12-2008

Movement Patterns and Multi-Scale Factors That Influence Exotic Brook Trout and Endemic Bonneville Cutthroat Trout Distribution and Abundance in the Mill Creek Drainage, Utah

Benjamin Keith Nadolski
Utah State University

MOVEMENT PATTERNS AND MULTI-SCALE FACTORS THAT INFLUENCE EXOTIC BROOK TROUT AND ENDEMIC BONNEVILLE CUTTHROAT TROUT DISTRIBUTION AND ABUNDANCE IN THE MILL CREEK DRAINAGE, UTAH

by

Benjamin K. Nadolski

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

of

MASTER OF SCIENCE

in

Fisheries Biology

Approved:

Phaedra Budy Major Professor	Fred Provenza Committee Member
Bob Greswell Committee Member	Byron R. Burnham Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2008

ABSTRACT

Movement Patterns and Multi-scale Factors that Influence Exotic Brook Trout and Endemic Bonneville Cutthroat Trout Distribution and Abundance in the Mill Creek Drainage, Utah

by

Benjamin K. Nadolski, Master of Science

Utah State University, 2008

Major Professor: Dr. Phaedra Budy
Department: Watershed Sciences

Introduced brook trout (*Salvelinus fontinalis*) are implicated as a primary factor leading to the decline in distribution and abundance of native cutthroat trout (*Oncorhynchus clarkii*). However, not all introductions are successful, suggesting local conditions influence the success of invasions. Therefore, I sought to determine the multi-scale factor(s) that influence brook trouts' invasion success of native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) habitats in Mill Creek, Utah. I conducted patch occupancy surveys to determine watershed-scale brook trout and cutthroat trout distribution. I also determined the relative abundance of brook trout and cutthroat trout at the reach-scale by conducting three-pass depletion electrofishing surveys at ten index sites throughout the drainage. Upon completion of those surveys, I collected key watershed and reach-scale biotic and abiotic data twice during base-flow conditions. In addition, to determine watershed-scale population connectivity and the potential for upstream invasion by brook trout, I assessed fish movement using two-way weir traps. At the watershed-scale, stream slope appeared to limit brook trout invasion into some portions of the drainage. Intermittent stream-flows and extreme levels of stream slope ($>$ 10%) appeared to limit cutthroat trout distribution. At the reach-scale, regression analyses indicated aquatic invertebrate abundance and low winter water temperatures may have influenced the abundance of brook trout, but my models explained little variation in cutthroat trout abundance overall. I observed high rates (74%) of site fidelity amongst brook trout, and mobile brook trout moved short distances (range=62-589 meters) overall. Cutthroat trout also exhibited high site fidelity (92%), but their movement was more variable, as few individuals moved long distances (up to 12.15 km). These findings will help prioritize cutthroat trout management actions in this watershed, and will be useful in determining why brook trout are successful invaders in some systems, yet remain in low and patchy abundance in others.

(91 pages)

DEDICATION

I dedicate this thesis to my wife, Jaynee Nadolski, whose tireless effort and unending patience allowed me to fulfill my academic, professional, and spiritual aspirations. I would also like to thank her for the emotional support she provided during the many periods of academic struggle and hardship.

ACKNOWLEDGMENTS

This research was funded by the Utah Division of Wildlife Resources (UDWR), Project XIII, Sport Fisheries Research, Grant Number F-47-R, Segment 20. Additional contributions were provided by the Utah State University, United States Geological Survey Utah Cooperative Fish and Wildlife Research Unit.

I acknowledge Craig Schaugaard for coordinating the implementation of this project, providing UDWR logistical support for my education and field research, and his mentorship throughout my program of study. Also, I would like to acknowledge Paul Thompson, Paul Burnett, Matthew McKell, and Aaron Webber for their logistical support and sage technical advice. I give special recognition to my peers Robert Al-Chokhachy, Kirk Dahle, Eriek Hansen, Jeremiah Wood, Sara Sidel, Tracy Bowerman, and Jared Botcher for their logistical support and technical advice. I wish to acknowledge the technicians that assisted with this project, including Peter MacKinnon, Amanda Taylor-Townsend, Corrie Wallace, Benjamin Schleicher, Silas Ratten, John Schinker, Michael Vasser, Michael Bolinski, Erin Van Dyke, Michael Pittinger, Christopher Kula, Marlie Johnson, and Weston Pearce. I acknowledge Paul Cowley and Earl O'Driscoll of the United States Forest Service for their project support. I would like to especially acknowledge Gary P. Thiede for his endless oversight, logistical support, and technical advice of this project. I acknowledge Susan Durham for her assistance with data analysis and reviewing previous drafts of this thesis. I acknowledge committee members Bob Gresswell and Fred Provenza for providing technical advice and reviewing previous drafts of this thesis. I would like to especially acknowledge Phaedra Budy for her unending technical support and guidance, and superb mentorship throughout my program of study. The use of trade or firm names in this paper is for reader information only and does not imply endorsement by the U.S. Geological Survey of any product or service.

Benjamin K. Nadolski

CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The worldwide proliferation of nonnative species invasions is well documented and poses one of the greatest threats to the persistence of native fauna (Williamson 1999). In fact, the introduction of nonnative species has been implicated in 49% of all species listings under the Endangered Species Act (Wilcove et al. 1998). For these reasons, the introduction of nonnative species is cited as one of the foremost causes of biotic impoverishment both worldwide (Scott and Helfman 2001), and in the United States. Historically, in an effort to increase species diversity amongst western streams, the United States Fish Commission used the transcontinental railway to transport eastern aquatic species to the west. As a result, one in four fish that occur in streams of 12 western states is nonnative (Schade and Bonar 2005). Despite the well documented impacts to native fish species, nonnative species introductions have continued.

The introductions of nonnative salmonid species, such as brook trout (*Salvelinus fontinalis*), have occurred since the late 1800's (MacCrimmon and Campbell 1969), and are implicated in the decline, and in some cases, loss of native trout species throughout the intermountain west (Gresswell 1988). The negative impacts of these introductions to native trout species include hybridization (Carmichael et al. 1993; Henderson et al. 2000; Hitt et al. 2003), agonistic behavioral interactions (Wang and White 1994), predation (McGrath and Lewis 2007), habitat use overlap (Gunckel et al. 2002), and diet overlap (Hilderbrand and Kershner 2004). Through interspecific competition, these negative interactions can lead to reduced body condition, growth, and ultimately fitness of native fish populations, including native cutthroat trout *(Oncorhynchus clarkii)*.

The cutthroat trout is a salmonid species native to portions of western North America (Trotter 1987), and has the broadest distribution of native western trout species (Behnke 1992). The details of its evolutionary origin are not clearly understood, but fossil records indicate that a divergence of a common ancestor, ancient "*Parasalmo*," occurred approximately 2-8 million years ago, and gave rise to ancient forms of cutthroat trout and rainbow trout (Behnke 1988; Smith et al. 2002). Natural dispersal of cutthroat trout followed by geographic isolation events led to the evolutionary divergence of multiple cutthroat trout subspecies. Currently, there are eight putative subspecies of cutthroat trout in western North America (Behnke 1992), including the Bonneville cutthroat trout *(Oncorhynchus clarkii utah*), which is a plesiomorphic sister group to all other native cutthroat trout subspecies (Smith et al. 2002). Extant populations of Bonneville cutthroat trout persist in portions of Utah, Idaho, Wyoming, and Nevada (Gresswell 1988), and have experienced reductions in historically occupied habitats, with populations primarily relegated to headwater tributary streams (Lentsch et al. 1997). Many factors have contributed to this decline, including habitat degradation (Binns and Remmich 1994), disease (de la Hoz Franco and Budy 2004), hybridization (Weigel et al. 2003), and negative interactions with nonnative fish species such as brook trout (Griffith 1988).

The introduction and subsequent invasion of brook trout has occurred throughout western United States (Behnke 1992; Adams et al. 2002; Dunham et al. 2002; Shepard 2004), often in drainages containing native cutthroat trout populations (Tyus and Saunders 2000; Shepard 2004; Meyer et al. 2006). Brook trout are native to portions of eastern Canada, the Atlantic, Great Lakes and Mississippi River Basins, Minnesota, and northern Georgia (Page and Burr 1991), and have been introduced into 35 out of 50 states to be used for sport fish purposes (Fuller et al. 1999). Negative competitive interactions between brook trout and cutthroat trout are well studied and include diet (Dunham et al. 2000; Hilderbrand and Kershner 2004) and habitat use overlap (Destaso and Rahel 1994; Peterson and Fausch 2003), as well as direct competition through agonistic behavioral interactions (Cunjak and Green 1984; Hutchison and Iwata 1997). These interactions often result in reduced body condition, growth, and fitness of native cutthroat trout populations, and can be so adverse that Behnke (1992), observed a virtual replacement of cutthroat trout by brook trout within Black Hollow Creek, Colorado during a five-year period.

Despite the prolific history of brook trout introductions, not all invasions are successful, suggesting that environmental factors can mediate brook trout invasion success. These environmental factors operate at multiple spatial and temporal scales (Poff 1997), and are important in determining local species assemblages by acting as a species "filter." According to this concept, species' pass through a hierarchy (i.e., large-scale to small-scale) of spatially and temporally-nested environmental filters, and as species' pass through increasingly finer filters, local biotic and abiotic conditions determine a species presence or absence. The declining status of brook trout in its native range (Hudy et al. 2005), and widespread invasion success outside its native range, have resulted in numerous studies of the biotic and abiotic variables that influence brook trout distribution and abundance at multiple hierarchical scales (e.g., filters). Some examples include geology and geomorphology (Nelson et al. 1992; Kocovsky and Carline 2006), stream slope (Chisholm and Hubert 1986; Adams et al. 2000; Isaak and Hubert 2000), macrohabitat characteristics (Lindstrom and Hubert 2004), water temperature (Shepard 2004; Mullner and Hubert 2005), stream pH (Cleveland et al. 1986; Jordahl and Benson 1987), fine sediment abundance (VanDusen et al. 2005; Hartman and Hakala 2006), invertebrate abundance (VanDusen et al. 2005), and life-history stage (Kennedy et al. 2003). In addition, large scale (i.e., watershed-scale) movement dynamics play an important role in determining the likelihood of successful invasion. Movement behaviors of potamadromous (i.e., migration within flowing freshwaters) brook trout are well studied, and include movements into and out of spawning, over-wintering, and feeding habitats (Northcote 1997; Gowan and Fausch 2002). These behaviors can be influenced by environmental factors including, stream discharge (Chrisholm et al. 1987), and frequency of pool habitats (Lindstrom and Hubert 2004). In addition, if suitable habitats are patchily distributed, connectivity amongst those areas through movement is an important mechanism for successful invasion, and in many cases, these movements promote the invasion of native cutthroat trout habitats (Adams et al. 2002; Peterson and Fausch 2003; Benjamin et al. 2007). However, the location, timing, duration, and distance of these movements can vary within and across populations, habitats, and diel periods (Gowan and Fausch 1996), making it important to understand large-scale, population-specific movement dynamics when investigating the factors that influence the success and spatial extent of brook trout invasion.

The goal of my research was to better understand why brook trout are successful invaders in some systems, yet, remain in low, patchy abundance in similar systems. To determine this, I 1) determined the watershed-scale biotic and abiotic factors that influence the distribution of brook trout and cutthroat trout in a northern Utah stream, 2) determined the reach-scale biotic and/or abiotic factors that influence the abundance of brook trout and cutthroat trout, and 3) characterized watershed-scale brook trout and cutthroat trout movement patterns and assessed the effects of movement on brook trout distribution and invasion.

STUDY AREA

Mill Creek is a tributary to the headwater portions of the Bear River, and is located approximately 2,740 meters above sea level in Summit County, Utah (Figure B.1). The Bear River Basin encompasses portions of Utah, Wyoming, and Idaho before terminating into the Great Salt Lake. The upper portions of Mill Creek has a single channel of low sinuosity and high slope, whereas the lower portion has greater sinuosity and less slope. Mill Creek supports a unique and diverse community of native fish species including Bonneville cutthroat trout, northern leatherside chub (*Lepidomeda copei*), longnose dace (*Rhinichthys cataractae)*, speckled dace (*Rhinichthys osculus*), sculpin (*Cottus spp*.), mountain whitefish (*Prosopium williamsoni*), mountain sucker (*Catostomus platyrhynchus*), Utah sucker (*Catostomus ardens*), and redside shiner (*Richardsonius balteatus hydroflox*). The only nonnative fish species in Mill Creek is brook trout. The Utah Division of Wildlife Resources considers the Bonneville cutthroat trout population in Mill Creek a "core conservation population," thereby warranting increased conservation protection (Lentsch et al. 1997). Mill Creek and its tributaries contain one of the largest remaining genetically pure metapopulations of Bonneville cutthroat trout. In addition, Mill Creek and its tributaries support one of only two extant populations of northern leatherside chub in Utah.

In 2003 and 2004, as part of a large-scale electrofishing survey to document the spatial distribution of northern leatherside chub in Mill Creek and its tributaries, the Utah Division of Wildlife Resources coarsely identified watershed-scale fish species distributions. Those findings suggested that cutthroat trout occupied large portions of the watershed, while brook trout were patchily distributed throughout the watershed and had not invaded some nearby tributary streams, despite no apparent physical or biological barrier(s). In addition, these surveys documented dynamic spatial and temporal differences in fish density at multiple locations, suggesting expansion and contraction of brook trout and cutthroat trout populations throughout the drainage. I used these pilot data to design my study of the watershed and reach-scale factors that influence the distribution and abundance of brook trout and Bonneville cutthroat trout in the Mill Creek drainage.

METHODS

Watershed-scale assessment

Watershed-scale patch occupancy surveys were conducted to describe large-scale brook trout and cutthroat trout distribution in Mill Creek and its tributaries. Survey methods were based on protocols developed by Peterson et al. (2002), but modified to meet the constraints and objectives of this project. Starting at the upstream extent of known brook trout occupancy (based on pilot study results) in Mill Creek and each of its tributaries, I measured a 50-meter electrofishing study unit. A one-pass electrofishing depletion survey was conducted within that 50-meter study unit. All fish were captured, identified, measured, weighed, and released. Upon completion of that survey, moving in an upstream direction, within another 50-meter study unit separated by a 500-meter stream segment, another one-pass electrofishing depletion survey was completed. This process was repeated until no brook trout or cutthroat trout were detected at three consecutive 50-meter study units, or when the water source was reached, whichever came first. At each study unit, Universal Transverse Mercator (UTM) coordinates were recorded. The lowest 50-meter study unit that contained brook trout represented the upstream extent of brook trout distribution. Likewise, the lowest 50-meter study unit that contained cutthroat trout represented the upstream extent of cutthroat trout distribution.

Watershed-scale stream slope was determined by using stream layers in ArcGIS software to divide Mill Creek and its tributaries into 250-meter stream segments. I then overlaid the stream layers with a 10-meter resolution digital elevation model, and assigned top and bottom elevation values (i.e., meters above mean sea level) to each stream segment. The difference between the top and bottom elevations was calculated and divided by the distance between the two points (i.e., 250-meters) to determine the percent slope of each stream segment. That process was repeated throughout the watershed to construct a watershed-scale longitudinal profile of stream slope.

Watershed-scale patterns of water chemistry were determined by measuring pH, salinity (ppm), conductivity (μ/cm), turbidity (NTU), and total dissolved solids (TDS; g/L) at multiple locations along the longitudinal gradient of Mill Creek and its tributaries (Figure B.2). All water chemistry measurements were collected using a YSI model 556 MPS multi-meter. Turbidity samples were collected and analyzed using a LaMotte model 2020e turbidimeter following the manufacturers guidelines.

Watershed-scale analysis

The results of patch occupancy surveys were used to determine if stream slope or water chemistry influenced large-scale brook trout and cutthroat trout distribution. I used the results of patch occupancy surveys to determine where brook trout and cutthroat trout occurred, and qualitatively compared that distribution to stream slope and water chemistry measurements.

Reach-scale assessment

Based on spatially explicit patch occupancy surveys, and to represent all habitat types present along the longitudinal stream gradient of Mill Creek and its tributaries, I identified ten permanent 100-meter index sites throughout the watershed that represented the lower, middle, and upper portions of Mill Creek (Mill Creek border, low, middle, and high), Deadman Creek (Deadman Creek low, middle, and high), and North Fork (North Fork low, middle, and high; Figure B.3). At each index site, I collected information describing key biotic and abiotic variables twice during base-flow summer conditions: once in July and August. Three-pass depletion electrofishing surveys were performed at each index site in order to understand the relationship of these variables to brook trout and cutthroat trout abundance.

Nutrient samples were collected using 250-milliliter amber bottles. Immediately following collection, all samples were placed in coolers containing dry ice. Samples were analyzed by High Sierra Water Lab in Truckee, California to determine the concentrations of ammonia, total nitrogen, Kjeldal nitrogen, nitrates, nitrites, dissolved phosphorous, soluble phosphorous, and total phosphorous. In addition, I measured stream pH, conductivity, salinity, and turbidity following the protocols described previously (see watershed-scale assessment).

To determine water temperature profiles at all ten index sites, hourly water temperature was measured using temperature data loggers. This data was summarized using yearly minimum, median, mean, and maximum values for each index site. Due to some incidence of logger loss or malfunction, I obtained temperature profiles for some index sites by regressing known temperatures of two "nearest neighbor" locations and applying the regression equation to areas of unknown temperature. For example, the temperature profiles of the Mill Creek middle and Mill Creek high index sites during 2007 were highly related ($n=5,521$, $R^2=0.98$), thus allowing me to predict temperature profiles where data were missing.

Pebble counts were used to characterize substrate composition. Each index site was divided into ten evenly spaced longitudinal stream segments. At one randomly selected location within each stream segment, I collected ten substrate particles across the width of the stream channel using the heel-toe method. Particle size was determined by recording the largest slot that retained the particle using an Albert Scientific field sieve-gravelometer (Bunte and Abt 2001).

