Fish life history and habitat use in the Northwest Territories: Arctic grayling (*Thymallus arcticus*)

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FISH LIFE HISTORY AND HABITAT USE IN THE NORTHWEST TERRITORIES: ARCTIC GRAYLING (*Thymallus arcticus*)

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ABSTRACT

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2007. Fish life history and habitat use in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2797: vi + 55 p.

Arctic grayling occur throughout the Mackenzie River System, where they are most abundant in the clear, swift tributaries that flow from the east side of the valley into the Mackenzie River. They require cold, clear water and undertake complex seasonal movements that differ among systems in response to local conditions. Their populations can be resident or migratory, and the latter can follow fluvial or adfluvial life histories. Differences in habitat use by these populations and in the seasonal requirements of eggs, fry, juveniles, and adults are summarized. Spawning occurs in shallow (<1 m), fast-flowing (<150 cm/s) tributary streams or in lake inlets or outlets, typically over unembedded gravel substrates at or shortly after spring ice breakup. Tributary streams also provide important feeding and rearing habitat for grayling during the open water period. To support the assessment, avoidance and mitigation of environmental impacts in the Mackenzie Valley, the potential impacts of development activities and climate change on survival of the species are reviewed. Key habitat requirements of Arctic grayling that may be particularly susceptible to impacts from human activities include: 1) clear water for visually locating prey; 2) unimpeded access between spawning, feeding, and overwintering areas -- particularly during the spring spawning period; and, 3) tributary streams with flow rates, water depths, and unembedded gravel substrate suitable for spawning and feeding. Spawning success appears to be strongly affected by stream obstructions that prevent or delay migrations, and flooding or drought during the two week period after hatching may cause high larval mortalities. Populations may be slow to recover from year-class failures. The species' ability to locate prey declines rapidly as turbidity increases, and fingerlings avoid water with turbidity >20 NTU. Activities such as gravel removal or log driving that rework the streambed in spawning areas can extirpate grayling from an area, as can the introduction of competitors and predators.

Key words: distribution; life history; habitat requirements; seasonal movements; reproduction; spawning; rearing; life cycle; Mackenzie watershed; hydrological integrity; fresh water; Salmonidae.

RÉSUMÉ

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2007. Fish life history and habitat use in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2797: vi + 55 p.

L'ombre arctique se trouve partout dans le réseau du fleuve Mackenzie, où il abonde le plus dans les tributaires aux eaux rapides et limpides qui coulent du versant est de la vallée jusque dans le Mackenzie. Il entreprend des déplacements saisonniers complexes qui diffèrent selon les réseaux, en réaction aux conditions locales. Ses populations peuvent être sédentaires ou migratrices et ces dernières peuvent être de nature fluviale ou adfluviale. Nous résumons ici les différences dans l'utilisation des habitats de ces populations et dans les besoins saisonniers des œufs, des alevins, des juvéniles et des adultes. La fraie se produit dans des tributaires peu profonds (< 1 m), à courant rapide (< 150 cm/s), ou dans les affluents ou les décharges des lacs, habituellement sur des substrats de gravier libre, au printemps, au moment du dégel ou peu après. Les tributaires constituent également un important habitat pour l'alimentation et l'alevinage durant la période des eaux libres. Nous examinons les incidences éventuelles des activités humaines et du changement climatique sur la survie de l'espèce en appui de l'évaluation, de l'évitement ou de l'atténuation des incidences environnementales dans la vallée du Mackenzie. Les principales exigences en matière d'habitat de l'ombre arctique qui peuvent être affectées par les activités humaines comprennent : 1) une eau limpide pour repérer les proies visuellement; 2) un accès libre d'obstacles entre les aires de fraie, d'alimentation et d'hivernage -- particulièrement à l'époque de la fraie au printemps et 3) des tributaires dont le débit, la profondeur et le substrat libre conviennent à la fraie et à l'alimentation. Le succès de la fraie semble fortement affecté par les obstructions dans les ruisseaux, ce qui empêche ou retarde les migrations, ainsi que par l'inondation ou la sécheresse au cours de la période de deux semaines qui suit l'éclosion, ce qui peut entraîner la mort d'un grand nombre de larves. Les populations peuvent être lentes à récupérer de l'échec d'une classe d'âge. La capacité de l'espèce à trouver ses proies décline rapidement à mesure que la turbidité augmente et les alevins d'un an évitent l'eau d'une turbidité > 20 uTN. Les activités comme l'enlèvement du gravier ou le flottage qui réaménagent le lit du cours d'eau dans les frayères peuvent causer la disparition de l'ombre d'une aire donnée, tout comme le fera l'introduction de compétiteurs et de prédateurs.

Mots clés : répartition; cycle vital; exigences en matière d'habitat; déplacements saisonniers; reproduction; fraie; alevinage; bassin versant du Mackenzie; intégrité hydrologique; eau douce; Salmonidés.

1.0 INTRODUCTION

Renewed interest in natural gas pipeline development along the Mackenzie Valley has raised the prospect that fish species in the watershed may be impacted by changes to their habitat. The proposed pipeline would extend from near the Beaufort Sea coast to markets in the south (http://www.mackenziegasproject.com/). Fishes in the Mackenzie River depend upon the integrity of their aquatic habitats, so it is important to summarize knowledge that can be used to assess potential impacts of this development proposal and others, and to facilitate efforts to avoid and mitigate these impacts.

This report reviews knowledge of the Arctic grayling, *Thymallus arcticus* (Pallas, 1776). These fish, with their rich blue colouration, showy dorsal fins and habit of leaping out of the water are a characteristic species of the Mackenzie River watershed. They are sought-after sport fish that attract anglers from Canada and abroad, and contribute significantly to the regional economy (DFO 1988).

Information is provided on the species' distribution, habitat use during the various stages of its life history, and about threats posed to the species and its habitat by development activities. Good information is available on the species' use of tributaries during the open water period for spawning and rearing, and on their movement patterns during the open water period, but relatively little is known of their use of lake and large river habitats, especially during the period of ice cover. Where gaps in knowledge of the species in the Northwest Territories (NT) are identified, supplementary information is included where possible from other regions.

This information was compiled to assist developers, habitat managers, and researchers. Similar reports have been prepared for other fishes that inhabit the Mackenzie River watershed.

1.1 Taxonomic units

Geographical differences in lateral line scale counts and mitochondrial DNA suggest that Arctic grayling survived the Wisconsin glaciation in at least two refugia: 1) the Bering Refuge, north of the ice sheets; and 2) either the Upper Missouri or southwest Alberta Refuge, south of the ice sheets (McCart and Pepper 1971; Redenbach and Taylor 1999). Other populations may have survived in a Nahanni Refuge or in a refuge on the north slope of the Brooks Range in Alaska (AK). The origins of fish that recolonized the Northwest Territories following deglaciation are uncertain, but likely represent a complex mixture of several refugial forms.

Hybridization can occur between Arctic grayling and European grayling (*T. thymallus*) in the contact zone of the species (Shubin and Zakharov 1984).

1.2 Distribution

The Arctic grayling has a **holarctic**[1] distribution in northern freshwater drainages (Scott and Crossman 1973; Lee *et al*. 1980). In North America it occurs in northern areas of Manitoba, Saskatchewan, Alberta, and British Columbia; in mainland drainages of Nunavut (NU) and Northwest Territories; and throughout the Yukon and Alaska. The species' natural distribution extends southward into the headwaters of the Missouri River above Great Falls, Montana, and formerly into rivers flowing into lakes Michigan, Huron, and Superior in northern Michigan (Lee *et al*. 1980). It has been introduced as far south as California, Arizona, and Nevada.

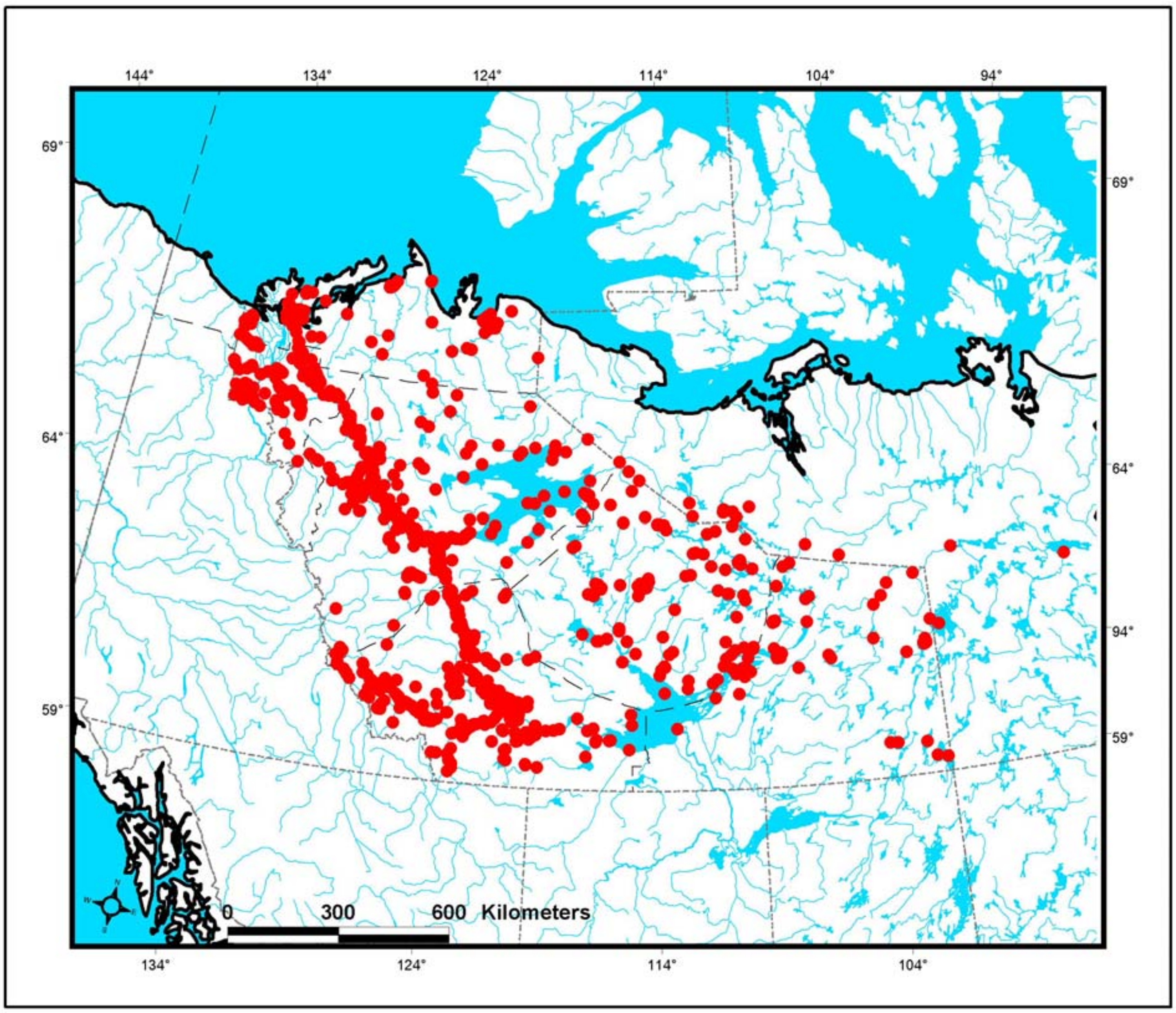

Figure 1. Arctic grayling distribution in the Northwest Territories (updated from Sawatzky *et al*. 2007).

[1] Terms in bold type are defined in the Glossary.

Arctic grayling inhabit many clear, cold streams, rivers and lakes of the mainland NT and NU but are rare in the northeastern Kivalliq Region and have not been recorded from the Arctic Islands (McPhail and Lindsey 1970; Scott and Crossman 1973; Stewart and MacDonald 1978; MacDonald and Fudge 1979; McCart and Den Beste 1979; Lee *et al*. 1980; MacDonald and Stewart 1980; Sawatzky *et al*. 2007). They are found throughout the Mackenzie System, where they are most abundant in the clear, swift tributaries that flow from the east side of the valley into the Mackenzie River (Figure 1) (Hatfield *et al*. 1972a,b; Dryden *et al*. 1973; Stein *et al*. 1973a,b; Jessop *et al*. 1974). Within the Northwest Territories, the species is widely distributed in the Taiga Shield, Taiga Plains, and Southern Arctic ecozones (Marshall and Schut 1999).

2.0 LIFE HISTORY TYPES

Stream-resident, **fluvial**, **adfluvial**, and **lacustrine** life histories have been observed among Arctic grayling populations (McPhail and Lindsey 1970; Scott and Crossman 1973; Jessop and Lilley 1975; Krueger 1981; Northcote 1995). Each of these population types exhibit somewhat different patterns of habitat use (Table 1). Arctic

Table 1. Habitat use by Arctic grayling populations with different life history types.

HABITAT	POPULATION		
	STREAM-RESIDENT	FLUVIAL	ADFLUVIAL/LACUSTRINE
Small (~10 m wide), medium gradient tributary streams	• Year-round use by all life history stages for all activities. • Overwinter in deep, often spring fed, pools.	• Spawning and rearing habitat. • Seasonal feeding habitat for all life stages. • Sometimes provide overwintering habitat for young-of-the-year. • Migratory corridors for juveniles and adults.	• Spawning and rearing habitat. • Seasonal feeding habitat for all life stages. • Sometimes provide overwintering habitat for young-of-the-year. • Migratory corridors for juveniles and adults.
Rivers		• Migration corridors and feeding and overwintering habitat for **fry**, juveniles, and adults. • Spawning by some populations where conditions are suitable.	• Migration corridors and feeding habitat for fry, juveniles, and adults. • Overwintering habitat for some juveniles. • Spawning by some populations where conditions are suitable.
Lakes		• Migration corridors for some adults.	• Year-round use by all life history stages for all activities. • Spawning typically occurs in small tributaries or near lake inlets or outlets.
Brackish or marine coastal waters		• Migration corridors for some adults and/or juveniles.	• Migration corridors for some adults and/or juveniles.

grayling spawn in the spring in both rivers and lakes (McPhail and Lindsey 1970; Scott and Crossman 1973; Dryden *et al*. 1973; Stein *et al*. 1973a,b; Ford *et al*. 1995; Northcote 1995). They also use streams as migration corridors between lakes (Martin 2001). Grayling are rarely reported from coastal waters, but individuals have been caught in weakly brackish water (~5 ppt) in Wood Bay near the outlet to the Anderson River, NT (Bond and Erickson 1992). Radio-tagging studies have also observed grayling using nearshore brackish waters to move between coastal drainages on Alaska's North Slope (West *et al*. 1992).

Grayling undertake complex seasonal movements that differ among systems in response to local conditions (Schallock 1966; Hatfield *et al*. 1972a; Craig and Poulin 1975; Northcote 1995). Figure 2 illustrates the seasonal movements of Arctic grayling **fry**, juveniles, and adults in small Alaskan streams in relation to the flow and ice regimes. While these movements occur later in the spring and earlier in the fall than those in the southern and central Mackenzie Valley, they serve to illustrate the general pattern of movements in response to flow and ice conditions, with the exceptions that in some streams spawners migrate upstream under the ice (Jessop *et al*. 1974) and fry may extend their stream residence (Deleray 1991). Over-ice movements have also been documented (W. Morris, Alaska Department of Natural Resources, pers. comm.).

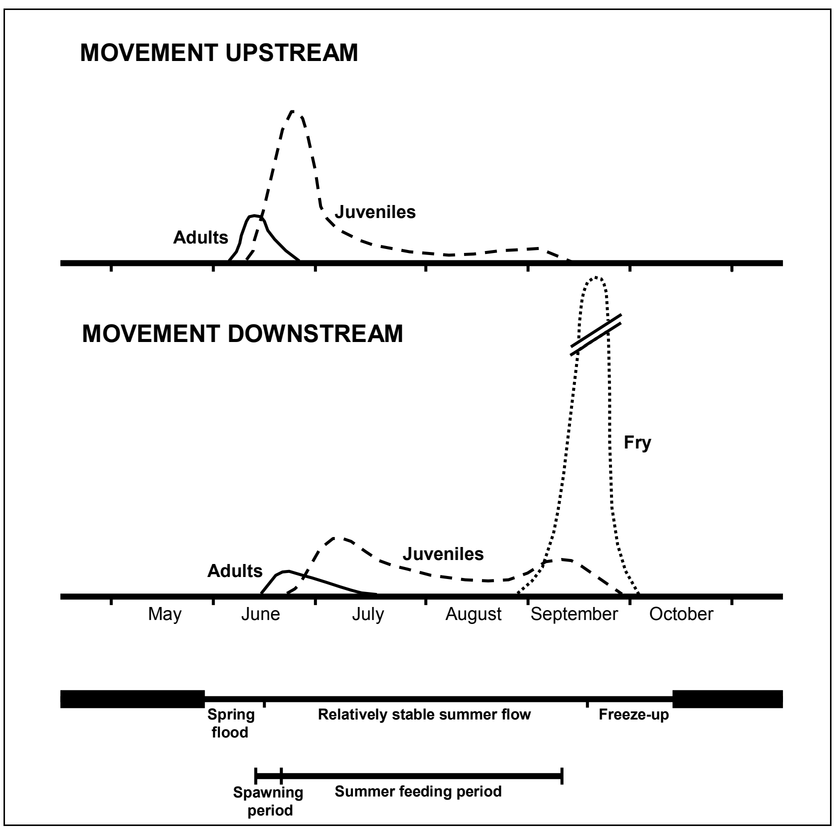

Figure 2. Schematic diagram of grayling movements in small Alaskan streams (after Craig and Poulin 1975, p. 696).

In Alaska, grayling were present in lower order lakes (0 to -3) connected to streams with an average gradient of <4.6% and depth of >5.9 m, and in lakes (order 1 to -3) with a higher stream gradient (>4.6%) where the depth was >15 m (Hershey *et al*. 2006; Figure 3). In northern Alberta, Tonn *et al*. (2004) found a tendency for Arctic grayling to be dominant in small mountain lakes with steep catchments and low phosphorus and chlorophyll-***a*** concentrations.

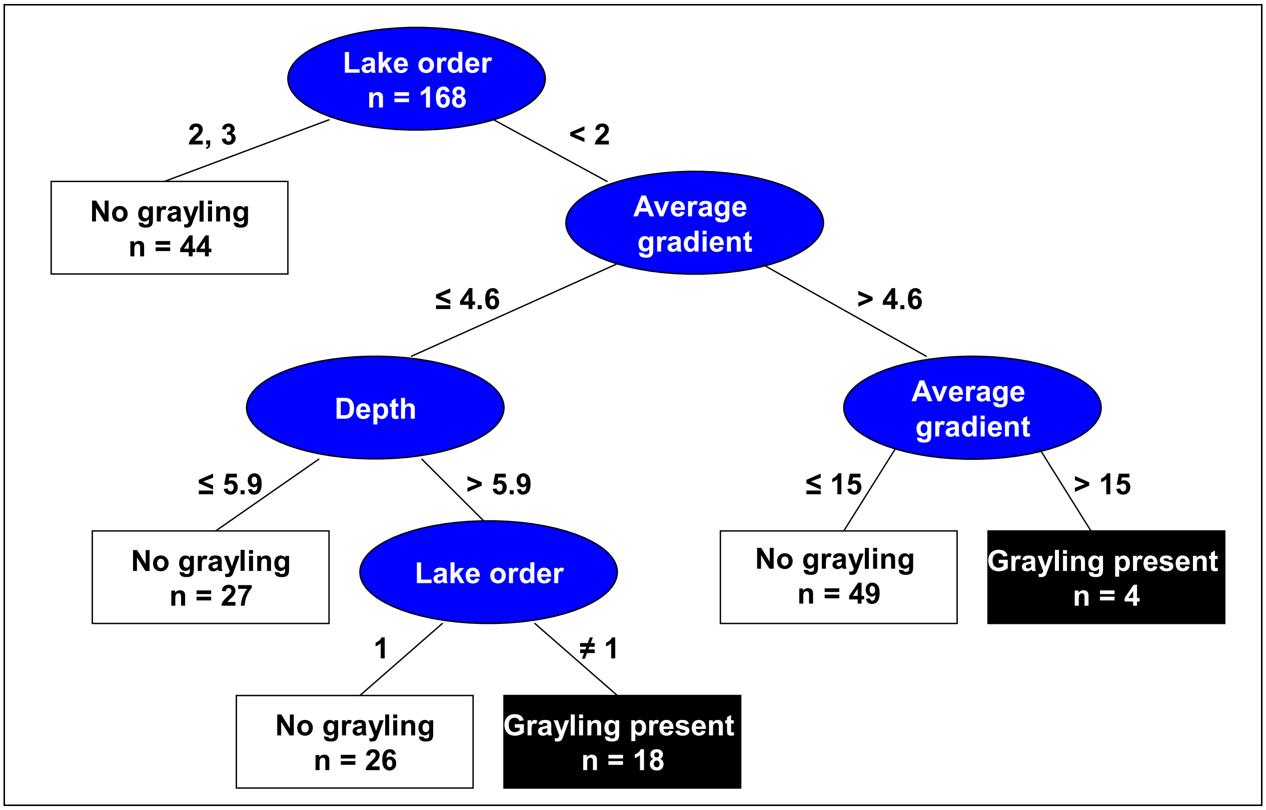

Figure 3. Classification and regression tree (CART) analysis for Arctic grayling (after Hershey et al. 2006, p. 47). Ovals show variable used as decision points and values of decision criteria are indicated along diagonal lines. Rectangles show nodes used in tree construction. Arctic grayling are predicted to be absent in cases to the left of a decision point if there are no further decision points, and present in cases to the right of a decision point if there are no further decision points. Sample sizes (n=) indicate the number of lakes; units are percent (%) for gradient and meters (m) for depth.

