Habitat use by fluvial Arctic Grayling (*Thymallus arcticus*) in mountain streams of the Little Nahanni watershed, Northwest Territories.

by

Morag Danine McPherson

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Conservation Biology

Department of Renewable Resources

University of Alberta

Abstract

Northern aquatic ecosystems face increasing pressures from climate change and natural resource development, raising conservation concerns for species in these vast and remote regions. Arctic Grayling (*Thymallus arcticus*) have a Holarctic distribution and are a sensitive freshwater fish that provide a good indication of general aquatic health. In the Northwest Territories (NWT), there has been little focus on studying riverine Arctic Grayling populations or their use of stream habitats within mountain river watersheds. The purpose of my research was to characterize fluvial Arctic Grayling distribution among mountain streams in the NWT, and to determine habitat characteristics that influence Arctic Grayling habitat use across life stages. Sampling sites (n=183) were selected in four sub-basins within the Little Nahanni River watershed in the southwest NWT. In the summer of 2015, each site (100 meters in length) was electrofished and stream habitat parameters were measured. Arctic Grayling were collected for analyses of age, size, weight, and reproductive development. Results showed shifts in Arctic Grayling development by size and age class that corresponded with shifts in distribution observed across the study streams. From these findings, four post-emergence life stages for Arctic Grayling were assigned: young-of-year (YOY), juvenile, sub-adult and adult. Step-wise logistic regression was used to explore the relationship between the occurrence of Arctic Grayling life stages and stream habitat characteristics. Multivariate regression tree (MRT) analysis was used to identify environmental thresholds and habitat-based life stage segregation, and redundancy analysis (RDA) was used to determine potential life stage-specific habitat correlations. Differences emerged in how Arctic Grayling life stages used habitat across a range of available stream conditions. YOY Arctic Grayling were found exclusively in low elevation, low gradient habitat dominated by silty-sand substrate with average water temperatures >10ºC. Similarly, juvenile Arctic Grayling occupied low elevation, warm water stream habitat, but associated strongly with run habitats, as well as showing movement into cooler water temperatures and more riffle dominated habitats. Sub-adult Arctic Grayling used the widest range of habitats across the study area, being found at a range of elevations and water temperatures, demonstrating the ability of this life stage to use a diversity of available habitats. Sub-adults showed a relationship to in-stream riffle, pool, and cascade-boulder habitats. Adults had a strong correlation to elevation and water temperature, using habitats with high elevation (>1200 m) and low temperature (7°C), and increased proportions of pool and boulder habitat. The four sub-watersheds studied provided distinct stream habitats and Arctic Grayling life stages separated across the habitat types, advancing our understanding of the life cycle habitat requirements for fluvial populations in mountain systems. It provides insight on the important and potential limiting factors, such as availability of warm water habitats, to population success in cold regions. The dynamic nature of Arctic Grayling summer habitat use in mountain streams highlights the need to consider habitat complexes at the watershed scale when defining species life stage requirements, managing habitats, monitoring populations, and assessing potential impacts into the future. Improved understanding of the distribution, habitat requirements and ecology of different life history types and life stages of Arctic Grayling in different ecozones is crucial for the effective management and monitoring of this species in northern environments.

Preface

This thesis is an original work by Morag D. McPherson. Some of the research conducted for this thesis forms part of a collaboration between Fisheries and Oceans Canada and Parks Canada Agency, led by Neil Mochnacz with the Arctic Aquatic Research Division of Fisheries and Oceans Canada. Fish dissection and measurement data compilation in the methods was assisted by Tannis Serben, Lab Coordinator for the Poesch Lab at the University of Alberta.

Research for this thesis received ethics approval by Fisheries and Oceans Canada's Freshwater Institute Animal Care Committee under the animal use protocol number: FWI-ACC-2015-016. Field collections were carried out under the approved Licence to Fish for Scientific Purposes number S-15/16-3013-YK issued pursuant to Section 52 of the Fishery (General) Regulations in the Northwest Territories, and Parks Canada Agency Research and Collection Permit number NAH-2014-16517 issued pursuant to Sections 7(5) and 11(1) of the National Parks General Regulations and Section 15(1)(a) of the National Parks Wildlife Regulations.

For my dad.

Acknowledgements

I feel very fortunate for the opportunities I've had to see and experience the beauty of the Northwest Territories working as a biologist with Fisheries and Oceans Canada (DFO) in Yellowknife. Through this work I learned about Arctic Grayling and through that learning that I made connections with DFO Science. I would like to thank Neil Mochnacz with DFO's Arctic Aquatic Research Division for seeing the potential in me and the chance to study Arctic Grayling while contributing to federal research. Investigating an iconic northern fish in the mountain ranges of two of Canada's remote northern National Park Reserves was a research project that I couldn't not do, and I'm grateful for the opportunity.

I wouldn't have been able to do this research if it were not for Dr. Pete Cott connecting me with Dr. Mark Poesch at the University of Alberta. Dr. Cott went above and beyond in his support as a co-supervisor and as a friend. The most difficult part of this MSc. was managing all that life threw at me along the way. His experience, advice, understanding, and friendship allowed me to keep my head up, so to speak, on this project and slog my way through both life and the post-graduate process. I wouldn't have completed this MSc. without his time and support. Thank you to Dr. Mark Poesch for taking me on, providing space in the lab, supporting data collection and analyses, and understanding when periods of leave were required. My time on campus in the Poesch lab was enjoyable, with a great group of people. Thank you all.

The cost, effort, and logistics required to undertake the field research were extensive. Funding, equipment and in-kind support for the field program were provided by DFO and Parks Canada. Natural Resources Canada Polar Continental Shelf funding covered the cost of helicopter time and fuel, without which it would have been cost-prohibitive to conduct field sampling at this scale in a remote northern region. Additional funding was also provided through the Government of the Northwest Territories Cumulative Impact Monitoring Program (CIMP), the W. Garfield Weston Fund, the University of Waterloo, and the University of Alberta.

People make things happen. I'd like to thank Stuart Dean and the late Julie Dahl with DFO for supporting me in this MSc. endeavor while I was still employed, allowing time to undertake the research and supporting staff to participate in the field research experience. The Little Nahanni watershed is one of the most beautiful and harsh places I've ever been to. Thank you to the field personnel for accepting the challenge of long soggy days hiking packs of equipment and supplies along and through mountain streams. The daily helicopter commutes and the scenery made up for the struggles. The crew included: Brianna Robinson, Melissa Carol, Ryan Boxem, Bonnie Deschene, Julian Sabourin, Dr. Julie Marentette, Mark D'Augair, Nathaniel, Dr. Mark Poesch, Dr. Pete Cott, Marie Veillard, Nathan Medinski, and last but definitely not least, Brent Lewis.

A special thank you to Brent Lewis with Parks Canada, who collaborated with me on this research. We spent many hours and long days together to get this research done, learning much from each other along the way. His positive energetic approach made it feel like no challenge was too big to tackle. Cass Docherty, Marie Veillard, and Nathan Medinski from the Poesch Lab were my cheerleaders and my friends, offering guidance, enthusiasm, and confidence when it was most needed. I have so many great people in my life that supported me through this process, you know who you are, thank you all.

Thank you to my family, my mom and sisters, for your love and support. It was not an easy time in my life. And last I'd like to thank my love, my wife Heather Keiller, for coming into my life, for loving me, and for providing date night incentives to get me to work on the final aspects of this project. Your patience and belief in me made the difference.

Table of Contents

List of Tables

List of Figures

1.0 Introduction

1.1 Species conservation and habitat relationships

To understand the relationship between a species and its environment, there is a need to identify the suite of conditions that define the species' habitat requirements for all life stages (Rosenfeld 2003), including how habitat use may shift over time, depending on life stage or the life history type. For species that are broadly distributed across variable landscapes, our incomplete understanding of habitat requirements and environmental factors remains a fundamental challenge for management and conservation (Fausch et al. 2002, Rosenfeld 2003). Identifying species habitat requirements at various spatial scales requires research that spans multiple levels of ecological organization, across different life history types and landscapes (Frissell et al. 1986; Rosenfeld 2003; Rosenfeld and Hatfield 2006). The concept of scale is recognized as a fundamental challenge in ecology, where locally measured environmental variables and patterns cannot be automatically scaled up to understand processes over larger areas and longer timeframes (Schneider 2001; Peckarsky et al. 1997). Conservation biology emphasizes the importance of understanding habitat heterogeneity to address ecological problems at larger spatial and temporal scales. In addition to the general challenges of scale, the nature of rivers and streams across diverse landscapes makes them challenging to study. Conducting research in streams and rivers often involves navigating broad and difficult landscapes, working in fast flowing waters, and attempting to measure and interpret the high variability created by the continuous and active movement of materials, organisms and energy (Fausch et al. 2002). How the varying aquatic habitats are used by stream fishes shifts with seasons and resource availability, making research and monitoring programs susceptible to misrepresent how habitats are used, or the timing and extent of a fishes' movements. Study at a landscape-scale to capture the heterogeneity of river environments is needed to understand the ecological processes at play for species, and to set the context for conservation of aquatic biota (Fausch et al. 2002; Polis et al. 1997). However, there are limitations in the ability of landscape scale research to identify underlying mechanisms that may drive species-specific habitat associations at watershed and stream-level scales, making research at finer scales an important and complimentary aspect of landscape-scale research (Falke et al. 2013; Rosenfeld and Hatfield 2006).

1.2 The nature of stream systems

Climate, geology and topography frame the geomorphic processes that create and maintain watersheds (Frissell et al. 1986). Within a watershed, stream habitats are hierarchical, that is they are spatially nested and organized in structural levels, and therefore aquatic species habitat associations can be evaluated and modeled across different scales (Frissel et al. 1986; Hawkins et al. 1993). The continuous, hierarchical and heterogeneous nature of linear aquatic habitats has to be considered and incorporated into both research and conservation (Schlosser 1991; Rosenfeld and Hatfield 2006; Fausch et al. 2002). Stream ecology recognizes the importance of spatial arrangement of habitats related to each life stage, and the pivotal role of fish movement in dispersing these life stages across watershed-scales to occupy critical habitats required to fulfill their life cycle (Schlosser 1991, 1995a, 1995b, Schlosser and Angermeier 1995; Peckarsky et al. 1997; Rosenfeld and Hatfield 2006).

The relationship of a stream system to the broader watershed makes it sensitive to changes in surrounding climate and landscape. The stream becomes a receptor for the watershed that concentrates and transmits environmental changes to rivers as they move through the landscape. Consequently, species relying on stream habitats have also evolved to be sensitive to changing environmental conditions and demonstrate a range of adapted responses for survival at each life stage (Bunn and Arthington 2002; Schlosser 1990; Schlosser 1985). This means that specific or rare habitats or narrow ranges of environmental conditions may regulate species population-level responses across landscapes (Torgersen et al. 1999; Pecakrsky et al. 1997).

1.3 Resource development impacts

In Canada's north, aquatic environments are becoming increasingly vulnerable to multiple cumulative natural and anthropogenic impacts including resource development and climate change

(Christiansen et al. 2013; Poesch et al. 2016). The Northwest Territories (NWT) continues to experience new development with road building, mining, seismic exploration, and oil and gas activity over the past 10 years, and the economy continues to depend on the non-renewable resource industry (GNWT 2019). The construction and extractive-based activities associated with these industries are known to impact aquatic ecosystems (Cott et al. 2015; Christiansen et al. 2013). Changes to water chemistry and temperature, sedimentation, underwater noise and pressure impacts, water withdrawals, barriers to stream flow and fish passage, exploitation and harvest of pristine fish populations, habitat fragmentation, habitat alteration and destruction, as well as introduction of non-native or invasive species and pathogens are all examples of known development impacts to freshwater systems (Cott et al 2015; Schindler 2001). Critical stream habitats, specific to a species life stage or time of year (e.g. spawning and overwintering), can be limited and isolated from other necessary habitats, making them particularly sensitive to perturbation (Schlosser 1990 and 1995a; Cunjak 1996; Rosenfeld and Hatfield 2006). Northern fish species that exhibit habitat specialization and migrate among a wide range of habitats are vulnerable to localized habitat disturbances which can have disproportionately greater effects at a wider scale for the population (Rosenfeld and Hatfield 2006; Christiansen et al. 2013). The dendritic nature of stream and river systems provides a network that collects and transports effects downstream, therefore stressors that may seem remote spatially on a watershed scale, can act cumulatively to affect stream fish populations.

1.4 Climate change impacts

In addition to direct effects on fish, such as siltation from improper road development, are the indirect impacts of climate change. Such impacts are complex and difficult to predict and measure in freshwater ecosystems. Temperatures across the Canadian Arctic are warming at three times the global rate, because of a combination of climate feedbacks over high-northern latitudes known as “Arctic amplification” (Bush and Lemmen 2019), and are projected to continue at an increased rate under future climate scenarios. Annual mean precipitation and daily extreme precipitation are also projected to increase in the north, impacting stream flows (Cohen et al. 2019). Northern freshwater systems are low productivity with limited light (e.g. ice free), temperature, nutrient, and food resources (Reist et al. 2006a; Christiansen 2013). Northern stream fish are adapted to these conditions, so changes in temperature and precipitation will cause shifts in the timing and range of habitat conditions available to freshwater fish species (Reist et al. 2006b; Rouse et al. 1997; Mantua et al. 2010; Christiansen et al. 2013).

Water temperature is a defining habitat characteristic for aquatic organisms and can affect the physiology and behavior of individuals (Reist et al 2006b). Stream fish use both thermal and hydrologic regimes as behavioral cues to trigger critical life history functions (Schlosser 1985; Taylor and Cooke 2012; Cassie 2006). In watersheds dominated by snowmelt, climate change is expected to alter the magnitude and timing of low- and peak-flow events, generating hydrographs comparable to regulated rivers (Adam et al. 2009; Stewart 2009; Mantua et al. 2010). Stream fishes have evolved life history strategies and habitat relationships linked to seasonal cycles of the natural flow regime (Bunn and Arthington 2002). Projected changes in temperature, precipitation, and hydrologic cycles may affect access to stream habitats, and the timing and success of key life functions such as migration and early life stage survival.

For northern freshwater systems, the potential impacts from climate change at the local habitat scale may cause a spectrum of effects on fish populations which span a wide range of habitats in the Arctic and have different life history strategies and sensitivities to biophysical factors (Reist et al. 2006b; Christiansen et al. 2013). Stream systems may be particularly susceptible because broad-scale changes in climate variables may become amplified within the stream channels (Reist et al 2006b). The Intergovernmental Panel on Climate Change (IPCC) concluded that fish populations in headwater streams and rivers, particularly on the margins of their geographic distributions, will be especially vulnerable to the effects of climate change because the temperature regimes in these systems are more closely correlated with air temperatures (Setelle et al. 2014 and Cassie 2006). The realized impacts of climate change will be species- and ecosystem-specific, making it challenging to predict consequences and assess both short and long-term trends for northern stream fish populations (Christiansen 2013; Poesch et al. 2016)

The ability of freshwater fish to adapt to changing environments is species-specific. Northern aquatic ecosystems are influenced by localized conditions, so there is a need to understand the ecological filters and watershed characteristics that may influence a species' distribution as aquatic environments change (Reist et al. 2006a). However, there are many data gaps related to associations between ecological processes and environmental factors for northern aquatic biota (Reist et al 2006b). Deficiencies in our basic knowledge of northern fish ecology and habitat interactions limits our ability to predict cumulative impacts to aquatic systems and prepare for challenges that climate change may present across the Arctic and Sub-Arctic landscape, from shifting climactic variables to increasing large-scale disturbances (Rouse et al. 1997; Reist et al 2006b; Poesch et al. 2016;).

An added challenge for assessing and managing northern freshwater ecosystems, alongside impacts from development and predicted effects of climate change, is the pre-disturbance conditions for these remote watersheds are often undocumented. Work to establish an environmental baseline and reference of fish populations in pristine northern aquatic systems can help to improve our understanding of ecological processes, to put impacted aquatic systems into context, and to inform habitat and species restoration efforts.

1.5 Northern salmonid fish species

Salmonidae is the most significant family of cold-water fish in the Arctic (Christiansen et al. 2013). Salmonids are widely distributed and abundant in the north, making this family of fish a key component of cold freshwater ecosystems, and featuring prominently in commercial, recreational and subsistence fisheries (Reist et al. 2006b; DFO 2012; Christiansen et al. 2013). Being stenothermic, salmonid species have temperature thresholds that are less variable making them particularly vulnerable to climate change (Linnansaari and Cunjak 2012).

One such species is the Arctic Grayling (*Thymallus arcticus* (Pallas 1776)). They are trout-like in appearance with an elongated oval-shaped body, but are distinguished from other salmonids by their large scales, large eyes, short heads with small mouths only containing teeth on the maxillary bone. However, their most striking feature, as shown in Figure 1, is their colourful, sail-like dorsal fin which is dark blue to black with a narrow orange or pinkish edge with a blue band beneath and has rows of orange-red and emerald green spots, the pelvic fins are black with wavy orange stripes and the caudal fin can be greyish to bronze in colour (McPhail and Lindsey 1970; Scott and Crossman 1973).

Figure 1. Arctic Grayling (*Thymallus arcticus*) 8-year old male in spawning colours taken from Baker Creek, Yellowknife, NWT. Illustration by Paul Vecsei 2008.

As adults their back is typically dark purple or blue, sides are grey to dark blue with pinkish iridescence and scattered black spots, and the belly is grey to white. Young Arctic grayling do not have a pronounced dorsal fin and are silvery grey in colour with par marks along the lateral line and more spots on their sides than adults. The average length of adult Arctic grayling ranges from 305-381mm with average weights at this size of 225 – 450 grams (Scott and Crossman 1973). The largest documented size was an Arctic grayling 757mm long and 2.7 kg (5 pounds, 15 ounces), captured in the Katseyedie River, which flows from the north into Great Bear Lake, NWT (Scott and Crossman 1973).

Arctic Grayling are an iconic northern species and have been described as, “a uniquely attractive fish, beautiful to look at, sporting to catch and quite palatable” (McPhail and Lindsey 1970). Scott and

Crossman (1973) note that, "the beautiful fish is a joy to behold and one of the few species over much of the northern part of Canada that will provide fly fishing". Their dramatic appearance, fighting qualities, and palatability has made Arctic grayling a highly sought after species by recreational anglers. Historically, Indigenous peoples in the Canadian north were able to exploit Arctic Grayling during their post-spawn migrations when other fish were scarce (Miller 1946; Scott and Crossman 1973), and were a reliable food source during mountain travel (Leon Andrews, Elder, Tulita, NWT, personal communication).

1.6 Arctic Grayling distribution

The range of graylings, genus *Thymallus,* extends across Eurasia and North America, giving it a Holarctic distribution. Based on the results of a recent review of the genus *Thymallus*, 18 species of grayling have been recognized using morphometric data and incorporating new data published on taxonomy, biology, ecology, and genetics (Dyldin et al. 2017). The systematic status of the species within the genus *Thymallus* has provided some controversy, as graylings show adaptivity in varying habitats and high polymorphism, reflecting their wide range of genotype responses (Dyldin et al. 2017). But, the ongoing identification of differences between individual species and native populations continues to be important for the understanding and conservation of genetic diversity within the grayling family.

The list of grayling species identified includes: European Grayling (*Thymallus thymallus*), Adriatic Grayling (*Thymallus aeliani*), Baikal Black Grayling (*Thymallus baicalensis*), Baikal White Grayling (*Thymallus brevipinnis*), Baikal-Lena Grayling (*Thymallus baicalolenensis*), Lake Markakol Grayling (*Thymallus brevicephalus*), Mongolian Grayling (*Thymallus brevirostris*), Bureya River Grayling (*Thymallus burejensis*), Yellow-Spotted Grayling (*Thymallus flavomaculatus*), Amur Grayling (*Thymallus grubii*), Lower Amur Grayling (*Thymallus* tugarinae), Kamchatka Grayling (*Thymallus mertensii*), Hovsgol Grayling (*Thymallus nigrescens*), Upper Ob Grayling (*Thymallus nikolskyi*), East-Siberian Grayling (*Thymallus pallasii*), Upper Yenisei Grayling (*Thymallus svetovidovi*), Alaska Grayling (*Thymallus signifier*), and Arctic Grayling (*Thymallus arcticus*).

Of all the grayling species, Arctic Grayling have the most extensive distribution, and occur throughout the northern parts of North America, Russia, Mongolia, China and North Korea, with the most southerly population being in Montana (Scott and Crossman 1973; Lee et al. 1980). Unfortunately, since 1992, the Montana population has required active stocking and habitat restoration to remain viable (USFWS 2015). In North America, Arctic Grayling occur in throughout Alaska, Yukon and the mainland areas of the NWT and Nunavut, and northern areas of Manitoba, Saskatchewan, Alberta and British Columbia (McPhail and Lindsey 1970: Scott and Crossman 1973; Sawatzky et al. 2007). Research on the genetic diversity of Arctic Grayling in North America has revealed that today's grayling descended from populations that persisted through the Pleistocene in three Arctic glacial refugia (Stamford and Taylor 2004). The results of samples analyzed from 32 different localities identified three separate assemblages of North American Arctic Grayling: a 'South Beringia' lineage, a 'North Beringia' lineage, and a distinct 'Nahanni' lineage confined to the Nahanni River area of the upper Mackenzie River drainage.

1.7 Life history types

Across diverse northern watersheds, Arctic Grayling populations have developed three main life history types; fluvial, adfluvial, and lacustrine. Each of these life history types has different patterns of habitat use (Scott and Crossman 1973; Northcote 1995; Stewart et al. 2007). <u>Fluvial</u> populations utilize streams and rivers year-round for all life stages, including overwintering, and migrate large distances to access other lotic habitats used for spawning, feeding or over-wintering (Scott and Crossman 1973; Armstrong 1986; West et al. 1992; Ford et al. 1995; Evans et al. 2002a; Stewart et al. 2007). <u>Lacustrine</u> populations utilize lake habitats year-round for all life stages, whereas <u>adfluvial</u> populations migrate from lakes into rivers and streams seasonally for spawning, feeding and rearing (Scott and Crossman 1973; Richardson et al. 2001; Stewart et al. 2007; Cahill et al. 2016).

1.8 Ecology

Regardless of life history type, Arctic Grayling require cold, clear, and well-oxygenated water. A characteristic that makes them sensitive to changes in water quality and a candidate indicator species

(Dyldin et al. 2017). Patterns of migration and habitat use differ among systems and across the life-stages of the fish (McPhail and Lindsey 1970; Scott and Crossman 1973; Stewart et al. 2007a; Northcote 1995). Like other salmonid species, they require different and distinct habitats for spawning, rearing, feeding and overwintering to complete their lifecycle (Stewart et al. 2007). Arctic Grayling are a typical rheophilous fish able to actively spread to adjacent stream and river habitats within a river system (Northcote 1995; Dyldin et al. 2017). Unique among northern salmonid species, Arctic Grayling spawn in the spring. Large migrations occur in the spring, associated with spawning and feeding, and then again in the fall with movement to suitable over-wintering habitats. These seasonal movement patterns occur in response to changes in environmental conditions such as discharge, water temperature or ice-cover, and responses vary depending on the eco-region, life stage or the life history type of the species (Armstrong 1986; Northcote 1995; Cahill et al. 2016; Heim et al. 2016). Arctic Grayling spawning can occur anytime from April to early July, but typically takes place from mid-May to mid-June (Scott and Crossman 1973; Stewart et al. 2007; Northcote 1995). They require clear, fast-flowing streams with un-embedded gravels for spawning, typically in riffle-run-pool habitats in tributaries or lake inlet and outlet streams. In general, spawning begins after ice break-up and when stream water temperatures reach a minimum of 4ºC (Reed 1964; Scott and Crossman 1973; Tack 1980; Northcote 1995; Stewart et al. 2007). The majority of spawning activity has been observed when water temperature daily means average 6-10ºC (McPhail and Lindsey 1970; Scott and Crossman 1973; Stewart et al. 2007; Northcote 1995) and the adult spawning period lasts for 2-3 weeks (Ford et al. 1995; Northcote 1995). Egg incubation within the interstitial spaces of stream gravels averages 13-18 days under natural stream conditions with daily water temperature averaging 8ºC (Stewart et al. 2007). The larvae hatch and remain protected in the gravels for a 3 to 4-day period before emerging approximately 3-4 weeks after fertilization (Scott and Crossman 1973; Northcote 1995). From this point on in the lifecycle, how each life stage of Arctic Grayling uses habitats varies and shows a range of differences depending on the ecoregion, life history type, and local conditions, with some life stages having been studied more than others.

1.9 Current understanding and focus

Habitat use by adults and young-of-year Arctic Grayling in spawning streams has been fairly well documented across life history types and in different ecoregions (Scott and Crossman 1973; Hubert et al. 1985; Armstrong et al. 1986; Ford et al 1995; Northcote 1995; Stewart et al. 2007a; Laroque et al. 2014). Through to the 1980s, the Government of Alaska focused on studying Arctic Grayling populations in the interior rivers but, despite that effort, significant gaps in life history information on the species remained (Armstrong 1986). Over the past two decades, there have been a number of studies in the NWT and Alaska focused on adfluvial Arctic Grayling populations in tundra streams and sub-Arctic lake systems, including studies on young-of-year habitat use and growth (Jones et al. 2003a, b, c; Jones and Tonn 2004; Deegan et al. 2005; Luecke and MacKinnon 2008; Heim et al. 2016; Baker et al. 2017) and movements of adults, juveniles and young-of-year into and out of streams connected to lake systems (West et al. 1992; Courtice et al. 2014; Cahill et al. 2016; Heim et al. 2016). Many of these studies are associated with assessing the impacts of mine developments or dam and reservoir creation on river systems like the Williston in BC, and others focus on evaluating the effectiveness of habitat restoration targeting Arctic Grayling (Blackman 2002; Clarke et al. 2007; Ballard and Shrimpton 2009; Stamford et al. 2017). The southernmost limit of the Arctic Grayling range in Canada is Alberta where populations have experienced declines due to multiple stressors including habitat loss, degradation and fragmentation, and overexploitation by anglers (Cahill 2015). Cold-water fish species at the southernmost extent of their range will be most vulnerable to changes in climate parameters, and climate modeling projections indicate that thermal stress will be a critical threat for suitable Arctic Grayling habitats across Alberta in the future (McCullough et al. 2009; Williams et al 2009).