Stream discharge was measured by placing a meter tape over the width of the stream channel. Total stream width was recorded at 20 equal distance locations across the stream channel. Stream velocity, depth, and distance from shore were also measured. Velocity measurements were recorded using a Marsh-McBirney Flo-Mate model 2000 electromagnetic flow-meter set at 0.6 of the total stream depth. I calculated stream discharge using methods outlined by Harrelson et al. (1994).

Stream slope was measured using an engineering level. At each index site, a staff gauge was placed at the downstream end of a riffle habitat near the downstream end of the index site, as well as at the downstream end of a riffle habitat near the upstream end of the index site. I estimated stream slope as the difference in elevation at the two staff gauges divided by the total stream distance between staff locations. When necessary, I used turning points to ensure direct line of sight between the laser and the staff gauge.

Aquatic invertebrates were collected both qualitatively and semi-quantitatively to determine species richness and species abundance. For qualitative samples, I used a 25cm x 46cm kick-net with 500-micron mesh to collect a sample from all habitat types (e.g., pool, riffle, run, beaver pond), present within each index site. For quantitative samples, I collected two kick-net samples from four riffle habitats within the index site.

As an index of algal abundance, periphyton samples from ten rocks were taken from each index site. Rocks were chosen randomly from ten evenly spaced longitudinal stream segments. Upon collection, rocks were placed on ice and transported to the laboratory. Two subsamples of the scrubbate were collected and filtered through a glass fiber filter to determine concentrations of chlorophyll *a*. After filtration, I froze all filters until they were processed using protocols outlined in Clesceri et al. (1989).

Brook trout and cutthroat trout abundance was estimated using standard 3-pass depletion techniques (Krebbs 1999). Stream distance of all 100-meter electrofishing survey locations was measured using a drag tape. A block net was placed at the lower and upper ends of each index site and electrofishing surveys were completed using battery powered backpack electrofishing units. Electrofishing settings varied depending upon levels of conductivity within the stream. In general, I set the pulse at J (70 Hz), the frequency at 4 (4 ms), and the voltage at 300 V. Electrofishing commenced with a crew ranging from 3-6 people. Three electrofishing passes were conducted and all the fish encountered were removed and placed into live cages. I identified all fish to species, weighed them to the nearest gram, and measured them to the nearest millimeter total length. Before release, I anesthetized all brook trout and cutthroat trout that measured ≥ 150 millimeters total length with a non-lethal dose of tricaine methanesulfonate (MS-222) and inserted an external anchor tag posterior to the dorsal fin. In addition, a 23-millimeter half-duplex radio frequency identification (RFID) transponder tag was surgically implanted into the ventral region slightly posterior to the pectoral fin. Upon completion of the survey, I measured wetted stream width at ten randomly selected locations along the longitudinal gradient of the index site to determine average stream width.

Reach-scale data analyses

To standardize fish abundance across index sites, all estimates were converted from linear abundance (i.e., number of fish per kilometer of stream) to aerial abundance (i.e., number of fish per hectare of stream) using average stream width values. To determine the variable(s) that influenced the magnitude of brook trout and cutthroat trout abundance at the reach-scale, I plotted each biotic and abiotic variable as continuous explanatory variables versus the log-transformed brook trout and cutthroat trout abundance estimates for each index site as the response variable. I used linear and quadratic regression models to determine the relationship between each explanatory variable and brook trout and cutthroat trout abundance estimates. Regression analyses were generated using the REG procedure in SAS/STAT software, Release 9.1.3 of the SAS System for Windows. P-values were assessed with significance determined *a priori* at a=.05, and I evaluated goodness of fit, homogeneity of variance, and influence.

Movement

To determine the extent of large-scale brook trout and cutthroat trout movement, and to identify the primary pathways of fish movement throughout the watershed, in-stream, two-way weir traps were deployed at two locations in Mill Creek, one location in

Deadman Creek, and one location in North Fork (Figure B.4). All traps were checked daily from June through September, 2007. I identified all captured fish to species, weighed them to the nearest gram, and measured them to the nearest millimeter total length. If a marked fish was captured (e.g., from index site sampling), the unique tag identification was recorded. In addition, for all fish captured I recorded the direction of movement (i.e., upstream or downstream) and the date of capture. All unmarked trout ≥ 150 millimeters total length were anesthetized with a non-lethal dose of tricaine methanesulfonate (MS-222), and internal and external tags were surgically administered. In addition, during September, 2007, I “spotshocked” portions of Mill Creek, North Fork, and Deadman Creek to supplement the movement data collected from index site and weir-trap sampling. All marked fish were identified to species, measured to the nearest millimeter total length, and weighed to the nearest gram. In addition, the date of capture and unique tag identification were recorded. Finally, the location of each capture was recorded using Universal Transverse Mercator (UTM) coordinates.

Movement model

A multi-strata mark/recapture model in Program MARK was used to estimate capture, survival, and movement probabilities for brook trout and cutthroat trout. Four main areas (i.e., strata) of brook trout and cutthroat trout occupancy throughout the drainage were identified (Figure B.5). I assigned each stratum a unique identification code (A, B, C, or D), then divided all six encounter occasions into six categories as follows: 1) index sites sampled during July, 2006, 2) index sites sampled during August, 2006, 3) two-way weir traps sampled from June through September, 2007, 4) index sites sampled during July, 2007, 5) index sites sampled during August, 2007, and 6) study streams spot electrofished during September, 2007. The individual encounter histories of all marked fish were used to determine which stratum each fish occupied during each encounter occasion. I expressed the encounter history of each fish as a contiguous series of locations (strata A-D) for each encounter occasion (1-6), and assigned a "0" to fish that were not observed in any strata for that particular encounter occasion. For example, a fish with encounter history "AA0BCD" was originally captured in stratum A during index site sampling in July of 2006, was recaptured in stratum A during index site sampling during August of 2006, was not seen in any strata during weir trap sampling from June through September of 2007, was recaptured in stratum B during index site sampling during July of 2007, was recaptured in stratum C during index site sampling in August of 2007, and was captured in stratum D during spot electrofishing surveys in September of 2007. All encounter histories were compiled into an input file (Table A.1), and I estimated the probability of capture (p), the probability of survival (Φ), and the probability of transition (i.e., movement; ψ) among all strata for brook trout and cutthroat trout. I started by estimating the best model (i.e., global model) for all three probability estimates (p, Φ, and ψ) by varying recapture, survival, and transition structure. Next, I calculated subsequent iterations with one probability structure varying at one time, while the remaining two probability structures remained constant. This was repeated for all combinations of all three probability estimates. I then used corrected Akaike's Information Criteria (AIC_c) to choose the most parsimonious top model of capture, survival, and transition probabilities.

RESULTS

Watershed-scale assessment

Despite the apparent lack of physical or biological barriers to fish movement, brook trout were patchily distributed throughout portions of the Mill Creek drainage and had not invaded some nearby tributary streams. More specifically, brook trout invaded and were established in approximately 24.68 of 30.92 km (80%) of Mill Creek, and were only sparsely distributed throughout an additional 4.69 km (15%) of Mill Creek. In addition, brook trout had invaded and were established in approximately 4.54 of 6.19 km (73%) of Deadman Creek, but had not invaded Carter Creek, Christmas Tree Creek, McKenzie Creek, the unnamed tributary near the headwater portions of Mill Creek, and the unnamed tributary adjacent to McKenzie Creek. In total, brook trout occupied approximately 33.91 of 71.12 total km (48%) of the Mill Creek drainage. Conversely, cutthroat trout were widely distributed throughout the drainage and occupied large portions of Mill Creek, Carter Creek, Christmas Tree Creek, Deadman Creek, McKenzie Creek, North Fork, and the unnamed tributary adjacent to McKenzie Creek. In total, cutthroat trout occupied approximately 55.52 of 71.12 total km (78%) of the Mill Creek drainage.

Based on watershed-scale stream slope profiles, patch occupancy surveys, and index-site abundance estimates, brook trout were established in areas with low to moderate stream slopes. More specifically, mean stream slope of all areas where brook trout were established was 0.019%, and ranged from 0.002% to 0.046% in Mill Creek, and 0.013% to 0.060% in Deadman Creek (Table A.2). In both streams, brook trout establishment ended at a point of precipitous increase in stream slope (Figure 1). Conversely, cutthroat trout were established in areas that ranged from low to high stream slope. More specifically, stream slope in areas where cutthroat trout were established averaged 0.035%, and ranged from 0.005 to 0.101% (Table A.2).

In general, conductivity, pH, and TDS measurements were lower in North Fork and McKenzie Creek than in Mill Creek, Deadman Creek, and Carter Creek, while turbidity and salinity measurements varied widely across sample sites and sample streams (Table A.3). Brook trout occupied some areas with higher levels of conductivity, pH, and TDS (i.e., portions of Mill Creek and Deadman Creek), and were generally absent in areas of low conductivity, TDS, and pH (i.e., North Fork and McKenzie Creek). Cutthroat trout were widely distributed throughout all sampled tributaries and occupied stream reaches that varied in turbidity, conductivity, salinity, pH, and TDS.

Overall, the density of brook trout ranged from 23 (North Fork low July, 2006) to 6084 (Deadman Creek middle August, 2007) individuals per hectare, and varied across sample periods and years (Figures 2, B.6, and B.7). Brook trout were detected at eight index sites, and in general, population abundance was lowest in North Fork, highest in Deadman Creek, and intermediate in Mill Creek. Overall, the density of cutthroat trout ranged from 59 (Deadman Creek low July, 2007) to 1870 (Mill Creek middle August, 2007) individuals per hectare, and varied within index sites and across sample periods and years (Figures 2, B.6, and B.7). Cutthroat trout were detected at all ten index sites and, in general, abundance was lowest in North Fork, highest in Mill Creek, and intermediate in Deadman Creek. Overall, cutthroat trout were more abundant than brook trout in Mill Creek and North Fork, and brook trout were more abundant than cutthroat trout in Deadman Creek.

Nutrient concentrations, water temperature, substrate, discharge, stream slope, and aquatic invertebrate abundance and diversity varied widely within and across all index sites and study streams (Tables 1, and A.4-A.10). Nutrient concentrations were generally higher in 2007 than in 2006, and differences across sites remained similar across years (Table A.4). Water temperatures were generally cooler in 2006 than in 2007, and were highest in Deadman Creek, lowest in North Fork, and intermediate in Mill Creek (Table A.5). In addition, median water temperature distribution was skewed towards cooler temperatures (Figure 3). In general, substrate size was greatest in North Fork, smallest in Deadman Creek, and intermediate in Mill Creek. Percent fines ranged from zero to 74, with the lowest values from the Mill Creek high index site and the highest values from the Deadman Creek low index site (Table A.6). Stream discharge measurements varied widely across index sites, sample periods, and sample years, but were generally highest in Mill Creek, lowest in Deadman Creek, and intermediate in North Fork (Table A.7). Stream slope varied across index sites and study streams, and was highest in North Fork, lowest in Deadman Creek, and intermediate in Mill Creek (Table A.8). Total invertebrate abundance was generally highest in Mill Creek, lowest in Deadman Creek, and intermediate in North Fork, and species diversity was highest in Deadman Creek, lowest in Mill Creek, and intermediate in North Fork (Table A.9). For watershed-scale water chemistry results, conductivity and pH values measured in Mill

Creek and Deadman Creek were similar, but were generally higher than those measured in North Fork (Table A.10).

Median temperature, dissolved phosphorous, minimum temperature, D16, and conductivity were significantly related to brook trout abundance based on a linear model, and total invertebrate abundance, percent fines, and mean temperature were significantly related to brook trout abundance based on a quadratic model (Table 2; Figure 4). I observed no other significant relationships among the remaining explanatory variables and brook trout abundance.

Maximum temperature, nitrate-nitrite, chlorophyll *a* abundance, D84, D90, D64, and D50 were significantly related to cutthroat trout abundance based on a linear model (Table 3; Figure 5). In addition, soluble reactive phosphorous was significantly related to cutthroat trout abundance based on a quadratic model. I observed no other significant relationships among the remaining explanatory variables and cutthroat trout abundance. However, due to low r^2, none of the explanatory variables measured appeared to explain a meaningful portion of the variation in cutthroat trout abundance.

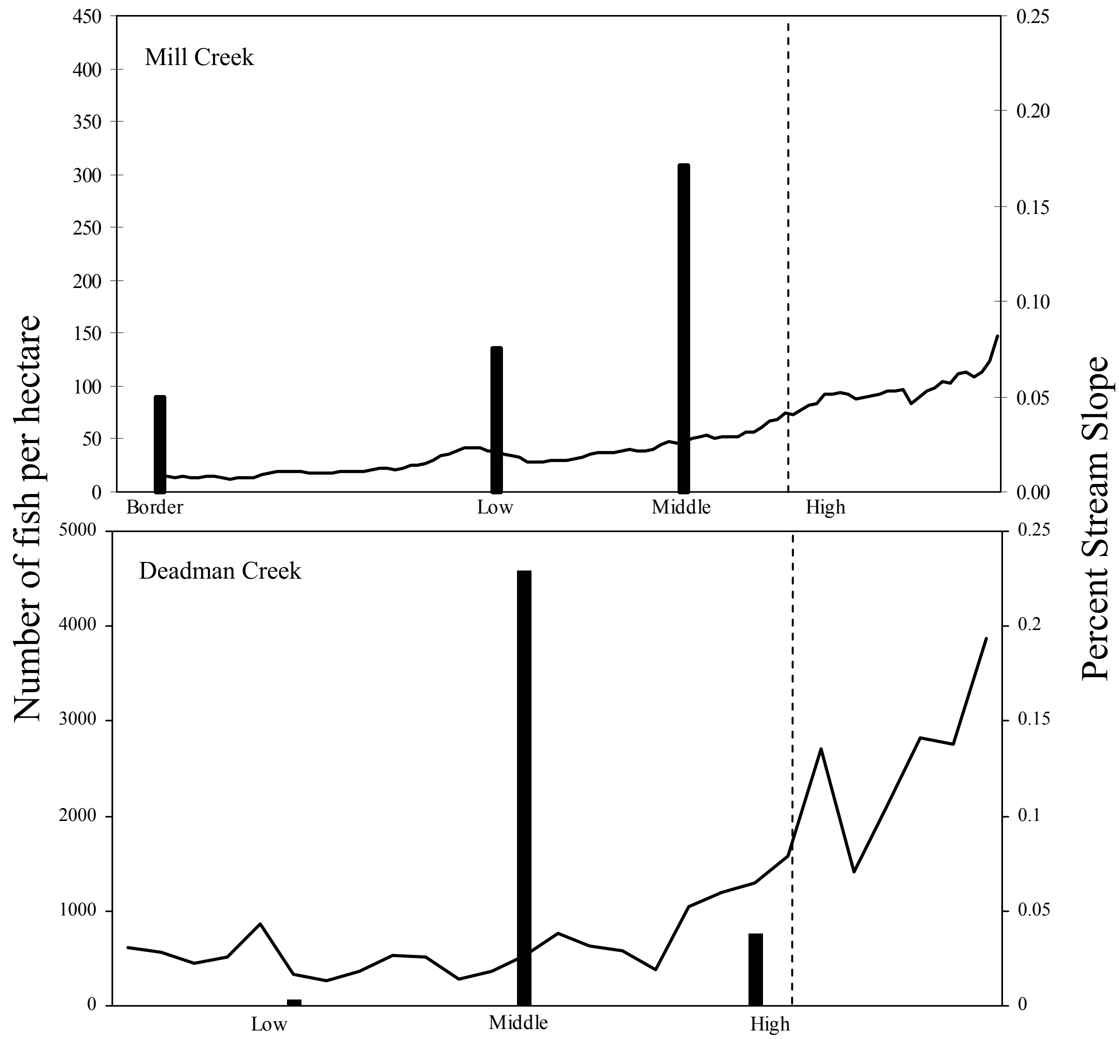

Figure 1. Longitudinal stream profile of percent stream slope (solid line) of Mill Creek and Deadman Creek (y-axes), with the location and number of brook trout per hectare (bars) at each index site positioned along the longitudinal stream profile (x-axes). Dashed vertical lines indicate the approximate upstream extent of brook trout establishment based on patch occupancy surveys.

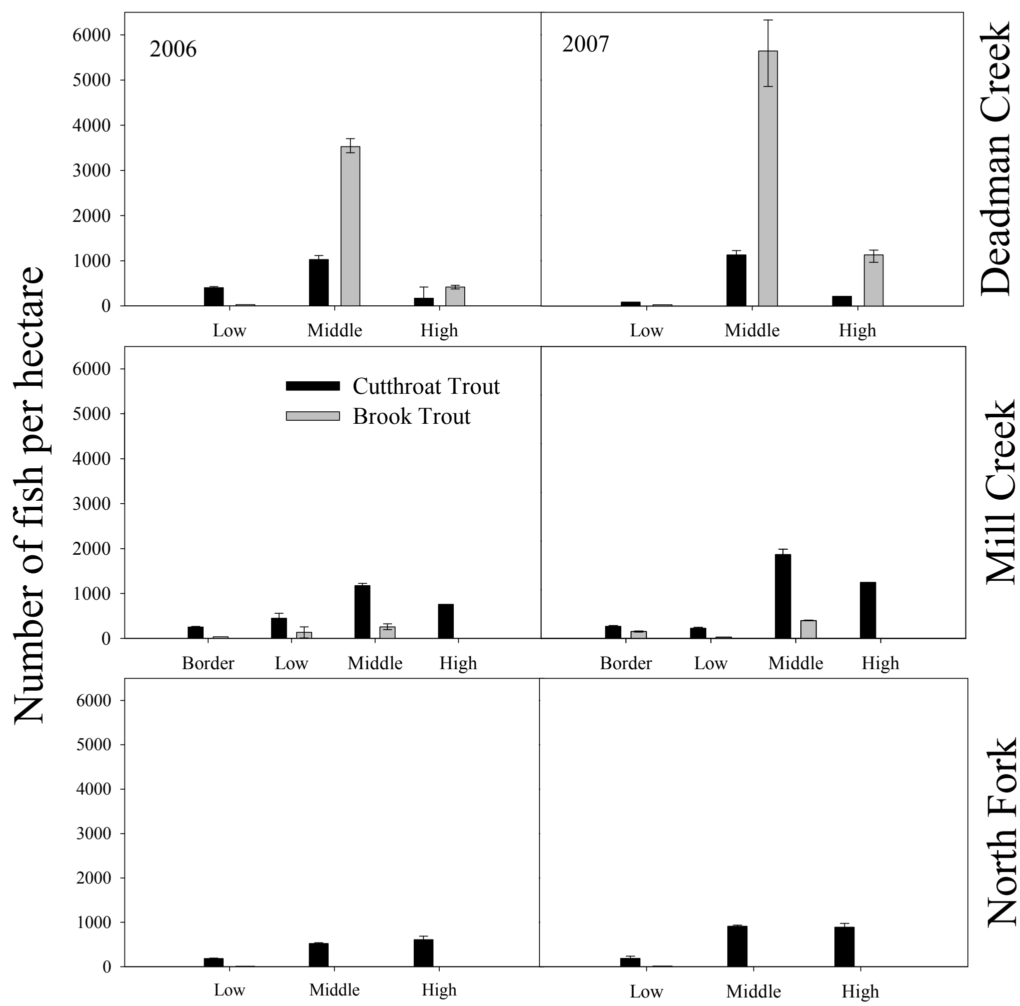

Figure 2. Mean brook trout and cutthroat trout abundance at all ten index sites during 2006 and 2007. Error bars represent 95% confidence intervals.

