TEMPERATURE PREFERENCE AND DISTRIBUTION OF JUVENILE ARCTIC GRAYLING (*THYMALLUS ARCTICUS*) IN THE WILLISTON WATERSHED, BRITISH COLUMBIA CANADA

by

Sarah C. F. Hawkshaw

B.Sc. The University of British Columbia (Integrated Sciences), 2005
B.Sc. The University of British Columbia (Marine Biology), 2007

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES (BIOLOGY)

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

May, 2011

Your file Votre référence
ISBN: 978-0-494-75161-9
Our file Notre référence
ISBN: 978-0-494-75161-9

ABSTRACT

The habitat requirements of juvenile Arctic grayling (*Thymallus arcticus*) were assessed in the Williston watershed, British Columbia, where the population is currently red-listed (critically imperiled). Temperature preference of juvenile Arctic grayling was assessed behaviorally using a shuttlebox system, and an information theoretic approach analysis of logistic regression models was used to evaluate the influence of environmental factors on the distribution of juvenile Arctic grayling throughout the Williston watershed. Temperature preference of juvenile Arctic grayling did not vary between the two tributaries in the watershed ($p = 0.77$) and the average preferred temperature was 16.84 ± 0.66 °C ($n = 28$). Comparisons of the preferred temperature to ambient water temperatures suggested that juvenile Arctic grayling will avoid areas where maximum water temperature is above the preferred temperature. There was a positive association between juvenile Arctic grayling occurrence and stream order (SO) and stream order multiplied by distance from the Williston reservoir (SDRxSO), as well as a negative association with the mean daily water temperature variance (varT) and average water temperature (aveT). Overall these findings suggest that large river systems are important juvenile Arctic grayling habitat and management decisions should be made to ensure protection of this habitat throughout the range of this species.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I want to express my sincere appreciation to my supervisor Dr. J. Mark Shrimpton for giving me the opportunity to work on this project with him. It is because of his enthusiasm, encouragement, guidance, advice and constant support that my experience at UNBC has by far exceeded my expectations. Thanks also to my thesis committee Dr. Michael Gillingham and Dr. Tom Johnson, for taking the time to work with me throughout my studies and for providing me with useful comments on this thesis.

This work would have been impossible without several individuals and organizations that supported this project. My sincere thanks go to Elizabeth Miller for preparing the initial proposal for this project, providing me with comments along the way and for helping me in the field. Also thank you to Brian Blackman, Ray Pillipow, Arne Langston, and Randy Zemlak for continuously supporting this project and sharing their knowledge of Arctic grayling and the Williston watershed with me. I am also thankful to Susanne Williamson for helping me with the historical Arctic grayling sampling records, for continuously assisting me with ArcGIS mapping and for allowing me access to her computer whenever I needed it. I would also like to thank Sarina Loots, Ben Pittman, Anne-Marie Flores, Kyla Warren and Lisa Henderson for their help in the field. I am also grateful to the Peace/Williston Fish and Wildlife Compensation Program, the BC Ministry of Environment, the Northern Scientific Training Program, the Natural Sciences and Engineering Research Council of Canada, and UNBC for providing funding for this project. To my family and friends I would like to thank you for your unwavering and unquestioning support in my scientific endeavors, especially my husband, Stephen, who has become my permanent field assistant and editor.

PROLOGUE

Arctic grayling (*Thymallus arcticus*) are a freshwater fish species from the Salmonidae Family that have a holarctic distribution. In North America, populations are commonly found in cold temperate waters in northern Manitoba, Saskatchewan, Alberta, British Columbia, Northwest and Yukon Territories, and Alaska, but a small remnant population is also found in Montana (Scott and Crossman 1973). These populations utilize two life-history strategies: fluvial and adfluvial. Fluvial populations are adapted to inhabit mainstem river and tributary systems, whereas adfluvial populations migrate between lake and river or tributary systems (Kaya 1991). In the Williston watershed, British Columbia, Arctic grayling primarily exhibit a fluvial life-history strategy and there is evidence that these grayling do not use lake-type habitat (Kaya and Jeanes 1995).

In the Williston watershed, Arctic grayling were red-listed (critically imperiled) by the BC Conservation Data Centre (CDC) in 1995. This conservation status was the result of a drastic decline over two decades in Arctic grayling abundance in the Williston watershed (Northcote 1993). The decline occurred after the construction of the WAC Bennett Dam by BC Hydro and subsequent flooding of the Upper Peace River forming the Williston reservoir in 1968. Given the paucity of information on populations of Arctic grayling before the dam was built (Bruce and Starr 1985), it is difficult to quantify the effects the dam has had on these populations. Recently, Clarke *et al.* (2007) demonstrated that Arctic grayling in the Williston watershed do not use the reservoir, indicating that flooding of the Upper Peace River resulted in a considerable loss of habitat. Genetic evidence has also recently suggested that distinct populations of Arctic grayling exist in different tributaries in the Williston watershed (Shrimpton *et al.* 2007).

The current red-listed conservation status of Arctic grayling populations in the Williston watershed has generated much effort in developing conservation and management plans to protect and rebuild these populations. Before these efforts can be effective it is important to understand what factors affect distribution positively or negatively to develop an understanding of how habitat changes have, but also may continue to impact grayling populations. The creation of the Williston reservoir altered Arctic grayling habitat, yet there is limited information on the physical and environmental requirements for this species, particularly for populations in this area (Ballard and Shrimpton 2009). Measurements of environmental factors across a broad geographic region in concert with current Arctic grayling distribution will provide insight into habitat use or avoidance. The environment in the Williston watershed has been and is continuing to be perturbed by habitat degradation associated with resource extraction (timber and minerals), water management, and changes in climatic conditions. Information is needed about the influence of environmental variables on the distribution of Arctic grayling in the Williston watershed. Such information is required to understand historical declines in abundance, plan future management of these populations, and prevent future declines in abundance, loss of biodiversity and potential extirpation.

My research was conducted in the Williston watershed during the low-flow summer months of 2009 and 2010 to assess temperature preference of juvenile Arctic grayling populations and describe the influence that temperature regimes and other environmental variables have on juvenile Arctic grayling distribution. The objectives of this study were to: (1) determine behavioral thermal preference of juvenile Arctic grayling from the Williston reservoir; (2) characterize the microhabitat and macrohabitat requirements of juvenile Arctic grayling in the Williston watershed; and (3) investigate the influence of large scale macrohabitat environmental variables on juvenile Arctic grayling occurrence in sub-watersheds within the Williston watershed; (4) investigate the influence of small scale microhabitat environmental variables on juvenile Arctic grayling occurrence in specific sites within tributaries of the Williston watershed.

Behavioral assessment in an electronic shuttlebox system (Loligo Systems, Tjele, Denmark) was used to determine temperature preference of juvenile Arctic grayling from the southern part of the Williston watershed (Chapter 1). Macrohabitat variables were extracted from a Geographic Information Systems (GIS) based analysis of the watersheds where Arctic grayling were present or absent. Field surveys and GIS analysis were used to measure microhabitat features at sites where Arctic grayling were present or absent. An information theoretic approach was used to compare candidate models and analyze the influence of habitat variables on Arctic grayling occurrence (Chapter 2). I then made general conclusions, management implication and recommendations based on the results of these studies.

CHAPTER 1

Temperature Preference of Arctic grayling (*Thymallus arcticus*) from Tributaries of the Williston Watershed, British Columbia*

* Throughout this chapter I use the first person plural to acknowledge the contribution of others to this work, which will be submitted for publication with the authorship of S.C.F. Hawkshaw and J.M. Shrimpton

ABSTRACT

Thirty juvenile Arctic grayling (*Thymallus arcticus*) from three different study sites across two tributaries of the Williston watershed were tested individually in a shuttlebox system to determine their preferred temperatures. The average temperature preference for juvenile Arctic grayling across all study sites was 16.84 ± 0.66 °C ($n = 28$). Temperature preference did not vary among study sites ($p = 0.77$) and there was no difference between individual fish ($p = 0.07$). Arctic grayling ranged in size from 5.3 cm to 7.3 cm, but there was no relationship between preferred temperature and size ($p = 0.53$), and there was no difference in size between study sites ($p = 0.22$). The results of this study provide valuable information on the thermal requirements for Arctic grayling from two tributaries of the Williston watershed. Findings can be used to make assumptions about the thermal requirements of Arctic grayling in different river systems throughout the Williston watershed and potentially in other systems throughout the range of the species.

INTRODUCTION

Temperature is an important environmental variable that influences fish distribution, life history and physiology (Reynolds and Casterlin 1979a; Bear *et al.* 2007; McMahon *et al.* 2008). Fish have evolved to deal with specific temperature regimes; consequently relatively small temperature changes can have measurable effects on community and population structure. These changes are largely rooted in the direct effect of temperature on the physiology of individual fish (Brett 1971; McCormick *et al.* 2002; Crossin *et al.* 2008). The thermal requirements of fish are often characterized by reference to critical thermal maxima, upper incipient lethal temperatures and temperature preferences (Fry 1947). The critical thermal maximum and upper incipient lethal temperature are avoided by fish while temperature preference represents temperatures actively selected by fish. Fish are ectothermic and behaviorally thermoregulate to seek out preferred temperatures in nature, an important consideration when predicting distribution (Reynolds and Casterlin 1979b; Reynolds and Casterlin 1981; Berman and Quinn 1991; Dunham *et al.* 2003). Consequently, considerable effort has been directed by fisheries scientists and managers toward characterizing the thermal preferences of freshwater fishes as it may be an important determinant for habitat selection. Knowledge of thermal preference, therefore, becomes increasingly important for species that are showing a decline in abundance that may be associated with change or loss of habitat.

Arctic grayling (*Thymallus arcticus*) populations in the Williston watershed of British Columbia were red-listed (critically imperiled) by the BC Conservation Data Centre in 1995 (Miller 2010). The designation was a result of habitat change following the completion of the WAC Bennett Dam, the flooding of the Upper Peace River, and the formation of the

Williston reservoir. Since 1995, surveys in the area have compiled a considerable amount of data for this species. Due to the size of the Williston watershed and limited resources, however, there has been little long-term monitoring or research conducted on Arctic grayling populations in this area. Spatial information is also disproportionate and important life-history information is still lacking (Ballard and Shrimpton 2009). To effectively manage these Arctic grayling populations and ensure long-term persistence over their native range at abundance levels capable of providing substantial society benefits, additional information is required.

The thermal requirements for Arctic grayling have not been adequately described and no studies have investigated the preferred temperature for this species. A single study conducted in Big Hole, Montana found the critical thermal maximum for juvenile Arctic grayling to be 26.4 to 29.3 °C when acclimated to 8.4 and 20.0 °C, respectively (Lohr *et al.* 1996). Lohr *et al.* (1996) also found upper incipient lethal temperatures to be 23 °C when Arctic grayling were acclimated at 16 °C and 25 °C when acclimated at 20 °C. Another study on European grayling (*Thymallus thymallus*) in Britain found that, when placed in a temperature gradient, these fish selected an average water temperature of 18 °C (Coutant 1977). The traditional approach for determining fish temperature preference was to allow fish to choose temperatures by positioning themselves in horizontal, vertical or annular temperature gradients (Wollmuth *et al.* 1987; Clutterham *et al.* 2004; Myrick *et al.* 2004; Lafrance *et al.* 2005). Neill *et al.* (1972) were the first to use a shuttlebox system to investigate thermal preferences for a number of fish species. Since the work of Neill et al. (1972), this system has been used to determine the preferred temperature of a number of fish species (Schurmann *et al.* 1991; Schurmann and Steffensen 1992; Mortensen *et al.* 2007).

The objective of this study was to behaviorally assess the temperature preference of juvenile Arctic grayling from the southern part of the Williston watershed in a shuttlebox system (Loligo Systems, Tjele, Denmark). We also aimed to compare the thermal preference of Arctic grayling from different geographic locations within the study area.

MATERIALS AND METHODS

STUDY AREA

Temperature preference studies were conducted on juvenile Arctic grayling captured in two locations from the Nation River and one location in the Table River. Both rivers are tributaries in the Williston watershed, BC (Figure 1-1). The Nation River is a larger system than the Table River and grayling were collected from two sites approximately 20 km apart: near the headwaters of the Nation River and at the mouth of Sylvester Creek (a tributary flowing into the Nation River). Both sites were similar in elevation, dissolved oxygen, conductivity and pH, but temperature was higher at the upper Nation River site during sampling (Table 1-1). Dissolved oxygen was measured using a handheld YSI 550A (Yellow Springs, OH), and conductivity, pH and temperature were measured using a HANNA pH/EC Combo meter (Woonsocket, RI). Water quality from the Table River site was similar to the Nation River sites, but the temperature was slightly lower during capture (Table 1-1). Arctic grayling from the Nation River also differ genetically from the population found in the Table River system (Shrimpton *et al.* 2007). Capturing fish from the three locations allowed us to investigate the influence of the ambient environment on temperature preference and also add to the demographic information for the different populations of Arctic grayling throughout the Williston watershed.

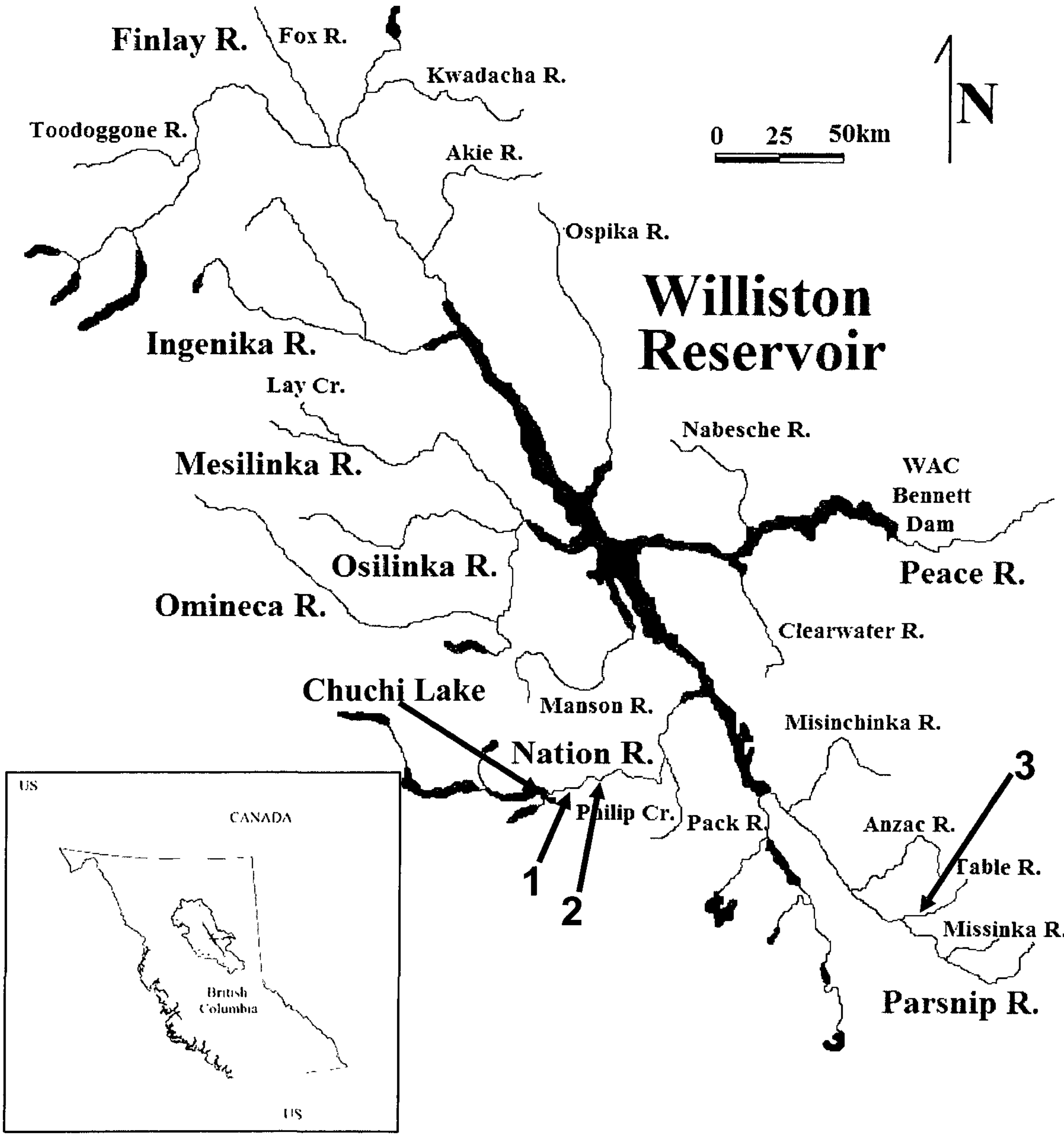


Figure 1-1. Map of juvenile Arctic grayling temperature preference study sites in the Williston watershed, BC (1: upper Nation River; 2: Nation River at Mouth of Sylvester Creek; 3: Table River).

Table 1-1. Ambient environmental characteristics at each temperature preference study sites in the Williston watershed, BC (1: upper Nation River, 2: Nation River at the mouth of Sylvester Creek, 3: Table River; T_A: Average ambient water temperature over the summer months (June 18 – August 18, 2010); T_C: Ambient water temperature during capture).

Site	$T_A \pm$ SD (Range) (°C)	T_C (°C)	Dissolved Oxygen (mg/l)	Conductivity (µS/cm)	pH	Elevation (m)	Watershed Area (km^2)
1	12.99 ± 2.51 (7.17 - 18.68)	18.02	8.7	77	8.85	836	6921
2	-	16.59	8.9	82	7.53	832	6921
3	13.55 ± 2.63 (6.74 - 18.12)	16.43	10.3	108	7.31	704	506

The Nation River (55°15′ N 125°15′ W) flows east through the four Nation Lakes as it drains the Nechako Plateau. It is 215.5 km long and has a watershed area of approximately 6921 km^2. Industrial activities (logging and mining) have occurred in the Nation River watershed in the past and have recently increased with the development of the Mount Milligan gold/copper mine (Terrane Metals Corp.) (55°07'N 124°01'W) (Hengeveld and Corbould 2000; Independent Mining Consultants 2007). In BC, the most southern populations of Arctic grayling are found in the Parsnip River and its tributaries. The Table River (54°42'N 122°17'W) is a tributary of the Parsnip River, 75 km upstream from the Williston Reservoir. It flows west out of the Misinchinka Range of the Rocky Mountains and is 56 km long with a watershed area of 506 km^2 (Blackman and Hunter 2001). Timber harvesting has impacted approximately 40% of the Table River (Mathias *et al.* 1998).

ARCTIC GRAYLING COLLECTION

Juvenile Arctic grayling (5.3 - 7.3 cm in length) were collected using a 0.6-cm, nylon-mesh seine net (50 m long and 1 m deep) in July 2010. Water quality (dissolved oxygen, conductivity and pH) and location coordinates were recorded at each study site during fish capture. Temperature data were recorded for two of the capture sites (HOBO Water Temp U22 loggers, Onset Corporation, Bourne, MA) as part of another study (Chapter 2). Captured Arctic grayling were transferred to the Chuchi Lake field site and held in separate large perforated flow through containers in the Nation River from one to 36 days until temperature preference analysis could be conducted (Figure 1-2). Substrate was placed in each container to simulate a natural environment. Although fish were not observed to feed, condition factor (weight / $length^3$ *100) did not decrease with time, suggesting that fish did not fast while being held. Water quality was monitored daily throughout the holding period.

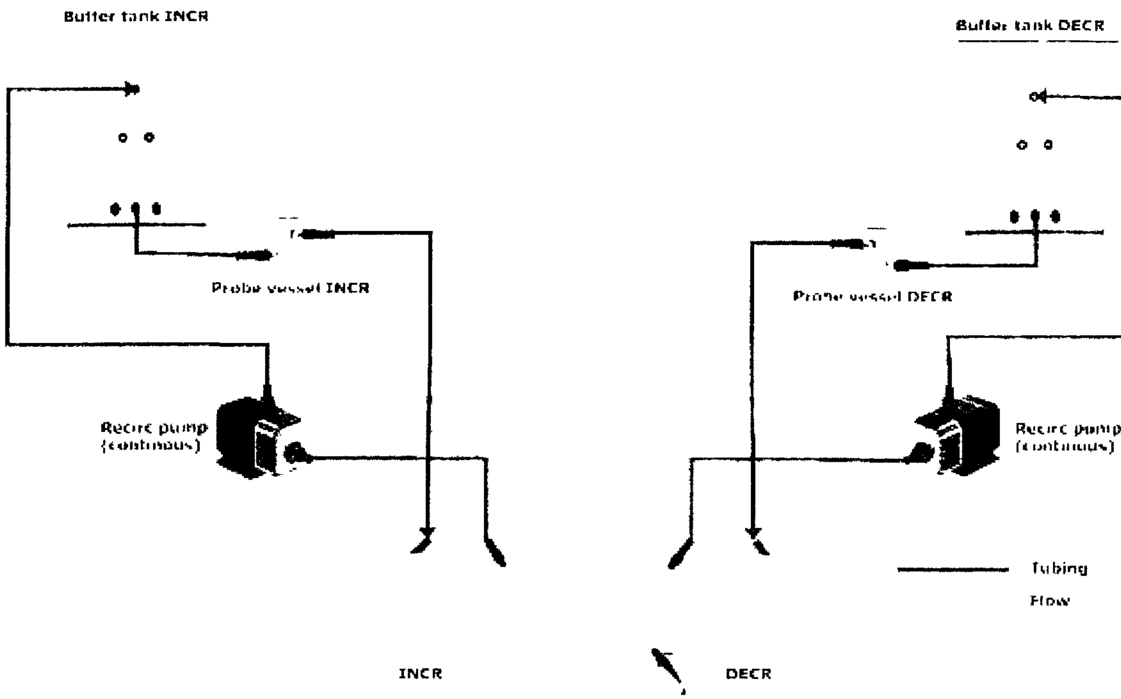
Figure 1-2. Arctic grayling holding containers in the Nation River

TEMPERATURE PREFERENCE ANALYSIS

To assess temperature preference of Arctic grayling, individual juvenile grayling were introduced to a "shuttlebox system" (Loligo Systems, Tjele, Denmark). The shuttlebox had two connected circular chambers with an opening between them (Figure 1-3a). Temperature was continuously monitored in each chamber and a difference of approximately 1.0 °C was maintained between the two chambers throughout the analysis; one chamber consistently warmer (INCR) than the other (DECR). Starting temperature of the experiment was set to the temperature at the time of capture (Table 1-1) and the starting chamber was alternated throughout the experiments to eliminate potential bias.

The shuttlebox system is designed to cool and warm each chamber independently using individual pumps controlled by the shuttlebox software (Loligo Systems, Tjele, Denmark). Each chamber was connected by these pumps to a cold (~2 °C) and warm (~27 °C) reservoir (Figure 1-3b). A Ueye 1640-C video camera (Imaging Development Systems, Dimbacher, Germany) was mounted over the tank and connected to a PC computer running the shuttlebox software (Figure 1-3c). Shuttlebox software recorded the location of the fish by pixel recognition and the location of the fish determined whether the system would be cooling or heating the water (Figure 1-4). When a fish occupied the cold (DECR) chamber the water temperature in both chambers cooled and when the fish occupied the warm (INCR) chamber the water temperature in both chambers warmed, continuously maintaining a 1.0 °C difference between chambers. The rate of cooling and warming was approximately 0.5 °C per min.

All temperature preference tests were conducted in a portable laboratory set up at Chuchi Lake, a lake at the headwaters of the Nation River (Figure 1-5). The system was a.



b.

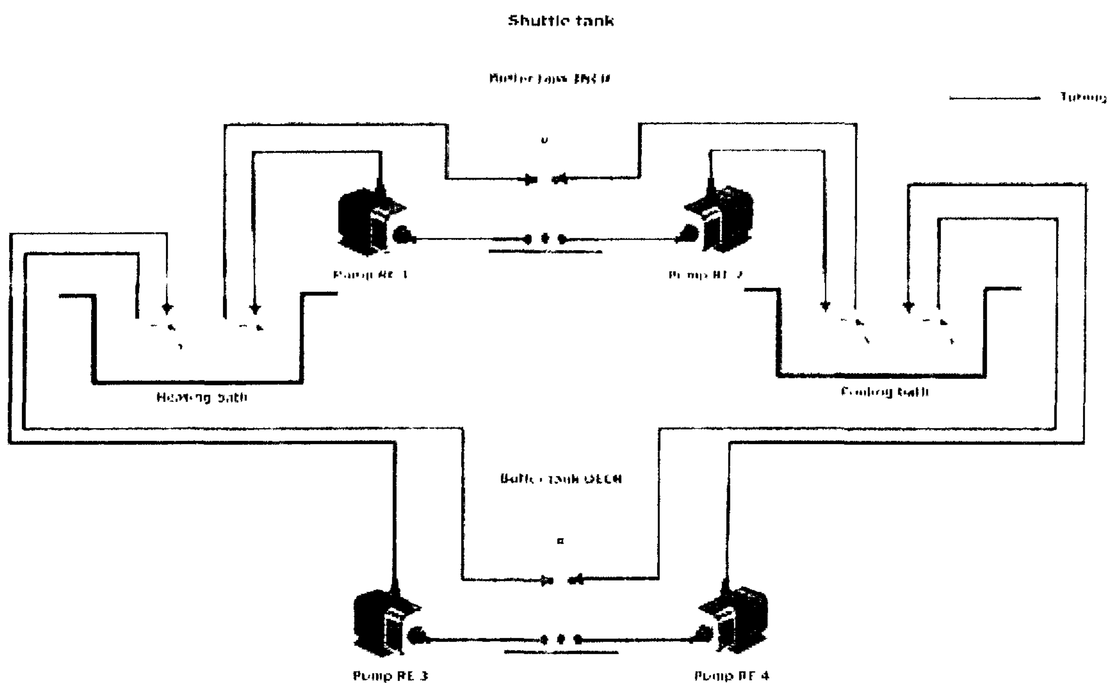


Figure 1-3. Shuttlebox system used to determine temperature preference; a. Shuttlebox tank; b. Shuttlebox buffer tank and temperature control pumps; c. Shuttlebox instruments, devices and connections (All diagrams provided by Loligo Systems, Tjele, Denmark).

c.

