particularly in large pools, before returning to lakes. Occasionally, adult grayling would be found trapped in pools by low summer water levels.

TABLE 5. Comparison of mean density and percentage composition of benthic invertebrates and drift. Benthos data are from nine Barrenland streams in 1998–2000, whereas drift data are from Polar-Vulture stream in 1999–2000 and Pigeon Creek in 2000. The composition of Diptera is further subdivided into four groups by percent composition. Invertebrate densities are shown as individuals per m^2 for benthos and as individuals per 100 m^3 for drift.

Benthic group	Benthos	Drift
Density (± SE)	23485 (5557)	11999 (2642)
Composition (%)		
Crustacea	11.8	90.4
Diptera	43.2	6.7
(*Diptera*)	(2.0)	(5.5)
(*Chironomidae*)	(84.1)	(34.7)
(*Simuliidae*)	(13.9)	(57.5)
(*Culicidae*)	(0.0)	(2.3)
ETP[1]	2.6	0.5
Nematodes, Oligochaetes, and Turbellaria	10.9	0.1
Hydracarina	1.7	2.0
Hemiptera, Coleoptera, and Hymenoptera	0.1	0.2
Mollusca	1.6	0.0
Other (mainly Coelenterata)	28.0	0.1

[1] ETP = Ephemeroptera, Trichoptera, and Plecoptera as a group.

Arctic grayling fry were first observed 21 to 24 days (183–192 degree-days) after spawning. At this time, young were 11 to 13 mm in length and yolk sacs were often visible. Young remained in their natal stream, although some were found inhabiting the margins of lakes in August. During the low flows in August, YOY grayling concentrated in the larger pools, some of which became hydraulically isolated from the main stem. However, by

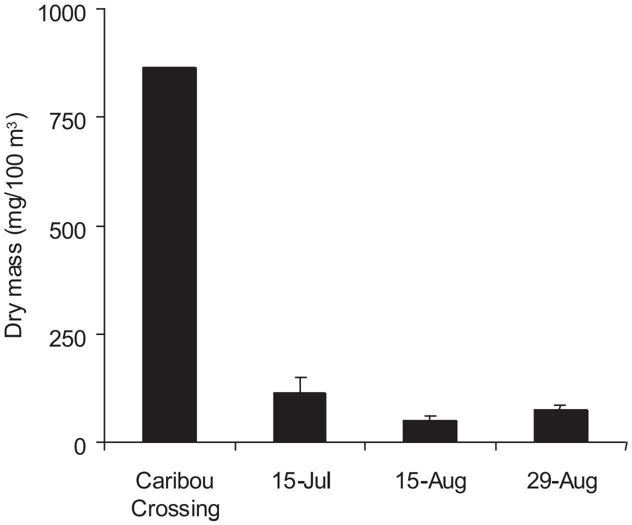

FIG. 3. Mean ± SE drift biomass found at Polar-Vulture Creek on 12 July, 15 July, 15 August, and 29 August 1999. Estimates for each date are based on 18 samples except for the caribou stream crossing estimate (July 12), which is from a single sample collected 30 minutes after a herd of ca. 100 caribou crossed Polar-Vulture Creek.

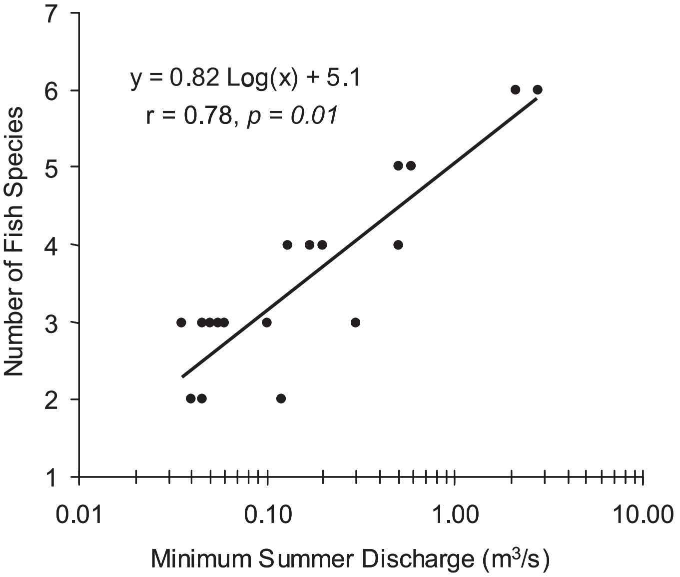

FIG. 4. Relationship between number of fish species found in 18 study streams and the minimum summer discharge, based on surveys in mid-August 2000.

mid-August, the combination of rains and cooler temperatures replenished lakes and streams, increasing discharges and reconnecting channels. At this time, YOY began migrating to the lakes to overwinter. YOY averaged 68.4 mm ± 4.8 SE in fork length and 3.0 g ± 0.5 SE in mass, but this varied among years in relation to differences in temperature, discharge, and invertebrate densities (Table 2).

