FACTORS INFLUENCING THE DISTRIBUTION OF BULL TROUT AND WESTSLOPE CUTTHROAT TROUT WEST OF THE CONTINENTAL DIVIDE IN GLACIER NATIONAL PARK

By

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A Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Environmental Studies

The University of Montana
Missoula, MT

December 2010

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The reported decline of native bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisi* populations west of the Continental Divide in Glacier National Park (GNP) prompted research to identify critical habitats and investigate factors influencing their distribution and relative abundance. I evaluated the association of six abiotic factors (stream width, elevation, gradient, large woody debris density, pool density, mean August stream temperature) and a biotic factor (the presence of nonnative lake trout, *Salvelinus namaycush*) with the occurrence and density of bull trout and westslope cutthroat trout in 79 stream reaches in five sub-drainages of the North Fork Flathead River in GNP. Logistic and linear regression models were used to quantify the influence of these independent variables on species occurrence (presence/absence) and density (age-1 or older fish/100m^2), and an information theoretic approach (AIC$_c$) was used to determine the most plausible combinations of variables in each case. The occurrence of westslope cutthroat trout was negatively associated with the presence of lake trout and positively associated with large woody debris and water temperature. Westslope cutthroat were detected throughout a wide range of water temperatures (8.5-16^{o}C), stream sizes and elevations, but were most abundant in small, complex streams that were not connected to lakes supporting lake trout. Bull trout occurrence was positively related to stream width and negatively related to channel gradient and water temperature. Bull trout were most abundant in narrow (< 10 m wetted width) streams with relatively cold mean August water temperatures (8 – 10^{o}C) and in stream reaches not affected by lake trout. The low densities and limited distribution of bull trout observed in this study reflect the imperiled status of adfluvial populations in GNP, owing to the invasion and establishment of nonnative lake trout from Flathead Lake. These data may be used to monitor critical habitats and populations, inform conservation and recovery programs, and guide suppression efforts to reduce the deleterious impacts of nonnative invasive fishes.

TABLE OF CONTENTS

Factors Influencing the Distribution of Bull Trout and Westslope Cutthroat Trout West of the Continental Divide in Glacier National Park

LIST OF FIGURES

LIST OF TABLES

GLOSSARY

adfluvial – Residing primarily in lakes but using rivers or streams for spawning. Migrating between lakes and rivers or streams.

admixture – The formation of novel genetic combinations through hybridization of genetically distinct groups.

AIC – Akaike's information criterion (AIC) – Developed by Hirotsugu Akaike (1973). A criterion for selecting among competing econometric models that incorporates sample size, the number of estimated parameters and overall model likelihood to generate the best approximating model(s).

AIC_c – Akaike's information criterion adjusted for small sample sizes, most often used when the ratio of sample size to the number of model parameters is < 40.

critical habitat – An area of habitat required for the conservation of a species listed under the Endangered Species Act.

detection probability – the probability of detecting a species when it is known to be present in a given area, specific detection probabilities will vary depending upon sampling methodology.

diel – Occurring on a 24 hour cycle.

fluvial – In reference to fish life history expression: living in larger rivers but using small streams for spawning. Migrating from rivers to streams.

global model – The model containing all of the variables and associated parameters thought to be important as judged from an a priori consideration of the problem at hand. The global model is often the basis for goodness-of-fit-evaluation.

goodness-of-fit-evaluation – A statistical test assessing the validity of a regression model by comparing observed Y-values with predicted Y-values.

hybridization – Mating between individuals of two genetically distinct populations.

incidence function – In ecology, a mathematical relationship explaining the probability of species occurrence in relation to a set of abiotic and/or biotic factors.

interspecific hybridization – Hybridization between species.

intraspecific hybridization – Hybridization via gene flow among populations of the same species.

introgressive hybridization – the incorporation of genes from one population to another through hybridization that results in fertile offspring that further hybridize and backcross to parental populations.

linear regression model – A statistical model that analyzes the linear relationship between a continuous response variable (Y) and one or more predictor variables (X_i) to describe the amount of variation in Y that can be explained by $\mathrm{X_i}$ and to predict new values of Y from new values of X_i.

logistic regression model – A statistical model that analyzes the relationship between a binary (eg. presence/absence) response variable (Y) and one or more predictor variables (X_i) to determine the probability that Y equals 1 for given values of X_i.

piscivorous – Fish eating.

stream resident – Residing in small streams, non-migratory.

Introduction

Aquatic species face projected extinction rates that exceed those of terrestrial species (Ricciardi and Rasumussen, 1999; Rahel, 2000) and, consistent with this trend, many native salmonid species in western North America have experienced range-wide declines over the last 150 years due to habitat fragmentation and degradation, competition with nonnative species, and climate change (Behnke, 2002; Moyle and Marchetti, 2006; Williams et al., 2009). Identifying the factors governing the distribution and abundance of declining salmonid species has become increasingly important and is necessary for the development of informed conservation and management programs.

In response to these challenges, research has assessed the influence of biotic and abiotic factors affecting the occurrence and abundance of increasingly rare native salmonids in stream networks (e.g. Bozek and Hubert, 1992; Rieman and McIntyre, 1995; Horan et al., 2000; Paul and Post, 2001; Young and Guenther-Gloss, 2004; Rieman et al., 2006; Muhlfeld et al., 2009a). These studies have often focused on threatened species, like the greenback cutthroat trout *Oncorhynchus clarkii stomias* (Young and Guenther-Gloss, 2004) and bull trout *Salvelinus confluentus* (Rieman and McIntyre, 1995), and have used incidence functions to develop predictive models of species occurrence (Paul and Post, 1991; Bozek and Hubert, 1992), investigate factors influencing detection probability (Bayley and Peterson, 2001; Peterson et al., 2002), and analyze nonnative species invasions (Hitt et al., 2003; Benjamin et al., 2007; Muhlfeld, 2009a).

The upper Flathead watershed has long been recognized as a regional and range-wide stronghold for native bull trout and westslope cutthroat trout *O. c. lewisi* populations (Liknes and Graham, 1988; Rieman et al., 1997; Fraley and Shepard, 2005; Shepard et al., 2005; Hauer and Muhlfeld, 2010). The rivers, lakes and streams of this largely pristine landscape provide cold, clean water, and silt-free streambeds necessary to support robust populations of these native species. However, despite the refugia provided by these diverse and connected habitats, threats to the long-term persistence of both species exist in this ecologically unique region.

Introgressive hybridization with introduced rainbow trout *O. mykiss* has contributed to the decline of all 14 cutthroat trout subspecies in western North America (Gresswell, 1988; Young, 1995; Trotter, 2008) and is the greatest threat to the persistence of westslope cutthroat trout (Allendorf and Leary, 1988; Allendorf et al., 2004; Shepard et al., 2005; Muhlfeld et al., 2009b). Interspecific hybridization may cause outbreeding depression in wild populations (Muhlfeld et al., 2009b) due to the break-up of co-adapted gene complexes and disruption of local adaptations (Rhymer and Simberloff, 1996; Epifanio and Philipp, 2001). Recent studies have documented the upstream spread of hybridization from downstream source populations in the lower Flathead River system to historic westslope cutthroat trout spawning tributaries in Glacier National Park (GNP; Hitt et al., 2003; Boyer et al., 2008; Muhlfeld et al., 2009c). Barriers to fish migration may be the only abiotic factor inhibiting the spread of hybridization and this threat will likely persist as long as hybrid source populations remain connected to non-hybridized westslope cutthroat trout strongholds.

Bull trout were listed as a threatened species under the U.S. Endangered Species Act (ESA) in 1998 (U.S. Fish and Wildlife Service, 1998) in response to widespread declines throughout their native range in the western United States. Habitat fragmentation and degradation (Fraley and Shepard, 1989; Rieman and McIntyre, 1995; Rieman et al., 1997), altered stream temperature regimes (Dunham et al., 2003), and competition with introduced species (Donald and Alger, 1993; Fredenberg, 2002) have all contributed to reductions in bull trout distribution, abundance, and genetic diversity. Bull trout populations in the upper Flathead watershed have been severely impacted by the establishment of nonnative lake trout *S. namaycush* in Flathead Lake and the subsequent invasion of numerous lakes in GNP (Fredenberg, 2002). Since their initial introduction to Flathead Lake in 1905, lake trout have radiated throughout the system; of the 17 lakes west of the Continental Divide in GNP that historically supported bull trout, nine have been compromised by lake trout, two remain vulnerable to invasion and just five are secure due to isolation by downstream barriers (Fredenberg, 2002; Fredenberg et al., 2007; Meeuwig et al., 2008). Ongoing gill netting surveys in these lakes and annual redd counts in associated spawning streams have documented dramatic declines in bull trout abundance in GNP (Fredenberg et al., 2007; Meeuwig et al., 2008; C. Downs, GNP, unpublished data).

The challenges faced by native fishes in western GNP underscore the importance of identifying critical habitat and current distributions. Although native species assemblages in western GNP lakes have been monitored by repeated gill netting surveys (Fredenberg, 2002; Meeuwig et al., 2008; C. Downs, GNP, unpublished data) and some studies have investigated fish distributions (Dux and Guy, 2004) and genetic status (Hitt et al., 2003; Muhlfeld et al., 2009a,b) in western GNP streams, no studies have systematically evaluated the factors influencing the distribution and abundance of westslope cutthroat trout and bull trout in these stream networks.

Therefore, I developed three primary objectives to fill this critical knowledge gap. First, I sought to determine westslope cutthroat trout and bull trout distributions in streams within five sub-drainages of the North Fork Flathead watershed in GNP that are used for spawning and rearing. Second, I evaluated the association of six abiotic factors (stream width, elevation, gradient, large woody debris density (LWD), pool density, mean August stream temperature) and a biotic factor (the presence of nonnative lake trout) with the occurrence and density of bull trout and westslope cutthroat trout using logistic and linear regression modeling techniques. Finally, I analyzed differences in habitat characteristics and fish densities among sub-drainages to examine variability at a larger scale. These data will help managers monitor and protect critical habitats and populations, inform conservation and recovery programs, and enhance nonnative species suppression/eradication efforts essential to the persistence of native salmonid populations in western GNP.

Methods

Study Area

The 621 km^2 study area included 19 first to fourth order streams in the Kintla (132 km^2), Akokala (106 km^2), Bowman (146 km^2), Quartz (136 km^2) and Logging (101 km^2) sub-drainages of the North Fork Flathead watershed in northwestern GNP (Figure 1). Streams in the Kintla (cumulative perennial stream length, 40.4 km), Bowman (64.5 km), Logging (53.4 km) and Quartz (67.1 km) sub-drainages begin in the Livingston Range (2,500-3,000 m) and descend quickly through narrow, glaciated valleys punctuated by numerous cirque and moraine lakes, most of which support populations of bull trout and westslope cutthroat trout (Marnell, 1988; Meeuwig et al., 2008). Total lake areas in these sub-drainages range from 476 ha (Quartz) to 898 ha (Kintla). The Akokala sub-drainage largely consists of stream habitat (60.1 km), including Akokala, Parke and Long Bow creeks. Akokala Lake, a small (lake area, 9.5 ha) and shallow (max depth, 7.0 m) lake located at the head of the sub-drainage, supports bull trout and westslope cutthroat trout populations (Marnell, 1988; Fredenberg et al., 2007).

The hydrologic regime is primarily driven by snowmelt, with peak runoff occurring in May or June (Baxter and Hauer, 2000). Streams are cold (mean August temperatures ~ 11.5 ^{o}C) and low in nutrient concentrations and suspended particulates (Baxter and Hauer, 2000). Cobble (7.5-30 cm maximum width) and large gravel (0.6-7.5 cm) substrates are prevalent, but boulders (>30 cm) and bedrock are common in higher gradient (>10%) reaches. Aggregates of LWD frequently occur within stream channels, especially in narrow (<5.0 m average wetted width) reaches in burned areas.

Bull trout express an adfluvial life history in the study area; they spawn and rear in small streams and spend the bulk of their adult lives in lakes (Fredenberg et al., 2007). Nine lakes (Kintla, Upper Kintla, Akokala, Bowman, Lower Quartz, Middle Quartz, Quartz, Cerulean, and Logging) in the study area support bull trout populations (Meeuwig et al., 2008), but only Upper Kintla, Cerulean, and Akokala have not been invaded by lake trout (Fredenberg et al., 2007). Spawning generally occurs in the uppermost stream reaches of each sub-drainage unless barriers prevent fish dispersal to such areas (C. Downs, GNP, unpublished data).

Bull trout exhibit a high degree of genetic diversity among populations, even those separated by relatively short geographic distances (Leary et al., 1993; Meeuwig et al., 2010). Early research showed that local bull trout populations in the study area are genetically distinct from migratory bull trout populations in the wider Flathead watershed (Leary et al., 1993), and recent genetic studies have shown substantial genetic differences among bull trout populations within GNP (Meeuwig et al., 2010).