1.10 Advancing our understanding across ecoregions

Our current ecological knowledge of Arctic Grayling shows that when and how habitats are used throughout the life-cycle of the species varies depending on life history type and ecoregion (Scott and Crossman 1973; Armstrong 1986; Northcote 1995; Stewart et al. 2007; Laroque et al. 2014; Baker et al.

2017; Lewis 2018). In northern mountain watersheds, Arctic Grayling are an important component of the food web and play an essential role in transferring energy resources throughout these high elevation, low productivity watersheds (Armstrong 1986). Stream fishes have evolved under the seasonally changing flow regimes of natural river systems (Bunn and Arthington 2002), and Arctic Grayling are no exception. They have adapted in mountain systems by moving within and among the networks of streams, utilizing different aquatic habitats and resources available to survive. In resource-constrained environments of northern mountains, a variety of available habitats are used across large areas to complete their life-cycle (Armstrong 1986). Given their wide range, improving our knowledge of Arctic Grayling distribution, life-cycle requirements, and essential habitats in mountain watersheds is important to be able to understand the variety of aquatic habitats and range of environmental conditions used by the species. Insights on natural baseline for a population of fluvial Arctic Grayling, in a relatively pristine northern mountain ecosystem, will help to evaluate effects of climate change and development, to assess trends over time, and to support conservation and restoration actions for the species.

1.11 Advancing our understanding for northern aquatic resource management

Improving baseline information and addressing gaps related to Arctic Grayling populations and their habitat requirements across life-stages is a priority for resource managers responsible for monitoring and conserving this species (Cahill 2015; Stamford et al. 2017). Although Arctic Grayling are found in a wide variety of northern freshwater habitats, they are recognized as a species sensitive to changes in environmental conditions (McPhail and Lindsey 1970; Scott and Crossman 1973; Northcote 1995; Stewart et al. 2007), and considered a fitting monitoring species for indicators of aquatic health and integrity (Cahill 2015; Stamford et al. 2017). Monitoring approaches for species are typically founded in an understanding of suitable and important habitats based on objective, repeatable and defensible biophysical criteria (MacKenzie et al. 2006 and Isaak et al. 2009). In the Mackenzie Mountain region of the western NWT, very little information exists on the aquatic ecosystems or Arctic Grayling distribution and habitat use in the river watersheds (Evans et al. 2002; Sawatzky et al. 2007; Stewart et al. 2007), and continued development of access roads, mines and oil and gas exploration is anticipated (GNWT 2019). There is a need to improve our understanding of the range of habitats used by fluvial Arctic Grayling populations in this region to identify, protect and manage important habitats for the species, to mitigate development impacts, and to effectively monitor the species over time.

1.12 Addressing knowledge gaps

Studies on Arctic Grayling habitat use and life-stage requirements have been summarized to aid in monitoring and management of the species in different regions (Reed 1964; Tack 1980; Armstrong 1986; Northcote 1995; Roberge et al. 2002; Stewart et al. 2007; AEP 2015; Stamford et al. 2017), and fish habitat models have been developed to evaluate habitat quality in rivers and lakes. Mathematical modelling is a common technique used in fisheries biology to analyze study results, interpret observed patterns and simulate ecological relationships in aquatic ecosystems (de Kerchove et al. 2008). It provides analytical methods to predict and evaluate the quality of habitats for fish species across different spatial and temporal scales. Modelling applications are often used by government and industry in the assessment of impacts to fish and fish habitat from developments, calculation of fish habitat loss, and measurement of the success of aquatic habitat restoration for species (de Kerchove et al. 2008; Laroque et al. 2014). At a landscape scale, occupancy modelling provides a method to assess fish population distribution in suitable habitats across watersheds (Isaak et al. 2009). By establishing parameters around habitat occupancy and detection efficiency these models allow for predictions of species presence in suitable habitats at a scale relevant to land and resource management, along with development of more efficient sampling designs and monitoring protocols representative of the spatial extent and variability for the species (Isaak et al. 2009; Baker et al. 2017; Lewis 2018). For the vast and remote un-surveyed areas of Canada's north, occupancy modelling offers a scientifically defensible approach to predict or infer the presence and distribution of a fish species within and among watersheds. However, the broad-scale habitat parameters required to accurately determine distribution, at a watershed level, need to be supported by a clear understanding of the species habitat requirements across life history types, life stages and ecoregions, as demonstrated by Baker et al. (2017) and Lewis (2018) for different Arctic Grayling populations in the NWT. The coarse level of environmental parameters used in species occupancy models limits the ability to account for and understand site-specific ecological or biophysical habitat factors that could affect this species' occurrence and distribution. Improving our understanding of local or site specific habitats and life stage specific habitat relationships for Arctic Grayling is needed to support the continued development and verification of occupancy models and distributional monitoring protocols for different ecoregions.

A common model used by resource managers for quantifying fish habitat loss or change using species-specific habitat values is based on Habitat Suitability Indices (HSIs). HSIs combine the resource selection and habitat preferences of a fish species for different biophysical variables to determine suitable or optimal habitat specific to that species (de Kerckhove et al. 2008). HSIs have been developed for Arctic Grayling and include indices specific to life stage or biologically significant periods in their lifecycle (Hubert et al. 1985; Jones and Tonn 2004; Golder Associates 2008; Laroque et al. 2014; Lewis 2018). However, these indices are based on available data often from different life history types or ecoregions, limiting the applicability to fluvial populations in northern mountain stream systems. There is also evidence of gaps and discrepancies in our understanding of juvenile habitat use and life stage requirements (Armstrong 1986; Northcote 1995; Laroque et al. 2014; Stamford et al. 2017). The variation in age-size structures and size at maturity reported for the species across life histories, river systems and regions, makes it difficult to delineate juvenile size-class for a population without previous study (Scott and Crossman 1973; Armstrong 1986; Stewart et al. 2007). Our limited understanding of the juvenile life stage has led to the grouping of juvenile life stage requirements with either young-of-year or adult fish when evaluating habitat, creating inconsistencies in descriptions of habitat needs as these grouping may be erroneous. Although common practice is to consider Arctic Grayling between young-of-year and sexually mature adults as juveniles (Hubert et al. 1985; Roberge et al. 2002; Stewart et al. 2007; Laroque et al. 2014), there are some reports where this phase is separated into juvenile and sub-adults (Tack 1980;

Armstrong 1986), based on observed differences in habitat use and biological characteristics. Data gaps related to the early life history of Arctic grayling have been acknowledged as a hindrance to management of the species for some time (Armstrong 1986). The paucity of data specific to juveniles and sub-adults has limited the development of comprehensive HSIs for the species (Laroque et al. 2014) and the accurate delineation of critical habitats (Stamford et al. 2017). Successful recruitment to adults requires survival through the early life stages, therefore understanding the dynamics of the life stage-specific habitat relationships and requirements is essential for the conservation and management of Arctic Grayling populations and its critical habitats.

1.13 Study objectives and hypotheses

Within this context, the objectives of my study are to:

a) improve our understanding of Arctic Grayling ecology and summer habitat use across life stages in pristine northern mountain streams, with a focus on the juvenile stage;
b) establish an ecological baseline of within-stream characteristics and Arctic Grayling habitat across sub-watersheds; and,
c) document Arctic Grayling summer distribution within and among mountain streams of the Little Nahanni River watershed.

Habitat characteristics - Hypothesis 1. Temperature, flow, and cover are the primary ecological drivers that determine habitat use for juvenile Arctic Grayling.

d) Prediction - Juvenile Arctic Grayling will use stream habitats with lower gradients, lower water velocities, and more complex available cover, to reduce the energetic cost of maintaining station in the current.
e) Prediction - Water temperature affects stream productivity and fish metabolism; therefore, juvenile Arctic Grayling will use stream habitats with warmer water temperatures that promote growth.

Distribution - Hypothesis 2. Due to differing swimming abilities and feeding requirements Arctic Grayling of different life stages will partition across the available summer stream habitats.

f) Prediction - Juvenile Arctic Grayling will occupy tributaries with lower gradients, water depths and velocities than those occupied by adults.

g) Prediction – Juvenile Arctic Grayling will occupy habitats within stream reaches that have more diverse velocities and available cover compared to areas used by young-of-year.

My research will increase our understanding of fluvial Arctic Grayling summer distribution across sub-watersheds, habitat use by life stage within available stream habitats, and the species lifecycle dynamics and requirements. At the stream scale, the data can contribute to the enhancement and validation of fish habitat models and life stage-specific HSIs for the species. At the watershed scale, data collected on habitat use across undisturbed mountain stream systems can help to better understand population-level dynamics, limitations and critical habitats. Information on Arctic Grayling life history requirements in this ecoregion will broaden our understanding of the range and variability of habitats used by the species in northern mountain systems, and the potential to adapt to changing environmental conditions. Establishing a baseline or reference habitat conditions for the species in pristine mountain streams will enhance our ability to monitor trends over time and assess cumulative impacts from climate change and resource development stressors. The long-term conservation and restoration of essential habitats for Arctic Grayling, including fluvial populations in pristine northern mountain streams, depends on our understanding of habitat requirements across life stages and the implications of changing environmental conditions over time.

2.0 Methods

2.1 Study area

The study area is located in the Little Nahanni River watershed in the southwest of the NWT, Canada, along the border of the Yukon Territory where the Sahtu and Dehcho traditional lands meet. The watershed is centered at approximately 512170 m E, 6897916 m N (UTM), a large portion of which is located within in the boundaries of the Nahanni and the Naats'ihch'oh National Park Reserves, respectively (Figure 2 in Results). The watershed of the Little Nahanni River is found within the Mackenzie and eastern Selwyn mountain ranges, at the northern limit of the Canadian Rocky Mountains (Ootes et al. 2013). The Little Nahanni River drains an area of approximately 1,670km^2 and is a branch of the headwater system for the South Nahanni River, a major tributary entering the Liard River, which flows into the Mackenzie River system. These watersheds are found within the Lower Mackenzie freshwater ecoregion and the Western Arctic national freshwater biogeographic zone, that comprise freshwaters draining into the Arctic Ocean (Mandrak 2003; Abell et al. 2008).

The Little Nahanni River watershed is part of the Greater Nahanni Ecosystem (Parks Canada 2015; Ponomarenko and Quirouette 2015), falling along the edge of the Taiga Cordillera Ecozone (ESRT Secretariat 2011) and within the Boreal Cordillera (Level II) Mid-Boreal (Level III) Ecoregions of the NWT (Ecosystem Classification Group 2010). Elevations within the watershed range from 800-2200 meters above sea level (masl) creating a mix of alpine, sub-alpine and boreal (forested) ecozones. Alpine areas are defined by shale and sandstone peaks, eroded plateaus and, at high elevations, glaciers and some small glacial lakes, with vegetation characterized by alpine fir-herb meadow and lichen tundra complexes (Ecosystem Classification Group 2010). Sub-alpine areas are distinguished by stands of stunted white spruce (*Picea glauca*), alpine fir (*Abies lasiocarpa*), willow (*Salix sp.*) and dwarf birch (*Betula nana*) (Ponomarenko and Quirouette 2015). Spruce woodlands and conifer forests are common on the lower valley slopes and floors, as well as sedge-dominated wetlands scattered within valley floors (Ecosystem Classification Group 2010).

The montane climate in this region is defined by short, wet summers and very cold, snowy winters. The average summer temperature in the region is 9.5ºC, July being the warmest summer month with daily maximums up to 34ºC. In winter temperatures average -20's ºC, with January being the coldest month having recorded a minimum of -59ºC (Cantung report EA02-003; Selwyn Chihong Mining Ltd. 2015). The average annual precipitation in the region is 400-600 mm, with snowfall comprising approximately 50%. The ecoregion of the Little Nahanni River is considered to be one of the wettest in NWT. The moisture-bearing Pacific systems that approach from the west are forced upward by the high mountain ranges depositing precipitation to the area year-round (Ecosystem Classification Group 2010).

Stream morphology in the sub-watersheds of the Little Nahanni River is highly variable from low gradient, low energy systems meandering through organic-rich broad valleys to high gradient, high energy channels that convey material loads through confined steep valley walls (Selwyn Chihong Mining Ltd. 2015). The range of stream gradients, channel configurations, streambed materials, bank characteristics and cover types (riparian and in-stream) creates a diversity of aquatic habitats. The hydrogeomorphology of this mountainous region provides a combination of lake and bog-fed water sources in low gradient systems, glacial-fed sources originating at higher elevations, spring-fed sources throughout the region, including thermal-springs, and precipitation-fed run-off systems that create a range of stream water temperatures throughout the sub-watersheds (Selwyn Chihong Mining Ltd. 2015). Annual and summer water temperatures in the streams within Little Nahanni watershed are also variable, governed by different source water inputs from surface-water, groundwater, glaciers and springs (Mochnacz et al. 2013), and influenced by summer air temperatures. Stream flows in the Little Nahanni watershed typically peak May through June, coinciding with snowmelt and rain-on-snow events that drive freshet (Selwyn Chihong Mining Ltd. 2015).

2.2 Study streams

Documentation of fish species distributions and aquatic habitat conditions in the Little Nahanni watershed is limited (Babaluk et al. 2015; Lewis 2018) and have focused on mining exploration and development activity in the region (Envirocon Ltd. 1976; Triton Environmental Consultants 2014). Fish species recorded during field sampling in 2014, included Arctic Grayling (*Thymallus arcticus*), Slimy Sculpin (*Cottus cognatus*), Burbot (*Lota lota*), Lake Trout (*Salvelinus namaycush*) and Lake Chub (*Couesius plumbeus*), with Arctic Grayling being the most commonly encountered species (Lewis 2018). For this study, Arctic Grayling distribution and habitat use in the Little Nahanni River watershed was evaluated at the sub-watershed scale across four creeks flowing into the Little Nahanni River: Guthrie, Fork, March and South Lened-Dozer creeks (Figure 2). These four creeks were selected based on surveys conducted in the summer of 2014 and were found to be representative of the variety of stream habitats available within the Little Nahanni River watershed.

Guthrie Creek has an approximate catchment area of 275 km^2 and flows from the west into the Little Nahanni River. The main channel of the creek is fed by a shallow lake-bog system creating a low gradient meandering channel with mid and side channel bars, both vegetated and gravel, conveying a broad flow pattern across the valley floor of the creek watershed. Several tributaries sourced from higher elevation alpine lake and run-off systems flow through narrow higher energy channels, from peaks on the north side, into the main channel, downstream of the lake-bog fed area (Lewis 2018; Selwyn Chihong Mining Ltd. 2015). Arctic Grayling, Slimy Sculpin and Burbot are known to occupy this sub-watershed (Triton Environmental Consultants 2014; Lewis 2018).

Fork Creek has an approximate catchment area of 341 km^2 and flows from the west into the Little Nahanni River. It is a higher gradient, higher energy system fed by several tributaries draining glaciers, alpine lakes and ridges. Its main channel and tributaries are characterized by high valley walls, and areas of confined channels with steep banks, narrow bedrock canyons and fans of alluvial outwash. The creek conveys high energy flows with active channel erosion contributing to large amounts of bed load material and substrate movement (Lewis 2018; Selwyn Chihong Mining Ltd. 2015). Arctic Grayling and Lake Trout are known to occupy this sub-watershed (Lewis 2018; Triton Environmental Consultants 2014).

March Creek has an approximate catchment area of 263 km^2 and flows from the west into the Little Nahanni River. It is also a higher gradient, higher energy system fed by tributaries draining from densely forested sub-alpine and boggy alpine areas. The creek is characterized by narrow, high valley walls confining the main channel into a relatively straight configuration. The prominent boulder substrate and absence of active erosion and deposition of channel materials are indicative of naturally high hydraulic conductance able to convey high volumes of water quickly (Selwyn Chihong Mining Ltd. 2015). Arctic Grayling have been documented in this sub-watershed (Lewis 2018)

South Lened-Dozer Creek (hereafter "Lened-Dozer") has a catchment area of approximately 497 km^2, flows from the south into the Little Nahanni River, and is comprised of three tributaries, one of which is Dozer, converging into a main stem channel. Lened-Dozer the most downstream sub-watershed draining into the Little Nahanni River prior to its confluence with the South Nahanni River. It is the largest of the four sub-watersheds studied and has a moderate gradient, lengthy and relatively confined main channel (South Lened) characterized by well vegetated narrow steep valley walls. Three tributaries converge and flow into the South Lened main channel at about the half-way point of the total creek length. Two are lengthy confined stream segments draining steep high elevation peaks from the north and east; the other tributary (Dozer) is a shorter segment of low gradient stream draining an organic rich lake-bog system confined by steep valley walls. Arctic Grayling and Lake Chub are known to occupy this sub-watershed (Lewis 2018).

2.3 Study design

The sampling design for this study was based on the watershed-scale distributional monitoring protocol developed by Isaak et al. (2009) to monitor bull trout (*Salvelinus confluentus*) occupancy in mountain streams in the northwestern United States. Distributional monitoring provides a means of monitoring or assessing a species distribution, or spatial patterns of occurrence, across a vast landscape by using less intensive sampling at each site and covering a larger spatial area (Isaak et al. 2009). Sampling at a watershed-scale allows for improved understanding of the important biophysical and habitat parameters needed to delineate suitable habitat patches for a species that is more representative and relevant to both the life history of fluvial fishes and the management of lands (Mackenzie et al. 2006; Guisan et al. 2006; Isaak et al. 2009). For this study, areas of suitable Arctic Grayling habitat (hereafter "habitat patches") across the four study streams were selected using pre-defined environmental criteria based on current understanding of salmonid habitat requirements in mountain systems. The criteria included catchment area >400ha, stream Strahler Order <4, stream gradient < 15%, and elevation <1600m above sea level (masl). Specifically, a habitat patch was defined as a continuous section of stream channel with similar environmental characteristics (elevation, grade, channel structure, hydrology, substrates, etc.) that was delineated using stream-specific conditions such as in-flows and out-flows of other tributaries or presence of physical channel barriers. Sampling sites were identified within the habitat patches using GIS and Generalized Random Tessellation Stratified design (GRTS; Stevens and Olsen 2004), a means of randomly selecting sample sites that are hierarchically and spatially represented (Isaak et al. 2009).

A total of 183 sites were identified within 35 habitat patches across the four sub-watersheds of the Little Nahanni River (Figure 2). Guthrie Creek had 64 sites within 14 patches. Fork Creek had 47 sites within 9 patches. March Creek had 36 sites within 6 habitat patches and Lened-Dozer Creek was the same, with 36 sample sites within 6 habitat patches (Table 2). Spatial replication was used (vs. temporal replication) where multiple sites along a continuous section of stream with comparable habitat patches are sampled to allow for more sites to be covered at a broader spatial scale across a watershed (MacKenzie and Royle 2005; Charbonnel et al. 2014). A recent study by Baker et al. (2017) on Arctic Grayling distribution in tundra streams showed that spatial replicates outperformed temporal replicates in estimating young-of-year (YOY) Arctic Grayling occupancy. For this study, each habitat patch had on average 4.6 to 6.0 sites that were sampled once to evaluate fish presence and habitat characteristics across the four study creeks (Table 2). Field sampling was conducted over three periods during the summer of 2015, from 5-10 July, 27 July–5 August, and 27 August-1 September. An *a priori* assumption was made that all sites within the habitat patches surveyed in the four sub-watersheds had equal probability of Arctic Grayling presence during the summer period.

2.4 Arctic Grayling occurrence and biological data

All sites across the four study creeks were surveyed to detect fish species and identify Arctic Grayling presence, as well as characterize important stream habitats at the watershed scale. Each site was 100m in length and was sampled for fish presence using a single-pass electrofishing survey (downstream to upstream) recommended by Isaak et al. (2009). Single-pass sampling was used to optimize sampling effort allowing more sites to be sampled over a larger scale and reduce potential harm to sensitive species and life stages (Bohlin et al. 1989; Meador et al. 2003; Poos et al. 2007; MacPherson et al. 2012; Reynolds and Kolz 2012). MacPherson et al. (2012) evaluated sampling techniques for low-density Arctic Grayling populations and, due to catch efficiency of different-sized grayling, recommended using angling for juvenile and adult fish in conjunction with electrofishing to target young-of-year. As such, angling was opportunistically used where adult Arctic Grayling were observed or where deep water precluded the safe use of electrofishing gear (e.g. patches in Fork and Dozer creeks).

Each site was electrofished by two personnel, wearing polarized sunglasses, moving from downstream to upstream in a zig-zap pattern from bank to bank, giving equal sampling effort to all habitat types (e.g. riffles, pools, insides and outsides of bends) as outlined in Meador et al. (2003) and Bonar and Willis (2009), with an average of 411 seconds of shock time per site. Fishes that were observed but not captured were recorded as a detection if both survey personnel positively identified the fish to species. Sampling was conducted with Smith-Root Inc. LR-24 Electrofishers using standard 11" anode rings and 16" x 16" dipnets. The units were set to a pulsed DC waveform with a frequency of 30Hz and 12% duty cycle. Before sampling each site, the quickset function was used to measure water conductivity and adjust the voltage, ranging from 185 to 475 volts across the sites. Fishes awaiting sampling were carried in buckets and then kept in holding bags, which allowed free flow of stream water. All fish species captured during the surveys were identified to species and measured to fork or total length (mm). Once biological data was recorded on each fish, it was released back into the stream in the same site where it was captured.

A sub-sample of fish captured were sacrificed to collect additional biological information or, in some instances, to confirm species identification. All sacrificed fish were frozen whole using a portable electric Engel™ freezer powered by a generator at the field camp location, then transported to freezers at DFO in Yellowknife and shipped to the University of Alberta for subsequent analysis. Sacrificed Arctic Grayling (n=174) were photographed and measured for fork length (mm) and weight (nearest 0.1g). Sex, maturity, and gonad weight (nearest 0.1g) were recorded where possible to evaluate size at maturity. Sexual maturity was determined by internal examination of gonads and each fish was assigned a maturity level (Table 1b). Otoliths were extracted for aging purposes. Scales, pectoral fin rays and caudal fin rays were collected and preserved for potential future analysis. Stomach and liver weight were recorded (nearest 0.1g) and samples preserved frozen. The gills, adipose fin, dorsal muscle and ventral muscle tissue samples were collected and archived frozen for potential future analysis.

Estimated ages for Arctic Grayling from whole otoliths have been found to be the most precise when compared to other aging methods (Sikstrom 1983; Merritt and Fleming 1991). Otoliths from a selection of 75 Arctic grayling samples covering the range of sizes captured were submitted to AAE Tech Services Inc. in La Salle, MB. Ages were determined using the read whole method, with a subset of 11 randomly selected otoliths sectioned and read again after being read whole to confirm age estimates. All otoliths were photographed using a microscope mounted camera system and reference markers were provided to highlight annuli and depicted age.

2.5 Site habitat characterization

Stream characteristics and habitat types for each sample site were documented using rapid habitat assessment field methods which provide broad characterization of stream environments (Bain and Stevenson 1999; Gordon et al. 2004; Environment Canada 2012). For each sample site, GPS coordinates were recorded at both the downstream and upstream locations of the 100m site. After the electrofishing survey was conducted, one transect (stream bank to stream bank, perpendicular to the flow) was selected at the upstream extent of the site to record habitat data representative of the entire site. Site photographs were taken looking downstream, upstream, left bank, right bank and underwater substrate at the transect location. At four equidistant points across the transect, water depth and velocity was measured with a meter stick (nearest 0.5cm) using the indirect surface water velocity-head rod method (Wilm and Storey 1944; Carufel 1980; Fonstad et al. 2005; Environment Canada 2012). The mean depth and velocity was determined for each site. Air and water temperature were recorded using a Fisherbrand™ pocket closed metal case liquid-in-glass thermometer. Stream water parameters (temperature, dissolved oxygen (DO), pH) were measured using a YSI™ ProDSS Multimeter with a 6000MS V2 sonde. The stream substrates, habitat types, riparian area and stream cover at each site were estimated visually as composition out of 100% for the site. Substrate types were estimated using particle size ranges (mm) from the modified Wentworth classification scale (Cummins 1962), documenting proportion of boulder, cobble, gravel, and silt/sand present using an area approximately two mean stream widths upstream and downstream of the transect location. Evaluation of stream habitat-types included estimation of the proportion of cascade, riffle, run and pool habitats out of 100% for the site. Similarly, riparian composition was documented by estimating the proportion of grass/moss, shrubs, and trees out of 100% for the site. Stream cover at the site was estimated as an area percentage of the total site and included aquatic vegetation, overhanging vegetation, boulder refuge, woody debris, undercut banks and eddies.

Water samples from each sub-watershed were collected during the second sampling period and submitted to Maxxam Analytics in Yellowknife, NWT for water quality analysis, including the standard suite of water quality parameters, nutrients and metals (total and dissolved).

2.6 Statistical analysis

Statistical analyses were undertaken to draw results related to Arctic Grayling habitat use at the watershed scale across the four study creeks. A variety of statistical tests were used to explore and analyze the data. Additional tests were performed as a redundant measure to confirm concurrence among tests and increase my confidence level in the subsequent interpretations. All statistical analyses were conducted using the open-source R software version 2.15.3 (R Core Team 2013). The project data was collected over three sampling periods during the summer of 2015 from July 5 to September 1. To account for these differences, the sampling dates were converted to Julian days (using the 2015 Julian calendar) and added as a conditional variable to the analyses.

