ECOLOGY AND LIFE HISTORY DIFFERENCES OF BULL TROUT (*Salvelinus confluentus*) LIVING ABOVE AND BELOW BARRIERS

by

JASON J. LADELL

B.Sc., University of British Columbia, 1991

A THESIS SUBMITTED IN PARTIAL FUFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE
in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
December 2003

© Jason J. Ladell

Library Authorization

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Jason Ladell — Name of Author *(please print)*

Dec 15/03 — Date

Title of Thesis: Ecology and life history differences of bull trout (Salvelinus confluentus) living above and below barriers

Degree: Masters of Science Year: 2003

Abstract

Bull trout populations in the Arrow Lakes exhibit two distinct life history patterns depending on whether they live above or below waterfall barriers. Migratory populations utilize the lower reaches of tributaries for spawning and rearing but resident populations carry out their entire life history upstream of waterfall barriers. Few studies have examined how these populations differ in terms of habitat preference or life history pattern. The specific objectives of this study were thus twofold. The first was to describe and quantify differences between habitat availability and use by resident versus migratory bull trout, and the second was to describe how certain life history parameters varied between the two populations.

The physical environments of these two habitats showed distinct variation in temperature and physical habitat variables including stream size, water velocity, pool composition and available cover. Maximum summer water temperature and average summer water temperature were both lower above the barriers. However, bull trout utilized similar habitats irrespective of whether they were above or below barriers, and appeared to maintain positions in shallow, low velocity areas of the stream. Daytime cover associated with above-barrier fish was typically logjams or other instream woody debris, while below-barrier cover usually consisted of large boulder substrates. Densities of bull trout at all sites were similar to those reported from other populations and were temporally variable within and between sites. Movements of bull trout determined by mark-recapture rates showed that above-barrier fish exhibited a more restricted movement pattern than below-barrier fish. Evidence of life history differentiation between bull trout populations occurring above and below barriers included differences

in growth rates, average lengths, morphology, and meristics. This study showed that bull trout populations occurring above and below waterfall barriers in the tributaries of the Arrow Lakes inhabit different physical environments, and that certain aspects of their life histories appear to reflect local adaptation to these distinct ecosystems.

Table of Contents

ABSTRACT ..... **II**

TABLE OF CONTENTS ..... **IV**

LIST OF TABLES ..... **VI**

LIST OF FIGURES ..... **VII**

ACKNOWLEDGEMENTS ..... **IX**

CHAPTER 1 – GENERAL INTRODUCTION **1**

Introduction to Life History Evolution *1*
Biology of Salvelinus confluentus *4*
Bull Trout in the Arrow Lakes Region *6*
Project background, relevance and objectives *7*

CHAPTER 2 – A COMPARISON OF PHYSICAL ENVIRONMENTS, HABITAT USE, AND MOVEMENTS OF BULL TROUT LIVING ABOVE AND BELOW WATERFALLS **11**

INTRODUCTION 11
MATERIALS AND METHODS 19
Study Sites *19*
Watershed morphometry *23*
Water temperature *23*
Habitat features *24*
Habitat use *26*
Density *26*
Movement *26*
DATA ANALYSES 27
RESULTS 29
Watershed morphometry *29*
Water temperature *30*
Habitat variables *35*
Habitat use by bull trout *41*
Density *49*
Movement *51*
DISCUSSION 54
Ecological consequences of differing stream environments *54*
Summary and conclusions *63*

CHAPTER 3 – EVIDENCE OF DIFFERENTIATION IN LIFE HISTORY AND MORPHOLOGY BETWEEN BULL TROUT LIVING ABOVE AND BELOW WATERFALLS. **66**

INTRODUCTION 66

MATERIALS AND METHODS 73
Data Collection *73*
Size and Growth *73*
Size at maturity *74*
Morphological and meristic variation *74*
DATA ANALYSIS 78
Size and growth *78*
Size at maturity *78*
Morphological and meristic variation *78*
RESULTS 81
Size and growth *81*
Size at maturity *86*
Morphological and meristic variation *87*
DISCUSSION 100
Size and growth *100*
Size at maturity *102*
Morphology and meristic variation *104*
CHAPTER 4 – CONCLUSIONS 109
Summary *109*
Conservation implications *109*
Management issues *111*
Habitat loss *112*
Introduced species *114*
Genetic legacy *115*
Future Research *116*
REFERENCES 118

List of Tables

Table 2.1. Categories used to classify substrate characteristics for bull trout in the Arrow Lakes tributaries (Sexauer 1994;Baxter 1997d).....25
Table 2.2 Categories used to classify cover characteristics for bull trout in the Arrow Lakes tributaries (Sexauer 1994;Baxter 1997d).....25
Table 2.3. Large scale habitat characteristics of study sites. Stream length indicates distance from study site to the outflow to lake.....29
Table 2.4. Summary of mean water temperature at study sites. 23 May – 19 Oct. 1998..31
Table 2.5. Nested ANOVA results for continuous habitat variables.....36
Table 2.6. Mean values (± SE) for channel dimensions of above- and below-barrier sites in the two study streams.....38
Table 2.7. Summary of habitat variable measurements. Woody debris represents actual counts of pieces within 100m study sections. Pool habitat, undercut bank and overhanging vegetation numbers are all mean proportions averaged from 5 m stream sections. (N=20).....39
Table 2.8. Distribution of substrate size classes (see Table 2.1). Values represent percentages of substrate size class within sample site.....39
Table 2.9. Summary of mean (SE) measurements taken for bull trout microhabitat use in Arrow Lakes study streams during summer 1998. Values for cover and substrate are modes.....48
Table 2.10. Summary of mean density (# fish/ha) and mean biomass (kg/ha) of bull trout (*Salvelinus confluentus*). June-September, 1998.....50
Table 2.11. Nested ANOVA results for density and biomass measurements on bull trout sampled from above- and below-barriers in two Arrow Lakes tributaries.....50
Table 3.1. Morphological measurements taken for morphometric analysis of bull trout (*Salvelinus confluentus*) from Arrow Lakes tributaries (Hubbs and Lagler 1958;Haas and McPhail 1991).....76
Table 3.2. Meristic measurements taken for analysis of bull trout (*Salvelinus confluentus*) from Arrow Lakes tributaries.....77
Table 3.3. Comparison of mean size adjusted[a] characters (mm) for each study population of bull trout in the Arrow Lakes.....89
Table 3.4. Nested ANOVA results comparing adjusted morphometric measurements taken from bull trout with the factor stream nested within barrier.....90
Table 3.5. Loadings for the first three principal components on adjusted morphological traits. See Table 3.1 for trait definitions.....91
Table 3.6. Nested ANOVA results comparing above and below barrier morphometric PCA scores for the first three components.....94
Table 3.7. Mean meristic counts within site and between life history type. Nested ANOVA results for above barrier versus below barrier.....95
Table 3.8. Factor loadings for principal components on meristics.....96
Table 3.9. Nested ANOVA results comparing above and below barrier meristic PCA scores for the first three components.....99

List of Figures

Figure 1.1. The Columbia River basin with the Arrow Lakes study region shaded. 10
Figure 2.1. Study site locations in tributaries of the Arrow Lakes. Below-barrier site on St. Leon Creek located approximately 100m downstream of waterfall barrier. 20
Figure 2.2. Maximum daily water temperature (°C) for 150 period 23 May and ending 19 October. AB= Above-barrier; BB= Below-barrier..... 31
Figure 2.3. Cumulative temperature units (CTU) in St. Leon Creek for 150 day period beginning May 23, 1998 and ending October 19, 1998. AB= Above-barrier; BB= Below-barrier..... 32
Figure 2.4. Cumulative temperature units (CTU) in Woden Cr. and Burton Cr. for 150 day period beginning May 23, 1998 and ending October 19, 1998. AB= Above-barrier; BB= Below-barrier. 33
Figure 2.5. Total accumulated thermal units for 150-day period beginning 23 May and ending 19 October 1998. BBB=Burton Creek, below-barrier; WAB=Woden Creek, above-barrier; SLBB=St. Leon Creek, below-barrier; SLAB=St. Leon Creek, above-barrier. 34
Figure 2.6. Bar chart of mean maximum depth measurements (±SE) in the four stream sites sampled. AB= Above-barrier; BB= Below-barrier. 37
Figure 2.7. Relative proportion of substrate types at each study site. 40
Figure 2.8. Frequency histogram of fork length for bull trout sampled for habitat use analyses from above- and below-barrier sites. 42
Figure 2.9. Comparison of focal point water depth (cm) and (log) fork length (mm) for bull trout sampled from above- and below-barrier study sites. 43
Figure 2.10. Comparison of focal point bottom velocity (m/s) and (log) fork length (mm) for bull trout sampled from above- and below-barrier study sites. 44
Figure 2.11. Substrate frequency histogram for bull trout (*Salvelinus confluentus*) measured for habitat use in above- and below-barrier sites. 45
Figure 2.12. Cover frequency histogram for bull trout (*Salvelinus confluentus*) measured for habitat use in above and below barrier sites. 46
Figure 2.13. Water depth frequency histogram for bull trout (*Salvelinus confluentus*) habitat use measured in above and below barrier sites. 47
Figure 2.14. Percentage of marked bull trout found during three-pass removal electrofishing in above-barrier sites in St. Leon and Woden Creeks. 52
Figure 2.15. Percentage of marked bull trout found during three-pass removal electrofishing in below-barrier sites in St. Leon and Burton Creeks..... 53
Figure 3.1. Above-and below-barrier comparisons of fork length (mm) plotted against consecutive sampling day. 82
Figure 3.2. Fork length frequency of bull trout (*Salvelinus confluentus*) captured during 1998 in St. Leon Creek. 83
Figure 3.3. Fork length frequency of bull trout (*Salvelinus confluentus*) captured during 1998 in Burton/Woden Creeks. 84
Figure 3.4. Length frequency of sexually mature resident bull trout from above-barrier populations. 85
Figure 3.5. Scatter plot of principal components performed on entire morphometric set along PC 1 and PC2 (Table 3.6). Circles are samples from St. Leon Creek and

inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols are from below-barrier samples 92
Figure 3.6. Scatter plot of principal components performed on entire morphometric set along PC1 and PC3 (Table 3.6). Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols are from below-barrier samples. 93
Figure 3.7.. Scatter plot of principal components performed on entire meristics set along PC1 and PC2 (Table 3.9). Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols are from below-barrier samples. 97
Figure 3.8. Scatter plot of principal components performed on entire meristics set along PC1 and PC3 (Table 3.9). Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols represent below-barrier samples. 98

Acknowledgements

This work could not have been completed without the assistance and support of a great number of people. I would like to thank everyone who assisted me in the West Kootenays: Grant Thorpe, Bob Millar, and Diane Koeller at the Hill Creek Hatchery and Spawning Channel provided accommodation and assistance. The staff of Columbia Basin Fish and Wildlife Compensation Program (CBFWCP), Maureen DeHaan, Harald Manson, Steve Arndt and Karen Bray, have been extremely helpful. I am grateful to all my committee members for their assistance and advice on this project: J.D. McPhail, Scott Hinch and Eric Parkinson.Thanks to all the people that have helped me in the field: Cory Suski, Mark Phillpotts, Steve Latham. I have appreciated all those here at the university who has made my experiences here invaluable: Steve Latham, Mike Stamford, Anna Elz, David O'Brien. A special thanks goes to Kate Willis for all that she has done for me personally and professionally.

This work has been funded by a generous grant from CBFWCP, Ministry of Water, Land & Air Protection (MWLAP) and BC Hydro Environment. Field equipment was kindly loaned to me by CBFWCP and MWLAP, Kootenay region.

Finally, I want to thank my thesis supervisor, Dr. Eric B. (Rick) Taylor, for taking me on as a student, providing support, and showing both patience and generosity over the course of my degree.

Chapter 1 – General Introduction

Introduction to Life History Evolution

An issue central in evolutionary biology is how natural selection acts in concert with genetic variation to produce adaptation in a species. Specific adaptations evolve as a result of improvement in survival and reproductive performance within their local environment. The concept of ecological speciation suggests that populations within different resource environments can diverge in phenotype and may ultimately develop reproductive isolation due to divergent natural selection (Schluter 2001). Life history traits are the phenotypic expression of those adaptations that affect the reproductive success of the animal. Generally these include survival, size and age at maturity, growth and fecundity.

The literature on life history evolution is broad and diverse. Published works include reviews (Stearns 1977;Roff 1984, 1992), mathematical models (Schaffer 1974;Roff 1986;Kozlowski 1992;Kawecki and Stearns 1993) as well as empirical studies (Schaffer and Elson 1975;Reznick and Endler 1982;Stearns 1983a;Hutchings 1993). Such studies attempt to give us a wider understanding of how trade-offs between growth, reproduction and survival influence lifetime fecundity. Life history traits vary as a function of the ecological setting in which an organism occurs, and as such ecological constraints will drive the particular set of traits found.

Within a local population, the suite of life history traits that has evolved is usually considered to be the result of optimization of survival and reproductive success. Trade-offs and constraints mediate the allocations of resources to specific traits within the life history framework. In addition, the environment within which the organisms live will have a direct effect upon mortality and fecundity, and life history traits must also have some genetically heritable variation. The combination of all these factors should serve to maximize the fitness of members of a local population, via natural selection on life history attributes.

Ecological divergence within a species is a function of isolation and natural selection. Divergence between populations may also be accompanied by shifts in resource use, morphology or physiology (Taylor 1991;Skulason and Smith 1995;Jonsson and Jonsson 2001). It is well known, however, that within a single species, phenotypes can be expressed differently depending on the environment in which that species lives (West-Eberhard 1989). This range of variation in expressed phenotypes from a single group of genetically related individuals has been termed a species reaction norm (Stearns 1992). Intraspecific variation can be found in allopatric, sympatric or parapatric populations, particularly in species of freshwater fishes where physical isolation among populations is often pronounced. Adaptation to the local environment is expressed in terms of various life histories, morphological variation, or differences in resource use (Lessios 1981;Currens et al. 1990;Dynes et al. 1999).

Local adaptation in phenotype has been well studied in fish (e.g.,Kume et al. 2003). For example, significant effects of environment were found to explain differences in life history parameters for mosquitofish (*Gambusia affinis*) in Hawaiian reservoirs

(Stearns 1983b, c), and in north temperate freshwater fish fauna there is a wide range of examples of intraspecific variation (Taylor 1999). In particular, the salmonids have shown a high degree of local adaptation that is reflected in unique life history and morphological characteristics (Taylor 1991;Willson 1997).

Fish of the genus *Salvelinus* ("char"; Salmonidae) have long been known to possess exceptionally plastic responses to environmental variation (Jonsson et al. 1988;Snorrason et al. 1989;Yamamoto et al. 1992;Baroudy and Elliot 1994;Hutchings 1996;Magnan et al. 2002), and studies of allopatric populations of brook trout (*Salvelinus fontinalis*) indicate that life history parameters can diverge within a small geographic area (Hutchings 1993;Hutchings and Myers 1994). There appears to be strong overwinter survival costs associated with reproduction that contribute to life history differences within local brook trout populations (Hutchings 1994). Numerous populations of Arctic char (*Salvelinus alpinus*) in postglacial Holarctic lakes have evolved specific local adaptations to different habitats (Klemetsen et al. 2003). These Arctic char populations often occur sympatrically within a single lake and yet remain differentiated in both morphology and life history characteristics (Jonsson et al. 1988). Similarly, adult brook trout in northern Quebec lakes show functional differences in body morphology related to habitat use (Bourke et al. 1997).

Although there have been many studies of divergence within the char family, the literature remains relatively sparse for bull trout (*Salvelinus confluentus*). Bull trout life history variation is commonly characterized in terms of migratory patterns, and the majority of research on this species has concentrated on the large-bodied, migratory forms. Studies of bull trout variation have focused on wide scale geographic patterns

(Haas and McPhail 1991;Taylor et al. 1999;Haas and McPhail 2001;Taylor et al. 2001), and intraspecific variation on local scales has largely been examined using molecular analyses (Leary et al. 1993;Latham 2000;Kanda and Allendorf 2001;Costello et al. 2003).

Biology of Salvelinus confluentus

Bull trout are a species of char endemic to western North America (Cavender 1978;Haas and McPhail 1991). In British Columbia (BC), this indigenous fish is distributed inland throughout the province, but its range is centered in southeastern BC. The extant range of the species extends south to Nevada, east into Alberta and northward into some watersheds of the Yukon and Northwest Territories. Bull trout have only recently been formally described as a species distinct from the Dolly Varden (*Salvelinus malma*). Initially this distinction was based on morphological evidence (Cavender 1978) and then expanded upon with Haas and McPhail's (1991) supplemental morphological work. Additionally, molecular studies have shown the two species to be discrete from one another, although there are regions of sympatry (Hagen and Taylor 2001) and cases of hybridization (Baxter et al. 1997;Redenbach and Taylor 2002;Redenbach and Taylor 2003).

Bull trout populations exhibit several distinct life history forms throughout their range (McPhail and Baxter 1996). The least understood (and likely ancestral) life history pattern occurs in populations that are anadromous. Populations that live entirely within large river systems and yet still make spawning migrations to smaller tributaries are described as 'fluvial'. In contrast, 'adfluvial' populations spawn and rear in the tributary

streams of large lakes and reservoirs, and comprise the predominant life history form of bull trout. The majority of the adfluvial bull trout's life is spent in the lacustrine environment where it is picivorous and attains a large body size at maturity (occasionally over 900 mm in length). Finally, 'stream resident' populations are usually confined to headwaters by geological barriers or environmental factors (Nelson et al. 2002), and are found in many areas throughout their native range. These headwater populations tend to show very small sizes at maturity (less than 300 mm in length).

Morphology has largely been used in bull trout for either species diagnosis or to place the species within a larger zoogeographic context (Haas and McPhail 2001). Cavender (1978) used morphological and meristic characters distinguish bull trout from Dolly Varden. Further validation of this work was done by Haas and McPhail (1991) where the two species were differentiated using multivariate analyses on a wide range of morphological characters. These studies, however, examined bull trout specimens from a wide geographic range, but did not consider local or small-scale variation in characters.

Although the pace of research has increased on the bull trout, there is still little known about many aspects of their life history. Few populations throughout the range in North America remain unaffected by anthropogenic influences, and many of the populations for which there are time-series data appear to be in decline (Rieman and McIntyre 1995;Rieman et al. 1997). The US Fish and Wildlife Service has formally listed all populations of bull trout in the coterminous United States as threatened (U.S. Federal Register November 1, 1999 vol. 64 (210): 58910-58933). In British Columbia, the bull trout has been blue listed as sensitive and vulnerable by the British Columbia Ministry of Environment, Lands and Parks Conservation Data Centre (Cannings and Ptolemy 1998).

Fisheries scientists and managers recognize the bull trout as an important regional indicator of the health of freshwater systems

Bull Trout in the Arrow Lakes Region

Bull trout populations in southeastern British Columbia have not been particularly well studied. With the advent of hydroelectric development in the 1970's and 1980's researchers and managers began to focus on this species primarily in response to potential population decreases through habitat inundation. The majority of bull trout that occur in the Arrow Lakes region (between Revelstoke and Castlegar, BC; Figure 1.1) are adfluvial migrants. Adults feed and grow to maturity in the relatively productive waters of the Arrow Lakes, where numerous tributaries are used to spawn, and where their progeny develop and feed as fry and juveniles. Sebastian et al (2000) list 18 and 6 streams in the Upper and Lower Arrow Lakes, respectively, that are known to support spawning adfluvial bull trout. Many adults undergo extensive migrations within the region bounded by the dams at the northern and southern ends of the Arrow Lakes, and adult fish return to their natal or spawning streams in the latter part of the summer.

Bull trout typically spawn in the months of September, October and November. McPhail and Murray (1979) observed that the majority of returning adfluvial adults entered Mackenzie Creek, a tributary to the Upper Arrow Lake, during the period from July 22 to August 20. They also found that this period coincided with the period of maximum water temperature and minimum water flow in their study stream. Adults may also enter the stream up to a month earlier (McPhail and Murray 1979); however, these fish are likely undergoing exploratory movements and may, in fact, drop back out to the

lake. Adult bull trout will spawn in areas of low water flow and loose gravel. Many of the tributaries to the Arrow Lakes are high gradient to their outlet and consequently adfluvial spawners need to be opportunistic in their selection of suitable spawning areas.

Bull trout juveniles feed and grow in the Arrow Lakes' tributaries for up to 3 years. There may be some migration by fry to the lake in the late spring, but typically juveniles move to the lake at 2 or 3 years of age (McPhail and Murray 1979;Ladell 1999). Upon entering the lake bull trout begin to grow quickly and can live for many years. McPhail and Murray (1979) examined otoliths from out-migrating and lake-caught adults and found that the majority of spawners were 4-7 years old. A large number of bull trout taken in the Upper Arrow Lake's sport fishery were also analyzed for age using otoliths. These data are summarized in Sebastian et al (2000), and show that over half of the fish were 5-7 years of age, with the maximum age being 15 years of age.

Project background, relevance and objectives

The zoogeography of British Columbia has been strongly influenced by Pleistocene glaciations (Lindsey and McPhail 1986;McPhail and Lindsey 1986). Throughout the province there are numerous examples of postglacial colonization of new environments leading to differentiation within species. The relatively short geological and biological history of the northern latitudes means that speciation processes are ongoing in many places (Taylor 1999). The British Columbian native freshwater fish assemblage, while relatively small in number, contains many of the most interesting examples of intraspecific postglacial ecological variation in the world. In many cases, studies have shown that evolution is occurring *in situ* around the province (e.g.,Schluter

1996;Taylor et al. 1999). In southeastern British Columbia, the Columbia River system is the main source of influence for the distribution of fish species. Post Wisconsinan recolonization of this region can be traced to refugia populations that occurred south of the glacial boundaries in the Columbia drainage basin (Taylor et al. 1999;Haas and McPhail 2001;Costello et al. 2003).

When organisms colonize new environments, life history theory predicts that they will evolve life history traits that maximize fitness. By studying different life history strategies and how they evolve in varied environments, ecologists can obtain a better understanding of how populations are maintained. Furthermore, detrimental influences on the aquatic environment force species to adapt or be extirpated. Understanding the components of life history and how they co-evolve can only serve to benefit both ecologists and managers. Teleosts and, in particular, salmonids have provided excellent examples of studies of life history evolution. Variation in age and size at maturity has been documented in guppies (*Poecilia reticulata*) in response to selection (Reznick et al. 1997), and the evolution of adaptive traits has been examined in many salmonids including sockeye salmon (*Oncorhynchus nerka*) (Hendry et al. 2000), coho salmon (*Oncorhynchus kisutch*) (Fleming and Gross 1989), Atlantic salmon (*Salmo salar*) (Schaffer and Elson 1975) and grayling (*Thymallus thymallus*) (Haugen and Vollestad 2000;Koskinen et al. 2002).

Over the past twenty years, fisheries researchers and managers have begun directing more of their energy towards accumulating information about bull trout populations. In the northwestern United States (Montana, Washington, Oregon and California), bull trout populations are being studied intensively, largely in response to

extirpations and range reductions. In the Canadian portion of the species' range, fisheries scientists are gathering data on populations that, while perhaps not as threatened, are facing similar problems. The migratory life history forms (fluvial and adfluvial) have received the bulk of attention as their particular characteristics (multiple habitat requirements, large size, angler value) make them significant to managers. Although the migratory forms are the most common, there appears to be a trend toward some of these populations becoming fragmented into headwater residents through changes in temperature regimes, loss of habitat and competition and hybridization with nonnative salmonids (Ziller 1992;Nelson et al. 2002). Further study on the resident life history form will provide a better foundation for our knowledge across the spectrum of bull trout life history variation.

The overall objective of this thesis is, therefore, to examine differences in life history and ecology between populations of stream resident and adfluvial bull trout from the upper Columbia River region (i.e., upstream of the Canada-US border) (Figure 1.1). An examination of the variation in strategies and their persistence in the context of life history evolution theory can elucidate how these populations have adapted for their specific environments postglacially. Specific objectives are to 1) establish a framework for life history evolution and provide a general introduction to bull trout biology and the Arrow Lakes Region (this Chapter); 2) address differences in the ecology of bull trout populations living above and below waterfalls (Chapter 2); 3) examine life history characteristic variation and its relationship to evolution and evolutionary theory (Chapter 3), and 4) offer management suggestions and general conclusions (Chapter 4).

Figure 1.1. The Columbia River basin with the Arrow Lakes study region shaded.

Chapter 2 – A comparison of physical environments, habitat use, and movements of bull trout living above and below waterfalls

Introduction

Salmonid life histories occur in a wide variety of patterns (Northcote 1997). The common method of describing salmonid life histories in fisheries biology has been to characterize their migration. Although many populations throughout the Salmonidae remain in the freshwater environment for their entire life cycle, anadromous populations make migrations between natal, freshwater habitats and the marine environment. For those life histories occurring entirely in freshwater, however, the extent of their migrations can vary considerably. Migratory populations may move between the spawning and natal habitats in small streams to the adult habitat in larger rivers or lakes. In some cases, populations with no large-scale migrations will remain within a single stream. Often, multiple life history types of a single species utilize a single watershed or basin. Most salmonids make some form of migration as part of their life cycle. Generally, movements increase in distance as the fish progresses through each life stage. The spectrum of variation in salmonid life histories with regards to migration and residency is a wide one. Large-scale freshwater spawning migrations can occur over hundreds of kilometers, and have been exhibited by some bull trout populations (O'Brien 1999). At the other extreme, stream resident populations may show restricted movement throughout their life. For example, brown trout (*Salmo trutta*) recaptured one year after marking showed home ranges of less than 800 m (Knouft and Spotila 2002). Resident populations may coexist with a migratory population where both types occur in sympatry (Yamamoto

et al. 1999) or maintain themselves in discrete regions of the stream (Goto 1998). This latter configuration occurs when a single species maintains different life history strategies within a stream, and a physical barrier separates them. Barriers can take both natural or anthropogenic forms but this study focuses on natural impassable waterfall barriers. This type of obstacle is unique in that it acts in a unidirectional manner allowing only downstream migration.

Many salmonid fishes in streams of the northern hemisphere have populations that can be found above an impassable waterfall barrier. Brown trout (Jonsson and Sandlund 1979;Jonsson 1982;Hindar et al. 1991), Atlantic salmon (Vuorinen and Berg 1989), cutthroat trout (Northcote and Hartman 1988;Griswold et al. 1997), Dolly Varden (Blackett 1973;Maekawa et al. 1993;Cavender 2001), Arctic char (McCart and Craig 1973) and rainbow trout (Northcote et al. 1970;Northcote 1981;Northcote and Kelso 1981;Parkinson et al. 1984;Northcote and Hartman 1988;Currens et al. 1990) have all been found to maintain resident populations above waterfalls. Populations living above waterfalls are typically much smaller in size than their adult counterparts below.

Instream migration barriers such as the waterfalls seen in tributaries of the Arrow Lakes divide populations into specific upstream and downstream habitats. Within a stream there are well known associations between the physical structure of the stream and its order (Platts 1979), and there appears to be a generally negative association between habitat quality as stream size increases (Kozel and Hubert 1989). Stream width, stream depth and substrate size all decrease as stream order decreases. In the case of habitat variables associated with the abundance of brook trout, there was a decrease in the amount of overhanging vegetation and consequent overhead cover as the size of the

stream increased (Kozel and Hubert 1989). Small streams have strong associations with large woody debris (LWD) (Fausch and Northcote 1992). Stream morphology is affected by the position and amount of LWD within the stream channel and LWD are major factors in pool formation (Andrus et al. 1988). Another association with stream size increase is the decline in the abundance of pool habitat (Kozel and Hubert 1989). Pool habitat is extremely important for bull trout, especially in the fry and juvenile stages (McPhail and Murray 1979;McPhail and Baxter 1996;Bonneau and Scarnecchia 1998). Pool habitats of increasing depth provide cover as well as velocity refuges, feeding areas and overwinter habitat for salmonids (Harvey and Stewart 1991;Jakober et al. 1998).

For salmonids, water temperatures in the stream environment have a strong influence on their distribution both among streams and along the thermal gradient of a single watercourse (Fausch et al. 1994;Rieman et al. 1997;McCullough 1999). The *Salvelinus* complex and, bull trout in particular, are cold water adapted and have relatively narrow thermal preferences (Goetz 1994a;Bonneau and Scarnecchia 1996). Water temperature appears to play a critical role in determining the distribution of small bull trout (<150 mm) in coldwater streams (Dunham et al. 2003). Field studies have characteristically found that a summer thermal maximum of 15°C is the upper limit of juvenile bull trout presence (McPhail and Murray 1979;Fraley and Shepard 1989;Saffel and Scarnecchia 1995), and fry are unable to survive warm temperatures for extended periods of time. The upper incipient lethal temperature (50 % mortality over 60 days) for fry raised in the laboratory is 20.9°C and maximum growth rates occur between 12 and 16°C (Selong et al. 2001).