Although there was considerable variation in the size of YOY grayling among streams (Table 4), grayling from the four groups of streams, identified by their physical characteristics, did not differ systematically in this respect ($F_{3,4}$ = 0.13, $p = 0.879$), nor did they differ in terms of catch-per-unit-effort of YOY grayling ($F_{3,13}$ = 1.56, $p = 0.399$), or % grayling in the fish community ($F_{3,13}$ = 0.11, $p = 0.955$). Similarly, individual physical variables did not correlate ($p > 0.05$) with YOY mass in late August or with % grayling within the fish community. However, CPUE for YOY grayling, in streams containing grayling, was negatively correlated with stream width (r = 0.64, $p = 0.020$).

DISCUSSION

Physicochemical Characteristics

Although virtually all Barrenland streams originate as lake outlets, and thus share some important attributes (see below), our analyses indicate that they have diverse physical characteristics, including length, width, and substrate composition. Because of covariation among stream attributes, however, we could identify four groups of streams with similar physical characteristics. For example, streams that drained areas of fine sediment tended to have a greater depth-to-width ratio and single, well-defined channels, whereas the boulder-filled streams were typically braided or, more accurately, multi-channelled. In contrast to the streams typically described as “braided,” Barrenland streams have very stable banks, low sediment loads, and discharges that are not highly variable. Sections of land between channels, the islands, are mainly the result of colluvial, not alluvial, processes. Channel degradation in many of the streams has armoured the beds with cobbles and boulders, and this material, by and large, is not embedded.

Streams of the Barrenlands appear to share hydrothermal characteristics with streams in Arctic Alaska, related to climatic similarities in the two regions (see Oswood et al., 1989; Milner et al., 1997). In streams of both regions, flows peak rapidly for several days as snow and ice melt in late May; then, stream discharge attenuates slowly as the active layer thaws. By early August, flows can be very low, ceasing altogether in some first-order streams (Craig and McCart, 1975). Precipitation in late August again increases water levels. Although daily averages are 10˚–14˚C in both regions (Craig and McCart, 1975; Oswood et al., 1989; Irons and Oswood, 1992), tundra streams in Alaska accumulate approximately 1000 degree-days in total (Irons and Oswood, 1992), whereas Barrenland streams achieve 1000 degree-days by 1 September, with still roughly a month (100–200 degree-days) of ice-free time before freeze-up.

Despite the occurrence of recognizable stream groups based on physical characteristics, we found little evidence of differences in water chemistry among the groups, probably because of the influence of lakes on stream chemistry (Kling et al., 2000). Nevertheless, both pH and TOC increased with stream size, likely reflecting an overall lower position in the catchment basin and the downslope processing of materials (Kling et al., 2000). The location within a stream (upstream vs. downstream) and the char-

TABLE 6. Frequency of occurrence (%) of fish species and average fish community composition (%) among 18 Barrenland study streams, NWT, Canada.

Species	n	Frequency of Occurrence (%)	Composition (%)
Slimy sculpin (*Cottus cognatus*)	17	94	34.3
Burbot (*Lota lota*)	16	89	19.4
Arctic grayling (*Thymallus arcticus*)	16	89	39.5
Lake trout (*Salvelinus namaycush*)	7	39	2.9
Northern pike (*Esox lucius*)	2	11	1.3
Lake chub (*Couesius plumbeus*)	2	11	0.4
Round whitefish (*Prosopium cylindraceum*)	1	6	0.3
Ninespine stickleback (*Pungitius pungitius*)	1	6	1.4
Longnose sucker (*Catastomus catastomus*)	1	6	0.4

acteristics of the upstream lake may have more bearing on water chemistry than the physical and biological characteristics of the stream itself.