2.6.1 Arctic Grayling habitat relationships

Distribution models relate the occurrence of an organism to habitat characteristics, identifying habitat preferences that can help predict species presence for monitoring and management (Guisan and Zimmermann 2000). It is recognized that these models are limited by their inability to account for imperfect detection, that is assuming that if a species is present it will be detected 100% of the time, which can limit inferences on true habitat use (Kery and Schmidt 2008). However, despite this limitation which occupancy modelling addresses, distributional models have proved valuable in predicting and assessing species habitat use in vast and remote areas (Jones and Tonn 2004). For my study, a step-wise logistic regression based on a logit model was used to analyze the relationship between the presence or absence of Arctic Grayling (binomial response variable) and the stream habitat characteristics (predictor variables) to find the probability of presence based on the combination of predictors. Using these relationships, probabilities were developed for predicting Arctic Grayling presence based on the habitat variables collected across sample sites.

Logistic regressions were run and probabilities plotted for each individual habitat variable to evaluate the strength of the potential relationship and its influence on the presence of Arctic grayling (Table 4). The significance factor ($p<0.05$) for each variable was used to identify those best suited to continue in model evaluation. Step-wise multiple logistic regressions based on a logit model were run on an *a priori* model set to select the best fit model for each life stage based on Akaike's Information Criterion (AIC) (Burnham and Anderson 2004). Step-wise logistic regression automatically tests variables by adding and eliminating forward selection, backward elimination, and bidirectional elimination approaches, all three of which were tested to examine outputs and select the best fit model. Additional model combinations of variables selected based on the variable significance factors from the individual regressions, the step-wise regression AIC outputs, and an understanding of ecologically important variables, were run and the results compared to select the top ranked model (lowest AIC value) for each life stage.

A binomial ANOVA was run on the output of each model to evaluate the variance and significance of the environmental variables used in the models. The predicted probabilities of Arctic Grayling presence from the model outputs were plotted against the most significant habitat variable influencing the model results. The relationship between that habitat variable and the probability of Arctic Grayling occurrence was plotted to determine thresholds related to the presence of grayling in varying habitat conditions found across the mountain watersheds. Logistic regression was used as a method to predict the probability of Arctic Grayling presence based on habitat variables by estimating maximum likelihoods. The logistic regression analysis was conducted broadly, using all Arctic Grayling detections together across the four sub-watersheds, but the focus of analyses was on the probability of predicting each life stage to evaluate habitat relationships across the sites occupied by Arctic Grayling.

2.6.2 Habitat use across life stages

Multivariate Regression Tree (MRT) method, using the 'mvpart' package in R (Therneau et al. 2013), was used as an additional method to understand what drives the relationships among the life stages of Arctic Grayling captured and the habitat variables in more detail. MRT was selected to better understand variation and identify environmental thresholds that separate the Arctic Grayling life stages and their use of available habitats across the sub-watersheds, therefore providing insight on causal relationships within the measured habitat variables. MRT provides a decision tree-type analysis that identifies specific thresholds within the habitat variables at the sample sites that may drive relationships between Arctic Grayling occupancy and stream characteristics, to predict distribution and suitable habitats for all life stages. MRT allows for the use of both categorical and continuous numeric response variables with bimodal distributions.

A redundancy analysis (RDA), using the 'vegan' package in R (Oksanen et al. 2013), was also conducted to identify which habitat variables are most important in structuring the response of the four life stages of Arctic Grayling across the sample sites. This rotation-based technique for constrained gradient analyses integrates ordination and multiple regression. RDA was selected as a multivariate approach to better understand the life stage-specific habitat associations by analyzing which linear combinations of environmental (predictor) variables represent the most variance in the relative abundance of life-stages, allowing for the interpretation of patterns in Arctic Grayling life stage occurrence from patterns in the habitat variables across the sample sites. It was used as an additional layer of information to try to garner a better understanding of the relationship between habitat variables and how Arctic Grayling life stages vary along key habitat gradients.

For the multivariate statistical analyses, Arctic Grayling abundances (response variables) per life stage were calculated as Catch Per Unit Effort (CPUE) by taking the total number of grayling per life stage at each site divided by the electrofishing effort (measured in seconds). The abundance values were then normalized using a Hellinger transformation.

3.0 Results

3.1 Fluvial Arctic Grayling life stages

Based on the analysis of fork lengths, weights, gonad development, and aging results, and guided by the size ranges and observations reported on fluvial Arctic Grayling populations in northern mountain systems (e.g. Armstrong 1986; Mochnacz and Reist 2007a), four life stages of Arctic Grayling were assigned: young-of-year, juvenile, sub-adult, and adult (Tables 1a and 1b). Differences in habitat distribution by size were observed across the four sub-watersheds (Figure 2). Although, as expected there is variation in individual fish sizes between ages, and therefore some overlap, it appears that fish < 80 mm in length, and age 0+ are YOY, and those > 80 mm and age 1 + are juveniles. In the fourth summer they move to the sub-adult stage (age 3+ or > 170 mm or >50 g) where the growth curve steepens and gonadal development begins, and in the seventh summer (age 6+ or > 250 mm or > 200 g) sexual maturity is reached as adults (Tables 1a and 1b). Only one fish was aged at 5 years and no fish at age 6, so there remains some uncertainty on the range of growth and reproductive development at age 5. The age 5 individual was smaller than some age 4 fish, but had greater gonadal development. It has been assumed, based on the annual growth and weights measured between age 5 and older fish, that age 6 fish would reach full maturity.

This age-size structure and evaluation of maturity provides a biological and physiological understanding of the developmental differences and demographic structure within this fluvial Arctic Grayling population. For the purposes of this study, the data was categorized using the four life stages for subsequent analyses of Arctic Grayling habitat use.

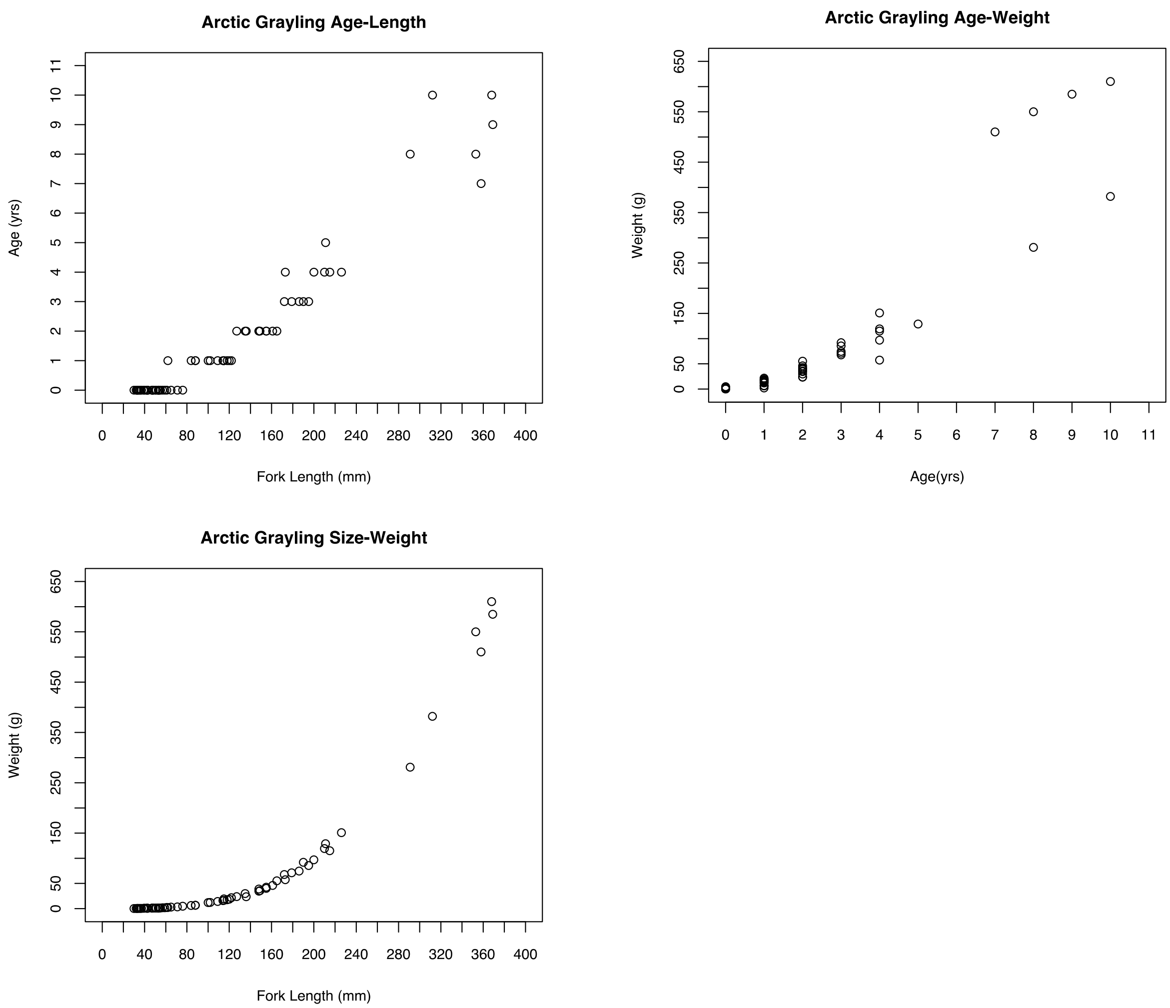


Figure 1 (a, b, and c). Plots of Age, length and weight results from a sub-set of Arctic Grayling collected in the four sub-watersheds of the Little Nahanni River, NWT (n=75). Plot a (top) is age-length, Plot b (middle) is age-weight, and Plot c (bottom) is length-weight.

Table 1a. Summary statistics of Arctic Grayling collected in the Little Nahanni watershed, NWT separated by sub-watershed. Age, fork length, weight, sexual maturity and gonad weight. Fork length and weight data are presented as mean ± standard deviation and range in parentheses.

Sub-watershed	Age (yrs)	n	Fork Length (mm)	Weight (g)	Sex	Maturity*	Gonad Weight (g)	Life stage
Dozer	0+	18	41±8 (30-54)	0.61±0.36 (0.17-1.26)	UNK	UND	NA	YOY
	1	9	96. ±18 (62-120)	10.46±5.65 (1.98-18.63)	UNK	UND	NA	Juvenile
	2	5	147±15 (127-161)	36.43±9.29 (23.69-45.91)	UNK	UND	NA	Juvenile
	3	1	186	74.52	F	IMM	0.32	Sub-adult
	4	1	173	57.45	F	IMM	0.35	Sub-adult
Guthrie	0+	13	56±10	1.78±1.22	UNK	UND	NA	YOY

			(39-76)	(0.55-4.68)				
	1	7	80±35 (47-122)	8.58±8.94 (1.03-21.54)	UNK	UND	NA	Juvenile
	2	3	150±15 (136-165)	37.80±16.0) (23.64-55.15)	UNK	UND	NA	Juvenile
	4	1	210	119.36	F	IMM	0.59	Sub-adult
Fork	1	1	115	19.25	UNK	UND	NA	Juvenile
	2	2	149±1 (148-149)	37.24±2.29 (35.62-38.86)	UNK	UND	NA	Juvenile
	3	4	184±10 (172-195)	79.03±11.50 (67.72-91.86)		IMM	0.22	Sub-adult
	4	3	214±13 (200-226)	120.98±27.47 (97-150.95)		IMM	0.42	Sub-adult
	8	1	291	281.00		MAT	3.15	Adult
March	10	1	312	382	F	MAT	6.63	Adult
Lened	5	1	211	128.98	F	IMM	1.37	Sub-adult
Mac Creek	7	1	358	510	M	MAT	NA	Adult
Little	8	1	353	550	F	MAT	NA	Adult
Nahanni	9	1	369	585	F	MAT	NA	Adult
River	10	1	368	610	M	MAT	NA	Adult

*UND=undeveloped, no gonad development; IMM=reproductively immature; MAT=reproductively mature

Table 1b. Characterization of four life stages of fluvial Arctic Grayling from the Little Nahanni River watershed, NWT based on results of age (from otoliths), length, weight, and developmental data.

Fork Length (mm)	Age (yrs)	Weight (g)	Gonad development	Life stage
0-80	0+	<5	Undeveloped	YOY
80-170	1-2	>5-50	Undeveloped	Juvenile
170-250	3-5	>50-200	Immature	Sub-adult
>250	6+	>200	Mature	Adult

3.2 Fluvial Arctic Grayling distribution across sub-watersheds

Over three sampling periods between July 5 and September 1, 2015, a total of 183 sites were surveyed across four sub-watersheds, of which 57 sites had Arctic Grayling present (~31%) (Figure 2). In general, adult Arctic Grayling were found further upstream in the tributaries of the sub-watersheds, particularly in Fork Creek, while primarily sub-adult Arctic Grayling occupied the further downstream habitat patches in the main stems of the sub-watersheds where they were present. Juvenile Arctic Grayling were detected in the fewest number of sampling sites (n = 11) compared to YOY (n = 21), sub-adult (n = 22) and adults (n = 22) (Table 2). Across the sample sites, there was separation in the distribution of Arctic Grayling by size both within and among the sub-watersheds (Figure 3). Sub-adult and adult Arctic Grayling occupied 27 (~57%) of the sites in the Fork Creek sub-watershed, whereas YOY and juvenile Arctic Grayling occupied 21 (~33%) of the sites in the Guthrie Creek sub-watershed. In the Lened-Dozer sub-watershed, YOY and juvenile Arctic Grayling used all five (100%) of the sites sampled within the Dozer Creek tributary, where as the sub-adults and adults occupied three out of 31 (~10%) of the sites sampled in Lened Creek proper. YOY Arctic Grayling were found in a total of 21 sites in seven patches between Guthrie and Lened-Dozer Creeks, all of which were in low elevation and low gradient channels downstream of lake and ponded marsh habitat. In March Creek, there was only one detection of a single adult Arctic Grayling, 310 mm in length, out of the 36 sites sampled in the sub-watershed.

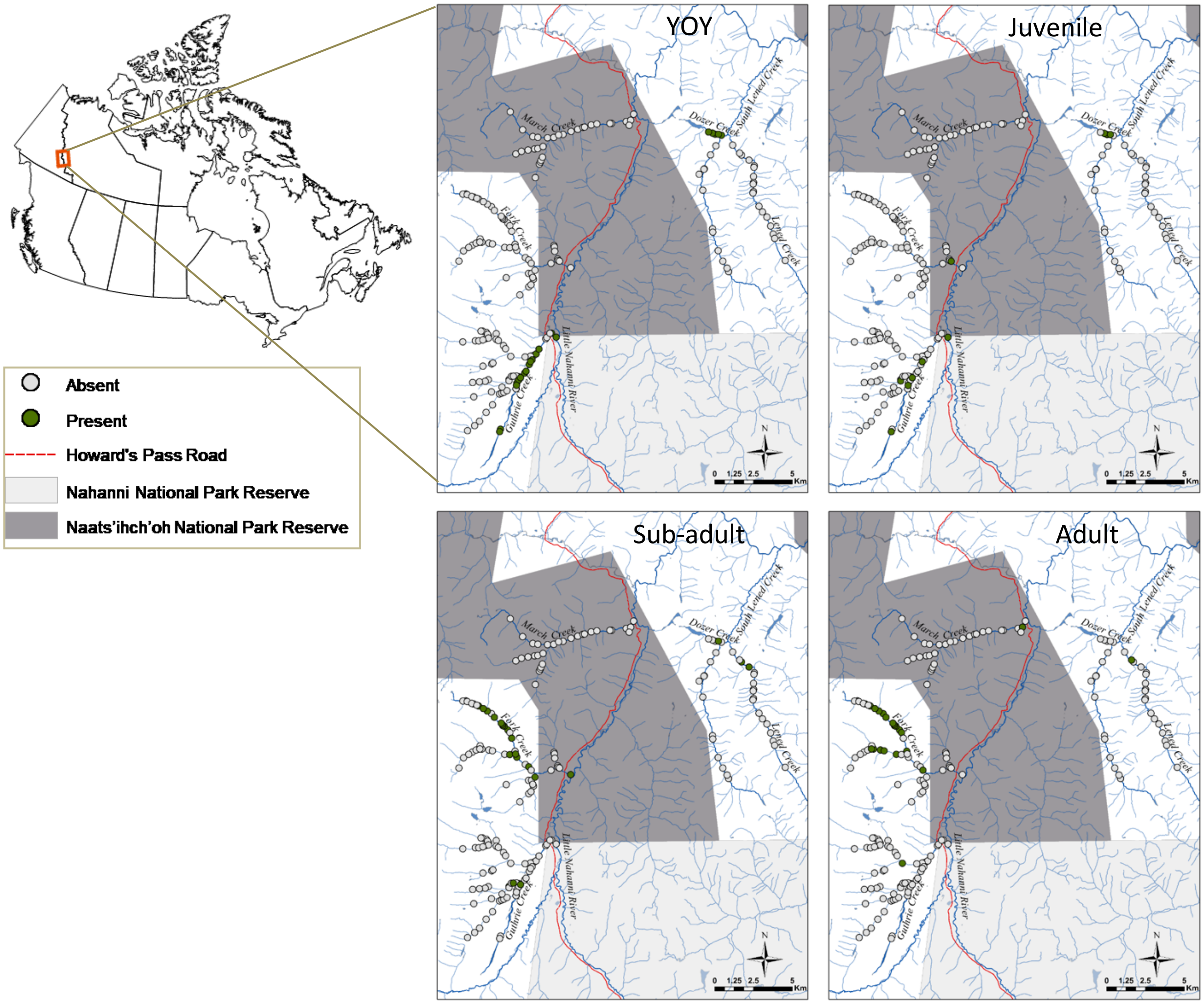


Figure 2. The Little Nahanni River watershed, NWT, Canada, showing the four sub-watersheds studied (Guthrie, Fork, March and South Lened-Dozer). Each sub-watershed contains sample sites selected using GIS and Generalized Random Tessellation Stratified Design (GRTS). The circles indicate sites that were sampled in the summer of 2015. Colored circles represent sites with Arctic Grayling occupancy by life stage: young-of-year (YOY), juvenile, sub-adult, and adult.

Table 2. The four sub-watersheds of Little Nahanni River, NWT sampled in 2015 for Arctic grayling occupancy. Sampling effort and occupancy per life stage is shown (modified from Lewis 2018).

Sub-watershed	Patches	Sites	Mean Sites per Patch	Patches Occupied	Sites Occupied	Sites YOY	Sites JUV	Sites SUB-AD	Sites ADULT
Guthrie	14	64	4.6	7	21	16	7	3	1
Fork	9	47	5.2	8	27	0	1	16	19
Dozer/Lened	6	36	6.0	2	8	5	3	3	1
March	6	36	6.0	1	1	0	0	0	1
Total	35	183	5.45	18	57	21	11	22	22

3.3 General characteristics of fluvial Arctic Grayling habitat

Data on a total of 19 stream habitat parameters was collected across all the sample sites (n = 183) (Table 3). When compared to the mean values and ranges of habitat parameters across all sample sites, the sites occupied by Arctic Grayling were similar in that they had water velocities < 0.8 m/s and water temperatures > 8 ºC. Sites occupied by YOY and juvenile Arctic Grayling had elevations < 1050 masl, water velocities < 0.7 m/s, water temperatures > 9 ºC, substrates with greater proportions of gravel and silt/sand (> 25%), and dominated by run habitat (> 50%). Sites occupied by sub-adult and adult Arctic Grayling had elevations > 1200 masl, water velocities > 0.75 m/s, water temperatures < 7.5 ºC, substrates with greater proportions of boulder (> 25%) and cobble (> 45%), and characterized by riffle (> 45%) and cascade (> 10%) stream habitats.

Table 3. Habitat variables (n = 19) measured at sampling sites across the four sub-watersheds of Little Nahanni River, NWT. Values in the ALL column are from all sample sites used in the analyses (n=180); ARGR values are from all sites with Arctic grayling present (n=58); YOY results are from sites with Arctic Grayling fork length 0-80 mm present (n=22); juvenile results are from sites with Arctic Grayling fork length 80-170 mm present (n=11); sub-adult results are from sites with Arctic Grayling fork length 170-250 mm present (n=22); and adult results are from sites with Arctic Grayling fork length >250 mm present (n=22). Data are presented as mean ± standard deviation and range in parentheses.

VARIABLE	ALL	ARGR	YOY	Juvenile	Sub-adult	Adult
Elevation (m)	1195 ± 138 (914-1478)	1153 ± 140 (939-1429)	1043 ± 49 (965-1103)	1040 ± 57 (965-1117)	1211 ± 142 (965-1416)	1280 ± 125 (939-1429)
Velocity (m/s)	0.81 ± 0.3 (0-1.93)	0.73 ± 0.26 (0-1.28)	0.65 ± 0.29 (0-1.12)	0.68 ± 0.29 (0.23-1.12)	0.77 ± 0.22 (0.32-1.12)	0.77 ± 0.24 (0.33-1.28)
Water Temp (ºC)	7.18 ± 2.19 (2.48-17.00)	8.20 ± 2.38 (4.32-17.00)	9.82 ± 2.51 (6.0-17.00)	9.22 ± 2.23 (6.6-13.00)	7.24 ± 1.83 (4.32-10.5)	6.91 ± 1.6 (4.32-10.6)
Depth (cm)	29.8 ± 11.2 (0-68.5)	34 ± 12 (11.6-68.5)	39.3 ± 14.5 (20.2-68.5)	39.6 ± 16 (19.1-68.5)	30.4 ± 9.9 (11.6-50.3)	28.9 ± 8.3 (16.3-42.3)
Width (cm)	436.3 ± 219.1 (77-1432)	475.3 ± 268.1 (77-1432)	413.6 ± 258.1 (132-998)	424.4 ± 350.8 (77-1190)	499.4 ± 280 (180-1432)	477.1 ± 138.3 (290-860)
Boulder (%)	26 ± 20 (0-78)	21± 19 (0-70)	5 ± 7 (0-25)	10 ± 10 (0-25)	29 ± 21 (0-70)	25 ± 17 (3-70)
Cobble (%)	48 ± 20 (0-85)	43 ± 20 (0-85	33 ± 23 (0-80)	35 ± 22 (0-60)	46 ± 19 (0-85)	51± 14 (15-70)
Gravel (%)	19 ± 14 (1-70)	24 ± 17 (1-70)	35 ± 20 (1-70)	29 ± 17 (1-65)	18 ± 11 (5-40)	20 ± 10 (10-40)
Silt-Sand (%)	8 ± 13 (0-89)	13 ± 19 (0-89)	27 ± 26 (0-89)	27 ± 30 (0-84)	7 ± 16 (0-10)	5 ± 3 (0-10)

VARIABLE	ALL	ARGR	YOY	Juvenile	Sub-adult	Adult
Run (%)	19 ± 26 (0-100)	33 ± 33 (0-100)	62 ± 31 (0-100)	54 ±35 (0-95)	23 ± 25 (0-95)	18 ± 19 (0-60)
Riffle (%)	52 ± 28 (0-100)	42 ± 30 (0-100)	23 ± 30 (0-90)	29 ± 31 (0-90)	49 ± 28 (0-100)	51 ± 19 (25-80)
Pool (%)	13 ± 8 (0-60)	15 ± 8 (0-40)	15 ± 11 (0-40)	15 ± 8 (5-30)	14 ± 6 (0-30)	17 ± 5 (10-30)
Cascade (%)	16 ± 22 (0-100)	8 ± 14 (0-75)	0.3 ± 1 (0-5)	3 ± 6 (0-20)	11 ± 17 (0-75)	13 ± 13 (0-50)
Aquatic veg (%)	5 ± 10 (0-50)	9 ± 13 (0-50)	9 ± 14 (0-50)	7 ± 10 (0-30)	10 ± 13 (0-50)	10 13 (0-50
Overhanging veg (%)	22 ± 20 (0-90)	16 ± 14 (0-70)	19 ± 20 (1-70)	20 ± 19 (5-70)	13 ± 7 (0-25)	14 ± 9 (5-35)
Woody debris (%)	7 ± 10 (0-60)	6 ± 6 (0-20)	7 ± 7 (0-20)	9 ± 7 (0-20)	5 ± 5 (0-20)	3 ± 2 (0-5)
Undercut bank (%)	30 ± 25 (0-95)	37 ± 30 (0-95)	56 ± 35 (0-95)	53 ± 30 (10-95)	22 ± 15 (0-70)	26 ± 19 (0-70)
Boulder cover (%)	9 ± 9 (0-40)	10 ± 10 (0-40)	1 ± 4 (0-15)	7 ± 11 (0-35)	13 ± 9 (0-30)	13 ± 10 (3-40)
Eddies (%)	6 ± 5 (0-25)	7 ± 5 (0-20)	6 ± 6 (0-20)	5 ± 4 (0-10)	7 ± 5 (0-20)	7 ± 5 (0-20)

Supplementary data on water quality parameters and mean values and ranges of habitat conditions by sub-watershed are presented in the Appendix, Tables A-1 and A-2. Dozer tributary and Guthrie Creek, where YOY and juvenile Arctic Grayling were present, provided the warmest mean water temperatures at 10.8 ºC ± 0.85 (9.7-12.0 ºC) and 7.9 ºC ± 2.19 (3.9-17.0ºC), the highest proportions of gravel substrates at 30% ± 19 (10-60%) and 24% ±18 (1-70%), and run habitat at 83% ± 15 (65-100%) and 24% ± 29 (0-100%) respectively (Table A-2). Fork Creek, which had the highest occupancy of sub-adult and adult Arctic Grayling, provided the highest proportion of boulder substrate at 34% ± 19 (3-78%) and cascade habitat at 24% ± (0-100%), of the sub-watersheds sampled (Table A-2). From a watershed perspective, March and Lened creeks, which had the lowest occupancies of Arctic Grayling, also had the lowest mean water temperatures at 6.4 ºC ± 1.6 (4-10 ºC) and 5.8 ºC ± 1.5 (2.5-8 ºC), the highest mean velocities at 0.97 m/s ± 0.25 (0.58-1.59 m/s) and 1.08 m/s ± 0.34 (0-1.93 m/s), and most abundant riffle habitat at 59%± 26 (0-95%) and 66% ± 21 (25-100%), respectively, compared to the other sub-watersheds (Table A-2). Across life stages, Arctic Grayling occupied sites that spanned a large range of the available stream elevations, water temperatures, velocities, widths and habitat types (Table 3). However, no Arctic Grayling were detected in sites with water temperatures < 4.3 ºC or water velocities >1.28 m/s (Table 3).