Salmonids are exceptionally adaptable in their ability to express differing life history forms. In many cases, stream resident populations are the result of historical (geological) deglaciation processes where migration to a more productive adult habitat was restricted and populations adapted to the new situation. Bull trout stream habitat requirements (Rieman and McIntyre 1995;Saffel and Scarnecchia 1995;Baxter and McPhail 1996;McPhail and Baxter 1996;Baxter 1997a;Baxter 1997c) have been studied over the past ten years, and it is clear that the species is vulnerable to environmental disturbance (Ratliff and Howell 1992;Rieman and McIntyre 1995). Bull trout in all stages of their life require clean, cold water and have strong associations with several abiotic habitat variables such as substrate and cover. For all life history forms, the stream environment provides critically important habitat for both spawning and rearing.

The char complex, like other salmonid groups, contains a high level of both inter- and intraspecific diversity. In order to maintain maximum levels of biodiversity, an understanding of adaptive variation down to, and including, local populations is essential. In recent years, the scientific and management communities have directed an increasing amount of research toward understanding the ecological requirements of bull trout. Much of this study was thus driven by concerns that anthropogenic, interspecific and possibly geoclimatic processes are negatively impacting the ability of bull trout populations to flourish throughout their range. Bull trout studies in the past have focused primarily on the large-bodied, migratory populations (Fraley and Shepard 1989;Swanberg 1991;Bond 1992;Brenkman et al. 2001;Post and Johnson 2002). These life history types tend to be recreationally important and the adults are top-level predators within their native range. If, however, we are concerned with the overall preservation of biodiversity in bull trout as

an entire species, then we must obtain information on as many different forms as possible. It is often the case that smaller, more marginal populations of a species are inherently valuable and may act as reservoirs of biodiversity (Scudder 1989;Costello et al. 2003). Resident populations of bull trout in the Arrow Lakes are relatively free of human influence and represent an important component of the freshwater fish fauna in the region.

For all bull trout life history types, the rearing phase is almost exclusively within the natal stream. Newly emerged fry remain strongly associated with slow moving water (channel margins, side channels), benthic orientation and submerged cover during their first summer (McPhail and Murray 1979;Saffel and Scarnecchia 1995;Baxter 1997c). In the migratory forms, bull trout juveniles remain within the stream for 1 to 3 years. Juveniles can occupy a range of habitats but their daytime summer preferences appear to be for pool habitat and larger cover such as woody debris and undercut banks (Fraley and Shepard 1989; Nakano et al 1992; Baxter 1997).

Directed movements in bull trout occur in differing life history forms and life stages. Adfluvial fish have complex and long distance movement patterns (Fraley and Shepard 1989;Brenkman et al. 2001). In general, juveniles and fry make directed downstream movements from the natal rearing area, and juveniles generally move into the lacustrine habitat at the end of their second or third summer (McPhail and Murray 1979;Ladell 1999). Fry may also move out of the stream in their first summer, although this movement may be due to increased water flow from the freshet (Pratt 1992). Upon sexual maturation, adults will migrate to the stream to begin spawning. Spawning migrations can involve distances of several hundred kilometers (O'Brien 1999).

For bull trout, many aspects of their stream ecology have been studied throughout the range. In the stream environment, temperature and habitat are the two most crucial factors that influence the early years of adfluvial bull trout life history. Resident bull trout populations in my area of study are confined exclusively to the stream environment, and consequently the influences of this environment are probably a major driving influence on the direction their life history. For both resident and adfluvial life history forms to persist, their respective populations presumably must track any changes in stream environments with life history changes.

A large number of previous studies on bull trout life history have focused on the adfluvial populations (Goetz 1994b;Kitano et al. 1994;Sexauer 1994;Rieman and McIntyre 1995;Baxter 1997b;Craig 1997;Brenkman et al. 2001). This was most likely due to a combination of factors such as size effects and incidence within the recreational fishery. Since they are larger in size, migratory populations of bull trout are an important recreational fisheries resource. As a result, studies were designed to focus on increasing our understanding of early life history patterns in order to meet conservation goals and help officials manage these larger populations more effectively. Bull trout, in all their life history types, are being influenced by human activities and no form is inherently more important than another. Therefore, under representation of information on the resident life history type clearly leaves a gap in the overall picture of bull trout biodiversity.

The objective of this component of my thesis is to provide a description of the ecological and habitat differences between the above and below barrier populations of bull trout. I have hypothesized that important differences in ecology between the stream component of the resident and migratory populations have driven the divergence in life

history forms. Longitudinal thermal patterns in streams are influenced by both local (geomorphology and hydrology) and regional (climate and altitude) factors. The general expectation is that water temperature decreases with increasing elevation (Ward 1985) although local factors (groundwater influences, riparian vegetation) will increase heterogeneity in this pattern (Torgersen et al. 1999;Arscott et al. 2001). I therefore predict that water temperatures in the above barrier sites should be colder than those of the below barrier sites.

Bull trout have a strong association with various components of habitat in the streams they utilize. Migratory populations require suitable substrate, cover, depth, and velocity for fry and juveniles (Shepard et al. 1984;Fraley and Shepard 1989;Sexauer 1994;Saffel and Scarnecchia 1995;Baxter and McPhail 1997). Stream resident populations have similar requirements, in addition to necessary suitable habitat for the adult phase of their life history. I hypothesize that above-barrier sites should be smaller in size but have a wider array of habitat diversity than below-barrier sites. I also predict that bull trout habitat use in the below-barrier sites should be more restricted as a result of a smaller proportion of available suitable habitat. This restriction in habitat use, coupled with potential competitive interactions with other native species in the below-barrier sites, leads to an expectation of lower densities of bull trout in these areas.

Resident populations of fish in streams are thought to exhibit relatively limited migratory movements (Gerking 1959;Knouft and Spotila 2002). More recently, some studies have suggested that the within-stream movements of salmonids may be more widespread than currently recognized (Gowan et al. 1994;Gowan and Fausch 1996). In high elevation streams, downstream movement can occur in the autumn as fish locate

overwintering areas that are ice-free (Cunjak 1996;Jakober et al. 1998). For bull trout populations located above waterfalls, however, downstream movement is limited by the 'knife-edge' selection of falling over the barrier (i.e., downstream dispersers can not contribute reproductively to the populations from which they originated). Therefore, long distance, directed, downstream movement should be strongly selected against (Northcote 1981;Jonsson 1982;Northcote and Hartman 1988;Hindar et al. 1991). This supposition has been supported by recent evidence showing adaptation of some char populations to a resident life history form within a short period of time (McCart 1997;Rieman et al. 1997;Nelson et al. 2002). Additionally, rapid adaptation to reduced downstream movement has been seen in populations of char isolated above dams for less than 50 years (Morita and Yamamoto 2000, 2001). Based on these findings, I hypothesized that bull trout from the above-barrier populations would exhibit less movement, as shown by greater site fidelity, than the below-barrier populations. If, as I am hypothesizing, habitat complexity is higher in the above-barrier sites, then bull trout from those areas will be less inclined to make directed movements in search of higher quality habitat. Therefore, by examining differences in the environment I hope to create a context within which to elucidate life history differences between these conspecifics.

Materials and Methods

Summer stream ecology of bull trout was studied in the St. Leon and Burton Creek systems, two watersheds of the Arrow Lakes. Water temperature, habitat use, density and movement were examined for adfluvial juveniles and fry and for resident juveniles and adults. In addition, the morphometry of the two watersheds was compared.

Study Sites

The Arrow Lakes constitute a long section of the upper Columbia River system in southeastern British Columbia (Figure 2.1). The system stretches to over 200 km in the north-south direction between the Revelstoke and Keenlyside dams. The Monashee and Selkirk mountain ranges bound the reservoir to the east and west, respectively. The majority of tributaries to the system are high gradient, low order streams. A large number of these streams contain velocity or waterfall barriers that block upstream migration within the first few kilometers.

No description of the Arrow Lakes region would be complete without a brief history of its hydroelectric development. Subsequent to the signing of the Columbia River Treaty in 1969, the Hugh Keenlyside Dam was built just upstream of the town of Castlegar. This impoundment flooded what were essentially two large oligotrophic lakes (Upper and Lower Arrow lakes) with sections of the Columbia River flowing freely in

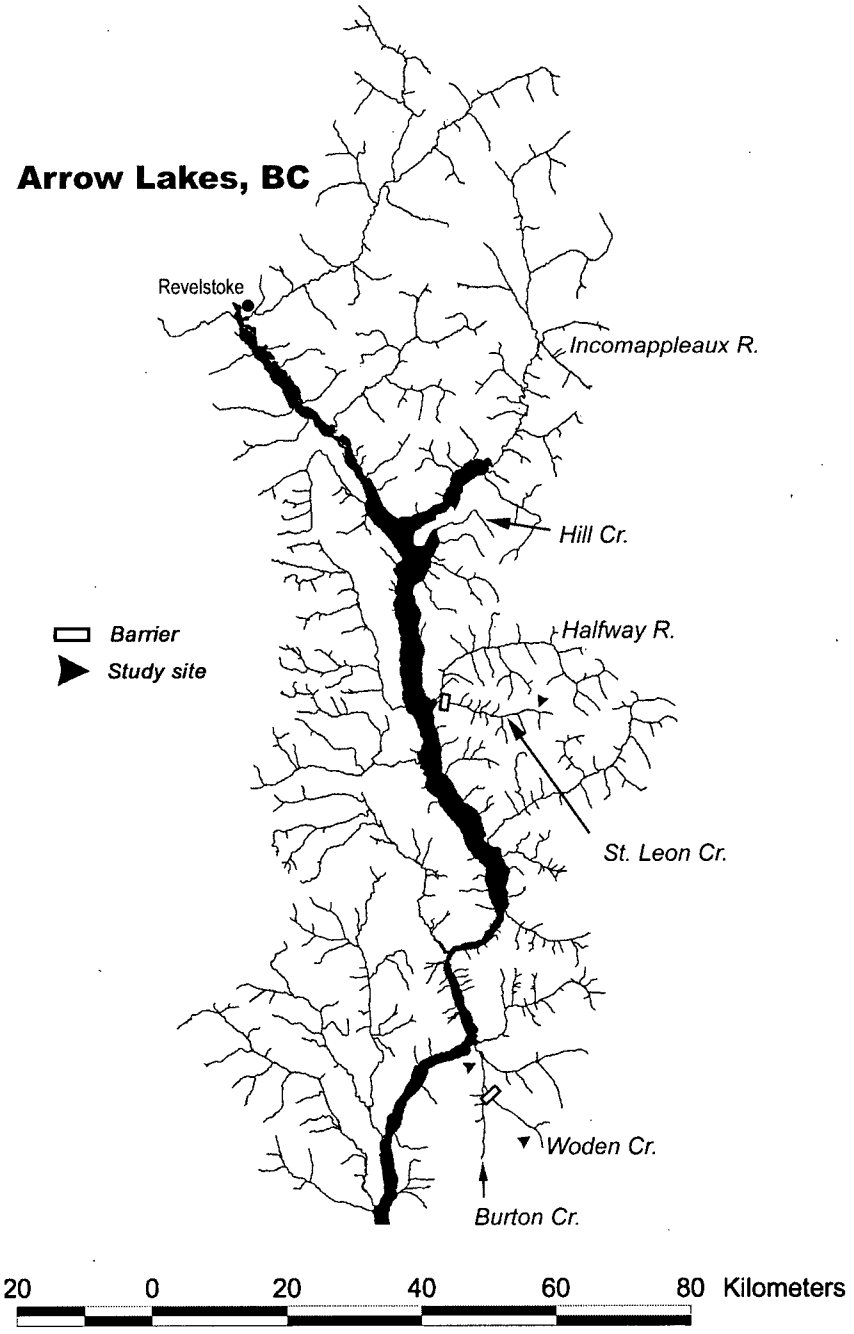

Figure 2.1. Study site locations in tributaries of the Arrow Lakes. Below-barrier site on St. Leon Creek located approximately 100 m downstream of waterfall barrier.

between. Water levels rose by 14 m and created a reservoir extending 230 km north to Revelstoke. In 1973 and 1984 the Mica and Revelstoke dams were built and blocked migration and utilization of upstream habitat. Little assessment was done with regards to loss of habitat for fish spawning and rearing. A rough estimate, however, indicated that the Revelstoke Dam (Martin 1976) would block 4000 bull trout spawners from access to their natal habitat.

Within this region there is a long history of introduction and enhancement. Fish species including eastern brook trout and lake whitefish (*Coregonus clupeaformis*) were introduced to the Arrow Lakes drainage and have become well established. Both the Upper and Lower Arrow Lakes have had the freshwater crustacean, *Mysis relicta*, introduced to their waters. The other major biological manipulation of the system has been the enhancement of native fish species. In the first half of the last century rainbow trout from various populations were introduced. After the completion of the Revelstoke and Keenlyside dams, regular stocking of rainbow trout and bull trout was carried out from the Hill Creek Spawning Channel and Hatchery.

Bull trout, rainbow trout (*Oncorhynchus mykiss*) and kokanee salmon (*Oncorhynchus nerka*) dominate fish populations existing in the lake accessible sections of the Arrow Lakes tributaries. In addition to these fish, lake whitefish, slimy sculpin (*Cottus cognatus*) and torrent sculpin (*Cottus rhotheus*) can be found in the lotic environment, and the introduced brook trout is found in many of the tributary streams. Headwater portions of the streams above waterfalls generally contain only bull trout, although there may also be some *Cottus* species.

Study sites were located in two stream systems situated approximately 60 kilometers apart on the eastern side of the reservoir (Figure 2.1). St. Leon Creek, the northernmost site, drains into the Upper Arrow Lake and contained both above- and below-barrier sites within its mainstem. The southern sites were located in Burton Creek and its tributary, Woden Creek, and served as below- and above-barrier sites, respectively. These streams were easily accessible and had sufficiently high densities of fish to permit study.

St. Leon Creek is a small watershed located on the eastern side of the reservoir. The watershed catchment area is 106 km^2. The below-barrier study site was located approximately one km upstream of the outlet at 1610 m above sea level. The waterfall barrier was approximately 100 m upstream of this site. The above-barrier site was 16 km upstream and was situated 4340 m above sea level. The average stream gradient between the two sites was approximately 17 %.

The Burton Creek study area drains to the northern part of the Lower Arrow Lake region of the reservoir. The below-barrier site was located in Burton Creek at about 1600 m elevation. The watershed area of Burton Creek, excluding Woden Creek, is 97 km^2. The above barrier site was located in Woden Creek, the largest tributary of Burton Creek. This site was 9.8 km upstream at an elevation of 3800 m. The area drained by the Woden Creek watershed is 76 km^2, and the average stream gradient between the two sites was 12 %.

Both of the watersheds in this study have been impacted to varying degrees by anthropogenic activities. Access roads and logging cutblocks follow the stream courses and reach to the extreme headwaters of these systems. Additionally, impoundment of the

Arrow Lakes served to raise water levels in the lake and inundate critical spawning and rearing habitat near stream outlets. In the case of St. Leon Creek, where the migration barrier is within a kilometer of the lake, this loss of habitat was likely more of a cost to the bull trout than on Burton Creek

Watershed morphometry

Both watersheds in this study were assessed for large-scale habitat features and processes. Total watershed area was calculated using a GIS database. Elevation at each study site was obtained by taking a reading using a handheld GIS unit and examination of 1:50,000 topographic maps. Stream gradient at each site was measured using a handheld clinometer.

Water temperature

Stream water temperatures were collected by placing a remote digital temperature recorder (Onset Instruments, Pocassett, MA, USA) in the water at all four study sites. The temperature logger took two daily records at 04:00 and 16:00. The second daily water temperature was used for analysis because maximum summer water temperature has been cited as a factor controlling juvenile bull trout distribution (Fraley and Shepard 1989;Goetz 1989;Saffel and Scarnecchia 1995). Temperature recorders were placed at the downstream end of each study site on 23 May and removed on 19 October 1998.

Over the course of this 150-day period water temperatures were periodically taken with a hand held alcohol thermometer to confirm the digital recordings.

Habitat features

During the 1998 summer field season (July – September) data were collected on habitat use and availability for above- and below-barrier populations of bull trout. At each study site, a measurement segment was established along the centerline of a 100 m section of the stream that encompassed all available habitat types. Transects perpendicular to the flow were taken at 5 m intervals. Channel dimensions recorded at each transect were wetted width and maximum depth.

In addition to channel dimensions, several habitat variables were measured along the segment within each study site. The number of LWD, pool composition (%), undercut banks (%), overhanging vegetation (%), and substrate composition were assessed over each 100 m section. Woody debris was defined as any woody object lying within the active channel along the transect and having dimensions in excess of 1 m long and 10 cm diameter. Undercut banks were defined as the length of any area along the stream bank that could provide overhead cover for bull trout. Overhanging vegetation included trees and shrubs less than 3 m in height that provided cover over the active stream channel. Substrate was assessed visually by estimating the majority size class (Table 2.1) occurring between each transect.

Table 2.1. Categories used to classify substrate characteristics for bull trout in the Arrow Lakes tributaries (Sexauer 1994;Baxter 1997d).

Code	Substrate Class
1	Detritus
2	Silt
3	Sand
4	Gravel (2-16 mm)
5	Pebble (17-64 mm)
6	Cobble (65-255 mm)
7	Boulder (256+ mm)
8	Bedrock

Table 2.2 Categories used to classify cover characteristics for bull trout in the Arrow Lakes tributaries (Sexauer 1994;Baxter 1997d).

Code	Cover Type
1	Submerged vegetation
2	Small wood <30 cm length
3	Large wood >30 cm length
4	Overhanging vegetation
5	Rootwad
6	Cobble (65-255 mm)
7	Boulder (256+ mm)
8	Turbulence
9	Undercut bank
10	No cover
11	Log jam

Habitat use

Individual fish were sampled for microhabitat use by marking their point of capture during electrofishing passes. Fish lengths were measured to the nearest mm and microhabitat variables (water depth, bottom velocity, substrate and cover) were taken at each focal point. Water depth was measured to the nearest cm. Water velocities were taken with a Marsh-McBirney current meter and measured to 0.01 $m \cdot s^{-1}$. Substrate classification is listed in Table 2.1 and was recorded as the predominant type within a 20 cm radius. Cover was recorded as the nearest available within 1 m and classes are listed in Table 2.2.

Density

Densities of bull trout in each study site were measured by counting all fish from a defined section of the stream and dividing that measurement by the area of the sampled section. Bull trout were counted by removing all fish during three pass-removal electrofishing sessions. Stop nets were placed at the downstream end of the stream section to block the movement of fish out of the reach.

Movement

During the summer of 1998 (23 May –20 September) each study site was sampled multiple times (7-11) via electrofishing. Each sampling event consisted of blocking the

site at the downstream end and collecting all bull trout caught. In the first sampling event, all bull trout were marked with a small fin clip to identify them as having been captured. On each subsequent sampling event the presence of a fin clip was recorded and unclipped fish were marked. By examining how the proportions of clipped to unclipped fish changed over time, I was able to infer movement to and from the study sites.

Between 22 August and 15 September, 1998 a total of 22 passive integrated transponder (PIT) tags were implanted in resident adult bull trout. PIT tags allow individual fish to be identified by scanning them with a PIT tag detector. After a study site was sampled by electrofishing, fish larger than 160 mm were selected for implantation. Bull trout were anesthetized with tricaine methanesulfonate (MS-222) after capture and a single PIT tag was inserted below the skin using a large gauge syringe. Thereafter all adult bull trout captured were scanned for PIT tags.

Data Analyses

Water temperatures recorded over the 150 day period from 23 May until 19 October were compared both within and between study streams. To test for differences in mean stream temperature between upstream and downstream sites, repeated measures analysis of variance (ANOVA) (α=0.05) were conducted on the above and below barrier sites within the two study streams (Zar 1999). I calculated accumulated thermal units (ATU) by summing the maximum daily water temperature within a particular site over the measurement period and comparing it with ATU's at other sites.

Measured habitat variables were compared between above and below barrier sites using a nested ANOVA, with sample sites nested within above and below barrier categories (Zar 1999). Substrate distribution between sites was compared using the Mann-Whitney test for ordinal data. In the case of woody debris, numbers consisted of a frequency of pieces and were compared within streams using a goodness of fit test. All tests had statistical significance assessed at α=0.05.

Because habitat use by stream-resident salmonids changes with body size (Keeley and Grant 1995;Hagen and Taylor 2001), an analysis of covariance (ANCOVA) was performed to correct for body size differences between bull trout with log transformed body size as the covariate. Discrete habitat variables were tested for differences between above and below barrier sites using a chi square (χ^2) analysis on the contingency table. In all tests the statistical significance was assessed at α=0.05.

Density estimates were compared between life history types (resident vs. migratory) using a nested ANOVA.

Results

Watershed morphometry

All of the sites in this study were located in third or higher order streams (Table 2.3). The sites were typically low gradient (near 4%) although the below-barrier site on St. Leon Creek was slightly higher gradient due to its proximity to the waterfall. The Woden Creek site was located at an elevation of 1158 m above sea level and was 670 m higher than its paired below-barrier site on Burton Creek at 488 m. Similarly, the elevation difference between the above- and below-barrier sites on St. Leon Creek was 833 m.

Table 2.3. Large scale habitat characteristics of study sites. Stream length indicates distance from study site to the outflow to lake.

Stream Site	Stream order	Elevation (m)	Site Gradient (%)	Stream Length (km)
St. Leon, Above	3rd	1323	4.2	20.64
St. Leon, Below	3rd	490	7.4	1.2
Woden, Above	3rd	1158	3.9	35.26
Burton, Below	4th	488	4.4	20.42

Water temperature

In the St. Leon Creek above-barrier site the average water temperature over the measurement period was 7.7°C (Table 2.4), and the maximum temperature reached over the summer was 12.4°C (Figure 2.2). Below the barrier in St. Leon Creek the average temperature was 11.0°C, and the maximum temperature attained was 17.8°C. Above the barrier in the Burton-Woden watershed, the mean water temperature was 8.6°C and the below-barrier site averaged 11.4°C over the 150 day measurement period. The maximum temperatures recorded were 12.3°C and 16.3°C in the above- and below-barrier sites, respectively.

Profiles of both the cumulative thermal units (CTU) (Figures 2.3, 2.4) and total accumulated thermal units (ATU) (Figure 2.5) showed differences between the above- and below-barrier sites within watersheds. Water temperatures between above- and below-barrier sites were significantly colder than the downstream water temperatures (Repeated measures ANOVA, ($F=1824.4$, $p<0.001$). However, there were no significant differences between streams (Repeated measures ANOVA, ($F=4.357$, $p=0.548$).

Table 2.4. Summary of mean water temperature at study sites. 23 May – 19 Oct. 1998.

Barrier	Stream	Mean (°C)	Std. Deviation (°C)	N
Above	Burton/Woden	8.65	2.23	150
	St.Leon	7.74	2.53	150
Below	Burton/Woden	11.44	2.63	150
	St.Leon	11.00	3.08	150

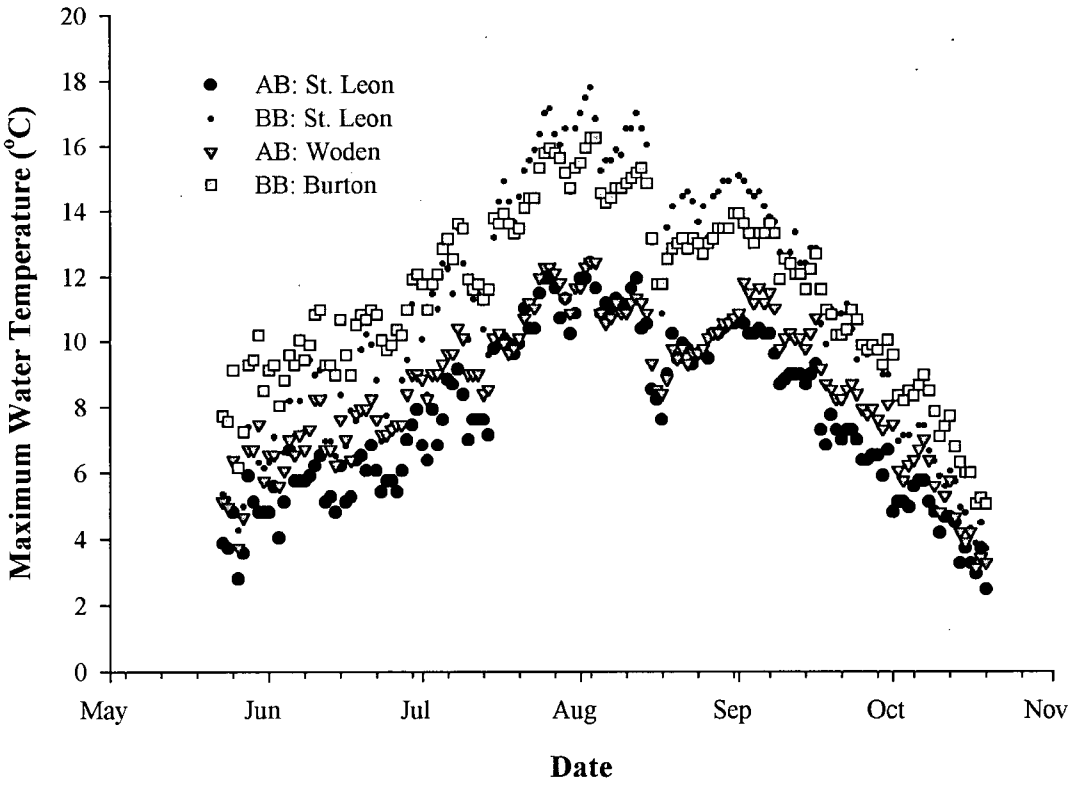

Figure 2.2. Maximum daily water temperature (°C) for 150 period 23 May and ending 19 October. AB= Above-barrier; BB= Below-barrier.

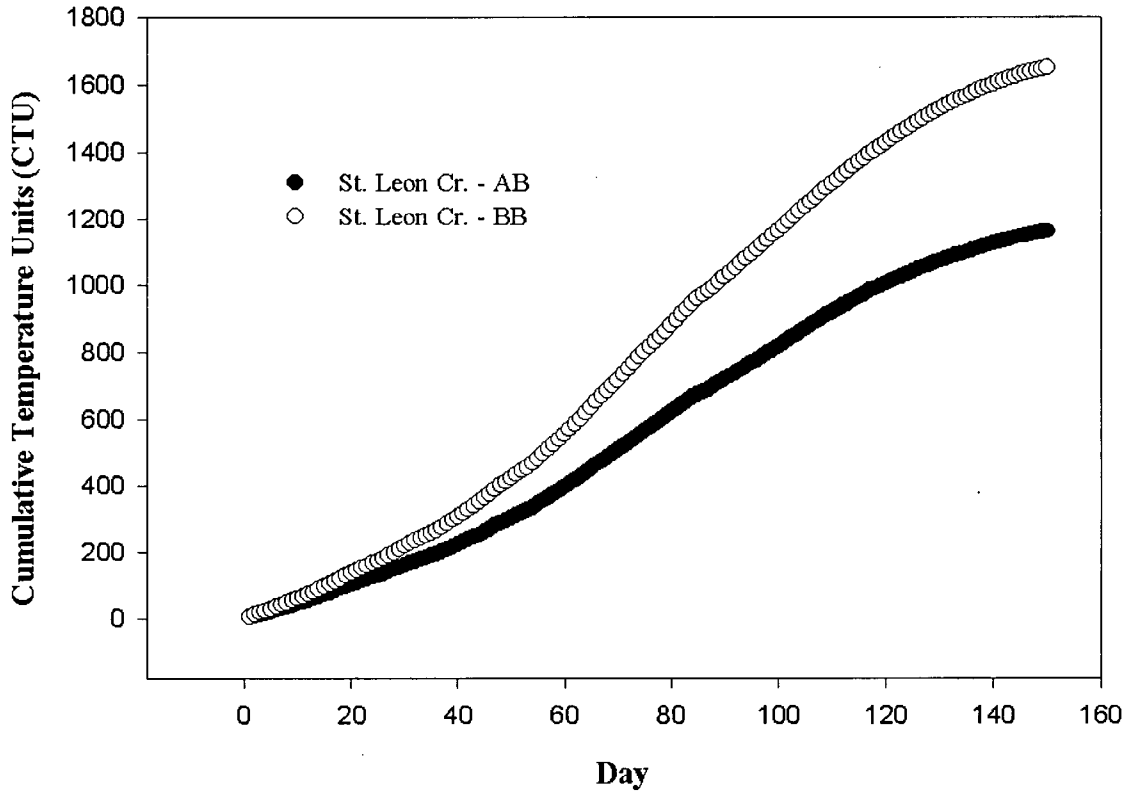

Figure 2.3. Cumulative temperature units (CTU) in St. Leon Creek for 150 day period beginning 23 May 1998 and ending 19 October 1998. AB = Above-barrier; BB = Below-barrier.

