Fish diets and food webs in the Northwest Territories: Arctic grayling (*Thymallus arcticus*)

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FISH DIETS AND FOOD WEBS IN THE NORTHWEST TERRITORIES: ARCTIC GRAYLING (*Thymallus arcticus*)

by

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TABLE OF CONTENTS

ABSTRACT .... **iv**
RÉSUMÉ .... **v**
1.0 INTRODUCTION **1**
2.0 FOOD WEB **2**
2.1 Predators 2
2.2 Prey 5
2.2.1 Young-of-the-year 6
2.2.2 Larger Juveniles and Adults 7
2.2.3 Seasonal 8
2.3 Competitors 9
3.0 SUMMARY **9**
4.0 ACKNOWLEDGEMENTS **10**
5.0 REFERENCES **10**
6.0 GLOSSARY **15**
7.0 APPENDICES **15**

LIST OF FIGURES

Figure 1. Generalized food web for Arctic grayling 3

LIST OF APPENDICES

Appendix 1. Stomach contents of Arctic grayling expressed as percent by volume or percent by number from rivers and lakes in the Northwest Territories (NT) 16
Appendix 2. Stomach contents of Arctic grayling expressed as percent frequency of occurrence, from rivers and lakes in the Yukon (YT) and Northwest Territories (NT) 19

ABSTRACT

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.

Arctic grayling prey opportunistically on a wide variety of seasonally available macroinvertebrate taxa and life stages that originate from aquatic and terrestrial habitats. They also eat 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; however, little is known of their fall and winter diet. Humans are a key predator on larger grayling while piscivorous fishes, particularly northern pike (*Esox lucius*), may be the key predators on smaller juveniles. Competition for food with other salmonid species may displace grayling from some regions and limit their growth in some stream habitats. Because grayling are visual predators, their feeding success is vulnerable to increases in water turbidity. This document provides a generalized food web for the species and reviews knowledge of its interactions with predators, prey, and competitors. Dietary differences related to geographical location, habitat type, life history stage, season, predation, and competition are discussed.

Key words: diet; life history; habitat use; fresh water; stream resident; fluvial; adfluvial; lacustrine; Salmonidae; feeding behaviour.

RÉSUMÉ

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L'ombre arctique s'alimente de façon opportuniste d'une vaste gamme de macroinvertébrés d'origine terrestre ou aquatique qui se présentent selon les saisons et le stade du cycle vital. Il mange également des œufs de poisson et des alevins, y compris de sa propre espèce. Il dépend à divers degrés sur les organismes qui dérivent à la surface de l'eau et les insectes terrestres durant la saison des eaux libres, mais on en sait peu à propos de son régime alimentaire au cours de l'automne et de l'hiver. L'homme est un important prédateur des grands ombres, tandis que les poissons ichtyophages, le grand brochet (*Esox lucius*) en particulier, peuvent constituer les principaux prédateurs des juvéniles les plus petits. La compétition pour la nourriture avec d'autres espèces de salmonidés peut mener au déplacement de l'ombre de certaines régions et limiter sa croissance dans certains habitats fluviaux. Comme il est un prédateur visuel, son succès à se nourrir peut être affecté par une augmentation de la turbidité de l'eau. Nous présentons un réseau trophique généralisé pour l'espèce et nous évaluons les connaissances sur ses interactions avec ses prédateurs, ses proies et ses compétiteurs. Nous examinons également les différences dans son alimentation reliées aux emplacements géographiques, aux types d'habitat, aux stades du cycle vital, aux saisons, à la prédation et à la compétition.

Mots clés : régime alimentaire; cycle vital; utilisation d'habitat; eau douce; sédentaire; fluvial; adfluvial; lacustre; Salmonidés; comportement alimentaire.

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 diet of the Arctic grayling, *Thymallus arcticus* (Pallas, 1776). This sought after sport fish inhabits many clear, cold streams, rivers and lakes of the mainland Northwest Territories and Nunavut but is rare in the northeastern Kivalliq Region and has not been recorded from the Arctic Islands (McPhail and Lindsey 1970; Scott and Crossman 1973; McCart and Den Beste 1979; Lee *et al*. 1980). It is found throughout the Mackenzie System, where it is most abundant in the clear, swift tributaries that flow from the east side of the valley into the Mackenzie River (Hatfield *et al*. 1972a,b; Stein *et al*. 1973a,b; Jessop *et al*. 1974). 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.

Stream resident, **fluvial**[1], **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). Young-of-the-year, juveniles, and adults often undertake seasonal migrations between spawning, feeding, and overwintering habitats. These movements vary with life stage and watershed. Stewart *et al.* (2007) provide a recent review of habitat use by Arctic grayling.