Table 1. Mean (SD) values of all biotic and abiotic variables measured at all ten index sites in Mill Creek, Deadman Creek, and North Fork during July and August, 2006 and 2007.

Variable	Mill Creek	Deadman Creek	North Fork
Conductivity	253.19 (38.96)	355.58 (93.65)	40.51 (12.53)
pH	8.21 (0.41)	8.11 (0.43)	7.56 (0.32)
Turbidity	0.96 (0.47)	1.68 (0.88)	1.66 (0.63)
Minimum Temperature	-0.12 (0.18)	-0.03 (0.33)	-0.33 (0.23)
Median Temperature	0.24 (0.18)	0.5 (0.36)	0.03 (0.13)
Mean Temperature	2.67 (0.54)	3.11 (0.32)	1.87 (0.01)
Maximum Temperature	20.03 (3.39)	18.85 (3.19)	17.94 (1.47)
Discharge	0.17 (0.19)	0 (0)	0.01 (0)
Soluble Reactive Phosphorous	2 (0.76)	1 (0)	2.67 (2.66)
Dissolved Phosphorous	7.75 (1.49)	8.67 (2.73)	7.33 (1.97)
Total Phosphorous	13.75 (3.73)	12.17 (3.54)	11.17 (3.25)
Nitrate-Nitrite	112.25 (109.57)	5.33 (3.08)	47.17 (47.13)
Total Keljdal Nitrogen	216.75 (43.27)	189.83 (69.43)	118.5 (15.76)
Total Nitrogen	329 (112.74)	195.17 (69.57)	165.67 (36.26)
Ammonia	5.25 (3.77)	2.17 (0.41)	17 (34.8)
Chlorohlyll a Abundance	3.33 (1.61)	36.4 (73.15)	1.36 (1.41)
Hill Eveness	0.56 (0.09)	0.58 (0.13)	0.6 (0.1)
Number OUT	27.13 (6.13)	38.17 (8.28)	30.83 (3.82)
Shannon Diversity	2.19 (0.22)	2.49 (0.53)	2.46 (0.27)
Simpson Diversity	0.19 (0.05)	0.16 (0.15)	0.14 (0.06)
EPT Abundance	361.88 (42.66)	185.33 (143.23)	337.5 (75.88)
Total Invertebrate Abundance	482.25 (51.64)	434.83 (76.21)	455.17 (54.35)
D16	37.44 (14.12)	4 (0)	38.5 (12.75)
D50	76.94 (30.38)	12.75 (9.1)	77.67 (21.91)
D64	98.06 (37.08)	20.75 (14.01)	104.17 (30.52)
D84	149.81 (50.13)	52.92 (22.88)	171 (35.06)
D90	183.56 (60.06)	78.5 (27.7)	220.17 (35.72)
Percent Fines	3.44 (3.44)	47.5 (23.88)	2.58 (2.27)
Percent Slope	0.03 (0.02)	0.02 (0.02)	0.06 (0.01)

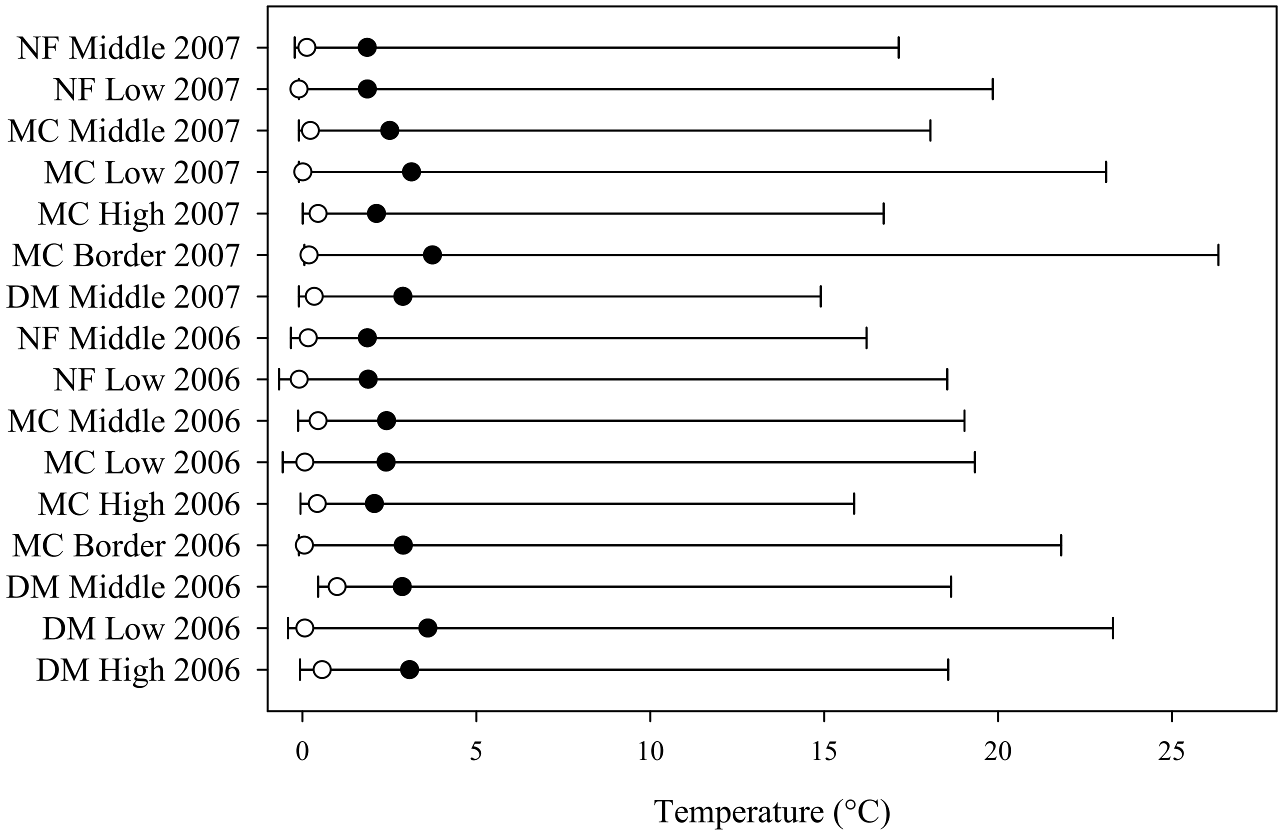

Figure 3. Median (open circles) and mean (dark circles) annual water temperatures at all index sites during 2006 and 2007. Bars represent minimum and maximum annual water temperatures.

Table 2. Outputs of all linear models and all significant quadratic models for brook trout. All models are ranked in descending order of r^2.

Variable	P-value	r2	Parameter Estimate	SE	Model Type
Total Invertebrate Abundance	*0.003	0.737	0.000	0.000	Quadratic
Median Temperature	*0.001	0.664	2.239	0.504	Linear
Percent Fines	*0.000	0.520	-0.001	0.000	Quadratic
Mean Temperature	*0.029	0.463	-1.510	0.581	Quadratic
Dissolved Phosphorous	*0.038	0.395	0.205	0.084	Linear
Minimum Temperature	*0.044	0.346	1.767	0.768	Linear
D16	*0.012	0.276	-0.017	0.006	Linear
Conductivity	*0.033	0.207	1.598	0.396	Linear
Simpson's Diversity	0.074	0.312	3.636	1.801	Linear
Hill Evenness	0.077	0.308	-3.361	1.680	Linear
Maximum Temperature	0.092	0.260	5.115	1.600	Linear
D50	0.054	0.173	-0.069	0.003	Linear
Shannon's Diversity	0.219	0.163	-0.641	0.485	Linear
D64	0.070	0.154	-0.005	0.003	Linear
D84	0.108	0.124	-0.004	0.002	Linear
Total Invertebrate Abundance	0.304	0.117	-0.004	0.004	Linear
D90	0.131	0.110	-0.003	0.002	Linear
Soluble Reactive Phosphorous	0.372	0.089	-0.325	0.347	Linear
Percent Slope	0.523	0.086	15.426	22.485	Linear
Percent Fines	0.262	0.062	0.008	0.007	Linear
Mean Temperature	0.444	0.060	0.362	0.454	Linear
Turbidity	0.304	0.053	0.213	0.202	Linear
Total Phosphorous	0.248	0.050	0.077	0.062	Linear
Discharge	0.594	0.019	-0.815	1.496	Linear
EPT Abundance	0.811	0.007	0.000	0.002	Linear
Number OTU	0.813	0.007	0.006	0.026	Linear
Chlorophyl *a*	0.744	0.005	0.015	0.046	Linear
pH	0.801	0.003	0.095	0.371	Linear
Nitrate-Nitrite	0.896	0.002	0.000	0.003	Linear
Total Keljdal Nitrogen	0.920	0.001	0.000	0.004	Linear
NH4_N	0.944	0.001	-0.007	0.090	Linear
Total Nitrogen	0.974	0.000	0.000	0.002	Linear

* significant ($p<.05$)

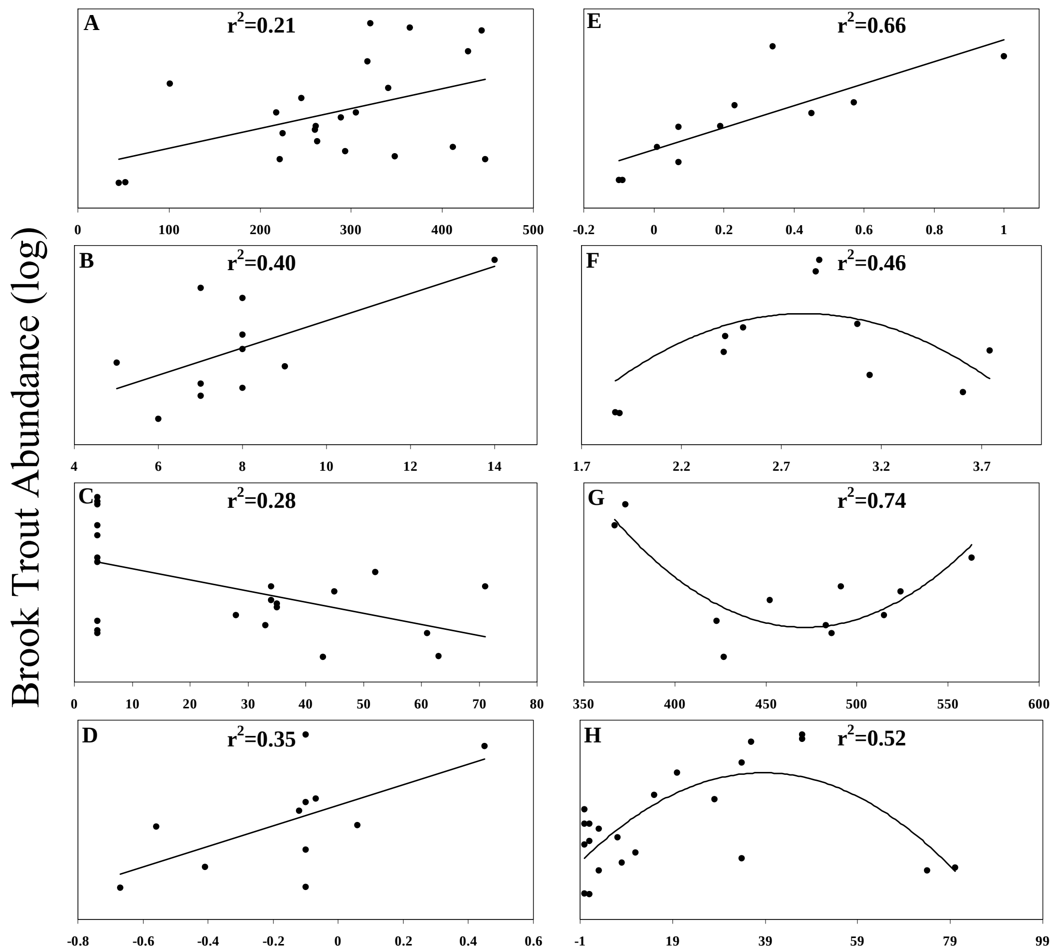

Figure 4. Log-transformed brook trout abundance (y-axes) plotted against conductivity (A; µ/cm), dissolved phosphorous (B; ppb), D16 (C), minimum yearly water temperature (D; °C), median yearly water temperature (E; °C), mean yearly water temperature (F; °C), aquatic invertebrate abundance (G; m^2), and percent fine substrate material (H) on the x-axes.

Table 3. Outputs of all linear and all significant quadratic models for cutthroat trout. All models are ranked in descending order of r^2.

Variable	P-value	r2	Parameter Estimate	SE	Model Type
Soluble Reactive Phosphorous	*0.030	0.289	-0.052	0.022	Quadratic
Maximum Temperature	*0.044	0.260	-0.056	0.025	Linear
Nitrate-Nitrite	*0.025	0.248	0.002	0.001	Linear
Chlorophyl *a*	*0.005	0.203	0.048	0.016	Linear
D84	*0.007	0.187	0.003	0.001	Linear
D90	*0.007	0.184	0.002	0.001	Linear
D64	*0.022	0.137	0.003	0.001	Linear
D50	*0.040	0.112	0.003	0.002	Linear
Median Temperature	0.067	0.220	0.554	0.279	Linear
Total Phosphorous	0.081	0.160	0.044	0.024	Linear
Total Nitrogen	0.133	0.121	0.001	0.001	Linear
Minimum Temperature	0.215	0.108	0.425	0.327	Linear
Percent Fines	0.071	0.088	-0.004	0.002	Linear
Percent Slope	0.414	0.085	4.563	5.301	Linear
pH	0.148	0.057	0.181	0.122	Linear
Soluble Reactive Phosphorous	0.326	0.054	0.056	0.056	Linear
Hill Evenness	0.516	0.048	-1.647	2.437	Linear
Simpson's Diversity	0.376	0.046	0.633	0.696	Linear
EPT Abundance	0.408	0.041	0.000	0.001	Linear
Mean Temperature	0.492	0.034	-0.100	0.142	Linear
D16	0.275	0.033	0.003	0.003	Linear
Total Invertebrate Abundance	0.462	0.032	0.001	0.001	Linear
Shannon's Diversity	0.475	0.031	-0.126	0.172	Linear
Dissolved Phosphorous	0.502	0.026	0.031	0.044	Linear
Number OTU	0.614	0.015	0.004	0.008	Linear
Turbidity	0.693	0.004	-0.033	0.082	Linear
Total Keljdal Nitrogen	0.786	0.004	0.000	0.001	Linear
Discharge	0.730	0.004	2.659	0.075	Linear
NH4_N	0.798	0.004	0.001	0.005	Linear
Conductivity	0.980	0.000	0.000	0.000	Linear

* significant ($p<.05$)

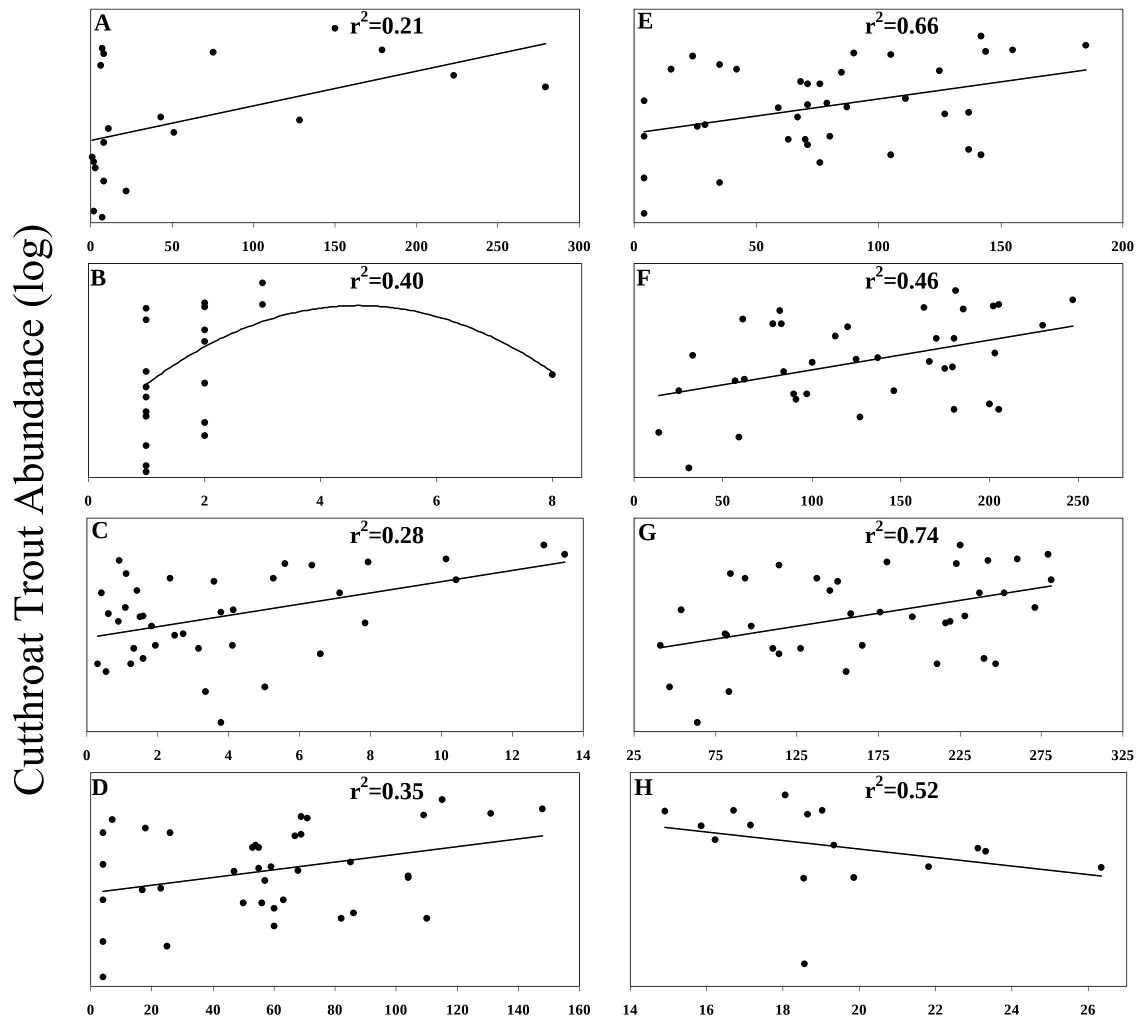

Figure 5. Log-transformed cutthroat trout abundance (y-axes) plotted against nitrates-nitrites (A; ppb), soluble reactive phosphorous (B; ppb), Chlorophyl *a* abundance (C; ug/cm^2), D50 (D), D64 (E), D84 (F), D90 (G), and maximum yearly water temperature (H; °C) on the x-axes.