Barrenland streams contain even lower concentrations of nutrients and major ions than Alaskan tundra streams (Table 3). Differences in water chemistry between Alaskan and Barrenland sites are likely related to geology, including the abundance of sedimentary rock in Alaska versus igneous rock in the Barrenlands. Because of extensive permafrost and a thin active layer, however, atmospheric inputs (wet and dryfall) likely supply the majority of the ions to streams within both regions (Everett et al., 1989).

Organic Matter

Quantities of CPOM in Barrenland streams are relatively high even though the region produces only small amounts of leaf litter. High biomass likely reflects low rates of decomposition resulting from an Arctic climate and a higher percentage of coarse substrate that fosters retention of CPOM. Unlike Naiman et al. (1987), we did not find that CPOM decreased with stream order or size, likely because the numerous lakes on the Barrenlands landscape capture downward-moving coarse organics, thus interrupting the stream processing of materials (Ward and Standford, 1983).

Vegetation in Barrenland catchments is similar to that in Alaska and supplies similar quantities of dissolved and total organic carbon (Peterson et al., 1986; Oswood et al., 1989; Hershey et al., 1997; Table 2).

Benthic Invertebrates

The composition of the benthic community in Barrenland streams was typical of tundra streams and rivers in Alaska (Oswood, 1989). Generally, the Arctic invertebrate fauna is depauperate, and some groups (Odonata and Megaloptera) are usually absent (Miller et al., 1986). Instead, stream invertebrate communities are generally dominated by a diverse group of dipterans, particularly Chironomidae, which can be as species-rich as in temperate streams (Oswood, 1989).

Despite the compositional similarity of the benthic communities, we found that benthic invertebrate densities were substantially higher in Barrenland streams (20 times those found in Alaska). For example, Craig and McCart (1975) found benthic densities of 126–2469 individuals/m^2 (mean 1025) in 18 streams, using a mesh of 9 threads/cm. Miller et al. (1986) reported average densities of 372–2128 individuals/m^2 in Imnavait Creek, using a 363 mm mesh, while Miller and Stout (1989) estimated benthic invertebrate density in Imnavait Creek at 334–917 individuals/m^2. In contrast, the lowest value we obtained, 1620 individuals/m^2, was at the higher end of those recorded from tundra streams in Alaska, and during the warm, dry year of 1998, densities averaged more than 31 000 individuals/m^2. It seems unlikely that our smaller mesh size (250 μm) accounts for differences in densities between Barrenland and Alaskan streams.

Benthic invertebrate densities were positively correlated to bankfull depth among Barrenland streams. Bankfull depth was generally greater in larger streams, which also tend to carry more flow. These streams (e.g., Norm's Camp, Ursula, and Slipper-Lac de Gras) are also less likely to freeze solid during the winter, or at least they freeze for a shorter period, and thus invertebrates may find refuge and survive. Large streams also likely moderate spring floods and heavy precipitation events, and thus provide more environmental stability than do smaller streams.

Invertebrate Drift

Relatively few studies have documented invertebrate drift in the Arctic, and most of this research was done in Alaska (e.g., Miller et al., 1986; Miller and Stout, 1989), where *Baetis* mayflies are often the dominant drifter (Hinterleitner-Anderson et al., 1992). In the lake-outlet streams of the Barrenlands, however, zooplankton dominate the drift, producing densities 40–150 times as high as those from Alaskan streams. Even without the microcrustacean component, drift densities were still 2–15 times as high as those recorded for Alaskan streams. If drift density is related to benthic density, as suggested by Miller and Stout (1989), then these differences in non-microcrustacean drift density support our findings of higher benthic invertebrate densities in Barrenland streams than in streams of Arctic Alaska.

Exceptionally high drift densities (16 607 individuals/ 100 m^3), of which 75% were Diptera, Ephemeroptera, Trichoptera, and Plecoptera, were observed just after Polar-Vulture stream was crossed by a small herd of caribou (ca. 100 individuals). This represents an unusual example of catastrophic drift elicited by a biotic factor (as opposed to the more typical abiotic forces, such as spates, pesticides, and acid pulses). Given the nature of the Barrenlands landscape, and the twice-per-year migration of the Bathurst caribou herd, however, it seems likely that this phenomenon is no more unusual for many Barrenland streams than seasonal spates are in other landscapes.