3.4 Predicting fluvial Arctic Grayling occupancy – life stage habitat relationships

Of the 183 sites and 19 habitat variables, 176 sites and 13 habitat variables were included in the analyses and modelling of Arctic Grayling habitat relationships. Logistic regressions were run and probabilities plotted for each habitat variable individually to evaluate the strength of the potential relationship and its influence on the presence of Arctic Grayling life stages (Table 4). Step-wise multiple logistic regressions (backward, forward and both), and additional model combinations, were tested, and the results of the top five ranked models, based on lowest AIC values for each life stage, are presented in Table 5.

Table 4. Results of logistic regressions on individual variables for presence of each life stage of fluvial Arctic Grayling used to build factors into the step-wise regression models tested and compared. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	YOY		Juvenile		Sub-adult		Adult	
Variable	P(>z)	AIC	P(>z)	AIC	P(>z)	AIC	P(>z)	AIC
ELEVATION	0.000***	84.77	0.001**	62.15	0.590	84.77	0.002**	111.58
WATER_TEMP	0.000***	91.64	0.002**	69.08	0.947	91.64	0.628	122.82
VELOCITY	0.011*	111.25	0.173	77.87	0.467	111.25	0.347	117.50
WIDTH	0.495	118.14	0.785	79.87	0.089	118.14	0.469	118.13
DEPTH	0.000***	102.38	0.002**	68.94	0.767	102.38	0.557	118.28
GRAVEL	0.000***	96.73	0.009**	74.13	0.889	96.73	0.723	122.94
SILTY_SAND	0.001**	90.66	0.001**	68.57	0.882	90.66	0.323	121.60
COBBLE	0.001**	106.18	0.030*	75.09	0.816	106.18	0.576	122.75
BOULDER	0.000**	82.25	0.011*	67.59	0.846	82.25	0.896	123.05
POOL	0.456	118.34	0.632	79.85	0.509	118.34	0.073 .	120.03
RUN	0.000***	69.18	0.000***	61.80	0.385	77.91	0.692	122.91
RIFFLE	0.000***	95.29	0.006**	71.12	0.525	95.29	0.835	123.02
CASCADE	0.062 .	79.75	0.074 .	70.71	0.248	79.75	0.385	122.19

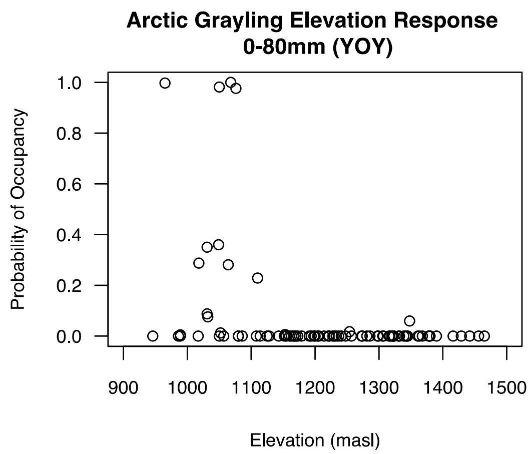
Table 5. Top five logistic regression models evaluated to predict occupancy of YOY, juvenile, sub-adult and adult Arctic Grayling in the Little Nahanni River, NWT during summer 2015. Models included had Δ AIC< 3.

Life stage	Rank	Model Variables	k	AIC	ΔAIC
YOY	1	Elevation, Width, Velocity, Silt Sand, Cascade	5	28.72	0
	2	Elevation, Width, Velocity, Gravel, Silt Sand, Cascade	6	28.96	0.24
	3	Elevation, Water Temp, Width, Gravel, Silt Sand, Cascade	6	29.73	1.01
	4	Elevation, Width, Silt Sand, Cascade	4	29.99	1.27
	5	Elevation, Water Temp, Width, Velocity, Gravel, Silt Sand, Cascade	7	30.07	1.35
JUV	1	Elevation, Run	2	52.08	0
	2	Elevation, Depth, Run, Boulder	4	52.41	0.33
	3	Elevation, Depth, Run	3	52.51	0.43
	4	Elevation, Water Temp, Depth, Cascade	4	52.6	0.52
	5	Elevation, Depth, Run, Cascade	4	52.69	0.61
SUB-ADULT	1	Run, Riffle, Pool, Cascade, Boulder	5	124.15	0
	2	Run, Riffle, Pool, Cascade	4	124.53	0.38
	3	Elevation, Riffle, Run, Pool, Cascade, Boulder	6	125.38	1.23
	4	Cobble, Run, Riffle, Pool, Cascade	5	126.13	1.98
	5	Velocity, Width, Run, Riffle, Pool, Cascade	6	126.54	2.39
ADULT	1	Elevation, Width, Depth, Silt Sand, Run, Pool	6	110.92	0
	2	Elevation, Width, Depth, Silt Sand, Run, Riffle, Pool	7	112.07	1.15
	3	Elevation, Width, Pool, Silt Sand	4	112.5	1.58
	4	Elevation, Width, Depth, Silt Sand, Cobble, Run, Riffle, Pool	8	113.82	2.9
	5	Elevation, Width, Depth, Pool	4	113.96	3.04

3.4.1 Logistic regression results for YOY Arctic Grayling

The top ranked logistic regression model for predicting YOY Arctic Grayling occurrence included: elevation, wetted width, velocity, percent silt-sand substrate, and percent cascade (Table 5). All five habitat variables showed significant results from the binomial ANOVA on the model outputs. However, elevation, cascade habitat, and silt-sand substrate came out as the most significant ($p = 0$)

(Table 6). From the model outputs, the predicted probabilities of YOY Arctic Grayling presence were plotted against habitat variables to show the nature of the relationship between habitat conditions and probability of occurrence. Figure 3 illustrates the relationship of YOY Arctic Grayling presence to elevation and water velocity, with maximum probabilities (100%) of occurrence at elevations < 1100 masl and velocities between 0.3-0.7 m/s.



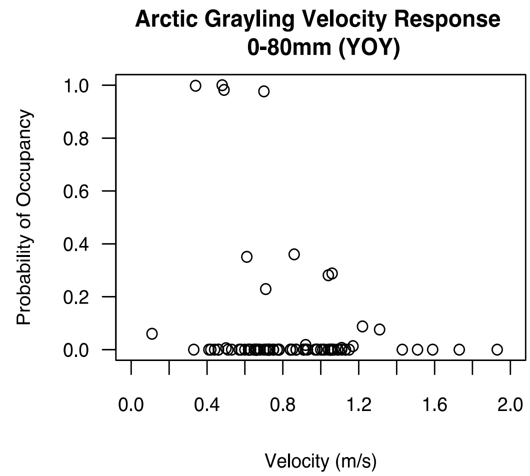
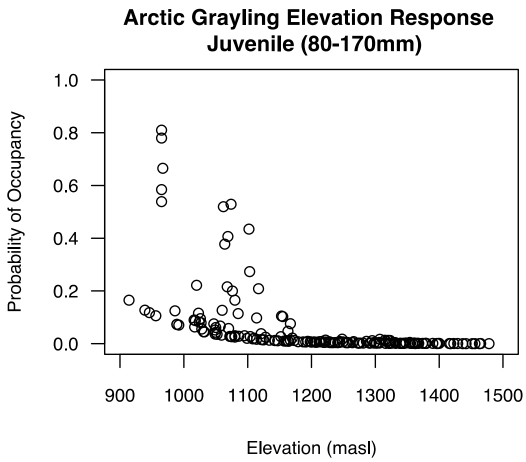


Figure 3 (a and b). Plots of the relationships between a) elevation and b) water velocity and the probability of YOY Arctic Grayling (0-80 mm) presence, Little Nahanni River watershed, NWT, 2015.

3.4.2 Logistic regression results for juvenile Arctic Grayling

The top ranked logistic regression model for predicting the occurrence of juvenile Arctic Grayling included: elevation and percent run habitat (Table 5). Both elevation and run habitat showed significant results ($p = 0$) from the binomial ANOVA on the model outputs explaining the probability of presence (Table 6). The predicted probabilities were plotted against elevation and run variables to show the influence of each habitat variable on the presence of juvenile Arctic Grayling (Figure 4). Maximum probabilities of 80% for the presence of juvenile size class were reached at sites with elevations < 1000 masl and proportion of run habitat > 90%.



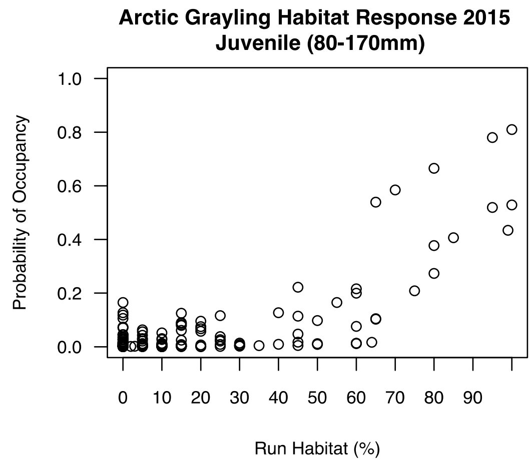


Figure 4 (a and b). Plot of relationship between a) elevation and b) run habitat and probability of juvenile Arctic Grayling (80-170 mm) presence, Little Nahanni River watershed, NWT, 2015.

3.4.3 Logistic regression results for sub-adult Arctic Grayling

The top ranked logistic regression model for predicting the occurrence of sub-adult Arctic Grayling included: percent run, riffle, pool, cascade, and boulder habitat (Table 5). The results of the binomial ANOVA run on the output of the model to evaluate the variance and significance of the selected predictor variables showed that the only significant habitat variable influencing the model results for presence of sub-adult Arctic Grayling was percent cascade habitat ($p = 0$) (Table 6). The predicted probabilities for occurrence of sub-adult Arctic Grayling from the model outputs were plotted against each habitat variable. Figure 5 illustrates the relationship between the presence of sub-adults and the proportion of cascade and run habitat. Probabilities reached 60% and greater for the presence of sub-adult Arctic Grayling at sites where the proportion of run habitat was < 50% and cascade habitat was 20%.

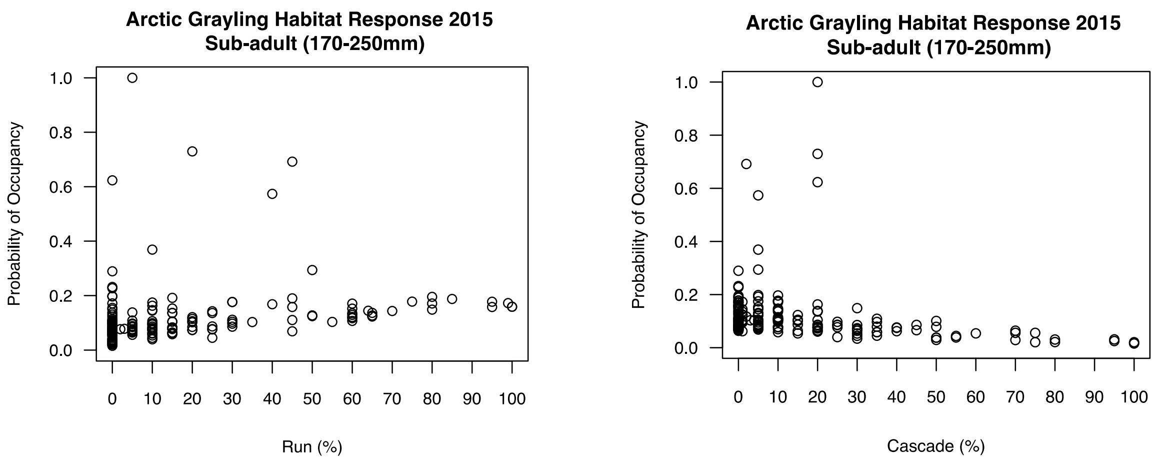
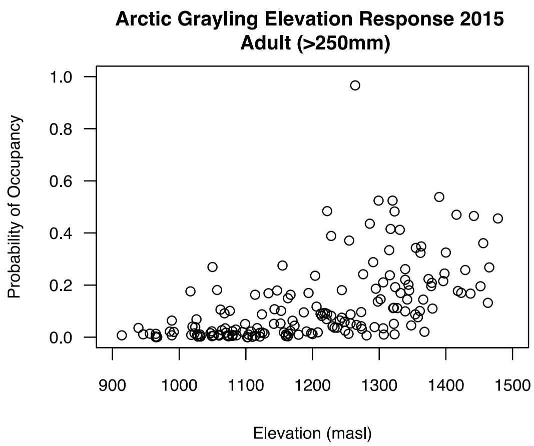


Figure 5 (a and b). Plot of relationship between a) run habitat and b) cascade habitat and the probability of sub-adult Arctic Grayling (170-250 mm) presence, Little Nahanni River watershed, NWT, 2015.

3.4.4 Logistic regression results for adult Arctic Grayling

The top logistic regression model for predicting the occurrence of adult Arctic Grayling included: elevation, wetted width, water depth, percent silt-sand substrate, percent run habitat, and percent pool habitat (Table 5). A binomial ANOVA run on the output of the model to evaluate the variance and significance of the selected predictor variables showed that the most significant habitat variable influencing the model results for the presence of Arctic Grayling adult was elevation ($p = 0$), followed by pool habitat ($p = 0.001$), and wetted width ($p = 0.01$) (Table 6). The predicted probabilities of occurrence of adult Arctic Grayling from the model outputs were plotted against elevation, and percent pool habitat (Figure 6). Probabilities of occurrence reached 50% at sites with elevations > 1200 masl and sites where the proportion of pool habitat was 20%.



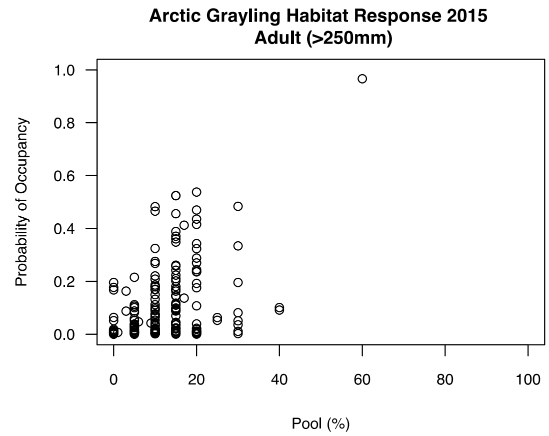


Figure 6 (a and b). Plot of relationship between a) elevation and b) pool habitat and the probability of adult Arctic Grayling (>250mm) presence, Little Nahanni River watershed, NWT, 2015.

Table 6. Analysis of deviance table - results of a binomial ANOVAs on logistic model outputs for presence of Arctic Grayling life stages. Significance codes = 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

Life stage	Model	Df	Deviance Resid.	Df	Resid. Dev	Pr(>Chi)	
YOY	NULL			173	120.001		
	ELEVATION	1	35.720	172	84.281	0.000	***
	WIDTH	1	8.716	171	75.565	0.003	**
	VELOCITY	1	9.212	170	66.354	0.002	**
	SILT SAND	1	19.343	169	47.010	0.000	***
	CASCADE	1	30.292	168	16.7193	0.000	***
JUV	NULL			172	76.425		
	ELEVATION	1	17.837	171	58.586	0.000	***
	RUN	1	12.506	170	51.435	0.000	***
SUB-ADULT	NULL			172	127.91		
	RUN	1	0.833	171	127.08	0.361	
	RIFFLE	1	0.000	170	127.08	0.999	
	POOL	1	0.254	169	126.82	0.614	
	CASCADE	1	12.291	168	114.53	0.000	***
	BOULDER	1	2.380	167	112.15	0.123	
ADULT	NULL			172	127.91		
	ELEVATION	1	11.331	171	116.58	0.000	***
	WIDTH	1	3.999	170	112.58	0.046	*
	DEPTH	1	3.598	169	108.98	0.058	.
	SILT SAND	1	1.974	168	107.01	0.160	
	RUN	1	2.218	167	104.79	0.136	
	POOL	1	7.873	166	96.918	0.005	**

3.4.5 Summary of logistic regression results

The results of the logistic regressions indicate that determining response thresholds for Arctic Grayling, related to consistent environmental variables at the watershed and sub-watershed scale, may be difficult because of the range of summer habitats that fluvial Arctic Grayling occupy. Figures 3-6 show the probability of fluvial Arctic Grayling occupancy for given stream habitat variables and demonstrate the different responses to different environmental conditions dependent on life stage. Stream elevation is an important predictor for Arctic Grayling presence, except for sub-adults. The proportion of run habitat factored into the top models, but only showed significance for predicting juvenile Arctic Grayling. The proportion of cascade habitat has a strong influence on predicting presence or absence of YOY and sub-adult Arctic Grayling, and the proportion of pool habitat plays a role in predicting adult Arctic Grayling. There are a number of stream habitat variables across a range of conditions that influence fluvial Arctic Grayling presence in summer mountain stream habitats throughout its lifecycle. The nature of the relationships between life stage and stream habitats was further explored through multivariate analyses, presented below.

3.5 Arctic Grayling habitat relationships

3.5.1 Multivariate Regression Tree (MRT)

The MRT (decision tree) method was used to analyze the relationships between the life-stages of Arctic Grayling and the various habitat conditions found across the sample sites in more detail. The analysis was conducted using 13 of the 19 habitat variables using 176 sample sites across the four sub-watersheds to understand which habitat parameters may drive or influence the relationships between Arctic Grayling size and habitat use. Julian days were not considered as a variable in this analysis along with the six cover variables (aquatic vegetation, overhanging vegetation, woody debris, undercut banks, boulder cover and eddies). A regression tree size of seven was selected, as no tree sizes below showed lower CV Error values (summarized relative error for all predictors), and the additional branches allowed further breakdown of the data to provide additional information on the habitat thresholds that explain smaller portions of the overall variation (Figure 7).

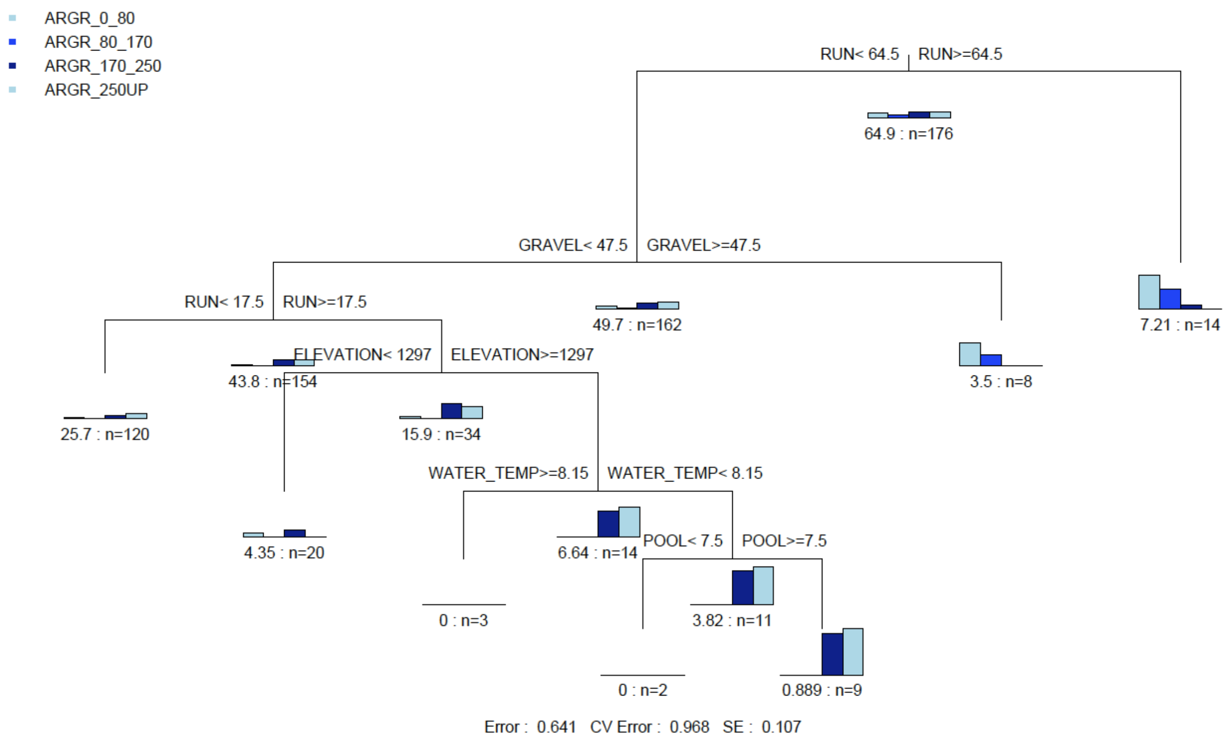


Figure 7. MRT results showing relationships between thresholds in habitat parameters and sites occupied by Arctic Grayling life stages from data collected on 176 sample sites, Little Nahanni River watershed, NWT, 2015. Bar graphs from left to right represent YOY, juvenile, sub-adult, then adult. Bars on the left side of the branch are YOY and juvenile and on the right side are sub-adult and adult.

The reported CV Error of 0.968 is high, indicating that the model is not a strong predictor for explaining the variation in the responses of fluvial Arctic Grayling life-stages to the stream habitat variables measured across the study sub-watersheds. The Error value of 0.641 (residual error) indicates that 64% of the variation is not explained by the MRT. But, it does provide a picture of which environmental thresholds, within the range of stream habitat data collected, explain up to 36% of the variation observed in habitat use across the life-stages of fluvial Arctic Grayling (Table 7). The first split in the regression tree (run habitat < or > 64.5%) identified 14 sites that had a high frequency of YOY and juvenile Arctic Grayling, and explained 12% of the variance. The second, third, and fourth splits (gravel, run habitat and elevation) together accounted for 15% of the variation, and identified an elevation threshold of 1297 masl, above which only sub-adult and adult Arctic Grayling were found. The fifth and sixth splits in the regression tree (water temperature and pool habitat) explained 9% of the variation, and indicate that colder water and pool habitats may distinguish the higher elevation sites where sub-adult and adults occur. Sub-adult Arctic Grayling were found in 22 sample sites across the four sub-watersheds (Table 2). The MRT result shows that these sites appear to span a range of habitat conditions compared to the sites of other life-stages, as sites with sub-adults found in all branches of the regression tree, indicating that this life-stage can make use of a broad variety of habitats.

Table 7. Variance output for each split (n=6) in the multivariate regression tree (MRT) explaining responses of Arctic Grayling size classes to stream habitat parameters (n=13) measured across sample sites (n=176).

	CP	nsplit	rel error	$\hat{p}$ error	xerror	xstd
1	0.123	0	1.000	0	1.014	0.113
2	0.049	1	0.877	0.123	1.033	0.112
3	0.044	4	0.730	0.147	0.985	0.106
4	0.041	6	0.641	0.089	0.968	0.107

3.5.2 Redundancy Analysis (RDA)

RDA analysis was conducted to evaluate the variance observed between the abundance of each Arctic Grayling life stage and the associated habitat measurements across the 167 sample sites and within the 46 occupied sites. The analysis was conducted using 13 of the 19 habitat variables collected at 167 sampling sites across the four sub-watersheds to draw correlations between Arctic Grayling life-stage and habitat variables. The six cover variables (aquatic vegetation, overhanging vegetation, woody debris, undercut banks, boulder cover and eddies) were not included in the analyses due to inconsistent data collection. To optimize the model parameters, the two RDA models were run using a step-wise process to remove variables showing linear dependencies among constraints and conditions, which reduced the 13 habitat variables down to a group of 10 variables (run, elevation, width, water temperature, depth, velocity, cascade, riffle, pool, silt sand) for Model 1 using all sample sites (n=167) and down to a group of three variables (elevation, boulder, cobble) for Model 2 using only the Arctic Grayling occupied sites (n=46) (Tables 8 and 9).

For Model 1, the constrained variance (how much of the variance in life stage response/presence is explained by the habitat variables) for RDA 1 was 20.5% and RDA 2 was 6%, indicating that this model using all sampling sites across the four sub-watersheds explained 20.5% of the variance observed in the presence of the fluvial Arctic Grayling by life-stage. For Model 2, the constrained variance for RDA 1 was 44% and RDA 2 was 5.7%, indicating that this model, looking within the 46 occupied sites across the four sub-watersheds, explained 44% of the variance observed among the Arctic Grayling life-stage.

ANOVAs on the model outputs were performed to evaluate whether a significant relationship exists between the presence of size classes (response) and the habitat variables. For the RDA Model 1 (n=167), all variables showed significance except for cascade habitat and silt-sand substrate, with run habitat and elevation having the most significant values ($p<0.001$) (Table 8). The RDA Model 2 (n=46), all three habitat variables (elevation, boulder, cobble) were significant (Table 9), with elevation and boulder habitat showing the strongest significance ($p<0.001$).