Movement model

In total, I marked 86 brook trout and 291 cutthroat trout. Recapture rates were relatively high: of those marked fish, 23 brook trout and 90 cutthroat trout were recaptured. For all recaptured brook trout, 17 were recaptured once, five were recaptured twice, and one was recaptured four times. All but six of those fish were recaptured at their initial capture location. Of those brook trout that were recaptured outside of their initial capture location, all were recaptured within the same stratum, and each of those fish moved from 62-589 meters (mean = 247 meters). For all recaptured cutthroat trout, 69 were recaptured once, 18 were recaptured twice, and three were recaptured three times. All but seven of those fish were recaptured at their initial capture location. Of those cutthroat trout that were recaptured outside of their initial capture location, five were recaptured within the same stratum, and each of those fish moved from 152-991 meters (mean = 508 meters).

I analyzed seven mark/recapture model combinations (Table 4). Based on ΔAIC_c values, the most parsimonious top model included capture and survival probability that varied by group with a constant transition probability structure [i.e., s(g) p(g) psi(.)]. The top-ranking model provided plausible estimates of survival and capture probability for both brook trout and cutthroat trout, and accounted for 66% of the Akaike weights. The next three models accounted for 13%, 10%, and 10% of the Akaike weights, respectively. Transition probability could not be estimated for brook trout with any model, as no brook trout transitioned amongst strata. Estimates of cutthroat trout transition probability were very low in all four top-ranking models, as only two out of 291 cutthroat trout transitioned amongst strata. Of the two cutthroat trout that moved amongst strata, one was initially captured in stratum A during index site sampling in July, 2006 and was recaptured in stratum C during spot electrofishing in September, 2007, for a total downstream movement of approximately 12.15 km. The other cutthroat trout was initially captured in stratum C during index site sampling in July, 2006, and was recaptured in stratum D during index site sampling in July, 2007, for a total downstream movement of approximately 6.37 km. The top ranking model did not plausibly estimate brook trout or cutthroat trout survival for most strata. Capture probability was higher for cutthroat trout than for brook trout in all four strata.

Table 4. Rankings of seven multi-strata mark/recapture models of survival (Φ), capture (p), and transition (ψ) probabilities for brook trout and cutthroat trout in the Mill Creek watershed based on program MARK output and AIC selection criteria, where AIC_c= corrected Akaike's information criterion, NP = number of parameters, (g) = grouped parameters, and (.) = constant parameters.

Model	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	NP	Deviance
Φ(g), p(g), ψ (.)	870.20	0	0.659	1	24	290
Φ(.), p(g), ψ (.)	873.41	3.21	0.132	0.2005	22	297
Φ(.), p(.),ψ (.)	873.87	3.68	0.105	0.1591	20	302
Φ(g), p(.),ψ (.)	873.89	3.69	0.104	0.1583	22	298
Φ(g), p(.),ψ (g)	886.75	16.56	0.000	0.0003	28	297
Global (no group effects)	887.28	17.08	0.000	0.0002	32	289
Φ(.), p(g), ψ (g)	898.38	28.18	0	0	35	293

DISCUSSION

Based on watershed and reach-scale surveys, brook trout distribution and establishment appeared to be limited by precipitous increases in stream slope in both Mill Creek and Deadman Creek. In Mill Creek, brook trout abundance increased in an upstream direction, but the upstream extent of brook trout establishment then terminated abruptly upstream of the Mill Creek middle index site. Within that same area, stream slope increased from approximately 0.027% to 0.046%. In addition, patch occupancy surveys suggest that brook trout were abundant just upstream of the Mill Creek middle index site, but were sparsely distributed near the Mill Creek high index site. With one exception (see Deadman Creek below), at the lower reaches of all tributaries, stream slopes exceeded those of most areas of brook trout establishment in this drainage.

A similar pattern persisted in Deadman Creek, where again, brook trout establishment ended at a point of a precipitous increase in stream slope. Therefore, the pattern of brook trout distribution and establishment observed here suggests that steep stream slopes in the upper reaches of Mill Creek and its tributary confluences may limit additional brook trout invasion and establishment.

Species segregation along a streams longitudinal gradient is not unique to this watershed (Rieman et al. 2006), and many studies have investigated the potential effect of stream slope on salmonid distribution (Chrisholm and Hubert 1986; Fausch 1989; Hilderbrand 1998; Isaak and Hubert 2000; Hicks and Hall 2003). Findings by Hilderbrand (1998) and Fausch (1989), for example, suggest that brook trout perform better in lower slope (< 3%) stream reaches, and struggle to establish populations in streams that exceed 4-7%. Additional studies suggest that higher slope stream reaches limit brook trout abundance (Chisholm and Hubert 1986; Kozel and Hubert 1989; Bozek and Hubert 1992), potentially limiting successful establishment in some areas. These findings are consistent with this study, as areas of brook trout establishment in the Mill Creek watershed ranged from 0.02% to 6% in stream slope, but averaged only 2%. Fausch (1989) hypothesized that brook trout are weaker swimmers compared to other salmonids, making it difficult for brook trout to ascend steep stream slopes (but see Adams et al. 2000). In addition, other habitat variables that are associated with steep stream slope (e.g., low water temperature) may pose demographic challenges to brook trout by limiting spawning, recruitment, and survival (Fausch 1989), and thus the potential for successful establishment in some areas.

Based on Utah Division of Wildlife Resources stocking records, brook trout were first introduced into this system in 1948, with eight additional stocking events that occurred between 1949 and 1966. The precise locations of these introductions are not known, but given the absence of public property near the lower portions of the watershed and poor vehicle access in the upper portions of Mill Creek, most fish were probably stocked at the road crossing near the Mill Creek middle index site. Despite the close proximity of those introductions to the confluences of North Fork and McKenzie Creek, as well as the upper portions of Mill Creek, brook trout have not become established in those areas. During patch occupancy surveys, only three brook trout were captured upstream of the apparent stream slope barrier in Mill Creek, and all were large adults (172-226) in good condition (mean Fulton's K=1.25; Anderson and Newman 1996).

These findings suggest brook trout can ascend steep slopes in this watershed, and are consistent with the findings of Adams et al. (2000) who observed brook trout ascending stream slopes as steep as 22%. However, the ability of few brook trout to ascend the apparent stream slope barrier does not indicate successful invasion of those areas.

Given the length of time since brook trout were initially introduced into this system, the close proximity of those introductions to the upper portions of Mill Creek and its tributaries, and the paucity of brook trout above the apparent stream slope barrier, it appears local conditions in the upper portions of this watershed have limited successful establishment, and therefore successful invasion of those areas. While stream gradient appears to be the factor that limits the upstream distribution of brook trout in this system, smaller-scale factors that are associated with steep stream gradient may be more influential in determining brook trout distribution and establishment in this watershed. Given the large size (i.e., absence of sub-adult fish) and good condition of the few fish captured above the apparent stream slope barrier, it appears that brook trout experience poor spawning and/or recruitment success in the upper portions of Mill Creek, thereby limiting successful invasion of those areas by brook trout. Therefore, factors that are known to be influential in the early life-history of salmonids, such as water temperature and groundwater discharge (see below), may limit brook trout invasion in this system.

While stream slope, or environmental attributes associated with steep stream slope, appeared to influence watershed-scale brook trout distribution, additional factors appeared to influence brook trout abundance at the reach-scale, and therefore successful establishment in some areas. Based on model relationships, invertebrate abundance appeared to be influential in determining brook trout abundance; a quadratic model was positively related to brook trout abundance and had the highest explanatory power of all models. However, two data points were highly influential in determining the curvilinear relationship, and both of those data points were from the Deadman Creek middle index site, where brook trout were the most abundant and aquatic invertebrates were the least abundant. While upon first examination, this relationship may make little biological sense, it is possible that invertebrate abundance in the Deadman Creek middle index site was low because brook trout abundance was high, as there were more fish present to consume invertebrate taxa and reduce invertebrate abundance (Bechara et al. 1993; Flecker and Townsend 1994; Huryn 1996). In addition, the Deadman Creek low and high index sites, which are located just upstream and downstream of the middle index site, contained among the highest densities of aquatic invertebrates, and brook trout abundance was markedly lower at both index sites compared to the middle index site, further suggesting that brook trout reduced the abundance of aquatic invertebrates in the middle index site. Finally, the data from all other index sites (i.e., excluding Deadman Creek middle) best represented a positive linear relationship between brook trout abundance and aquatic invertebrate abundance, suggesting that indeed, invertebrate abundance may influence brook trout abundance in this watershed.

Despite the potentially confounding effects of other factors, a positive relationship between invertebrate abundance and trout biomass has also been observed in other systems (Murphy et al. 1981; Bowlby and Roff 1986; Jowett 1992; VanDusen et al. 2005). In fact, Bowlby and Roff (1986) and Jowett (1992) modeled the effects of multiple biotic and abiotic variables simultaneously, and both studies concluded that invertebrate abundance is among the most important factors influencing the biomass of stream-dwelling salmonids, further suggesting that invertebrate abundance may influence brook trout abundance in this watershed. However, while invertebrate abundance may influence brook trout abundance in this watershed, this factor alone cannot fully explain why brook trout were so abundant in the Deadman Creek middle index site compared to other areas in the watershed.

Of the remaining variables evaluated, the abundance of fine substrate material (i.e., percent fines) appeared to positively influence brook trout abundance as well. However, it appears that again, two data points were highly influential. Both influential data points were from the Deadman Creek low index site where the substrate was composed of a much higher percentage of fine material relative to the other index sites, and brook trout were detected only twice during this study and at very low abundance both times. When those data points were excluded from the analysis, the linear model was highly significant (p-value=<0.001) with reasonable model fit (r^2=0.579). Nevertheless, in this watershed the abundance of fine substrate material was positively related to brook trout abundance, regardless of the model.

This relationship may not make biological sense, as increased fine substrate material is often associated with low trout biomass. Some studies suggest that abundance of fine substrate material negatively affects salmonid reproduction by reducing the rate of intergravel flow, thereby reducing the levels of dissolved oxygen delivered to developing embryos (Waters 1995). Hall (1986) and Tagart (1984) both report an inverse relationship between survival of salmonid eggs and abundance of percent fines, observing minimal survival when the percent of fine substrate material was greater than 10% and 20%, respectively. Percentage of fine substrate material in Deadman Creek exceeded 30% during all sample periods. In fact, in the Deadman Creek middle index site where brook trout were the most abundant, the percent of fine substrate material far exceeded detrimental levels during all sample periods (mean = 41%, range = 34-47%). In addition to the detrimental effects of fine sediment abundance on early life stages of salmonids, excess levels can also negatively affect aquatic invertebrate communities, the primary forage for stream-dwelling salmonids. More specifically, by altering substrate composition, excess fine substrate material can decrease aquatic invertebrate standing stock and alter invertebrate community structure (see Lenat et al. 1979). These findings suggest that fine substrate material may not influence brook trout abundance at the reach-scale in this watershed.

Of the remaining explanatory variables evaluated, minimum, mean, and median annual water temperatures were related to brook trout abundance. In this watershed, the distribution of water temperature is skewed towards cooler temperatures, as cold winter periods are prolonged and warm summer periods are protracted. These data suggest that cold winter water temperatures may negatively influence brook trout abundance. The effects of winter stream conditions on salmonid habitat selection and movement have been firmly established (Chrisholm et al. 1987; Lindstrom and Hubert 2004), and in addition, some authors have linked (Reiser and Wesche 1979; Wood 2008) or postulated a link (Harshbarger and Porter 1979; Wiley et al. 1993) between low early life-history survival rates of fall spawning salmomids (e.g., brook trout), and cold winter water temperature. Those studies suggest that eggs that are deposited in the fall rather than spring or summer are exposed to harsh winter conditions (e.g., anchor and frazile ice) shortly after deposition. In the Mill Creek study area, it appears that water temperatures were below freezing for extended periods during the winter at most index sites, excluding the Deadman Creek middle index site during 2006. These data suggest that warm winter water temperatures in the Deadman Creek middle index site may positively influence early life-stage survival of brook trout.

The stream channel at the Deadman Creek middle index site was narrow and deeply incised, and riparian vegetative cover was dense relative to channel width. These conditions may have facilitated snow-bridging during winter months, thereby insulating the stream channel and recently deposited brook trout eggs from harsh winter conditions (Chisholm et al. 1987). Conversely, at North Fork and some areas of Mill Creek, the stream channel was shallow and wide, and riparian vegetation was less dense in relation to its channel width, leaving those stream channels exposed to harsh winter conditions. The formation of anchor ice occurred in some areas of Mill Creek as early as mid-November, while in Deadman Creek anchor ice was comparatively absent. While winter stream conditions were not a focus of this study, field observations suggest that anchor ice did not form in all areas of this drainage, perhaps a result of groundwater discharge (Prowse 1994). In the midst of harsh winter conditions, brook trout as well as other fall-spawning salmonids can spawn successfully in areas of groundwater upwelling (Webster and Eiriksdottir 1976; Curry and Noakes 1995; Baxter and Hauer 2000). However, like other stream systems (e.g., Baxter and Hauer 2000), these areas of upwelling may be patchily distributed throughout the Mill Creek watershed, a factor that may explain, in part, the patchy distribution and abundance of brook trout throughout this system.

Cutthroat trout were widely distributed throughout the watershed making it difficult to elucidate the factors that limit their watershed-scale distribution and reach-scale abundance, if any. All significant models explained little variation in cutthroat trout abundance, making it difficult to determine with a high degree of confidence, the variables that influence cutthroat trout abundance at the reach-scale. Given the high abundance of cutthroat trout in this watershed compared to other streams within its historical range, this result is not surprising, as Mill Creek and its tributaries likely represent high quality, suitable habitats for Bonneville cutthroat trout.

However, it does appear that extreme levels of stream slope (>10%) may limit cutthroat trout distribution in this system, and in some cases, upstream cutthroat trout distribution was limited only when tributaries became intermittent. Other research suggests that Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) rarely occur in stream reaches that exceed 10% (Kruse et al. 1997), however; Lohantan cutthroat trout (*Oncorhynchus clarkii henshawi*) can occupy stream reaches as steep as 26% (Dunham et al. 1999). Stream slope tolerance is not well studied for Bonneville cutthroat trout, but based on research of other closely related subspecies, it is possible that cutthroat trout distribution in this watershed could transcend stream slopes that exceed 10%, given adequate in-stream flows.

Despite the patchy abundance and limited distribution of brook trout in this watershed, movement dynamics can facilitate their continued upstream invasion by providing source populations from areas with suitable spawning and rearing habitats (Peterson and Fausch 2003; Peterson et al. 2004; Benjamin et al. 2007). In this study, I evaluated population-level movement dynamics to determine if areas of core brook trout occupancy were connected through movement. My results suggest that few brook trout move long distances in this watershed, as no brook trout were observed moving from one stratum to another. In addition, a relatively high percentage (74%) of brook trout were recaptured at their initial capture location, indicating high site fidelity. Finally, of the brook trout that were captured outside their initial capture location, but within the same stratum as their initial capture location, all had moved relatively short distances (mean=247 meters).

Salmonid movement, and in particular brook trout movement is well studied, but divisive contradictions exist amongst researchers (Gowan et al. 1994; Gowan and Fausch 1996). Gowan et al. (1994) reviewed the extensive literature that studied salmonid movement and concluded that most stream-dwelling salmonids are sedentary, later coining the term, “restricted movement paradigm”. These findings were consistent with the restricted movements of fish first described by Gerking (1959). However, subsequent research by Gowan and Fausch (1996) urged a reconsideration of this paradigm, suggesting that sampling bias is responsible for the observed patterns of restricted movement amongst many studies. To date, refuting studies report that brook trout are largely sedentary (i.e., typical movement <1.61-river kilometers; Shetter 1968), or highly mobile (Riley et al. 1992). However, it may be misleading to describe a population as entirely sedentary or entirely mobile. Some studies suggest that seasonal variations in movement amongst stream dwelling salmonids exists, and populations contain primarily sedentary individuals, with few individuals moving over long distances (Hilderbrand and Kershner 2000). While these contradictions have not been resolved, movement patterns across populations appears variable, and are likely influenced by both environmental factors and life-history characteristics (Lindstrom and Hubert 2004; Diana et al. 2004; Colyer et al. 2005), suggesting that movement is dependant upon local conditions. When compared to other studies, movement of brook trout in this watershed was primarily, if not entirely restricted, as no individuals were observed moving over long distances (i.e., >1.61-river kilometers). While sampling bias may have played a role in these findings (see Gowan and Fausch 1996), the high rate of site fidelity and short distance of movement amongst recaptured brook trout in this study is compelling evidence that brook trout movement was restricted.

