ECOLOGY OF WESTSLOPE CUTTHROAT TROUT (ONCORHYNCHUS CLARKI LEWISI) POPULATIONS IN THREE SMALL ROCKY MOUNTAIN HEADWATER STREAMS

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Bachelor of Science, University of Lethbridge, 2015

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfilment of the
Requirements for the Degree

MASTER OF SCIENCE

Department of Biological Sciences
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

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Date of Defence: April 11, 2019

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Abstract

Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* (WCT) are a threatened species in Alberta, Canada, where almost all remaining pure populations are restricted to small headwater streams. Field based methods were used to first describe the general habitat and WCT populations in three headwater streams, and secondly look at how habitat and populations changed seasonally. Well connected, deep pools with suitable cover provided the best WCT habitat during summer low flows. During winter, small WCT (< 20 cm) concealed and large WCT (> 20 cm) used pools for winter refuge. Summer habitat metrics (depth, area, geomorphology) in addition to seasonal changes in water temperature were drivers of large WCT presence-absence in pools during winter. Large WCT winter abundance in pools was further driven by water velocity, ice cover, and connectivity. Overall, this thesis highlights attributes of critical WCT habitat that can be used to help manage threatened populations in small headwater streams.

Acknowledgements

During the time of my master's thesis I have been fortunate to have had the opportunity to work within a system and on a species that was a big part of my bringing up in the Kootenays. I have pursued this thesis project to the best of my ability, however, I would have never been able to complete this project on my own and I am thankful of all those that have helped make that possible.

I would first like to thank my supervisors Dr. Joseph Rasmussen and Dr. Andreas Luek. I could probably never list the entirety of all that I have learned during these few years thanks to the opportunity I was given with this project. It was truly great to have the knowledge and resources available to me throughout this experience. Also, to my committee members, Dr. Cameron Goater and Dr. Stefan Kienzle, thank you for all of your advice and always being available when I needed others insight.

I would like to extend my thanks to those that provided technical assistance and advice during this project: Paul Harper (Parks Canada), Jason Blackburn (Alberta Conservation Association), and Matthew Coombs. Furthermore, funding for this project was through the Natural Sciences and Engineering Research Council of Canada collaborative research development grant (NSERC CRD). Thank you Riversdale Resources Limited for your collaboration and resources you have provided throughout this research project. I would like to thank Trout Unlimited Canada, specifically the Oldman Chapter, also for their support.

During this project, field work tested the best in people. From long, hot summer days slogging through headwater creeks, tangled in alder and biting insects, to the frigid and laborious winter days snowshoeing through the flurry of deep snow and ice laden canyons. Certainly, it may not be fully possible to explain all of these experiences, however there will always be the stories from those who lived it. I would like to give a special thanks to Conner Burdett, Michael Campen, and Kip Jay for all the good times working out in the mountains.

I would like to thank all of my friends and fellow graduate students for always providing opportunity for a time away from the tedious workings of data analysis and writing. Your comic relief and understanding were always appreciated.

Finally, I would like to thank my family. Justin Benson, who’s always been someone I could count on and to the best hunting and fishing partner a guy could ever ask for. To my parents, Linda and Westy Benson who always believed in what I was doing even when circumstances tested me. Your support over the years has been enormous in comparison to others and I couldn’t have done it without you.

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List of Abbreviations

AIC: Akaike Information Criterion

AWCTRT: The Alberta Cutthroat Trout Recovery Team

ALTPOOL: Alternate number of pools

ANOVA: Analysis of variance

AREA: Pool area

BCOND: Bank condition

BKCH: Brook Char

BLCH: Bull Char

CANOPY: Canopy coverage

COND: Conductivity

COSEWIC: The Committee on the Status of Endangered Wildlife in Canada

CREEK: Study streams

DAM: Dammed pool

DEM: Digital elevation model

DISNBD: Distance to the nearest barrier downstream

DISNBU: Distance to the nearest barrier upstream

DISNPD: Distance to the nearest pool downstream

DISNPU: Distance to the nearest pool upstream

DO: Dissolved oxygen

DOMSUB: Dominant substrate

ELEV: Elevation

GIS: Geographic information system

GPS: Global positioning system

HABCOV: Available habitat cover

HSD: Honestly significant difference test (Tukey's)

LATSC: Lateral scour pool

LONG: Longitudinal distance downstream

NMDS: Non-metric multidimensional scaling

MAX_DEPTH: Maximum depth

MID: Mid-channel pool

MNWH: Mountain Whitefish

OHV: Off highway vehicle

PermANOVA: Permutation analysis of variance

PLUNGE: Plunge pool

POOLTYPE: Pool type

RNTR: Rainbow Trout

SARA: Species at Risk Act

SE: Standard error

SEGMENT: Geomorphic segment

SIDE_CHAN: Side channel pool

SILT: Silt cover

SPDIVERSITY: Species diversity

STEP: Step pool

TRENCH: Trench pool

TURB: Turbidity

VEL: Pool velocity

VMR: Variance mean ratio

WCT: Westslope Cutthroat Trout

WTEMP: Water temperature

WTEMP_DIFF: Seasonal water temperature difference

WTSH: Watershed area

Chapter 1 - Introduction

Land Use and Ecological Impacts to Streams and Rivers – Surface Mining

There is substantial cause for threat on water resources and aquatic biodiversity globally due to physical and chemical impairment by human activities (Malmqvist and Rundle 2002, Sanderson et al. 2002, Vörösmarty et al. 2010). The leading cause of species extirpations and extinctions are changes in land use resulting in habitat loss and alteration (Baillie et al. 2004, Venter et al. 2006). Out of the many different forms of land use changes, resource extraction through mining can be regarded as one of the most influential to aquatic ecosystems (Wilcove et al. 1998, Malmqvist and Rundle 2002). This is because impacts from mining compared to other land uses such as agriculture for example, are generally more severe considering the amount of land directly altered (Sojka 1999, Cooke and Johnson 2002). Overtime the extent of mining has increased globally as the demand for metals and minerals to sustain national economic stability and growth has increased (Mudd 2007, 2010, Krausmann et al. 2009). Sustainability in light of climate change has also led to an increased push in the decarbonisation of energy systems (Hodgkinson and Smith 2018). As we shift to more renewable sources of energy, the demand for mined materials, particularly metals, will continue so to support the required infrastructure and technologies (Hodgkinson and Smith 2018). Concurrently, as larger scale surface mines become more prevalent, their activities across the globe and North America has become of increased interest due to the negative effects on aquatic ecosystems (Palmer et al. 2010).

Effects from surface mining (e.g. strip mining, open-pit mining, and mountaintop removal) can drastically influence water quality (Palmer et al. 2010). For example, water draining mined waste rock can contain elevated concentrations of chemical elements such as selenium (Lindberg et al. 2011, Kuchapski and Rasmussen 2015a, Wellen et al. 2015) and metals (Sullivan and

Drever 2001, Harding 2005, Palmer et al. 2010, Lindberg et al. 2011, Langman et al. 2018), while also affecting pH and conductivity in nearby streams and rivers (Raymond and Oh 2009, Palmer et al. 2010, Lindberg et al. 2011, Kuchapski and Rasmussen 2015a, Niu et al. 2018). Changes in water chemistry often result in changes to macroinvertebrate communities, such as reduced abundance, reduced species richness, and shifts in composition (Clements 1996, Hogsden and Harding 2012, Kuchapski and Rasmussen 2015a). Additionally, toxic effects to fish due to food chain transfer or direct exposure of contaminants (Dallinger et al. 1987, Miller et al. 2013, Kuchapski and Rasmussen 2015b) can result in altered behaviour (Atchison et al. 1987), reduced growth (McKim and Benoit 1971, Mount 1973, Menendez 1976, Ogle and Knight 1989, Sfakianakis et al. 2015), reduced reproduction (Mount 1973, Menendez 1976, Speranza et al. 1977, Sfakianakis et al. 2015) and direct mortality (Jezierska et al. 2009, Sfakianakis et al. 2015).

Surface mining also alters physical habitat in streams and rivers. Mining activities that modify watershed characteristics such as vegetation, soils, and subsurface materials, can significantly alter the basin hydrology and streamflow (Bonta et al. 1997, Negley and Eshleman 2006, Ferrari et al. 2009, Bernhardt and Palmer 2011), which can lead to changes in channel morphology (Bunn and Arthington 2002), sediment delivery and transport (Wood and Armitage 1997), and biogeochemistry (Mulhollan et al. 1990). Furthermore, surface mining can impact groundwater characteristics by altering flow paths and the location of discharge (Bonta et al. 1992, Evans et al. 2015). Consequently, by altering groundwater resources by surface mining, stream water temperatures can be affected (Rautio et al. 2018). Increased fine sediment loading caused from water draining off disturbed sites can increase turbidity and fill interstitial spaces of substrate (Wood and Armitage 1997) needed by spawning and overwintering fish (Bjornn and Reiser 1991), as well as aquatic invertebrates (Richards and Bacon 1994). In addition, contaminated sediments may facilitate further transport of other pollutants downstream (Dabney et al. 2018).

Coal Mining in Southern Alberta

Throughout the East Slopes of the Rocky Mountains in Alberta, Canada, different forms of land use, most notably mining, oil and gas, logging, grazing, and recreational off highway vehicle (OHV) use are common and can have substantial impact to aquatic ecosystems (Farr et al. 2017, 2018). Particularly, large scale surface mining along the mountains and foothills of Alberta has developed over time as a more commonly used practice for the removal of coal, as opposed to historic underground coal mining (Government of Alberta 2018). Recently, a coal mining development (Grassy Mountain Coal Project) was proposed near Blairmore, Alberta (**Figure 1.1**). The open pit mine (proposed by Benga Mining Limited) is to be located on Grassy Mountain (**Figure 1.2**) which encompasses two main watersheds Gold Creek and Blairmore Creek (**Figure 1.3**). The mine will be primarily targeting coking coal (metallurgical coal) which is an essential component of steel production (Díez et al. 2002, Price et al. 2002). Steel being an important component of infrastructure and other essential commodities that make our lifestyle possible. Currently, construction is projected to begin in early 2019 following regulatory timelines, where the production of cleaned metallurgical coal could start by early 2021 (Alberta Energy 2017). It is estimated that this mine would produce 4.5 million tonnes of clean coal per year over a 24 year mine life (Alberta Energy 2017). In comparison to other coal mines located nearby in British Columbia, Canada, Teck Resources operates five metallurgical coal surface mines in the Elk River watershed, which produced 27.6 million tonnes of coal in 2016 and 26.6 million tonnes of coal in 2017 (Teck Resources 2018). Teck's largest mine, Fording River, producing up to 9.5 million tonnes of coal annually and is expected to further persist for an additional 45 years (Teck Resources 2018).

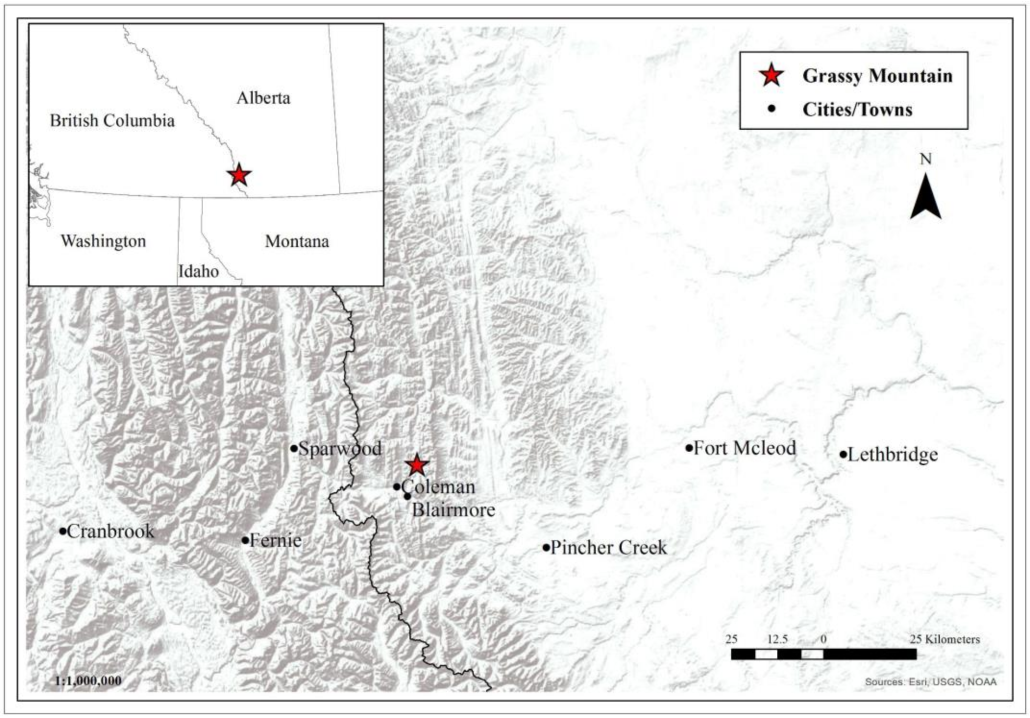

Figure 1.1 Grassy Mountain Coal Project Site and nearby cities and towns of Southern Alberta and British Columbia.

Figure 1.2 Grassy Mountain as viewed from Lille historic town site facing North. Grassy Mountain being the site for the proposed open pit coal mine.

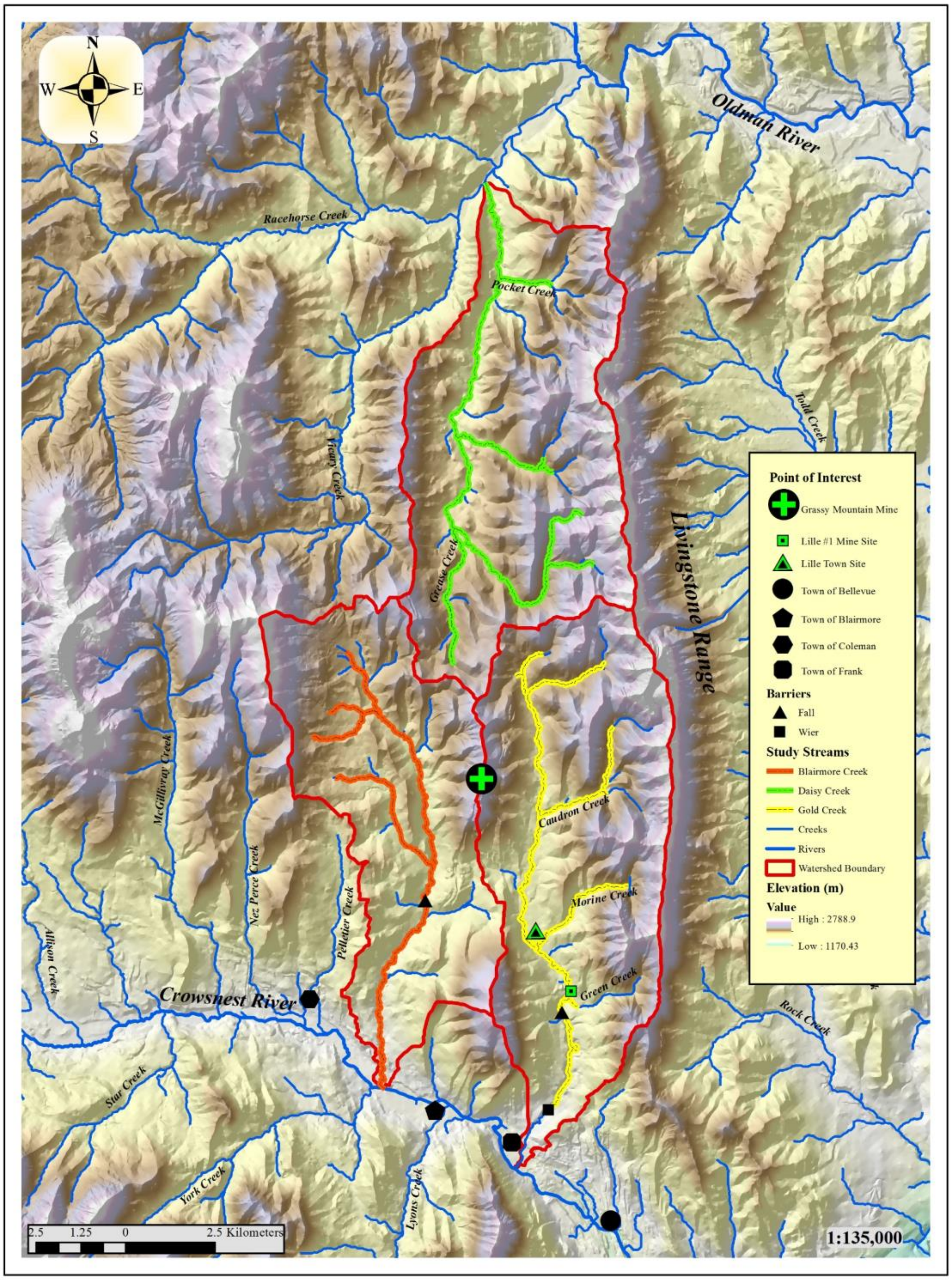

Figure 1.3 Study area map showing study streams and their watersheds. All highlighted study stream area was surveyed for fish habitat between years 2016 and 2017. Barriers are those that are previously documented and permanent. Points of interest include Grassy Mountain (site of the proposed Grassy Mountain Coal Mine), the historical town of Lille, Lille #1 mine site, and the current towns of the Crowsnest Pass.

Although this coal mining development is recently proposed, coal mining within the Crowsnest Pass is not new, dating back over 100 years (Felske 1991, Porter 2006). Historical coal mining taking place on Grassy Mountain itself, but also throughout scattered portions of the surrounding watersheds. From the early 1900's to the 1960's, at least six different coal mines and processing plants ran throughout the Crowsnest Pass in Alberta, including the famed Frank mine, the site of the tragic Turtle Mountain Disaster of 1903 (Felske 1991). Specifically within the Gold Creek watershed, there was significant coal mining development leading to the establishment of the town Lille (also known as "French Camp") in 1901 (Porter 2006) (**Figure 1.4**). From 1903 on, tipple facilities (i.e. structures used for loading and unloading extracted coal) were constructed with the addition of coking ovens and a wet coal washery (Felske 1991). A seven mile long railway line along the creek bed was used for transporting coal from Lille to the town of Frank, involving 23 train trestles through the narrow and steep canyon (Felske 1991). The town and facility ran for 11 years (1901-1912) and at its peak was producing an average of 600 tons of coal a day from the #1 seam (Porter 2006). After the market collapsed for Lille's coke in 1912, the town and facilities were moved (Porter 2006). The towns location later became a Provincial Historic Site in the 1970's (Porter 2006). Further strip mining has taken place on Grassy Mountain since Lille (**Figure 1.5**), however these ventures were not long lasting. Many past mining relics remain throughout the study watersheds, including end-pit lakes, machinery, infrastructure (**Figure 1.6**), and large coal deposits along Gold Creeks' main stem and tributaries (**Figure 1.7**).

Figure 1.4 Historic town site, railway line and coking ovens of Lille (1906-1909). Photograph retrieved from Glenbow Archives NA-2197-1.

Figure 1.5 Strip mining on Grassy Mountain looking southwest towards the Crowsnest Pass (1940's). Photograph retrieved from Glenbow Archives NA-3381-24.

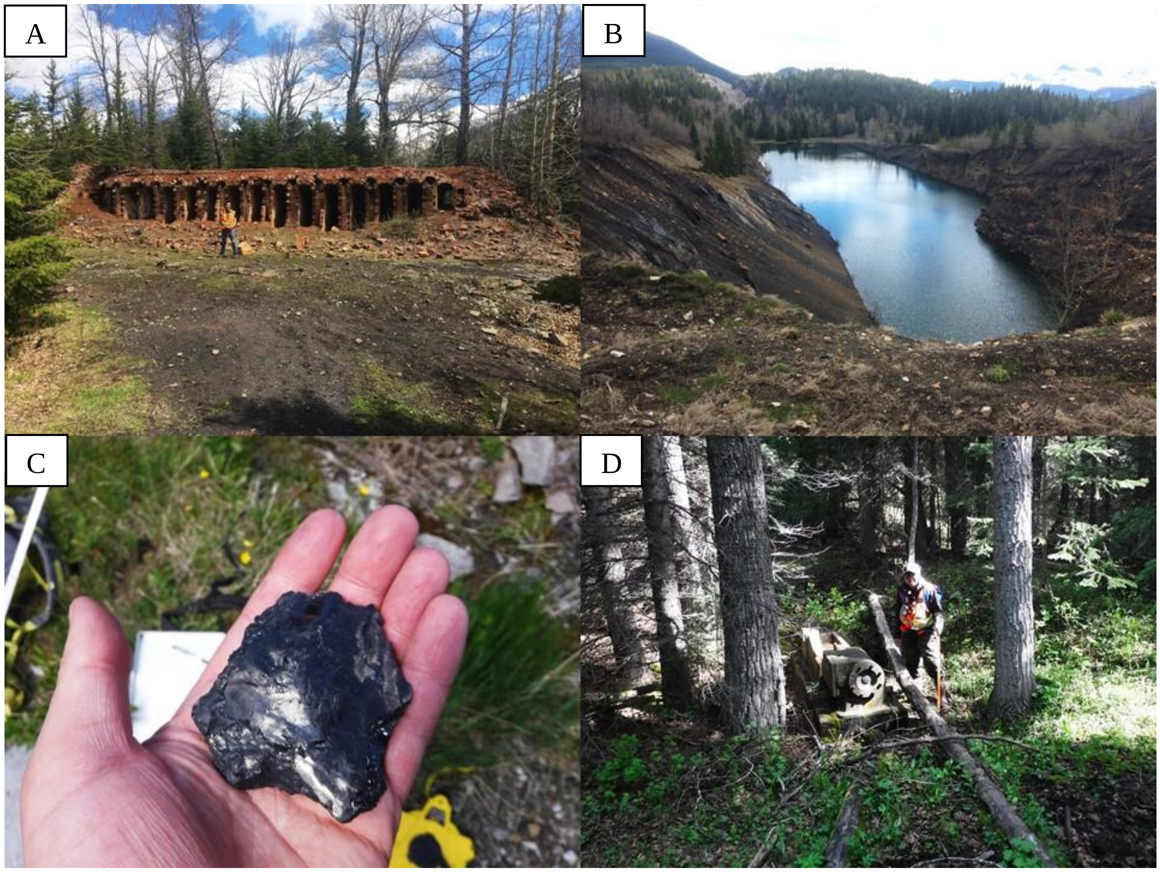

Figure 1.6 Past mining relics within the study streams: A) coking ovens of Lille, B) end-pit lake on Grassy Mountain, C) coal fragment, D) machinery left behind, located near the Morine Creek coal pile.

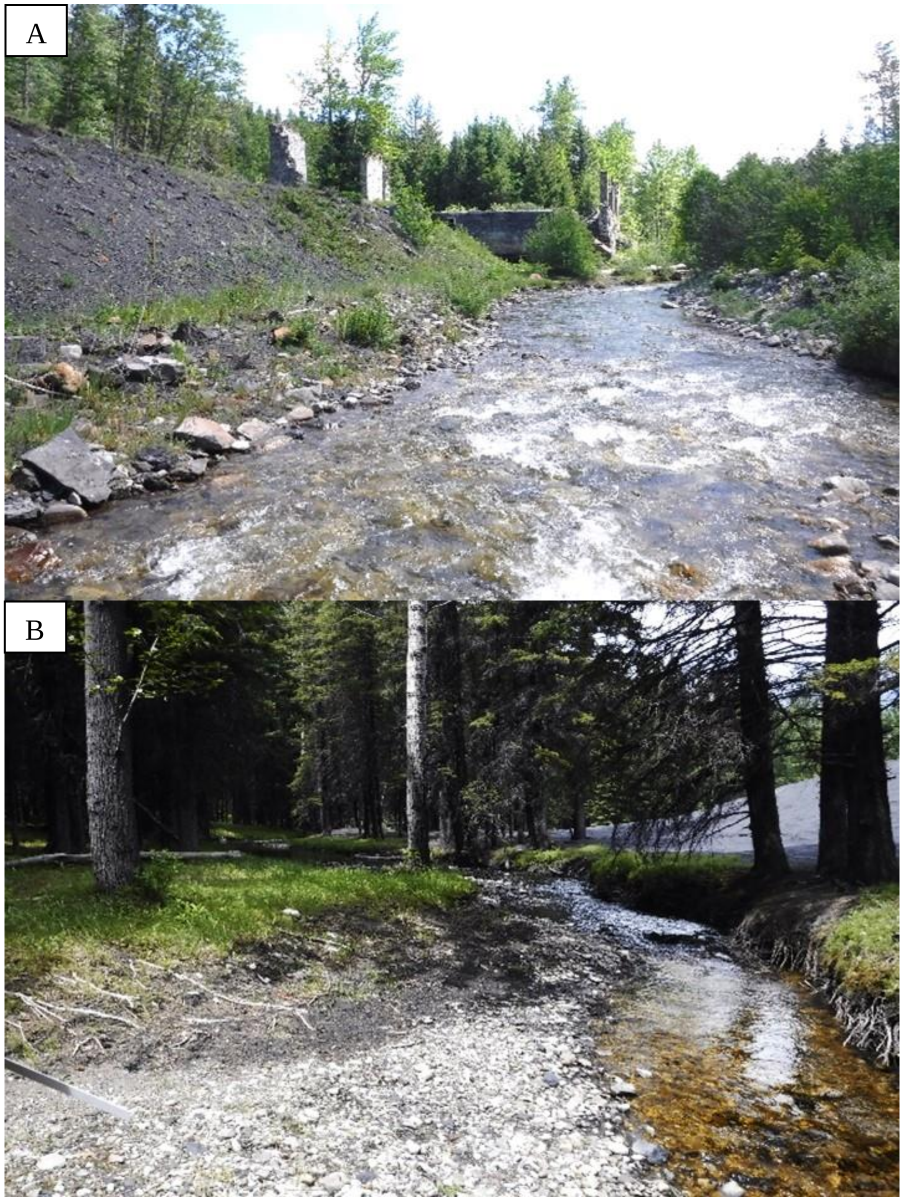

Figure 1.7 Photos showing two of four historic coal piles found along Gold Creek and its tributaries during this study: A) Lille #1 mine site, coal pile on the left stream bank; B) Lille town site, coal pile on the right stream bank.

The recently proposed coal mining development is expected to further impact aquatic resources within the two focal streams, Gold Creek and Blairmore Creek. It is expected that these activities will influence and alter the hydrology of both basin catchments (SRK Consulting Inc. 2016) and thus impact stream habitat. The potential future coal mine impacts are of particular interest due to the presence of threatened Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* (WCT) in both surrounding streams (Fisheries and Oceans Canada 2014). With mining activities having the potential to impact fish habitat, this presents an opportunity to study potentially pre and post-mine impacted headwater stream systems in an area where threatened species populations are present.

Westslope Cutthroat Trout

WCT are a subspecies of Cutthroat Trout *Oncorhynchus clarki* and are found throughout the mid Rocky Mountains, occupying a range of fluvial and adfluvial habitats (Behnke 2002) (**Figure 1.8**). In the United States, WCT distribution extends from Eastern Montana to Northern Idaho, with some disjunct populations occurring in Washington and Oregon (Behnke 2002). In Canada, WCT are found in Southern British Columbia and South Western Alberta (Behnke 2002). Despite this species being historically widespread and successful in a variety of habitats, it is under serious decline throughout most of its range (COSEWIC 2016).

Figure 1.8 Westslope Cutthroat trout *Oncorhynchus clarki lewisi* in their native habitat. Photograph taken during late winter in Gold Creek, Alberta.

In Alberta, WCT are listed as Threatened under the Canadian Federal *Species at Risk Act* (SARA) (Fisheries and Oceans Canada 2014, COSEWIC 2016). This status reflects threats due largely to habitat loss and alteration, competition with non-native species, as well as genetic introgression of Rainbow Trout *Oncorhynchus mykiss* (AWCTRT 2013). These combined threats have reduced pure WCT populations to only 5 % of the historical range in Alberta, which is restricted to primarily high elevation headwater streams (Mayhood and Taylor 2011). Often the sole mechanism in maintaining many genetically pure WCT populations are physical barriers, isolating WCT populations from downstream Rainbow Trout populations (Rasmussen et al. 2010).

Due to the current state of many pure WCT populations in Alberta, a recovery strategy was prepared by the Alberta Westslope Cutthroat Trout Recovery Team (2013), which provided a strategy to support, maintain and expand current WCT habitat and identified knowledge gaps associated with WCT in Alberta. Particularly, there is need for more research towards understanding general population health, but also identifying attributes of critical habitat in headwater streams (AWCTRT 2013, Fisheries and Oceans Canada 2014). Critical habitat being defined as habitat that is important for the survival and recovery of WCT in Alberta (AWCTRT 2013, Fisheries and Oceans Canada 2014). Defining critical habitat is a requirement for threatened or endangered listed species listed under the SARA (AWCTRT 2013, Fisheries and Oceans Canada 2014). This means baseline information needs to be collected on the quality and extend of critical WCT habitat (AWCTRT 2013). A complete inventory on barriers is needed to identify populations and critical habitats that are at risk to upstream invasion by non-native species and to better understand connectivity issues for future recovery actions (AWCTRT 2013). Furthermore, impacts of land use and disturbance on aspects of critical WCT habitat are not well understood, where analyses at the landscape and watershed scale are needed (AWCTRT 2013).

Within the critical habitat order (AWCTRT 2013), several key knowledge gaps were identified. Winter is a time, in which all live stages of WCT are under higher stress, yet, knowledge about critical habitat requirements and its occupation during that time are limited (AWCTRT 2013, Fisheries and Oceans Canada 2014). Research describing winter habitat use by different WCT life stages and their competition during that time with invasive species that pose risk to WCT populations is needed (AWCTRT 2013). This information is becoming more important as anthropogenic activities are increasing on the landscape, increasing the impact on aquatic resources within critical habitats. My thesis focuses on WCT populations in headwater streams in winter and their use of critical habitat. Furthermore, my research will address the potential impacts of further mine developments and climate change on this fragile landscape and threatened WCT populations.

Stream Geomorphology and Spatial Distribution of Habitat

Relationships between physical and biological components of fluvial environments, such as in streams and rivers, are becoming increasingly important in understanding ecological processes (Rieman and Dunham 2000, Belletti et al. 2017). Abiotic and biotic interactions can vary spatially and temporally, making fluvial environments dynamic and complex systems. Furthermore, fluvial environments contain numerous subsystems, related to the processes and forms at different scales of organization (Frissell et al. 1986, Belletti et al. 2017). Scale in this case refers to the size or level of the subsystem and dictates the relationship between spatial units and physical habitat (**Figure 1.9**). Consequently, a hierarchy of scale occurs because the smaller scale systems develop within constraints set by larger scaled systems (Frissell et al. 1986, Belletti et al. 2017). For example, a riffle-pool sequence is determined by water and sediment input from the catchment basin, which is further controlled by climate and geologic process (Frissell et al. 1986, Charlton 2008). Geomorphology of fluvial environments thus can create a mosaic of habitats within a single stream and river system (Belletti et al. 2017). Influences like slope, substrate, vegetation, valley setting, and even human activities, further drive these processes (Charlton 2008, Belletti et al. 2017).

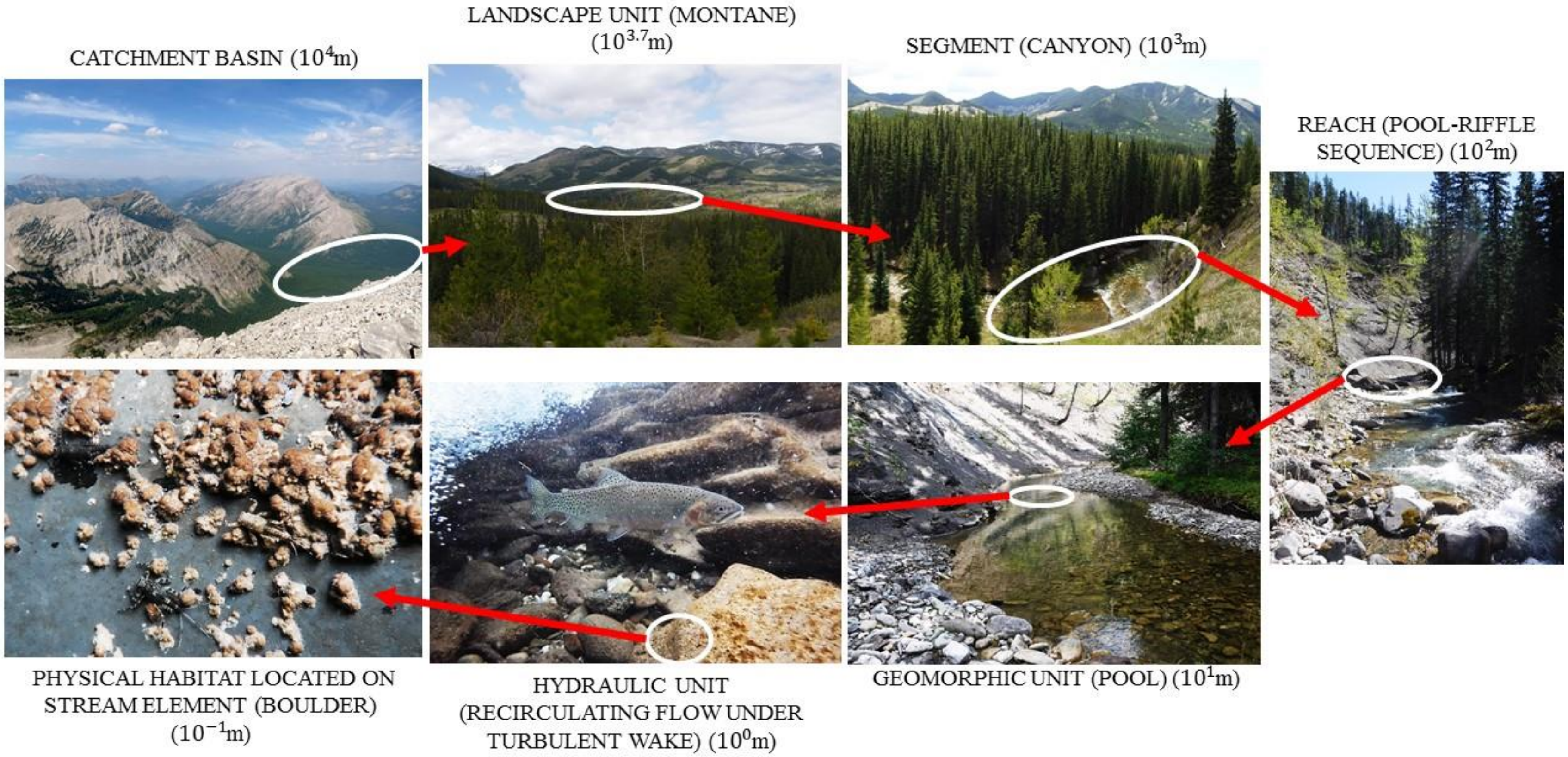

Figure 1.9 Nested relationships between spatial units and physical habitats (indicated by approximate linear distance) within a 3rd order montane headwater stream (adapted and modified from figures in Belletti et al. 2017 and Frissell et al. 1986).

Within the geomorphic mosaic of rivers and streams lie more specific hydraulic patches, such as riffles, pools, bars, etc. (Frissell et al. 1986, Belletti et al. 2017), which constitute distinct habitat features for aquatic and riparian plants and animals. Microhabitat features such as water velocity, depth, and substrate type all vary within different habitat patches (Frissell et al. 1986). These features are critical elements of salmonid ecology (i.e. for trout, char, salmon) (Bjornn and Reiser 1991). Requirements for these features by salmonids change under different conditions, such as during different seasons and life stages, including spawning, rearing, and overwintering (Bjornn and Reiser 1991). For example, obligate stream spawning salmonids require specific components of water temperature, velocity, depth, and substrate to facilitate upstream migration to spawning grounds, egg deposition, incubation, and survival of embryos (Bjornn and Reiser 1991, Quinn 2005). Microhabitat features also effect the amount of space available for feeding and cover within streams, particularly influencing carrying capacity of salmonid populations (Bjornn and Reiser 1991). Changes in water depth and velocity alter the amount of available cover (e.g. undercut banks, woody debris, and substrate) to avoid predation and competition. Often then it is found that in fluvial environments fish populations are influenced by the underlying geomorphology (Lanka et al. 1987, Kruse et al. 1997, Baxter and McPhail 1999). This is because geomorphology at larger scales influences those specific hydraulic patches (i.e. habitat patches) at smaller scales, those of which influence the microhabitat features that fish require.

Rivers or streams are contained within a linear stream network, and habitat patches occur along the network at varying degrees of distance. Obligate aquatic organisms, such as fish, are restricted to movement only within this network. Factors that resist movement within the fluvial network further determine dispersal opportunity between habitat patches (Rieman and Dunham 2000). Different types of barriers (e.g. water falls, cascades, hanging culverts, a dry creek bed), can be thought of as resistance factors as they partially impede or completely block movement within the stream network. Thus, in order to find habitat that facilitates survival, the overall spatial position of suitable and non-suitable habitat patches within stream networks has significant influence on fish populations (Rieman and Dunham 2000, Falke and Fausch 2010). For example, habitat patches closer together and unimpacted by barriers allow increased dispersal among different habitats that are required for different life stages, which leads to higher survival and population persistence over time (Falke and Fausch 2010). In contrast, habitat patches that are farther apart and impacted by barriers decrease or block dispersal, inhibiting fish populations to utilize the full range of required habitat. In the latter case, subpopulations or satellite populations could result and may act as sinks due to the absence of critical habitats required for persistence (Falke and Fausch 2010).

The idea that fish populations can be constrained by the spatial position and availability of habitats leads to the concept of spatially structured populations (i.e. metapopulation theory) (Rieman and Dunham 2000, Falke and Fausch 2010). As described by Falke and Fausch (2010), in fluvial environments, spatially structured populations result when there are strong effects of spatial scale, habitat heterogeneity, and dispersal on fish populations. If we consider a basin scale approach for analysing headwater systems and salmonid populations, it is apparent that in mountainous environments all the required elements for spatially structured populations are present. Furthermore, spatial structuring may change temporally, specifically as flow changes seasonally activating different barriers (**Figure 1.10**).

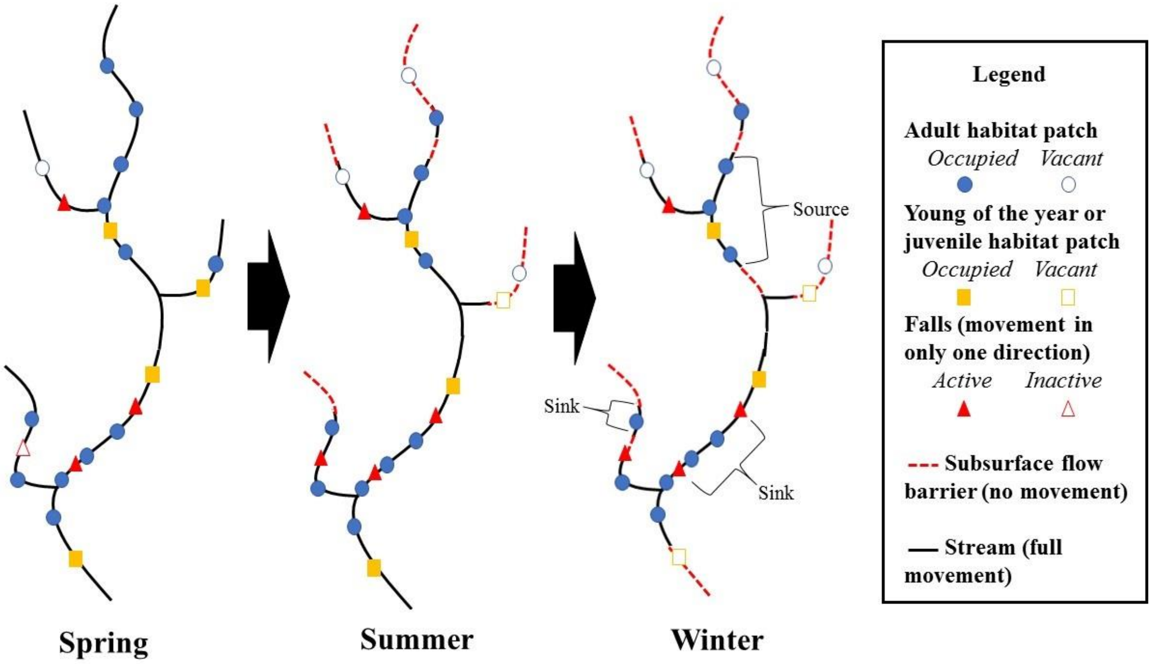

Figure 1.10 Conceptual representation of the complex spatial influence of habitat patches and barriers on fish populations in a headwater stream (basin/watershed scale) under different seasons. In this example from spring to winter, changes in flows have increased the number of vacant and isolated habitat patches. Furthermore, source and sink subpopulations become more distinct. Source populations have access to all required habitat. Sink populations do not have access to all required habitat.

Rieman & Dunham (2000) suggest that spatial structuring within salmonid populations is likely strong for most species, particularly for those that show local adaptation to facilitate their life cycle. This idea of spatially structured populations becomes increasingly important as habitat loss and fragmentation across landscapes forces managers to prioritize, conserve and restore habitat within watershed networks. As important as this may be for management and conservation for threatened species, little empirical work has been done to apply this theory to many salmonid populations (Rieman and Dunham 2000).

The consideration of required stream habitat patches and how they are spatially arranged within high elevation headwater stream networks is then important to understanding critical habitat for threatened WCT populations. Past glacial and tectonic forces have shaped many of the watersheds along the Rocky Mountains of Southern Alberta (Beaty 1975). This has produced a wide variety of geomorphic features within high elevation headwater streams such as steep and highly constricted bedrock channels to lower gradient and highly braided alluvial channels (**Figure 1.11**, **Figure 1.12**, **Figure 1.13**). These differing stream morphologies dictate the amount and the spatial position of different habitat patches (e.g. riffles and pools) within stream networks. In addition, barriers such as water falls, cascades, subsurface flow sections, debris jams, and man-made barriers (**Figure 1.14**) are common in these headwater streams and further restrict movement and dispersal. Therefore, because WCT populations within these environments are exposed to habitats that contain a high degree of spatial scale and heterogeneity, as well as lowered dispersal opportunities, we can expect these populations to be spatially structured.