Very little is known of the species' diet within the Mackenzie watershed outside the summer season, about energy flow, or predation rates. This limits the ability to assess the effects of environmental changes on the species, particularly impacts related to pipeline development and climate change. This report presents a generic food web for Arctic grayling, based largely on data from the Mackenzie River watershed within the Northwest Territories. It reviews knowledge of how the species' diet varies with geographical location, habitat type, season, life history stage, and competition. It also considers predation pressures and identifies knowledge gaps.

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

2.0 FOOD WEB

Quantitative data from Arctic grayling populations in the Northwest Territories, and Yukon were used to construct the generic food web (Appendix 1; Appendix 2). Most of these studies were conducted during the summer, and small sample sizes often resulted in lumping together of juvenile and adult dietary data. These limitations make it difficult to compare dietary differences among populations, life stages, and seasons. They also limit what can be said about the energetic importance of each pathway.

The methods used to quantify Arctic grayling diet are not directly comparable among studies. Some studies have used percentage by volume or percent by number to quantify the stomach contents (Appendix 1), while others have used percent frequency of occurrence (Appendix 2). The percent frequency of occurrence was determined based on all fish caught, except at the Firth River (de Bruyn and McCart 1974), where they were based only on fish with food in their stomachs. Based on these data, a generalized food web has been constructed for the species (Figure 1). Aspects of this food web, including predators and dietary differences related to life history stage, habitat, and season are discussed below, as are the effects of inter- and intraspecific competition.

2.1 Predators

Predation of Arctic grayling by other species has not been well documented. As adults, they are seldom reported in the stomach contents of predatory fishes. Whether this is simply a sampling artefact is unknown. By erecting their large dorsal fin they may be able to deter predators by appearing too large to swallow (Bishop 1967). Bite marks on the fragile fin suggest that it may also be used to lure attackers away from the fish’s body. By spawning in swift, shallow streams at break-up and feeding at the surface along shallow, rocky shorelines they may also reduce predation by **piscivorous** fishes. Burbot (*Lota lota*) predation on grayling eggs has been inferred by the presence of juvenile burbot at Arctic grayling spawning congregations during late May in Alaska (Ott and Morris 1999). Predation on fry and juveniles is likely higher, and may be poorly documented in part due to the difficulty of distinguishing between partially digested graylings and coregonids.

Grayling in the Chatanika River of Alaska are eaten by northern pike (*Esox lucius*), inconnu (*Stenodus leucichthys*), and burbot (Schallock 1966). Pike in Indin Lake, Northwest Territories, also eat grayling (Jessop *et al*. 1993). In Great Slave Lake they are eaten on occasion by lake trout (*Salvelinus namaycush*), but are rare in their stomach contents and otherwise appear to have few predators (Bishop 1967).