3.0 LIFE HISTORY STAGES AND HABITAT USE

Stream habitat use by Arctic grayling has been studied in detail (Table 2) but the specifics of habitat use and requirements in larger rivers and lakes are poorly known (Table 3). Key transitions in the Arctic grayling life history are illustrated schematically in Figure 4 and discussed below. Life history and habitat parameters are defined in

Table 2. Observed stream habitat use by Arctic grayling (data from NT populations in bold type; numbers in brackets refer to sources cited below). Habitat features (e.g., substrate types) are defined in Appendix 1. Abbreviations are defined in Section 8.0.

HABITAT FEATURES		LIFE STAGE			
		Spawn/egg	**Young of the year**	**Juvenile**	**Adult**
Habitat type		**Clear, fast-flowing streams** (1, 18-22)	Shallow pools and side channels of clear streams (12, 20, 28-33, 52)	Middle and lower reaches of small, clear tributaries in riffles, slow-moving shallows, and pools (20, 28, 41, 42, 43)	Middle and upper reaches of small, clear tributaries in riffles, slow-moving shallows, and pools (20, 28, 41, 42)
Stream gradient					0.17-0.18% on overwintering grounds (51)
Depth range (m)		**A few cm to over 1 m** (1, 11)	0.05-0.5 m (12, 20, 28-33, 52)	0.2-0.8 m (28, 41, 43)	1.1-1.52 (28, 41, 43)
Substrate		**Unembedded gravel, sometimes sand, rubble,** (1, 5, 7- 10, 13-16) or clay (2)	Silt to boulder, with a preference for sand and fine gravel (12, 20, 28-33, 52)	Silt to boulder, with a preference for sand and fine gravel (28, 41, 43)	Silt to boulder, with preference for gravel and rubble (28, 41, 43)
Cover		**Spawning sometimes occurs under ice cover** (21); **eggs in the interstices of gravel substrate to a depth of 5 cm** (1, 2, 5, 6, 8, 9, 11)	Alevins spend first 3-5 d in the interstices of the substrate (6, 8, 33); later use overhead vegetation and boulders (12, 28, 30, 33)	When used, cover consists of rocks or, less often, cut banks or overhanging or instream vegetation (28, 41, 43)	**When used, cover consists of rubble and cobble or, less often, cut banks, deadfall, overhanging or instream vegetation** (1, 28, 41, 44, 45, 53)
Velocity range (cm/s)		**<150 cm/s, typically at means of 30-80 cm/s** (1, 5, 7-10)	<80 cm/s (12, 20, 28-33, 52)		**<150 cm/s, typically at means of 50-110 cm/s** (1, 7-10, 28, 31, 41, 43, 53)
Turbidity (NTU)	Range		Avoid turbidity of >20 NTU (34);	Naturally present at suspended sediment levels of ≤100 mg/L (31)	Naturally present at suspended sediment levels of ≤100 mg/L (31). More common at turbidities <30 NTU (53)
	Limits	No significant difference observed in egg mortality during 96 h test comparing clear (NTU 1.4) and placer mined (NTU = 445) streams.	<1% mortality during 96 h test at 445 NTU (34); feeding success impaired during longterm exposure to 100-1000 mg/L (47); can survive short term exposure (4-5 d) to ≤250 g/L inorganic or ≤50 g/L organic sediment (47).	Water quality standard of 5 NTU over natural recommended due to the adverse effects on feeding of loss of water clarity (34)	Water quality standard of 5 NTU over natural recommended due to the adverse effects on feeding of loss of water clarity (34)
Oxygen (mg/L)	Range				
	Limits		1.5 mg O_2/L for fish acclimated to 5°C and held at 10°C; 2.0 mg O_2/L for fish acclimated to 15°C and held at 20°C (48)		

Temperature (°C)	Range	Spawning: **~4-16°C fluctuating about daily means of ~6-10°C** (1, 5, 13, 18, 19, 21-23) Incubation: successful in the laboratory at constant temperatures of 5.8 to 15.5°C (3, 6,8,9)		5-17°C (28, 41)	0.3 to at least 16.7°C (26, 49)
	Limits	Spawning: daily low of 2°C (27), daily high of 16.7°C (26) Incubation: unknown	MTL = 21.5-24.2 for sac fry acclimated to 8.5±1°C (50) UILT = 27.5-27.9°C for young-of-the-year acclimated to 15°C; 24.8-24.9 for fish acclimated to 5°C (48)	CTM ranges from 26.4°C for fish acclimated to 8.4°C to 29.3°C for fish acclimated to 25°C (17) UILT ranges from 23°C for fish acclimated to 8.4°C to 25.0°C for fish acclimated to 20.0°C (17).	
Prey items	Primary	-	**Aquatic insect larvae** (1, 5, 52)	**Aquatic and terrestrial insects** (1, 5, 19, 20, 39, 40)	**Aquatic and terrestrial insects** (1, 5, 19, 20, 39, 40)
	Secondary	-	**Crustacean zooplankton** (1, 5, 52)	**Crustacean zooplankton, fish, small mammals** (1, 5, 19, 20, 39, 40)	**Crustacean zooplankton, fish, small mammals** (1, 5, 19, 20, 39, 40)
Period		**Spawning: usually mid-May to mid-June, can extend from late April into early July** (5, 10, 18, 19, 21, 23, 24, 25, 26, 27) **Incubation: 13-18 d under natural stream conditions that fluctuated about a daily mean of 8.8°C** (1, 5)	Fry emergence: 3-4 d after hatch (6); first year.	**1 to 8 y** (1, 5, 10, 19, 20, 23, 35-38)	**13 to 20 y** (1, 5, 10, 19, 20, 23, 35-38)
Size/age range (Note: fish are considered to be age 0 until December 31 of the year they are hatched)		Egg diameter: **unhardened 2.5-2.6 mm (1,** 3); water hardened 2.7 mm (2), 3.5-4.0 mm (4)	7-15 mm at emergence; mean length of yearlings 75-140 mm (46)	**Both sexes typically mature to adults at age 2 to 6, range 2 to 9** (1, 5, 10, 19, 20, 23, 35-38)	**Female: Maximum: 515 mm FL (1)** **Male: Maximum: 488 mm FL (1)**

1 = Bishop 1967—Providence Creek, NT;
2 = Reed 1964—Tanana River drainage, Alaska;
3 = Wojcik 1955—Tanana River drainage, Alaska;
4 = Vincent 1962—review; data from various southerly populations;
5 = Bishop 1971—Providence Creek, NT;
6 = Kratt and Smith 1977—Fond du Lac River, SK;
7 = McPhail and Lindsey 1970—review;
8 = Kratt 1977—Fond du Lac River, SK;
9 = Krueger 1981—Tyee Lake, Alaska;
10 = Barndt and Kaya 2000—Montana;

11 = Tack 1971 cited in Armstrong 1986—Tanana River, Alaska;
12 = Deleray 1991—Deer Creek, Montana;
13 = Rawson 1950—Reindeer Lake, SK;
14 = Beauchamp 1990—Upper Granite Lake, Washington;
15 = Stuart and Chislett 1979—Adsett Creek, BC;
16 = Machniak *et al*. 1980—MacKay River, AB;
17 = Lohr *et al*. 1996—laboratory, Montana fish.
18 = Falk *et al*. 1982—Providence Creek, NT;
19 = Tripp and McCart 1974—Donnelly River, NT; Vermillion Creek, NT;
20 = de Bruyn and McCart 1974—Babbage River, YT;
21 = Jessop *et al*. 1974—Trail River, NT;
22 = Katopodis *et al*. 1978—Redknife River, NT;
23 = Stein *et al*. 1973a—Mackenzie Valley, NT;
24 = Jessop and Lilley 1975—Mackenzie Valley, NT;
25 = Scott and Crossman 1973—review;
26 = Craig and Poulin 1975—Kavik River system, Alaska;
27 = Netsch 1975—Alaska, Yukon;
28 = Vascotto 1970—McManus Creek, Alaska;
29 = Deegan *et al*. 2005—Kuparuk River and Oksrukuyik Creek, Alaska;
30 = McClure and Gould 1991—laboratory, Montana fish;
31 = Birtwell *et al*. 1984—Minto Creek, Yukon;
32 = Kaya 1989—laboratory, Montana fish;
33 = Ford *et al*. 1995—review;
34 = Scannell 1988—laboratory;
35 = Armstrong 1986—review;
36 = Falk *et al*. 1980—Kakisa River, NT;
37 = Carl *et al*. 1992—Beaverlodge River, AB;
38 = Hatfield *et al*. 1972a—Mackenzie Valley, NT;
39 = Chang-Kue and Cameron 1980—Great Bear River area, NT;
40 = McKinnon and Hnytka 1979—Liard River tributaries, NT;
41 = Evans *et al*. 2002—review;
42 = Hughes and Reynolds 1994; Hughes 1998a, 1999—Tanana River drainage, Alaska;
43 = Den Beste and McCart 1984—Alaskan streams north of the Yukon River;
44 = Schmidt *et al*. 1984—Alaska;
45 = Liknes and Gould 1987—Montana;
46 = Northcote 1995—review;
47 = McLeay *et al*. 1984, 1987—laboratory, Yukon fish;
48 = McLeay *et al*. 1983—laboratory, Yukon fish;
49 = Kane *et al*. 1989—Fish Creek, Alaska;
50 = LaPerriere and Carlson 1973—laboratory, Alaskan fish;
51 = Stanislawski 1997—Little Smokey River, AB;
52 = Jones *et al*. 2003a—Lac du Gras area streams, NU.
53 = Suchanek *et al*. 1984—Susitna River, Alaska

Table 3. Observed lake habitat use by Arctic grayling (data from NT populations in bold type; numbers in brackets refer to sources cited below). Habitat features (e.g., substrate types) are defined in Appendix 1.

HABITAT FEATURES		LIFE STAGE			
		Spawn/egg	**Young of the year**	**Juvenile**	**Adult**
Habitat type		Lake inlets or outlets of clear-water lakes (1)	Shallow littoral habitats and shallow, quiet pools of inlet streams (1)		**Rocky shorelines, often in bays near stream inflows, or in lake outlets** (1, 9, 13)
Depth range (m)		0.15 to 0.9 m (1, 2)	0.02-0.46 m (1)		**Typically <4 m** (1, 4, 13) **but a few have been taken between 6-10 m** (13)
Substrate		Coarse sand, gravel, silt, organic (1, 2)			**Sand, silt, gravel, cobble** (4-8)
Cover				Overhanging boulders (3)	**Overhanging vegetation** (1, 4)
Prey items	Primary				**Terrestrial and aquatic insects, amphipods** (4, 10-12)
	Secondary				**Other crustacean zooplankton, fish** (4, 10-12)

1 = Krueger 1981—Tyee Lake, Alaska;
2 = Reed 1964—Tanana River drainage, Alaska;
3 = Beauchamp 1982—Upper Granite Lake, Washington;
4 = Bishop 1967—Great Slave Lake, NT
5 = Rawson 1950—Reindeer Lake, SK;
6 = McPhail and Lindsey 1970—review;
7 = Lawrence and Davies 1979—NU;
8 = Hatfield *et al*. 1972a—Mackenzie Valley, NT;
9 = Miller 1947—Great Bear Lake, NT
10 = de Bruyn and McCart 1974—Trout Lake and “Lake 100”, YT;
11 = Jessop *et al*. 1993—Indin Lake, NT;
12 = Miller 1946—Great Bear Lake, NT;
13 = Rawson 1951—Great Slave Lake, NT.

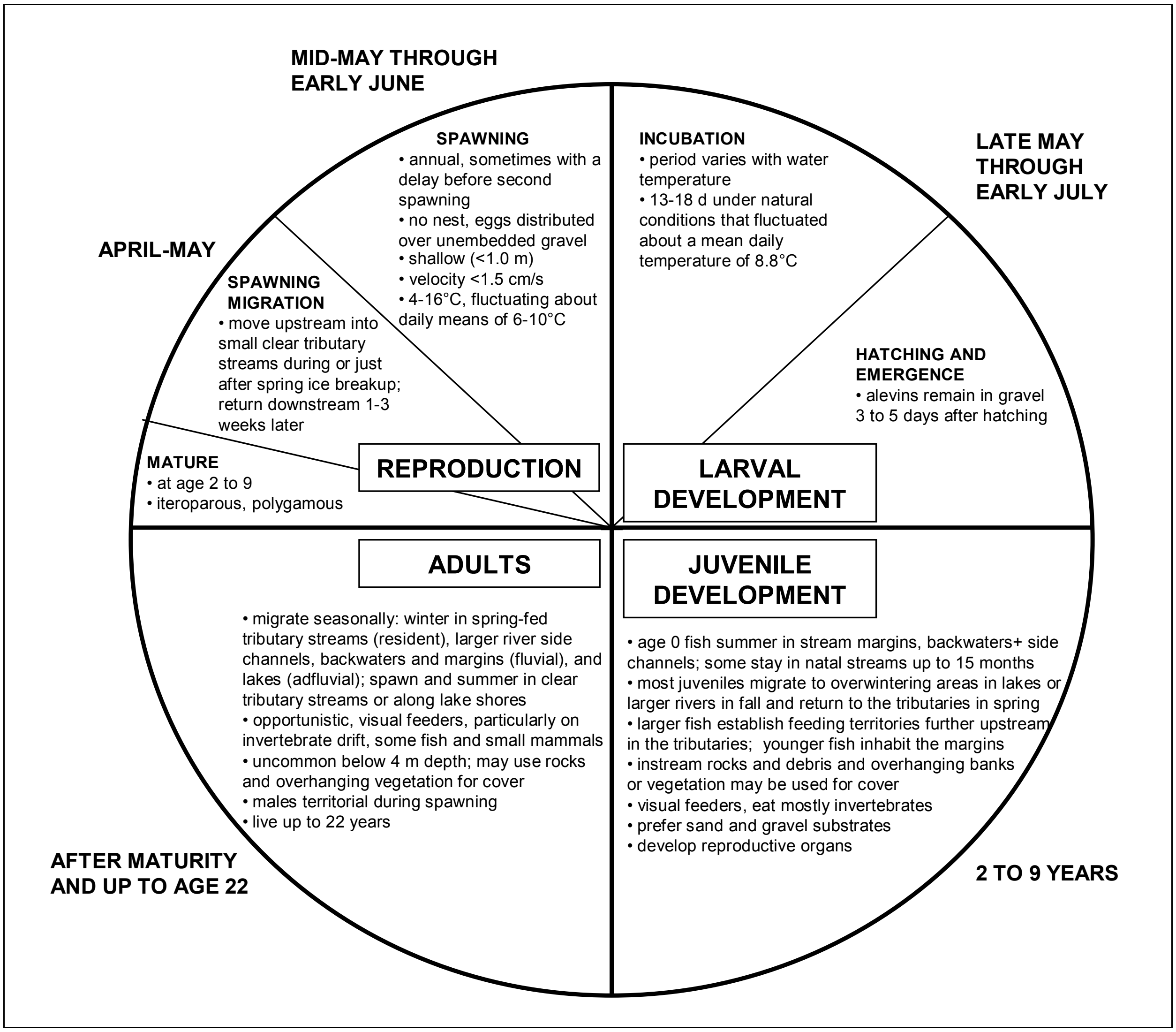

Figure 4. Generic life cycle of Arctic grayling.

Appendix 1. Stream and lake habitat requirements are summarized in Appendices 2 and 3, respectively.

Grayling populations are capable of surviving and reproducing in stream, river, and lake environments. These populations are particularly vulnerable to habitat fragmentation that prevents access to and from spawning and overwintering areas, to increases in water turbidity that prevent fish from visually locating prey, and to harvesting or other disturbances at the spawning streams.

3.1 Eggs (Spawning and incubation habitat)

Arctic grayling spawn in a variety of habitats, including mainstem rivers, large and small tributaries to rivers and lakes, intermittent streams, and in lakes—usually at the mouths of tributaries (Table 4) (Armstrong 1986). Fish that spawn in the Mackenzie River valley generally migrate from lakes and larger rivers into small, clear, fast-flowing

Table 4. Habitat and life history parameters related to Arctic grayling reproduction, with data from the Northwest Territories (NT) in bold type. Numbers in brackets refer to data sources listed below.

PARAMETER	STREAM (data source)
Reproductive strategy:	**Iteroparous, polygamous** (2, 5-7,10, 18)
Age at maturity:	**Typically age 2 to 6 for both sexes, sometimes as late as age 9** (2-4, 6, 8, 12, 19, 22-24)
Fecundity (eggs/female):	Mean: **11,107 (12,359 eggs/kg body wt)** (1); **9,670 (10,965 eggs/kg body wt; n = 15 fish**) (2); **6,518 ± 1,455 (n=33 fish**)(4a) and **7,051 ± 2,780 (n=11 fish)** (4b); Range **4,694-15,867 (6,475 to 16,887 ova/kg body wt)** (1); **6,120-15,905** (2); **3,243-9,230 (4a); 2,646-10,230** (4b).
Spawning:	Typically, annually after maturity (5-7), sometimes skip a year after the first spawning (23)
Habitat type	**Clear, fast-flowing tributaries** (1, 2, 4, 6, 8, 20, 21)
Builds nest	**No, but defends territory** (2, 8-10)
Temperature (°C)	**4-16°C** (1, 2, 4a+b, 8, 19-21)
Depth (m)	**Several cm to over 1 m** (8, 13)
Substrate	**Unembedded gravel, sometimes sand or rubble** (2, 8-10, 12, 14-17)
Current velocity (cm/s)	**<150 cm/s** (8-12, 18)
Maximum age:	Age 29, sex not stated, aged by otolith (25)
Age at senescence:	No evidence of senescence

1 = Falk *et al*. 1982—Providence Creek, NT;
2 = Bishop 1971—Providence Creek, NT;
3 = Armstrong 1986—review;
4 = Tripp and McCart 1974—a=Donnelly River, NT; b=Vermillion Creek, NT;
5 = Williams 1969—Tolsona and Moose lakes, Alaska;
6 = de Bruyn and McCart 1974—Babbage River, YT;
7 = Deleray 1991—Deer Creek, Montana;
8 = Bishop 1967—Providence Creek, NT;
9 = McPhail and Lindsey 1970—review;
10 = Kratt 1977—Fond du Lac River, SK;
11 = Krueger 1981—Tyee Lake, Alaska;
12 = Barndt and Kaya 2000—Montana;
13 = Tack 1971 cited in Armstrong 1986—Tanana River, Alaska;
14 = Rawson 1950—Reindeer Lake, SK;
15 = Beauchamp 1990—Upper Granite Lake, Washington;
16 = Stuart and Chislett 1979—Adsett Creek, BC;
17 = Machniak *et al*. 1980—MacKay River, AB ;
18 = Beauchamp 1990—Upper Granite Lake, Washington;
19 = Stein *et al*. 1973a—Mackenzie Valley, NT;
20 = Jessop *et al*. 1974—Trail River, NT;
21 = Katopodis *et al*. 1978—Redknife River, NT;
22 = Falk *et al*. 1980—Kakisa River, NT;
23 = Carl *et al*. 1992—Beaverlodge River, AB;
24 = Hatfield *et al*. 1972a—Mackenzie Valley, NT.
25 = DeCicco and Brown 2006—Eldorado River, Alaska.

tributaries during (Jessop *et al*. 1974), or just after (Stein *et al*. 1973b), the breakup of river ice. These spawning areas are often located considerable distances upstream on the tributaries (Jessop and Lilley 1975). Spawners seem to continue moving upstream until the temperature conditions are right or until they are unable to proceed further (W. Morris, pers. comm.). Spawning can begin in April and extend into early July but usually occurs from mid-May to mid-June (Stein *et al.* 1973a,b; Tripp and McCart 1974; Jessop and Lilley 1975; Read and Roberge 1989). The same general pattern holds in other areas of the species' distribution (e.g., YUKON: de Bruyn and McCart 1974; ALASKA: Wojcik 1955, Schallock 1966, Vascotto 1970, Craig and Poulin 1975; Netsch 1975; Armstrong 1986; ALBERTA: Kratt 1977; WASHINGTON: Beauchamp 1990; MONTANA: Deleray 1991; Barndt and Kaya 2000). Some fish return to their natal streams to spawn (Tripp and McCart 1974). Most male and female grayling spawn each year after they reach sexual maturity (Williams 1969; de Bruyn and McCart 1974; Deleray 1991). Some coastal streams along the Alaskan North Slope are used by adults only during the spring for spawning (W. Morris, pers. comm.). Fish from larger river systems access them by migrating through brackish nearshore coastal waters.