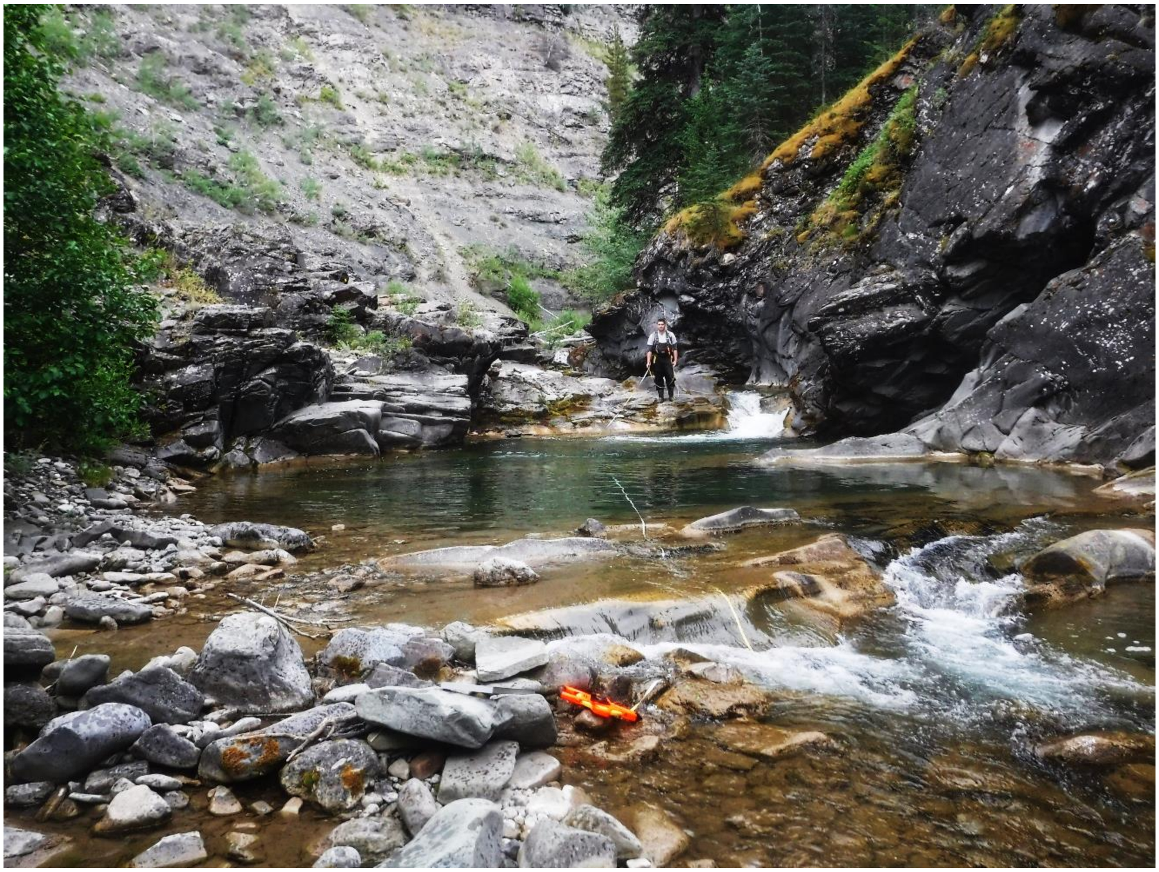

Figure 1.11 Example of the typical geomorphology found within canyon segments within study streams. Note the canyon segment is highly confined within the valley, has a cobble and bedrock dominated channel, and is 3rd order in size. Photograph taken on Daisy Creek, looking upstream.

Figure 1.12 Example of the typical geomorphology found within alluvial segments within study streams. Note the alluvial segment is relatively unconfined within the valley, has alluvium (fluvial or glacial) dominated channel, and is 2nd-3rd order in size (depending on stream location). Photograph taken on Blairmore Creek, looking upstream.

Figure 1.13 Example of the typical geomorphology found within headwater segments within study streams. Note the headwater segment is moderately confined within the valley, in this case has a boulder dominated channel, and is 1st-2nd order in size (depending on stream location). Photograph taken on Gold Creek, looking downstream.

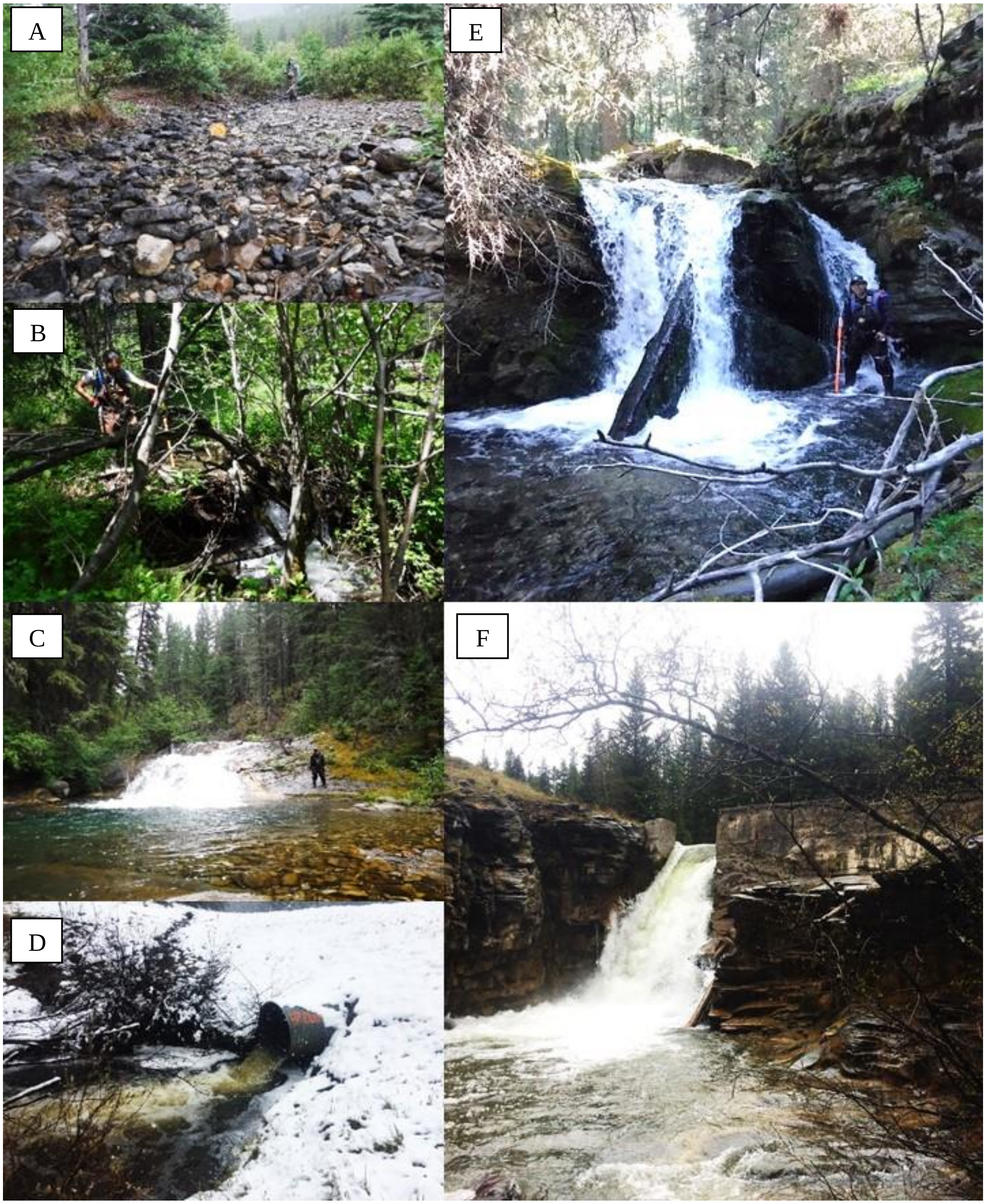

Figure 1.14 Some examples of typical barriers present in the study streams. Movement across barriers is variable, being either limited in both directions (e.g. passability limited by the size of fish and/or flow level), one-way, or none. Furthermore, barriers can restrict movement either permanently or temporarily. Examples included above: A) subsurface flow section (none, temporal); B) debris jam (none or one-way, temporal); C) cascade (limited, permanent); D) hanging culvert (limited, permanent); E) water fall (one-way, permanent); and F) weir (one-way, permanent).

Salmonid Winter Ecology in Streams

It has long been known that the winter period is a significant portion of many animals' life history in temperate regions of the northern hemisphere, inducing physiological and behavioural changes (Willmer et al. 2009). Although, the definition of winter relevant to ecology is more than what is determined by calendar dates (i.e. astronomical definition) and furthermore, may change considerably depending on the location (e.g. latitude or elevation) or system in question (e.g. rivers or lakes). Cunjak (1996) provides a relevant definition of winter within streams from an ecological and biological standpoint, which accounts for significant periods during the life cycle of salmonids and the physical changes in habitat: The onset of winter in streams is marked by the reduction in air temperature and the formation of ice, often following egg deposition by fall spawning salmonids; the end of winter in streams is extended until the loss of all surface ice and prior to reproductive activity of spring spawning salmonids, often followed shortly after by spring flooding. Applying Cunjak's definition of winter to high elevation headwater streams in Southern Alberta, winter begins around early November after fall spawning of native Bull Char *Salvelinus confluentus* has ended (usually taking place from September to October (Nelson and Paetz 1992, Behnke 2002), and ice starts to form. Winter then lasts until early April, prior to WCT spawning (usually taking place from April to June (Nelson and Paetz 1992, Behnke 2002)), when most ice has melted and just prior to spring flooding. Following Cunjak's definition would then extend winter in the headwater streams to up to six months, meaning that salmonid species occurring in these areas are living up to 50 % of their life history under winter conditions. Yet, this significant time period remains one of the most understudied parts of the salmonid life cycle, specifically for salmonid species such as WCT in headwater streams (AWCTRT 2013).

Ice Formation in Streams

Although streams and rivers are considered lotic systems (i.e. composed of flowing water), the quantity of ice formed in small, steep mountain streams in comparison to much larger rivers can be considerably different due to the varying differences in ice forming processes (Calkins 1989)(**Figure 1.15**). As this thesis focuses on smaller streams, I will only make limited reference to larger rivers when ice forming processes are similar.

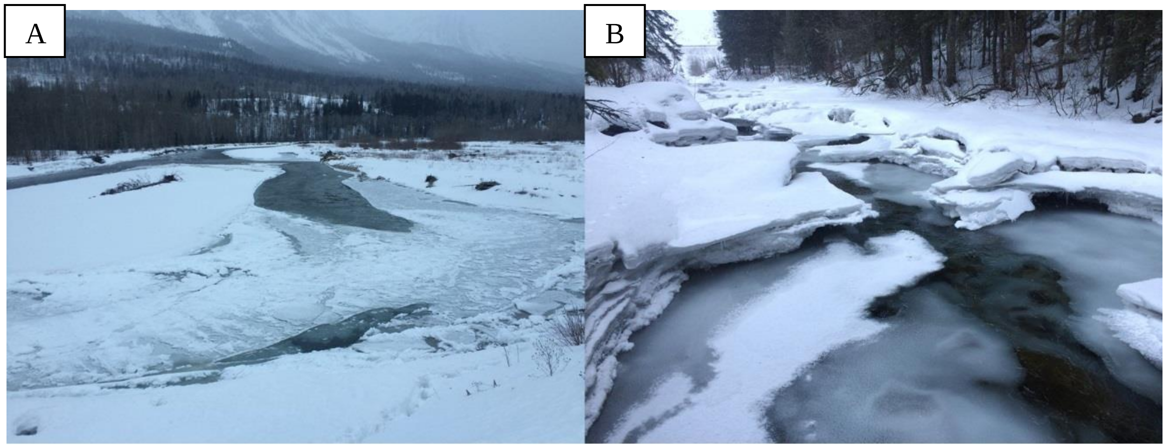

Figure 1.15 Comparison of ice formation in a large river (A: Elk River, 5th order) to that of a small stream (B: Alexander Creek, 3rd order) in British Columbia (at 1:250,000 map scale). Photos were taken on the same day during mid winter under a severe cold period with air temperatures between -25 and -30 °C. Note that the volume of ice formed within the channel of the small creek over winter in comparison to the volume of flowing water is considerably greater than that of the larger river. In addition, floating ice, in this case frazil floes (Prowse 1994), is dominant in the larger river and absent in the small creek.

Stream habitat is altered significantly by ice formation in winter (Cunjak 1996, Huusko et al. 2007, Brown et al. 2011). Ice formation in streams can be described within two main groups: static and dynamic (Huusko et al. 2007). However, in order to further and properly classify ice types, understanding the history of ice formation and its structure is fundamentally important (Michel and Ramseier 1971). The simplest and probably most widely recognized type of ice formation is through static means, which occurs on calm, density-stratified water bodies with little to no turbulence (e.g. lakes, ponds and pools) (Prowse 1994, Brown et al. 2011). Static ice formation results in ice that is uniform in structure and texture (Michel and Ramseier 1971), such as most types of surface ice. Here, static surface ice formation begins when the water temperature drops below the freezing point and ice crystals grow horizontally within a supercooled layer (initially only a few tenths of a millimeter thick) across the water surface (Michel and Ramseier 1971). The initial ice formation is termed the primary ice layer, also known as skim ice (Michel and Ramseier 1971). Further ice development occurs perpendicular to the primary ice layer, which thickens surface ice downwards in the water column (Michel and Ramseier 1971, Prowse 1994). Surface ice usually first occurs on stream and river margins, as well as around exposed cold objects (e.g. exposed boulders), growing laterally outward into flow (Prowse 1994) (**Figure 1.16**). Conversely, flooding on top of the primary surface ice will form superimposed ice growth, continually thickening surface ice upwards away from the stream bed (Michel and Ramseier 1971).

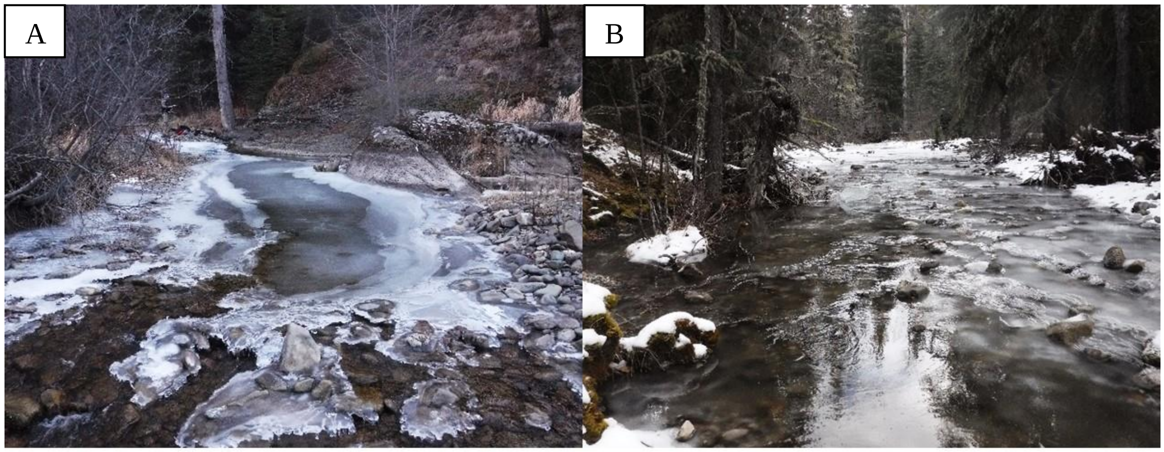

Figure 1.16 Early winter ice formation during the freeze-up period. A) Static surface ice formation on a pool. B) Dynamic frazil and anchor ice formation in a turbulent riffle.

However, the mechanism behind most ice formation in streams and rivers is much more dynamic because these environments lack widespread density-stratification due to turbulent mixing (Martin 1981, Stickler et al. 2010, Brown et al. 2011). In this case, water is cooled at the surface and is not allowed to stratify due to physical turbulence mixing the water column vertically (Prowse 1994, Brown et al. 2011). This mixing generates supercooled water throughout the entire river or stream depth (Prowse 1994, Brown et al. 2011). Specifically, at sub-freezing air temperatures supercooled water in streams and rivers can be at or near 0.01 to 0.1 °C below the freezing point (Martin 1981). Where conditions permit, the introduction of ice crystals from the surrounding environment at the water surface initiates ice formation (Martin 1981, Brown et al. 2011). The introduction of ice crystals in supercooled water subsequently leads to a chain reaction, where a process called "collision breeding" causes the formation of more and larger ice crystals (Martin 1981, Brown et al. 2011). Turbulence causes the growing crystals to remain suspended in the water column, which is termed frazil ice (Martin 1981, Brown et al. 2011) (**Figure 1.17**). During this time, the crystals are referred to as being "active" and may stick to many different cold surfaces or objects, such as rock substrate and woody debris (Martin 1981, Brown et al. 2011). It is when the ice crystals are deposited on the bottom substrate, that it is termed anchor ice (Martin 1981, Stickler and Alfredsen 2009, Brown et al. 2011). Anchor and frazil ice are typically formed in more turbulent areas of streams and rivers, such as riffles, as these areas contain enough physical turbulence to enable water to become supercooled and allow ice crystals to be mixed in the water column (Martin 1981, Brown et al. 2011). However, frazil and anchor ice may collect and accumulate in slower stream habitats such as runs (Stickler and Alfredsen 2009) and pools (Cunjak 1996). Where habitats and obstacles capture active ice (i.e. frazil ice) and slow its movement on the surface, further surface ice development can occur (Brown et al. 2011).

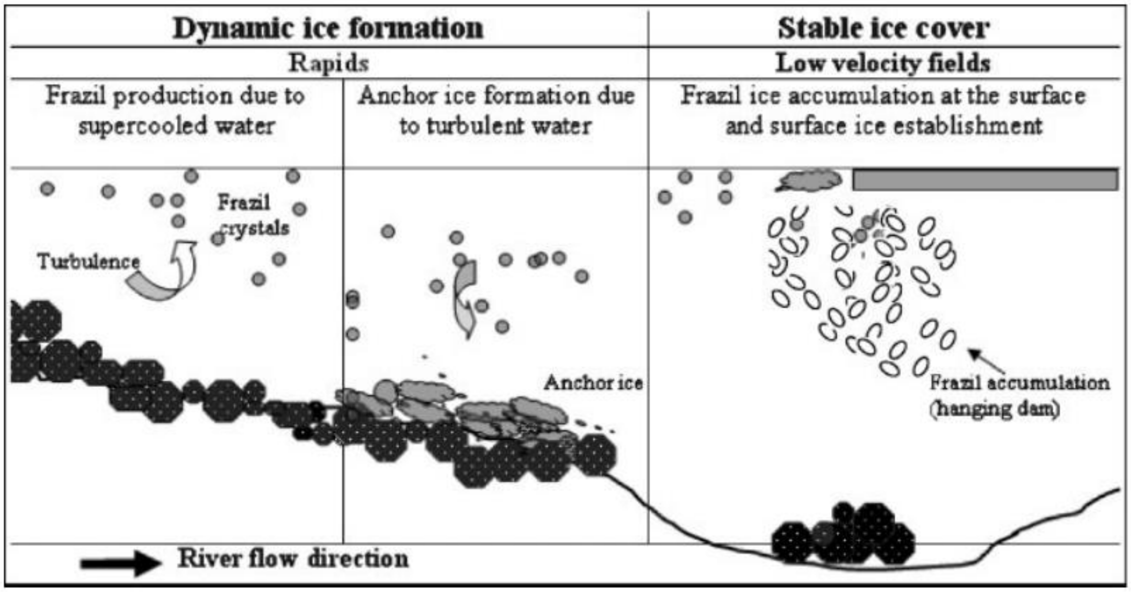

Figure 1.17 Ice formation in streams and rivers under dynamic and static conditions (Huusko 2007).

As ice forms in steep mountain rivers and streams, it can produce significant, dynamic and often challenging environmental conditions for aquatic organisms (Huusko et al. 2007, Stickler et al. 2010, Brown et al. 2011) (**Figure 1.18**). For example, numerous and growing frazil ice crystals can be hazardous to fish because they can abrade and plug the gills (Brown et al. 1993). Ice growth that penetrates deep enough into the substrate may freeze incubating eggs and alevins of fall spawning salmonids (Reiser and Wesche 1979, Curry et al. 1995, Baxter and McPhail 1999). Anchor ice can be resuspended into the water column, transporting course sediments (Martin 1981, Kempema et al. 2002) and aquatic invertebrates downstream (Benson 1955, Martin et al. 2000). Further frazil ice accumulation which is deposited downstream under surface ice cover leads to hanging ice dam formation (Brown et al. 2000, Huusko et al. 2007). Hanging ice dams can substantially restrict flow and increase water velocity, reducing available habitat and increasing fish movement (Brown et al. 2000, Huusko et al. 2007). Alternatively, when the current is fast enough and anchor ice becomes increasingly thick, anchor ice dams can be generated (Stickler et al. 2010). Anchor ice dams effectively block or limit all the stream or river discharge, leading to large fluctuations in water levels (Stickler et al. 2010). Furthermore, as water level and storage increase upstream of dams, water velocity is decreased (termed backwater effects), allowing surface ice formation in even high gradient and normally faster flowing areas (e.g. riffles) (Stickler et al. 2008, 2010). However, the stability of anchor ice dams can be reduced, due to increases in water pressure and temperature, leading to dams to drain or break during winter (Huusko et al. 2007). Consequently, because anchor ice dams significantly alter in-stream habitat, anchor ice dams have been linked to increased movement and changes in habitat use by juvenile salmonids during winter (Stickler et al. 2008). However, hanging surface ice left by lowering water levels, those areas especially were surface ice is supported by exposed boulders or narrow banks, causes sub-ice air gaps (Calkins 1989, Cunjak 1996) (**Figure 1.19**). Sub-ice air gaps can be ecologically significant stream habitats in winter because they limit further ice growth (i.e. acting as an insulating layer), allow aeration, provide an exit for winter emerging macroinvertebrates and corridors for sub-ice movement by small mammals (Calkins 1989, Cunjak 1996). In high elevation streams where snow accumulation is substantial, snow bridging across small streams also provide open-water conditions under ice (Chisholm et al. 1987, Calkins 1989).

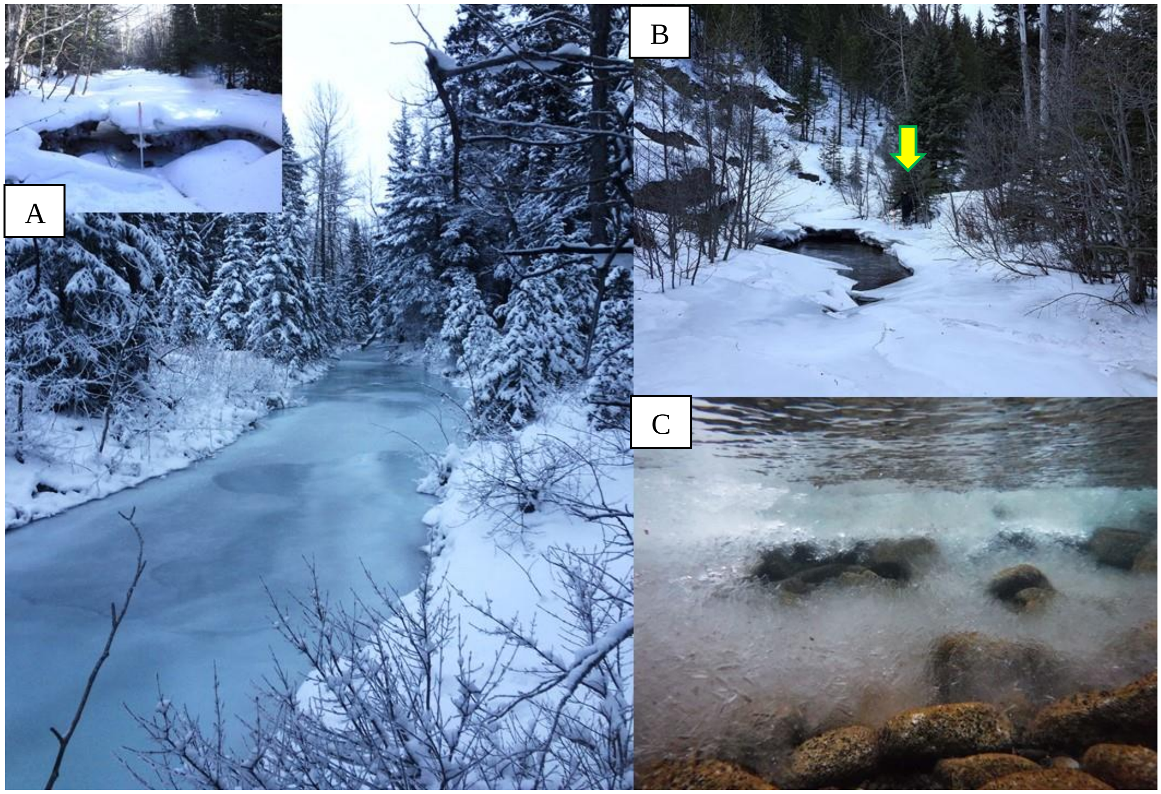

Figure 1.18 Some examples of substantial ice forming events including: A) during and after severe frazil and anchor ice formation; B) significant flooding and release as a result of an anchor ice dam (arrow pointing to the subject of scale, indicating the water level was raised over 1 m at just the head of a pool); C) Underwater view of frazil and anchor ice accumulation limiting available habitat.

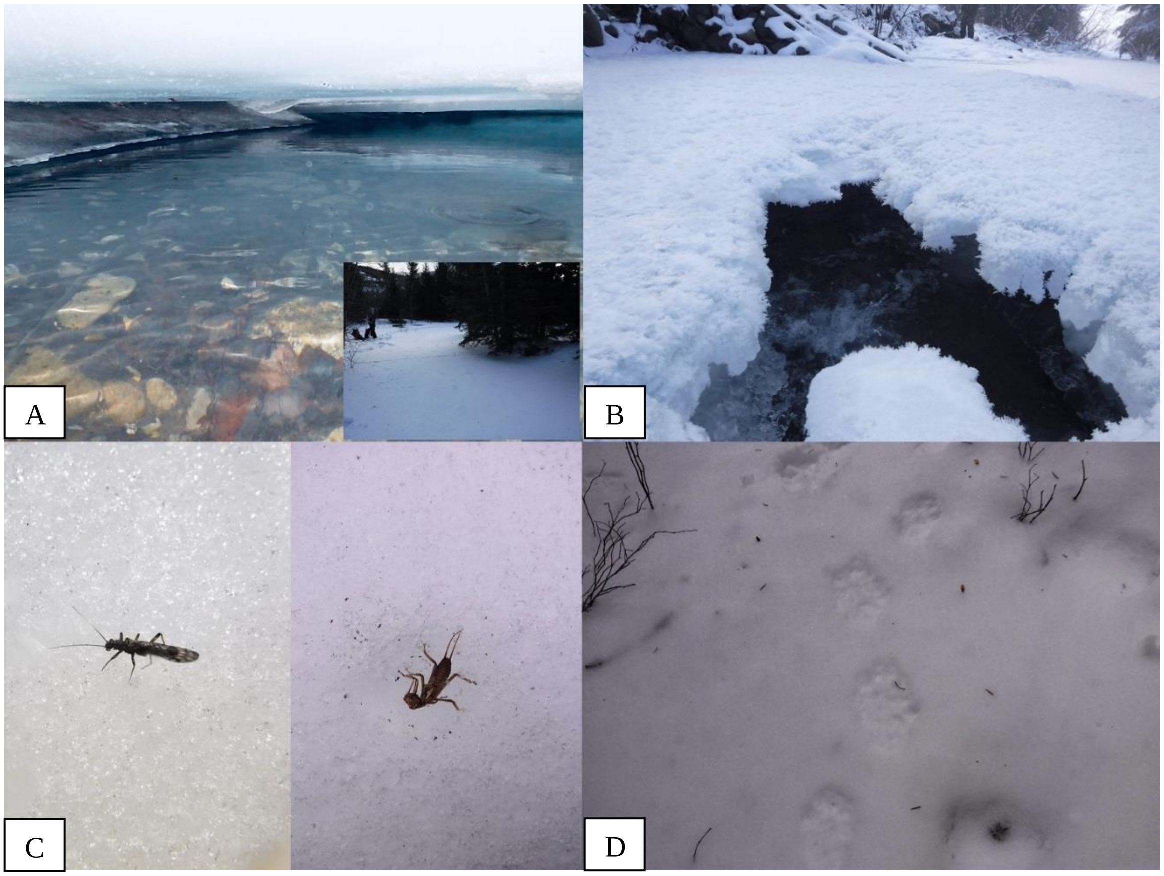

Figure 1.19. Sub-ice air gaps in winter, such as shown in A and B, are ecologically significant habitat features because they limit further ice growth (i.e. acting as an insulating layer), allow aeration, providing an exit for winter emerging macroinvertebrates (C), and may provide corridors for sub-ice movement by small mammals (e.g. mink) (D) (Calkins 1989, Cunjak 1996).

Typically, the most dynamic ice development occurs during the onset of winter, known as the freeze-up period (Prowse 2001, Huusko et al. 2007, Stickler et al. 2010). Once ice is formed and becomes stable, it can persist as long as air temperatures remain cold and discharge remains steady or declines (Brown et al. 2011). However, under certain conditions significant ice development can continue over winter reducing or completely eliminating usable habitat (Craig and Poulin 1975, Craig 1989, Schmidt et al. 1989, West et al. 1992). For instance in extremely cold environments such as the arctic, ice formation can continue and freeze streams completely (Craig 1989, Schmidt et al. 1989). In contrast, if air or water temperatures are warmed or rise during periods in winter, the stability of ice can be compromised (Lindstrom and Hubert 2011) and possibly initiate thermal ice break-up (Prowse 1994, Scrimgeour et al. 1994).

Groundwater can have a significant effect on ice persistence and development over winter in streams (Power et al. 1999, Lindstrom and Hubert 2011). Groundwater is water that is stored in underground aquifers, such as within the pore spaces of glacial-alluvial deposits, which gradually drains towards the valley bottom forming streams (Power et al. 1999). In contrast to surface water which is highly influenced by daily and seasonal air temperatures, groundwater is stored underground and is maintained at much more stable temperatures (e.g. near the mean annual air temperature) (Power et al. 1999, Kalbus et al. 2006). In areas where sufficient amounts of groundwater meet the surface, this leads to cooler stream water temperatures during the summer and relatively warmer water temperatures during winter (Power et al. 1999). If water temperatures are high enough in winter, this may lead to areas with little or no ice formation (Power et al. 1999). Due to the higher water temperatures and little ice formation, often groundwater influenced areas provide thermal refuge for fish during winter (Brown and Mackay 1995, Power et al. 1999). In some arctic systems the only overwintering habitat available to fish are those influenced by groundwater seeps (Craig 1989). Although, in areas located below groundwater inputs, dynamic ice forming processes can continue throughout winter, particularly during cold periods and may induce significant mid winter movements by salmonids (Brown 1999, Lindstrom and Hubert 2011). In cold arctic and alpine regions, continual flow of springs and groundwater influence over winter may form large accumulations of ice known as icings (Prowse 1994, Power et al. 1999). Icings may be several times the normal depth of the open-channel flow and 2-3 times the maximum thickness of ice formed due to regular thermal processes (Prowse 1994).

Salmonid Behaviour in Winter

In addition to ice, cold water temperature itself also limits usable habitat in winter due to the physiological constraints of fish. Fish are poikilotherms, meaning that a fish's body temperature closely matches that of the environment (i.e. water), influencing metabolism and thus activity (Cunjak 1988a). Consequently, at lower water temperatures a fish's ability to respond to a predator or changing environmental conditions is reduced, making fish particularly vulnerable in winter (Cunjak 1996, Huusko et al. 2007). However, salmonids do not hibernate and instead remain active during winter at low and near freezing water temperatures (Cunjak 1988a, 1996, Huusko et al. 2007). Continued activity during winter is crucial in order to respond to changing environmental conditions, such as avoiding the effects from dynamic ice formation. Activity level may vary among different salmonid life stages and species, giving rise to multiple strategies to increase survival under different water temperature and ice formation regimes (Cunjak 1996, Huusko et al. 2007).

The "squeezing effect" forces stream dwelling salmonids into alternative habitats due to ice formation and lowered water temperatures (i.e. physical exclusion of space) (Cunjak 1996, Power et al. 1999) (**Figure 1.20**). Once forced into alternative habitats, stream dwelling salmonids then seek and select conditions that facilitate reduced energy demand and predation risk (Cunjak 1996, Jakober et al. 1998). In fluvial environments, this often leads to large single or mixed species aggregations, which has been observed for many different salmonid species such as: Chinook Salmon *Oncorhynchus tshawytscha* (Hillman et al. 1987), Coho Salmon *Oncorhynchus kisutch* (Hartman 1965, Bustard and Narver 1975, Roni and Fayram 2000), Atlantic Salmon *Salmo salar* (Whalen et al. 1999, Mäki-Petäys et al. 2004), Rainbow Trout (Riehle and Griffith 1993), Brown Trout *Salmo trutta* (Cunjak and Power 1986, Heggenes et al. 1993, Dieterman et al. 2018), Cutthroat Trout (Brown and Mackay 1995, Jakober et al. 1998, 2000, Brown 1999, Harper and Farag 2004), Brook Char *Salvelinus fontinalis* (Cunjak and Power 1986), Bull Char (Jakober et al.

1998, Brown 1999), Arctic Char *Salvelinus alpinus* (Bendock 1981), Arctic Grayling *Thymallus arcticus* (Bendock 1981), Round Whitefish *Prosopium cylindraceum* (Bendock 1981), and Mountain Whitefish *Prosopium williamsoni* (Harper and Farag 2004, Carlson and Quinn 2005). Aggregation by salmonids, which is a type of shoaling behaviour, may be composed of smaller juveniles, but most often they are composed of larger adults (Heggenes et al. 1993, Jakober et al. 2000). Aggregations typically form in pools (Brown 1999, Jakober et al. 2000). Pools are the primary refuge for many stream dwelling salmonids during winter, as the increased depth and lowered water velocity allow for reduced energy demand and predation risk (Cunjak 1996, Brown et al. 2011).

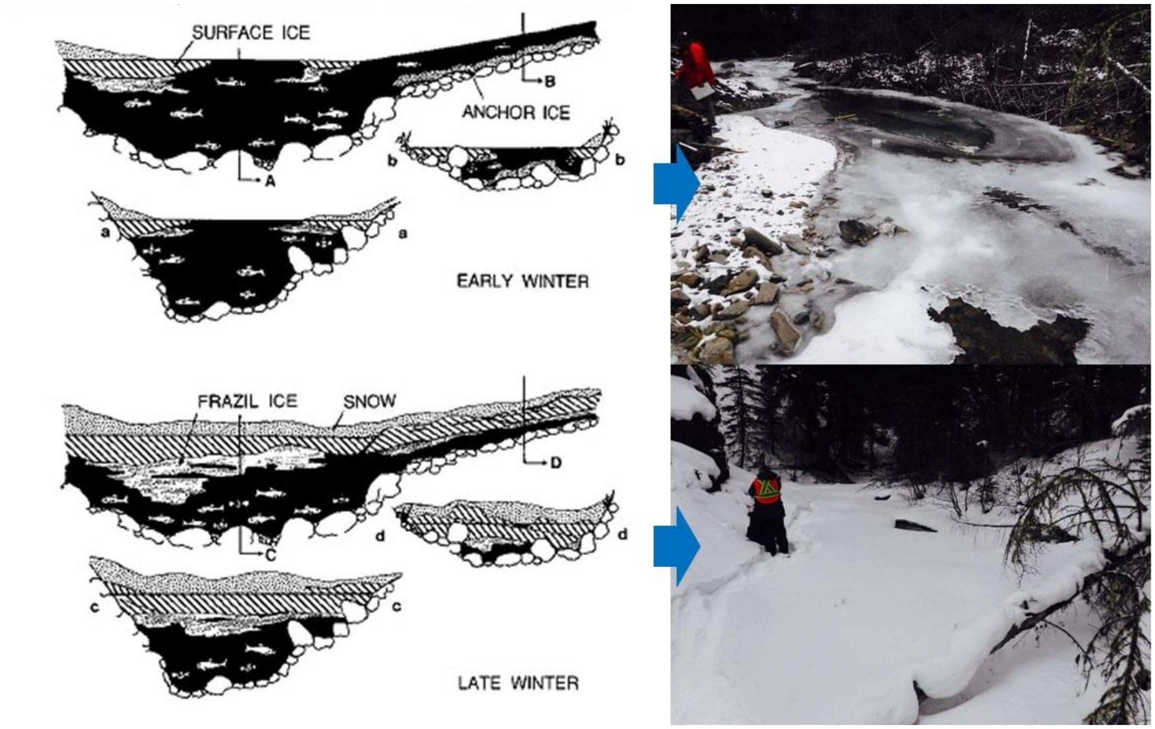

Figure 1.20 Conceptual and field representation of the changes in habitat availability in temperate streams (pool-riffle sequence) as winter progresses and ice accumulates. Figure adapted from (Cunjak 1996).

In contrast to aggregating in pools during winter, some species at early life stages and smaller body sizes may hide or conceal themselves in the interstitial spaces of substrate during winter

(Cunjak 1996, Huusko et al. 2007). Furthermore, concealment can be within shallow and faster flowing habitats alternative to pools, such as riffle-run habitats (Cunjak 1988b). This strategy is most often observed in young-of-year and juveniles less than 25 cm (Cunjak 1988b, Heggenes et al. 1993, Jakober et al. 2000) but has also been observed to occur in larger adults (e.g. up to 43 cm) (Meyer and Gregory 2000). During concealment, some individuals may even make movements down to 30 cm below the substrate surface in clean gravel and cobble (Erkinaro et al. 1994). Accompanying the concealment strategy is often a strong photonegative response, where salmonids hide during the day and emerge in large numbers at night (Jakober et al. 2000, Meyer and Gregory 2000). In many cases emergence at night is suggested to be due because of the need to feed (Contor and Griffith 1995, Griffiths et al. 2003) even at water temperatures approaching 0 °C (Murphy et al. 2006), but also because ice formation is greatest during the night (Heggenes et al. 1993). Because of the importance of concealment in winter, when interstitial spaces are limited, intra- and inter-specific competition can be high in salmonids (Gregory and Griffith 1996, Armstrong and Griffiths 2001, Harwood et al. 2002). In some cases where limited concealment habitat is available, mass exodus of smaller salmonids out of habitats or entire streams can occur (Armstrong and Griffiths 2001).

Conclusion

Winter is a critical period of survival for many salmonids residing in temperate streams (Cunjak 1996, Huusko et al. 2007). However, there is still limited knowledge for salmonid winter ecology in general (Cunjak 1996, Huusko et al. 2007), but specifically within high elevation mountain streams containing WCT (AWCTRT 2013). Land use and climate change impacts are major factors that may influence and alter winter habitat (Cunjak 1996). Improper land use practices within agriculture, forestry and mining can result in decreased habitat complexity in winter, which is needed by salmonids at different life stages to facilitate overwintering survival (Cunjak 1996). Furthermore, improper land use can alter streamflows during winter, inducing increased dynamic ice formation and stress on salmonid populations (Cunjak 1996). Even stream "enhancement" projects can have deleterious effects on salmonid populations if winter conditions are not considered (Cunjak 1996). Climate change in northern regions is expected to increase winter temperatures (Corell 2006), further altering winter regimes related to freeze and thaw cycles (Magnuson et al. 2000). Therefore, in order to properly manage and protect critical habitat and species at risk occurring in headwater streams now and into the future, a greater understanding into the dynamics of winter ecology is needed.

Thesis Objectives and Organization

Threatened pure WCT populations are currently under threats related to anthropogenic activities within the last remaining critical habitat for the species in Alberta (AWCTRT 2013). This thesis responds to the limited body of knowledge for WCT ecology within small, high elevation, mountain streams and is intended to help properly understand, assess and manage critical habitat for the last remaining pure populations of WCT in Alberta. The project will focus on and aim to understand the winter ecology of WCT and asses the potential effects of anthropogenic and global change, especially due to the direct impacts of proposed mining activities and development. The field sites were then selected accordingly and focus on the streams, Gold Creek and Blairmore Creek. Daisy Creek, a tributary within the upper Oldman watershed, and bordering the northern edges of drainage basin with Gold Creek and Blairmore Creek (**Figure 1.3**), will be used as an additional study stream. Specifically, this thesis will cover two important and broad objectives within those study streams:

1. How does the current habitat (physical, chemical, biological, and spatial) relate to WCT populations in small, high elevation, Rocky Mountain streams?
2. How do WCT populations of small streams respond to seasonal changes in habitat?

Chapter two of this thesis addresses the first main objective of describing and investigating the habitat and WCT populations in the study streams. Specifically, environmental aspects of specific habitat patches (pools) in relation to spatial considerations will be investigated. Further, environmental and spatial aspects of habitat will be related to WCT populations and their distributions within each study stream. Chapter three of this thesis addresses seasonal changes of WCT populations in relation to pool habitat in the study streams. Here, the winter period will be the focus, using summer habitat and population distributions as reference, then characterizing the main factors driving winter habitat use. Finally, chapter four will highlight the key findings of each previous chapter and present recommendations for managing WCT habitats and populations, and those specifically that are subject to potential future impairment by anthropogenic change.