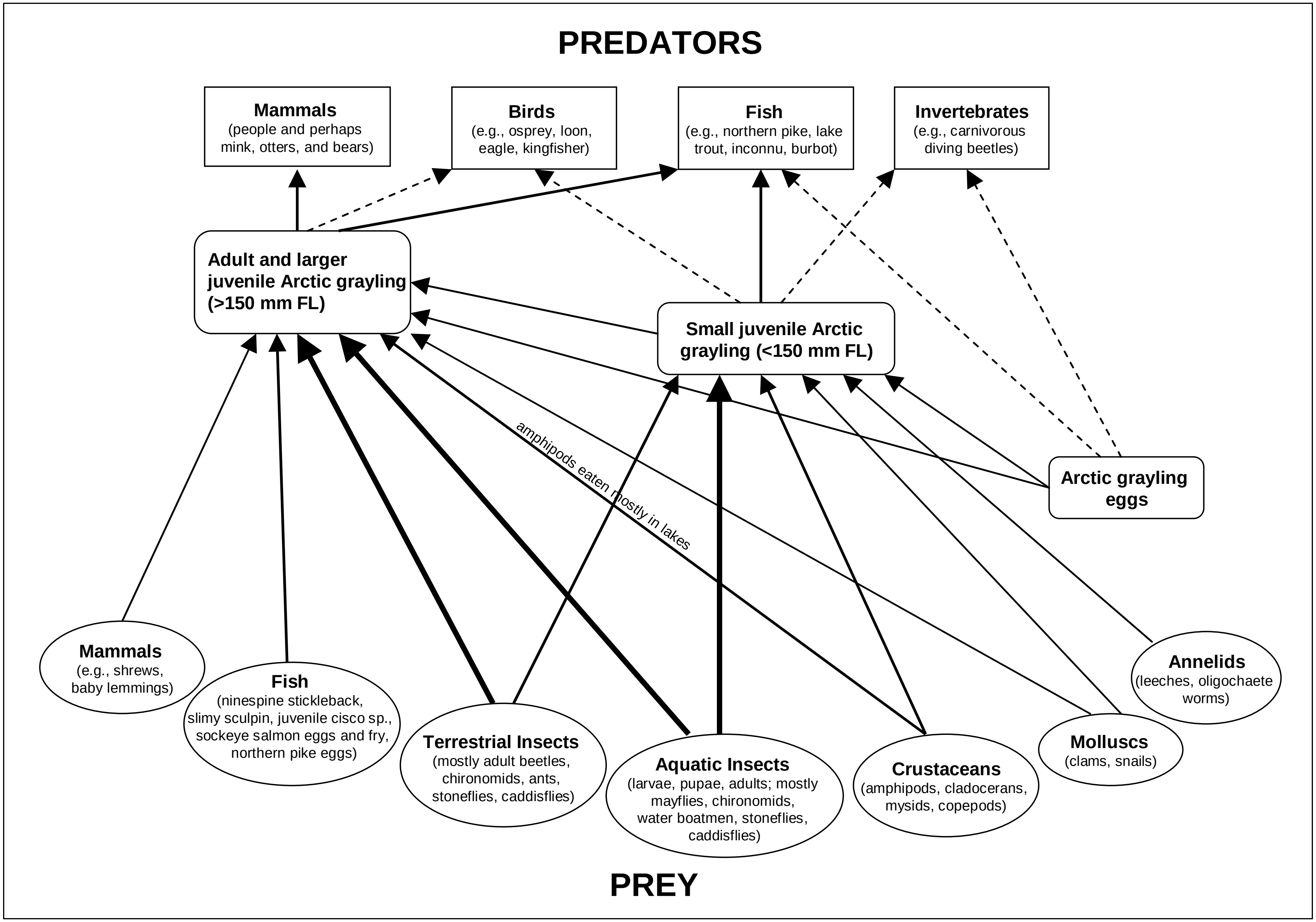

Figure 1. Generalized food web for Arctic grayling showing the direction of energy flow. Bold lines indicate major food pathways, in comparison to thinner lines; solid lines indicate demonstrated and dashed lines indicate putative pathways.

The low abundance of grayling in tundra streams occupied by northern pike suggests that these species do not coexist well (Jones *et al*. 2003b). Tonn *et al*. (2004) also found a negative relationship between the presence of northern pike and grayling in small mountain lakes. There is little or no survival of grayling fry when they are stocked into lakes that support predators such as northern pike (Tack 1972 cited in Armstrong 1986). However, grayling appear to be adept at avoiding pike predation in stream environments (Bishop 1967; Barndt and Kaya 2000). Bull trout (*Salvelinus confluentus*) in the Northwest Territories have been observed attempting to prey upon Arctic grayling, but successful predation has not been confirmed (N. Mochnacz, pers. obs.).

Under captive and natural conditions larger grayling will eat smaller grayling (McLeay *et al*. 1983). In the wild, grayling in the spawning streams eat eggs, some of which may be grayling eggs (Bishop 1967, 1971). Adults will eat eggs when the opportunity presents, and will actively prey on fry (Miller 1946; Deleray 1991).

Arctic 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*. 1980, 1982; Dahlke 1983; Moshenko and Low 1983; Armstrong 1986; Dunn and Roberge 1989; Northcote 1995). 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). Wojcik (1955) cited overfishing as the primary cause for a decline in the grayling population in the Fairbanks area of Alaska. 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%). Grayling are harvested incidentally by subsistence fishers but only make up a significant portion of the harvest in the central portions of the Mackenzie Valley (McCart and Den Beste 1979). They are sometimes eaten but are used mostly for dog food, as they spoil very quickly (Scott and Crossman 1973; D.B. Stewart, pers. obs.).

Piscivorous birds, such as loons (*Gavia* spp.), grebes (*Podiceps* spp.), the bald eagle (*Haliaeetus leucocephalus*), osprey (*Pandion haliaetus*) and belted kingfisher (*Ceryle alcyon*); and mammals, such as the mink (*Mustela vison*), river otter (*Lontra canadensis*) and bears (*Ursus* spp.), probably eat grayling on occasion (Scott and Crossman 1973; W. Morris, Alaska Department of Natural Resources, pers. comm.). These fish may be particularly susceptible to bird and mammal predation during spring, when large numbers of adult fish congregate in the clear, shallow spawning streams, and during winter when wintering congregations of fish are accessible to mink and otter.

2.2 Prey

Grayling are visual feeders that prey primarily at the surface and at midwater depths, often on **drift** (Bishop 1967; Vascotto 1970). They are opportunistic in their feeding habits and their diet is extremely variable (Bishop 1967; de Bruyn and McCart 1974). During the breeding season only larger adult male grayling maintain territories, but during the summer feeding season females and smaller males also maintain territories (Vascotto 1970; Vascotto and Morrow 1973; Kratt and Smith 1979). Positions are maintained by means of ritualistic displays. Feeding behaviour varies with the size of the individual and its hierarchical status, and also appears to be related to the degree of competition from other grayling (Vascotto and Morrow 1973). The larger fish are more deliberate in their movements to capture prey than the smaller fish, which face more competition and must move quickly.

