Evaluation and action plan for protection of 15 threatened adfluvial populations of bull trout in Glacier National Park, Montana

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Executive Summary

Fish assemblages in 17 lakes in Glacier National Park, Montana, were sampled as part of an ongoing project designed to develop an action plan for management of bull trout *Salvelinus confluentus* in Glacier National Park. Sampling occurred during the periods of June through October in the years 2004, 2005, and 2006. Sampling consisted of gill net surveys, lake shoreline electrofishing surveys, hook and line surveys, stream electrofishing surveys, stream habitat characterization, migratory barrier surveys, and bull trout redd surveys. Additionally, age structure was examined with a limited sample of bull trout otoliths, population genetic analyses were conducted, and samples were collected and prepared for examination of food-web structure among lakes.

Gill-net surveys provided information on the relative abundance of bull trout in Glacier National Park waters and effects of lake trout presence on bull trout relative abundance. Hook and line surveys were used to increase sample sizes of target species (e.g., bull trout and lake trout). Juvenile bull trout (i.e., 37 to 148 mm total length) used shoreline habitat in some lakes. Low numbers of bull trout are present in stream reaches in close proximity to lakes in Glacier National Park. Physical habitat quantification associated with stream electrofishing surveys provided information about habitat characteristics associated with potential bull trout spawning and rearing sites. Barrier surveys provided information about the location of potential barriers to migration or invasion among study lakes. Low numbers of bull trout redds, limited habitat available for spawning bull trout, and high temporal variability in the number of bull trout redds was observed in spawning streams for Bowman Lake, Harrison Lake, Logging Lake, Lower Quartz Lake, Middle Quartz Lake, and Quartz Lake.

Basic information regarding the age structure of bull trout populations was examined by aging 185 bull trout otoliths. Bull trout age varied from 2 to 16 among study lakes. A high degree of variability in population differentiation was observed among lakes based on 10 microsatellite loci. Lakes located above migratory barriers were highly differentiated from other study lakes, and lakes within the same drainage appeared to have a high degree of gene flow among and between populations. Muscle samples were collected from 475 fish and prepared for stable isotope analysis to examine food-web structure among lakes; analyses are currently being conducted.

These data, as well as forthcoming data, will be synthesized to develop a comprehensive action plan for the long-term monitoring, management, and recovery of bull trout resources in Glacier National Park, Montana.

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Introduction

The bull trout *Salvelinus confluentus* is a species of char endemic to western North America. The bull trout is generally considered to be an inland salmonid that is distributed west of the Great Divide and from northern California and Nevada northward to the southeastern headwaters of the Yukon system. The core distribution of bull trout is east of the Cascade mountain range, including most of Oregon (from the Willamette system east), Washington, inter-mountain Idaho and Montana, and British Columbia; however, some coastal populations exist in Washington and British Columbia. Some populations of bull trout also exist east of the Great Divide in northern Montana and Alberta. Declining trends in bull trout populations have prompted increased interest in this species since the late 1970s. Additionally, recent negative trends in bull trout abundance led to designation of this species as threatened under the US Endangered Species Act in 1998.

Prior to the late 1970s there was relatively little interest in the biology of bull trout. However, available information regarding bull trout has increased dramatically in recent years (McPhail and Baxter 1996). There have been great advances in our understanding of bull trout biology, both basic and applied, spanning a variety of topics such as general life history characteristics (Fraley and Shepard 1989; McPhail and Baxter 1996), habitat use and requirements (Swanberg 1997; Rich et al. 2003; Bahr and Shrimpton 2004), population genetics (Kanda and Allendorf 2001; Neraas and Spruell 2001; Costello et al. 2003; Spruell et al. 2003), community interactions (Donald and Alger 1993), and survey methods (Dunham et al. 2001).

Bull trout have been shown to exhibit a variety of life history strategies, including resident, fluvial, adfluvial, and anadromous strategies. Resident individuals spend their entire lives within small streams. Fluvial individuals live in large rivers and migrate to small streams where spawning and rearing occur. Adfluvial individuals live in lakes and reservoirs and migrate to streams where spawning and rearing occur. Anadromous individuals, like adfluvial individuals, spawn and rear in streams, but spend extended periods of time in seawater environments.

Regardless of life history strategies, all bull trout appear to spawn in lotic habitats and are iteroparous; however, reproductively mature individuals often spawn biennially or potentially less frequently (Fraley and Shepard 1989). Spawning generally occurs in low gradient streams with low water velocity and gravel substrate (McPhail and Baxter 1996). Evidence suggests that spawning will not occur until stream temperatures are at or below 9° C, and that spawning behavior may cease below 5° C (McPhail and Baxter 1996). Bull trout redds are constructed by females and may be 10-20 cm deep and over one meter long (McPhail and Baxter 1996). After excavation, eggs are deposited, fertilized, and covered by gravel displaced from upstream by the female (McPhail and Baxter 1996). Empirical studies indicate that bull trout eggs hatch at 350 CTU (Celsius Temperature Units), that optimal development occurs at temperatures from 2° C to 4° C, and that bull trout emerge from gravel approximately three weeks after hatching. In a field study, emergence of bull trout fry occurred at 223 days after egg deposition (Fraley and Shepard 1989).

After emergence, bull trout fry are most abundant in side-channels and pools and may be associated with submerged cover (McPhail and Baxter 1996). Bull trout fry are generally bottom oriented and feed mainly on aquatic insects. Juvenile bull trout (ages 1 to 3) are believed to rear in streams regardless of adult life history strategy (McPhail and Baxter 1996). Juvenile bull trout are most commonly associated with pool habitat, but habitat use can be variable over diel periods and seasonally (McPhail and Baxter 1996). As juvenile bull trout grow they shift from an insectivorous diet to a piscivorous diet (McPhail and Baxter 1996).

Because of the variety in life history strategies, few generalizations can be made about the biology of adult bull trout. However, it is accepted that bull trout are a coldwater species and they are usually confined to waters that do not exceed approximately 15° C for extended periods of time (McPhail and Baxter 1996; Selong et al. 2001). Adult bull trout also commonly adopt a piscivorous feeding strategy when they reach a sufficient size (approximately 100 mm to 200 mm; McPhail and Baxter 1996); however, exception to adult piscivory may occur. For example, bull trout may subsist on aquatic invertebrates in communities that contain no other fish species (Marnell 1985) and some resident populations may feed predominantly on aquatic invertebrates; however, this may be a function of prey availability (McPhail and Baxter 1996).

Several studies have been conducted that provide insight into the habitat requirements of stream dwelling bull trout. Shepard et al. (1984) and McPhail and Baxter (1996) suggest that stream dwelling bull trout are associated with pools and in-stream cover. At the landscape level the occurrence of bull trout in the Boise River Basin, Idaho, was positively related to habitat patch size and negatively related to the distance to the nearest occupied habitat patch and road density (Dunham and Rieman 1999). At a finer spatial scale, the occurrence of bull trout was positively related to stream width (Dunham and Rieman 1999). In the upper Bitterroot River Drainage, Montana, stream width and the presence of large woody debris were positively related to the occurrence of bull trout and stream gradient was negatively related to the occurrence of bull trout (Rich et al. 2003). Also in their model, the presence of nonnative brook trout *Salvelinus fontinalis* was negatively related to the occurrence of bull trout.