Spawning has been documented in many streams and rivers of the Mackenzie Valley (Figure 5) (Bishop 1971; Hatfield *et al*. 1972a; Dryden *et al*. 1973; Stein *et al*. 1973a,b; Jessop *et al*. 1974; Tripp and McCart 1974; Jessop and Lilley 1975; Katopodis *et al*. 1978; Chang-Kue and Cameron 1980; Falk *et al*. 1982; EIS Mackenzie Gas Project 2004). Spawning is suspected to occur in many other streams and rivers (Dryden *et al*. 1973; Stein *et al*. 1973a; Jessop *et al*. 1974; EIS Mackenzie Gas Project 2004).

The timing of spawning varies within and among systems, and from year to year, but typically commences in mid-May in the southern Mackenzie Valley to mid-June in the north, at water temperatures of 4 to 16°C (8-10°C Bishop 1971; 7-15°C Stein *et al*. 1973a; 8-16°C Jessop *et al*. 1974; 8-12°C Jessop and Lilley 1975; 4-11.5°C Tripp and McCart 1974; 4-10°C Falk *et al*. 1982). Similar temperature ranges have been observed during the spawning period elsewhere (e.g., Reindeer R., SK: 7-9.5°C, Rawson 1950; 7-10°C, Scott and Crossman 1973; 3.9-16.7°C, Craig and Poulin 1975; Jim R., Alaska daily lows of 2 to 6°C to daily highs of 4 to 7°C, 28 May – 11 June, Netsch 1975; Barndt and Kaya 2000).

A rise in water temperature to 4°C and spring flooding may be factors that stimulate grayling to spawn (Tack 1972; Tripp and McCart 1974; Falk *et al*. 1982; Armstrong 1986). Spawners may arrive in the spawning areas a few days before spawning (Bishop 1967; Jessop *et al*. 1974). In some systems, such as the Trail River, they migrate upstream to the spawning grounds under the ice, and may spawn under the ice (Jessop *et al*. 1974; Jessop and Lilley 1975). Annual variations in the spawning

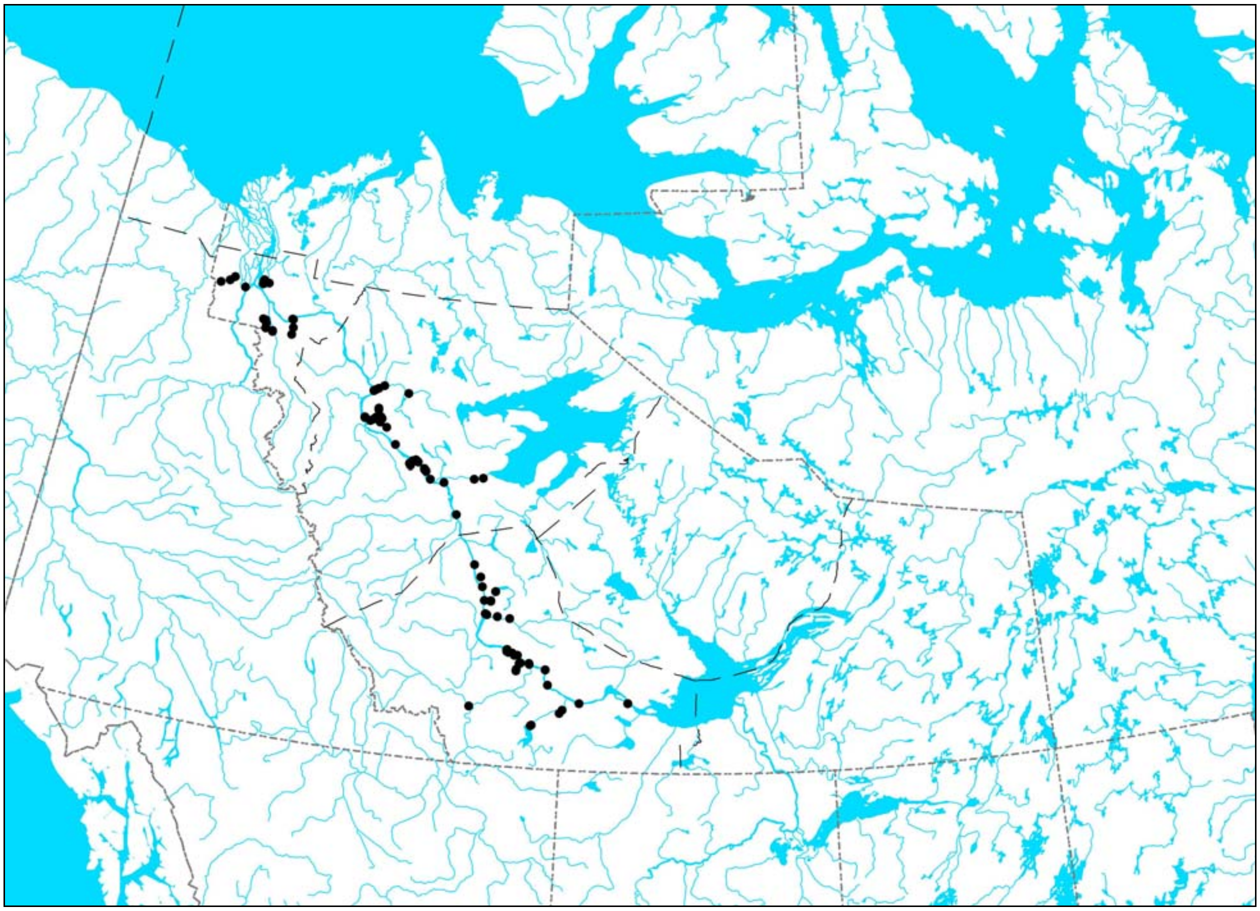

Figure 5. Locations in the Mackenzie Valley where Arctic grayling spawning has been reported.

period are dependant on breakup dates, stream flows, and water temperatures (Jessop and Lilley 1975). Fish in the Trail River, NT, spawned two weeks later in 1974 than in 1973 when breakup was earlier.

In the southern Mackenzie Valley, the upstream spawning migration in Providence Creek in 1979 extended from 17 to 21 May at water temperatures of 5.0 to 8.7°C (peak on 18 May at 5.5°C), although some fish may have moved upstream before the trap was installed to monitor the migration (Falk *et al*. 1982). Spawning was first observed on 19 May when water temperatures ranged from 4.5 to 9°C (mean 7.0°C). It peaked on 21 May at 7.0 to 10.0°C (mean 8.7°C), and ended about 23 May. The downstream migration was from 21 to 26 May, peaking on 22 May at 9.8°C. Migratory activity was greatest in the late evening and early morning (2200 to 0400 h). In the Redknife River, nearby, the upstream spawning migration in late April and early May of 1976, corresponded almost exactly to the peak flow of spring runoff (Katopodis *et al*. 1978). The first ripe female arrived at the highway crossing on 29 April, when the mean daily water temperature was about 6.3°C; the first spent female was observed on 6 May at 7.7°C; and the first fry on 22 May at about 10.7°C.

Further to the north, grayling spawning in the Donnelly River, NT, was closely associated with a sudden rise in temperature from 4°C on May 27 to 11.5°C on June 2 as the ice cover left the lake upstream (Tripp and McCart 1974). Spawning of grayling in Vermillion Creek, NT, evidently occurred at a temperature of 5 to 6°C from May 21 to 25. Shotton (1971) captured gravid females on 5 July in the Ontaratue River, NT.

Similar spawning patterns have been observed in Alaska, north of Fairbanks and on the Seward Peninsula, with the onset of spawning occurring at about 4°C (Ott and Morris 2005, 2006; W. Morris, pers. comm.). When peak daily temperatures remain close to 4°C the duration of the spawning period is extended, while when they are at or above 10°C it may be shortened to a couple of days. Spawning is abandoned or fails during years when the temperatures stay too low after fish have arrived on the spawning grounds. Some fish will move to other streams with warmer water while others hold and ultimately fail if the water does not warm soon enough.

Both fluvial and adfluvial grayling populations spawn primarily in shallow water (<1.0 m), with surface current velocities less than 150 cm/s (Bishop 1967; McPhail and Lindsey 1970; Tack 1971 cited in Armstrong 1986; Kratt 1977; Lawrence and Davies 1979; Krueger 1981; Falk *et al.* 1982; Stewart *et al*. 1982 cited in Northcote 1995; Barndt and Kaya 2000). Spawning substrates range from silt to cobble and boulders, but most spawning occurs over relatively small, unembedded gravels about 2.5 cm in diameter (Rawson 1950; Bishop 1967, 1971; Kratt 1977; Stuart and Chislett 1979; Machniak *et al*. 1980; Beauchamp 1990). In artificial channels they will spawn at depths of 0.15 to 0.45 m (mean 0.24 m), in current velocities of 17 to 43 cm/s (mean 30 cm/s), and over gravel ranging in diameter from 0.2 to 5.0 cm (Barndt and Kaya 2000). Suitable spawning conditions are found below riffles in Providence Creek, NT (Bishop 1967, 1971), and at the tails of long runs in Adsett Creek, BC (Stewart *et al*. 1982 cited in Northcote 1995).

While stream riffles with gravel to rubble bottom are the most commonly reported spawning habitat, other sites have been reported (Kratt 1977; Armstrong 1986). In an inlet of Fielding Lake, Alaska, grayling spawned primarily in slow, shallow backwater areas (Wojcik 1955), and in some northern Alaskan lakes spawning occurred in the lake over substrates ranging from large rubble to vegetated silt (Armstrong 1986). They have also been seen spawning among sedges over an organic bottom in a nearly stagnant pond (Tack 1980 cited in Armstrong 1986), and over mud in a slough (Reed 1964). In Alaska, spawning also occurs in lake inlets or outlets (Roguski and Tack 1970; Tack 1972; Armstrong 1986) and highway culverts (Kratt 1981).

Males arrive on the spawning ground first and establish and defend a rectangular territory with the long axis parallel to the stream flow, about 2 m by 3.5 m (Bishop 1967, 1971; Kratt 1977). They do not build a redd (Bishop 1967, 1971; McPhail and Lindsey

1970; Barndt and Kaya 2000). Males that cannot establish a territory move downstream into a refuge area where females wait too. Females cruise through the males' territories looking for mates. The majority of spawning occurs from mid-day through late afternoon, when the water temperature peaks for the day (Bishop 1967, 1971; Beauchamp 1990; Ford *et al*. 1995). After many lateral displays the male drapes his dorsal fin over the female and they spawn (Beauchamp 1990). This can disturb the bottom sediment slightly due to the vigorous vibrating by both fish.

Observations at Providence Creek, NT, suggest that females release all of their eggs in one act, but that males may spawn more than once during the season (Bishop 1967, 1971). This pattern may differ among systems since both male and female grayling in the Fond du Lac River of Saskatchewan were polygamous (Kratt 1977). The orange eggs are about 2.5 to 2.6 mm in diameter at spawning (Wojcik 1955; Bishop 1971), but quickly swell to 2.7 mm on hardening (Reed 1964). They continue to swell over the next 3 or 4 days and reach diameters of between 3.5 and 4.0 mm (Vincent 1962). The eggs are very adhesive when expressed and adhere to the substrate, but gradually lose this property as they water harden (Bishop 1971). They may be covered by up to 5 cm of substrate (Reed 1964; Tack 1971; Kratt 1977; Kratt and Smith 1977; Krueger 1981). Some eggs drift downstream from the spawning areas (Kratt 1977).

Spawning takes place over a 2 to 3 week period, after which the adults return to larger rivers or lakes (Lawrence and Davies 1979; Chang-Kue and Cameron 1980; Tack 1980 cited in Armstrong 1986; Ford *et al*. 1995). There is no parental care of the eggs or young (Ford *et al*. 1995). Fecundity varies depending upon the size of fish and locality (range 1,700 to 15,867) (Schallock 1966; Williams 1969; Tripp and McCart 1974; Falk *et al*. 1982). Schallock (1966) suggested that fecundity may be better correlated with condition than length, but Tripp and McCart (1974) found strong correlations with length. In Providence Creek, NT, the number of eggs per individual ranged from 4,694 to 15,867 (6,475 to 16,887 eggs per kg body weight) (Falk *et al*. 1982). Populations where most spawners are generally smaller produce fewer eggs on average per individual but have a similar egg:body weight ratio (e.g., Deer Creek, Montana, Deleray 1991).

The time required for incubation of the eggs varies with mean water temperature, ranging from 8 days at 15.5°C and 16 to 18 days at 9°C, to 25 to 29 days at 7.1°C and 32 days at 5.8°C, (Wojcik 1955; Kratt 1977; Kratt and Smith 1977; Krueger 1981). However, typical incubation times were 13 to 18 days under natural stream conditions that fluctuated about a mean daily temperature of 8.8°C (Bishop 1967, 1971). Water temperatures during the egg development period often vary widely. In the Fond du Lac River, SK, they ranged from 1.0 to 11.5°C (Kratt and Smith 1977).

Estimates of the number of **thermal units** for hatching time vary widely (Northcote 1995). No carefully controlled measurements of hatch time appear to have been made, and those based on average stream temperature records may be misleading. Kratt (1977) found that grayling eggs hatched in 176.75 degree-days at a mean temperature of 7.07°C, Kratt and Smith (1977) in 186.24 degree-days at a mean daily temperature of 5.82°C, Bishop (1971) in 216.5 degree-days, and Ward (1951) in about 250 degree-days. Young grayling emerge from the gravel 3 to 4 days after they hatch (Kratt and Smith 1977).

There is little information on lake spawning by Arctic grayling in the NT and NU. However, grayling from the Great Bear River do spawn in “Three Day Lake” in the spring and then return to the river to feed and overwinter (Chang-Kue and Cameron 1980). Lake spawning by grayling has been observed in Alaska over coarse sand, gravel, silt and organic substrates in water 0.15 to 0.9 m deep (Reed 1964; Tack 1980 cited in Armstrong 1986; Krueger 1981). It usually occurs in the vicinity of inlet or outlet streams (Krueger 1981).

3.2 Alevins and fry (Rearing habitat)

Nursery areas for Arctic grayling have been located in streams and rivers down the length of the Mackenzie Valley (Hatfield *et al*. 1972a; Dryden *et al*. 1973; Stein *et al*. 1973a; Jessop *et al*. 1974; Tripp and McCart 1974; EIS Mackenzie Gas Project 2004).

Newly hatched grayling **alevins** spend three to five days under the substrate (Kratt 1977; Kratt and Smith 1977; Ford *et al*. 1995) before emerging from the gravel in late May to early July (Tripp and McCart 1974; Craig and Poulin 1975; Katopodis *et al*. 1978; Chang-Kue and Cameron 1980). Their length at emergence varies among systems, ranging from about 7 to 15 mm (Northcote 1995). Newly emerged fry are usually found in shallow, calm water with little flow. Such areas include very shallow riffles between rocks at the lower end of gravel bars (Vascotto 1970), backwaters, side channels (Tack 1971 cited in Armstrong 1986; de Bruyn and McCart 1974; Northcote 1995), marginal habitats along banks (Jones *et al*. 2003a), shallow shorelines, quiet side pools (Lee 1985), and bushy or grassy areas of adjacent sloughs (Armstrong 1986). In areas with current, larval grayling use sand drifts and rocks as velocity barriers (Lee 1985). Larvae are found over silt or sand substrates within 10 to 20 mm of the bottom. They do not use rocks and debris in these areas for cover.

In Providence Creek, NT, grayling began eating about 9 days after hatching (Bishop 1967, 1971). Mayfly nymphs and diptera pupae were important food items for 4 to 5 week-old fry, which also ate cladocerans. Older grayling have a more varied diet.

Young-of-the-year grayling in tundra lake-outlet streams on the NT barrens consumed primarily Chironomidae and Simuliidae (Jones *et al*. 2003a). Production capacity of grayling in the streams was determined primarily by in-stream production of invertebrates, despite the abundance of lake-derived microcrustacea in the drift. They selected the larger individuals among these taxa. As they grew the fish ate larger numbers of prey, but the range of prey size did not change after mid-July. The selection of pupae and avoidance of Ephemeroptera suggested that prey characteristics other than size also contribute to selectivity by young-of-the-year grayling. Artificial streams provided less productive feeding habitat than natural streams (Jones *et al*. 2003c).

Because fry are helpless in water currents for two weeks after hatching, flooding or drought during this period may cause high mortalities, either by washing them downstream into unfavourable habitat or by stranding them in shallow, isolated pools (de Bruyn and McCart 1974; Armstrong 1986). Grayling fry are most susceptible to downstream displacement shortly after swimup, particularly at night (Kratt 1977; Deleray 1991; Deleray and Kaya 1992). In Deer Creek, Montana, between 4 and 7% of the fry produced may have been displaced downstream annually. Year class failures in Alaska's Chena River may have resulted from heavy larval mortality due to flooding (Tack 1974 cited in Armstrong 1986).

Initially the fry school together but within three weeks begin to exhibit some antagonistic behaviour toward one another, become territorial and solitary, and move into deeper water (Vascotto 1970; de Bruyn and McCart 1974; Kratt 1977; Kratt and Smith 1979; Lee 1985; Jones *et al*. 2003a). Young grayling (11-41 d after swim-up) tend to swim downstream (Kaya 1989). However, the tendency to maintain position is greater among fluvial than lacustrine fish, perhaps as a means of maintaining stream residence (Kaya 1991).

Later in the season, once they become more mobile, young-of-the-year in streams inhabit shallow pools and side channels with water velocities less than 80 cm/s and depths of 5 to 50 cm, over silt to boulder substrates (Vascotto 1970; de Bruyn and McCart 1974; Stuart and Chislett 1979; Lee 1985; Kaya 1989; Deleray 1991; McClure and Gould 1991; Ford *et al*. 1995; Jones *et al*. 2003a). Within this range of habitat they show strong preference for slower water velocities (0-25 cm/s), shallow depths (6-31 cm), and silt to fine gravel substrates (Birtwell *et al*. 1984; Lee 1985; McClure and Gould 1991; Deleray 1991; Deegan *et al*. 2005). In **allopatry** they may make more use of gravel to cobble and less use of sand substrates than when they are in **sympatry** with round whitefish or chinook salmon (Lee 1985).

Young-of-the-year grayling in Alaskan streams occupied current velocities between 15 and 25 cm/s or 4 L_T/s (total lengths per second) (Deegan *et al*. 2005). This is about half their potential prolonged swimming speed (10 L_T/s), which is usually slightly higher than, but close to their sustained swimming speed and much lower than burst speed (Hammer 1995 cited in Deegan *et al*. 2005). Oxygen consumption increases with fish mass and temperature (6-23°C), with a steep increase in metabolic rate between 12 and 16°C (Deegan *et al*. 2005).

The availability of cover in the form of overhead vegetation or boulders is also an important factor in stream habitat use by young-of-the-year grayling (Vascotto 1970; McClure and Gould 1991; Ford *et al*. 1995). In Deer Creek, Montana, over 80% of the fry remained within 60 cm of overhead cover (vegetation), and over 90% remained within 10 cm of the stream bottom (focal point depth) (Deleray 1991). As summer progressed and the fry grew, more of them strayed further from cover and occupied areas with higher water velocities and a deeper water column (Lee 1985; Deleray 1991). However, when age 0 grayling were disturbed they swam to another location rather than hide under cover, whereas age 1 fish used cover when disturbed (Deleray 1991).