Adult grayling feeding on drift in streams appear to position themselves on the basis of water depth and flow 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 their distribution patterns in stream habitats, by determining the location and ranking of the most profitable feeding positions. Higher water velocities preferred by larger young may provide them with better feeding stations (Deleray 1991).

Grayling appear to be sight feeders and to feed mostly during the day (Bishop 1967; Vascotto 1970). Their ability to locate prey increases with fish size and light intensity (Schmidt and O'Brien 1982). Their reactive distance is greater than other fish species and increases dramatically at light intensities higher than 100 lux. Wind or rain storms that roil the surface waters or increase turbidity can disturb surface feeding by grayling (Reed 1964; Bishop 1967).

Planktivorous Arctic grayling appear to employ a stop and go search strategy (saltatory strategy) rather than ambushing their prey or cruising continuously in search of prey (Evans and O'Brien 1988; O'Brien and Evans 1992). Fish larger than 130 mm show little interest in **zooplankton**, presumably because prey less than 1.5 mm in body length often slip between their gillrakers and are difficult for them to retain (Schmidt and O'Brien 1982).

Arctic grayling in the Kuparuk River, Alaska, show strong interannual fidelity to summer feeding sites -- both river zones and specific locations (Buzby and Deegan 2000). This may reflect the limited time these fish have to explore for alternative resources during the short Arctic summer, and their need to acquire sufficient energy to sustain them through the longer (9 month) Arctic winter.

In an Alaskan stream, grayling growth, energy storage, and reproductive response of females declined with increasing fish density (Deegan *et al*. 1997). Fish growth and energy storage were strongly correlated with per capita insect availability, suggesting that production is limited by food competition. A 10-fold increase in the density of fishes in a particular area reduced the growth rate of adults to half (Deegan *et al*. 1997), and of age 0 fish to one-third (Golden and Deegan 1998).

2.2.1 Young-of-the-year

Grayling fry in Providence Creek 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 Cladocera. Older grayling have a more varied diet.

Dietary differences among streams and lakes are probably related to the relative and seasonal abundance of the prey (Jessop *et al*. 1974), although some prey selection does occur (Jones *et al*. 2003a). The stomachs of fry taken from Mackenzie River tributaries contained, in order of frequency of occurrence, dipterans, hemipterans, formicids, trichopterans, and ephemeropterans (Jessop *et al*. 1974). Trichopterans and dipterans were important in the diet of grayling from Oscar Creek, while hymenopterans and corixids were important to Trail River grayling. Coleopterans and ephemeropterans were important foods of grayling in both systems. Two fry taken from Providence Creek about 8 weeks after hatching had fed on immature Baetidae, Hydropsychidae, and Simuliidae (Bishop 1967). In August, stream-dwelling age 0 grayling in the Minto Creek drainage, Yukon, fed primarily on Diptera larvae and, to a lesser extent, on Ephemeroptera nymphs (Birtwell *et al*. 1984). Grayling fry in Great Slave Lake, Northwest Territories, ate mainly Cladocera and small Ephemeroptera nymphs (Bishop 1967).

Young-of-the-year grayling in tundra lake-outlet streams on the Northwest Territories 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).

The ability of young grayling to feed successfully depends in part on the turbidity of the water. The reactive distance of grayling fingerlings (~45 mm FL) to prey diminishes proportional to the natural logarithm of turbidity, and they avoid water with a turbidity of over 20 NTU (Scannell 1988). The feeding success of age 0 grayling in high turbidity waters below an Alaskan placer mine was low and confined to chironomid pupae (Reynolds *et al*. 1989).

2.2.2 Larger Juveniles and Adults

Adult and larger juvenile grayling feed voraciously during the summer on a wide variety of terrestrial insects, benthic organisms, fish, plankton, and plant material (Appendix 1, Appendix 2). They eat a wide variety of aquatic and terrestrial insect taxa (Rawson 1950; Bishop 1967). Larger grayling in the tributaries of Great Slave Lake and the lake itself, for example, ate insects from 46 families, and 15 species of non-insect foods (Bishop 1967). Terrestrial insects are an important contributor to the species' diet, and grayling will position themselves beneath overhanging vegetation to capture insects that fall into the water (Rawson 1951; Bishop 1967; Hatfield *et al*. 1972a,b). They are opportunists that will also consume feathers, pine needles, ham sandwiches, corn and onions from tugboat refuse, and small mammals (Miller 1947; Rawson 1950; Bishop 1967; de Bruyn and McCart 1974). While many fish contain vegetable matter it is not known whether they graze upon it or consume it incidentally with their prey (Bishop 1967).