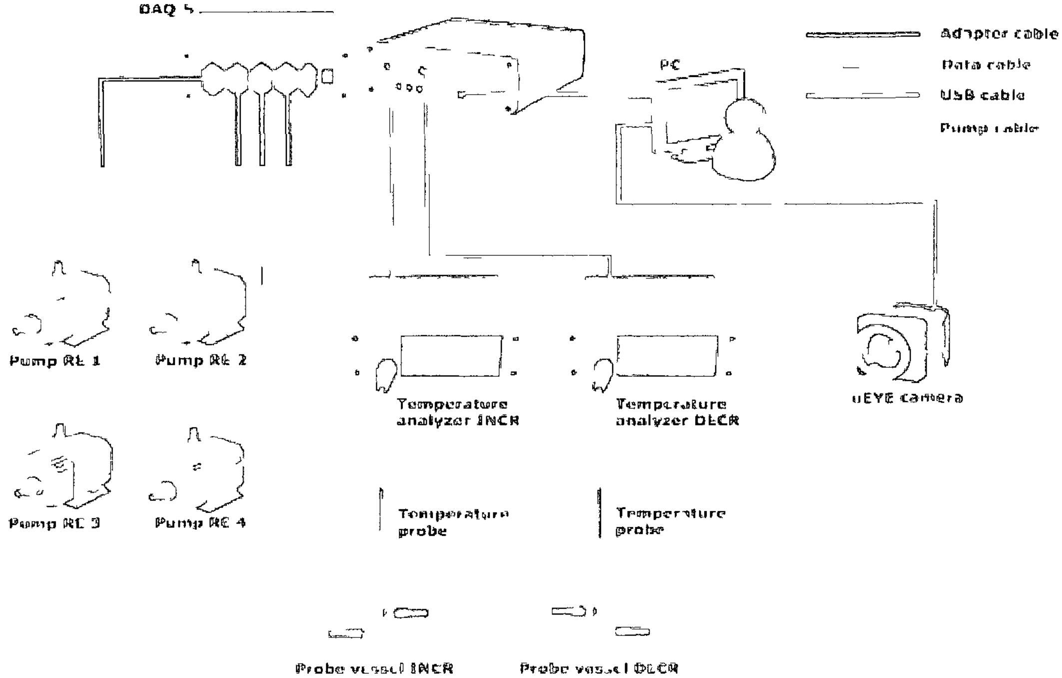


Figure 1-3 cont'd.

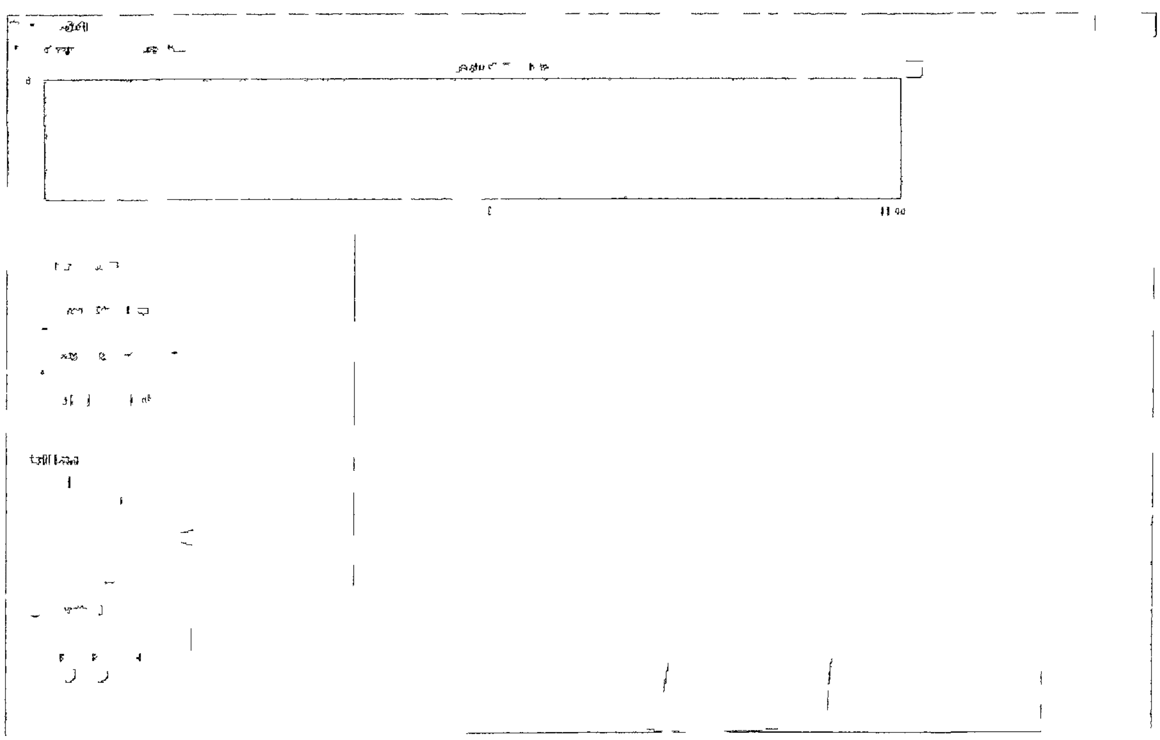
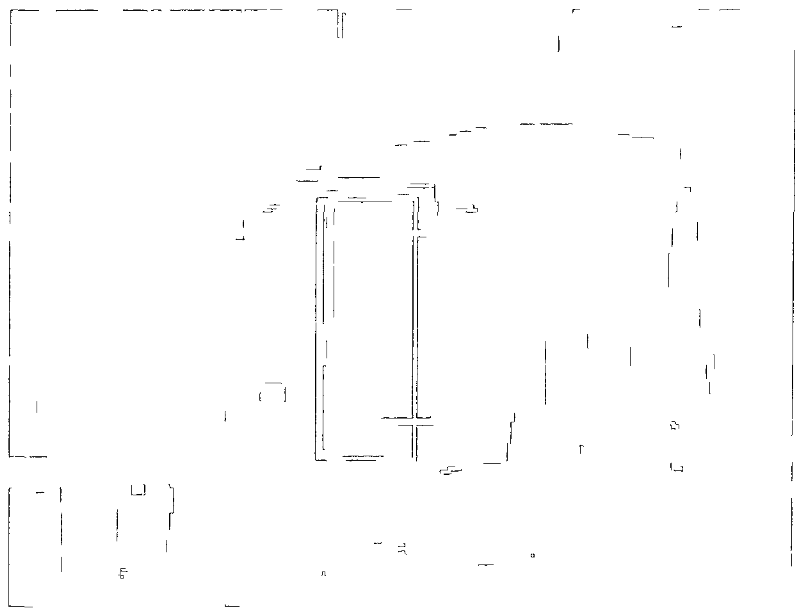


Figure 1-4 Shuttlebox software display (Loligo Systems, Tjele, Denmark)

a.



b.

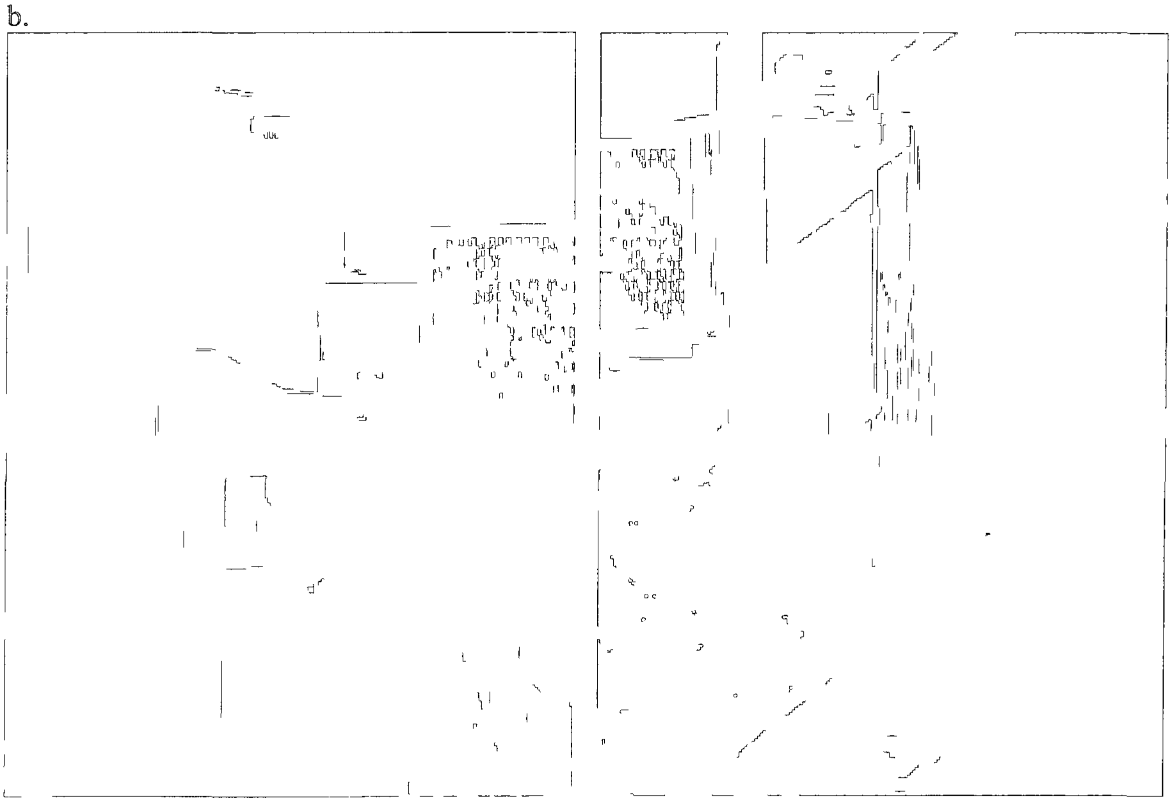


Figure 1-5. Portable shuttlebox laboratory at Chuchi lake field site. a. Enclosed portable trailer; b. Shuttlebox setup inside trailer.

powered by a 6500W generator (American Honda Power Equipment Division, Alpharetta, GA) and two 400W NOMA® Back Up Systems (Canadian Tire Corporation, Toronto, ON) were used to supply continuous power and protect against power surges. Water used in each shuttlebox experiment came from the Nation River and was replaced after each behavioral test. Water quality measurements were taken once starting temperature was obtained, before each fish was placed into the system. Previous work has suggested that temperature selected by fish within the first 2 hours of a temperature preference study is an acute preferred temperature influenced by the ambient temperatures. If fish are observed for a longer period, usually within 24 hours, then the preferred temperature is no longer influenced by the acclimation temperature (Fry 1947; Reynolds and Casterlin 1979a). Each Arctic grayling, therefore, was analyzed in the shuttlebox system for 24 hours. Movement of a fish between the cold and warm chambers revealed the temperature preference of the fish. The first 18 hours were used as an acclimation period for the fish to learn to behaviorally regulate the temperature of the chambers and the last 6 hours were used to determine temperature preference of the fish.

STATISTICAL ANALYSIS

The water temperature of the shuttlebox chamber occupied by the fish was recorded every second and the average of these temperature recordings during the last six hours of the experiment was considered the temperature preference for the fish. An analysis of covariance (ANCOVA) was used to analyze the potential differences in temperature preference between study sites and the potential influence of fork length on the preferred temperatures. A t-test was then used to determine the difference between temperature preference and the corresponding ambient water temperature during capture. Probability levels less than 0.05 were considered significant in all tests.

RESULTS

Behavioral experiments conducted in this study found that the average temperature preference for Arctic grayling across all study sites was 16.84 ± 0.66 °C (mean ± standard deviation, n = 28; See Appendix A for individual fish details). The Arctic grayling tested ranged in size from 5.3 cm to 7.3 cm. An ANCOVA with study site and fish fork length revealed no effect of study site ($F_{2,24} = 0.2655$, $p = 0.7691$) or fork length ($F_{2,25} = 0.23$, $p = 0.80$) on Arctic grayling temperature preference.

Average temperature preference for upper Nation Arctic grayling was 16.83 ± 0.64 °C (n = 9; Figure 1-6). One Arctic graying from this site was unable to learn to behaviorally thermoregulate in the system and was therefore excluded from the analysis. Arctic grayling sampled from the lower site on the Nation River at the mouth of Sylvester Creek had an average temperature preference of 16.74 ± 0.66 °C (n = 10; Figure 1-7). Average temperature preference of Arctic grayling from the Table River study site was 16.97 ± 0.74 °C (n = 9; Figure 1-8). One fish from the Table River study site died during the shuttlebox experiment and was excluded from the analysis.

Ambient water temperature during capture was the highest at the upper Nation River study site, 18.02 °C, which was significantly different from the average temperature preference of the Arctic grayling from this study site (n = 9, $t(8) = -5.56$, $p \sim 0.00$; Figure 1-6). The ambient water temperatures at the lower Nation and Table River sites were similar, 16.59 °C and 16.43 °C, respectively (Figures 1-7 and 1-8) and neither differed significantly

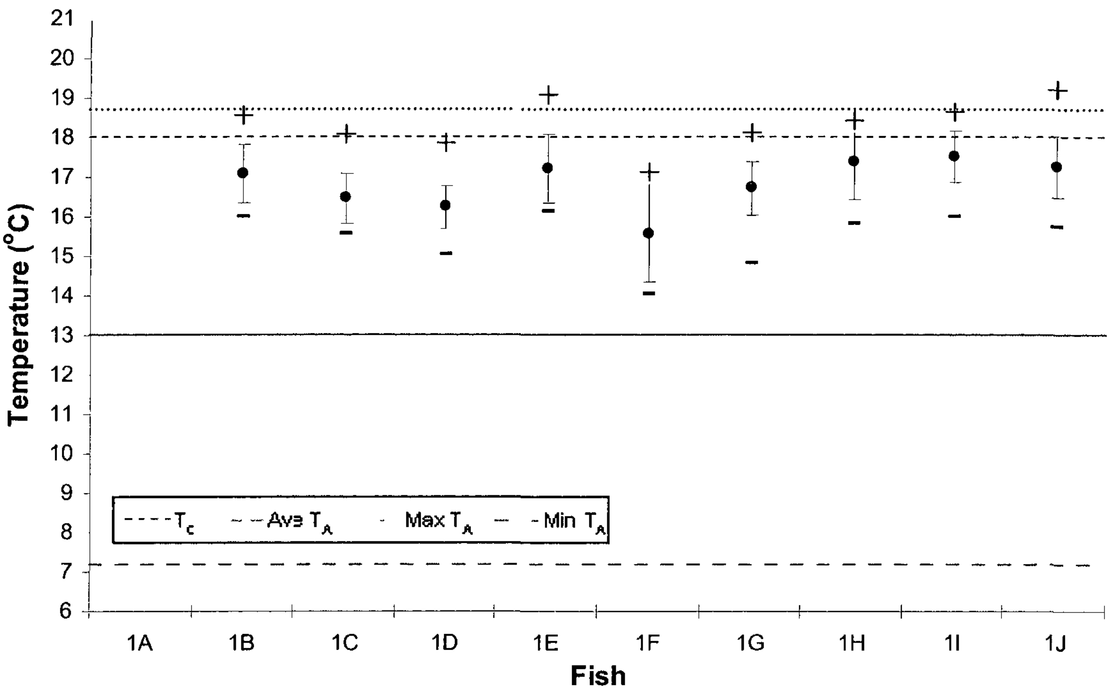


Figure 1-6. Summary of the temperature preferences for Arctic grayling from study site 1 on the upper Nation River (Error bar represent standard deviation of the temperatures recordings taken every second during last 6 hours of each experiment; '+' maximum and '-' minimum by fish during the last 6 hours of experiment; T_C: Ambient water temperature during capture; Ave T_A: Average ambient water temperature during summer months (June 18 - August 18, 2010); Max T_A: Maximum ambient water temperature during summer months; Min T_A: Minimum ambient water temperature during summer months).

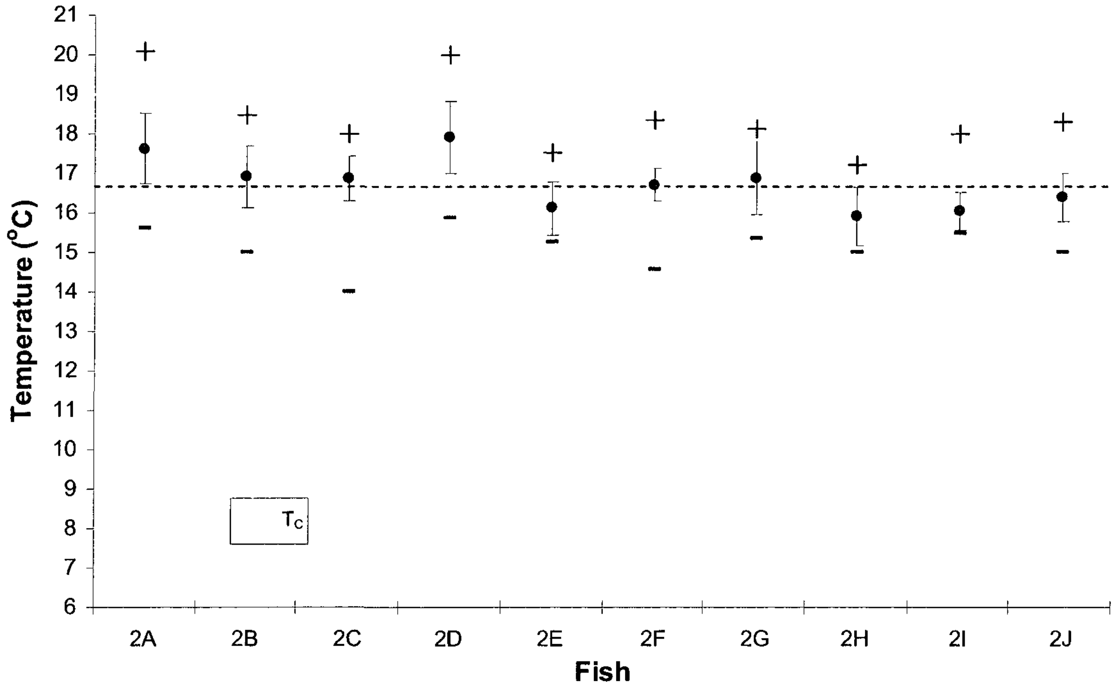


Figure 1-7. Summary of the temperature preferences for Arctic grayling from study site 2 on the lower Nation River near the mouth of Sylvester Creek (Error bar represent standard deviation of the temperatures recordings taken every second during last 6 hours of each experiment; '+' maximum and '-' minimum temperatures experienced by fish during the last 6 hours of experiment; T_C: Ambient water temperature during capture).

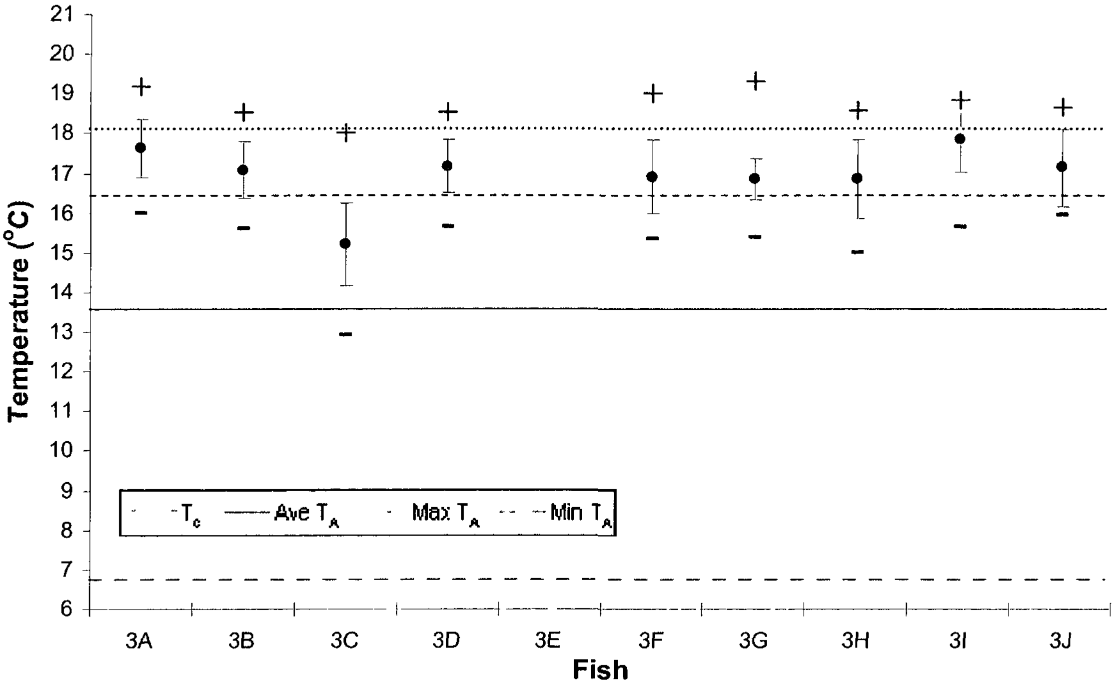


Figure 1-8. Summary of the temperature preferences for Arctic grayling from study site 3 on the Table River (Error bar represent standard deviation of the temperatures recordings taken every second during last 6 hours of each experiment; '+' maximum and '-' minimum temperatures experienced by fish during the last 6 hours of the experiment; T_C: Ambient water temperature during capture; Ave T_A: Average ambient water temperature during summer months (June 18 - August 18, 2010); Max T_A: Maximum ambient water temperature during summer months; Min T_A: Minimum ambient water temperature during summer months).

from the average temperature preference of the Arctic grayling sampled at these study sites ($n = 10$, $t(9) = 0.71$, $p = 0.50$ and $n = 9$, $t(8) = 2.17$, $p = 0.06$, respectively).

DISCUSSION

Temperature preference has been investigated for a number of salmonid species (Neill *et al.* 1972; Coutant 1977; Mortensen *et al.* 2007; McMahon *et al.* 2008; Muhfeld *et al.* 2009), but this study was the first to investigate the thermal preferences for Arctic grayling. We found juvenile Arctic grayling from the Williston watershed to have an average temperature preference of 16.84 ± 0.66 °C. This temperature is high compared to previous sampling records in streams throughout British Columbia that reported average ambient water temperatures of 10.41 ± 3.71 °C where Arctic grayling were caught (Ballard and Shrimpton 2009). Juvenile European grayling (*Thymallus thymallus*) selected water temperatures of 18 °C when placed in a temperature gradient (Coutant 1977), a temperature higher than the results of our study. Using the shuttlebox system on fed juvenile rainbow trout (*Onchorhynchus mykiss*), we found a preferred temperature of 17.66 °C (Hawkshaw and Shrimpton, unpublished); slightly higher than our results for juvenile Arctic grayling. As rainbow trout are typically found in warmer waters than other salmonids (Peterson *et al.* 1979; McMahon *et al.* 2008; Muhfeld *et al.* 2009), preference for a warmer temperature than grayling was not unexpected.

Preferred temperatures are related to the thermal experience of the fish. Previous research has suggested a strong association between acclimation temperatures and temperature preference (Reynolds and Casterlin 1979a; Wagner *et al.* 2001; Mortensen *et al.* 2007). In the present study, preferred temperatures of Arctic grayling from the lower Nation River site and from the Table River site did not differ from the ambient water temperatures recorded where fish were captured. The preferred temperature of Arctic grayling from the upper Nation River the warmest study site, however, was significantly different from the ambient water temperature recorded where fish were captured. All the fish were, however, held in the Nation River for one to 36 days and the average water temperature in the holding containers during the morning was 17.4 ± 1.2 °C; a finding that suggests our protocol determined temperature preference independent of acclimation temperature.

Temperature preference is believed to reflect the optimum temperature for several physiological functions within a fish (Jobling 1981; Brett 1971) and is, therefore, influenced by many different factors (Reynolds and Casterlin 1976; Clark and Green 1991). For example, differences in temperature preference have been reported between species, age, sex, seasons, and time of day (Mortensen *et al.* 2007; McMahon *et al.* 2008; Muhfeld *et al.* 2009). Environmental stresses such as increased levels of hypoxia and decreased availability of food can also influence the temperature preferences of fish (Zdanovich 2006). Experiments by Schurmann *et al.* (1991) found that there was a physiological advantage for rainbow trout to select lower temperatures in hypoxic environments. It is also possible that competitive or predator interactions of fish species with the same temperature preferences may displace one species from their suitable habitat (Byorth and Magee 1998; Bear *et al.* 2007).

In a preliminary study on rainbow trout, we found that fasted fish preferred significantly colder water temperature (12.96 ± 4.05°C) than fed fish (17.66 ± 0.06 °C) (Hawkshaw and Shrimpton unpublished). Fish are naturally subjected to periods of fasting in the environments and will reduce their energy consumption processes. One way fish can conserve energy is by decreasing their body temperature and this can be achieved by behaviorally seeking out cooler water temperatures (Zdanovich 2006; Van Dijk *et al.* 2002).

This ultimately influences the final temperature preference of the fish and must be considered when interpreting the Arctic grayling temperature preference results of this study. In the present study, Arctic grayling were held in flow-through holding containers in an attempt to allow feeding to occur during holding, however stomach contents were not examined and feeding was not confirmed in the study. Condition factor of fish did not change with time and no fish died during the holding period, therefore, it is likely that fish fed while being held in the Upper Nation River.

In the natural environment, temperature regimes where Arctic grayling are found may not be reflecting their preferred temperatures due to limited availability of these temperatures or other environmental factors may be influencing distribution. In this study, temperature preference was closer to the maximum water temperature than average or minimum temperatures. Ambient water temperature records were collected throughout the summer months (June 18 – August 18, 2010) from the upper Nation River and the Table River study sites for the microhabitat analysis in Chapter 2. Although, the average, maximum and minimum water temperatures over this period were significantly different ($p < 0.05$) from the preferred temperatures of Arctic grayling at each study sites, ambient temperatures during the time of capture were near the maximum water temperatures. Water temperature in the shuttlebox during the experiments rarely exceeded the maximum temperature recorded for the two study locations where we had temperature measurements throughout the low-flow summer months. We expect, therefore, that the maximum temperature will determine Arctic grayling occurrence and Arctic grayling will avoid areas where the maximum temperature is above their preferred temperature. The findings of a binary logistic regression model for Arctic grayling occurrence, however, do not support maximum temperature as a limiting factor for Arctic grayling distribution (Chapter 2). It is likely that other factors are also influencing grayling distribution and Chapter 2 of this investigation indicates that other aspects of temperature are important.