Some fry (age 0) and juveniles (age 1) leave the stream habitats in late summer and fall (mid-August through mid-October), while others extend their stream residence into the fall and leave under the ice, possibly to avoid predation by larger grayling in the lake (Deleray 1991). Some young-of-the-year remain in their natal stream for up to 15 months (Ford *et al*. 1995). Fish exiting the streams may move upstream or downstream depending upon their location in relation to the overwintering habitat (Kratt 1977), typically larger rivers or lakes, or (on the North Slope) spring fed areas (Armstrong 1986). In the Mackenzie Valley, fry move downstream from the hatching areas earlier in the south, mid-June through early July in small tributaries near Fort Simpson; and later in the north, in mid-July though early August, peaking in late July in Bluefish Creek near Norman Wells (Jessop *et al*. 1974; Jessop and Lilley 1975).

Little is known of habitats selected by young-of-the-year grayling associated with lakes (Armstrong 1986). Young-of-the year grayling in Tyee Lake, Alaska, occupied shallow **littoral** habitats ranging in depth from 0.02–0.46 m, and shallow, quiet pools in delta regions of the inlet streams (Krueger 1981).

3.3 Juveniles (Rearing habitat)

Yearling and juvenile grayling undertake yearly migrations between feeding areas in small tributaries and overwintering areas (Ford *et al*. 1995). Some juveniles remain in their natal stream feeding, while others move to other areas of the river system. In Alaska they begin moving into some streams at the end of the adult spawning migration, sometimes with the latest arriving adults (Morris and Winters 2002; W. Morris, pers. comm.). In the Fort Simpson area (NT) they typically arrive 2 to 4 weeks after the adults have spawned, moving into tributaries there in early summer (Jessop and Lilley 1975).

In Alaska, those that stay in their natal streams all summer leave in the middle of September, with numbers dropping by the end of September, to go to their overwintering areas (Craig and Poulin 1975). Fidelity to small overwintering ponds has been observed in age 0 and 1 fish (Barndt and Kaya 2000). Some juvenile grayling (80-157 mm) overwinter in spring fed areas of tributary streams such as Prohibition, Vermillion, and

Hodgson creeks, Little Smith and Willowlake rivers, and unnamed stream at milepost 519 (McCart 1974). They also overwinter in small spring fed lakes.

Juveniles prefer areas with sand and gravel substrates (Vascotto 1970; Den Beste and McCart 1984; Evans *et al*. 2002). In Alaska juveniles were found in water temperatures ranging from 5 to 17°C. Cover, when used, was most often rocks and, to a lesser extent, cutbanks, loose gravel, overhanging vegetation, instream vegetation and shade. Juveniles were found in the highest densities in slow-moving, shallow water over silt, gravel and rubble substrates with some sand, especially in still water areas with silt substrates at depths of 20 to 80 cm. Some juveniles were also caught in riffle areas with boulders and cobble in water 20 to 30 cm deep. They appeared to select for channels that are 1 to 8 m wide and against channels wider than 14 m (Den Beste and McCart 1984).

Juvenile grayling are seldom observed schooling, but schools have been seen seeking cover under an overhanging boulder in Upper Granite Lake, British Columbia (Beauchamp 1982). Boulders are also used as cover by stream populations (Ford *et al.* 1995).

Age 1 fish are territorial throughout the summer feeding period (Kratt and Smith 1979). Initially, juveniles are distributed in the middle and lower reaches and delta areas of small tributaries during the summer (de Bruyn and McCart 1974). As they grow larger individuals tend to maintain territories further upstream (Vascotto 1970; Hughes and Reynolds 1994; Hughes 1998a, 1999). In McManus Creek, Alaska, older juveniles and adults inhabited the mainstem stream pools, with the largest fish occupying the uppermost portions of the pools and the smallest ones the periphery (Vascotto 1970). The average habitat area used by juvenile grayling in some Alaskan streams was 125 m^2, although habitats as small as 1 m^2 were used in boulder-controlled pools in some mountain streams (Den Beste and McCart 1984).

3.4 Adults

Arctic grayling can mature as early as age 2 or as late as age 9 (Schallock 1966; Bishop 1967; de Bruyn and McCart 1974; Tripp and McCart 1974; Chang-Kue and Cameron 1980; Armstrong 1986; Ford *et al*. 1995; Barndt and Kaya 2000). In the Donnelly River, NT, individuals of both sexes mature as early as age 2 (Tripp and McCart 1974). Fish in this population may mature earlier and grow faster than those in other nearby populations, although this was not confirmed by multi-year sampling. In the Great Bear River, NT the youngest mature female was age 3 and male was age 2 (Chang-Kue and Cameron 1980), while in Great Slave and Great Bear lakes and their tributaries, most fish matured between the ages of 3 and 6 (Miller 1946; Bishop 1967;

McPhail and Lindsey 1970; Falk and Dahlke 1974; Falk *et al*. 1980; Moshenko and Low 1983; Low and Read 1987; Read and Roberge 1989; Jessop *et al*. 1993).

After their first spawning, grayling sometimes skip a year before spawning again (Carl *et al*. 1992). The species' variable time to first maturity and the delay in second spawning may be an adaptation to highly variable juvenile recruitment, and limit the population's ability to withstand exploitation. Successful recruitment appears to be very infrequent in some populations on the Alaskan North Slope, possibly only once in every 4 to 7 years (W. Morris, pers. comm.).

Grayling age estimates have historically been under-estimated due to the use of scales for age determination and the possible resorption of annuli (Bishop 1967; Chang-Kue and Cameron 1980; DeCicco *et al*. 1997). Many studies have relied on scale ages, which only yield reliable estimates up to about the time of maturity. Annulus formation on scales may be delayed in northern populations for a year and may not be visible in fish over 10 years old, so scale readings can underestimate ages by up to 20 years (de Bruyn and McCart 1974; Armstrong 1986; Northcote 1995; DeCicco and Brown 2006). Accurate age estimations are fundamental to the management of fish populations, so otoliths should be used for aging until a non-lethal method (e.g., fin rays) can be validated for age determination in grayling (DeCicco and Brown 2006).

The maximum age for grayling ranges from age 10 to age 29 depending on the river system and method of age determination. Based on scale ages, the oldest grayling captured from the Mackenzie system by Hatfield *et al*. (1972a) was age 8 and by Stein *et al*. (1973b) age 10. The oldest fish in the Kakisa River, a tributary of Great Slave Lake were age 11 (Falk *et al*. 1980; Moshenko and Low 1983; Low and Read 1987; Read and Roberge 1989), while those in Great Slave and Great Bear lakes live to at least age 12 (Bishop 1967; Falk and Dahlke 1974; Falk and Gillman 1974). Based on otolith readings, fish in the Donnelly and Great Bear rivers live to at least age 21 (Tripp and McCart 1974; Chang-Kue and Cameron 1980), and those in northern Alaska to at least age 29 (DeCicco and Brown 2006). Age differences among systems may be related to differences in environmental conditions or in aging techniques (scales cf. otoliths).

During the summer feeding period, after spawning, adults in rivers prefer areas of rubble and gravel (Vascotto 1970; Den Beste and McCart 1984; Evans *et al*. 2002). They are found over fine grained and coarse substrates, but avoid medium-grained substrates. They prefer water velocities of 61 to 108 cm/s and depths of 110 to 152 cm, but also occur in currents of 0 to 130 cm/s and in shallows with depths of 23 to 91 cm (Evans *et al*. 2002). Grayling habitat in the Minto Creek drainage of the Yukon had August surface water velocities ranging from 48 to 97 cm/s (Birtwell *et al*. 1984).

Adult grayling often use debris, rubble (7.62-12.7 cm) and cobble (>12.7 cm) as cover (Schmidt *et al*. 1984; Suchanek *et a*l. 1984; Liknes and Gould 1987; Evans *et al*. 2002). They sometimes use overhanging riparian vegetation, undercut banks, and deadfall as cover, and seldom use aquatic or emergent vegetation. When disturbed, grayling in stream pools seek the deepest water first and then move to the downstream end of the pool (Vascotto 1970).

During the spring breeding season only larger adult male grayling maintain territories, but during the summer feeding season females and smaller males also maintain territories (Vascotto 1970; Kratt and Smith 1979). They adopt a larger-older-fish-upstream distribution pattern (Vascotto 1970; Hughes and Reynolds 1994; Hughes 1998a, 1999). This process begins with the concentration of spawning fish and the resultant fry in the lower reaches (Hughes 1999). As cohorts age their distribution in the river gradually increases as they move upstream, with the fastest growing fish in the upper reaches and slower growing fish in the lower reaches. Substantial interannual movements are required to maintain this gradient (Hughes 1998a). Headwater positions appeared to be preferred by grayling, and the larger fishes were more successful competing for these positions (Hughes and Reynolds 1994).

The summer distribution of Arctic grayling is significantly influenced by flow and water temperature (Ott and Morris 2006; W. Morris, pers. comm.). In a small Alaskan interior lake and at streams in northwestern Arctic Alaska, fish older than age 0 congregate in large numbers at the outflows of cooler or better oxygenated systems during years with low water and/or high water temperatures.

In some Alaskan streams, the average habitat area used by adult grayling was 170 m^2, but habitats as small as 1.5 m^2 were used in a few small mountain streams (Den Beste and McCart 1984). The average stream width used by adults was 10 m, and channels less than 6 m wide were selected against. Over half the fish observed were found within 10 cm of the stream bed.

Adult grayling feeding on drift in streams appear to position themselves on the basis of water depth and flow so as to maximize their net energy intake, not on the proximity to overhead cover (Hughes and Dill 1990; Hughes 1992a,b). Physical habitat forms the template for distribution patterns by determining the location and ranking of the most profitable feeding positions. Manifestation of summer territoriality appears to depend upon the presence of adequate current, as otherwise there is little advantage to maintaining an upstream position so as to have the first opportunity to capture food carried downstream into a pool.

In fall, entire populations of grayling migrate out of small headwater lakes and small streams to overwinter in larger rivers or lakes (Chang-Kue and Cameron 1980;

Armstrong 1986; West *et al*. 1992; Ford *et al*. 1995). The timing of these migrations varies from early summer through December depending upon the local conditions (Stein *et al*. 1973a; Pearse 1974; Porter *et al*. 1974; Netsch 1975; Armstrong 1986; Stanislawski 1997). The direction may be up or down stream depending upon where the spawning grounds are in relation to suitable overwintering habitat.

Some fish overwinter in deeper spring-fed pools while others leave the spring-fed tributaries, perhaps due to the risk of injury or death from frazil ice (Armstrong 1986). The use of spring-fed tributaries by grayling for overwintering and perhaps spawning may be relatively common (McCart 1974; Jessop and Lilley 1975; N. Mochnacz, pers. obs.). Areas fed by perennial springs are used by adult grayling overwintering in Cache Creek, NT (Feb. 21-23, 1974, depth 0.5-1.5 m, 2-8°C Jessop and Lilley 1975) and in various streams and rivers in the Yukon (e.g., upper Firth River, Joe Creek, Canoe Creek, Babbage River, de Bruyn and McCart 1974) and Alaska (Kavik River, Craig and Poulin 1975; North Slope, West *et al*. 1992). Grayling in some streams can be more abundant in headwater reaches with significant groundwater discharge than in lower reaches without detectable groundwater discharge (N. Mochnacz, unpubl. data). Arctic grayling in Alaska's Tanana River system winter in the main river and by April are aggregating at the mouths of small tributary streams (Craig and Poulin 1975).

Some grayling may spend part or all of their lives near their overwintering areas. These fish may include stocks in some lakes, those living near major groundwater sources, and perhaps some of those that spawn in mainstem areas of larger unsilted runoff rivers such as the Chena in Alaska (Armstrong 1986). Other stocks undertake extensive migrations between spawning and overwintering areas (Reed 1964; Pearse 1974; Jessop *et al*. 1974; Tripp and McCart 1974; Chang-Kue and Cameron 1980; West *et al*. 1992; Stanislawski 1997). Some migrants enter estuarine waters enroute to overwintering habitats in other systems (West *et al*. 1992).

In the Donnelly River system, NT, adults remained in the Chick Lake area for about a month after spawning (Tripp and McCart 1974). They moved downstream into other areas of the river in early to mid July, and then into the Mackenzie River by the beginning of October. Post-spawning adults in the Trail River, NT moved downstream in mid to late May, within a week or so of spawning (Jessop *et al*. 1974). Fish from Mackenzie tributaries such as the Donnelly, Rabbitskin, and Trail rivers undertake extensive post-spawning movements upstream or downstream in the Mackenzie mainstem (Jessop *et al*. 1974; Tripp and McCart 1974). A grayling tagged at Chick Lake on the Donnelly River moved 320 km to the Great Bear River between 9 July and 4 October 1972 (Tripp and McCart 1974).

Limited tagging data suggest that individual grayling show fidelity to both spawning and overwintering areas (Jessop *et al*. 1974; Tripp and McCart 1974; Jessop and Lilley

1975; Kratt 1977), but whether this extends to populations is unknown. Arctic grayling will also move from the Donnelly River to Oscar Creek, and may do so between other tributaries (Jessop *et al*. 1974). The Great Bear River attracts adult grayling from the Mackenzie mainstem and other tributaries to feed during the summer (McCart 1982).

In lakes, adult Arctic grayling occur over sand, silt, gravel and rubble substrates (Bishop 1967; Hatfield *et al.* 1972a) and along rocky shorelines (Rawson 1951; McPhail and Lindsey 1970), typically at depths of < 4.0 m (Bishop 1967; Lawrence and Davies 1979; Scott and Crossman 1973; Krueger 1981), although Rawson (1951) caught a few in Great Slave Lake at depths of between 6 and 10 m. In Great Bear Lake, they were often found in bays near stream inflows (Miller 1947). During the summer, grayling are abundant in the Brabant and Lobstick islands area, where Great Slave Lake flows into the Mackenzie River (Bishop 1967). These islands have trees that overhang the water, a rubble bottom that is generally free of vegetation and drops off sharply, and current. Grayling are often found under trees overhanging the water feeding on insects in streams (Bishop 1967), and may use similar overhead cover in lakes.

Arctic grayling are opportunistic, visual predators (Bishop 1967; Vascotto 1970; de Bruyn and McCart 1974; Stewart *et al*. 2007). Throughout their distribution, both adults and juveniles eat a wide variety of seasonally available macroinvertebrate taxa and life stages (eggs, larvae, pupae, nymphs, adults) that originate from both aquatic and terrestrial habitats (Miller 1946; Bishop 1967, 1971; Jessop *et al*. 1974; Tripp and McCart 1974; McKinnon and Hnytka 1979; Chang-Kue and Cameron 1980). Juveniles eat an increasing variety of taxa as they approach adulthood, and prey opportunistically on fish eggs and fry, including those of their own species. Their reliance on surface drift and on terrestrial insects changes over the open water season in response to food availability (Vascotto 1970; Vascotto and Morrow 1973; Morrow 1980). Little is known of their fall and winter diet, but it will shift away from terrestrial biota to almost entirely aquatic biota, and foraging patterns will likely shift from a surface and mid-water focus to mid-water and bottom focus (Stewart *et al*. 2007). Amphipods may constitute a greater proportion of the diet of grayling in lakes than in streams.

Humans are a key predator on adult and large juvenile grayling, while piscivorous fishes, particularly northern pike (*Esox lucius*), may be the key predators on smaller juveniles (Schallock 1966; Bishop 1967; Jessop *et al*. 1993; Stewart *et al*. 2007). Competition for food with other salmonid species may be a factor in the displacement of Arctic grayling from some regions, and may limit their growth in some stream habitats (Vincent 1962; Armstrong 1986). Because grayling are visual predators, their feeding success is vulnerable to increases in water turbidity (Bishop 1967; Vascotto 1970; Schmidt and O'Brien 1982; Birtwell *et al*. 1984; Lloyd *et al*. 1987; Scannell 1988).

Long term (17 y) variance in survival rates among adult grayling in the Kuparak River, Alaska was not strongly correlated to environmental (stream temperature, discharge, winter severity, and incidence of drought) or population parameters (growth, condition factor, and mean fish size) (Buzby and Deegan 2004). This lack of responsiveness to annual environmental conditions suggests that survival may be determined by multiyear factors or life history tactics that maintain survival at the expense of growth and fecundity. Lack of evidence that the mortality rate was density dependant suggests that fishing mortality should be added to, rather than substituted for, natural mortality when managing grayling stocks to avoid population depletion.

4.0 HABITAT IMPACTS ON FISH BIOLOGY

Activities with the potential to affect key aspects of Arctic grayling habitat and thereby the species' biology are discussed below and summarized in Table 5. Habitat degradation, habitat fragmentation, species introductions, and improved access are all aspects of development that could affect the species, and their effects might also be modified by climate change. Grayling may be slow to recover from year class failures, as they are relatively slow-growing and there are relatively few adult age classes (Stein *et al*. 1973a). It may be considerably more difficult to restore Arctic grayling populations than to maintain them (Buzby and Deegan 2004).

In Montana, loss of hydrological integrity and the introduction of non-native fish species have played an important role in the disappearance of native salmonids, including Arctic grayling (Van Kirk and Benjamin 2001). The species was once abundant in northern Michigan, where logging, pollution, the introduction of competitors such as brown trout (*Salmo trutta*), and overfishing may have contributed to its extirpation by the late 1930s (McPhail and Lindsey 1970).

4.1 Habitat degradation

4.1.1 Organic contaminants

Because they feed heavily on terrestrial insects at the surface, grayling may be particularly susceptible to insecticide sprays and chemical spills that reduce or contaminate these sources of food (Stein *et al*. 1973a).

Concentration ranges for organochlorine pesticides and polychlorinated biphenyls (PCBs) in grayling muscle and liver from lakes in the Alaskan Arctic have been similar to those observed for other Arctic freshwater fishes (1-100 ng/g wet wt), but one to two orders of magnitude lower than Great Lakes salmonids (Wilson *et al*. 1995; Allen-Gil *et*

Table 5. Activities with the potential to affect key aspects of Arctic grayling habitat and their potential effects on the species.

Activity	Potential impact		
	Habitat	**Species**	**Directly affected life stage(s)**
• water removal • drainage alterations • seismic testing	• reduced groundwater flow • altered **baseflow** and ice and temperature regimes	• degradation, reduction or loss of spawning, rearing and feeding habitats • increased winter mortality of stream resident fish	• all
• placer mining • construction of roadways, pads, and structures • stream crossings	• streambed alteration by removal or disturbance of sand, gravel, and cobble substrates • sediment mobilization • streambed destabilization	• degradation, reduction or loss of spawning, rearing, and feeding habitat • increased mortality or physiological stress to all life stages from increased turbidity, physical damage, exposure, and/or loss of cover • decreased ability of adults to withstand other stressors, such as toxicants • emigration of adults and larger juveniles	• all
• logging • clearing for right-of-ways, camps, etc. • stream crossings	• inland clearing • loss of riparian and instream cover (i.e., shoreline, large woody debris) • streambed reworking • altered hydrological regime with more abrupt runoff • warming, increased sediment inputs	• degradation of spawning, rearing, and feeding habitat • higher mortality rates for all life stages	• all
• culvert installation for stream crossings • dam construction • in-stream construction	• flow impoundment • changes in seasonal flow regimes, water depth, and water velocity • habitat fragmentation	• interruption of spawning and feeding migrations • inundation or dewatering of spawning areas • population extirpation • creation of new overwintering areas	• yearling and older fish
• road and right-of way construction • population growth	• improved access to Arctic grayling habitat	• increasing harvest pressure on adults and large immature fish • visual and physical disturbance of fish and fish eggs • changes in population structure, possibly leading to extirpation • increased potential for species introductions	• adults and large juveniles by harvesting • all life stages by introductions
• contaminants releases	• chemical pollution	• reduction in fish quality • increased mortality	• all
• nutrient additions	• stimulated production	• higher production by young-of-the-year and adults, no detectable difference in egg production or fitness	• young-of-the-year and older fish
• climate change	• changes in the temperature and precipitation regimes that alter seasonal streamflow regimes • warming	• changes in the seasonal access to and suitability of stream habitats for spawning, rearing, and feeding • increasing competition and predation by warmer water species	• all

al. 1997). These contaminants are carried into the north by long-range transport, and their biomagnification factors are similar to ratios reported for other aquatic systems.