Adult Arctic grayling feed effectively on drift (i.e., *Daphnia middendorffiana*) in a variety of stream habitats with different current velocities (O'Brien *et al*. 2001). In laboratory experiments, their feeding rate increased with prey density but did not change over the range of current velocities tested, 0.25 to 0.4 m/s. The latter may reflect a trade-off between increasing likelihood of encounter and decreasing location efficiency. The addition of debris decreased location efficiency (O'Brien and Showalter 1993).

Small grayling (n = 75; 32-142 mm FL) captured in the Mackenzie River and its tributaries during the summer contained mostly aquatic and terrestrial insects, particularly chironomids, plecopterans, and coleopterans; larger juvenile and adult grayling (n=144; 119-402 mm FL) captured there contained a wider variety of aquatic and terrestrial insects, mostly trichopterans, corixids, hymenopterans, coleopterans, and dipterans of aquatic origin (Hatfield *et al*. 1972a,b; Stein *et al*. 1973b). Fish in the Mackenzie River area of Great Slave Lake also fed mainly on aquatic insects, with Trichoptera being the single most important food item, while those in the Stark River area of the lake, to the south east, had a more varied diet, with aquatic and terrestrial insects and fish being the most important items (Bishop 1967). In Great Slave Lake, young grayling in the 2 to 5 year age classes eat the same foods as older, larger grayling.

During the summer, grayling in two small lakes on the Yukon North Slope relied heavily on surface insects for food and also fed extensively on trichopteran larvae, amphipods, and ninespine stickleback (*Pungitius pungitius*) (de Bruyn and McCart

1974). Grayling in small Alaskan lakes also eat small benthic snails (Cl. Gastropoda: *Lymnaea* sp., *Valvata* sp.) (Merrick *et al*. 1992).

Grayling vary in their piscivory. At the spawning streams they will eat drifting fish eggs, including those of salmon, inconnu (Alt 1969 cited in Armstrong 1986), northern pike, and grayling (Miller 1946; Rawson 1950; Bishop 1967). They also prey actively on fry of their own (Miller 1946; Deleray 1991) and other species, including sockeye salmon (*Oncorhynchus nerka*) in the Gulkana River of Alaska (Williams 1969 cited in Armstrong 1986). Ninespine stickleback are an important prey species (Bishop 1967; McPhail and Lindsey 1970; Stein *et al*. 1973b; de Bruyn and McCart 1974; Jessop *et al*. 1974), and they also eat slimy sculpin (*Cottus cognatus*) (Bishop 1967; Birtwell *et al*. 1984) and cisco (*Coregonus* sp.) (Miller 1946; Bishop 1967).

Small mammals such as lemmings (Miller 1946, 1947; Reed 1964) and shrews (*Sorex* spp.) are also eaten opportunistically by Arctic grayling (de Bruyn and McCart 1974; Moore and Kenagy 2004).

In Russian reservoirs created by river impoundment, grayling switched their diets from predominately Trichoptera and Chironomidae to Amphipoda and Chironomidae, and their abundance declined (Kupchinskaya *et al*. 1983).

2.2.3 Seasonal

Adult grayling in Providence Creek fed only incidentally before and during spawning, but actively afterwards (Bishop 1967, 1971). Before and during spawning they ate food items that drifted past but did not actively search for food, and were not vulnerable to angling. Afterwards they fed actively in riffles on mayfly larvae and fish eggs (either grayling or northern pike). The presence of large numbers of grayling in small streams at spawning 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).

During the summer grayling in streams depend mostly on drifting organisms and flying insects for food, and feed mostly at the surface and at midwater depths (Vascotto 1970; Vascotto and Morrow 1973). They become more dependant on benthic drift and less selective as fall approaches and food availability decreases (Morrow 1980 cited in Armstrong 1986). Later in the season, when benthic drift is reduced, they may feed on the bottom. Terrestrial insects are most important during the early spring and other periods of high water, and in late fall when fewer aquatic insects may be available (Schallock 1966). Little is known of the species' late fall and winter diet, although a fish taken from Great Slave Lake in March contained mostly fish remains (Bishop 1967).

2.3 Competitors

The introduction of rainbow (*Oncorhynchus mykiss*), brook (*Salvelinus fontinalis*), or brown trout (*Salmo trutta*) has caused grayling numbers to decline in some systems (Vincent 1962). However, grayling fry can compete successfully with rainbow trout fingerlings when both are stocked into a previously barren lake (Van Hulle and Murray 1975 cited in Armstrong 1986), and may compete successfully with lake chub (*Couesius plumbeus*) (Roguski and Tack 1970 cited in Armstrong 1986).