Relatively little information is available regarding the specific habitat requirements of adfluvial bull trout. Adfluvial bull trout occupy lakes and reservoirs throughout their native range. These lakes are often high elevation alpine lakes; however, some low elevation oligotrophic lakes also contain bull trout (e.g., Flathead Lake, Montana; McPhail and Baxter 1996). Native fish assemblages within these lakes are variable, but it is not uncommon for bull trout to be the only fish species present (Donald and Stelfox 1997). In lakes that contain other fish species, bull trout are often the dominant piscivore (Donald and Alger 1993). Within the Columbia River Basin (US) there are approximately 100 lakes inhabited by adfluvial bull trout of which only a small proportion are natural lakes (8% of combined surface area), the majority being reservoirs; of these 100 lakes, 42% are located within Montana. Additionally, there are only 15 natural lakes greater than 350 ha in surface area; five of which are located within Glacier National Park, Montana (GNP; Lake McDonald, Bowman Lake, Kintla Lake, Logging Lake, and Quartz Lake). Based on these statistics, GNP stands out as an important resource for preserving the adfluvial life history of bull trout.

Recent research (Fredenberg 2002) has identified dramatic declines of bull trout over the last 30 years in the four largest lakes on the west side of the Great Divide in GNP; Bowman Lake, Kintla Lake, Lake McDonald, and Logging Lake. These declines are associated with corresponding increases in numbers of invasive lake trout *Salvelinus namaycush* (Figure 1), which have colonized these waters from downstream sources in the Flathead River Drainage. Native distributions of bull trout and lake trout are generally allopatric; however there is some overlap (Donald and Alger 1993). Donald and Alger (1993) observed that where bull trout and lake trout distributions do overlap, the species appear to be separated based on elevation. However, elevation did not appear to limit species presence; therefore, they suggested that patterns of post-glacial colonization and competitive interactions resulted in these species separation.

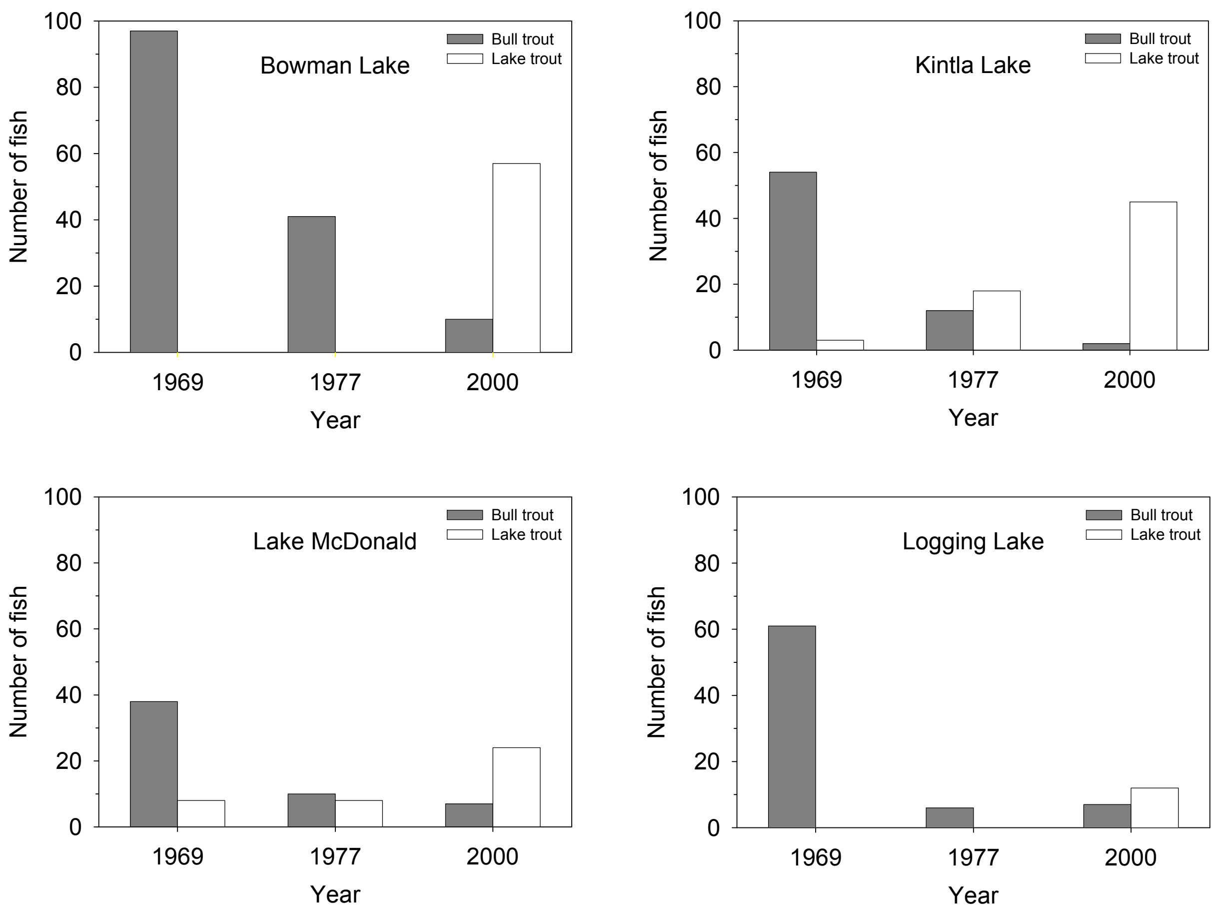

Figure 1. Number of bull trout and lake trout sampled in 1969, 1977, and 2000 during gill net surveys in Bowman Lake, Kintla Lake, Lake McDonald, and Logging Lake, Glacier National Park (reproduced from Fredenberg 2002).

Lake trout were introduced to the Flathead River-Lake ecosystem in 1905 (Spencer et al. 1991) and have since been dispersing throughout the upper Columbia River Basin. The chronology of lake trout invasion within GNP includes documentation of lake trout in Lake McDonald in 1959, Kintla Lake and Bowman Lake in 1962, Logging Lake in 1984, and Harrison Lake in 2000 (Fredenberg 2000). Furthermore the invasion of Lower Quartz Lake by lake trout was verified in 2003 (W. A. Fredenberg, US Fish and Wildlife Service, unpublished data), and lake trout were documented in Quartz Lake and Rogers Lake in 2005 (M. H. Meeuwig, MT Cooperative Fishery Research Unit, unpublished data) indicating that the spread of lake trout is ongoing. Furthermore, bull trout and lake trout appear to occupy a similar trophic niche, and lake trout introductions may result in displacement of bull trout from the position of dominant piscivore (Donald and Alger 1993). Best available science indicates that conversion of these unique native bull trout ecosystems to lake trout-dominated systems is a common result once lake trout invade and become established (Donald and Alger 1993, Fredenberg 2002). Extirpation of bull trout from at least some of these lakes is likely to occur in the near future.