Although defining temperature preference for Arctic grayling has been important, there is still little known about other habitat requirements for Arctic graying – and specifically for populations in the Williston watershed (Ballard and Shrimpton 2009). The similar thermal preferences, regardless of capture location, for Arctic grayling in the present study indicates that we can make assumptions about the thermal preference of fish from different river systems throughout the Williston watershed. Caution must be used when making inferences about suitable habitat for Arctic grayling using only temperature preference, however, because temperature preference can vary with other environmental variables and the distribution of fish is influenced by multiple environmental factors (Schurmann *et al.* 1991; Zdanovich 2006; Muhlfeld *et al.* 2009).

CHAPTER 2

Habitat Characteristics that affect Occurrence of a Fluvial Species in a Watershed Impacted by a Large Reservoir: Microhabitat and Macrohabitat Requirements for Arctic Grayling (*Thymallus arcticus*) in the Williston Watershed, British Columbia†

† Throughout this chapter I use the first person plural to acknowledge the contribution of others to this work, which will be submitted for publication with the authorship of S C F Hawkshaw, M P Gillingham and J M Shrimpton

ABSTRACT

Arctic grayling (*Thymalus arcticus*) populations in the Williston watershed, British Columbia, are provincially red-listed (critically imperiled) by the BC Conservation Data Centre (CDC) and currently managed as a catch-and-release fishery. Little is known about Arctic grayling distribution throughout the Williston watershed or the environmental variables that influence their distribution. We evaluated the association of environmental macrohabitat (elevation, gradient, watershed area, Strahler's stream order, migration barriers and road disturbances) and microhabitat (temperature, pH, dissolves oxygen, conductivity, width, depth, velocity, elevation, substrate, large woody debris, reservoir influence, migration barriers, presence of other salmonids species, and road disturbances) scale features with the occurrence of juvenile Arctic grayling using an information theoretic approach. The top macrohabitat model indicated an association between stream order (SO) and Arctic grayling occurrence, but this model validated poorly and had low predictive ability. The top microhabitat models showed a positive association between juvenile Arctic grayling occurrence and distance from the Williston reservoir multiplied by stream order (SDRxSO), as well as a negative association with the mean daily water temperature variance (varT) and average water temperature (aveT). Microhabitat models all validated well and had strong predictive ability. Both scales of analysis indicated the size of the stream system to be the important influence on the occurrence of juvenile Arctic grayling in the Williston watershed. Large river systems, therefore, represent important juvenile Arctic grayling habitat and management decisions should be made to ensure protection of the large river tributaries that flow into the reservoir.

INTRODUCTION

Understanding fish habitat requirements in streams is a major concern for fisheries managers and biologists. By identifying habitat conditions that limit stream fish distribution, management efforts can be focused on specific practices that protect and potentially enhance critical habitat. Logistic regression models are commonly used to model the association between habitat variables and animal occurrence (Bozek and Rahel 1991; Rieman and McIntyre 1995; Rich and McMahon 2003; Rosenfeld 2003; Rashleigh *et al.* 2005; Turgeon and Rodriguez 2005; Fansen *et al.* 2006; McCleary and Hassan 2008). Stream systems are complex, however, and assessing the effects of habitat on fish distribution at a single scale can be misleading. Many studies have suggested that the patterns of fish distribution are the result of multiple scales of habitat conditions and microhabitat and macrohabitat variables are often assessed (Bozek and Rahel 1991; Bozek and Hubert 1992; Porter *et al.* 2000; Rosenfeld 2003). Traditionally microhabitat models have identified stream width, depth, velocity, gradient, substrate, cover, and temperature as important variables influencing stream fish distribution (Shirvell and Dungey 1983; Kozel and Hubert 1989; Bardonnet *et al.* 1991; Rieman and McIntyre 1995; Paul and Post 2001; Rashleigh *et al.* 2005; Turgeon and Rodriguez 2005). Several studies have also identified elevation, channel gradient, and stream size in macrohabitat models as important influences on fish distribution (Platts 1979; Lanka *et al.* 1987; Bozek and Rahel 1991; Hubert and Kozel 1993; Kruse and Hubert 1998; Porter *et al.* 2000; Fansen *et al.* 2006; McCleary and Hassan 2008).

Two of these variables, gradient and stream size, are irreversibly altered when fluvial systems are ponded following the construction of dams. Declines in species abundance and diversity have been reported following flooding of a reservoir, while some species have been shown to increase (Sebastian *et al.* 2003). Of further concern is that freshwater biodiversity is generally recognized to be more threatened than terrestrial biodiversity by global changes (Ricciardi and Rasmussen 1999; Jenkins 2003). Thus, increased efforts are needed to gather better data on patterns of habitat use by freshwater species and how they respond to environmental change.

A species of concern in north-central British Columbia is Arctic grayling (*Thymallus arcticus*). Arctic grayling populations in the Williston watershed are provincially red-listed (critically imperiled) by the BC Conservation Data Centre (CDC) and currently managed as a catch-and-release fishery (Miller 2010). This conservation status was the result of a drastic decline in Arctic grayling abundance over two decades in the Williston watershed (Northcote 1993). The decline occurred after the construction of the WAC Bennett Dam by BC Hydro and subsequent flooding of the Upper Peace River forming the Williston reservoir in 1968. The creation of the Williston reservoir changed a fluvial system into an adfluvial environment. Arctic grayling in the Williston watershed exhibit a fluvial life-history strategy and there is evidence that this population does not use adfluvial habitat (Kaya and Jeanes 1995). Recently, Clarke *et al.* (2007) demonstrated that Arctic grayling in the Williston Watershed do not use the reservoir, indicating that flooding of the Upper Peace resulted in considerable loss of habitat. It is, however, difficult to quantify the effects of the dam on populations of Arctic grayling given the paucity of information on Arctic grayling before the dam was built (but see Bruce and Starr 1985) and there is limited information on the physical and environmental requirements for this species.

The aim of this study was to examine the influence of environmental characteristics on juvenile Arctic grayling occurrence in the Williston watershed. Little is known about

Arctic grayling distribution in the Williston watershed or about the environmental variables that influence this distribution. We used an information-theoretic approach to identify which environmental variables have the greatest influence on juvenile Arctic grayling distribution at both macrohabitat and microhabitat scales of analysis. It is important to understand what factors affect distribution positively or negatively to develop an understanding of how habitat changes have, but also may, impact Arctic grayling populations.

MATERIALS AND METHODS

MACROHABITAT

Study Area

The Williston watershed is approximately 70,000 km^2 and supports a number of Arctic grayling populations. Several sub-watersheds make up the Williston watershed. We selected 97 sub-watersheds for analysis of Arctic grayling macrohabitat requirements (Figure 2-1). Watersheds were selected to represent the potential range of habitats available to Arctic grayling in the Williston watershed. These watersheds ranged in size from 2.23 km^2 to 19024.07 km^2.

Arctic Grayling Presence/Absence

Juvenile Arctic grayling presence or absence in the study watersheds during the low flow summer months was primarily (74%) determined for this macrohabitat analysis from previous sampling records (Williamson and Zimmerman 2005). Electrofishing and seine-net surveys were conducted for some of the study sites in the Parsnip, Nation and Manson

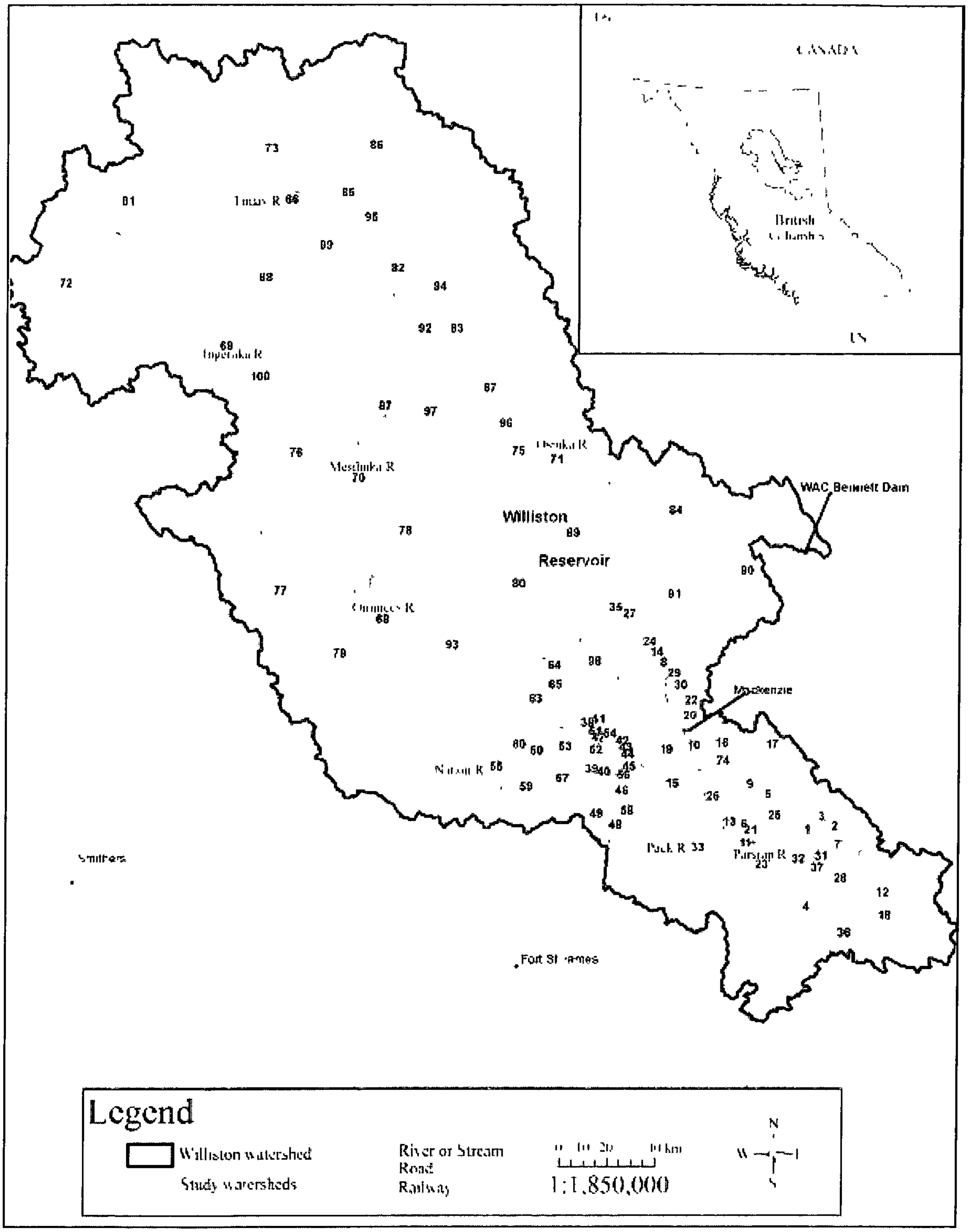


Figure 2-1. Map of the Williston watershed, indicating approximate location of each watershed included in macrohabitat analysis (n = 97; Sites 34, 61 and 62 correspond to second microhabitat sites in a watershed and were excluded from this analysis).

watersheds in summer of 2010 for the microhabitat analysis (see below). Where available, the results of the field surveys were cross referenced with previous sampling records. If survey results did not agree with previous sampling records Arctic grayling were considered to be present because of the limitations of using previous surveys that were not targeting Arctic grayling. Previous sampling records were not available for 25 study watersheds in the southern part of the Williston watershed. The electrofishing and seine-net surveys conducted in the summer of 2010, therefore, were used to designate juvenile Arctic grayling presence or absence in these watersheds.

Macrohabitat Variables

Eleven macrohabitat variables (Table 2-1) were collected using information derived from the Terrain Resource Information Management (TRIM) watershed atlas digital elevation model (DEM), a digital base map of British Columbia on a 1:20,000 scale in Geographic Information Systems (GIS) software, ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA) (Spatial Vision Consulting Ltd. 1996; Caslys Consulting Ltd. 2010), and databases of fish sampling records provided by the British Columbia Ministry of Environment (Williamson and Zimmerman 2005). The variables selected for this analysis were previously identified as important influences on the distribution of Arctic grayling and/or other salmonid species (Platts 1979; Beecher *et al.* 1988; Rieman and McIntyre 1995; Kruse *et al.* 1997; Porter *et al.* 2000; Blackman and Hunter 2001; Cowie and Blackman 2003; Cowie and Blackman 2004; Williamson and Zimmerman 2004; Fransen *et al.* 2006; Scrimgeour et al. 2008; McCleary and Hassan 2008).

Macrohabitat variables were based on a watershed scale and categorized as watershed or disturbance variables. Watershed variables included average, maximum and minimum

Table 2-1. Variables used to characterize macrohabitat in the Williston watershed.

Category	Code	Type	Units	Description
Watershed	aveE	Map	m	Average Stream Elevation
	maxE	Map	m	Maximum Stream Elevation
	minE	Map	m	Minimum Stream Elevation
	aveG	Map	%	Average Stream Gradient
	maxG	Map	%	Maximum Stream Gradient
	minG	Map	%	Minimum Stream Gradient
	SO	Map	SO Units	Strahler (1952) stream order extracted from 1:20,000 TRIM maps.
	WSA	Map	km^2	Watershed Area
	OWSD	Map	$\#/km^2$	Density of known migration barriers in watershed
Disturbance	WSR	Map	km/km^2	Road density in watershed (including all roads and railroads)
	WSSX	Map	$\#/km^2$	Stream crossing density in watershed (includes all road and railroad crossings)

stream elevation, average, maximum and minimum stream gradient, stream order (Strahler 1952), watershed area, and migration barriers (density of known migration barriers in each watershed). Disturbance variables included road density and stream crossing density in each watershed. The z-coordinates on the 1:20,000 TRIM base map of British Columbia represent the elevation from sea level and were used to calculate the elevation variables (aveE, maxE and minE) for each watershed. Gradient variables were calculated using the difference in elevation, z-coordinates, between the two end points of a stream divided by the total stream length, measured using the 'Measure' tool in ArcGIS 9.3. Watershed area and stream order from the TRIM freshwater atlas DEM database were used in the analysis (Caslys Consulting Ltd. 2010). A database with locations of known fish migration barriers (falls, cascades, bridges, beaver dams, culverts and large rocks) (Williamson and Zimmerman 2005) was mapped on the TRIM freshwater atlas DEM and used to determine the watershed density of barriers (number of barriers in a watershed / watershed area). Road density was determined by measuring the length of all roads within a watershed, using the 'Measure' tool in ArcGIS 9.3, divided by the watershed area. Stream crossing density was determined by counting the number of times roads crossed streams within a watershed, divided by the watershed area.

MICROHABITAT

Study Area

Sixty five microhabitat study sites were selected in the southern part of the Williston watershed from the Parsnip, Nation and Manson watersheds (Figure 2-2). Sites were initially selected based on previous Arctic grayling sampling records from 1975 to 2009 (Williamson

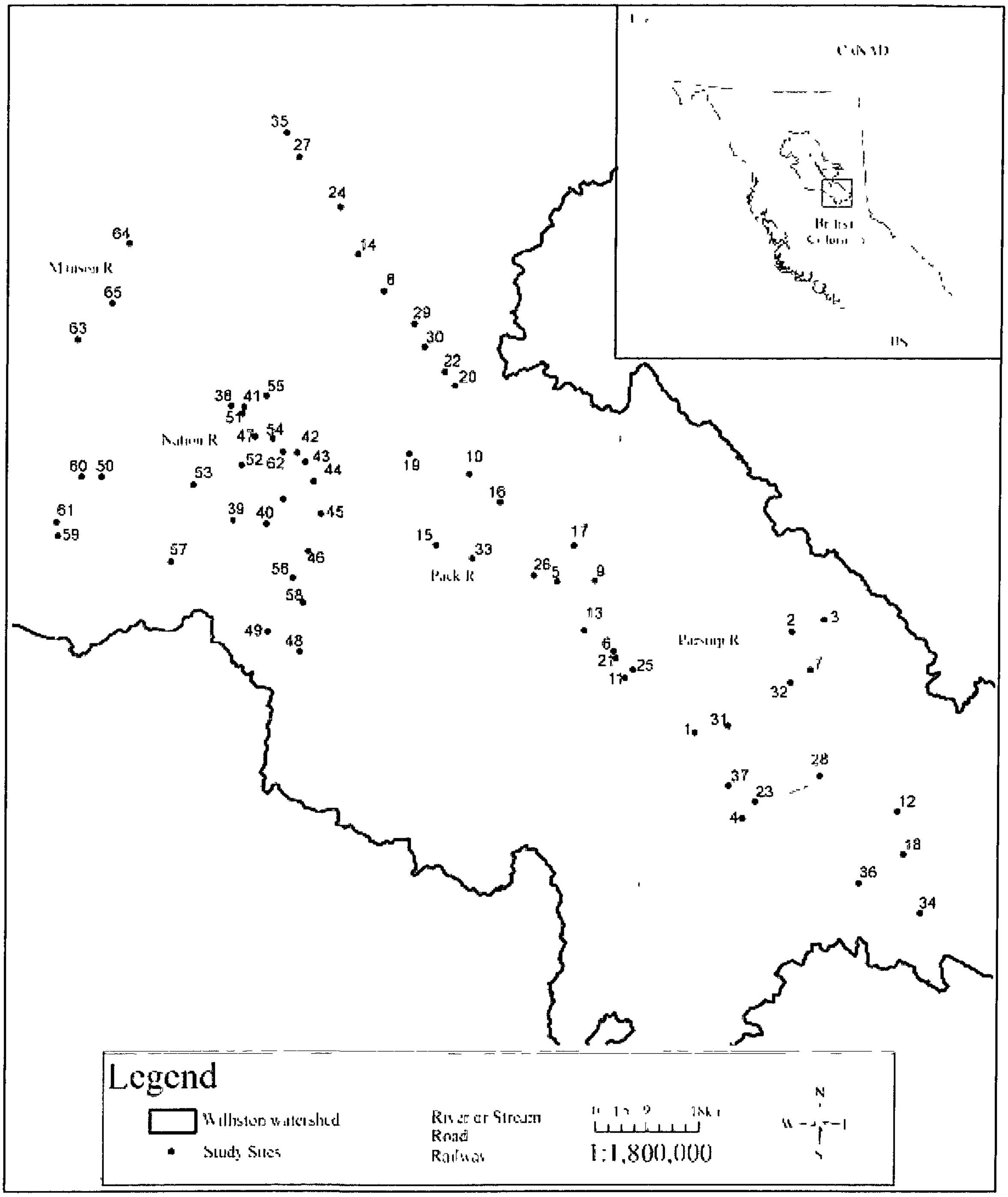


Figure 2-2. Map of the southern part of the Williston watershed, indicating the locations of the microhabitat study sites (n = 65).

and Zimmerman 2005). The Parsnip watershed is the southern periphery of the Arctic grayling range in BC. Each study site was located on a different stream system (with the exception of upper and lower sites, >100 km apart, on the Parsnip River, Nation Rivers and Philip Creek) and we assumed that the sites were independent of each other and fish would not migrate between sites during the study. Study sites were chosen to represent a variety of environmental characteristics available in the major watersheds. Some sites were located in streams fed by large lake systems, and other sites were in streams influenced by snowmelt. The study sites were also located in streams associated with anthropogenic disturbances such as road development, mining, and forest harvesting. Pictures of the microhabitat study sites are provided in Appendix B.

Arctic Grayling Presence/Absence

Juvenile Arctic grayling presence or absence was determined by field surveys conducted in the low flow summer months (June-September) in 2010 and previous sampling records from 1994 - 2004 (Williamson and Zimmerman 2004). In the field, a battery-powered backpack electrofisher (Smith-Root, Vancouver, WA) was used to conduct single-pass surveys on the stream reaches containing each study site to confirm presence or absence (Kruse *et al.* 1998; Peterson *et al.* 2002). We assumed juvenile Arctic grayling to be present in the study site if at least one individual of any size was observed and the presence of all fish species was recorded. Electrofishing methods could not safely be used at three sites (depth > 1 m). A beach seine net survey, therefore, was conducted on each stream reach containing a study site. The results of field surveys were cross referenced with previous sampling records. Previous sampling records were only available for forty of the microhabitat sites. The field survey results were in agreement with previous sampling records for the majority (88%) of these sites, with the exception of five study sites. Juvenile Arctic grayling were not reported at these five study sites in the previous sampling records, but were sampled in our field surveys. Juvenile Arctic grayling were considered to be present at these sites because of the limitations of using previous surveys that did not necessarily target Arctic grayling. Furthermore, the conditions at two study sites were unsuitable for both electrofishing and seine net surveys (depth > 1 m and water velocity too high) so the most recent sampling records were used to determine presence or absence of juvenile Arctic grayling.

Microhabitat variables

Twenty microhabitat variables were either measured directly in the field or derived from the 1:20,000 TRIM watershed atlas DEM (Williamson and Zimmerman 2005; Caslys Consulting Ltd. 2010) (Table 2-2). Similar to the macrohabitat variables, all microhabitat variables have been recognized in the literature as important influences on Arctic grayling and/or other salmonid species distribution (See Appendix D for specific references). All field measurements were taken during the low flow summer months (June-September) in 2010 and were collected at sites that were representative for the stream reach.

Microhabitat variables were taken from four main categories: water quality, physical habitat, biological and disturbance. To capture the range of thermal conditions, as well as seasonal high and low temperatures at each site, which are thought to influence Arctic grayling distribution, temperature data loggers (HOBO Water Temp U22, Onset Corporation, Bourne, MA) were installed at 65 microhabitat study sites, between June and September in 2009. All temperature loggers were placed into a protective steel casing and attached to a strong, permanent feature with wire cable and placed in flowing water at the bottom of the

Table 2-2. Microhabitat variables used in analysis ('Field' variables measured at time of Arctic grayling presence/absence surveys; 'Map' variables derived from the TRIM watershed atlas DEM, a digital base map of British Columbia on a 1:20,000 scale.

Category	Variable	Type	Units	Description
Water Quality	varT	Field	$^oC^2$	Mean daily water temperature variance
	aveT	Field	^oC	Mean daily average water temperature
	maxT	Field	^oC	Mean daily maximum water temperature
	DO	Field	mg/l	Dissolved oxygen
	COND	Field	μS/cm	Electrical conductivity
	pH	Field		pH at study site
Physical Habitat	DEPTH	Field	m	Stream depth
	WIDTH	Field	m	Wetted stream width
	VEL	Field	m/s	Velocity of 60% of depth
	ELEV	Field	m	Elevation GPS unit measure
	GRAD	Map	%	Average site gradient
	aveS	Field	1-6	Average substrate coarseness (1=clay and silt (<0.059); 2=sand (0.06-1); 3=fine gravel (2-16mm); 4=coarse gravel (16-64mm); 5=cobble (64-256mm); 6=boulders)
	sdS	Field	1-6	Substrate heterogeneity (standard deviation of average coarseness)
	LWD	Field	#/site	Number of large woody debris
	SDRxSO	Map	km*SO	Stream distance from Williston reservoir multiplied by stream order
	OUPD	Map	#/km	Density of known migration barriers upstream of study site.
	ODOWND	Map	#/km	Density of known migration barriers downstream of study site
Biological	OTHER	Field	Y/N	Presence or absence of other fish species
Disturbance	K1R	Map	km/km^2	Road density (including all roads and railroads)
	K1SX	Map	$\#/km^2$	Stream crossing density (includes all road and railroad crossings)

stream. Water temperature was logged every hour for one year. The temperature data logged in 2010 during the summer months (June 18, 2010 - August 18, 2010) was used to calculate three temperature variables (mean daily average water temperature, mean daily water temperature variance, and mean daily maximum water temperature). A single point measurement of dissolved oxygen, conductivity and pH were measured during temperature logger collection (2010) at the bottom of the water column. Dissolved oxygen was measured using a handheld YSI 550A (Yellow Springs, OH). Conductivity and pH were measured using a HANNA pH/EC Combo meter (Woonsocket, RI).

Physical habitat variables included water depth, wetted-stream width, water velocity, elevation, stream segment gradient, substrate composition, quantity of large woody debris, distance of study site from the Williston reservoir, density of barriers upstream of the study site, and density of known barriers downstream of the study sites. Site depth and wetted stream width were measured at each study site where the temperature logger was installed in a single representative transect. Water velocity was measured using a Swoffer Velocity Meter (Model 2100, Seattle, WA) at 60% of depth at each temperature logger site (Bain and Stevenson 1999). A handheld Garmin eTrex Legend GPS unit (Olathe, KS) was used to measure elevation at each site during temperature logger installation. Visual estimation of the percentage of each substrate category (from a modified Wentworth scale (1 = clay and silt (<0.059 mm); 2 = sand (0.06 – 1 mm); 3 = fine gravel (2 – 16 mm); 4 = coarse gravel (16 – 64 mm); 5 = cobble (64 – 256 mm); 6 = boulders (> 256 mm)) within a 0.5 m^2 transect centered at each temperature logger was recorded and used to determine average substrate coarseness and heterogeneity (Cummins 1962; Bain and Stevenson 1999). We quantified large woody debris by a visual count of all large woody debris ($\geq$ 1 m long and 10 cm diameter) fully or partially submerged in the stream and visible from where the temperature logger was installed.

Stream-segment average gradient, distance of study site from the Williston reservoir, stream order, the density of obstacles upstream and downstream of the study site were all extracted from the TRIM watershed atlas DEM, the digital base map of British Columbia on a 1:20,000 scale (Williamson and Zimmerman 2005; Caslys Consulting Ltd. 2010). Stream segments defined in the BC freshwater atlas were used in this analysis (Caslys Consulting Ltd. 2010). The average gradient of stream segments containing microhabitat study sites were calculated using the difference in elevation, z-coordinates, between the two end points of a stream segment divided by the distance along the stream segment, measured using the 'Measure' tool in ArcGIS 9.3. The influence of the Williston reservoir on each study site was quantified using a measure of stream distance from the reservoir to each site, measured using the 'Measure' tool in ArcGIS 9.3 and multiplied by the stream order extracted from the TRIM watershed atlas DEM (Caslys Consulting Ltd. 2010). A database with locations of known fish migration barrier (falls, cascades, bridges, beaver dams, culverts and large rocks) (Williamson and Zimmerman 2005) was mapped on the TRIM freshwater atlas DEM and used to determine the density of barriers upstream and downstream of each study site (number of barriers divided by stream length).

The only biological variable measured was the presence or absence of other salmonid species at each field site and this was coded as a binary response variable. This information was collected during the Arctic grayling presence/absence surveys in the 2010 field season. Previous sampling records (Williamson and Zimmerman 2005) were cross referenced with the presence/absence results of the survey. Where presence/absence surveys could not be conducted previous survey data was used to determine presence or absence of other salmonid species at a study site (Williamson and Zimmerman 2005).