In contrast, cutthroat trout movement was more variable, as two individuals were observed moving amongst strata and both fish moved considerably long distances (12.15 km and 6.37 km). However, based on transition probabilities attained from my top mark/recapture model, the overall probability of cutthroat trout movement amongst all strata remained low. The five cutthroat trout captured outside of their initial capture location, but within the same stratum, moved longer distances on average (508 meters) than brook trout (247 meters). However, I recaptured 92% of cutthroat trout at their initial capture location, indicating relatively high site fidelity by many individuals within this population (but see Budy et al. 2007). Overall, it appears that cutthroat trout in this watershed moved more often and over longer distances than brook trout; however, the spatial-scale of cutthroat trout movement in this watershed remains minimal compared to similar systems (Hilderbrand and Kershner 2000; Colyer et al. 2005).

Financial and logistic restraints precluded the evaluation of all explanatory variables for all sample periods. As a result, my dataset contained missing observations for some explanatory variables, making more rigorous statistical testing (e.g., multiple regression and model selection techniques) impossible. Nevertheless, I provide evidence of the factors that influence brook trout and cutthroat trout distribution and abundance at multiple spatial scales. Additional research should further investigate the affects of low winter water temperature on brook trout egg and fry survival in this watershed, given fine-scale heterogeneity in habitats. Finally, the temporal-scale of this movement study, from late-spring to early-fall, may not have adequately assessed spawning migrations. Despite these limitations, I observed a relatively high rate of sight fidelity by both species, and movement patterns did not appear to facilitate additional upstream invasion by brook trout, nor limit watershed-scale cutthroat trout movement.

The results of this study will aid in prioritizing management actions for cutthroat trout in this watershed. More specifically, continued upstream invasion by brook trout does not pose an immediate threat to cutthroat trout in the headwater portions of Mill Creek or Deadman Creek, as local conditions appear to limit brook trout invasion of those areas. Based on those findings, the use of artificial barriers to prevent additional upstream brook trout invasion is not necessary in this watershed. In addition, I observed some cutthroat trout moving long distances in this watershed, therefore; the use of artificial barriers could impede watershed-scale cutthroat trout movement and hinder their natural dispersal and migration patterns (Peterson et al. 2008). Finally, if resource managers decide to eradicate brook trout from this system, my species distribution and establishment data will help identify and prioritize areas where those projects should occur.

In conclusion, the results from this study suggest that stream slope, or smaller-scale factors associated with stream slope, limits the upstream distribution of brook trout at the watershed-scale, and aquatic invertebrate abundance and low winter water temperatures influence the magnitude of brook trout abundance at the reach-scale. Within this watershed, brook trout movement appeared minimal overall, as I observed relatively high site fidelity and no movement across strata. I could not explain the variation in cutthroat trout abundance at the reach-scale based on the explanatory variables I measured, but given the high abundance of cutthroat trout in this watershed relative to other historically occupied habitats, this system likely represents high quality habitat for cutthroat trout. In addition, while small-scale cutthroat trout movement was more variable than that of brook trout, few individuals within the population moved long distances. These results provide resource managers with critical demographic data and information describing the invasion potential of a ubiquitous and often aggressive nonnative species. Mill Creek contains one of the largest remaining genetically pure metapopulations of Bonneville cutthroat trout. Protection of this metapopulation is critical for the future persistence of this subspecies, and the results of this study aid in prioritizing cutthroat trout management actions in this watershed.

REFERENCES

Adams, S.B., C.A. Frissell, and B.E. Rieman. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions of the American Fisheries Society 129(3): 623-638.

Adams, S.B., C.A. Frissell, and B.E. Rieman. 2002. Changes in distribution of nonnative brook trout in an Idaho drainage over two decades. Transactions of the American Fisheries Society 131: 561-568.

Anderson, R.O., and R.M. Newman. 1996. Length, weight, and associated structural indices. Pages 114-482 in B. R. Murphy and D. W. Willis, editors. Fisheries Techniques, Second Edition. American Fisheries Society. Bethesda, Maryland.

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

Bechara, J.A., G. Moreau, and L. Hare. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. The Journal of Animal Ecology 62: 451-464.

Behnke, R.J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Behnke, R.J. 1988. Phylogeny and classification of cutthroat trout. American Fisheries Society Symposium 4: 1-7.

Benjamin, J.R., J.B. Dunham, and M.R. Dare. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance, and connectivity to source habitats. Transactions of the American Fisheries Society 136: 875-888.

Binns, A.N., and R. Remmick. 1994. Response of Bonneville cutthroat trout and their habitat to drainage-wide habitat management at Huff Creek, Wyoming. North American Journal of Fisheries Management 14: 669-680.

Bowlby, J.N, and J.C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. Transactions of the American Fisheries Society 115: 503-514.

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

Budy, P., G.P. Thiede, and P. McHugh. 2007. Quantification of the vital rates, abundance, and status of a critical, endemic population of Bonneville cutthroat trout. North American Journal of Fisheries Management 27: 593-604.

Bunte, K., and S.R. Abt. 2001. Sampling surface and subsurface particle-size distributions in wadable gravel-and cobble-bed streams for analyses in sediment transport, hydraulics, and streambed monitoring. U.S. Forest Service, General Technical Report RMRS-GTR-74.

Carmichael, G.T., J.N. Hanson, M.E. Schmidt, and D.C. Merizot. 1993. Introgression among Apache, cutthroat, and rainbow trout in Arizona. Transactions of the American Fisheries Society 122: 121-130.

Chisholm, I.M., and W.A. Hubert. 1986. Influence of Stream Gradient on Standing Stock of Brook Trout in the Snowy Range, Wyoming. Northwest Science 60: 137-139.

Chisholm, I.M., W.A. Hubert, and T.A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society 116: 176-184.

Cleveland, L., E.E. Little, S.J. Hamilton, D.R. Buckler, and J.B. Hunn. 1986. Interactive toxicity of aluminum and acidity to early life stage of brook trout. Transactions of the American Fisheries Society 115: 610-620.

Clesceri, L.S., A.E. Greenberg, and R.R. Trussell. 1989. Standard methods for the examination of water and wastewater. A. P. H. A. American Public Health Association, American Water Works Association, editor. Water Pollution Control Federation, Washington, D.C.

Colyer, W.T., J.L. Kershner, and R.H. Hilderbrand. 2005. Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho-Wyoming. North American Journal of Fisheries Management 25: 954-963.

Cunjak, R.A., and J.M. Green. 1984. Species Dominance by Brook Trout and Rainbow-Trout in a Simulated Stream Environment. Transactions of the American Fisheries Society 113: 737-743.

Curry, R.A., and D.L.G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 52: 1733-1740.

de la Hoz Franco, E.A., and P. Budy. 2004. Linking environmental heterogeneity to the distribution and prevalence of *Myxobolus cerebralis*: a comparison across sites in a northern Utah watershed. Transactions of the American Fisheries Society 133: 1176-1189.

Destaso, J., and F.J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Transactions of the American Fisheries Society 123: 289-297.

Diana, J.S., J.P. Hudson, and R.D. Clark Jr. 2004. Movement patterns of large brown trout in the mainstem Au Sable River, Michigan. Transactions of the American Fisheries Society 133: 34-44.

Dunham, J.B., S.B. Adams, R.E. Schroeter, and D.C. Novinger. 2002. Alien invasions in aquatic ecosystems: Toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12: 373-391.

Dunham, J.B., M.M. Peacock, B.E. Rieman, R.E. Schroeter, and G.L. Vinyard. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Transactions of the American Fisheries Society 128: 875-889.

Dunham, J.B., M.E. Rahn, R.E. Schroeter, and S.W. Breck. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. Western North American Naturalist 60: 304-310.

Fausch, K.D. 1989. Do gradient and temperature affect distributions of, and interaction between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiology and Ecology Japan Special Volume 1: 303-332.

Flecker, A.S., and C.R. Townsend. 1994. Community-wide consequences of trout introduction in New Zealand streams. Ecological Applications 4: 798-807.

Fuller, P.L., L.G. Nico, and J.D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Special Publication 27, Bethesda, Maryland.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Reviews 34: 221-242.

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

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

Gowan, C., and K.D. Fausch. 2002. Why do foraging stream salmonids move during summer? Environmental Biology of Fishes. 64: 139-153.

Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society Symposium 4.

Griffith, J.S. 1988. Review of competition between cutthroat trout and other salmonids. American Fisheries Society Symposium 4: 134-140.

Gunckel, S.L., A.R. Hemmingsen, and J.L. Li. 2002. Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. Transactions of the American Fisheries Society 131: 1119-1130.

Hall, T. J. 1986. A laboratory study of the effects of fine sediments on survival of three species of Pacific salmon from eyed to egg to fry emergence. National Council of the Paper Industry for Air and Stream Improvement, Technical Bulletin 482, New York.

Harrelson, C.C., C.L. Rawlins, and J.P. Potyondy. 1994. Stream channel reference sites: an illustrated guide to field technique. General Technical Report RM-245. Fort Collins, CO: U.S. Departement of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Harshbarger, T.J., and P.E. Porter. 1979. Survival of brown trout eggs: two planting techniques compared. The Progressive Fish Culturist 41: 206-209.

Hartman, K., and J.P. Hakala. 2006. Relationships between fine sediment and brook trout recruitment in forested headwater streams. Journal of Freshwater Ecology 21(2): 215-230.

Henderson, R., J.L. Kershner, and L.A. Toline. 2000. Timing and location of spawning by nonnative wild rainbow trout and native cutthroat trout in the South Fork Snake River, Idaho, with implications for hybridization. North American Journal of Fisheries Management 20: 584-596.

Hicks, B.J., and J.D. Hall. 2003. Rock type and channel gradient structure salmonid populations in the Oregon coast range. Transactions of the American Fisheries Society 132: 468-482.

Hilderbrand, R.H. 1998. Movements and conservation of cutthroat trout. Doctoral dissertation. Utah State University, Logan, Utah.

Hilderbrand, R.H., and J.L. Kershner. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. Transactions of the American Fisheries Society 129: 1170-2000.

Hilderbrand, R.H., and J.L. Kershner. 2004. Influence of habitat type on food supply, selectivity, and diet overlap of Bonneville cutthroat trout and nonnative brook trout in Beaver Creek, Idaho. North American Journal of Fisheries Management 24: 33-40.

Hitt, N.P., C.A. Frissell, C.C. Muhlfeld, and F.W. Allendorf. 2003. Spread of hybridization between native westlope cutthroat trout, *Oncorhynchus clarkii lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Science 60: 1440-1451.

Hudy, M., T.M. Thieling, N. Gillespie, and E.P. Smith. 2005. Distribution, status, and threats to brook trout within eastern United States. Report submitted to the Eastern Brook Trout Joint Venture, International Association of Fish and Wildlife Agencies, Washington, D. C.

Huryn, A.D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnological Oceanography 41: 243-252.

Hutchison, M.J., and M. Iwata. 1997. A comparative analysis of aggression in migratory and non-migratory salmonids. Environmental Biology of Fishes 50: 209-215.

Isaak, D.J., and W.A. Hubert. 2000. Are trout populations affected by reach-scale stream slope? Canadian Journal of Fisheries and Aquatic Sciences 57: 468-477.

Jordahl, D.M., and A. Benson. 1987. Effect of low pH on survival of brook trout embryos and yolk-sac larvae in West Virginia streams. Transactions of the American Fisheries Society 116: 807-816.

Jowett, I.G. 1992. Models of the abundance of large brown trout in New Zealand rivers. North American Journal of Fisheries Management. 12: 417-432.

Kennedy, B.M., D.P. Peterson, and K.D. Fausch. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. Western North American Naturalist 63: 215-223.

Kocovsky, P.M., and R.F. Carline. 2006. Influence of landscape-scale factors in limiting brook trout populations in Pennsylvania streams. Transactions of the American Fisheries Society 135: 76-88.

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

Krebbs, C.J. 1999. Ecological methodology, 2nd edition, Addison-Welsey Educational Publishers, Menlo Park, California.

Kruse, C.G., W.A. Hubert, and F.J. Rahel. 1997. Geomorphic influence on distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. Transactions of the American Fisheries Society 126: 418-427.

Lenat, D.R., D.L. Penrose, and K.W. Eagleson. 1979. Biological evaluation of non-point source pollutants in North Carolina streams and rivers. North Carolina Department of Natural Resources and Community Development, Biological Series 102, Raleigh.

Lentsch, L., Y. Converse, and J. Perkins. 1997. Conservation agreement and strategy for Bonneville cutthroat trout in the State of Utah. Publication Number 97-19 Utah Department of Natural Resources, Division of Wildlife Resources. Salt Lake City, Utah.

Lindstrom, J.W., and W.A. Hubert. 2004. Ice processes affect habitat use and movements of adult cutthroat trout and brook trout in a Wyoming foothills stream. North American Journal of Fisheries Management 24: 1341-1352.

MacCrimmon, H.R., and J.S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. Journal of Fisheries Research 26: 1699-1725.

McGrath, C.C., and W.M. Lewis Jr. 2007. Competition and predation mechanisms for displacement of greenback cutthroat trout by brook trout. Transactions of the American Fisheries Society 136: 1381-1392.

Meyer, K.A., J.A. Lamansky, and D.J. Schill. 2006. Evaluation of an unsuccessful brook trout electrofishing removal project in a small rocky mountain stream. North American Journal of Fisheries Management 26: 849-860.

Mullner, S.A., and W.A. Hubert. 2005. Low summer water temperatures influence occurrence of naturalized salmonids across a mountain watershed. North American Journal of Fisheries Management 25: 1034-1040.

Murphy, M.L., C.P. Hawkins, and N.H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society 110: 469-478.

Nelson. R.L., W.S. Platts, D.P. Larsen, and S.E. Jensen. 1992 Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Transactions of the American Fisheries Society 121: 405-426.

Northcote, T. G. 1997. Potammodromy in Salmonidae-living and moving in the fast lane. North American Journal of Fisheries Management 17: 1029-1045.

Page, L.M., and B.M. Burr. 1991. A field guide to freshwater fishes of North American north of Mexico. The Peterson Field Guide Series 42 Houghton Mifflin, Boston.

Peterson, D.P., and K.D. Fausch. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60: 1502-1516.

Peterson, D.P., K.D., Fausch, and G.C. White. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecological Applications 14: 754-772.

Peterson, D.P., B.E. Rieman, J.B. Dunham, K.D. Fausch, and M.K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout *(salvelinus fontinalis)* and intentional isolation for native westslope cutthroat trout *(Oncorhynchus clarkii lewisi)*. Canadian Journal of Fisheries and Aquatic Sciences 65: 557-573.

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

Poff, L.N. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16(2): 391-409.

Prowse, T.D. 1994. Environmental significance of ice to streamflow in cold regions. Freshwater Biology 32: 241-259.

Rieman, B.E., J.T. Peterson, and D.L. Meyers. 2006. Have brook trout (*salvelinus fontinalis*) displaced bull trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams? Canadian Journal of Fisheries and Aquatic Sciences 63: 63-78.

Reiser, D.W., and T.A. Wesche. 1979. *In situ* freezing as a cause of mortality in brown trout eggs. The Progressive Fish Culturist 41(2): 58-60.

Riley, S.C., K.D. Fausch, and C. Gowan. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fishes 1: 112-122.

Schade, C.B., and S.A. Bonar. 2005. Distribution and abundance of nonnative fishes in streams of the western United States. North American Journal of Fisheries Management 25: 1386-1394.

Scott, M., and G.S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26(11): 6-15.

Shepard, B.B. 2004. Factors that may be influencing nonnative brook trout invasion and their displacement of native westslope cutthroat trout in three adjacent southwestern Montana streams. North American Journal of Fisheries Management 24: 1088-1100.

Shetter, D.S. 1968. Observations on movements of wild trout in two Michigan stream drainages. Transactions of the American Fisheries Society 97: 472-480.

Smith, G.R., T.E. Dowling, K.W. Gobalet, T. Lugaski, D.K. Shiozawa, and R.P. Evans. 2002. Biogeography and timing evolutionary events among Great Basin fishes. Pages 175-234 in R. Hershler, E. O. Wiley, and anonymous, editors. Great Basin Aquatic History Smithsonian Contribution to Earth Sciences, Washington, D. C.

Taggart, J.V. 1984. Coho salmon survival from egg deposition to fry emergence. Pages 173-182 in J.M. Walton and D.B Houston, editors. Proceedings of the Olympic Wild Fish Conference. Peninsula College, Port Angeles, Washington.

Trotter, P. 1987. Cutthroat: Native trout of the west. Colorado Associated University Press, Boulder, Colorado.

Tyus, H.M., and J.F. Saunders III. 2000. Nonnative fish control and endangered fish recovery: lessons from the Colorado River. Fisheries 24: 17-24.

VanDusen, P.J., C.J.F. Huckins, and D.J. Flashpohler. 2005. Associations among selection logging history, brook trout, macroinvertebrates, and habitat in northern Michigan headwater streams. Transactions of the American Fisheries Society 134: 762-774.

Wang, L., and R.J. White. 1994. Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. North American Journal of Fisheries Management 14: 475-487.

Waters, T.F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7: 53.

Webster, D.A., and G. Eiriksdottir. 1976. Upwelling as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 105: 416-421.