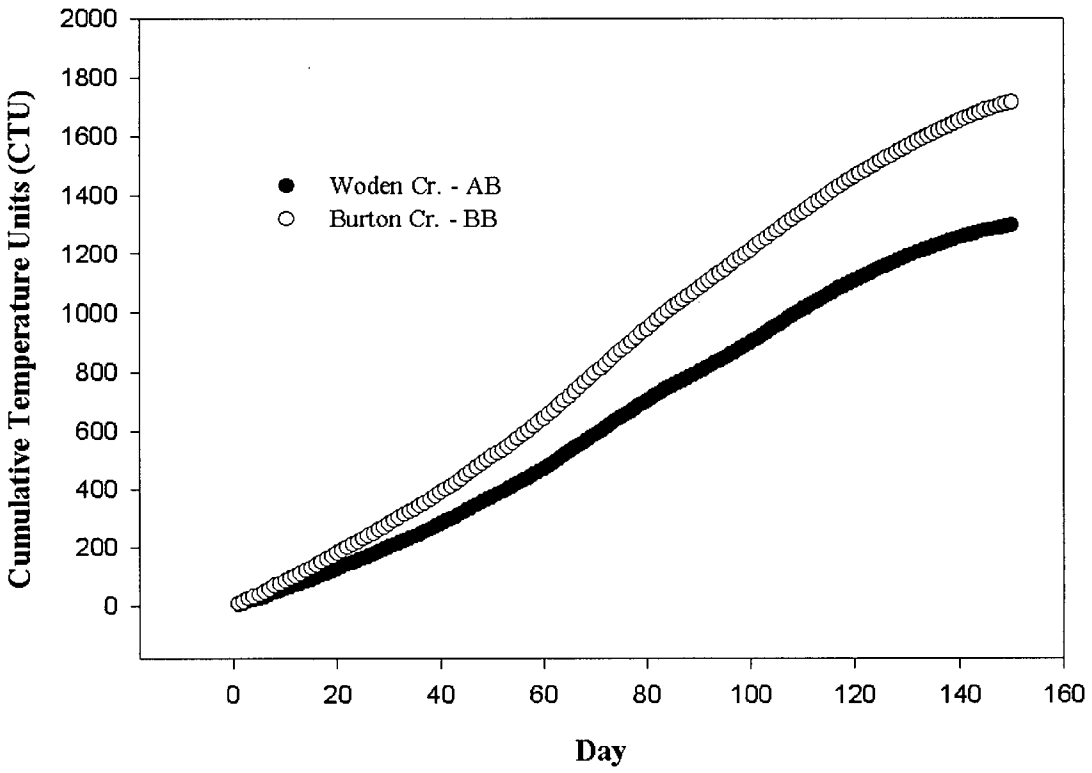

Figure 2.4. Cumulative temperature units (CTU) in Woden Cr. and Burton Cr. for 150 day period beginning 23 May 1998 and ending 19 October 1998. AB = Above-barrier; BB = Below-barrier.

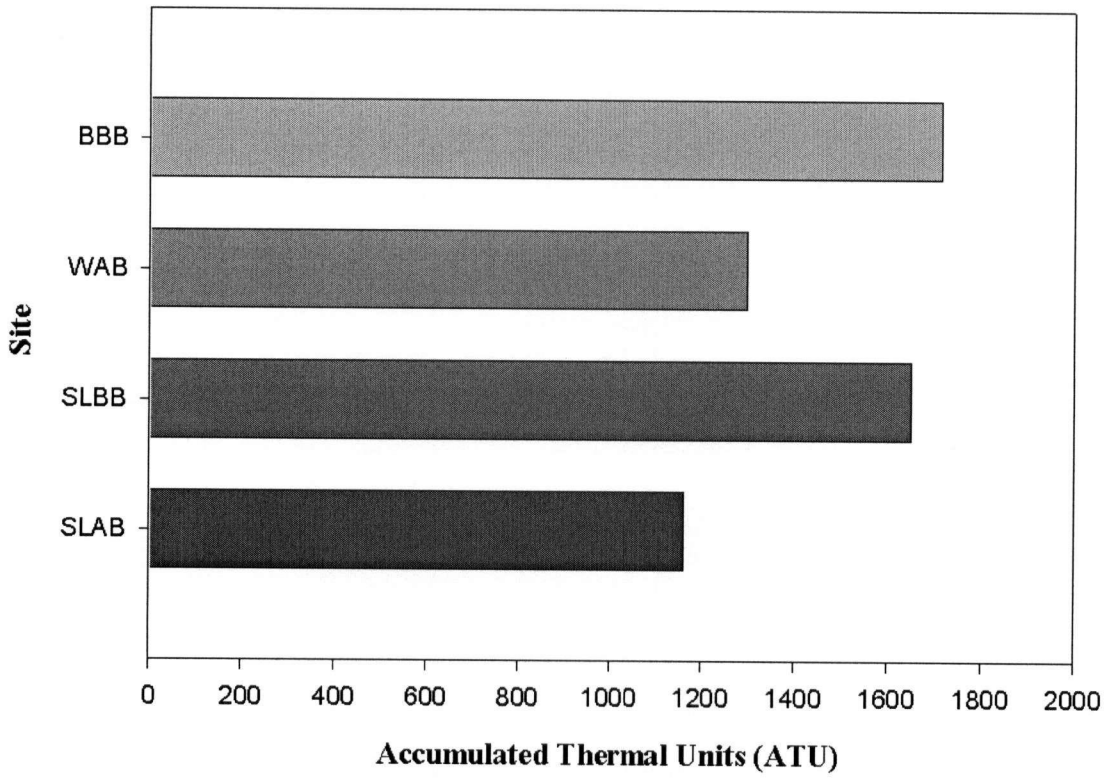

Figure 2.5. Total accumulated thermal units for 150-day period beginning 23 May 1998 and ending 19 October 1998. BBB = Burton Creek, below-barrier; WAB = Woden Creek, above-barrier; SLBB = St. Leon Creek, below-barrier; SLAB = St. Leon Creek, above-barrier.

Habitat variables

Habitat characteristics of the above- and below-barrier streams showed slight differences. The wetted width of the above-barrier sites was significantly narrower (Nested ANOVA, F=18.65, p=0.0497) than the width of the downstream sites (Table 2.5). The average maximum depth of the study sites was lower (F=299.12, p=0.003) for the headwater areas than in the below-barrier sites (Table 2.5, Figure 2.6). Measurements of stream cover as shown by overhanging vegetation were much higher (F=61.02, p=0.016) in the above-barrier sites than in the below-barrier sites (Table 2.5). The amount of undercut bank was higher (Table 2.6) in the above-barrier sites, although not significant (Nested ANOVA, F=18.08, p=0.051). The proportion of stream that constituted pool habitat was not statistically higher (Nested ANOVA, F=9.46, p=0.092), but was numerically larger in the above-barrier sites (Table 2.6).

The absolute numbers of pieces of woody debris in the above-barrier sites of Woden and St. Leon Creeks was 3.3 and 7.3 times higher, respectively (Table 2.7). There was also a significantly higher number of large woody debris within the active stream channel in above- versus below-barrier sites. In St. Leon Creek there were 87 pieces of woody debris along the 100 m transect above-barrier compared to 12 pieces below-barrier (Chi-squared goodness of fit test, χ^2=56.8, p<0.0001). In Woden Creek, there were 61 pieces above-barrier, while below-barrier there were only 18 (Chi-squared goodness of fit test, χ^2=23.4, p<0.0001). Substrate distributions (Table 2.8) were significantly different between above- and below-barrier sites within St.Leon Creek (Mann-Whitney test, U=3425, p<0.0001). Similarly, between the Woden and Burton

Creek sites there was a significantly different substrate distribution in above- versus below-barrier sites (Mann-Whitney test, U=3737.5, p=0.001) (Figure 2.7).

Table 2.5. Nested ANOVA results for continuous habitat variables.

Variable	**Group**	**F**	**p**
Wetted Width	Barrier	18.65	0.0497
	Stream[Barrier]	9.21	0.0003
Maximum Depth	Barrier	299.12	0.003
	Stream[Barrier]	0.13	0.88
Bottom Velocity	Barrier	36.1	0.0266
	Stream[Barrier]	0.1774	0.8378
Pool	Barrier	9.46	0.09
	Stream[Barrier]	8.02	0.0007
Overhanging Vegetation	Barrier	61.02	0.016
	Stream[Barrier]	48.81	<0.0001
Undercut Bank	Barrier	18.08	0.051
	Stream[Barrier]	24.33	<0.0001

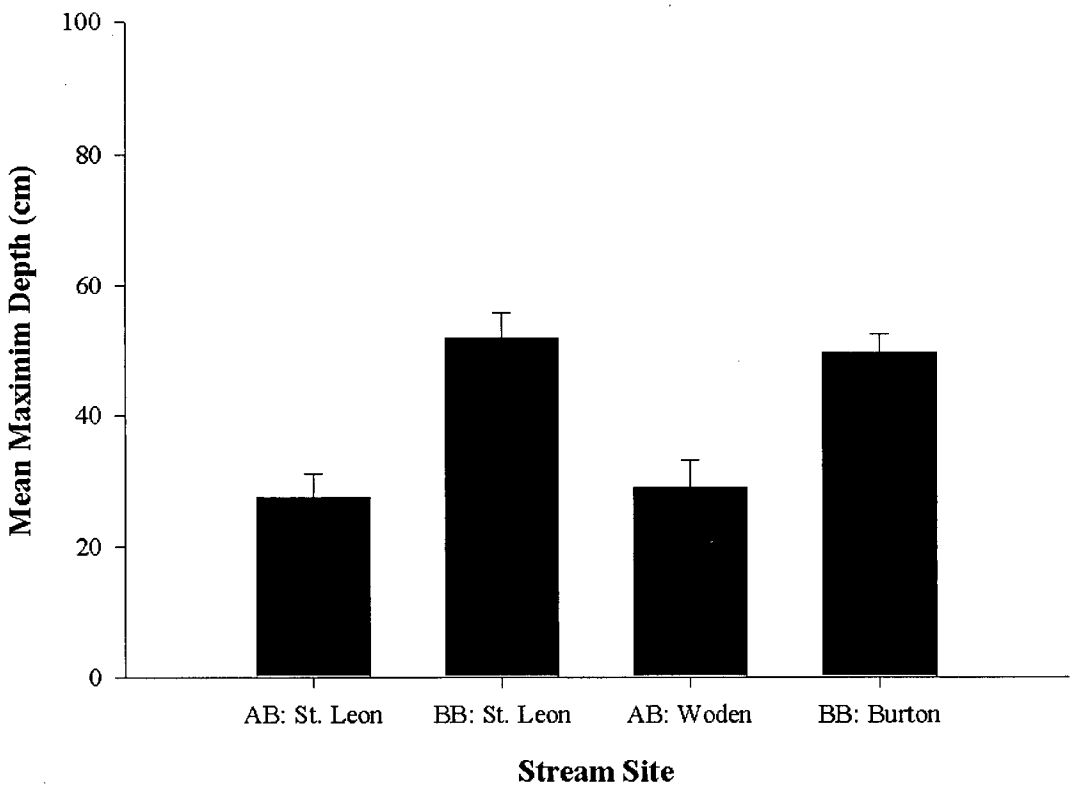

Figure 2.6. Bar chart of mean maximum depth measurements (±SE) in the four stream sites sampled. AB = Above-barrier; BB = Below-barrier.

Table 2.6. Mean values (± SE) for channel dimensions of above- and below-barrier sites in the two study streams.

Stream	Wetted width (m)	Maximum depth (m)	Bottom velocity (m/s)	N
AB: St. Leon Creek	5.4 (0.35)	0.28 (0.037)	0.034 (0.008)	20
BB: St. Leon Creek	8.8 (0.39)	0.52 (0.038)	0.059 (0.012)	20
AB: Woden Creek	4.4 (0.18)	0.29 (0.043)	0.037 (0.008)	20
BB: Burton Creek	9.6 (0.28)	0.50 (0.028)	0.068 (0.015)	20

Table 2.7. Summary of habitat variable measurements. Woody debris represents actual counts of pieces within 100 m study sections. Pool habitat, undercut bank and overhanging vegetation numbers are all mean proportions averaged from 5 m stream sections. (N=20)

Stream	Woody Debris (#/100m)	Pool Habitat (%)	Undercut Bank (%)	Overhang Vegetation (%)
AB: St. Leon Creek	87	29	11	69
BB: St. Leon Creek	12	13	0	5
AB: Woden Creek	61	40	15	83
BB: Burton Creek	18	19	1	15

Table 2.8. Distribution of substrate size classes (see Table 2.1). Values represent percentages of substrate size class within sample site.

Stream	Size Class							
	1	2	3	4	5	6	7	8
AB: St. Leon Creek	0	5	8	13	21	34	19	0
BB: St. Leon Creek	5	2	6	8	11	26	42	0
AB: Woden Creek	4	8	12	6	14	41	15	0
BB: Burton Creek	2	5	5	6	11	35	36	0

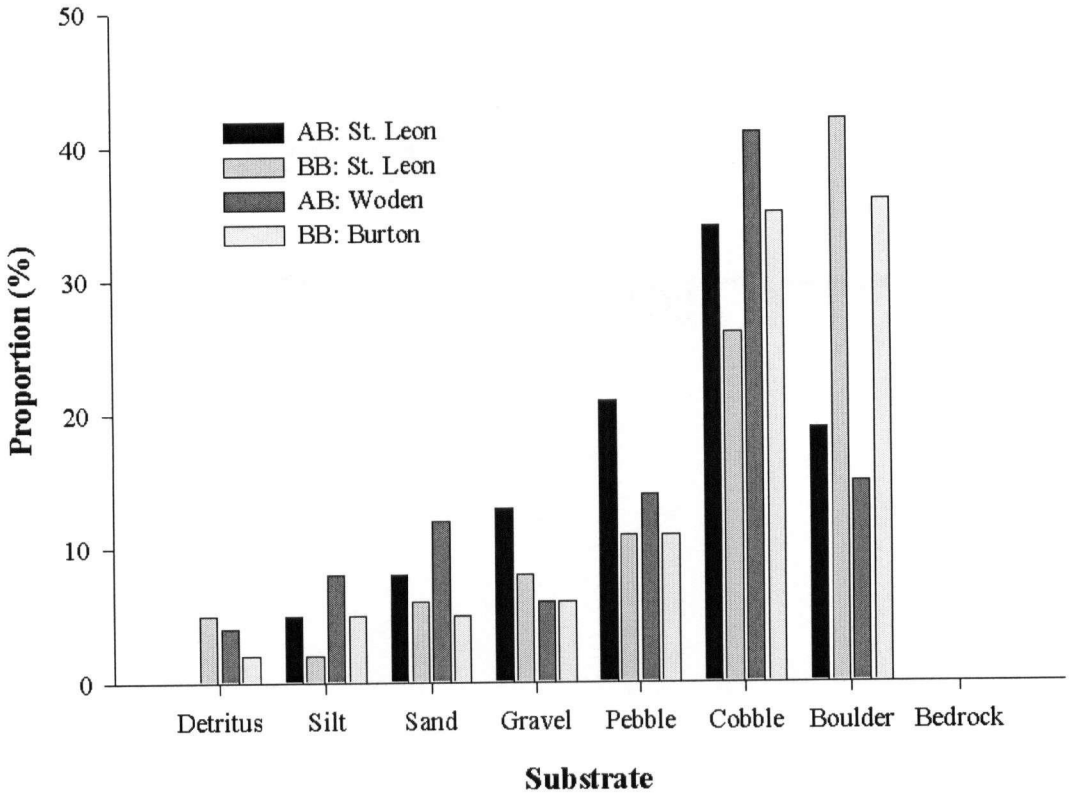

Figure 2.7. Relative proportion of substrate types at each study site.

Habitat use by bull trout

Microhabitat data was collected for a total of 196 juvenile bull trout. Fish were sampled from two above-barrier (St. Leon and Woden Creeks) and two below-barrier (St. Leon and Burton Creeks) sites. All data pertain only to daytime summer microhabitat use. Lengths of bull trout (Figure 2.8) sampled for habitat use analyses did not differ significantly (Nested ANOVA, $F=3.63$, $p=0.197$).

Bull trout habitat use differences between above- and below-barrier populations were not statistically significant after correcting for body size differences. Above-barrier fish were caught in slightly deeper water (Figure 2.9) than below-barrier fish, but this difference was not statistically significant (ANCOVA, $F=0.006$, $p=0.94$). Bull trout from all locations utilized low water velocities (Figure 2.10), but no significant differences between above- and below-barrier sites were found (ANCOVA, $F=0.323$, $p=0.57$). The substrate where bull trout were observed to hold focal points showed similar size class distributions between headwater and downstream sites (Mann-Whitney test, $U=4290$, $p=0.210$). Below the barriers, larger, boulder-cobble substrate was found to be associated with juveniles and in the majority of cases it was the nearest available cover (Figures 2.11, 2.12) The use of cover by bull trout was, however, significantly different (Mann-Whitney test, $U=5718.5$, $p=0.015$) between the above- and below-barrier sites. Bull trout above the barriers tended to be associated with instream woody debris and logjams as cover (Figure 2.12). Juveniles from the adfluvial populations were found primarily along the stream margins. They utilized mainly shallow water (Figure 2.13) that had low bottom velocity.

By contrast, bull trout resident above barriers were caught throughout the stream. They generally held positions in water that was deeper (Figure 2.10) than below barrier fish. Water velocities utilized were low (Table 2.9). The main substrate type was gravel and logjams were the predominant cover used (Figures 2.11, 2.12).

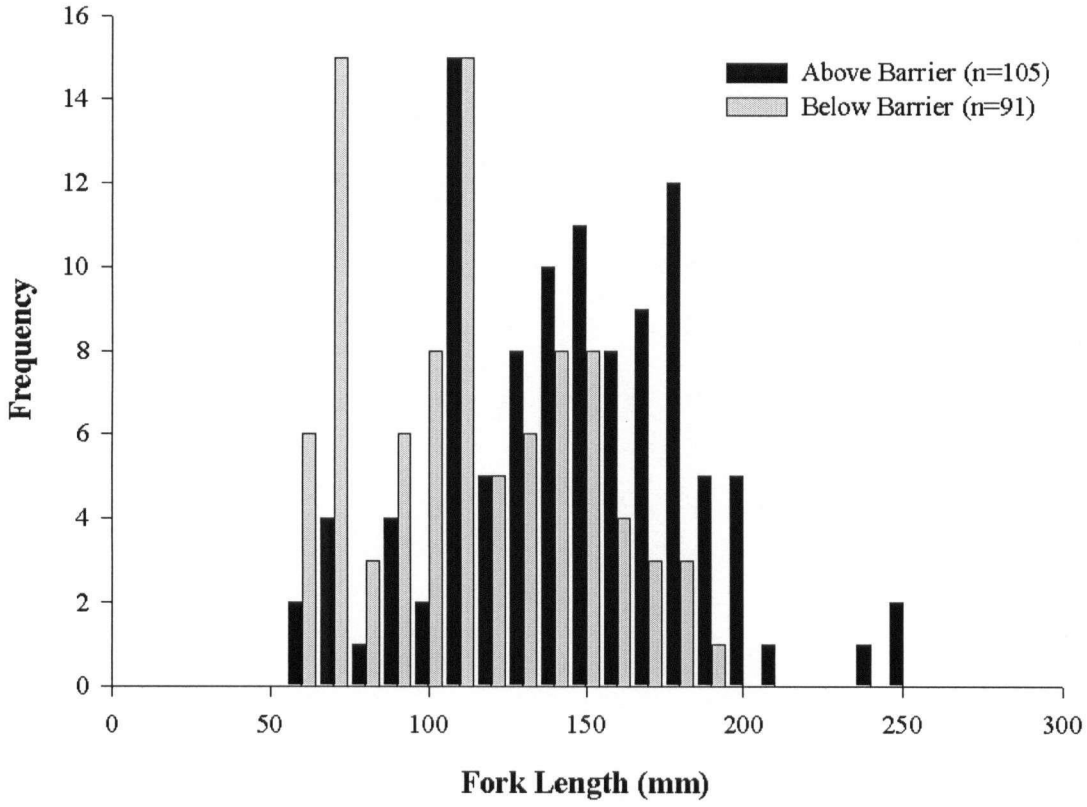

Figure 2.8. Frequency histogram of fork length for bull trout sampled for habitat use analyses from above- and below-barrier sites.

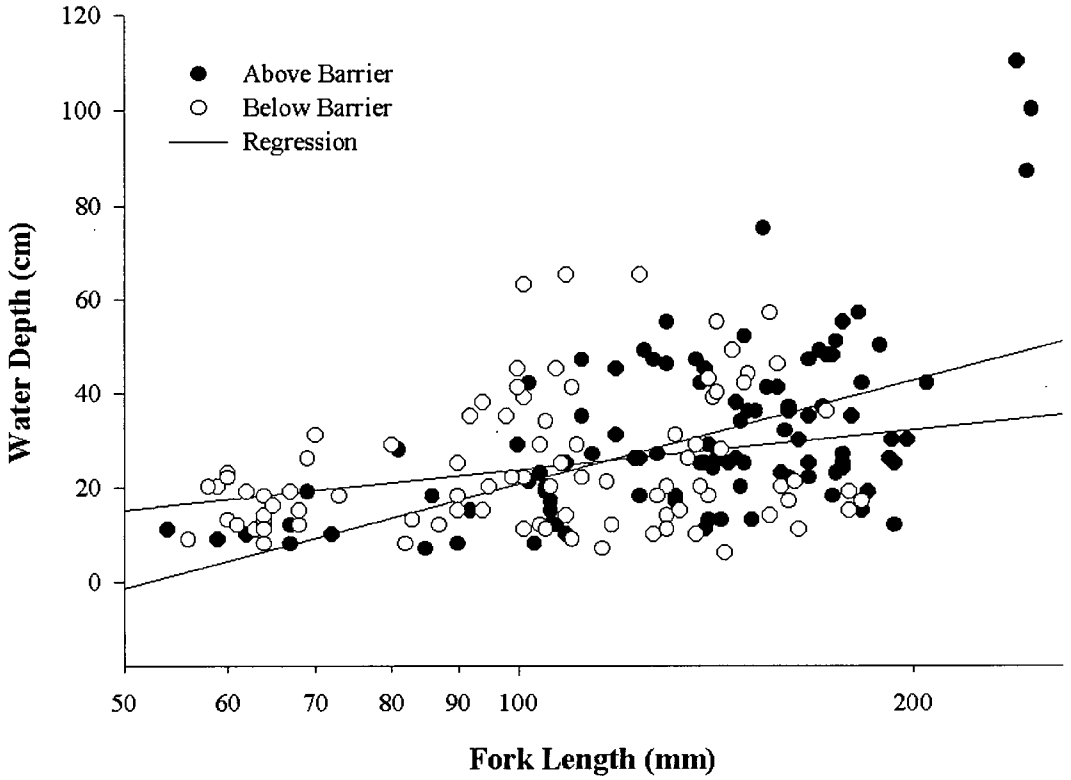

Figure 2.9. Comparison of focal point water depth (cm) and (log) fork length (mm) for bull trout sampled from above- and below-barrier study sites.

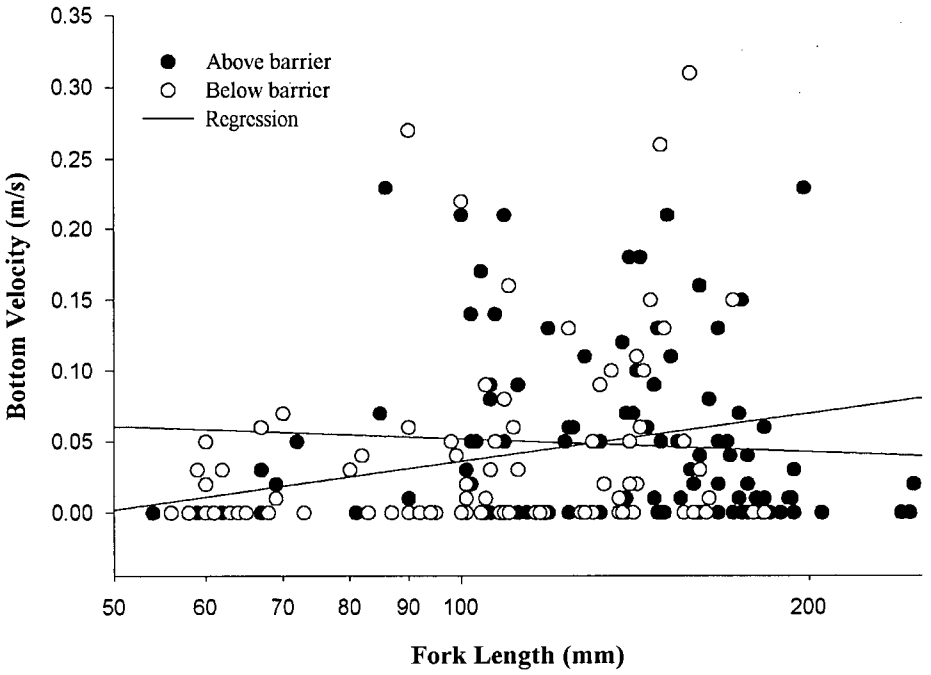

Figure 2.10. Comparison of focal point bottom velocity (m/s) and (log) fork length (mm) for bull trout sampled from above- and below-barrier study sites.

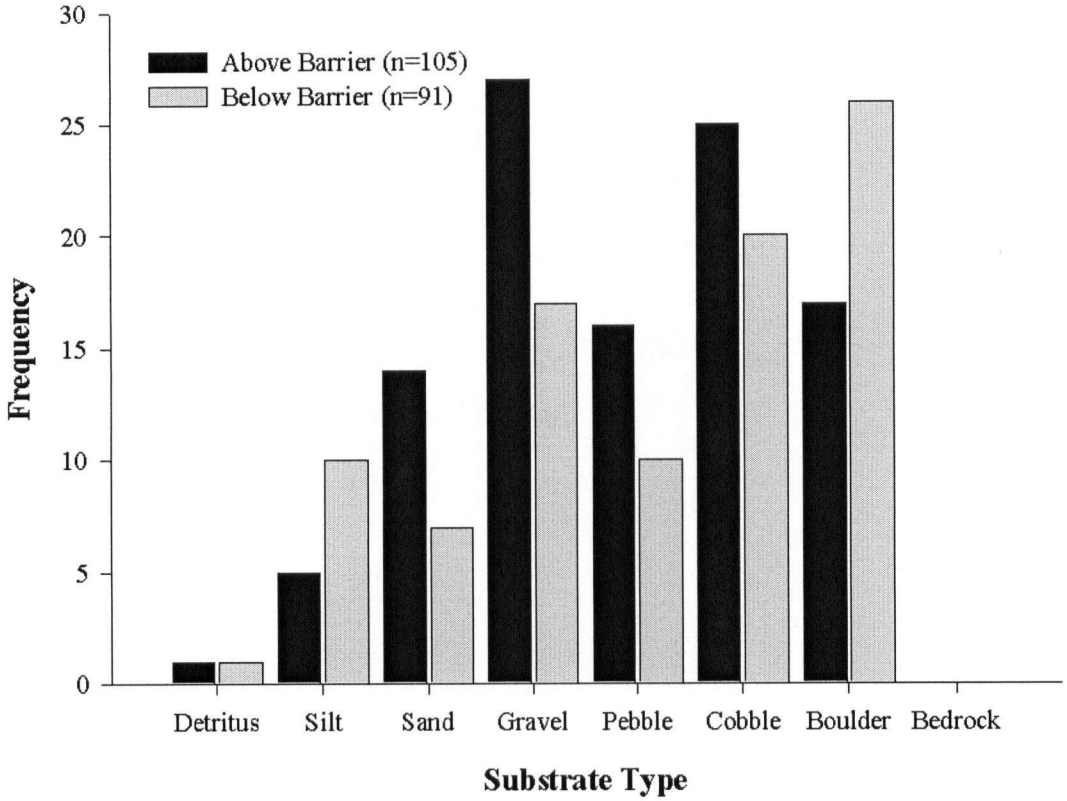

Figure 2.11. Substrate frequency histogram for bull trout (*Salvelinus confluentus*) measured for habitat use in above- and below-barrier sites.