Strong dietary similarities between slimy sculpin and Arctic grayling suggest that they may compete for food resources (Schallock 1966), although the sculpins are more apt to feed at the bottom and grayling at the surface. There is also dietary overlap between grayling and round whitefish (*Prosopium cylindraceum*) and white sucker (*Catostomus catostomus*), although the latter species feed mostly on benthic biota. Arctic grayling coexist with bull trout in the Northwest Territories but appear to exploit different food niches.

3.0 SUMMARY

Arctic grayling are opportunistic predators. 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. 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. 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. 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, may be the key predators on smaller juveniles. 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. Because grayling are visual predators, their feeding success is vulnerable to increases in water turbidity.

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6.0 GLOSSARY

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

Drift is comprised of plant and animal material that is carried by the current.

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

Lacustrine fish populations live and reproduce in lakes.

Macroinvertebrates are animals that lack a backbone (i.e., invertebrates) and are big enough to be seen by the naked eye (e.g., insects larvae and crayfish).

Piscivorous species eat fish.

Planktivorous species eat small to microscopic plants (**phytoplankton**) and animals (**zooplankton**) that float or swim weakly in the water column.

7.0 APPENDICES

Stomach contents of Arctic grayling reported by volume or numbers are summarized in Appendix 1, and by frequency of occurrence in Appendix 2.

Key to Appendices 1 and 2:

Where organisms of various life stages or terrestrial origin were consumed they are denoted as follows: **A** = Adult, **L** = Larvae, **P** = Pupae, **N** = Nymph, **T** = Terrestrial origin. All other organisms were aquatic adult forms.

OS = Indicates additional taxa reported by McKinnon and Hnyka (1979) from smaller sample sizes of grayling taken from other streams flowing into the Liard River.

+ = present in small amounts.

* = The combined total for Copepoda and Cladocera in the original has been allocated equally to the groups here.

** = fish stomachs likely empty due to holding for 3-4 days prior to sampling.

*** = fish are considered to be age 0 until December 31 of the year they are born.

References:

1 = Bishop 1967; **2** = Bishop 1971; **3** = de Bruyn and McCart 1974; **4** = Tripp and McCart 1974; **5** = Miller 1946; **6** = Jessop *et al*. 1993; **7** = Chang-Kue and Cameron 1980; **8** = McKinnon and Hnytka 1979.

Notes:

a = % frequency of occurrence based on all fish caught except for the Firth River, where percentages were based only on fish with food in their stomachs, **b** = % by volume (Note: Due to trace amounts and rounding errors totals in Bishop (1967) do not always total 100%. **c** = % by number.

Appendix 1. Stomach contents of Arctic grayling expressed as percent by volume or percent by number from rivers and lakes in the Northwest Territories (NT). See above for explanatory key.

	"Providence Creek", NT	Kakisa River, NT	Liard River tributary, NT (mile 63)	Liard River tributary, NT (mile 115.7)	Mackenzie River, NT		Great Slave Lake, NT
Season	May 4-28	22 May-9 June	Summer 1977		19 Jun-31 Jul, 1965	6-29 Jul, 1966	4 Aug-9 Sep
Coordinates	61°15'N, 117°34'W	61°04'N, 117°09W	61°06'50"N, 122°50'W	60°29'N, 123°27'W	(116°W to 118°W)--Beaver Lake/Brabant Island area		61°04'N, 116°38'W
Elevation (m asl)							156
Life history type	Fluvial	Fluvial	Fluvial	Fluvial	Fluvial	Fluvial	Adfluvial
Life stage (J = juvenile; A = Adult)	A	A?	J	J, A	A?	A?	A?
Age range***			0	>0			
Length range (mm)			22-64	146-298			
# of stomachs examined (# empty)	39	16	21(0)	16(0)	66	47	18
Plant Material	10.4				3.1	3.2	
Invertebrates							
Ph. Nemata (round worms)			0.3	0.8			
Ph. Nematomorpha				0.4			
F. Gordiidae (horsehair worms)					0.3	0.3	
Ph Annelida							
SubCl. Hirudinea (leeches)				OS		+	
SubCl. Oligochaeta				OS	+		
Ph. Arthropoda							
Cl. Arachnida (arachnids, water mites)			OS	1.8	+	+	
Cl. Entognatha							
O. Collembola			OS				
Cl. Insecta (insects)		0.4 (T)					0.4 (T)
O. Coleoptera (beetles)	0.3 (L) 1.2 (A)	0.4 (T)	OS	22.0	0.5 (T)	0.1 (T)	8.3 (T)
F. Dytiscidae (predaceous diving beetles)		1.5 (L)			0.3 (L) 0.1 (A)	+ (L)	1.8 (A)
O. Diptera (gnats, mosquitoes, flies)	0.1 (T)	1.2 (T)	10.3 (P) 51.3 (A)	0.4 (L) 20.9 (A)	+ (T)	+ (T)	0.8 (T)
F. Ceratopogonidae (biting midges)			4.4 (L)	0.8 (L)			