Table 8. Results of a binomial ANOVA on the RDA Model 1 output for all sample sites (n=167) using 10 optimized habitat variables, Significance codes = 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

Model	Df	Var	F	N.Perm	Pr(>F)	
RUN	1	0.029067	29.2575	999	0.001	***
ELEVATION	1	0.007057	7.1036	999	0.001	***
WIDTH	1	0.004964	4.9969	999	0.007	**
WATER_TEMP	1	0.004678	4.7087	999	0.010	**
DEPTH	1	0.003244	3.2649	999	0.033	*
VELOCITY	1	0.003687	3.7111	999	0.017	*
CASCADE	1	0.002652	2.6695	999	0.055	.
RIFFLE	1	0.003449	3.4719	999	0.027	*
POOL	1	0.003671	3.6951	999	0.037	*
SILTY_SAND	1	0.002248	2.2630	999	0.107	
Residual	155	0.15398				

Table 9. Results of a binomial ANOVA on the optimized RDA Model 2 output for the Arctic Grayling occupied sites (n=46) and three optimized habitat variables, Significance codes = 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' '

Model	Df	Var	F	N.Perm	Pr(>F)	
ELEVATION	1	0.123692	30.6020	999	0.001	***
BOULDER	1	0.033542	8.2985	999	0.001	***
COBBLE	1	0.015332	3.7931	999	0.016	*
Residual	42	0.169762				

The RDA biplot, using all sample sites, shows a shift in habitat association from the smaller Arctic Grayling to the largest across environmental gradients (Figure 8). YOY Arctic Grayling associated with stream environments that had a greater proportion of silt-sand substrate, run habitat and warm water temperatures, and were in low elevation stream environments. Juvenile Arctic Grayling did not show strong directional positive or negative correlations, but did associate with greater water depths than YOY. This life-stage appears to associate with environmental characteristics similar to the YOY, such as warmer water temperature and run habitat, as compared to the larger fish, but not as positively to silt sand. Sub-adult and adult Arctic Grayling showed almost equal associations to higher elevation stream habitats with colder water, greater wetted widths and larger proportions of pool habitat. Sub-adults showed a slightly greater association to increased width and pool habitats, and the adults to slightly higher elevation.

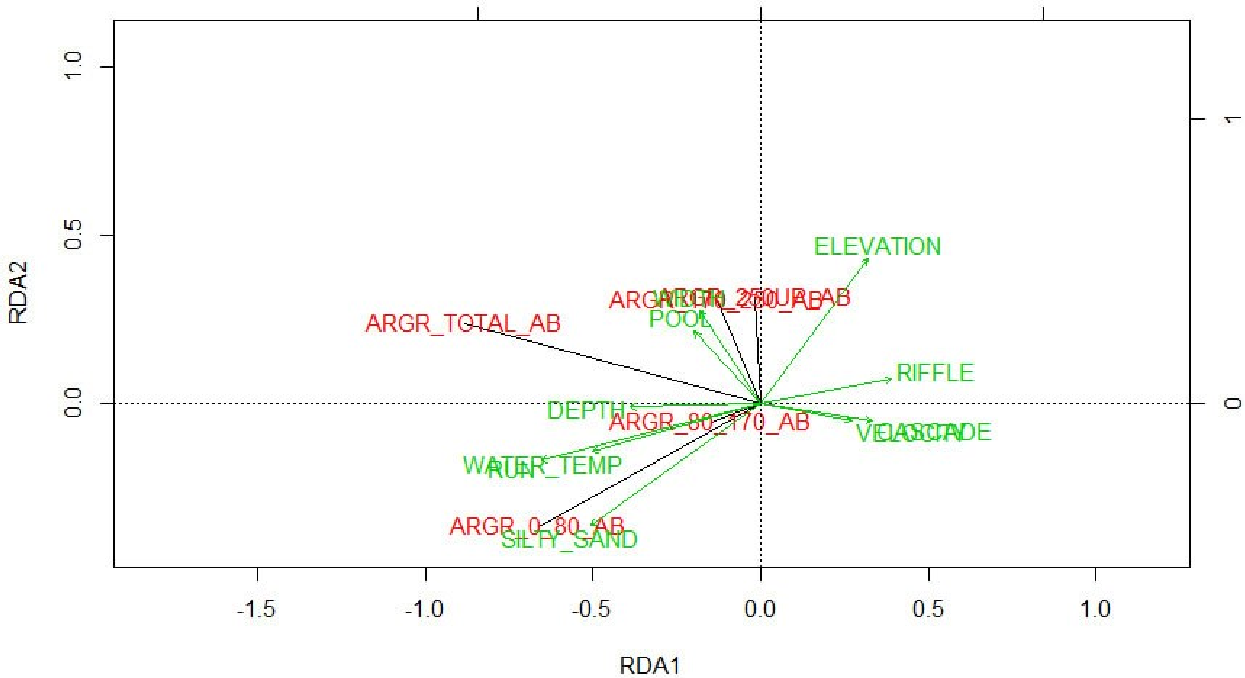


Figure 8. Biplot of RDA scores showing the correlations between the four life stages of Arctic Grayling and the 10 habitat variables selected in the model for xxx sample sites, Little Nahanni River watershed, NWT, 2015.This model explained 20% of the variance observed in the response of the life-stages.

From the RDA biplot focusing on the 46 sites with Arctic Grayling present (Figure 9), the strength of correlations driving differences among the size class habitat associations within the occupied sites can be seen. YOY have a clear negative correlation to elevation and stream habitats with greater proportions of cobble and boulder substrate. Similar to Figure 8, juveniles did not show a clear positive or negative correlations; however, like the smaller size class, they did not associate with higher elevations or cobble and boulder habitats. Sub-adult Arctic Grayling showed a stronger association to sites with greater proportions of cobble and boulder substrate than the larger Arctic Grayling. The clear distinction in these results for adults, compared to the other life stages, are higher elevation sites used as summer habitat.

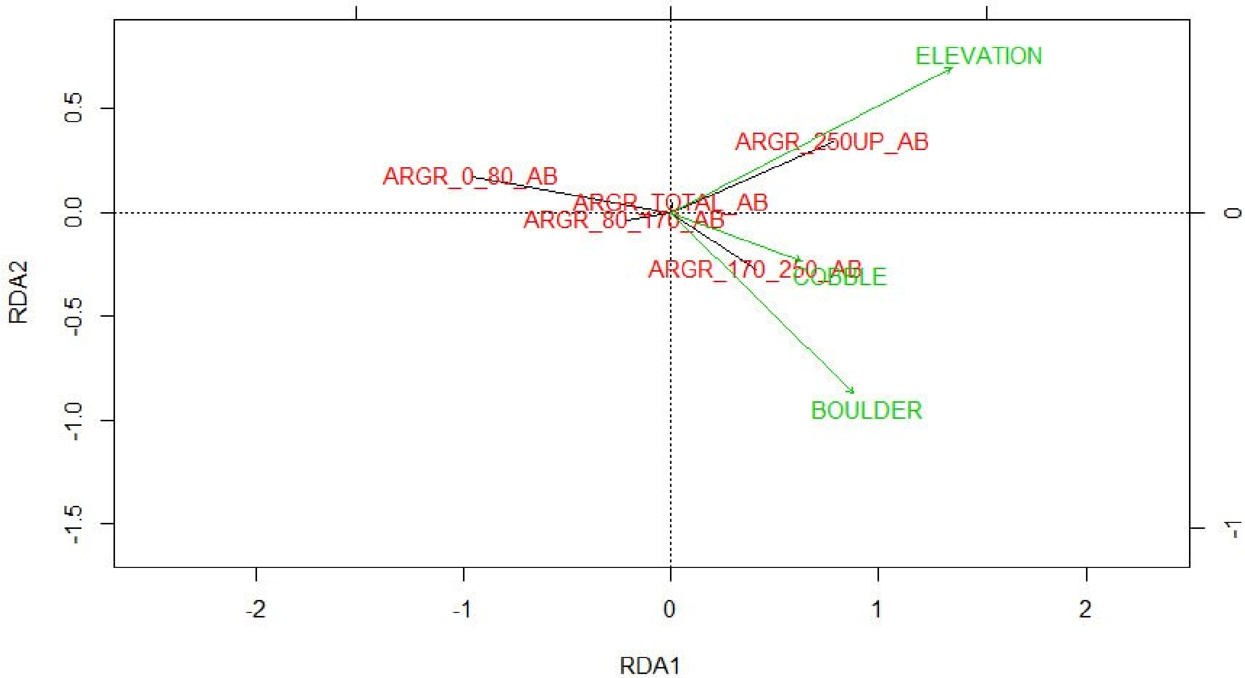


Figure 9. Biplot of RDA scores showing the correlations between the four life stages of Arctic Grayling and the three habitat variables selected in the model for the 46 Arctic Grayling occupied sites, Little Nahanni River watershed, NWT, 2015. This model explained 44% of the variance observed in the response of the size-classes within the occupied sites.

4.0 Discussion

4.1 Fluvial Arctic Grayling size classes and life stages

To better understand habitat requirements of fluvial Arctic Grayling in northern mountain ecosystems, the population demographics in the sub-watersheds of the Little Nahanni River needed to be understood to evaluate habitat relationships at each stage of the species lifecycle. Arctic Grayling growth differs between regions and habitats (Scott and Crossman 1973; Armstrong 1986) and they reach sexual maturity at different ages, showing a general trend of slower growth, later maturity, longer life span, and larger size at the northern limit of their range (Reed 1964; Northcote 1995). Studies in Alaska have shown that there is considerable variation in size at age and age at first maturity in different stream systems. The maturity of Arctic Grayling is thought to be more closely related to size than to age (Armstrong 1986; Northcote 1995). This can lead to incorrect assumptions of age class and maturity, based on size alone, when comparing between populations in different regions. Accordingly, the age composition, size at age, and size at maturity of the Arctic Grayling captured in this study were evaluated to better understand the size classes of this fluvial population to assess life stage-specific distribution and habitat associations. Based on biological data, distribution patterns across the study area, I identified four post-emergence life stages for Arctic Grayling in the Little Nahanni study area: young-of-year, juvenile, sub-adult and adult (Table1; Figure 10). The results of the distributional data and the analyses of habitat associations by life stage indicate that there are not only biological but ecological differences across the life stages of fluvial Arctic Grayling. During the summer, they used different habitats within a range of habitat conditions that separated the life stages across available stream habitats.

Figure 10. Life stages of Arctic Grayling with representative habitats, Little Nahanni River watershed, NWT, 2015. Left to right: YOY Dozer Creek (tributary of South Lened Creek), juvenile Guthrie Creek (main stem), sub-adult Guthrie Creek (tributary) and adult Fork Creek (main stem).

My findings are supported by several Alaskan studies. Reporting on size at age for fluvial Arctic Grayling in northern regions has primarily come from Alaska, using scales to determine fish age. Hallberg (1982) reported on the age-length composition of 384 grayling from the Tanana River drainage in interior Alaska. The mean fork length and ranges for age 1 were 112 mm (80-149 mm), age 2 was 162 mm (130-199 mm), age 3 was 187 mm (160-219 mm), age 4 was 215 mm (190-239 mm), age 5 was 239 mm (220-279 mm), and age 6+ had fork lengths > 250 mm. Almost identical age-length compositions for Arctic Grayling from the Tanana River was also reported by Tack (1973) and Holmes (1983), with the exception of age 5 fish having a larger mean fork length of > 250 mm. Population structure in these reports was presented in terms of age classes only, with no discussion of life stages.

The 1985 U.S Fish and Wildlife habitat suitability indices for riverine populations of Arctic Grayling in Alaska outlines young-of-year fish having fork lengths of 45-70 mm, and calculates an annual growth rate of 40 mm up to age 6; juveniles were considered 50-250mm and adults >250mm (Hubert et al. 1985). The report indicates that most fish mature at lengths 200-380mm, demonstrating how delineation of either juvenile or mature adult life stage, between the sizes of 200-250 mm, may become unclear. The habitat requirements for fluvial Arctic Grayling described in the report are provided in four stages, outlined as embryo, fry, juvenile, and adult. In the Stewart et al. (2007a) report on life history and habitat use of Arctic Grayling in the NWT, mean lengths for young-of-year were reported at 75-114 mm, juveniles ranged from 80-157 mm, and adults were identified by sexual maturity, anywhere from ages 2-6. The Arctic Grayling life history stages were also described in this report using four life stages of egg, young-of-year, juvenile, and adult. These summaries on habitat requirements for egg development and embryo survival are useful for describing essential spawning and incubation habitat for fluvial Arctic Grayling; however, there remain discrepancies in the information presented on fork lengths, ages and sexual maturity between juvenile and adult life stages, which creates uncertainty in deciphering the specific habitat requirements across life stages.

Mochnacz and Reist (2007b) reported data on fork lengths, weights, and otolith ages from fluvial Arctic Grayling collected during mountain stream surveys in the Sahtu region of the NWT. The age-size class ranges found were similar to my study results, where young-of-year captured were <80 mm, age 1 fish ranged from 85-120 mm, age 2 fish ranged from 123-170 mm, age 3 and 4 fish were >175 mm. Three life stages were used to group the Arctic Grayling into either young-of-year, juvenile, or adult, based on measures of sexual maturity. All fish reported between 80-277 mm in length (ages 1-4) were considered juveniles. Gonadal development and weight was recorded on fish >170 mm, similar to the findings of reproductive development in Arctic Grayling from the Little Nahanni watershed.

Designating the juvenile life stage for fluvial Arctic Grayling using broad size classes alone, such as 80-250 mm (Hubert et al. 1985; Mochnacz and Reist 2007b), becomes incongruous with age and developmental data used to identify sexually mature individuals. For example, mean lengths of age 4 fish can be 215 mm (Hallberg 1982), gonadal development can start at ages 2-3 or fish ≥ 170 mm (Mochnacz and Reist 2007b), and sexually mature adults can be identified anywhere from ages 2-6 (Hubert et al. 1985; Stuart et al. 2007a). This issue of life stage designation between the juvenile and adult phase for Arctic Grayling ages 2-5 (170-250 mm) was identified by Tack (1980) as an important consideration in the management of fluvial populations in the interior of Alaska. He found that shifts in reproductive development during the life cycle between the juvenile and adult phase, coincided with shifts in the summer feeding distribution, leading to the designation of four life stages for these fluvial populations. Tack (1980) described four life stages, using size, age, maturity, and summer distribution data, identified as young-of-year (age 0+), juvenile (ages 1, 2, 3), sub-adult (ages 4,5) and adult (age 6+). Armstrong's 1986 review of Arctic Graying studies in Alaska also adopted these four life stages, and found that the age at maturity was typically at age 4, and they identified mature fish as >270mm (age 4-6), which is similar to the size at maturity results I found for the Little Nahanni Arctic Grayling.

More recently, life history characteristics of fluvial Arctic Grayling populations were compiled by Ballard and Shrimpton (2009) for the Omineca region in northern British Columbia from 1956 to 2007. A considerable range of sizes for each age class was determined, with substantial overlap in size between age classes. Size at age for this population appears to be larger than the Little Nahanni River fluvial population, with age 1 fish ranging up to 150mm, age 2 up to 250mm and age 3 up to 350mm. This aligns with our understanding that growth rates slow for fish further north in latitude, and this watershed may be more productive because it's in a reservoir system. But, it may also be an artifact of the discrepancies found in using scales to age Arctic Grayling compared to otoliths. Evidence shows that age determination from otoliths is more accurate for Arctic Grayling, and that age estimates from scales tend to underestimate age compared to results from otoliths (Silkstrom 1983, DeCicco and Brown 2006). Growth rates were not developed as part of this study, but size at age ranges suggest an annual growth rate for young-of-year, juvenile and sub-adult fish similar to the 40mm/yr used by Hubert et al. (1985) for riverine Arctic Grayling in Alaska, with growth leveling out at approximately 300-350mm once full sexual maturity is reached (age 6). Studies are limited on age and growth of fluvial Arctic Grayling populations across size classes using otoliths. Information collected in this study on the relationship between size and maturity by specific age groups using otoliths improves our baseline understanding of the demographics for a pristine northern fluvial population. Such information can help improve the accuracy of life stage-specific habitat suitability evaluations, population monitoring, and bioenergetics modelling for the species (Laroque et al. 2014; Hartman and Jensen 2017).

4.2 Juvenile ecology

Our incomplete understanding of different life stages of fluvial Arctic Grayling may also be attributed to the difficulty of capturing juvenile fish. Arctic Grayling in northern regions are found in relatively low densities and, based on the available literature, fish between 100-200 mm are the least captured size class. Length-frequency histograms reported in other studies on fluvial Arctic Grayling populations show a bimodal distribution, similar to the results of this study, with young-of-year (<80 mm) Arctic Grayling having the highest frequency, a very low or zero frequency of juveniles and then increased frequency of sub-adults and adults (>200 mm) (Ballard and Shrimpton 2009). Results presented on the fork length and distribution in the Tanana River drainage in interior Alaska showed very few juvenile fish captured <200 mm and none <150 mm (Reed 1964), and no fish <170 mm (Tack 1980). Liknes and Gould (1987) found that age 1 (mean length 116 mm) fish made up only 12.2% of the total sample of Arctic Grayling in the upper Big Hole River in Montana. Baccante (2010) summarized results of size class distribution from studies on fluvial Arctic Grayling watersheds in Alaska, BC and Alberta, but had few data points for fish < 200 mm. The small sample sizes of juveniles captured, measured and aged has hampered our understanding of this early life stage.

The low capture numbers and limited data on age-stage determinations for juvenile fish may be a direct result of our poor understanding of the summer distribution and movements of juvenile Arctic Grayling in fluvial populations. The potential for temporal and spatial variation in summer movements and distribution of juveniles may make them more elusive in these fluvial systems. MacPherson et al. (2012b) evaluated sampling techniques for low-density Arctic Grayling in wadeable streams in the watershed of the Athabasca River in Alberta. Their study compared backpack electrofishing and angling, and found that both gear type and timing of sampling influenced the size of Arctic Grayling captured. Juveniles were captured with some efficiency using electrofishing, whereas the number of Arctic

Grayling >110 mm captured/km was 3.1 times greater using angling. These results led them to recommend using both gear types over a wide sampling period to effectively sample for all life stages of Arctic Grayling. In a recent study by Bentley et al. (2015), inter-tributary movements and habitat use by adfluvial Arctic Grayling were monitored in the Wood River basin in Alaska. Fish were collected in four tributary creeks using a fine-meshed stick seine, with results showing >87% of Arctic Grayling captured between 100-300 mm. The large proportion of fish between 100-200 mm collected in this study, compared to others, demonstrates the need to include various sampling methods to increase the probability of capturing juveniles and sub-adults in smaller tributary creeks. Ballard and Shrimpton (2009) analyzed data from 1956-2007 on fluvial Arctic Grayling in the Omineca Region of BC and presented the combined length-frequency results, as well as results separated by sampling methods. Their results showed a bimodal distribution of lengths, similar to my results in the Little Nahanni watershed, with the lowest frequency of Arctic Grayling captured between 150-250 mm. However, when separated by sampling method, the highest frequency of fish captured between 100-200 mm were from studies where seining was used, and fish between 200-300mm where angling was used. These studies demonstrate that in Arctic Grayling surveys, neither electrofishing nor angling were effective for capturing juveniles. Again, the use of multiple gear types, and those appropriate for the life-stage of interest, will increase the capture of Arctic Grayling across life stages.

In addition to sampling bias, juvenile grayling may have been missed due to the study design itself and the criteria used to select suitable stream habitats for sampling. The seasonal migrations and summer distribution of fluvial Arctic Grayling in the Tanana River drainage in Alaska were described where juvenile and sub-adult fish followed the adult fish in pre-spawn migrations to spawning habitats and post-spawn migrations to summer feeding areas. Summer feeding distribution for fluvial Arctic Grayling changed during the life cycle, with juvenile fish (age 1-3) occupying the lower portions of rivers and tributaries compared to sub-adults in mid-reaches and adults in the upper reaches (Tack 1980). This size and age gradient along river and stream habitats created a summer feeding distribution pattern of increasingly larger, older fish as you move upstream. The size gradient pattern of summer distribution along stream lengths has been supported in further studies of fluvial Arctic Grayling populations (Hughes 1999; Baccante 2010). While Tack (1980) observed that juvenile Arctic Grayling followed the movements of adult fish into spawning and feeding areas in lower portions of stream, he speculated that smaller tributary streams may be important rearing habitats for juvenile fish. Arctic Grayling in the Kuparuk River of northern Alaska have been studied for decades, where juvenile fish are more often observed in smaller streams (Buzby and Deegan 2000). Additional study on the juvenile Arctic Grayling life stage to improve our understanding of habitat use in small tributaries connected to mainstem river habitats, was identified as a need for assessing impacts within BC's Williston Reservoir and Upper Peace River watershed (Stamford et al. 2017). In a more recent study, juvenile and sub-adult Arctic Grayling (100-300mm) were observed to conduct inter-tributary movements across a network of four small tributaries in the Wood River basin in Alaska (Bentley et al. 2015). They found that, within a summer, juvenile Arctic Grayling undertook large-scale movements, and that approximately 50% of individual fish moved among two or more tributaries separated by seven km or more. Although these Arctic Grayling are using tributary streams that flow into a larger lake within a river system, this inter-stream movement indicates that juvenile fish may use and move between numerous small tributary streams within a single summer season. Large-scale movements using multiple streams throughout a single season suggests that juvenile grayling may have habitat requirements with greater temporal and spatial variation than previously thought. Over the summer, changes in foraging opportunities and temperature resources among tributaries may drive juvenile grayling movement to different habitats to maximize growth (Werner and Gilliam 1984; Gowan and Fausch 2002; Armstrong et al. 2013). Summer movement among tributaries by juvenile Arctic Grayling suggests that these fish may have been missed in my study, where criteria used to identify suitable habitat patches (e.g. catchment area or stream order) did not included sampling of multiple smaller tributary habitats connected to the Little Nahanni River. As we continue to learn more about capture efficiency, summer distribution, movement, and behavior of juvenile Arctic Grayling, sampling designs and methods targeting this life stage can be adapted and refined.

The paucity of data on juveniles is a likely result of the lack of emphasis put on this life stage in Arctic Grayling studies, compared to adults, spawning requirements, and YOY development, so it is underrepresented in the literature. Study designs and sampling gear may unintentionally exclude juveniles. Similar to taxonomic bias that occurs for select species in ecological studies (Link, 2007; Pysek et al. 2008), the interpretation of information for a species can be biased towards the specific life stage that has been emphasized in the research. Consequently, for Arctic Grayling, the importance of the juvenile life stage may be understated and the distinction of a sub-adult life stage may be absent, misrepresenting and misinforming our understanding of habitat and ecology for the lifecycle of the species. Identifying a shift in reproductive development and habitat use from juvenile to sub-adult within the life cycle has implications for other salmonids and fish species, as it likely occurs in others. Ontogenetic dietary shifts over the life span of individual fish are recognized as providing key insights into the biological and ecological processes at play for individuals, populations, and communities (Sanchez-Hernandez et al. 2019).

4.3 Distribution of Arctic Grayling life stages across sub-watersheds

Differences in summer habitat distribution and habitat use of the Arctic Grayling life stages were apparent in my study results, where different life stages used separate sub-watersheds (Figure 3). The Guthrie sub-watershed and Dozer tributary provided suitable spawning habitat, rearing areas for YOY, and juvenile habitat. Both of these systems are distinct from other sub-watersheds in that they are fed by small lake and bog areas, rich in organic matter, with low elevation and gentle gradient stream habitats. Both streams provided warmer water temperatures, and an abundance of gravel substrate and run habitat required for Arctic Grayling spawning and rearing. Juveniles were found in the fewest number of sites across the four sub-watersheds (n=11), indicating that they may have been missed in the study design. Of the sites occupied by juveniles, they were found primarily in the spawning tributaries, but also utilized lower portions of creeks and tributaries near the confluences of colder tributaries in Guthrie Creek and into lower Fork Creek. The presence of juveniles in the lower reaches of the sub-watersheds agrees with the findings of other researchers on size-gradients of larger fish upstream in Arctic Grayling distribution along stream lengths (Tack 1980; Hughes 1999; and Baccante 2010). Fork and Lened sub-watersheds provided suitable summer habitat for sub-adult and adult grayling. Both are high energy stream systems characterized by high elevation and cold water, and dominated by cobble-riffle and boulder-pool habitats. Sub-adults occupied sites with all other life stages indicating that habitat use during this developmental stage is dynamic and variable. But, they were found in highest abundance in the same systems as adult fish, occupying sites along with adults, but also using a broader range of downstream sites. The presence of sub-adults across the sub-watersheds provides some additional insight into movement of Arctic Grayling across life stages, and supports observations that sub-adults follow the movements of adult fish as a potential mechanism for imprinting to both spawning and summer feeding habitats (Tack 1980; Armstrong 1986).