In the laboratory, the acute lethal tolerance (96 h LC50) for pentachlorophenol was 67 µg/L (95% CI = 57-77) at 15°C, and 61 µg/L (95% CI = 48-71) at 5°C (McLeay *et al*. 1983, 1987). The species' ability to withstand this reference toxicant was similar to that for other healthy salmonids.

4.1.2 Sediment mobilization

Grayling that are unable to escape from streams carrying sediments mobilized by placer mining die at high rates (sac fry) or suffer gill damage, starvation, and slowed maturation (age 0 fingerlings and age 2 juveniles) (Reynolds *et al*. 1989). In Birch Creek, Alaska, the turbidity two kilometers downstream from the nearest placer mine averaged 727 NTU (SD = 419), as compared to 1.3 NTU (SD=1.4) in a nearby unmined stream. The direct effects of sedimentation on health and survival of individual fish may be less damaging to grayling populations than the indirect effects of sedimentation, through loss of summer habitat for feeding and reproduction (see also Weber and Post 1985). While grayling often live in large, turbid, glacial-fed rivers, these systems are used primarily for overwintering—when they are clear of sediment, and as migratory routes to other systems. However, areas of glacial rivers with significant spring upwellings likely provide some feeding habitat within the clear water lens and plume (W. Morris, pers. comm.). Arctic grayling prefer clear, bog-fed streams with rapid runoff for spawning.

In naturally and artificially turbid aquatic systems in Alaska, Lloyd *et al*. (1987) observed reduced abundance of zooplankton, macroinvertebrates, and Arctic grayling. They collected many grayling in streams without placer mines but none in placer mined streams, except during the presumed autumn migration of some fish through streams influenced by mining. Adult and juvenile grayling were present in Sulphur Creek, Yukon, where suspended sediment levels were about 100 mg/L, but absent from Clear, Johnson, and Duncan creeks which were being actively placer mined (Birtwell *et al*. 1984).

Gill damage, possibly related to high suspended sediment exposure, has been observed in juvenile and adult grayling that inhabit the Yukon's Minot Creek drainage, where a placer mine was operating on Highet Creek (Birtwell *et al*. 1984). Fewer age 0 grayling were found in Highet Creek than elsewhere in the system, suggesting that they were displaced by the mining activities. Turbidity values in Highet Creek ranged from 4.6 to 395 Formazin Turbidity Units (FTU), reflecting the variability of placer mining activities and associated sediment releases.

Age 0 grayling fry survived short term (4-5 d) exposure to very high levels of suspended inorganic (≤ 250 g/L) and organic (≤ 50 g/L) sediment from a Yukon placer mine (McLeay *et al*. 1983, 1987). Their lethal tolerance may decrease slightly when they are acclimated to lower temperatures (5°C). They are stressed physiologically by acute exposure to these high suspended sediment concentrations. Prolonged exposure (6 weeks) to lower concentrations (100, 300, and 1000 mg/L) had little effect on their survival but significantly impaired growth and feeding success (surface and subsurface), particularly at the highest concentration (McLeay *et al*. 1984, 1987). Fish were also displaced downstream at the higher concentrations (300 and 1000 mg/L), and were paler in colour. Their ability to withstand increases in temperature or decreases in oxygen was unchanged; indicating that exposure to the suspended sediments had not impaired gill function. However, their ability to withstand concentrations of the reference toxicant pentachlorophenol decreased.

Arctic grayling fingerlings (~45 mm FL) suffered less than 1% mortality during a 96 h toxicity test in both clear (mean NTU = 1.4) and placer mined (mean NTU = 445) streams, and egg mortality did not differ significantly ($p \geq 0.1$) between the streams (Scannell 1988). However, the fingerlings avoided water with turbidity >20 NTU, and their reactive distance to prey diminished proportional to the natural logarithm of turbidity. This rapid degradation of Arctic grayling habitat with loss of clarity supports use of a water quality standard of 5 NTU above natural conditions as an appropriate standard for protecting grayling habitat (Scannell 1988).

4.1.3 Inorganic contaminants

Acute toxicity tests on Arctic grayling (96 h LC50) of trace inorganics associated with placer mining found that toxicities varied by four orders of magnitude among compounds, juveniles are generally more sensitive than alevins, and that the sensitivity of grayling is similar to that of rainbow trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) (Buhl and Hamilton 1990, 1991). From most toxic to least toxic the overall rank orders for these species were, for three compounds: $CuSO_4{\cdot}5H_2O > ZnCl_2 > As_2O_5{\cdot}xH_20$ (Buhl and Hamilton 1990), and for nine other compounds: $CdCl_2 = AgNO_3 > HgCl_2 > NiCl_2{\cdot}6H_2O = HAuCl_4{\cdot}3H_2O > NaAsO_2 = Na_2SeO_3 > Na_2SeO_4 = Na_2CrO_4{\cdot}4H_20$ (Buhl and Hamilton 1991). The copper concentrations in five Alaskan streams were higher than acutely toxic concentrations, but chemical speciation in the presence of sediments suspended by the mining operations may alter their toxicities (Buhl and Hamilton 1990). Arsenic and mercury may also pose a hazard to salmonids inhabiting streams with active placer mines (Buhl and Hamilton 1991).

Acidic aluminum-rich water, 369 µg/L (SD=33) as inorganic, monomeric Al-species, is acutely toxic to juvenile Arctic grayling, but acidic (pH 5.0) Al-poor water is not (Poléo *et al*. 1997). Grayling are more sensitive to Al than Arctic charr (*Salvelinus alpinus*), but much less sensitive than Atlantic salmon (*Salmo salar*).

4.1.4 Nutrient additions

Whole-river fertilization with phosphoric acid (Deegan and Peterson 1992), phosphorus, or phosphorus and nitrogen (Harvey *et al*. 1998) stimulated production by young-of-the-year and adult grayling. In some years, the size of the age 0 fish increased 1.4 to 1.9 fold, while adults showed a 1.5 to 2.4 fold increase in the weight gain with a 1.3 to 3.4 fold increase in neutral lipid storage (Deegan and Peterson 1992). Fertilization did not cause a detectable difference in gonad mass, percent lipid in eggs, or egg size.

4.1.5 Physical disturbances

During and following the open-cut installation of a natural gas pipeline under the Wildhay River in Alberta, radio-tagged adult grayling were often sedentary (Reid *et al*. 2002). Suspended sediment concentrations were relatively low before and during construction, with background levels of 12 to 42 mg/L and concentrations during the blasting peak of 408 mg/L at 150 m downstream, 136 to 162 mg/L during trenching, and 50 to 150 mg/L during backfilling. The fish did not exhibit a pattern of avoidance to increased sediment load, and the few movements by downstream fish were probably motivated by disturbances such as blasting or equipment movement. However, sediment concentrations were not augmented by natural events such as spring runoff or storms. To avoid conflicts with Arctic grayling reproduction, construction activities that affect spawning activity should be avoided from the beginning of breakup until after hatching is completed (Netsch 1975).

Construction methods that reduce or eliminate groundwater discharge in grayling streams could also stress populations. A reduction or cessation of groundwater could increase stream temperature in the summer and eliminate overwintering refuges in the winter. Groundwater discharge areas may also be used by Arctic grayling for spawning as they provide a stable environment for egg incubation.

4.1.6 Entrainment

At a hydroelectric development on the Chatanika River in Alaska, grayling passing through the turbines did not survive, but those following diversion ditches and entering large siphons were able to pass downstream successfully (Schallock 1966).

4.1.7 Logging

Log driving in streams during spawning or larval development contributed to the extripation of grayling in Michigan (Hubbs and Lagler 1958; Vincent 1962). It likely did so by reworking the streambed in the swift, shallow areas where the grayling spawned, dislodging eggs and destabilizing the spawning substrate.

4.2 Habitat fragmentation

Grayling spawning success appears to be strongly affected by stream obstructions which are, in part, dependent on the timing and magnitude of the spring discharge (Carl *et al*. 1992). Highway culvert installations that are narrow or steep can have interior flow velocities that obstruct upstream Arctic grayling spawning runs because their peak spring flows are too high to permit fish passage (Katopodis *et al*. 1978; Derksen 1980). Elevated culvert outlets, beaver dams, and hydroelectric impoundments can also prevent fish from accessing spawning habitats. When spawning runs are delayed, females continue to ripen and once released do not move as far upstream as control fish (Fleming and Reynolds 1991). This distance reduction suggests that delays may force them to spawn in suboptimal habitats, which could decrease recruitment. The most marked changes in spawning condition occur among females during the first 3 days of delay. Consequently, spawning delays for Arctic grayling should not exceed 3 days. The effects of delays on egg viability are unknown.

In Alaska's Fish Creek, Arctic grayling migrating upstream congregated beneath a road culvert on 13 May in water temperatures ranging from 0.3 to 3.1°C (Kane *et al*. 1989). They moved upstream through the corrugated metal culvert (length 18.1 m, diameter 2.9 m) from 14 to 22 May, at water temperatures ranging from 3.01 to 7.34°C. During this period the average water velocity in the culvert ranged from 170 to 213 cm/s, and at the culvert outlet ranged from 168 to 293 cm/s. Migrants included both mature and immature fish, which ranged in fork length from 30 to 383 mm. They appeared to have more difficulty swimming against the current in the immediate vicinity of the culvert outlet. Once inside they appeared to swim more easily. Most movement through the culverts occurred between 1500 and 2400h. Sustained swimming velocities (n=24 grayling, 114-305 mm FL) ranged from 42 to 125 cm/s, and burst speeds from 162 to 213 cm/s (n = 3). Grayling were unable to pass through a highway culvert on Poplar Grove Creek, Alaska when the water velocity was 370 cm/s and temperature ~7°C but 70% were able to pass through when it dropped to 225 cm/s at 7.7°C, and 95% passed at velocities of 213 cm/s and temperatures of 9.5°C (Tilsworth and Travis 1987).

Dryden and Stein (1975) recommended that the average cross-sectional velocity through any fish culvert not exceed 91 cm/s unless there is a section in the culvert wherein velocities are low enough to pass fish upstream.

Stream blockages can also impede grayling fry as they emigrate downstream from small tributaries into the Mackenzie River (Jessop *et al*. 1974). Such blockages should be avoided during this critical migration period, which is typically mid-June to the end of July but varies somewhat among systems and years.

The effects of impoundment on grayling populations range widely depending on the scale and type of impoundment, the extent and kind of unaffected habitat left in the watershed, and on the potential downstream changes (Northcote 1995). Turbidity levels, access to spawning habitat, and the introduction of predators are some important determinants of the long term effects of impoundment. In Russian reservoirs created by river impoundment, grayling abundance declined and the fish switched their diets from predominately Trichoptera and Chironomidae to Amphipoda and Chironomidae (Kupchinskaya *et al*. 1983). The absence of Arctic grayling was noted after impoundment of the Snare River, NT (Weagle and Cameron 1974).

4.3 Species introductions

Competition from or predation by non-native species may have been an important contributor to the decline of fluvial Arctic grayling in Montana (Barndt and Kaya 2000). The introduction of rainbow, brook (*Salvelinus fontinalis*), or brown trout also contributed to the extirpation of grayling from some systems in Michigan (Vincent 1962).

The introduction of parasites or diseases into systems could alter fish populations and should be discouraged (Arthur *et al*. 1976).

4.4 Improved access

Grayling have a well-deserved reputation as a sport fish and are much sought after by anglers (Wojcik 1955; Falk and Gillman 1980; Falk *et al*. 1982; Dahlke 1983; Moshenko and Low 1983; Armstrong 1986; Dunn and Roberge 1989; Northcote 1995). However, increased angler harvests afforded by improved access can affect the structure of Arctic grayling populations by causing a decline in average size and age (Falk and Gillman 1974; Armstrong 1986), and may cause fish to mature earlier and at a smaller size (Tack 1974 cited in Armstrong 1986). Grayling may also be increasingly vulnerable to angling as they age and grow larger (Carl *et al*. 1992). Consequently, the size structure of previously unexploited populations may change rapidly when fishing is allowed under liberal regulations (DeCiccio *et al*. 1997).

Wojcik (1955) cited overfishing as the primary cause for a decline in the grayling population in the Fairbanks area of Alaska. However, loss of warm, slack water rearing areas due to road construction may also have contributed to the decline of the stock in the Chena River at Fairbanks, which has not yet recovered despite 20 years of catch and release fishing (W. Morris, pers. comm.).

Angling for grayling in the Brabant Island area of Great Slave Lake, where it empties into the Mackenzie River, in the 1960s and early 1970s impacted the population by reducing the average size and age of fish caught (Falk and Gillman 1974, 1980). In addition to harvest mortalities by fisheries, there is a mortality rate among fish that are caught and then released of 11.8% for barbed lures and 5.1% for barbless lures (Falk and Gillman 1975). The mortality rate is higher for fish caught on spinning lures (11.7%) than on flies (8.6%).

The presence of large numbers of grayling in small streams at spawning time and their indifference to angling, before and during spawning, frustrates anglers who sometimes resort to illegal methods, such as snagging and spearing, to catch these fish (Falk *et al*. 1982). Fish and eggs in the shallow, clear spawning streams are also vulnerable to disturbance by anglers wading in the streams.

Closure of the grayling sport fisheries during and immediately following the spawning runs, when fish are congregated in small streams and voracious after spawning, combined with low harvest limits, size restrictions, and the use of barbless hooks may offer the best protection for the species from angler overfishing (Northcote 1995).

In the past, during years of poor fishing, First Nations sometimes harvested large quantities of post-spawning grayling by constructing a weir across the stream to capture fish as they returned downstream (Preble 1908). Grayling are seldom targeted by subsistence fisheries for food as they spoil quickly, although they may be used for dogfood.

Electrofishing for scientific sampling does not have a substantial detrimental effect on grayling populations over the short term (Holmes *et al*. 1990) but, combined with tagging, it can reduce annual growth and thereby the extent of upstream movements (Hughes 1998b).

4.5 Climate change

River discharge and water temperature are two important habitat variables that may be altered by climate change, and may influence the long-term survival and population dynamics of grayling in Arctic tundra streams (Deegan *et al*. 1999; Jones *et al*. 2003b). Discharge has been positively correlated with the growth of adult grayling, and negatively correlated with the average weight of young-of-the-year grayling. Because adult grayling growth is reduced in years of low flows and high temperatures (Deegan *et al*. 1999), climatic warming may stress Arctic grayling populations along the North Slope of Alaska (Hobbie *et al*. 1999) and in the Mackenzie Valley. Their ability to adapt is unknown.

Stream flow during spawning, emergence, and the larval stage is also a significant descriptor of variability in recruitment ($r = 0.751$, $P = 0.005$) (Clark 1992). Low flow rates in spring may affect cohort size indirectly by first reducing growth, followed by a strong size-dependent mortality, such that only fish that grow well survive; or directly by isolating young-of-the-year in beaver ponds or pools and subjecting them to increased natural mortality through predation or some other mechanism (Carl *et al*. 1992). As water levels in tundra streams decline over the summer, young-of-the-year grayling can also become trapped in side channels (Jones *et al*. 2003b). The combination of increased precipitation and cooler temperatures in the Arctic fall may enable these fish to return to main branches or lakes before freeze-up, and be critical for many populations. During low water periods the contribution of groundwater inflows may be important for maintaining suitable flow and avoiding stranding in streams.

Thermal bioassays of grayling from Alaska found median tolerance limits (96 h LD 50) of 21.5 to 24.2°C for sac fry and >24.5°C for young-of-the-year acclimated to 8.5°C±1°C; 20.0 to 24.0°C for >10 cm fish acclimated to 4°C±1°C; and 22.5 to 24.5°C for >20 cm fish acclimated to 8.0°C±1°C (LaPerriere and Carlson 1973). The thermal tolerance of juvenile grayling (mean TL = 133.0 mm, Sd = 8.7) from Montana increased with acclimation temperature (Lohr *et al*. 1996). The mean critical thermal maximum (CTM) was 26.4°C for fish acclimated to 8.4°C, 28.5°C for fish acclimated to 16.0°C, and 29.3°C for fish acclimated to 25°C. The upper incipient lethal temperature was 23°C for fish acclimated to 8.4°C and 16°C, and 25.0°C for those acclimated to 20.0°C.

The mean critical thermal maxima (upper lethal temperature=ULT) for groups of age 0 grayling acclimated to 15°C and tested in fresh water were 27.5 to 27.9°C with small variances (SD) (McLeay *et al*. 1983). For fish acclimated to 5°C the ULT was 24.8 to 24.9°C. The highest concentrations of suspended sediments tested, 50,000 to 100,000 mg/L, reduced the ULT by only 1°C for fish acclimated to 15°C and had no effect on that of fish acclimated to 5°C. The critical residual dissolved oxygen level for fish acclimated to 15°C and held in freshwater at 20°C was about 2.0 mg O_2/L, and for fish acclimated to 5°C and tested at 10°C it was 1.5 mg O_2/L.

Another of the predictions under climate change scenarios is an increasing frequency of forest fires in the north. Tonn *et al*. (2004) did not find direct evidence that forest fires affected Arctic grayling populations in small mountain lakes. However, forest fires may have indirect affects by increasing sediment inputs in runoff.

4.6 Habitat remediation

Artificial stream habitats constructed for habitat compensation have been used successfully to reconnect fragmented grayling habitats (Jones *et al*. 2003c). They also provided spawning and nursery habitat for grayling, but were less productive feeding habitat than natural streams. Physical structures placed in these habitats to increase productive capacity (e.g., ramps, V-weirs, vanes, and groins) attracted significantly higher fish densities than nearby reference sections, suggesting that they provide energetically favourable microhabitats, but their benefits may not be fully realized until more organic matter is available for **benthic** fauna and fish (Jones and Tonn 2004a). The more complex habitat demands of larger young-of-the-year were not met as well as those of the smaller fish (Jones and Tonn 2004b). Arctic grayling have also established reproducing populations in other suitable artificial habitats, such as test structures designed to mitigate the loss of spawning habitat due to dam construction (Elwell 1989), and intermittently-flowing irrigation canals (Barndt and Kaya 2000).

In Alaska, the Fort Knox Gold Mine built a reservoir that flooded portions of several streams that had been heavily mined since the early 1920's (W. Morris, pers. comm.). A population of stunted grayling was present in the streams and captured by the reservoir. Prior to impoundment, males in this population matured as small as 148 mm FL, females 165 mm, and individuals seldom reached 220 mm (Ott *et al*. 1995; Ott and Weber Scannell 1996). Age 0 production was low and recruitment was very low. Once the reservoir flooded the population structure immediately changed, with mature fish growing 30 to 40 mm per year (Ott and Morris 1999, 2006). The structure is now more typical to interior populations, although some individuals still mature at small sizes. Spawning success remained low in the main tributary to the reservoir following impoundment due to significant **aufeis** build-up that caused channel shifts and cold water temperatures during the spawning season. To remedy this, a channel was cut to connect a wetland system with constant discharge to the reservoir. When the sediment settled (that same day) Arctic grayling were already moving into the system. Spawning in the newly constructed channel and constructed wetlands channels has been successful and recruitment has been strong. By late August or early September, age 0 fish from the wetlands tend to be nearly twice as large as those from the original spawning stream. Better survival of the larger fish during their first winter likely accounts for the high productivity of this population (Ott and Morris 1999, 2006).

Stocking newly hatched grayling into rivers has not been successful, but stocking with fry (age > 3 months) has been successful in creating self-sustaining populations, as has transplanting adult and subadult grayling into barren lakes (Armstrong 1986). There is little or no survival of grayling fry when they are stocked into lakes with predators such as northern pike (*Esox lucius*) (Tack 1972). They will, however, compete successfully with rainbow trout fingerlings when both are stocked into a previously barren lake (Van Hulle and Murray 1975), and may compete successfully with lake chub (*Couesius plumbeus*) (Roguski and Tack 1970).

Grayling introduced to a rehabilitated gravel extraction site in Alaska overwintered successfully for at least two years, albeit with significant mortality (Hemming 1997). Their reproductive success in a small tributary stream was very limited, perhaps due to egg or fry predation by grayling or ninespine sticklebacks (*Pungitius pungitius*), so stocking may not have produced a self-sustaining population. Long term work suggests that the likelihood of establishing a self-sustaining grayling population is increased by stocking adult fish, provided they stay in the system (Ott and Townsend 2003; W. Morris, pers. comm.). The combination of successful spawning, good growth conditions for age 0 fish, and good winter survival is uncommon. If adult fish are stocked and available to spawn when the conditions are favourable, the resulting successful cohort appears to be able to sustain the population until favourable conditions next occur. However, if only age 0 fish are planted the numbers that survive to take advantage of favourable spawning conditions may not produce a cohort large enough to sustain the population. Further work to assess stocking success is ongoing in Alaska (W. Morris, pers. comm.).