Disturbance variables, road density and stream crossings, were also extracted from the 1:20,000 TRIM watershed atlas DEM for this analysis. Road density was calculated by measuring the length of road within a 0.5-km-radius of each study site, using the 'Measure' tool in ArcGIS 9.3, divided by the area of the 0.5-km-radius circle. Stream crossing density was measured by counting the number of road-stream crossings, divided by the area of the 0.5-km-radius circle. Logging roads, highways, and railroads were included for both variables.

STATISTICAL ANALYSIS

We used an information theoretic approach (Burnham and Anderson 2002) to construct and rank candidate models from a set of predictor variables recognized as important for explaining habitat use by Arctic grayling. Models were developed from previous studies on Arctic grayling; however, literature on Arctic grayling habitat requirements is limited and information on other salmonid species was used to supplement any important data gaps (Ballard and Shrimpton 2009). Models were developed at two scales; a watershed-scale (macrohabitat) and a smaller stream-reach scale (microhabitat). For the large scale modeling approach, 15 ecologically plausible macrohabitat candidate models were created. For the small scale modeling approach, 35 ecologically plausible microhabitat candidate models were developed. A summary of hypotheses used to form the candidate macrohabitat models is provided in Appendix C and a summary of hypotheses used to form the candidate microhabitat models is provided in Appendix D.

Each candidate model, fit with the data collected for each variable and using presence (1) / absence (0) of Arctic grayling as the response variable, was assessed with logistic regression. Akaike's Information Criterion (AIC), regression coefficients (β) and standard error terms were calculated for each variable to evaluate the components of each candidate model (Burnham and Anderson 2002). Variance inflation factors (VIF) for each variable were examined to assess the model covariates for multicollinearity, which may influence coefficients and error terms (O'Brien 2007). No variables were dropped due to multicollinearity. Temperature variables and elevation were evaluated for potential non-linear relationships by fitting models with the individual variable and comparing the fit to models with the quadratic form of the variable. Due to a better fit, elevation was included as a quadratic in microhabitat models only. Each variable was also evaluated for complete or near-complete separation (Menard 2002).

AIC values for each candidate model were corrected for small sample size (AIC_c) (Burnham and Anderson 2002) and used to rank macrohabitat and microhabitat models separately. Akaike weight (w_i) was also calculated for each model to support the evidence for the top models in each model set. When competing models had similar levels of support, top models with w_i summing to ≥ 0.95 were averaged and inferences were made using the averaged model (Burnham and Anderson 2002). The area under the receiver operating characteristic (ROC) curve is typically calculated to evaluate the predictive ability of logistic regression models (Pearce and Simon Ferrier 2000). The data in this study, however, does not represent true absence data, limiting the reliability of our interpretation of the ROC scores when making predictions (Bozek and Rahel 1991; Bozek and Hubert 1992; Nelson *et al.* 1992; Reiman *et al.* 1997; Dunham *et al.* 2003; Peterson and Dunham 2003). The validation of the top models therefore was evaluated using a k-fold cross validation procedure for five random subsets of the data and a Spearman's rank correlation ($\bar{r}_s$) was produced for each subset with a significance p-value (Boyce *et al.* 2002). Average $\bar{r}_s >$ 0.648 with a p-value < 0.05 was considered valid (Zar 1972). Statistical analysis was performed using R (version v.2.8.1; R Foundation for Statistical Computing, Vienna, Austria) and STATA statistical software (version 9.2; StataCorp, College Station, Texas).

RESULTS

MACROHABITAT

Watersheds used in the analysis of Arctic grayling macrohabitat selection (n = 97) ranged considerably in size (ie. Strahler stream order 1-8 and watershed area 2-19024 km^2). Arctic grayling were present in 42% of these watersheds (Appendix E). There was scarce evidence of collinearity between the variables (VIF < 10); therefore, all of the original ecologically plausible candidate models were included in the analysis. The top two ranked macrohabitat models had AIC_c weights (w_i) of 0.692 and 0.251, respectively (Table 2-3). A summary of the variables measured for the macrohabitat analysis is presented in Appendix F.

Stream order appeared to be the most ecologically plausible model with the highest w_i, low standard error for all parameters (Table 2-4). Both top models identified stream order as an important variable for predicting the occurrence of Arctic grayling; the second-ranked model also identified watershed area. The second-ranked model, however, did not appear to perform better than the simpler model with only stream order. Watershed area had a very low coefficient (Table 2-4). Additionally, when watershed area modeled individually it had a high ΔAIC_c value, ranking it 7th, indicating that it was a poor fit for the data.

Table 2-3. Summary of macrohabitat logistic regression models ranked by Akaike weights (w_i) (n = 97; k = number of variables, including intercept).

Rank	Model	k	AIC_c	ΔAIC_c	w_i
1	SO	2	119.0	0.0	0.692
2	SO + WSA	3	121.0	2.0	0.251
3	aveE + maxE + minE + aveG + maxG + minG	7	126.6	7.6	0.015
4	aveG + maxG + minG + WSR + WSSX	6	126.9	7.9	0.013
5	OWSD + aveG + aveE	4	127.4	8.5	0.010
6	aveE + maxE + minE + aveG + maxG + minG + WSA	8	127.8	8.9	0.008
7	WSA	2	130.2	11.3	0.002
8	aveG + maxG + minG + WSA	5	129.9	10.9	0.003
9	aveG + maxG + minG	4	130.6	11.7	0.002
10	aveE + maxE + minE	4	130.9	12.0	0.002
11	WSR + WSSX	3	133.2	14.2	0.001
12	aveE + maxE + minE + WSR + WSSX	6	132.7	13.7	0.001
13	OWSD + aveE	3	135.4	16.4	0.000
14	OWSD	2	136.2	17.3	0.000
15	OWSD + aveG	3	137.3	18.4	0.000

Table 2-4. Summary of the top ranked logistic regression macrohabitat models (n = 97; β = Coefficient; OR = odds ratio; SE = standard error; z = z-score; p = p-value).

Rank	Parameter	β	OR	SE	z	p	β 95% CI	
							Lower	Upper
1	Intercept	-4.302	0.01	1.125	-3.825	0.000	-6.686	-2.247
	SO	0.765	2.15	0.208	3.669	0.000	0.383	1.206
2	Intercept	-4.139	0.02	1.215	-3.405	0.001	-6.730	-1.921
	SO	0.727	2.07	0.236	3.078	0.002	0.292	1.226
	WSA	0.000	1.00	0.000	0.32	0.749	0.000	0.000

The simpler model with only stream order was selected as the best macrohabitat model, however, the k-fold cross validation analysis for this top ranked model suggested that the model had very low predictive ability for the occurrence of Arctic grayling in the Williston watershed ($\bar{r}_s = 0.298 \pm 0.260$, $n = 5$, $p = 0.351$). The data suggest that Arctic grayling are likely to be absent from rivers with a small stream order (< 4), but they may be present or absent in the larger stream order streams (≥ 4), making the model's predictive ability weak for larger stream order rivers (Figure 2-3).

MICROHABITAT

Microhabitat study sites chosen for the analysis were limited to streams that were accessible in the field. Study sites were in watersheds that ranged in size from approximately 3.0 to 6921.2 km^2 and sites were located on rivers that ranged in stream order from 2 to 8. Eight of the initial 65 study sites were not included in the analysis because temperature data from the loggers were lost ($n = 57$). Arctic grayling were present in 47% of the remaining study sites (Appendix E). There was little collinearity between microhabitat variables used in this analysis (VIF < 10) and all originally considered candidate models were included in the analysis. A summary of the variables measured for the macrohabitat analysis is presented in Appendix G.

The top three microhabitat models had w_i of 0.772, 0.151 and 0.077, respectively (Table 2-5). All three top models included SDRxSO indicating that stream distance from the reservoir multiplied by stream size had a positive effect on the presence of Arctic grayling in the study area (Table 2-6). The top ranked model, SDRxSO + varT, also suggested that mean daily water temperature variance had a strong negative effect on the presence of Arctic grayling. The k-fold cross validation for this model suggested that it had strong predictive

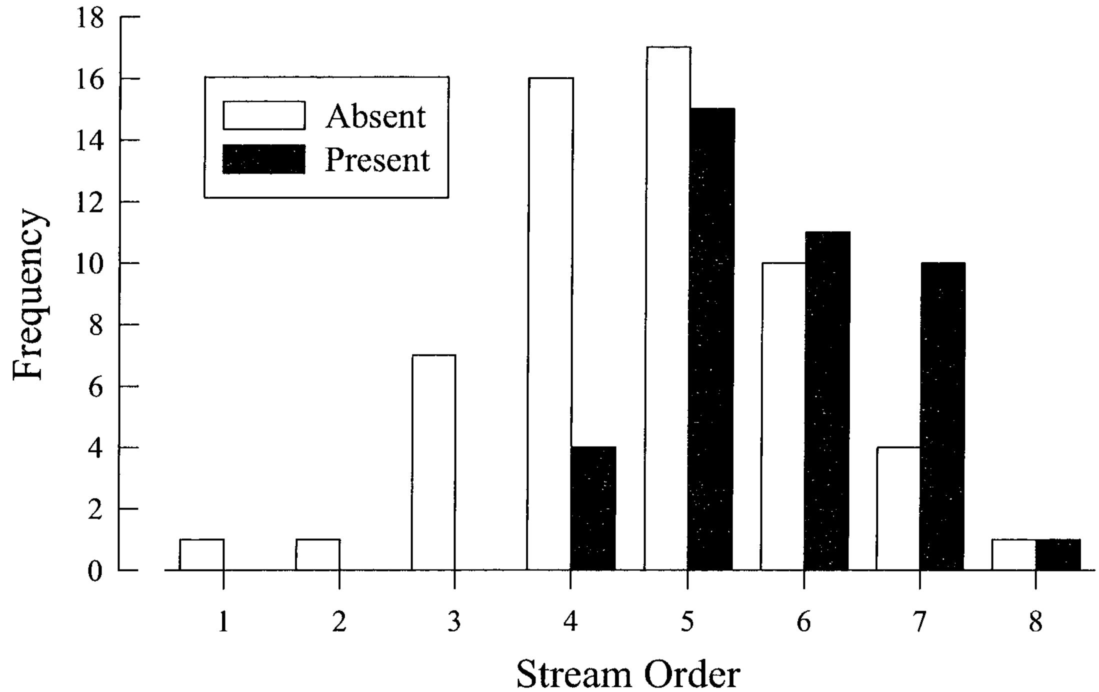


Figure 2-3. Frequency of watersheds with Arctic grayling absent or present for each stream order.

Table 2-5. Summary of microhabitat logistic regression models ranked by Akaike's weights (w_i) (n = 57; k = number of variables, including intercept).

Rank	Model	k	AIC_c	ΔAIC_c	w_i
1	SDRxSO + varT	3	46.2	0.0	0.772
2	SDRxSO + aveT	3	49.5	3.3	0.151
3	SDRxSO	2	50.8	4.6	0.077
4	WID + E + E^2	4	64.4	18.3	0.000
5	varT	2	64.5	18.3	0.000
6	varT + aveT + maxT	4	64.6	18.5	0.000
7	maxT + WID + E + E^2 + GRAD	6	64.7	18.5	0.000
8	varT + COND	3	65.0	18.9	0.000
9	varT + aveT + maxT + DEP + aveS + sdS + LWD	8	66.0	19.8	0.000
10	varT + aveT + maxT + K1SX	5	66.8	20.6	0.000
11	varT + aveT + maxT + DO	5	66.9	20.7	0.000
12	WID + E + E^2 + K1R + K1SX	6	68.6	22.4	0.000
13	OUPD + GRAD + E + E^2 + WID	6	69.3	23.1	0.000
14	varT + aveT + maxT + DO + COND + PH	7	70.2	24.1	0.000
15	WID + E + E^2 + GRAD + aveS + sdS	7	71.0	24.8	0.000
16	WID + COND	3	71.8	25.6	0.000
17	OUPD + WID	3	74.6	28.4	0.000
18	OUPD + E + E^2	3	75.5	29.3	0.000
19	WID + E + E^2 + GRAD + aveS + sdS + K1R + K1SX	9	75.8	29.7	0.000
20	WID + LWD + OTHER	4	75.9	29.7	0.000
21	OTHER	2	77.9	31.7	0.000
22	COND	2	78.2	32.1	0.000
23	GRAD	2	79.0	32.8	0.000
24	VEL + GRAD	3	79.4	33.2	0.000
25	maxT	2	80.3	34.1	0.000
26	DEP + aveS + sdS	4	80.9	34.7	0.000
27	OUPD + GRAD	3	81.0	34.9	0.000
28	VEL + DEP + aveS + sdS	5	81.6	35.4	0.000
29	aveT	2	81.6	35.4	0.000
30	LWD	2	82.1	35.9	0.000
31	aveS + sdS	3	82.2	36.0	0.000
32	VEL	2	82.5	36.3	0.000
33	VEL + DEP + aveS + sdS + LWD	6	83.1	36.9	0.000
34	OUPD + ODOWND	3	83.9	37.7	0.000
35	K1R + K1SX	3	84.5	38.3	0.000

Table 2-6. Summary of the top ranked logistic regression microhabitat models (n = 57; β = Coefficient; OR = odds ratio; SE = standard error; z = z-score; p = p-value).

Rank	**Parameter**	**β**	**OR**	**SE**	**z**	**p**	**β 95% CI**	
							Lower	**Upper**
1	Intercept	-0.665	0.51	1.05	-0.634	0.526	-2.828	1.378
	SDRxSO	0.009	1.01	0.00	3.594	0.000	0.005	0.015
	varT	-1.658	0.19	0.75	-2.202	0.028	-3.393	-0.371
2	Intercept	3.204	24.64	3.51	0.912	0.362	-3.194	10.703
	SDRxSO	0.011	1.01	0.00	4.014	0.000	0.007	0.018
	aveT	-0.550	0.58	0.33	-1.680	0.093	-1.277	0.019
3	Intercept	-2.803	0.06	0.72	-3.898	0.000	-4.407	-1.540
	SDRxSO	0.010	1.01	0.00	4.133	0.000	0.006	0.016

ability for the occurrence of Arctic grayling in the Williston watershed at the microhabitat scale ($\bar{r}_s$ = 0.691 ± 0.106, n = 5, p = 0.039). The second-ranked model, SDRxSO + aveT, suggested a negative association between the mean daily average water temperature and the occurrence of Arctic grayling. The k-fold cross validation for this model suggested that it also had reasonable predictive ability for the occurrence of Arctic grayling in the Williston watershed at the microhabitat scale ($\bar{r}_s$ = 0.662 ± 0.081, n = 5, p = 0.045). The third-ranked model was the simplest or most parsimonious model containing only SDRxSO. The k-fold cross validation for this model suggested that it also had reasonable predictive ability for the occurrence of Arctic grayling in the Williston watershed ($\bar{r}_s$ = 0.650 ± 0.160, n = 5, p = 0.071).

Because all three top models had reasonable validation and appeared to have high predictive ability, an average model was created to make inferences about Arctic grayling occurrence in the study area (Table 2-7). The averaged model was (-0.256 + (0.009) SDRxSO – (1.277) varT – (0.0825) aveT). This model indicated that the SDRxSO and varT appeared to be the largest influences on Arctic grayling occurrence in the study area with a smaller effect of aveT. Arctic grayling primarily occurred in study sites with low average daily temperature variance (< 1.65 $^{o}C^{2}$) and increased distance from the Williston reservoir with large stream order (> 151.2 km*SO) (Figure 2-4).

DISCUSSION

This study was the first analysis of Arctic grayling habitat selection in the Williston watershed. The incomplete information describing habitat use and selection by Arctic grayling has limited management and conservation options for populations in the Williston watershed, hence the fishery has been catch-and-release since 1995 (Northcote 1993;

Table 2-7. Summary of the averaged microhabitat model (β = averaged coefficient; SE = standard error; z = z-score; p = p-value).

Parameter	β	Variance	SE	z	p	β 95% CI	
						Lower	Upper
Intercept	-0.256	5.319	1.201	-0.213	0.831	-2.610	2.098
SDRxSO	0.009	0.000	0.002	5.008	0.000	0.006	0.013
varT	-1.277	1.356	0.606	-2.105	0.035	-2.465	-0.088
aveT	-0.083	0.028	0.088	-0.938	0.348	-0.255	0.090

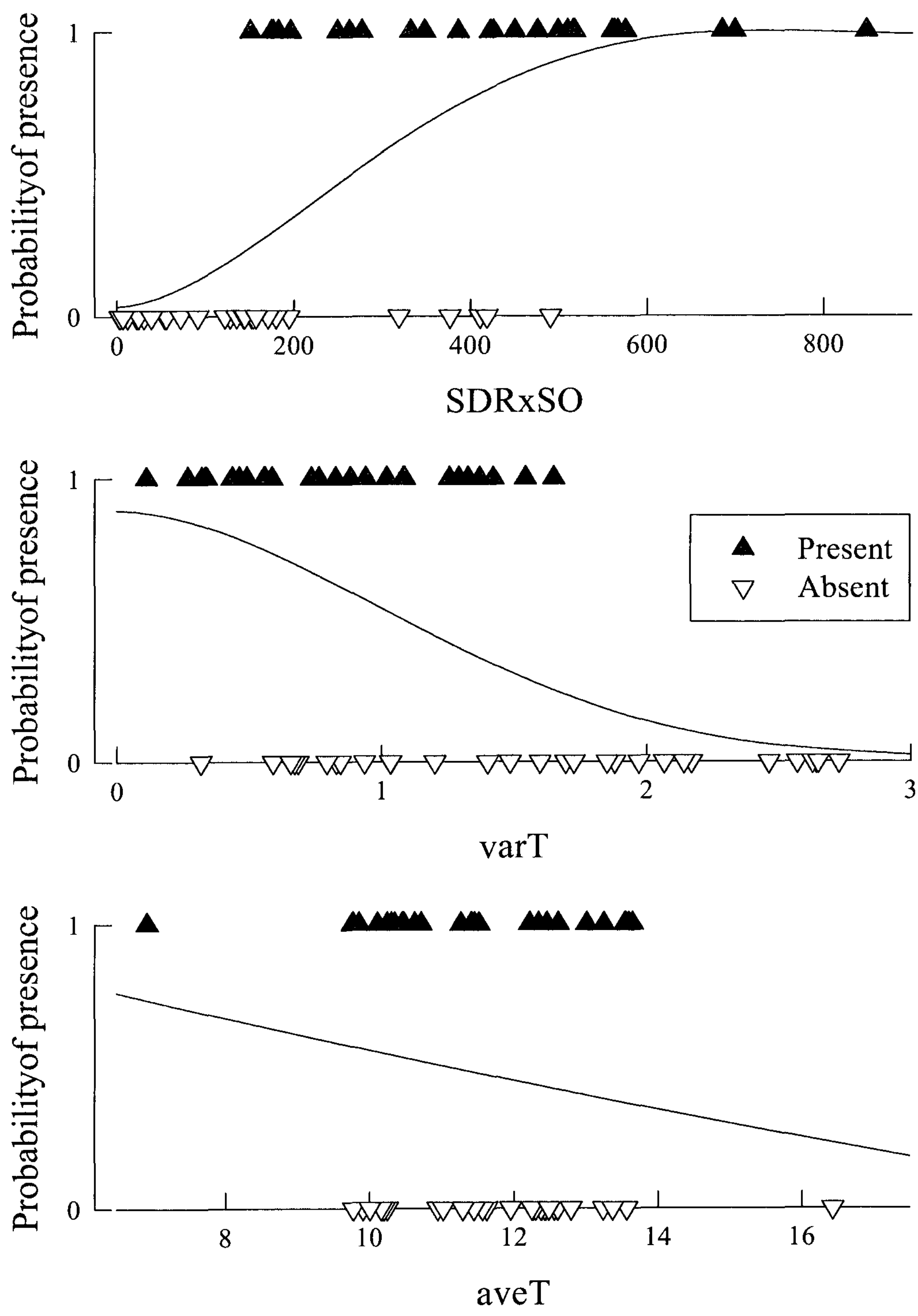


Figure 2-4. Arctic grayling presence (n = 27) and absence (n = 30) in relation to the influence of the Williston reservoir (SDRxSO), the mean daily temperature variance (varT) and mean daily average temperature (aveT).

Northcote 1995; Ballard and Shrimpton 2009; Miller 2010). Understanding the environmental conditions influencing Arctic grayling occurrence in the Williston watershed has been a challenge in the past because of the size of the region and the lack of baseline information available on the population. Often the influences of environmental conditions on the occurrence of fish species are not all explained at the same habitat scale, therefore, we assessed the importance of environmental conditions on the occurrence of Arctic grayling at both macrohabitat and microhabitat scales.

MACROHABITAT

The macrohabitat analysis model provides insight into why juvenile Arctic grayling are present in some rivers within the Williston watershed over others. Past analyses of the influence of large-scale habitat features on the occurrence of salmonids species have had mixed results (Hawkins *et al.* 2000; Porter *et al.* 2000; Harig and Fausch 2002; Rich *et al.* 2003). The results of this study indicated stream order to be important for predicting Arctic grayling occurrence in the Williston watershed, a finding consistent with previous work on grayling and other salmonid species (Platts 1979; Beecher 1988; Tautz *et al.* 1992; Rieman and McIntyre 1995; Williamson and Zimmerman 2004). Stream order is an indicator of stream size and is related to a number of physical characteristics of a stream (ie. width, depth and discharge). It is relatively easy to determine stream order from topographic maps, therefore, it is often used to identify the occurrence of salmonid species in a system (Tautz *et al.* 1992; Rieman and McIntyre 1995). Increasing stream order has been associated with increased species diversity and fish abundance (Platts 1979; Beecher 1988). A comprehensive review of historical Arctic grayling data was conducted for the Williston watershed (Williamson and Zimmerman 2004) and suggested that Arctic grayling preferred fourth-order streams or larger. The review also recognized that little is known about Arctic grayling spawning and early rearing habitat requirements in this area which may alter this perceived relationship with steam order.

The predictive ability of the model with stream order was very poor, however, suggesting restricted utility for predicting Arctic grayling occurrence. Juvenile Arctic grayling were absent from study streams with small stream order (<4), but were both present and absent in large stream order streams (≥4). Inferences, therefore, can be made about Arctic grayling absence from small order streams, but this model can not be used to predict Arctic grayling occurrence in larger streams. Such a finding does not discount the influence of watershed scale habitat features on Arctic grayling occurrence because it is possible that Arctic grayling are sensitive to indirect watershed differences or differences that were not measured in this study.

Watershed area was present in the second-ranked macrohabitat model combined with stream order. This model was found to be an even poorer predictor of Arctic grayling occurrence in the Williston watershed than stream order on its own. Previous studies on other stream dwelling salmonids suggested that presence was positively associated with watershed area (Rieman and McIntyre 1995; Porter *et al.* 1999; Harig and Fausch 2002; McCleary and Hassan 2008). The conflicting results of our study compared to previous work may indicate a difference in preference between salmonid species as the influence of watershed area has not been previously investigated for Arctic grayling. It is also possible that the predictive ability of watershed area found in other studies was due to collinearity with a small-scale habitat variable. In our study area the majority of the watersheds (81 %)

were small (<1000 km^2) and the lack of larger watersheds also likely limited the predictive ability of the second ranked model.

Arctic grayling are also absent from all the major watersheds on the eastern side of the Williston reservoir regardless of stream order. The eastern side of the Williston reservoir is composed primarily of cascades and canyons through the Rocky Mountains; terrain that creates high velocity from steep gradients. Research has suggested that Arctic grayling prefer lower velocities and shallower gradient (McPhail and Lindsey 1970; Cowie and Blackman 2003) and it has been suggested that this is likely the reason for Arctic grayling absence from these systems (Williamson and Zimmerman 2004). We investigated the influence of three gradient variables (aveG, maxG and minG) on Arctic grayling occurrence in the Williston watershed in a single model. These variables showed no collinearity with one another and the model ranked poorly. In addition to gradient, elevation, watershed area, fish migration barriers, road construction and stream crossings have been shown to have a significant influence on the occurrence of salmonids (Bozek and Hubert 1992; Kruse *et al.* 1997; Byorth and Magee 1998; Paul and Post 2001; Fransen *et al.* 2006; Scrimgeour *et al.* 2008; Rich *et al.* 2003; McCleary and Hassan 2008). We found that these variables measured at a macrohabitat scale were poor predictors of Arctic grayling occurrence in the Williston watershed. The third-ranked macrohabitat model contained a combination of average, maximum and minimum stream elevation, and gradient, but this model had poor predictive ability and did not validate well.

There are several factors that could account for the poor predictive ability of these macrohabitat models. In the study area the majority of watersheds had intermediate average stream gradients, low maximum gradients (<2.6 %) and minimum gradients were commonly zero, indicating a lack of watersheds with overall high gradients. Arctic grayling were both present and absent over the entire range of stream elevations in the study area (671 – 2820 m). It is likely that the effects of stream gradient and elevation would be more evident at a smaller scale of analysis. For example the occurrence of Arctic grayling has been associated with low elevation at the stream reach scale in the Big Hole Drainage, Montana and two boreal forest watersheds of Alberta (Byorth and Magee 1998; Scrimgeour *et al.* 2008). Furthermore, the distribution of many salmonid species has also been associated with stream gradient at local habitat scales (Porter *et al.* 1999; Rich *et al.* 2003; McCleary and Hassan 2008).

Barriers to movement have also been shown to significantly influence fish distribution (Kruse *et al.* 1997; Thompson and Rahel 1998; Novinger and Rahel 2003). Kaya (2000) found that Arctic grayling in Yellowstone National Park were unable to establish areas upstream of migration barriers. The density of migration barriers was expected to be associated with Arctic grayling occurrence in the study watersheds because barriers create fragmentation in a stream and limit distribution. Contrary to expectations, the results of this macrohabitat analysis did not suggest any association between the watershed density of migration barriers and the occurrence of Arctic grayling in the study area. A possible explanation for the difference is that the Yellowstone Park study was conducted at a reach scale and it is likely that watershed scale used in our study was too coarse to show any influence on Arctic grayling and barriers limiting upstream/downstream movement at a local scale may be more important.

The density of roads and stream crossings were similar in watersheds where Arctic grayling were present and absent indicating that this level of anthropogenic disturbance does not influence the occurrence of Arctic grayling in the study area. These results conflict with a study conducted on two boreal forest watersheds of Alberta which suggested that road density was positively related to the occurrence of Arctic grayling and mountain whitefish (Scrimgeour *et al.* 2008). This study also reported that Bull trout in these watersheds were negatively associated with road density and the positive relationship with Arctic grayling occurrence may be from the reduced rates of predation.