Westslope cutthroat trout populations in the study area primarily display adfluvial life histories, although fluvial and stream resident life histories are also expressed (Read et al., 1982; Shepard et al., 1984; Marnell, 1988; Fraley and Shepard, 1989). Indigenous populations exist in eight lakes (Kintla, Akokala, Bowman, Lower Quartz, Middle Quartz, Quartz, Cerulean, and Logging) and westslope cutthroat trout are believed to occupy the majority of accessible stream habitat in the study area (Read et al., 1982; Marnell, 1988; Meeuwig et al., 2008). Stream resident forms have been observed in the Akokala and Quartz sub-drainages (Read et al., 1982). The majority of westslope cutthroat trout populations in the study area are non-hybridized, with a few that contain less than 10% rainbow trout admixture (Hitt et al. 2003; Shepard et al., 2005; Boyer et al. 2008; C. Muhlfeld, USGS, unpublished data); westslope cutthroat x rainbow trout hybrids have been detected in the lower portion of Akokala Creek (Muhlfeld et al., 2009c) and Logging Creek downstream of Logging Lake (Hitt et al., 2003). The spread of introgressive hybridization from sources on the mainstem Flathead River remains a major concern and may not be limited by environmental factors (Hitt et al., 2003; Muhlfeld et al., 2009a).

Other native fish species in the study area include mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coutleri*, longnose sucker *Catostomus catostomus*, large scale sucker *Catostomus macrocheilus,* and slimy sculpin *Cottus cognatus* (Fredenberg, 2002). Native cyprinid species, such as northern pike minnow

Ptychocheilus oregonensis, peamouth *Myocheilus caurinus,* and redside shiner *Richardsonius balteatus*, are uncommon in western GNP lakes (Fredenberg, 2002).

From the early 1900s through the 1950s, several nonnative salmonid species were stocked in GNP lakes and streams by the National Park Service (NPS) (Morton, 1968; Fredenberg et al., 2007). Remnant populations of stocked kokanee salmon *O. nerka* exist in Kintla, Bowman and Logging Lakes (Fredenberg, 2002; Meeuwig et al., 2008). Chinook salmon *O. tshawytscha* and steelhead *O. m. irideus* were sporadically stocked in western GNP in the early 1900s, but did not become established (Morton, 1968; Fredenberg et al., 2007). Brook trout *S. fontinalis* occur in several lakes and in tributaries to the Middle Fork Flathead River (Fredenberg et al., 2007; Meeuwig et al., 2008). Records also document the stocking of "black spotted trout" and "cutthroat trout" (Morton, 1968). The majority of these fish were likely Yellowstone cutthroat trout *O. c. bouvieri,* which became established in Grace Lake, a small lake (lake area, 33 ha) in the upper Logging sub-drainage that is isolated by a natural barrier falls on Logging Creek. Six lakes (Kintla, Bowman, Lower Quartz, Middle Quartz, Quartz, and Logging lakes) within the study area have been colonized by lake trout that likely dispersed from Flathead Lake (Fredenberg, 2002; Fredenberg et al., 2007; Meeuwig et al., 2008).

<u>Sampling Design and Dependent Variables</u>

Fish and habitat data were collected at 79 stream reaches throughout the five sub-drainages. Reaches were distributed longitudinally along streams to include the full extent of habitat variability within and among streams (Figure 1). Most reaches were located on sub-drainage mainstems (e.g., Quartz Creek) but tributaries were sampled as logistics allowed. Sampling occurred at or near base flow discharges (July-September) in 2008 and 2009.

The occurrence (presence or absence) and density (fish/100m^2) of bull trout and westslope cutthroat trout were the dependent (response) variables. The capture and positive identification of a bull trout or westslope cutthroat trout qualified as presence for each species at a given sample reach. Fish densities were calculated for each species in each reach as a function of sample reach area (reach length (m) x average stream width (m)) and were standardized (fish/100m^2) to account for variation in reach area. Based on previous length frequency data for Flathead watershed tributaries, westslope cutthroat trout less than 55 mm in total length (TL) and bull trout less than 60 mm were considered young-of-the-year (YOY) individuals (Fraley and Shepard, 1989; Fraley and Shepard, 2005). Due to poor sampling efficiency and differing emergence times among streams, YOY fish were not included in density calculations (Muhlfeld et al., 2009a).

Fish sampling was conducted during daylight hours using single-pass electrofishing with one or two backpack electrofishing units (Smith-Root Model L-24). Electrofishing was performed moving upstream and in a manner designed to draw fish out of optimum habitat. Adjustments to electrofisher settings were made in response to stream conditions (i.e., temperature and conductivity) and fish behavior. The bounds of the sample reaches were defined by a pool at the downstream limit and a natural habitat break (riffle, substrate, or LWD aggregate) on the upstream end (Rieman et al., 2006). Reaches were at least 50 m in length and extended to a maximum of 150 m to include a minimum of two pools. Pools were defined as low velocity areas spanning at least half the channel width and were assumed to be preferable habitat for westslope cutthroat trout and bull trout (Rieman et al., 2006).

The TL (mm) for each captured fish was recorded and all individuals were identified to species. Previous research (Marnell et al., 1987; Hitt et al., 2003; Boyer et al., 2008; Muhlfeld et al., 2009a) confirmed the presence of westslope cutthroat trout x rainbow trout and westslope cutthroat x Yellowstone cutthroat trout hybrids in some lakes and lower elevation stream reaches within the study area and technicians attempted to identify these individuals using morphological characteristics. Only fish suspected to be non-hybridized were classified as westslope cutthroat trout and hybrids were not included in occurrence and density analyses.

Independent Variables

Six abiotic factors were estimated in each sample reach: gradient (%), stream width (m), elevation (m), pool density (pools/100m^2), LWD density, and August mean temperature (^{o}C) (Table 1). Channel gradient (%) was obtained by averaging two measurements (upstream and downstream) taken with a handheld clinometer. Stream width (m) was the average of at least five wetted stream width measurements taken every 10 m with a handheld tape measure. Elevation (m) was determined from topographic maps within ArcGIS 9.3 (ESRI, Redlands, CA). Pools were enumerated and pool density was calculated (pools/100m^2). Woody material within the wetted channel width that was at least 10 cm in diameter and at least 3 m in length was considered LWD. Large woody debris was counted for the entire length of each reach and a standardized density was calculated (LWD/100m^2). Twenty-four HOBO U22 temp pro v2 thermographs were deployed in selected reaches and recorded hourly water temperatures during August 2008

(Figure 2). A predictive temperature model (see below) was generated from these data to estimate August mean temperature for each reach (Figure 3). Finally, a biotic component was included to represent the influence of nonnative lake trout in the study area. A binary (0 or 1) dummy variable for “lake trout presence/absence” was assigned to each fish sampling reach. The lake trout effect was “present” for 41 stream reaches that were connected to lakes inhabited by lake trout populations (Quartz, Middle Quartz, Lower Quartz, Kintla, Bowman, Logging) and “absent” for 38 reaches that were connected to lakes that did not support lake trout populations (Cerulean, Akokala, Upper Kintla, and Grace lakes) (Fredenberg et al., 2007; Meeuwig et al., 2008).

Statistical Analysis

SYSTAT 12 (SYSTAT Inc., Chicago, IL) was used for all statistical analyses. August mean stream temperatures were estimated for each reach using a predictive model based on empirical temperature data recorded throughout the study area in 2008 (Figure 3). The August mean temperature (average of all hourly measurements in August) was calculated for each of 24 thermographs, and stepwise multiple linear regression was used to explain the variation in stream temperatures using three predictor variables: site elevation (m), gradient (%; estimated from ArcGIS 9.3), and lake influence. To capture the influence of lakes on downstream temperature regimes, each thermograph site was placed in one of three “lake effect categories” based on upstream lake area estimates obtained from ArcGIS 9.3: high (>100 ha), moderate (5-100 ha), and low (<5 ha). Only lakes below 2,000 m in elevation were included to avoid including frozen lakes in high elevations. All three variables were included in both forward and backward regression procedures. The final stepwise model included elevation and lake effect (Figure 3).

Mann-Whitney *U* tests ($\alpha = 0.05$) were used to test for differences in habitat characteristics between reaches in which westslope cutthroat trout and bull trout were present or absent. While other studies have used similar tests to eliminate non-significant variables (Kruse et al., 1997; Rich et al., 2003), we chose to use these tests to explore the data prior to linear and logistic regression model construction. Multiple logistic and linear regression models were generated independently for westslope cutthroat trout and bull trout to evaluate the influence of the independent variables on species occurrence and density, respectively. Logistic regression models included data from all sample reaches ($N = 79$), whereas linear regression models only included data from reaches where age-1 or older westslope cutthroat trout (TL ≥ 55 mm, $N = 43$ reaches) or bull trout (TL ≥ 60 mm, $N = 10$ reaches) were captured.

Initially, all predictor variables were included in global models and regression assumptions were validated using normal probability plots and residual analyses. Hosmer and Lemeshow tests were performed on global logistic regression models to ensure an adequate fit to the data (Quinn and Keough, 2002). Log_{10} transformations were performed on several independent variables (LWD density, stream width, gradient) and fish densities to meet normality and homogeneity of variance assumptions. Global models were then subjected to forward entry and backward removal methods to generate candidate models. Additional variable combinations were developed based on observations from scatterplots and previous research on factors affecting salmonid distributions in stream networks (Rieman and McIntyre, 1995; Horan et al., 2000; Rich et al., 2003; Rieman et al., 2006). Pearson's product-moment correlations among the independent variables were used to ensure that highly correlated variables ($r \geq 0.50$) were not included in the same models (Bozek and Hubert, 1992; Horan et al., 2000). This method was preferable to an exhaustive all subsets approach considering the relatively small sample size (N = 79) (Olden and Jackson, 2000). The relative plausibility of logistic and linear models was determined by Akaike's Information Criterion adjusted for small sample size (AIC_c; Hurvich and Tsai, 1989; Burnham and Anderson, 1998). Models with ΔAIC_c scores within 2.0 of the best model were considered equally plausible (Burnham and Anderson, 2002). The classification cutoff was 0.5 for each logistic model, and all models included a constant and error term.

Results

Fish Distributions and Sub-drainage Habitat Variability

Westslope cutthroat trout (TL range, 32-282 mm) were widely distributed throughout the study area; they were detected in 47 of 79 (59.5%) reaches, 13 of 19 (68.4%) streams, and all five sub-drainages (Figure 4). Westslope cutthroat trout occupied the full range of stream sizes and elevations among sample reaches (Figure 5). In the Akokala sub-drainage, westslope cutthroat trout were widespread (20 of 24 reaches (83.3%), including Akokala, Parke and Long Bow creeks), but not detected upstream of Akokala Lake. Their distribution was limited in the Kintla sub-drainage; westslope cutthroat trout were detected in 3 of 11 reaches (27.2%), but were only found downstream of Kintla Lake. Two waterfall barriers, located approximately 0.5 km upstream of Kintla Lake, likely preclude the presence of the species in the upper Kintla sub-drainage (Fredenberg et al., 2007; Meeuwig et al., 2008). Westslope cutthroat trout were detected throughout the Quartz sub-drainage (12 of 15 reaches (80.0%), including Quartz, Cummings and Rainbow creeks), from lower reaches near the North Fork

Flathead River to upper reaches between Quartz and Cerulean lakes. In the Logging sub-drainage, westslope cutthroat trout were found throughout the length of Logging Creek to a barrier falls upstream of Grace Lake and in two unnamed tributaries to Logging Creek (6 of 16 reaches, 37.5%). Westslope cutthroat trout were found in 6 of 13 reaches (46.2%) in the Bowman sub-drainage, including Bowman and Pocket creeks, but were encountered less frequently upstream of Bowman Lake (1 of 7 reaches, 14.3%). When all reaches were considered, westslope cutthroat trout were detected in significantly (P = 0.003) warmer reaches as compared to those in which they were not detected (Table 2). No significant differences in LWD density, pool density, stream width, gradient, or elevation were observed among detection and non-detection reaches (Table 2).

When all reaches were considered (N = 79), the average density of westslope cutthroat trout was 1.20 fish ≥ 55mm/100m^2 (range, 0 to 10.33). In the 43 reaches containing fish ≥ 55 mm TL, the average density was 2.20 fish/100m^2 (range, 0.03 to 10.88). Densities of westslope cutthroat trout differed significantly among sub-drainages (Kruskall-Wallis, X^2 = 29.6, P < 0.001), with sub-drainage averages ranging from 0.03 fish/100m^2 in Kintla to 3.19 fish/100m^2 in Akokala (Table 2; Figure 6). Pairwise comparisons revealed that Akokala had significantly higher westslope cutthroat trout densities than all other sub-drainages (Mann-Whitney P-values: Kintla < 0.001; Bowman < 0.001; Quartz = 0.007; Logging < 0.001; Figure 6) and that average densities were significantly lower in Kintla than in Quartz (P = 0.010; Figure 6). In the 43 reaches containing age-1 or older fish, westslope cutthroat trout densities exhibited an inverse relationship with stream width (Figure 7).

Bull trout were detected in 10 of 79 (12.6%) stream reaches, 6 of 19 (31.6%) streams, and 4 of 5 sub-drainages (Figure 8). Only juveniles were captured (TL range, 45–224 mm), but all reaches where bull trout were observed contained fish ≥ 60 mm in TL. In the Bowman sub-drainage, bull trout were detected in 3 of 13 reaches (23.1%); one reach downstream of Bowman Lake and in two reaches in Jefferson Creek, a cold (estimated August mean temperature < 10^{o}C) tributary to Bowman Creek upstream of Bowman Lake. In the Kintla sub-drainage, bull trout were detected in 2 of 11 reaches (18.1%); both were upstream of Upper Kintla Lake (one reach in Kintla Creek and one in Agassiz Creek, a glacier fed stream that drains directly into Upper Kintla Lake) and were upstream of the two waterfall barriers that preclude upstream fish movement. Bull trout were detected in 3 of 24 (12.5%) reaches in the Akokala sub-drainage, including two reaches in Akokala Creek downstream of Akokala Lake and one reach in Akokala Creek upstream of the lake. In the Quartz sub-drainage, bull trout were detected in 2 of 15 reaches (13.3%); one reach in Quartz Creek between Middle Quartz and Quartz lakes and one reach in Quartz Creek between Quartz and Cerulean lakes. Bull trout were not detected in any of the 16 reaches sampled in the Logging sub-drainage.