Chapter 2 - Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*) Habitat and Populations in Three Headwater Streams

Abstract

Due to anthropogenic change many species have become threatened or endangered across the globe. In western Canada, Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*; WCT) are a species that have been severely impacted by anthropogenic change and are currently restricted to small headwater mountain streams and listed as threatened in Alberta. Recently, a coal mining project (Grassy Mountain Coal Project) was proposed near Blairmore, Alberta. Due to possible impacts to headwater stream habitat containing threatened WCT populations, research investigating the potential impacts were needed. Because of their importance to salmonids in small streams, pools were chosen as the main habitat patch of interest. The objectives of this research were to: 1) determine how landscape features at different scales influenced summer pool habitat characteristics within the chosen headwater streams; 2) determine which environmental, spatial, and biological factors composed of summer pool habitat influenced WCT populations. Among the three headwater streams studied, pool habitat only made up approximately 6 % of the available habitats during late summer. Large scale stream features related to differences in watersheds and geomorphology gradients were found to have a superimposed influence on smaller scale pool habitat characteristics. Specifically, characteristics, such as those related to physical habitat, water quality and connectivity, influenced pool habitat characteristics. Lastly, analysis of WCT populations showed that these pool characteristics significantly influenced WCT abundance and biomass. Changes in pool characteristics such as further decreased connectivity, shallowing of pools, and reduced cover due to further anthropogenic change will have negative effects to threatened WCT populations in these headwater streams.

Introduction

Due to anthropogenic change, many species across the world are threatened to become extinct (Baillie et al. 2004, Venter et al. 2006). Canada currently lists 521 species as endangered or threatened under the federal *Species at Risk Act* (SARA) (COSEWIC 2018). In the mountain ranges of western Canada, Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*; WCT) are a species that have been severely impacted by anthropogenic change, specifically urbanization, agricultural and industrial development (AWCTRT 2013). The combined threats of habitat loss and alteration, competition with non-native species (e.g. Brook Char *Salvelinus fontinalis*), as well as genetic introgression with Rainbow Trout *Oncorhynchus mykiss* have reduced pure WCT populations to only 5 % of the historical range in Alberta (Mayhood & Taylor 2011; AWCTRT 2013). This has led to WCT being listed as threatened in Alberta and as of special concern in BC under SARA (COSEWIC 2016). Most WCT populations are now restricted to high elevation headwater streams, and the sole mechanism in maintaining genetic purity among many WCT populations are physical barriers, isolating WCT populations from downstream Rainbow Trout populations (Rasmussen et al. 2010).

Anthropogenic activities on the landscape are increasing the pressure and impact on aquatic resources within critical habitats of WCT (Farr et al. 2017, 2018). Habitat loss and fragmentation across landscapes forces managers to prioritize, conserve and restore habitat for threatened species within watershed networks (Rieman and Dunham 2000). One of the principle land-uses within the Eastern Slopes of the Rocky Mountains that impact aquatic environments is large scale surface mining. In contrast to the underground mining methods of the past (Felske 1991), large scale surface mining along the mountains and foothills of Alberta has developed over time as commonly used practice for the removal of coal (Government of Alberta 2018). Concurrently, surface mining activities across North America have become of increased interest due to the growing amount of evidence indicating the negative effects on aquatic ecosystems, namely altered hydrology and water pollution (Palmer et al. 2010). Recently, a coal mining development (Grassy

Mountain Coal Project) was proposed near Blairmore, Alberta. It is expected that these activities will influence and alter the hydrology of nearby basin catchments (SRK Consulting Inc. 2016), likely impacting fish habitat. The future coal mine impacts are of particular interest due to the presence of threatened WCT in both headwater streams surrounding the mine site, Blairmore Creek and Gold Creek (Fisheries and Oceans Canada 2014).

Differences in landscape features (e.g. vegetation, geology, land use, climate) play an important role in influencing characteristics of streams and rivers (Charlton 2008), which ultimately influences habitat. Landscape features influence how water enters and exits streams and how sediment erosion, transport, and deposition occur, which all influence channel formation (Charlton 2008). Headwater streams, particularly those in mountainous areas, provide highly heterogeneous and complex systems due to the considerable spatial and temporal variability among landscape features, those of which determine local habitat conditions. Often, salmonids (i.e. trout, char, salmon) require specific microhabitat features during different seasons and life stages, such as for spawning, rearing, and overwintering (Bjornn and Reiser 1991). The microhabitat features water velocity, cover, depth, and substrate vary among specific habitat patches (e.g. riffles, runs, pools) and are considered to be critical components of salmonid ecology (Bjornn and Reiser 1991).

Spatial considerations of habitat are often lacking in ecological research, particularly regarding salmonids in fluvial environments (i.e. streams and rivers) (Rieman and Dunham 2000, Falke and Fausch 2010). Suitable habitat patches that fish require are contained within a linear network of less suitable habitat. Within the stream network, required habitat patches also occur at varying distances from one another. Barriers within the network further restrict movement among habitat patches, either completely or temporarily. Spatial position of needed habitat patches within stream networks have a significant influence on obligate aquatic organisms, such as fish, as movement by those organisms is restricted to only within the network (Rieman and Dunham

2000). Thus, when there are strong effects of habitat heterogeneity, spatial scale, and dispersal in fluvial environments, fish populations may become spatially structured (i.e. metapopulation theory) (Rieman and Dunham 2000, Falke and Fausch 2010). The headwater stream habitats that are currently occupied by WCT along the Rocky Mountains of southern Alberta, have been shaped by past glacial and tectonic forces which provide a wide range of landscape features (Beaty 1975). These features in landscape likely dictate the characteristics and spatial position of habitat patches within these headwater stream networks and thus influence WCT populations.

This study investigates the ecological impacts of environmental and spatial factors influencing WCT populations within potentially mine impacted headwater streams. Pools were identified as the main habitat patch of interest, as they are often noted in the literature to be the primary habitat of many stream dwelling salmonids (Bjornn and Reiser 1991). The objectives of this study are to: 1) describe how landscape features at different scales influence summer pool habitat characteristics within the chosen headwater streams and 2) determine which environmental, spatial, and biological factors composed of summer pool habitat influence WCT populations. The overall goal of this study is to make recommendations to aid in the conservation of WCT in headwater stream habitats, specifically considering a proposed large-scale surface coal mine.

Materials and Methods

Study Area

The study area is located along the east slopes of the Rocky Mountains of Southern Alberta, Canada (**Figure 2.1**). I selected three study streams within the larger Oldman watershed drainage system. Specifically, the study streams Gold Creek and Blairmore Creek are located within the Crowsnest River sub-watershed, and Daisy Creek within the Upper Oldman River sub-watershed. All three streams share drainage basin borders at their headwaters and occur around the proposed Grassy Mountain Coal Project site. Total watershed area is similar among streams, with the largest being Daisy Creek (64 km^2), followed by Gold Creek (63 km^2), and Blairmore Creek (51 km^2). At their largest point and considering only perennial tributaries, all streams are 3rd order in size (Strahler 1964, Bain and Stevenson 1999). Study sites are located along the length of all study streams at elevations between 1340 m to 1880 m, with main channel slopes ranging between 19.8 m/km to 22.5 m/km. Presence of pure and near pure WCT occur among all streams, with other species including native Bull Char *Salvelinus confluentus* (Daisy Creek), introduced Brook Char (Blairmore Creek and Gold Creek), native Mountain Whitefish *Prosopium williamsoni* (Blairmore Creek and Daisy Creek), and introduced Rainbow Trout (Blairmore Creek).

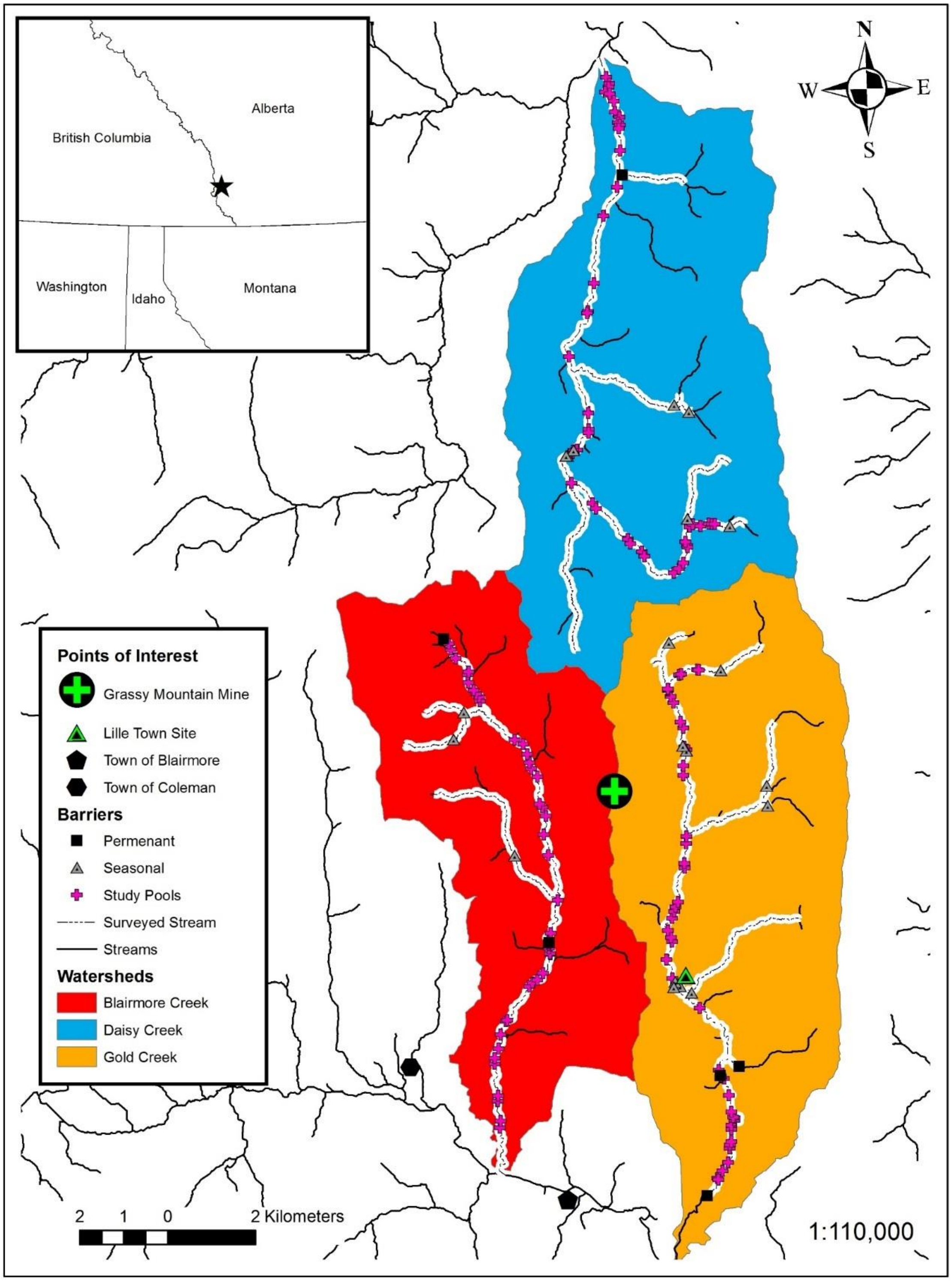

Figure 2.1 Study area map showing study stream watersheds, study sites (pools, *N* = 133), and barriers used in summer analysis. Surveyed stream area includes data from summers 2016 and 2017. Points of interest include Grassy Mountain (site of the proposed Grassy Mountain Coal Mine), the historical town of Lille, and the towns of Coleman and Blairmore of the Crowsnest Pass.

Habitat

Sampling Strata

All streams where surveyed along their entire length to quantitatively characterize habitat within the streams' main stems. Wetted width was measured to the nearest meter at 100 m transects along the entire length of the study streams and was later used to estimate wetted area (m^2) of each stream. Each stream was stratified into three geomorphic segments, designated here as: canyon, alluvial, and headwater. Each segment contains characteristics of differing geomorphology, dictating the formation and characteristics of pool habitat. Each segment occurs in a consistent sequential order on each stream where the canyon is characterized by a highly confined, bed rock dominated channel (lowest elevations, 3rd order); the alluvial is characterized by an unconfined and alluvium (fluvial or glacial) dominated channel (mid elevations, 3rd to 2nd order); and the headwater is characterized by a moderately confined, boulder dominated channel (highest elevations, 2nd to 1st order).

The study focuses on pools as the main habitat patch of interest. Pools were defined as areas within the stream with an average lower velocity and greater depth than the surrounding habitat. All pools throughout each of the streams entire length were identified, georeferenced with a global positioning system (GPS)(GARMIN, model 64s), characterized by type using a habitat classification system (modified from Flosi *et al.* 1998), and rated for habitat quality. Pool types included: dammed pool, lateral scour pool, mid-channel pool, plunge pool, side channel pool, step pool, and trench pool. The rating for habitat quality (low, medium, high) was based on subjective sampling (Brown and Austen 1996), where measured habitat values and the available literature suggested the most favourable habitat for stream dwelling salmonids. Suitable pool habitat was rated based on the maximum pool depth and available cover. Pools that were very deep and had the presence of cover were classified as high-quality pools. Pools that had diminished factors of depth or cover were classified as medium-quality. If pools were shallow and had little or no cover, these pools were classified as low-quality pools. Since high-quality pools were limited, all high-quality pools were sampled. Thirty randomly selected low and medium-quality pools were sampled among each stream, which were divided equally among geomorphic segments (5 low and 5 medium quality pools each per stratum). Habitat and fish population data were collected for each selected pool during the summer low flow period (mid to late August and early September) of 2016 and 2017.

Pool Habitat

Pool length (longest axis) and wetted width (widest axis) were measured to the nearest meter, and later were used to estimate pool area (m^2). Pool area was estimated using a standard ellipse area equation:

$$A = \pi \, w \, l$$

Equation 2.1

where π = constant; *w* = wetted width divided by two; *l* = length divided by two. This was assumed to better approximate the typical oval shape observed among pools since only one length and width measurement were made (modified from Heifetz *et al.* 1986). Maximum depth was measured with a meter stick or measuring pole to the nearest centimetre at the deepest point within the pool. Pool water velocity (m/s) was estimated using the float method (Bain and Stevenson 1999). In this case, a neutrally buoyant object (an orange), was randomly placed upstream of the pool and floated through the length of the pool a minimum of five times. The average water velocity for the pool was then calculated. A multimeter (YSI Inc., model 556 MPS) was used to measure water quality parameters such as temperature (nearest 0.1 °C), conductivity (µS/cm), and dissolved oxygen (mg/L). Canopy coverage (%) was measured directly above the center of the pool, approximately 30 cm from the water surface with a densiometer (Bain and Stevenson 1999).

Qualitative estimates of habitat that were visually estimated consisted of available habitat cover, bank condition, turbidity, silt cover, and dominant substrate. Available habitat cover was visually estimated in relation to pool area (aerial estimate) (Department of Fisheries and Oceans and British Columbia Ministry of Environment 1989, Harper and Farag 2004). Habitat cover was defined here as the proportional area (%) of small woody debris (diameter < 30 cm), large woody debris (diameter > 30 cm), root mass, vegetation overhang, boulder, and undercut bank. Each cover type was estimated individually, and the percentages were then summed and converted to an available habitat cover score. The percent available habitat cover was scored as follows: 0-20 % (1), 21-40 % (2), 41-60 % (3), 61-80 % (4), 81-100 % (5). Each pool bank (river right, river left) was separately evaluated for bank condition, rated as being low (no to little vegetation cover and/or loose small rocky material), moderate (moderate vegetation cover with some root mass and/or moderate rocky material cover including larger cobbles and boulders), or highly stable (high vegetation cover with deep root mass, multiple species and age classes and/or complete rocky material cover with larger boulders or bedrock). Bank type and habitat evaluation was modified from descriptions provided by Bain & Stevenson (1999). These ratings were later converted to a numeric value (low = 1, moderate = 2, high = 3) and an average was taken for the pool. Presence-absence of silt cover was noted by visually inspecting fine sediment cover over the substrate surface area. Turbidity was indirectly assessed based on visibility assessments during snorkel surveys and rated as: none, low, moderate, high, or very high (see fish surveys for further detail). Dominant substrate was classified as the substrate material that covered the greatest proportion of pool area. Dominant substrate was based off of a modified Wentworth classification system (Bain and Stevenson 1999), where substrate types were categorized as either bedrock, boulder (> 256 mm), cobble (256 – 64 mm), pebble (63 – 16 mm), gravel (15 – 2 mm), sand (1 – 0.06 mm), silt (< 0.059 mm) or organic material.

Water velocity was only assessed during the summer of 2017 and held constant for the missing year assuming no significant change in flow. No flow data was available at the time of this study to allow comparisons between years 2016 and 2017. Available habitat cover, canopy cover and dominant substrate were assessed in detail during the summer of 2016, and reassessed if there was significant change to the pool in 2017 (e.g. due to spring flooding).

Spatial Data

Spatial data were derived from the geographic information system (GIS) software ArcMap (ESRI 2016) and field collected georeferenced data. Data were collected during summer surveys of 2016 and 2017 with a handheld global positioning system (GPS). Key tributaries to the study streams' main stems were also surveyed for additional information on pool habitat and barriers during the summer of 2017. During initial surveys all pools identified were georeferenced. During the same time, streams and barriers were also georeferenced. For this study, only barriers previously known or obvious were considered, as full assessments to determine passability for all potential barriers encountered were not possible during the time period of this study. Barrier types for analysis included: water falls, weirs, debris jams and subsurface flow areas (dry sections of creek bed). Debris jams were frequently encountered on smaller tributaries in high gradient areas and were only considered when a full drop was greater than one meter (Kondratieff and Myrick 2006) and/or had flow through the structure (i.e. no water passing over the barrier). Georeferenced data collected in the field consisted of: pools (points), streams (lines), and barriers (points). These data were then later used in GIS for network analysis and watershed analysis.

Network analysis allowed the calculation of distances regarding spatial position among pools within the stream network. Longitudinal position (km) of each pool was determined by measuring the distance from the upstream most boundary (end of all surface flow or other impassable barrier), to each downstream pool. To assess connectivity for each study pool, the distance to the nearest pool upstream and downstream (m), and distance to the nearest barrier upstream and downstream (m) were measured. Different barrier types were set as either “active” (i.e. fish are not able to pass the barrier) or “inactive” (i.e. fish are able to pass the barrier) during the nearest pool analysis depending on flow direction and fish movement. For example, waterfalls and weirs allow fish movement in the downstream direction, but no fish movement in the upstream direction, so these barriers would be set as “inactive” for downstream calculations and set as “active” for upstream calculations. In contrast, subsurface flow sections do not allow any fish movement in either direction and so these barriers would always be set as “active”. Lastly, the total number of alternate pools was also counted for each study pool. In this case all barriers, including falls and weirs, were kept “active” during the analysis. Even though fish can access pools downstream of falls and weirs, if they were to go over the barrier, they would not be able to return to the former pool, effectively removing itself from the previous population. In the cases were no barrier was present below the study pool and connectivity extended into the larger watersheds (Crowsnest and Oldman), the maximum value plus a 50 % increase was used as the limit. This was done for both distance calculations and pool counts to avoid adding disproportionate weight to the analysis for those pools, yet still reflect the greater connectivity present.

Watershed area (km^2) and elevation (m) were also determined by GIS. This was done using a 10-meter digital elevation model (DEM) (Canadian GIS & Geomatics 2017) and the georeferenced stream and pool data. Elevation was determined by extracting DEM elevation values with matched pool location data. Watershed analysis was done to calculate watershed area for each pool using a flow direction raster derived from the DEM.

Fish Survey

Fish population surveys were performed using the least invasive methods possible, due to WCT being a threatened species (COSEWIC 2016). Snorkel surveys have been used as a non-invasive technique to estimate population size, size-class, and habitat use (Thurow 1994, O'Neal 2007). Snorkel surveys for selected pools occurred just prior to habitat sampling with the snorkeler entering the stream from the downstream end of the pool so to not spook or disturb fish. Visibility was periodically checked by measuring the distance from a stationary object resembling a salmonid silhouette (a 20 cm long trout fishing lure with parr marks was used) to the maximum distance where the snorkeler could no longer see the object (Thurow 1994). Snorkel surveys were only performed if visibility in the pool was at a minimum of 2-4 m depending on stream size (Thurow 1994). When snorkel surveys encountered complex cover (e.g. undercut banks, log jams, boulder crevasses) that had limited amounts of light, an under-water flash light was used.

Within pools fish were identified to species, counted, and put into size classes of 10 cm increments (< 10 cm, < 20 cm… to < 80 cm), with the exception of < 5 cm individuals, as suggested by Thurow (1994). Species identification during snorkel surveys were done using the key characteristics described for each species present in the study streams (Nelson and Paetz 1992, Thurow 1994, Behnke 2002). Genetically pure WCT have been recorded above the lowest barrier (weir) located on Gold Creek, and in the headwaters of both Daisy Creek (Rasmussen et al. 2010) and Blairmore Creek (Fisheries and Oceans Canada 2014). However, the ability to distinguish WCT hybrids during these surveys based on phenotypic characteristics (i.e. morphological characteristics) such as coloration and spotting pattern are unreliable (Allendorf et al. 2004, Robinson 2007) and thus unless fish provided all phenotypic characteristics of positive Rainbow Trout identification, they were counted as WCT.

Abundance within each pool and for each species was calculated based on the number of individuals per estimated surface area (m^2). Biomass (g/m^2) was estimated for WCT in each study pool using an equation derived from length-weight relationships of 1,235 WCT (Robinson 2007), predicting the mass (g) of an individual WCT based on the mean size class length (cm). The equation is:

$$WCT\ mass\ (g) = 0.0122x^{3.0009}$$

Equation 2.2

where x is WCT length (cm). Individual WCT masses were then summed and the total mass was divided by the pool area. Finally, a species diversity score was given to each pool, calculated as the sum of all possible species observed occurring to the point of last observation in the upstream direction. Here it is assumed if at the last point a species was observed along the length of the stream, it could be present in all pools below that point. Thus, a species did not need to be present during the time of sampling to be counted in species diversity score.

Statistical Analysis

To identify patterns among streams and geomorphic segments, a multivariate analysis approach was used. The environmental and spatial variables varied greatly by scale and in magnitude. As data often did not meet assumptions of linearity and normality, non-metric multidimensional scaling (NMDS) was chosen as the most appropriate method. Specifically, NMDS was used to assess the underlying gradients among study pools surveyed during the summer of 2016. The R package *vegan* was used to perform the NMDS analysis (Oksanen et al. 2018). Essentially NMDS transforms the variable information into distances (Bray-Curtis was used) and maps them in a multidimensional space (ordination space) (Oksanen 2013). Data were square root transformed and then subjected to Wisconsin double standardization (Oksanen 2013). Wisconsin double standardization divides observations by their maxima and standardizes by the sites unit totals (Oksanen 2013). This transformation results in dissimilarity indices becoming identical in rank ordering (Oksanen 2013). All environmental and spatial variables were used for the NMDS analysis except those variables found highly colinear (e.g. $r > 0.85$ among elevation, longitudinal distance, and watershed area) based on Spearman Rank correlation. In this case the variable that had the highest correlation with WTC abundance and biomass was chosen for the analysis. Lastly, significance of factors within NMDS analysis are derived from class centroids, where a goodness of fit statistic is calculated from R^2 values and tested with permutations (e.g. 999 permutations) (Oksanen 2013).

Once gradients were visually assessed and key environmental and spatial variables identified, differences among creek and geomorphic segment groups were tested with one-way permutation analysis of variance (permANOVA) using the package *LmPerm* in R (Wheeler and Torchiano 2016). PermANOVA was used as some data remained non-normally distributed after transformations (using Shapiro-Wilk test (Quinn and Keough 2002)). A set number of permutations (10,000), was used to derive the likelihood (P) of group mean differences. When comparing means WCT abundance and biomass among streams, one-way analysis of variance (ANOVA) was used. To make multiple comparisons between means, Tukey’s honestly significant difference (HSD) test was used (Quinn and Keough 2002).

Multiple Linear Regression Model

To identify key variables influencing WCT abundance and biomass in pools during the summer of 2016, a multiple linear regression approach was used. A total of 133 observations were used for model development, to identify key variables influencing WCT abundance and biomass in pools during the summer of 2016. Correlation analysis was used to determine the correlation (and its significance) between each independent variable and WCT abundance and biomass in pools using the R package *Hmisc* (Harrell 2017). Some independent variables remained non-normally distributed and so the robust Spearman Rank based correlation was used (Quinn and Keough 2002). Significant correlations ($P \leq 0.05$) between independent variables and dependant variables were investigated further. If a pair of independent variables were highly colinear ($r \geq 0.75$) one of the two variables was eliminated from the analysis. The remaining variables were used for model development.

All categorical variables (i.e. factors) for which have values that range on a scale (e.g. available habitat cover score, bank condition, turbidity, and silt cover) were treated as continuous variables and transformed into numeric values (Quinn and Keough 2002). Other categorical variables such as creek, geomorphic segment, pool type, and dominant substrate were instead interpreted using their factor levels (Quinn and Keough 2002). For example, coefficients for categorical variables in the model were derived through a partial regression slope, which measures the difference in the adjusted mean of the dependant variable between each level of the category to the reference category (e.g. reference category being the highest adjusted mean) (Quinn and Keough 2002). For the remaining independent variables with highly skewed distributions logarithmic transformations ($X = \log_{10}$ or $X = \log_{10} [X + 1]$ if zeros were present) were able to approximate normality and linearity (Quinn and Keough 2002). To confirm if normality and linearity was achieved through transformation, histograms were visually assessed, and a Shapiro-Wilk test was performed.

Stepwise regression procedures using the R package *MASS* (Venables and Ripley 2002), utilized forward and backward selection to provide the most parsimonious model as determined by the lowest Akaike Information Criterion (AIC) (Quinn and Keough 2002). Multicollinearity was checked after model development by the variance inflation factor using the R package *car* (Fox and Weisberg 2011), where values less than 5 were considered optimal (Craney and Surles 2002). Further, model assumptions were evaluated using diagnostic plots for normality, linearity, and influential observations (Zuur et al. 2007). Relative importance of model variables (%) were calculated using the R package *relaimpo*, in which the R^2 partitioned averaging over orderings method was used (Grömping 2006).

After a model was produced and assumptions met, to see if observed trends were consistent through time, the equation derived from the summer 2016 data was used to predict WCT abundance and biomass in pools using data values from the summer of 2017. The predictive ability was determined similar to common cross-validation techniques (Hair et al. 2006), where the accuracy of estimates were evaluated by comparing predicted and actual values through: (1) assessing the root mean square error; (2) assessing the mean absolute error; and (3) examining Pearson correlation coefficients between observed and predicted values (Wiley et al. 2004, Walther and Moore 2014). Root mean square error and mean absolute error were calculated using the R package *Metrics* (Hamner and Frasco 2017).

All statistical analyses were conducted using the programming language R (R Core Team 2016) running within RStudio (RStudio Team 2015). The package *ggplot2* was used for graphical display of data (Wickham 2009). All independent variables encompassing environmental, spatial and biological components of pool habitat were also given variable codes (**Table 2.1**).

Table 2.1 Descriptions and codes for all independent variables used in analyses.

Component of Pool Habitat	#	Independent Variable Description (Units)	Code
Spatial	1	Study Streams *	CREEK
	2	Geomorphic Segment *	SEGMENT
	3	Elevation (m)	ELEV
	4	Longitudinal Distance Downstream (km)	LONG
	5	Watershed Area (km^2)	WTSH
	6	Distance to Nearest Pool Downstream (m)	DISNPD
	7	Distance to Nearest Pool Upstream (m)	DISNPU
	8	Distance to Nearest Barrier Downstream (m)	DISNBU
	9	Distance to Nearest Barrier Upstream (m)	DISNBD
	10	Alternate Number of Pools	ALTPOOL
Chemical	11	Conductivity (µS)	COND
	12	Dissolved Oxygen (mg/L)	DO
	13	Water Temperature (°C)	TEMP
Physical	14	Pool Type *	POOLTYPE
	15	Maximum Depth (m)	MAX_DEPTH
	16	Area (m^2)	AREA
	17	Pool Velocity (m/s)	VEL
	18	Turbidity [c]	TURB
	19	Dominant Substrate *	DOMSUB
	20	Silt Cover [a]	SILT
	21	Available Habitat Cover (%)	HABCOV
	22	Canopy Coverage (%)	CANOPY
	23	Bank Condition [b]	BCOND
Biological	24	Species Diversity	SPDIVERSITY
	25	Bull Char Abundance (BLCH/m^2)	BLCH_ABUND
	26	Brook Char Abundance (BKCH/m^2)	BKCH_ABUND
	27	Mountain Whitefish Abundance (MNWH/m^2)	MNWH_ABUND

* variable is a factor – see methods for level classification
[a] values are scores ranging 1 to 2
[b] values are mean scores ranging 1 to 3
[c] values are scores ranging 1 to 5

Results

Habitat

A total of 602 pools were identified across the three study streams (Blairmore *N* = 172, Daisy *N* = 177, and Gold *N* = 253), from which a total of 133 pools were sampled (Blairmore *n* = 42, Daisy *n* = 44, Gold *n* = 47). During the summer of 2017, 4 study pools on Blairmore were not surveyed due to increased turbidity from a tributary draining off Grassy Mountain. The increase in turbidity did not meet the required minimum visibility for snorkel surveys to take place.

A total of 12 barriers were identified in the mainstems of the study streams during the summer of 2016 and a total of 11 barriers identified during the summer of 2017 (**Table 2.2**). In addition, a total of 10 barriers limiting upstream movement by WCT were observed on main tributaries to the study streams during the summer of 2017, which included fall, debris, and subsurface flow barriers.

Table 2.2 Barriers identified on study stream mainstems during the summers of 2016 and 2017.

Barrier Type	Blairmore Creek	Daisy Creek	Gold Creek
2016			
Subsurface Flow	0	4	4
Falls	2	0	1
Weir	0	0	1
Debris Dams	0	0	0
2017			
Subsurface Flow	0	3	4
Falls	2	0	1
Weir	0	0	1
Debris Dams	0	0	0

Among all study streams, pools within channel mainstems only accounted for on average 6 % of the entire stream surface area. Lateral scour pools were the most common pool type among pools sampled for habitat (35.3 %), followed by step pools (30.1 %), mid-channel pools (20.3 %), plunge pools (9.8 %) and all other pool types (5.2 %) (**Figure 2.2**). There was no statistical difference among streams for pool type (permANOVA: $F_{2,130} = 0.899$, $P = 0.409$), however, pool type differed significantly among geomorphic segments (permANOVA: $F_{2,130} = 6.05$, $P = 0.003$). Pool type was significantly different between canyon and alluvial segments ($P = 0.002$), but not between alluvial and headwater segments ($P = 0.245$) or between canyon and headwater segments ($P = 0.143$). Alluvial segment pools were predominantly lateral scour pools (44.7 %). In contrast, canyon segment pools were predominantly step pools (48.0 %). Headwater segment pools were comprised of mixed pool types including lateral scour pools (31.1 %), mid-channel pools (26.6 %), step pools (24.4 %), and plunge pools (17.7 %).

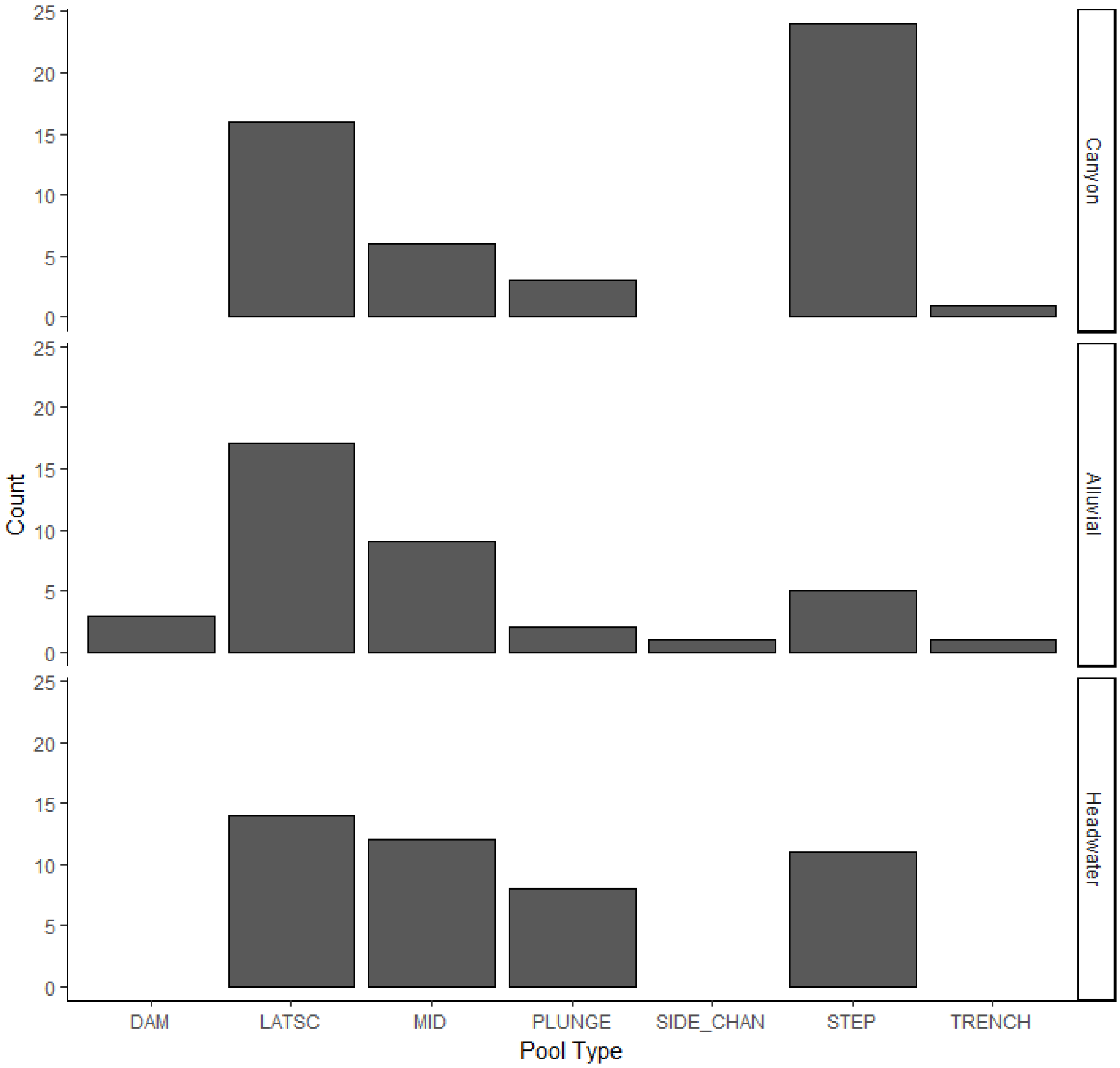

Figure 2.2 Total count of pool types sampled in all study streams among geomorphic segments during the summer of 2016 (*N* = 133). For pool type code descriptions: DAM = dammed pool; LATSC = lateral scour pool; MID = mid-channel pool; PLUNGE = plunge pool; SIDE_CHAN = side channel pool; STEP = step pool; and TRENCH = trench pool.

Cobble was the most common dominant substrate found among all study pools (47.4 %) (**Figure 2.3**). There was no statistical difference among streams for dominant substrate (permANOVA: $F_{2,130}$ = 2.14, P = 0.122), however, dominant substrate differed significantly among geomorphic segments (permANOVA: $F_{2,130}$ = 4.06, P = 0.019). Dominant substrate was significantly different between canyon and headwater segments (P = 0.016), but not between canyon and alluvial segments ($P = 0.205$) or between alluvial and headwater segments ($P = 0.611$). Pool dominant substrate in alluvial segments was mainly comprised of cobble (71.1 %). Pools within canyon segments were dominated by cobble (46.0 %) and bedrock (24.0 %). Pools within headwater segments had mixed dominant substrate including: gravel (31.1 %), cobble (28.9 %), boulder (20.0 %), and pebble (17.8 %).

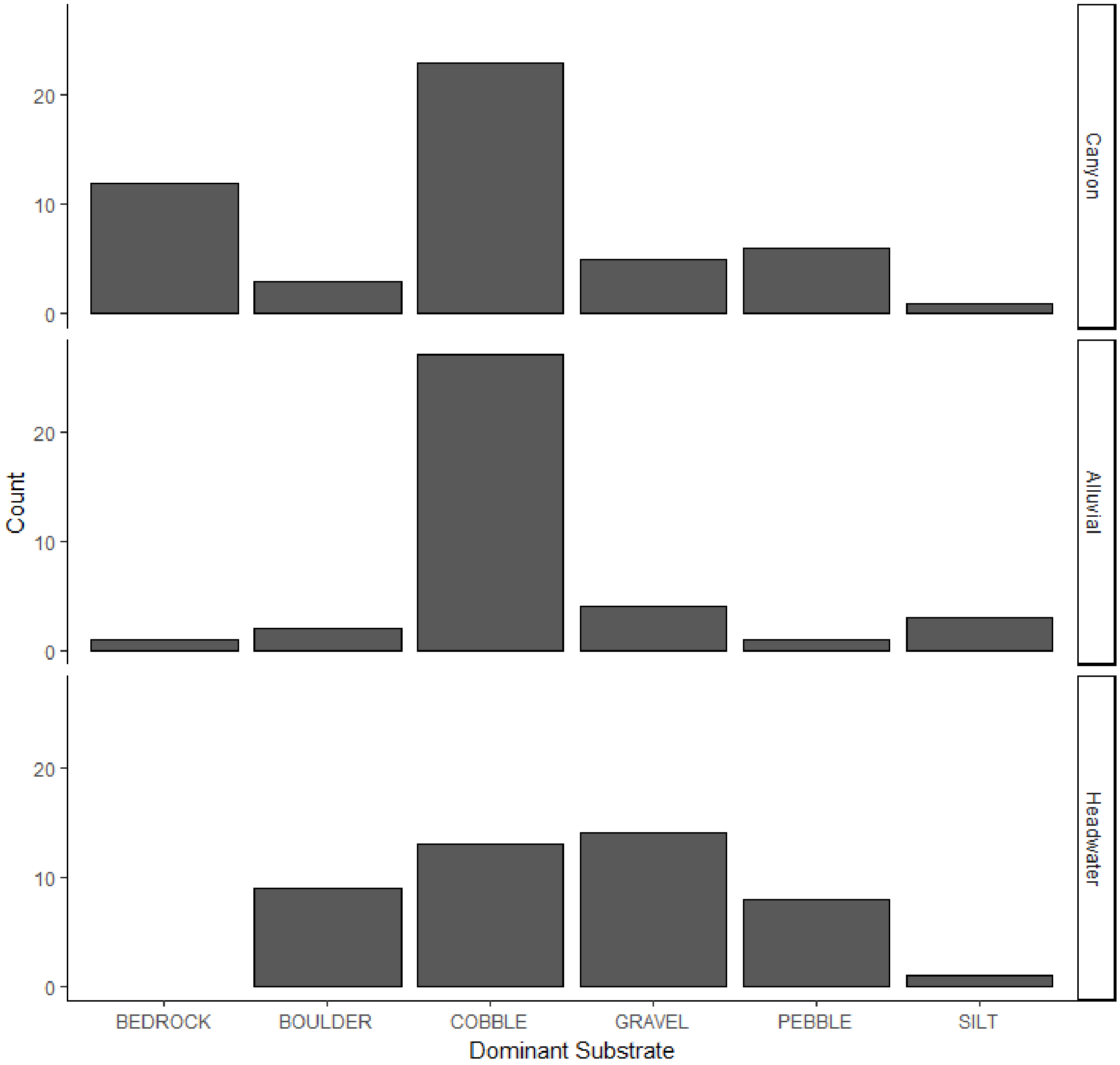

Figure 2.3 Total count of dominant substrate types sampled in all study streams among geomorphic segments during the summer of 2016 ($N = 133$). See methods for dominant substrate classification.

Only three variables, including elevation, longitudinal position downstream, and watershed area, were determined to be highly colinear (all having $r > 0.85$). Because the inclusion of all three variables overpowered the analysis and made determining gradients of other variables difficult, only watershed area was chosen for the NMDS analysis. Watershed area was chosen over the other variables because it was found to have the greatest correlation with WCT abundance. All variables, excluding elevation and longitudinal distance downstream, were then used in the analysis.

The final results of the NMDS analysis separated all study sites by the difference within their environmental and spatial data matrix. Separately, I asked questions on how the environmental and spatial variables describe variations first among study sites between streams (**Figure 2.4**) and second, variations of the same study sites between geomorphic segments (**Figure 2.5**). Post-hoc analysis revealed that stream groups identified among pools by NMDS were significant ($r = 0.16$, $P < 0.001$). Similarly, geomorphic segment groups identified among pools by NMDS were also significant ($r = 0.16$, $P < 0.001$). Further post-hoc analysis of significant vectors ($P < 0.05$) determined by NMDS were further assessed.