MICROHABITAT

The microhabitat analysis study sought to explore small-scale attributes that may define habitat suitability for Arctic grayling and predict occurrence across the whole Williston watershed. The results indicated an average microhabitat model with significant validation and predictive ability. The average model showed a positive association between Arctic grayling occurrence and stream size multiplied by distance from the Williston reservoir, as well as a negative association with the mean daily water temperature variance and mean daily average water temperature. This suggests that Arctic grayling in the study area prefer larger river systems with habitat that extends far from the Williston reservoir and in large- stream systems with stable cool water temperatures.

The top three microhabitat models all included the influence of the Williston reservoir variable, indicating that the Williston reservoir has a strong negative influence on Arctic grayling occurrence. The variable used to assess the influence of the Williston reservoir was an interaction between the stream distance from the Williston reservoir and stream order. The inclusion of stream order made it possible to distinguish between study sites on large and small streams that were the same distance from the reservoir. In the average model, SDRxSO was the most important influence on Arctic grayling occurrence compared to varT and aveT.

The distance from a study site to a reservoir downstream has not been measured as an environmental variable affecting salmonid habitat selection. The Williston reservoir, however, has previously been identified as a major influence on Arctic grayling distribution. Gillnet and trawl-net surveys failed to capture any Arctic grayling in the Williston reservoir suggesting that they do not utilize it (Pillipow and Langston 2002; Sebastian *et al.* 2003). Furthermore, Arctic grayling otolith microchemistry from six major tributaries in the Williston watershed showed no signature indicative of the reservoir and the authors concluded that grayling never entered the reservoir (Clarke *et al.* 2007). The significance of the SDRxSO variable at the microhabitat scale may be indicative of the availability of important habitat and suggests that fluvial fish require considerable habitat downstream of locations where they are commonly found – potentially for critical life-history stages. Fluvial Arctic grayling in the Williston watershed (Kaya and Jeanes 1995) may be displaced downstream into an undesirable lake-type environment and lost if the spawning population is too close to the reservoir.

Our results also indicated that Arctic grayling occurrence was negatively associated with daily water temperature variance and average stream temperatures. Water temperature has a direct effect on behavior, physiology and the ecological interactions of salmonids and has long been shown to influence their distribution (Thomas *et al.* 1986; Deegan *et al.* 1999; Lohr *et al.* 1996; Porter *et al.* 2000; Dunham et al. 2003; Johnstone and Rahel 2003; Lobon-Cervia 2003; Wehrly *et al.* 2007; Meeuwig *et al.* 2004; De la Hoz Franco and Budy 2005). Species-specific work has also demonstrated the influence of water temperature on Arctic grayling distribution (LaPerriere and Carlson 1973; Lohr *et al.* 1996; Deegan *et al.* 1999). The pattern of Arctic grayling distribution in the Big Hole River, Montana, appeared to be influenced by a behavioral avoidance of waters close to their upper incipient lethal temperature limit (Lohr *et al.* 1996).

Many studies have linked average and maximum stream temperatures to the distribution of salmonids (Deegan *et al.* 1999; Porter *et al.* 2000; Dunham *et al.* 2003; Rashleigh *et al.* 2005; Muhlfeld *et al.* 2009), but daily stream temperature variance has not commonly been investigated in habitat selection models. We found that the mean daily stream temperature variance had a significant influence on Arctic grayling occurrence in the study area. Streams typically undergo daily variation in temperature and the magnitude of this variation is usually associated with stream size and/or the nature of the headwaters (Vannote and Sweeney 1980; Thomas *et al.* 1986). In our study, daily water temperatures fluctuated up to 14.8 °C in the low flow summer months and afternoon maximum temperatures reached up to 23.0 °C. Such ranges are similar to data for other western Canadian streams in the Rocky Mountains where water temperatures fluctuated by 10 to 13 °C in the summer and maximum water temperatures exceeded 24 °C (Schrank *et al.* 2003).

High diel-temperature variations could be beneficial; however, if stream temperatures exceed the upper incipient lethal temperature because the cool temperatures will allow fish to recover as has been shown in Bonneville cutthroat trout (Johnstone and Rahel 2003). Arctic grayling from the Big Hole River, Montana had upper incipient lethal temperatures of 23 °C when acclimated at 16 °C and 25 °C when acclimated at 20 °C (Lohr *et al.* 1996). It is, therefore, unlikely that Arctic grayling in the study area were limited by the maximum water temperatures and high temperature variations would not benefit them in this environment. In fact, a previous study on juvenile coho salmon suggested that large fluctuations in diel temperatures (6.5 - 20 °C) produced elevated levels of plasma cortisol and glucose, indicating increased stress (Thomas *et al.* 1986).

Average daily water temperatures appeared to have a smaller influence on Arctic grayling occurrence in the study area than daily temperature variance. Mean daily average temperatures in the study area ranged from 6.9 - 16.4 °C, however, the majority of sites had intermediate temperatures (mean ± SD, 11.61 ± 1.48 °C). In chapter 1 we determined that the average preferred temperature of Arctic grayling from the southern part of the Williston reservoir was 16.84 ± 0.66 °C. Yet, Arctic grayling were absent from the study site with the highest mean daily average temperature, 16.4 °C. This suggests that other factors are affecting occurrence and our model indicates that the most notable variables are the influence of the reservoir and the mean daily temperature variance.

Habitat variables traditionally used to predict presence/absence of stream fish were also evaluated in this analysis. Interestingly several of the traditional candidate models were considered poor predictors of occurrence of Arctic grayling in the study area. Given that there is a lack of information on the unique habitat requirements for fluvial Arctic grayling populations in the study area, it is possible that Arctic grayling in the Williston watershed do not respond to these variables. Some variables from the poorly ranked models (water quality variables other than temperature) did not differ significantly across study sites and the lack of effect on Arctic grayling occurrence could be the result of sampling over a narrow range of measurements for these variables.

MODELLING LIMITATIONS

Although presence/absence logistic regression models are commonly used to predict the occurrence of fish species, limitations of these models must also be considered. One of the most commonly addressed limitations of presence/absence logistic regression models is the correct designation of absence (Bozek and Rahel 1991; Bozek and Hubert 1992; Nelson *et al.* 1992; Reiman *et al.* 1997; Dunham *et al.* 2003; Peterson and Dunham 2003). Presence of a fish species can often be confirmed at a location, but it is very difficult, if not impossible, to confirm absence of a species. Absence may be the result of failing to detect the presence of the species that is actually present at that site. Caution must be used when making inferences using models developed using data with potentially false absences. Particularly, when interpreting ROC scores, which are dependent on true absence data (Fielding and Bell 1997; Pearce and Ferrier 2000).

In this study we conducted a single-pass electrofishing or seine net survey at each microhabitat study site and cross referenced the survey results with previous sampling records to establish Arctic grayling presence or absence. There was no previous fish sampling records for 22 (39%) of the final microhabitat sites used in the analysis and Arctic grayling were determined to be absent from 16 (28%) of these sites by single-pass electrofishing surveys. Conducting multiple surveys at these study sites would have minimized the chances of false absences; however we did not have the resources to do so during this study. Further confirmation of Arctic grayling absence in a stream system would increase our confidence in the top models identified in this study.

Data used to determine presence and absence from Williamson and Zimmerman (2005) and from our sampling used methods that tend to target juveniles and small species. Consequently, our models do not reflect habitat use by adult Arctic grayling. Earlier work showed that this species segregated in streams during the summer based on size and age; older and larger fish found further upstream (Hughes and Reynolds 1994; Hughes 1999;

Baccante 2011). We cannot conclude, therefore, that smaller and lower order streams are not important habitat for other Arctic grayling life stages. The focus of our study on juveniles, however, represents an important contribution to understanding habitat needs for the critical juvenile life stage.

Another potential limitation to consider when making inferences using the models developed in this study is validation. Assessing the predictive ability of the top models is essential to evaluate the strength of the model. In this study the top models were validated by sub-sampling the original dataset and testing the predictive ability on each subset. This limits our confidence in applying the top models to different geographic locations because they may have different environmental gradients. Furthermore different populations of Arctic grayling may have different habitat requirements and until tested, it is uncertain whether the model is transferable.

MANAGEMENT IMPLICATIONS

Both scales of analysis, macrohabitat and microhabitat, identified the size of a stream system as an important influence on the occurrence of juvenile Arctic grayling in the Williston watershed. Although the top macrohabitat model did not validate well and had low predictive ability, it indicated a higher probability of juvenile Arctic grayling occurrence in large streams. The microhabitat analysis results suggest that in the summer months juvenile Arctic grayling are likely to be present in sites further away from the Williston reservoir in large streams with low daily temperature variance. Overall both analyses suggest a similar finding; large systems are needed for juvenile Arctic grayling to be present throughout the Williston watershed. The negative association of juvenile Arctic grayling occurrence with daily temperature variance identified in the microhabitat analysis further supports the need to protect large streams as important habitat for juvenile Arctic grayling. Large streams are less vulnerable to heat loading due to their higher thermal capacity and exhibit less daily variation in temperature (Caissie 2006). Conservation and management efforts to benefit juvenile Arctic grayling populations, therefore, would be most effective if existing areas with the characteristics of large stream systems and low daily temperature variance in the summer months were identified. Implementation of stream restoration to provide these conditions could also potentially sustain long-term health of juvenile Arctic grayling populations in the Williston watershed. The influence of the Williston reservoir reflects the impacts of a large anthropogenic disturbance and can only be assessed indirectly. Increased monitoring of habitat characteristics at sites near and far from the Williston reservoir would give managers a better understanding of the influence of the reservoir and lead to more comprehensive planning and decision making for Arctic grayling populations across the study area. For predictive habitat models to be useful in fisheries management they should include variables that can be monitored and/or affected directly or indirectly by management decisions and practices.

Temperature varies in natural aquatic systems but it may also be altered directly or indirectly by anthropogenic activities (Webb *et al.* 2008) and our work suggests that management decisions should be made to prevent increases in variance of summer temperature would benefit Arctic grayling populations. Ongoing and future disturbances in the Williston watershed that will affect stream temperature include forest harvesting and mining. To mitigate for potential effects associated with resource extraction, riparian vegetation should be protected in watersheds where Arctic grayling are present as lost riparian shade through deforestation leads to increases in stream temperature (Beschta and

Taylor 1988; Macdonald *et al.* 2003). Consequently an effect of timber removal is greater daily temperature variation – a response that our analysis indicates would negatively affect grayling. Artificially low flows may also increase water temperatures by increasing the area of air-water interface per unit volume of water (Webb *et al.* 2003). Water extraction that results in discharge reduction can lead to significant temperature changes particularly for systems with gradual slope where the influence of solar radiation is stronger (Meier *et al.* 2003). For this reason, extraction of water from Arctic grayling streams and clear-cut practices adjacent to Arctic grayling streams (or tributaries flowing into these streams) that might reduce mid-summer discharge should be minimized.

The information from this study can be used for predicting changes in habitat suitability associated with proposed future disturbances, such as the construction of additional dams, forest harvesting or mining activities in the study area. The top models developed in our analysis, however, are specific to juvenile Arctic grayling in the Williston watershed and caution should be used if attempting to apply these models to other populations. Similar models can be applied to other systems to develop population specific models but the specific requirements of these populations need to be considered.

EPILOGUE

Historically, the Upper Peace River was formed as the Parsnip and Finlay Rivers flowed together. Following the creation of the Williston reservoir the Upper Peace River and the lower sections of the Parsnip and Finlay were flooded. Additionally, the lower reaches of a large number of the tributaries flowing into these river systems were also flooded and the fluvial environment drastically changed. The change in habitat has long been speculated to be the cause for changes in species abundance; most notably the decline in Arctic grayling. Scarce information has been documented on the physical and environmental habitat requirements of Arctic grayling before and after the creation of the reservoir, limiting management and conservation initiatives for these populations. The objectives of this research were to assess temperature preference requirements of juvenile Arctic grayling populations in the Williston watershed and describe the influence that temperature regimes and other environmental variables have on their distribution. These objectives were designed to address important information gaps and help us to define habitat requirements for Arctic grayling throughout the Williston watershed.

The results of this investigation will be integrated into the BC provincial management plan for Arctic grayling and used to make inferences about other Arctic grayling populations, as well as other stream dwelling salmonid species. Fluvial Arctic grayling have been suggested as an indicator species of the health of stream ecosystems (Vincent 1962; Kaya 1992; Blackman 2001). When habitat requirements for this species are not met their abundance declines, indicating that they are extremely sensitive to habitat alterations and disturbances. Examples of declines due to habitat loss have been seen in the Williston watershed, where Arctic grayling populations declined drastically after the reservoir was built (Northcote 1995); in Michigan where Arctic grayling populations have been extirpated since the 1930s (Vincent 1962); and in Montana where Arctic grayling populations have declined significantly in range and abundance (Kaya 1991; Clark 1996). My thermal preference investigation (Chapter 1) suggested that juvenile Arctic grayling from the Nation and Table Rivers had similar temperature preferences across all study sites; 16.84 ± 0.66 °C. Temperature preference experiments were independent of prior thermal acclimation, therefore, inferences can be made about the preferred temperatures of other Arctic grayling populations based on the results of this study. I further compared preferred temperature to ambient water temperatures at sample locations during the summer and from this I expected juvenile Arctic graying occurrence to be influenced by the thermoregulatory behavior to avoid areas where the maximum temperature exceeds their preferred temperature. A binary logistic regression juvenile Arctic graying distribution modeling analysis, however, did not support this theory, but indicates that other aspects of environmental temperature were more important (Chapter 2).

I investigated a number of other important environmental factors at multiple habitat scales that could potentially influence juvenile Arctic grayling distribution throughout the Williston watershed using binary logistic regression modeling with an information theoretic approach (Chapter 2). Both scales of analysis indicated a positive association between stream size and juvenile Arctic grayling occurrence, suggesting that large river systems represent critical habitat. The creation of the Williston reservoir flooded a large portion of one of the major river systems in northern BC. Because fluvial Arctic grayling in the area do not utilize the lake-type habitat of the reservoir these populations lost large stretches of critical fluvial habitat. Future management planning should focus on protecting the remaining large river systems where juvenile Arctic grayling are currently distributed. Furthermore, the microhabitat scale analysis of this study indicated a negative association between juvenile Arctic grayling occurrence and the mean daily water temperature variance and average water temperature. Long-term monitoring of water temperatures throughout the year would therefore provide baseline information regarding water quality for these populations of Arctic grayling and enhancement efforts can be focused.

Within the Williston watershed there are a number of anthropogenic disturbances that continue to degrade stream habitat and threaten Arctic grayling and also other fish populations. For example logging and mining activities have recently increased in the Nation River watershed with the development of the Mount Milligan gold/copper mine (Terrane Metals Corp.). Mandatory environmental assessments have been conducted for Mount Milligan mine under provincial legislation and the Canadian Environmental Assessment Act (CEAA), indicating that the mine is not likely to cause significant adverse effects on fish and their habitats. The activities of this mine are concentrated in the southern part of the Nation River watershed, primarily affecting Rainbow Creek. Arctic grayling have been captured only in the lower part of Rainbow Creek near mouth entering into the Nation River and the mining activity is located near the middle of this stream. The comprehensive study report prepared by Fisheries and Oceans Canada and Natural Resources Canada therefore indicated that Arctic grayling are not expected to be impacted by the mine. The findings of our study, however, suggest that Rainbow Creek represents a large river system that potentially represents critical habitat for Arctic grayling. The water temperature throughout this stream system should be monitored and further Arctic grayling occurrence surveys should be conducted to confirm Arctic graying potential utilization of this watershed.

The BC Hydro Site C hydroelectric dam, proposed to be constructed downstream of the WAC Bennett dam on the Peace River, is another example of an anthropogenic disturbance that will impact Arctic grayling populations negatively. The proposed dam will create a reservoir smaller than the Williston reservoir, but it will flood a portion of the lower Peace River and a number of important large stream order tributaries where Arctic grayling are found, such as the Halfway and Moberly Rivers. BC Hydro is currently conducting an environmental study to inventory fish and stream habitat in areas that will be impacted directly by the flooding in the Peace, Halfway and Moberly Rivers. Construction of the Site C dam, however, will result in loss of juvenile Arctic grayling habitat in more than just the flooded areas. The results of my investigation suggest that the probability of juvenile Arctic grayling occurrence increases with stream size and that shorter tributaries (< 79 km) are not likely to be used by juvenile Arctic grayling. Flooding will displace juvenile Arctic grayling from the lower flooded reaches of tributaries into habitat further upstream if it is suitable. If the remaining stream habitat in rivers and streams that are flooded following the creation of a reservoir from the Site C dam is not suitable, however, grayling populations within these systems are likely to be lost. At the very least species composition is likely to be altered and it has been suggested that Arctic grayling do not do well when crowded by other competing or predatory salmonid species (Vincent 1962). Even if suitable habitat is available upstream, juvenile grayling may be precluded; Arctic grayling in the summer months segregate in streams according to size and age, getting larger and older going upstream (Hughes and Reynolds 1994; Hughes 1999; Baccante 2011). Downstream movement during the first year of life concentrates younger fish in the lower reaches of rivers (Hughes 1999). It is not known what will happen to juveniles that move downstream if the lower reaches of the rivers are flooded, but I speculate that they are lost from the population based on my microhabitat model results. It will, therefore, be important to also monitor population densities, life history distribution and species composition over many years in areas upstream of the proposed flooding. This will allow the true impact of dam construction on Arctic grayling and other fish populations to be evaluated.

My study strongly suggests that large river systems represent important habitat for fluvial juvenile Arctic grayling and that they avoid short river systems that only have fluvial habitat close to the reservoir. The Williston watershed, however, represents a unique ecosystem dominated by tributaries flowing into a reservoir and only fluvial Arctic grayling have been recognized in this area. Throughout the range of this species, including other management regions in BC, both fluvial and adfluvial life histories have been identified. The results of my study can only be used to make inferences about fluvial Arctic grayling populations. Nevertheless, management decisions and planning for Arctic grayling should be made to ensure protection of large river systems throughout the range of this species and further research should be conducted to confirm habitat requirements of adfluvial Arctic grayling populations.

REFERENCES

Baccante DA 2011 Further evidence of size gradients in Arctic grayling (*Thymallus arcticus*) along stream length. BC Journal of Ecosystems and Management, 11:13-17.

Ballard S and Shrimpton JM 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 and Wildlife Compensation Program Report No. 337, 66 pp. Prince George, BC.

Bain MB and Stevenson NJ 1999 Aquatic habitat assessment: common methods. American Fisheries Society, Bethesda, MD.

Bardonnet A, Gaudin P and Persat H 1991 Microhabitat and diel downstream migration of young grayling (*Thymallus thymallus L.*). Freshwater Biology, 26:365-376.

Bear EA, McMahon TE and Zale AV 2007 Comparative thermal requirements of westslope cutthroat trout: Implications for species interactions and development of thermal protection standards. Transactions of the American Fisheries Society, 136:1113-1121.

Beecher HA, Dott ER and Fernau RF 1988 Fish species richness and stream order in Washington State streams. Environmental Biology of Fishes, 22:193-209.

Berman CH and Quinn TP 1991 Behavioural thermoregulation and homing by spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. Journal of Fish Biology, 39:301-312.

Beschta RL and Taylor RL 1988 Stream temperature increases and land use in a forestred Oregon watershed. Journal of the American Water Resources Association, 24:19-25.

Boyce MS, Vernier PR, Nielsen SE, and Schmiegelow FK 2002 Evaluating resource selection functions. Ecological Modeling, 157:281-300.

Blackman BG 2001 A strategic plan for the conservation and restoration of Arctic grayling in the Williston Reservoir Watershed. Peace/Williston Fish and Wildlife Compensation Program, Report No. 241, 16 pp. Prince George, BC.

Blackman BG and Hunter MJ 2001 Arctic grayling (*Thymallus arcticus*) Surveys in the Table Anzac and Parsnip Rivers. Peace/Williston Fish and Wildlife Compensation Program, Report No. 237, 39 pp. Prince George, BC.

Bozek MA and Hubert WA 1992 Segregation of resident trout in streams as predicted by three habitat dimensions. Canadian Journal of Zoology, 70:886-890.

Bozek MA and Rahel FJ 1991 Assessing habitat requirements of young Colorado River cutthroat trout by use of macrohabitat and microhabitat analysis. Transactions of the American Fisheries Society, 120: 571-581.

Brett JR 1971 Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist, 11:99-113.

Bruce PG and Starr PJ 1985 Fisheries resources and fisheries potential of Williston Reservoir and its tributaries streams. Vol. II. Fisheries resources potential of Williston Lake tributaries – a preliminary overview. Prov. B.C. Fish. Tech. Circ. No. 69. 100 pp.

Burnham KP and Anderson DR 2002 Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, NY, 488 pp.

Byorth PA and Magee JP 1998 Competitive Interactions between Arctic Grayling and Brook Trout in the Big Hole River Drainage, Montana. Transactions of the American Fisheries Society, 127:921-931.

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

Caslys Consulting Ltd. 2010 GeoBC freshwater atlas user guide. Prepard for BC Integrated Land Management Bureau. Saanichton, BC.

Clark DS and Green JM 1991 Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. Canadian Journal of Zoology, 69:1302-1307.

Clarke AD, Telmer KT and Shrimpton JM 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. Journal of Applied Ecology, 44:1156-1165.

Clutterham S, Gamperl AK, Wallace HL, Crawshaw LI and Farrell AP 2004 Exhaustive exercise does not affect the preferred temperature for recovery in juvenile rainbow trout (*Oncorhynchus mykiss*). Physiological and Biochemical Zoology, 77:611-618.

Coutant CC 1977 Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada, 34:739-745.

Cowie DM and Blackman BG 2003 2001-2002 Arctic grayling (*Thymallus arcticus*) Fry Surveys in the Omineca and Osilinka Rivers. Peace/ Williston Fish and Wildlife Compensation Program Report No. 276, 18 pp. Prince George, BC.

Cowie DM and Blackman BG 2004 2003 Arctic grayling (*Thymallus arcticus*) Fry Surveys in the Ingenika River. Peace/ Williston Fish and Wildlife Compensation Program Report No. 291, 19 pp. Prince George, BC.

Crossin GT, Hinch SG, Cooke SJ, Welch DW, Patterson DA, Jones SRM, Lotto AG, Leggatt RA, Mathes MT, Shrimpton JM, Van Der Kraak G and Farrell AP 2008 Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Canadian Journal of Zoology, 86:127-140.

Cummins KW 1962 An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist, 67:477-504.

Deegan LA, Golden HE, Harvey CJ and Peterson BJ 1999 Influence of environmental variability on the growth of age-0 and adult Arctic grayling. Transactions of the American Fisheries Society, 128:1163-1175.

De la Hoz Franco EA and Budy P 2005 Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environmental Biology of Fishes, 72:379-391.

Dunham J, Rieman BE and Chandler G 2003 Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management, 23:894-904.

Eklov AG, Greenberg LA, Bronmark C, Larsson P and Berglund O 1998 Response of stream fish to improved water quality: a comparison between the 1960s and 1990s. Freshwater Biology, 40:771-782.

Eriksen CH 1975 Physiological ecology and management of the rare "southern" grayling *Thymallus arcticus tricolor* Cope. International Association of Theoretical and Applied Limnology, 19:2448-2455.

Fielding AH and Bell JF 1997 A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24:38-49.

Feldmeth CR and Eriksen CH 1978 A hypothesis to explain the distribution of native trout in a drainage of Montana's Big Hole River. International Association of Theoretical and Applied Limnology, 20:2040-2044.

Fransen BR, Duke SD, McWethy LG, Walter JK and Bilby RE 2006 A Logistic Regression Model for Predicting the Upstream Extent of Fish Occurrence Based on Geographical Information Systems Data. North American Journal of Fisheries Management, 26:960-975.

Fry FEJ 1947 Effects of the environment on animal activity. University of Toronto Studies, Biological Series No. 55, 1-62; Publications of the Ontario Fisheries Research Laboratory No. 68, 1-62.

Harig AL and Fausch KD 2002 Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications, 12:535-551

Hawkins CP, Norris RN, Hogue JN and Feminella JW 2000 Development and Evaluation of Predictive Models for Measuring the Biological Integrity of Streams. Ecological Applications, 10:1456-1477.

Hengeveld PE and Corbould FB 2000 Winter moose surveys of the Omineca, Nation, and Ospika River drainages, 1999. Peace/Williston Fish and Wildlife Compensation Program, Report No. 232, 19 pp. Prince George, BC

Hughes NF 1999 Population processes responsible for larger-fish-upstream distribution patterns of Arctic grayling (*Thymallus arcticus*) in interior Alaskan runoff rivers. Canadian Journal of Fisheries and Aquatic Sciences, 56:2292-2299.

Hughes NF and Reynolds JB 1994 Why do Arctic grayling (*Thymallus arcticus*) get bigger as you go upstream? Canadian Journal of Fisheries and Aquatic Sciences, 51:2154-2163.

Hubert WA and Kozel SJ 1993 Quantitative relations of physical habitat features to channel slope and discharge in unaltered mountain streams. Journal of Freshwater Ecology, 8:177-83.

Independent Mining Consultants, INC. 2007 Technical Report on the Mt. Milligan Project, Omenica Mining District, British Columbia, Prepared for Terrane Metals Corperation. Tuscon, AZ.

Jenkins M 2003 Prospects for Biodiversity. Science, 302:1175-1177.

Jobling M 1981 Temperature tolerance and the final preferendum--rapid methods for the assessment of optimum growth temperatures. Journal of Fish Biology, 19:439-455.

Johnstone HC and Rahel FJ 2003 Assessing temperature tolerance of Bonneville cutthroat trout based on constant and cycling thermal regimes. Transactions of the American Fisheries Society, 132:92-99.

Jones NE and Tonn WM 2004 Resource selection functions for age-0 Arctic grayling (*Thumallus arcticus*) and their application to stream habitat compensation. Canadian Journal of Fisheries and Aquatic Sciences, 61:1736-1746.

Kaya CM 1991 Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (*Thymallus arcticus*), and implications for the only remaining indigenous population of fluvial "Montana grayling". Canadian Journal of Fisheries and Aquatic Sciences, 48:53-59.

Kaya CM 1992 Review of the decline and status of Fluvial Arctic grayling, *Thymallus arcticus*, in Montana. Proceedings of the Montana Academy of Sciences, 52:43-70.

Kaya CM 2000 Arctic grayling in Yellowstone: status, management, and recent restoration efforts. Yellowstone Science, 8:12-17.