This document summarizes activities and data collected in GNP during the years 2004, 2005, and 2006 related to adfluvial bull trout populations. Included in this document are summaries of gill net, electrofishing, habitat, and redd count surveys, as well as preliminary analyses of population genetic characteristics of bull trout populations and a list of ongoing and future activities. Ultimately, these data will be used to develop an action plan for the long-term monitoring, management, and recovery of bull trout resources in GNP.

Study Area

Fifteen lakes in GNP were originally identified as areas of limited information in need of examination; additionally, Rogers Lake and Upper Lake Isabel were sampled opportunistically (Figure 2). These seventeen lakes are located in the North Fork Flathead (USGS Cataloging Unit: 17010206) and Middle Fork Flathead (USGS Cataloging Unit: 17010207) watersheds (USEPA 2006). Situated in glaciated valleys, lakes within GNP can generally be classified as cirque and moraine lakes (Gallagher 1999a). These glacial lakes vary from round and deep to long and narrow, and are fed by headwater streams originating from glaciers and snowfields (Schneider 1998). Fish assemblages within GNP lakes vary from monospecific, such as Upper Kintla Lake (inhabited only by bull trout), to lakes containing intact native species assemblages, such as Cerulean Lake (inhabited by bull trout, westslope cutthroat trout *Oncorhynchus clarkii lewisi*, and mountain whitefish *Prosopium williamsoni*), to lakes containing complex fish assemblages marked by multiple nonnative introductions, such as Lake McDonald (inhabited by 14 fish species; five of which are nonnative). The selected lakes represent the known distribution of adfluvial bull trout within the Columbia River Basin portion of GNP. Characteristics defining the morphometry of the study lakes were obtained either from available map and GIS data or on site and are summarized in Table 1.

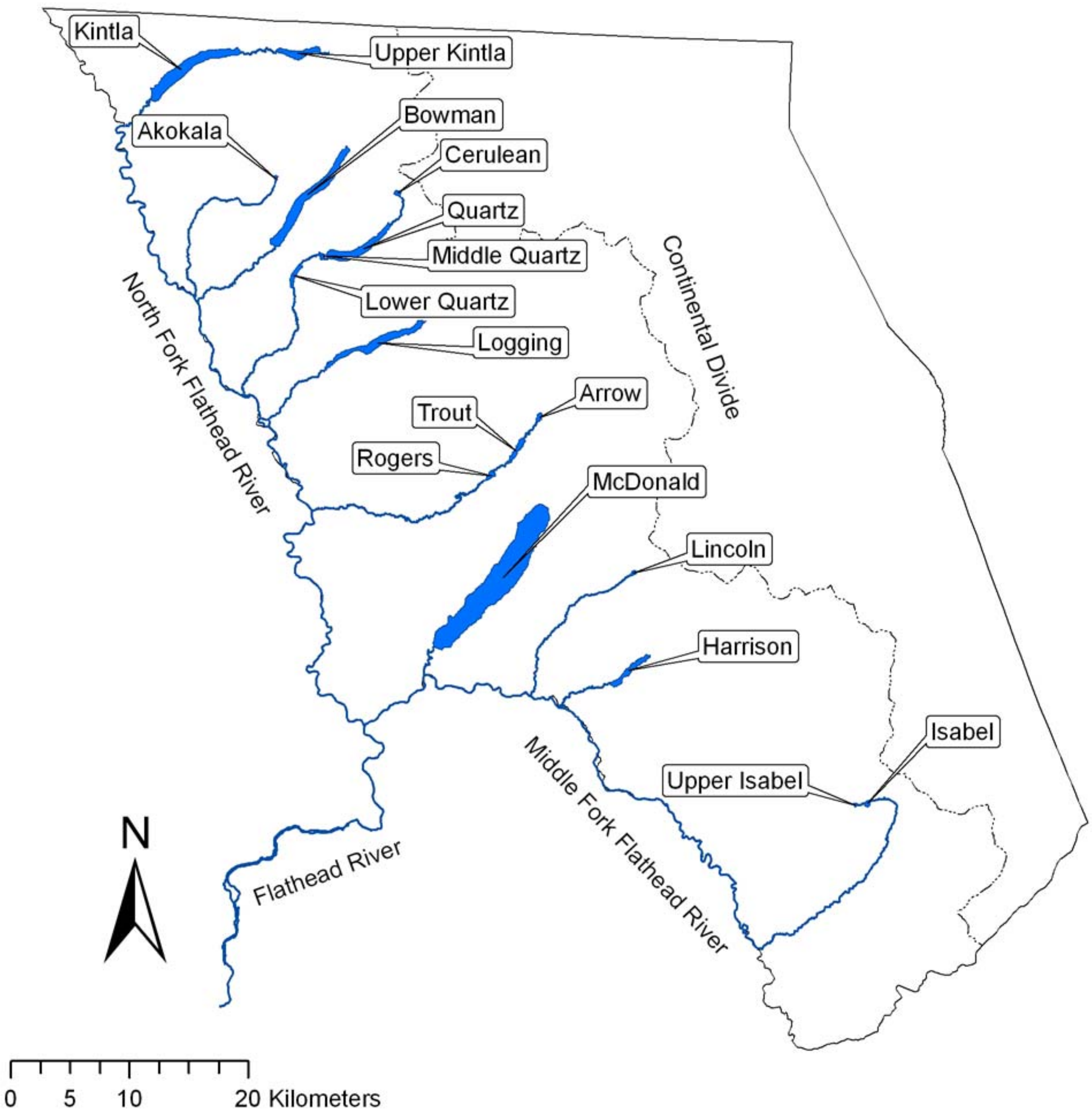

Figure 2. Seventeen lakes sampled in Glacier National Park during the years 2004, 2005, and 2006. The border of Glacier National Park is represented by a solid line (black), the Great Divide is represented by a dashed line (black), the North Fork Flathead River, Middle Fork Flathead River, and the mainstem Flathead River are represented by a bold solid line (blue), and the 17 lakes are labeled.

Table 1. Elevation, surface area, maximum length, maximum depth, and shoreline development for the 17 study lakes in Glacier National Park. Maximum depth was not measured at Upper Lake Isabel.