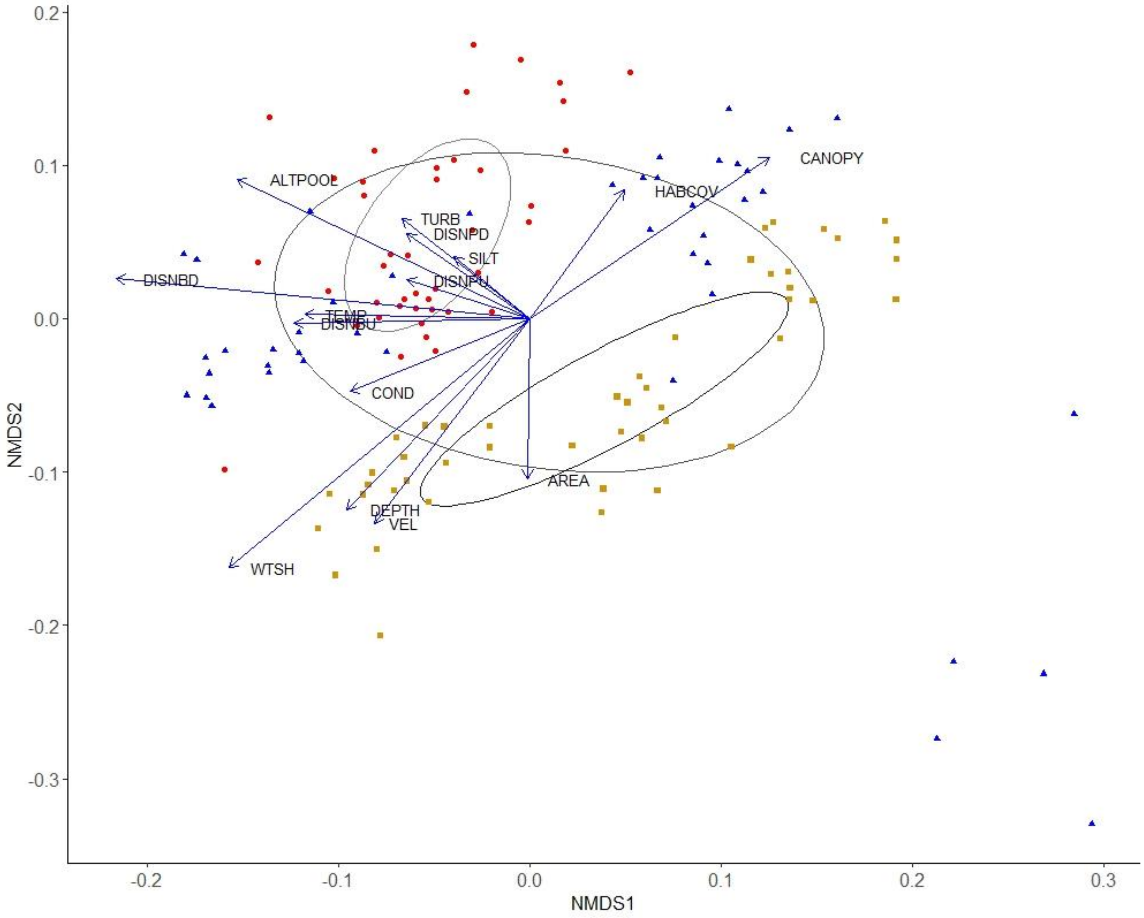

Figure 2.4 Non-metric multidimensional scaling (NMDS) plot showing environmental and spatial vectors (*P* < 0.05) among pools during the summer of 2016 (*N* = 133). Colour denotes the factor level within the variable Creek: Blairmore Creek (●), Daisy Creek (▲), and Gold Creek (■). Ellipses are drawn at one standard deviation and show group fitting between creeks. Blue arrows indicate the strength and direction of each environmental and spatial variable. For environmental and spatial variable code descriptions, see methods (Table 2.1).

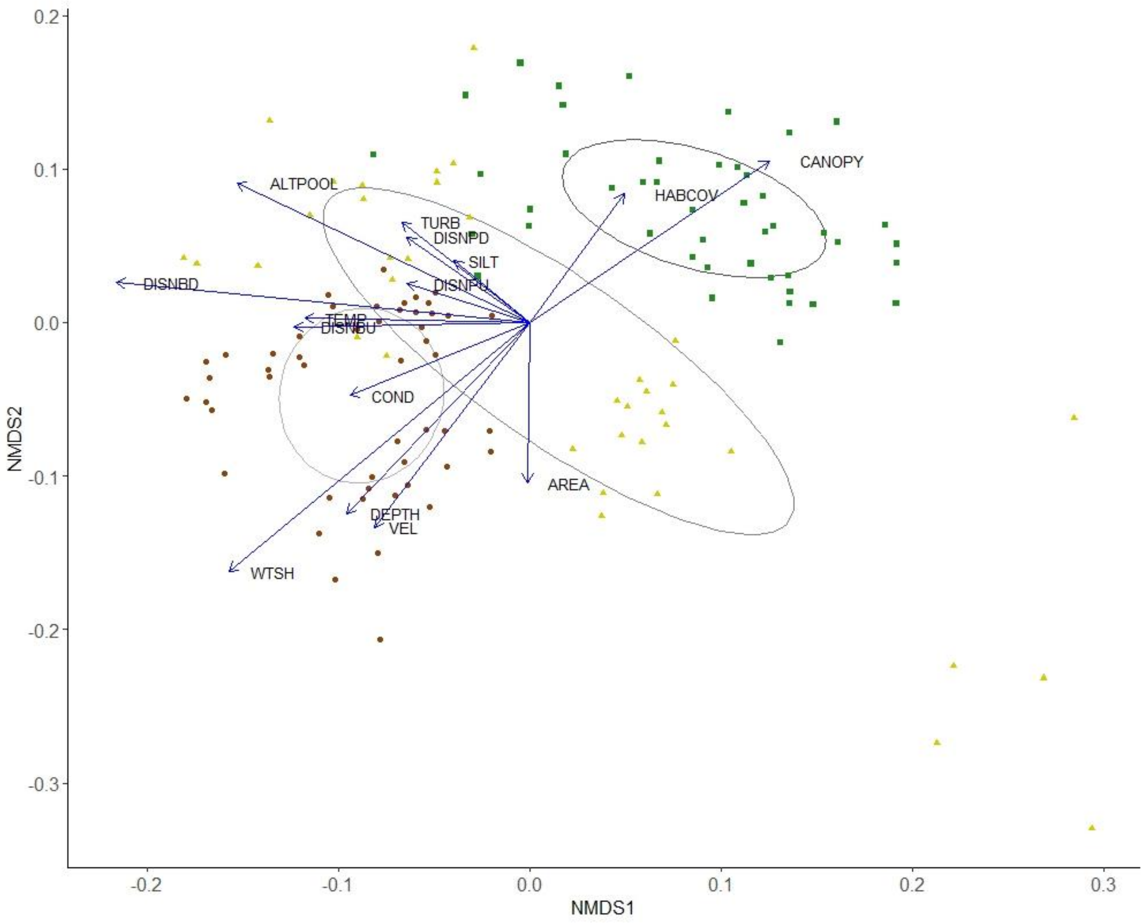

Figure 2.5 Non-metric multidimensional scaling (NMDS) plot showing environmental and spatial vectors ($P < 0.05$) among pools during the summer of 2016 ($N = 133$). Colour denotes the factor level within the variable geomorphic segment: canyon (●), alluvial (▲), and headwater (■). Ellipses are drawn at one standard deviation and show group fitting between geomorphic segments. Blue arrows indicate the strength and direction of each environmental and spatial variable. For environmental and spatial variable code descriptions, see methods (Table 2.1).

Environmental and spatial components of pool habitat were found to be significantly different among streams. The only variables showing no significant difference among streams were maximum depth, area, mean bank condition, and habitat cover score (**Table 2.3**). Tukeys HSD test further revealed significant differences between streams. Generally, Gold Creek pools during summer were characterized by having low turbidity, little silt cover, cold water temperatures, low conductivity, higher dissolved oxygen, and higher water velocity. In contrast, Blairmore Creek pools during summer were characterized by having higher turbidity, higher silt cover, higher water temperatures, higher conductivity, lower dissolved oxygen, and lower water velocity. Daisy Creek pool characteristics remained intermediate in comparison to both streams, but generally had the highest conductivity and lowest canopy cover.

Table 2.3 Descriptive statistics, and permutations analysis of variance (permANOVA: $F_{2,130}$) results for environmental and spatial variables in study pools between Blairmore Creek (*n* = 42), Daisy Creek (*n* = 44), and Gold Creek (*n* = 47) during the summer of 2016.

	Blairmore Creek	Daisy Creek	Gold Creek		
Variables		Mean ± SE		*F* value	*P*
Environment					
Maximum Depth (m)	0.82 ± 0.05	0.79 ± 0.06	0.90 ± 0.06	1.02	0.365
Area (m^2)	23.9 ± 2.5	65.4 ± 21.5	40.3 ± 4.6	2.65	0.075
Pool Velocity (m/s)	0.13 ± 0.01^{b}	0.11 ± 0.02^{b}	0.27 ± 0.03^{a}	16.50	**<0.001**
Conductivity (µS)	218.0 ± 5.5^{b}	319.1 ± 7.8^{a}	211.3 ± 7.1^{b}	76.02	**<0.001**
Turbidity ***	2.0 ± 0.1 ^{a}	1.0 ± 0.0^{b}	1.2 ± 0.1^{b}	59.22	**<0.001**
Water Temperature (C°)	10.3 ± 0.4^{b}	9.5 ± 0.3^{b}	7.7 ± 0.3^{a}	19.63	**<0.001**
Dissolved Oxygen (mg/L)	11.1 ± 0.2^{a}	11.6 ± 0.2^{ab}	11.8 ± 0.2^{c}	3.96	**0.021**
Silt Cover *	2.0 ± 0.0^{a}	1.4 ± 0.1^{b}	1.4 ± 0.1^{b}	30.19	**<0.001**
Mean Bank Condition **	2.4 ± 0.1	2.5 ± 0.1	2.6 ± 0.1	1.85	0.161
Habitat Cover Score ***	1.7 ± 0.2	1.6 ± 0.1	1.7 ± 0.1	0.11	0.899
Canopy Coverage (%)	27.9 ± 3.4^{ab}	19.4 ± 3.3^{a}	35.0 ± 3.5^{c}	5.36	**0.006**
Space					
Elevation (m)	1496.7 ±17.8^{b}	1628.4 ±19.6^{a}	1501.7 ±17.8^{b}	16.26	**<0.001**
Watershed Area (km^2)	27.8 ± 2.4	29.6 ± 3.6	35.0 ± 2.9	1.72	0.183
Longitudinal Distance (km)	7.4 ± 0.7	8.5 ± 0.9	8.2 ± 0.8	0.44	0.648
Nearest Pool Upstream (m)	98.8 ± 12.2	79.6 ± 10.9	80.1 ± 11.3	0.90	0.410
Nearest Pool Downstream (m)	84.6 ± 11.7	82.8 ± 11.7	69.0 ± 8.0	0.68	0.508
Nearest Barrier Upstream (km)	3.3 ± 0.4^{a}	4.1 ± 0.5^{a}	2.3 ± 0.3^{a}	5.00	**0.008**
Nearest Barrier Downstream (km)	23.7 ± 0.0^{ab}	12.8 ± 1.5^{c}	10.6 ± 1.5^{a}	28.94	**<0.001**
Total Number of Alternate Pools	380.9 ± 14.5^{b}	346.7 ± 30.7^{b}	105.7 ± 6.3^{a}	59.73	**<0.001**

Means that do not share a letter are significantly different
* values are scores ranging 1 to 2
** values are mean scores ranging 1 to 3
*** values are scores ranging 1 to 5

Elevation, distance to the nearest barrier upstream, distance to the nearest barrier downstream, and the total number of alternate pools were statistically significant among streams (**Table 2.3**). Elevation was highest in Daisy Creek pools, in comparison to both Gold Creek and Blairmore Creek pools. Out of all three streams, Blairmore Creek pools had the highest degree of connectivity, while Gold Creek pools had the lowest degree of connectivity. Daisy Creek pools were intermediate to both Blairmore Creek and Gold Creek in terms of connectivity. Specifically, Blairmore Creek pools had longer distances on average to the nearest barrier downstream and access to the highest number of alternate pools. In contrast, Gold Creek had the shortest distances on average to the nearest barrier downstream and upstream, and access to the lowest number of alternate pools.

Environmental and spatial components of pool habitat were also found to be significantly different among geomorphic segments. The only variables showing no significant difference among geomorphic segments were dissolved oxygen, turbidity and silt cover (**Table 2.4**). Tukeys HSD test further revealed differences between geomorphic segments. Generally, canyon segment pools during summer were characterized by having the greatest maximum depth, higher surface area, highest water velocity, highest water temperature, highest conductivity, lowest habitat cover score, and low canopy coverage. In contrast, headwater segment pools during summer were characterized by having the lowest maximum depth, lowest pool area, lowest water velocity, lower conductivity, highest habitat cover score, and highest canopy coverage. Alluvial segment pools were intermediate to both canyon and headwater segments, however, pools located here on average had the lowest bank condition.

Table 2.4 Descriptive statistics, and permutations analysis of variance (permANOVA: $F_{2,130}$) results for environmental and spatial variables in study pools between geomorphic segments canyon (n = 50), alluvial (n = 38), and headwater (n = 45) during the summer of 2016.

	Canyon	Alluvial	Headwater		
Variables		Mean ± SE		*F* value	*P*
Environment					
Maximum Depth (m)	1.14 ± 0.06^{c}	0.75 ± 0.04^{b}	0.58 ± 0.02^{a}	41.10	**<0.001**
Area (m^{2})	58.2 ± 5.1^{b}	59.4 ± 24.4^{b}	13.6 ± 1.3^{a}	4.35	**0.015**
Pool Velocity (m/s)	0.27 ± 0.03^{c}	0.18 ± 0.02^{b}	0.06 ± 0.01^{a}	26.09	**<0.001**
Conductivity (µS)	287.5 ± 9.7^{a}	222.2 ± 8.8^{b}	229.1 ± 8.4^{b}	16.09	**<0.001**
Turbidity ***	1.5 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.49	0.229
Water Temperature (C°)	10.1 ± 0.3^{a}	8.8 ± 0.5^{b}	8.3 ± 0.3^{b}	9.44	**<0.001**
Dissolved Oxygen (mg/L)	11.7 ± 0.2	11.5 ± 0.3	11.4 ± 0.1	0.58	0.561
Silt Cover *	1.6 ± 0.1	1.6 ± 0.1	1.5 ± 0.1	0.96	0.384
Mean Bank Condition **	2.6 ± 0.1^{b}	2.2 ± 0.1^{a}	2.7 ± 0.1^{b}	14.13	**<0.001**
Habitat Cover Score ***	1.3 ± 0.1^{a}	1.7 ± 0.2^{ab}	2.0 ± 0.1^{c}	7.09	**0.001**
Canopy Coverage (%)	16.1 ± 2.0^{b}	24.9 ± 3.8^{b}	42.8 ± 3.6^{a}	20.13	**<0.001**
Space					
Elevation (m)	1403.7 ± 6.8^{a}	1544.2 ± 9.7^{b}	1693.9 ± 10.4^{c}	281.00	**<0.001**
Watershed Area (km^{2})	53.28 ± 1.3^{c}	28.7 ± 1.2^{b}	8.5 ± 0.2^{a}	459.90	**<0.001**
Longitudinal Distance (km)	13.9 ± 0.3^{c}	7.5 ± 0.3^{b}	2.0 ± 0.5^{a}	431.00	**<0.001**
Nearest Pool Upstream (m)	79.0 ± 10.7^{b}	119.2 ± 14.6^{a}	65.3 ± 7.8^{b}	5.89	**0.004**
Nearest Pool Downstream (m)	69.0 ± 7.9^{b}	108.9 ± 14.2^{a}	64.1 ± 8.9^{b}	5.16	**0.007**
Nearest Barrier Upstream (km)	3.9 ± 0.5^{b}	4.06 ± 0.4^{b}	1.7 ± 0.2^{a}	11.50	**<0.001**
Nearest Barrier Downstream (km)	23.7 ± 0.0^{a}	12.01 ± 1.8^{b}	9.2 ± 1.3^{b}	44.01	**<0.001**
Total Number of Alternate Pools	354.7 ± 32.5^{a}	97.2 ± 25.3^{b}	207.8 ± 10.6^{b}	9.92	**<0.001**

Means that do not share a letter are significantly different
* values are scores ranging 1 to 2
** values are mean scores ranging 1 to 3
*** values are scores ranging 1 to 5

A significant difference was found for all spatial variables among geomorphic segments (**Table 2.4**). The canyon segment pools were generally characterized as having the lowest elevation, largest watershed area, and greatest longitudinal distance downstream. In addition, canyon segment pools typically had the highest degree of connectivity, such as having farther distances to the nearest barrier downstream and having the greatest access to more alternate pools. In contrast, headwater segment pools had the highest elevation, smallest watershed area, and shortest longitudinal distance downstream. Although both alluvial and headwater segments had a lower degree of connectivity, such as having shorter distances to the nearest barrier downstream and less access to alternate pools. However, alluvial segments further differed from headwater segments by having significantly farther distances to nearest pools upstream and downstream.

Fish Communities and Populations

Out of the total fish counted (2016 $N = 2375$; 2017 $N = 1860$), WCT (including hybrids) were found to be the most abundant species among all study streams during both summers (2016 = 94.6 %; 2017 = 92.2 %). Furthermore, within individual streams among both summers, WCT were still the most abundant species: Blairmore Creek (2016 = 92.2 %; 2017 = 95.9 %), Daisy Creek (2016 = 99.2 %; 2017 = 97.8 %), Gold Creek (2016 = 89.8 %; 2017 = 72.4 %). In Blairmore Creek the remainder of fish counted were composed of Brook Char (2016 = 7.7 %; 2017 = 4.1 %), Mountain Whitefish (2016 = < 0.1 %; 2017 = 0 %), and Rainbow Trout (2016 = 0.3 %; 2017 = 0 %). In Gold Creek the remainder of fish counted were composed of only Brook Char (2016 = 10.2 %; 2017 = 27.6 %). Finally, in Daisy Creek the remainder of fish counted were composed of only Bull Char (2016 = 0.8 %; 2017 = 2.2 %).

Among streams, ranges of species diversity were from one to five. Only salmonid species were found in these headwater streams. Increased species diversity was significantly correlated to decreasing elevation ($r = -0.59$, $P < 0.001$), increasing longitudinal distance downstream ($r = 0.80$, $P < 0.001$), and increasing watershed area ($r = 0.72$, $P < 0.001$). WCT were the only salmonid species found at the highest elevations among all streams.

During both summers, Brook Char in both streams were not found above 1445 m of stream elevation (Blairmore 1444 m, Gold Creek 1445 m). Brook Char abundance in pools (Blairmore Creek and Gold Creek, $N = 89$) was correlated to elevation ($r = -0.59$, $P < 0.001$), longitudinal distance downstream ($r = 0.42$, $P < 0.001$), and watershed area ($r = 0.41$, $P < 0.001$). Furthermore, elevation ($R^2 = 0.35$, $P < 0.001$), longitudinal distance downstream ($R^2 = 0.38$, $P < 0.001$), and watershed area ($R^2 = 0.37$, $P < 0.001$) strongly explained cube root transformed Brook Char abundance.

During both summers, Bull Char in Daisy Creek were found up to 1717 m of stream elevation. Bull Char abundance in pools (Daisy Creek, $N = 44$) was correlated to elevation ($r = -0.34$, $P = 0.0012$), longitudinal distance downstream ($r = 0.34$, $P = 0.0012$), and watershed area ($r = 0.34$, $P = 0.0012$). Elevation ($R^2 = 0.13$, $P < 0.001$), longitudinal distance downstream ($R^2 = 0.14$, $P < 0.001$) and watershed area ($R^2 = 0.15$, $P < 0.001$) did only weakly explain cube root transformed Bull Char abundance. Both Brook Char abundance ($R^2 = 0.31$, $P < 0.001$) and Bull Char abundance ($R^2 = 0.13$, $P < 0.001$) significantly increased with increasing pool depth.

Westslope Cutthroat Trout

Mean WCT abundance and biomass in pools among all streams in 2016 was 0.63 ± 0.07 WCT/m^2 and 17.7 ± 1.59 g/m^2 and in 2017 was 0.42 ± 0.04 WCT/m^2 and 20.3 ± 1.89 g/m^2. However, WCT abundance and biomass varied considerably among pools during both summers 2016 and 2017, with values ranging from 0 to as high as 4.0 WCT/m^2 and 109.0 g/m^2. Although pools with zero WCT present were recorded, only 10 pools (3.8 %) out of all pools sampled had zero WCT observed for both 2016 and 2017 summer surveys. Nine of the fishless pools were located on Gold Creek. In pools, WCT abundance differed significantly between summers 2016 and 2017 (ANOVA: $F_{1,260} = 5.33$, $P = 0.022$), however WCT biomass did not differ significantly between summers 2016 and 2017 (ANOVA: $F_{1,260} = 0.257$, $P = 0.613$).

WCT abundance in pools was significantly different among streams (**Table 2.5**). During both summers Blairmore Creek had significantly more WCT present per pool compared to Daisy Creek and Gold Creek. WCT were also more abundant in Daisy Creek than Gold Creek during both summers. WCT biomass in pools was also significantly different among streams during both summers. Biomass in pools did not differ significantly between Blairmore Creek and Daisy Creek. Gold Creek had significantly lower WCT biomass in pools compared to both, Blairmore Creek and Daisy Creek. Mean WCT abundance and biomass among geomorphic segments was not significantly different (**Table 2.6**).

Table 2.5 Estimated Westslope Cutthroat Trout abundance (WCT/m^2) and biomass (g/m^2), descriptive statistics, and analysis of variance (ANOVA: $F_{2,130}$) results between study streams during the summer of 2016 and 2017.

	Blairmore Creek	Daisy Creek Mean ± SE	Gold Creek	*F* value	*P*
Summer 2016					
N	42	44	47		
Abundance (WCT/m^2)	1.12 ± 0.14^c	0.66 ± 0.10^b	0.17 ± 0.04^a	46.01	**<0.001**
Biomass (g/m^2)	22.94 ± 2.84^b	20.65 ± 2.69^b	10.29 ± 2.40^a	13.91	**<0.001**
Summer 2017					
N	38	44	47		
Abundance (WCT/m^2)	0.82 ± 0.09^c	0.35 ± 0.06^b	0.15 ± 0.03^a	32.75	**<0.001**
Biomass (g/m^2)	30.32 ± 4.13^b	21.94 ± 2.78^b	10.76 ± 2.36^a	15.62	**<0.001**

Means that do not share a letter are significantly different

Table 2.6 Estimated Westslope Cutthroat Trout abundance (WCT/m^2) and biomass (g/m^2), descriptive statistics, and analysis of variance (ANOVA: $F_{2,130}$) results between geomorphic segments during the summer 2016 and 2017.

	Canyon	Alluvial Mean ± SE	Headwater	*F* value	*P*
Summer 2016					
N	50	38	45		
Abundance (WCT/m^2)	0.41 ± 0.06	0.70 ± 0.14	0.83 ± 0.14	2.276	0.107
Biomass (g/m^2)	15.68 ± 2.30	22.24 ± 3.47	16.14 ± 2.58	0.908	0.406
Summer 2017					
N	46	38	45		
Abundance (WCT/m^2)	0.31 ± 0.06	0.43 ± 0.09	0.51 ± 0.08	1.331	0.268
Biomass (g/m^2)	19.19 ± 2.89	24.78 ± 3.84	17.76 ± 3.16	1.695	0.188

WCT Regression Model

Nine variables were significantly correlated to summer 2016 WCT abundance and three variables were significantly correlated to summer 2016 WCT biomass (**Table 2.7**). Spearman rank correlation identified three variables to be colinear: WTSH – LONG ($r = 0.98$, $P < 0.001$), WTSH – ELEV ($r = -0.89$, $P < 0.001$) and LONG – ELEV ($r = -0.87$, $P < 0.001$). Elevation and longitudinal distance were subsequently removed from further analyses as watershed area had a higher significant correlation with WCT abundance. The remaining variables significantly correlated with WCT abundance and biomass were used for multiple linear regression model development. WCT abundance and biomass distributions were highly right skewed (Poisson distributed), thus cube root transformations ($X = X^{1/3}$) were used instead of logarithmic transformations to approximate normality and linearity (Quinn and Keough 2002). Normality and linearity were achieved through transformation, as indicated through visually assessing the histograms and the Shapiro-Wilk test statistic (Abundance $W = 0.97$, $P < 0.001$; Biomass $W = 0.95$, $P < 0.001$).

Table 2.7 Correlation analysis (Spearman rank correlation coefficients (*r*)) results for summer 2016 data. Relationships are among environmental, spatial and biological variables by Westslope Cutthroat Trout abundance (WCT/m^2) and biomass (g/m^2) in pools (*N* = 133). For environmental, spatial and biological variable code descriptions, see methods.

Variable	Abundance (WCT/m^2)	Biomass (g/m^2)
CREEK	-0.65**	-0.37**
STRATUM	0.07	-0.11
POOLTYPE	-0.05	0.03
DEPTH	0.00	0.30**
AREA	-0.22*	0.09
VEL	-0.31**	-0.14
CONDUCT	0.04	0.08
TURB	0.27**	0.12
TEMP	0.28**	0.17
DO	-0.17	-0.03
DOMSUB	0.23**	0.09
SILT	0.25**	0.18*
HABCOV	0.23**	0.04
CANOPY	0.01	-0.14
BCOND	-0.04	0.02
ELEV	0.20*	0.07
WTSH	-0.27**	-0.05
LONG	-0.20*	0.00
DISNPU	0.17	0.07
DISNPD	0.07	0.09
DISNBU	0.12	0.11
DISNBD	0.22*	0.17*
ALTPOOLS	0.50**	0.31**
SPDIVERSITY	-0.07	0.04
BKCH_ABUND	-0.03	0.02
BLCH_ABUND	-0.01	0.22*
MNWH_ABUND	0.03	-0.05

**Indicates significance at $P < 0.01$
*Indicates significance at $P < 0.05$

Stepwise procedures (forward and backward) were used to developed two multiple linear regression models, one model to explain WCT abundance in pools, and another model to explain

WCT biomass in pools. The best predictor model for WCT abundance in pools during the summer of 2016 consisted of four variables: Stream with levels Blairmore Creek, Daisy Creek, and Gold Creek (CREEK), log transformed pool area (AREA), habitat cover score (HABCOV), watershed area (WTSH), and the number of alternate pools (ALTPOOLS) (**Equation 2.3**). The WCT abundance model accounted for 49.6 % (adjusted R^2) of the variation in WCT abundance in pools ($R_a^2 = 0.496$; $F = 22.66$; $P < 0.001$). CREEK was proportionally the most important variable in the model, explaining 53.5 % of the variance. AREA and ALTPOOLS explained 2.6 % and 20.9 % of the variance but were both not significant in the model ($P = 0.105$; $P = 0.092$). HABCOV and WTSH were both significant in the model ($P < 0.001$; $P = 0.009$) and explained 13.7 % and 11.1 % of the variance.

$$Y = 0.628 - 0.159DAISY - 0.447GOLD + \ 0.124\, log_{10}(AREA) + 0.098HABCOV \\ - 0.005WTSH + 0.0004ALTPOOLS$$

Equation 2.3 Multiple linear regression equation predicting cube root transformed WCT abundance (WCT/m^2) in pools during the summer of 2016 ($R_a^2 = 0.496$; $F = 22.66$; $P < 0.001$). Variables include: Daisy Creek (DAISY), Gold Creek (GOLD), log transformed area (m^2) (AREA), habitat cover score (HABCOV), watershed area (km^2) (WTSH), and the number of alternate pools (ALTPOOLS).

Using the summer 2017 data set ($N = 129$) the WCT abundance model accounted for 35.3 % (adjusted R^2) of the variation in WCT abundance in pools. Root mean square error was calculated at 0.30 or 0.03 WCT/m^2, and mean absolute error was calculated at 0.23 or 0.01 WCT/m^2. A significant correlation between model predictions and observed WCT abundance was also found ($r = 0.59$, $P < 0.001$). These measures indicate that this model was successful in predicting observed trends in WCT abundance in pools during the summer of 2017.

The best predictor model for WCT biomass consisted of 3 variables: Stream with levels Blairmore Creek, Daisy Creek, and Gold Creek (CREEK), maximum depth (MAX_DEPTH) and the number of alternate pools (ALTPOOLS) (**Equation 2.4**). The WCT biomass model accounted for 29.0 % (adjusted R^2) of the variation in WCT biomass in pools ($R_a^2 = 0.290$; $F = 14.48$; $P < 0.001$). CREEK explained 54.1 % of the variance in the model. MAX_DEPTH was the second significant variable in the biomass model ($P < 0.001$) and explained 33.1 % of variance. ALTPOOLS was the third variable in the model ($P = 0.068$) and explained the least amount of variance (12.9 %).

$$Y = 2.072 - 0.089DAISY - 1.506GOLD + 1.155MAX\_DEPTH \; - \; 0.001ALTPOOLS$$

Equation 2.4 Multiple linear regression equation predicting cube root transformed WCT biomass (g/m^2) in pools during the summer of 2016 ($R_a^2 = 0.290$; $F = 14.48$; $P < 0.001$). Variables include: Daisy Creek (DAISY), Gold Creek (GOLD), maximum depth (m) (MAX_DEPTH), and the number of alternate pools (ALTPOOLS).

Using the summer 2017 data set ($N = 129$) the WCT biomass model accounted for 24.3 % (adjusted R^2) of the variation in WCT biomass in pools. Root mean square error was calculated at 1.91 or 1.29 g/m^2 and mean absolute error was calculated at 1.67 or 0.67 g/m^2. A significant correlation between model predictions and observed WCT biomass was also found ($r = 0.40$, $P < 0.001$). These measures indicate that this model also was successful in predicting observed trends in WCT biomass in pools during the summer of 2017.

Discussion

This study investigated the ecological impacts of the environmental and spatial factors of pool habitat and how they influenced WCT populations within potentially mine impacted headwater streams. Specifically, the objectives of this study were to first determine how landscape features at different scales influence pool characteristics within the chosen headwater streams. The second objective was to determine which environmental, spatial, and biological factors that constituted pool habitat influenced WCT abundance and biomass.

Among the three headwater streams studied, large scale stream features have a superimposed influence on smaller scale habitat characteristics. Specifically, a hierarchy of habitat scale emerged, with watersheds and geomorphology superimposing pool habitat features. Study streams were found to have differing watershed characteristics and a gradient of geomorphological characteristics, such as those related to physical habitat, water quality and connectivity, which in turn influenced pool habitat characteristics. Lastly, analysis of WCT populations showed that as pool characteristics changed under different watershed and geomorphological conditions, they significantly influenced WCT abundance and biomass.

Pool Habitat Among Landscapes and Watersheds

The most influential variable associated with both WCT abundance and biomass was related to the specific watershed in which the population was contained. Due to the significant differences in pool habitat found among and within study streams, landscape features strongly influenced pool habitat. Differences in landscape features (e.g. vegetation, geology, land use, climate) play an important role in influencing characteristics of streams and rivers (Charlton 2008), which ultimately influences habitat. Landscape features influence how water enters and exits streams or how sediment erosion, transport, and deposition occurs (Charlton 2008). These features therefore influence channel formation and the habitats contained within them. The main differences in habitat observed among my study streams (i.e. watersheds) was related to water quality variables such as temperature, silt cover, and turbidity.

Summer Water Temperature

Water temperature influences habitat quality among streams and geomorphic segments. Stream shading by canopy cover, including vegetation and other overhead cover, reduces the amount of direct radiation entering streams, effectively moderating maximum water temperatures (Amaranthus et al. 1989, Rutherford et al. 1997, Johnson 2004). In my study streams, the increased canopy cover in the headwater segments was reflected in the cooler water temperatures. Johnson (2004) reported in addition to shade, differences in substrate type also affect water temperature. Specifically, bedrock substrates could increase daily maximum water temperatures over alluvial substrates due the limited amount of hyporheic exchange (Johnson 2004). Hyporheic exchange is the mixing of surface and shallow subsurface water through porous sediment (i.e. re-emergent surface water) (Kalbus et al. 2006). Another and possibly more significant source of cooler water in streams is groundwater (i.e. water stored in deep underground aquifers) (Kalbus et al. 2006). Groundwater contributions to streams significantly reduce stream temperatures and maintain streamflow during summer, consequently influencing stream salmonid populations (Power et al. 1999).

Cold water streams are often found to be positively associated with WCT and are highlighted as critical remaining habitat for the species persistence (Muhlfeld et al. 2009, Yau and Taylor 2013, 2014). Interestingly, the warmest streams (i.e. Blairmore Creek and Daisy Creek) had significantly higher WCT abundance and biomass. In contrast, Gold Creek had the lowest water temperatures among pools and had significantly lower WCT abundance and biomass. However, hybridization between WCT and Rainbow Trout has occurred in Blairmore Creek (Fisheries and Oceans Canada 2014) and Daisy Creek, while no hybridization has occurred in Gold Creek above permanent barriers (Rasmussen et al. 2010). WCT-Rainbow Trout hybrids have a higher water temperature tolerance and optimum than pure WCT (Yau and Taylor 2014). Thus, the relationship between higher WCT abundance and higher water temperatures could be a result of hybridization with Rainbow Trout within the study streams. Yet, the greatest proportion of hybridization in Blairmore Creek and Daisy Creek has occurred in the lowest elevations while pure WCT in those streams remain in the higher elevations (Rasmussen et al. 2010, Fisheries and Oceans Canada 2014). Stream temperatures in higher elevations of Blairmore Creek and Daisy Creek are both warmer than the mean temperature of all Gold Creek, and yet still have higher abundance and biomass of WCT.

A study by Isaak and Hubert (2004) found summer stream temperature, trout densities and biomass relationships were non-linear among 24 first to fourth order montane streams. That is, there was an upper and lower temperature threshold that could no longer support trout populations (Isaak and Hubert 2004). It may be also possible that among my study streams, the colder water temperatures that negatively affect WCT abundance and biomass were captured in Gold Creek. Bear *et al.* (2007) found the optimal growth temperature range of wild stock WCT in Montana was between 13 – 15 °C and that the upper lethal water temperatures were near 20 °C. Average water temperature during both summers within the Gold Creek study pools was only 7.5 °C, nearly half of the optimal reported by Bear *et al.* (2007). Cold water temperatures reduce growth rates of trout in streams, due to reduced metabolism rates (Xu et al. 2010). WCT require water temperatures approaching 8 °C for optimal spawning (Nelson and Paetz 1992, Behnke 2002). In Gold Creek, water temperatures in some areas were never higher than 5 °C during both summers. Colder water temperatures in Gold Creek could limit or delay spawning opportunity. Late spawning would induce late fry emergence and reduced growth, which could result in poor overwintering success (Smith and Griffith 1994, Magee et al. 1996, Coleman and Fausch 2007a). Cold summer temperature regimes (mean July water temperatures of 7.4 °C) have been shown to limit recruitment of age-0 Cutthroat Trout (*O. c. pleuriticus* and *O. c. stomias*) in high-elevation streams (Coleman and Fausch 2007b). Furthermore, cold summer temperature regimes caused recruitment bottlenecks in age-0 Colorado River Cutthroat Trout (*O. c. pleuriticus*) reared in laboratory streams (Coleman and Fausch 2007a). Therefore, extremely cold summer water temperatures could have contributed to the lower observed WCT abundance and biomass in Gold Creek pools. In contrast, Blairmore Creek and Daisy Creek both had significantly higher summer water temperatures than Gold Creek, much closer to optimum, even in the highest elevations where pure WCT occur (8 – 12 °C). Warmer water temperatures in Blairmore Creek and Daisy Creek in comparison to Gold Creek, likely contribute to better recruitment, growth and survival.

Silt Cover and Turbidity

Silt cover and turbidity significantly influenced WCT abundance and biomass among streams. Specifically, study streams with increased silt cover and turbidity (Blairmore Creek and Daisy Creek) had higher WCT abundance and biomass (**Figure 2.6**). These results are in contrast to literature that suggests increased siltation and turbidity negatively affect trout in streams due to lower reproductive success and food production (Tebo Jr. 1955, Waters 1983, 1995). Siltation in particular is often associated with naturally erosive geology (Magee et al. 1996), natural disturbances such as wild fire (Florsheim et al. 1991) and increased land-use (Rabeni and Smale 1995, Wagenhoff et al. 2011). Berkman and Rabeni (1987) found that as fine sediment increased, the distinction between habitats such as riffles, runs and pools decreased, reducing invertebrate diversity and altering food resources for fish. Sedimentation fills interstitial spaces between gravel, effectively reducing spawning success and embryo survival (Jensen et al. 2009). However, Magee *et al.* (1996) found in spite of increased fine sediment levels within naturally sediment-rich stream basins and low predicted emergence success of fry, Cutthroat Trout recruitment was unaffected and densities were high (32.5 – 43.5 Cutthroat Trout / 100 m^2). High fry mortality due to low emergence success, could have led to decreased fry densities, and consequently, may have resulted in decreased competition, increased growth, and compensatory survival (Magee et al. 1996). In addition, Magee *et al.* (1996) also suggested that the small, resident Cutthroat Trout may have been adapted to high fine-sediment loading because small egg sizes survive better than large eggs in highly sedimented substrates (van den Berghe and Gross 1989). The majority of WCT observed in Blairmore Creek were small (93 % ≤ 20 cm). It may be possible that in this case, the increased silt cover and turbidity in Blairmore Creek was not enough to negatively effect the resident WCT and may have contributed to the smaller sizes observed and thus increased abundance.

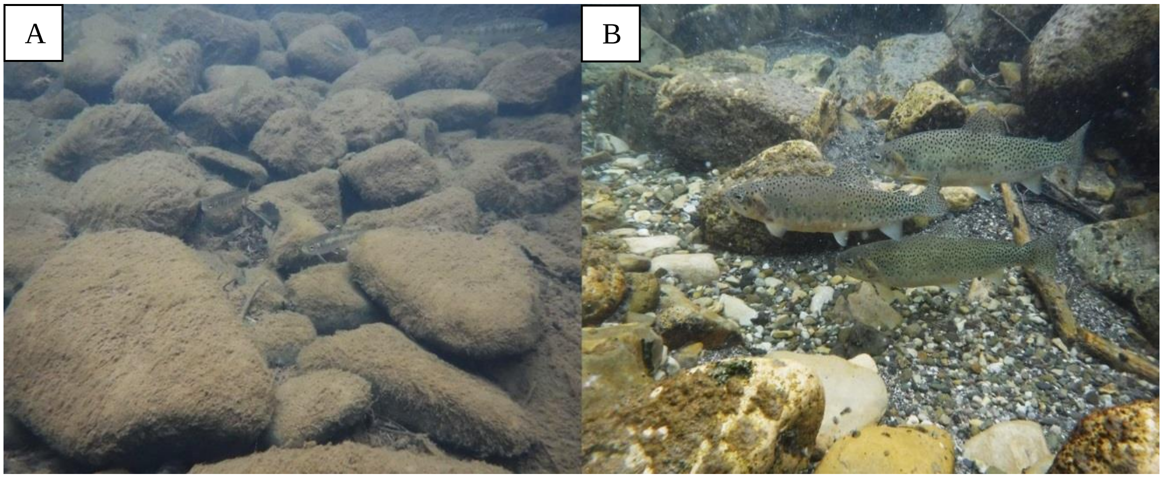

Figure 2.6 Examples of different levels of silt cover and turbidity observed in study streams during summer. A) Blairmore Creek canyon segment pool with extensive silt cover on substrate and moderate to high turbidity; B) Gold Creek alluvial segment pool with no silt cover on substrate and turbidity at low to none.

Physical Habitat

Generally, streams and rivers most often increase in size moving downstream in a watershed as water flow accumulates (Strahler 1964). Thus, it is no surprise certain physical variables measured among pools, such as maximum depth and water velocity were closely related to longitudinal position, elevation and watershed area. In addition to stream size, stream habitat on a small scale is often found to be a function of larger geologic processes (Lanka *et al.* 1987). Lanka *et al.* (1987) presented evidence that drainage basin morphology and trout standing stock were related through a functional link between geomorphic features and stream habitat. When they compared geomorphic variables of forest and rangeland streams they found that larger scale geomorphic variables (e.g. basin area, basin relief, channel slope, drainage density, elevation, stream order) easily explained smaller scale stream measurements (e.g. average reach width, reach gradient, reach velocity, substrate type, width:depth ratio), which together best explained trout biomass (Lanka *et al.* 1987). Specifically, stream measurements such as increased width:depth ratio (i.e. increasingly wider and shallower stream channels) were negatively correlated with trout biomass (Lanka *et al.* 1987). However, in rangeland streams for example, increased width:depth ratio was significantly related to decreasing reach elevation and increasing stream order (Lanka *et al.* 1987). In my study streams, maximum depth in pools was found to significantly influence WCT biomass, however geomorphic segments significantly influenced pool type (e.g. lateral scour, step, plunge) which is a function of channel formation, velocity, substrate and depth (Flosi et al. 1998). Furthermore, canyon segment channels were dominated by bed rock which is conducive for forming long lasting, deep pools. In contrast, alluvial segment channels were dominated by alluvium, which is easily moved when banks are unstable, which is less conducive for forming deep pools. Physical pool characteristics, such as depth of pools, reflect the differences in landscape between canyon and alluvial segments, specifically features related to geology, rather than stream size alone. Therefore, incorporating landscape features such as geomorphology at various scales in analyses of headwater stream habitats are important in interpreting responses by stream dwelling salmonid populations such as WCT.

Deeper pools supported higher WCT biomass. Since biomass did not differ among geomorphic segments, depth was the most important physical characteristic of pools influencing WCT biomass. In manipulation experiments, Brown Trout *Salmo trutta* biomass (Greenberg et al. 2001) and Cutthroat Trout biomass (Gowan and Fausch 1996) increased when pool depth increased. The increased biomass I observed in deeper pools is likely due to higher numbers of larger WCT being present in those pools, as the relationship between length and weight is exponential. In particular, other studies have often noted that larger, adult trout use deeper pools (Baltz et al. 1991, Vondracek and Longanecker 1993, Gowan and Fausch 1996). Greenberg *et al.* (2001) suggests that large trout use pools with greater depth during the day to avoid predation.

In contrast to biomass, my results show that WCT abundance was not related to pool depth, and instead cover was the most important factor. Similar to my results, other studies have reported that variability in trout abundance in streams is not related to pool depth (Lewis 1969, Horan et al. 2000). Instead, Lewis (1969) identified habitat cover in pools as the most important factor describing variation in Brown Trout densities. However, in Lewis' (1969) study the pool depths investigated were within a narrower range (mean pool depth range 0.4 – 0.8 m) compared to the wider range of pool depths in my study (max pool depth range 0.3 – 2.3 m), yet with a similar conclusion. In contrast to larger trout, smaller juvenile trout often use shallower habitats (Baltz et al. 1991, Vondracek and Longanecker 1993) and are usually more abundant than larger fish (Anderson and Neumann 1996). Therefore, in my study streams, increased cover within pools is more important for smaller WCT as they use shallower habitats (indicated by high abundance), while increased pool depth is more important for larger WCT as they prefer deeper habitats (indicated by higher biomass). Since cover in pools was increasingly limited in the downstream canyon segments, particularly with less undercut banks and woody debris, depth becomes increasingly more important to larger WCT further downstream. In contrast, alluvial and headwater segments may have provided habitat more suitable for the smaller WCT as even though pools are shallower, they contained higher amounts of cover.