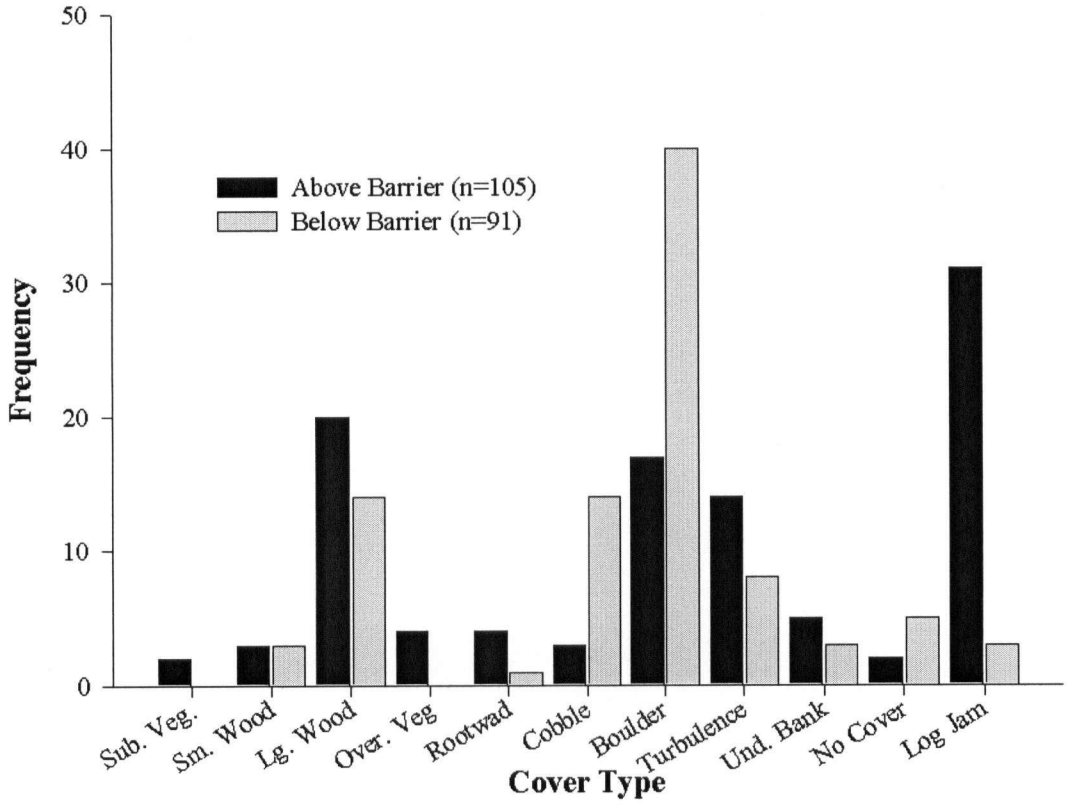

Figure 2.12. Cover frequency histogram for bull trout (*Salvelinus confluentus*) measured for habitat use in above- and below barrier-sites.

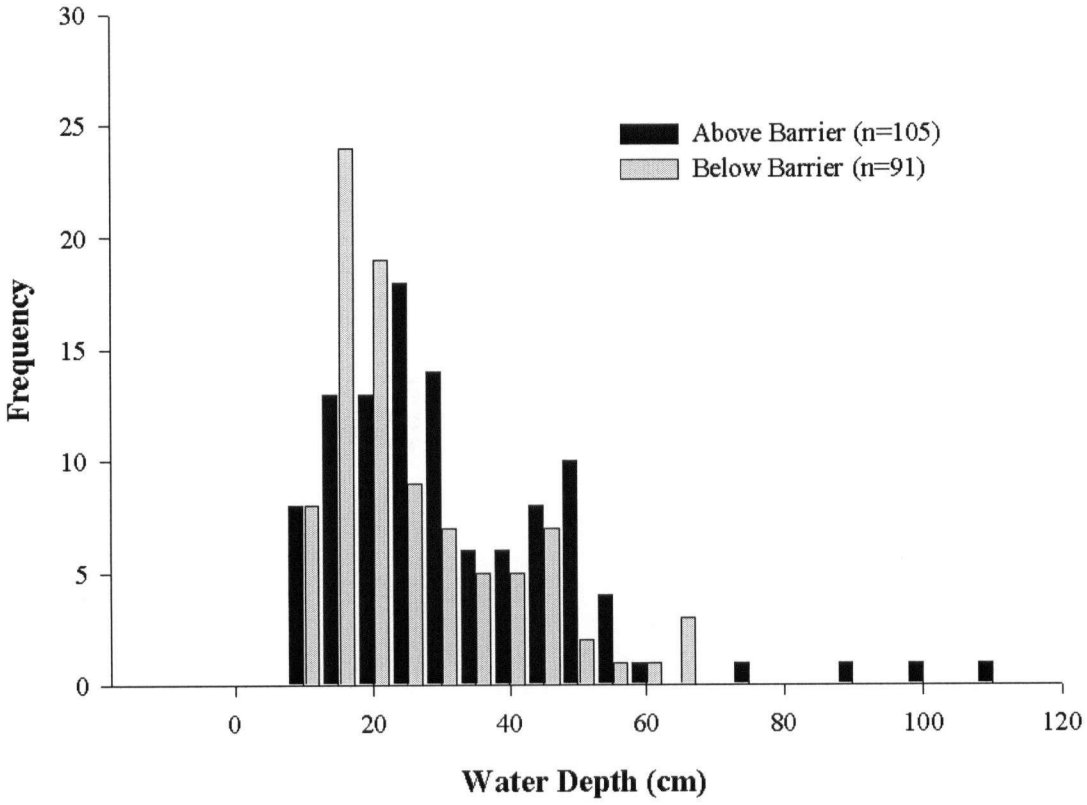

Figure 2.13. Water depth frequency histogram for bull trout (*Salvelinus confluentus*) habitat use measured in above- and below-barrier sites.

Table 2.9. Summary of mean (SE) measurements taken for bull trout microhabitat use in Arrow Lakes study streams during summer 1998. Values for cover and substrate are modes.

Stream	N	Water Depth (cm)	Bottom Velocity (m/s)	Cover	Substrate
AB: St. Leon Creek	56	27.7 (1.73)	0.05 (0.009)	Turbulence	Cobble
BB: St. Leon Creek	45	22.9 (2.14)	0.03 (0.009)	Turbulence	Boulder
AB: Woden Creek	49	33.1 (3.22)	0.04 (0.007)	Log jam	Gravel
BB: Burton Creek	46	25.2 (2.04)	0.04 (0.01)	Turbulence	Gravel

Density

During the summer of 1998, a number of discrete sampling events were performed on each of the four stream sites. Both density and biomass were calculated from results of these events by evaluating the total number and weight of fish captured.

Densities (nested ANOVA, F=7.44, p=0.1107) and biomass (nested ANOVA, F=5.99, p=0.1331) of bull trout from the above-barrier sites were not significantly different from below-barrier sites. Densities (nested ANOVA, F=6.48, p=0.0056) and biomass (nested ANOVA, F=9.59, p=0.0009) of bull trout in both sites of the St. Leon were, however, significantly higher than in Woden and Burton Creeks (Table 2.11, 2.12).

Table 2.10. Summary of mean density (# fish/ha) and mean biomass (kg/ha) of bull trout (*Salvelinus confluentus*) captured June-September, 1998. Number in parentheses represents SE.

Stream	Mean density (#/ha)	Density range (#/ha)	Average Biomass All species (kg/ha)	Average Biomass Bull trout (kg/ha)	Average proportion bull trout (%)
AB: St. Leon Creek (N=10)	640 (40)	440 - 810	N/A	23.25 (1.56)	100
BB: St. Leon Creek (N=6)	210 (70)	60 - 510	3.93 (1.05)	0.93 (0.23)	26
AB: Woden Creek (N=7)	410 (60)	230 - 610	N/A	11.01(3.64)	100
BB: Burton Creek (N=5)	140 (40)	50 - 260	1.60 (0.35)	0.36 (0.13)	23

Table 2.11. Nested ANOVA results for density and biomass measurements on bull trout sampled from above- and below-barriers in two Arrow Lakes tributaries.

Variable	Group	F	p
Density	Barrier	7.4362	0.1107
	Stream[Barrier]	6.4787	0.0056
Biomass	Barrier	5.9887	0.1331
	Stream[Barrier]	9.5937	0.0009

Movement

Bull trout in the above-barrier populations appear to have a highly restricted movement pattern (Figure 2.14). In St. Leon Creek a total of 101 out of 280 (36.1 %) fish captured over the entire period had been previously marked. The recapture percentage in Woden Creek was 12.4 % (20/161).

Recaptures in the below-barrier sections of the study streams were lower than those in the comparable above-barrier sites (Figure 2.15). In St. Leon Creek, out of a total of 104 bull trout encountered, only 7 (6.7 %) had been marked in previous sampling events. The other site in Burton Creek had 4 out of 75 (5.3 %) that were fin clipped. Chi-square goodness of fit analysis showed that at all sites except Woden Creek (χ^2=8.41, p=0.3947) there was significant variation from random movement within study sites.

A total of 24 PIT tags were implanted into bull trout in the above-barrier site on St. Leon Creek in the summer of 1998. Subsequent sampling in the same location over 2 days in August of 1999 yielded 32 bull trout, two of which contained PIT tags from the previous year.

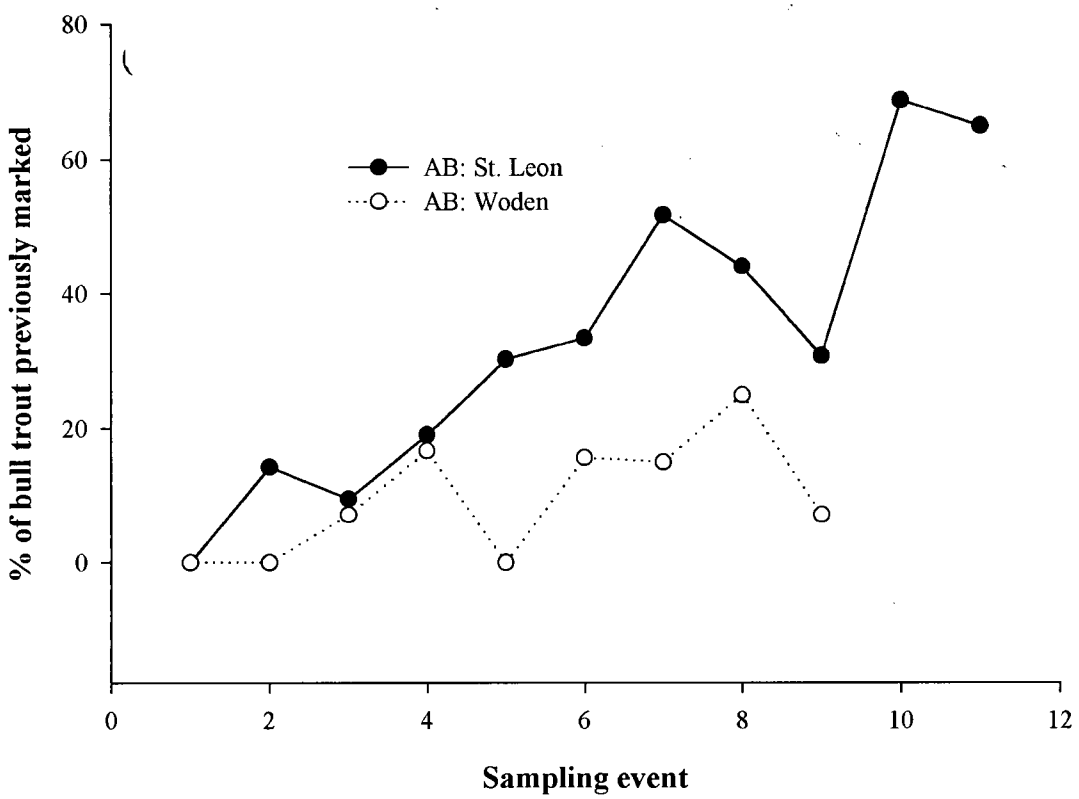

Figure 2.14. Percentage of marked bull trout found during three-pass removal electrofishing in above-barrier sites in St. Leon and Woden Creeks.

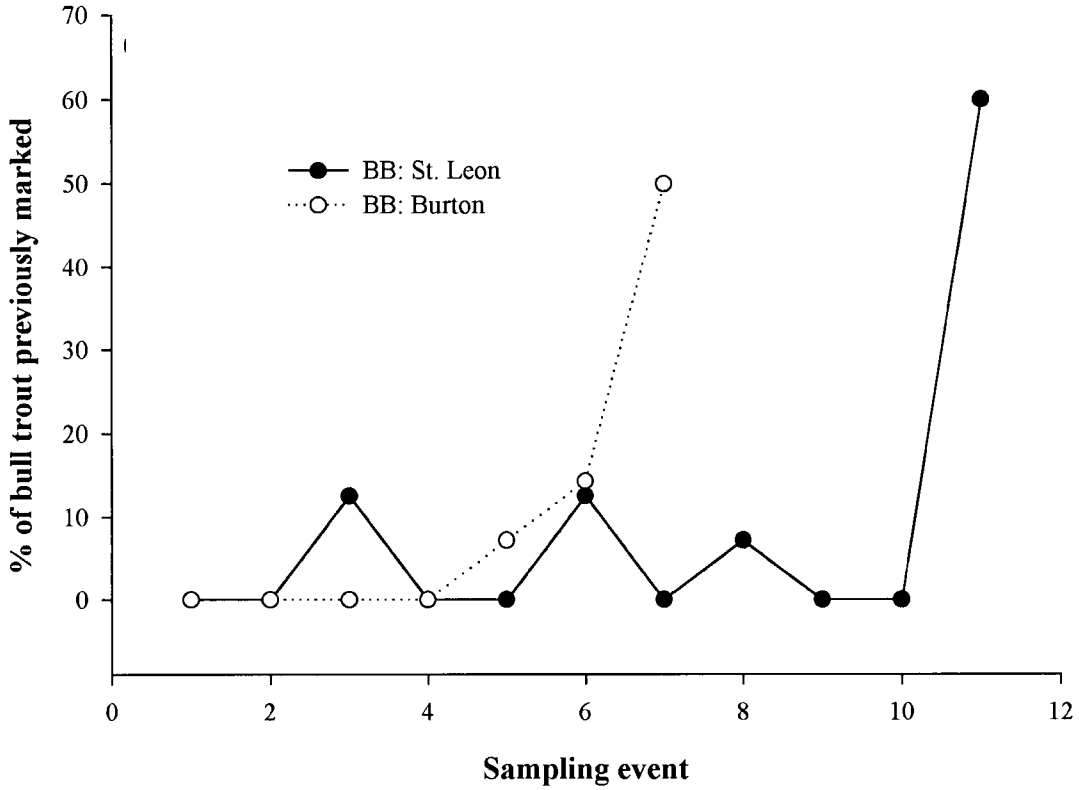

Figure 2.15. Percentage of marked bull trout found during three-pass removal electrofishing in below-barrier sites in St. Leon and Burton Creeks.

Discussion

Ecological consequences of differing stream environments

Results from the present study were consistent with my prediction and with empirical data for other systems in terms of differences along stream lengths and between above- and below-barrier habitats (Northcote 1981;Jonsson 1982;Northcote and Hartman 1988;Kozel and Hubert 1989;Heggenes et al. 1991;Fausch and Northcote 1992;Harvey et al. 1999). The resident population above-barriers and the adfluvial population below the falls were both limited by the area of stream reaches available to them. The migratory populations, however, did not have as stringent a constraint on habitat selection compared to the resident populations, most likely because they eventually migrate to the lake. Clearly, above- and below-barrier habitats presented very different environments for juvenile bull trout.

River systems, from the headwaters to the mouth, show a continuous gradient of physical habitat variables. The continuum of these variables can be seen in width, depth, velocity, flow volume and temperature (Vannote et al. 1980). Habitat variables that are strongly associated with bull trout differed both between above- and below-barrier sites, and among sites within above-and below-barrier areas. The proportion of stream that was pool habitat, the amount of overhead cover and the amount of undercut bank was higher in above-barrier sites compared to below-barrier ones (Table 2.6). Within above-barrier sites, these measures of habitat complexity were higher in Woden Creek than in St. Leon Creek. Similarly, amount of pool habitat, overhanging vegetation and undercut bank

proportions were higher in the Burton Creek below-barrier site than in the St. Leon Creek site above the waterfall. These results indicate that there is a decline in habitat quality as stream size increases for bull trout living within tributaries of the Arrow Lakes.

Another measure of stream habitat complexity is the amount of woody debris located within the stream channel, and other studies have found that bull trout are strongly associated with woody debris, undercut bank and overhanging vegetation (Shepard et al. 1984;Fraley and Shepard 1989;Sexauer 1994;Baxter 1997c). Results from this study indicate that there were three and seven times more debris pieces in the upstream sites of Woden and St. Leon Creeks, respectively. The lack of habitat complexity in the below-barrier sites is illustrated by bull trout from those sites using primarily substrate material (cobble and boulder) as cover (Figure 2.12). Above the barriers, bull trout cover was mainly associated with woody debris and the structure it conferred upon the stream (pool formation) (Figure 2.12), a finding similar to that of Baxter (1995) in the Chowade River. Both of the above-barrier sites in the present study were at least partially located alongside areas of timber harvest, and habitat complexity in streams, whether logged or unlogged, appears to be strongly associated with in-stream woody debris (Fausch and Northcote 1992;Ralph et al. 1994). This helps explain, in part, why bull trout in the present study, occurred in higher densities in the above-barrier sites. The stream channels in the headwater sites were regularly broken up by instream woody debris that created velocity breaks, pools and undercutting that are critical for cover and feeding.

In both study creeks, water was significantly deeper, and stream width was greater below the barrier than above. There were no statistical differences, however, between

water depths where bull trout were found to hold daytime positions(Figure 2.9). Below the barriers, juveniles were found along the margins in water that was shallower (Table 2.10) than the average available depth (Table 2.6). In the below-barrier study sites the majority of the deeper water areas were not in velocity-reduced pool habitat but consisted of fast flowing large riffle areas associated with large boulder substrate. This result was consistent with other studies where bull trout water depth selection was measured; During the day, bull trout preferred to hold positions in shallower, lower velocity areas that are associated with cover (Goetz 1994b;Bonneau et al. 1995;Baxter 1997d;Baxter and McPhail 1997), and generally moved from deeper water positions during the night to shallower water depths during the day (Goetz 1994b;Baxter and McPhail 1997). In the present study, bull trout that occupied the above-barrier sites held in water throughout the entire range of available depths. This lack of preference for any particular depth could be due to the fact that bull trout densities were four to six times higher in the above barrier sites (Table 2.12), and as a consequence they may have used a wider range of available depths than below the barrier. Furthermore, intraspecific competition due to higher densities above the barriers may have caused fish to become more evenly spread throughout the stream.

The average water velocity along the bottom of the stream was significantly slower above the barriers than below, and bull trout from all study sites, regardless of life history type, selected positions in slow velocity microhabitat (Table 2.10). Below the barriers, juveniles preferred the slowest water velocities available. These findings are consistent with those of other studies that found bull trout exhibited distinct preferences for lower velocity areas of the stream, such as backwater pools or side channels (Sexauer

1994;Baxter 1997c;Baxter and McPhail 1997). Additionally, fry tend to be found in extremely shallow areas along the stream margins that have little or no water velocity, while larger juveniles occupy faster pool and run habitat (McPhail and Murray 1979;Pratt 1992).

Bull trout juveniles are benthically oriented and are often found feeding on the stream bottom or resting on or within the substrate (Bonneau and Scarnecchia 1998;Hagen and Taylor 2001). Results from the present study showed that the distribution of substrate size classes in the both the downstream and upstream sites ranged across the entire distribution of size classes. Below the barriers there was a higher proportion of boulder substrate and above the barriers there were more smaller size classes (cobble and smaller). Juveniles below the barrier were associated with all substrate sizes, but were strongly associated with boulders. Fish from above the barrier sites were found above mainly gravel and cobble substrate (Figure 2.11). These findings support those of previous studies (Bonneau and Scarnecchia 1998;Hagen and Taylor 2001), and indicate that substrate is an important physical variable in juvenile bull trout habitat. Larger cobble and boulder substrates provide concealment, velocity breaks and habitat complexity necessary for bull trout foraging and predator evasion during the day. Baxter and McPhail (1997) demonstrated that in an artificial stream channel juvenile bull trout would move into areas where the substrate consisted of smaller silt and gravel during the night. Watson and Hillman (1997) also showed that over a wide geographical range, bull trout occurrence was positively associated with the presence, in part, of large boulder substrate.

Densities and biomass of bull trout above-barriers were higher than below-barriers, although not statistically so. This was likely due to small sample size and high variance in density estimates within each individual site. Bull trout densities below the barriers were similar to those measured by other researchers for adfluvial juveniles (Sexauer 1994). Sexauer (1994) found overall average density to be 0.94 fish/100m^2, a finding similar to those of 2.1 and 1.4 fish/100 m^2 measured in the St. Leon and Burton Creek sites, respectively. Snorkeling surveys done by Fraley and Shepard (1989) estimated that there was an average of 1.5 juveniles/100 m^2 in the Flathead River (Montana) system, however, other authors have encountered much higher densities of bull trout. For example, one study in north central British Columbia found bull trout density as high as 12.12 fish/100 m^2 (Hagen and Taylor 2001). Above the barriers, higher densities of bull trout were likely due to fish from all stages of maturity occupying the stream.

Water temperatures in streams are controlled by a variety of natural factors that can be split into both climatic (air temperature, precipitation) and geographic (topography, groundwater discharge, lithology, riparian vegetation) factors (Poole and Berman 2001). The overall pattern seen in longitudinal stream temperature is one where there is a downstream warming trend as the groundwater influenced headwaters equilbrate with atmospheric temperature (Lowe and Hauer 1999;Torgersen et al. 1999;Poole and Berman 2001).

Headwaters are often more strongly influenced by riparian vegetation than are the larger downstream areas of rivers. Downstream reaches tend to be less shaded than headwaters, and consequently have higher autotrophic production and lower amounts of

allochthonous detritus entering the stream. Several factors should combine to make headwater reaches a more stable environment than those found toward the stream mouth. The stronger terrestrial-aquatic interface in the smaller stream reaches tends to put greater amounts of woody debris into the stream. Once these elements become stable in the stream channel, they result in localized scouring and pool formation (Beschta and Platts 1986).

Water temperature can serve to limit a species' distribution within a particular aquatic environment at both geographic (Fausch et al. 1994) and regional (Bonneau and Scarnecchia 1996) scales. High water temperatures can have deleterious physiological effects on fish, including stress and decreased oxygen availability, which can be limiting or lethal. For most salmonids, there appears to be distinct thermal maxima, beyond which growth and survival decrease (McCullough 1999). In the case of char, prolonged periods of such exposure also have detrimental effects (Takami et al. 1997), with feeding and growth declining as temperature increases beyond a critical point. Over an extended period of time, bull trout exposed to temperatures above 20.9°C will ultimately die (Selong et al. 2001).

Bull trout tend to be coldwater specialists in the southern portion of their range. While temperature may not be the sole abiotic character defining the distribution of bull trout, it undoubtedly plays a critical role. Other studies have examined water temperature effects on juvenile bull trout (ages 0+ to 3+ years), with the majority of research conducted on adfluvial bull trout in the northern United States (Shepard et al. 1984;Nakano et al. 1992;Ziller 1992;Saffel and Scarnecchia 1995). Saffel and Scarnecchia (1995) found that in tributary streams of Lake Pend Oreille in Idaho, there

were definitive declines in abundance where maximum summer water temperatures exceeded 13.9°C; No bull trout found at sites where the summer water temperatures were over 20°C. In the Flathead system of Montana, Fraley and Shepard (1989) found that juvenile bull trout were uncommon in waters where highest summer temperatures exceeded 15°C. In southeast British Columbia, Haas (2001) was unable to find bull trout in sites above 16°C, and showed that the highest densities of fish occured in water temperatures less than 13.9°C. Results from my study were consistent with these findings, with adfluvial bull trout fry and juveniles present where the maximum summer water temperature did not exceed 18°C. In both above-barrier study sites, the maximum summer temperature never exceeded 12.5°C, and the two study sites located in headwater areas had significantly lower mean temperatures than their respective below barrier populations over the summer. Throughout this study, I also obtained water temperatures from small back channels and marginal pools opportunistically. The below-barrier temperatures in these microhabitats were often much higher than 20°C throughout the latter portion of the summer. Such temperatures may further limit the amount of habitat that is available to bull trout in the below barrier reaches of the streams. Similarly, Northcote and Hartman (1988) showed that cutthroat trout populations in the West Kootenays lived in comparable habitat conditions to those found in this study. Waterfall barriers were located in the downstream reaches of their study streams, and water temperatures were consistently lower in the above-barrier sections of the stream, with summer maxima occurring in mid-August

The clear relationship between bull trout distribution and water temperature suggests that any increases in temperature could have an influence on the availability of

habitat for bull trout (Nakano et al. 1996;Rahel et al. 1996). It is certainly possible that the phenomenon of global warming is increasing the overall temperature in the Northern Hemisphere. Furthermore, the more localized effects of clearcut logging can increase instream water temperatures by several degrees through the loss of riparian cover (Johnson and Jones 2000). In many of the watersheds of the Arrow Lakes there exists a limited amount of stream available to adfluvial bull trout due to the constriction of waterfall barriers and the loss of habitat associated with impoundment. Compounded with the effects of clearcut logging, which occurs in virtually every tributary watershed, and water temperature increases, detrimental effects such as declining availability of suitable cold-water habitat appear inevitable.

Results from this portion of the study show that stream resident populations of bull trout exhibit a more restricted movement pattern than below-barrier populations. Bull trout that are migratory (adfluvial or fluvial) rear in their natal streams for up to three summers. Within the below-barrier sites, bull trout displayed less site fidelity over the summer months than bull trout from above the barrier (Figures 2.14, 2.15). Resident fish must be limited in their directed downstream movements, and many salmonid fish species have some intraspecific variation in juvenile movement patterns within streams. For example, in white spotted char, chinook salmon (*Oncorhynchus tshawytscha*), and Arctic grayling, local adaptations in rheotaxis consistent with life history type have been found (Taylor 1990;Kaya 1991;Morita and Yamamoto 2001). Populations of rainbow trout that occur above and below waterfall barriers in the same stream have also showed divergence in movement patterns (Northcote 1981;Northcote and Kelso 1981), with above-falls fish displaying less downstream movement than below-falls stocks.

The typical paradigm of movement patterns of stream salmonids has been one where resident fish show restricted spatial movement (Gerking 1959). However, some authors (Gowan and Fausch 1996) have argued that many mark-recapture studies are inherently biased towards detecting limited movement and as such, researchers should be wary of previous studies. One recent study (Knouft and Spotila 2002) has attempted to overcome some of these shortcomings by sampling an entire stream with mark-recapture and telemetry. The authors found, however, that resident brown trout (*Salmo trutta*) exhibited highly conservative movement patterns consistent with the restricted movement paradigm.

Similarly, bull trout from the two above-barrier populations in this study showed a pattern of restricted movement. Since each of the sites were resampled over the course of the summer, all unmarked bull trout were given a fin clip to indicate that they had been encountered at least once. In the above barrier sites, the recapture percentages after the first sampling event ranged from 0 – 60 %. In St. Leon Creek, above the barrier, there was an increasing trend of recaptures over time (Figure 2.13). This is consistent with a pattern of limited movement, where in each subsequent sampling event the number of marked fish in the stream increases. This pattern was also evident in Woden Creek, but to a less consistent degree. A likely explanation for this difference is that Woden Creek contained small side channels and inaccessible areas of water that could allow fish lateral routes away from the main sampling site, whereas in St. Leon Creek the entire channel was contained.