F. Chironomidae (midges)		0.1 (L,P)	19.7 (L)	2.0 (L)	8.5 (L,P) + (A)	0.5 (L,P) + (A)	0.5 (L,P)
F. Simuliidae (blackflies)			6.3 (L)	1.3 (L)			
F. Tipulidae (crane flies)							
O. Ephemeroptera (mayflies)	50.2 (N)	7.4 (N)	6.3	1.2	1.0 (N)	5.6 (N)	
O. Hemiptera (true bugs)		+	0.6	8.7	+ (T)		0.3
F. Corixidae (water boatmen)	0.9	+			+	+	
O. Hymenoptera (bees and ants)	0.1 (T)	1.2 (T)	OS (T)	17.9 (T)	0.4 (T)	0.2 (T)	7.1 (T)
O. Lepidoptera (butterflies and moths)				0.2			
O. Odonata (dragonflies)	2.6 (naiads)	18.7 (naiads)		1.7	0.1 (A)		0.9 (A)
O. Orthoptera (grasshoppers)				OS			
O. Plecoptera (stoneflies)	2.1 (N)	35.0 (N) 0.1 (A)	OS (A)		7.9 (N) 1.7 (A)	0.6 (N) 0.2 (A)	
O. Trichoptera (caddisflies)	2.0 (L,P)	10.6 (L,P)	OS (A)	17.7 (L)0.8 1.3 (A)	12.3 (L,P) 42.5 (A)	3.1 (L,P) 30.0 (A)	
SubPh. Crustacea							
Cl. Branchipoda							
O. Anostraca (fairy shrimp)							
O. Conchostraca (clam shrimp)							
Cl. Malacostraca							
O. Amphipoda (e.g., *Gammarus lacutris, Hyalella azteca, Pontoporeia affinis)*)	1.6	+					42.6
SubO. Cladocera (water fleas)							
O. Mysida							
F. Mysidae (opossum shrimp)							
Cl. Maxillopoda							
SubCl. Copepoda			0.6				
Cl. Ostracoda (seed shrimp)			0.3				
Ph. Mollusca							
Cl. Bivalvia (clams)							
Cl. Gastropoda (snails)				OS			

Appendix 1. Continued.

	"Providence Creek", NT	Kakisa River, NT	Liard River tributary, NT (mile 63)	Liard River tributary, NT (mile 115.7)	Mackenzie River, NT		Great Slave Lake, NT
Fishes		3.3	OS		0.7	0.7	
F. Salmonidae (salmonids)							
Coregonus sp.							
Thymallus arcticus (Arctic grayling)							
F. Cottidae (sculpins)							
Cottus cognatus (slimy sculpin)						3.6	
F. Gasterosteidae (sticklebacks)							
Pungitius pungitius (ninespine stickleback)							
Fish eggs	10.7	1.8			0.3	0.3	
Mammals							
F. Soricidae (shrews)							
Debris (includes unidentified insect parts, baby lemmings, refuse, caribou hair, feathers, sticks, plastic ribbon, rocks)	17.6	18.1			18.7	47.4	37.0
Miscellaneous (e.g., parasitic nematodes)							
Reference:	1	1	8	8	1	1	1
Notes:	b	b	c	c	b	b	b

Appendix 2. Stomach contents of Arctic grayling expressed as percent frequency of occurrence, from rivers and lakes in the Yukon (YT) and Northwest Territories (NT). See above for explanatory key.

	Firth River, YT	Donnelly River, NT	Great Bear River, NT	Providence Creek, NT	Trout Lake, YT	"Lake 100", YT	Great Slave Lake, NT	Indin Lake, NT
Season	13 Jun- 12 Sep	May-Jun	29 Jun-20 Sep.	Jun 19	9 Jul- 12 Sep	2 Jul- 25 Aug	Jul-Aug	Jun-Sep
Coordinates	69°33'N, 139°32'W	65°50'N, 128°46'W	64°54'N, 125°35'W	61°15'N, 117°34'W	68°51'N 138°43'W	69°20'N, 139°00'W	61°04'N, 116°38'W	64°15'N, 115°05'W
Elevation (m asl)			156				156	273
Life history type	Fluvial?	Fluvial?	Fluvial-Adfluvial	Fluvial	Adfluvial	Adfluvial	Adfluvial	Adfluvial--Lacutsrine
Life stage (J = juvenile; A = Adult)	A, J?	A?	J,A	YOY	A	J?	A?	J, A
Age range***			2 - 11	0 (4-5 weeks)				2 - 7
Length range (mm)			160-460	Mean 25.1				165-422
# of stomachs examined (# empty)	136	119 (34)	138 (4)	48 (22)	115 (5**)	78 (5**)	103 (1)	101 (0)
Plant Material						6.4		
Invertebrates			52.2					
Ph. Nemata (round worms)			2.9					
Ph. Nematomorpha								
F. Gordiidae (horsehair worms)							6.9	
Ph Annelida								
SubCl. Hirudinea (leeches)		4.2						
SubCl. Oligochaeta								
Ph. Arthropoda								
Cl. Arachnida (arachnids, water mites)	0.7		2.9			2.7		12.9 (H) 8.9 (A)
Cl. Entognatha								
O. Collembola								1.0
Cl. Insecta (insects)	36.0 (T)	5.9 (T)	58.0 (T)		22.6 (T)	35.9 (T)		
O. Coleoptera (beetles)	8.8 (A) 14.7 (T)	3.4 (L) 5.0 (A)	2.2 (A)		12.2 (A) 0.9 (T)	9.0 (A) 3.9 (T)	14.6	10.9 (L) 58.4 (A) 3.0 (T)
F. Dytiscidae (predaceous diving beetles)								