Spatial Variation in Abundance – Watershed Area and Connectivity

Variation in WCT abundance in pools was not only explained among the different streams, but the model also suggested variation in WCT abundance in pools was related to spatial position within streams. Specifically, as watershed area decreased WCT abundance increased. WCT biomass however was not related to watershed area. This means there were fewer fish in lower stream segments, but they were larger. In contrast, there were more fish in the upper stream segments, but they were smaller. The higher abundance further up in the watershed may reflect differences in population recruitment. For example, Magee *et al.* (1996) found that recruitment was most successful in the higher elevation sub basins (1st – 2nd order) and lowest in the lower elevation sub basins. They attributed this difference to better spawning substrate found in the higher elevations within streams, leading to higher numbers of younger juvenile trout (Magee et al. 1996). In my study streams, pools with substrate conducive for spawning (i.e. clean gravels) were more abundant within the headwater segments and could have granted greater recruitment and higher numbers of WCT.

Lower WCT abundance in pools with larger watershed areas could also be due to cumulative effects from human activities such as the number of roads and trails, cattle grazing, and recreational activity (e.g. off-road vehicle use and angling) (**Figure 2.7**). Lanka *et al.* (1987) noted that an increase in human impacts in higher order streams could result in the lower observed trout biomass in their streams. Increasing road density has been shown to negatively impact trout and char populations due to decreased suitable spawning substrate (i.e. through sedimentation) and reduced connectivity (Rieman et al. 1997, Baxter and McPhail 1999, McCaffery et al. 2007). For example, in my study watersheds there are a number of off-road trails and roads that are regularly used, many of which have stream crossings. Along just Daisy Creek's mainstem alone, there were a total of thirteen stream crossings observed, all with no bridge or culvert present. Furthermore, increased access due to roads may increase angling pressure within lower elevation segments of my study streams, which may be impacting WCT more than in higher elevation segments. Increased road access has been found to increase angling pressure in a number of systems and effect population structure (Gunn and Sein 2000, Parker et al. 2007, Kaufman et al. 2009). In addition, in even catch and release fisheries, increased exploitation and recapturing of individuals can have the potential to induce stress and mortality on salmonid populations (Schill et al. 1986). Lastly, another prominent impact throughout these watersheds were concentrations of cattle, which in most areas had direct access to the streams and their tributaries. Increased grazing intensity can have substantial impacts to water quality, including increased fine sediment and excess nutrients (Meehan and Platts 1978). Additionally, increased grazing intensity around streams can alter stream habitat by reducing streamside cover (e.g. undercut banks and vegetation) whereby increasing stream temperatures and reducing bank stability (Meehan and Platts 1978, Platts 1991). Altered stream habitats through excessive grazing can also reduce the amount of pool habitat (Meehan and Platts 1978).

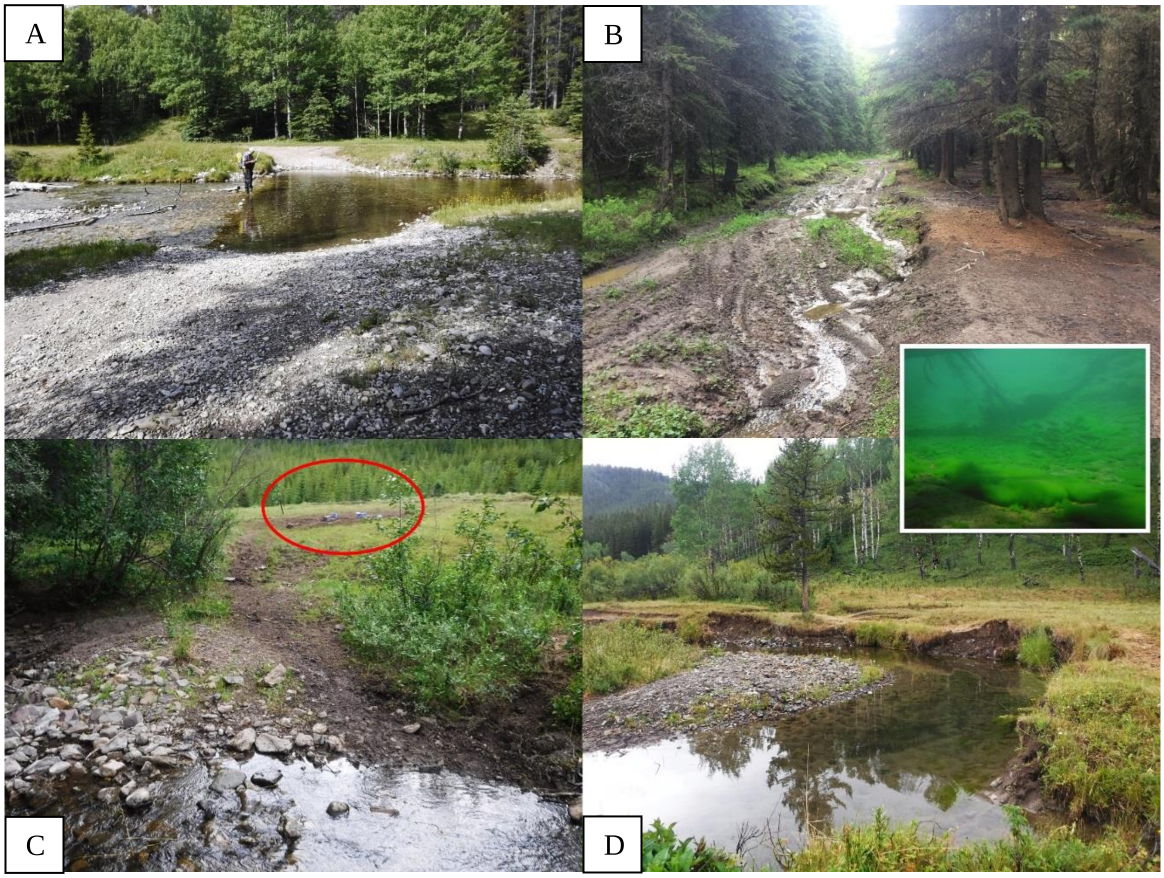

Figure 2.7 Examples of road and trail crossings, as well as cattle impacts within study streams. A) Typical road/trail crossing (Gold Creek). B) Old road/off-highway vehicle trail near unnamed tributary to Blairmore Creek. C) Cattle impacted area located on Blairmore Creek. Note the presence of salt blocks in close proximity to the creek in C. D) Heavy grazing impacts on the banks of Daisy Creek leading to reduced bank stability. Inset photo showing a large algae bloom in a pool during the summer (Daisy Creek), likely as a result of increased nutrient loading.

Reduced connectivity in the headwater and alluvial segments may have led to increased WCT abundance within smaller watershed areas. Increased rocky, shallow and poorly developed soils, smaller watershed area, and increased slope, are all characteristics of higher elevation montane catchments and contribute to variable flows seasonally, particularly those catchments dominated by snowmelt (Sueker et al. 2000). Seasonal flow variability is then higher as water storage capacity decreases with increasing elevation and decreasing watershed size in these streams. Decreased flow and resulting decreased connectivity during summer among all streams was evident (i.e. apparent by the prevalence of subsurface flow barriers) and was especially pronounced in the upstream segments (e.g. alluvial and headwater segments). Decreased connectivity due to low flows and subsurface barriers could be acting to increase WCT abundance (densities) in pools because alternate habitats are reduced or not accessible. Furthermore, the effect that low flows have on connectivity becomes further exasperated when pools are much farther apart, as was shown within alluvial segments. In contrast, low flows may impact WCT less in canyon segments as there are a greater amount of alternate pools which are closer together.

Connectivity or the degree of isolation among habitats, on large scale (landscape) and small scale (habitat patches), influence dispersal, colonization, and gene flow within and among local populations (Rieman and Dunham 2000). Accessibility to high-quality pool habitat (i.e. availability of alternate accessible pools without impedance by a barrier) positively affected WCT abundance and biomass among streams and geomorphic segments. Blairmore Creek habitat was the best connected, as barriers were very limited, in turn granting greater access to more pool habitat. In contrast, Gold Creek contained multiple barriers, which limited access to alternate pool habitat, significantly reducing connectivity. Gowan & Fausch (1996) found that when pool habitat was artificially added to streams, abundance and biomass of large trout increased. However, immigration was the primary reason for the increase in their study and regional factors were likely influencing fish populations over large spatial scales (Gowan and Fausch 1996). Thus, even if deep pool habitat with enough cover is present within a stream, if fish cannot immigrate to those habitats due to barriers, effective habitat to those populations is reduced. As a negative consequence of increased connectivity to larger watersheds, the threat of hybridization with Rainbow Trout increases (Rasmussen et al. 2010), evident by current pure WCT populations in Gold Creek above barriers and hybridized WCT in lower elevations of Blairmore Creek (Rasmussen et al. 2010, Fisheries and Oceans Canada 2014).

Warming by climate change is expected to increase the variability of streamflows in mountainous areas of southern Alberta, particularly reducing summer and fall flows (Rood et al. 2008) and increasing summer water temperatures (MacDonald et al. 2014). In addition, increased land use along the east slopes of southern Alberta is also expected to alter basin hydrology and reduce stream base flows in the future (Wijesekara et al. 2012). This may further decrease connectivity in these streams and increase the importance of high quality pool habitat as refuge during summer low flows.

Fish Communities

When Brook Char are introduced into an ecosystem, they often displace Cutthroat Trout from their native habitats (Krueger and May 1991, McIntyre and Rieman 1995, Thompson and Rahel 1996, Shepard 2004, Roberts et al. 2017). However, WCT abundance and biomass was not significantly related to introduced Brook Char abundance in pools during my study. Instead, my results show WCT as the dominant species in both Blairmore Creek and Gold Creek and that Brook Char distribution was limited to the lowest elevations. In Blairmore Creek, the current distribution of Brook Char is likely the result of the permanent water fall barrier, which is limiting further upstream movement (**Figure 2.8**). In contrast, there is no permanent barrier blocking any further upstream movement of Brook Char in Gold Creek.

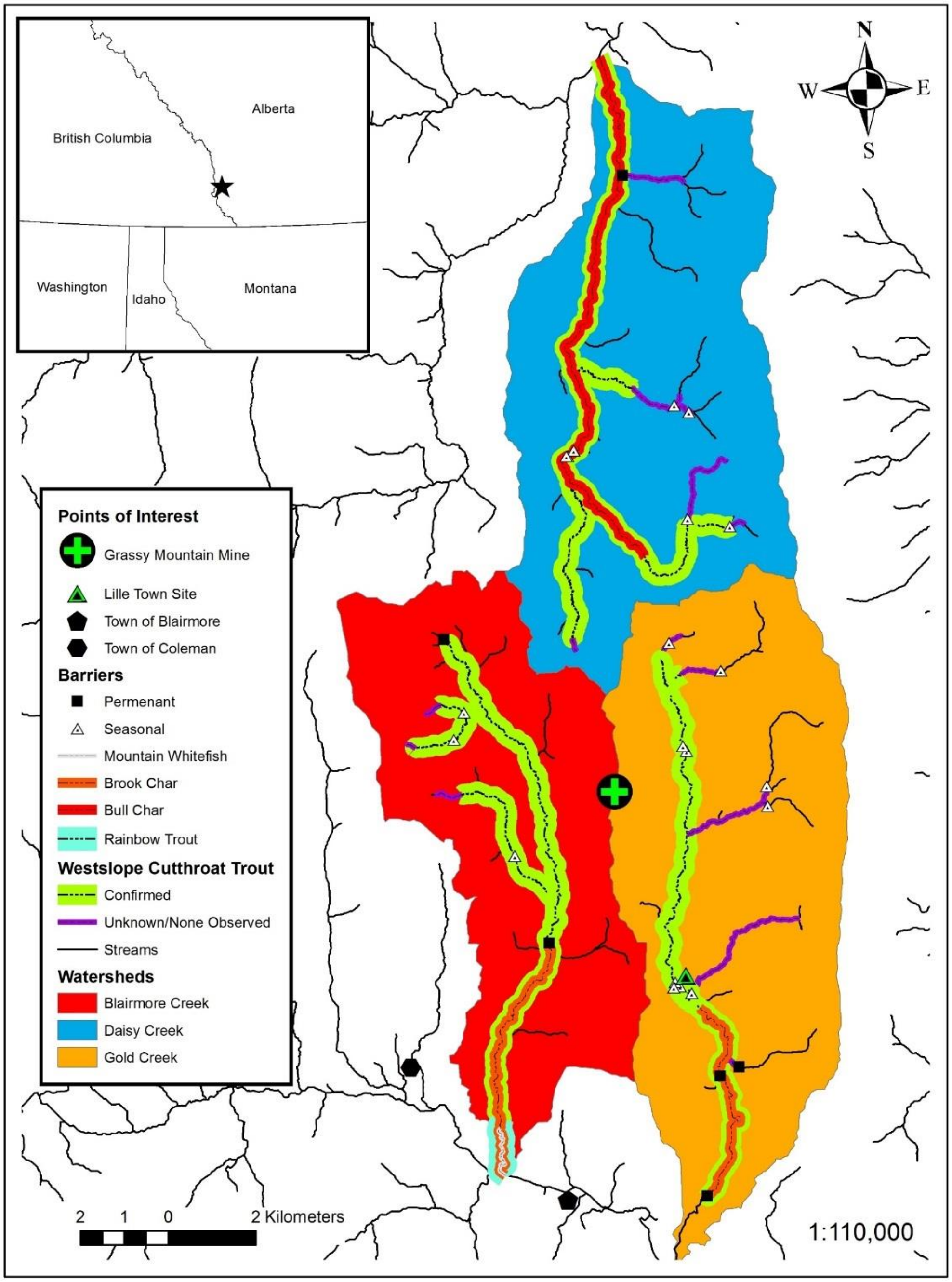

Figure 2.8 Species distributions within the study streams Blairmore Creek, Daisy Creek, and Gold Creek. Westslope cutthroat trout distributions are classified here as confirmed (positive identification during all survey types) or unknown/none observed (occurring on tributary locations were no positive identification occurred, mainly due to limited surveys, i.e. bank surveys). Barriers (seasonal and permanent) used in summer analysis are included. Also shown is Grassy Mountain (site of the proposed Grassy Mountain Coal Mine) of the Crowsnest Pass, Alberta. Note, this map does not consider or provide species distributions from other or historical sources. Data are derived from summer snorkel and bank surveys during the duration of this study (2016 – 2017).

Increased undercut bank cover and suitable stream temperature are primary abiotic variables supporting increased Brook Char invasions in mountainous streams of Southern Alberta (Warnock and Rasmussen 2013). Undercut bank cover increased further in the headwaters among all of my study streams. Thus, even though habitat cover is likely more than suitable for Brook Char farther in the headwaters of Gold Creek, the current distribution of Brook Char does not reflect this. Invasion ability of Brook Char into Cutthroat Trout habitat increases with higher water temperatures (De Staso and Rahel 1994, Dunham et al. 2002). However, at lower water temperatures (approximately ≤ 15 °C), Brook Char have no competitive advantage over similar sized Cutthroat Trout (Griffith, 1972; De Staso & Rahel 1994). Thus, Brook Char distribution in Gold Creek may be determined by the colder water temperatures in the upper stream segments as Brook Char have a limited ability to compete with WCT at those water temperatures. With future warming of the environment by climate change, Brook Char's distribution and invasion ability is expected to increase (Roberts et al. 2017). In addition to illegal stocking above barriers (Thompson and Rahel 1998), this could extend Brook Char distribution further upstream in these watersheds.

Currently, there are also habitats that lie outside of Gold Creeks' mainstem and above permeant barriers that may be providing key source areas for the Brook Char population, those providing little competition with WCT (**Figure 2.9**). Letcher et al. (2007) found in their study of native Brook Char, that small tributaries with open access to larger stream networks provided reproductive sources and can be a significant factor in the population's persistence. Within the distribution of Brook Char on Gold Creek, there is a small tributary named Green Creek which has been found to contain Brook Char in the lower gradient reaches and has been previously looked at as a possible reproductive source for the population (Hatfield Consultants 2016). Another possibly significant source of Brook Char is a pond, of which is directly connected to Gold Creek. This pond was dammed, possibly during the time the historic town of Lille and railway line was active (1902-1912) (Felske 1991, Porter 2006), but has since been used by beaver *Castor canadensis*. In May of 2017, Brook Char fry were observed in abundance near a ground water seep located at the southwest corner of the pond.

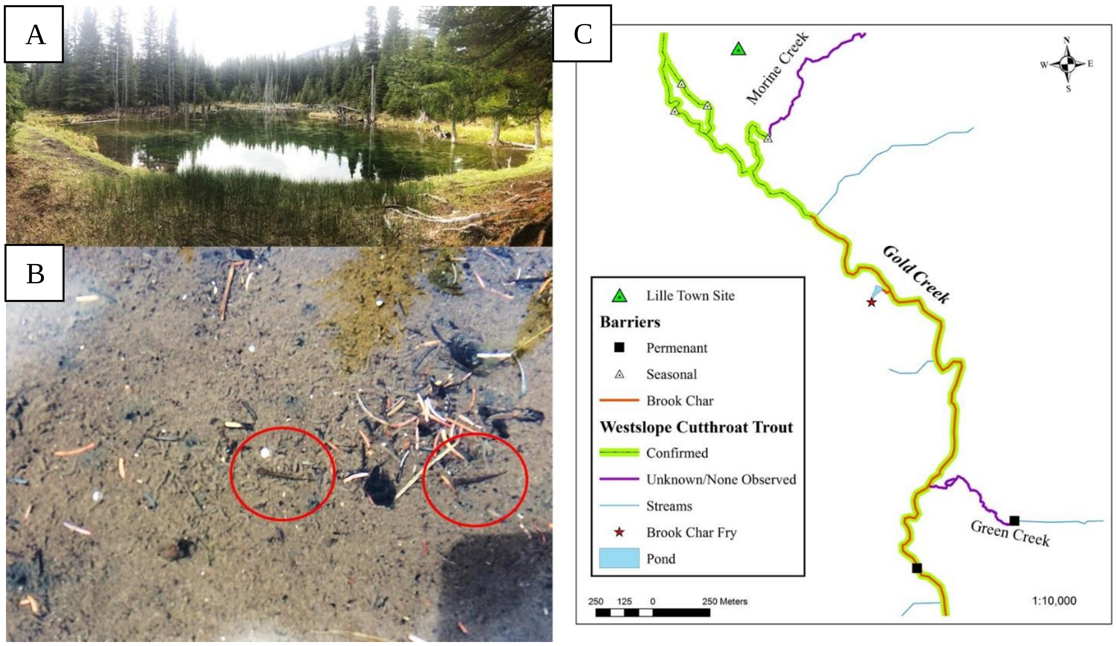

Figure 2.9 Possible reproductive sources of Brook Char on Gold Creek above a permanent barrier (waterfall). A) Pond near Gold Creek looking south-southwest. B) Brook Char fry observed in the pond during May of 2017 as indicated by red circles. C) Map showing pond location and Green Creek in relation to the historic town of Lille, barriers, and current Brook Char distribution within Gold Creek.

Conclusion

Pools in these headwater mountain streams makes up a very small proportion of total stream habitats but have a disproportionally high importance for WCT survival. Pool habitat characteristics can also vary considerably among watersheds and geomorphic segments. Sufficient cover in pools is one of the most important habitat features for WCT, however pool depth is an increasingly important habitat feature when cover is limited. In addition, physical barriers to movement are a significant influence, and specifically sections of subsurface flow and high waterfalls decrease connectivity and reduce fish presence in pools of separated stream sections. During low seasonal base flows in mountain streams, pool habitats are of increased importance as seasonal refugia. However, future changes in the landscape and climate may further exacerbate or impair habitat in Rocky Mountain headwater streams in Alberta. These factors will likely increase isolation among and within WCT populations, and management of headwater stream habitat should consider the conservation and protection of deep and well-connected pool habitats in conserving threatened WCT populations.

Chapter 3 - Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*) Winter Pool Use in Three Small, Steep, Rocky Mountain Headwater Streams in Southern Alberta.

Abstract

Westslope Cutthroat Trout (WCT) *Oncorhynchus clarki lewisi* are a threatened species in Alberta, where most remaining WCT populations are restricted to small headwater streams along the Rocky Mountains' eastern slopes. Winter is a critical time, where anthropogenic effects such as land-use, resource extraction, and climate change may have amplified effects on the survival of WCT populations. Comprehensive habitat surveys and non-invasive population estimate techniques, such as snorkeling and underwater cameras, were used to identify key features of WCT overwintering habitat quality, quantity and its use by WCT. This research focused on pools as the primary winter habitat for adult WCT, which is of increased importance for winter survival in small, high gradient mountainous streams. Using both habitat and spatial characteristics of pools, I investigated the feasibility of developing a two-step modelling approach to predict WCT winter habitat use within study watersheds. The first step in modeling incorporated multiple logistic regression methods, where summer habitat metrics in addition to seasonal changes in water temperature were able to reliably predict large WCT (> 20 cm) presence-absence in pools during mid winter by 82%. Where large WCT were present, the second step of modeling used multiple linear regression methods to predict large WCT abundance in winter. Here, generally the observed large WCT abundance during summer was not an indicator of winter large WCT abundance. However, during winter large WCT abundance responded to pool velocity, surface ice cover, and connectivity. The models identified key overwintering features and locations for threatened WCT within the study watersheds, which will lead to better informed decisions on the management of critical WCT habitat considering different land use practices and climate change.

Introduction

Anthropogenic impacts across the world threaten water resources and aquatic biodiversity through physical and chemical impairment (Malmqvist and Rundle 2002, Sanderson et al. 2002, Vörösmarty et al. 2010). In particular, habitat loss and effects of increased land use are the leading causes of species extirpations and extinctions globally (Baillie et al. 2004, Venter et al. 2006). However, changes in land use that negatively effect habitat may only be apparent within a seasonal context, for example during reproduction or environmentally challenging times of year (e.g. higher summer water temperatures vs. colder winter water temperatures) (Hicks et al. 1991, Cunjak 1996). Due to seasonal changes in the environment, what may be considered suitable habitat in one season, may not be suitable in another. In this case, although land use may not have a significant negative effect on summer habitat, negative effects may be more pronounced during winter (Cunjak 1996).

Winter is often considered a critical time of year for stream dwelling salmonids because of the significant changes to stream habitat (Cunjak 1996, Huusko et al. 2007). Near freezing water temperatures and the resulting ice formation in streams and rivers is the main source of habitat change from summer to winter (Cunjak 1996, Huusko et al. 2007, Stickler et al. 2010, Brown et al. 2011). For example, cold water temperatures lower fish's metabolism and thus activity (Cunjak 1988a) and consequently, reducing fish's ability to respond to a predator or changing environmental conditions. Ice formation physically alters stream habitat by altering streamflow (Stickler and Alfredsen 2009, Stickler et al. 2010) and excluding available habitats (Craig 1989, Whalen et al. 1999). These changes to stream habitat in winter make salmonid populations particularly vulnerable to the effects from land use and other environmental change (Cunjak 1996).

In streams and rivers, ice can be described within three main groups: frazil, anchor, and surface ice (Huusko et al. 2007, Brown et al. 2011). Surface ice is formed at the water surface within low velocity areas, such as slow runs and pools (Prowse 1994, Brown et al. 2011). In contrast, frazil and anchor ice are usually formed in turbulent areas of streams, such as riffles, which support sufficient supercooling (i.e. the cooling of water below 0 °C due to physical movement) throughout the water column (Martin 1981, Brown et al. 2011). Ice crystals that are suspended in the water column are termed frazil ice (Martin 1981, Brown et al. 2011). When the ice crystals are deposited on the bottom substrate, it is termed anchor ice (Martin 1981, Stickler and Alfredsen 2009, Brown et al. 2011). Frazil ice can be hazardous to fish due to the direct physiological effects to the respiratory system (e.g. abrading and plugging of the gills), caused by numerous and growing ice crystals (Brown et al. 1993). Frazil ice and anchor ice development also can cause substantial and rapid changes to habitat, physically altering water velocities and water depth (Brown et al. 1993, Stickler and Alfredsen 2009, Stickler et al. 2010). Ice growth that penetrates deep enough into the substrate can freeze incubating eggs and alevins of fall spawning salmonids (Reiser and Wesche 1979, Curry et al. 1995, Baxter and McPhail 1999).

In general, groundwater influence in streams has a moderating effect on surface water, maintaining colder water temperatures during summer and warmer water temperatures during winter (Power et al. 1999). Since groundwater discharge is water that is stored in underground aquifers, in winter it usually maintains higher temperatures than that of surface water, dictating ice persistence and development in streams (Power et al. 1999, Lindstrom and Hubert 2011). For example, in stream segments with high groundwater influence, little or no ice formation occurs which can provide thermal refuge for fish during winter (Brown and Mackay 1995, Power et al. 1999). However, as groundwater discharge moves downstream from the original source, it is cooled by air temperatures resulting in dynamic ice forming processes (Brown 1999, Lindstrom and Hubert 2011).

To avoid near freezing water temperatures and ice formation, smaller salmonids, usually young of the year and juveniles, seek concealment in the interstitial space of substrate and may move to shallower habitats (Cunjak 1988b, Bjornn and Reiser 1991, Heggenes et al. 1993, Gregory and Griffith 1996, Jakober et al. 2000). In contrast, deep pools are the primary habitat used by larger bodied salmonids (mainly adults) in winter (Heifetz et al. 1986, Brown and Mackay 1995, Cunjak 1996, Bonneau and Scarnecchia 1997, Jakober et al. 1998, Brown 1999, Dieterman et al. 2018) because they are too large to conceal within cover interstices and must congregate in limited open habitat (Cunjak and Power 1986, Brown and Mackay 1995, Cunjak 1996). Pool habitats contain lowered water velocities and increased physical space (e.g. in contrast to riffles), which provide conditions that facilitate reduced activity and predation risk (Cunjak 1996). The congregating behaviour of salmonids during winter in pools (a type of shoaling behaviour) is caused by habitat limitation, also called the “squeezing effect”, when salmonids are forced from alternative summer habitats due to further decreasing water temperatures and ice formation (Cunjak 1996, Brown 1999, Power et al. 1999). Although deep pools may often seem to provide conditions to facilitate refuge habitats in winter, not all deep pools are suitable. Even in deep pools, habitat suitability can be compromised by frazil and anchor ice development (Cunjak 1996).

Spatial position of habitat and connectivity within stream networks plays an important role in the ecology of many stream dwelling salmonids (Rieman and Dunham 2000). For example, in order to avoid deleterious ice conditions, some fish make large migrations between summer and winter habitats (Brown and Mackay 1995, Cunjak 1996). Cutthroat Trout in an Idaho river system moved greater than 80 km to winter habitat (Bjornn and Mallet 1964). In less migrant life history forms of Cutthroat Trout, movements up to 2.5 km are not uncommon (Brown and Mackay 1995, Brown 1999). Continual dynamic ice forming processes throughout winter can further induce significant movements of salmonids (Brown 1999, Lindstrom and Hubert 2011). Thus, connectivity among habitats that provide winter refuge must be available when environmental conditions change.

Even though winter is considered a critical time, there is still limited knowledge surrounding winter salmonid ecology (Cunjak 1996, Huusko et al. 2007). The lack of knowledge of specific components of winter ecology is especially significant as we start to find land use practices and climate change have the ability to drastically alter winter habitats (Cunjak 1996, Quayle et al. 2002). Improper land use management can lead to a loss of habitat complexity and altered streamflows (Bonta et al. 1997, Negley and Eshleman 2006, Ferrari et al. 2009, Bernhardt and Palmer 2011). Climate change in northern regions is expected to increase winter temperatures (Corell 2006), altering winter freeze and thaw cycles (Magnuson et al. 2000). Therefore, it is important to be able to describe winter habitats before they are altered which is imperative for proper fisheries management.

Currently, little information exists for describing threatened Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* (WCT) winter habitat, and what stream features are conducive for winter survival in small and steep mountain headwater streams (AWCTRT 2013). In Alberta, these major knowledge gaps have been identified in the recovery plan for the species (AWCTRT 2013). Limits of technology and gear, as well as reduced accessibility to remote headwater streams in winter has hindered research in this area. Consequently, studies have mainly focused on rivers and larger streams (> 3rd order) (e.g. Brown & Mackay 1995; Brown 1999), and very few have looked at smaller and steep mountain headwater streams (≤ 3rd order) (e.g. Jakober *et al.* 1998, 2000; Muhlfeld *et al.* 2001).

Although deep pool habitat may be primarily suitable for WCT during winter (Brown and Mackay 1995, Jakober et al. 1998, 2000, Brown 1999), other factors, such as seasonal changes in environmental conditions, as well as spatial position within the stream network, may become important in explaining habitat use during winter. The main objectives of this study are to: 1) describe the seasonal changes in pool habitat, specifically focusing on water temperature, ice conditions, and the extent of barriers limiting movement among pools; 2) describe the seasonal changes in size class specific WCT abundance in pools, which may be related to differences in concealment or aggregation in winter; 3) develop predictive models to explain WCT pool use, including presence-absence and abundance, from summer and winter habitat metrics.

Materials and Methods

Study Sites

The study area is located along the east slopes of the Rocky Mountains of Southern Alberta, Canada (see Chapter 2, **Figure 2.1**). I selected three study streams within the larger Oldman watershed drainage system. Specifically, the study streams Gold Creek and Blairmore Creek are located within the Crowsnest River sub-watershed, and Daisy Creek within the Upper Oldman River sub-watershed. During the summer of 2016, streams were surveyed and stratified into three geomorphic segments: canyon, alluvial, and headwater. Pools are the main habitat patch of interest, where a total of 133 pools (randomly selected from a larger subset of all pools = 602) were identified for summer and winter sampling: Blairmore N = 43, Daisy N = 44, Gold N = 47. All of the study pools were georeferenced with a global positioning system (GPS)(GARMIN, model 64s) and characterized by type using a habitat classification system (modified from Flosi *et al.* 1998). For a full description of the study area, streams and geomorphic segments, see Materials and Methods in Chapter 2 (**pg. 41**).

Summer habitat and fish surveys for all study pools were conducted within the low flow periods during mid to late August and early September. For the winter analysis, habitat and fish surveys took place during two main winter periods: early winter (November – December) and mid winter (January – February). Late winter surveys (March – April) were attempted for all streams, however, high variability of turbidity in Blairmore Creek due to partial snow melt led to conditions not adequate for snorkel surveys (e.g. visibility often < 0.5 m). Because late winter surveys contained incomplete fish and habitat data for Blairmore Creek, this period was not used for this analysis.

Stream Habitat

Quantitative and qualitative stream habitat variables were assessed in pools during the summer of 2016 including but not limited to: maximum depth (cm), area (m^2), pool velocity (m/s), dominant substrate, silt cover, available habitat cover, and bank condition (see Chapter 2, Materials and Methods, **pg. 44**, for descriptions on how variables were derived and **Table 2.1** for a complete list of variables). Several summer habitat variables were not expected to change across the seasons and were held constant from summer 2016 to be used to predict WCT pool use during winter. These qualitative habitat variables held constant over winter were: available habitat cover, bank condition, silt cover, and dominant substrate. Maximum depth, area, and pool velocity were also held constant from summer to winter. Pool dimensions and velocity were kept constant because complete or accurate measurements for these variables in winter was difficult due to complete or partial ice and snow cover. Moreover, the removal of ice and snow cover to measure these variables was not conducted because of the threatened status of WCT in Alberta (Fisheries and Oceans Canada 2014). In this case, priority was given to minimize disturbance of critical habitat.

During both summer and winter, water quality parameters were measured. Water temperature (nearest 0.1 °C), conductivity (µS/cm), and dissolved oxygen (mg/L) were measured with a multimeter (YSI Inc., model 556 MPS). Turbidity was assessed indirectly in a similar manner as summer fish surveys and rated as: none, low, moderate, high, or very high. In winter, the addition of air temperature and seasonal water temperature difference was used for analysis. Air temperature was measured to the nearest 1.0 °C using a standard outdoor thermometer. Seasonal water temperature difference was estimated by subtracting the observed average winter water temperature (mean water temperature taken between early and mid winter) by the summer water temperature. The difference between winter and summer water temperatures (i.e. seasonal variation) was used to estimate the moderating effect of groundwater on stream temperatures for each pool, since groundwater temperatures are much more stable throughout the year (i.e. small seasonal temperature variation) in contrast to stream water temperatures, which vary strongly on a daily and seasonal basis (i.e. larger seasonal temperature variation) (Kalbus et al. 2006). Therefore, each study pool was assigned the calculated seasonal water temperature difference value for both summer and winter analyses to indicate groundwater influence.

To further obtain detailed seasonal water temperature data in pools, water temperatures were also recorded using pendant temperature loggers (Onset-Hobo®, model numbers UA-002-64 and UA-001-08). A subset of pools was randomly chosen (*N* = 55) with priority given to pools classified as potentially high quality (see Chapter 2, Materials and Methods, **pg. 44)**. Loggers were attached to rebar and placed near the deepest part of the pool to avoid removal during spring flooding or ice scour. Loggers were set to record water temperature every hour for approximately one year (August 2016 to August 2017). Furthermore, because groundwater temperatures were not directly measured and later comparisons to stream temperature profiles were intended, to approximate groundwater temperature the average yearly air temperature was used (Power et al. 1999, Kalbus et al. 2006, Menberg et al. 2014). Generally, the average yearly air temperature above the ground surface is equal to the temperature of groundwater (Power et al. 1999, Kalbus et al. 2006, Menberg et al. 2014). Data were used from five stations surrounding the study area (Pelletier Creek, Crowsnest River, Blairmore, Vicary Creek, Chapel Rock) and the mean average yearly air temperature was calculated for years 2016 and 2017 (Government of Alberta Agriculture and Forestry 2018).

Measured winter habitat characteristics consisted of mean surface ice thickness and mean snow depth. Surface ice thickness was taken at the thickest and thinnest point found within the pool, measured to the nearest millimeter, and an average then taken for the pool. Snow depth was measured at the deepest and shallowest point within the pools' surface area, measured to the nearest centimeter, and measurements were averaged for the pool. Percent surface ice cover (%), percent snow cover (%), presence of frazil ice and anchor ice, and cumulative ice exclusion were assessed visually for each pool as metrics for qualitative winter habitat. Percent surface ice and snow cover were visually estimated in relation to the pools' surface area and transformed into a scale as follows: 0-25 % (1), 26-50 % (2), 51-75 % (3), 76-100 % (4). The presence of frazil ice and anchor ice were both noted for the pool individually. Individually, percent surface ice, percent frazil ice, and percent anchor ice exclusion were visually estimated relative to the pool volume and summed up. Cumulative ice exclusion was then transformed into a scale in the same manner as surface ice and snow cover.

Spatial Data

Spatial data were derived from field collected georeferenced data and the use of geographic information system (GIS) software ArcMap (ESRI 2016). During summer surveys pools, barriers and streams were georeferenced with a handheld GPS. In addition to spatial data collected within the study streams' mainstems, key tributaries were also surveyed for additional information on pool habitat and barriers during the following summer of 2017. Only barriers previously known or obvious were considered, as full assessments to determine passability for all potential barriers encountered were not possible during the time period of this study. Barriers to fish movement were reassessed during winter surveys and the new barrier extent was georeferenced and used for winter analyses. Barrier types identified included: water falls, weirs, debris jams and subsurface flow areas (i.e. dry sections of creek bed). Debris jams were frequently encountered on smaller tributaries in high gradient areas and were only considered when a full drop was greater than one meter (Kondratieff and Myrick 2006) and/or had flow through the structure (i.e. no water passing over the barrier).

To assess connectivity for each study pool, the distance to the nearest pool upstream and downstream (m), and distance to the nearest barrier upstream and downstream (m) were measured. Different barrier types were set as either "active" (i.e. fish are not able to pass the barrier) or "inactive" (i.e. fish are able to pass the barrier) during the nearest pool analysis depending on flow direction and fish movement. For example, waterfalls and weirs allow fish movement in the downstream direction, but no fish movement in the upstream direction, so these barriers would be set as “inactive” for downstream calculations and set as “active” for upstream calculations. In contrast, subsurface flow sections do not allow any fish movement in either direction and so these barriers would always be set as “active”. Additionally, the total number of alternate pools were also counted for each study pool. In this case all barriers, including falls and weirs, were kept “active” during the analysis. Even though fish can access pools downstream of falls and weirs, if they were to go over the barrier, they would not be able to return to the originating pool, effectively removing themselves from the previous population. In the cases were no barrier was present below the study pool and connectivity extended into the larger watersheds (Crowsnest or Oldman River), the maximum value recorded plus a 50 % increase was used as the limit. This was done for both distance calculations and pool counts to avoid adding disproportionate weight to the analysis for those pools, yet still reflect the greater connectivity present.

Other variables used during analysis to describe spatial position in streams included: longitudinal position (e.g. the distance from the upstream most boundary, downstream to each pool), watershed area, and elevation. For more detail on how spatial variables were derived see Materials and Methods section in Chapter 2 (**pg. 44**).

Fish Surveys

Due to WCT being a threatened species (COSEWIC 2016), fish population surveys during summer were performed using the least invasive methods possible. Snorkel surveys were first used as a non-invasive technique to estimate population size, size-class, and habitat use (Thurow 1994, O’Neal 2007). Snorkel surveys for selected pools occurred just prior to habitat sampling with the snorkeler entering the stream from the downstream end of the pool so to not spook or disturb fish. Visibility was periodically checked by measuring the distance from a stationary object resembling a salmonid silhouette (a 20 cm long trout fishing lure with parr marks was used) to the maximum distance where the snorkeler could no longer see the object (Thurow 1994). Snorkel surveys were only performed if visibility in the pool was at a minimum of 2-4 m depending on stream size (Thurow 1994). When snorkel surveys encountered complex cover that had a limited amount of light (e.g. undercut banks, log jams, boulder crevasses), an under-water flash light was used. Lastly, because exceptionally large aggregations of WCT were encountered during winter, to make the most accurate count, a mean of five repeated snorkeling counts per pool was taken. Exceptionally large aggregations were defined as containing 50 or more individuals.

Similar to summer surveys, the least invasive methods to minimize disturbance to threatened WCT were employed during winter. Thus, in winter snorkel surveys continued to be the primary means of fish surveys, however video camera surveys (Carlson and Quinn 2005, Mueller et al. 2006) and bank surveys supplemented snorkeling whenever surface ice conditions (e.g. full surface ice cover) and extremely low temperatures (e.g. -20 to -30 °C) prevented snorkel surveys. Where there was no surface ice present, visibility was excellent, and the entire pool could be viewed to the bottom (i.e. only in the shallowest pools), some surveys were conducted at the stream bank using polarized glasses (**Figure 3.1**) to limit disturbance on threatened overwintering fish. However, because the combination of these characteristics was rare, the majority of sites were surveyed using a camera.

For camera surveys a commercial ice-fishing camera (Aqua-vu®, model 760cz) was used in combination with either an ice fishing tripod (Aqua-vu® Mo-Pod) or a modified four-meter-long collapsible painting pole (**Figure 3.2**). When surface ice was present, the tripod was used to suspend the camera through a hole in the ice. If a hole through the ice was needed, a single hole was drilled through the center of the pool using a 16 cm diameter hand auger. If visibility was obstructed by features preventing a full view of the pool, additional holes were made. Using the tripod allowed for a horizontal 360° view of the pool under ice cover. When surface ice was limited but air temperatures where too cold for snorkeling, the camera was mounted to a bracket on a painting pole (i.e. the bracket allowing the camera to pivot). Like snorkel surveys, the camera entered the pool from the downstream end near the shore so to not spook or disturb fish and then was moved up through the pool as needed. In both cases of camera use, the real time video captured in the field allowed counts, identification of species, and estimates of size classes on the adjacent 17.8 cm, full colour, Aqua-vu® fishing camera LCD monitor. To make the most accurate count, fish surveys were conducted a minimum of 15 min after the hole was drilled to allow fish to settle after being disturbed. However, fish were often observed in normal behaviour within a few minutes of the hole being drilled in the ice or the camera entering the pool. In cases were snow was sufficiently deep or ice sufficiently thick and the amount of light reaching the pool was limited, the used model of Aqua-vu® camera included an infrared lighting feature to capture video in low light conditions. If this feature was still not enough to view the pool due to extremely low light conditions, an under-water flood light (Aqua-vu®) was attached to the camera to aid in viewing. Fish had low fright response to light, a similar observation made by other studies (Jakober et al. 1998). After all surveys were completed, if holes in the ice were present or a hole in the snow was dug to access the pool, these features were carefully filled in and/or covered with snow or ice to ensure there was limited effect to habitat and fish. To limit any detection bias between the snorkel and camera surveys, cover that may provide concealment for fish (e.g. cobbles, wood debris) were not moved during snorkel surveys during summer or winter.

Figure 3.1 An example of a study pool that provided conditions for bank surveys. Note the aggregation of WCT can be seen in the center of the pool (indicated by the yellow circle), uninterrupted by cover or turbulence.