Lake	Elevation (m)	Surface area (ha)	Maximum length (km)	Maximum depth (m)	Shoreline development
Akokala Lake	1443	9.45	0.71	6.9	1.60
Arrow Lake	1241	23.87	0.78	16.5	1.17
Bowman Lake	1228	697.54	10.50	77.1	2.43
Cerulean Lake	1423	20.34	0.74	35.9	1.23
Harrison Lake	1126	162.62	2.29	41.1	2.16
Kintla Lake	1222	694.12	6.76	118.9	2.07
Lake Isabel	1742	18.29	0.61	16.0	1.08
Lake McDonald	961	2780.95	15.18	141.4	1.85
Lincoln Lake	1401	13.86	0.65	22.7	1.34
Logging Lake	1161	450.60	7.94	60.4	2.88
Lower Quartz Lake	1277	67.52	2.03	18.9	1.64
Middle Quartz Lake	1340	19.02	0.66	12.5	1.43
Quartz Lake	1346	351.80	4.75	83.2	2.08
Rogers Lake	1156	34.47	1.02	3.2	1.43
Trout Lake	1190	87.36	2.79	49.8	2.17
Upper Kintla Lake	1332	189.48	3.67	55.8	2.14
Upper Lake Isabel	1826	5.31	0.30		1.16

Methods

Gill Net Surveys

Gill net surveys were conducted in 16 of the 17 study lakes. Upper Lake Isabel was not sampled using gill nets because of logistic constraints (i.e., transporting netting gear with limited personnel). Surveys were conducted with sinking experimental gill nets that were 38-m long and 2-m deep and that were constructed of multifilament nylon with five panels; 19-, 25-, 32-, 38-, and 51-mm bar mesh. Gill nets were configured as either single (one 38-m net) or double (two 38-m nets tied end-to-end) and the number of gill nets set varied among lakes (Appendix 1) based on scientific collection permit requirements. Gill nets set as double nets had an identical surface area to single 76-m long by 2-m deep gill net used in previous surveys of some lakes in GNP (Fredenberg 2002). Gill nets were set in locations where target species were likely to be encountered (i.e., gill nets were non-randomly set near point bars and tributary inflows). Gill nets were set perpendicular to the lake shoreline with one end anchored near the shore. Gill nets were set from a float tube, canoe, or motorboat depending on accessibility and lake-specific boating regulations. In 2004 and 2006, some nets were set with the smallest mesh near shore and some were set with the largest mesh near shore. In 2005, all nets were set with the smallest mesh near shore to duplicate previous sampling efforts (Fredenberg 2002). Gill nets were set during the late afternoon and evening, allowed to soak overnight, and pulled in the morning beginning at sunrise. Gill net set time, soak time, pull time, and depth varied among lakes because of seasonality (i.e., day length in relation to different sampling dates), lake morphometry (i.e., size, depth profile), and accessibility (Appendix 1).

Fish sampled were identified to species and measured for total length (mm) and weight (g). Live fish were anesthetized in 30 mg/L of clove oil prior to measuring (Prince and Powell 2000). If more than 100 fish of a given species were encountered at a lake, a subsample of 100 fish was measured for length and weight and the remaining fish were counted. Size structure data were summarized as length-frequency histograms for bull trout and lake trout by lake. Catch per unit effort (C/*f*) was calculated for each gill net for bull trout and lake trout separately as:

$$\mathrm{C}/f = \frac{N}{\text{soak time} \cdot \text{net configuration}},$$

where *N* is the number of fish sampled, soak time is the number of hours that the net was set, and net configuration is 1 (one 38 m gill net) or 2 (two 38 m gill nets tied end-to-end and set as one).

Ten separate linear regression models were used to examine the influence of environmental variables (i.e., lake surface area, lake maximum depth, lake maximum length, shoreline development, and available spawning habitat) on bull trout relative abundance (mean C/*f*) for lakes where lake trout are absent and for lakes where lake trout are present (PROC REG; SAS Institute 1999). Lake surface area, maximum length, and shoreline development were obtained from existing GIS data. Lake maximum depth was determined either on-site or from existing bathymetric data. Available spawning habitat was measured as the kilometers of stream habitat of the primary inlet of each lake with a gradient of less than or equal to 2% (Fraley and Shepard 1989). Stream elevation profiles were derived by obtaining elevation data at increments of 0.05 km along each stream reach (e.g., Figure 3) using TOPO! Mapping Software (National Geographic Maps, Evergreen, CO). Gradient for each increment was calculated as:

$$\text{Gradient} = \left(\frac{elevation_j - elevation_i}{0.05} \right) \cdot 100\%$$

where $elevation_j$ is the elevation at the upstream end of the 0.05 km increment and $elevation_i$ is the elevation at the downstream end of the 0.05 km increment. The number of increments with a slope equal to or less than 2% were summed and multiplied by 0.05 km and recorded as available spawning habitat. Stream reaches included in this analysis were those between the lake of interest and the stream origin, the next lake in an upstream direction, or a known migratory barrier (see below). Additionally, if a stream had an average gradient greater than or equal to 15% for at least 0.50 km, only habitat downstream of the high gradient reach was included in the analysis (e.g., Figure 4).