Average gradient was significantly lower in reaches where bull trout were detected as compared to reaches where they were not detected (Table 3). Reaches where bull trout were detected were also significantly higher in elevation as compared to reaches where bull trout were not detected (Table 3). Throughout the study area, bull trout were not found below 1,250 m in elevation (Figure 9). Reaches where bull trout were detected were colder than reaches where bull trout were not detected, although this difference was not statistically significant (P = 0.058; Table 3). There were no significant differences in average stream width, pool density, or LWD density between detection and non-detection reaches (Table 3).

Bull trout densities were consistently low throughout the study area. Overall, the average bull trout density was 0.03 fish/100m^2 (range, 0.00 to 0.70), and in the 10 reaches where bull trout were detected the average density was 0.25 fish/100m^2 (range, 0.03 to 0.70). Bull trout densities were not significantly different among sub-drainages (Kruskall-Wallis $X^2 = 3.63$, $P < 0.458$), but the two highest densities (0.70 fish/100m^2 and 0.42 fish/100m^2) were observed in Akokala Creek downstream of Akokala Lake. Bull trout and westslope cutthroat trout were detected in sympatry in four reaches; one reach in Bowman Creek downstream of Bowman Lake, two reaches in Akokala Creek downstream of Akokala Lake, and one reach in Quartz Creek between Middle Quartz and Quartz lakes.

Habitat characteristics varied among sub-drainages (Figure 6). Kruskall-Wallis tests indicated that LWD density ($P = 0.041$), stream width ($P = 0.021$), pool density ($P = 0.002$), and elevation ($P = 0.040$) were significantly different among sub-drainages, while gradient ($P = 0.174$) and estimated August mean temperature ($P = 0.130$) were not significantly different among sub-drainages. Pairwise Mann-Whitney U tests indicated that Akokala was the source of variation for several metrics (Figure 6). The Akokala sub-drainage had the highest average LWD density (4.49/100m^2), which was significantly different from the Kintla ($P = 0.003$) and Logging ($P = 0.044$) sub-drainages. Average LWD differences between Akokala and Quartz were nearly significant ($P = 0.058$). Akokala also had the highest pool densities (mean, 1.41/100m^2), significant as compared to Kintla ($P < 0.001$), Bowman ($P < 0.001$), and Quartz sub-drainages ($P = 0.007$).

Average stream width was narrowest (6.1 m) in the Akokala sub-drainage and significantly narrower than the Kintla (P = 0.004), Bowman (P = 0.003), and Quartz (P = 0.012) sub-drainages. On average, Akokala had the lowest predicted August mean temperature (10.0 ^{o}C), and was significantly colder than the Quartz sub-drainage (P = 0.013). The Logging sub-drainage was also a source of variability with the lowest average elevation (1,198 m) and the highest average gradient (6.9 %).

Occurrence and Density Models

Pool density was highly correlated with stream width (r = - 0.674) and LWD density (r = 0.621), and thus eliminated from regression analyses (Table 4). Also, estimated August mean temperature was strongly correlated with stream width (r = 0.715) and elevation (r = - 0.707) (Table 4). Estimated August mean temperature was only included with either of these two variables in global models.

The best approximating westslope cutthroat trout occurrence model contained the abiotic factors of LWD density and estimated August mean temperature and the biotic factor of lake trout presence, with an overall classification accuracy of 75.9 % (Table 5). The occurrence of westslope cutthroat trout was positively associated with LWD density and estimated August mean temperature, and negatively associated with the presence of lake trout (Table 6). The best approximating westslope cutthroat trout density model contained the abiotic factors of gradient, stream width, and the biotic variable of lake trout presence (Table 7). However, an equally plausible model contained the additional abiotic factor of elevation (Table 7). Both of these models had adjusted r-square values greater than 0.65. The density of westslope cutthroat trout was positively associated with gradient and elevation, and negatively associated with stream width and the presence of lake trout (Table 8; Figure 7).

The best approximating bull trout occurrence model contained the abiotic variables gradient, elevation, and stream width (Table 9). Another model containing only gradient and elevation was equally plausible. Both models had overall classification accuracies greater than 87% (Table 9). Bull trout occurrence was negatively associated with gradient and was positively associated with elevation and stream width (Table 10). Linear regression models for bull trout density were handicapped by a very small sample size (10 reaches, 19 total fish). The best approximating bull trout density model included the abiotic factors elevation and stream width ($r^2 = 0.848$; Table 11). Bull trout density was positively associated with elevation and negatively associated with stream width (Table 12).

Discussion

Westslope Cutthroat Trout

Westslope cutthroat trout were detected throughout the full range of measured stream sizes and elevations, but their occurrence was more likely and abundances higher in relatively warm reaches with abundant LWD that were not connected to lakes supporting lake trout populations (Figure 4). These results suggest that complex habitats disassociated from nonnative lake trout populations are critical for the persistence of westslope cutthroat trout in western GNP.

Westslope cutthroat trout exhibit high levels of genetic diversity and variable life histories among populations, suggesting that local adaptations among populations are important for persistence (Allendorf and Leary, 1988). Fortunately, stream networks in

GNP contain high quality habitat, which may serve as refugia from nonnative species invasions and projected climate change threats (Bozek and Hubert, 1992; Rieman and McIntyre, 1993; Paul and Post, 2001; Rieman et al., 2006; Muhlfeld et al., 2009a; Williams et al., 2009). The importance of such areas is likely a function of habitat quality, maintenance of local adaptations to harsh and dynamic environments, and the benefits associated with isolation (by distance or physical barriers) from competitor species (Liknes and Graham, 1988; Muhlfeld et al., 2009a).

The relative importance of these factors differs among remaining watersheds that harbor native species; in some cases separation from nonnative competitors may be more important than occupying reaches with ideal habitat. For example, in a study investigating stream temperature and westslope cutthroat trout growth potential in the Madison River basin, Sloat et al. (2005) observed that although westslope cutthroat trout persist only in the basin's headwater reaches, temperatures most conducive to maximum growth potential occurred more frequently in low elevation areas that were compromised by nonnative competitors, such as rainbow trout and brown trout *Salmo trutta*. In the Greater Yellowstone region, Bozek and Hubert (1992) found that cutthroat trout were more frequently detected in higher gradient reaches; low gradient reaches in lower elevations were more susceptible to invasion by nonnative brook trout and brown trout. In this study, the Akokala sub-drainage was the largest stream network not connected to a local lake trout population and contained abundant complex habitat. Not surprisingly, westslope cutthroat trout densities and detection frequency were highest in this sub-drainage.

Given the common occurrence of westslope cutthroat trout in small, relatively high elevation reaches, the positive relationship between presence and stream temperature appears contradictory. However, it is important to note that this association is probably not indicative of a true preference for “warm” water temperatures. Summer temperatures in most GNP streams are extremely cold (average predicted August mean temperature = 11.2^{o}C) and daily maximum temperatures observed in the study area rarely exceeded upper lethal limits for the species (19.6^{o}C ± 0.5; Bear et al., 2007). Therefore, it is plausible that relatively warm temperatures coincide with increased stream productivity and fish growth potential in GNP streams. Similarly, Young et al. (2005) observed a positive relationship between Colorado River cutthroat trout *O. c. pleuriticus* and greenback cutthroat trout *O. c. stomias* abundance and stream temperature in high elevation streams in Utah and attributed these findings to higher productivity and a potentially larger macroinvertebrate forage base in warmer stream reaches.

Research on the competitive interactions between westslope cutthroat and nonnative lake trout is lacking, but my results suggest that lake trout are negatively impacting the distribution and abundance of westslope cutthroat trout in western GNP. The negative effects of lake trout on westslope cutthroat trout are apparent in the regression model results and in the comparative density and distribution information. Indeed, the highest densities and highest frequency of westslope cutthroat trout occurrence were observed in the Akokala sub-drainage, the only sub-drainage apparently free of lake trout during the time of this study (Fredenberg et al., 2007; Meeuwig et al., 2008).

Declines of adfluvial Yellowstone cutthroat trout in Yellowstone Lake following the establishment of lake trout are well documented and associated declines of returning adults have been observed in important spawning tributaries (Koel et al., 2004). Whether lake trout will similarly impact westslope cutthroat populations in western GNP remains to be seen. Westslope cutthroat trout throughout western GNP are primarily adfluvial, a characteristic that could exacerbate the negative effects of lake trout invasion. However, unlike the Yellowstone subspecies, westslope cutthroat trout in the upper Flathead system co-evolved with bull trout, a highly piscivorous predator, and this component of their evolutionary history may help populations persist in the face of lake trout invasion. Obtaining robust estimates of lake trout population size in study area lakes would provide additional insight into predictions of their effects on native fish assemblages.

Bull Trout

The limited distribution and abundance of bull trout observed in the study area is likely the result of a combination of several biotic and abiotic factors. Most importantly, adfluvial bull trout populations in Bowman, Kintla and Logging lakes were known to be in decline due to competition with lake trout prior to sampling and this undoubtedly affected the frequency bull trout detection in the stream environment (Fredenberg, 2002; Fredenberg et al., 2007; Meeuwig et al., 2008). For example, Logging Lake historically supported a strong population of adfluvial bull trout that used upper Logging Creek for spawning and rearing, but bull trout were not captured in the Logging sub-drainage during this study. Similar instances of bull trout population declines associated with the invasion and establishment of nonnative lake trout have been documented elsewhere in North America (Donald and Alger, 1993; Martinez et al., 2009). Although lake trout and bull trout are naturally sympatric in the St. Mary River watershed on the east side of the Continental Divide in northeastern GNP, bull trout exhibit a fluvial life history in that watershed (Mogen and Kaeding, 2005), which may make it possible for bull trout to persist in sympatry with lake trout in areas where they co-evolved. Such spatial and/or temporal segregation of bull trout and lake trout is not known to occur in western GNP and adfluvial bull trout populations have declined substantially over the last 50 years (Fredenberg et al., 2002).

Prior to the human-mediated spread of nonnative competitor species like lake trout, the distribution and abundance of bull trout in western GNP may also have been limited by environmental conditions. The bull trout occurrence models presented here suggest that the current distribution of bull trout is closely tied to spawning habitat availability. Bull trout were more likely to occur in high elevation, relatively wide, low gradient reaches with cold summer temperatures, which is in agreement with other studies (Fraley and Shepard, 1989; McPhail and Baxter, 1996; Baxter and Hauer, 2000; Rich et al., 2003). However, accessible habitats that meet these criteria are rare in western GNP (Fredenberg, 2002), and this limitation has likely influenced bull trout distribution and abundance. Early anecdotal observations in GNP documented the small reaches where bull trout congregated to spawn (Hazzard, 1935) and surveys of the wider Flathead watershed estimated that only 28% of 750 km of accessible stream were used for spawning by migratory bull trout from Flathead Lake (Fraley and Shepard,1989). Fish access can also be precluded in some headwater reaches due to sub-surface stream flows during spawning (late summer, early fall) and lake outlet temperatures are often too high to accommodate spawning (Fredenberg, 2002; Fredenberg et al., 2007). Additionally, headwater streams in GNP are prone to sudden rain-on-snow and scouring events that may negatively impact spawning habitat availability and bull trout recruitment. The cumulative effects of these factors on the quantity and quality of bull trout spawning habitat in GNP likely contributed to the low abundances and sporadic distribution of bull trout observed in this study.

Finally, bull trout are notoriously difficult to detect using daytime electrofishing methods, owing to their diel habitat use patterns and the general remoteness of streams that contain known populations (Thurow and Schill, 1996; Bonneau and Scarnecchia, 1998; Muhlfeld et al., 2003; Thurow et al., 2006). Adult and subadult bull trout often spend most of the daylight hours in deep, complex habitats that are difficult to sample, and they may not emerge from cover until after dark (Bonneau and Scarnecchia, 1998; Jakober, 2000; Muhlfeld et al., 2003). Furthermore, pools greater than 2 m in depth are fairly common in western GNP streams and were difficult to effectively sample with a backpack electrofishing unit. As a result, capture efficiencies were likely low in these areas.

Study Limitations

Spatial autocorrelation may have affected my results; a problem perhaps illustrated best by the significant differences in habitat metrics among sub-drainages. As a result, the physical habitat and fish population characteristics of proximate reaches within sub-drainages were not independent and additional error was likely introduced to occurrence and density models. Rieman et al. (2006) detected spatial autocorrelation in a similarly designed study and used hierarchical modeling to account for this limitation. However, due to varying sample sizes among streams and sub-drainages, hierarchical techniques were not appropriate for this study. Nonetheless, despite additional error introduced by spatial autocorrelation, the results of this study are concordant with other research that has analyzed the distribution of salmonid species with measurable abiotic and biotic factors (Kershner et al., 1997; Rich et al., 2003; Young et al., 2005; Muhlfeld et al., 2009a).