The nature of the stream habitats in the four sub-watersheds studied along the Little Nahanni River, and the distribution of Arctic Grayling life stages across these systems, follows a similar pattern to what has been documented in other mountain river systems (Wojcik 1955; Reed 1964; and Tack 1980). The importance of relating observed Arctic Grayling migrations and distribution to functional stream types, has long been recognized. For example, Wojcik (1955) proposed four different stream types for interior Alaskan river systems: bog-fed streams, spring-fed streams, rapid runoff streams and glacier-fed streams. Other researchers consistently found that most bog-fed streams of interior Alaska are used for spawning by Arctic Grayling, as they are the warmest part of the system. Juvenile and sub-adult fish followed the spawning migration of adult fish into the bog-fed streams. Post-spawn, most adult and sub-adult fish left the bog-fed streams and migrated to either the parent river or moved into spring-fed or un-silted rapid runoff streams for summer feeding (Tack 1980; Armstrong 1986). Tagging studies on Alaskan Arctic Grayling populations showed a pattern of adult and sub-adult fish returning to the same un-silted rapid runoff streams for summer feeding over successive years, with larger fish dominating the further upstream reaches and sub-adults typically in mid to lower reaches of the stream (Schallock and

Roguski 1967; Pearse 1974; Tack 1975). Juveniles were almost exclusively in the lower stream sections, and the numerous tiny tributary streams were noted to likely be important for juvenile rearing (Tack 1980). The results of my study provide additional insight on the nature of fluvial Arctic Grayling summer habitat use in mountain watersheds throughout their life cycle. My findings are supported by other Arctic Grayling studies, particularly those from Alaska, related to the spatial extent of migrations undertaken from the main stem river system into tributary streams, and the diversity of stream habitats used throughout its life history.

4.4 Characteristics of sub-watersheds and patterns of stream types

Viewing the broader watershed of the Little Nahanni, the patterns of Arctic Grayling occupancy in relation to stream types available in the four study systems raises interesting questions regarding why certain tributaries are occupied with higher abundance, and others are not. The low elevation, gentle gradient, lake and bog-fed streams found in valleys provided warm water spawning and nursery habitat for Arctic Grayling, however it is not as clear for adults. At the watershed scale, the course-level environmental criteria used to develop this study design do not appear to capture the variation among the sub-watersheds that separates suitable summer habitats for adult Arctic Grayling. Much time and effort was spent sampling March and Lened Creeks with low success.

The majority of adult Arctic Grayling were captured in Fork Creek. When the results of adult Arctic Grayling occupancy of Fork, March and Lened Creeks are compared to the stream pattern morphologies and site-specific data on each sub-watershed, differences emerge between the physical characteristics of the channels and the abundances of adult fish. The drainage basin of Fork Creek is spread across a wider area with longer tributary patches, that are more frequent along the length of the creek, dividing up the main channel. The valley walls of the March Creek drainage basin are narrow having a steeper relief, with three shorter tributaries all converging in close proximity at a higher elevation in the headwaters, confining the creek to one long straight main channel (Figure 3). The characteristics of the Lened Creek sub-watershed are similar to those of March Creek, with the drainage system being confined within narrow steep valley walls, having two long straight tributaries without any other major tributaries converging along their lengths. Hydraulically, the drainage configuration of Fork Creek offers more diversity because of the substantial tributary inputs along its length and a broader basin for the channels to move within. This complexity was observed from the site-specific data collected on Fork Creek where eroding banks contributed to the active movement of materials into the channel creating areas of alluvial outwashes, riffles and boulder-pool cascades. The hydraulic characteristics of Fork Creek may offer greater velocity refugia, allowing fish to move upstream in the system, and more opportunity to hold and feed in cascade pools. The dynamic erosion and deposition in Fork Creek opens the active channel offering substrate types, hydraulic conditions, and light environment that may allow for slightly warmer water and greater macroinvertebrate productivity, which was supported by field observations of higher biomass of mayfly larvae captured in the nets while electrofishing (Figure 11). In contrast, March and Lened Creeks had straight channel configurations, showed no evidence of active erosion and deposition along the stream banks, indicating that the channels likely have high conductance that can move water quickly downstream. These two creeks had higher mean velocities, colder mean water temperatures, and contained few Arctic Grayling compared to Fork Creek.

Figure 11. Mayfly larvae captured in electrofishing nets during fish survey in Fork Creek, Little Nahanni River watershed, NWT, July 2015. Photos taken by Dr. Pete Cott.

Identifying natural habitat variability across lotic systems and linking those variables to the various life-cycle requirements of fish, is a challenge (Schlosser 1991), but is needed for the effective monitoring and assessment of stream-dwelling species. Spatial criteria for evaluating watersheds can be useful indices of stream habitat subsystems, natural variability in a stream, and the potential capacity for suitable fish habitats (Frissell et al. (1986). However, this approach is not without its difficulties. For example, stream size estimated by catchment area can overestimate the actual surface area inhabited by fish; whereas, evaluating the potential for habitat heterogeneity and diversity available in a watershed can help to better predict the possible resources and niches available (Hugueny et al. 2010). Broad morphological characterization of a watershed, such as valley morphology, channel longitudinal profile, dimensions and patterns of channel networks, evaluates variables that help to identify stream types and physical habitat features (Davies et al. 2000). These spatial criteria for evaluating watersheds can be useful indices of stream habitat subsystems, natural variability in a stream, and the potential capacity for suitable fish habitats (Frissell et al. (1986). Discharge has been found to provide a better surrogate of the surface area of habitat available for fishes than catchment area (de Wit and Stankiewicz 2006). Looking at the watershed to stream relationship, and the stream to channel relationship, across these Little Nahanni study creeks, may help to identify the potential suitability of habitat patches, at a broad scale, for different life stages of Arctic Grayling within sub-watersheds with greater accuracy. Distinguishing habitats at a watershed-scale and relating those to the different life stage requirements of Arctic Grayling would lead to more effective methods of evaluating stream ecosystems, improved accuracy for targeted fish assessments in un-surveyed mountain regions, and ecologically relevant criteria for distributional monitoring of fluvial Arctic Grayling.

4.5 Landscape influence on fish population dynamics

Large-scale spatial relationships between different stream types within a watershed is also recognized as having an effect on resource use and movement of fluvial fish populations (Schlosser 1995a). The patch dynamics concept in stream community ecology and the landscape ecology view of rivers as a mosaic of habitat patches that can determine ecological processes across multiple spatial scales, were put forward as frameworks to enhance the understanding lotic systems (Pringle et al. 1988 and Townsend 1989). Various life stages of stream fish require different kinds of physical habitat, therefore spatial heterogeneity and connectivity between habitat patches are recognized as critical components for reproduction and survival of fish (Schlosser 1991). The spatial arrangement of habitats within the landscape or riverscape can influence the persistence of populations, where different habitat patches required by a species that are closer together will support more stable populations, therefore increasing the population size in that region of the watershed (Dunning et al. 1992). In my study area, this could provide additional explanation for the greater occupancy and abundance of Arctic Grayling in Fork Creek, because of its proximity to different stream habitats provided by Guthrie Creek.

The concept of optimal habitat ratios has been used to assess habitat requirements of stream fishes. It evaluates not only the abundance of different habitat types (e.g. riffle and pools) within a stream, but the proportional abundance of essential and potentially limiting habitats (e.g. spawning, rearing, overwintering) required for different life stages over a broader watershed-scale (Rosenfeld 2003). For fluvial Arctic Grayling, with life stages occupying different habitats and sub-watersheds across lotic systems, the concept of optimal habitat ratios or configurations may be useful to identify suitable habitat patches across a broad watershed. The results of my study perhaps shed some light on the potential scale of fluvial Arctic Grayling migration and ranging behaviour, and distances moved among sub-watersheds to reach suitable habitats required throughout their lifecycle. It may help to understand potential limiting habitat factors, such as proximity and connectivity of suitable spawning and rearing habitat to suitable streams with summer habitat for adults. Informed species management requires knowledge of which habitat factors may limit a population, and how these factors vary over space and time within a species range (Schlosser 1995a). My study has provided an opportunity to look at correlations between different life stages of Arctic Grayling and stream habitat types within the context of intact mountain watersheds. It also provides a natural reference or baseline to evaluate habitat requirements and identify suitable habitats required for fluvial populations in northern mountain regions.

4.6 Fluvial Arctic Graying habitat use across life stages

Similar to what has been found at larger spatial scales, habitat use within streams can be dynamic and have strong associations to particular in-stream habitat types throughout the life cycle of the fish (Schlosser 1991). By sampling entire sub-watersheds and ground-truthing stream characteristics, my study has provided an intermediate level to evaluate habitat use. From stream sub-watershed to reach scale, I was able to identify patterns of in-stream habitat use and garner information on the relationships between Arctic Grayling life stages and habitat variables.

4.6.1 YOY

My results on YOY habitat use support the findings of Lewis (2018) where water temperature and elevation were the most important drivers of YOY presence across the sub-watersheds. YOY were not found in any sites were water temperatures were <6 ºC and showed the highest probability of occupancy at water temperatures >8 ºC. The mean water temperature was 7 ºC across all sites sampled in the sub-watersheds of the Little Nahanni, demonstrating that these northern mountain systems are warm water limited, and highlighting the different conditions facing northern versus southern Arctic Grayling populations. The importance of warm water temperatures in the spring for Arctic Grayling spawning has be documented across northern regions for both fluvial and adfluvial populations (Scott and Crossman 1973; Northcote 1995; Stewart et al. 2007a). Spawning areas also provide important nursery habitat required to rear YOY fish after emergence. In my study, YOY fish were only found in habitat patches in Guthrie and Dozer creeks, which were the only two sub-watersheds sampled that provided suitable spawning habitat conditions, based on our current understanding of fluvial Arctic Grayling habitat requirements. Temperature and elevation, along with the increased probability of YOY presence associated with run habitat and gravel substrate, indicate that Guthrie and Dozer creeks likely provide critical spawning and rearing habitat. In this study, the correlation of YOY to silt-sand substrate, and their absence in cobble and boulder habitats, provides data that can be used to refine life stage-specific habitat suitability indices (HSIs) for the Arctic Grayling fluvial life history. Arctic Grayling HSIs have been developed to provide indices of suitability to different substrates for each life stage, where YOY are given a relatively high suitability (i.e. 0.6+) to boulder, cobble and rubble substrate (Laroque et al. 2014). However, my findings indicate that for YOY in northern mountain fluvial populations, the suitability of stream habitats with boulder and cobble substrate may be much lower. Existing HSIs specific to Arctic Grayling riverine populations identify important habitat variables associated with spawning success and embryo survival, where the percentage of silt-sand substrate (fines) is negatively correlated with embryo survival prior to emergence, and the percentage of pool habitat downstream from spawning areas is important as nursery habitat (Hubert et al. 1985). However, my results did not show a strong relationship between YOY and pool habitat in the streams studied, rather the proportion of silt-sand substrate consistently arose as an important variable for YOY presence.

Guthrie and Dozer Creeks are both located in wide, low gradient, organic rich mountain valleys fed by lake and bog systems that are heavily influenced by beaver (*Castor canadensis*) (pers. obs.). Both creeks had the highest mean water temperatures and the most abundant run habitat available across the sub-watersheds studied. The open flat nature of these streams, with dark organic substrates, would allow for greater light and heat absorption, warming the water faster than the other study streams. These factors indicate that low-lying, organic-rich systems provide important warm water, hydraulic conditions, and substrates suitable for spawning and rearing, and may be key limiting habitats for the production of Arctic Grayling and success of local fluvial populations. Similar results from studies conducted in interior Alaskan watersheds, found that lake and bog-fed systems were used predominantly as spawning and rearing habitat by Arctic Grayling (Tack 1980; Armstrong et al. 1986). The results of my study show that northern mountain watersheds are likely warm water limited, therefore stream habitats that warm first in the spring, providing stable warm water temperatures and low-gradient flow, likely provide critical habitat for reproduction.

4.6.2 Juveniles

Juvenile Arctic Grayling were not found in water temperatures <6 ºC. Similar to YOY fish, juvenile presence showed a strong response to elevation, indicating that lower elevation stream habitats provide important summer habitat for the juvenile life stage. Interestingly, and contrary to what I had predicted, run habitat came out as a significant factor for juveniles. Cover variables and substrate did not show a strong influence on the presence of juvenile Arctic Grayling in available stream habitats across the four sub-watersheds. They primarily used the same tributaries as YOY, suggesting that putative spawning streams are important for juveniles, as well as YOY. The value of run habitat for juveniles, versus water velocity or cover, may be an indicator of the productivity of run habitat in these warmer spawning streams. The energetic cost of holding in run habitat may be outweighed by increased food availability required for growth of early life stages. These findings for juvenile Arctic Grayling provides support for the recommendation that HSI models be refined to fit local conditions (USFWS 1981). As an example, HSIs based on existing data for juveniles in other regions provide very low suitability values (<0.3) to run habitat for juveniles and YOY (Laroque et al. 2014), in contrast, I determined the probability of juvenile presence >60% when the proportion of run habitat exceeds 50%.

The results of my analyses also show that within the juvenile life stage there appears to be movement towards cooler water temperatures and wider more riffle dominated habitats relative to those used by YOY, which may be the first signs of ontogenetic separation. In Guthrie Creek, juveniles were captured in the same patches as YOY fish, with the exception of a small colder tributary draining to the main channel. One juvenile Arctic Grayling was captured in a downstream site in the main channel of Fork Creek. It is likely that this juvenile moved into Fork Creek from the Little Nahanni River, as the results of sampling in the Fork Creek sub-watershed did not find habitat patches with typical or suitable Arctic Grayling spawning or rearing habitat, based on our current understanding, and no other juvenile fish were captured in the upstream habitats sampled in Fork Creek. Although these data are from only one sample site, it provides some indication of the movement and swimming ability of juvenile Arctic

Grayling, and similar to other observations, the immature fish may be following the spring and summer migrations of mature fish to find suitable feeding habitats (Tack 1980; Hughes 1999; Baccante 2010).

It should be noted that there may be a diurnal aspect to juvenile habitat use that was undetected. Sampling was conducted between 9:00-19:00h, so there may be other suitable habitats that are used by juveniles at other times of the day, as movement by juveniles has been observed in Arctic Grayling populations and other salmonid species. For example, in tundra streams the majority of Arctic Grayling movements between suitable habitats occurred at night (Cahill et al. 2016). Although in northern latitudes there isn't full darkness during summer months, the sun is at a lower angle providing less light. In addition to Arctic Grayling, other salmonids are known move daily or seasonally. Juvenile Arctic Grayling and Rainbow Trout have been shown to make kilometer-scale movements within and between different tributary streams to take advantage of summer foraging opportunities (Bentley et al. 2015). Juvenile Coho Salmon were found to make diel horizontal migrations of 350-1300m to exploit different thermal and trophic resources within a stream (Armstrong et al. 2013).

4.6.3 Sub-adults

Sub-adult Arctic Grayling showed a wider distribution among the sub-watersheds than other life stages. They were most frequently captured in cold, cascading boulder-pool habitats along with adult fish in Fork and Lened creeks. However, they were also captured in smaller tributary streams feeding into Guthrie Creek, warm run habitats with YOY and juvenile fish in Dozer Creek, and wide riffle-dominated areas further downstream in Fork Creek. Evidence of the dynamic nature of the sub-adult habitat use is clear, with their presence detected in a wide range of elevations and stream widths and in each habitat type. Sub-adult Arctic Grayling are large enough to move into a variety of habitats, but small enough that factors such as competition with adult fish for food resources, and avoidance of predators may play an important role in determining which stream habitats they use. Dominant feeding behavior based on size has been documented for riverine Arctic Grayling and is thought to drive both within-pool distribution patterns and upstream to downstream size gradients, where larger fish have a competitive advantage over smaller fish for the most desirable upstream feeding positions (Hughes 1992; Hughes 1999; Baccante 2010). Smaller Arctic Grayling have been found to colonize downstream areas because of exclusion from upstream habitats by larger Arctic Grayling (Hughes and Reynold 1994). As with other animals, territorial adults force the sub-adults to roam into different habitats to find sufficient resources. In this study, sub-adults occupied the widest range of habitats of the Arctic Grayling life stages, demonstrating a stronger swimming ability than juveniles allowing them to cover more territory and tolerate higher velocities, lending itself to the evidence that sub-adults are a distinct life stage.

Elevation and temperature were not factors influencing the probability of sub-adult presence, as they were for the other life stages; however, on average, sub-adults were found in sites >1200 masl and <8 ºC. Sub-adult Arctic Grayling showed similar correlations to habitats used by adults, indicating that during this stage of growth and reproductive development, they likely move with adult fish on pre-and post-spawn migrations to summer habitats, similar to what has been observed by others in other fluvial Arctic Grayling populations (Armstrong 1986). My study demonstrated that sub-adults can take advantage of a diversity of available stream habitat conditions, as they mature and move to seek out suitable habitats. A recent example of this includes a study by Heim et al. 2016 on Arctic Grayling seasonal migrations between habitats along the coastal plains of Alaska, where fish with fork lengths up to 279 mm were classified as juveniles, but the juveniles were found to have two distinct migrations: one of larger juveniles in the spring coinciding with adults, and another of smaller juveniles in September. Both groups of juveniles, considered the same life stage in this study, are using different summer habitats making it difficult to identify and describe distinct summer habitat requirements for the juvenile life stage when defined this broadly. However, results from my study indicate that the sub-adults, which likely composed the first migration of larger juveniles, represent a distinct life stage with its own suite of habitat requirements. Understanding these distinctions between life stages has important implications for management of the species, and ensuring the conservation and restoration of appropriate habitats to support population success.

4.6.4 Adults

Adult Arctic Grayling found in my study occupied specific streams in high elevation habitats during the summer, similar to those reported for fluvial populations in interior Alaska (Tack 1980; Armstrong 1986). No adult Arctic Grayling were observed or captured in either Guthrie or Dozer creeks, even during the first week of July, where spawning had taken place and YOY had emerged. Adult fish are known to move into warm water, low gradient streams in early spring to feed prior to spawning, and may remain to feed post-spawn. In my study area, spawning likely takes place in early June, so adults would be present in warmer, low elevation, low gradient spawning streams through May and June prior to migrating to summer habitats, such as Fork and Lened creeks. Adult Arctic Grayling had more specific habitat associations than sub-adults, occupying sites with elevations >1200 masl, water temperatures averaging 7°C, and higher proportions of pool and boulder habitat. The mean water velocity at sites where adults were observed was 0.8 m/s. Water velocity is recognized as an important habitat variable for stream fish, and is often evaluated in terms of both habitat suitability for species and life stages, as well as in-stream flow requirements for impact assessments. Adult Arctic Grayling in the Little Nahanni area were captured in sites with water velocities up to 1.3m/s, but were more abundant in sites with water velocities <0.9m/s during the summer, similar to what is reported from other studies (e.g. Laroque et al. 2014). Fork Creek offered a wide active channel with a variety of substrates, and more tributary habitat contributing to diverse hydraulic conditions. It supported the highest abundance of adult Arctic Grayling and can serve as a template to identify adult summer habitats for other fluvial populations in northern mountain regions.

4.7 Management implications

Studying Arctic Graying habitat use in regions across its range continues to provide new insights on how different life stages and life history types use their environment. By better understanding the relationship of size-age-life stage for these populations it enables more accurate interpretation of population data. Evaluation of watershed-scale characteristics of Arctic Grayling distribution is important to determine patterns at broader spatial scales to improve our ability to identify suitable habitat, to design more efficient monitoring programs, and to develop ecologically relevant occupancy models for fluvial populations in northern watersheds. From the watershed to the sub-watershed to the stream-scale, it is important to understand how each life stage of Arctic Grayling uses the available stream habitats and what habitat conditions are required to complete its lifecycle. Identifying upper and lower bounds and thresholds within the stream habitat variables for each Arctic Grayling life stages will help to refine life stage-specific models, therefore improving our ability to support decisions by land and resource managers that make ecological sense for the species.

4.8 Conservation and protection of fluvial Arctic Grayling

The Little Nahanni watershed, like other northern ecosystems, is experiencing the realities of multiple stressors. New access routes are opening up the Little Nahanni area to increased resource development and recreational activity. Seismic exploration for shale oil in the mountain ranges of the Sahtu Settlement Area, north of the Little Nahanni watershed, has been ongoing for years. Impacts of climate change in the north are affecting permafrost at the landscape-scale with megaslumps impacting watersheds and the having dramatic effects on the aquatic life within (Kokelj et al. 2013, Chin et al. 2016, Kokelj et al. 2017), temperature and hydrologic regimes are shifting, and increased forest fire activity is changing landscapes (Box et al. 2019; Bush and Lemmen 2019). At the circumpolar level, government agencies, Indigenous organizations, non-government organizations, and academia across the Arctic have worked to coordinate efforts for the long-term monitoring of Arctic freshwater biodiversity to effectively measure and compare biodiversity status and trends (Culp et al. 2011). Frameworks for the approaches, spatial scales, metrics and standardized methods for freshwater biodiversity monitoring have been proposed, including linking population and ecosystem approaches to understand effects to freshwater biota in a changing environment.

Myers et al. (2017) conducted an extensive review of existing studies on documented and projected effects of climate change on inland fish. They identified a discrepancy between the focus of research on projected effects of climate change (being primarily on predicting distributional shifts species range and community assemblage) and the focus of studies that documented effects on individuals (emphasizing phenological changes, such as migration, spawning, emergence). They identified a need for future research that includes long-term studies and monitoring networks to supply data that documents effects, both distributional and phenological. In response to a changing climate, salmonids are predicted to exhibit increased growth, yet results to date have found a greater decrease in abundance for salmonids than what was projected (Myers et al. 2017). My study provides useful information on the dynamics of fluvial Arctic Grayling summer habitat use both within and across mountain watersheds. The data on fish distribution and abundance, along with stream habitat evaluations provide an environmental baseline reference from which to monitor change.

The spatial extent of the sampling design implemented in my study, allowed for the collection of spatially continuous data on fish distributions and stream habitats across four sub-watersheds, providing a broader picture of Arctic Grayling habitat use across the Little Nahanni watershed. This helped to identify summer habitats important to different life-stages of Arctic Grayling at a scale at that reflects their life-history, and a scale relevant to decision-making by resource managers and future monitoring programs in this area and elsewhere fluvial Arctic Grayling occur. Improved understanding of the different and shifting habitat requirements throughout its fluvial life history, at a broad watershed scale, may allow resource management, land use planning and habitat protection decisions to be more effective in meeting conservation objectives for this species.

4.9 Environmental assessment, regulatory review, and monitoring

The Little Nahanni River and its tributaries are located in a region that has become a patchwork of jurisdictional boundaries and competing land use interests. The traditional territories of the Dehcho and Kaska Dena, and the Sahtu Settlement Area converge in the Little Nahanni River watershed. In 2008, the Nahanni National Park Reserve was expanded and the Naats'ihch'oh National Park Reserve was established to protect the headwaters of the South Nahanni River, including areas of the Little Nahanni

River watershed. However, historic winter access road easements for mineral exploration and existing mining lease areas have been grandfathered in, leaving the majority of the tributary systems within the watershed, including Guthrie, Fork, Dozer and Lened creeks outside of the park boundaries.

The Little Nahanni is located in the Selwyn Mountains where there are extensive lead-zinc deposits. In 2014 and 2015, the Howard's Pass Access Road (HPAR) was built, of which 48km (of the 79km long all-season road) runs along the southwest side of the Little Nahanni River, to access the Selwyn Project, a proposed lead-zinc mine located on the Yukon side of Howard's Pass. There are plans to upgrade the Nahannni Range Road to improve access to the Little Nahanni River area from the Yukon. A proposal to expand the HPAR is currently undergoing environmental assessment and regulatory review in the NWT (MVRB EA-1516-01, MV2015F0012, and MV2015L8-0005). The proposed upgrade to HPAR includes 32 watercourse crossings (8 bridges and 24 culverts) and will require widening of the right-of-way, upgrading of crossings, development of borrow sources along the route, as well as camps and staging areas along the length of the Little Nahanni River. Linear developments in northern areas have documented affects on sensitive aquatic ecosystems and important fish habitat (Cott et al. 2015). The current regulatory framework used to assess watercourse crossing requirements for roads does not focus on the smaller drainages when evaluating potential impacts to fish and aquatic habitat. Spring freshet high water flows and aquatic assessments have not been conducted for all small tributaries flowing into the Little Nahanni that are crossed by HPAR (Selwyn Chihong Mining Ltd. 2015). The potential importance of small tributary streams to the juvenile life stage of Arctic Grayling, and the need to understand both spring and summer flows in the small drainages is of immediate relevance to the evaluation of watercourse crossings for continued road development. The baseline information collected in my study, and the results presented, will have direct application to the evaluation of potential impacts to fish and aquatic resources, and mitigation and monitoring requirements for the expansion of HPAR and other development projects in the watershed.

In 2017, mining exploration activity began on a mine lease area located in the Guthrie Creek sub-watershed (MV2017C0021). The exploration work is taking place in the headwater cirques that feed multiple tributaries flowing into the main channel of Guthrie Creek. The downstream areas of Guthrie Creek are known fish habitat. Arctic Grayling and Slimy Sculpin were captured in the tributaries immediately downstream of the mine exploration activity. My study demonstrates that Guthrie Creek provides an important Arctic Grayling spawning area, and summer habitat for YOY, juvenile and sub-adult life stages. The ecological baseline I have established can be used by resource management agencies for evidence-based decision making and enable monitoring for change over time. Improved understanding of fish species present, Arctic Grayling distribution, and fish habitat use in creeks that overlap with the Howard Pass Access Road and mine lease areas can inform current and future assessments of northern mountain watersheds.

4.10 Fluvial Arctic Grayling habitat restoration

There have been a number of fish habitat compensation and restoration projects in the north focused on Arctic Grayling, primarily related to habitat loss from the impacts of diamond mines to adfluvial populations in the barrenland regions of the NWT (Jones et al. 2003c; Jones and Tonn 2004; Courtice et al. 2014; Baker et al. 2017). As development continues, the need to offset Arctic Grayling habitat losses and to restore impacted habitats will also continue. Large-scale mine remediation projects in Canada's north, like Giant and Faro mines, must manage previously impacted aquatic habitats, and consider ways to protect and restore Arctic Grayling habitats. The results of my study provide additional insights, at a watershed-scale, on important habitat relationships and requirements for fluvial Arctic Grayling that can inform the evaluation of restoration needs and habitat suitability for various life stages of the species.