Kaya CM and Jeanes ED 1995 Retention of adaptive rheotactic behavior by F1 fluvial Arctic grayling. Transactions of the American Fisheries Society, 124:453-457.

Kozel SJ and Hubert WA 1989 Habitat features and trout abundance relative to gradient in some Wyoming streams. Northwest Science 63:175-182.

Kruse CG, Hubert WA and Rahel FJ 1997 Geomophic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. Transactions of the American Fisheries Society, 126:418-427.

Kruse CG, Hubert WA and Rahel FJ 1998 Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. North American Journal of Fisheries Management, 18:940-946.

Lafrance P, Castonguay M, Chabot D and Audet C 2005 Ontogenetic changes in temperature preference of Atlantic cod. Journal of Fish Biology, 66:553-567.

Lanka RP, Hubert WA and Wesche TA 1987 Relation s of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society, 116:21-28.

LaPerriere JD and Carlson RF 1973 Thermal tolerances of interior Alaskan Arctic grayling (*Thymallus arcticus*). Institute of Water Resources, University of Alaska, Fairbamks, AK.

Liknes GA and WR Gould 1987 The distribution, habitat and population characteristics of fluvial Arctic grayling (*Thymallus arcticus*) in Montana. Northwest Sciences, 61:122-129.

Lobon-Cervia J 2003 Spatiotemporal dynamics of brown trout production in a Cantabrian stream: effects of density and habitat quality. Transactions of the American Fisheries Society, 132:621-637.

Lohr SC, Byorth PA, Kaya CM and Dwyer WP 1996 High-temperature tolerances of fluvial Arctic grayling and comparisons with summer river temperatures of the Big Hole River, Montana. Transactions of the American Fisheries Society, 125:933-939.

Macdonald JS, MacIsaac EA and Herunter HE 2003 The effect of variable-retention riparian buffer zones on water temperatures in small headwater streams in sub-boreal forest ecosystems of British Columbia. Canadian Journal of Forest Research, 33:1371-1382.

Mathias KL, Langston AR and Zemlak RJ 1998 A summary report of the Table River surveys 1996 status report. Peace/Williston Fish and Wildlife Compensation Program, Report No. 180, 62 pp. Prince George, BC.

McCleary RJ and Hassan MA 2008 Predictive modeling and spatial mapping of fish distributions in small streams of the Canadian Rocky Mountain foothills. Canadian Journal of Fisheries and Aquatic Sciences, 65:319-333.

McCormick SD, Shrimpton JM, Moriyama S and Björnsson BT 2002 Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. The Journal of Experimental Biology, 205:3553-3560.

McMahon TE, Bear EA and Zale AV 2008 Use of an annular chamber for testing thermal preference of westslope cutthroat trout and rainbow trout. Journal of Freshwater Ecology, 23:55-63.

McPhail JD and Lindsey CC 1970 Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada, 173:360-373.

Meeuwig MH, Dunham JB, Hayes JP and Vinyard GL 2004 sEffects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variables sizes. Ecology of Freshwater Fishes, 13:208-216.

Meier W, Bonjour C, Wüest A, and Reichert P 2003 Modeling the effect of water diversion on the temperature of mountain streams. Journal of Environmental Engineering, 129, 755-764.

Menard SW 2002 Applied logistic regression analysis (Second Edition). Thousand Oaks, CA: Sage Publications. Series: Quantitative Applications in the Social Sciences, No. 106

Meyer KA, Elle FS and Lamansky JA 2009 Environmental factors related to the distribution, abundance, and life history characteristics of mountain whitefish in Idaho. North American Journal of Fisheries management, 29:753-767.

Miller E 2010 Arctic grayling (*Thymallus arcticus*) species management plan: freshwater fisheries program, DRAFT. British Columbia Ministry of Water, Land, and Air Protection.

Mortensen A, Ugedal O and Lund F 2007 Seasonal variation in the temperature preference of Arctic charr (*Salvelinus alpinus*). Journal of Thermal Biology, 32:314-320.

Muhlfeld CC, McMahon TE, Boyer MC and Gresswell RE 2009 Local Habitat, Watershed, and Biotic Factors Influencing the Spread of Hybridization between Native Westslope Cutthroat Trout and Introduced Rainbow Trout. Transactions of the American Fisheries Society, 138:1036-1051.

Myrick CA, Folgner DK and Cech JJ 2004 An annular chamber for aquatic animal preference studies. Transactions of the American Fisheries Society, 133:427-433.

Neill WH, Magnuson JJ and Chipman GG 1972 Behavioral Thermoregulation by Fishes: A New Experimental Approach. American Association for the Advancement of Science, 176:1443-1445.

Nelson RL, Platts WS, Larsen DP and Jensen SE 1992 Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Transactions of the American Fisheries Society, 121:405-426.

Northcote TG 1993 A review of management and enhancement options for the Arctic grayling *(Thymallus arcticus)* with special reference to the Williston Reservoir watershed in British Columbia. Peace/Williston Fish and Wildlife Compensation Program Report No. 78, 69pp. Prince George, BC.

Northcote 1995 Comparative biology and management and Arctic and European grayling (*Salmonidae, Thymallus*). Reviews in Fish Biology and Fisheries, 5:141-194.

Novinger DC and Rahel FJ 2003 Isolation Management with Artificial Barriers as a Conservation Strategy for Cutthroat Trout in Headwater Streams. Conservation Biology, 17:772-781.

Nykänen M and Huusko A 2003 Size-related changes in habitat selection by larval grayling (*Thymallus thymallus L.*). Biology of Freshwater Fish, 12:127-133.

O'Brien 2007 A caution regarding rules of thumb for variance inflation factors. Quality and Quantity, 41:673-690.

Paul AJ and Post JR 2001 Spatial distribution of native and nonnative salmonids in streams of the Eastern slopes of the Canadian Rocky Mountains. Transactions of the American Fisheries Society, 130:417-430.

Pearce J and Ferrier S 2000 Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modeling, 133:225-245.

Peterson RH, Sutterlain AM and Metcalfe JL 1979 Temperature preference of several species of Salmo and Salvelinus and some of their hybrids. Journal of Fisheries Research Board of Canada, 36: 1137-1140.

Peterson JT and Dunham J 2003 Combining inferences from models of capture efficiency, detectability, and suitable habitat to classify landscapes for conservation of threatened bull trout. Conservation Biology, 17:1070-1077.

Peterson JT, Dunham J, Howell P, Thurow R and Bonar S 2002 Protocol for determining bull trout presence. Bull Trout Committee, Western Division, American Fisheries Society, Bethesda, Maryland.

Platts WS 1979 Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries (Bethesda), 4(2):5-9.

Pillipow RA and Langston AR 2002 Williston Reservoir fish assessments 2000, pelagic netting summary. Peace/Williston Fish and Wildlife Compensation Program Report No. 261, 12 pp. Prince George, BC.

Porter MS, Rosenfeld J and Parkinson EA 2000 Predictive models of fish species distribution in the Blackwater drainage, British Columbia. North American Journal of Fisheries Management, 20:349-359.

Rashleigh B, Parmar R, Johnston JM and Barber MC 2005 Predictive Habitat Models for the Occurrence of Stream Fishes in the Mid-Atlantic Highlands. North American Journal of Fisheries Management, 25:1353-1366.

Reynolds WW and Casterlin ME 1976 Thermal preferenda and behavioral thermoregulation in three centrarchid fishes. In Thermal Ecology H (Edited by Esch G. W. and McFarlane, RW), pp. 185-190. U.S. National Technical Information Service, Springfield, VA.

Reynolds WW and Casterlin ME 1979a Behavioral thermoregulation and the "final preferendum" paradigm. American Zoology, 19: 211-224.

Reynolds WW and Casterlin ME 1979b Thermoregulatory behaviour of brown trout, *Salmo trutta.* Hydrobiologia, 62: 79-80.

Reynolds WWR and Casterlin ME 1981 Thermoregulatory behavior of the triggerfish *Balistes fuscus* in an electronic shuttlebox. Hydrobiologia, 83: 255-256.

Ricciardi A and Rasmussen JB 1999 Extinction Rates of North American Freshwater Fauna. Conservation Biology, 13:1220-1222.

Rich CF, McMahon TE, Rieman BE and Thompson WL 2003 Local-habitat, watershed, and biotic features associated with bull trout occurrence in Montana streams. Transactions of the American Fisheries Society, 132:1053-1064.

Rieman BE, Lee DC and Thurow RF 1997 Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath basins. North American Journal of Fisheries Management, 17:1111-1125.

Rieman BE and McIntyre JD 1995 Occurrence of Bull Trout in Naturally Fragmented Habitat Patches of Varied Size. Transactions of the American Fisheries Society, 124:285-296.

Rosenfeld J 2003 Assessing the Habitat Requirements of Stream Fishes: An Overview and Evaluation of Different Approache. Transactions of the American Fisheries Society, 132:953-968.

Schrank AJ, Rahel FJ and Johnstone HC 2003 Evaluating laboratory-derived thermal criteria in the Field: An example involving Bonneville cutthroat trout. Transactions of the American Fisheries Society, 132:100-109.

Schurmann H and Steffensen JF 1992 Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod. *Gadus morhua L.* Journal of Fish Biology, 41:927-934.

Schurmann H, Steffensen JF and Lomholt JP 1991 The influence of hypoxia on the preferred temperature of rainbow trout, *Oncorhynchus mykiss*. Journal of Experimental Biology, 157:75-86.

Scott and Crossman 1973 Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, 966 pp.

Scrimgeour GJ, Hvenegaard PJ and Tchir 2008 Cumulative industrial activity alters lotic fish assemblages in two boreal forest watersheds of Alberta, Canada. Environmental Management, 42:957-970.

Sebastian DC, Scholten GH and Woodruff PE 2003 Williston Reservoir fish assessment: results of hydroacoustic, trawl and gill net surveys in August 2000. Peace/ Williston Fish and Wildlife Compensation Program Report No. 274, 34pp. Prince George, BC.

Shirvell CS and Dungey RG 1983 Microhabitats chosen by brown trout for feeding and spawning in rivers. Transactions of the American Fisheries Society, 112:355-367.

Shrimpton JM, Roberts SL and Clarke AD 2007 Genetic analysis of Arctic grayling population structure in the Williston Watershed. Peace/Williston Fish and Wildlife Compensation Program Report No. 311, 12 pp. Prince George, BC.

Skaugstad C 1988 Evaluation of Arctic grayling enhancement in Alaska during 1987. Alaska Department of Fish and Game, Fisheries Data Series No. 48, Fairbanks, AK.

Spatial Vision Consulting Ltd. 1996 An introduction to the British Columbia watershed atlas. Fisheries Branch, British Columbia Ministry of Environment, Lands and Parks, Victoria, BC.

Strahler AN 1952 Dynamic basis of geomorphology. Geological Society of America Bulletin, 63:923-938.

Tautz AF, Ward BR and Ptolemy RA 1992 Steelhead trout productivity and stream carrying capacity for rivers of the Skeena drainage. Ministry of Environment, Land and Parks Fisheries Branch, Pacific Stock Assessment Review Committee, S92:6-8. Vancouver, BC.

Thomas RE, Gharrett JA, Carls MG, Rice SD, Moles A and Korn S 1986 Effects of fluctuating temperature on mortality, stress, and energy reserves of juvenile coho salmon. Transactions of the American Fisheries Society, 115:52-59.

Thompson PD and Rahel FJ 1998 Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout. North American Journal of Fisheries Management, 18:206-210.

Turgeon K and Rodriguez MA 2005 Predicting microhabitat selection in juvenile Atlantic salmon *Salmo salar* by the use of logistic regression and classification trees. Freshwater Biology, 50: 539-551.

Van Dijk PLM, Staaks G and Hardewig I 2002 The effects of fasting and refeeding on temperature preference, activity and growth of roach, *Rutilus rutilus*. Oecologia, 130: 496-504.

Vannote RL and Sweeney BW 1980 Geographic Analysis of Thermal Equilibria: A Conceptual Model for Evaluating the Effect ofNatural and Modified Thermal Regimes on Aquatic Insect Communities. The American Naturalist, 115:667-695.

Vehanen T, Huusko A, Yrjana T, Lahti M and Maki-Petays A 2003 Habitat preference by graylng (*Thymallus thymallus*) in an artificially modified, hydropeaking riverbed: a contribution to understanding the effectiveness of habitat enhancement measures. Journal of Applied Ichthyology, 19:15-20.

Vincent RE 1962 Biogeographical and ecological factors contributing to the decline of Arctic grayling, *Thymallus arcticus* Pallas, in Michigan and Montana. Doctoral dissertation. The University of Michigan, Ann Arbor, MI.

Wagner EJ, Arndt RE and Brough M 2001 Comparative tolerance of four stocks of cuttthroat trout to extremes in temperature, salinity, and hypoxia. Western North American Naturalist, 61:434-444.

Webb BW, Clack PD and Walling DE 2003 Water- air temperature relationships in a Devon river system and the role of flow. Hydrological Processes, 17:3069-3084.

Webb WB, Hannah DM, Moore RD, Brown LE and Nobilis F 2008 Recent advances in stream and river temperature research. Hydrological Processes, 22:902-918.

Wehrly KE, Wang L and Mitro M 2007 Field-based estimates of thermal tolerance limits for trout: incorporating exposure time and temperature fluctuation. Transactions of the American Fisheries Society, 136:365-374.

Williamson SA and Zimmerman JT 2005 Region 7a, Omineca Arctic Grayling (*Thymallus arcticus*): Data Consolidation Review and Gap Analysis. Ministry of Water, Land and Air Protection, 13 pp. Prince George, BC.

Wollmuth LP, Crawshaw LI and Panayiotides-Djaferis H 1987 Thermoregulatory effects of intracranial norepinephrine injections in goldfish. American Physiological Society, 253: 821-826.

Zar JH 1972 Significance Testing of the Spearman Rank Correlation Coefficient. Journal of the American Statistical Association, 67: 578-580.

Zdanovich 2006 Alteration of thermoregulation behavior in juvenile fish in relation to satiation level. Journal of Ichthyology, 46: S188-S193.

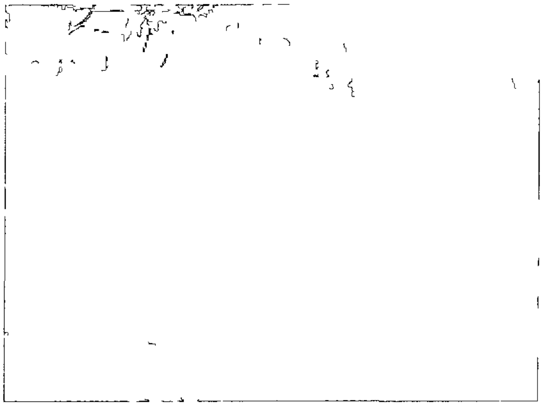
APPENDICES

Appendix A: Summary of temperature preference experiments (Ts = water temperature in starting chamber; Tpref = temperature preference; SD (Range) = standard deviation and range of the temperatures recordings taken every second during last 6 hours of each experiment; FL = fork length; 1: upper Nation River; 2: Nation River at the Mouth of Sylvester Creek; 3: Table River).

Fish	Date	Start Chamber	Ts (°C)	Tpref (°C)	SD (Range) (°C)	FL (cm)
2A	21Jul10	Cold	16.69	17.62	0.88 (15.60 - 20.07)	5.4
2B	22Jul10	Warm	16.57	16.91	0.79 (15.01 - 18.46)	5.5
2C	23Jul10	Cold	16.58	16.86	0.57 (14.00 - 17.99)	5.3
3A	24Jul10	Cold	16.41	17.63	0.72 (15.99 - 19.18)	5.6
3B	25Jul10	Warm	16.40	17.07	0.72 (15.59 - 18.53)	5.4
3C	26Jul10	Cold	16.40	15.21	1.04 (12.90 - 18.02)	6.1
2D	27Jul10	Warm	16.64	17.91	0.91 (15.85 - 19.98)	6.6
2E	3Aug10	Cold	16.63	16.11	0.66 (15.24 - 17.53)	5.1
3D	4Aug10	Warm	16.42	17.17	0.67 (15.66 - 18.54)	5.3
3E	5Aug10	Cold	16.39	-	-	6.3
1A	6Aug10	Cold	18.06	-	-	5.4
1B	7Aug10	Warm	18.03	17.09	0.74 (16.01 - 19.56)	6.6
3F	8Aug10	Warm	16.41	16.90	0.93 (15.32 - 18.99)	7.1
3G	9Aug10	Cold	16.40	16.86	0.53 (17.36 - 19.31)	7.1
1C	10Aug10	Cold	17.98	16.47	0.63 (15.05 - 19.58)	7.3
1D	11Aug10	Warm	18.00	16.24	0.55 (14.96 - 19.35)	6.8
3H	12Aug10	Warm	16.45	16.86	0.99 (14.99 - 18.57)	7.0
3I	13Aug10	Cold	16.39	17.84	0.83 (15.63 - 18.82)	6.5
1E	14Aug10	Cold	18.03	17.23	0.87 (16.12 - 19.07)	6.1
1F	15Aug10	Warm	18.01	15.57	1.24 (14.87 - 17.14)	7.2
3J	16Aug10	Warm	16.42	17.15	0.97 (15.93 - 18.68)	6.7
2F	17Aug10	Warm	16.61	16.71	0.43 (14.57 - 18.36)	5.9
2G	18Aug10	Cold	16.60	16.89	0.93 (15.33 - 18.11)	6.4
1G	19Aug10	Cold	17.99	16.73	0.68 (14.83 - 18.14)	7.0
1H	20Aug10	Warm	18.03	17.38	0.93 (15.84 - 18.42)	6.5
2H	22Aug10	Warm	16.59	15.92	0.74 (15.02 - 17.22)	7.2
2I	23Aug10	Cold	16.62	16.05	0.48 (15.48 - 17.99)	5.8
1I	24Aug10	Cold	18.02	17.53	0.66 (15.99 - 18.64)	7.1
2J	25Aug10	Warm	16.60	16.39	0.59 (14.98 - 18.29)	6.9
1J	26Aug10	Warm	18.00	17.26	0.78 (15.76 - 19.22)	6.9

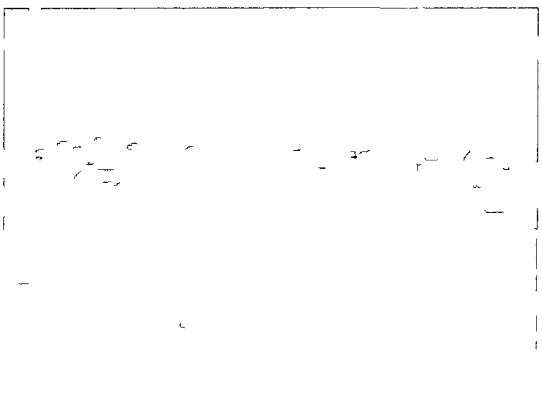
Appendix B. Pictures of microhabitat study sites.

1. Anzac River

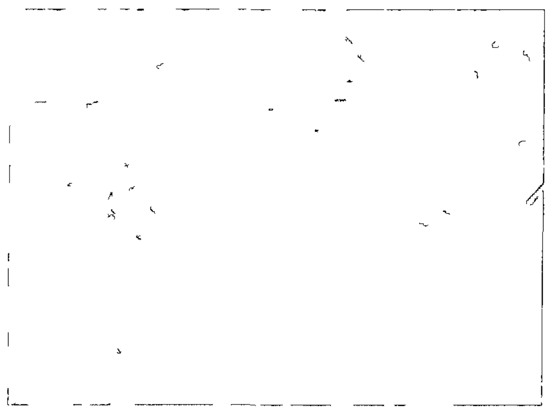


2. AnzacTrib1

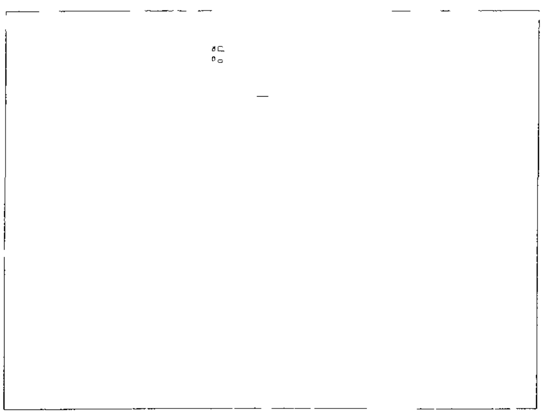
3. AnzacTrib2



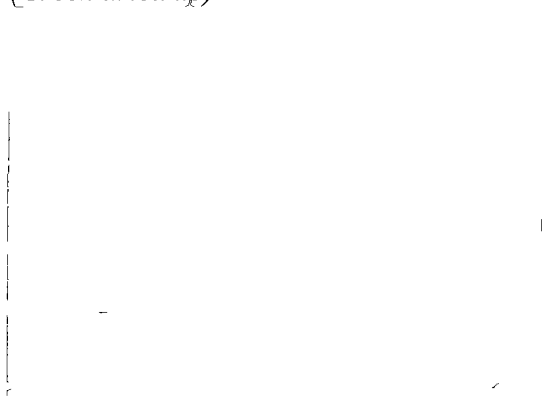
4. Bill's Creek



5. Colbourne Creek

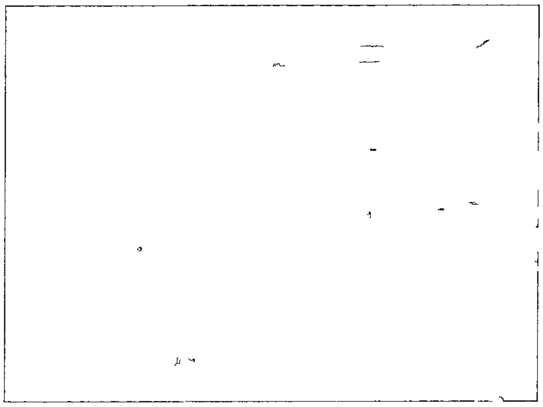


6. Condemned Bridges Creek
(Creek dried up)

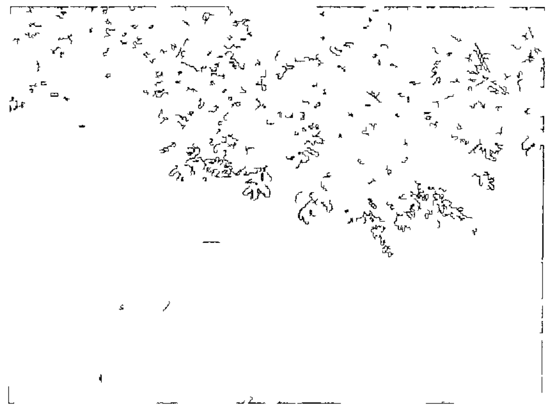


Appendix B cont'd.

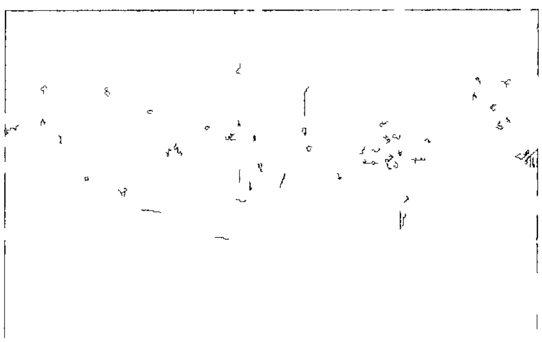
7. Crocker Creek



8 Cutthumb Creek

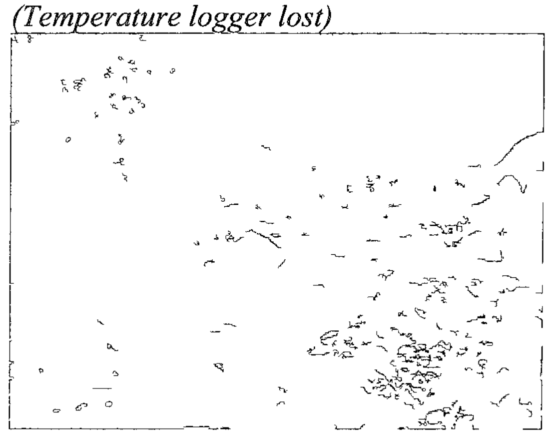


9 Fast Creek

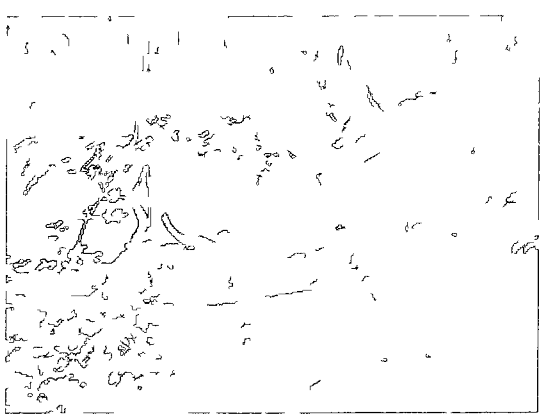


10. Gagnon Creek

(Temperature logger lost)



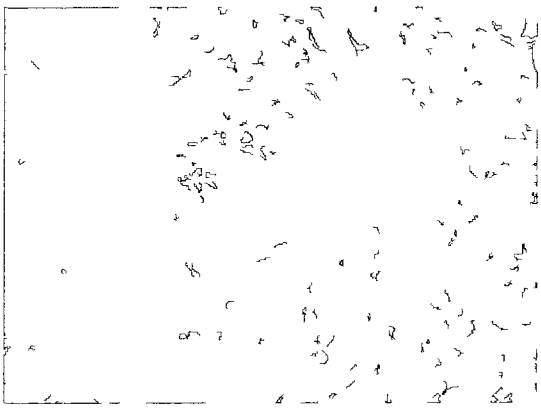
11 Hodda River



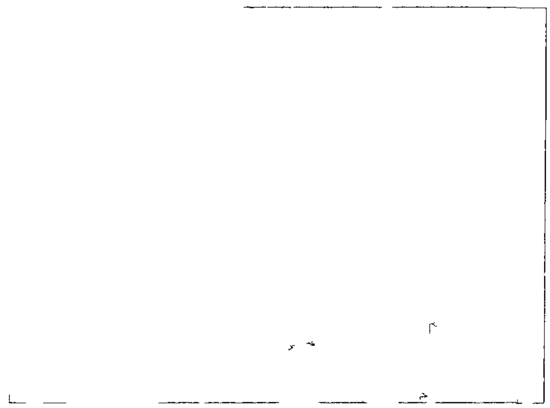
12 Hominka River

Appendix B cont'd

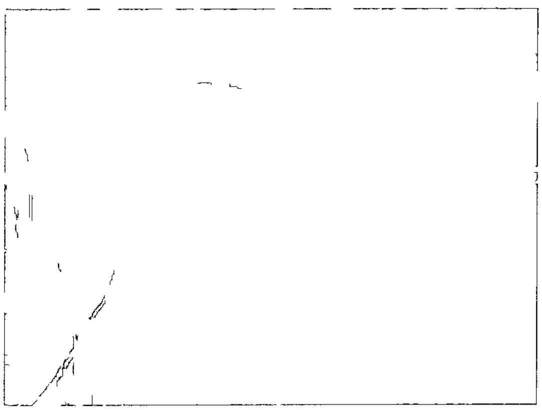
13 Isador Creek



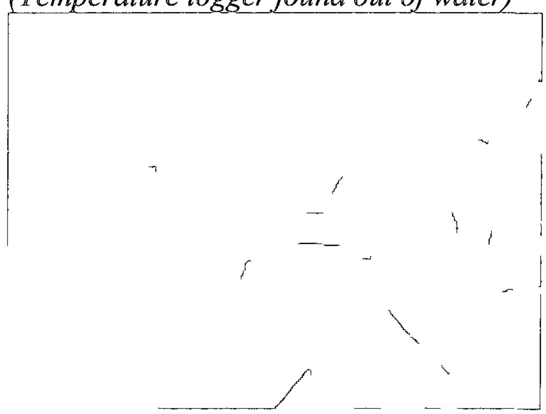
14 Lamonti Creek



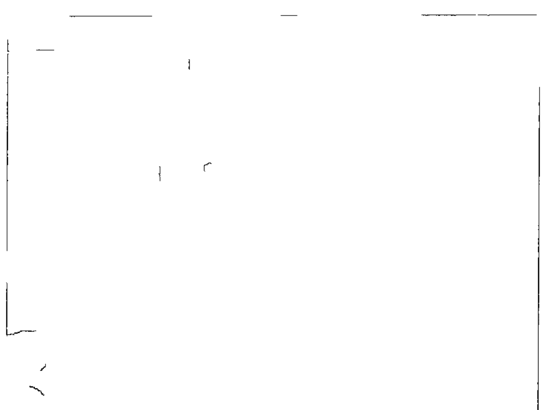
15 Lignite Creek



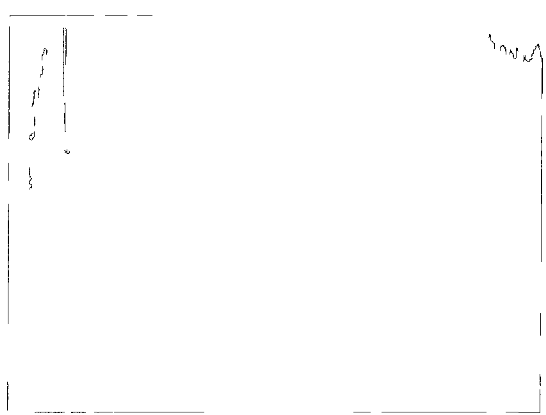
16 Mischinsinlinka River
(Temperature logger found out of water)



17 Misinchinka Creek



18 Missinka Creek



Appendix B cont'd.