5.0 SUMMARY

Arctic grayling occur throughout the Mackenzie System, where they are most abundant in the clear, swift tributaries that flow from the east side of the valley into the Mackenzie River. They require cold, clear water and undertake complex seasonal movements that differ among systems in response to local conditions. Their populations can be resident or migratory, and the latter can follow fluvial or adfluvial life histories. Most juvenile and adult grayling undertake annual migrations between spawning, feeding, and overwintering areas. Individuals show fidelity to both spawning and overwintering habitats that may be hundreds of kilometers apart, and require uninterrupted migratory corridors that connect them. Good information is available on the species' use of tributaries during the open water period for spawning and rearing, and on their movement patterns during the open water period, but relatively little is known of their use of lake and large river habitats, especially during the period of ice cover.

Spawning occurs in shallow (<1 m), fast-flowing (<150 cm/s) tributary streams or in lake inlets or outlets, at or shortly after spring ice breakup. The timing of spawning varies within and among systems, and from year to year, occurring from mid-May in the southern Mackenzie Valley to mid-June in the north, at water temperatures of 4 to 16°C. Eggs are usually distributed over unembedded gravel substrates, and fry emerge two or three weeks later. Because fry are helpless in water currents for two weeks after hatching, flooding or drought during this period may cause high mortalities, either by washing them downstream into unfavourable habitat or by stranding them in shallow, isolated pools.

Tributary streams also provide important feeding and rearing habitat for grayling during the open water period. These fish are opportunistic, visual predators that eat mostly aquatic and terrestrial insects, crustacean zooplankton, and fish. Instream rocks and debris and overhanging vegetation provide important cover for the species. Entire populations of grayling migrate out of small headwater lakes and small streams to overwinter in larger rivers or lakes. These migrations can occur from early summer through December depending upon the local conditions. Some fish overwinter in deeper spring-fed pools while others leave the spring-fed tributaries, perhaps due to the risk of injury or death from frazil ice. In lakes, adult grayling occur over sand, silt and gravel substrates and along rocky shorelines, typically at depths of <4.0 m.

Arctic grayling mature between ages 2 and 9. Most spawn annually but some skip a year before spawning again. The species' variable time to first maturity and the delay in second spawning may be adaptations to highly variable juvenile recruitment, and limit the ability of populations to withstand exploitation. The maximum age for grayling ranges from 11 to 29 years depending on the river system and whether the fish were aged using scales, which tend to underestimate ages, or otoliths.

Habitat degradation and fragmentation, species introductions, improved access, and climate change all have the potential to damage or extirpate Arctic grayling populations. Grayling may be slow to recover from year class failures, and populations may be considerably more difficult to restore than to maintain. Key habitat requirements of Arctic grayling that may be particularly susceptible to impacts from human activities include: 1) clear water for visually locating prey; 2) unimpeded access between spawning, feeding, and overwintering areas--particularly during the spring spawning period; and 3) tributary streams with flow rates, water depths, and unembedded gravel substrate suitable for spawning and feeding.

Activities such as placer mining and right-of-way construction that increase turbidity can alter the feeding success of grayling, causing them to leave an area. The species' ability to locate prey declines rapidly as turbidity increases, and fingerlings avoid water with turbidity >20 NTU. A water quality standard of 5 NTU above natural conditions has been recommended for protecting grayling habitat. Because they feed heavily on terrestrial insects at the surface, grayling may also be particularly susceptible to insecticide sprays and chemical spills that reduce or contaminate these sources of food.

Grayling spawning success appears to be strongly affected by stream obstructions, such as improperly designed or installed highway culverts that prevent or delay migrations. Spawning delays for Arctic grayling should not exceed 3 days. The effects of delays on egg viability are unknown. The effects of flow impoundment on grayling populations range widely depending on the scale and type of impoundment, the extent and kind of unaffected habitat left in the watershed, and on the potential downstream changes. Turbidity levels, access to spawning habitat, and the introduction of predators are some important determinants of the long term effects of impoundment.

Activities such as gravel removal or log driving that rework the streambed in the swift, shallow tributaries where grayling spawn, dislodging eggs and destabilizing the spawning substrate, can ultimately extirpate them from an area, as can the introduction of competitors and predators. Arctic grayling do not, for example, compete well with some trout species, and juveniles may be particularly vulnerable to predation by northern pike. Increased angler harvests afforded by improved access can affect the structure of Arctic grayling populations by causing a decline in average size and age, and may cause fish to mature earlier and at a smaller size. The species' ability to adapt to changes in river discharge and water temperature related to climate change is unknown.

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7.0 REFERENCES

Allen-Gil, S.M., Gubala, C.P., Landers, D.H., Wade, T.L., Sericano, J.L., and Curtis, L.R. 1997. Organochlorine pesticides and polychlorinated biphenyls (PCBs) in the sediments and biota from four US Arctic lakes. Arch. Environ. Contam. Toxicol. **33**: 378-387.

Armstrong, R.H. 1986. A review of arctic grayling studies in Alaska, 1952-1982. Biol. Pap. Univ. Alsk. **23**: 3-17.

Arthur, J.R., Margolis, L., and Arai, H.P. 1976. Parasites of fishes of Aishihik and Stevens lakes, Yukon Territory, and potential consequences of their interlake transfer through a proposed water diversion for hydroelectrical purposes. J. Fish. Res. Board Can. **33**: 2489-2499.

Barndt, S.A., and Kaya, C.M. 2000. Reproduction, growth, and winter habitat of Arctic grayling in an intermittent canal. Northwest Sci. **74**: 294-305.

Beauchamp, D.A. 1982. The life history, spawning behaviour, and interspecific interactions of the Arctic grayling (*Thymallus arcticus*) in Upper Granite Lake. M.Sc. Thesis, University of Washington, Seattle, Washington. 130 p.

Beauchamp, D.A. 1990. Movements, habitat use, and spawning strategies of Arctic grayling in a subalpine lake tributary. Northwest Sci. **64**: 195-207.

Birtwell, I.K., Hartman, G.F., Anderson, B., McLeay, D.J., and Malick, J.G. 1984. A brief investigation of Arctic grayling (*Thymallus arcticus*) and aquatic invertebrates in the Minto Creek drainage, Mayo, Yukon Territory: an area subjected to placer mining. Can. Tech. Rep. Fish. Aquat. Sci. **1287**: xi + 57 p.

Bishop, F.G. 1967. The biology of the Arctic grayling, *Thymallus arcticus* (Pallas), in Great Slave Lake. M.Sc. Thesis, Department of Zoology, University of Alberta, Edmonton, AB. xvi + 165 p.

Bishop, F.G. 1971. Observations on spawning habits and fecundity of the Arctic grayling. Prog. Fish-Cult. **27**: 12-19.

Bond, W.A., and Erickson, R.N. 1992. Fishery data from the Anderson River estuary, Northwest Territories, 1990. Can. Manuscr. Rep. Fish. Aquat. Sci. **2171**: vi + 46 p.

Buhl, K.J., and Hamilton, S.J. 1990. Comparative toxicity of inorganic contaminants released by placer mining to early life stages of salmonids. Ecotoxicol. Environ. Saf. **20**: 325-342.

Buhl, K.J., and Hamilton, S.J. 1991. Relative sensitivity of early life stages of Arctic grayling, coho salmon, and rainbow trout to nine inorganics. Ecotoxicol. Environ. Saf. **22**: 184-197.

Buzby, K.M. and Deegan, L.A. 2004. Long-term survival of adult Arctic grayling (*Thymallus arcticus*) in the Kuparuk River, Alaska. Can. J. Fish. Aquat. Sci. **61**: 1954-1964.

Carl, L.M., Walty, D., and Rimmer, D.M. 1992. Demography of spawning grayling (*Thymallus arcticus*) in the Beaverlodge River, Alberta. Hydrobiologia **243/244**: 237-247.

Chang-Kue, K.T.J., and Cameron, R.T. 1980. A survey of the fish resources of the Great Bear River, Northwest Territories, 1974. Can. Fish. Mar. Serv. Manuscr. Rep. **1510**: vi + 59 p.

Clark, R.A. 1992. Influence of stream flows and stock size on recruitment of Arctic grayling (*Thymallus arcticus*) in the Chena River, Alaska. Can. J. Fish. Aquat. Sci. **49**: 1027-1034.

Craig, P.C., and Poulin, V.A. 1975. Movements and growth of Arctic grayling (*Thymallus arcticus*) and juvenile Arctic char (*Salvelinus alpinus*) in a small Arctic stream, Alaska. J. Fish. Res. Board Can. **32**: 689-697.

Dahlke, L.W. 1983. Data on the Arctic grayling sport fishery at Kakisa River, Northwest Territories, 1980. Can. Data Rep. Fish. Aquat. Sci. **390**: iv + 11 p.

de Bruyn, M., and McCart, P. 1974. Life history of the grayling (*Thymallus arcticus*) in Beaufort Sea drainages in the Yukon Territory. Canadian Arctic Gas Study Limited (Calgary, AB), Biological Report Series **15**: iv + 41 p.

DeCicco, A.L., and Brown, R.J. 2006. Direct validation of annual growth increments on sectioned otoliths from adult Arctic grayling and a comparison of otoliths and scale ages. N. Am. J. Fish. Manage. 26: 580-586.

DeCicco, A.L., Merritt, M.F., and Bingham, A.E. 1997. Characteristics of a lightly exploited population of Arctic grayling in the Sinuk River, Seward Peninsula, Alaska. Am. Fish. Soc. Symp. **19**: 229-239.

Deegan, L.A., and Peterson, B.J. 1992. Whole-river fertilization stimulates fish production in an Arctic tundra river. Can. J. Fish. Aquat. Sci. **49**: 1890-1901.

Deegan, L.A., Golden, H.E., Harvey, C.J., and Peterson, B.J. 1999. Influence of environmental variability on the growth of age-0 and adult Arctic grayling. Trans. Am. Fish. Soc. **128**: 1163-1175.

Deegan, L.A., Golden, H.E., Harrison, J., and Kracko, K. 2005. Swimming performance and metabolism of 0+ year *Thymallus arcticus*. J. Fish Biol. **67**: 910-918.

Deleray, M.A. 1991. Movement and utilization of fluvial habitat by age-0 Arctic grayling, and characteristics of spawning adults, in the outlet of Deer Lake, Gallatin County, Montana. M.Sc. Thesis, Montana State University, Bozeman, Montana. xii + 75 p.

Deleray, M.A., and Kaya, C.M. 1992. Lakeward and downstream movements of age-0 Arctic grayling (*Thymallus arcticus*) originating between a lake and a waterfall. Great Basin Nat. **52**: 344-351.

Den Beste, J., and McCart, P. 1984. Overview of studies on the long-term effects of the Trans Alaska Pipeline system on fish and aquatic habitats. Aquatic Environments Limited, Anchorage, Alaska. Vol. 1, 51 p.

Derksen, A.J. 1980. Evaluation of fish passage through culverts at the Goose Creek road crossing near Churchill, Manitoba, in April and May, 1977. Manit. Dep. Nat. Resour. MS Rep. **80-4**: xi + 103 p.

DFO. 1988. Sport fishing in the Northwest Territories, 1985. Prepared by Information and Publication Branch, Communications Directorate, Canada Department of Fisheries and Oceans, Ottawa, ON. 12 p. (DFO/3778).

Dryden, R.L., and Stein, J.N. 1975. Guidelines for the protection of the fish resources of the Northwest Territories during highway construction and operation. Can. Fish. Mar. Serv. Tech. Rep. Ser. CEN-T **75-1**: vi + 32 p.

Dryden, R.L., Sutherland, B.G., and Stein, J.N. 1973. An evaluation of the fish resources of the Mackenzie River valley as related to pipeline development, Volume 2. Environmental-Social Committee Northern Pipelines, Task Force on Northern Oil Development Rep. **73-2**: iii + 176 p.

Dunn, J.B., and Roberge, M.M. 1989. Creel census and biological data from the sport fisheries occurring at Great Bear and adjacent areas, N.W.T., 1984-5. Can. Data Rep. Fish. Aquat. Sci. **757**: v + 48 p.

EIS Mackenzie Gas Project [Environmental Impact Statement for the Mackenzie Gas Project]. 2004. Vol. 3. Biophysical Baseline, Part C - Aquatic Resources: Fish and Fish Habitat. 520 p. [Available at: http://www.ngps.nt.ca/upload/eis/EIS-oct-08-05.html#threec, Accessed 28 December 2006]

Elwell, G. 1989. Arctic grayling coexist with dam safety improvements, p. 83-93. In Proceedings of the Symposium on Headwaters Hydrology. American Water Resources Association, Bethesda, Maryland.

Evans, C.L., Reist, J.D., and Minns, C.K. 2002. Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on riverine habitat requirements. Can. Manuscr. Rep. Fish. Aquat. Sci. **2614**: viii + 169 p.

Falk, M.R., and Dahlke, L.W. 1974. Data on the lake and round whitefish, lake cisco, northern pike, and Arctic grayling from Great Bear Lake, N.W.T., 1971-1973. Can. Fish. Mar. Serv. Data Rep. Ser. CEN-D **74-1**: vi + 52 p.

Falk, M.R., and Gillman, D.V. 1974. Impact of a sport fishery on Arctic grayling in the Brabant Island area, Northwest Territories. Can. Fish. Mar. Serv. Tech. Rep. Ser. CEN-T **74-7**: v + 21 p.

Falk, M.R., and Gillman, D.V. 1975. Data on the lake and round whitefish, lake cisco, northern pike, Arctic grayling and longnose sucker from the east arm of Great Slave Lake, N.W.T., 1971-74. Can. Fish. Mar. Serv. Data Rep. Ser. CEN-D **75-2**: 95 p.

Falk, M.R., and Gillman, D.V. 1980. Status of the Arctic grayling and northern pike sport fisheries in the Brabant Island-Beaver Lake area of the Mackenzie River, Northwest Territories. Can. Manuscr. Rep. Fish. Aquat. Sci. **1553**: v + 48 p.

Falk, M.R., Low, G., Gillman, D.V., and Carder, G.W. 1980. Data from the Arctic grayling sport fishery on the Kakisa River, Northwest Territories, 1979. Can. Data Rep. Fish. Aquat. Sci. **199**: iv + 13 p.

Falk, M.R., Roberge, M.M., Gillman, D.V., and Low, G. 1982. The Arctic grayling, *Thymallus arcticus* (Pallas), in Providence Creek, Northwest Territories, 1976-79. Can. Manuscr. Rep. Fish. Aquat. Sci. **1665**: vi + 27 p.

Fleming, D.F., and Reynolds, J.B. 1991. Effects of spawning-run delay on spawning migration of Arctic grayling. Am. Fish. Soc. Symp. **10**: 299-305.

Ford, B.S., Higgins, P.S., Lewis, A.F., Cooper, K.L., Watson, T.A., Gee, C.M., Ennis, G.L., and Sweeting, R.L. 1995. Literature reviews of the life history, habitat requirements and mitigation/compensation strategies for thirteen sport fish species in the Peace, Liard, and Columbia river drainages of British Columbia. Can. Manuscr. Rep. Fish. Aquat. Sci. **2321**: xxiv + 342 p.

Hammer, C. 1995. Fatigue and exercise tests with fish. Comparative Biochemistry and Physiology **112A**: 1-20.

Harvey, C.J., Peterson, B.J., Bowden, W.B., Hershey, A.E., Miller, M.C., Deegan, L.A., and Finlay, J.C. 1998. Biological responses to fertilization of Oksrukuyik Creek, a tundra stream. J. N. Am. Benthol. Soc. **17**: 190-209.

Hatfield, C.T., Stein, J.N., Falk, M.R., and Jessop, C.S. 1972a. Fish resources in the Mackenzie River Valley, Interim Report 1, Volume 1. Department of the Environment, Fisheries Service, Winnipeg, MB. xiii + 249 p.

Hatfield, C.T., Stein, J.N., Falk, M.R., Jessop, C.S., and Shepherd, D.N. 1972b. Fish resources in the Mackenzie River Valley, Interim Report 1, Volume 2. Department of the Environment, Fisheries Service, Winnipeg, Manitoba. x + 289 p.

Hemming, C.R. 1997. Experimental introduction of Arctic grayling to rehabilitated gravel extraction site, North Slope, Alaska. Am. Fish. Soc. Symp. **19**: 208-213.

Hershey, A.E., Beaty, S., Fortino, K., Keyse, M., Mou, P.P., O'Brien, W.J., Ulseth, A.J., Gettel, G.A., Lienesch, P.W., Luecke, C., McDonald, M.E., Mayer, C.H., Miller, M.C., Richards, C., Schuldt, J.A., and Whalen, S.C. 2006. Effect of landscape factors on fish distribution in arctic Alaskan lakes. Freshwater Biol. **51**: 39-55.

Hobbie, J.E., Peterson, B.J., Bettez, N., Deegan, L., O'Brien, J., Kling, G.W., Kipphut, G.W., Bowden, W.B., and Hershey, A.E. 1999. Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. Polar Res. **18**: 207-214.

Holmes, R., McBride, D.N., Viavant, T., and Reynolds, J.B. 1990. Electrofishing induced mortality and injury to rainbow trout, arctic grayling, humpback whitefish, least cisco, and northern pike. Alaska Dep. Fish Game Fishery Manuscr. **90**: viii + 95 p.

Hubbs, C.L., and Lagler, K.F. 1958. Fishes of the Great Lakes region. Cranbrook Inst. Sci. Bull. **26**: 213 p.

Hughes, N.F. 1992a. Ranking of fish positions by drift-feeding Arctic grayling (*Thymallus arcticus*) in dominance hierarchies. Can. J. Fish. Aquat. Sci. **49**: 1994-1998.

Hughes, N.F. 1992b. Selection of positions by drift feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **49**: 1999-2008.

Hughes, N.F. 1998a. Use of whole-stream patterns of age segregation to infer the interannual movements of stream salmonids: a demonstration with Arctic grayling in an interior Alaskan stream. Trans. Am. Fish. Soc. **127**: 1067-1071.

Hughes, N.F. 1998b. Reduction in growth due to electrofishing and tagging may change interannual movement behaviour of stream salmonids: evidence from Arctic grayling in an interior Alaskan stream. Trans. Am. Fish. Soc. **127**: 1072-1077.

Hughes, N.F. 1999. Population processes responsible for larger-fish-upstream distribution patterns of Arctic grayling (*Thymallus arcticus*) in interior Alaskan runoff rivers. Can. J. Fish. Aquat. Sci. **56**: 2292-2299.

Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **47**: 2039-2048.

Hughes, N.F., and Reynolds, J.B. 1994. Why do Arctic grayling (*Thymallus arcticus*) get bigger as you go upstream? Can. J. Fish. Aquat. Sci. **51**: 2154-2163.

Jessop, C.S., and Lilley, J.W. 1975. An evaluation of the fish resources of the Mackenzie River valley based on 1974 data. Can. Fish. Mar. Serv. Tech. Rep. Ser. CEN-T **75-6**: x + 97 p.

Jessop, C.S., Chang-Kue, K.T.J., Lilley, J.W., and Percy, R.J. 1974. A further evaluation of the fish resources of the Mackenzie River valley as related to pipeline development. Environmental-Social Committee, Northern Pipelines, Task Force on Northern Oil Development Rep. **74-7**: xii + 94 p.

Jessop, E.F., Chang-Kue, K.T.J., and MacDonald, G. 1993. Fish resource data from Indin Lake, Northwest Territories. Can. Data Rep. Fish. Aquat. Sci. **907**: v + 52 p.

Jones, N.E., and Tonn, W.M. 2004a. Enhancing productive capacity in the Canadian Arctic: assessing the effectiveness of instream habitat structures in habitat compensation. Trans. Am. Fish. Soc. **133**: 1356-1365.

Jones, N.E., and Tonn, W.M. 2004b. Resource selection functions for age-0 Arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation. Can. J. Fish. Aquat. Sci. **61**: 1736-1746.

Jones, N.E., Tonn, W.M., and Scrimgeour, G.J. 2003a. Selective feeding of age-0 Arctic grayling in lake-outlet streams of the Northwest Territories, Canada. Environ. Biol. Fish. **67**: 169-178.

Jones, N.E., Tonn, W.M., Scrimgeour, G.J., and Katopodis, C. 2003b. Ecological characteristics of streams in barrenlands near Lac de Gras, N.W.T., Canada. Arctic **56**: 249-261.