Species of fish that are derived from or similar to life history forms that are migratory are subject to 'knife-edge' selection when found upstream of a one-way barrier

(Northcote 1981). Both of the above-barrier sites in this study are located several kilometers upstream of the waterfall barriers. In order for these populations to persist for several thousand years, there has probably been strong selection against the directed downstream migration patterns. Such selection may explain the very restricted movements of above-barrier bull trout that I encountered.

Summary and conclusions

For migratory salmonids, the stream phase of their life cycle may be the limiting factor in the production of adults. For adfluvial bull trout in the Arrow Lakes, the lotic environment supports three critical phases of their life history:1) Adult fish return to the stream to locate and spawn in suitable habitat, 2) fertilized eggs overwinter and develop to hatching and 3) fry and juveniles rear in the stream for up to 3 years.

Habitat requirements for the stream phase of the adfluvial juvenile bull trout have been well studied by many researchers (Baxter and McPhail 1996). Water depth, water velocity, substrate and cover have all been identified as environmental factors that are associated with the early life history of bull trout. These physical variables are strongly associated with each other and also with water temperature (McPhail and Murray 1979;Fraley and Shepard 1989;Nakano et al. 1992;Pratt 1992;Saffel and Scarnecchia 1995;Haas and Parkinson 1997). Water velocity at the bottom of the stream is the most appropriate measure of water velocity for bull trout juveniles. Most studies have found that bull trout juveniles are found in slow moving waters (Pratt 1992;Sexauer 1994;Saffel and Scarnecchia 1995;Watson and Hillman 1997).

My study indicated that bull trout spend the daylight hours in areas with greater cover, and both instream cover characteristics and the extent of overhead cover are associated with juvenile bull trout in streams. Undercut banks and riparian trees and shrubs have been found to occur at sites where bull trout live, although extreme overhead canopy cover may reduce primary productivity enough to reduce fish numbers (Watson and Hillman 1997). Juvenile bull trout studied by Baxter and McPhail (1997) showed a marked diel shift in preference from a strong association with cover (daytime) to areas of no cover (night). Hagen and Taylor (2001) found that bull trout and Dolly Varden juveniles preferred areas of low current velocity near the stream bottom and exhibited little diel variation in habitat use. McPhail and Murray (1979) studied the habitat requirements of bull trout fry (0+) and juveniles (1+ & 2+) in Mackenzie Creek, a tributary of Upper Arrow Lake, and found bull trout fry primarily in shallow, low velocity backwaters and side channels. The majority of juveniles occurred in pool habitats and to a lesser extent in low turbulence runs. Similarly, I found that that smaller young-of-the-year held in shallow water (Figure 2.13). Above the barriers, bull trout were strongly associated with pool habitats created by instream woody debris structure, whereas below the barriers juveniles had little pool habitat available and utilized whatever low velocity areas were available.

In conclusion, physical characteristics of habitats vary both within and among the tributaries leading to the Arrow Lakes. Moreover, two life history forms of bull trout utilize distinct parts of the streams depending on whether they are above or below barriers. Above waterfalls, the streams were much colder, smaller in size and more complex in terms of habitat diversity. Overall, above-barrier sites were shallower in

depth, slower in water velocity, had smaller substrate and a wider range of cover available. Similar relationships (where habitat quality decreases as stream size increases) have been shown for other high altitude lotic environments (Kozel and Hubert 1989), and additional studies found that bull trout juveniles in streams have relatively specific environmental preferences (Swanberg 1991;Saffel and Scarnecchia 1995;Watson and Hillman 1997;Polacek and James 2003). These appear to be shallow, low velocity waters associated with good cover and large substrate.

My study revealed that juvenile bull trout that utilize the below-barrier reaches of the Arrow Lakes tributaries are limited to, at most, three years in the stream. These juveniles occupy relatively limited areas of suitable habitat and coexist with resource competitors while maintaining high growth and survival in order to migrate to the lacustrine environment. Furthermore, this research supported initial hypotheses that populations of resident and migratory bull trout are exposed to differing stream environments. Such variation within a relatively small region of the upper Columbia River system has consequences for bull trout habitat use, density, movements, and possible enhancement programs (discussed above), and these are all important factors driving differential selection. In the next chapter, I thus test for effects of differing above- and below-barrier environments on life history, growth, and morphology of bull trout.

Chapter 3 – Evidence of differentiation in life history and morphology between bull trout living above and below waterfalls.

Introduction

When conspecific populations are successful in new environments there is often adaptive divergence in life history parameters. If gene flow between populations is restricted, then directional selection should promote divergence in those characteristics that impact individual fitness. In this way adaptive divergence can increase the overall level of biodiversity within a species. In several ways, however, isolation may ultimately be detrimental for populations. Vicariant populations are subject to an increased risk of extinction through environmental disturbances. Extreme climactic events, anthropogenic influences or invasive/introduced species may all have disproportionate effects upon marginal populations (Murphy et al. 1986;Leary et al. 1995;Rahel et al. 1996). Furthermore, the ability of small, isolated populations to respond to changes in the environment can be limited by reduced genetic diversity resulting from bottlenecks or few original colonizers (Frankham 1997).

Distributions of Holarctic fish species were heavily influenced during the last period of the Pleistocene glaciations. Native fish species in the northern (British Columbia) portion of the Columbia River drainage recolonized watersheds from ice-free refugia south of the glacial maxima (McPhail and Lindsey 1986), and postglacial recolonization occurred through a complex series of proglacial lakes and drainage connections. Contemporary patterns of differentiation within species are a result of the effects of differentiation within the glacial refuge and/or postglacial differentiation.

Bull trout populations in the northern Columbia River are thus a good example of such life history diversity, as adults can exhibit fluvial, adfluvial, or resident life history patterns whereby they spend their adult lives in large rivers, lakes, or their natal streams, respectively. In tributaries to the Arrow Lakes, impassable waterfall barriers allow both adfluvial and resident forms to utilize the same stream, the result of which is partially isolated populations that inhabit different environments (Chapter 2).

Within a species, local adaptation resulting from natural selection should be able to evolve in geographically neighboring populations. If, in the case of bull trout populations in the Arrow Lakes, partial allopatry is enforced through a one-way barrier, then it is not unreasonable to expect phenotypic differentiation as a result of local adaptation. Several recent studies provide evidence that such microevolution can occur at high rates in natural settings. Guppies (*Poecilia reticulata*) in Trinidad have been studied extensively to determine their responses to changes in mortality schedules (Reznick and Endler 1982), and results indicated that life history traits evolved after only 11 years. In addition, studies by Haugen and Vollestad (2001) showed that populations of European grayling (*Thymallus thymallus*) diverged adaptively in early life history traits after only 13-18 generations. And in two populations of sockeye salmon (*Oncorhynchus nerka*) with a common ancestor living in Lake Washington, partial reproductive isolation evolved in less than 13 generations (Hendry et al. 2000).

An important life history trait that affects an organism's lifetime fitness is its age and size at maturity (Roff 1992;Stearns 1992). What is more, an important tradeoff exists between early or delayed maturation. Whereas the former allows for shortened generation times and decreases the probability of mortality before first reproduction, the latter allows

for improved growth, larger body sizes and corresponding increases in fecundity (Morita and Takashima 1998). Freshwater fish show evidence of adaptive phenotypic plasticity in age at maturity (Stearns 1983a;Hutchings 1996;Morita and Morita 2002), and life history theory predicts that when juvenile growth is high a delay in maturation should be favored to allow for an increase in fecundity (Hutchings 1997). Furthermore, compared to adfluvial fish that have higher lake survival, resident populations are expected to mature earlier as a result of detrimental effects of winter conditions (Power et al. 1993). As a result, I hypothesized that adfluvial bull trout should mature at an older age and larger body size than bull trout populations from above the barriers.

Because the growth of an organism is limited by the amount of obtained energy (Stearns and Koella 1986;Roff 1992;Stearns 1992), local population differences are also the result of differences in growth rates acting directly upon age specific life history parameters. For example, Hutchings (1993) showed that small scale, local variation in brook trout growth rate had predictable effects upon age specific survival and fecundity, with low adult and high juvenile growth rates favoring earlier reproductive ages. This negative association between growth rate and age at maturity appears to be an adaptive response to environmental heterogeneity (Reznick 1990;Hutchings 1993, 1996), and growth rate appears to be positively correlated with temperature and negatively with density (Vollestad et al. 2002). In addition, populations of fish that maintain an exclusively resident life history are much smaller in size as adults than migratory conspecifics (Jonsson and Sandlund 1979;Morita and Takashima 1998), because migration to large rivers and lakes enables adults to exploit a plentiful and varied food base that allows for greater growth and fecundity (Gross 1987;Hagen and Taylor 2001).

Based on this theory, I hypothesized that resident bull trout populations, having low adult growth, as compared to adfluvial fish should show smaller sexually mature body size.

Bull trout growth in the juvenile period is rapid in migratory populations bull trout (reviewed in Goetz 1989;McPhail and Baxter 1996). By the end of their first summer, fry average about 60-70 mm; they are over 100 mm and approach 200 mm by the end of their second and third summers, respectively (McPhail and Murray 1979;Fraley and Shepard 1989;Ziller 1992). Fluvial and adfluvial bull trout will begin to utilize fish as a portion of their diet in the 100 mm to 200 mm size range (Boag 1987). Generally, this is coincident with the emigration of juveniles to their adult habitat (McPhail and Murray 1979;Fraley and Shepard 1989). Additionally, relative to their juvenile life history phase, growth rates are higher if adults are piscivorous, especially in lakes (Fraley and Shepard 1989), and McPhail and Murray (1979) found that adults exhibited an increase in growth rate after emigration to the lake but prior to sexual maturity (5-6 years old). This life history shift by adfluvial bull trout and its associated increase in adult growth rate suggests that adfluvial bull trout should delay maturity relative to above-barrier fish. This supposition, coupled with the expectations of low adult growth rate in above-barrier populations resulting from lower water temperatures (Chapter 2) leads to the current hypothesis that resident populations will be smaller in size over their first summer of growth and ultimately mature at a much reduced body size.

Morphological and meristic features in fish have strong relationships with the environment that they inhabit. In many cases, sympatric populations exhibit trophic polymorphisms (Skulason and Smith 1995) that differ morphologically. These

morphological differences often relate to the capture and handling of prey items. For polymorphic Holarctic freshwater fish, one morph may exploit the benthic environment whereas another will be more planktivorous (Lavin and McPhail 1987;Skulason et al. 1989;Ehlinger 1990). Differences in foraging habitat are thus accompanied by unique morphologies including head size and shape, jaw size, gill raker number and eye diameter (Svedang 1990;Hindar and Jonsson 1993;Adams et al. 1998;Adams and Huntingford 2002). In addition to foraging ecology, head morphology, body shape and fin size reflect adaptations to local environmental conditions such as water flow (Gosline 1971;Swain and Holtby 1989;Claytor and Verspoor 1991;Pakkasmaa and Piironen 2001b).

Swimming performance is also strongly affected by body shape in many species and streamlining increases swimming ability for species that feed in open waters, live in faster-flowing waters, or undergo long distance migrations (Webb 1977;Riddell and Leggett 1981;Taylor and McPhail 1985b). Body shapes that are more robust are better suited for foraging in more structurally complex environments (Taylor and McPhail 1986;Pakkasmaa et al. 1998), and fish that occupy higher velocity environments will often have larger paired fins to assist in maneuverability and holding position at the substrate (Riddell and Leggett 1981;Bisson et al. 1988;Beacham et al. 1989;Pakkasmaa and Piironen 2001b).

Adfluvial bull trout in the study systems of the present study lived in higher gradient habitats (Chapter 2) and migrated to a lake environment. They also made extensive within-lake movements and migrated back upstream to spawn. As a result,I expected that selection for an efficient body shape would be stronger in adfluvial compared to resident, above-barrier populations of fish. Specifically, I expected that

adfluvial bull trout would be more streamlined in shape and have larger paired fins for holding position or resting in currents (Webb 1984).

Laboratory studies of many fish species have shown that fish reared in colder water have higher mean vertebral counts, as well as other meristic features, than those in warmer water (Lindsey et al. 1984). The very different water temperatures in above- and below-barrier environments (Chapter 2), therefore, suggest differentiation between populations in meristic traits. Specifically, I predicted that above barrier bull trout would have consistently higher meristic counts than below barrier char.

Aspects of trophic morphology, such as head size, jaw length, gill raker number, spacing, and length appear to be subject to strong selection depending on the average particle size that is exploited within populations (Skulason et al. 1989;Jonsson and Jonsson 2001). Many species exhibit morphological differences related to trophic feeding habitats, especially between pelagic and littoral forms, and gill raker spacing is typically narrower in populations of fish that exploit open water habitats (Bodaly 1979;Gillespie and Fox 2003). For instance, juvenile rainbow trout from lacustrine environments feeding on small zooplankton typically have smaller and more numerous gill rakers compared to fish feeding on larger sized invertebrates in streams (Behnke 1992), and different forms of Arctic char show distinct segregation in gill raker counts, mouth shape, body size and shape (Skulason et al. 1989;Snorrason et al. 1994;Jonsson and Skulason 2000). Similarly, threespine sticklebacks from coastal lakes have a benthic form (with robust body shape, wide mouth and fewer gill rakers) and a limnetic, open water form (with a narrow mouth and longer, more numerous gill rakers) (Schluter 1993). Because adfluvial bull trout switch to feeding on fish after they emigrate to lake environments, I predicted that above-

and below-barrier bull trout would exhibit differentiation in trophically relevant morphological characters. Specifically, I expected that adfluvial bull trout would generally have larger heads and jaws, with fewer, more widely spaced gill rakers than stream-resident char.

The bull trout populations that exist as residents above waterfalls have likely been selected for traits suited to a non-migratory life history pattern. In the process, above- and below-barrier populations have probably differentiated in traits that are important to persistence in their respective, and divergent, environments. The objective of this portion of my thesis is to test for several critical components of life history and morphological variation for both resident and adfluvial populations. Furthermore, I intend to test predictions of responses to selection since postglacial recolonization by examining differences between these ecotypes in the context of current life history evolution theory.

Materials and Methods

Data Collection

All data were collected from 23 May to 27 September 1998. St. Leon and Burton Creeks were the first and second study systems, respectively, and both above-and below-barrier sampling sites in St. Leon Creek were located on the mainstem. The below-barrier site for the second system was located on a section of the mainstem of Burton Creek, and the above-barrier site was situated in Woden Creek, a tributary to Burton Creek. The locations of these systems are outlined in Chapter 2 of this thesis. All study sites were consistent for each sampling event, and upon completion of sampling an effort was made to return all fish to the same areas from which they were collected.

Size and Growth

Individual bull trout were sampled by electrofishing and minnow trapping. All bull trout captured were measured for fork length (mm) and weight (g), and each captured fish was given a fin clip to identify it as having been captured and released at least once. Adfluvial bull trout young-of-the-year do not generally reach more than 70 mm in length by the end of their first summer (McPhail and Murray 1979;Fraley and Shepard 1989;Ratliff 1992;Ziller 1992). Consequently, I used lengths of bull trout fry over the period from 23 May to 27 September to compare early growth. Histograms comparing length frequencies of bull trout from above-and below-barrier populations were created for each study system.

Size at maturity

Bull trout spawn during a period from early September until late October (McPhail and Baxter 1996). In the Arrow Lakes region, McPhail and Murray (1979) found that bull trout first began spawning in mid-September. As a result, in above-barrier study sites, bull trout were examined for characteristics of maturity at the beginning of September. All bull trout that were captured were surveyed for changes in coloration and kype development, both of which are secondary external characteristics commonly found in maturing bull trout. Furthermore, each adult fish was gently squeezed along the belly to look for gamete extrusion.

In order to examine body size at maturity for adfluvial bull trout, I obtained data on broodstock that was collected for the Hill Creek Hatchery. Bull trout broodstock for hatchery production has been collected since 1992 and data on sex, length and weight were recorded. Broodstock data in this analysis came from a number of known adfluvial populations in both the upper and lower Arrow Lakes. Only data on fish that were successfully spawned and released were included in the analysis.

Morphological and meristic variation

Bull trout were collected from two above-barrier sites (St. Leon Creek and Woden Creek) and two below-barrier sites (St. Leon Creek and Burton Creek) during the summer of 1998. Minimums of 30 fish were collected from each site, and fish were initially preserved in formalin and then transferred to isopropyl alcohol after fixation.

Morphometric measurements (Table 3.1) consisted of 26 body measurements taken to the nearest 0.01 mm with Mitutoyo CD-8 digital calipers. Body measurements expected to relate to hydrodynamics and swimming performance followed methods outlined in Hubbs and Legler (1958) and Haas and McPhail (1991). All measurements taken were linear and from the left side of the body (Haas and McPhail 1991). Accuracy was verified by repeating each measurement until the same value was obtained twice.

Table 3.1. Morphological measurements taken for morphometric analysis of bull trout (*Salvelinus confluentus*) from Arrow Lakes tributaries (Hubbs and Lagler 1958;Haas and McPhail 1991).

Body Measurement (mm)	Symbol	Definition
Fork length	FL	Length from tip of snout to fork in caudal fin
Standard length	SL	Length from tip of snout to end of hypural plate
Body depth	BD	Depth of body at dorsal fin insertion
Body Width	BW	Width of body at point BD is measured
Peduncle length	PEDL	Length from end of hypural plate to fork in caudal fin
Peduncle width	PEDW	Least width of caudal peduncle
Pre-dorsal length	PDORL	Length from tip of snout to insertion of dorsal fin
Dorsal fin height	DORH	Distance from origin of dorsal fin to tip of longest ray
Dorsal fin base	DORB	Length of dorsal fin from origin to insertion
Anal fin base	ANAL	Length of anal fin from origin to insertion
Body-caudal length	BCFL	Distance from insertion of adipose fin to end of hypural plate
Pectoral fin base	PEC	Length of pectoral fin from origin to insertion
Pelvic fin base	PEL	Length of pelvic fin from origin to insertion
Gape width	GAPE	Greatest transverse distance across opening of mouth
Snout length	SNLEN	Length from tip of snout to anterior edge of eye orbit
Upper jaw length	UJLEN	Distance from tip of snout to posterior point of maxillary
Head length	HEAD	Distance from snout tip to posterior edge of operculum
Preopercle length	POPLEN	Distance from posterior margin of eye orbit to posterior edge of preoperculum
Opercle length	OPLEN	Distance from posterior edge of preopercle to posterior edge of operculum
Orbit length	ORBIT	Greatest distance between the orbital rims
Eye diameter	EYE	Greatest distance across the cornea
Snout width	SNWID	Distance between inside edges of nostrils
Head width	HWID	Greatest distance across opercles
Head depth	HDEP	Depth of the head at posterior edge of operculum
Postorbital head length	POHL	Distance from posterior margin of eye orbit to posterior edge of operculum
Interorbital width	IORW	Distance between inside edges of orbits

Eight meristic traits (Table 3.2) were measured from a total of 71 above-and 63 below-barrier bull trout. The above-barrier sample consisted of 39 and 32 fish from Woden Creek and St. Leon Creek, respectively. Below-barrier samples consisted of 32 and 31 fish from Burton Creek and St. Leon Creek, respectively. All fin ray counts were made on the left side of the specimen under a binocular dissecting microscope. Fins were pulled open to an expanded position and all branched and unbranched rays were counted. Branchiostegal ray and mandibular pore counts are combined numbers from the left and right sides of the fish. Gill raker counts are of the first arch from the left side of the specimen and include all rudimentary rakers.

Table 3.2. Meristic measurements taken for analysis of bull trout from Arrow Lakes tributaries.

Body Count	**Symbol**
Dorsal fin rays	DFR
Anal fin rays	AFR
Caudal fin rays	CFR
Pectoral fin rays	PECFR
Pelvic fin rays	PELFR
Branchiostegal rays	BRAN
Mandibular pores	MANPOR
Gillrakers	GILLRK

Data Analysis

Size and growth

Bull trout fry (<70 mm) fork lengths were plotted by day (beginning 23 May 1998) and ANCOVA was used to determine if there were differences in the slopes (growth rates).

Size at maturity

Mature bull trout were only encountered in the above barrier sections of this study. Males and females were tested for difference in average size using the two sample *t* test. Data pertaining to sexually mature adfluvial bull trout was obtained from the Hill Creek Hatchery. Fork lengths and sex of bull trout broodstock that were collected between 1991 and 1998 were used to test for differences between life history types and sexes using the two-sample *t* test.

Morphological and meristic variation

Principal components analysis is a multivariate data analysis technique that is used for large data sets. This method of analysis allows for the transformation of large multivariate data sets into a set of uncorrelated variables. The new sets of variables created by PCA are termed eigenvectors and are defined by the dimensions of the data

set. By examining a two dimensional view of eigenvectors, a representation of the data containing the maximum amount of variation from the multivariate data set can be observed along each axis. Each component of the orthogonal matrix has a specific contribution from each variable of the data set, and these contributions, or eigenvalues, are expressed as loading values that indicate the significance of each variable on an eigenvector (Jolliffe 1986).

Principal components analysis on the morphometric data was conducted on the correlation matrix. The reasons for the use of this matrix, as opposed to the covariance matrix, were twofold. First, the correlation matrix standardizes all the variances within the data set and reduces the influence of variables with large variance on the PCA (Jolliffe 1986;Somers 1986). The second reason for the use of the correlation matrix was that although body measurements were standardized to a common body size, the PCA is more efficient in separating size and shape in the resulting components (Somers 1986).

Obtaining the correct number of components to analyze is often an ad hoc procedure involving several criteria (Jolliffe 1986). Typically, one tries to account for 80-90% of the observed variance by using the graphical Scree test and Kaiser's rule (Jolliffe 1986). The Scree test plots the component number against the eigenvalue and suggests using the number of components up to the point where the plot line breaks its downward slope. Kaiser's rule advocates the dismissal of any eigenvalue less than 1, as it will contain less information than was in the original data set. Principal components were analysed for differences using a nested ANOVA, in which the streams were nested within life history type (resident or migratory).

Fish that were used in the morphometric and meristic analysis differed in size between sites (one-way ANOVA, standard length: $F_{3,130} = 15.44$, $p < 0.0001$) In order to minimize effects of size differences between bull trout used in this study, all morphometric data were converted to a size adjusted structure (Taylor 1986;Steel et al. 1997;Pakkasmaa and Piironen 2001a). Size adjusted measures (e) were calculated using the formula:

$$e = \log_{10}Yi - \beta(\log_{10}Xi - \log_{10}X_{SL})$$

where Yi is the value of the measured trait, β is the allometric coefficient defined by the common within form relationship, Xi is the body length (standard length) of the individual, and X_{SL} is the mean standard length of the sample (Thorpe 1976;Reist 1985, 1996). Final size adjusted values were obtained by taking the antilog of the data obtained from the above formula.

Mean meristic counts were compared between forms (migratory vs. resident) using nested ANOVA with statistical significance set at $\alpha=0.05$. In addition, meristic measurements multivariate PCA was performed on all meristic counts to reduce variation to a set of independent variables. Nested ANOVAs were performed to compare factors (barrier type and stream location) on PCA scores.

Results

Size and growth

ANCOVA on growth rate indicated that below-barrier bull trout grew faster than above-barrier fish over the summer ($F=38.27$, $p<0.001$, Figure 3.1). There was no significant interaction effect between the factor and the independent variable ($F=2.81$, $p=0.095$), and the effect of stream nested within barrier was also not significant ($F=1.81$, $p=0.167$).

Data collected from above-barrier bull trout in this study indicated that these populations attained a larger maximum size in the stream compared to fish captured below barrier. Above-barrier fish ranged in size from 21–246 mm in total fork length, whereas below-barrier fish ranged in size from 25–183 mm (Figures 3.2 and 3.3).

Adults were captured only in the above-barrier sites. Maximum lengths attained by these fish were 236 mm in St. Leon Creek and 246 mm in Woden Creek. The average length of mature fish was 181 ± 2.4 mm (N=51) in St. Leon Creek and 194 ± 5.1 mm (N=26) in Woden Creek (Figure 3.4).

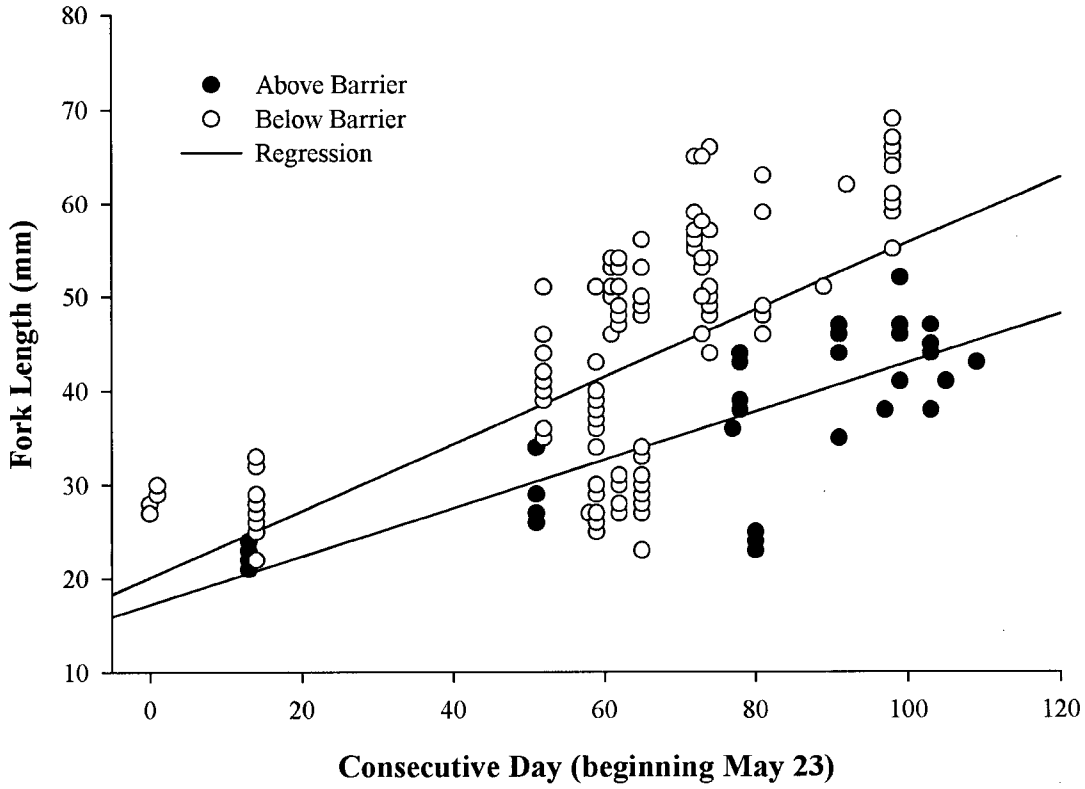

Figure 3.1. Above-and below-barrier comparisons of fork length (mm) plotted against consecutive sampling day.

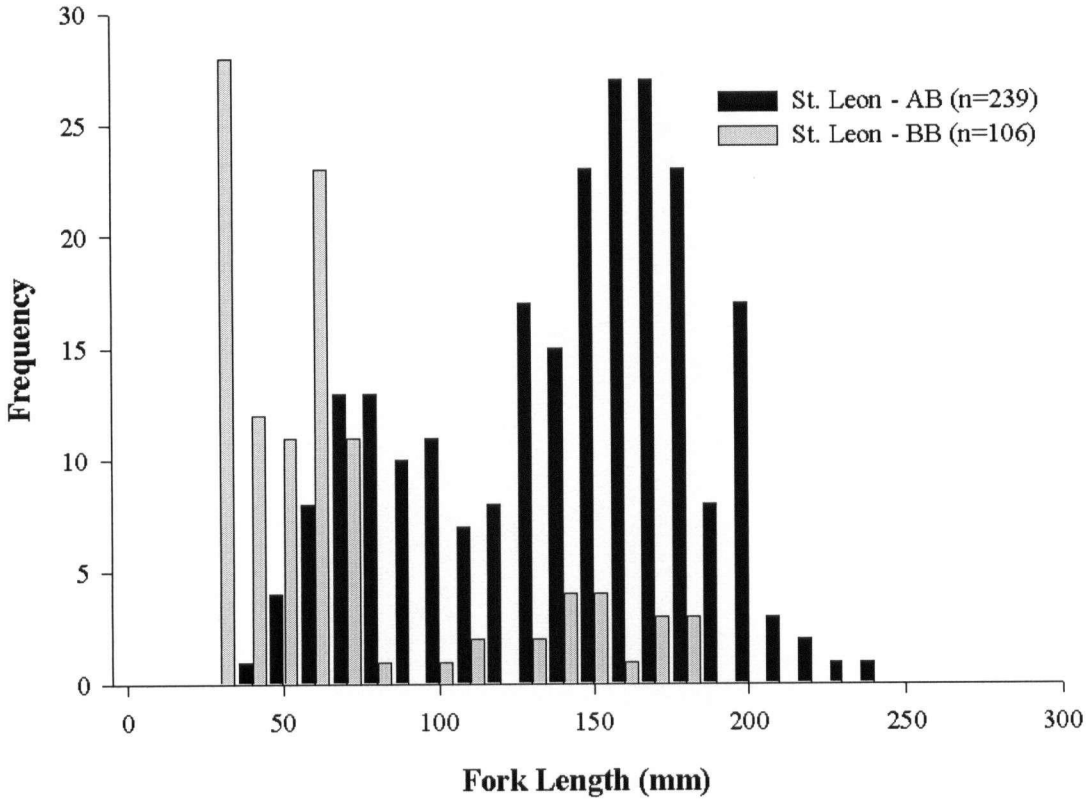

Figure 3.2. Fork length frequency of bull trout (*Salvelinus confluentus*) captured during 1998 in St. Leon Creek.