4.11 Southern population habitat impacts

My study of a fluvial population, in nearly un-impacted habitats, provides insight on the challenges faced in trying to manage, protect and restore essential stream habitats and habitat complexes at watershed-scales that are required by Arctic Grayling to complete its lifecycle. This information helps to identify potentially limiting habitats for life stages that could be restricting the success and stability of populations in other regions (e.g., the Williston Reservoir in northern BC).

Of particular interest is the importance of cold-water resources to adult Arctic Grayling. The adults (and most of the sub-adults) were found in separate tributaries using high elevation cold water habitats. Northern river systems are warm-water limited and southern rivers are becoming increasingly cold-water limited. The mean water temperature for all sites sampled across the Little Nahanni between July-August was 7°C. The only sub-watersheds within the study area that reached mean temperatures >8 °C were the low elevation bog and lake fed systems. These areas were used as spawning habitat and rearing areas for early life stages, highlighting the importance of warm water resources for the reproductive success of these northern populations. In contrast, no sub-adult or adult Arctic Grayling were captured in any sites with measured water temperatures >11°C, as they selected sites with mean water temperatures of about 7 °C. So, although warmer water was available within the study sub-watersheds, sub-adult and adult Arctic Grayling were not found to use them over the summer. The selection of colder stream habitats in the summer by sub-adults and adults, in a cold northern watershed, adds evidence to the importance of cold-water resources to the fitness of later life stages of fluvial Arctic Grayling.

In Alberta, the loss of access to higher elevation stream habitats and land use disturbance that changes temperature regimes in tributaries and watersheds that support Arctic Grayling populations, may affect the overall fitness, survival and reproductive capacity of adult fish. Compounded with the projection of continued warming from climate change, cold water is likely to become a significant limiting habitat for Arctic Grayling populations in the southern portions of their range (Cahill 2015). Conservation and protection of existing summer cold water resources for sub-adult and adult Arctic Grayling, restoring connectivity to high elevation habitats, and restoration of areas that can help to naturally cool streams (e.g. those with groundwater inputs and riparian cover) may become increasingly important for southern populations.

4.12 Recovery and re-establishment of populations

Populations of Arctic Grayling in Michigan were extirpated in 1936, primarily due to overfishing, introductions of non-native fish, and large-scale habitat loss (Vincent 1962). Recently, interest by Indigenous groups in the potential re-establishment of fluvial Arctic Grayling to the Big Manistee River has led to abiotic assessments of suitable stream habitats and evaluation of methods for re-introduction of the species within the watershed (Danhoff et al. 2017, Wilson 2017). The upper Big Hole River drainage in Montana hosts the last remaining population of native Arctic Grayling in the USA, outside of Alaska. The historic range of Arctic Grayling in Montana has been significantly reduced the current population has required active management and restoration efforts for over 20 years, including re-introduction attempts using brood stock (USFW 2015). Understanding of the watershed-scale distribution for fluvial Arctic Grayling in the Little Nahanni River, as well as population structure and life stage specific habitat use, can provide a natural reference for comparison. It provides an important picture of a population that has evolved in the absence of non-native species competition, fishing pressures, and habitat disturbance. My study provides insights on the intraspecific variation between northern and southern fluvial populations, and can help with the active management of populations at the limits of the species range.

5.0 Conclusions

My study advances what we know about the summer distribution and habitat use of fluvial Arctic Grayling, specifically those living in northern mountain streams. The results present evidence of the range of stream systems and habitat types used throughout the species' life cycle, including the potential niche breadth of life stages.

A key finding of this study was the identification of four distinct post-emergence life stages for Arctic Grayling in the Little Nahanni watershed. Specifically, the establishment of a sub-adult life stage and documenting the differences between the juvenile, sub-adult, and adult life stages based on biological data, distribution patterns, and habitat use. The results provide additional data on the relationship between size, age, and maturity, improving our understanding of the demographics of a fluvial population in northern mountain systems. Demographic information is important to not only to fisheries management and population monitoring, but can improve our evaluation of life stage-specific habitat requirements and understanding of the ecology of the species throughout its lifecycle. This can lead to refinements and adaptations of sampling designs and methods to target understudied life stages, like juveniles, so we can continue to learn more about their distribution, behaviour, and ecology.

The four life stages of Arctic Grayling used the available summer habitat differently within the study area, distributing into separate sub-watersheds. The YOY and juveniles primarily used warm water stream systems that meandered through low elevation, gentle gradient valleys fed by small lake and bog areas, rich in organic matter. The sub-adults and adults used high elevation, cold water stream systems, characterized by cobble-riffle and boulder-pool habitats. The distribution of the life stages across the different stream types in the study area of the Little Nahanni River followed similar patterns to what has been documented in other northern mountain river systems in Alaska. The nature of the Fork Creek drainage basin, the variety of habitat patches provided within it, and its hydraulic conditions, supported the highest abundance of sub-adult and adult Arctic Grayling of the sub-watersheds studied. The large-scale spatial arrangement of the different streams used by the life stages within the Little Nahanni watershed lends itself to the patch dynamic and optimal habitat ratio concepts of landscape ecology, where the connectivity and proximity of different habitats required by the species, across its life stages, may play an important role in predicting and identifying occupancy and abundance of Arctic Grayling in these systems. These results provide insight on watershed-scale characteristics that could help to develop ecologically relevant criteria to improve how we evaluate stream systems for Arctic Grayling occupancy and distributional monitoring in un-surveyed regions.

My results indicate that, similar to at the landscape-scale, habitat use within the study streams was dynamic and life stages showed associations to particular in-stream habitats. Arctic Grayling YOY were only found in low elevation, warm water streams, and showed a correlation to silt-sand substrate. Similarly, juvenile Arctic Grayling occupied low elevation, warm water stream habitat, but associated strongly with run habitats, as well as showing movement towards cooler water temperatures and more riffle dominated habitats. Sub-adult Arctic Grayling showed the widest range of habitat use across the sub-watersheds, being found at different elevations and water temperatures, demonstrating the dynamics of the life stage and its ability to take advantage of a diversity of stream habitat types and conditions. This life stage showed the strongest correlation to in-stream habitat types, primarily to riffle, pool, cascade-boulder habitats. For adult Arctic Grayling, there was a strong correlation to elevation and water temperature, and in this study, adults were only found in high elevation and cold water stream sections, with high proportions of pool and boulder habitat.

My study has provided additional information on the juvenile and sub-adult life stages, furthering our knowledge of early Arctic Grayling development and habitat use. It provided evidence that sub-adults can use a wide variety of available summer habitats, and it brings attention to the need to refine data collection specific to these early life stages, particularly for juveniles, so we can improve our understanding and interpretation of the life cycle of fluvial Arctic Grayling. Our limited understanding of these life stages may be hindering the ability of study designs to accurately evaluate juvenile ecology and habitat use, such as the use of smaller drainages within broader watersheds.

Of the sub-watersheds studied in the Little Nahanni River watershed, 35% of the total sites sampled had water temperatures above 8ºC, and only 15% had water temperatures above 10ºC, indicating that these northern mountain watersheds are warm-water limited, unlike watersheds in the southern portion Arctic Grayling range. The use of high elevation areas and cold water by adult Arctic Grayling during the summer months, when relatively warmer water was available, demonstrates the importance of cold water habitats to mature fish, even in cold water systems.

In addition to providing some insights on Arctic Grayling distribution and life stage-habitat relationships in a northern mountain river system, this study has established an ecological baseline in a relatively un-impacted watershed. The Little Nahanni River watershed continues to draw attention as it is recognized for both its ecological and mineral resource wealth. This baseline can be used to monitor aquatic health and assess potential impacts from a changing climate and expanding development in the watershed. The uncertainty related to the effects of climate change, the deficiency in basic knowledge on fish ecology and habitat requirements, and the lack of watershed baseline or reference conditions in a rapidly changing north, reinforces the need for improved monitoring of freshwater fish populations to understand their vulnerability to environmental variability and assess ongoing development impacts (Reist et al. 2006b; Culp et al. 2011; Christiansen et al. 2013; Poesch et al. 2016).

6.0 Research directions

Studies of fluvial Arctic Grayling populations that focus on improving our basic ecological understanding of life histories and life stages are needed. With the differing habitat requirements of different life history types and life stages, there is much to learn about this dynamic and sensitive cold-water species. Continued research on fluvial Arctic Grayling distribution and habitat use in other northern mountain watersheds may reveal patterns of summer habitat use similar to what was found in my study, and improve our understanding of the relationships between stream type, habitat characteristics, and distribution of fluvial Arctic Grayling life stages within watersheds. Relationships between environmental heterogeneity and fish behaviour are complex, requiring additional research focused on understanding differences between individuals and ontogenetic shifts within a species life cycle (Sanchez-Hernandez et al. 2019). I have summarized research questions identified through this study in Table 10, that I feel should be addressed in future studies on fluvial Arctic Grayling habitat use and distribution in northern mountain watersheds.

Table 10. Opportunities and questions for future research on fluvial Arctic Grayling in northern mountain watersheds.

Topic	Research Question	Source
Fluvial Arctic Grayling – adult habitat use	Do springs or ground-water inputs provide important temperature and habitat conditions within the streams selected by adult Arctic Grayling over other tributaries in the Little Nahanni watershed? Is this true for adult Arctic Grayling habitat use in other northern mountain watersheds? How does the aquatic productivity compare between the different sub-watersheds of the Little Nahanni River, specifically Fork, Lened, and March creeks? Do differences in productivity between tributaries influence summer occupancy by adult Arctic Grayling?	Tack 1980; Mochnacz et al. 2013; Dunmall et al. 2016; Lewis 2018; McPherson 2020
Fluvial Arctic Grayling – sub-adult life stage	Is there a shift in reproductive development and habitat use for Arctic Grayling approximately 170mm in length in other northern fluvial populations? What are the age ranges where this shift is found? Is the variability of stream habitats used by the sub-adult life stage found in other northern mountain populations? Is there a trophic difference or ontogenetic shift between juvenile and sub-adult life stages and sub-adult and adult life stages that could provide an additional line of evidence to evaluate the distinctiveness of the sub-adult life stage for fluvial Arctic Grayling?	Tack 1980; Sanchez-Hernandez et al. 2019; McPherson 2020

Topic	Research Question	Source
Fluvial Arctic Grayling – juvenile habitat use	Do juvenile Arctic Grayling use smaller first or second order tributaries draining directly into the Little Nahanni River as spring and summer habitat? How are the smaller drainages being impacted by road crossings and mining development in the Little Nahanni watershed? Does the inclusion of angling and seining in the sampling techniques improve the capture efficiency for juvenile Arctic Grayling in these fluvial mountain systems? Is it feasible and effective to include seining as a sampling method in lower portions of tributary systems or smaller drainages?	Tack 1980; Bentley et al 2015; Stamford et al. 2017; McPherson 2020 MacPherson et al. 2012; Bentley et al. 2015; McPherson 2020
Fluvial Arctic Grayling – spawning and YOY habitat	How important are low-gradient lake and bog-fed sub-watersheds to fluvial Arctic Grayling spawning and YOY rearing in northern mountain watersheds? Do they provide the only available spring habitat in these watersheds with warm enough water for spawning? Does spawning occur in other habitats? Is this pattern or link between lake and bog-fed tributaries and Arctic Grayling spawning also found in other northern mountain watersheds?	Tack 1980; Lewis 2018; McPherson 2020
Fluvial Arctic Grayling occupancy and distribution in northern watersheds	Are the patterns of fluvial Arctic Grayling summer occupancy and distribution observed in the sub-watersheds of the Little Nahanni River also found in other northern watersheds with similar properties? What are the relationships between drainage basin characteristics, stream habitat types and fluvial Arctic Grayling occupancy, distribution, and habitat use? Do these watershed-scale indices influence the probability of Arctic Grayling presence in other northern mountain watersheds? Are the relationships between life stages and habitat types across sub-watersheds in other river drainage systems similar to the Little Nahanni River? Is there a relationship between low elevation warm water bog-fed streams and the proximity of high elevation cold water run-off streams to the patterns of occupancy and habitat use by Arctic Grayling life stages within a watershed?	Brown 1995; Hugueny et al. 2010; McPherson 2020 Tack 1980; McPherson 2020
Fluvial Arctic Grayling - occupancy models and distributional monitoring	Can the inclusion of drainage dimensions, channel configuration, and spatial analyses across sub-watersheds improve the criteria used for identifying suitable habitats for fluvial Arctic Grayling in northern watersheds? Does it improve our ability to accurately predict the occupancy and distribution of populations in un-surveyed watersheds? Can these indices or criteria be incorporated into life-stage specific occupancy modelling and distributional monitoring for the species?	Schlosser and Angermeier (1995); Faucsh et al. 2002; Falke et al. 2013; Kirsch and Peterson 2014; McPherson 2020

References

Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., et al. 2008. Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. BioSci. 58, 403–414.

Adam, J.D. Hamlet, A.F., Lettenmaier, D.P. 2009. Implications of global climate change for snowmelt hydrology in the twenty-first century. Hydrol. Processes 23, 962-972.

Angermeier PL, Krueger KL, Dolloff CA. 2001. Discontinuity in stream-fish distributions: Implications for assessing and predicting species occurrence. Pages. 51-527 in Scott JM, Heglund PJ, Morrison ML, eds. *Predicting Species Occurrences: Issues of Accuracy and Scale*. Covelo (CA): Island Press.

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

Armstrong, J.B., Schindler, D.E., Ruff, C.P., Brooks, G.T., Bentley, K.E., Torgersen, C.E. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94,2066-2075.

Baccante, D. 2010. Further evidence of size gradients in Arctic grayling (*Thymallus arcticus*) along stream length. BC Journal of Ecosystems and Management 11, 13–17.

Baker, L.F., Artym, K.J., Swanson, H.K. 2017. Optimal sampling methods for modelling the occupancy of Arctic grayling (*Thymallus arcticus*) in the Canadian barrenlands. Can. J. Fish. Aquat. Sci. 74, 1564-1574.

Ballard, S., Shrimpton, J.M. 2009. Summary report of Arctic grayling management and conservation 2009: A synopsis of the information available on Arctic grayling in the Omineca region of northern British Columbia and identification of additional information needs. Peace/Williston Fish Wildl. Compens. Prog. Rep. 337, 66 pp.

Bentley, K.T., Schindler, D.E., Armstrong, J.B., Cline, T.J., Brooks, G.T. 2015. Inter-tributary movements by resident salmonids across a boreal riverscape. PLoS ONE 10, e0136985.doi:10.1371/journal.pone.0136985

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

Blackman, B.G. 2002. An information summary on Arctic grayling from the Williston Reservoir Watershed with data gap analysis and recommendations. Peace/Williston Fish Wildl. Compens. Prog. Rep. 258, 26 pp.

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, 46 pp.

Box, J.E. et al. 2019. Key indicators of Arctic climate change: 1971-2017. Environ. Res. Lett. 14 045010.

British Columbia Ministry of Water, Land and Air Protection. 2002. Williston watershed Arctic grayling. Prepared by the Biodiversity Branch. 6 pp. http://wlapwww.gov.bc.ca/wld

Brown, J.H. 1995. Macroecology. The University of Chicago Press, Chicago, 270pp. ISBN 0-226-07614-8.

Bryant, M.D. 2009. Global climate change and potential effects on pacific salmonids in freshwater ecosystems of southeast Alaska. Climatic Change 95, 169-193.

Bunn, S.E., Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30, 492-507.

Burnham, K.P., Anderson, D.R. 1998. Model Selection and Inference. Springer-Verlag, New York, NY, US.

Burnham, K.P., Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd ed. edn. Springer-Verlag, New York, NY, USA.

Burnham, K.P., Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. Social Method Res., 33, 261–304.

Bush, E., Lemmen, D.S., editors. 2019. Canada's Changing Climate Report; Government of Canada, Ottawa, ON. 444 pp.

Buzby, K.M., Deegan, L.A. 2000. Environmental Biology of Fishes 59, 319. https://doi.org/10.1023/A:1007626507936

Cahill, C.L. 2015. Status of the Arctic Grayling (*Thymallus arcticus*) in Alberta: Update 2015. Alberta Environment and Parks. Alberta Wildlife Status Report No. 57 (Update 2015). Edmonton, AB. 96 pp.

Cahill, C.L., Howland, K.L., Hulsman, M.F., Noddin, F., Tonn, W.M. 2016. Arctic grayling movements through a nature-like fishpass in northern Canada. Trans. Am. Fish. Soc.145, 951-963.

Cassie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51, 1389-1406.

Chin, K.S., Lento, J., Culp, J.M., Lacelle, D., Kokelj, S.V. 2016. Permafrost thaw and intense thermokarst activity decreases abundance of steam benthic macroinvertebrates. Global Change Biology 22, 2715-2728.

Christiansen, J.S., Reist, J.D., Brown, R.J., Brykov, V.A., Christensen, G., Christoffersen, K., et al. 2013. Fishes. In Arctic biodiversity assessment. Status and trends in Arctic biodiversity. Chapt. 6. Edited by Meltofte, H. pp. 192–245. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Christie, K., R. McCleary, S. Ouellet. 2010. Estimating Arctic grayling population size in mid-size streams with night snorkeling. Foothills Research Institute Fish & Watershed Program. 37 pp.

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.

Clarke, A.D., Telmer, K.H., Shrimpton, J.M. 2007. Habitat use and movement patterns for a fluvial species, the Arctic grayling, in a watershed impacted by a large reservoir: evidence from otolith microchemistry. J. Appl. Ecol. 44, 1156-1165.

Cohen, S., Bush, E., Zhang, X., Gillett, N., Bonsal, B., Derksen, C., Flato, G., Greenan, B., Watson, E. 2019. Synthesis of Findings for Canada's Regions; Chapter 8 in Canada's Changing Climate Report, (ed.) E. Bush, D.S. Lemmen; Government of Canada, Ottawa, Ontario, p. 424–443.

Cott, P.A., Schein, A., Hanna, B.W., Johnston, T.A., MacDonald, D.D., Gunn, J.M. 2015. Implications of linear developments on northern fishes. Environ. Rev. 23, 177-190.

Courtice, G., Basar, A.M., Zhu, D.Z., Cahill, C., Tonn, W.M. 2014. Stream modifications to enhance system connectivity for fish habitat compensation: a case study in the barrenlands region of Canada. Can. J. Civ. Eng. 41, 650-659.

Coutant, C.C. 1987. Thermal preference: when does an asset become a liability? Env. Biol Fishes 18, 161-172.

Craig, P.C., 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.

Culp, J., Gantner, N., Gill, M., Reist, J.D., Wrona, F. 2011. Development of an Arctic Freshwater Biodiversity Monitoring Plan: Framework Document. Circumpolar Biodiversity Monitoring Programme. CAFF Monitoring Series Report 4, 4 pp.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Can. J. Fish. Aquat. Sci. 53, 267-282.

Cutting, K.A., Cross, W.F., Anderson, M.L., Reese, E.G. 2016. Seasonal change in trophic niche of adfluvial Arctic grayling (*Thymallus arcticus*) and coexisting fishes in a high-elevation lake system. PLoS ONE 11, 19 pp. e0156187. doi:10.1371/journal.pone.0156187.

Danhoff, B.M., Huckins C.J., Auer, N.A., Goble, C.W., Ogren, S.A., Holtgren, J.M. 2017. Abiotic Habitat Assessment for Arctic Grayling in a Portion of the Big Manistee River, Michigan, T. Am. Fish. Soc., 146, 645-662, DOI: 10.1080/00028487.2017.1301995.

Davies, N.M., Norris, R.H., Thoms, M.C. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. Freshwater Biol. 45, 343-369.

de Bruyn, M., 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. Biol. Rep. Series. 15, xii + 41 pp.

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

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

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

de Kerckhove, D.T., Smokorowski, K.E., Randall, R.G. 2008. A primer on fish habitat models. Can. Tech. Rep. Fish. Aquat. Sci. 2817, 65 pp.

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 pp.

de Wit, M., Stankiewicz, J. 2006. Changes in Surface Water Supply across Africa with Predicted Climate Change. Science 311, 1917-1921. https://doi.org/10.1126/science.1119929

Dunmall, K. M., Mochnacz, N. J., Zimmerman, C. E., Lean, C., Reist, J. D. 2016. Using thermal limits to assess establishment of fish dispersing to high-latitude and high-elevation watersheds. Can. J. Fish. Aquat. Sci. 73, 1750–1758.

Dunn, C.G., Angermeier, P.L. 2016. Development of habitat suitability indices for the Candy darter, with cross-scale validation across representative populations. T. Am. Fish. Soc.145, 1266-1281.

Dunning, J.B., Danielson, B.J., Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–175.

Dyldin, Yu. V., Hanel, L., Romanov, V.I., Plesník, J. 2017. A review of the genus Thymallus (Pisces: Salmoniformes, Salmonidae, Thymallinae) with taxonomic notes. Bull. Lampetra, ZO ČSOP Vlašim 8, 103-126.

Environment Canada. 2012. Canadian Aquatic Biomonitoring Network Field Manual - Wadeable Streams. Manual. ISBN 978-1-100-20816-9. 52 pp.

Envirocon Ltd. 1976. Environmental Overview Howard's Pass Access Road for Canex Placer Ltd. Prepared by Envirocon Ltd., Vancouver, BC.

Evans, C.E., Reist, J.D., 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, 169 pp.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52, 483-498.

Falke JA, Dunham JB, Jordan CE, McNyset KM, Reeves GH. 2013. Spatial Ecological Processes and Local Factors Predict the Distribution and Abundance of Spawning by Steelhead (Oncorhynchus mykiss) across a Complex Riverscape. PLoS ONE 8(11): e79232. doi:10.1371/journal.pone.0079232

Fisheries and Oceans Canada (DFO). 2012. Survey of Recreational Fishing in Canada 2010. Published by Economic Analysis and Statistics Strategic Policy, Resource Management, Ecosystems and Fisheries Management. 33 pp.

Ford, B.S., Higgins, P.S., Lewis, A.F., Cooper, K.L., Watson, T.A., Gee, C.M., Ennis, G.L., 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, 342 pp.

Frissell, C.A., Liss, W.J., Warren, C.E., Hurley, M.D. 1986. A heirarchical framework for stream habitat classification: viewing streams in a watershed context. Env. Manag. 10, 199-214.

Golden, H.E., Deegan, L.A. 1998. Trophic interactions of young Arctic grayling (*Thymallus arcticus*) in an Arctic tundra stream. Freshwater Biol. 39. 637-648.

Golder Associates Ltd. 2008. Fish species habitat suitability index models for the Alberta oil sands region. Version 2.0. 93 pp.

Gordon, N.D, McMahon, T.A., Finlayson, B.L., Gippel, C.J., Nathan, R.J. 2004. Stream hydrology: An introduction for ecologists. Second Edition. John Wiley & Sons Ltd.

Gowan, C., Fausch, K.D. 2002. Why do foraging stream salmonids move during summer? Environ. Biol. Fish. 64, 139-153.

GNWT. 2019. Northwest Territories Budget Paper - Economic Review. Department of Finance, Government of Northwest Territories, Yellowknife, NT. 24 pp.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I., … Buckley, Y. M. 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189

Hallberg, J. 1982. Population structure, migration and habitat of Arctic grayling. Alaska Department of Fish and Game. Federal Aid in Fish Restoration and Anadromous Fish Studies. Volume 23. 28 pp.

Hartman, K.J., Jensen, O.P. 2017. Anticipating climate change impacts on Mongolian salmonids: bioenergetics models for lenok and Baikal grayling. Ecol. Freshw. Fish 26, 383-396.

Hawkins, C.P., Kershner, J.L., Bisson, P.A., Bryant, L.M., Decker, L.M., Gregory, D.A., McCullough, C.K., Overton, G.H., Reeves, G.H., Steedman, R.J., and Young, M.K. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18, 3-12.

Heim, K.C., Wipfli, M.S., Whitman, M.S., Arp, C.D., Adams, J., Falke, J.A. 2016. Seasonal cues of Arctic grayling movement in a small arctic stream: the importance of surface water connectivity. Environ. Biol. Fish 99, 49-65.

Heim, K. C., Wipfli, M. S., Whitman, M. S., Seitz, A. C. 2014. Body size and condition influence migration timing of juvenile Arctic grayling. Ecol. Freshw. Fish 25, 156–166.

Holmes, R.A. 1983. Grayling migration and habitat. Alaska Department of Fish and Game. Federal Aid in Fish Restoration and Anadromous Fish Studies. Volume 24, 36 pp.

Holmes, R.A. Ridder, W.P., Clark, R.A. 1986. Tanana Arctic grayling study. Alaska Department of Fish and Game. Federal Aid in Fish Restoration and Anadromous Fish Studies. Volume 27, 73pp.

Hubert, W.A., Helzner, R.S., Lee, L.A., Nelson, P.C. 1985. Habitat suitability index models and instream flow suitability curves: Arctic grayling riverine populations. U.S. Fish Wildl. Serv. Biolog. Rep. 82, 34 pp.

Hugueny, B., Oberdorff, T., Tedescco, P.A. 2010. Community ecology of river fishes: a large-scale perspective, in K.B. Gido and D.A. Jackson, editors. Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society, Symposium 73, 29-62.

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 dominanc 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. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79, 281-294.

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

Huntington, H.P., and contributing authors. 2013. Provisioning and Cultural Services. In Arctic biodiversity assessment. Status and trends in Arctic biodiversity. Chapt. 18. pp. 592-626. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Isaak, D., B. Rieman, Horan, D. 2009. A watershed-scale monitoring protocol for bull trout. Gen. Tech. Rep. RMRSGTR-224. Fort Collins, CO: U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station. 25 pp.

Isaak, D., Horan, D., Wollrab, S. P. 2013. A simple protocol using underwater epoxy to install annual temperature monitoring sites in rivers and streams. Gen. Tech. Rep. RMRS-GTR-314. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 21 pp.