Appendix 2. Continued.

	Firth River, YT	Donnelly River, NT	Great Bear River, NT	Providence Creek, NT	Trout Lake, YT	“Lake 100”, YT	Great Slave Lake, NT	Indin Lake, NT
O. Diptera (gnats, mosquitoes, flies)	5.9 (L) 12.5 (A)	0.8 (L) 4.2 (A)	18.1 (L) 60.9 (A)	21 (L,P)				61.4 (L) 76.2 (P)
F. Ceratopogonidae (biting midges)								
F. Chironomidae (midges)	29.4 (L) 1.5 (P) 3.5 (A)	11.8 (L)	29.0 (L)		1.7 (L) 0.9 (P)	1.3 (L)	2.9	
F. Simuliidae (blackflies)	2.9 (L)							
F. Tipulidae (crane flies)	19.8 (L)				0.9 (L)	5.1 (L)		
O. Ephemeroptera (mayflies)	8.8 (N)	0.8 (L)	13.0 (L)	23 (N)	0.9 (N)		5.9 (N)	2.0 (N)
O. Hemiptera (true bugs)								27.7 (A)
F. Corixidae (water boatmen)	5.2	21.0 (A)	24.6 (A)		9.6			
O. Hymenoptera (bees and ants)	9.6 (A)						32.3	42.6
O. Lepidoptera (butterflies and moths)								
O. Odonata (dragonflies)		2.5 (N)	0.7 (N)					
O. Orthoptera (grasshoppers)	2.2						16.6	
O. Plecoptera (stoneflies)	19.1 (N) 5.2 (A)	1.7 (L)	36.2 (L)					8.9 (L)
O. Trichoptera (caddisflies)	7.4 (L) 8.1 (A)	15.1(L)	0.7 (L)	6 (L,P)	51.0 (L)	20.5 (L)	3.9 (L)	8.9 (L) 5.0 (P) 1.0 (A)
SubPh. Crustacea								
Cl. Branchipoda								1.0
O. Anostraca (fairy shrimp)			1.4					
O. Conchostraca (clam shrimp)			1.4					
Cl. Malacostraca								
O. Amphipoda (e.g., *Gammarus lacutris, Hyalella azteca, Pontoporeia affinis)*)		33.6	3.6		6.1	25.6	7.8	9.9
SubO. Cladocera (water fleas)				6			~10.3*	6.9
O. Mysida								
F. Mysidae (opossum shrimp)							5.9	
Cl. Maxillopoda								
SubCl. Copepoda							~10.3*	11.9

Cl. Ostracoda (seed shrimp)								
Ph. Mollusca								
Cl. Bivalvia (clams)		0.8						
Cl. Gastropoda (snails)	0.7				1.7	1.3	0.9	1.0
Fishes			1.4				8.8	2.0
F. Salmonidae (salmonids)								
Coregonus sp.							0.9	
Thymallus arcticus (Arctic grayling)							0.9	
F. Cottidae (sculpins)								
Cottus cognatus (slimy sculpin)			0.7					
F. Gasterosteidae (sticklebacks)								
Pungitius pungitius (ninespine stickleback)	1.5				20.9	12.8		
Fish eggs	1.5						0.9	
Mammals								
F. Soricidae (shrews)	5.2							
Debris (includes unidentified insect parts, baby lemmings, refuse, caribou hair, feathers, sticks, plastic ribbon, rocks)	8.6	26.1	31.9		2.4	0.9	1.8	
Miscellaneous (e.g., parasitic nematodes)	3.7	2.4		10		1.3		
Reference:	3	4	7	1, 2	3	3	5	6
Notes:	a	a	a	a	a	a	a	a