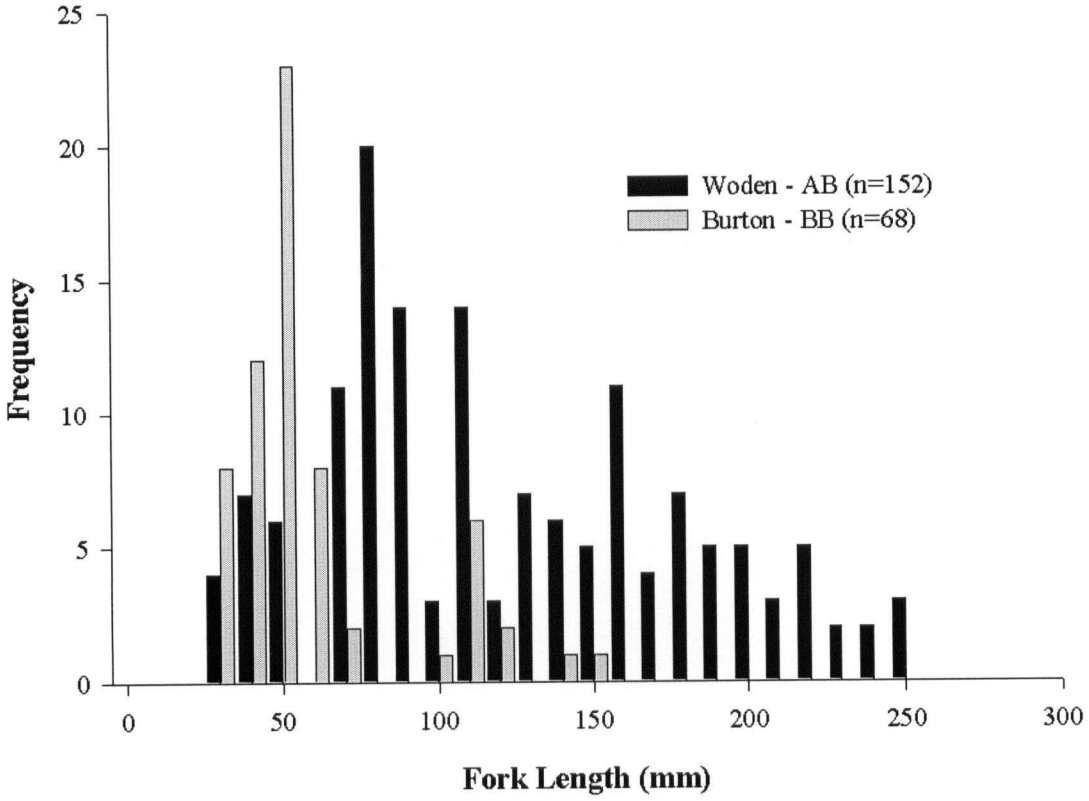

Figure 3.3. Fork length frequency of bull trout (*Salvelinus confluentus*) captured during 1998 in Burton and Woden Creeks.

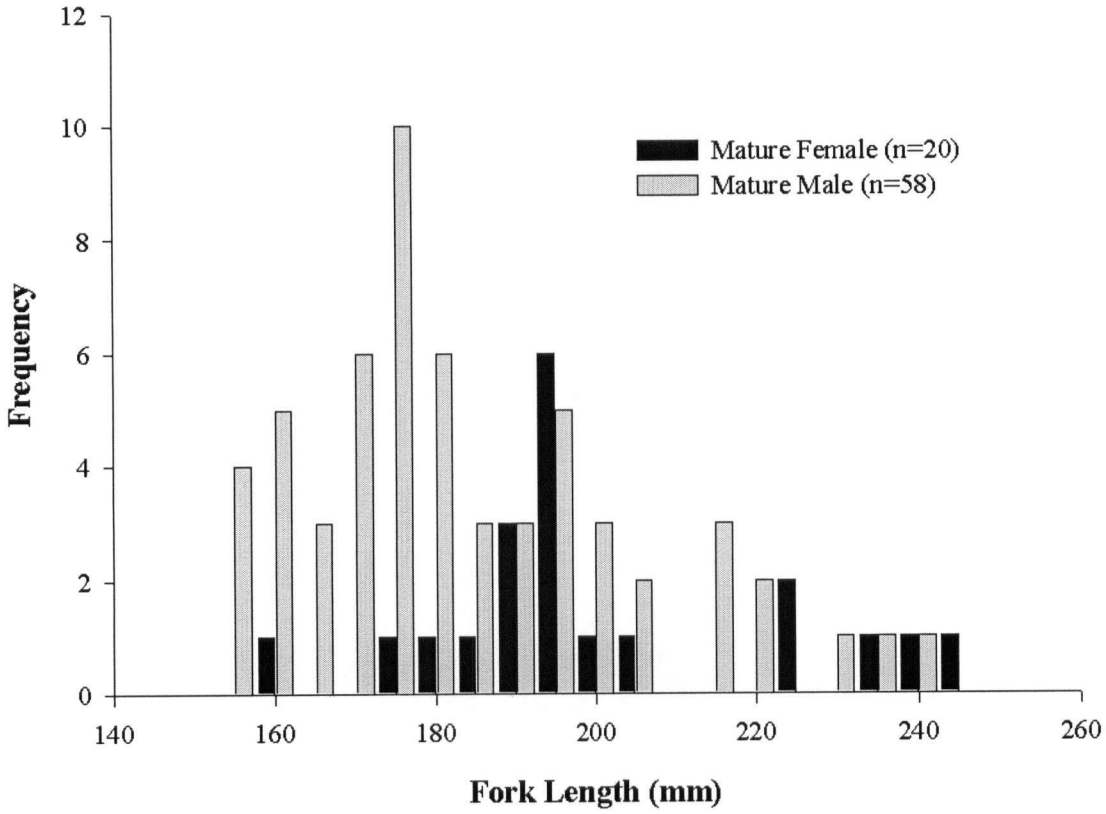

Figure 3.4. Length frequency of sexually mature resident bull trout from above-barrier populations.

Size at maturity

There was a significant difference between the fork lengths of sexually mature bull trout from adfluvial and resident populations (two sample *t* test, t=38.71, p<0.0001).

A total of 78 sexually mature, resident bull trout were measured during the late summer of 1998. Of these, 58 were male and 20 were female, resulting in a 2.9:1 ratio of males to females. The mean size ± standard error for a mature female from the above-barrier sites was 198.4 ± 5.0 mm. Mature resident males were significantly smaller (two sample *t* test, t=2.98, p=0.0039) than females and had a mean fork length of 182.0 ± 2.8 mm (Figure 3.4). The average length of males and females combined was 186.2 ± 9.2 mm.

Fork lengths of a total of 260 mature adfluvial bull trout collected as broodstock for the Hill Creek Hatchery averaged 591.9 ± 5.0 mm for both sexes. Males and females did not significantly differ in length (two sample *t* test, t=1.86, p=0.065). Females averaged 585.2 ± 6.7 mm (n=185) in length while males were 608.4 ± 10.5 mm (n=75).

Morphological and meristic variation

Within streams, most size-adjusted characters were qualitatively larger in above-barrier fish compared to below-barrier fish (Table 3.3). However, univariate nested ANOVAs of size-adjusted characters showed few statistically significant differences between above- and below-barrier populations, with gape width, head width and head depth the only measurements exhibiting significant differences at α=0.05 (Table 3.4).

Principal components analysis (PCA) resulted in the first six components having eigenvalues over 1. The first three components accounted for 53% of the variation and standard criteria for retention of components (Jolliffe 1986) indicated that these contained relevant morphological information. Principal component one (PC1) accounted for 28.5% of the variation in the data set and loaded positively on all characters (Table 3.5). The first principal component loaded most strongly on body depth, body width and measures of head size. The second principal component (PC2) accounted for 15.5% of the variation and had high positive loadings on head and jaw size. Strongly negative loadings for PC2 were seen for body depth and width (Table 3.5). Nested ANOVA on the first three component scores showed no significant difference between above and below barrier measures (Table 3.6). Bivariate plots of PC1, PC2, and the third principal component (PC3) showed considerable overlap among both streams and life history types (Figures 3.5 and 3.6). Above-barrier char, however, tended to score positively along PC2 and negatively along PC3.

Mean meristic counts did not differ significantly between above- and below-barrier populations, and mean anal fin ray and caudal fin ray were higher for above- versus below-barrier populations (Table 3.7). Although these differences were not statistically significant, average fin ray counts for the dorsal, pectoral and pelvic fins were all higher for the resident fish. Both average branchiostegal ray and mandibular pore counts were lower for fish taken from below the barrier than from above. Compared with bull trout from adfluvial populations, above-barrier fish had higher average gill raker number (Table 3.7).

In the multivariate anaysis of the meristic data (Figures 3.7 and 3.8), PC1 accounted for comparatively little of the total variation (19.8%) and loaded positively on all traits except branchiostegal rays and mandibular pores (Table 3.8). PC2 and PC3 accounted for 19.0 and 16.5% of the total variation, respectively. The strongest loadings on PC2 and PC3 were on the dorsal, anal, branchiostegal, pectoral (+) and pelvic (-) rays (Table 3.8). Nested ANOVA showed that none of the first three principal components differed statistically between above- and below-barrier fish (Table 3.9).

Table 3.3. Comparison of mean size adjusted[a] characters (mm) for each study population of bull trout in the Arrow Lakes.

	AB	BB	AB	BB
	Woden (*N*=39)	**Burton (*N*=32)**	**St. Leon (*N*=32)**	**St. Leon (*N*=31)**
Body depth	19.3	18.4	19.0	17.6
Body width	13.7	13.2	13.8	12.1
Peduncle length	16.6	13.2	18.7	16.5
Peduncle width	9.7	7.7	10.9	8.4
Pre-dorsal length	47.7	48.3	48.1	46.7
Dorsal fin base	10.7	10.9	11.6	10.7
Dorsal fin height	16.4	16.7	17.3	16.9
Anal fin base	8.9	8.9	9.5	8.8
Body-caudal length	12.5	12.6	13.0	12.5
Pectoral fin base	4.1	4.1	4.0	3.7
Pelvic fin base	3.4	3.3	3.4	3.1
Gape width	9.3	8.4	9.3	8.4
Snout length	4.3	4.4	4.3	4.6
Upper jaw length	11.6	11.9	12.3	12.1
Head length	25.7	25.8	26.0	26.1
Preopercle length	7.8	8.6	8.4	8.3
Opercle length	7.3	6.8	7.1	7.0
Orbit length	6.9	6.7	7.1	7.1
Eye diameter	5.8	5.7	6.0	6.0
Snout width	4.7	4.7	4.9	4.6
Head width	15.2	14.4	15.4	14.1
Head depth	8.0	7.5	7.8	7.4
Postorbital head length	15.0	15.3	15.4	15.1
Interorbital width	7.3	7.5	7.7	7.3

[a] Adjusted to 100mm standard length

Table 3.4. Nested ANOVA results comparing adjusted morphometric measurements taken from bull trout with the factor stream nested within barrier.

	Barrier		**Stream**	
	F	***p***	***F***	***p***
Body depth	9.06	0.094	5.68	0.004
Body width	4.19	0.177	13.61	<0.001
Peduncle length	2.05	0.288	13.29	<0.001
Peduncle width	10.94	0.081	7.02	0.001
Pre-dorsal length	0.21	0.695	13.42	<0.001
Dorsal fin base	0.58	0.525	20.31	<0.001
Dorsal fin height	0.01	0.939	16.70	<0.001
Anal fin base	1.12	0.401	25.69	<0.001
Body-caudal length	0.68	0.496	2.50	0.086
Pectoral fin base	0.44	0.574	14.23	<0.001
Pelvic fin base	6.56	0.124	4.59	0.012
Gape width	780.54	<0.001	0.08	0.919
Snout length	2.59	0.248	1.87	0.158
Upper jaw length	0.02	0.895	12.23	<0.001
Head length	0.29	0.645	1.57	0.211
Preopercle length	1.59	0.334	10.81	<0.001
Opercle length	7.82	0.107	1.86	0.160
Orbit length	0.07	0.813	10.26	<0.001
Eye diameter	0.005	0.949	10.48	<0.001
Snout width	2.73	0.241	6.66	0.002
Head width	32.03	0.030	1.56	0.214
Head depth	22.58	0.041	0.62	0.538
Postorbital head length	0.14	0.748	4.08	0.019
Interorbital width	0.22	0.686	16.71	<0.001

Table 3.5. Loadings for the first three principal components on adjusted morphological traits. See Table 3.1 for trait definitions.

Trait	PC1 (28.5%)	PC2 (15.5%)	PC3 (9.5%)
BD	0.602	-0.609	-0.105
BW	0.619	-0.576	-0.228
PEDL	0.171	-.0111	0.520
PEDW	0.461	-0.320	0.366
PDORL	0.697	0.007	-0.349
DORB	0.589	0.071	-0.321
DORH	0.525	0.299	-0.204
ANAL	0.503	-0.098	-0.261
BCFL	0.494	0.163	-0.126
PEC	0.468	-0.343	-0.294
PEL	0.503	-0.435	-0.104
GAPE	0.592	-0.449	0.454
SNLEN	0.175	0.525	0.396
UJLEN	0.568	0.570	0.110
HEAD	0.614	0.508	0.211
POPLEN	0.467	0.586	-0.450
OPLEN	0.312	-0.198	0.389
ORBIT	0.454	0.529	0.351
EYE	0.447	0.545	0.348
SNWID	0.660	0.061	0.078
HWID	0.670	-0.527	0.226
HDEP	0.297	-0.210	0.468
POHL	0.640	0.331	-0.226
IORW	0.762	0.051	-0.111

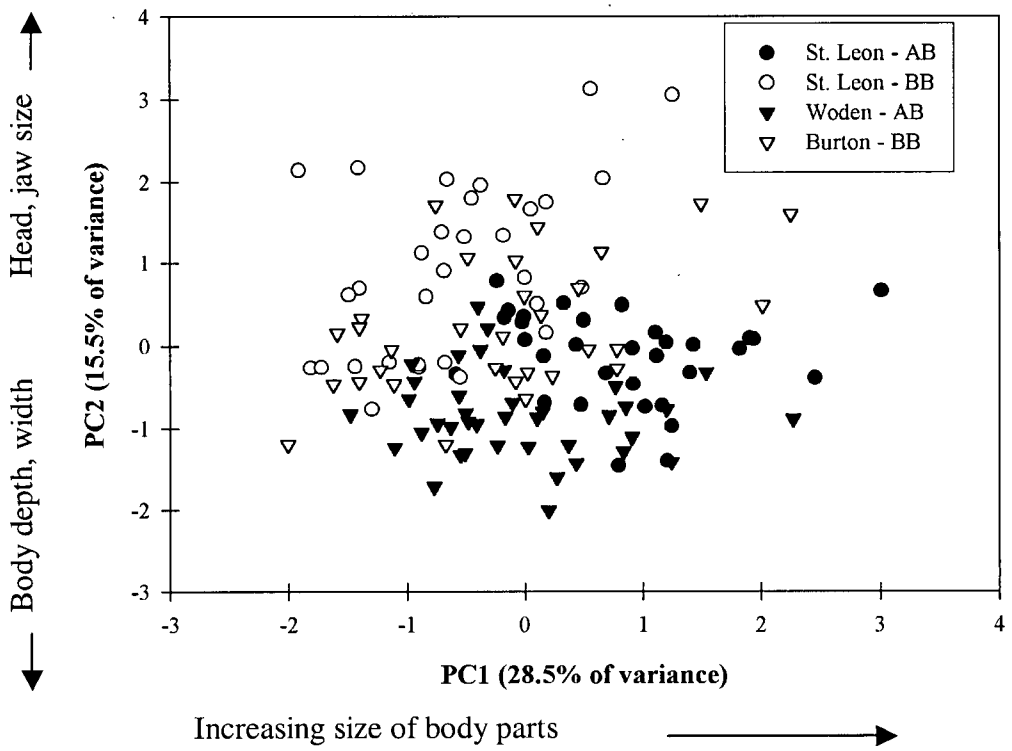

Figure 3.5. Scatter plot of principal components performed on entire morphometric set along PC1 and PC2. Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols are from below-barrier samples

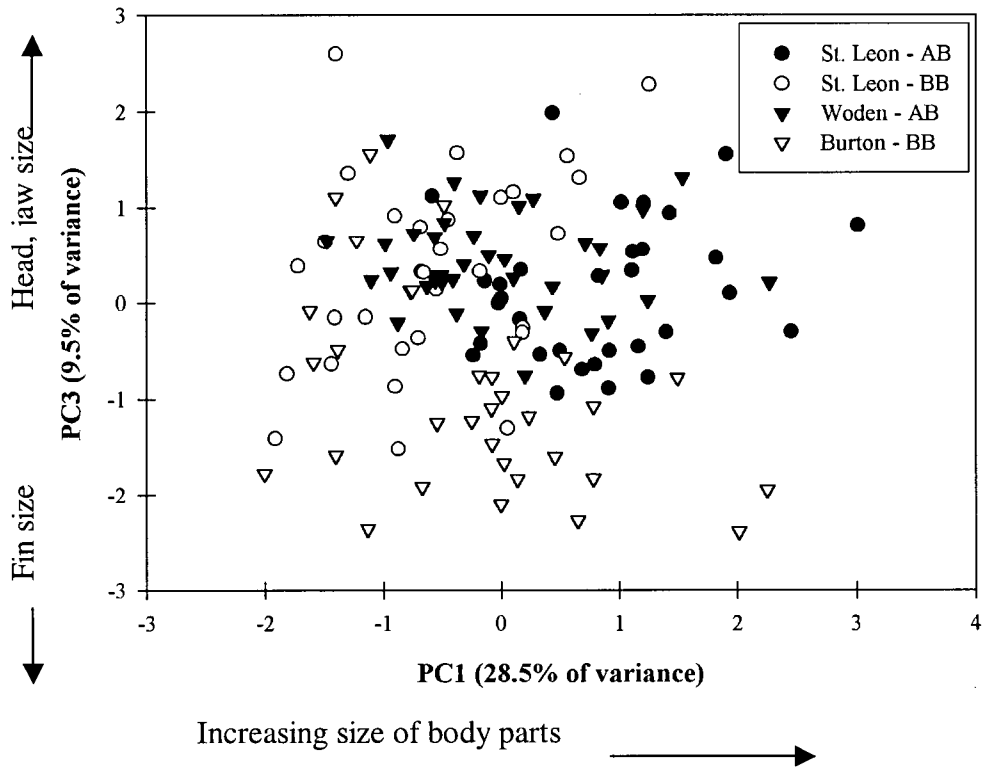

Figure 3.6. Scatter plot of principal components performed on entire morphometric set along PC1 and PC3. Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols are from below-barrier samples.

Table 3.6. Nested ANOVA results comparing above and below barrier morphometric PCA scores for the first three components.

	Barrier		Stream	
Component	**F**	***p***	**F**	***p***
PC 1	2.58	0.250	10.95	<0.001
PC 2	4.79	0.160	14.50	<0.001
PC 3	0.79	0.468	21.11	<0.001

Table 3.7. Mean meristic counts within sites and between life history types. Nested ANOVA results are for above-barrier (AB) versus below-barrier (BB) fish

Trait	AB			BB			P(AB vs BB)
	St.Leon Cr. (N=32)	Woden Cr. (N=39)	Mean	St. Leon Cr. (N=31)	Burton Cr. (N=32)	Mean	
Dorsal fin rays	11.5	10.9	11.2	10.8	10.9	10.9	0.409
Anal fin rays	9.8	9.2	9.5	9.0	8.9	9.0	0.190
Caudal fin rays	22.8	23.4	23.2	23.1	22.8	22.9	0.606
Pectoral fin rays	13.7	13.6	13.6	13.6	13.7	13.7	0.790
Pelvic fin rays	9.7	9.9	9.7	9.6	9.7	9.7	0.917
Branchiostegal rays	25.6	24.8	25.2	25.7	25.6	25.6	0.368
Mandibular pores	15.1	14.3	14.6	15.4	16.5	15.0	0.200
Gillrakers	14.1	14.2	14.2	13.8	13.4	13.6	0.096

Table 3.8. Factor loadings for principal components on meristics.

Trait	PC1 (19.8%)	PC2 (19.0%)	PC3 (16.5%)
DFR	0.239	0.817	0.023
AFR	0.558	0.609	0.172
CFR	0.463	-0.224	-0.238
PECFR	0.399	-0.232	0.740
PELFFR	0.384	-0.538	0.360
BRAN	-0.153	0.274	0.555
MANPOR	-0.544	0.050	0.486
GILLRK	0.612	-0.104	-0.122

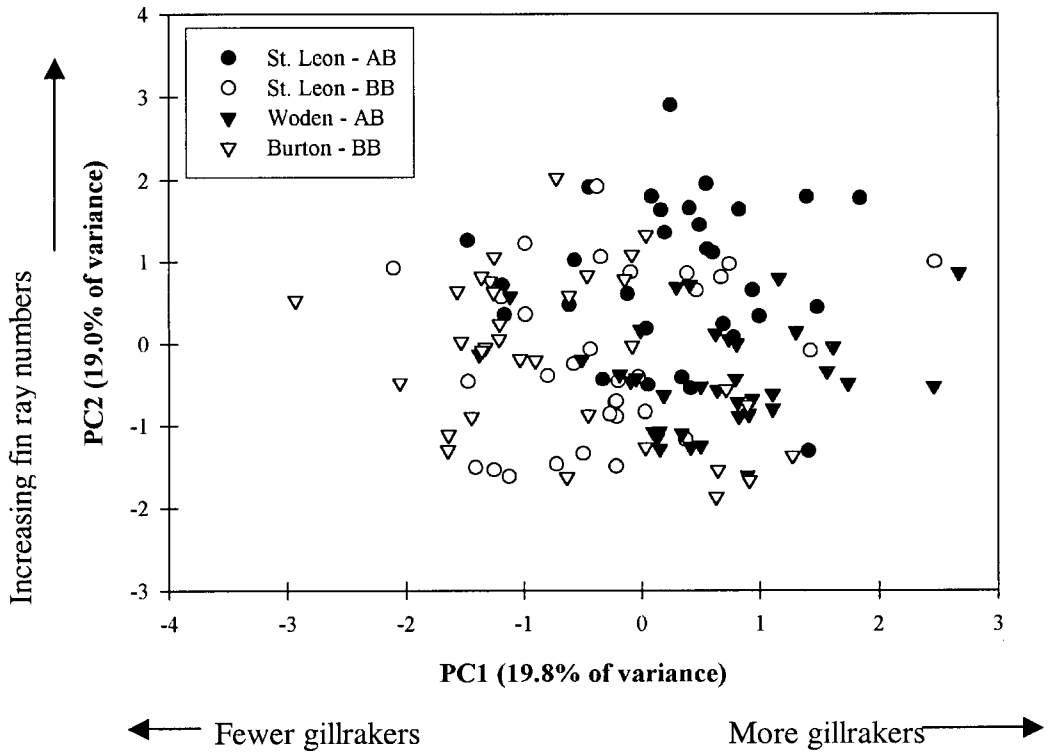

Figure 3.7. Scatter plot of principal components performed on entire meristics set along PC1 and PC2. Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols are from below-barrier samples.

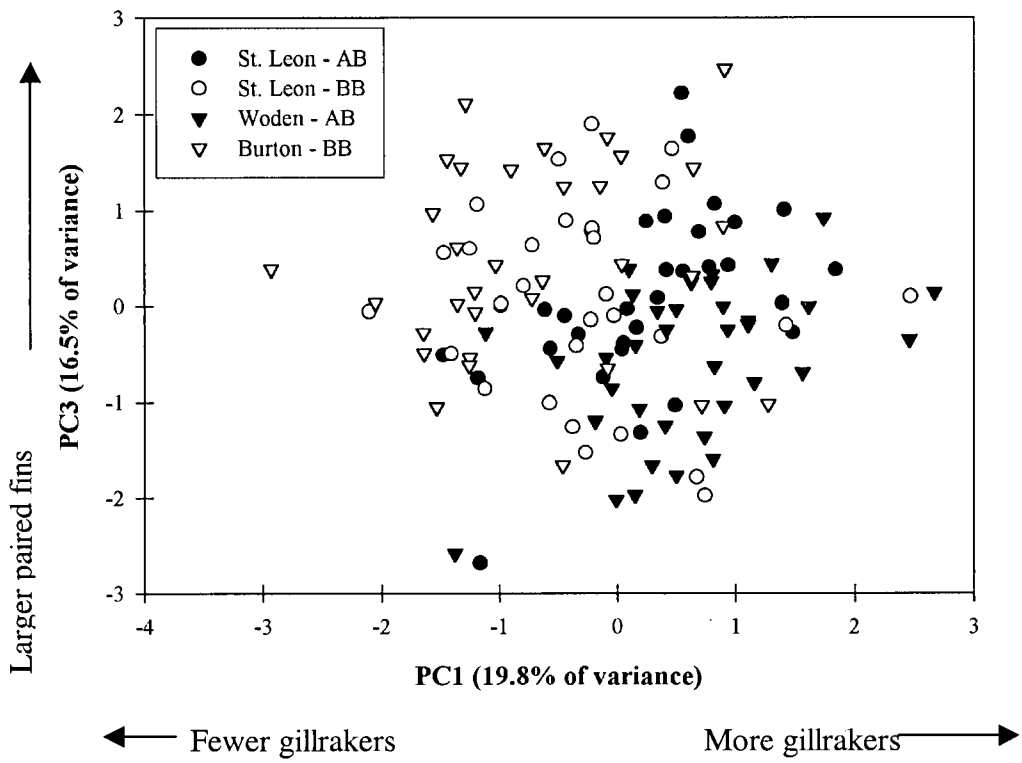

Figure 3.8. Scatter plot of principal components performed on entire meristics set along PC1 and PC3. Circles are samples from St. Leon Creek and inverted triangles are samples from the Burton Creek watershed. Filled symbols represent above-barrier samples and empty symbols represent below-barrier samples.

Table 3.9. Nested ANOVA results comparing above and below barrier meristic PCA scores for the first three components.

	Barrier		Stream	
Component	**F**	***p***	**F**	***p***
PC 1	11.86	0.075	3.76	0.026
PC 2	0.241	0.672	15.34	<0.001
PC 3	1.48	0.348	6.21	0.003

Discussion

Size and growth

Results from this portion of the study indicated that growth rates for bull trout during their first summer were higher in below- versus above-barrier populations. By the end of their first summer, migratory young-of-the-year had reached lengths of 60-70 mm, whereas resident fish were less than 50 mm in length. These findings were consistent with those of McPhail and Murray (1979), who documented similar growth trajectories of adfluvial young-of-the-year bull trout in the Arrow Lakes' tributaries. In their study, recently emerged fish were between 20-30 mm in June, and by late September they had reached 60-70 mm in length.

The differences in growth exhibited by bull trout in the present study during the early stages of life history have also been seen in populations of both Arctic char (Jonsson et al. 1988) and grayling (Haugen 2000) in northern lakes. Additionally, rainbow trout from below waterfall barriers have been found to consistently grow at a faster rate early in life compared to individuals from above-barrier populations (Northcote 1981;Northcote and Hartman 1988), and brown trout within a single watershed have exhibited higher growth in the mainstem compared to fish from tributaries (Jonsson and Sandlund 1979).