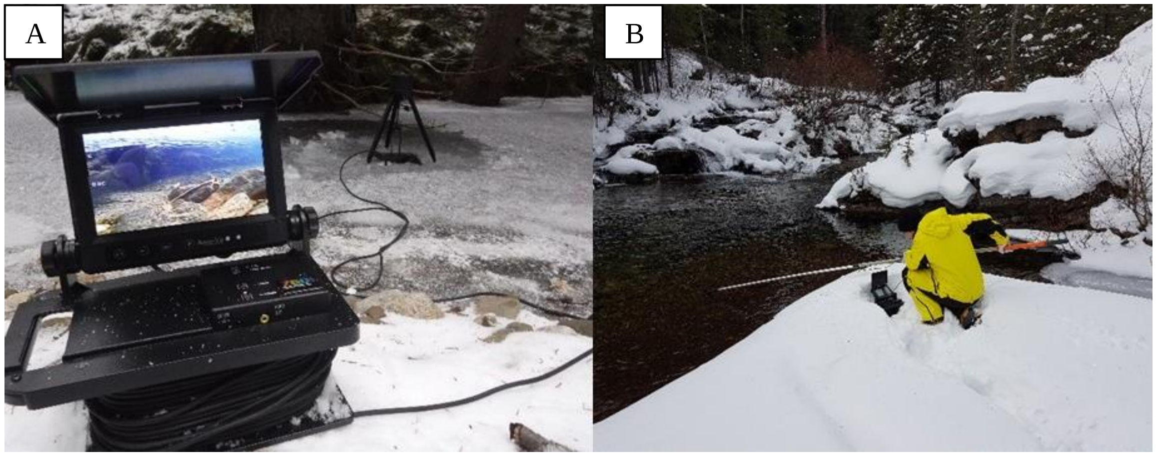

Figure 3.2 Photos showing A) ice cover set up with camera and tripod (Aqua-vu®) used in fish surveys; B) pole set up used in fish surveys for remote sites when no ice cover was present and air temperatures posed a risk to the snorkeler.

Fish within pools were identified to species, counted, and put into size classes of 10 cm increments (< 10 cm, < 20 cm… to < 80 cm), with the exception of < 5 cm individuals (Thurow 1994). Species identification during surveys was done using the key characteristics described for each species present in the study streams (Nelson and Paetz 1992, Thurow 1994, Behnke 2002). Genetically pure WCT have been recorded above the lowest barrier (weir) located on Gold Creek, and in the headwaters of both Daisy Creek (Rasmussen et al. 2010) and Blairmore Creek (Fisheries and Oceans Canada 2014). However, the ability to distinguish WCT hybrids during these surveys based on phenotypic characteristics (i.e. morphological characteristics) such as coloration and spotting pattern are unreliable (Allendorf et al. 2004, Robinson 2007) and thus unless fish provided all phenotypic characteristics of positive Rainbow Trout identification, they were counted as WCT.

When conditions permitted both snorkel and camera surveys to take place (e.g. only partial ice cover), camera surveys were calibrated with snorkel surveys to ensure comparable counts. Here camera surveys were conducted first, then after a brief rest period (15-20 minutes), snorkel surveys took place. Camera surveys took place first as they were assumed to be less intrusive within the pool compared to snorkel surveys and because of this, camera surveys may detect less fish. Between these two methods, no significant difference among fish counts were found (see Results **pg. 115**).

Abundance within each pool and for each species was calculated based on the number of individuals per estimated surface area (m^2). Finally, a species diversity score was given to each pool, calculated as the sum of all possible species observed occurring to the point of last observation in the upstream direction. Here it is assumed if at the last point a species was observed along the length of the stream, it could be present in all pools below that point. Thus, a species did not need to be present during the time of sampling to be counted in species diversity score.

Statistical Analysis

WCT abundance was checked for normality using Shapiro-Wilk test (Quinn and Keough 2002), and due to zero inflation (variable containing high numbers of zeros and having a highly skewed Poisson distribution) transformations to include zeros were not possible. Thus, to test if salmonid abundance was statistically different among sample periods (summer, early winter, and mid winter) while still including “true” zeros, one-way permutation analysis of variance (permANOVA) using the package *LmPerm* in R (Wheeler and Torchiano 2016) was used. To make multiple comparisons between means, Tukey’s honestly significant difference (HSD) test was used (Quinn and Keough 2002). Further investigation of winter habitat characteristics also used this approach as many habitat variables were also non-normally distributed.

Due to zero inflation of winter WCT abundance estimates in pools, a two-step modelling approach was used. The first step involves using multiple logistic regression to predict the probability of a pool having WCT present or absent (binomial function) based on its environmental and spatial variables. Where WCT are present, the second step of the analysis models WCT abundance in pools using multiple linear regression based on the same environmental and spatial variables. In other words, these analyses asked two separate questions regarding pool use by WCT where the first analysis explains the probability of suitability by a single individual and the second analysis explains suitability by a number of individuals.

Multiple Logistic Regression

The underlying basis of logistic regression is to discriminate between two groups or outcomes (i.e. in this case presence and absence) based on the relationship with the independent variable (Hair et al. 2006). Therefore, to select independent variables for multiple logistic model development, emphasis was given to those that had significant group differences (i.e. were highly discriminant) (Hair et al. 2006). In this case, correlation analysis was only used to help identify variables that may differ significantly among groups as well as identify collinearity. Significant correlations ($P \leq 0.05$) between independent variables and dependant variables were investigated further. If a pair of independent variables were highly colinear ($r \geq 0.75$) one of the two variables was eliminated from the analysis. Independent variables were then further assessed through permANOVA, and only variables found significantly different among groups presence and absence ($P \leq 0.05$) were used for model development. Where transformation increased logistic model fit, independent variables were logarithmic transformed ($X = \log_{10}$ or $X = \log_{10} [X + 1]$ if zeros were present) (Rieman and McIntyre 1995, Quinn and Keough 2002). Models were developed using the logistic function form:

$$P_i = \frac{e^{g(x_i)}}{1 + e^{g(x_i)}}$$

Equation 3.1

where P_i = probability of WCT presence or absence, e = the inverse natural logarithm of 1, and $g(x_i)$ = linear model:

$$g(x_i) = \alpha + \beta_1 X_{1i} + \ldots + \beta_p X_{pi},$$

Equation 3.2

where α = regression constant, β_p = regression coefficients, and X_{pi} = independent variables (Zuur et al. 2007). The maximum (-2) log likelihood method was used to estimate regression coefficients and probabilities of those regression coefficients are given by:

$$P_i = \left(\frac{e^{\beta}}{1 + e^{\beta}}\right) \times 100$$

Equation 3.3

where β is the regression coefficient in log odds (Hair et al. 2006, Zuur et al. 2007).

Stepwise regression procedures, using forward and backward selection provided the most parsimonious model determined by the lowest Akaike Information Criterion (AIC) (Quinn and

Keough 2002, Zuur et al. 2007). In R the package *MASS* was used for stepwise regression (Venables and Ripley 2002). Multicollinearity was checked after model development by the variance inflation factor using the R package *car* (Fox and Weisberg 2011), where values less than five were considered optimal (Craney and Surles 2002). Further, model assumptions were evaluated using diagnostic plots for influential observations (Zuur et al. 2007). Statistical significance of models were assessed using a chi-square test using the (-2) log-likelihood statistic (Quinn and Keough 2002, Hair et al. 2006, Zuur et al. 2007). In addition to chi-square tests and for ease of interpretation, McFadden R^2 measures were also calculated for the logistic regression model to asses model fit (Hair et al. 2006), using the R package *DescTools* (Signorell et al. 2018). McFadden R^2 measures are categorized as a pseudo R^2 measure that has similar interpretation to linear R^2 measures (i.e. coefficient of determination).

After the logistic regression model (based on summer habitat values collected during 2016) was produced and assumptions met, it was used to try and predict WCT presence-absence in winter. The model was tested using both winter data sets independently (i.e. early and mid winter data sets). The predictive ability was determined by the percentage of correctly or incorrectly classified predictions (Newcomb et al. 2007). In this case, large WCT presence-absence probabilities were predicted by the logistic model and compared with observed values. Predicted probabilities of ≥ 0.50 indicated WCT were present and predicted probabilities of ≤ 0.50 indicated WCT were absent. Model accuracy for the logistic regression model considered: (1) the proportion of observations correctly classified; (2) the proportion of WCT presence correctly classified, providing a measure of model sensitivity; (3) the proportion of WCT absence correctly classified, providing model specificity; (4) the proportion of presences incorrectly classified as false positives; and (5) the proportion of absences incorrectly classified as false negatives (Newcomb et al. 2007). Lastly, the Cohen’s kappa statistic expresses the proportion of sites correctly classified by the selected model after removing the effect of correct classification by chance (Titus and Mosher 1984, Beauchamp et al. 1992, Kruse et al. 1997). Kappa values with 95 % confidence limits were tested to determine if WCT presence-absence classifications by the logistic model were significantly different than random classifications (Titus and Mosher 1984). In R, the package *fmsb* was used to calculate and test Kappa values (Nakazawa 2018).

Multiple Linear Regression

To identify key variables influencing WCT abundance in pools during the summer of 2016 and both winter periods, a multiple linear regression approach was used. A total of 133 observations were used for model development. Correlation analysis was used to determine the correlation (and its significance) between each independent variable and WCT abundance in pools using the R package *Hmisc* (Harrell 2017). Some independent variables remained non-normally distributed and so the robust Spearman Rank based correlation was used (Quinn and Keough 2002). Significant correlations ($P \leq 0.05$) between independent variables and dependant variables were investigated further. If a pair of independent variables were highly colinear ($r \geq 0.75$) one of the two variables was eliminated from the analysis (e.g. the independent variable least correlated to the dependant variable was removed). The remaining variables were used for model development.

All categorical variables (i.e. factors) for which have values that range on a scale (i.e. available habitat cover score, bank condition, turbidity, and silt cover) were treated as continuous variables (Quinn and Keough 2002). Other variables such as creek, geomorphic segment, pool type, and dominant substrate were instead interpreted as categorical variables and transformed into numeric “dummy variables” (Quinn and Keough 2002). For the remaining independent variables with highly skewed distributions logarithmic transformations ($X = \log_{10}$ or $X = \log_{10} [X + 1]$ if zeros were present) were able to approximate normality and linearity (Quinn and Keough 2002). To confirm if normality and linearity was achieved through transformation, histograms were visually assessed, and a Shapiro-Wilk test was performed.

Similar to multiple logistic regression analysis, stepwise regression procedures used the R package *MASS* (Venables and Ripley 2002) to help select the most parsimonious model. Models were further assessed through their adjusted R^2 to select the best model (Hair et al. 2006). After model development multicollinearity and model assumptions were checked by evaluating the variance inflation factor and diagnostic plots (Zuur et al. 2007).

Large WCT Aggregation

Often large bodied salmonids aggregate in winter (Cunjak and Power 1986, Brown and Mackay 1995, Cunjak 1996). Therefore, to assess if aggregation of WCT in pools took place within each of the study streams an index of dispersion (variance-mean ratio) (VMR) was calculated using the total count for each pool:

$$VMR = \frac{\sigma^2}{\mu}$$

Equation 3.4

where σ^2 is the variance and μ is the mean (McGrew and Monroe 2000). In this case, a larger ratio ($VMR > 1$) indicates a higher degree of aggregation in pools, while a smaller ratio ($VMR < 1$) indicates a smaller degree of aggregation in pools (McGrew and Monroe 2000). VMR of one would indicate a random distribution (McGrew and Monroe 2000). The VMR was calculated for each stream during summer, early winter and mid winter sample periods. To compare changes in aggregation among streams and sample periods, the percent change in the VMR was calculated.

All statistical analyses were conducted using the programming language R (R Core Team 2016) running within RStudio (RStudio Team 2015). The package *ggplot2* was used for graphical display of data (Wickham 2009).

Results

During the summer of 2016 a total of 133 pools were assessed: Blairmore *N* = 42, Daisy *N* = 44, Gold *N* = 47. Due to changes in flow and ice formations, some sample sites were lost over the course of the winter. During early winter, 132 sites were sampled. One site in Gold Creek was lost due to upstream expansion of a subsurface flow area below the site. Partial surface ice formed over the pool indicates the loss of flow may have been sudden. By mid winter, the number of sites sampled declined to 129. Further dynamic ice formation through back water effects (Stickler et al. 2010) left thin or hanging surface ice layers on pools and in combination with heavy snow loading, caused conditions in two pools to be very unstable (both on Daisy Creek) and ultimately leading to surface ice collapse. In another pool located on Gold Creek, the ice formation became too thick for the hand auger to fully drill through the ice (surface ice thickness was > 80 cm).

Water Temperature and Ice

Out of the 55 temperature loggers deployed, five loggers had data logging errors, and 13 loggers were not recovered during the second summer. As indicated by the temperature loggers, water temperature in pools varied by season, stream and geomorphic segment (**Figure 3.3**). Furthermore, the average yearly air temperature (approximating groundwater temperatures) was approximately 3.0 °C during 2016 and 2017. Examining the average yearly air temperature on **Figure 3.3**, we find some pools during winter closely match this temperature, particularly in alluvial segments. Many other pools, particularly those in headwater segments and occurring in Blairmore Creek, remain near or at sub-freezing temperatures (i.e. near 0 °C) throughout winter. The time of year when the average water temperature in pools becomes colder than the groundwater temperature (i.e. when the average water temperature lines intersect and cross the average yearly air temperature line) occurs earlier for higher elevation segments (headwater - mid to late October), and later for lower elevation segments (canyon - early November).

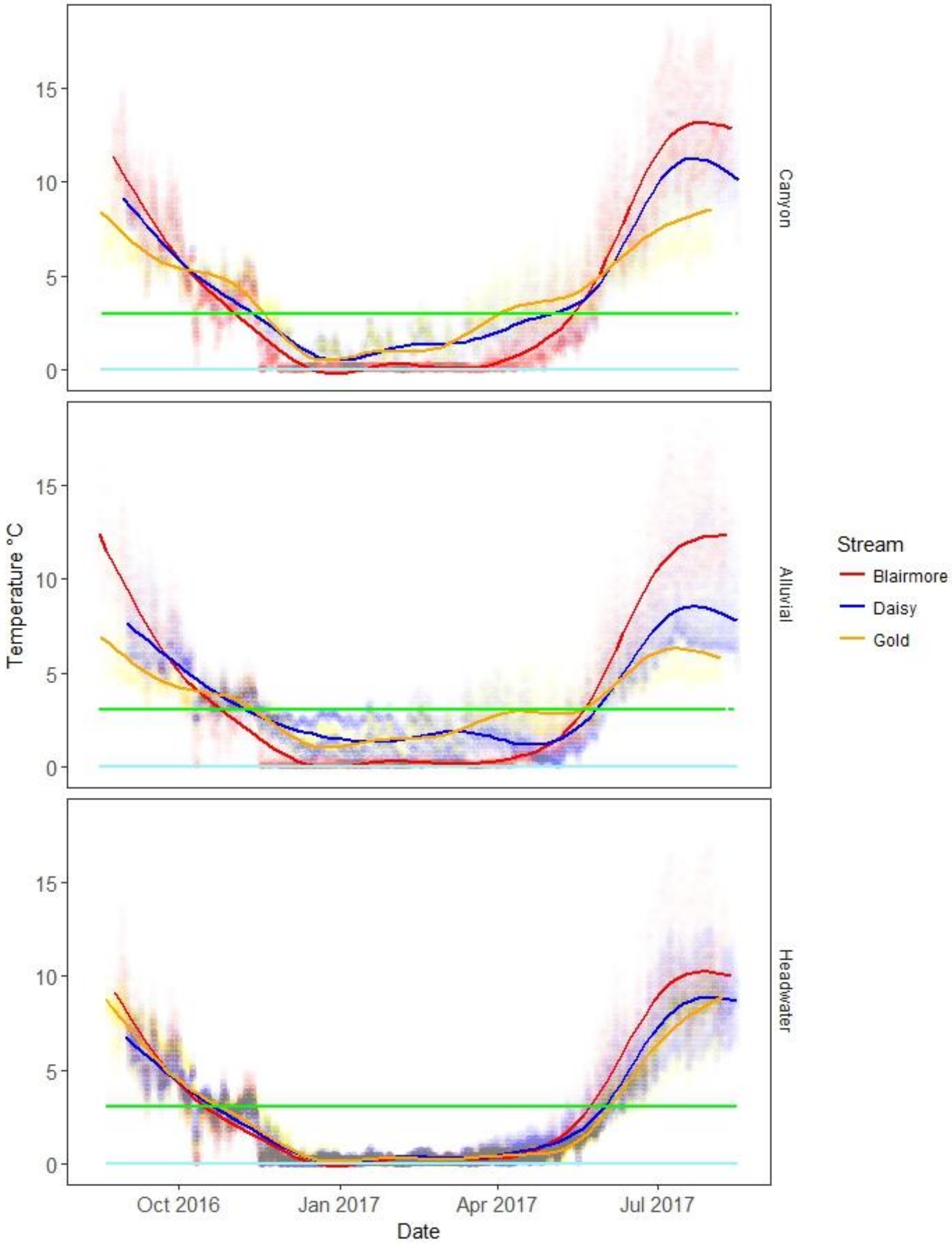

Figure 3.3 Hourly mean water temperature (°C) in pools for streams Blairmore Creek (*N* = 13), Daisy Creek (*N* = 10), and Gold Creek (*N* = 14) recorded over a one year period (approx. from August 2016 to August 2017). Faceting is by geomorphic segment and coloured lines indicate mean water temperature for each study stream. The green line indicates average yearly air temperature (2016-2017) at 3.03 °C, which is approximating groundwater temperature. The light blue line indicates freezing temperatures at 0.0 °C.

Water temperature recorded during field surveys show that it was significantly colder from summer to winter periods (**Table 3.1**). Although early winter had significantly colder air temperature than mid winter ($P < 0.001$), water temperature was not significantly different between early and mid winter. Among individual streams, water temperature was significantly different in summer of 2016, early winter and mid winter (**Table 3.2**). Among all sample periods, Tukey's HSD test revealed no significant difference in mean water temperature between Blairmore Creek and Daisy Creek, except during mid winter. However, Gold Creek was found to be significantly colder during summer than both Blairmore Creek and Daisy Creek and was significantly warmer during winter.

Table 3.1 Descriptive statistics, and permutations analysis of variance (permANOVA) results for environmental variables in study pools between summer 2016 (*N* = 133), early winter (*N* = 132) and mid winter (*N* = 129) periods. Where no units of measure are specified, values are score ranges.

	Summer 2016			Early Winter			Mid Winter				
Variable	Mean ± SE	Max	Min	Mean ± SE	Max	Min	Mean ± SE	Max	Min	*F* value	*P*
Conductivity (μS)	249.1 ±5.8^{c}	421.0	148.0	155.6 ±2.1^{a}	209.0	94.0	182.2 ± 3.1^{b}	286.0	113.0	144.30	**<0.001**
Dissolved Oxygen (mg/L)	11.5 ±0.1^{a}	13.7	7.0	16.1 ±0.1^{c}	18.3	10.1	15.4 ±0.1^{b}	18.7	10.7	357.70	**<0.001**
Turbidity ***	1.4 ±0.1^{b}	4.0	1.0	1.0 ±0.0^{a}	1.0	1.0	1.0 ±0.0^{a}	2.0	1.0	49.85	**<0.001**
Water Temperature (C°)	9.1 ±0.2^{b}	16.7	4.2	0.8 ±0.1^{a}	3.6	-0.1	0.7 ±0.1^{a}	3.6	-0.1	1180.00	**<0.001**
Air Temperature (C°)	13.2 ±0.4^{c}	31.0	5.0	-6.5 ±0.7^{b}	3.0	-25.0	-2.1 ±0.6^{a}	10.0	-18.0	314.00	**<0.001**
Surface Ice Thickness (mm)				75.3 ±7.8^{a}	400.0	0.0	123.7 ±13.9^{b}	720.0	0.0	9.33	**0.003**
Snow Depth (cm)				4.1 ±0.6^{a}	29.0	0.0	20.0 ±1.6^{b}	96.0	0.0	85.18	**<0.001**
Surface Ice Cover **				2.9 ±0.1	4.0	1.0	3.1 ±0.1	4.0	1.0	1.83	0.178
Snow Cover **				2.4 ±0.1^{a}	4.0	1.0	3.0 ±0.1^{b}	4.0	1.0	11.85	**0.001**
Frazil Ice Presence *				1.2 ±0.0^{b}	2.0	1.0	1.0 ±0.0^{a}	1.0	1.0	22.86	**<0.001**
Anchor Ice Presence *				1.0 ±0.0^{b}	2.0	1.0	1.0 ±0.0^{a}	1.0	1.0	5.04	**0.026**
Cumulative Ice Exclusion **				1.0 ±0.0	3.0	1.0	1.2 ±0.0	4.0	1.0	1.42	0.235

Means that do not share a letter are significantly different
* values are scores ranging 1 to 2
** values are scores ranging 1 to 4
*** values are scores ranging 1 to 5

Table 3.2 Descriptive statistics, and permutations analysis of variance (permANOVA) results for water temperature (°C) in study pools between Blairmore Creek, Daisy Creek , and Gold Creek during summer 2016 (*N* = 133), early winter (*N* = 132) and mid winter (*N* = 129).

Sample Period	Blairmore	Daisy Mean ± SE	Gold	*F* value	*P*
Summer	10.35 ±0.38^{b}	9.48 ±0.27^{b}	7.53 ±0.23^{a}	24.56	**<0.001**
Early Winter	0.01 ±0.03^{a}	0.28 ±0.09^{a}	2.13 ±0.18^{b}	94.98	**<0.001**
Mid Winter	0.05 ±0.04^{a}	0.74 ±0.16^{b}	1.37 ±0.14^{c}	29.04	**<0.001**

Means that do not share a letter are significantly different

When water temperature that was collected in the field was then further plotted against longitudinal distance downstream (**Figure 3.4**), we find that water temperatures varied spatially within streams. Specifically, during summer point sources of colder water temperature are present. During winter, point sources of higher water temperature become even more clearly visible. In Blairmore Creek water temperatures remained homogenous throughout the majority of the stream length during winter, while Daisy Creek, and further Gold Creek, became increasingly more heterogeneous in water temperature throughout the stream length.

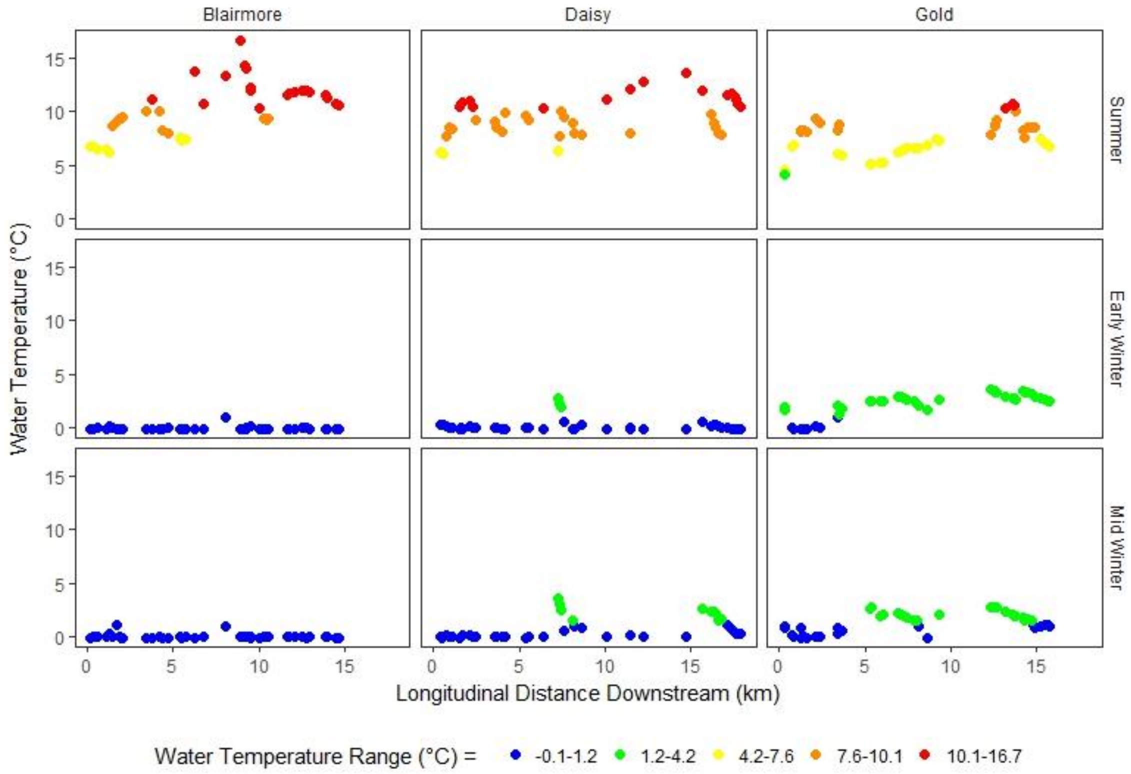

Figure 3.4 Water temperature (°C) in relation to longitudinal distance downstream (km). Here, streamflow is from left to right or from 0 km (highest elevation) to 15 km or greater (lowest elevation). For aid in visual interpretation, water temperature is also broken into classes using natural breaks (Coulson 1987). All observations are included. Faceting is by study stream and sample period (summer *N* = 133, early winter *N* = 132, mid winter *N* = 129).

When the seasonal water temperature difference in pools was calculated, means were found significantly different among streams (**Table 3.3**). Temperature variations in Gold Creek were significantly smaller, while temperature variations in Blairmore Creek and Daisy Creek were significantly larger (Tukey HSD, *P* < 0.001; **Figure 3.5**).

Table 3.3 Descriptive statistics, and permutations analysis of variance (permANOVA: $F_{2,130}$) results for seasonal water temperature difference (°C) in study pools between Blairmore Creek (N = 42), Daisy Creek (N = 44), and Gold Creek (N = 47).

	Blairmore Creek	Daisy Creek	Gold Creek		
Variable		Mean ± SE		*F* value	*P*
Water Temperature Difference	10.34 ± 0.38^b	9.40 ± 0.28^b	5.75 ± 0.28^a	61.85	<0.001

Means that do not share a letter are significantly different

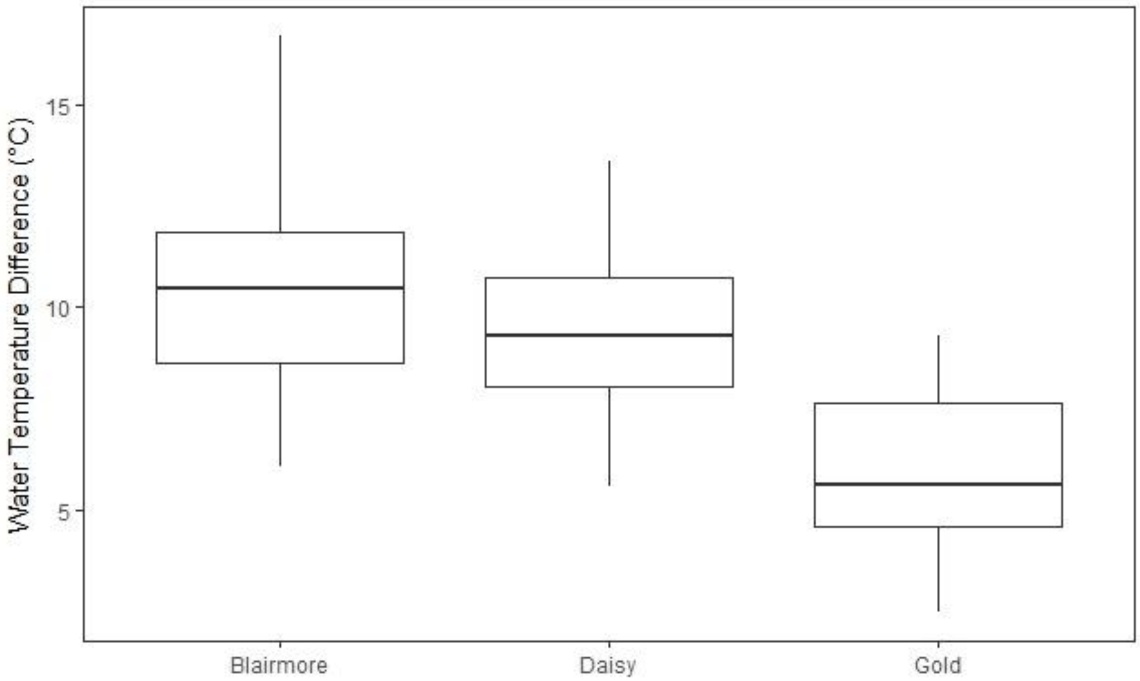

Figure 3.5 Seasonal water temperature difference (°C) in pools from summer to winter. Outliers are indicated (○) and lines indicate mean standard error.

In early winter, surface ice cover score (r = -0.78, $P < 0.001$) and mean surface ice thickness (r = -0.76, $P < 0.001$) significantly increased with falling water temperature (**Figure 3.6**). By mid winter, surface ice cover score was found not significantly different from early winter (**Table 3.1**) and water temperature was still significantly correlated (r = -0.71, $P < 0.001$).

In contrast, mean surface ice thickness had increased significantly from early winter, however water temperature and mean surface ice thickness became less correlated ($r = -0.21$, $P < 0.019$).

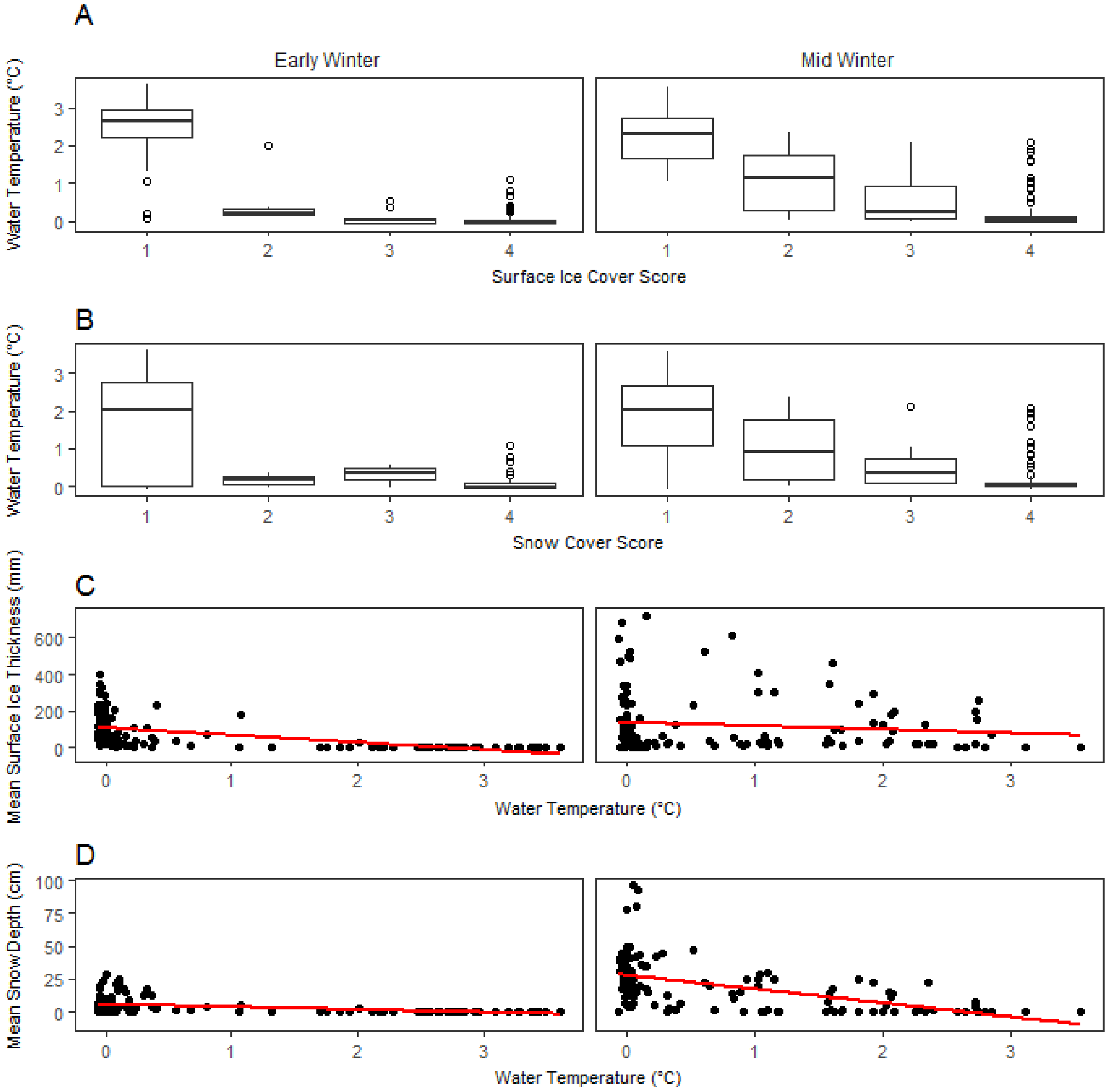

Figure 3.6 Mean water temperature (°C) by (A) surface ice cover score; (B) snow cover score; (°C) mean surface ice thickness (mm); and (D) mean snow depth (cm). Percent pool surface area cover scores range from: 1 = 0-25 %, 2 = 25-50 %, 3 = 50-75 %, and 4 = 75-100 %. All observations (pools) were used, where outliers are indicated (○) and lines indicate mean standard error. Faceting is by winter periods early winter (*N* = 132) and mid winter (*N* = 129).

Snow cover significantly increased on top of pools over the winter (**Table 3.1**). In mid winter, both snow cover ($r = 0.29$, $P = 0.001$) and snow depth ($r = 0.38$, $P < 0.001$) increased with increasing elevation. Both snow cover ($r = 0.90$, $P < 0.001$) and snow depth ($r = 0.62$, $P < 0.001$) also increased with increasing surface ice cover. Both snow cover ($r = -0.69$, $P < 0.001$) and snow depth ($r = -0.62$, $P < 0.001$) decreased with increased water temperature. Frazil ice and anchor ice presence was significantly higher in pools during early winter compared to mid winter (**Table 3.1**). No significant difference in habitat exclusion by ice (cumulative ice exclusion) in pools was found between early and mid winter.

Other water quality measurements were also found to be significantly different from summer to winter periods (**Table 3.1**). Both conductivity and turbidity were significantly lower in winter compared to summer. Dissolved oxygen was significantly higher in winter compared to summer and no measurements were observed below 10 mg/L during both winter periods. The lowest dissolved oxygen measurements observed during winter and summer were in pools directly below strong groundwater seeps.

Seasonal Changes in Barriers

A total of 12 barriers were identified in the mainstems of the study streams during the summer of 2016 (**Table 3.4**) and a total of 10 barriers limiting upstream movement by WCT were observed on main tributaries to the study streams during the summer of 2017. Two additional barriers were identified during the winter period on the main stems. These two additional barriers were subsurface flow areas located on Blairmore Creek near the confluence of the Crowsnest River and Gold Creek near the historic town of Lille. All subsurface flow barriers observed in summer persisted into winter and further increased in size, both in the upstream and downstream direction. The most extensive subsurface flow barrier located on Gold Creek had not yet developed during summer, but by early winter was approximately 600 m in length. The number of alternate pools was significantly lower during winter periods compared to summer (permANOVA: $F_{2,391} = 4.91$, $P = 0.008$; early winter $P = 0.016$; mid winter $P = 0.023$), but not between early and mid winter periods.

Table 3.4 Barriers identified on study stream mainstems during the summer of 2016 and both combined early and mid winter periods.

Barrier Type	Blairmore Creek	Daisy Creek	Gold Creek
Summer			
Subsurface Flow	0	4	4
Falls	2	0	1
Weir	0	0	1
Debris Dams	0	0	0
Winter			
Subsurface Flow	1	4	5
Falls	2	0	1
Weir	0	0	1
Debris Dams	0	0	0

Camera and Snorkel Counts

Due to large areas free of ice cover and mild temperature periods, snorkel surveys continued into winter making up 30 % of surveys during early winter and 21 % of surveys during mid winter. Because surface ice completely covered the majority of pools or air temperatures were often too cold for snorkeling, camera surveys became the main survey type over winter (early winter = 70 %; mid winter = 77 %). Eleven pools provided conditions for calibration between camera and snorkel surveys. Presence and absence between snorkel and camera surveys were in agreement 100 % of the time within size categories of small fish (< 20 cm) and 91 % of the time within the large fish category (> 20 cm). No difference in total fish counts (both WCT and Brook Char combined) or counts among size classes were found between snorkel or camera surveys (**Table 3.5**). Furthermore, significant relationships between log transformed total snorkel counts and log transformed total camera counts were found within size categories of small fish (< 20 cm) ($N = 11$, $R^2 = 0.98$, $P < 0.001$) and large fish (>20 cm) ($N = 11$, $R^2 = 0.81$, $P < 0.001$).

Bank surveys only occurred three times during winter in very shallow pools with little to no cover present. Visibility in early and mid winter was excellent, often greater than 10 m.

Table 3.5 Total, mean, standard deviation and one-way analysis of variance (permANOVA) results for fish counts (WCT and Brook Char combined) among snorkel and camera surveys in pools (*N* = 11). Fish are also grouped by categories small (<20 cm) and large (>20 cm).

	Snorkel Survey	**Camera Survey**		
Size Class	Mean ± SE		*F* value	*P*
TOTAL	2.64 ±0.97	2.36 ±0.81	0.047	0.831
0-5 cm	0.09 ±0.09	0.00 ±0.00	1.000	0.329
5-10 cm	0.09 ±0.09	0.27 ±0.19	0.714	0.408
10-20 cm	1.63 ±0.69	1.45 ±0.61	0.039	0.845
20-30 cm	0.54 ±0.25	0.36 ±0.20	0.323	0.576
30-40 cm	0.27 ±0.27	0.27 ±0.27	0.000	1.000
SMALL	1.82 ±0.84	1.73 ±0.73	0.007	0.936
LARGE	0.82 ±0.33	0.64 ±0.31	0.164	0.690

* indicates significant difference detected ($P < 0.05$).

Seasonal Changes in Salmonid Communities

Out of the total fish counted among all streams during the summer of 2016 ($N = 2375$), WCT (including hybrids) were the most abundant species among all study streams during both summers (94.6 %). Furthermore, within individual streams, WCT were still the most abundant species: Blairmore Creek (92.2 %), Daisy Creek (99.2 %), Gold Creek (89.8 %). In Blairmore Creek the remainder of fish counted were composed of Brook Char (7.7 %), Mountain Whitefish (< 0.1 %), and Rainbow Trout (0.3 %). In Gold Creek the remainder of fish counted were only Brook Char (10.2 %). Finally, in Daisy Creek the remainder of fish counted were only Bull Char (0.8 %).

By early winter the total fish count among streams had decreased by 53 % ($N = 1119$). Brook Char observations declined in Blairmore Creek by 100 % (i.e. none observed) and Gold Creek by 94 % from summer. Bull Char observations in Daisy Creek remained similar to summer counts making up 1.7 % of the fish count. In mid winter the total fish count had further decreased by 32 % from early winter (*N* = 845). Brook Char observations remained absent in Blairmore Creek and low in Gold Creek (only one single individual was observed in Gold Creek). In Daisy Creek Bull Char observations remained about the same making up 1.1 % of the total count. During both winter periods, WCT remained the most abundant fish species (early winter = 97.9 %, mid winter = 99.2 %). Nine mountain whitefish where observed during early winter in a single pool on Daisy Creek, however none were observed by mid winter. No individuals identified where observed to display complete phenotypic characteristics consistent with Rainbow Trout during winter periods.

During the summer of 2017, the total number of fish counted among all streams had doubled from mid winter counts (*N* = 1860), and WCT were still the most abundant species among all study streams (92.2 % of the total fish counted). Summer Brook Char observations increased from winter in both Blairmore Creek and Gold Creek, making up 4.1 % and 27.6 % of the fish count. Bull Char observations in Daisy Creek remained similar to previous sampling periods making up 2.2 % of the fish count.

Seasonal Changes in WCT Size Class Specific Abundance

In general, differences in mean total WCT abundance and size specific WCT abundance in pools were found among sample periods (**Table 3.6**). Total WCT abundance was significantly different among sample periods in pools, where specifically, WCT abundance significantly decreased from summer to winter (early winter $P < 0.0000$; mid winter $P < 0.0000$), and that there was no significant difference among early and mid winter ($P = 0.8385$). Only WCT size classes < 20 cm were significantly different among sample periods. WCT size classes > 20 cm did not differ significantly among sample periods. Subsequently, WCT size classes were grouped into categories small (< 20 cm) and large (> 20 cm) based on these differences and used in these groupings for further analysis. Abundance for small WCT was higher during summer, while large

WCT did not show significant differences among sampling periods. Including WCT survey data from the summer of 2017 with the first years WCT data (summer of 2016, early winter and mid winter) reveals that most small size classes (< 20 cm) return to similar mean abundance levels, while large size classes (> 20 cm) remain the same (**Figure 3.7**).

Table 3.6 Mean, standard deviation and permutations one-way analysis of variance (permANOVA) results for WCT abundance (WCT/m^{2}) among sample periods in pools.