The physical habitat characteristics of a reach are known to impact the efficiency of any sampling method and wide, fast flowing streams can be extremely difficult to sample via backpack electrofishing (Bayley and Peterson, 2001). In light of this issue, the inverse relationship between the density of westslope cutthroat trout and stream width may be partially explained by an increased sampling efficiency in smaller streams. Although the importance of small streams (first and second order) to westslope cutthroat is supported by these results and other research (Bozek and Hubert 1992; Sloat et al., 2005), estimates of fish density in wider stream reaches (>8 m) are likely biased low.

Finally, bull trout density models were limited by a small sample size (N = 10) which reduced the statistical power of these results. That bull trout were most abundant in narrow, high elevation streams was not surprising given the limited distribution of bull trout in the study area and the importance of headwater refugia since arrival of lake trout (Fredenberg, 2002). However, these findings may also be related to the inefficiency of backpack electrofishing in wide, low gradient areas that my occurrence models, and those of other studies (Rich et al., 2003), suggest are important. In the future, snorkeling surveys may help alleviate this discrepancy; snorkeling is more logistically feasible in backcountry locations and likely more effective at detecting bull trout in deep water. A rigorous comparative study examining the efficacy of these methods would contribute greatly to the development of detection probability estimates for bull trout in western GNP streams and would lead to more insight on how best to monitor trends in these threatened populations.

Conclusions and Recommendations for Conservation

The headwater streams of the upper Flathead in western GNP remain a stronghold for westslope cutthroat trout despite the threats posed by the spread of hybridization with rainbow trout and habitat loss in the wider Flathead watershed. In contrast, bull trout are becoming increasingly rare in western GNP due to a complex combination of habitat limitations and competitive interactions with nonnative lake trout. Stream networks disassociated from lake trout populations, such as those in the Akokala sub-drainage, will become increasingly valuable and pro-active recovery efforts will ultimately be necessary to ensure the persistence of these native species in GNP.

In areas that have yet to be compromised by nonnative species, isolation may be a viable preemptive management tool to preserve native fish assemblages. For example, the Akokala sub-drainage contains high quality stream habitat, supports non-hybridized westslope cutthroat trout, and one contains of the few remaining bull trout lakes west of the Continental Divide in GNP that has not been compromised by lake trout. This sub-drainage presents a unique opportunity for managers to test the viability of isolation management in GNP to conserve native fish populations threatened by nonnative fish invasions (Fredenberg et al., 2007; C. Muhlfeld, USGS, unpublished data).

Isolating the Akokala sub-drainage may preclude the advance of introgressive hybridization and prevent the establishment of lake trout in Akokala Lake. However, this measure may also impose increased extinction risks for westslope cutthroat trout and bull trout populations. Natural and human constructed barriers can cause a reduction of genetic diversity within isolated populations, resulting in a high degree of genetic divergence among neighboring populations, and may increase the probability of demographic and environmental stochasticity (Neville et al., 2006; Meeuwig et al., 2010). This can be problematic in situations where migratory life history forms are prevalent, but whether a substantial reduction in diversity occurs, and how it affects the population in question, depends on the quantity and quality of the isolated habitat and life history characteristics of the isolated populations (Neville et al., 2006; Peterson et al., 2008).

Meeuwig et al. (2010) found that Akokala Lake bull trout were genetically divergent from populations in all 15 western GNP lakes tested. Considering the well documented bull trout declines following lake trout invasion and the unique genetics of this population, it is reasonable to conclude that isolation may be beneficial for the long term persistence of bull trout in the Akokala sub-drainage. Isolation may also benefit westslope cutthroat trout in the Akokala sub-drainage, albeit with the permanent loss of migratory life history forms upstream of the barrier point. Genetic analyses indicate some reproductive overlap among populations within the Akokala sub-drainage (Parke, Long Bow and Akokala Creeks) and maintaining the connectivity of this relatively large stream network may counteract the loss of migratory forms (C. Muhlfeld, USGS, unpublished data). Positioning the barrier on the mainstem of Akokala Creek near the North Fork Flathead confluence would ensure upstream connectivity while preventing the spread of hybridization.

In addition to preventing further lake trout dispersal via strategic barrier construction, preserving adfluvial bull trout populations in western GNP will require lake trout suppression in one form or another. To this end, the NPS implemented mandatory kill regulations for lake trout west of the continental divide in 2008. While this measure is undoubtedly a positive development in light of bull trout declines, angling efforts alone have proven insufficient in reducing lake trout numbers in large lakes throughout the western U.S. (Martinez et al., 2009). For the nine bull trout lakes in western GNP that have already been compromised by lake trout, suppression of lake trout using intensive gill netting coupled with bull trout restoration efforts is the most viable management option currently available.

The primary disadvantage of mechanical removal in GNP is the incidental catch and subsequent mortality of bull trout and westslope cutthroat trout. Additionally, long term mechanical removal projects are expensive, especially in large, remote bodies of water; annual suppression costs in Yellowstone Lake have approached $400,000 (Martinez et al., 2009). The relatively small size of bull trout supporting lakes in western GNP (Lake McDonald is the largest at 2761 ha) will help mitigate both of these negative factors; small lakes can be covered by fewer personnel and gill nets can be checked more frequently in order to reduce by-catch mortality.

Experimental gill netting to remove juvenile and adult lake trout was initiated by the USGS in Quartz Lake during the fall of 2009 and results have been encouraging thus far. Mature lake trout implanted with sonic tags have successfully been used to identify several spawning locations and gill netting in these areas during spawning (late October) appears to be effective (Muhlfeld and Fredenberg, 2009). Efforts continued during the spring and fall of 2010, concentrating on juveniles and adults, respectively. Preliminary catch results from 2010 indicate a sizeable reduction in mature lake trout as compared to

2009 and potential disruption of the sex ratio (Muhlfeld and Fredenberg, 2009; C. Muhlfeld, USGS, unpublished data)

Quartz Lake was selected for this experimental project due to its recent invasion (lake trout were not detected until 2005) and the relative strength of its adfluvial bull trout population as compared to others in western GNP (Fredenberg et al., 2007). If lake trout suppression proves feasible in Quartz Lake, expansion of similar mechanical removal to additional lakes in GNP is a logical next step. However, in lakes like Logging and Bowman, where bull trout numbers have been reduced to drastically low levels, lake trout removal efforts will need to be paired with an extensive bull trout translocation/re-establishment effort.

Naturally fishless lakes or lakes that currently contain mixtures of native and nonnative cutthroat species present ideal locations for the development of bull trout source populations that can ultimately be used for re-establishment elsewhere in GNP. Raising bull trout in western GNP, in habitats remarkably similar to those where fish will be re-established, is preferable to releasing hatchery fish that may carry diseases or may not share genetic characteristics allowing for local adaptation. Zooplankton, macroinvertebrate, fish composition and spawning habitat surveys are currently underway in Grace Lake in the upper Logging sub-drainage, Pocket Lake in the upper Bowman sub-drainage, and Lake Ellen Wilson in the upper Lincoln sub-drainage (Middle Fork Flathead watershed). These data will be used to assess the ability of candidate lakes to support bull trout source populations for future translocation efforts (C. Muhlfeld and B. Galloway, USGS, personal communication).

Although watersheds in GNP have been protected from development and resource extraction by the NPS since 1910, many of the streams and lakes of western GNP are connected to the wider Flathead watershed and are affected by policies implemented outside park boundaries. Native fish communities in GNP remain vulnerable to invasion by nonnative species and will continue to be affected by climate change. Isolation of intact native fish assemblages when appropriate and an aggressive lake trout suppression/bull trout re-establishment program will be necessary to ensure that GNP's native fish communities persist beyond the 21^{st} century.

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FIGURES

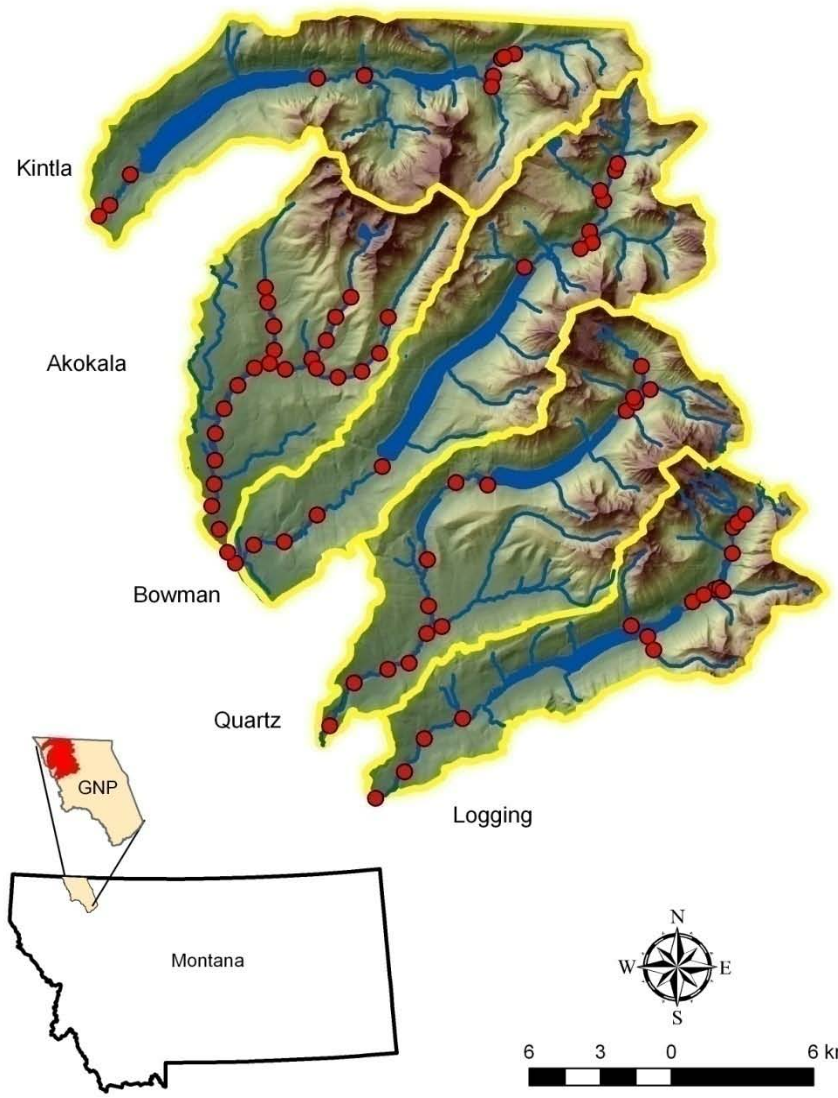

Figure 1: Locations of sample reaches (N = 79) in five sub-drainages of the North Fork Flathead watershed in GNP, 2008-2009.

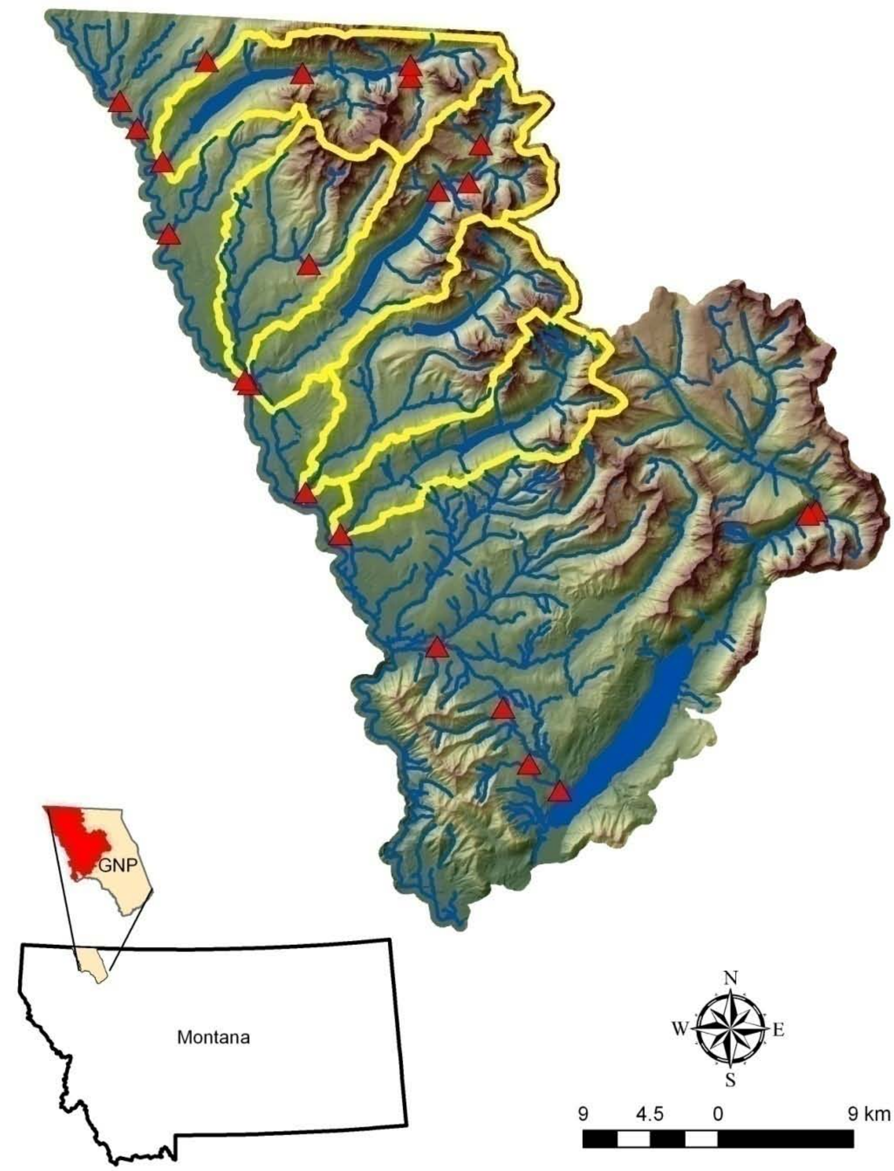

Figure 2: Locations of HOBO U22 temp pro v2 thermographs (N = 24) used to estimate August mean temperature (^{o}C) at sample reaches.