Fish

In comparison to temperate streams, which can have 15–101 species of fish in a stream (e.g., Horwitz, 1978), the streams of the Barrenlands contain few species. A combination of biogeographic and life history constraints creates this impoverished condition (Power, 1997). Although stream size (minimum summer discharge and drainage area) was a good predictor of species richness on a regional scale, the occurrence of some uncommon species, e.g., northern pike, depended more on proximity to colonization sources. Interestingly, pike-bearing streams also contained an abundance of mare's tail, while streams without pike did not. These pike streams also had very low grayling abundance, suggesting that these species do not coexist well.

Many streams serve as spawning, nursery, and juvenile habitat for arctic grayling. Adult grayling, lake trout, and round whitefish use small streams primarily in the spring, when flows are sufficient for fish passage, but were occasionally found trapped in pools below barriers such as waterfalls, rapids, and boulders. Some may also have been inadvertently swept downstream below barriers at this time, where they subsequently became trapped. By midsummer, most stream sections contain primarily YOY grayling, along with slimy sculpin and burbot. Some of these YOY grayling can also become trapped in side channels as water levels decline during the summer. The combination of increased precipitation and cooler temperatures in the Arctic fall, therefore, might be critical for many populations, allowing fish to migrate back to main branches or lakes before freeze-up.

Variability Among Years

Invertebrate drift and benthic invertebrate density and biomass varied considerably among the three study years in relation to air and water temperature, rainfall, and discharge. Correspondingly, YOY grayling were larger in the warm, dry year (1998) when food (i.e., invertebrates) was plentiful. Conversely, epilithon abundance was low, perhaps because of high invertebrate numbers. The opposite pattern was observed in the cool, wet year (1999). This pattern is consistent with relationships among growth of YOY grayling, discharge, and water temperature recently observed in Alaska (Deegan et al., 1999), suggesting climatic trade-offs; during warm, dry years, fish may experience good growth but also a greater risk of being trapped in an isolated side channel.

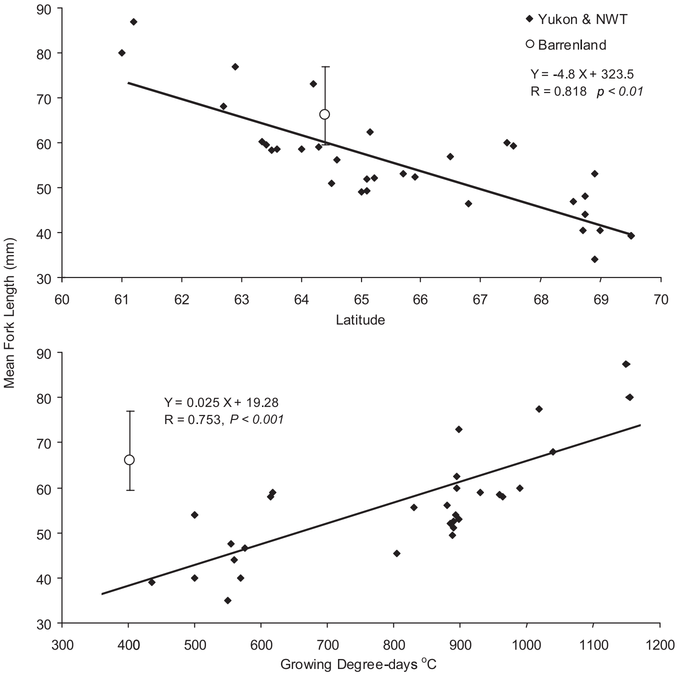

FIG. 5. Relationships of mean fork length of YOY arctic grayling in late August to latitude (upper) and growing degree-days (lower) in northwestern Canada (black diamonds) and Barrenland streams (open circle). Error bars are ranges from 10 Barrenland streams during 1998–2000. Comparison data and linear regressions are from the Mackenzie Valley and Yukon North Slope drainages (figure modified from McCart, 1986). Barrenland climate data are from Contwoyto Lake, Northwest Territories (65˚29′N, 110˚22′W) (Environment Canada 1991), adjusted to match McCart (1986), who defined growing degree-days from a base of 4.4˚C (40˚F).

Tundra Streams, Lake Outlets, and Fish Growth

Craig and McCart (1975) classified streams of the Beaufort Sea drainage into three categories (mountain, spring, and tundra streams) on the basis of their physical, chemical, and biological properties. The general characteristics of their tundra streams were intermediate between spring and mountain streams. With a few exceptions, this description applies to Barrenland streams, and perhaps to tundra streams in general.