WCT Size Class	Summer 2016	Early Winter	Mid Winter	*F* value	*P*
		Mean ± SE			
ALL	0.638 ±0.067^{a}	0.227 ±0.034^{b}	0.178 ±0.025^{b}	30.36	<0.001*
0-5 cm	0.090 ±0.018^{a}	0.000 ±0.000^{b}	0.000 ±0.000^{b}	25.12	<0.001*
5-10 cm	0.290 ±0.043^{a}	0.059 ±0.014^{b}	0.036 ±0.009^{b}	27.16	<0.001*
10-20 cm	0.218 ±0.024^{a}	0.123 ±0.019^{b}	0.113 ±0.018^{b}	8.05	<0.001*
20-30 cm	0.035 ±0.004	0.039 ±0.009	0.024 ±0.004	1.49	0.227
30-40 cm	0.002 ±0.001	0.006 ±0.002	0.004 ±0.001	2.97	0.052
SMALL	0.602 ±0.066^{a}	0.182 ±0.030^{b}	0.150 ±0.023^{b}	32.37	<0.001*
LARGE	0.036 ±0.005	0.045 ±0.010	0.028 ±0.005	1.48	0.228
N	133	132	129		

* indicates significant difference detected
Means that do not share a letter are significantly different

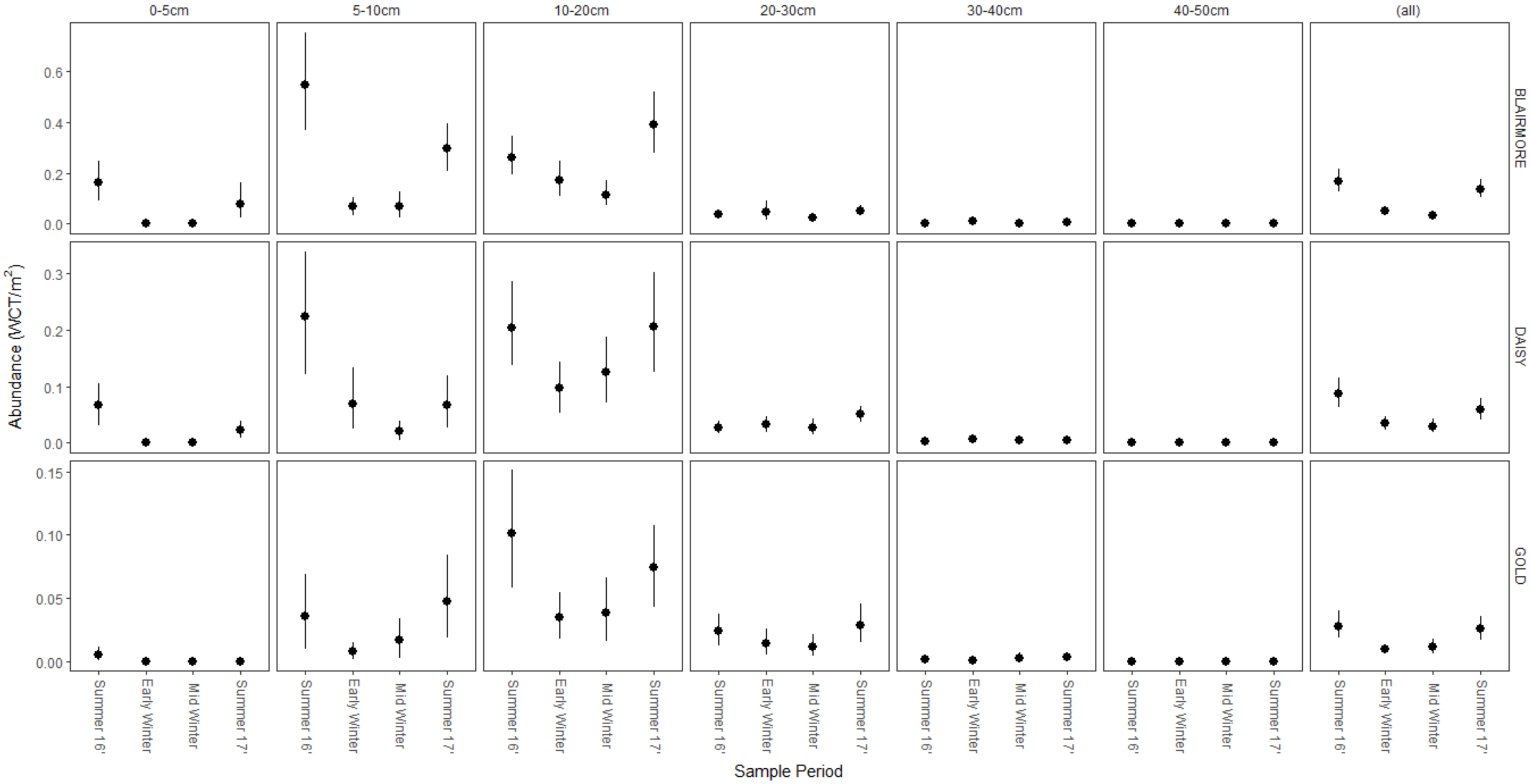

Figure 3.7 Mean Westslope Cutthroat Trout abundance (WCT/m^2) in pools by study stream and size class, among sample periods summer 2016 (*N* = 133), early winter (*N* = 132), mid winter (*N* = 129). Data from the summer of 2017 (*N* = 129), second chapter of this thesis is included. Lines indicate mean standard error.

Because many of the barriers (e.g. subsurface flow areas or large water falls) do not allow any mass migrations to occur for most of the study streams, the reduced small (< 20 cm) WCT abundances from summer to winter was thought to be due to concealment (Cunjak 1988b, Bjornn and Reiser 1991, Heggenes et al. 1993, Gregory and Griffith 1996, Jakober et al. 2000, Valdimarsson et al. 2000). Therefore, to approximate this change in abundance of small WCT less than 20 cm, an estimate of concealment was considered. Estimated concealment was calculated as the difference in abundance for each pool between two periods: 1) from summer to early winter and 2) from early winter to mid winter (**Table 3.7**).

Table 3.7 Mean, standard error and permutations one-way analysis of variance (permANOVA) results for small (< 20 cm) WCT estimated concealment (difference) among streams in pools for two periods: summer to early winter (SEW) and early winter to mid winter (EMW). Note that a negative difference indicates decreased concealment, while a positive difference indicates increased concealment.

Period	WCT Size Class	Blairmore	Daisy	Gold	*F* value	*P*
			Mean ± SE			
SEW	COMBINED	0.817±0.119^{c}	0.394 ±0.103^{b}	0.094 ±0.031^{a}	16.22	**<0.001***
	0-5 cm	0.178±0.043^{b}	0.096 ±0.030^{ab}	0.006 ±0.003^{a}	8.35	**<0.001***
	5-10 cm	0.529±0.098^{b}	0.189 ±0.063^{a}	0.028 ±0.015^{a}	14.95	**<0.001***
	10-20 cm	0.111±0.040	0.110 ±0.044	0.060 ±0.023	0.648	0.525
EMW	COMBINED	-0.066±0.054	-0.008 ±0.055	0.011 ±0.019	0.79	0.458
	0-5 cm	-0.001±0.001	-0.000 ±0.000	-0.000 ±0.000	2.00	0.140
	5-10 cm	-0.008±0.028	-0.046 ±0.025	0.010 ±0.009	1.67	0.192
	10-20 cm	-0.057±0.040	0.037 ±0.035	0.001 ±0.012	2.316	0.103
	N	42	42	45		

* indicates significant difference detected
Means that do not share a letter are significantly different

Including all WCT less than 20 cm, the number of individuals concealing was highest in Blairmore Creek and lowest in Gold Creek from summer to early winter (**Figure 3.8**). Furthermore, when looking at specific size classes, only estimated concealment of WCT 10-20 cm was not significantly different. WCT size classes 0-5 cm and 5-10 cm had significantly higher estimated concealment in Blairmore Creek compared to Daisy Creek and Gold Creek. In comparison, there was no difference in estimated concealment for the combined or specific size classes of small WCT from early winter to mid winter (**Figure 3.9**). When the estimated concealment was scaled for differences in population density (e.g. dividing estimated concealment by the total number of fish counted) no significant differences were found for the combined or size specific classes.

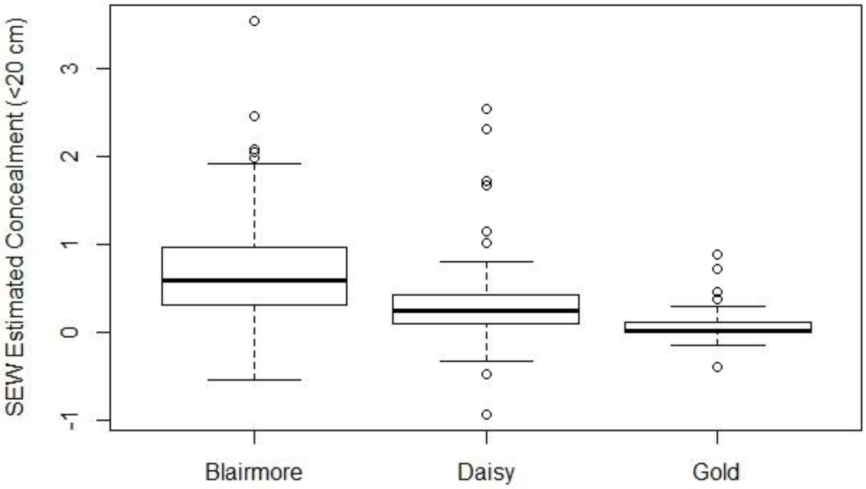

Figure 3.8 Summer – early winter (SEW) estimated concealment of combined small WCT (< 20 cm) among study streams Blairmore Creek (*N* = 42), Daisy Creek (*N* = 42), and Gold Creek (*N* = 45).

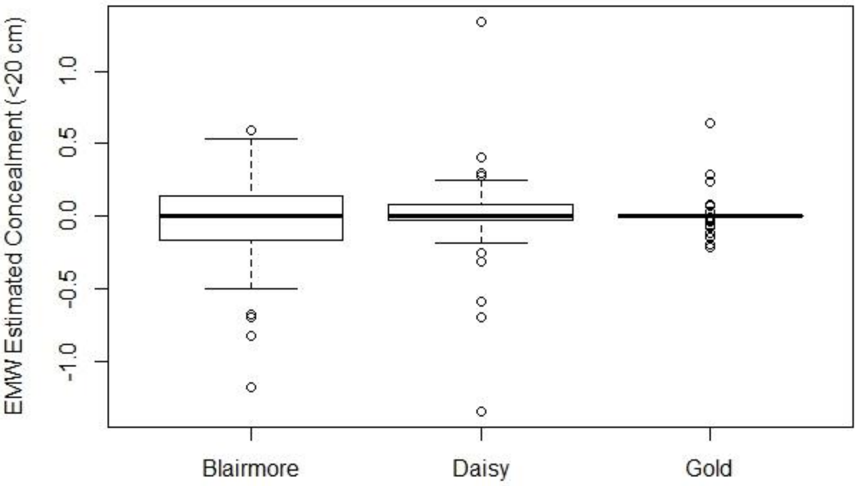

Figure 3.9 Early winter – mid winter (EMW) estimated concealment of combined small WCT (< 20 cm) among study streams Blairmore Creek (*N* = 42), Daisy Creek (*N* = 42), and Gold Creek (*N* = 45).

Summer and Winter WCT Presence-Absence in Pools

All together, WCT were present in all but 15 of the 133 pools sampled during the summer of 2016, 14 of those pools being located on Gold Creek. By early winter, WCT resided in 82 of 132 pools and in mid winter in 76 of 129 pools. Small WCT were present in 114 of the 133 pools sampled during summer of 2016. In early winter small WCT occupied 73 of the 132 pools sampled and by mid winter were present in 68 of the 129 pools sampled. When developing a multiple logistic model, ideally group proportions closer to a 50:50 ratio are best (e.g. pools divided by 50 % WCT presence: 50 % WCT absence) (Hair *et al.* 2006). Due to the group bias presented by presence-absence groups of small WCT in summer (i.e. 11 % absent to 89 % present), a multiple logistic model predicting presence-absence in winter could not be developed for this size category. In contrast, large WCT were present in only 55 of 133 pools sampled during summer of 2016. In early winter, large WCT were present in 39 of the 132 pools sampled and by mid winter were present in 38 of the 129 pools sampled. Because there was little group bias between presence and absence for large WCT (41 % absent to 59 % present) in summer, a multiple logistic model was developed for this size category.

A total of 133 observations were used for multiple logistic regression model development, only for the large WCT group. The best predictor model accounted for 43.2 % (McFadden R^2) of the variation in large WCT presence-absence during the summer of 2016 and was statistically significant (log-likelihood = -55.23; X_2 *(5)* = 77.9, P < 0.001) (**Equation 3.5**). This model consisted of 4 variables: the categorical variable geomorphic segment (SEGMENT); and the continuous variables log maximum depth (MAX_DEPTH), log area (AREA), and seasonal water temperature difference (WTEMP_DIFF). SEGMENT was significant in the model for two factor levels (Canyon P = 0.0580, Headwater P = 0.0027). The probability of large WCT presence in canyon segment pools was 22.6 % compared to the alluvial segment pools. The probability of large WCT presence in headwater segment pools was further reduced to only 6.7 % compared to the alluvial segment pools. Log MAX_DEPTH was significant in the model (P = 0.0007) where a one-unit increase in log MAX_DEPTH increased the probability of large WCT presence in a pool by 99.9 %. Log AREA was not significant in the model (P = 0.0549), however a one-unit increase in log AREA increased the probability of WCT presence in a pool by 86.9 %. Lastly, WTEMP_DIFF was significant in the model (P = 0.0316) where a one-unit increase in WTEMP_DIFF decreased the probability of WCT presence in a pool by 45.2 %.

$$Logit\ (p) = -2.970 - 1.230\ CANYON - 2.627\ HEADWATER + 6.823\ log_{10}(MAX\_DEPTH) + 1.894\ log_{10}(AREA) - 0.191\ WTEMP\_DIFF$$

Equation 3.5 Multiple logistic regression equation predicting the probability (*p*) of large (> 20 cm) WCT presence-absence in pools during summer (McFadden R^2 = 0.43; log-likelihood = -55.23; X_2 (5) = 77.9, *P* < 0.001). Variables include: canyon segment (CANYON), headwater segment (HEADWATER), log transformed maximum depth (m) (MAX_DEPTH), log transformed area (m^2) (AREA), and seasonal water temperature difference (°C) (WTEMP_DIFF).

Log maximum depth and log area were correlated ($r = 0.69$, $P < 0.001$) but not colinear. Alone, log maximum depth had the greatest influence in predicting large WCT distributions during the summer of 2016, however, including log area further improved the model. While log maximum depth and log area continue to influence large WCT distributions during winter, the predictive ability was slightly reduced (**Figure 3.10**). Some large WCT did seek lower velocity pools in canyon segments, particularly in early winter, however, overall pool velocity was not a great predictor of large WCT presence-absence.

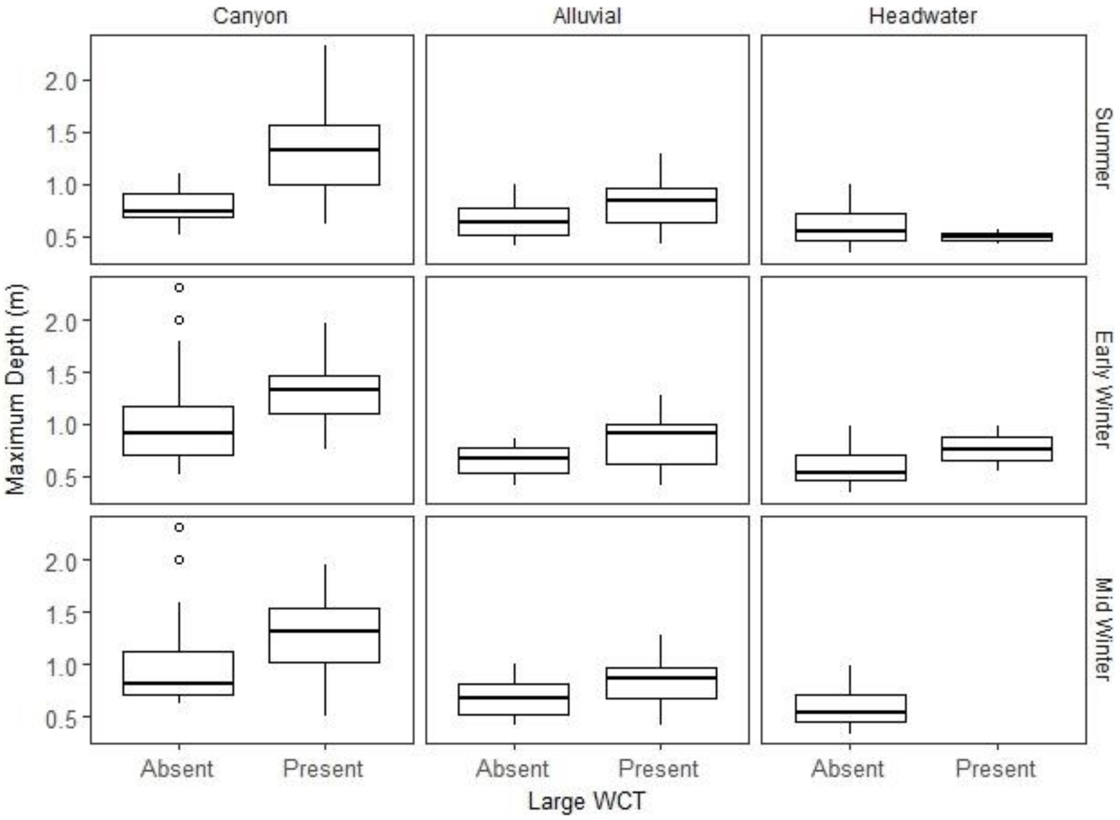

Figure 3.10 Presence and absence of large Westslope Cutthroat Trout (>20 cm) in relation to maximum depth (m) in pools. All observations are included, where outliers are indicated (○) and lines indicate mean standard error. Faceting is by geomorphic segment and sample period (summer *N* = 133, early winter *N* = 132, mid winter *N* = 129).

Seasonal water temperature also influenced large WCT distributions during the summer of 2016. In Blairmore Creek, large WCT presence was more associated with larger seasonal water temperature differences in pools. Between pools predicting large WCT presence and absence in Blairmore Creek, a significant difference in seasonal water temperature difference was found during summer (ANOVA: $F_{1,40} = 6.82$, $P = 0.0126$) and early winter (ANOVA: $F_{1,40} = 4.10$, $P = 0.0496$). No significant difference was detected for seasonal water temperature difference between pools predicting large WCT presence and absence during mid winter in Blairmore Creek. In contrast, large WCT presence was more closely associated with decreased seasonal water temperature difference in Gold Creek pools. Between pools predicting large WCT presence and absence in Gold Creek, a significant difference in seasonal water temperature difference was found during early winter (ANOVA: $F_{1,44} = 7.851$, $P = 0.008$). Seasonal water temperature difference was not significantly different between pools with large WCT present and absent in Daisy Creek.

The categorical variable geomorphic segment influenced large WCT presence and absence. One of the largest differences among geomorphic segments was the distance to the nearest pool upstream and downstream (**Figure 3.11**). During summer, the distance to the nearest pool upstream and downstream was significantly farther in the alluvial segment than both canyon and headwater segments (**Table 3.8**). On average the distance to the nearest pool in the alluvial segment was 1.5 to 1.8 times farther than within both canyon and headwater segments. The distance to the nearest pool upstream and downstream did not significantly differ by sample period.

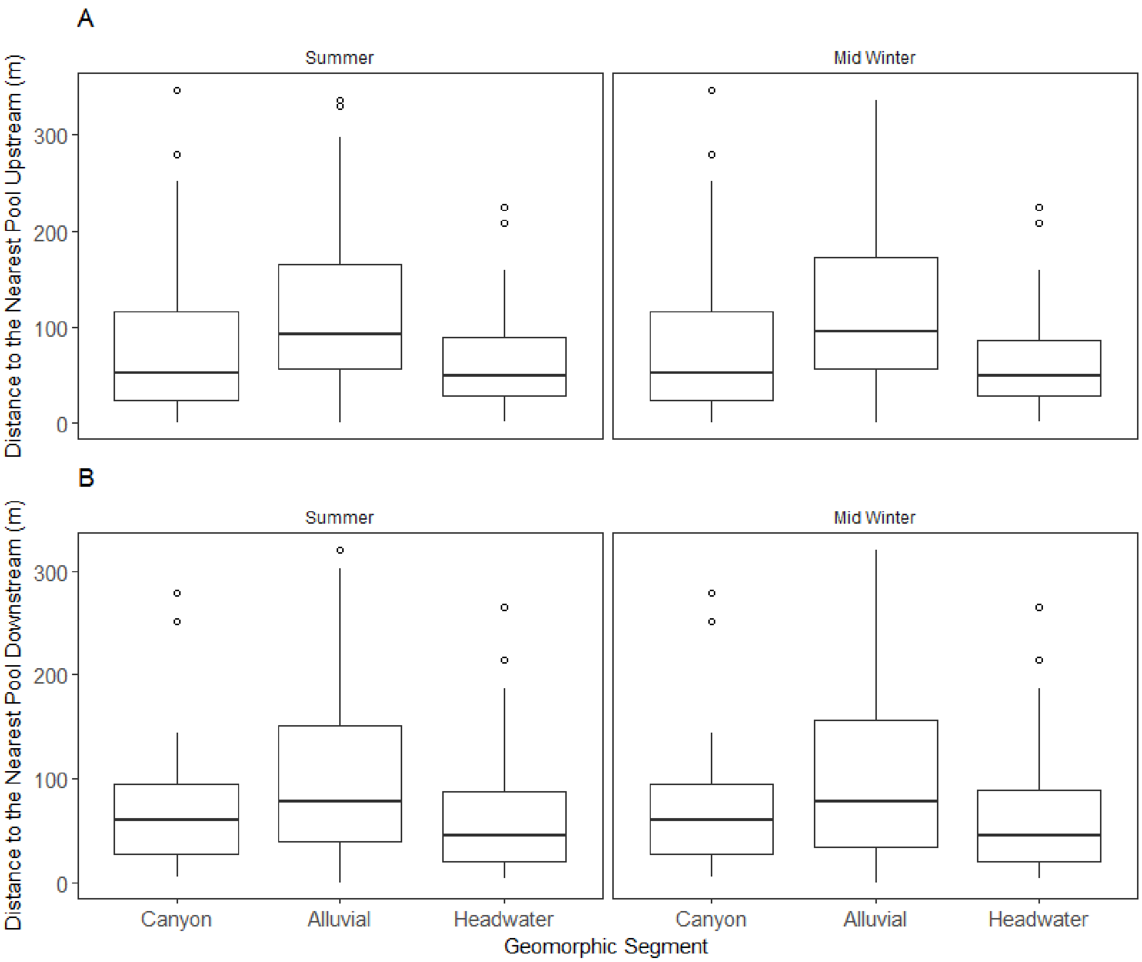

Figure 3.11 Distance to the nearest pool upstream (m) (A) and distance to the nearest pool downstream (m) (B) in relation to geomorphic segments. All observations (pools) were used, where outliers are indicated (○) and lines indicate mean standard error. Faceting is by sample periods summer (*N* = 133) and mid winter (*N* = 129).

Table 3.8 Mean, standard deviation and permutations one-way analysis of variance (permANOVA) results for distance to the nearest pool upstream (m) (DISTNPU) and distance to the nearest pool downstream (m) (DISTNPD) among geomorphic segments in pools during the summer of 2016.

	Canyon	Alluvial	Headwater		
Variable		Mean ± SE		*F* value	*P*
DISTNPU	79.0 ±10.7^{b}	119.2 ±14.6^{a}	65.3 ±7.8^{b}	5.89	0.004*
DISTNPD	69.0 ±7.9^{b}	108.1 ±14.2^{a}	64.1 ±8.9^{b}	5.16	0.007*
N	50	37	45		

* indicates significant difference detected
Means that do not share a letter are significantly different

Large group differences between presence and absence existed for large WCT in winter, presenting the potential for group bias in predictions (Titus and Mosher 1984, Hair et al. 2006). For example, large WCT were only present in 39 of the 132 pools sampled during early winter (30 % present : 70 % absent) and by mid winter were present in 38 of the 129 pools sampled (30 % present : 70 % absent). In this case, the absent group within the large WCT category is over represented. To remediate this, observations within the absent group were randomly selected for removal to match the present group (i.e. maintain group ratios closer to 50:50) (Hair et al. 2006). Selections were based on random numbers assigned to each observation, where the highest numbered observations were chosen for removal. The remaining observations were used to test the models.

The best predictor model correctly classified presence-absence in pools 79.5 % of the time in early winter (**Table 3.9**). The Cohens Kappa statistic of the model predictions strongly supported a non-random effect. Here the model correctly classified large WCT presence-absence in pools 75.0 % of the time in Blairmore Creek, 89.7 % of the time in Daisy Creek, and 72.0 % of the time in Gold Creek. Out of all predicted classifications, a total of 11.5 % of incorrect classifications were false positives. False positives were mainly comprised by pools located in Gold Creek (56 %). Among streams, false positives also occurred predominantly in pools located within canyon segments (89 %). Out of all predicted classifications, a total of 9.0 % of incorrect classifications were false negatives. False negatives were mainly comprised by pools located in Blairmore Creek (43 %). Among streams, false negative predictions were mainly associated with pools in alluvial segments (71 %).

Table 3.9 Model prediction results, between actual and predicted large (> 20 cm) Westslope Cutthroat Trout (WCT) in pools during early winter (*N* = 78, Present = 39, Absent = 39) and mid winter (*N* = 76, Present = 38, Absent = 38). Cohen's kappa statistics calculated at 95 % confidence.

Sample Period	Misclassification Error (%)	Correct Classification (%)			
		Present	Absent	Overall	Kappa
Early Winter	16 (20.5)	32 (82.1)	30 (76.9)	62 (79.5)	0.590*
Mid Winter	14 (18.4)	33 (86.8)	29 (76.3)	62 (81.6)	0.632*

*indicates significance at P < 0.001

In midwinter, the model correctly classified presence-absence in pools 81.6 % of the time. Again, the Cohens Kappa statistic of the model predictions strongly supported a non-random effect. The best model correctly classified large WCT presence-absence in pools 82.6 % of the time Blairmore Creek, 76.9 % of the time in Daisy Creek, and 85.2 % of the time in Gold Creek. Out of all predicted classifications, a total of 11.8 % of incorrect classifications were false positives. False positives were primarily comprised by pools located in Daisy Creek (44 %) and Gold Creek (33 %). Among streams, almost all false positives occurred in pools located within canyon segments (89 %). Out of all predicted classifications, a total of 6.6 % of incorrect classifications were false negatives. False negative predictions were mainly associated with pools located in Blairmore Creek (40 %) and Daisy Creek (40 %). Among streams, false negatives in pools where largely located in alluvial segments (80 %).

Large WCT Abundance in Pools

Among all pools (i.e. pools with large WCT present and absent) correlation analysis revealed cube root transformed large WCT abundance in summer was only moderately correlated to cube root transformed large WCT abundance in early winter (Pearson's $r = 0.49$, $P < 0.001$) and mid winter (Pearson's $r = 0.63$, $P < 0.001$). Pools with only large WCT present between sample periods revealed a weaker correlation between log large WCT abundance in summer and log large WCT abundance in early winter (Pearson's $r = 0.40$, $P = 0.0471$) and mid winter

(Pearson's $r = 0.42$, $P = 0.0364$). However, there was a significant positive correlation between log large WCT abundance in early winter and log large WCT abundance in mid winter (Pearson's $r = 0.83$, $P < 0.001$). The linear relationship in pools with large WCT present during both winter sampling periods was also significant ($N = 25$, $R^2 = 0.67$, $P < 0.001$). In contrast, the linear relationship between summer and both winter periods was found to be weak ($N = 25$, $R^2 = 0.12$, $P = 0.047$; $N = 25$, $R^2 = 0.14$, $P = 0.036$).

Investigation of environmental and spatial characteristics of pools during the summer of 2016 only found two variables significantly correlated to large WCT abundance (**Table 3.10**). However, none of these variables identified provided any strong predictors of large WCT abundance in winter. Further investigation of environmental and spatial characteristics of pools during early winter found no variables significantly correlated to large WCT abundance. Variables were found significantly correlated to large WCT abundance during mid winter (**Table 3.10**).

Table 3.10 Correlation analysis (Spearman rank correlation coefficients (*r*)) results for summer 2016 ($N = 55$) and mid winter ($N = 38$). Relationships are only those that are significant ($P < 0.05$) among environmental, spatial and biological variables by large (> 20 cm) Westslope Cutthroat Trout abundance (WCT/m^2). Only pools with large WCT present were used.

	Large WCT Abundance (WCT/m^2)	
Variable	*r*	*P*
Summer		
Area (m^2)	-0.37	0.006
Species Diversity Score [a]	-0.30	0.026
Mid Winter		
Creek	-0.34	0.034
Velocity (m/s)	-0.37	0.022
Conductivity (µS)	0.43	0.007
Mean Surface Ice Thickness (mm)	-0.38	0.020
Number of Alternate Pools	0.40	0.013
Bull Char Abundance (BLCH/m^2)	0.41	0.011

[a] values are scores ranging 0 to 4

Stepwise procedures (forward and backward) were used to find the linear regression model that best explained large WCT abundance in pools during mid winter. The best model that accounted for the variation in large WCT abundance in pools among all streams consisted of just one variable: water velocity (VELOCITY). When an outlier was removed, this model accounted for 23.1 % (adjusted R^2) ($P = 0.0015$) of the variation in large WCT abundance in pools during mid winter (**Figure 3.12**).

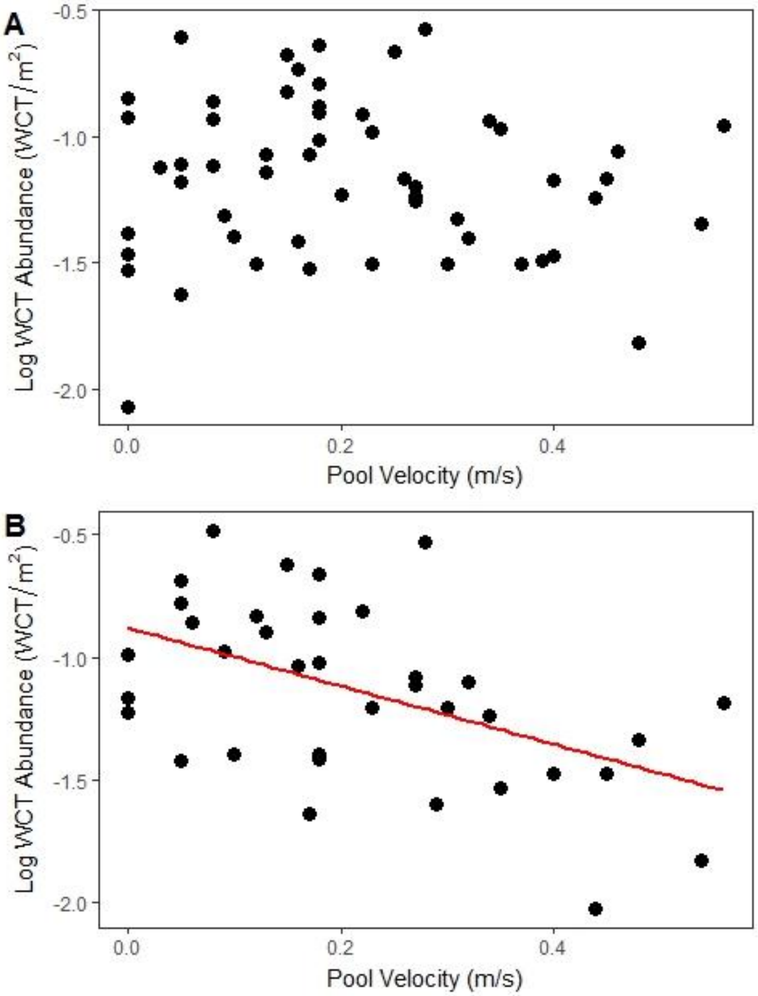

Figure 3.12 Log transformed large (>20 cm) Westslope Cutthroat Trout (WCT) abundance (WCT/m^2) in relation to pool velocity (m/s). All observations (pools) with large WCT present were used. A) no significant linear relationship was found for summer: $N = 55$, $R^2 = 0.005$, $P = 0.6218$. B) a line of best fit indicates the linear relationship for mid winter: $N = 37$, $R^2 = 0.23$, $P = 0.0015$.

VMR calculations in summer and winter for large WCT counts indicate that even the lowest VMR for pools was non-random (VMR = 3.03, $\chi^2 = 387.84$, $P < 0.001$) and that only certain pools contained increased numbers of large WCT (**Table 3.11**). Furthermore, VMR's substantially increased from summer to winter, confirming that large WCT did aggregate more in pools during winter compared to summer. The stream which had the greatest increase in aggregation of large WCT from summer to early winter was Blairmore Creek, while Gold Creek had the lowest increase in aggregation from summer to early winter. From early winter to mid winter, aggregation by large WCT had decreased in Blairmore Creek but aggregation was still higher than in summer by 38.6 %. Large WCT aggregation in both Daisy Creek and Gold Creek had increased from early winter to mid winter by 22 to 24 %. Throughout winter, aggregation by large WCT was consistently high in Daisy Creek and lowest in Gold Creek.

Table 3.11 Calculated index of dispersion and percent change (%) from the previous sampling period of large (> 20 cm) WCT total counts in pools. In addition, the combined mean winter dispersion and percent change (%) from summer is included. Observations are by each sample period for study streams Blairmore Creek (*N* = 42), Daisy Creek (*N* = 42), and Gold Creek (*N* = 45).

Creek	Summer	Early Winter	Mid Winter	**Mean Winter Dispersion**
	Index of Dispersion (Percent Change %)			**and Percent Change (%)**
Blairmore	3.03	10.70 (253.1)	4.20 (-60.7)	**7.45 (145.9)**
Daisy	8.37	20.83 (148.9)	25.49 (22.4)	**23.16 (176.7)**
Gold	7.07	8.49 (20.1)	10.49 (23.6)	**9.49 (34.2)**

Among all streams from summer to early winter, large WCT abundance increased in 16.3 % of study pools, decreased in 25.6 % of study pools; and 58.1 % of study pools had no change (i.e. where pools had both zero abundance in summer and early winter). When excluding pools that had no change in large WCT abundance and further grouping pools into categories of "increased" (*n* = 21) or "decreased" (*n* = 33) large WCT abundance, a multiple logistic regression model was developed to find the variables which most accounted for this difference. Using early winter environmental and spatial habitat data to derive the model, and step wise procedures (forward and backward) to find the best model, the three top variables identified to explain the increase or decrease in large WCT abundance were: mean surface ice thickness (SURF_ICE), average pool velocity (VEL), and the number of alternate pools (ALT_POOLS) (**Equation 3.6**). This model accounted for 18.7 % (McFadden R^2) ($P = 0.0037$) of the variation in pools that had either an increase or decrease in large WCT abundance from summer to early winter.

$$Logit\ (p) = -1.087 + 0.006\, SURF\_ICE + 0.003\, ALTPOOLS - 7.808\, VEL$$

Equation 3.6 Multiple logistic regression equation predicting the probability (*p*) of large (> 20 cm) WCT abundance increase or decrease in pools from summer to early winter (McFadden $R^2 = 0.187$; log-likelihood = -29.35; X_2 (3) = 13.46, $P = 0.0037$). Variables include: surface ice thickness (mm) (SURF_ICE), the number of alternate pools (ALTPOOLS), and average pool water velocity (m/s) (VEL).

The multiple logistic regression results indicate that a one unit increase in mean surface ice thickness would increase the probability that large WCT abundance would increase in that pool by 50.1 % (**Figure 3.13**). Similar to mean surface ice thickness, a one unit increase in the total number of alternate pools would further increase the probability that large WCT abundance would increase in that pool by 50.1 %. For water velocity however, a one-unit increase would actually decrease the probability that large WCT abundance would increase in that pool by 93.9 %.

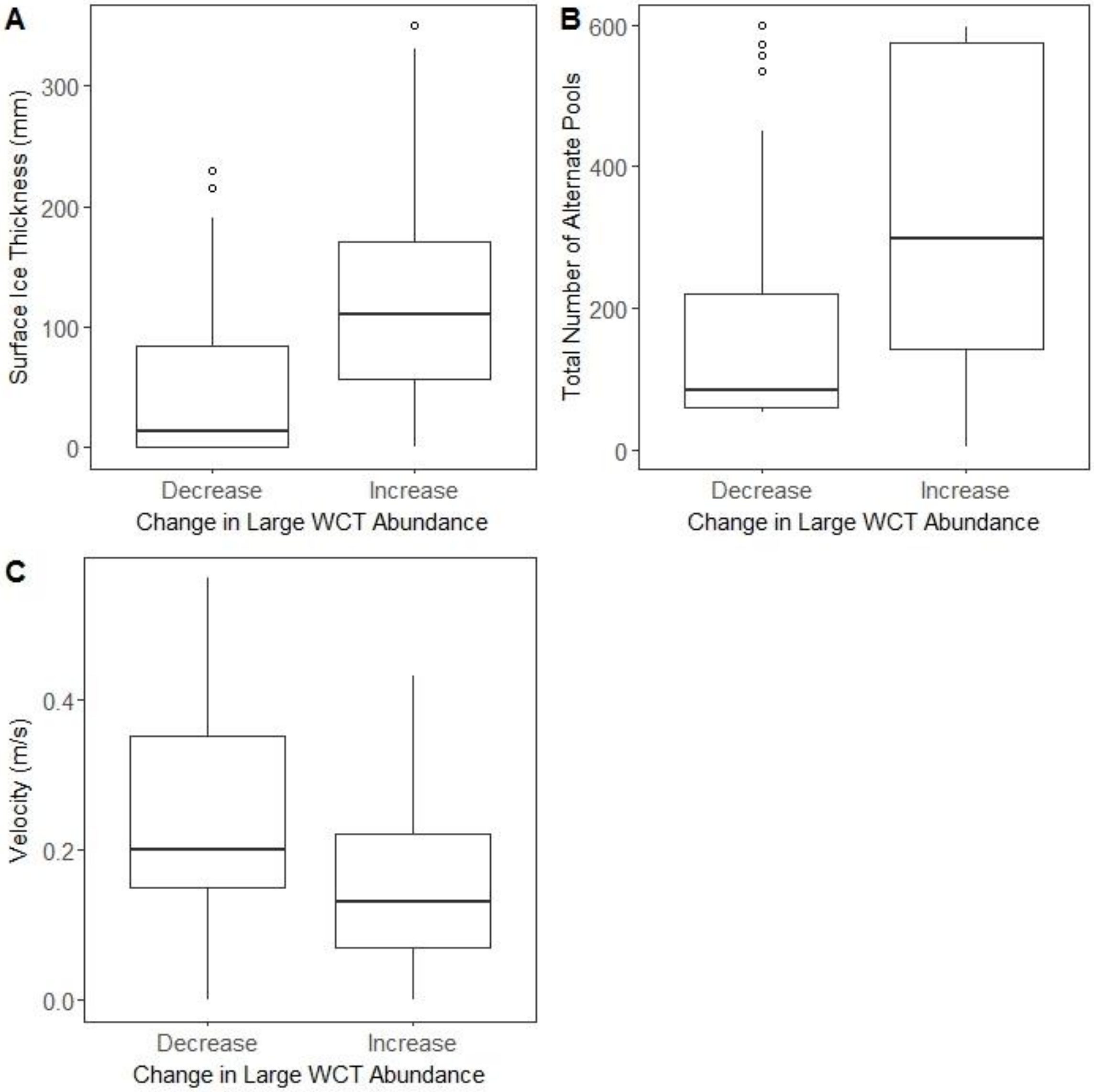

Figure 3.13 Change in large (> 20 cm) WCT abundance (increase or decrease) from summer to early winter for pools (*N* = 54) in relation to: A) surface ice thickness (mm); B) the total number of alternate pools unimpeded by a barrier; C) average water velocity (m/s) of the pool.

Further visual examination into differences in mean surface ice thickness and surface ice cover in early and mid winter revealed three categories in relation to seasonal water temperature difference: 1) stable warm = 0-4 °C, 2) dynamic = 4-8.5 °C, 3) stable cold = 8.5-17 °C (**Figure 3.14**). Stable warm conditions yielded very little or no surface ice formation on pools throughout winter. In contrast, stable cold conditions yielded moderate surface ice thickness on pools but had complete surface ice cover throughout winter. Pools under dynamic conditions had variable surface ice cover in early winter, and by mid winter yielded the thickest surface. Mean large WCT abundance was found to be higher in both stable pool conditions, however due to limited sample size was not found to be significantly different.

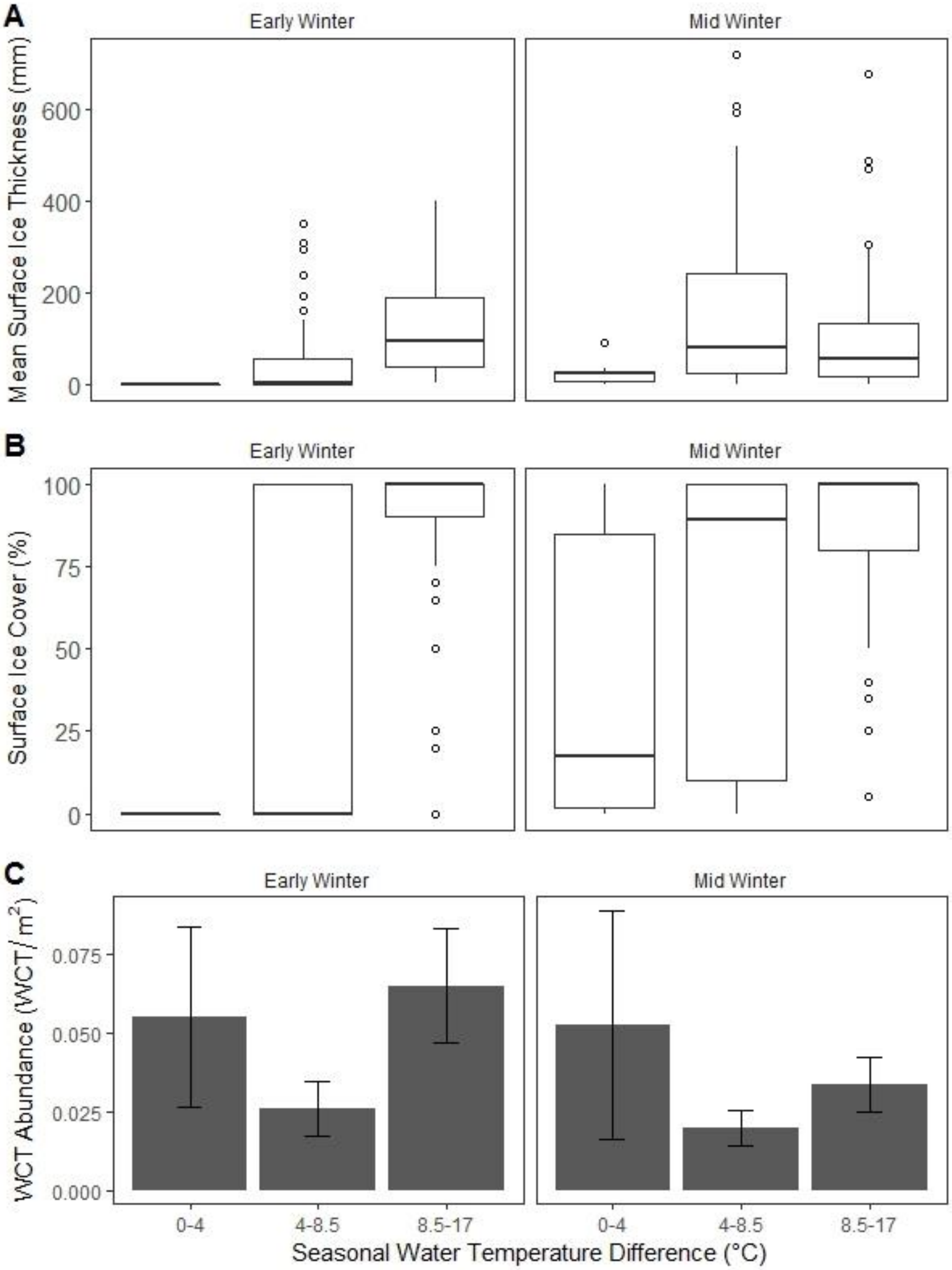

Figure 3.14 Seasonal water temperature difference categories (stable warm = 0-4 °C, *N* = 8; dynamic = 4-8.5 °C, *N* = 60; stable cold = 8.5-17 °C, *N* = 61) of pools in relation to (A) mean surface ice thickness (mm) (B) surface ice cover (%) and (C) mean large (> 20 cm) WCT abundance (WCT/m^2). All observations (pools) were used, where outliers are indicated (○) and lines indicate mean standard error. Faceting is by winter periods early winter and mid winter.