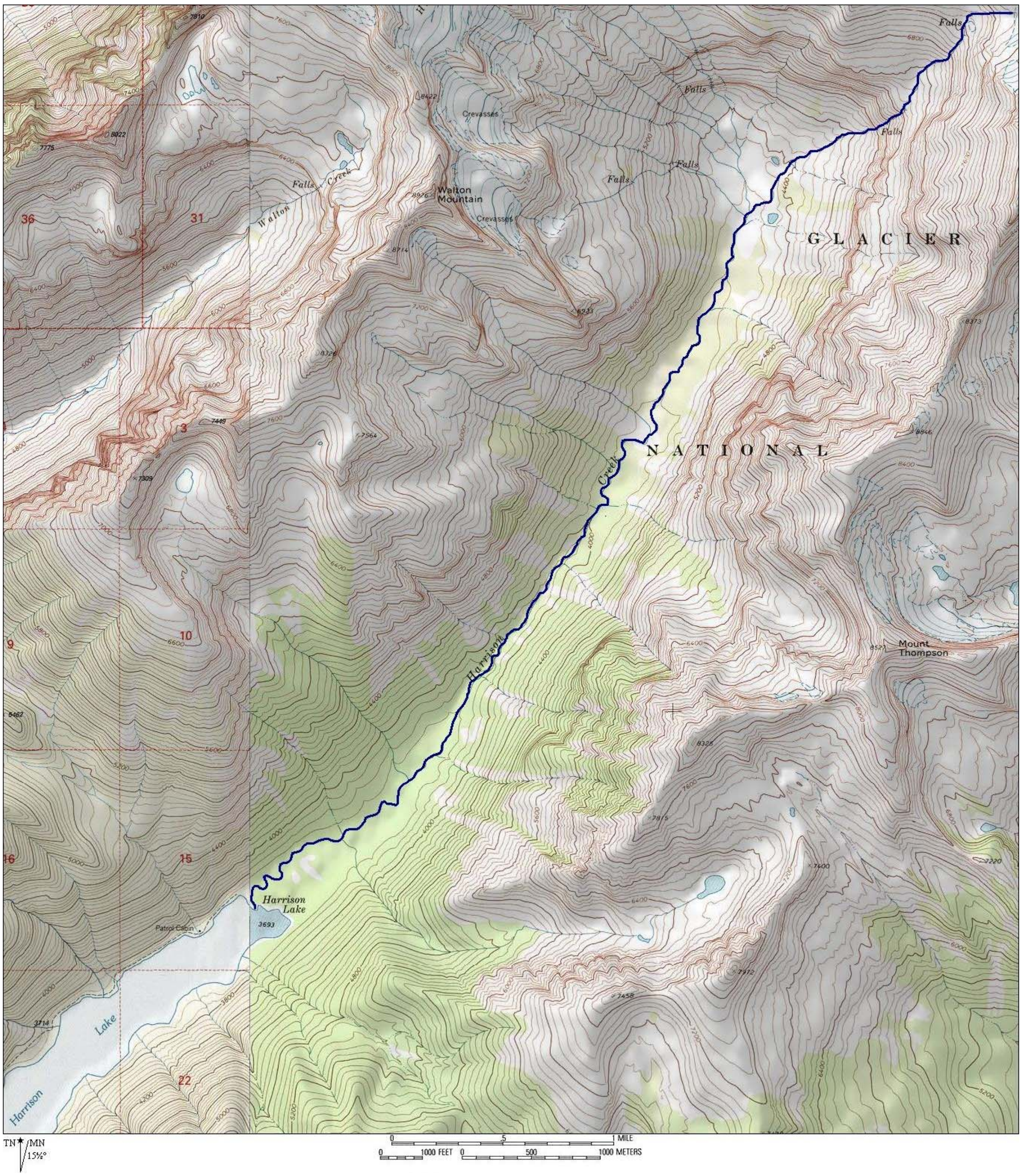

Figure 3. Stream reach (bold line) for which elevation data were derived to determine stream gradient and available spawning habitat (example from Harrison Creek).

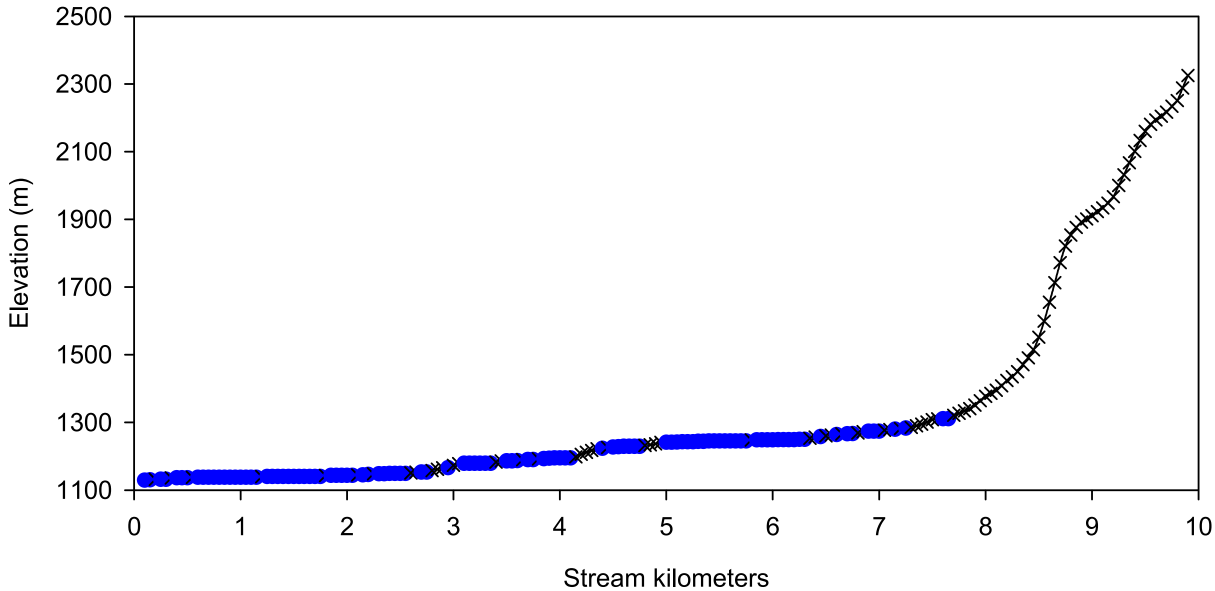

Figure 4. Elevation as a function of stream kilometer (measured from lake; example from Harrison Creek). Available spawning habitat (filled circle) based on 0.05 km stream reaches with a gradient less than or equal to 2%. Unavailable spawning habitat (X) based on 0.05 km stream reaches with a gradient greater than 2% or areas above a 0.50 km reach with an average gradient greater than 15%.

The statistical model for each regression model examining the influence of environmental variables on bull trout relative abundance was:

$$Y = \beta_0 + \beta_1 X + \varepsilon ,$$

where Y is the value of the response variable, β_0 is the parameter of the intercept, β_1 is the parameter for the slope, X is the value of the predictor variable, and ε is the random error term. Lake surface area, lake maximum length, and available spawning habitat were normalized using a $\log_{10}$ transformation. For each model examining the influence of environmental variables on bull trout relative abundance, outliers were detected using a Bonferroni test procedure on the absolute value of the studentized deleted residuals (Neter et al. 1996). The influence of each observation determined to be an outlier was examined using *DFFITS* values (Neter et al. 1996). Observations that were both outliers and influential on the predicted value of Y in the regression model were removed from the model.

Three separate analysis of variance (ANOVA) models were used to compare bull trout relative abundance between lake trout absent and lake trout present lakes (PROC MIXED; SAS Institute 1999). Each model included the presence or absence of lake trout as a fixed effect, one environmental variable (i.e., surface area, maximum depth, shoreline development) as a quantitative predictor, and the interaction between these two terms. Models including lake maximum length and available spawning habitat were not examined as they did not have a significant effect on bull trout relative abundance (see below). The statistical model for each analysis was:

$$y_{ijk} = \mu + \tau_i + e_{ij} + d_{ijk} \text{ ,}$$

where μ is the general mean, τ_i is the fixed effect of the i^{th} treatment, e_{ij} is the random experimental error effect for the j^{th} experimental unit of the i^{th} treatment, and d_{ijk} is the random effect for the k^{th} subsample of the j^{th} experimental unit of the i^{th} treatment. For these analyses, individual lakes were treated as the experimental unit and individual gill nets were treated as random subsamples within the experimental unit (Kuehl 1994).

Hook and Line Surveys

Hook and line sampling was conducted opportunistically in an effort to increase sample sizes of target species (i.e., bull trout and lake trout) for genetic and stable isotope analyses. Fish were anesthetized in 30 mg/L of clove oil (Prince and Powell 2000), identified to species, and measured for length (mm) and weight (g).