Weigel, D.E., J.T. Peterson, and P. Spruel. 2003. Introgressive hybridization between native cutthroat trout and introduced rainbow trout. Ecological Applications 13: 38-50.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Wiley, R.W., R.A. Whaley, J.B. Stake, and M. Fowden. 1993. Assessment of stocking hatchery trout: a Wyoming perspective. North American Journal of Fisheries Management 13: 160-170.

Williamson, M. 1999. Invasions. Ecography 22: 5-12.

Wood, J. R. 2008. An investigation of the early life-history of brown trout (*Salmo trutta*) and potential influences on invasion success in the Logan River, Utah. Masters thesis. Utah State University, Logan, Utah.

APPENDICES

APPENDIX A

Table A.1. Input file for multi-strata mark-recapture model in Program MARK, including unique fish ID and capture history (stratas A-D) for each recaptured cutthroat trout (1 0) and brook trout (0 1).

/*	087C518D	*/	AA0A00	1	0	;
/*	087C518A	*/	A00000	1	0	;
/*	087C518E	*/	A00000	1	0	;
/*	087C518F	*/	A00000	1	0	;
/*	087C5191	*/	AA0000	1	0	;
/*	087C5192	*/	A00000	1	0	;
/*	087C5193	*/	AA0000	1	0	;
/*	087C5190	*/	AA0000	1	0	;
/*	087C5195	*/	AA0000	1	0	;
/*	087C518C	*/	AA0A00	1	0	;
/*	087C5108	*/	0A0AA0	1	0	;
/*	087C5107	*/	0A0A00	1	0	;
/*	0876472A	*/	00AA00	1	0	;
/*	08764723	*/	000AA0	1	0	;
/*	08764724	*/	000A00	1	0	;
/*	0876472B	*/	000AA0	1	0	;
/*	087643F8	*/	0000A0	1	0	;
/*	087643F7	*/	0000A0	1	0	;
/*	087643F9	*/	0000A0	1	0	;
/*	087643FA	*/	0000A0	1	0	;
/*	087C5183	*/	CC0000	1	0	;
/*	087C5188	*/	C00000	1	0	;
/*	087C5186	*/	C00000	1	0	;
/*	087C5189	*/	CC000C	1	0	;
/*	087C5194	*/	C00000	1	0	;
/*	087C511F	*/	0C0000	1	0	;
/*	08764726	*/	000C00	1	0	;
/*	08764728	*/	000CC0	1	0	;
/*	087643FC	*/	0000C0	1	0	;
/*	087643FE	*/	0000CC	1	0	;
/*	087643FF	*/	0000CC	1	0	;
/*	087C518B	*/	A00A00	1	0	;
/*	087C5185	*/	A00A00	1	0	;
/*	087C517F	*/	A00000	1	0	;
/*	087C5182	*/	A0000C	1	0	;
/*	087C5184	*/	A00000	1	0	;
/*	087C516C	*/	A00000	1	0	;
/*	087C516D	*/	A00000	1	0	;
/*	087C5181	*/	A00A00	1	0	;

/*	087C5197	*/	A00000	1	0	;
/*	087C5187	*/	A00000	1	0	;
/*	087C50E0	*/	0A0000	1	0	;
/*	087C511A	*/	0A0000	1	0	;
/*	0876471F	*/	000A00	1	0	;
/*	08764729	*/	00AA00	1	0	;
/*	08764722	*/	00AA00	1	0	;
/*	08764727	*/	00AA00	1	0	;
/*	087C518B	*/	0000A0	1	0	;
/*	087C5157	*/	CC000C	0	1	;
/*	087C50E3	*/	C00000	1	0	;
/*	087C5105	*/	CC0000	1	0	;
/*	087C514C	*/	CC0000	1	0	;
/*	087C5145	*/	CC000C	1	0	;
/*	087C5144	*/	C00000	1	0	;
/*	087C5142	*/	CC0000	1	0	
/*	087C513D	*/	CC0000	1	0	;
/*	087C5118	*/	CC0C0C	1	0	;
/*	087C512A	*/	CC0000	1	0	;
/*	087C5149	*/	C00000	1	0	;
/*	087C5148	*/	C00000	1	0	;
/*	087C514A	*/	C00000	1	0	;
/*	087C5143	*/	C00000	1	0	;
/*	087C5106	*/	C00000	1	0	;
/*	087C5104	*/	C00000	1	0	;
/*	087C50E1	*/	CC0000	1	0	;
/*	087C5147	*/	CC0C00	1	0	;
/*	087C5148	*/	C00000	1	0	;
/*	087C515D	*/	CC0C00	1	0	;
/*	087C514E	*/	C00000	1	0	;
/*	087C512E	*/	C00000	1	0	;
/*	087C515C	*/	C00000	0	1	;
/*	087C5150	*/	C00000	0	1	;
/*	087C5156	*/	C00000	0	1	;
/*	087C5111	*/	C00000	1	0	;
/*	087C5159	*/	CC0000	1	0	;
/*	087C516A	*/	C00000	1	0	;
/*	087C514F	*/	C0000C	0	1	;
/*	087C5131	*/	0C0000	1	0	;
/*	087C5120	*/	0C0000	1	0	;
/*	087C5125	*/	0C0000	1	0	;
/*	087C5123	*/	0C0000	1	0	;
/*	087C5113	*/	0C0000	1	0	;

```
/*   087C5119   */   0C0000   1   0   ;
/*   087C5124   */   0C0000   1   0   ;
/*   087C5116   */   0C0000   1   0   ;
/*   087C5129   */   0C0000   1   0   ;
/*   087C5121   */   0C0000   0   1   ;
/*   087C5122   */   0C0000   0   1   ;
/*   087C5127   */   0C0000   0   1   ;
/*   087C511E   */   0C0000   1   0   ;
/*   087C511B   */   0C0C00   1   0   ;
/*   087643A4   */   000C00   1   0   ;
/*   087643A6   */   000CCC   1   0   ;
/*   087643A5   */   000CCC   1   0   ;
/*   087643A3   */   000CC0   1   0   ;
/*   08763955   */   000C00   1   0   ;
/*   087643AC   */   000C00   1   0   ;
/*   087643A7   */   000C0C   1   0   ;
/*   087643A8   */   000CCC   1   0   ;
/*   087643AF   */   000CC0   1   0   ;
/*   087643B2   */   000CC0   1   0   ;
/*   087643B0   */   000C00   1   0   ;
/*   087643B3   */   000C00   1   0   ;
/*   087643AE   */   000CC0   1   0   ;
/*   087643B6   */   000CC0   1   0   ;
/*   087643D7   */   000CC0   1   0   ;
/*   087643B1   */   000C00   1   0   ;
/*   087643B4   */   000CCC   1   0   ;
/*   087643AA   */   000C00   1   0   ;
/*   087643A9   */   000CCC   1   0   ;
/*   087643B5   */   000C00   1   0   ;
/*   087643AD   */   000CC0   1   0   ;
/*   087643B9   */   000C00   1   0   ;
/*   087643AB   */   000C00   0   1   ;
/*   087643B8   */   000C00   1   0   ;
/*   087643BB   */   000CCC   1   0   ;
/*   087643BA   */   000CC0   1   0   ;
/*   087643BD   */   000CC0   1   0   ;
/*   0876440E   */   0000C0   1   0   ;
/*   08764408   */   0000C0   1   0   ;
/*   0876440B   */   0000C0   1   0   ;
/*   08764409   */   0000C0   1   0   ;
/*   0876440C   */   0000C0   1   0   ;
/*   08764418   */   0000C0   1   0   ;
/*   08764414   */   0000C0   1   0   ;
```

/*	08764416	*/	0000C0	1	0	;
/*	08764411	*/	0000C0	1	0	;
/*	08764413	*/	0000C0	1	0	;
/*	08764417	*/	0000C0	1	0	;
/*	0876440D	*/	0000C0	1	0	;
/*	08764412	*/	0000CC	1	0	;
/*	08764415	*/	0000C0	1	0	;
/*	0876441B	*/	0000C0	1	0	;
/*	08764419	*/	0000C0	1	0	;
/*	0876441A	*/	0000C0	1	0	;
/*	0876440F	*/	0000C0	1	0	;
/*	0876440A	*/	0000CC	0	1	;
/*	08764410	*/	0000C0	1	0	;
/*	0876441D	*/	0000C0	1	0	;
/*	0876441C	*/	0000CC	1	0	;
/*	08764294	*/	0000C0	1	0	;
/*	08764420	*/	0000C0	1	0	;
/*	08764290	*/	0000CC	1	0	;
/*	0876441F	*/	0000C0	1	0	;
/*	08764293	*/	0000C0	1	0	;
/*	087C5154	*/	DD0000	1	0	;
/*	087C5158	*/	DD0000	1	0	;
/*	087C515A	*/	DD0000	1	0	;
/*	087C515E	*/	D00000	1	0	;
/*	087C5117	*/	D00000	1	0	;
/*	087C5153	*/	D00000	1	0	;
/*	087C5155	*/	DD0000	1	0	;
/*	087C515B	*/	D00000	1	0	;
/*	08764355	*/	D00000	1	0	;
/*	08764354	*/	D00000	1	0	;
/*	087C5140	*/	D00000	1	0	;
/*	087C514B	*/	D00000	1	0	;
/*	087C512C	*/	DD0000	1	0	;
/*	087C50E4	*/	D00000	1	0	;
/*	087C515F	*/	D00000	1	0	;
/*	087C514D	*/	D00000	1	0	;
/*	087C510E	*/	D00000	1	0	;
/*	087C5161	*/	D00000	1	0	;
/*	087C5110	*/	DD0000	0	1	;
/*	087C5151	*/	D00000	0	1	;
/*	087C510D	*/	D00000	0	1	;
/*	087C510E	*/	D00000	0	1	;
/*	087C5104	*/	C00D00	1	0	;

/*	087C50F6	*/	0D0000	1	0	;
/*	087C50EB	*/	0D0000	0	1	;
/*	087C50FF	*/	0D0000	1	0	;
/*	087C50EE	*/	0D0000	1	0	;
/*	087C50FE	*/	0D0000	1	0	;
/*	087C50FC	*/	0D0000	0	1	;
/*	087C5102	*/	0D0000	1	0	;
/*	087C50FD	*/	0D0000	1	0	;
/*	087C5100	*/	0D0000	0	1	;
/*	087C50FB	*/	0D0000	1	0	;
/*	087C50FA	*/	0D0000	1	0	;
/*	087C512F	*/	0D0000	1	0	;
/*	087C513B	*/	0D0000	1	0	;
/*	087C5141	*/	0D0000	0	1	;
/*	087C5133	*/	0D0000	1	0	;
/*	087C5134	*/	0D0000	1	0	;
/*	087C5130	*/	0D0000	0	1	;
/*	087C5132	*/	0D0000	1	0	;
/*	087C5135	*/	0D0000	0	1	;
/*	NONE	*/	0D0000	1	0	;
/*	08763932	*/	0D0000	1	0	;
/*	08763934	*/	0D0000	1	0	;
/*	08763938	*/	0D0000	1	0	;
/*	087643D4	*/	00D0D0	1	0	;
/*	08763936	*/	0000D0	1	0	;
/*	0876393A	*/	0000D0	1	0	;
/*	08763975	*/	0000D0	1	0	;
/*	08763961	*/	0000D0	1	0	;
/*	08763965	*/	0000D0	1	0	;
/*	087643C7	*/	0000D0	1	0	;
/*	087643C9	*/	0000D0	1	0	;
/*	087643C8	*/	0000D0	1	0	;
/*	08763976	*/	0000D0	1	0	;
/*	087643C4	*/	0000D0	0	1	;
/*	087643C6	*/	0000D0	0	1	;
/*	087C5175	*/	B00000	1	0	;
/*	087C516E	*/	BB0000	1	0	;
/*	087C5174	*/	B00000	1	0	;
/*	087C5172	*/	B00000	1	0	;
/*	087C5171	*/	B00000	1	0	;
/*	087C517A	*/	BBB000	1	0	;
/*	087C5162	*/	BB0000	1	0	;
/*	087C517B	*/	B00000	1	0	;

```
/*	087C5101	*/	BB0BB0	1	0	;
/*	087C5164	*/	B00000	1	0	;
/*	087C5103	*/	BB0000	1	0	;
/*	087C50E5	*/	B00BB0	1	0	;
/*	087C50E6	*/	BB0000	1	0	;
/*	087C5126	*/	0B0000	1	0	;
/*	087C512B	*/	0B0000	1	0	;
/*	087C511C	*/	0B0000	1	0	;
/*	087C5112	*/	0B0000	1	0	;
/*	087C5114	*/	0B0000	1	0	;
/*	087C511D	*/	0B0000	1	0	;
/*	0876470A	*/	000B00	1	0	;
/*	0876470B	*/	000BB0	1	0	;
/*	08764707	*/	000B00	1	0	;
/*	08764709	*/	000B00	1	0	;
/*	08764708	*/	000BB0	1	0	;
/*	08764700	*/	000BB0	1	0	;
/*	08764701	*/	000BB0	1	0	;
/*	087C5172	*/	000B00	1	0	;
/*	08764702	*/	000B00	1	0	;
/*	08764703	*/	000B00	1	0	;
/*	08764705	*/	000BB0	1	0	;
/*	08764704	*/	000B00	1	0	;
/*	087646FF	*/	000B00	1	0	;
/*	08764706	*/	000BB0	1	0	;
/*	08764403	*/	0000B0	1	0	;
/*	087643FB	*/	0000B0	1	0	;
/*	08764400	*/	0000B0	1	0	;
/*	087643FD	*/	0000B0	1	0	;
/*	08764402	*/	0000B0	1	0	;
/*	08764404	*/	0000B0	1	0	;
/*	08764407	*/	0000B0	1	0	;
/*	08764406	*/	0000B0	1	0	;
/*	08764401	*/	0000B0	1	0	;
/*	087C5146	*/	D00000	1	0	;
/*	087C5138	*/	D00000	1	0	;
/*	087C51F	*/	D00000	1	0	;
/*	087C513C	*/	D00000	1	0	;
/*	087C5137	*/	D00000	1	0	;
/*	087C5139	*/	D00000	1	0	;
/*	087C5136	*/	D00000	1	0	;
/*	087C513A	*/	D00000	1	0	;
/*	087C513E	*/	DD0D00	1	0	;
```

/*	087C510B	*/	D00000	1	0	;
/*	087C512D	*/	D00000	1	0	;
/*	087C5115	*/	D00000	1	0	;
/*	087C50EC	*/	0D0000	1	0	;
/*	187C50E9	*/	0D0000	1	0	;
/*	087C50EF	*/	0D0000	1	0	;
/*	087C50ED	*/	0D0000	1	0	;
/*	087C50F4	*/	0D00D0	1	0	;
/*	087C50F9	*/	0D0000	1	0	;
/*	087C50F5	*/	0D0000	1	0	;
/*	087C50F1	*/	0D0000	1	0	;
/*	087C50F2	*/	0D0DD0	1	0	;
/*	087C50F3	*/	0D0000	0	1	;
/*	087C50F0	*/	0D0000	0	1	;
/*	087C50F7	*/	0D0000	1	0	;
/*	087C50F8	*/	0D0000	1	0	;
/*	0876471A	*/	000D00	1	0	;
/*	08763953	*/	000D00	1	0	;
/*	0876395C	*/	000D00	1	0	;
/*	08763957	*/	000D00	1	0	;
/*	08763940	*/	000D00	1	0	;
/*	08763968	*/	000D00	1	0	;
/*	0876395A	*/	000D00	0	1	;
/*	08763964	*/	000DD0	0	1	;
/*	08764717	*/	000D00	0	1	;
/*	08763962	*/	000D00	0	1	;
/*	0876470F	*/	000D00	1	0	;
/*	08764711	*/	000DDD	1	0	;
/*	08764299	*/	0000D0	1	0	;
/*	08764298	*/	0000D0	1	0	;
/*	0876429A	*/	0000D0	1	0	;
/*	0876428F	*/	0000D0	1	0	;
/*	08764296	*/	0000D0	1	0	;
/*	08764295	*/	0000D0	1	0	;
/*	08764297	*/	0000D0	1	0	;
/*	08764291	*/	0000D0	1	0	;
/*	087C5165	*/	DD0000	1	0	;
/*	087C5168	*/	DD0000	1	0	;
/*	087C5169	*/	D00D00	0	1	;
/*	087C5177	*/	DD0000	0	1	;
/*	087C5179	*/	DD0D00	0	1	;
/*	087C5176	*/	D00000	0	1	;
/*	087510C	*/	D00000	0	1	;

/*	087C517C	*/	DD0DDD	0	1	;
/*	087C517D	*/	D00000	0	1	;
/*	087C517E	*/	D00DD0	0	1	;
/*	087C5165	*/	D00000	0	1	;
/*	087C5163	*/	D00DD0	0	1	;
/*	087C5166	*/	D00000	0	1	;
/*	087C5173	*/	D00000	0	1	;
/*	087C5167	*/	DD0DD0	0	1	;
/*	087C5178	*/	D00DD0	0	1	;
/*	087C5109	*/	0D0D00	0	1	;
/*	087C50E8	*/	0D0D00	0	1	;
/*	087C50CB	*/	0D0000	0	1	;
/*	08764710	*/	000DD0	0	1	;
/*	0876470D	*/	000D00	0	1	;
/*	0876470C	*/	000DD0	0	1	;
/*	08764718	*/	000DD0	0	1	;
/*	08764719	*/	000D00	0	1	;
/*	0876470E	*/	000DD0	0	1	;
/*	08764716	*/	000DD0	1	0	;
/*	08764712	*/	000DD0	1	0	;
/*	08764714	*/	000DD0	0	1	;
/*	08764715	*/	000D00	0	1	;
/*	08764713	*/	000D00	0	1	;
/*	087643CD	*/	0000D0	0	1	;
/*	08763951	*/	0000D0	0	1	;
/*	08764302	*/	0000D0	0	1	;
/*	0876395FT	*/	0000D0	0	1	;
/*	087643D1	*/	0000DD	0	1	;
/*	087643CFT	*/	0000D0	0	1	;
/*	087643CE	*/	0000D0	0	1	;
/*	087643D3	*/	0000D0	0	1	;
/*	087643CB	*/	0000D0	0	1	;
/*	087C5198	*/	DD0DD0	1	0	;
/*	087C5199	*/	DD0000	1	0	;
/*	087C5160	*/	DD0000	1	0	;
/*	087C5170	*/	DD0000	1	0	;
/*	087643C0	*/	000D00	0	1	;
/*	087C519A	*/	D00000	0	1	;
/*	087C5180	*/	D00000	0	1	;
/*	087C516E	*/	D00000	0	1	;
/*	087C510A	*/	0D0000	0	1	;
/*	08764721	*/	000DD0	0	1	;
/*	0876471E	*/	000D00	0	1	;