Nevertheless, important differences exist between tundra streams of Alaska and those of the Barrenlands, derived ultimately from differences in physical geography. Except on portions of the coastal plain, the Alaskan tundra generally has few lakes. As a consequence, the majority of Alaskan Arctic streams are long (30–65 km), continuous, single channelled, and sinuous. Many of those in the foothills region are called "beaded" streams (Oswood et al., 1989). Conversely, our study area lies on the Canadian Shield, in a landscape that consists of numerous chains of lakes, with outlet streams that follow highly irregular drainage patterns over a multitude of glacial features.

The presence of lakes in the Barrenlands modifies the physical, chemical, and especially biological characteristics of the outlet streams in a way consistent with the serial discontinuity concept (Ward and Stanford, 1983; see also Richardson and Mackay, 1991; Kling et al., 2000). Diel temperature fluctuations in Barrenland streams were small (~3˚C) relative to the considerable amplitude (11.6˚C) noted in Alaska (Craig and McCart, 1975; Irons and Oswood, 1992). Similarly, lakes can stabilize stream discharge and provide water flow throughout the summer. Drift in Barrenland streams was dominated (90%) by planktonic microcrustaceans of lake origin, compared with *Baetis* in Alaska (Hinterleitner-Anderson et al., 1992). The presence of lakes also concentrates migrating caribou, causing minor stream bank erosion, adding woody debris to the stream, and provoking catastrophic drift. Finally, because of the tight lake-stream relationship, grayling in the Barrenlands exhibit an adfluvial life history (Northcote, 1978), residing mainly in the lakes and ascending streams primarily to spawn. Thus their migratory sequence is relatively simple compared to the mainly fluvial arctic grayling in Alaska, which make distinct and complex spawning, feeding, and overwintering migrations (Craig and Poulin, 1975).

Such differences in the characteristics of Alaskan and Barrenland tundra streams propagate to higher trophic levels, ultimately increasing the capacity of the streams to support fish production. To illustrate, the growth of YOY grayling in streams of northwestern North America varies greatly in relation to latitude and climate (growing degree-days) (McCart, 1986; Fig. 5). Arctic grayling in Barrenland streams, however, achieve first-year growth rates that are well above the level predicted from McCart's climatic gradient. Because of their more central, continental location, the Barrenlands have a climate comparable to that of the Yukon's North Slope (Environment Canada, 1991), which is well to the north, yet YOY grayling grow there to a size comparable to that expected from a region with three times the growing degree-days. Because climate generally has a strong influence on the growth of fish (Conover and Present, 1990), the discrepancy between observed and predicted growth suggests that specific abiotic and biotic characteristics of Barrenland streams allow YOY to attain larger sizes.

Nutrient levels do not resolve the discrepancy, as Barrenland streams contain some of the most nutrient-poor waters of North America, considerably lower than Alaskan and Yukon streams (Watson et al., 1966; Craig and McCart, 1975; Oswood et al., 1989; Peterson et al., 1992; Hershey et al., 1997). Rather, the most striking difference is the lake-outlet nature of Barrenland streams. The characteristics and properties of lake outlets may promote higher productivity than would be observed in continuous streams (see Haraldstad et al., 1987; Hillbricht-Ilkowska, 1999; Hieber et al., 2002). Outlet stream temperatures, determined largely by the source lake's epilimnion, are often warmer and less variable than those of continuous streams. For arctic grayling on the tundra, higher temperatures inevitably mean longer periods near their thermal optima, resulting in higher growth rates. Most important, perhaps, is the addition of lake-derived energy sources, including the high quality/quantity of seston upon which filter-feeding lotic insects depend (Richardson and Mackay, 1991). Although this lake-outlet effect generally attenuates within a few hundred meters (McCreadie and Robertson, 1998), most Barrenland streams are relatively short; therefore, influences of the upstream lake should remain significant throughout most of their length. Each of these factors likely contributes to Barrenland outlet streams' ability to support benthic densities and rates of grayling growth and production higher than those found in climatically similar streams in Alaska and the Yukon. Given that impacts of industrial development on aquatic ecosystems are largely determined in Canada on the basis of effects on their productive capacity for fish (e.g., Minns, 1996), it is vital that we understand reference conditions for Barrenlands so that we can account for these differences.

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