Jackson, L. 1987. Terrain inventory and quaternary history of the Nahanni map area, Yukon and Northwest Territories. Geol. Surv. Can., 86-18, 1-23.

Jensen, A.J., Forseth, T., Johnson, B.O. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. J. Anim. Ecol. 69, 1010-1020.

Jiménez Cisneros, B.E., T. Oki, N.W. Arnell, G. Benito, J.G. Cogley, P. Döll, T. Jiang, Mwakalila, S.S. 2014: Freshwater resources. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D.

Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L.White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 229-269 pp.

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

Jones, N.E., Tonn, W.M., Scrimgeour G.J. 2003b. Selective feeding of age-0 Arctic grayling in lake-outlet streams of the Northwest Territories, Canada. Environ. Biol. Fishes 67, 169–78.

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

Jones, N.E., Tonn, W.M. 2004. 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.

Kéry, M., Schmidt, B. R. 2008. Imperfect detection and its consequences for monitoring for conservation. Community Ecol. 9, 207–216.

Kirsch, J.E., Peterson, J.T. 2014. A Multi-Scaled Approach to Evaluating the Fish Assemblage Structure Within Southern Appalachian Streams. T. Am. Fish. Soc. 143, 1358-1371.

Kokelj, S.V., Lacelle, D., Lantz, T.C., Tunnicliffe, J., Malone, L., Clark, I.C., Chin, K.S. 2013. Thawing of massive ground ice in mega slumps drives increases in stream sediment and solute flux across a range of watershed scales. J. Geophys. Res.- Earth 118, 681-692.

Kokelj, S.V., Lantz, T.C., Tunnicliffe, J., Segal, R., Lacelle, D. 2017. Climate-driven thaw of permafrost preserved glacial landscapes, northwestern Canada. Geology 45, 371-374.

Larocque, S.M., Hatry, C., Enders, E.C. 2014. Development of habitat suitability indices and bioenergetics models for Arctic grayling (*Thymallus arcticus*). Can. Tech. Rep. Fish. Aquat. Sci. 3097, vi + 57 pp.

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

Lewis, J.B. 2018. Comparing habitat use and mercury accumulation in Arctic Grayling (*Thymallus arcticus*) from two northern ecosystems. MSc. thesis, University of Waterloo, Waterloo, ON.

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

Link, J. S. 2007. Underappreciated species in ecology: ''Ugly fish'' in the northwest Atlantic Ocean. Ecol. Appl. 17, 2037–2060.

Linnansaari, T., Cunjak, R.A. 2012. Fish: Freshwater Ecosystems (Chapter 6), pp 80-97. In Temperature Adaptation in a Changing Climate: Nature at Risk. K.B. Storey and K. Tanino (eds.). Climate Change Series, No.3, CAB International Publishing, Wallingford, UK, 248pp.

Luecke, C., MacKinnon, P. 2008. Landscape effects on growth of age-0 Arctic grayling in tundra streams. T. Am. Fish. Soc. 137, 236–243.

MacKenzie, D. I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E. 2006. Occupancy estimation and modeling. Academic Press, New York.

MacPherson, L.M., Sullivan, M.G., Foote, A.L., Stevens, C.E. 2012a. Effects of Culverts on Stream Fish Assemblages in the Alberta Foothills, N. Am. J. Fish. Manage. 32, 480–490.

MacPherson, L.M., Sullivan, M.G., Foote, L., and Stevens, C.E. 2012b. Evaluating sampling techniques for low-density populations of Arctic Grayling (*Thymallus arcticus*). Northwestern Nat. 93, 120-132.

Mandrak, N. E. 2003. COSEWIC National Freshwater Biogeographic Zones. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., 1993. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Chapman & Hall, London, 177 pp.

Mantua, N., Tohver, I., Hamlet, A. 2010. Climate change impacts on stream flow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Clim. Change 102, 187-223.

McClure, W. V., 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.

McCullough, D.A., Bartholow, J. M., Jager, H.I., Beschta, R.L., Cheslak, E.F., Deas, M.L., Ebersole, J.L, Foott, J.S., Johnson, S.L., Marine, K.R., Mesa, M.G., Petersen, J. H., Souchon, Y., Tiffan, K.F., Wurtsbaugh, W.A. 2009. Research in thermal biology: burning questions for coldwater stream fishes. Rev. Fish. Sci.17, 90–115.

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

Meltofte, H. (ed.) 2013. Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Akureyri.

Miller, R.B. 1946. Notes on the Arctic grayling, *Thymallus signifier* Richardson, from Great Bear Lake. Copeia. 4, 227-236.

Minns, C. K., Moore, J. E. 1995. Factors limiting the distributions of Ontario's freshwater fishes: the role of climate and other variables, and the potential impacts of climate change. Can. J. Fish Aquat Sci. 121, 137–160.

Mochnacz, N. J, Reist, J. D. 2007a. Biological and habitat data for fish collected during stream surveys in the Deh Cho Region, Northwest Territories, 2006. Can. Data Rep. Fish. Aquat. Sci. 1190, vii + 21 pp.

Mochnacz, N. J, Reist, J. D. 2007b. Biological and habitat data for fish collected during stream surveys in the Sahtu Settlement Region, Northwest Territories, 2006. Can. Data Rep. Fish. Aquat. Sci. 1189, vii + 40 pp.

Mochnacz, N.J., Backhouse, S.M., Banjo, R., Reist, J.D. 2009. Biological and habitat data for fish collected during stream surveys in the southern (Dehcho) and central (Sahtu) Northwest Territories, 2007. Can. Data Rep. Fish. Aquat. Sci. 1209, vii + 29 pp.

Mochnacz, N.J., Bajno, R., Reist, J.D., Low, G., Babaluk, J.A. 2013. Distribution and biology of Bull Trout (*Salvelinus confluentus*) in the Mackenzie Valley, Northwest Territories, with notes on sympatry with Dolly Varden (*Salvelinus malma*). Arctic 86, 79-93.

Muhlfeld, C.C., Kovach, R.P., Jones, L.A., et al. 2014. Invasive hybridization in a threatened species is accelerated by climate change. Nat. Clim. Chang 4, 620–624. doi:10.1038/NCLIMATE2252.

Myers, B.J.E., Lynch, A.J., Bunnell, D.B. et al. 2017. Global synthesis of the documented and projected effects of climate change on inland fishes. Rev Fish Biol Fish. doi: 10.1007/s11160-017-9476-z.

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

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M. H., Wagner, H. 2013. vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan.

Ootes, L., Gleeson, S.A., Turner, E., Rasmussen, K., Gordey, S., Falck,…Pierce, K. 2013. Metallogenic evolution of the Mackenzie and eastern Selwyn Mountains of Canada's northern cordillera, Northwest Territories: A compilation and review. Geosci. Can. 40, 40-69.

Park, D., Sullivan, M., Bayne, E., Scrimgeour, G. 2008. Landscape level stream fragmentation caused by hanging culverts along roads in Alberta's boreal forest. Can. J. Forest Res. 38, 566– 575.

Paul, A.J., Post, J.R. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. T. Am. Fish. Soc.130, 417–430.

Pearse, G. A. 1974. A study of a typical spring fed stream of Interior Alaska. Alaska Dept. of Fish and Game. Federal Aid in Fish Restoration, Annual Report of Progress, 1973-1974, Project F-9-6, 15(G-111), 49 pp.

Peckarsky, B.L., Cooper, S.D., McIntosh, A.R. 1997. Extrapolating from individual behavior to populations and communities in streams. J. N. Am. Benthol. Soc. 16, 375-390.

Pendray, T. 1983. Life history and habitat utilization of Arctic grayling (*Thymallus arcticus*) in two central Yukon drainages. Yukon River Basin Study Rep. Fisheries No. 8, 44 pp. + appendices.

Poesch, M.S., Chavarie, L., Chu, C., Pandit, S.N., Tonn, W. 2016. Climate change impacts on freshwater fishes: a Canadian perspective. Fisheries 41, 385-391.

Polis, G.A., Anderson, W.B., Holt, R.D. 1997. Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. 28, 289-316.

Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L., Winterbourne, M.J. 1988. Patch dynamics in lotic systems: The stream as a mosaic. J. N. Am. Benthol. Soc. 7, 503–524.

Ponomarenko, S., Quirouette, J. 2015. Ecotype mapping report for Nahanni National Park Reserve. Monitoring and Ecological Information, Protected Areas Establishment and Conservation Directorate. Parks Canada. Gatineau, QC.

Prowse, T. D., Wrona, F. J., Reist, J. D., Gibson, J. J., Hobbie, J. E., Levesque, L. M., Vincent, W. F. 2006. Climate change effects on hydroecology of arctic freshwater ecosystems. Ambio 35, 347–358.

Prowse, T., Alfredsen, K., Beltaos, S., Bonsal, B.R., Bowden, W.B., Duguay, C.R., Korhola, A., McNamara, J., Warwick, F.V., Vuglinksky, V., Anthony, K.M.W., Weyhenmeyer, G.A. 2011. Effects of changes in arctic lake and river ice. Ambio 40, 63-74.

Pyseˇk, P., Richardson, D. M., Pergl, J., Jarosˆ ıÅLk, V., SixtovaÅL , Z., Weber, E. 2008. Geographical and taxonomic biases in invasion ecology. Trends Ecol. Evol. 23, 237–244.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/.

Rathert, D., White, D., Sifneos, J.C., Hughes, R.M. 1999. Environmental correlated of species richness for native freshwater fish in Oregon, U.S.A. J. Biogeogr. 26, 257-273.

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 pp.

Reilly, J. R., C. A. Paszkowski, D. W. Coltman. 2014. Population genetics of Arctic Grayling distributed across large, unobstructed river systems. T. Am. Fish. Soc. 143, 802-816.

Reist, J.D, Wrona, F. J., Prowse, T.D., Power, M., Dempson, J.B., King, J.R., Beamish, R.J. 2006a. An overview of effects of climate change on selected arctic freshwater and anadromous fishes. Ambio 35, 381-387.

Reist, J.D, Wrona, F. J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J., Sawatzky, C.D. 2006b. General effects of climate change on arctic fishes and fish populations. Ambio 35, 370-380.

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

Richardson, E.S., Reist, J.D., Minns, C.K. 2001. Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on lake habitat requirements. Can. Manuscr. Rep. Fish. Aquat. Sci. 2567, vii+146 pp.

Roberge, M., Hume, J.M.B., Minns, C.K., Slaney, T. 2002. Life history characteristics of freshwater fishes occurring in British Columbia and the Yukon, with major emphasis on stream habitat characteristics. Can. Manuscr. Rep. Fish. Aquat. Sci. 2611, 248 pp.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. T. Am. Fish. Soc. 132, 953-968.

Rosenfeld, J.S., Hatfield, T. 2006. Information needs for assessing critical habitat of freshwater fish. Can. J. Fish. Aquat. Sci. 63, 683-698.

Rosgen, D.L. 1994. A classification of natural rivers. Catena 22, 169–199.

Rouse, W.R, Douglas, M.S.V, Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., Smol, J.P. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrol. Process. 11, 873-902.

Sanchez-Hernandez, J., Nunn, A.D., Adams, C.E., Amundsen, P.A. 2019. Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. Biol. Rev. 94, 539-554.

Sawatzky, C.D., Michalak, D., Reist, J.D., Carmichael, T.J., Mandrak, N.E., 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 pp.

Schallock, E. W., Roguski, E. A. 1967. Investigations of the Tanana River and Tangle Lakes fisheries: Migratory and population study. Alaska Dept. of Fish and Game. Federal Aid in Fish Restoration, Annual Report of Progress 1966-1967, Project F-5-R-8, 8(16-B), 89 pp.

Schlosser, I.J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66, 484-1490.

Schlosser, I.J. 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. Environ. Manage. 14, 621-628.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. Bioscience 41, 704-712.

Schlosser, I.J. 1995a. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303, 71-85.

Schlosser, I.J. 1995b. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology 67, 908-925.

Schlosser, I.J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. Oecologia 11, 260-268.

Schlosser. I.J., Angermeier, P.L. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392-401 in J.L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Schindler, D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Can. J. Fish. Aquat. Sci. 58, 18–29.

Schindler, D.E, Scheuerell, M.D. 2002. Habitat coupling in lake ecosystems. Oikos 98, 177-189.

Schneider, D.C. 2001. The rise of the concept of scale in ecology. Bioscience 51, 545-553.

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

Scrimgeour, G.J., Hvenegaard, P.J., Tchir, J. 2008. Cumulative industrial activity alters lotic fish assemblages in two boreal forest watersheds of Alberta, Canada. Environ. Manage. 42, 957–970.

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T., Taboada, M.A. 2014. Terrestrial and inland water systems. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 271-359.

Selwyn Chihong Mining Ltd. 2015. Howard's Pass Access Road Upgrade Project 2015 Land Use and Water Licence Application Package. Volume 2: Project Description Report. Prepared by SLR Consulting (Canada) Ltd. Vancouver, B.C.

Shuter, B., Meisner, J. 1992. Tools for assessing the impact of climate change on freshwater fish populations. GeoJournal 28, 7–20.

Shuter, B.J., Finstad, A.G., Helland, I.P., Zweimuller, I., Holker, F. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. Aquat. Sci. 74, 637-657.

Silkstrom, C.B. 1983. Otolith, pectoral fin ray and scale age determinations for Arctic grayling. Prog. Fish Cult. 45(4).

Simonson, T.D., Lyons, J., Kanehl, P.D. 1994. Quantifying fish habitat in streams: transect spacing, sample size and a proposed framework. N. Am. J. Fish. Manag. 14, 07-615.

Slavik, K., Peterson, B.J., Deegan, L.A., Dowden, W.B., Hershey, A.E., Hobbie, J.E. 2004. Long-term responses of the Kuparuk river ecosystem to phosphorus fertilization. Ecology 85, 939-954.

Spangler, G. R., Berst, A. H., Koonce, J. F. 1981. Perspectives and policy recommendations on the relevance of the stock concept to fishery management. Can. J. Fish. Aquat. Sci. 38, 1908–1914.

Stamford, M. D., Taylor, E. B. 2004. Phylogeographical lineages of Arctic Grayling (*Thymallus arcticus*) in North America: divergence, origins and affinities with Eurasian *Thymallus*. Mol. Ecol. 13, 1533–1549.

Stamford, M., Hagen, J., Williamson, S. 2017. Limiting factors, enhancement potential, conservation status, and critical habitat for Arctic grayling in the Williston reservoir watershed, and information gaps limiting potential conservation and enhancement actions. Prepared for: Fish and Wildlife Compensation Program (FWCP) Peace Region. 148 pp.

Stevens, D. L., Jr., Olsen, A. R. 2004. Spatially-balanced sampling of natural resources. J. Am. Stat. Assoc. 99, 262-278.

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

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

Stewart, I. T., 2009. Changes in snowpack and snowmelt runoff for key mountain regions. Hydrol. Processes 23, 8-94.

Tack, S.L. 1972. Distribution, abundance, and natural history of the Arctic grayling in the Tanana River drainage. Alaska Dept. Fish Game, Fed. Aid Fish Restor., Annu. Perf. Rep., 1971-1972. Project F-9-4, 14 (R-I), 36 pp.

Tack, S. L. 1975. Distribution, abundance, and natural history of the Arctic grayling in the Tanana River drainage. Alaska Dept. of Fish and Game, Fed. Aid Fish Restor., Annu. Perf. Rep., 1974-1975, Project F-9-7, 16(R-I): 35 pp.

Tack, S.L. 1980. Migrations and distribution of Arctic grayling in interior and arctic Alaska. Alaska Dept. Fish Game, Fed. Aid Fish Restor., Annu. Perf. Rep., 1979-1980. Proj. F-9-12, 21 (R-I), 32 pp.

Taylor, M.K., Cooke, S.J. 2012. Meta-analysis of effects of river flow on fish movement and activity. Environ. Rev. 20, 211-219.

Taylor, M.K., Cook, K.V., Hasler, C.T., Schmidt, D.C., Cooke, S.J. 2012. Behaviour and physiology of mountain whitefish (*Prosopium williamsoni*) relative to short-term changes in river flow. Ecol. Freshw. Fish 21, 609-616.

Therneau, T.M, Atkinson, B., Ripley, B., Oksanen, J., De'ath, G. 2013. mvpart: Multivariate partitioning. R package version 1.6-1. http://CRAN.R-project.org/package=mvpart.

Torgersen, C.E., Price, D.M., Li, H.W., McIntosh, B.A. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecol. Appl. 9, 301-319.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. J. N. Am. Benthol. Soc. 8, 36–50.

Triton Environmental Consultants. 2014. Fish and Fish Habitat Inventory of the Howard’s Pass Access Road. Prepared for Selwyn Chihong Mining Ltd. Vancouver, BC.

USFWS (U.S. Fish and Wildlife Service). 1981. Standards for the development of habitat suitability index models 103 ESM. Div. Ecol. Serv., USFWS, Washington. 171 pp.

USFWS. 2015. Endangered species: Fish, Arctic Grayling. Recent Actions and links. US Fish and Wildlife Service, Mountain-Prairie Region. Retrieved February 23, 2019. https://www.fws.gov/mountain-prairie/es/arcticGrayling.php

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E. 1980. The river continuum concept. J. Fish Aquat. Sci. 37, 130-137.

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

Dana R. Warren, Jason B. Dunham & David Hockman-Wert (2014) Geographic Variability in Elevation and Topographic Constraints on the Distribution of Native and Nonnative Trout in the Great Basin, T. Am. Fish. Soc.143, 205-218, DOI: 10.1080/00028487.2013.833551

Wenger, S.J., Isaak, D.J., Luce, C.H., Neville, H.M., Fausch, K.D., Dunham, J.B., Dauwalter, D.C., Young, M.K., Elsner, M.M., Rieman, B.E., Hamlet, A.F., Williams, J.E. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. P. Natl. Acad. Sci. USA. 108, 14175–14180.

Werner, E.E., Gilliam, J.E. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15, 393-425.

West, R.L., Smith, M.W., Barber, W.E., Reynolds, J.B., 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, J.E., Haak, A.L., Neville, H.M., Colyer, W.T. 2009. Potential consequences of climate change to persistence of cutthroat trout populations. N. Am. J. Fish. Manage. 29, 533–548.

Wilson, S. 2017. Using remote site incubators for re-introduction of Arctic Grayling (*Thymallus arcticus*) to the Big Manistee watershed. Open Access Master's Thesis, Michigan Technological University, http://digitalcommons.mtu.edu/etdr/391

Wojcik, F. 1955. Life history and management of the grayling in interior Alaska. Unpubl. M.S. Thesis, Univ. Alaska, Fairbanks. 54 pp.

Zurr, A.F., Leno, E.N., Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. Meth. Ecol. Evol. 1, 3-14.

Appendix – Supplementary Data

Table A-1 Mean values for habitat variables measured at sites sampled in Fork Creek (n = 47), March Creek (n = 36), Lened Creek (n = 31), Dozer Creek (n = 5), and Guthrie Creek (n = 64).

VARIABLE	FORK	MARCH	LENED	DOZER	GUTHRIE
Elevation (m)	1270 ± 132 (989-1478)	1132 ± 126 (914-1361)	1168 ± 101 (986-1342)	965 ± 0.89 (965-967)	1196 ± 131 (1020-1463)
Velocity (m/s)	0.75 ± 0.25 (0.33-1.45)	0.97 ± 0.25 (0.58-1.59)	1.08 ± 0.34 (0-1.93)	0.59 ± 0.41 (0.23-1.12)	0.69 ± 0.22 (0-1.35)
Water Temp (ºC)	7.21 ± 2.19 (3.87-13.00)	6.36 ± 1.60 (4.00-10.00)	5.76 ± 1.49 (2.48-8.00)	10.83 ± 0.85 (9.66-12.00)	7.86 ± 2.19 (3.94-17.00)
Depth (cm)	28 ± 8.90 (11.75-51.25)	30 ± 8.80 (12.75-51)	34 ± 10.5 (0-51.25)	33.24 ± 17.75 (20.2-62.75)	28.96 ± 13.1 (9.25-68.5)
Width (cm)	480.8 ± 250 (130-1432)	445.7 ± 202.3 (150-870)	505.7± 155.8 (270-890)	478.2 ± 250.7 (291-910)	363.9 ± 207.2 (77-998)
Boulder (%)	34 ± 19 (3-78)	26± 18 (1-70)	23 ± 15 (2-55)	1 ± 2 (0-5)	22 ± 22 (0-75)
Cobble (%)	46 ± 15 (15-75)	53 ± 18 (10-85)	60 ± 14 (25-80)	30 ± 34 (0-80)	43 ± 22 (0-85)
Gravel (%)	16 ± 9 (1-45)	16 ± 8 (5-40)	13 ± 6 (3-20)	30 ± 19 (10-60)	24 ± 18 (1-70)
Silt-Sand (%)	5 ± 3 (0-15)	5 ± 4 (0-15)	4 ± 3 (0-10)	39 ± 27 (10-80)	11 ± 17 (0-89)
Run (%)	16 ± 26 (0-60)	13 ± 18 (0-80)	18 ± 22 (0-65)	83 ± 15 (65-100)	24 ± 29 (0-100)
Riffle (%)	51 ± 24 (0-100)	59 ± 26 (0-95)	66 ± 21 (25-100)	4 ± 4 (0-10)	45 ± 30 (0-100)
Pool (%)	13 ± 7 (0-30)	12 ± 7 (3-30)	11 ± 5 (0-17)	14 ± 12 (0-30)	15 ±10 (0-60)
Cascade (%)	24 ± 25 (0-100)	16 ± 22 (0-95)	5 ± 7 (0-20)	0 ± 0 (0-1)	16 ± 23 (0-100)

Table A-2. Water quality - Results of chemical analyses of water samples taken from the downstream main channel of the four sub-watersheds. Values with < in front of them are below reportable detection limits.

PARAMETERS	UNITS	GUTHRIE	FORK	MARCH	DOZER
Hardness ($CaCO_3$)	mg/L	150	120	150	300
N (Nitrate + Nitrite)	mg/L	0.043	0.023	0.045	<0.02
TDS	mg/L	160	130	200	320
TSS	mg/L	<1.0	<1.0	2.7	3.3
Conductivity	uS/cm	270	230	280	500
pH)	pH	7.90	7.86	7.89	8.03
Dissolved Cadmium (Cd)	ug/L	<0.02	<0.02	0.048	<0.02
Total Cadmium (Cd)	ug/L	0.027	<0.02	0.079	0.067
Dissolved Sulphate (SO_4)	mg/L	42	37	90	110
Elements					
Total Aluminum (Al)	mg/L	0.014	0.016	0.88	0.026
Total Arsenic (As)	mg/L	0.00094	0.00021	0.0007	0.00031
Total Barium (Ba)	mg/L	<0.010	<0.01	0.024	0.082
Total Calcium (Ca)	mg/L	56	43	43	85
Total Cobalt (Co)	mg/L	<0.0003	<0.0003	0.019	<0.0003
Total Copper (Cu)	mg/L	<0.0002	<0.0002	0.0054	<0.0002
Total Iron (Fe)	mg/L	<0.06	<0.06	0.37	0.1
Total Lithium (Li)	mg/L	<0.02	<0.02	0.021	<0.02
Total Magnesium (Mg)	mg/L	4.1	2.8	10	23
Total Manganese (Mn)	mg/L	<0.004	<0.004	0.59	0.027
Total Molybdenum (Mo)	mg/L	0.0002	0.00025	0.00026	0.0017
Total Nickel (Ni)	mg/L	<0.0005	0.00079	0.12	0.0079
Total Potassium (K)	mg/L	1.1	0.93	0.9	0.68
Total Selenium (Se)	mg/L	<0.0002	0.00023	0.00042	0.00053
Total Silicon (Si)	mg/L	2.7	2.5	2.9	2.0
Total Sodium (Na)	mg/L	1.1	1.1	1.2	0.98
Total Strontium (Sr)	mg/L	0.2	0.15	0.17	0.16
Total Sulphur (S)	mg/L	14	13	31	36
Total Uranium (U)	mg/L	0.00089	0.00063	0.0005	0.0036
Total Vanadium (V)	mg/L	<0.001	0.0011	<0.001	0.0012
Total Zinc (Zn)	mg/L	<0.003	<0.003	0.053	0.013
Lab Filtered Elements					
Dissolved Aluminum (Al)	mg/L	<0.003	<0.003	0.048	<0.003
Dissolved Arsenic (As)	mg/L	0.00061	<0.0002	0.00039	<0.0002
Dissolved Barium (Ba)	mg/L	<0.01	<0.01	0.023	0.071
Dissolved Calcium (Ca)	mg/L	53	42	42	83
Dissolved Cobalt (Co)	mg/L	<0.0003	<0.0003	0.017	<0.0003
Dissolved Copper (Cu)	mg/L	<0.0002	<0.0002	0.00087	<0.0002
Dissolved Magnesium (Mg)	mg/L	4.0	2.9	10	23
Dissolved Molybdenum (Mo)	mg/L	0.0003	0.00035	0.00021	0.0018
Dissolved Nickel (Ni)	mg/L	<0.0005	0.00065	0.1	0.0061
Dissolved Potassium (K)	mg/L	1.1	0.93	0.9	0.68
Dissolved Silicon (Si)	mg/L	2.6	2.5	2.6	1.9
Dissolved Sodium (Na)	mg/L	1.0	1.1	1.2	0.97
Dissolved Strontium (Sr)	mg/L	0.2	0.15	0.17	0.16
Dissolved Sulphur (S)	mg/L	13	13	31	36
Dissolved Uranium (U)	mg/L	0.00081	0.00055	0.00031	0.0031
Dissolved Zinc (Zn)	mg/L	<0.003	<0.003	0.027	0.0076