/*	0876471C	*/	000D00	0	1	;
/*	087643D0	*/	0000D0	0	1	;
/*	087643D4	*/	0000D0	0	1	;
/*	08764734	*/	00D000	0	1	;
/*	08764732	*/	00D000	0	1	;
/*	08764730	*/	00D000	0	1	;
/*	0876472E	*/	00D000	1	0	;
/*	0876472F	*/	00D000	1	0	;
/*	0876472D	*/	00D000	1	0	;
/*	087643A1	*/	00C000	1	0	;
/*	08764733	*/	00C000	1	0	;
/*	0876472C	*/	00C00C	1	0	;
/*	0876471D	*/	00C000	0	1	;
/*	087643BE	*/	00C000	1	0	;
/*	087643BF	*/	00C000	0	1	;
/*	08763948	*/	00C000	0	1	;
/*	087643C1	*/	00C000	1	0	;
/*	08763946	*/	00C000	1	0	;
/*	08763943	*/	00C00C	0	1	;
/*	08763952	*/	00C000	0	1	;
/*	0876392B	*/	00C000	0	1	;
/*	087643C2	*/	00C000	1	0	;
/*	0876392E	*/	00C000	1	0	;
/*	087643C3	*/	00D000	1	0	;
/*	08764731	*/	00D000	0	1	;
/*	087643A2	*/	00C000	1	0	;
/*	08764735	*/	00C000	1	0	;
/*	08764720	*/	00C000	1	0	;
/*	087643BC	*/	00C000	1	0	;
/*	0876394A	*/	00C000	1	0	;
/*	08763930	*/	00C000	1	0	;
/*	08763930	*/	00C00C	1	0	;
/*	0876393B	*/	00C00C	0	1	;
/*	0876396B	*/	00C000	0	1	;
/*	08764731	*/	00D000	0	1	;
/*	08763946	*/	00D000	0	1	;
/*	0876393C	*/	00D000	0	1	;
/*	0876395B	*/	00D00D	1	0	;

Table A.2. Minimum, mean, median, and maximum percent slope values at all stream reaches that contained brook trout (BKT) and Bonneville cutthroat trout (BCT) during patch occupancy sampling.

Stream Name	Minimum % Slope	Mean % Slope	Median % Slope	Maximum % Slope	Species
Deadman Creek	0.013	0.028	0.027	0.060	BKT
Mill Creek	0.002	0.017	0.016	0.046	BKT
Carter Creek	0.029	0.051	0.047	0.092	BCT
Christmas Tree Creek	0.022	0.039	0.034	0.089	BCT
Deadman Creek	0.013	0.030	0.027	0.064	BCT
McKenzie Creek	0.025	0.047	0.049	0.083	BCT
Mill Creek	0.023	0.023	0.018	0.060	BCT
North Fork	0.005	0.054	0.056	0.101	BCT
Unnamed Tributary 1	0.027	0.057	0.048	0.099	BCT

Table A3. Water chemistry measurements collected along the longitudinal gradient of Mill Creek, North Fork, Deadman Creek, McKenzie Creek, and Carter Creek.

Stream Location	Turbidity	Conductivity (ms/cm3)	Conductivity (ms/cm)	Salinity	pH	TDS
Mill Creek High	0.38	279	209	0.13	8.6	181
Mill Creek Middle	1.55	308	235	0.15	7.51	200
Mill Creek Low	1.19	286	274	0.14	8.72	0.186
North Fork High	0.99	33	24	0.01	7.51	0.021
North Fork Middle	0.8	60	48	0.04	7.89	0.4
North Fork Low	2.53	60	60	40	6.84	0.035
Deadman High	0.33	427	344	0.21	8.52	0.277
Deadman Middle	1.49	437	350	0.21	8.65	14.45
Deadman Low	3.03	423	336	0.2	8.43	0.275
McKenzie High	1.56	309	226	0.1	7.96	0.058
McKenzie Middle	1.58	68	54	0.02	8.18	0.034
McKenzie Low	0.44	77	64	0.1	6.86	122.3
Carter Creek High	4.3	329	281	0.16	7.73	0.214
Carter Creek Middle	1.71	325	278	0.16	7.81	211
Carter Creek Low	1.58	332	280	0.16	7.83	0.216

Table A4. Nutrient concentrations collected at all ten index sites during August, 2006 and 2007, measured in parts per billion.

Index Site	Year	Ammonia	Nitrates-Nitrites	Soluble Reactive Phosphorous	Dissolved Phospohorous	Total Phosphorous	Total Keljdal Nitrogen	Total Nitrogen
Deadman Creek High	2006	3	8	1	7	8	192	200
Deadman Creek Low		2	1	1	7	11	181	182
Deadman Creek Middle		2	6	1	7	10	71	77
Mill Creek Creek Border		2	2	1	8	8	146	148
Mill Creek Creek High		3	279	2	10	17	211	490
Mill Creek Creek Low		6	51	1	5	10	206	257
Mill Creek Creek Middle		2	223	2	8	18	206	429
North Fork High		88	128	8	11	17	105	233
North Fork Low		2	22	1	6	7	128	150
North Fork Middle		5	43	1	8	11	114	157
Deadman Creek High	2007	2	7	1	8	11	181	188
Deadman Creek Low		2	2	1	9	16	237	239
Deadman Creek Middle		2	8	1	14	17	277	285
Mill Creek Creek Border		4	3	2	9	12	239	242
Mill Creek Creek High		11	179	3	7	14	233	412
Mill Creek Creek Low		3	11	2	7	13	298	309
Mill Creek Creek Middle		11	150	3	8	18	195	345
North Fork High		2	75	2	6	11	100	175
North Fork Low		2	8	2	6	11	143	151
North Fork Middle		3	7	2	7	10	121	128

Table A.5. Minimum, mean, median, and maximum yearly water temperatures collected at all ten index sites during 2006 and 2007.

Index Site	Year	Min. Temp.	Mean Temp.	Median Temp.	Max. Temp
Deadman High	2006	-0.07	3.08	0.57	18.56
Deadman Low		-0.41	3.61	0.07	23.30
Deadman Middle		0.45	2.87	1	18.65
Mill Creek Border		-0.10	2.90	0.06	21.81
Mill Creek High		-0.05	2.07	0.43	15.86
Mill Creek Low		-0.56	2.41	0.07	19.33
Mill Creek Middle		-0.12	2.42	0.45	19.03
North Fork High		*	*	*	*
North Fork Low		-0.67	1.89	-0.09	18.54
North Fork Middle		-0.33	1.87	0.17	16.22
Deadman High	2007	*	*	*	*
Deadman Low		*	*	*	*
Deadman Middle		-0.10	2.89	0.34	14.90
Mill Creek Border		0.06	3.74	0.19	26.33
Mill Creek High		0.01	2.13	0.45	16.71
Mill Creek Low		-0.10	3.14	0.01	23.10
Mill Creek Middle		-0.10	2.51	0.23	18.05
North Fork High		*	*	*	*
North Fork Low		-0.10	1.87	-0.10	19.85
North Fork Middle		-0.22	1.86	0.13	17.14

* Measurements not collected

Table A.6. Substrate characteristics collected at all ten index sites during 2006 and 2007.

Index Site	Year	Sample period	Percent Fines	D16	D50	D64	D84	D90
Deadman High	2006	July	15	4	17	27	50	62
Deadman Low			74	4	4	4	33	54
Deadman Middle			36	4	26	42	78	93
Mill Creek Border			5	24	56	70	90	110
Mill Creek High			6	15	53	71	170	237
Mill Creek Low			11	28	59	79	137	176
Mill Creek Middle			3	45	131	155	205	260
North Fork High			2	25	55	76	180	252
North Fork Low			1	43	86	137	200	240
North Fork Middle			6	35	85	111	203	271
Deadman High		August	34	4	23	29	62	81
Deadman Low			74	4	4	4	25	41
Deadman Middle			34	4	18	35	61	84
Mill Creek Border			8	33	50	63	97	127
Mill Creek High			0	33	54	68	113	145
Mill Creek Low			7	34	57	67	84	97
Mill Creek Middle			1	34	67	85	120	150
North Fork High			2	25	47	59	100	196
North Fork Low			3	36	60	76	127	155
North Fork Middle			8	30	55	71	125	158
Deadman High	2007	July	28	4	17	26	57	82
Deadman Low			80	4	4	4	31	64
Deadman Middle			47	4	4	15	83	137
Mill Creek Border			0	35	63	80	146	165
Mill Creek High			0	31	69	125	230	281
Mill Creek Low			6	42	76	91	148	175
Mill Creek Middle			0	71	148	185	247	279
North Fork High			2	24	68	87	166	228
North Fork Low			1	48	82	105	180	211
North Fork Middle			3	52	104	137	179	219
Deadman High		August	20	4	25	35	59	83
Deadman Low			81	4	4	4	14	47
Deadman Middle			47	4	7	24	82	114
Mill Creek Border			1	35	60	71	91	114
Mill Creek High			4	26	69	90	163	180
Mill Creek Low			3	61	104	127	175	216
Mill Creek Middle			0	52	115	142	181	225
North Fork High			1	30	71	105	185	223
North Fork Low			0	63	110	142	205	247
North Fork Middle			2	51	109	144	202	242

Table A.7. Stream discharge measurements collected at all ten index sites during 2006 and 2007.

Index Site	Year	Sample Period	Discharge (m3/s)
Deadman High	2006	July	*
Deadman Low			0.0030
Deadman Middle			*
Mill Creek Border			0.7392
Mill Creek High			0.0477
Mill Creek Low			0.263
Mill Creek Middle			0.4751
North Fork High			0.0005
North Fork Low			0.0157
North Fork Middle			0.0066
Deadman High		August	*
Deadman Low			0.0025
Deadman Middle			*
Mill Creek Border			*
Mill Creek High			0.0355
Mill Creek Low			0.0862
Mill Creek Middle			0.0861
North Fork High			0.0021
North Fork Low			0.0047
North Fork Middle			*
Deadman High	2007	July	0.0012
Deadman Low			0.0106
Deadman Middle			0.0027
Mill Creek Border			0.1000
Mill Creek High			0.1011
Mill Creek Low			0.1000
Mill Creek Middle			0.0887
North Fork High			0.0063
North Fork Low			0.0125
North Fork Middle			0.0065
Deadman High		August	0.0039
Deadman Low			0.0097
Deadman Middle			0.0035
Mill Creek Border			0.1293
Mill Creek High			0.0391
Mill Creek Low			0.1200
Mill Creek Middle			0.0657
North Fork High			0.0125
North Fork Low			0.0067
North Fork Middle			0.0046

* Measurement not collected

Table A.8. Percent stream slope values measured at all ten index sites.

Index Site	Percent Slope
Deadman High	0.040
Deadman Low	0.003
Deadman Middle	0.032
Mill Creek Border	0.013
Mill Creek High	0.053
Mill Creek Low	0.023
Mill Creek Middle	0.032
North Fork High	0.069
North Fork Low	0.056
North Fork Middle	0.058

Table A9. Number of organizational taxonomic units, Shannon's diversity index, Simpson's diversity index, and Hill evenness calculated from all qualitative and semi-quantitative invertebrate samples at all ten index sites during 2006.

Index Site	Sampling Period	Organizational Taxonomic Units	Shannon's Diversity Index	Simpson's Diversity Index	Hill Evennes	Total Invert. Abundance	EPT Taxa Abundance
Deadman High	July	31	2.649	0.113	0.599	563	406
Deadman Low		46	2.921	0.080	0.655	486	37
Deadman Middle		30	1.432	0.458	0.371	373	197
Mill Creek Border		22	2.308	0.160	0.579	495	359
Mill Creek High		27	2.407	0.150	0.561	370	303
Mill Creek Low		28	2.362	0.146	0.609	515	376
Mill Creek Middle		33	1.970	0.271	0.436	524	317
North Fork High		29	2.406	0.140	0.608	483	387
North Fork Low		34	2.463	0.131	0.618	427	239
North Fork Middle		29	2.740	0.084	0.755	469	373
Deadman High	August	32	2.660	0.096	0.707	423	198
Deadman Low		41	2.635	0.101	0.684	397	21
Deadman Middle		49	2.655	0.138	0.470	367	253
Mill Creek Border		29	2.124	0.221	0.479	483	404
Mill Creek High		34	2.408	0.135	0.632	528	398
Mill Creek Low		29	2.061	0.234	0.478	452	325
Mill Creek Middle		15	1.840	0.209	0.716	491	413
North Fork High		33	2.477	0.131	0.607	523	395
North Fork Low		25	1.989	0.262	0.446	364	241
North Fork Middle		35	2.705	0.115	0.554	465	390

Table A.10. Conductivity, pH, and turbidity measurements at all ten index sites during 2006 and 2007.

Location	Year	Conductivity (μ/cm)	pH	Turbidity (NTU)
Deadman Creek High	2006	101	8.34	0.53
Deadman Creek Low		447	8.32	1.95
Deadman Creek Middle		443	8.23	2.10
Mill Creek Border		309	8.36	1.49
Mill Creek High		258	8.53	1.13
Mill Creek Low		263	8.42	1.13
Mill Creek Middle		289	8.35	1.27
North Fork High		21	7.19	2.16
North Fork Low		45	7.70	2.22
North Fork Middle		38	7.47	2.26
Deadman Creek High		412	8.35	0.68
Deadman Creek Low		415	8.37	1.43
Deadman Creek Middle		428	8.35	2.82
Mill Creek Border		293	8.41	0.15
Mill Creek High		301	8.38	0.48
Mill Creek Low		261	8.49	0.84
Mill Creek Middle		305	8.34	0.91
North Fork High		39	7.72	0.97
North Fork Low		52	7.87	1.29
North Fork Middle		46	7.75	2.16
Deadman Creek High	2007	341	8.32	0.72
Deadman Creek Low		348	8.44	1.43
Deadman Creek Middle		364	8.41	1.58
Mill Creek Border		225	8.13	0.37
Mill Creek High		197	7.62	0.74
Mill Creek Low		192	7.94	1.66
Mill Creek Middle		218	8.73	0.27
North Fork High		47	8.07	1.37
North Fork Low		36	6.85	1.51
North Fork Middle		57	7.72	1.08
Deadman Creek High		318	7.37	1.00
Deadman Creek Low		329	7.42	3.02
Deadman Creek Middle		321	7.39	2.86
Mill Creek Border		260	7.38	1.50
Mill Creek High		213	8.41	0.79
Mill Creek Low		222	7.38	1.15
Mill Creek Middle		245	8.48	1.50
North Fork High		14	7.47	1.88
North Fork Low		52	7.46	2.50
North Fork Middle		40	7.49	0.48

APPENDIX B

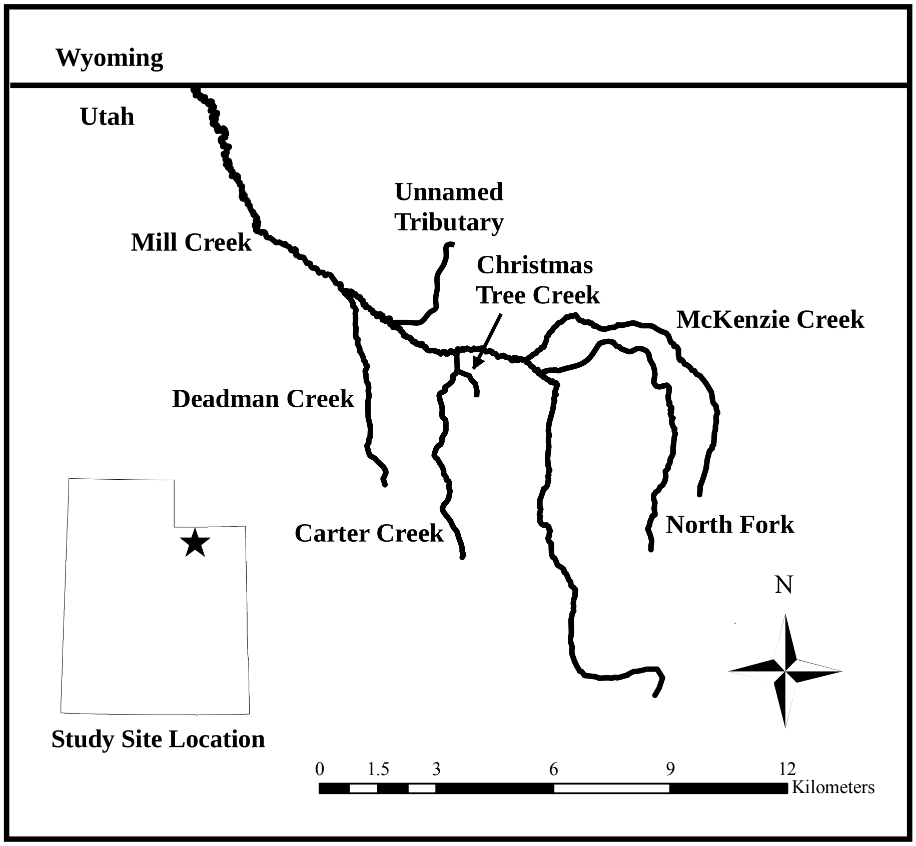

Figure B.1. Map of the Mill Creek watershed located in northern Utah.