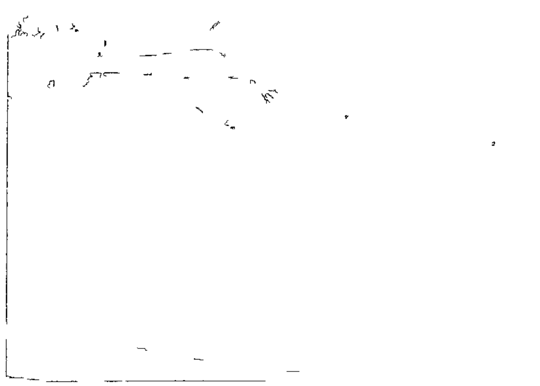
19. Modeste Lake Creek

20. Morfee Creek

21. Mossy Creek

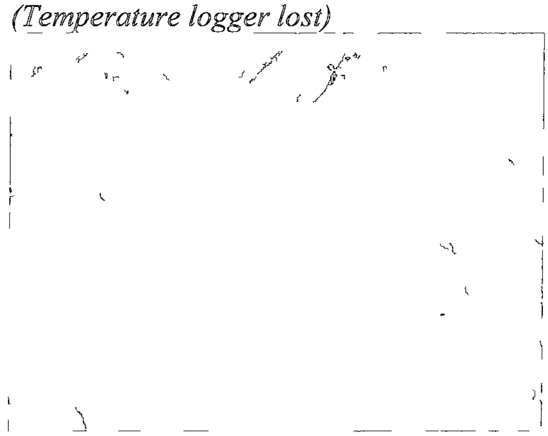
22. Mugaha Creek

23. Parsnip River



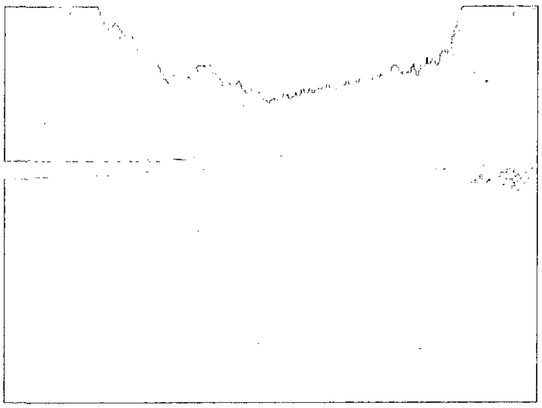
24. Patsuk Creek

(Temperature logger lost)

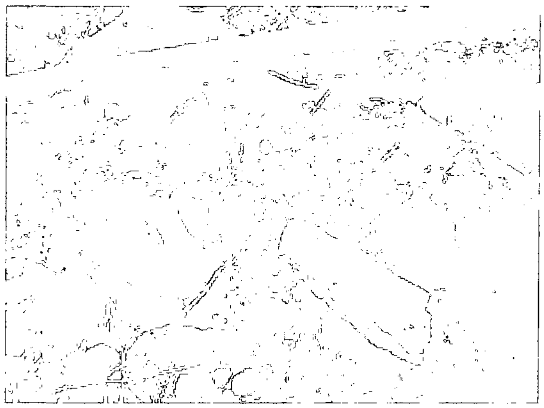


Appendix B cont'd.

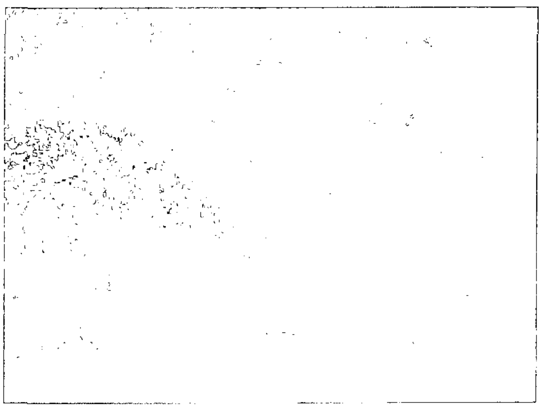
25. Reynold's Creek



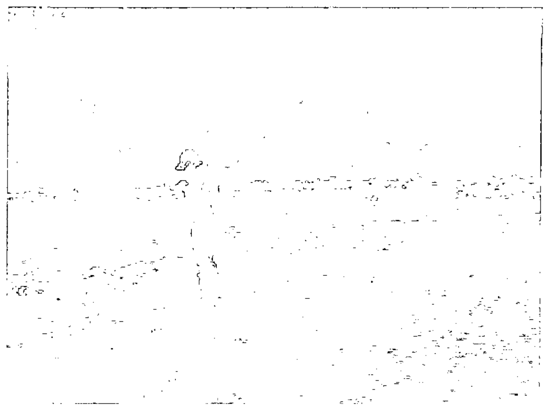
26. Rockslide Creek



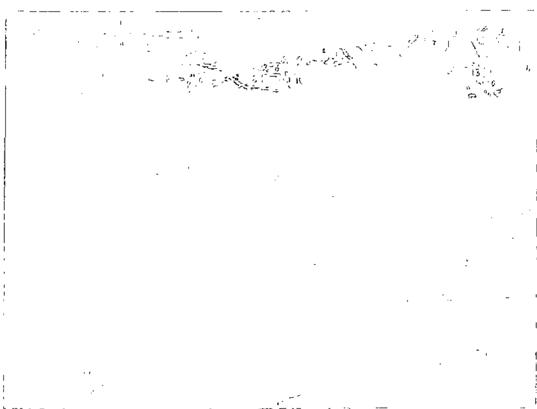
27. Scott Creek



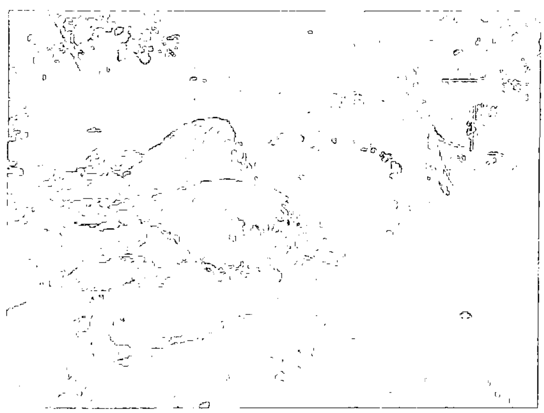
28. Table River



29. Tony Creek

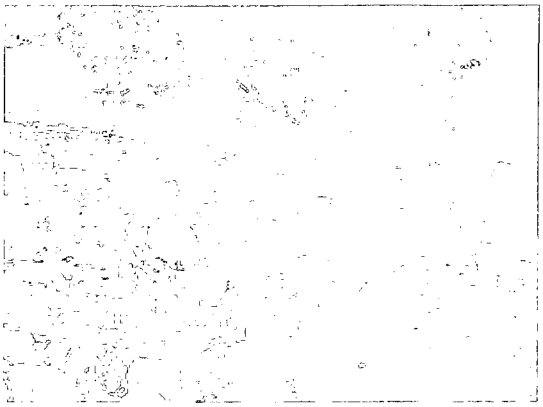


30. Tutu Creek

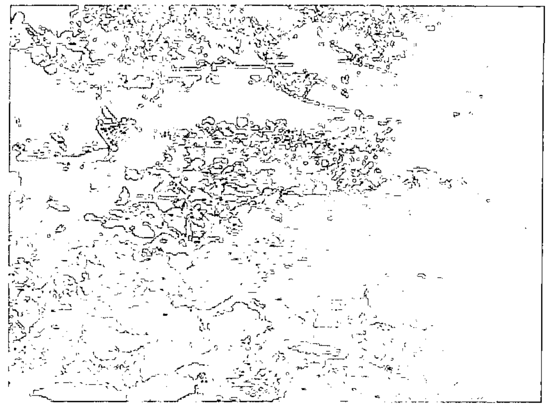


Appendix B cont'd.

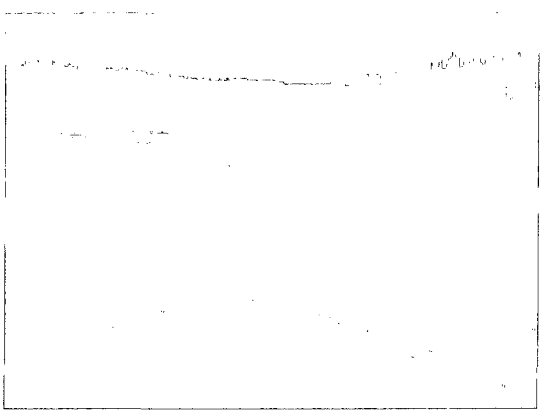
31. Twilight Zone Creek



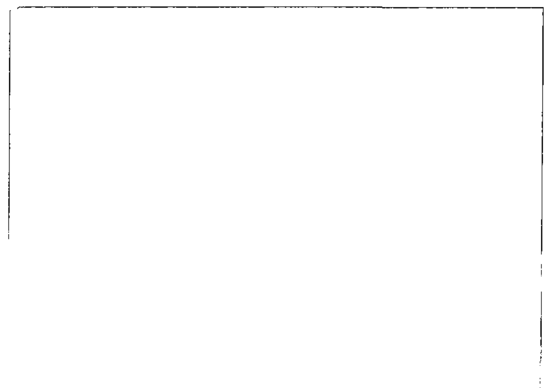
32. Two Stream Creek



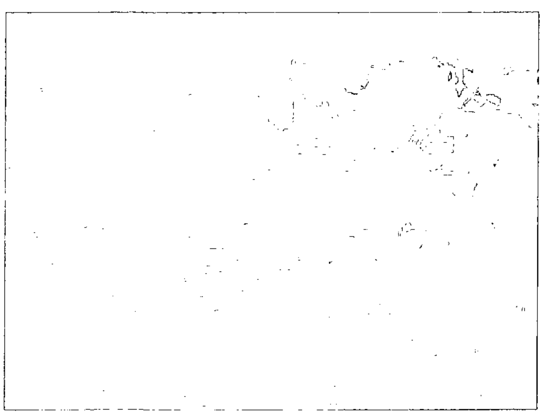
33. Upper Pack River



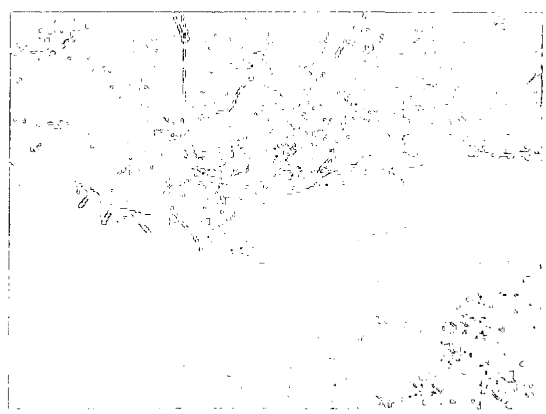
34. Upper Parsnip River



35. Weston Creek



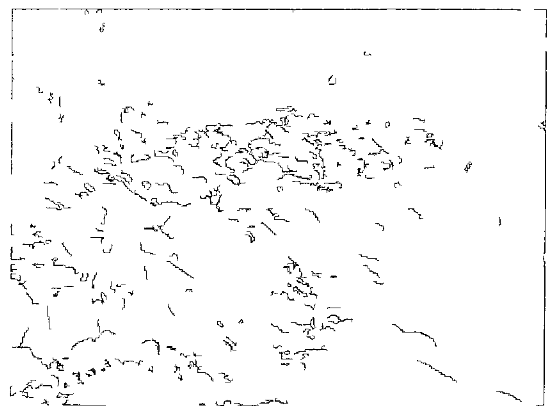
36. Wichcika Creek



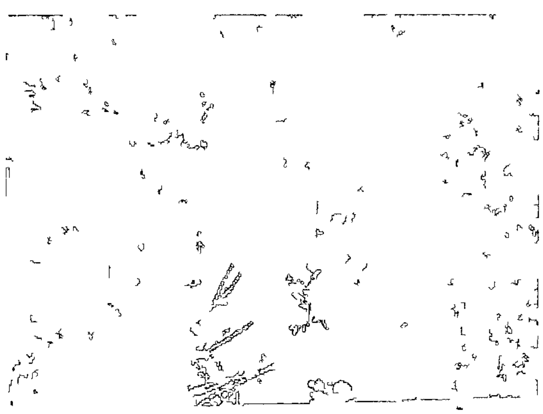
Appendix B cont'd

37 Wooyadilinka Creek

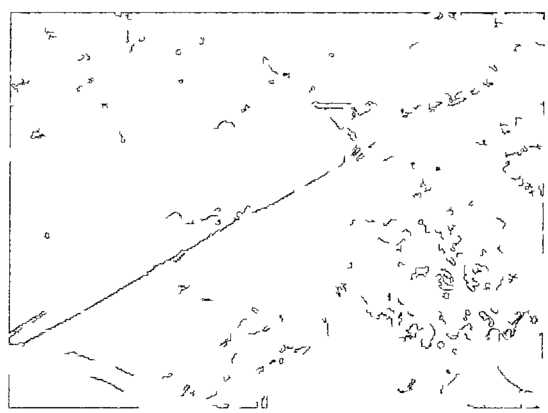
38 Mystery Creek



39 N12



40. N13

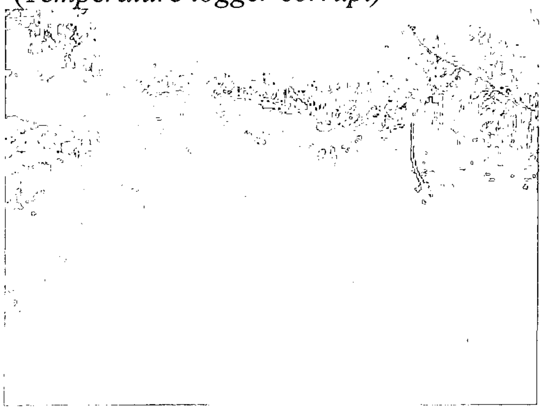


41 N2

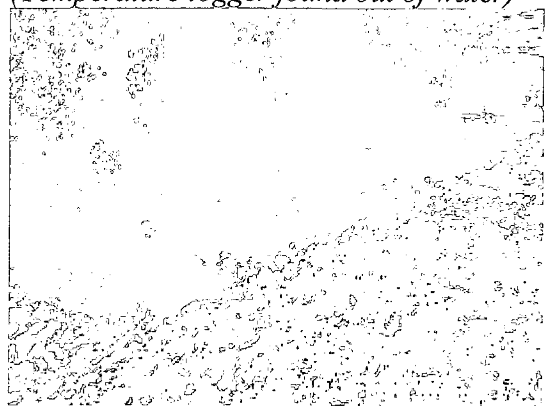
42 N25

Appendix B cont'd.

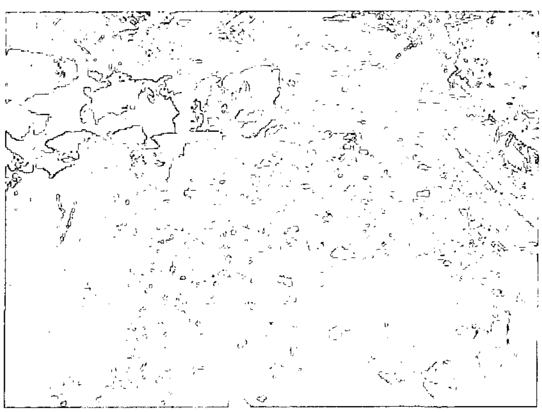
43. N26
(Temperature logger corrupt)



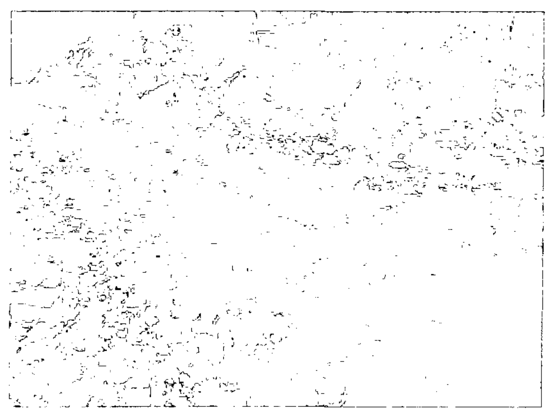
44. N27
(Temperature logger found out of water)



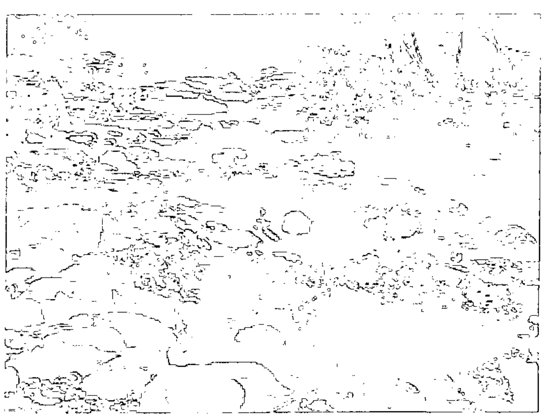
45. Wheel Creek



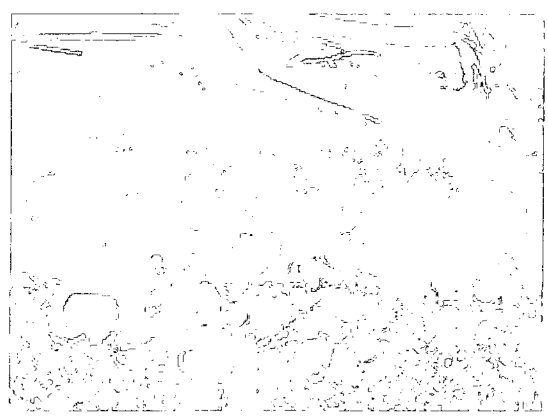
46. N31



47. N4

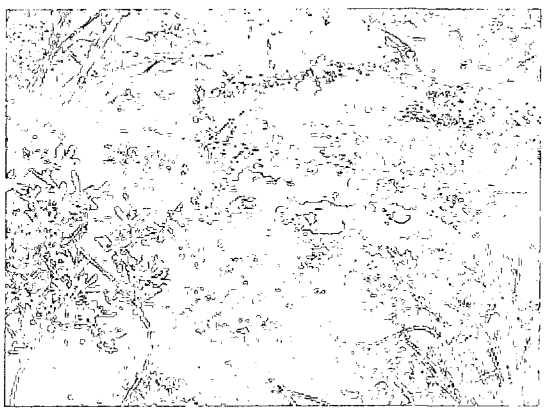


48. N40

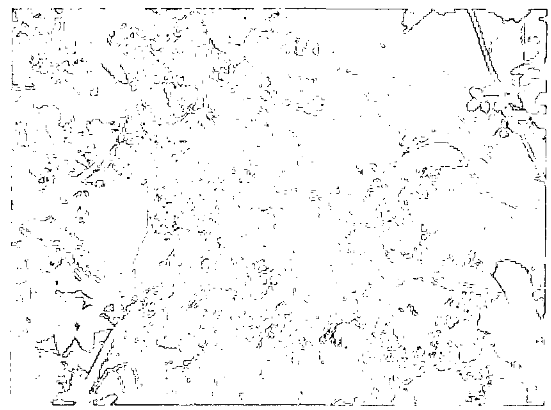


Appendix B cont'd.