One factor that helps explain why bull trout from above-barrier populations were smaller than migratory juveniles at the end of the first summer is temperature. Water temperature has important effects on egg development rate and alevin size, and lower

temperature has been negatively correlated with time-to-emergence for bull trout eggs reared under laboratory conditions (McPhail and Murray 1979). This same study also showed that eggs raised in colder temperatures produced larger alevins than those in warmer temperatures. If water temperatures were colder in the headwater sections of tributaries in the present study, similar spawning timing between above- and below-barrier fish, in conjunction with comparable developmental rates, would lead to a much-reduced growing season for above- versus below-barrier char. Since water temperatures were colder in above-barrier sections of tributaries in the present study (see Chapter 2), it follows that bull trout from these sections were smaller in size. This explanation is supported by studies of coldwater salmonids such as Arctic char and Atlantic salmon which showed declining growth rates as water temperature decreased below their growth optima (Jobling 1983;Saunders 1986;Brannas and Wilklund 1992). Additionally, in Arctic char, growth rates approached zero as water temperatures dropped below 4°C (Brannas and Wilklund 1992). If we define growth potential as the total number of days over 5°C (Selong et al. 2001), the above-barrier char had approximately 14% fewer days of growth available to them. As fish are poikilothermic, this clear difference in growth opportunity helps explain the differences in growth between the two populations.

Aside from a purely phenotypic response, it is possible that the increased growth rate of below-barrier char reflects the work of differential selection. For instance, selection for fast growth may be typical in adfluvial fish to allow for maximum exploitation of their piscivorous diet in the lake, or as an adaptation to reduce risk of mortality from cannibalistic conspecifics. Future studies should investigate whether the

growth differences documented in the present study are strictly phenotypic responses to differing growth opportunities, or whether they are, at least partially, genetically based.

In many species of freshwater fish stunted populations exist that exhibit much reduced body sizes. The basic cause of this stunting is a reduction in growth rate and size at maturity of one population compared to another. Typically, reduced growth rates are associated with decreases in the quantity or quality of food available to an individual. This pattern is often observed in conspecific populations where one population is unable to switch to piscivory upon attaining a certain body size (Thorpe 1987). In his analysis of stunting, however, Roff (1986) suggested that for a population to persist in a stunted form, there must be a commensurate increase in density dependent survival rates as well as a decrease in age and size at maturity. In the present study, bull trout that became established above waterfall barriers likely experienced reduced growth due to decreases in available food, thus leading to smaller sexually mature fish. Theoretical life history frameworks have shown that for a population to remain stable over time, the product of the probability of surviving and producing offspring at age must be at least equal to one. Therefore, if growth (and consequent fecundity) is reduced, then population size will decrease until there is a commensurate increase in the probability of surviving

Size at maturity

In natural populations, migratory bull trout begin maturing after they have moved from the natal stream into larger lakes or rivers. First sexual maturity can occur as early as the fifth summer of its life (McPhail and Murray 1979;Fraley and Shepard 1989).

Adfluvial bull trout from populations in the West Kootenays have been found to begin spawning within several years of migrating to the lacustrine environment. McPhail and Murray (1979) aged mature adults returning to Mackenzie Creek (a tributary to upper Arrow Lake) as being in their fifth (4+) or sixth (5+) summer. Bull trout adults caught in the Arrow Lakes sport fishery range in length from 350-950 mm and in age from 5-14 years (Sebastian et al. 2000;Arndt 2002). Other authors have also determined that sexual maturity may begin as early as the fifth summer (4+), but typically occurs in the sixth or seventh year (Fraley and Shepard 1989).

Results from this portion of the study suggest that resident bull trout from above-barrier populations mature at much smaller sizes than their adfluvial counterparts. The smallest sexually mature adult sampled from above the barrier was 155 mm, and the largest was 245 mm (Figure 3.4). The lengths of sexually mature fish collected for the Hill Creek Hatchery ranged from 395 – 848 mm. The body lengths of the mature adfluvial bull trout in this study should be looked at with a certain degree of caution. Broodstock was collected for the hatchery from a variety of tributaries in both the upper and lower Arrow Lakes. The body sizes of these fish are to be taken as a surrogate for body size of migratory bull trout populations from St. Leon and Burton Creeks.

Body size has been shown to have indirect effects upon a variety of critical life history traits including fecundity, development time and survival (Roff 1981, 1984, 1986). In fish, migratory species (or populations) show a tendency to grow faster, delay maturity, and consequently, attain a larger body size than residents (Roff 1991). For example, Meyer et al (2003) found that there were clear differences between lengths at maturity for Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) exhibiting

different life histories across their range in Idaho, with sexually mature residents more likely to mature at smaller body sizes than fish from migratory populations. Similarly, for bull trout in the present study, the differences in observed body sizes between above- and below-barrier populations could have implications for fecundity, development time, and survival. Given the positive correlation between female body size and fecundity (McPhail and Murray 1979;Beacham and Murray 1985;Elliot 1994;Morita and Takashima 1998), it is likely that resident females have substantially lower fecundity than adfluvial bull trout. Although this study did not address possible differences in egg size between forms, other authors have found that differences in life history type (resident versus migratory) were not reflected by differences in egg size (Morita and Takashima 1998). Therefore, the major reproductive differences between the two forms in this study should be in fecundity and temperature effects upon development. McPhail and Murray (1979) found that for bull trout decreasing incubation temperatures increased hatching time, increased survival to hatching, and also increased alevin size.

Morphology and meristic variation

In addition to the documented differences in body size between above- and below-barrier fish, adult bull trout in the present study also exhibited differences in morphology and meristics between populations. Multivariate analyses on measurements relating to body, head and fin sizes showed that bull trout collected from above- and below-waterfall barriers were representative of distinct life history patterns.

Many of the morphometric and meristic differences between above- and below-barrier populations in this study were subtle. Characters associated with body size, head size and station-holding ability all showed differences within and between streams. Resident fish were more robust for a given body size than adfluvial bull trout,and exhibited consistently larger body depths and widths, peduncle lengths and widths, head depths and widths, and gape widths. Adfluvial bull trout were more streamlined than above-barrier fish and had longer snouts and, in general, smaller head sizes.

In many salmonids, overall body shape is reflected in these characters, with the degree of slenderness expected to reduce drag and increase overall swimming performance while a more robust body shape is related to strong burst swimming (Webb 1984;Taylor and McPhail 1985a). Larger paired fin sizes have also been shown to be related to position maintenance and swimming ability (Riddell and Leggett 1981;Pakkasmaa and Piironen 2001a). Finally, differences in head morphology are often associated with selection along trophic gradients (Skulason et al. 1989), and show variation in feeding characters. Although morphological differences in above- versus below-barrier fish in the present study were slight, they do indicate that resident populations were more robust in their fin and body proportions.

Variation in trophic morphology is expressed by differences in mouth position, fin size, head shape, gillraker number and overall body length (Snorrason et al. 1994;Bjoru and Sandlund 1995;Adams et al. 1998). Intraspecific morphological divergence is a common feature in salmonids, especially in species of the genus *Salvelinus* (Parkinson et al. 1984;Taylor and McPhail 1985a;Fleming and Gross 1989;Snorrason et al. 1989;Hendry and Quinn 1997;Dynes et al. 1999), and distinctive morphotypes within

species are often related to segregation along habitat and feeding axes (Skulason and Smith 1995). For example, Arctic char may show as many as four distinctive morphs within some postglacial lakes in the Holarctic region (Hindar and Jonsson 1993;Snorrason et al. 1994). Additionally, studies on trout populations with differing migratory patterns showed that resident populations had a more robust body shape, shorter fins, smaller heads, and smaller mouth parts than migratory lake-run populations (Pakkasmaa and Piironen 2001a). Meristic characters of bull trout in the present study showed regular differentiation between life history types. Although these differences were not statistically significant, most fin ray and gillraker counts were consistently higher in above-barrier fish (Table 3.7), a finding that was in line with original predictions. High gillraker counts characterize fish populations that utilize an invertebrate diet base and fail to make a diet switch to piscivory (Lindstrom 1989), which is consistent with the invertebrate diet of above-barrier bull trout in this study.

Bull trout in the Arrow Lakes region differentiated as a result of historic glaciations and subsequent recolonization and isostatic rebound of landforms. These events isolated multiple populations above impassable waterfalls and resulted in the emergence of two distinctive life history forms: stream-resident and adfluvial. This particular set of historic biogeographic circumstances is common in the northern hemisphere (Griswold et al. 1997;Olsen and Vollestad 2001), and above- and below-barrier populations are common in many salmonids and other families (McGlashan and Hughes 2000).

Results from the present study have provided evidence of this differentiation in life history and morphology between bull trout in these distinct environments. For both

above- and below-barrier stream environments, most of the differences reported are in directions predicted to be advantages to survival and reproduction, and likely reflect adaptive responses to differing selective environments. However, controlled breeding studies are needed to test the genetic basis for these differences. Such "local adaptation" is well documented in salmonids (Ricker 1972;Taylor 1991) but has, in general, been poorly studied in char, especially bull trout. Not only is such adaptation important to persistence of populations in specific environments, but bull trout are also a species of special conservation concern throughout their range. As a result, more specific study of local adaptation and responses of populations to environmental change are warranted for this species.

Management of bull trout in the Arrow Lakes has typically focused exclusively on the adfluvial life history form for two reasons. First, the impoundment of the Columbia River and the creation of the reservoir caused a loss of traditional migration routes and flooded spawning and rearing habitats, making study of adfluvial fish more important for the maintenance and survival of the population. Second, large bull trout of the Arrow Lakes partially fuel an active sport fishery in the area, and as shown from data in the present study, adfluvial fish are, on average, larger than their resident counterparts and thus more popular to catch and study. However, above-barrier bull trout deserve as much study as below-barrier fish. This portion of my study has provided a more comprehensive and realistic appraisal of bull trout biodiversity in the Arrow Lakes, along with a description of above-barrier populations and a discussion of the factors that may have promoted resident differentiation from adfluvial char. If more representative biodiversity

conservation of bull trout is to be accomplished, then greater consideration must be given to above-barrier populations in conservation planning (cf. Costello et al. 2003).

Results from this study indicate that distinctive bull trout populations exist above and below waterfalls in the same watershed within two streams tributary to the Arrow Lakes. Care must be taken, however, in the extrapolation of this pattern to other streams within this region that are structured similarly. In the West Kootenays there are many streams that show a similar pattern (bull trout above and below waterfalls) to those found in this study (Latham 2000; Sebastian 2000). Further study on a larger number of populations within the Arrow watershed and, perhaps, in other watersheds (Kootenay Lake) would help substantiate many of the results and questions raised in this thesis.

In summary, this chapter examined several characteristics of life history and morphology for bull trout from above- and below-barriers. I expected that resident and migratory bull trout populations would have adapted to the divergent environments and that this would be reflected in characteristics of their life history and morphology. These hypotheses were supported by results, as above-barrier and stream resident bull trout showed lower growth rates, reduced body sizes and younger ages at maturity compared to below-barrier fish. They also had consistently more robust bodies and higher meristic counts except for some features of the head and mouth (i.e., they had fewer gill rakers, mandibular pores and branchiostegal rays). In general, these results were consistent with my expectations and likely reflect differences that are important for persistence in the differing environments of above- and below-barrier habitats.

Chapter 4 – Conclusions

Summary

The overall objective of this project was to document the extent to which bull trout life history types have diverged in the Arrow Lakes regions of British Columbia. Habitat differences were documented above and below waterfall barriers, and data on morphology, body size, and growth were analyzed to determine how these characteristics corresponded to the respective populations of resident and migratory bull trout.

Not only were there distinct differences in above- and below-barrier environments, but these differences also helped explain the variation in life history patterns exhibited by the fish populations in those areas. Whereas resident populations confined to the cold, above-barrier headwater sections of these tributaries had more robust body shapes, larger fins and more gillrakers, migratory populations in warmer, below-barrier sections had fusiform body shapes, smaller head sizes and smaller gapes. These morphological differences, in conjunction with the clear habitat differences between above- and below- barrier environments, suggest that above- and below-barrier populations of bull trout have adapted to their environments by selecting for morphologies that are adapted to their differing migratory and feeding patterns.

Conservation implications

In the past 20 years, the importance of bull trout as a freshwater fish worth conserving has been increasingly recognized in North America . The degree of sensitivity

this species exhibits in response to ecosystem alterations reveals how the collection of baseline life history information can serve as a crucial ally in their conservation. As the extent of diversity in bull trout is still largely unknown, it is extremely important that such data be collected and incorporated into current reports.

It has been argued that the preservation of biodiversity has not been particularly important historically (Williams et al. 1989), and many locally adapted groups of salmon, trout and char have already been lost. Regardless of what they are called (sub-species, population, etc.), the loss of these sub-groups represents an irreplaceable legacy for each individual species and for Salmonidae as a whole. Not only is the scope of bull trout biodiversity already being eroded in many places, but some populations have also become extinct at edges of their range.

The accelerated rate of global warming is perhaps one of the most detrimental effects to cold-water specialists such as bull trout (Nakano et al. 1996). In some watersheds, this warming may contribute to the loss of a migratory bull trout life history by increasing water temperatures in downstream, higher order reaches, resulting in isolated headwater populations that would have otherwise migrated (Nelson et al. 2002). Bull trout conservation thus requires that all those with a stake in the species to continue to work together and gather data on these char populations as well as the problems facing them. This includes responsible management practices that allow for monitoring of stream temperatures in the region with regards to forest harvest activities and other anthropogenic manipulation.

Management issues

Bull trout are an integral component of Arrow Lakes aquatic fauna, occupying an important niche in both stream and reservoir ecosystems. The history of the adfluvial population has been strongly influenced by human manipulation through impoundment, enhancement and angling. Currently, anglers target these fish in the reservoir, and nearly 1000 adults are harvested every year (Sebastian et al. 2000). Furthermore, impoundment of the reservoir in the southern end of the lakes in 1969 raised water levels and resulted in significant losses of spawning and rearing habitats. Additional impoundments at the Mica and Revelstoke dams in 1973 and 1984, respectively, blocked migrations for adults, which are known to travel hundreds of kilometers from their natal stream (McPhail and Baxter 1996;O'Brien 1999). The resultant loss of spawners in the adfluvial population from these impoundments prompted managers to initiate compensation activities, including habitat enhancements and hatchery releases. The consequences of these actions were minimal, as recruitment of hatchery-produced bull trout to the population appears to be negligible (Arndt 2002).

The geological history of the Arrow Lakes region has resulted in many of the tributary streams being fairly high in gradient and blocked by natural waterfall barriers near their mouths. The removal of these waterfall barriers has been suggested by some as an option that could open up extensive areas of habitat to the adfluvial population. For the most part, the management authorities have rejected this enhancement effort and current management strategies appear to changing. In the past, stream habitat availability was considered to the limiting factor in bull trout production in the Arrow Lakes. The new paradigm appears to one in which lake productivity is the limiting aspect of fish

production and is currently being addressed through a program of lake fertilization (Arndt 2002). The data from my study suggests that bull trout from the above-barrier populations are divergent in several important characteristics from the below-barrier bull trout. The elimination of migration barriers could lead to the differences between the life history forms becoming less distinct and ultimately reducing the overall biodiversity of Arrow Lakes bull trout.

Habitat loss

Habitat loss is an extremely important issue, especially for migratory bull trout populations for whom the majority of lotic habitat in the tributaries is unavailable for spawning and rearing. Bull trout, like some other salmonids that select pool habitats over other types of habitat (Bonneau and Scarnecchia 1998), may be heavily impacted by the loss of any pools. There are several threats to resident bull trout populations, the most important of which is the continued loss or alteration of available habitat as a result of logging activities. Forestry activities within watersheds negatively affect streams by increasing water temperatures due to the removal of riparian vegetation (Holtby 1988). Few tributary valleys to the Arrow lakes have not had forest harvest activities within them, and logging in these valleys has created a multifaceted threat to all bull trout in the area. First, logging roads provide public access to reaches of the streams that were otherwise inaccessible. In many cases, adfluvial bull trout 'stack up' beneath the waterfall barriers prior to spawning, and anecdotal evidence suggests that poachers may target these concentrations of fish for illegal harvest. Furthermore, while the stunted, headwater

populations may not provide the sport enjoyment of the larger adfluvial adults, family groups targeting these resident char have been encountered on several occasions (J. Ladell, personal observation).

Second, both past and present forest harvest practices continue to directly impact bull trout habitat, and there is evidence that harvesting in riparian areas contributes to increased stream temperatures (Holtby 1988;Johnson and Jones 2000). Since bull trout are a temperature sensitive species, the potential combination of hemisphere and local scale thermal increases could be detrimental.

Finally, logging practices often leave behind large and small woody debris within stream channels that increase stream complexity. This may be beneficial to populations by increasing cover and pool habitat. However, many of the streams in high gradient areas can become clogged with debris jams and may ultimately negatively impact habitat availability.

Although this study did not directly address spawning habitat characteristics for these populations, they are still of critical importance to bull trout conservation efforts. To date, little information exists on the habitat requirements, timing, behavior, sex ratio or fecundity of sexually mature resident bull trout in the Arrow Lakes. Bull trout appear to spawn in highly specific reaches that have a combination of groundwater upwelling (Baxter 1997b;Baxter and Hauer 2000) and specific habitat characters. Given the paucity of habitat available to both life history types due to the high gradients and waterfall barriers of streams in the region, it is likely that high quality spawning habitat could be limiting.

Introduced species

Perhaps most important, the non-indigenous eastern brook trout (*Salvelinus fontinalis*) has been introduced to the system and is now well established. Moreover, introduced brook trout pose a significant threat to native bull trout populations. Not only do introduced brook trout appear to outcompete bull trout when they occur together (Dambacher et al. 1992;Ratliff and Howell 1992), but sterile hybrids are also produced when there is interspecific mating (Markle 1992;Kitano et al. 1994). Brook trout only appear to be occurring in sympatry with the adfluvial populations in the Arrow Lakes, and no brook trout were encountered in this study above waterfall barriers.

Brook trout are known to have an excellent ability to ascend high gradient headwater streams (Adams et al. 2000), and it is likely that mitigation efforts that would allow adfluvial bull trout to access headwaters would also open those habitats to brook trout invasion. Although the establishment of viable brook trout populations within the Arrow Lakes region increases the overall biodiversity of the fauna, introductions, in combination with the loss of lotic habitat, may contribute to the phenomena of biotic homogenization in this region (Rahel 2002;Taylor 2003).

In addition to brook trout, other biological introductions to the Arrow Lakes have also affected bull trout. The introduction of opossum shrimp (*Mysis relicta*) to the system has been implicated in the decline in numbers of kokanee salmon (*Oncorhynchus nerka*), and this has affected bull trout populations because kokanee are an important food source for bull trout in the lake. Additionally, there is a fertilization program in place on the Upper Arrow Lake designed to increase productivity within the reservoir. The

implications for bull trout as these nutrients move up the food chain have yet to be determined.

In southeastern British Columbia, isolated populations of resident bull trout share a biogeographic history. Postglacial recession likely provided access for recolonization of char to high altitude, headwater sections of streams. Further glacial scouring and isostatic rebounding along the valley bottoms resulted in impassable waterfall barriers essentially locking these fish into the headwater sections of their streams. Consequently, in order to survive, these isolated populations needed to locally adapt to a unique set of circumstances. Isolated populations of resident bull trout are found with regularity throughout the Arrow lakes reservoir portion of the Columbia River. Historically, these disjunct populations have held little interest for managers of the resource. The adults are too small to serve the interests of the angling community and the habitat is too difficult to provide access to the adfluvial populations. However, in the past 20 years, the scientific community has come to understand that these small, peripheral populations are significant in their own right (Scudder 1989).

Genetic legacy

This thesis has shown that populations of isolated, resident bull trout in the Kootenay region of British Columbia are distinct in their ecology and life history. Other authors (Latham 2000;Costello et al. 2003) have studied the genetic distinctiveness between populations of bull trout from the Arrow Lakes and elsewhere. Their studies found that resident populations of bull trout located above waterfall barriers contained

genetic variation that was unique not only to their within-stream migratory counterparts, but also to other resident populations in neighboring streams. Similarly, isolated, headwater populations of rainbow trout on Vancouver Island have been shown to contain a small amount of morphometric and genetic differentiation as well (Northcote 1981;Parkinson et al. 1984;Griswold et al. 1997). Small, isolated populations can lose genetic variation over time and may face greater threats than larger, more connected populations (Rieman and Allendorf 2001). In and of itself, some degree of genetic individuality for a population residing above a barrier does not necessarily mean that it is adaptive in the context of the species. However, divergence in small populations may provide insight into local adaptation.

Future Research

For adfluvial bull trout, information concerning the location, numbers and timing of natural adult spawners is sorely lacking. Sebastian et al (2000) looked at various data sources and determined that the spawning population falls somewhere within the range of 2500-4000 fish. Since reproductively viable adults have been removed from the population for several decades through angling and broodstock capture it is likely that the average size of adult adfluvial bull trout are decreasing (Ricker 1981). Furthermore, bull trout spawn in highly specific areas of streams and often return to the same locations year after year (James and Sexauer;Baxter 1994;Baxter 1997b;Essington et al. 1998;Baxter and Hauer 2000). Critical information on the relative contributions of the spawning areas of Arrow lakes tributaries and their habitat will thus benefit efforts to protect bull trout and the important biological legacy that they represent.

Information on life history and demographics for resident populations of bull trout in the Arrow Lakes is deficient. This study examined two well-established, self-perpetuating populations of bull trout located above waterfall barriers. These populations, and many more like them in the region, have existed undisturbed for thousands of years. It is likely that these populations are uniquely adapted to the particular set of abiotic conditions within their natal stream. The inherent value in these populations of bull trout lies in allowing them to remain as undisturbed as possible for the future of biodiversity in the Arrow Lakes and, indeed, for *Salvelinus confluentus* in general.

References

Adams, C. E., D. Fraser, F. A. Huntingford, R. B. Greer, C. M. Askew, and A. F. Walker. 1998. Trophic polymorphism amongst Artic charr from Loch Rannoch, Scotland. Journal of Fish Biology **52**:1259-1271.

Adams, C. E., and F. A. Huntingford. 2002. The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. Evolutionary Ecology **16**:15-25.

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions Of The American Fisheries Society **129**:623-638.

Andrus, C. W., B. A. Long, and H. A. Froehlich. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Canadian Journal of Fisheries & Aquatic Sciences. **45**:2080-2086.

Arndt, S. 2002. Arrow Lakes reservoir creel survey and contribution of hatchery production in 1998 and 1999. Columbia Basin Fish and Wildlife Compensation Program, Nelson, BC.

Arscott, D. B., K. Tockner, and J. V. Ward. 2001. Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy). Canadian Journal of Fisheries and Aquatic Sciences **58**:2359-2373.

Baroudy, E., and J. M. Elliot. 1994. Racial differences in eggs and juveniles of Windermere charr, *Salvelinus alpinus*. Journal of Fish Biology **45**:407-415.

Baxter, C. V. 1997a. Geomorphology, land-use, and groundwater-surface water interaction: a multi-scale, hierarchical analysis of the distribution and abundance of bull trout (*Salvelinus confluentus*) spawning. M. Sc. University of Montana, Missoula.

Baxter, C. V., and F. R. Hauer. 2000. Geomorphology, hypoheic exchange, and selection of spawning habitat by bull trout (Salvelinus confluentus). Canadian Journal of Fisheries and Aquatic Sciences **57**:1470-1481.

Baxter, J. S. 1994. Adult bull trout (*Salvelinus confluentus*) surveys and assessment in the Chowade river (1994).

Baxter, J. S. 1995. Chowade River bull trout studies 1995: habitat and population assessment. British Columbia Ministry of Environment, Lands and Parks, Fort St. John, British Columbia.

Baxter, J. S. 1997b. Aspects of the reproductive ecology of bull trout (*Salvelinus confluentus*) in the Chowade river, British Columbia. M.Sc. University of British Columbia, Vancouver, B.C.

Baxter, J. S. 1997c. Summer daytime microhabitat use and preference of bull trout fry and juveniles in the Chowade river, British Columbia. 107, B.C. Ministry of Environment, Lands and Parks, Vancouver, B.C.

Baxter, J. S. 1997d. Summer daytime microhabitat use and preferences of bull trout fry (Age 0+) and juveniles (Age 1+ to 3+) in the Chowade river, British Columbia. Fisheries Management Report:34.

Baxter, J. S., and J. D. McPhail. 1996. Bull trout spawning and rearing habitat requirements: Summary of the literature. B.C. Ministry of Environment, Lands and Parks, Vancouver, B.C.

Baxter, J. S., and J. D. McPhail. 1997. Diel microhbitat preferences of juvenile bull trout in an artificial stream channel. North American Journal of Fisheries Management **17**:975-980.

Baxter, J. S., E. B. Taylor, D. R. H., J. Hagen, and J. D. McPhail. 1997. Evidence for natural hybridization between Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in a northcentral British Columbia watershed. Canadian Journal of Fisheries and Aquatic Sciences **54**:421-429.

Beacham, T. D., and C. B. Murray. 1985. Effect of female size, egg size, and temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitnat River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **42**:1755-1765.

Beacham, T. D., C. B. Murray, and R. E. Withler. 1989. Age, morphology, and biochemical genetic variation of Yukon River chinook salmon. Transactions Of The American Fisheries Society **118**:46-63.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph **6**:1-275.

Beschta, R. L., and W. S. Platts. 1986. Morphological features of small streams: significance and function. Water Resources Bulletin **22**:369-379.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead and cutthroat trout in streams. Transactions Of The American Fisheries Society **117**.

Bjoru, B., and O. T. Sandlund. 1995. Differences in morphology and ecology within a stunted Arctic char population. Nordic Journal of Freshwater Research **71**:163-172.

Blackett, R. F. 1973. Fecundity of resident and anadromous Dolly Varden (Salvelinus malma) in southeastern Alaska. Journal Of The Fisheries Research Board Of Canada **30**:543-548.

Boag, T. D. 1987. Food habits of the bull char, *Salvelinus confluentus*, and rainbow trout, *Salmo gairdneri*, coexisting in a foothills stream in northern Alberta. Canadian Field-Naturalist **101**:56-62.

Bodaly, R. A. 1979. Morphological and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) species complex in Yukon Territory. J. Fish. Res. Board Can. **36**:1214-1222.

Bond, C. 1992. Notes on the nomenclature and distribution of the bull trout and the effects of human activity on the species. Pages 1-4 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

Bonneau, J. L., and D. L. Scarnecchia. 1996. Distribution of juvenile bull trout in a thermal gradient of a plunge pool in Granite Creek, Idaho. Transactions Of The American Fisheries Society **125**:628-630.

Bonneau, J. L., and D. L. Scarnecchia. 1998. Seasonal and diel changes in habitat use by juvenile bull trout (Salvelinus confluentus) and cutthroat trout (Oncorhynchus clarki) in a mountain stream. Canadian Journal of Zoology **76**:783- 790.

Bonneau, J. L., R. Thurow, F., and D. L. Scarnecchia. 1995. Capture, marking, and enumeration of juvenile bull trout and cutthroat trout in small, low conductivity streams. North American Journal of Fisheries Management **15**:563-568.

Bourke, P., P. Magnan, and M. A. Rodriguez. 1997. Individual variations in habitat use and morphology in brook charr. Journal of Fish Biology **51**:783-794.

Brannas, E., and B.-S. Wilklund. 1992. Low temperature growth potential of Arctic charr and rainbow trout. Nordic Journal of Freshwater Research **67**:77-81.

Brenkman, S., J., G. L. Larson, and R. E. Gresswell. 2001. Spawning migration of lacustrine-adfluvial bull trout in a natural area. Transactions Of The American Fisheries Society **130**:981-987.

Cannings, S. G., and J. Ptolemy. 1998. Rare Freshwater Fish of British Columbia. BC Ministry of Environment, Lands and Parks, Victoria, BC.

Cavender, T. M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American northwest. California Fish and Game **64**:139-174.

Cavender, T. M. 2001. Taxonomic characteristics of the Dolly Varden, *Salvelinus malma*, isolated above the Soleduck falls, Olympic National Park, Washington. Pages 27-32 *in* M. K. Brewin, A. J. Paul, and M. Monita, editors. Bull Trout II conference proceedings : ecology and management of northwest salmonids, Canmore, Alberta.