Shoreline Electrofishing Surveys

Shoreline electrofishing surveys were conducted at 15 of the 17 study lakes. Shoreline electrofishing surveys were not conducted at Cerulean Lake or Upper Lake Isabel. Electrofishing surveys occurred during the late afternoon and evening crepuscular period using a backpack electrofishing unit (model LR-24 Electrofisher, Smith-Root, Inc., Vancouver, WA). The LR-24 Quick Setup option was used to produce a 30 Hz, 12% duty cycle at 25 W power output with the exception of Arrow Lake where a 10% duty cycle was used. Output voltage was increased if fish were not exhibiting taxis and varied from 275 to 810 V among shoreline electrofishing sites. Preliminary data suggest that juvenile bull trout are more likely to be detected in shoreline habitat consisting of cobble and boulder substrate (i.e., ≥ 64 mm particle size; M. H. Meeuwig, MT Cooperative Fishery Research Unit, unpublished data); therefore, sample sites were non-randomly selected in an attempt to maximize the likelihood of bull trout detection (Rieman and McIntyre 1995). Shoreline electrofishing sites were 100-m long by 3-m wide with the exception of Arrow Lake and Lake Isabel (Appendix 2). The number of sites sampled per lake varied from two to 10 (Appendix 2). Sites were not closed systems (i.e., nets were not used to confine individuals within the site) and sampling methods consisted of a single pass through the site with the backpack electrofishing unit. Fish were anesthetized in 30 mg/L clove oil (Prince and Powell 2000), identified to species, measured for total length (mm) and weight (g), and returned to the lake.

Habitat characteristics of shoreline electrofishing sites were quantified at evenly spaced transects arranged perpendicular to the shoreline. Transects were spaced at 10-m intervals from the beginning of the site to the end of the site. At each transect, depth measurements were recorded at 0.25, 0.50, and 0.75 times the width of the site (held constant at 3.0 m). Mean transect depth was calculated as:

$$\text{Mean transect depth} = \frac{\sum \text{depth}}{N+1},$$

where depth is the three depth measurements and *N* is the number of depth measurements made (Peterson et al. 2002). Mean site depth was calculated as the arithmetic mean of the average transect depths (Peterson et al. 2002). At each transect substrate type and embeddedness were quantified at 0.25, 0.50, and 0.75 times the width of the site. Substrate type was classified as silt and clay (particle size less than 0.059 mm), sand (0.06-1 mm), gravel (2-15 mm), pebble (16-63 mm), cobble (64-256 mm), boulder (greater than 256 mm) (Bain 1999), bedrock, and other (e.g., woody debris and bryopsids). Substrate embeddedness was classified as negligible (less than 5% of substrate covered by fine sediment), low (5-25% of substrate covered by fine sediment), moderate (25-50% of substrate covered by fine sediment), high (50-75% of substrate covered by fine sediment), and very high (greater than 75% of substrate covered by fine sediment) (Bain 1999). Substrate type and embeddedness were coded following Bain (1999; Table 2).

Table 2. Substrate type and embeddedness classifications and associated codes following Bain (1999).

Substrate type			Substrate embeddedness	
Classification	Code		Classification	Code
Silt and clay	0		Negligible	0
Sand	1		Low	1
Gravel	2		Moderate	2
Pebble	3		High	3
Cobble	4		Very high	4
Boulder	5			
Bedrock	6			
Other	7			

For each site, mean substrate type was calculated as:

$$\text{Mean substrate type} = \frac{\sum \text{type code}}{N},$$

where type code is given in Table 2 and *N* is the number of substrate type measurements made (Bain 1999). Dominant substrate type was calculated as the modal substrate type observed in the site. Mean substrate embeddedness was calculated as:

$$\text{Mean substrate embeddedness} = \frac{\sum \text{embeddedness code}}{N},$$

where embeddedness code is given in Table 2 and *N* is the number of substrate embeddedness measurements made (Bain 1999). Temperature (° C), dissolved oxygen (mg/L), conductivity (µS/cm), and salinity (ppt) were measured once at each electrofishing site.

Stream Electrofishing Surveys

Primary inlet and outlet streams for the study lakes, within close proximity to the lake (e.g., < 200 m from the lake), were sampled using a backpack electrofishing unit (model LR-24 Electrofisher, Smith-Root, Inc., Vancouver, WA). The electrofishing unit was set up as above and output voltage varied from 450 to 990 V among stream electrofishing sites. Inlet and outlet streams of Cerulean Lake, Harrison Lake, Lake McDonald, Rogers Lake, and Upper Lake Isabel, and the outlet stream of Kintla Lake were not sampled. Only one site was sampled between Quartz Lake and Middle Quartz Lake because of their close proximity (less than 0.4 m); this site is referred to as the inlet of Middle Quartz Lake. Sampling consisted of a single pass through a stream section approximately 100 m in length. All fish sampled were anesthetized in 30 mg/L clove oil (Prince and Powell 2000), identified to species, measured for total length (mm) and weight (g), and returned to the stream.

Habitat was quantified at transects spaced at 10-m intervals along the thalweg within each stream section. Maximum depth (m), and wetted width (m) were measured along each transect. Depth (m), substrate type, and substrate embeddedness were measured at three points along each transect (0.25, 0.50, and 0.75 times the wetted width of the transect). Mean transect depth, mean site depth, mean and dominant substrate type, and mean substrate embeddedness were calculated as above. Percent slope was calculated as:

$$\text{Percent slope} = \frac{\text{rise}}{\text{run}} \cdot 100\%,$$

where rise is the highest elevation minus the lowest elevation and run is the length of the site.

Within each site the number of pieces of woody debris was counted. Woody debris was defined as pieces of wood lying above or within the active channel. Woody debris was classified as single (a piece of wood at least 3 m long and 10 cm in diameter), aggregate (more than four pieces of wood acting as a single component), or root wad (Peterson et al. 2002). Undercut banks, defined as areas beneath the stream banks, boulders, bedrock, or wood that are at least 5 cm wide and within 0.5 m above or below the water surface (Peterson et al. 2002), were measured within each site. The length and three width measurements (at 0.25, 0.50, and 0.75 times the length) were recorded for each undercut bank. Temperature (° C), dissolved oxygen (mg/L), conductivity (µS/cm), and salinity (ppt) were measured once for each electrofishing site.

Barrier Surveys

Barrier surveys were conducted in drainages between the study lakes and the North Fork or Middle Fork Flathead rivers for all study lakes. Additionally, barrier surveys were conducted between Arrow Lake and Camas Lake and between Logging Lake and Grace Lake to determine if natural colonization of these waters by bull trout is possible. Camas Lake and Grace Lake are currently uninhabited by bull trout, but contain populations of Yellowstone cutthroat trout *O. clarkii bouvieri* as a result of stocking efforts. Barrier surveys consisted of either examining potential barriers at single locations along a stream (point surveys) or walking along entire stream reaches (reach surveys) and quantifying the location and morphometry of potential salmonid dispersal barriers (i.e., waterfalls and cascades with a vertical drop greater than 1.8 m; Evans and Johnston 1980, cited by Powers 1984). For each potential dispersal barrier, the height and width of the structure was measured (Gallagher 1999b), it was photographed, and its location was recorded using a hand-held global positioning system (GPS) receiver (model GPSmap 60CS; Garmin International Inc., Olathe, Kansas).