Discussion

This study investigated the ecological impacts of environmental, spatial, and biological characteristics of pool habitat and how these variables influenced WCT populations during winter in small Rocky Mountain headwater streams. Conducting field work in the study area during winter from November of 2016 to March of 2017 proved challenging due to periods of freezing temperatures (e.g. the coldest day being -35 °C), but especially due to the remoteness of sites, some of which were more than 20 km one-way from any winter-maintained highways or forestry roads. By mid winter the only way to access the study area was by snowmobile. Furthermore, many sites were not fully accessible by snowmobiles during winter because of the terrain and the lack of roads near the streams. For example, within canyon segments snowshoeing to and from many of the sites was the main means of access. Despite these challenges, with the appropriate gear I was successfully able to collect winter habitat and fish data in my study streams.

The first objectives of this study was to investigate the seasonal changes in pool habitat within these headwater streams, specifically focusing on water temperature, ice formation, and changes in barrier extent. The second objective was to investigate seasonal pool use by different size classes of WCT. The third objective was to predict WCT winter habitat use from summer and winter habitat metrics. Within pool habitat, ice conditions were found to be significantly affected by the seasonal changes in water temperature, which is related to groundwater influence. Increased barrier extent in winter significantly reduced connectivity among pool habitats. Expectedly, seasonal pool use by WCT was different among size classes which impacted how predictive models were derived. Pool characteristics classified in the summer sampling season were able to inform on large WCT pool use in winter. However, summer habitat variables were limited in their ability to make predictions of large WCT abundance in winter. Winter specific conditions, such as variable ice formation and changes in habitat connectivity influenced winter habitat use of large WCT in the three small headwater streams.

Seasonal Changes in Fish Communities

Changes in seasonal species abundance were apparent throughout these small mountain stream fish communities. The observed changes in WCT abundance were primarily within size classes less than 20 cm. During summer, small WCT less than 20 cm were present in almost all pools, however, by winter a significant decrease in abundance was observed. During winter young of the year and juvenile salmonids seek concealment in the interstitial space of substrate or other cover and in some cases may move to shallower habitats (Cunjak 1988b, Bjornn and Reiser 1991, Heggenes et al. 1993, Gregory and Griffith 1996, Jakober et al. 2000, Stickler et al. 2008). For example, Brown Trout juveniles *Salmo trutta* < 25 cm seek shelter in interstitial space of substrate and vegetation during the day to emerge at night (Heggenes et al. 1993), and young Atlantic Salmon *Salmo salar* < 15 cm (fork length), hide beneath rocks during the day in shallow riffle-run habitats instead of pools (Cunjak 1988b). While my study was not designated to detect fish in interstitial spaces, the disappearance of young of the year and juvenile WCT from study pools during winter and the re-emergence of the same size classes the next summer indicates that small WCT concealed during winter to avoid stress from predation, cold water, and ice conditions. This is further enforced due to the presence of barriers which did not allow any long-distance migration to occur.

From the data collected from this study there does not appear to be a significant difference in the amount of concealment by small WCT among the different streams and concealment may have occurred at lower temperatures than were previously reported. Most research has found that small salmonids increase daytime concealment during winter when water temperatures fall below 7 and 10 °C (Cunjak 1988b, Bjornn and Reiser 1991, Heggenes et al. 1993, Gregory and Griffith 1996, Jakober et al. 2000, Valdimarsson et al. 2000). However, in comparison to the highest water temperatures observed in my study streams during winter (maximum of 3.6 °C), many of these studies referenced above have much higher reported maximum winter water temperatures (7.0-8.3). Furthermore, even mean summer water temperatures in my streams were within the reported range of concealment (9.1 ± 2.3 °C) and small WCT were still observed and abundant. Local adaptation to different water temperature regimes and habitats can invoke different responses in concealment behaviour (Valdimarsson et al. 2000, Bradford and Higgins 2001). Therefore, if water temperature is one of the main factors driving concealment behaviour in WCT, it might be expected that locally adapted populations within colder systems might have lower water temperature thresholds which induce daytime concealment. In addition, concealment behaviour may still differ among WCT populations in headwater stream systems with different temperature regimes.

During summer, the mean water temperature among Gold Creek pools was only 7.7 °C, but water temperatures as low as 4-5 °C were recorded. In this case, the extremely low numbers of small WCT observed in Gold Creek in summer, in comparison to the other study streams Blairmore Creek and Daisy Creek, could be due to the extremely low water temperatures (at or below 7 °C) which induced concealment in small WCT. Other studies have noted that concealment at colder water temperatures is not only restricted to winter and that increased daytime concealment may occur at decreasing water temperatures ranging from 2 to 20 °C in fall and summer (Hillman et al. 1987, Fraser et al. 1995, Gries et al. 1997). For example, juvenile Atlantic Salmon in glacial fed rivers where water temperatures during summer are as low as 2.0 to 8.4 °C, were only detected at night in both summer and winter (Fraser et al. 1995). Thus, in the coldest headwater streams, small WCT may be concealed during the day even during the warmer seasons.

Photic response further dictates concealment behaviour in young of the year and juvenile salmonids during winter (Cunjak 1988b, Heggenes et al. 1993, Jakober et al. 2000). Specifically, Jakober *et al.* (2000) provided evidence for strong photonegative response in smaller WCT during winter in Montana headwater streams. Here, the amount of concealment during the day from fall to winter increased as water temperatures decreased for both Cutthroat Trout and Bull Char (Jakober et al. 2000). Although Jakober *et al.* (2000), as well as other studies (e.g. Meyer & Gregory 2000) have detected these behavioural changes in salmonids during winter, many were not conducted under full surface ice and snow cover. Yet, surface ice alters salmonid activity (Linnansaari et al. 2008) and reduces concealment behaviour (Gregory and Griffith 1996, Meyer and Griffith 1997). For example, as surface ice thickens (e.g. from 50 to 300 mm) juvenile Atlantic Salmon increase diurnal activity (Linnansaari et al. 2008). This reduced need to conceal during the day is linked to lowered predation risk due to increased overhead cover (Gregory and Griffith 1996). Except for groundwater influenced areas, most pools in my study streams were completely covered by surface ice and snow cover. In addition, surface ice thickness by mid winter was on average 124 mm, but in some locations was greater than 800 mm in thickness. Added snow by mid winter was on average 20 cm deep, but ranged as high as 96 cm. Therefore, added snow and ice cover during my study may have positively influenced the detection of small WCT during the day in some pools even when water temperatures were near freezing.

WCT greater than 20 cm did not show any significant change in mean abundance from summer to winter collectively among pools. However, the number of pools observed to have large WCT present decreased from summer to winter. This suggests not all pools used in summer were suitable WCT winter habitat. In fact, from summer to early winter the proportion of pools that saw large WCT abundance decrease was 1.5 times higher than the proportion of pools that saw large WCT abundance increase (i.e. more pools lost large WCT than gained large WCT). Furthermore, the highest density of large WCT in pools nearly tripled during winter (e.g. from 0.23 WCT/m^2 to 0.64 WCT/m^2). This suggests that large WCT simply redistributed to certain pools in winter that supported favourable conditions. These observations also then support the habitat limitation hypothesis, which suggests, that fish too large to conceal within interstitial cover must congregate in limited open habitat (Cunjak and Power 1986, Brown and Mackay

1995, Cunjak 1996). Specifically, congregation increases when alternative habitats become unusable due to cold water temperatures and/or increased dynamic ice conditions (Cunjak and Power 1986, Brown and Mackay 1995, Cunjak 1996).

Large WCT Pool Use

Large WCT presence in pools during summer and winter was largely dependent on pool maximum depth and area. As pool size increases within the respected geomorphic segment, the probability of large WCT presence increases. Furthermore, pools with slower water velocities had higher WCT abundance. Depth alone had the greatest influence among all other pool characteristics in determining suitability for large WCT in both summer and winter. Deep pools are often optimal habitat for large bodied salmonids in summer (Lewis 1969, Baltz et al. 1991, Bjornn and Reiser 1991, Gowan and Fausch 1996, Bonneau and Scarnecchia 1997) and winter (Heifetz et al. 1986, Brown and Mackay 1995, Cunjak 1996, Bonneau and Scarnecchia 1997, Dieterman et al. 2018). In winter, deep pools with low velocity allow for reduced activity and predation risk when water temperatures are low (Cunjak 1996).

Although predictive logistic models using only summer habitat values did predict large WCT presence in both winter periods reasonably well, in some cases classification errors by false positives occurred. In Blairmore Creek and Gold Creek, the model expectedly predicted a high probability of large WCT presence in five pools with maximum depths ranging from 0.8 to 2.3 m, yet there were no large WCT observed in those pools consistently during both winter periods. Hence, deep pools do not necessarily imply suitable winter habitat for larger salmonids.

Geomorphic segments further determined large WCT presence and absence. When pools were more abundant and closer together, such as within canyon segments, other factors (e.g. depth) had relatively more influence in determining presence or absence. However, when pools were less abundant and the distance to the nearest pool was large such as within alluvial segments (e.g. up to 347 m), large WCT were also detected in smaller and shallower pools (i.e. false negatives by the model predictions). Consequently, although pool depth may be the dominant deciding habitat characteristic, when habitats are limited in availability or connectivity, larger salmonids may be forced to use less preferred winter habitats.

Pools with increased connectivity also supported greater numbers of large WCT during winter. However, connectivity also differed between geomorphic segments due to differences in the extent of barriers. From the summer low-flow period to winter, the number and extent of barriers increased which further reduced connectivity to habitats (i.e. alternate pools) offering winter refugia. The most extensive subsurface flow barrier (approximately 600 m in length) developed rapidly during early winter. Other subsurface flow barriers had increased in extent by nearly 2.5 times from summer to winter. This change in extent of subsurface flow barriers from summer to winter is a result of low flows and dynamic ice formation during freeze up. As steep streams start to freeze, fast-flowing habitats (e.g. riffles) can be transformed to slow-flowing habitats (e.g. pools) independent of discharge (Stickler et al. 2010). Due to ice forming processes slowing down water velocities and reducing streamflows, water infiltration into stream beds may increase in areas already prone to subsurface flow barriers, for instance within alluvial channels (Winter 2007). In contrast to alluvial channels, canyon channels are composed of bed rock, allowing little to no water infiltration and continued flow (Winter 2007). Thus, the changes in connectivity and the effect it has on WCT populations is greater in alluvial segments compared to canyon segments and if low flows are severe, alluvial segments will experience the greatest reduction in connectivity and present the greatest stress to WCT populations.

Ice conditions can also have a large influence on winter habitat use (Cunjak 1996). Stickler *et al.* (2010) suggested temporarily, dynamic ice formation in northern stream systems may even become the most important factor for physical habitat characterisation. The results of my study further indicate that seasonal water temperature differences influenced large WCT pool use, due to varying ice formation conditions. Groundwater input to streams has a significant moderating effect on water temperatures in streams and influences ice conditions in winter (Cunjak 1996, Power et al. 1999, Brown et al. 2011, Lindstrom and Hubert 2011). In my study two different stable winter conditions were apparent (**Figure 3.15**). One of the study streams, Gold Creek, is an example of a strongly groundwater influenced stream. Seasonally, Gold Creek has colder water temperatures during the summer and comparatively warmer temperatures in the winter, reducing overall seasonal variation in water temperature. During cold periods, strong groundwater influence produces heterogenous water temperatures throughout the length of the stream (e.g. due to large diffuse point sources of input), providing areas with little or no ice formation. Furthermore, during milder periods water temperatures may allow the entire stream to be free of ice formation. In contrast, Blairmore Creek was less influenced by groundwater. Seasonally, Blairmore Creek has warmer water temperatures during summer and comparatively colder water temperatures in winter, producing higher seasonal water temperature variability. During cold periods, weak groundwater influence produces homogeneous water temperatures throughout the length of the stream, producing stable ice conditions. However, it was apparent between these stable conditions, there were areas with substantial and dynamic ice formation over winter, particularly below groundwater influenced areas. This is analogous with Lindstrom and Hubert (2011), who found that areas without groundwater input maintained stable surface ice conditions and allowed snow to accumulate (Lindstrom and Hubert 2011). In contrast, areas with groundwater input increased water temperatures and kept stream segments ice free (Lindstrom and Hubert 2011). However, areas downstream of groundwater input had the greatest amount of hazardous and dynamic ice formation (i.e. frazil and anchor ice) (Lindstrom and Hubert 2011). The more constant and dynamic ice conditions below groundwater influenced areas are the result of water cooling because there is no surface ice or snow cover to insulate it from cold air temperatures (Lindstrom and Hubert 2011). In addition, Brown (1999) suggested that in cases were sources of warm groundwater discharge are minimal, these areas may not provide suitable winter habitat because water temperatures are not enough to overcome the effects of supercooling during cold periods and increased dynamic ice formation can occur.

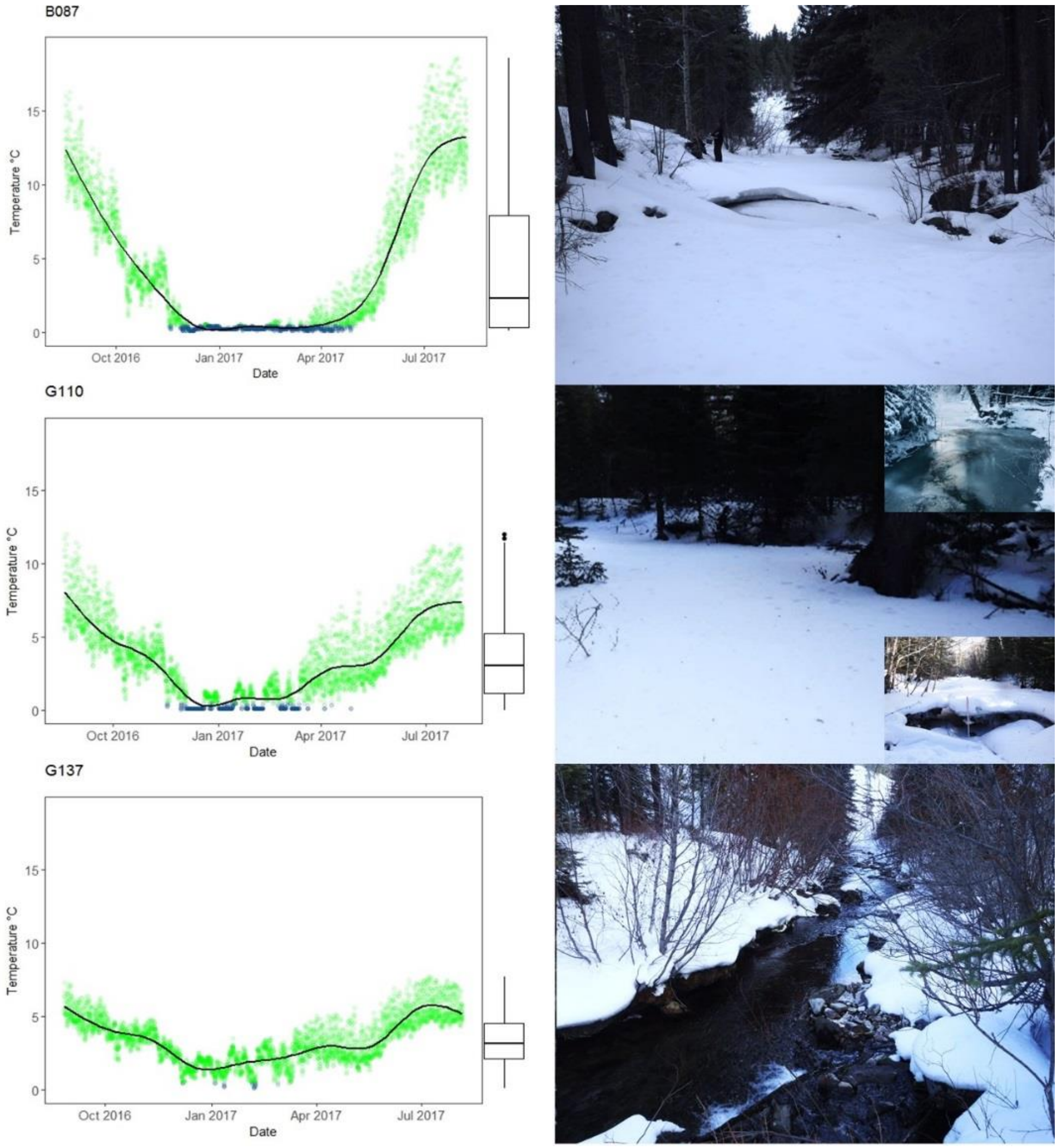

Figure 3.15 Winter stream conditions observed during this study using specific pools as examples: B087, G110, G137. Yearly water temperature (°C) plots are shown for each pool, where blue indicates subfreezing temperatures (≤ 0 °C), green indicates above freezing temperature (> 0 °C). Marginal plots further show seasonal variation in water temperature, where lines indicate standard error. B087) area with no groundwater influence and complete surface ice and snow cover throughout winter (Blairmore Creek); G110) area with only moderate groundwater influence which has had substantial dynamic ice formation during cold periods during winter (Gold Creek); G137) area with strong groundwater influence and no ice formation throughout winter (Gold Creek).

Pools with less groundwater influence (i.e. those with the largest seasonal water temperature difference) had a higher probability of large WCT being present due to factors related to ice formation and the physical exclusion of habitat. For example, in early winter during initial freeze-up periods, streams without strong groundwater influence may have widespread dynamic ice forming processes, forcing larger bodied fish to seek refuge in pools throughout the entire stream (e.g. Blairmore Creek). In contrast, in streams with strong groundwater influence dynamic ice forming processes are only localized within certain areas during initial freeze-up, thus only forcing larger bodied fish to seek refuge in areas affected by dynamic ice formation (e.g. Gold Creek).

In addition to ice formation driving large WCT pool use, effects of lower water temperatures on fish metabolism may further influence pool choice. At lower water temperatures fish metabolism and thus activity is decreased (Elliott 1976, Cunjak 1988a, Clarke and Johnston 1999). Cunjak (1988b) found that for stream dwelling Brook Char and Brown Trout, lipid levels were most rapidly depleted during the onset of early winter, followed by decreased serum protein levels and increased serum glucose levels as winter progressed. The trends in body composition and hematological conditions were also most apparent during an exceptionally cold and harsh winter (Cunjak 1988a). Cunjak (1988b) concluded that acclimation costs can be high during the onset of winter when environmental conditions change with rapidly dropping water temperatures and increased ice formation. In my streams, differences in summer to winter water temperatures in areas that are not moderated by groundwater input can be large (e.g. up to 10 to 16 °C difference). Therefore, if water temperatures are not moderated greatly and there is a large amount of variation in seasonal water temperatures particularly in the direction of near freezing, there is more cost to acclimation during the transition to winter for WCT and more of a requirement to move to pools. This was seen in Blairmore Creek which had the largest increase in aggregation from summer to early winter and coincidingly also had the greatest amount of seasonal water temperature variation and sharpest drop in water temperatures during the onset of winter. In contrast, largely groundwater influenced stream sections, such as those in Gold Creek, maintained water temperatures at or near 3.5 °C. Consequently, in these areas daytime seasonal water temperature differences (e.g. August vs December) were as low as 2.5 °C. Therefore, if water temperatures are moderated greatly and there is little variation in seasonal water temperatures, there is less cost to acclimation during the transition to winter for WCT.

Food may become more important to fish in these winter "warm" conditions later in winter, as increased water temperature increases the rate of metabolism, and thus increases energy demands (Cunjak 1988a). In small headwater streams, pool habitats can contain lower abundance of benthic invertebrates in comparison to riffle habitats (Brown and Brussock 1991, Kobayashi, Sohei; Kagaya 2002). Therefore, under warmer conditions there may actually be less of a requirement for WCT to move to pools and in some cases motivation to find food within other habitats such as shallow runs or even riffles. During mid winter within highly groundwater influenced areas on Gold Creek, large WCT were observed outside of pool habitats, such as in slow riffles and runs, actively feeding.

Changes in Habitat Use Throughout Winter

Generally, large WCT habitat use did not differ among early and mid winter periods and fish tended to stay within the chosen pool after the onset of winter. WCT movement is usually greatest during the onset of winter and WCT usually remain stationary throughout winter (Jakober et al. 1998). Movement by WCT during winter is usually caused by anchor and frazil ice excluding habitats (Brown and Mackay 1995, Jakober et al. 1998). Throughout most of my study streams, only short term and sudden early winter drops in air temperature lead to frazil and anchor ice formation. Similarly, Stickler *et al.* (2010) observed freeze up in small, steep streams during early winter coincided with significant drops in air temperature and that dynamic ice formation occurred within very short temporal scales (<12 h). By mid winter, further cold periods lead to stable ice conditions on most pools which allowed large WCT to maintain similar habitat use as in early winter. Surface ice and snow cover on many pools had increased or remained stable, which resulted in frazil and anchor ice formation in or near most pools to be absent. Generally, deep snow insulates small headwater streams preventing further frazil and anchor ice formation (Chisholm et al. 1987, Jakober et al. 1998). Therefore, if large WCT were present within a pool that had stable surface ice and snow cover to prevent further frazil ice formation there was little need for increased movement throughout winter.

As stable snow cover prevented further frazil ice formation in my study streams, areas of strong groundwater influence also prevented ice formation and allowed WCT to remain in those pools during mid winter. However, open water allowed access to endothermic predators. Endothermic predators such as River Otters *Lontra canadensis*, Mink *Neovison vison*, and Common Mergansers *Mergus merganser* occur along streams and rivers and prey on wintering salmonids (Salyer and Lagler 1940, Dolloff 1993, Lindstrom and Hubert 2004). During the fall of my study, River Otters were captured on video preying on trout in pools just below the study area on Gold Creek (Darren Lefort, Riversdale Resources, Blairmore, Alberta, personal communication), although by early winter no further sign was observed. Mink sign (i.e. tracks and scat) was common throughout the study streams and on one particular occasion during winter, scat in one location near open water was found to contain the remains of multiple WCT (**Figure 3.16**). Open water conditions due to groundwater influence may be areas frequented by endothermic predators in winter. I frequently observed WCT within these areas to respond strongly when the pool was approached during surveys. However, when the stream is completely enclosed by surface ice, predation risk by endothermic predators is limited or altogether removed (Linnansaari et al. 2008, Watz et al. 2016). Watz *et al.* (2016) found with increased simulated surface ice cover Brown Trout used more stream habitat, increasing survival and growth over winter. By midwinter in Blairmore Creek, aggregation by large WCT had largely decreased from early winter (by approximately 60 %) and coincided with increasing mean surface ice thickness (increased by 1.5 times) and mean snow depth on pools (increased by 6.3 times). In, contrast aggregation continued to increase or remain stable over winter in both Daisy Creek and Gold Creek, both of which contained groundwater influenced areas with no or only partial surface ice and snow cover. Thus, WCT populations my face trade offs in winter for survival when under different stream conditions. Although strong groundwater influenced areas my have little to no ice formation, predation risk can be disadvantageous to survival. On the other hand, weak groundwater influenced areas also provide little ice formation when stable and provide little predation risk.

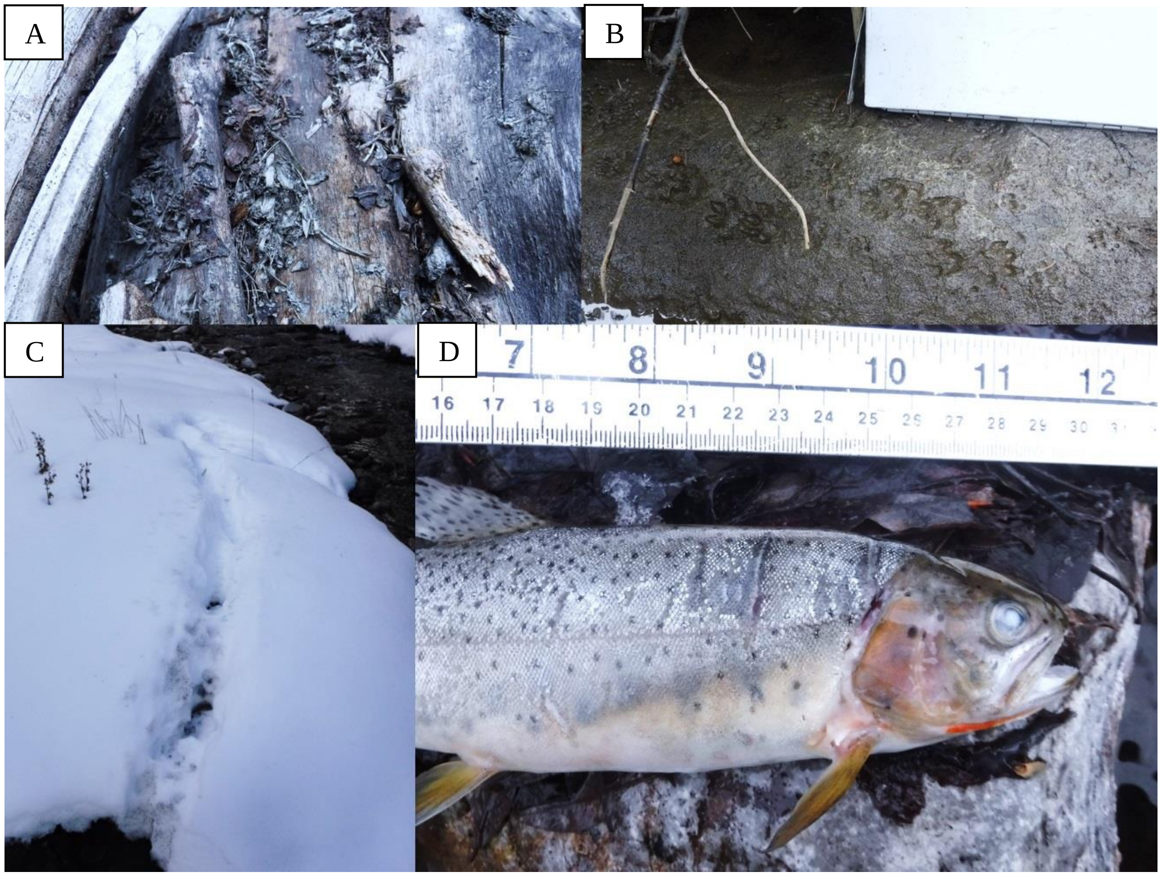

Figure 3.16 Mink sign in study streams. A) Mink scat with WCT remains. B) and C) Mink tracks on stream bank. D) Adult WCT found dead with deep cuts and puncture wounds likely from a mink.

In sections of my study streams, usually downstream of a groundwater source, the development of very thick surface ice (up to 80 cm +) occurred. Continued ice growth reduces available habitat in winter and in extreme cases, streams can even freeze completely (Cunjak 1996, Stickler et al. 2010). However, in my streams the occurrence of the thickest surface ice did not seem to develop by thermal ice growth (i.e. surface ice growing down towards the stream bed) (Michel and Ramseier 1971). Instead, the source of thickening surface ice was related to flooding during early winter. Flooding was caused by anchor and frazil ice accumulation in riffles above pools, which forced water to flow over a pre-existing surface ice layer already developed on the pool. This produced superimposed ice growth on top of the primary surface ice layer (surface ice growing upwards from the stream bed in layers). Thus, significant surface ice formation by itself did not seem to exclude pool habitat during winter in these streams and once static may have even prevented further frazil and anchor ice formation. In contrast, exclusion of pool habitat by ice in mid winter was only observed when a large amount of heavy and wet snow was present, whereby weighing down thinner surface ice into pools (**Figure 3.17**). If snow was present on top of the primary surface ice layer, it became saturated by the flooding and froze, forming what is known as snow ice or white ice (Gherboudj et al. 2007).

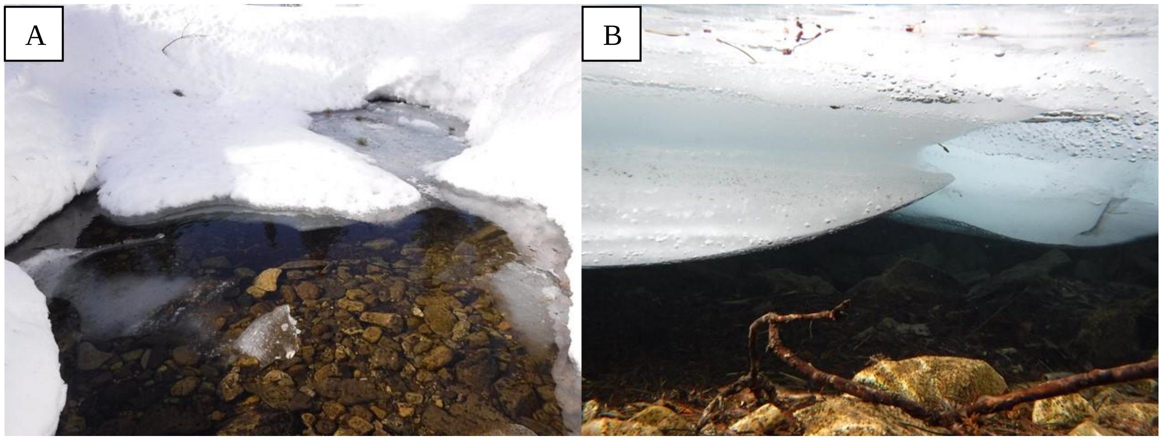

Figure 3.17 Heavy snow loading forcing ice into pools excluding habitat. A) Look from above the pool; B) Underwater view of white ice.

Brook Char

Abundance of Brook Char, the second most abundant fish species in the study streams, drastically decreased in pools from summer to winter. Many salmonid populations make long distance movements from smaller tributaries to overwintering habitats in larger rivers (Craig and Poulin 1975, Cunjak 1996). However, large falls and subsurface flow sections located near or at the lowest elevations of my study streams, make any mass out-migration very unlikely.

Therefore, a more likely explanation to the change in Brook Char abundance is that Brook Char exhibited a different behavioural strategy from WCT, such that they became inactive and concealed during winter. Meyer & Gregory (2000) found that Brook Char, even larger adults > 20 cm, were often concealed in winter during the day in pools and increased concealment behaviour was related to colder water temperature. Meyer & Gregory (2000) also found that concealment behaviour was expressed differently among species and that concealment was higher for Brook Char than for Rainbow Trout. Differences in concealment behaviour and activity may be a key behavioural distinction among adult WCT and Brook Char during winter.

Consequently, because seasonal behaviour may differ among species in winter, species interactions may also be affected. In my study streams, large WCT were observed to remain active during winter regardless of water temperature or time of day, often even observed feeding. In contrast, Brook Char, even the largest adults (>30 cm), were almost never observed during winter surveys, and none were observed in aggregations with large WCT. Thus, competition among larger WCT and Brook Char >20 cm, may even be reduced or non-existent during winter when water temperatures are cold for extended amounts of time. On the other hand, intra- and inter-specific competition for concealment spaces can be high in salmonids during winter (Gregory and Griffith 1996, Armstrong and Griffiths 2001, Harwood et al. 2002). Thus, if most Brook Char are in fact seeking concealment spaces during winter, it is possible that competition among Brook Char and small WCT < 20 cm may become heightened seasonally when water temperatures are cold.

Implications for Management

In the small headwater streams studied here, multiple logistic models using summer habitat data, such as maximum depth, area and the underlying geomorphology, were only able to reasonably predict large WCT presence and absence in pools for two winter periods. However, late summer abundances for large WCT were not indicative of winter habitat use. Here certain variables indicating increases in large WCT abundances were only made apparent during winter, such as surface ice thickness and velocity. Furthermore, considering the geomorphology and changes in connectivity between habitats during winter is imperative in understanding winter habitat use. Even though suitable winter habitat may be provided in a stream, if fish cannot move to that habitat in winter, it does not benefit the population. Other pool habitat characteristics such as seasonal changes in water temperature must also be considered in assessing winter habitat for larger adult WCT. For example, water temperature and the location of groundwater point sources should be considered in winter habitat surveys. Water temperatures can significantly influence snow and ice conditions and thus influence suitable habitats in winter. The assumption of increased depth in pools providing better habitat for large WCT may not always hold true in winter and traditionally assumed lower quality pools may become more important under seasonal changes in connectivity and water temperature (i.e. related to ice conditions).

Being able to assess the amount of winter habitat during summer is important considering the collection of fish and habitat data due to environmental conditions during winter can be difficult and expensive, particularly in remote areas. Although a good idea of possible locations for overwintering large adult WCT can be made from evaluating summer habitats in combination with seasonal water temperature data, it is strongly urged that those habitats be validated during winter to ensure they actually support the population. This is because in these mountain streams, slight changes in water temperature can have significant effects on ice conditions and miss classifying a pool as "good" winter habitat could be detrimental in evaluating habitats. Furthermore, conditions can change throughout winter and fish populations respond to these changes. For example, barriers may expand substantially during winter, such as subsurface flow barriers, either completely eliminating possible wintering pools or access to others. Ice conditions also change throughout winter in response to warming and cooling, influencing pool habitat conditions. Lastly, winter stream conditions can vary among years, either being milder or harsher. Properly evaluating winter habitats becomes vitally important in prioritization of areas for restoration or conservation of threatened species such as WCT. This emphasises the importance of including winter as a part of our regular field season (Cunjak 1996).

Land use practices such as mining, agriculture and forestry can alter basin hydrology and streamflow responses (Bent 2001, Blann et al. 2009, Ferrari et al. 2009, Bernhardt and Palmer 2011), which can lead to changes in channel morphology (Bunn and Arthington 2002, Blann et al. 2009) and sediment delivery and transport (Wood and Armitage 1997, Blann et al. 2009, Anderson and Lockaby 2011). Improper land use practices may lead to the loss of winter habitat for WCT through infilling, sedimentation and altered flows (Cunjak 1996). Furthermore, altered streamflows may further increase the extent of winter barriers, further reducing connectivity among possible winter refugia or even completely eliminating them. Surface mining and logging impact groundwater characteristics by altering flow paths and the location of discharge (Bonta et al. 1992, Bari et al. 1996, Evans et al. 2015). By altering groundwater inflow to streams, seasonal temperature regimes can be altered, impacting ice conditions and stream habitat. Additionally, climate change is also expected to alter streamflows and increase winter temperatures in the future (Rood et al. 2008, 2016, MacDonald et al. 2014), possibly leading to increased amount of freezing and thawing events, making some streams more dynamic throughout winter (Stickler et al. 2010) (**Figure 3.18**).

Figure 3.18 A possible look into the effects of future climate change on winter habitat in small mountain streams of southern Alberta. Although Blairmore Creek (shown above) had stable ice cover for most of winter, during late winter under mild conditions dynamic ice formation was evident and constant. With only weak groundwater influence, mild winters in streams like Blairmore Creek may cause harsh and stressful overwintering conditions.

The dynamic nature of ice formation in these steep mountain streams remains largely unexplored and is an important source of future study. Further detailed research within ice formation under different headwater stream conditions and how this effects habitat and fish populations over winter would be beneficial. Additionally, work studying the effects that non-native species have on WCT during other seasons such as winter, is also important, as the dynamics of competition may change seasonally. Lastly, more research investigating other barrier types during winter, such as those restricting movement by certain size classes and species, could be important in further understanding how WCT and other stream dwelling salmonids utilize stream habitats.

Chapter 4 - General Conclusion

This thesis described the components (physical, chemical, biological, and spatial) of current habitat in relation to WCT populations in three small montane headwater streams. Here I have demonstrated the importance of including spatial scale in assessing headwater stream habitats and salmonid populations. Specifically, in the study streams large landscape scale factors have a superimposed influence on small scale habitat patches, such as pools. Because of this, the ability for direct comparisons of fish populations within these systems may be limited when landscape features differ greatly. Here even though study streams share watershed borders, there are substantial differences in physical and chemical habitat characteristics, thus affecting WCT populations. However, when those differences in specific streams are accounted for, general habitat features that are required by WCT populations become apparent, such as pools with suitable cover, depth, and connectivity.

This thesis specifically focused on the seasonal changes in habitat and WCT populations in the same three small montane headwater streams. Here I have determined there are size-specific differences in how WCT overwinter within these smaller streams, which is similar to observations made in other larger stream and river systems studied in Alberta (Brown and Mackay 1995, Brown 1999). Specifically, most small WCT (< 20 cm) conceal themselves in winter and large WCT (> 20 cm) aggregated, while continuing to use pools for winter refuge.

My work suggests that critical WCT winter pool habitat can possibly be assessed during summer sampling while also incorporating seasonal water temperature data. Specifically, summer habitat metrics included the geomorphology (related to connectivity and stream size), pool depth, and pool area. Moreover, the addition of seasonal changes in water temperature, which is accounting for groundwater influence, further improved predictions for WCT habitat suitability because groundwater influence significantly effects ice conditions. However, when considering changes in abundance of large WCT in pools (i.e. large aggregations), ice formation, velocity and connectivity were further important in describing winter habitat use. The most significant variable that was able to predict presence and absence of large WCT, maximum depth, was not related to large WCT abundance all together among study streams. Consequently, although increased pool depth is the main preferred winter habitat characteristic for an individual large WCT, even shallow pools can become more important during winter for large aggregations of adults if sections of stream are highly groundwater influenced or isolated.

Predictions of winter habitat suitability can be made for adult WCT from summer habitat in combination with seasonal water temperature data. Although, in order to fully assess the importance of particular pools as winter refuge for WCT populations as a whole, surveys throughout winter should still be conducted to validate predictions and continued use. Misclassification of pools as suitable winter habitat could be detrimental in prioritization of habitats for restoration, conservation or enhancement projects for threatened populations. This emphasises the importance of still including winter as a part of our regular field season and to ensure predicted suitable habitat actually supports fish populations (Cunjak 1996). Yet, with the appropriate habitat assessments during summer, sampling efforts in winter can be greatly reduced.

The results from this study suggest that identifying winter refuge pools is vital for the successful management of a threatened species within these small headwater streams. In the streams studied, pool habitat made up only a small percentage of all other habitats available (6 %). Furthermore, out of the total number of pools available, only a small number of these actually supported even a single adult WCT during winter (< 30 %). Yet, these pools facilitate the survival of the majority of the breeding segment of threatened WCT populations during at least half of the year, without many alternatives. This makes pool habitats extremely important in the conservation of threatened WCT populations in small headwater streams and attention should be given to measures that allow protection of these habitats.

Anthropogenic impacts within headwater streams from land use and climate change are an important factor to consider. Specifically, land use activities that negatively impact or reduce pool habitat in these streams will have substantial effects on threatened WCT populations. With climate models predicting altered streamflows and increased stream temperatures into the future (Rood et al. 2008, 2016, MacDonald et al. 2014), the importance of refuge habitats such as pools will be enforced.

This thesis contains information that will help make better informed decisions regarding the potential effects from land use on small Rocky Mountain headwater streams. Particularly, the potential impacts to fish habitat surrounding the proposed Grassy Mountain Coal Project, such as altered streamflows and water quality (e.g. altered water temperatures and increased sedimentation) could have significant effects on WCT populations if not mitigated properly. This thesis highlights a few points that can inform and compliment projects related to mine offsetting plans and monitoring programs before and during operation, such as:

- Maintaining or improving water quality. Specifically, anthropogenically caused erosion and fine sediment deposition in stream water bodies.
- Maintaining or improving connectivity, which includes maintaining sufficient flows, number of and distances to pools. Particularly, this applies to areas that have been anthropogenically altered.
- Maintaining and conserving critical refuge pools during summer low flows and winter conditions for larger adult WCT.

Furthermore, before any proposed enhancement projects related to winter habitat are conducted, they must first identify how areas will be affected by ice formation and groundwater influence. Lastly, any projects done to enhance WCT habitat and populations in these watersheds need to consider the possibility of inadvertently improving habitat conditions for introduced species such as Brook Char and Rainbow Trout.

Further research investigating the full range of barriers and how this effects dispersal within headwater stream populations of WCT would be beneficial. For example, further research in this area would help in identifying the extent of source-sink populations in headwater streams allowing managers to assess key areas to focus restoration efforts and protection. My results show that these assessments however should be conducted throughout the seasons, particularly encompassing the winter period when barriers are at the greatest extent.

The Crowsnest Pass has experienced significant alterations of habitat due to historic mining, and anthropogenic development, and therefore, lessons from the past can be learned. As these WCT populations clearly have adapted to many of these changes (not measured in this thesis), it is important to recognize that past activities have led to the rapid decline of pure WCT populations and any measures possible to be taken now would be helpful to preserve this species into the future. The research that has been presented in thesis has filled in some of the previous knowledge gaps surrounding WCT ecology and will help make relevant management decisions and protect this iconic species of the Canadian Rocky Mountains into the future.

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