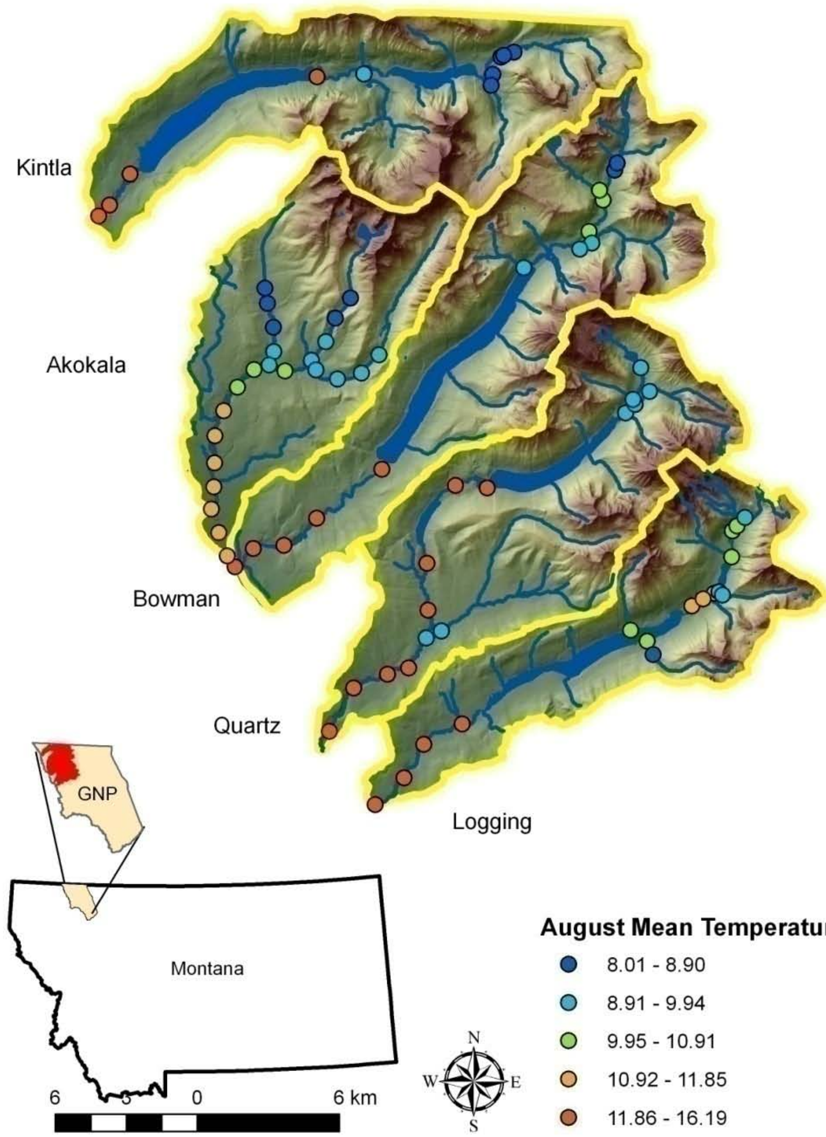

Figure 3: Predicted August mean temperature for sample reaches (N = 79) as obtained from the multiple regression model containing the variables elevation (m) and lake influence category (Low, <5 ha; Moderate, 5-100 ha; High, >100 ha) for each sample reach.

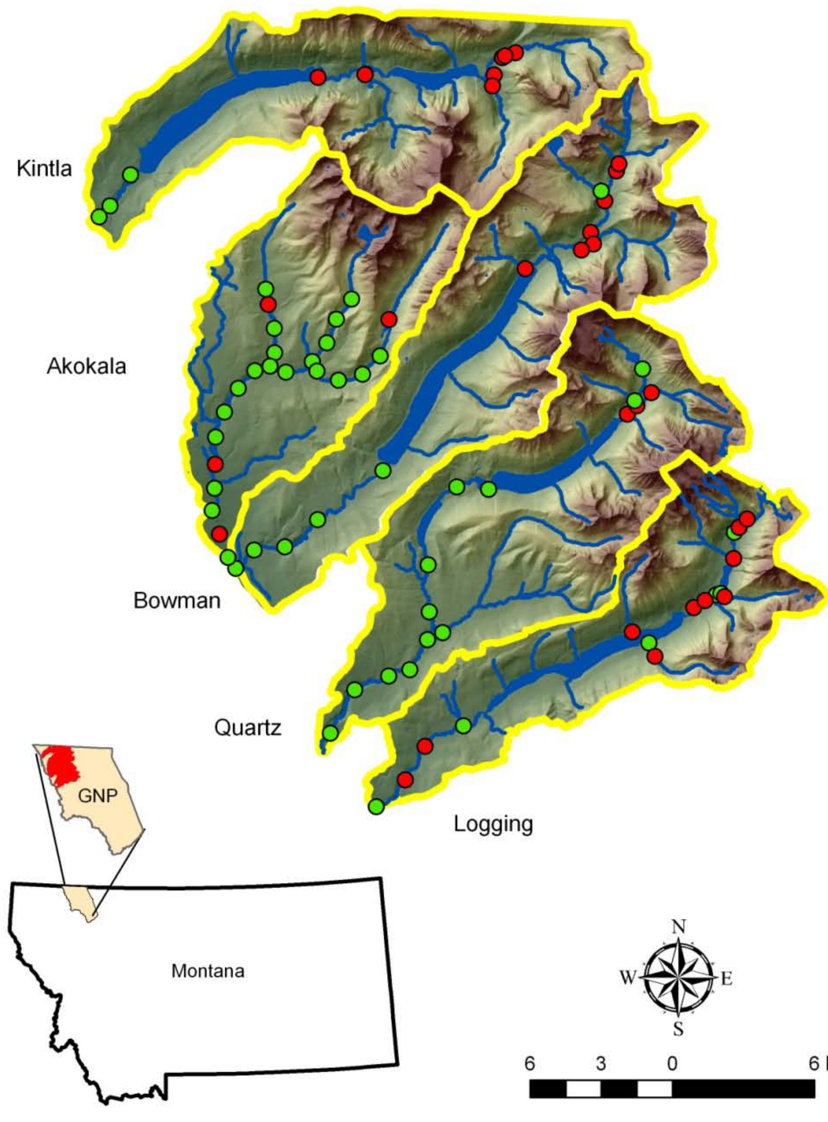

Figure 4: Distribution of westslope cutthroat trout detections (green dots, $N = 47$) in the 79 sample reaches.

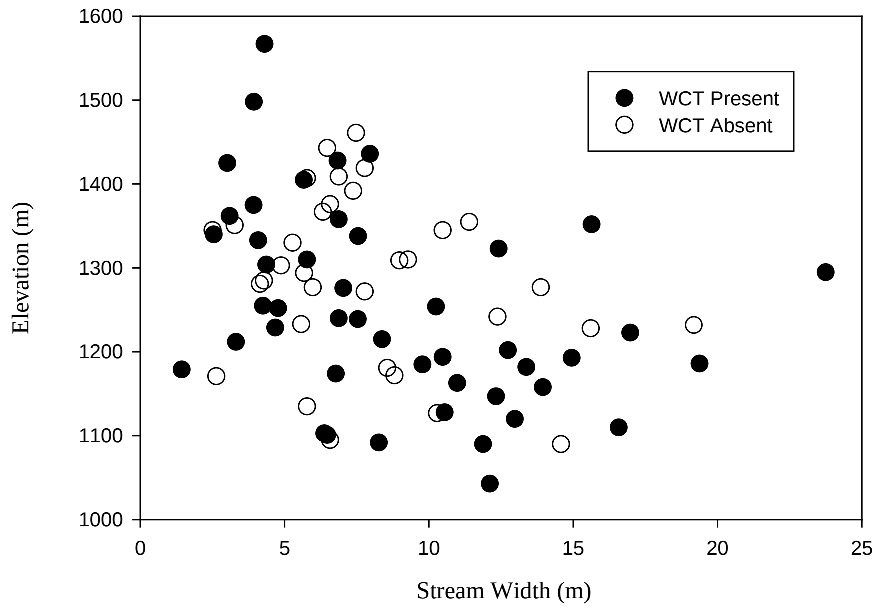

Figure 5: Occurrence of westslope cutthroat trout (WCT) in relation to stream width (m) and elevation (m) in the 79 sample reaches.

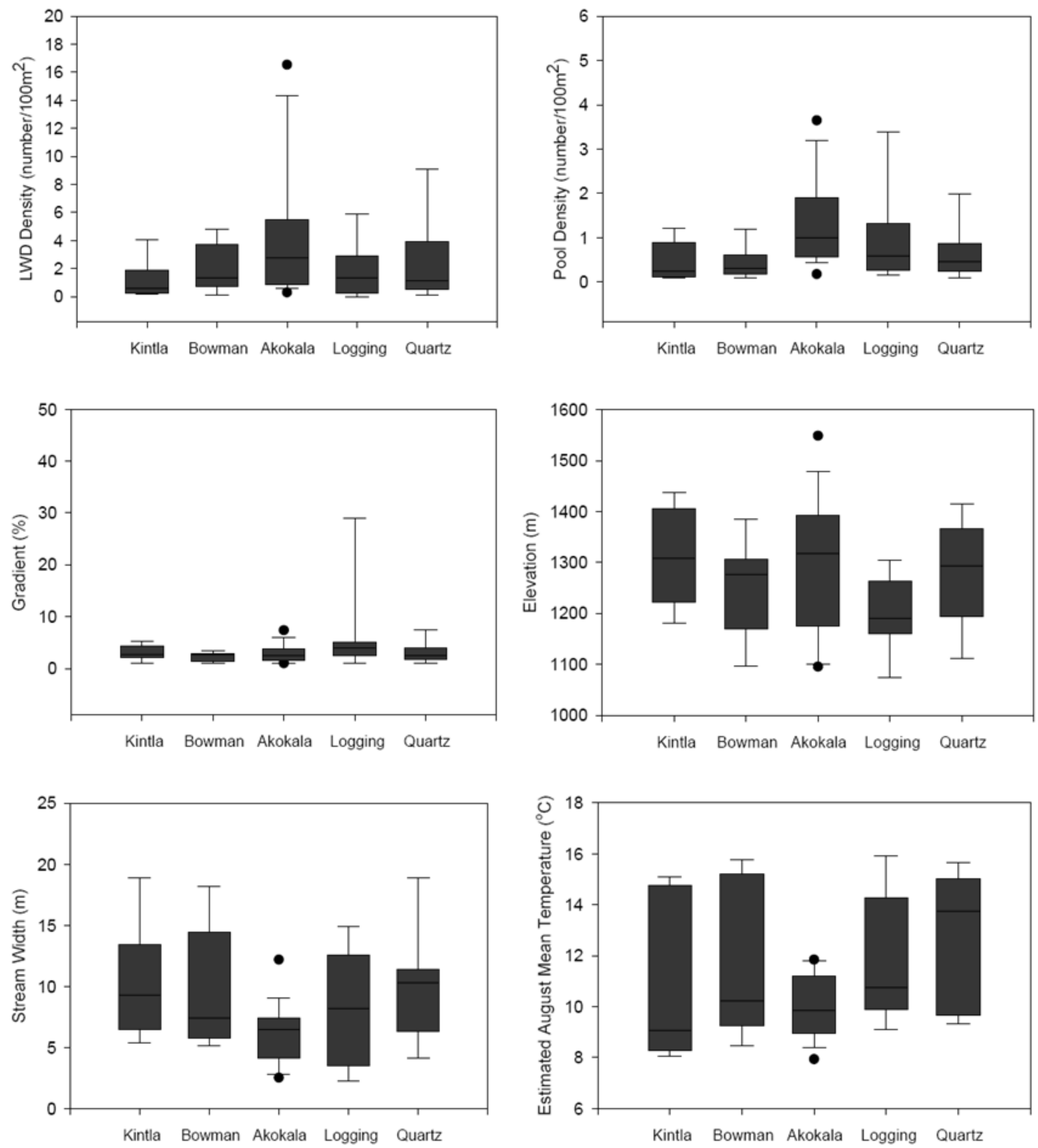

Figure 6: Boxplots of the abiotic factors LWD density (no./100m^2), pool density (no./100m^2), gradient (%), elevation (m), stream width (m) and estimated August mean temperature (^{o}C) for each sub-drainage. Boxes show the 25th and 75th percentiles, horizontal lines show median values and the whiskers show the 10th and 90th percentiles.