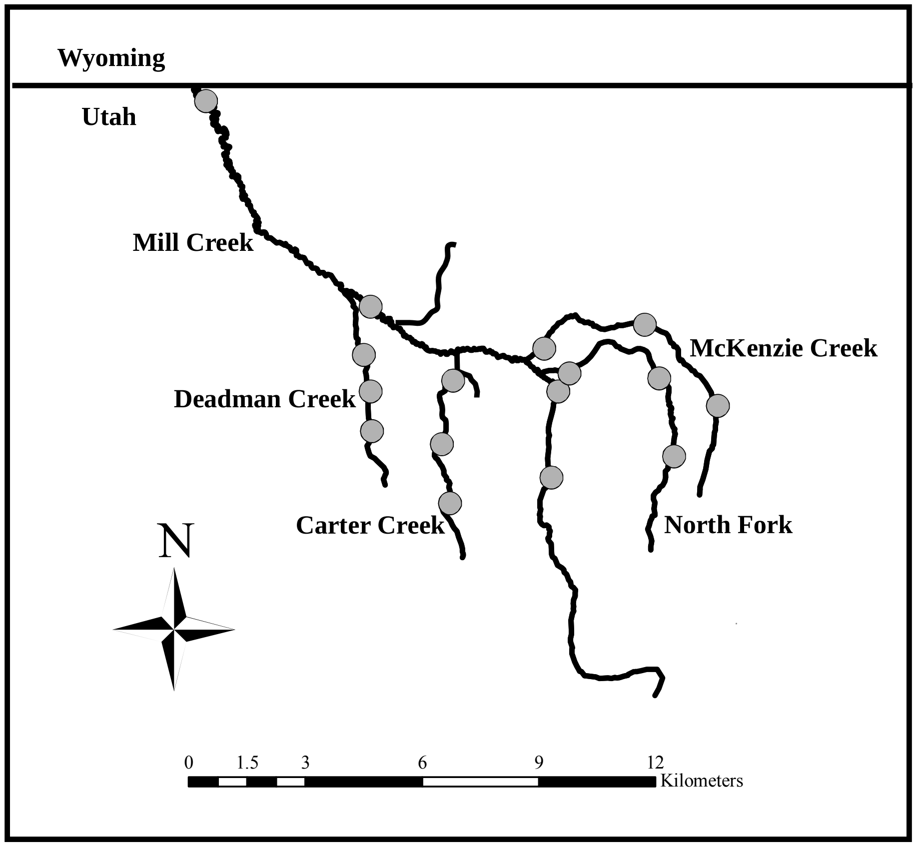

Figure B.2. Map of the Mill Creek watershed, with watershed-scale water chemistry sampling locations marked by shaded circles.

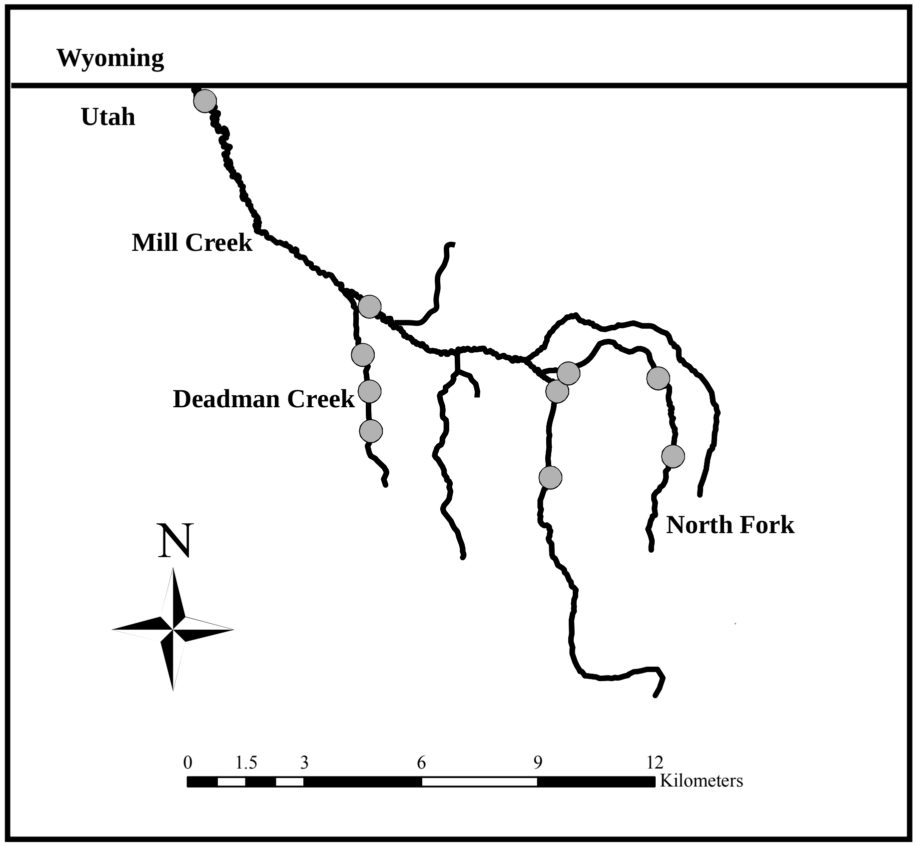

Figure B.3. Map of the Mill Creek watershed with the locations of ten permanent index sites marked by shaded circles.

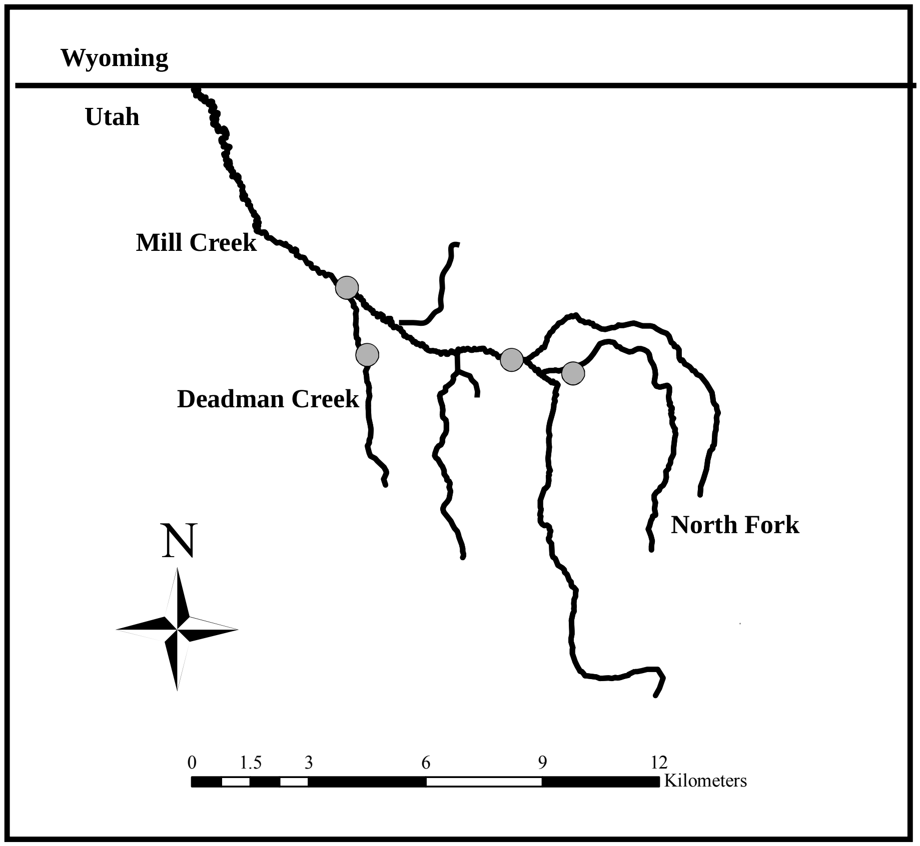

Figure B.4. Map of the Mill Creek watershed with two-way weir trap locations marked by shaded circles.

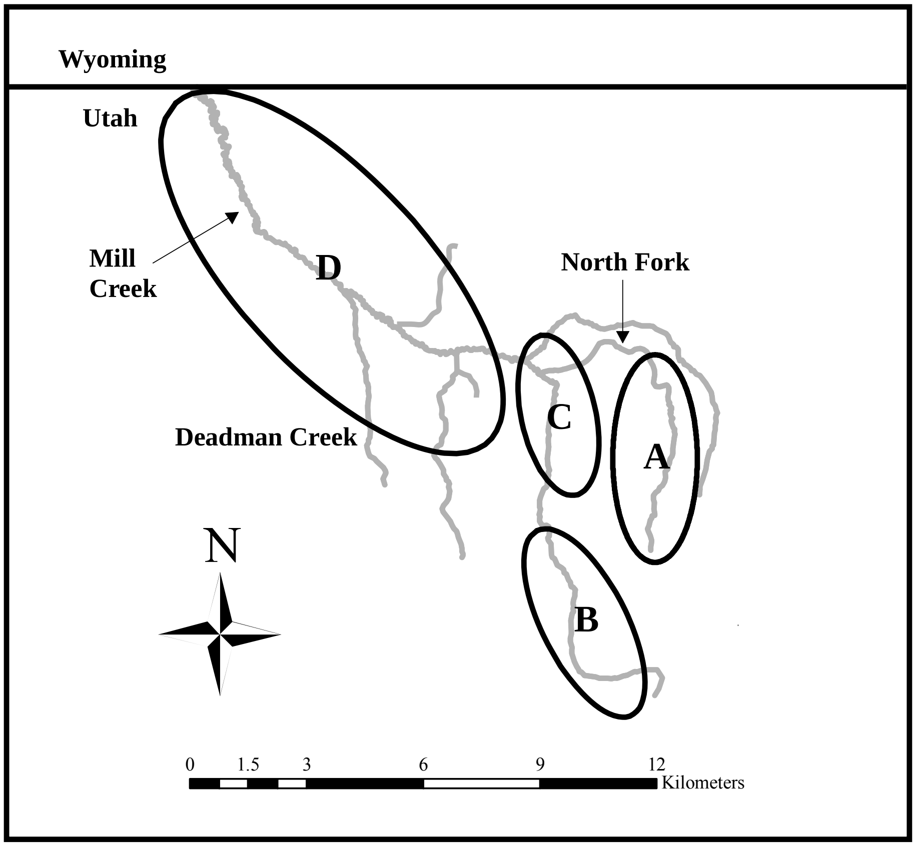

Figure B.5. Map of the Mill Creek watershed with the locations of four mark/recapture stratum marked by ovals. Letters within each stratum indicate the unique stratum identification.

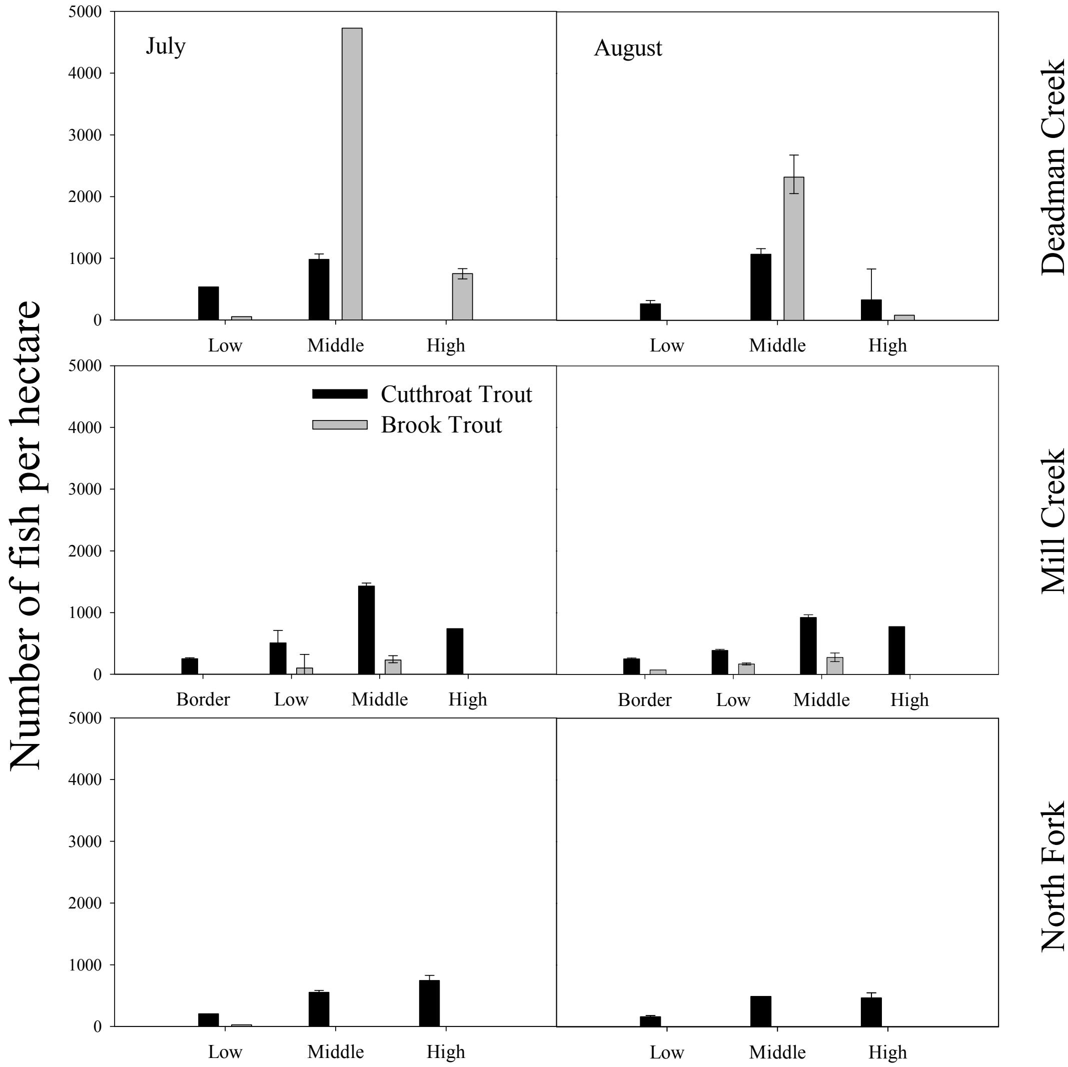

Figure B.6. Brook trout and cutthroat trout abundance (number of fish per hectare) at all ten index sites during July and August, 2006. Error bars represent 95% confidence intervals.

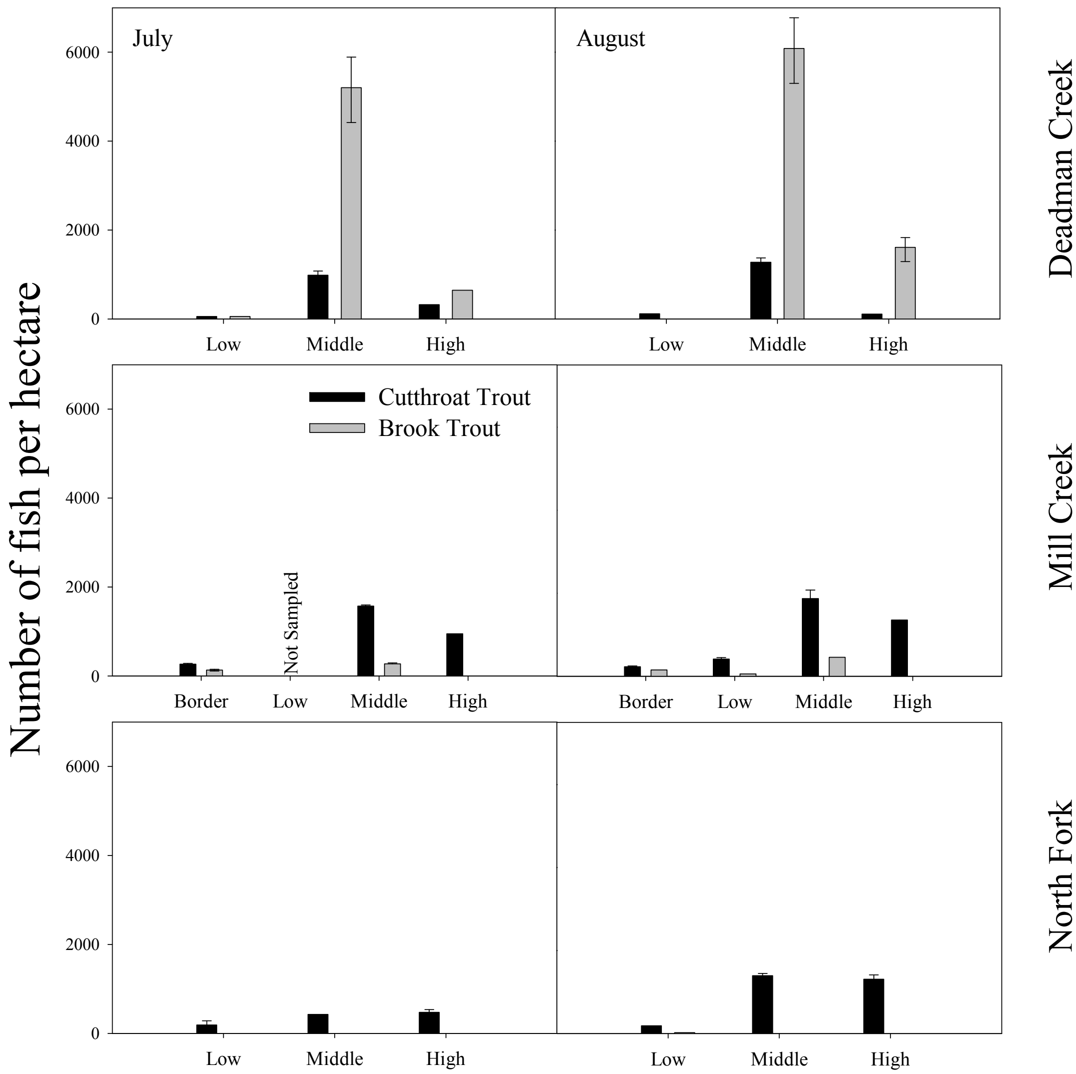

Figure B.7. Brook trout and cutthroat trout abundance (number of fish per hectare) at all ten index sites during July and August, 2007. Error bars represent 95% confidence intervals.