Jones, N.E., Tonn, W.M., Scrimgeour, G.J., and Katopodis, C. 2003c. Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of fish habitat compensation. Can. J. Fish. Aquat. Sci. **60**: 849-863.

Kane, D.L., Behlke, C.E., Basketfield, D.L., Gieck, R.E., McLean, R.F., and Travis, M.D. 1989. Hydrology, hydraulics and fish passage performance of Arctic grayling (*Thymallus arcticus*) at Fish Creek, Denali Highway near Cantwell Alaska. Alaska Department of Transportation and Public Facilities, Report No. **FHWA-AK-89-03**: viii + 180 p.

Katopodis, C., Robinson, P.R., and Sutherland, B.G. 1978. A study of model and prototype culvert baffling for fish passage. Can. Fish. Mar. Serv. Tech. Rep. **828**: v + 78 p.

Kaya, C.M. 1989. Rheotaxis of young Arctic grayling from populations that spawn in inlet or outlet streams of a lake. Trans. Am. Fish. Soc. **118**: 474-481.

Kaya, C.M. 1991. Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (*Thymallus arcticus*), and implications for the only remaining indigenous population of fluvial "Montana Grayling". Can. J. Fish. Aquat. Sci. **48**: 53-59.

Kratt, L.F. 1977. The behaviour of Arctic grayling, *Thymallus arcticus* Pallas, of the Fond du Lac River, Saskatchewan, with observations on early life history. M.Sc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan. xiii + 204 p. + app.

Kratt, L.F. 1981. Evidence of Arctic grayling (*Thymallus arcticus*) spawning in a highway culvert. Can. Field-Nat. **95**: 358.

Kratt, L.F., and Smith, R.J.F. 1977. A post-hatching sub-gravel stage in the life history of the Arctic grayling, *Thymallus arcticus*. Trans. Am. Fish. Soc. **106**: 241-243.

Kratt, L.F., and Smith, R.J.F. 1979. Agonistic behaviour of age 0, age 1 and non-breeding adult Arctic grayling *Thymallus arcticus* (Pallas). J. Fish Biol. **15**: 389-404.

Krueger, S.W. 1981. Freshwater habitat relationships - Arctic grayling (*Thymallus arcticus*). Alaska Department of Fish and Game, Habitat Division, Anchorage, Alaska. 65 p.

Kupchinskaya, Ye.S., Kupchinskiy, B.S., Ryzhova, L.N., Tugarina, P.Ya., and Tyutrina, L.I. 1983. Biology of the Arctic grayling, *Thymallus arcticus* (Thymallidae), in Ust' -Ilim Reservoir. J. Ichthyol. **23**: 47-56.

LaPerriere, J.D., and Carlson, R.F. 1973. Thermal tolerances of interior Alaskan Arctic grayling (*Thymallus arcticus*). University of Alaska (Fairbanks), Institute of Water Resources, Report No. **IWR-46**: vii + 36 p.

Lawrence, M., and Davies, S. 1979. Aquatic resources survey--Keewatin and Franklin districts. Canada Department of Indian and Northern Affairs, ESCOM Report No. **AI-31**: xii + 108 p.

Lee, K.M. 1985. Resource partitioning and behavioral interactions among young-of-the-year salmonids, Chena River, Alaska. M.Sc. Thesis, University of Alaska, Fairbanks, Alaska. ix + 75 p.

Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E., and Stauffer, J.R. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, NC. 854 p.

Liknes, G.A., and Gould, W.R. 1987. The distribution, habitat and population characteristics of fluvial Arctic grayling (*Thymallus arcticus*) in Montana. Northwest. Sci. **61**: 122-129.

Lloyd, D.S., Koenings, J.P., and LaPerriere, J.D. 1987. Effects of turbidity in fresh waters of Alaska. N. Am. J. Fish. Manage. **7**: 18-33.

Lohr, S.C., Byworth, P.A., Kaya, C.M., and Dwyer, W.P. 1996. High-temperature tolerances of fluvial Arctic grayling and comparisons with summer river temperatures of the Big Hole River, Montana. Trans. Am. Fish. Soc. **125**: 933-939.

Low, G., and Read, C.J. 1987. Data from the Arctic grayling sport fishery on the Kakisa River, Northwest Territories, 1983 and 1984. Can. Data Rep. Fish. Aquat. Sci. **642**: iv + 12 p.

MacDonald, G., and Fudge, R. 1979. Arctic Land Use Research Program 1978: a survey of the fisheries resources of the Kazan Upland (southeastern District of Mackenzie, southern District of Keewatin, NWT). Can. Dep. Ind. N. Aff. Environ. Stud. **11**: iii + 161 p.

MacDonald, G., and Stewart, D.B. 1980. Arctic Land Use Research Program 1979: a survey of the aquatic resources of the central Keewatin region of the Northwest Territories. Can. Dep. Ind. N. Aff. Environ. Stud. **17**: iii + 111 p.

Machniak, K., Bond, W.A., Orr, M.R., Rudy, D., and Millar, D. 1980. Fisheries and aquatic habitat investigations in the MacKay River watershed of northeastern Alberta. Alberta Oil Sands Environmental Research Program (AOSERP) Report **93**: 173 p.

Marshall, I.B. and Schut, P.H. 1999. A national ecological framework for Canada. Ecosystems Science Directorate, Environment Canada and Research Branch, Agriculture and Agri-Food Canada, Ottawa, ON. [http://sis.agr.gc.ca/cansis/nsdb/ecostrat/intro.html, Accessed 28 May 2007].

Martin, K.A. 2001. A limnological study of selected lakes in the Lac de Gras area, Northwest Territories with special reference to fish contaminants. Can. Tech. Rep. Fish. Aquat. Sci. **2385**: viii + 78 p.

McCart, D. 1982. An assessment of the fisheries resources of the Great Bear and Mackenzie Rivers in the vicinity of proposed IPL Pipeline crossings. Aquatic Environments Limited for Inter Provincial Pipelines Ltd, Calgary, AB. 33 p. + tables, figures.

McCart, P.J. 1974. Chapter 1. Late winter surveys of lakes and streams in Canada and Alaska along the gas pipeline routes under consideration by Canadian Arctic Gas Study Limited, 1972-1973, p.17-183. In P.J. McCart (ed.) Life histories of anadromous and freshwater fish in the western Arctic. Arctic Gas Biological Report Series **15**.

McCart, P.J., and Den Beste, J. 1979. Aquatic resources of the Northwest Territories. Prepared for Science Advisory Board of the Northwest Territories. Published by Department of Information, Government of the Northwest Territories, Yellowknife, Northwest Territories. vi + 55 p.

McCart, P.J., and Pepper, V.A. 1971. Geographic variation in the lateral line scale counts of the Arctic grayling, *Thymallus arcticus*. J. Fish. Res. Board Can. **28**: 748-754.

McClure, W.V., and Gould, W.R. 1991. Response of underyearling fluvial Arctic grayling (*Thymallus arcticus*) to velocity, depth, and overhead cover in artificial enclosures. Northwest Sci. **65**: 201-204.

McKinnon, G.A., and Hnytka, F.N. 1979. A survey of the fish resources of Liard River tributaries as related to highway construction and operation, 1976-77. Can. Fish. Mar. Serv. Manuscr. Rep **1483**: vii + 84 p.

McLeay, D.J., Knox, A.J., Malick, J.G., Birtwell, I.K., Hartman, G., and Ennis, G.L. 1983. Effects on Arctic grayling (*Thymallus arcticus*) of short-term exposure to Yukon placer mining sediments: laboratory and field studies. Can. Tech. Rep. Fish. Aquat. Sci. **1171**: xvii + 134 p.

McLeay, D.J., Ennis, G.L., Birtwell, I.K., and Hartman, G.F. 1984. Effects on Arctic grayling (*Thymallus arcticus*) of prolonged exposure to Yukon placer mining sediment: a laboratory study. Can. Tech. Rep. Fish. Aquat. Sci. **1241**: xiii + 96 p.

McLeay, D.J., Birtwell, I.K., Hartman, G.F., and Ennis, G.L. 1987. Responses of Arctic grayling (*Thymallus arcticus*) to acute and prolonged exposure to Yukon placer mining sediment. Can. J. Fish. Aquat. Sci. **44**: 658-673.

McPhail, J.D., and Lindsey, C.C. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Board Can. Bull. **173**: 381 p.

Miller, R.B. 1946. Notes on the Arctic grayling *Thymallus signifer* Richardson, from Great Bear Lake. Copeia **1946**: 227-236.

Miller, R.B. 1947. Great Bear Lake. Bull. Fish. Res. Board Can. **72**: 31-44.

Morris, W.A., and Winters, J. 2002. Red Dog Mine spring Arctic grayling sampling, May/June 2002. Alaska Department of Natural Resources, Fairbanks, AK. 8 p.

Morrow, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage, Alaska. 248 p.

Moshenko, R.W., and Low, G. 1983. Data from the Arctic grayling sport fishery on the Kakisa River, Northwest Territories. Can. Data Rep. Fish. Aquat. Sci. **388**: iv + 27 p.

Netsch, N.F. 1975. Fishery resources of waters along the route of the Trans-Alaska Pipeline between Yukon River and Atigun Pass in north-central Alaska. U.S. Dep. Interior, Fish. Wildl. Serv. Resour. Publ. **124**: v + 45 p.

Northcote, T.G. 1995. Comparative biology and management of Arctic and European grayling (Salmonidae, *Thymallus*). Rev. Fish Biol. Fish. **5**: 141-194.

Ott, A.G., and Morris, W.A. 1999. Fish use of the Fort Knox water supply reservoir 1995-1998. Alaska Department of Fish and Game, Habitat and Restoration Division, Tech. Rept. **99-2**: v + 28 p.

Ott, A.G., and Morris, W.A. 2005. Arctic grayling and burbot studies at the Fork Knox Mine, 2005. Alaska Department of Natural Resources, Office of Habitat Management and Permitting, Tech. Rep. **05-06**: iv + 33 p.

Ott, A.G., and Morris, W.A. 2006. Arctic grayling and burbot studies at the Fork Knox Mine, 2006. Alaska Department of Natural Resources, Office of Habitat Management and Permitting, Tech. Rep. **06-05**: v + 31 p.

Ott, A.G., and Townsend, A.H. 2003. A transplant of Arctic grayling to Bons Pond at the Red Dog Mine. Alaska Department of Natural Resources, Office of Habitat Management and Permitting, Tech. Rep. **03-06**: 43 p.

Ott, A.G., and Weber Scannell, P. 1996. Baseline fish and aquatic habitat data for Fort Knox Mine 1992 to 1995. Alaska Department of Fish and Game, Habitat and Restoration Division, Tech. Rep. **96-5**: ix + 165 p.

Ott, A.G., Weber Scannell, P., and Townsend, A.H. 1995. Aquatic habitat and fisheries studies upper Fish Creek, 1992-1995. Alaska Department of Fish and Game, Habitat and Restoration Division, Tech. Rep. **95-4**: vi + 61 p.

Pearse, G.A. 1974. Study G-III Lake and stream investigations: Job G-III-G A study of a typical spring fed stream of interior Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1973-1974, Project F-9-6, Volume **15**: 49 p.

Poléo, A.B.S., Østbye, K., Øxnevad, S.A., Andersen, R.A., Heibo, E., and Vøllestad, L.A. 1997. Toxicity of acid aluminum-rich water to seven freshwater fish species: a comparative laboratory study. Environ. Pollut. **96**: 129-139.

Porter, T.R., Rosenberg, D.M., and McGowan, D.K. 1974. Winter studies of the effects of a highway crossing on the fish and benthos of the Martin River, N.W.T. Can. Fish. Mar. Serv. Tech. Rep. Ser. CEN-T **74-3**: vii + 50 p.

Preble, E.A. 1908. A biological investigation of the Athabaska-Mackenzie Region. U.S. Department of Agriculture, Bureau of Biological Survey (Washington), North American Fauna No. **27**: 501-515.

Rawson, D.S. 1950. The grayling (*Thymallus signifer*) in northern Saskatchewan. Can. Fish. Cult. **6**: 3-10.

Rawson, D.S. 1951. Studies of the fish of Great Slave Lake. J. Fish. Res. Board Can. **8**: 207-240.

Read, C.J., and Roberge, M.M. 1989. Enumeration and biological data on Arctic grayling, *Thymallus arcticus*, Kakisa River, N.W.T., 1984. Can. Data Rep. Fish. Aquat. Sci. **750**: iv + 15 p.

Redenbach, Z., and Taylor, E.B. 1999. Zoogeographical implications of variation in mitochondrial DNA of Arctic grayling (*Thymallus arcticus*). Mol. Ecol. **8**: 23-35.

Reed, R.J. 1964. Life history and migration patterns of Arctic grayling, *Thymallus arcticus* (Pallas), in the Tanana River drainage of Alaska. Alaska Department of Fish and Game Research Report No. **2**: 30 p.

Reid, S.M., Metikosh, S., and Evans, J. 2002. Movement of Arctic grayling and mountain whitefish during an open-cut pipeline water crossing of the Wildhay River, Alberta. J. Freshwater Ecol. **17**:363-368.

Reynolds, J.B., Simmons, R.C., and Burkholder, A.R. 1989. Effects of placer mining discharge on health and food of Arctic grayling. Wat. Resour. Bull. **25**: 625-635.

Roguski, E.A., and Tack, S.L. 1970. Investigation of the Tanana River and Tangle Lakes grayling fisheries: migratory and population study. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress, 1969-1970. Project F-9-2, **11 (16-B)**: 303-319.

Sawatzky, C.D., Michalak, D., Reist, J.D., Carmichael, T.J., Mandrak, N.E., and Heuring, L.G. 2007. Distributions of freshwater and anadromous fishes from the mainland Northwest Territories, Canada. Can. Manuscr. Rep. Fish. Aquat. Sci. 2793: xiv + 239 p.

Scannell, P.O. 1988. Effects of elevated sediment levels from placer mining on survival and behavior of immature Arctic grayling. M.Sc. Thesis, Univ. of Alaska Fairbanks, Fairbanks, Alaska. ix + 84 p.

Schallock, E.W. 1966. Grayling life history related to a hydroelectric development on the Chatanika River in interior Alaska. M.Sc. Thesis, University of Alaska. xii + 113 p.

Schmidt, D., and O'Brien, W.J. 1982. Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. **39**: 475-482.

Schmidt, D.C., Hale, S.S., Crawford, D.L., and Suchanek, P.M. 1984. Resident and juvenile anadromous fish investigations (May/October 1983). Alaska Power Authority, Anchorage, Alaska. 98 p.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. **184**: xi + 966 p.

Shotton, R.T. 1971. Towards and environmental impact assessment of a gas pipeline from Prudhoe Bay, Alaska, to Alberta. Appendix II. Fish. Unpublished report prepared by Inter-disciplinary Systems Ltd, Winnipeg for the Environment Protection Board. Interim Rep. 1. variously paginated.

Shubin, P.N., and Zakharov, A.B. 1984. Hybridization between European grayling, *Thymallus thymallus*, and Arctic grayling, *Thymallus arcticus*, in the contact zone of the species. J. Ichthyol. **24**: 159-162.

Stanislawski, S.S. 1997. Fall and winter movements of Arctic grayling (*Thymallus arcticus* (Pallas)) in the Little Smokey River, Alberta. M.Sc. Thesis, University of Alberta, Edmonton, Alberta. ix + 91 p.

Stein, J.N., Jessop, C.S., Porter, T.R., and Chang-Kue, K.T.J. 1973a. An evaluation of the fish resources of the Mackenzie River valley as related to pipeline development. Environmental-Social Committee, Northern Pipelines, Task Force on Northern Oil Development Rep **73-1**: xv + 121 p.

Stein, J.N., Jessop, C.S., Porter, T.R., and Chang-Kue, K.T.J. 1973b. Fish Resources of the Mackenzie River Valley, Interim Report II. Environmental-Social Committee, Northern Pipelines, Task Force on Northern Oil Development Rep. xvii + 260 p.

Stewart, D.B., and MacDonald, G. 1978. Arctic Land Use Research Program 1977: a survey of the fisheries resources of the central Northwest Territories. Can. Dep. Ind. N. Aff. Environ. Stud. **8**: ii + 123 p.

Stewart, D.B., Mochnacz, N.J., Reist, J.D., Carmichael, T.J., and Sawatzky, C.D. 2007. Fish diets and food webs in the Northwest Territories: Arctic grayling (*Thymallus arcticus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2796: vi + 21 p.

Stewart, R.J., McLenehan, R.E., Morgan, J.D., and Olmsted, W.R. 1982. Ecological studies of Arctic grayling (*Thymallus arcticus*), Dolly Varden char (*Salvelinus malma*), and mountain whitefish (*Prosopium williamsoni*) in the Liard River drainage, B.C. Prepared by E.V.S. Consultants Ltd. for Westcoast Transmission Company Ltd. and Foothills Pipe Lines (North B.C.) Ltd., 99 p.

Stuart, K.M., and Chislett, G.R. 1979. Aspects of the life history of the Arctic grayling in the Sukunka drainage. Prepared by British Columbia Fish and Wildlife Branch, Prince George, BC. 111 p.

Suchanek, P.M., Sundet, R.L., and Wenger, M.N. 1984. Susitna Hydro Aquatic Studies 1984 Report No. 2, Part 6, Resident fish habitat studies. Alaska Department of Fish and Game, Anchorage, Alaska. iv + 40 p.

Tack, S.L. 1971. Distribution, abundance, and natural history of the Arctic grayling in the Tanana River drainage. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress, 1970-1971. Project F-9-3, **12 (R-I)**: 35 p.

Tack, S.L. 1972. Distribution, abundance, and natural history of the Arctic grayling in the Tanana River drainage. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress, 1971-1972. Project F-9-4, **13 (R-I)**: 36 p.

Tack, S.L. 1974. Distribution, abundance, and natural history of the Arctic grayling in the Tanana River drainage. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1973-1974. Project F-9-6, **15 (R-I)**: 52 p.

Tack, S.L. 1980. Migrations and distribution of Arctic grayling in interior and arctic Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, 1979-1980. Project F-9-12, **21 (R-I)**: 32 p.

Tilsworth, T., and Travis, M.D. 1987. Fish passage through Poplar Grove Creek. Alaska Department of Transportation and Public Facilities, Report No. **FHWA-AK-RD-87-15**: vii + 108 p.

Tonn, W.M., Boss, S.M., Aku, P.K.M., Scrimgeour, G.J., and Paszkowski, C.A. 2004. Fish assemblages in subarctic lakes: does fire affect fish-environment relations in northern Alberta? Trans. Am. Fish. Soc. **133**: 132-143.

Tripp, D.B., and McCart, P.J. 1974. Life histories of grayling (*Thymallus arcticus*) and longnose suckers (*Catostomus catostomus*) in the Donnelly River system, N.W.T., p. 1-19. In P.J. McCart (ed.) Life histories of anadromous and freshwater fish in the western Arctic. Arctic Gas Biological Report Series **15**.

Van Hulle, F., and Murray, J. 1975. Inventory and cataloguing of sport fish and sport fish waters in southwest Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Report of Progress, 1974-1975. Project F-9-7, **16 (G-I-B)**: 26 p.

Van Kirk, R.W., and Benjamin, L. 2001. Status and conservation of salmonids in relation to hydrologic integrity in the Greater Yellowstone ecosystem. West. N. Am. Nat. **61**: 359-374.

Vascotto, G.L. 1970. Summer ecology and behavior of the grayling of McManus Creek, Alaska. M.Sc. Thesis, University of Alaska, Fairbanks, Alaska. ix + 131 p.

Vascotto, G.L., and Morrow, J.E. 1973. Behaviour of the Arctic grayling, *Thymallus arcticus*, in McManus Creek, Alaska. Biol. Pap. Univ. Alsk. **13**: 29-38.

Vincent, R.E. 1962. Biogeographical and ecological factors contributing to the decline of Arctic grayling, *Thymallus arcticus* (Pallas), in Michigan and Montana. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan. 169 p.

Ward, J.C. 1951. The biology of the Arctic grayling in the southern Athabaska drainage. M.Sc. Thesis, University of Alberta, Edmonton, AB. 71 p.

Weagle, K.V., and Cameron, R.A. 1974. The impact of the Strutt Lake Hydro Project on the Snare River, N.W.T. Can. Fish. Mar. Serv. Tech. Rep. Ser. CEN-T **74-6**: vi + 32 p.