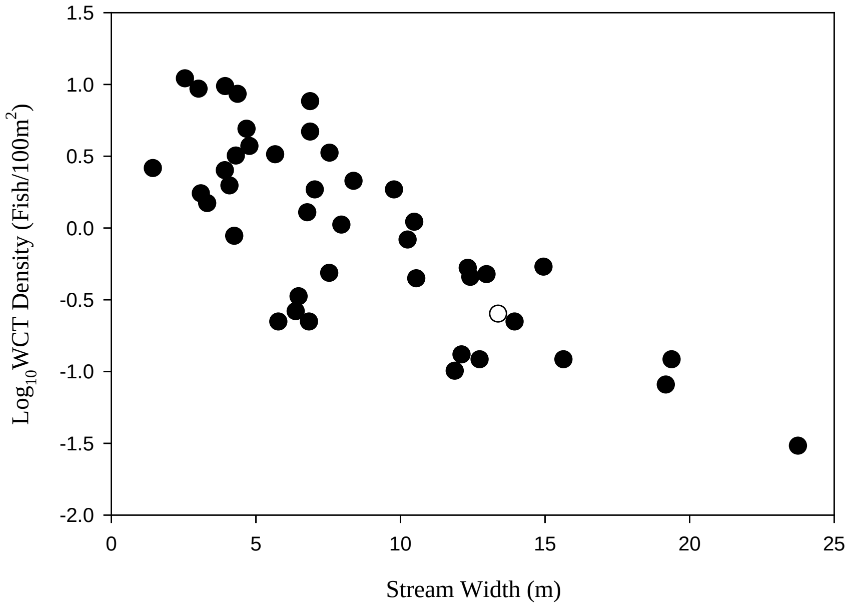

Figure 7: Density of westslope cutthroat trout (fish/100m^2; $\log_{10}$ transformed) against stream width (m) for the 43 sample reaches containing fish ≥ 55 mm TL.

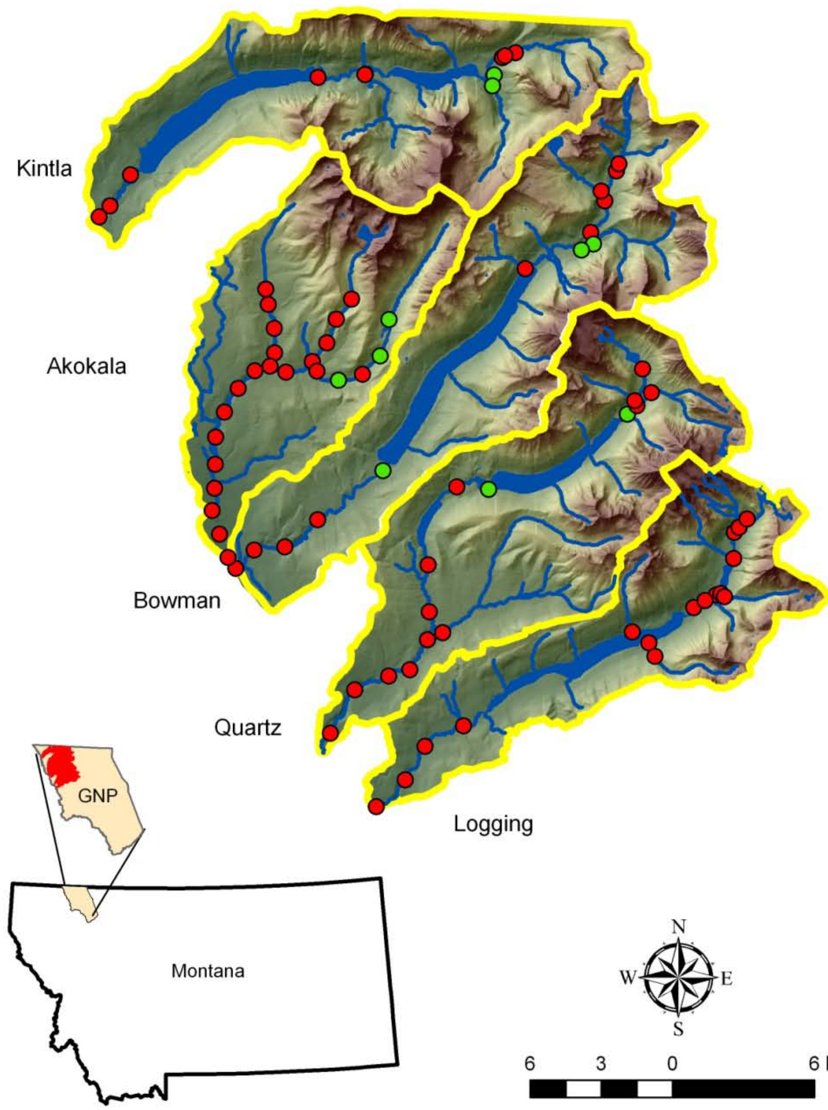

Figure 8: Distribution of bull trout detections (green dots; N = 10) in the 79 sample reaches.

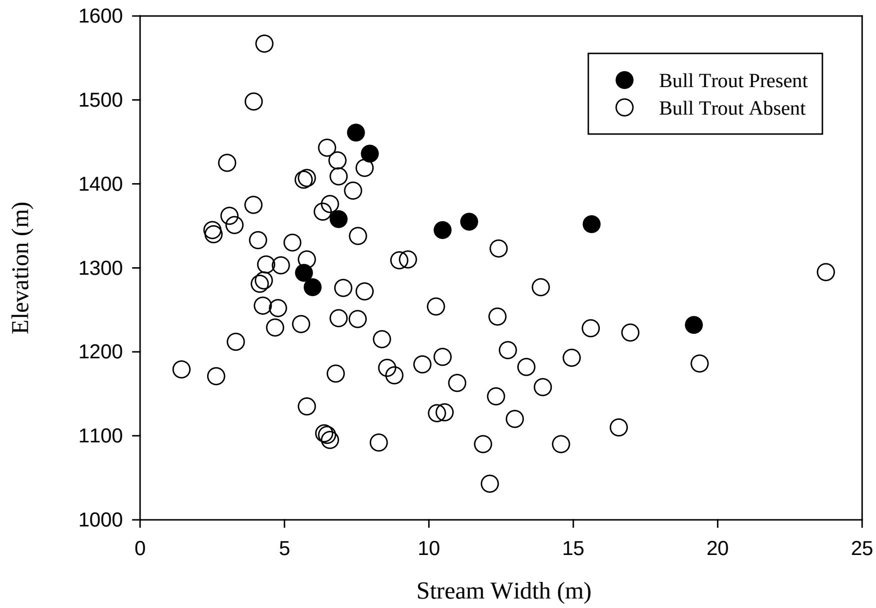

Figure 9: Occurrence of bull trout relative to average stream width (m) and elevation (m) in the 79 sample reaches.

TABLES

Table 1: The number of sample reaches (N), mean, and standard deviation (in parentheses) of abiotic factors and fish densities (fish/100m^2) segregated by sub-drainage.

	N	Elevation (m)	August Mean Temperature (°C)	Average Stream Width (m)	Pool Density (no/100^2)	LWD[a] Density (no./100m^2)	Gradient (%)	WCT[b] Density (no./100m^2)	Bull Trout[c] Density (no./100m^2)
Kintla	11	1308 (92)	11.36 (3.25)	10.58 (4.58)	0.48 (0.43)	1.15 (1.34)	3.02 (1.43)	0.03 (0.08)	0.04 (0.09)
Bowman	13	1248 (94)	11.73 (3.02)	10.07 (4.94)	0.45 (0.37)	2.00 (1.68)	2.20 (0.82)	0.11 (0.19)	0.04 (0.09)
Akokala	24	1294 (135)	10.01 (1.26)	6.07 (2.44)	1.41 (1.02)	4.49 (4.90)	2.86 (1.76)	3.19 (3.41)	0.06 (0.17)
Logging	16	1198 (78)	11.60 (2.55)	8.21 (4.67)	1.05 (1.29)	1.90 (2.14)	6.89 (10.1)	0.31 (0.71)	------
Quartz	15	1280 (104)	12.33 (2.74)	9.80 (5.10)	0.74 (0.67)	2.41 (3.08)	3.31 (2.31)	0.76 (1.31)	0.01 (0.04)

[a] LWD = Large woody debris ≥ 10cm in diameter, ≥ 3m in length.
[b] Westslope cutthroat trout ≥ 55mm.
[c] Bull trout ≥ 60mm.

Table 2: Results of Mann-Whitney U tests for variation abiotic factors between reaches where westslope cutthroat trout were detected and not detected.

Abiotic Factor	Detected (N = 47)	Not Detected (N = 32)	U	P-value	df
LWD Density (no/100m^2)	3.13 (3.88)	2.07 (2.61)	590.00	0.106	1
Gradient (%)	3.08 (1.78)	4.55 (7.48)	736.00	0.873	1
Stream Width (m)	9.10 (5.10)	7.62 (3.31)	652.00	0.318	1
August Mean Temperature (°C)	11.94 (2.63)	10.22 (2.12)	455.00	0.003	1
Elevation (m)	1251 (116)	1289 (101)	922.00	0.090	1
Pool Density (no/100m^2)	1.01 (1.10)	0.80 (0.66)	772.00	0.842	1

Table 3: Results of Mann-Whitney *U* tests for variation abiotic factors between reaches where and bull trout were detected and not detected.

Abiotic Factor	Detected (N = 10)	Not Detected (N = 69)	*U*	*P*-value	*df*
LWD Density (no/100m^2)	1.80 (1.46)	2.83 (3.64)	353.50	0.09	1
Gradient (%)	2.07 (1.27)	3.91 (5.26)	482.00	0.043	1
Stream Width (m)	9.62 (4.64)	8.34 (4.49)	283.50	0.364	1
August Mean Temperature (^{o}C)	10.13 (2.24)	11.41 (2.59)	473.50	0.058	1
Elevation (m)	1343 (69)	1255 (112)	174.00	0.012	1
Pool Density (no/100m^2)	0.59 (0.49)	0.97 (0.99)	409.00	0.345	1

Table 4: Pearson's product moment correlation coefficients (*r*) among abiotic factors measured at each fish sampling reach.

	LWD Density	Gradient	Stream Width	Elevation	August Mean Temperature
Gradient	0.062 (1.00)				
Stream Width	− 0.443 (0.001)	− 0.257 (1.00)			
Elevation	0.281 (0.180)	0.138 (1.00)	− 0.358 (0.018)		
August Mean Temperature	− 0.332 (0.042)	− 0.177 (1.00)	0.715 (<0.001)	− 0.707 (<0.001)	
Pool Density	0.621 (<0.001)	0.297 (0.117)	− 0.674 (<0.001)	0.310 (<0.001)	− 0.486 (<0.001)

Table 5: Model selection results for logistic regression models containing various combinations of abiotic factors (stream width, LWD, gradient, August mean temperature, elevation) and a biotic factor (lake trout presence) in relation to the occurrence of westslope cutthroat trout in 79 stream reaches in the North Fork Flathead watershed, Glacier National Park. The number of parameters (*k*) includes intercept and error terms. Models were ranked according to their corrected Akaike Information Criterion values (AIC_c)

Model	*k*	AIC_c	ΔAIC_c
LWD, Temperature, Lake Trout	5	92.77	0.00
LWD, Temperature	4	95.17	2.39
LWD, Temperature, Width, Lake Trout, Elevation, Gradient	8	97.92	5.15
Temperature, Lake Trout	4	100.36	7.58
Temperature	3	101.72	8.94
LWD, Elevation	4	106.59	13.82
LWD, Elevation, Width, Lake Trout	6	107.99	15.21
LWD	3	108.35	15.58
LWD, Width, Lake Trout	5	108.54	15.76
LWD, Elevation, Lake Trout	5	108.63	15.86
Elevation, Lake Trout	4	110.47	17.70
LWD, Lake Trout	4	110.57	17.80
Lake Trout	3	110.94	18.16
Elevation, Width, Lake Trout,	5	112.49	19.71

Table 6: Coefficients (*B*) and standard errors (SE) for the most plausible logistic regression model explaining the occurrence of westslope cutthroat trout in 79 stream reaches of the North Fork Flathead watershed in Glacier National Park (see Table 4).

Variable	*B*	SE
Model 1		
LWD	2.938	1.044
Temperature	0.585	0.152
Lake Trout	- 1.274	0.614

Table 7: Model selection results for linear regression models containing various combinations of abiotic factors (stream width, LWD, gradient, August mean temperature, elevation) and a biotic factor (lake trout presence) in relation to the density (fish/100m^2) of westslope cutthroat trout in 43 stream reaches in the North Fork Flathead watershed, Glacier National Park. The number of parameters (*k*) includes intercept and error terms. Models were ranked according to their corrected Akaike Information Criterion values (AIC_c)

Model	*k*	AIC_c	ΔAIC_c
Gradient, Width, Lake Trout	5	46.06	0.00
Gradient, Width, Lake Trout, Elevation	6	46.74	0.68
Width, Lake Trout, Elevation	5	49.78	3.72
Width, Lake Trout	4	50.26	4.20
Gradient, Width, Lake Trout, Temperature, Elevation, LWD	8	50.78	4.72
Gradient, Width	4	54.41	8.35
Width	3	55.97	9.91
Gradient, Lake Trout , Temperature	5	56.38	10.32
Gradient, Lake Trout, Elevation	5	59.73	13.67
Gradient, Lake Trout	4	61.01	14.95
Temperature	3	62.91	16.85
Lake Trout, Elevation, LWD	5	67.09	21.03
Gradient	3	77.66	31.60
Lake Trout	3	78.88	32.83

Table 8: Coefficients (*B*) and standard errors (SE) for the two most plausible linear regression models explaining the density (fish/100m^2) of westslope cutthroat trout in 43 stream reaches in the North Fork Flathead watershed in Glacier National Park (see Table 7).