Redd Surveys

Bull trout redd surveys were conducted on Bowman Creek, Quartz Creek, Logging Creek, and Harrison Creek in 2004, 2005 and 2006. Bowman Creek was surveyed from the inlet of Bowman Lake upstream to a point where the creek went subsurface. Harrison Creek was surveyed from the inlet of Harrison Lake upstream to a point where the stream gradient rapidly increases. Logging Creek was surveyed from the inlet of Logging Lake upstream to Grace Lake in 2004 and to a dispersal barrier located between Logging Lake and Grace Lake in 2005 and 2006. Quartz Creek was surveyed from the inlet of Lower Quartz Lake upstream to Middle Quartz Lake in 2004 and to a point where the stream gradient rapidly increases in 2005 and 2006. Quartz Creek was surveyed from the inlet Middle Quartz Lake upstream to Quartz Lake. Quartz Creek was surveyed from the inlet of Quartz Lake upstream past its confluence with Rainbow Creek in 2004 and to its confluence with Rainbow Creek in 2005 and 2006.

Redd surveys where conducted by two or three trained technicians in a downstream to upstream direction. The length of the survey reach was determined by a qualitative assessment of spawning habitat suitability (e.g., substrate type and stream gradient), and the location of the reach starting and ending points were recorded (UTM). The date and water temperature (° C) were recorded at the beginning of the survey. When redds were encountered, a location was recorded (UTM). The location and number of redds observed in each reach were summarized by sample year.

Age Estimates

Sagittal otoliths were removed from bull trout, lake trout, and a subsample of cutthroat trout that died during gill net surveys. Bull trout otoliths were embedded in epoxy resin, and sectioned in the transverse plane to a thickness of 0.58 mm using a low speed saw

(IsoMet Low Speed Saw, Buehler, Lake Bluff, IL). Sectioned otoliths were mounted to a standard microslide and sanded (400 grit sandpaper) and polished (1200 grit sandpaper) to increase transparency as needed. The transverse section was observed under a compound microscope at 100 to 200X and annuli were counted to determine fish age. Fish age was determined without knowledge of fish size (length or weight).

Two independent age readings were made for each otolith and the precision of the age readings was calculated as the percent coefficient of variation (CV);

$$\mathrm{CV} = 100\% \cdot \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(X_{ij} - X_j\right)^2}{R-1}}}{X_j},$$

where X_{ij} is the i^{th} age determination of the j^{th} fish, X_j is the mean age of the j^{th} fish, and R is the number of times each fish is aged (Campana and Jones 1992).

Population Genetics

A non-lethal fin-clip (approximately 25 mm^2) was collected from the anal fin of all bull trout, lake trout, and a subsample of cutthroat trout encountered during gill net and hook and line surveys. Fin clips were stored in 95% ethanol and archived at Montana State University.

DNA was extracted from 195 bull trout fin clips comprising 16 lakes using a QIAGEN DNeasy Tissue Extraction Kit (QIAGEN Inc., Valencia, CA). Ten microsatellite loci were amplified using the polymerase chain reaction (PCR) method in a DNA Engine DYAD thermal cycler (Bio-Rad Laboratories, Hercules, CA). Allele lengths were measured using an ABI 3100-*Avant* Genetic Analyzer (Applied Biosystems, Foster City, CA) and bull trout were genotyped using GeneMapper software (Applied Biosystems, Foster City, CA).

Observed heterozygosity (H_o), a measure of genetic diversity, was calculated for each lake as:

$$H_o = \frac{\sum_{i=1}^{\text{Number of loci}} \left(N_i \text{ individuals heterozygous} / N_i \text{ individuals sampled}\right)}{N \text{ loci}},$$

where N_i individuals heterozygous is the number of individuals heterozygous at the ith locus, N_i individuals sampled is the number of individuals sampled at the ith locus, and N loci is the number of loci examined. Expected heterozygosity (H_e) was calculated for each lake as:

$$H_e = \frac{\sum_{i=1}^{\text{Number of loci}} \left(1 - \sum_{j=1}^{\text{Number of alleles}} p_j^2\right)}{N \text{ loci}},$$

where p_j is the observed frequency of the *j*th allele at the *i*th locus and *N* loci is the number of loci examined. Deviation from Hardy-Weinberg equilibrium was calculated based on observed and expected heterozygosity for each population using the software package GENEPOP (GENEPOP on the Web, http://wbiomed.curtin.edu.au/genepop/). Allelic diversity (*A*), a measure of genetic diversity, was calculated for each population as:

$$A = \frac{\text{total number of alleles over all loci}}{\text{number of loci}}.$$

Pairwise F_{st} values for each pair of lakes were computed using the software package GENEPOP. Pairwise F_{st} values were used as a measure of genetic distance to compare the divergence between lakes (Frankham et al. 2002). A neighbor joining tree was produced to provide a visual representation of the divergence among lakes based on observed F_{st} values for each pair of lakes using the software package MEGA (Kumar et al. 2004; http://www.megasoftware.net/).

Stable Isotope Analysis

White muscle samples were collected from a subsample of fish encountered at each lake for stable isotope analysis to examine trophic relationships among species and lakes. Equipment available for field storage (freezing) of samples limited sample storage to approximately 80 samples. Therefore, subsampling was used to provide a representative sample of all fish species present in a lake. Fish were subsampled based on the following protocol:

- A minimum of 10 bull trout, if available,
- A minimum of 10 lake trout, if available,
- Equal numbers of all other fish species present until a total of 80 samples were collected.

Additionally, only bull trout and lake trout individuals large enough to be considered likely piscivores were sampled (e.g., > 200 mm; McPhail and Baxter 1996). Because few samples are required for stable isotope analyses (generally less than 10 individuals per species; Vander Zanden and Rasmussen 2002), subsampling should allow for sufficient statistical power. A 14-gauge soft tissue biopsy needle (Achieve Soft Tissue Biopsy Needle, Cardinal Health, McGaw Park, IL) was used to non-lethally extract a sample of white muscle approximately 2 mm in diameter and 15-mm long. Muscle samples were collected from the dorsal musculature by inserting the needle in a posterior to anterior direction into the dorsal musculature near the insertion of the dorsal fin. Immediately following extraction, muscle samples were placed in a portable cryogenic freezer (CX100, Taylor Wharton, Theodore, AL). Samples were transported to Montana State University, dried for 48 h at 60° C, and ground to a fine powder. Approximately 2 to 3 mg of the dried and ground sample was placed into a 4 by 6 mm tin capsule and sent to South Dakota State University for $\delta^{13}C$ and $\delta^{15}N$ analysis (South Dakota State University – Plant Science Department, Brookings, South Dakota).