Weber, P. and Post, R. 1985. Aquatic habitat assessments in mined and unmined portions of the Birch Creek watershed. Alaska Dep. Fish Game Tech. Rep. **85-2**: ix + 55 p.

West, R.L., Smith, M.W., Barber, W.E., Reynolds, J.B., and Hop, H. 1992. Autumn migration and overwintering of Arctic grayling in coastal streams of the Arctic National Wildlife Refuge, Alaska. Trans. Am. Fish. Soc. **121**: 709-715.

Williams, F.T. 1969. Grayling investigations on Tolsona and Moose Lakes. Alaska Department of Fish and Game Annual Report of Progress, 1968-1969. Federal Aid in Fish Restoration Project F-9-1: Sport Fish Investigations of Alaska, Volume **10**: 291-300.

Wilson, R., Allen-Gil, S., Griffin, D., and Landers, D. 1995. Organochlorine contaminants in fish from an Arctic lake in Alaska, USA. Sci. Total Environ. **160/161**: 511-519.

Wojcik, F.J. 1955. Life history and management of the grayling in interior Alaska. M.Sc. Thesis, University of Alaska. viii + 53 p.

8.0 ABBREVIATIONS

CTM = mean critical thermal maximum = upper lethal temperature (ULT)

FL = fork length—distance from the tip of the fish's snout to the notch in its tail.

MTL = median tolerance limits (i.e., 96 h LD 50)

NTU = Nephelometric turbidity units or NTU are a measure of light scattered by suspended particles in water. High NTU measurements indicate low water clarity (i.e. high turbidity).

TL = total length—distance from the tip of the fish's snout to the tip of its tail.

UILT = upper incipient lethal temperature

9.0 GLOSSARY

Adfluvial fish populations move between lake and river or stream environments.

Alevins are newly hatched, incompletely developed fishes (usually salmonids) still in the nest or inactive on the bottom and living off stored yolk.

Allopatric fish species do not inhabit the same waterbody.

Aufeis is the ice formed when water from a spring or stream emerges and freezes on top of previously formed ice.

Baseflow is stream flow derived from groundwater.

Benthic habitats in waterbodies are on or near the bottom.

Fluvial fish populations remain in rivers and streams throughout their lives.

Fry are young fish, newly hatched, after yolk has been used up and active feeding has commenced.

Holarctic species occur around the globe in Arctic regions.

Iteroparous fish spawn more than once in their lives.

Lacustrine species live and grow in lakes or ponds.

Larval fishes (plural larvae) are young fish, newly hatched, before the yolk has been used up (see also **Alevins**).

Littoral habitats in waterbodies are near the shore.

Pelagic habitats in waterbodies are not near the bottom or shore.

Sympatric species occur in the same or overlapping areas.

Thermal units are Centigrade degree-days above 0°C.

Appendix 1. Life history and habitat parameters

The emphasis of this work is on observations from within the Mackenzie Valley region. Terms such as “dominant”, “preferred” and “optimum”, which have been used in other summaries (e.g., Ford *et al*. 1995; Roberge *et al*. 2002), are avoided unless they are supported by directed research studies. This is because sampling observations may not accurately reflect a species’ preferences unless the spatial and temporal biases related to sampling design and gear are carefully controlled. The following sections define what is meant by the various life history and habitat use parameters used in the text and tables and in the appendices that follow. Some parameters described here may not be used in this report because this description applies to all of the habitat use reports in the series.

TABLES 2 and 3

Habitat use and requirements

These tables summarize habitat associations during the life history stages of the species. Separate tables may be included for stream, river, and lake environments. Observations from areas within the Mackenzie River watershed are in bold type. The following parameters are included, with the units of measurement typically used:

- **Habitat type** – habitat type most commonly associated with observations of the life history stage (e.g., streams–pools, runs, riffles; lakes–littoral, **pelagic**, benthic);
- **Stream gradient** – percent (%) slope;
- **Depth range (m)** – range of depths from which the species has been reported;
- **Substrate** – substrate type(s) most commonly associated with observations of the species;
- **Cover** – cover type(s) most commonly associated with observations of the species:
- **Habit** – typical distribution within the habitat type (e.g., surface, midwater, benthic, above or below thermocline, inshore or offshore);
- **Velocity range** – water velocities (cm/s) wherein the species is most commonly observed;
- **Turbidity (NTU):**
    - o **range** – turbidity range wherein the species has been reported;
    - o **limits** – upper and lower lethal limits as tested experimentally;
- **Oxygen (mg/L):**
    - o **range** – dissolved oxygen levels wherein the species has been reported;
    - o **limits** – upper and lower lethal limits as tested experimentally;
- **Temperature (°C):**
    - o **range** – water temperatures wherein the species has been reported;
    - o **limits** – upper and lower lethal limits as tested experimentally;
- **Prey:**
    - o **Primary** – taxa or taxon typically comprising the majority (by weight/volume/food value) of the food found in the stomachs of fishes sampled, or that were seen to be eaten during *in situ* behavioural studies;
    - o **Secondary** – taxa or taxon comprising the minority (by weight/volume/food value) of food found in the stomach of fish sampled, or that were seen to be eaten during *in situ* behavioural studies. [Note: Differences in prey selection (i.e., primary/secondary) may reflect changes in the seasonal availability rather than the relative importance of food items.];
- **Duration** –number of seasons, months, or years in which each specific life stage exists or occurs;
- **Size/Age range** – average and/or maximum size range (mm) of the life history stage; or maximum size range (mm); FL = fork length, SL = standard length, TL = total length. A fish is age 0 until December 31 of the year it was hatched unless otherwise indicated.

Reproduction

This table summarizes habitat and life history parameters related to the species' reproduction. Observations from areas outside the Mackenzie River watershed are italicized. The following parameters are included:

- **Reproductive strategy** – *oviparous* species produce eggs that hatch outside the body of the mother; *iteroparous* species produce their young in annual or seasonal batches (most fishes); *semeloparous* species (e.g., salmon) produce all of their offspring at one time and then usually die; *annual* spawners reproduce each year following maturity until they die or reach reproductive senescence; under marginal conditions a portion of the reproductive population may rest for a year or more between spawning events (*% resting*);
- **Age at maturity** – range of ages at which males (M) and females (F) become sexually mature, with any estimate of the most common age at maturity provided in brackets;
- **Fecundity** – range in the number of eggs produced by females;
- **Spawning habitat** – habitat types wherein spawning has been observed, ripe and running fish have been caught, ripe and spent fish have been caught together, or eggs or sac larvae have been found. The presence of mobile young-of-the-year was used to identify nursery areas, and sometimes "suspected" spawning areas;
- **Spawning habit** – some species *build a nest* by altering the bottom substrates to meet their requirements before spawning; others *use existing nests* constructed by other species; *broadcast spawners* spread their eggs over suitable areas of unaltered bottom substrates; some species *care for the eggs* or *care for the young*;
- **Spawning temperature** – temperature range at which spawning has been observed;
- **Spawning depth** – depth range at which spawning has been observed;
- **Spawning substrate** – substrate type(s) observed at spawning locations;
- **Spawning current velocity** – current velocity observed at spawning locations;
- **Maximum age** – life expectancy of the species;
- **Reproductive senescence** – age at which the species stops reproducing.

APPENDICES 2 and 3

The seasonal habitat requirements for each life history stage are presented below in separate appendices for stream and lake environments. Within these appendices, observations from the Mackenzie River watershed are in bold type.

Life history stage

Observations on habitat use are summarized by life history stage. Four stages are recognized:

- **Spawning/eggs** – includes habitats on the spawning grounds where adults spawn and eggs mature and hatch;
- **Young of the year (YOY)** – larvae and fry less than age 1 (age 0 until December 31 of the year they are hatched);
- **Juveniles** – sexually immature fish older than age 1;
- **Adults** – include fish that have attained sexual maturity.

Seasons

Habitat use was divided into four seasons, which correspond to the environmental conditions rather than to the calendar seasons. Calendar months are also provided if possible, but the correspondence between environmental variables and calendar months varies from south to north and from year to year. In the north of the Mackenzie watershed (Inuvik; S. Stephenson, DFO, pers. comm.), the seasons used are:

- **Spring (Sp)** – the period of ice breakup and spring runoff, typically late April to mid June;
- **Summer (Su)** – the period of open water, typically mid-June to late September;

- **Fall (Fa)** – the period of ice formation, typically late September to late November;
- **Winter (Wi)** – the period of ice cover, typically late November to late April.

In the south (Hay River; G. Low, DFO, pers. comm.) they are:

- **Spring (Sp)** – the period of ice breakup and spring runoff, mid-April to early June;
- **Summer (Su)** – the period of open water, typically early June to late-September;
- **Fall (Fa)** – the period of ice formation, typically late-September to mid-November;
- **Winter (Wi)** – the period of ice cover, typically mid-November to mid-April.

These date ranges are averages, since the timing of breakup varies from river to river and lake to lake depending upon factors such as stream gradient, exposure to sunlight, and lake size.

Water depth

Five water depth categories are used for stream environments: 0-0.2, >0.2-0.6, >0.6-1, >1–2, and >2 m. Depth represents the distance from the surface of the water downwards. The depth association of a fish found in the upper metre of the water column, for example, would be reported as 0–0.2, >0.2-0.6 and >0.6–1.0. Depth is reported as stated in the reference, but if "shallow" water was the only descriptor, a depth of 0–20 cm was used to represent "shallow" water. A broader range of depths is used to describe lake environments: 0–1, >1–2, >2–5, >5–10, and >10 m.

Substrate type

Substrate type was reported as stated in the reference. However, if particle size was not provided, substrate type was classified as follows:

- **bedrock** = uniform continuous substrate;
- **boulder** = >25 cm;
- **cobble** = 17–<25 cm;
- **rubble** = 6.4–<17 cm;
- **gravel** = 0.2–<6.4 cm;
- **sand** = <0.2 cm;
- **silt/clay** = finer than sand with fine organic content;
- **muck (detritus)** = mud with coarse organic content;
- **hard-pan clay** = clay; and
- **pelagic** = open water.

Cover type

Cover features that may provide protection, or a refuge, from predators, competitors, and adverse environmental conditions include:

- **None** – no cover;
- **Submergent vegetation** – aquatic plants that grow entirely below the surface and are attached to the bottom by roots or rhizomes;
- **Emergent vegetation** – aquatic plants with foliage that is partly or entirely borne above the water surface (e.g., cattail *Typha* spp.) or float on the surface of the water (e.g., milfoil);
- **Algae** – aquatic algae present on the bottom or within the water column;
- **Wood** – large (LWD) or smaller woody debris (SWD) on the bottom or within the water;
- ***In situ*** – submerged cavities and/or crevices, undercut banks;
- **Substrate** – interstitial spaces between any size of substrate (boulder–sand);
- **Overhead** – cover originating outside the riparian zone that overhangs the stream and/or banks, which includes overhanging banks or riparian vegetation, woody debris outside the channel, or anything above the surface that provides shade.

Habitat

In flowing water, habitat refers to the type of channel unit, and typical water velocity within the unit that the species inhabits, including:

- **Pool** – velocity range <0.25 $m \cdot s^{-1}$;
- **Run** – velocity range 0.25 – 0.50 $m \cdot s^{-1}$;
- **Riffle** – velocity range 0.50 – 1.00 $m \cdot s^{-1}$;
- **Rapid** – velocity range >1.00 $m \cdot s^{-1}$;
- **River margin** – habitat along the banks of the mainstem channel, often low velocity;
- **Off-channel** – any habitat that is outside the mainstem flow including side channels, backwaters, and off channel habitats, often low or no velocity.

Water velocity differences are not used to differentiate lake habitats; rather they are differentiated on the basis of their proximity to flowing water or shorelines, as follows:

- **Lake inlet** – near or within stream or river plumes entering the lake;
- **Lake outlet** – near or within the channel that drains the lake;
- **Inshore** – typically associated with littoral habitat along the edges, rather than the middle of the lake;
- **Offshore** – typically associated with the middle, rather than the edges of the lake. Where possible their typical position in the water column is described (e.g., surface, midwater, benthic, above or below thermocline).

Appendix 2. Stream habitat requirements for Arctic grayling. Habitat features are defined in Appendix 1.

Stream habitat features:	LIFE STAGES [Season of use (reference)]				LEGEND/COMMENTS/REFERENCES
	Spawn/egg	**YOY**	**Juvenile**	**Adult**	
Depth (m)					
0-0.2	Sp (7)	**Sp-Fa** (5, 16, 18-21)			**Season of use:**
>0.2-0.6	**Sp** (1, 2)	**Sp-Fa** (1, 2, 22-28)	Sp-Fa (22, 30, 33-35)	**All** (1, 2, 14, 30, 33-35)	Sp = spring
>0.6-1	**Sp** (1, 2)	**Sp** (1, 2)	Sp (22, 30, 33-35)	**All** (1, 2, 14, 30, 33-35)	Su = summer
>1-2				**All** (14, 30, 33-35)	Fa = fall
>2					Wi = winter
Substrate					All = all seasons
Bedrock					
Boulder		Sp-Fa (22-29)	Sp-Fa (22, 30)	Sp-Fa (22, 30, 33)	
Cobble		Sp-Fa (22-29)	Sp-Fa (22, 30)	Sp-Fa (22, 30, 33)	
Rubble	**Sp** (1, 2-12)	**Sp-Fa** (1, 2-12, 22-29)	Sp-Fa (22, 30)	**Sp-Fa** (1-12, 22, 30, 33)****	*Most spawning over unembedded gravel. ** Strong preference by YOY for silt to fine gravel. ****Adult preference for gravel and rubble.
Gravel	**Sp** (1, 2-12) *	**Sp-Fa** (1, 2-12, 22-29)**	Sp-Fa (22, 30)	**Sp-Fa** (1-12, 22, 30, 33)****	
Sand	**Sp** (1, 2-12)	**Sp-Fa** (1, 2-12, 22-29, 37)**	Sp-Fa (22, 30)	**Sp-Fa** (1-12, 22, 30, 33)	
Silt/Clay	Sp (15)	**Sp-Fa** (22-29, 37)	Sp-Fa (22, 30)	Sp-Fa (15, 22, 30, 33)	
Muck (Detritus)					
Hard-pan clay					
Pelagic					
Cover					
None			Sp-Fa (22, 30)	**Sp-Fa** (22, 30, 33-35)	
Submergents			Sp-Fa (22, 30, 33)	**Sp-Fa** (22, 30, 33-35)	
Emergents					
Algae					
Wood					
In situ		**Sp-Fa** (22, 25, 26, 29)	Sp-Fa (22, 30, 33)	**Sp-Fa** (22, 30, 33-35)	
Substrate	**Sp** (1-3, 5, 6, 15, 16)*		Sp-Fa (22, 30, 33)	**Sp-Fa** (22, 30, 33-35)	*Eggs in the interstices of gravel substrates.
Undercut bank/overhang			Sp-Fa (22, 30, 33)	**Sp-Fa** (22, 30, 33-35)	

Stream habitat features:	LIFE STAGES [Season of use (reference)]				LEGEND/COMMENTS/REFERENCES
Overhead		**Sp-Fa** (22, 25, 26, 29)	Sp-Fa (22, 30, 33)	**Sp-Fa** (22, 30, 33-35)	
Other	**Sp** (13, 14) *				* Sometimes spawn under the ice.
Velocity/Habitat					
Pool		Sp-Fa (22-29)	Sp-Fa (22, 30, 32)	**Sp-Fa** (27, 30, 32, 36)	
Run	Sp (1, 3)*		Sp-Fa (22, 30)	**Sp-Fa** (1, 3, 17, 27, 30, 32)	*Spawn just below riffles (1, 3). In areas with current, larval grayling use sand drifts and rocks as velocity barriers (37).
Riffle	Sp (17)*				*Spawn at the end of long runs.
Rapid					
River Margin		Sp-Fa (22-29)	Sp-Fa (22, 30)*		*Juveniles also occupy delta habitats.
Off-channel		Sp-Fa (22-29)			

1 = Bishop 1967—Providence Creek, NT;
2 = Tack 1971 cited in Northcote 1995—Tanana River, Alaska;
3 = Bishop 1971—Providence Creek, NT;
4 = McPhail and Lindsey 1970—review;
5 = Kratt 1977—Fond du Lac River, SK;
6 = Krueger 1981—Tyee Lake, Alaska;
7 = Barndt and Kaya 2000—Montana;
8 = Rawson 1950—Reindeer Lake, SK;
9 = Beauchamp 1990—Upper Granite Lake, Washington;
10 = Stuart and Chislett 1979—Adsett Creek, BC;
11 = Machniak *et al*. 1980—MacKay River, AB;
12 = Lohr *et al*. 1996—laboratory, Montana fish.
13 = Jessop *et al*. 1974—Trail River, NT;
14 = Jessop and Lilley 1975—Mackenzie Valley, NT;
15 = Reed 1964—Tanana River drainage, Alaska;
16 = Kratt and Smith 1977—Fond du Lac River, SK;
17 = Stewart *et al.* 1982 cited in Northcote 1995—Adsett Creek, BC.
18 = Tripp and McCart 1974—a=Donnelly River, NT; b=Vermillion Creek, NT;
19 = Craig and Poulin 1975—Kavik River system, Alaska;
20 = Chang-Kue and Cameron 1980—Great Bear River area, NT;
21 = Katopodis *et al*. 1978—Redknife River, NT;
22 = Vascotto 1970—McManus Creek, Alaska;
23 = de Bruyn and McCart 1974—Babbage River, YT;
24 = Kaya 1989—laboratory, Montana fish;
25 = Deleray 1991—Deer Creek, Montana;
26 = McClure and Gould 1991—laboratory, Montana fish;
27 = Birtwell *et al*. 1984—Minto Creek, Yukon;
28 = Deegan *et al*. 2005—Kuparuk River and Oksrukuyik Creek, Alaska;
29 = Ford *et al*. 1995—review;
30 = Evans *et al*. 2002—review;
32 = Hughes and Reynolds 1994; Hughes 1998a, 1999—Tanana River drainage, Alaska;
33 = Den Beste and McCart 1984—Alaskan streams north of the Yukon River;
34 = Schmidt *et al*. 1984—Alaska;
35 = Liknes and Gould 1987—Montana;
36 = Hughes and Dill 1990; Hughes 1992a+b—Tanana River drainage, Alaska;
37 = Lee 1985—Chena River, Alaska.

Appendix 3. Lake habitat requirements for Arctic grayling. Habitat features are defined in Appendix 1.

Lake habitat features:	LIFE STAGE [Season of use (reference number)]				LEGEND/COMMENTS/REFERENCES
	Spawn/egg	YOY	Juvenile	Adult	LEGEND
Depth (m)					
0-1	Sp (1, 2)	Su (1)		**Su** (1, 4, 10)	
>1-2				**Su** (1, 4, 10)	
>2-5				**Su** (1, 4, 10)	
>5-10				**Su** (10)**	**Few adults caught below 4 m depth.
>10					
Substrate					**Season of use:**
Bedrock					Sp = spring
Boulder					Su = summer
Cobble					Fa = fall
Rubble				**Su** (4-8)	Wi = winter
Gravel	Sp (1, 2)			**Su** (4-8)	All = year-round
Sand	Sp (1, 2)			**Su** (4-8)	
Silt/Clay	Sp (1, 2)			**Su** (4-8)	
Muck (Detritus)					
Hard-pan clay					
Pelagic					
Cover					
None					
Submergents				**Su** (4)**	**Adults may occur in or near submergent vegetation.
Emergents					
Algae					
Wood					
In situ					
Substrate					
Undercut bank/overhang			Su (3)		
Overhead				**Su** (1, 4)**	**Adults common beneath tree branches that overhang the water.
Other					
Habitat					
Lake inlet	Sp (1)	Su (1)		**Su** (1, 4, 9)	
Lake outlet	Sp (1)			**Su** (1, 4, 9)	
Inshore (littoral)		Su (1)		**Su** (1, 4, 9)	
Offshore-surface					
Offshore-midwater					
Offshore-benthic					

1 = Krueger 1981—Tyee Lake, Alaska;
2 = Reed 1964—Tanana River drainage, Alaska;
3 = Beauchamp 1982—Upper Granite Lake, Washington;
4 = Bishop 1967—Great Slave and Stark lakes, NT;
5 = Rawson 1950—Reindeer Lake, SK;
6 = McPhail and Lindsey 1970—review;
7 = Lawrence and Davies 1979—NU;
8 = Hatfield *et al*. 1972a—Mackenzie Valley, NT;
9 = Miller 1947—Great Bear Lake, NT;
10 = Rawson 1951—Great Slave Lake, NT.