Claytor, R. R., and E. Verspoor. 1991. Discordant phenotypic variation in sympatric resident and anadromous Atlantic salmon (*Salmo salar*) populations. Canadian Journal of Zoology **69**:2846-2852.

Costello, A. B., T. E. Down, S. M. Pollard, C. J. Pacas, and E. B. Taylor. 2003. The influence of history and contemporary stream hydrology on the evolution of genetic diversity within species: an examination of microsatellite DNA variation in bull trout, Salvelinus confluentus (Pisces: Salmonidae). Evolution **57**:328-344.

Craig, S. D. 1997. Habitat conditions affecting bull trout, *Salvelinus confluentus*, spawning areas within the Yakima river basin, Washington. Master of Science. Central Washington University.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activities. Canadian Journal of Fisheries and Aquatic Sciences **53**:267-298.

Currens, K. P., C. B. Schreck, and H. W. Li. 1990. Allozyme and morphological divergence of rainbow trout (*Oncorhynchus mykiss*) above and below waterfalls in the Deschutes River, Oregon. Copeia **3**:730-746.

Dambacher, J. M., M. W. Buktenica, and G. L. Larson. 1992. Distribution, abundance, and habitat utilization of bull trout and brook trout in Sun creek, Crater Lake National Park, Oregon. Pages 30-36 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop, Corvallis, Oregon.

Dunham, J., B. E. Rieman, and G. Chandler. 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.

Dynes, J., P. Magnan, L. Bernatchez, and M. A. Rodriguez. 1999. Genetic and morphological variation between two forms of lacustrine brook charr. Journal of Fish Biology **54**:955-972.

Ehlinger, T. A. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. Ecology **71**:886-896.

Elliot, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford.

Essington, T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus confluentus*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability. Canadian Journal of Fisheries and Aquatic Sciences **55**:2310-2316.

Fausch, K. D., S. Nakano, and K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia **100**:1-12.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries & Aquatic Sciences. **49**:682-693.

Fleming, I. A., and M. R. Gross. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution **43**:141-157.

Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead lake and river system, Montana. Northwest Science **63**:133-143.

Frankham, R. 1997. Do island populations have less genetic variation than mainland populations? Heredity **78**:311-327.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Reviews:221-242.

Gillespie, G. J., and M. G. Fox. 2003. Morphological and life-history differentiation between littoral and and pelagic forms of pumpkinseed. Journal of Fish Biology **62**:1099-1115.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. U.S.D.A., Eugene, Oregon.

Goetz, F. 1994a. Distribution of bull trout in Cascade Mountain streams of Oregon and Washington. Pages 237-248 *in* W. C. MacKay, M. K. Brewin, and M. Monita, editors. Friends of the Bull Trout Conference proceedings, Calgary, Alberta.

Goetz, F. A. 1994b. Distribution and juvenile ecology of bull trout (*Salvelinus confluentus*) in the Cascade mountains. Master of Science. Oregon State University.

Gosline, W. A. 1971. Functional morphology and classification of teleostean fish. The University Press of Hawaii, Honolulu.

Goto, A. 1998. Life-history variations in the fluvial sculpin, Cottus nozawae (Cottidae) along the course of a small mountain stream. Environmental Biology of Fishes **52**:203-212.

Gowan, C., and K. D. Fausch. 1996. Mobile brook trout in two high elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences **53**:1370-1381.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences **51**:2626-2637.

Griswold, K. E., K. P. Currens, and G. H. Reeves. 1997. Genetic and meristic divergence of coastal cutthroat trout residing above and below barriers in two coastal basins. *in* Sea-Run Cutthroat Trout: Biology, Management, and Future Conservation. Oregon Chapter, American Fisheries Society.

Gross, M. R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium:14-25.

Haas, G. 2001. The mediated associations and preferences of native bull trout and rainbow trout with respect to maximum water temperature, its measurement standards, and habitat. Pages 53-55 *in* M. K. Brewin, A. J. Paul, and M. Monita, editors. Bull Trout II Conference Proceedings.

Haas, G., and E. A. Parkinson. 1997. Mediation of bull trout and rainbow trout interactions and abundances by temperature and habitat. *in* 127th Annual Meeting of the American Fisheries Society, Monterey, CA (USA).

Haas, G. R., and J. D. McPhail. 1991. Systematics and distribution of Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in North America. Canadian Journal of Fisheries and Aquatic Sciences **48**:2191-2211.

Haas, G. R., and J. D. McPhail. 2001. The post-Wisconsinan glacial biogeography of bull trout (*Salvelinus confluentus*): a multivariate morphometric approach for conservation biology and management. Canadian Journal of Fisheries and Aquatic Sciences **58**:2189-2203.

Hagen, J., and E. B. Taylor. 2001. Resource partitioning as a factor limiting gene flow in hybridizing populations of Dolly Varden char (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences **58**:2037-2047.

Harvey, B. C., R. J. Nakamoto, and J. L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (Oncorhynchus clarki) during fall and winter. Canadian Journal of Fisheries and Aquatic Sciences **56**:2161-2166.

Harvey, B. C., and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia **87**:336-342.

Haugen, T. O. 2000. Early survival and growth in populations of grayling with recent common ancestors - field experiments. Journal of Fish Biology **56**:1173-1191.

Haugen, T. O., and A. Vollestad. 2001. A century of life-history evolution in grayling. Genetica **112**:475-491.

Haugen, T. O., and L. A. Vollestad. 2000. Population differences in early life-history traits in grayling. Journal of Evolutionary Biology **13**:897-905.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Seasonal Habitat Selection and Preferences by Cutthroat Trout (Oncorhynchus-Clarki) in a Small, Coastal Stream. Canadian Journal of Fisheries and Aquatic Sciences **48**:1364-1370.

Hendry, A. P., and T. P. Quinn. 1997. Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities. 54:75-84.

Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon. Science **290**:516-518.

Hindar, K., and B. Jonsson. 1993. Ecological polymorphism in Arctic charr. Biological Journal of the Linnean Society **48**:63-74.

Hindar, K., B. Jonsson, N. Ryman, and G. Stahl. 1991. Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. Heredity **66**:83-91.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences **42**:505-515.

Hubbs, C. L., and K. F. Lagler. 1958. Fishes of the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan.

Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology **74**:673-684.

Hutchings, J. A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos **70**:12-20.

Hutchings, J. A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. Ecoscience **3**:25-32.

Hutchings, J. A. 1997. Life history responses to environmental variability in early life. Pages 139-167 *in* R. C. Chambers and E. A. Trippel, editors. Early Life History and Recruitment in Fish Populations. Chapman & Hall, London.

Hutchings, J. A., and R. A. Myers. 1994. The evolution of alternative mating strategies in variable environments. Evolutionary Ecology **8**:256-268.

Jakober, M. J., T. E. McMahon, R. Thurow, F., and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions Of The American Fisheries Society **127**:223-235.

James, P. W., and H. M. Sexauer. 1997. Spawning behavior, spawning habitat and alternative mating strategies in an adfluvial population of bull trout. *In* Proceedings of Friends of the Bull Trout conference, Calgary, Alberta.

Jobling, M. 1983. Influence of body weight and temperature on growth rates of Arctic charr, *Salvelinus alpinus* (L.). Journal of Fish Biology **22**:471-475.

Johnson, S. L., and J. A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences **57**:30-39.

Jolliffe, I. T. 1986. Principal Components Analysis. Springer-Verlag, New York.

Jonsson, B. 1982. Diadromous and resident trout Salmo trutta: is their difference due to genetics? Oikos **38**:297-300.

Jonsson, B., and N. Jonsson. 2001. Polymorphism and speciation in Arctic charr. Journal of Fish Biology **58**:605-638.

Jonsson, B., and O. T. Sandlund. 1979. Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta* m. *fario*) in Sore Osa river system, Norway. Environmental Biology of Fishes **4**:43-54.

Jonsson, B., and S. Skulason. 2000. Polymorphic segregation in Arctic charr Salvelinus alpinus (L.) from Vatnshlidarvatn, a shallow Icelandic lake. Biological Journal of the Linnean Society [Biol. J. Linn. Soc.]. **69**:55-74.

Jonsson, B., S. Skulason, S. S. Snorrason, O. T. Sandlund, H. J. Malmquist, P. M. Jonasson, R. Gydemo, and T. Lindem. 1988. Life history variation of polymorphic Arctic charr (Salvelinus alpinus) in Thingvallavatn, Iceland. Canadian Journal of Fisheries and Aquatic Sciences **45**:1537-1547.

Kanda, N., and F. W. Allendorf. 2001. Genetic population structure of bull trout from the flathead river basin as shown by microsatellites and mitochondrial DNA markers. Transactions Of The American Fisheries Society **130**:92-106.

Kawecki, T. J., and S. C. Stearns. 1993. The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. Evolutionary Ecology **7**:155-174.

Kaya, C. M. 1991. Rheotactic differentiation between fluvial and lacustrine populations of Arctic grayling (*Thymallus arcticus*), and implications for the only remaining indigenous population of fluvial 'Montana grayling'. Canadian Journal of Fisheries and Aquatic Sciences **48**:53-58.

Keeley, E. R., and W. A. Grant. 1995. Allometric and environmental corrleates of territory size in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **52**:186-196.

Kitano, S., K. Maekawa, S. Nakano, and K. D. Fausch. 1994. Spawning behavior of bull trout in the upper Flathead drainage, Montana, with special reference to hybridization with brook trout. Transactions Of The American Fisheries Society **123**:988-992.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish **12**:1-59.

Knouft, J. H., and J. R. Spotila. 2002. Assessment of movements of resident stream brown trout, *Salmo trutta* L., among contiguous sections of stream. Ecology of Freshwater Fish **11**:85-92.

Koskinen, M. T., T. O. Haugen, and C. R. Primmer. 2002. Contemporary fisherian life-history evolution in small salmonid populations. Nature **419**:826-830.

Kozel, S. J., and W. A. Hubert. 1989. Factors influencing the abundance of brook trout (Salvelinus fontinalis) in forested mountain streams. Journal of Freshwater Ecology **5**:113-122.

Kozlowski, J. 1992. Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. Trends in Ecology and Evolution **7**:15-19.

Kume, G., A. Yamaguchi, and I. Aoki. 2003. Variation in life history parameters of the cardinalfish *Apogon lineatus*. Fisheries Science **69**:249-259.

Ladell, J. J. 1999. Life history variation in Upper Arrow Lake bull trout. CBFWCP, Nelson, BC.

Latham, S. J. 2000. Historical and anthropogenic influences on genetic variation in bull trout (*Salvelinus confluentus*) in the Arrow Lakes, British Columbia. Masters. University of British Columbia, Vancouver, BC.

Lavin, P. A., and J. D. McPhail. 1987. Morphological divergence and the organization of trophic characters among lacustrine populations of the threespine stickleback (Gaterosteus aculeatus). Canadian Journal of Fisheries and Aquatic Sciences **44**:1820-1829.

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath river drainages. Conservation Biology **7**:856-865.

Leary, R. F., F. W. Allendorf, and G. K. Sage. 1995. Hybridization and introgression between introduced and native fish. American Fisheries Society Symposium **15**:91-101.

Lessios, H. A. 1981. Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the isthmus of Panama. Evolution **35**:618-634.

Lindsey, C. C., A. M. Brett, D. P. Swain, and A. N. Arnason. 1984. Responses of vertebral numbers in rainbow trout to temperature changes during development. Canadian Journal of Zoology **62**:391-396.

Lindsey, C. C., and J. D. McPhail. 1986. Zoogeography of fishes of the Yukon and Mackenzie basins. Pages 639-674 *in* C. H. Hocutt and E. O. Wiley, editors. The zoogeography of North American freshwater fishes. Wiley, New York.

Lindstrom, T. 1989. On the morphological differentiation of juvenile whitefish (0+, 1+), *Coregonus sp.*, and juvenile char (1+), *Salvelinus sp.*, with particular regard to population ecology of closely related species. Nordic Journal of Freshwater Research **65**:5-33.

Lowe, W. H., and F. R. Hauer. 1999. Ecology of two large, net-spinning caddisfly species in a mountain stream: distribution, abundance, and metabolic response to a thermal gradient. Canadian Journal of Zoology **77**:1637-1644.

Maekawa, K., T. Hino, S. Nakano, and W. W. Smoker. 1993. Mate preference in anadromous and landlocked Dolly Varden (*Salvelinus malma*) females in two Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences **50**:2375-2379.

Magnan, P., C. Audet, H. Glemet, M. Legault, M. A. Rodriguez, and E. B. Taylor. 2002. Developments in the ecology, evolution, and behavior of charrs, genus *Salvelinus*: relevance for their management and conservation. Environmental Biology of Fishes **64**:9-14.

Markle, D. F. 1992. Evidence of bull trout x brook trout hybrids in Oregon. Pages 58-67 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

Martin, A. D. 1976. Interim report of investigations on fish populations that will be affected by the Revelstoke 1880 dam.31.

McCart, P. 1997. Bull trout in Alberta: a review. Pages 191-207 *in* W. C. MacKay, M. K. Brewin, and M. Monita, editors. Friends of the Bull Trout Conference Proceedings, Calgary.

McCart, P., and P. Craig. 1973. Life history of two isolated populations of Arctic char (Salvelinus alpinus) in spring-fed tributaries of the Canning River, Alaska. Journal Of The Fisheries Research Board Of Canada **30**:1215-1220.

McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime of freshwater life stages of salmonids, with special reference to chinook salmon. EPA 910-R-99-010, U.S. Environmental Protection Agency, Seattle, Washington.

McGlashan, D. J., and J. M. Hughes. 2000. Reconciling patterns of genetic variation with stream structure, earth history and biology in the Australian freshwater fish *Craterocephalus stercusmuscarum* (Atherinidae). Molecular Ecology **9**:1737-1751.

McPhail, J. D., and J. S. Baxter. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. Fisheries Management Report:35.

McPhail, J. D., and C. C. Lindsey. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia system and rivers north to the Stikine). Pages 615-637 *in* C. H. Hocutt and E. O. Wiley, editors. The Zoogeography of North American Freshwater Fish. John Wiley and Sons Inc., New York.

McPhail, J. D., and C. B. Murray. 1979. The early life-history and ecology of Dolly Varden *Salvelinus malma* in the Upper Arrow lakes.113.

Meyer, K. A., D. J. Schill, F. S. Elle, and J. A. Lamansky, Jr. 2003. Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. Transactions Of The American Fisheries Society **132**:183-195.

Morita, K., and S. H. Morita. 2002. Rule of age and size at maturity: individual variation in the maturation history of resident white-spotted charr. Journal of Fish Biology **61**:1230-1238.

Morita, K., and Y. Takashima. 1998. Effect of female size on fecundity and egg size in white-spotted charr: comparison between sea-run and resident forms. Journal of Fish Biology **53**:1140-1142.

Morita, K., and S. Yamamoto. 2000. Extreme life history change of white-spotted char (Salvelinus leucomaenis) after damming. Fisheries Science **67**:179-181.

Morita, K., and S. Yamamoto. 2001. Contrasts in movement behavior of juvenile white-spotted charr between stocks above and below a dam. Fisheries Science **67**:179-181.

Murphy, M. L., J. Heifetz, K. V. Koski, and J. F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries & Aquatic Sciences. **43**:1521-1533.

Nakano, S., K. D. Fausch, T. Furukawa-Tanaka, K. Maekawa, and H. Kawanabe. 1992. Resource utilization by bull char and cutthroat trout in a mountain stream in Montana, U.S.A. Japanese Journal Of Ichthyology **39**:211-216.

Nakano, S., F. Kitano, and K. Maekawa. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. Freahwater Biology **36**:101-112.

Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environmental Biology of Fishes **64**:321-332.

Northcote, T. G. 1981. Juvenile current response, growth and maturity of above and below waterfall stocks of rainbow trout, *Salmo gairdneri*. Journal of Fish Biology **18**:741-751.

Northcote, T. G. 1997. Why sea-run? An exploration into the migration/residency spectrum of coastal cutthroat trout. Pages 20-26 *in* J. D. Hall, P. A. Bisson, and R. E. Gresswell, editors. Sea-run cutthroat trout: biology, management and future conservation. Oregon Chapter, American Fisheries Society, Corvallis.

Northcote, T. G., and G. H. Hartman. 1988. The biology and significance of stream trout populations (*Salmo* spp.) living above and below waterfalls. Polshie Archiwum Hydrobiologii **35**:409-442.

Northcote, T. G., and B. W. Kelso. 1981. Differential response to water current by two homozygous LDH phenotypes of young rainbow trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences **38**:348-352.

Northcote, T. G., S. N. Williscroft, and H. Tsuyuki. 1970. Meristic and lactate dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. Journal Of The Fisheries Research Board Of Canada **27**:1987-1995.

O'Brien, D. S. 1999. The Duncan Bull Trout Telemetry Project. Columbia Basin Fish & Wildlife Compensation Program, Nelson, BC.

Olsen, E. M., and L. A. Vollestad. 2001. Within-stream variation in early life-history traits in brown trout. Journal of Fish Biology **59**:1579-1588.

Pakkasmaa, S., and J. Piironen. 2001a. Morphological differentiation among local trout (Salmo trutta) populations. Biological Journal of the Linnean Society **72**:231-239.

Pakkasmaa, S., and J. Piironen. 2001b. Water velocity shapes juvenile salmonids. Evolutionary Ecology **14**:721-730.

Pakkasmaa, S., E. Ranta, and J. Piironen. 1998. A morphometric study on four land-locked salmonid species. Ann. Zool. Fennici **35**:131-140.

Parkinson, E., R. J. Benhke, and W. Pollard. 1984. A morphological and electrophoretic comparison of rainbow trout (*Salmo gairdneri*) above and below barriers on five streams on Vancouver island, B.C. Fisheries Management Report:15 pp.

Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries **4**:5-9.

Polacek, M. C., and P. W. James. 2003. Diel microhabitat use of age-0 bull trout in Indian Creek, Washington. Ecology of Freshwater Fish **12**:81-86.

Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management **27**.

Post, J. R., and F. D. Johnson. 2002. Status of the bull trout (*Salvelinus confluentus*) in Alberta. Wildlife Status Report 39, Alberta Sustainable Resource Development, Fish and Wildlife Division and Alberta Conservation Division, Edmonton, AB.

Power, G., R. A. Cunjak, J. Flannagan, and C. Katopodis. 1993. Biological effects of river ice. Pages 97-120 *in* T. D. Prowse and N. C. Gridley, editors. Environmental aspects of river ice. Environment Canada, Saskatoon, Saskatchewan.

Pratt, K. L. 1992. A review of bull trout life history. Pages 5-9 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics **33**:291-315.

Rahel, F. J., C. J. Keleher, and J. A. Anderson. 1996. Potential habitat loss and fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: Response to climate warming. Limnology and Oceanography **41**:1116-1123.

Ralph, S. J., G. C. Poole, L. L. Conquest, and R. J. Naiman. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. Canadian Journal of Fisheries & Aquatic Sciences. **51**:37-51.

Ratliff, D. E. 1992. Bull trout investigations in the Metiolus River-Lake Billy Chinook system. Pages 37-44 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop, Corvallis, Oregon.

Ratliff, D. E., and P. J. Howell. 1992. The status of bull trout populations in Oregon. Pages 10-17 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.

Redenbach, Z., and E. B. Taylor. 2002. Evidence for historical introgression along a contact zone between two species of char (Pisces: Salmonidae) in northwestern North America. Evolution **56**:1021-1035.

Redenbach, Z., and E. B. Taylor. 2003. Evidence for bimodal hybrid zones between two species of char (*Salvelinus*) in northwestern North America. Journal of Evolutionary Biology **In Press**.

Reist, J. D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Canadian Journal of Zoology **63**:1429-1439.

Reist, J. D. 1996. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. Canadian Journal of Zoology **64**:1363-1368.

Reznick, D. N. 1990. Plasticity in age and size at maturity in male guppies (Poecilia reticulata): an experimental evaluation of alternative models of development. Journal of Evolutionary Biology **3**:185-203.

Reznick, D. N., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution **36**:160-177.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (Poecilia reticulata). Science **275**:1934-1937.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 19-160 *in* R. C. Simon and P. A. Larkin, editors. The stock concept in Pacific salmon. H. R. MacMillian Lectures in Fisheries, Vancouver, B.C.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences **38**:1636-1656.

Riddell, B. E., and W. C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **38**:308-320.

Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. North American Journal of Fisheries Management **21**:756-764.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management **17**:1111-1125.

Rieman, B. E., and J. D. McIntyre. 1995. Occurence of bull trout in naturally fragmented habitat patches of varied size. Transactions Of The American Fisheries Society **124**:285-296.

Roff, D. A. 1981. On being the right size. American Naturalist **118**:405-422.

Roff, D. A. 1984. The evolution of life history parameters in teleosts. Canadian Journal of Fisheries and Aquatic Sciences **41**:989-1000.

Roff, D. A. 1986. Predicting body size with life history models. BioScience **36**:316-323.

Roff, D. A. 1991. Life history consequences of bioenergetic and biomechanical constraints on migration. American Zoologist **31**:205-215.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York, NY.

Saffel, P. D., and D. L. Scarnecchia. 1995. Habitat use by juvenile bull trout in belt-series geology watersheds northern Idaho. Northwest Science **69**:304-317.

Saunders, R. L. 1986. The thermal biology of Atlantic salmon: Influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. Rep. Inst. Freshw. Res., Drottningholm **63**:77-91.

Schaffer, W. M. 1974. Selection for optimal life histories: The effects of age structure. Ecology **55**:291-303.

Schaffer, W. M., and P. f. Elson. 1975. The adaptive significance of variations in the life history among local populations of Atlantic salmon in North America. Ecology **56**:577-590.

Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape, and habitat use efficiency. Ecology **74**:699-709.

Schluter, D. 1996. Ecological speciation in postglacial fishes. Phil. Trans. R. Soc. Lon. B **351**:807-814.

Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology and Evolution **16**:372-380.

Scudder, G. G. E. 1989. The adaptive significance of marginal populations: A general perspective. Canadian Special Publications of Fisheries and Aquatic Sciences **105**:180-185.

Sebastian, D., H. Andrusak, G. Scholten, and L. Brescia. 2000. Arrow reservoir fish summary. Stock Management Report.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions Of The American Fisheries Society **130**:1026-1037.

Sexauer, H. M. 1994. Life history aspects of bull trout, *Salvelinus confluentus*, in the eastern Cascades, Washington. M.Sc. Central Washington University, Ellensburg, Washington.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the Upper Flathead Basin, Montana. R008224-01-5, Montana Department of Fish Wildlife and Parks, Helena.

Skulason, S., D. L. G. Noakes, and S. S. Snorrason. 1989. Ontogeny of trophic morphology in four sympatric morphs of Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. Biological Journal of the Linnean Society **38**:281-301.

Skulason, S., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trends in Ecology and Evolution **10**:366-370.

Snorrason, S. S., S. Skulason, B. Jonsson, H. J. Malmquist, P. M. Jonasson, O. T. Sandlund, and T. Lindem. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shift. Biological Journal of the Linnean Society **52**:1-18.

Snorrason, S. S., S. Skulason, O. T. Sandlund, H. J. Malmquist, B. Jonsson, and P. M. Jonasson. 1989. Shape polymorphism in Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. Physiol. Ecol. Japan **1**:393-404.

Somers, K. M. 1986. Multivariate allometry and removal of size with principal component analysis.

Stearns, S., C. 1983a. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: Rates of evolution, heritabilities, and developmental plasticity. American Zoologist **23**:65-75.

Stearns, S. C. 1977. The evolution of life history traits: A critique of the theory and a review of the data. Annual Review of Ecology and Systematics **8**:145-171.

Stearns, S. C. 1983b. The genetic basis of differences in life-history traits among six populations of mosquitofish (*Gambisia affinis*) that shared ancestors in 1905. Evolution **37**:618-627.

Stearns, S. C. 1983c. A natural experiment in life-history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. Evolution **37**:601-617.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. Evolution **40**:893-913.

Steel, R. G. D., J. H. Torrie, and D. A. Dickey. 1997. Principles and procedures of statistics: a biometrical approach., 3rd ed. edition. McGraw-Hill, New York.

Svedang, H. 1990. Genetic basis of life-history variation of dwarf and normal Arctic charr, *Salvelinus alpinus* (L.), in Stora Rosjon, central Sweden. Journal of Fish Biology **36**:917-932.

Swain, D. P., and L. B. Holtby. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and its tributary stream. Canadian Journal of Fisheries and Aquatic Sciences **46**:1406-1414.

Swanberg, T. 1991. The movement and habitat use of fluvial bull trout in the Upper Clark Fork river drainage. Master of Science. University of Montana, Bozeman, Montana.

Takami, T., F. Kitano, and S. Nakano. 1997. High water temperature influences on foraging responses and thermal deaths of Dolly Varden *Salvelinus malma* and white-spotted charr *S. leucomaenis* in a laboratory. Fisheries Science **63**:6-8.

Taylor, E. B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. Progressive Fish-Culturist **48**:171-176.

Taylor, E. B. 1990. Phenotypic correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. Journal of Animal Ecology **59**:455-468.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture **98**:185-207.

Taylor, E. B. 1999. Species pairs of north temperate freshwater fishes: Evolution, taxonomy, and conservation. Reviews in Fish Biology and Fisheries **9**:299-324.

Taylor, E. B. 2003. An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **in press**.

Taylor, E. B., and J. D. McPhail. 1985a. Variation in body morphology among British Columbia populations of coho salmon, Oncorhynchus kisutch. Canadian Journal of Fisheries and Aquatic Sciences **42**:2020-2028.

Taylor, E. B., and J. D. McPhail. 1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences **42**:2029-2033.

Taylor, E. B., and J. D. McPhail. 1986. Prolonged and burst swimming in anadromousand freshwater threespine stickleback, *Gasterosteus aculeatus*. Canadian Journal of Zoology **64**:416-420.

Taylor, E. B., S. Pollard, and D. Louie. 1999. Mitochondrial DNA variation in bull trout (Salvelinus confluentus) from northwestern North America: implications for zoogeography and conservation. Molecular Ecology **8**:1155-1170.

Taylor, E. B., Z. A. Redenbach, A. B. Costello, S. J. Pollard, and C. J. Pacas. 2001. Nested analysis of genetic diversity in northwestern North American char, Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences [Can. J. Fish. Aquat. Sci.]. **58**:406-420.

Thorpe, J. E. 1987. Smolting versus residency: developmental conflict in salmonids. American Fisheries Society Symposium **1**:244-252.

Thorpe, R. S. 1976. Biometric analysis of geographic variation and racial affinities. Biological Reviews **51**:407-452.

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

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Vollestad, L. A., E. M. Olsen, and T. Forseth. 2002. Growth-rate variation in brown trout in small neighbouring streams: evidence for density-dependence? Journal of Fish Biology **61**:1513-1527.

Vuorinen, J., and O. K. Berg. 1989. Genetic divergence of anadromous and nonanadromous Atlantic salmon (*Salmo salar*) in the River Namsen, Norway. Canadian Journal of Fisheries and Aquatic Sciences **46**:406-409.

Ward, J. V. 1985. Thermal characteristics of running waters. Hydrobiologia **125**:31-46.

Watson, G., and T. W. Hillman. 1997. Factors affecting the distribution and abundance of bull trout: An investigation at hierarchical scales. North American Journal of Fisheries Management **17**:237-252.

Webb, P. W. 1977. Effects of median-fin amputation on fast start performance of rainbow trout. Journal of Experimental Biology **68**:123-135.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist **24**.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics **20**:249-278.

Williams, J. E., J. E. Johnson, D. A. Hendrickson, S. Contreras-Balderas, J. D. Williams, M. Navarro-Mendoza, D. E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. Fisheries **14**:2-20.

Willson, M. F. 1997. Variation in salmonid life histories: patterns and perspectives. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Yamamoto, S., K. Morita, and A. Goto. 1999. Geographic variations in life-history characteristics of white-spotted char (*Salvelinus leucomaenis*). Canadian Journal of Zoology **77**:871-878.

Yamamoto, S., S. Nakano, and Y. Tokuda. 1992. Variation and divergence of the life-history of Japanese charr *Salvelinus leucomaenis* in an artificial lake-inlet stream system. Japanese Journal of Ecology **42**:149-157.

Zar, J. H. 1999. Biostatistical Analysis. Prentice Hall, Upper Saddle River, New Jersey.

Ziller, J. S. 1992. Distribution and relative abundance of bull trout in the Sprague river subbasin, Oregon. Pages 18-29 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis, Oregon.