Variable	*B*	SE
Model 1		
Gradient	0.738	0.286
Width	- 1.208	0.273
Lake Trout	- 0.215	0.064
Model 2		
Gradient	0.671	0.288
Width	- 1.130	0.276
Lake Trout	- 0.201	0.064
Elevation	0.001	0.001

Table 9: Model selection results for logistic regression models containing various combinations of abiotic factors (stream width, LWD, gradient, August mean temperature, elevation) and a biotic factor (lake trout presence) in relation to the occurrence of bull trout in 79 stream reaches in the North Fork Flathead watershed, Glacier National Park. The number of parameters (k) includes intercept and error terms. Models were ranked according to their corrected Akaike Information Criterion values (AIC_c)

Model	k	AIC_c	ΔAIC_c
Gradient, Elevation, Width	5	51.14	0.00
Gradient, Elevation	4	51.37	0.23
Gradient, Temperature	3	56.64	5.50
Gradient, Width, Temperature, Lake Trout, Elevation, LWD	8	56.75	5.61
Gradient	3	58.38	7.24
Elevation	3	58.74	7.60
Gradient, Width	5	60.36	9.22
Temperature	3	61.84	10.70
Width	3	63.14	12.00
Lake Trout	3	64.32	13.18

Table 10: Coefficients (B) and standard errors (SE) for the two most plausible logistic regression models of the occurrence of bull trout in the North Fork Flathead watershed in Glacier National Park (see Table 9).

Variable	B	SE
Model 1		
Gradient	- 4.602	1.922
Elevation	0.013	0.005
Width	3.006	2.000
Model 2		
Gradient	- 4.882	1.814
Elevation	0.011	0.004

Table 11: Model selection results for linear regression models containing various combinations of abiotic factors (stream width, LWD, gradient, August mean temperature, elevation) and a biotic factor (lake trout presence) in relation to the density (fish ≥ 55mm/100m^2) of bull trout in 10 reaches in the North Fork Flathead watershed, Glacier National Park. The number of parameters (*k*) includes intercept and error terms. Models were ranked according to their corrected Akaike Information Criterion values (AIC_c)

Model	*k*	AIC_c	ΔAIC_c
Elevation, Width	4	2.87	0.00
Gradient, Width	4	7.26	4.39
Width	3	10.05	7.18
Temperature	3	10.59	7.72
Elevation	3	11.17	8.30
Gradient, Width, Elevation	5	11.84	8.97
Lake Trout	3	13.61	10.74
Temperature, Gradient	4	16.36	13.49
Elevation, Gradient	4	16.95	14.08
Elevation, LWD, Gradient, Width, Temperature, Lake Trout	8	143.01	140.14

Table 12: Coefficients (*B*) and standard errors (SE) for the most plausible linear regression model explaining the density (fish/100m^2) of bull trout in the North Fork Flathead watershed in Glacier National Park (see Table 11).

Variable	*B*	SE
Model 1		
Elevation	- 0.003	0.001
Width	- 1.278	0.271

APPENDIX

Additional Tables of Field Data

Table 13: Geographic data and upstream lake area (including lakes > 9 ha in area and below 2000 m in elevation) associated with sample reaches (*N* = 79). Reach codes correspond to those in the USGS Glacier Field Station fisheries database.

Reach Code	Sub-drainage	Stream	UTM Zone 12 X (m)	UTM Zone 12 Y (m)	Elevation (m)	Upstream Lake Area (ha)
6	Kintla	Kintla Creek	253287	5423701	1181	883.61
7	Kintla	Kintla Creek	253744	5424151	1185	883.61
8	Kintla	Kintla Creek	254603	5425471	1222	883.61
9	Kintla	Kintla Creek	262512	5429575	1241	189.48
10	Kintla	Kintla Creek	264505	5429712	1309	189.48
11	Kintla	Kintla Creek	269938	5429684	1329	0.00
12	Kintla	Kintla Creek	270277	5430409	1418	0.00
13	Kintla	Kintla Creek	270827	5430611	1442	0.00
14	Kintla	Agassiz Creek	269869	5429219	1344	0.00
15	Kintla	North Fork Kintla Creek	270397	5430489	1406	0.00
16	Kintla	Red Medicine Bow Creek	264485	5429688	1308	0.00
22	Akokala	Akokala Creek	265503	5419360	1460	0.00
27	Bowman	Bowman Creek	259049	5408879	1089	730.93
28	Bowman	Bowman Creek	259815	5409652	1109	730.93
29	Bowman	Bowman Creek	265253	5413001	1231	730.93
30	Bowman	Bowman Creek	273999	5423046	1276	33.39
31	Bowman	Bowman Creek	274589	5424362	1302	33.39
32	Bowman	Bowman Creek	275082	5425628	1391	0.00
33	Bowman	Bowman Creek	275193	5425930	1375	0.00
34	Bowman	Jefferson Creek	274119	5422545	1293	0.00
35	Bowman	Jefferson Creek	273608	5422304	1276	0.00
36	Bowman	Numa Creek	271245	5421512	1232	0.00
37	Bowman	Pocket Creek	274447	5424776	1309	33.39

Table 13 Continued:

Reach Code	Sub-drainage	Stream	UTM Zone 12 X (m)	UTM Zone 12 Y (m)	Elevation (m)	Upstream Lake Area (ha)
63	Akokala	Akokala Creek	258714	5409334	1100	39.90
64	Akokala	Akokala Creek	258363	5410313	1094	39.90
65	Akokala	Akokala Creek	258043	5411316	1102	39.90
66	Akokala	Akokala Creek	258154	5412250	1119	39.90
67	Akokala	Akokala Creek	258179	5413265	1134	39.90
68	Akokala	Akokala Creek	258203	5414404	1173	39.90
69	Akokala	Akokala Creek	258561	5415461	1184	39.90
70	Akokala	Akokala Creek	259150	5416463	1214	39.90
71	Akokala	Akokala Creek	259852	5417209	1239	39.90
72	Akokala	Parke Creek	260680	5417971	1303	0.00
73	Akokala	Parke Creek	260664	5419000	1332	0.00
74	Akokala	Parke Creek	260406	5420002	1344	0.00
75	Akokala	Parke Creek	260310	5420645	1361	0.00
76	Akokala	Akokala Creek	261164	5417145	1275	39.90
77	Akokala	Long Bow Creek	262271	5417601	1339	30.45
78	Akokala	Long Bow Creek	262889	5418390	1424	30.45
79	Akokala	Long Bow Creek	263287	5419383	1497	30.45
80	Akokala	Long Bow Creek	263924	5420225	1566	30.45
81	Akokala	Akokala Creek	262463	5417194	1337	9.45
82	Akokala	Akokala Creek	263372	5416811	1357	9.45
83	Akokala	Akokala Creek	264392	5417062	1404	9.45
84	Akokala	Akokala Creek	265134	5417825	1435	9.45
85	Akokala	Parke Creek	260483	5417395	1251	0.00
86	Bowman	Bowman Creek	261110	5409778	1146	730.93
87	Bowman	Bowman Creek	262497	5410930	1192	730.93
91	Logging	Logging Creek	264968	5398824	1042	483.92
92	Logging	Logging Creek	266186	5399957	1089	483.92
93	Logging	Logging Creek	267019	5401370	1126	483.92
94	Logging	Logging Creek	268638	5402230	1157	483.92

Table 13 Continued:

Reach Code	Sub-drainage	Stream	UTM ZONE 12 X (m)	UTM ZONE 12 Y (m)	Elevation (m)	Upstream Lake Area (ha)
95	Logging	Logging Creek	279303	5407751	1201	33.32
96	Logging	Barrier Creek	279487	5407819	1211	0.00
97	Logging	Barrier Creek	279643	5407686	1284	0.00
98	Logging	Logging Creek	280065	5410396	1238	0.00
99	Logging	Logging Creek	278353	5407228	1171	0.00
100	Logging	Logging Creek	278829	5407512	1180	33.32
101	Logging	Adair Creek	275761	5406190	1170	0.00
102	Logging	Logging Creek	280246	5410605	1271	0.00
103	Logging	Logging Creek	280596	5410960	1280	0.00
104	Logging	Logging Creek	280027	5409296	1227	0.00
105	Logging	Wolf Gun Creek	276453	5405731	1178	0.00
106	Logging	Wolf Gun Creek	276715	5405161	1350	0.00
109	Quartz	Quartz Creek	263032	5401928	1091	458.68
110	Quartz	Quartz Creek	264055	5403758	1127	458.68
111	Quartz	Quartz Creek	265488	5404331	1162	458.68
112	Quartz	Quartz Creek	266378	5404602	1193	458.68
113	Quartz	Quartz Creek	267205	5407043	1253	458.68
114	Quartz	Quartz Creek	267148	5409026	1294	458.68
115	Quartz	Quartz Creek	268363	5412307	1322	391.16
116	Quartz	Quartz Creek	275544	5415380	1354	20.34
117	Quartz	Quartz Creek	275949	5415729	1366	20.34
118	Quartz	Rainbow Creek	276195	5417277	1427	20.34
119	Quartz	Quartz Creek	276562	5416286	1408	0.00
120	Quartz	Square Creek	275864	5415939	1374	0.00
121	Quartz	Cummings Creek	267123	5405871	1228	0.00
122	Quartz	Cummings Creek	267760	5406161	1254	0.00
123	Quartz	Quartz Creek	269693	5412208	1351	372.14

Table 14: Abiotic and biotic factors associated with sample reaches (*N* = 79). LKT = lake trout presence, marked 1 for reaches connected to lake trout populations and 0 for reaches not connected to lake trout populations. Reach codes correspond to those in the USGS Glacier Field Station fisheries database.

Reach Code	Sub-drainage	Stream	Reach Length (m)	Average Width (m)	Reach Area (m^2)	Average Gradient (%)	Pools/ $100m^2$	LWD/ $100m^2$	August Mean Temperature (^oC)	LKT
6	Kintla	Kintla Creek	151	13.4	2023.4	2.62	0.10	1.48	15.10	1
7	Kintla	Kintla Creek	89	19.4	1729.1	1.75	0.12	0.17	15.07	1
8	Kintla	Kintla Creek	153	17.0	2601.0	2.18	0.12	0.27	14.77	1
9	Kintla	Kintla Creek	82	12.4	1014.8	2.18	0.20	1.87	14.62	1
10	Kintla	Kintla Creek	67	9.3	623.1	3.49	0.32	0.32	14.09	0
11	Kintla	Kintla Creek	71	5.3	373.3	0.87	0.80	4.55	8.90	0
12	Kintla	Kintla Creek	86	7.8	668.7	5.24	1.05	0.15	8.20	0
13	Kintla	Kintla Creek	135	6.5	870.8	2.18	0.23	0.23	8.01	0
14	Kintla	Agassiz Creek	80	10.5	836.6	3.06	0.24	0.60	8.79	0
15	Kintla	North Fork Kintla Creek	69	5.8	399.3	4.37	1.25	0.75	8.30	0
16	Kintla	Red Medicine Bow Creek	75	9.0	677.1	5.24	0.89	2.22	9.07	0
22	Akokala	Akokala Creek	64	7.5	480.0	1.75	0.83	0.83	7.87	0
27	Bowman	Bowman Creek	82	11.9	973.8	3.06	0.31	2.57	15.82	1
28	Bowman	Bowman Creek	123	16.6	2041.8	2.62	0.10	0.93	15.66	1
29	Bowman	Bowman Creek	203	19.2	3897.6	1.31	0.08	1.05	14.70	1
30	Bowman	Bowman Creek	67	13.9	934.2	1.31	0.32	0.64	10.42	1
31	Bowman	Bowman Creek	81	4.9	396.0	2.62	1.01	3.79	10.21	1
32	Bowman	Bowman Creek	64	7.4	471.5	1.75	0.42	4.03	8.42	1
33	Bowman	Bowman Creek	61	6.6	400.0	3.49	0.50	0.00	8.54	1
34	Bowman	Jefferson Creek	97	5.7	549.0	3.06	0.73	3.64	9.19	1
35	Bowman	Jefferson Creek	122	6.0	735.7	0.87	0.27	1.36	9.32	1
36	Bowman	Numa Creek	80	5.6	451.0	2.62	1.33	5.32	9.67	1
37	Bowman	Pocket Creek	78	5.8	450.2	2.62	0.44	1.55	10.16	1
63	Akokala	Akokala Creek	93	6.5	607.3	1.25	1.32	1.32	11.81	0
64	Akokala	Akokala Creek	60	6.6	395.7	1.00	0.51	0.76	11.85	0

Table 14 Continued:

Reach Code	**Sub-drainage**	**Stream**	**Reach Length (m)**	**Average Width (m)**	**Reach Area (m^2)**	**Average Gradient (%)**	**Pools/ 100m^2**	**LWD/ 100m^2**	**August Mean Temperature (^oC)**	**LKT**
65	Akokala	Akokala Creek	61	6.4	391.0	1.50	0.51	1.53	11.79	0
66	Akokala	Akokala Creek	65	13.0	844.5	2.50	0.12	0.83	11.66	0
67	Akokala	Akokala Creek	55	5.8	319.6	1.00	0.94	0.94	11.54	0
68	Akokala	Akokala Creek	58	6.8	393.2	1.00	0.76	0.25	11.23	0
69	Akokala	Akokala Creek	56	9.8	546.4	3.75	0.37	2.75	11.14	0
70	Akokala	Akokala Creek	57	8.4	476.2	1.50	1.05	2.52	10.91	0
71	Akokala	Akokala Creek	53	6.9	367.2	3.00	0.54	1.91	10.71	0
72	Akokala	Parke Creek	51	4.4	224.0	7.50	1.79	6.25	9.11	0
73	Akokala	Parke Creek	50	4.1	205.5	2.00	1.95	5.35	8.88	0
74	Akokala	Parke Creek	51	2.5	129.0	1.00	3.10	11.63	8.79	0
75	Akokala	Parke Creek	56	3.1	174.7	5.00	2.86	17.17	8.65	0
76	Akokala	Akokala Creek	62	7.1	437.7	2.50	0.69	0.46	10.43	0
77	Akokala	Long Bow Creek	93	2.6	239.0	2.25	3.77	14.64	9.92	0
78	Akokala	Long Bow Creek	50	3.0	152.0	7.00	3.29	5.26	9.25	0
79	Akokala	Long Bow Creek	50	4.0	198.0	4.00	2.53	5.56	8.68	0
80	Akokala	Long Bow Creek	66	4.3	285.8	3.50	1.40	3.50	8.13	0
81	Akokala	Akokala Creek	52	7.6	393.6	3.25	0.76	3.30	9.94	0
82	Akokala	Akokala Creek	50	6.9	345.0	4.25	1.74	0.87	9.78	0
83	Akokala	Akokala Creek	60	5.7	341.4	2.25	1.46	14.06	9.41	0
84	Akokala	Akokala Creek	72	8.0	574.6	3.50	0.52	3.31	9.17	0
85	Akokala	Parke Creek	68	4.8	326.4	2.50	0.92	2.76	9.52	0
86	Bowman	Bowman Creek	108	12.4	1333.8	1.75	0.15	0.37	15.37	1
87	Bowman	Bowman Creek	100	15.0	1497.0	1.50	0.20	0.80	15.01	1
91	Logging	Logging Creek	63	12.1	764.5	2.50	0.52	3.01	16.19	1
92	Logging	Logging Creek	62	14.6	905.2	4.00	0.22	0.11	15.82	1
93	Logging	Logging Creek	69	10.3	711.0	4.00	0.42	5.06	15.53	1
94	Logging	Logging Creek	64	14.0	894.2	2.00	0.22	1.79	15.29	1
95	Logging	Logging Creek	132	12.8	1684.6	2.50	0.18	0.53	11.01	0
96	Logging	Barrier Creek	61	3.3	203.7	2.75	1.47	1.96	9.83	0

Table 14 Continued:

Reach Code	Sub-drainage	Stream	Reach Length (m)	Average Width (m)	Reach Area (m^2)	Average Gradient (%)	Pools/ $100m^2$	LWD/ $100m^2$	August Mean Temperature (^oC)	LKT
97	Logging	Barrier Creek	53	4.3	228.4	25.00	2.63	7.88	9.26	0
98	Logging	Logging Creek	82	7.6	619.9	4.00	0.81	1.45	10.72	0
99	Logging	Logging Creek	90	8.8	794.7	1.00	0.50	3.40	11.25	1
100	Logging	Logging Creek	99	8.6	849.8	3.00	0.59	1.18	11.18	1
101	Logging	Adair Creek	83	2.7	220.8	5.00	0.91	0.91	10.16	1
102	Logging	Logging Creek	59	7.8	460.2	4.50	0.65	0.00	10.46	0
103	Logging	Logging Creek	79	4.2	329.4	5.00	0.61	0.00	9.29	0
104	Logging	Logging Creek	115	15.6	1797.6	1.00	0.11	0.00	10.81	0
105	Logging	Wolf Gun Creek	53	1.5	77.5	5.50	5.16	2.58	10.09	1
106	Logging	Wolf Gun Creek	50	3.3	164.9	38.50	1.82	0.61	8.74	1
109	Quartz	Quartz Creek	52	8.3	431.1	4.00	0.46	0.46	15.81	1
110	Quartz	Quartz Creek	130	10.6	1374.1	2.00	0.15	1.82	15.52	1
111	Quartz	Quartz Creek	146	11.0	1607.3	2.00	0.12	0.12	15.25	1
112	Quartz	Quartz Creek	61	10.5	640.7	2.16	0.31	0.78	15.00	1
113	Quartz	Quartz Creek	71	10.3	729.5	9.78	0.27	0.55	14.53	1
114	Quartz	Quartz Creek	152	23.8	3613.3	1.50	0.06	1.36	14.21	1
115	Quartz	Quartz Creek	72	12.4	895.7	5.00	0.78	0.11	13.99	1
116	Quartz	Quartz Creek	93	11.4	1062.1	1.00	0.47	1.13	9.80	1
117	Quartz	Quartz Creek	66	6.4	419.1	2.50	0.72	1.67	9.71	1
118	Quartz	Quartz Creek	67	6.9	459.8	1.75	0.87	8.48	9.23	1
119	Quartz	Quartz Creek	50	6.9	345.2	4.00	0.87	0.58	9.38	1
120	Quartz	Square Creek	61	4.0	241.0	3.50	1.66	4.57	9.65	1
121	Quartz	Cummings Creek	57	4.7	267.9	6.00	1.87	10.08	9.70	1
122	Quartz	Cummings Creek	54	4.3	230.9	3.50	2.17	3.90	9.50	1
123	Quartz	Quartz Creek	52	15.7	814.3	1.00	0.25	0.61	13.76	1

Table 15: Fish occurrence and density data for sample reaches (*N* = 79). WCT = westslope cutthroat trout, reach codes correspond to those in the USGS Glacier Field Station fisheries database.

Reach Code	Sub-drainage	Stream	Total WCT	WCT Density (fish/100m^2)	Total Bull Trout	Bull Trout Density (fish/100m^2)
6	Kintla	Kintla Creek	12	0.25	0	0.00
7	Kintla	Kintla Creek	5	0.12	0	0.00
8	Kintla	Kintla Creek	4	0.00	0	0.00
9	Kintla	Kintla Creek	0	0.00	0	0.00
10	Kintla	Kintla Creek	0	0.00	0	0.00
11	Kintla	Kintla Creek	0	0.00	1	0.27
12	Kintla	Kintla Creek	0	0.00	0	0.00
13	Kintla	Kintla Creek	0	0.00	0	0.00
14	Kintla	Agassiz Creek	0	0.00	1	0.12
15	Kintla	North Fork Kintla Creek	0	0.00	0	0.00
16	Kintla	Red Medicine Bow Creek	0	0.00	0	0.00
22	Akokala	Akokala Creek	0	0.00	2	0.42
27	Bowman	Bowman Creek	4	0.10	0	0.00
28	Bowman	Bowman Creek	4	0.00	0	0.00
29	Bowman	Bowman Creek	4	0.08	1	0.03
30	Bowman	Bowman Creek	0	0.00	0	0.00
31	Bowman	Bowman Creek	0	0.00	0	0.00
32	Bowman	Bowman Creek	0	0.00	0	0.00
33	Bowman	Bowman Creek	0	0.00	0	0.00
34	Bowman	Jefferson Creek	0	0.00	1	0.18
35	Bowman	Jefferson Creek	0	0.00	5	0.27
36	Bowman	Numa Creek	0	0.00	0	0.00
37	Bowman	Pocket Creek	1	0.22	0	0.00
63	Akokala	Akokala Creek	2	0.33	0	0.00
64	Akokala	Akokala Creek	0	0.00	0	0.00
65	Akokala	Akokala Creek	1	0.26	0	0.00
66	Akokala	Akokala Creek	6	0.47	0	0.00
67	Akokala	Akokala Creek	0	0.00	0	0.00

Table 15 Continued:

Reach Code	Sub-drainage	Stream	Total WCT	WCT Density (fish/100m^2)	Total Bull Trout	Bull Trout Density (fish/100m^2)
68	Akokala	Akokala Creek	5	1.27	0	0.00
69	Akokala	Akokala Creek	10	1.83	0	0.00
70	Akokala	Akokala Creek	13	2.10	0	0.00
71	Akokala	Akokala Creek	20	4.63	0	0.00
72	Akokala	Parke Creek	19	8.49	0	0.00
73	Akokala	Parke Creek	4	1.95	0	0.00
74	Akokala	Parke Creek	0	0.00	0	0.00
75	Akokala	Parke Creek	3	1.72	0	0.00
76	Akokala	Akokala Creek	8	1.83	0	0.00
77	Akokala	Long Bow Creek	29	10.88	0	0.00
78	Akokala	Long Bow Creek	14	9.21	0	0.00
79	Akokala	Long Bow Creek	19	9.60	0	0.00
80	Akokala	Long Bow Creek	8	3.15	0	0.00
81	Akokala	Akokala Creek	13	3.30	0	0.00
82	Akokala	Akokala Creek	27	7.54	1	0.29
83	Akokala	Akokala Creek	12	3.22	0	0.00
84	Akokala	Akokala Creek	11	1.04	4	0.70
85	Akokala	Parke Creek	14	3.68	0	0.00
86	Bowman	Bowman Creek	9	0.52	0	0.00
87	Bowman	Bowman Creek	10	0.53	0	0.00
91	Logging	Logging Creek	3	0.13	0	0.00
92	Logging	Logging Creek	0	0.00	0	0.00
93	Logging	Logging Creek	0	0.00	0	0.00
94	Logging	Logging Creek	2	0.22	0	0.00
95	Logging	Logging Creek	2	0.12	0	0.00
96	Logging	Barrier Creek	3	1.47	0	0.00
97	Logging	Barrier Creek	0	0.00	0	0.00
98	Logging	Logging Creek	3	0.48	0	0.00
99	Logging	Logging Creek	0	0.00	0	0.00

Table 15 Continued:

Reach Code	Sub-drainage	Stream	Total WCT	WCT Density (fish/100m^2)	Total Bull Trout	Bull Trout Density (fish/100m^2)
100	Logging	Logging Creek	0	0.00	0	0.00
101	Logging	Adair Creek	0	0.00	0	0.00
102	Logging	Logging Creek	0	0.00	0	0.00
103	Logging	Logging Creek	0	0.00	0	0.00
104	Logging	Logging Creek	0	0.00	0	0.00
105	Logging	Wolf Gun Creek	2	2.58	0	0.00
106	Logging	Wolf Gun Creek	0	0.00	0	0.00
109	Quartz	Quartz Creek	6	0.00	0	0.00
110	Quartz	Quartz Creek	6	0.44	0	0.00
111	Quartz	Quartz Creek	2	0.00	0	0.00
112	Quartz	Quartz Creek	9	1.09	0	0.00
113	Quartz	Quartz Creek	13	0.82	0	0.00
114	Quartz	Quartz Creek	1	0.03	0	0.00
115	Quartz	Quartz Creek	4	0.45	0	0.00
116	Quartz	Quartz Creek	0	0.00	2	0.09
117	Quartz	Quartz Creek	0	0.00	0	0.00
118	Quartz	Quartz Creek	1	0.22	0	0.00
119	Quartz	Quartz Creek	0	0.00	0	0.00
120	Quartz	Square Creek	6	2.49	0	0.00
121	Quartz	Cummings Creek	13	4.85	0	0.00
122	Quartz	Cummings Creek	2	0.87	0	0.00
123	Quartz	Quartz Creek	1	0.12	1	0.12

Table 16: Geographic data, average August temperature and upstream lake area (lakes ≥ 9 ha in area and < 2000 m in elevation) for thermograph locations (N = 24) used to develop a predictive August mean temperature model at sample reaches (N = 79).

Location Name	Sub-drainage	UTM Zone 12 X (m)	UTM Zone 12 Y (m)	Elevation (m)	Average August Temperature (^{o}C)	Upstream Lake Area (ha)
Agassiz Creek Lower	Kintla	270277	5430409	1418	8.07	0.00
Akokala Creek Lower	Akokala	275193	5425930	1375	11.59	39.90
Akokala Creek Upper	Akokala	270827	5430611	1442	13.53	9.45
Bowman Creek Lower	Bowman	275082	5425628	1391	15.97	730.93
Bowman Creek Upper	Bowman	269869	5429219	1344	8.48	33.39
Camas Creek Lower	Camas	265253	5413001	1231	16.16	195.45
Fern Creek Lower	Fish	264505	5429712	1309	10.58	0.00
Fish Creek	Fish	253287	5423701	1181	10.58	0.00
Ford Creek Lower	Ford	271245	5421512	1232	11.60	0.00
Harrison Creek Lower	Harrison	262512	5429575	1241	15.86	162.62
Jefferson Creek Lower	Bowman	270397	5430489	1406	7.32	0.00
Kintla Creek Lower	Kintla	274447	5424776	1309	16.24	883.61
Kintla Creek Upper 1	Kintla	264485	5429688	1308	11.95	189.48
Kintla Creek Upper 2	Kintla	265503	5419360	1460	8.75	0.00
Kishenehn Creek Lower	Kishenehn	273608	5422304	1276	11.94	0.00
Lincoln Creek Lower	Lincoln	254603	5425471	1222	12.76	98.03
Logan Creek	McDonald	253744	5424151	1185	10.47	0.00
Logging Creek Lower	Logging	273999	5423046	1276	17.48	494.45
McDonald Creek Lower	McDonald	269938	5429684	1329	10.63	0.00
McGee Creek Lower	Camas	258714	5409334	1100	7.62	0.00
Pocket Creek	Bowman	259049	5408879	1089	8.84	33.39
Quartz Creek Lower	Quartz	274589	5424362	1302	16.59	458.68
Starvation Creek Lower	Starvation	274119	5422545	1293	11.02	0.00
Starvation Creek Upper	Starvation	259815	5409652	1109	10.73	0.00