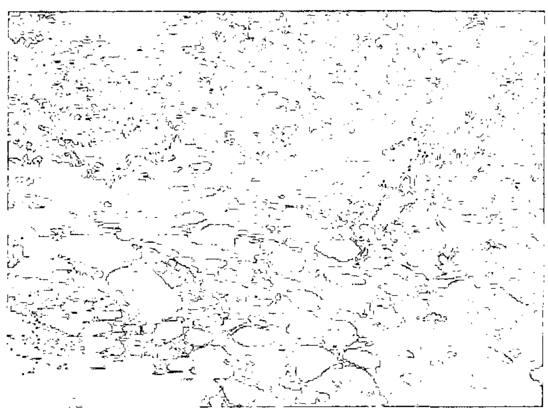
49. N41



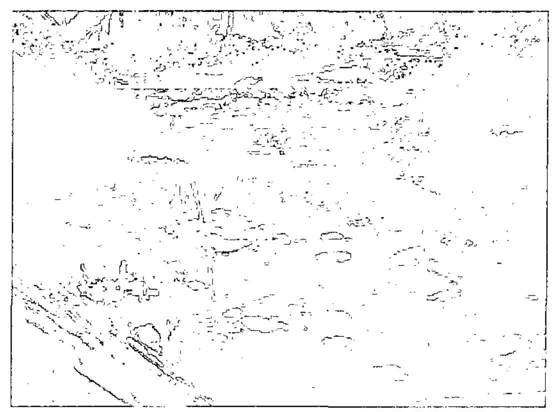
50. N5



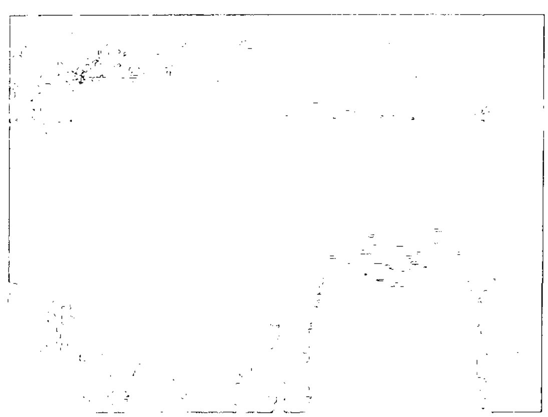
51. N6



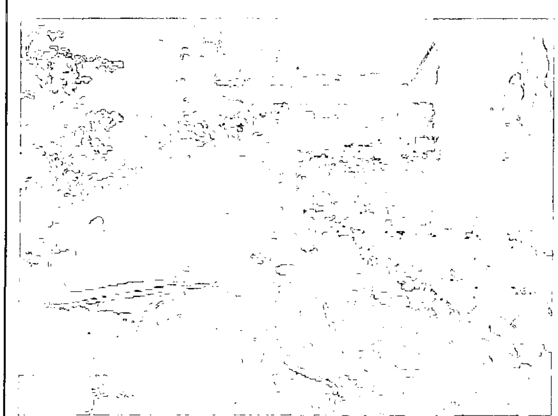
52. N7



53. N8

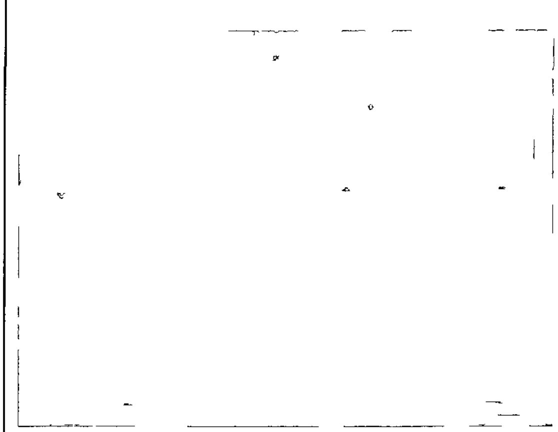


54. N9

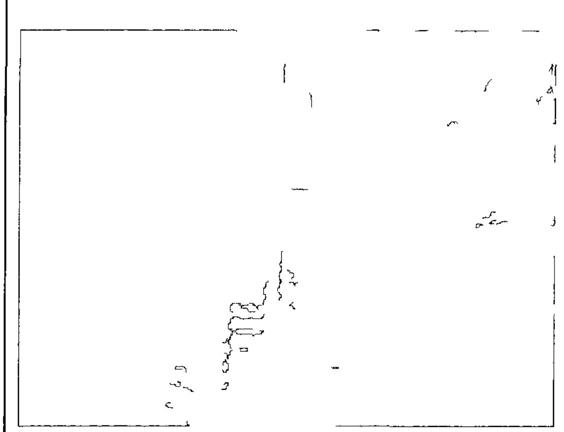


Appendix B cont'd

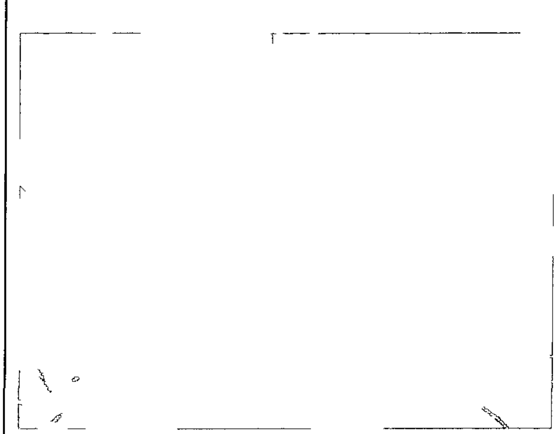
55 Nation River



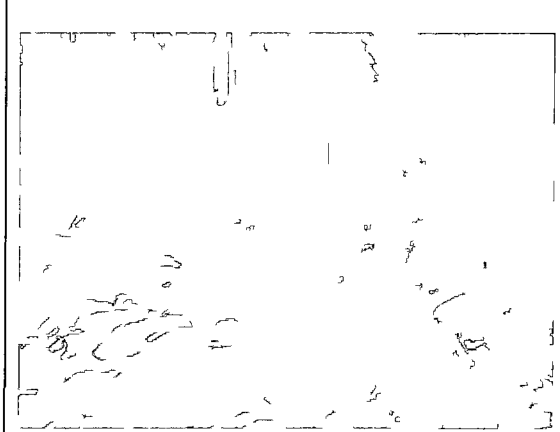
56 Philip Creek



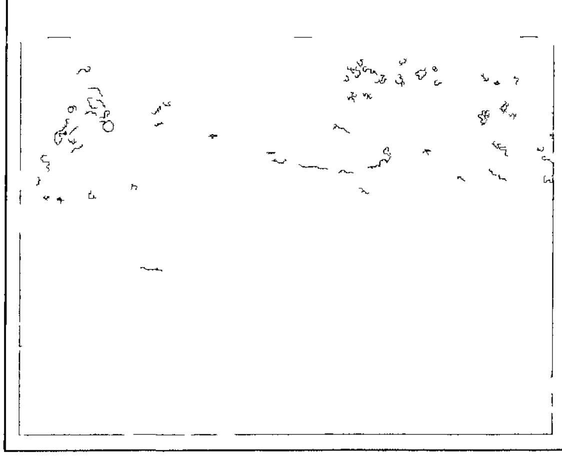
57 Rainbow Creek



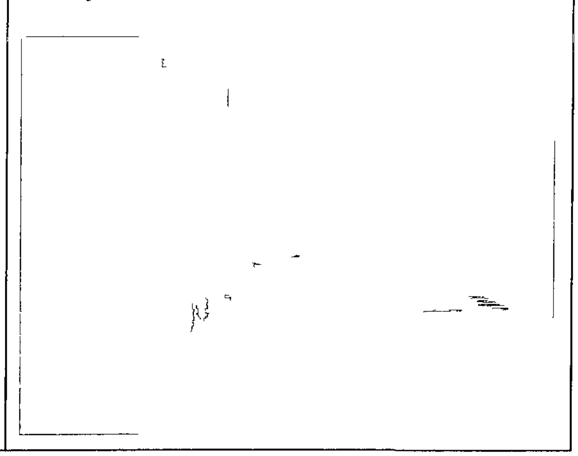
58 Robinson Creek



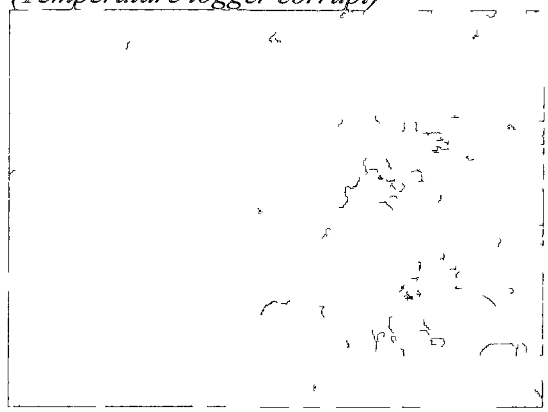
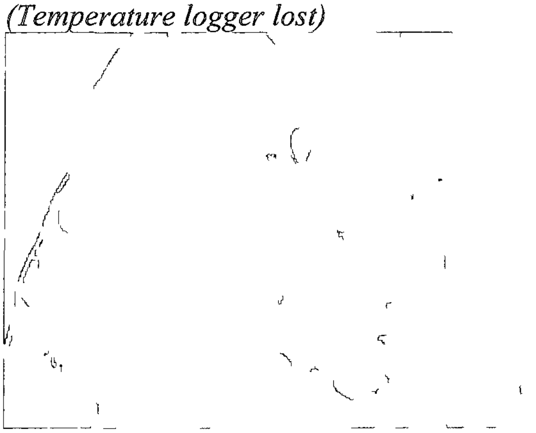
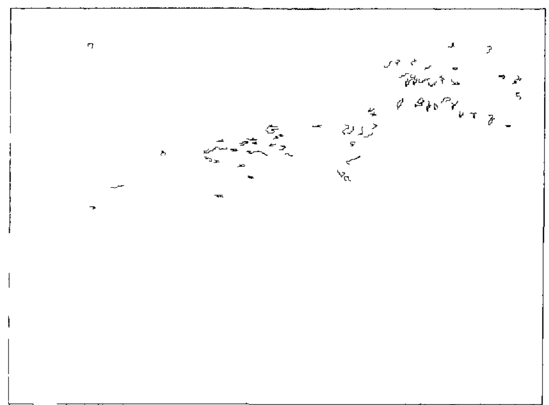
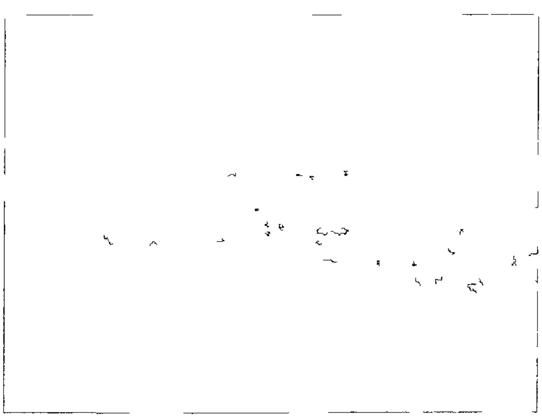
59 Suchona Creek



60 Sylvester Creek



Appendix B cont'd

61. Upper Nation River 	62. Upper Philip Creek *(Temperature logger corrupt)* 
63. Gaffney Creek *(Temperature logger lost)* 	64. Manson River 
65 Munro Creek 	

Appendix C. Summary of hypotheses used to form 15 ecologically plausible candidate macrohabitat models.

Model	Hypotheses	Reference
aveE + maxE + minE	Occurance of Arctic grayling is influenced by elevation	Kruse *et al.* 1997* Porter *et al.* 2000*; Scrimgeour *et al.* 2008
aveG + maxG + minG	Occurance of Arctic grayling is influenced by slope	Kruse *et al.* 1997* Porter *et al.* 2000*; Blackman 2001; Cowie and Blackman 2003 Cowie and Blackman 2004; Scrimgeour *et al.* 2008
aveE + maxE + minE + aveG + maxG + minG	Occurance of Arctic grayling is influenced by elevation and slope	Scrimgeour *et al.* 2008
aveE + maxE + minE + aveG + maxG + minG + WSA	Watershed elevation, gradient and drainage area influence salmonid distributions	Porter *et al.* 2000* McCleary and Hassan 2008; Fransen *et al.* 2006
WSA	Watershed area influences salmonid distributions	Porter *et al.* 2000*
aveG + maxG + minG + WSA	Watershed gradient and watershed area influence salmonid distribution	McCleary and Hassan 2008*
SO	Salmonid occurrence is influenced by stream order	Platts 1979*; Beecher *et al.* 1988*
SO + WSA	Stream size influences Arctic grayling distribution	Williamson and Zimmerman 2004; Kruse *et al.* 1997*
OWSD	Migration barriers limit salmonid distribution	Rieman and McIntyre 1995*; Kruse *et al.* 1997*
OWSD + aveG + aveE	Gradient, elevation, width and upstream fish migration barriers influence the occurrence of salmonids	Kruse *et al.* 1997*
OWSD + aveG	Upstream fish migration barriers and gradient influence salmonid occurrence	Kruse *et al.* 1997*
OWSD + aveE	Upstream fish migration barriers and elevation influence salmonid occurrence	Kruse *et al.* 1997*

Appendix C cont'd.

Model	Hypotheses	Reference
WSR + WSSX	Disturbance due to roads has a detectable impact on Arctic grayling occurance	Scrimgeour *et al.* 2008
aveE + maxE + minE + WSR + WSSX	Arctic grayling occurance is influenced by elevation and road disturbance	Scrimgeour *et al.* 2008
aveG + maxG + minG + WSR + WSSX	Arctic grayling occurance is influenced by slope and road disturbance	Scrimgeour *et al.* 2008

* Hypotheses include references from studies on other riverine salmonid species selectively used to supplement data gaps on the habitat requirements of Arctic grayling.

Appendix D. Summary of hypotheses used to form 35 ecologically plausible candidate microhabitat models.

Model	Hypotheses	Reference
varT + aveT + maxT	Arctic grayling distribution is influenced by water temperature.	Deegan *et al.* 1999; Lohr *et al.* 1996; Dunham *et al.* 2003*; Porter *et al.* 2000*
varT	Daily water temperature fluctuations affect salmonid distiribution.	Thomas *et al.* 1986*; Johnstone and Rahel 2003*; Lobon-Cervia 2003*; Wehrly *et al.* 2003*; Meeuwig *et al.* 2004*; de la Hoz Franco and Budy 2005*
aveT	The distribution of salmonids is influenced by preferred temperatures.	Muhlfeld *et al.* 2009*
maxT	Salmonids avoid maximum temperature thresholds.	Porter *et al.* 2000* Muhlfeld *et al.* 2009*
varT + aveT + maxT + DO + COND + PH	Salmonid have water quality preferences.	Eklov *et al.*1998*
COND	Arctic grayling distribution is influenced by water conductivity.	McRae, Warren and Shrimpton, unpublished data*; Ballard and Shrimpton 2009
varT + aveT + maxT + DO	Water temperature and dissolved oxygen influence Arctic grayling distribution.	Feldmuth and Eriksen 1978
varT + COND	Daily temperature variance and conductivity can influence salmonid distribution.	Ballard and Shrimpton 2009
WIDTH + ELEV	Occurrence of Arctic grayling is influenced by a stream's physical attributes, wetted width and site elevation.	Scrimgeour *et al.* 2008
WIDTH + ELEV + GRAD + aveS + sdS	The physical attributes of a stream influence the occurrence of salmonids.	Scrimgeour *et al.* 2008
VEL	Arctic grayling have preference criteria for water velocity.	Bardonnet 1991; Vehanen *et al.* 2003; Jones and Tonn 2004; Nykänen and Huusko 2004

Appendix D cont'd.

Model	Hypotheses	Reference
VEL + DEPTH + aveS + sdS + LWD	Arctic grayling occurrence is influenced by water velocity, depth, substrate and cover.	Jones and Tonn 2004
aveS + sdS	Substrate coarseness has an influence on Arctic grayling occurrence.	Vincent 1962; Liknes 1981
GRAD	Stream gradient influences distribution of Arctic grayling.	Blackman 2001; Cowie and Blackman 2003; Cowie and Blackman 2004
VEL + GRAD	Stream flow characteristics influence the occurrence of Arctic grayling.	Liknes 1981
VEL + DEPTH + aveS + sdS	Velocity, depth and substrate influence Arctic grayling occurrence.	Vehanen *et al.* 2003
DEPTH + aveS + sdS	Salmonid habitat selection is influenced by depth and substrate.	Turgeon and Rodriguez 2005*
LWD	Availability of large woody debris cover influences the distribution of salmonids.	Jones and Tonn, 2004; Rich *et al.* 2003*
OUPD + ODOWND	Salmonid distribution is limited by migration barriers.	Rieman and McIntyre 1995*; Kruse *et al.* 1997*
OUPD + GRAD + ELEV + WIDTH	Gradient, elevation, width and upstream fish migration barriers influences the occurrence of salmonids.	Kruse *et al.* 1997*
OUPD + GRAD	Upstream fish migration barriers and gradient influence salmonid occurrence.	Kruse *et al.* 1997*
OUPD + ELEV	Upstream fish migration barriers and elevation influence salmonid occurrence.	Kruse *et al.* 1997*
OUPD + WIDTH	Upstream migration barriers and stream size influence salmonid occurrence.	Kruse *et al.* 1997*
SDRxSO	Fluvial Arctic grayling distribution is influenced by the Williston reservoir.	Clarke *et al.* 2007

Appendix D cont'd.

Model	Hypotheses	Reference
OTHER	The presence of other salmonid species has an influence on occurrence of Arctic grayling.	Vincent 1962; Skaugstad 1988; Byorth and Magee, 1998
K1R + K1SX	Road disturbances have an impact on Arctic grayling occurrence.	Scrimgeour *et al.* 2008
WIDTH + ELEV + K1R + K1SX	Physical stream attributes and road disturbance have an influence on Arctic grayling occurrence.	Scrimgeour *et al.* 2008
WIDTH + ELEV + GRAD + aveS + sdS + K1R + K1SX	Physical stream attributes and road disturbance have an influence on Arctic grayling occurrence.	Scrimgeour *et al.* 2008
varT + aveT + maxT + DEPTH + aveS + sdS + LWD	Temperature, depth, substrate, and cover can be used to characterize suitable habitat for salmonids	Rashlaigh *et al.* 2005*
varT + aveT + maxT + K1SX	Stream temperature and disturbance from road stream crossings influence salmonid distribution	Muhlfeld *et al.* 2009*
maxT + WIDTH + ELEV + GRAD	Temperature, stream width, elevation and gradient combined influence occurrence of salmonids.	Porter *et al.* 2000*
WIDTH + COND	Width and conductivity have an influence on salmonid distribution.	Meyer *et al.* 2009*
WIDTH + LWD + OTHER	Width, cover and presence of other species influences salmonids distribution.	Rich *et al.* 2003*
SDRxSO + varT	Arctic grayling distribution is influenced by the Williston reservoir and daily temperature variation.	Clarke *et al.* 2007; Meeuwig *et al.* 2004*
SDRxSO + aveT	Arctic grayling distribution is influenced by the Williston reservoir and average temperatures.	Clarke *et al.* 2007; Muhlfeld *et al.* 2009*

* Hypotheses include references from studies on other riverine salmonid species selectively used to supplement data gaps on the habitat requirements of Arctic grayling.

Appendix E. Arctic grayling presence (P) / absence (A) for microhabitat and macrohabitat study sites, determined by previous sampling records, 1994 - 2004 (H) and/or summer 2010 field electrofishing (EF) and seine net (SN) field surveys (Method: Survey method used to determine presence or absence).

Site	Name	H	EF	SN	Macro	Micro	Method
1	Anzac	P	A	A	P	P	H
2	Anzac Trib1	P	P	-	P	P	EF
3	Anzac Trib2	P	P	-	P	P	EF
4	Bills	P	P	-	P	P	EF
5	Colbourne	A	A	A	A	A	EF
6	Condemned Bridges	-	A	-	A	A	EF
7	Crocker	P	P	-	P	P	EF
8	Cut thumb	A	A	-	A	A	EF
9	Fast	A	A	-	A	A	EF
10	Gagnon	A	A	-	A	A	EF
11	Hodda	A	P	-	P	P	EF
12	Hominka	P	A	A	P	P	H
13	Isador	-	A	-	A	A	EF
14	Lamonti	-	A	-	A	A	EF
15	Lignite	A	A	-	A	A	EF
16	Mischinsinlinka	A	P	-	P	P	EF
17	Misinchinka	A	P	-	P	P	EF
18	Missinka	P	P	-	P	P	EF
19	Modeste Lake	-	A	-	A	A	EF
20	Morfee	A	A	-	A	A	EF
21	Mossy	-	A	-	A	A	EF
22	Mugaha	A	A	-	A	A	EF
23	Parsnip	P	-	P	P	P	SN
24	Patsuk	A	A	-	A	A	EF
25	Reynolds	P	P	-	P	P	EF
26	Rockslide	-	A	-	A	A	EF
27	Scott	A	A	-	A	A	EF
28	Table	P	P	P	P	P	EF
29	Tony	A	A	-	A	A	EF
30	Tutu	A	A	-	A	A	EF
31	Twilight	-	P	-	P	P	EF
32	Two Stream	-	P	-	P	P	EF
33	Upper Pack	A	-	A	A	A	SN
34	Upper Parsnip	P	-	P	-	P	SN
35	Weston	A	A	-	A	A	EF
36	Wichcika	P	P	-	P	P	EF
37	Wooyadilinka	A	P	P	P	P	EF
38	Mystery	-	A	-	A	A	EF
39	N12	-	A	-	A	A	EF
40	N13	-	A	-	A	A	EF

Appendix E cont'd.

Site	Name	H	EF	SN	Macro	Micro	Method
41	N2	-	A	-	A	A	EF
42	N25	-	A	-	A	A	EF
43	N26	-	A	-	A	A	EF
44	N27	-	A	-	A	A	EF
45	Wheel	-	P	-	P	P	EF
46	N31	-	A	-	A	A	EF
47	N4	-	A	-	A	A	EF
48	Formula	-	A	-	A	A	EF
49	N41	-	A	-	A	A	EF
50	N5	-	P	-	P	P	EF
51	N6	-	A	-	A	A	EF
52	N7	-	A	-	A	A	EF
53	N8	-	P	-	P	P	EF
54	N9	-	P	-	P	P	EF
55	Nation	P	P	P	P	P	EF
56	Upper Philip	P	P	-	P	P	EF
57	Rainbow*	P	A	A	P	A	EF/H
58	Robinson	A	A	A	A	A	EF
59	Suchona	P	P	-	P	P	EF
60	Sylvester	P	-	P	P	P	SN
61	Upper Nation	P	P	P	-	P	EF
62	Philip	P	P	-	-	P	EF
63	Gaffney	A	A	A	A	A	EF
64	Manson	A	P	P	P	P	EF
65	Munro	A	A	-	A	A	EF
66	Finlay	P	-	-	P	-	H
67	Davis	A	-	-	A	-	H
68	Omineca	P	-	-	P	-	H
69	Ingenika	P	-	-	P	-	H
70	Mesilinka	P	-	-	P	-	H
71	Ospika	A	-	-	A	-	H
72	Firesteel	P	-	-	P	-	H
73	Fox	P	-	-	P	-	H
74	Izaac	A	-	-	A	-	H
75	Lafferty	A	-	-	A	-	H
76	Lay	P	-	-	P	-	H
77	Ominicetla	P	-	-	P	-	H
78	Osilinka	P	-	-	P	-	H
79	Silver	P	-	-	P	-	H
80	Strandberg	A	-	-	A	-	H
81	Toodoggone	P	-	-	P	-	H
82	Akie	P	-	-	P	-	H
83	Chowika	A	-	-	A	-	H

Appendix E cont'd.

Site	Name	H	EF	SN	Macro	Micro	Method
84	Nabesche	A	-	-	A	-	H
85	Paul	A	-	-	A	-	H
86	Kwadacha	A	-	-	A	-	H
87	Swannell	P	-	-	P	-	H
88	Pelly	A	-	-	A	-	H
89	LostCabin	A	-	-	A	-	H
90	Carbon	A	-	-	A	-	H
91	Clearwater	A	-	-	A	-	H
92	Ivor	A	-	-	A	-	H
93	Germansen	P	-	-	P	-	H
94	Pesika	A	-	-	A	-	H
95	Del	A	-	-	A	-	H
96	Collins	A	-	-	A	-	H
97	Factorross	A	-	-	A	-	H
98	Blackwater	A	-	-	A	-	H
99	Russel	A	-	-	A	-	H
100	Wrede	A	-	-	A	-	H

*No Arctic grayling were sampled (H, EF or SN) at the microhabitat study site on Rainbow Creek, but Arctic grayling have been recorded in other parts of this watershed.

Appendix F. Summary of macrohabitat variables for all study watersheds (n = 97) and the range of each variable observed where Arctic grayling were absent (n = 56) or present (n = 41).

Variable	Units	Average ± SD (Range)		
		All (n = 97)	**Absent (n = 41)**	**Present (n = 56)**
aveE	m	1217 ± 174 (816 - 1610)	1191 ± 177 (816 - 1580)	1252 ± 168 (909 - 1610)
maxE	m	1754 ± 398 (884 - 2820)	1677 ± 383 (884 - 2820)	1859 ± 403 (994 - 2820)
minE	m	777 ± 97 (671 - 1110)	768 ± 93 (671 - 997)	789 ± 102 (671 - 1110)
aveG	%	0.279 ± 0.107 (0.09 - 0.52)	0.29 ± 0.11 (0.10 - 0.52)	0.27 ± 0.09 (0.90 - 0.47)
maxG	%	0.02 ± 0.61 (0.18 - 4.01)	0.86 ± 0.64 (0.18-4.01)	1.03 ± 0.58 (0.25 - 2.61)
minG	%	0.929 ± 0.036 (0.00 - 0.18)	0.03 ± 0.04 (0.00 - 0.18)	0.01 ± 0.03 (0.00 - 0.12)
SO	SO	5 ± 1 (1 - 8)	4.7 ± 1.3 (1 - 8)	5.7 ± 1 (4 - 8)
WSA	km^2	1002 ± 2440 (2 - 19024)	530 ± 1293 (2 - 8320)	1648 ± 3376 (15 - 19024)
OWSD	$\#/km^2$	0.02 ± 0.03 (0.00 - 0.23)	0.02 ± 0.03 (0.00-0.14)	0.02 ± 0.04 (0.00 - 0.23)
WSR	km/km^2	0.514 ± 0.724 (0.01-5.93)	0.59 ± 0.92 (0.01-5.93)	0.42 ± 0.33 (0.05 - 1.28)
WSSX	$\#/km^2$	0.67 ± 1.06 (0.00 - 7.00)	0.84 ± 1.34 (0.00 - 7.00)	0.43 ± 0.37 (0.03 - 1.50)

Appendix G. Summary of microhabitat variables for all study sites (n = 57) and the range of each variable observed where Arctic grayling were absent (n = 30) or present (n = 27).

Variable	Units	Average ± SD (Range)		
		All	Absent	Present
varT	$^{o}C^{2}$	1.23 ± 0.72 (0.111 - 2.729)	1.59 ± 0.75 (0.32 - 2.73)	0.82 ± 0.44 (0.11 - 1.65)
aveT	^{o}C	11.61 ± 1.48 (6.92 - 16.43)	11.84 ± 1.40 (9.78 - 16.43)	11.36 ± 1.58 (6.93 - 13.64)
maxT	^{o}C	13.11 ± 1.89 (7.76 - 17.64)	13.50 ± 1.84 (9.44 - 17.64)	12.67 ± 1.92 (7.76 - 17.56)
DO	mg/l	10.4 ± 1.1 (7.6 - 12.3)	10.5 ± 1.0 (8.5 - 12.3)	10.4 ± 1.2 (7.6 - 11.9)
COND	μS/cm	155 ± 67 (54 - 354)	173 ± 73 (54 - 354)	135 ± 56 (61 - 276)
pH		7.74 ± 0.73 (6.29 - 8.97)	7.65 ± 0.66 (6.48 - 8.96)	7.83 ± 0.81 (6.29 - 8.97)
DEP	m	0.44 ± 0.48 (0.04 - 2.40)	0.33 ± 0.30 (0.06 - 1.23)	0.55 ± 0.61 (0.04 - 2.40)
WID	m	10.74 ± 10.70 (0.80 - 43.00)	6.57 ± 6.64 (0.80 - 32)	15.37 ± 12.62 (0.96 - 43)
VEL	m/s	0.35 ± 0.42 (0.00 - 1.61)	0.39 ± 0.50 (0.00 - 1.61)	0.30 ± 0.32 (0.01 - 1.13)
E	m	806 ± 90 (675 - 1003)	794 ± 101 (675 - 989)	820 ± 78 (718 - 1003)
GRAD	%	1.81 ± 2.27 (0.00 - 12.55)	2.35 ± 2.65 (0.00 - 12.55)	1.22 ± 1.66 (0.00 - 6.96)
aveS	1-6	3.48 ± 0.89 (1.60 - 4.75)	3.40 ± 0.91 (1.75 - 4.70)	3.57 ± 0.89 (1.60 - 4.75)
sdS	1-6	0.95 ± 0.24 (0.40 - 1.60)	0.99 ± 0.25 (0.50 - 1.60)	0.90 ± 0.23 (0.40 - 1.38)
LWD	#/site	3.1 ± 2.7 (0 - 10)	3.4 ± 3.0 (0.0 - 10.0)	2.7 ± 2.3 (0.0 - 7.0)
SDRxSO	km*SO	273.99 ± 211.52 (3.05 - 848.02)	138.08 ± 136.82 (3.05 - 490.32)	425 ± 179.47 (151.15 - 848.02)

Appendix G cont'd.

Variable	Units	Average ± SD (Range)		
		All	**Absent**	**Present**
OUPD	#/km^2	0.02 ± 0.03 (0 - 0.17)	0.01 ± 0.02 (0 - 0.09)	0.02 ± 0.04 (0.00 - 0.17)
ODOWND	#/km^2	0.01 ± 0.02 (0 - 0.14)	0.01 ± 0.03 (0 - 0.14)	0.01 ± 0.01 (0.00 - 0.06)
OTHER	Y/N	-	-	-
KIR	km/km^2	2.76 ± 1.01 (0.34 - 5.27)	2.78 ± 0.79 (1.22 - 4.73)	2.74 ± 1.24 (0.34 - 5.27)
KISX	#/km^2	2.86 ± 1.85 (0 - 7.64)	2.67 ± 1.75 (0 - 6.37)	3.07 ± 2.01 (0 - 7.64)