Results and Discussion

Gill Net Surveys

Bull trout sampled varied from approximately 110 to 770 mm among lakes (Figure 5). Gill nets generally sampled a broad range of bull trout sizes with exception of the Lower Quartz Lake 2005 (*N* = 4) and Rogers Lake (*N* = 1) samples, each of which had low sample sizes, and Lake Isabel (*N* = 57), which had the largest sample size, and C/*f* (see below), among bull trout sampled. Similarly, lake trout sampled varied from approximately 130 to 830 mm among lakes and the size range of lake trout sampled within lakes was related to the sample size (Figure 6).

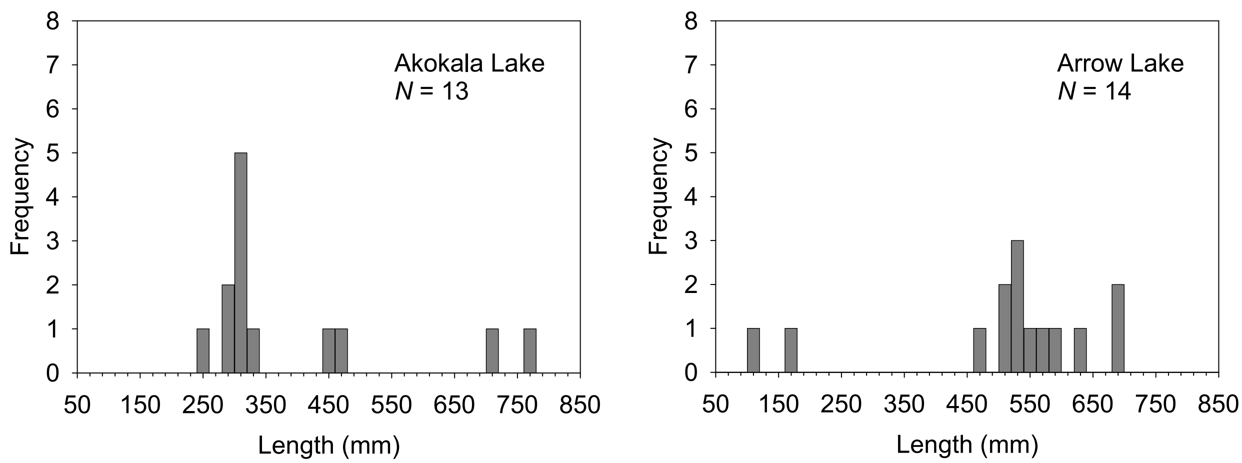

Figure 5a. Length frequency-histograms for bull trout sampled in Akokala Lake and Arrow Lake, Glacier National Park, using experimental gill nets. Length categories binned over 20 mm intervals.

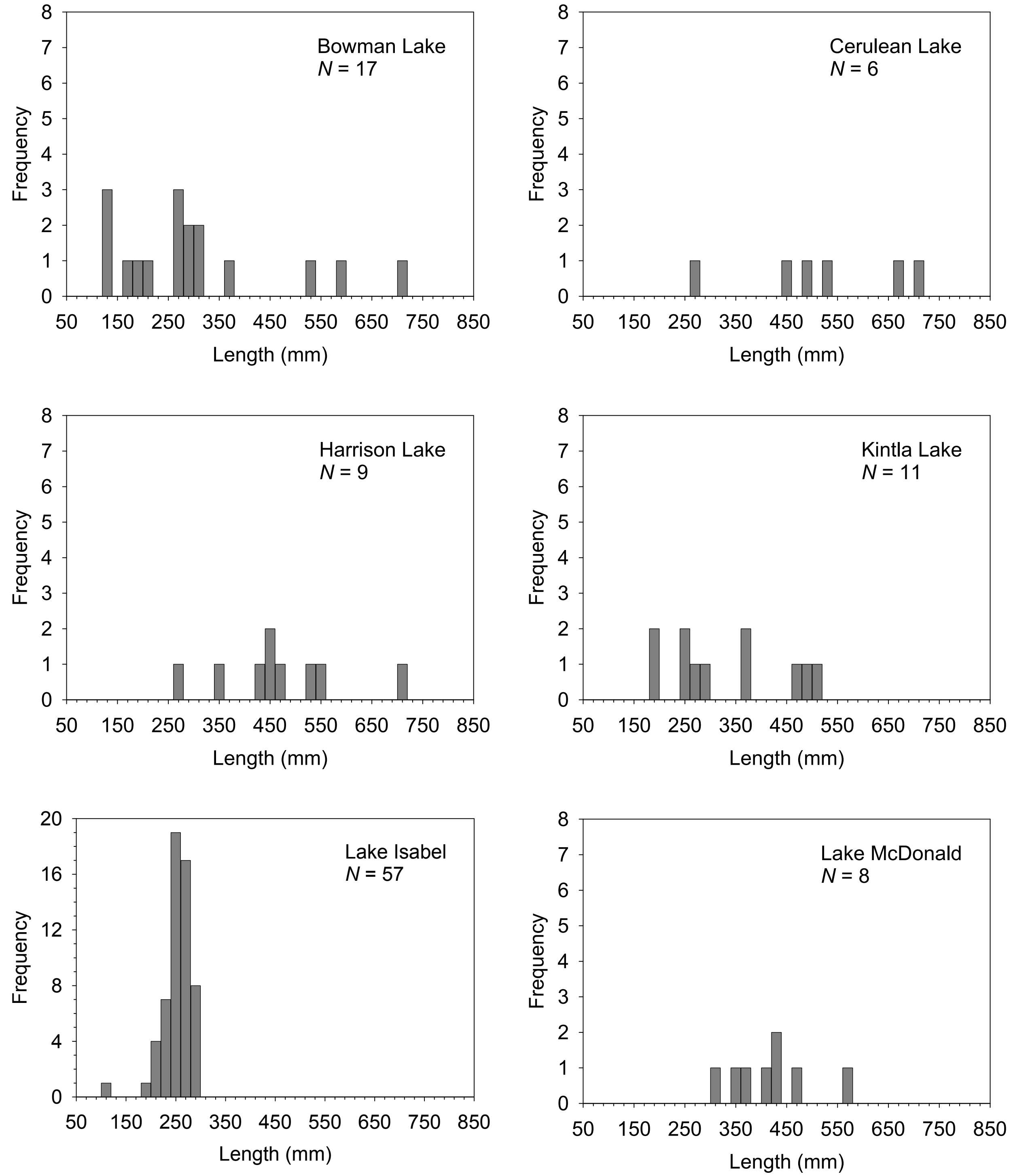

Figure 5b. Length-frequency histograms for bull trout sampled in Bowman Lake, Cerulean Lake, Harrison Lake, Kintla Lake, Lake Isabel, and Lake McDonald, Glacier National Park, using experimental gill nets. Length categories binned over 20 mm intervals.

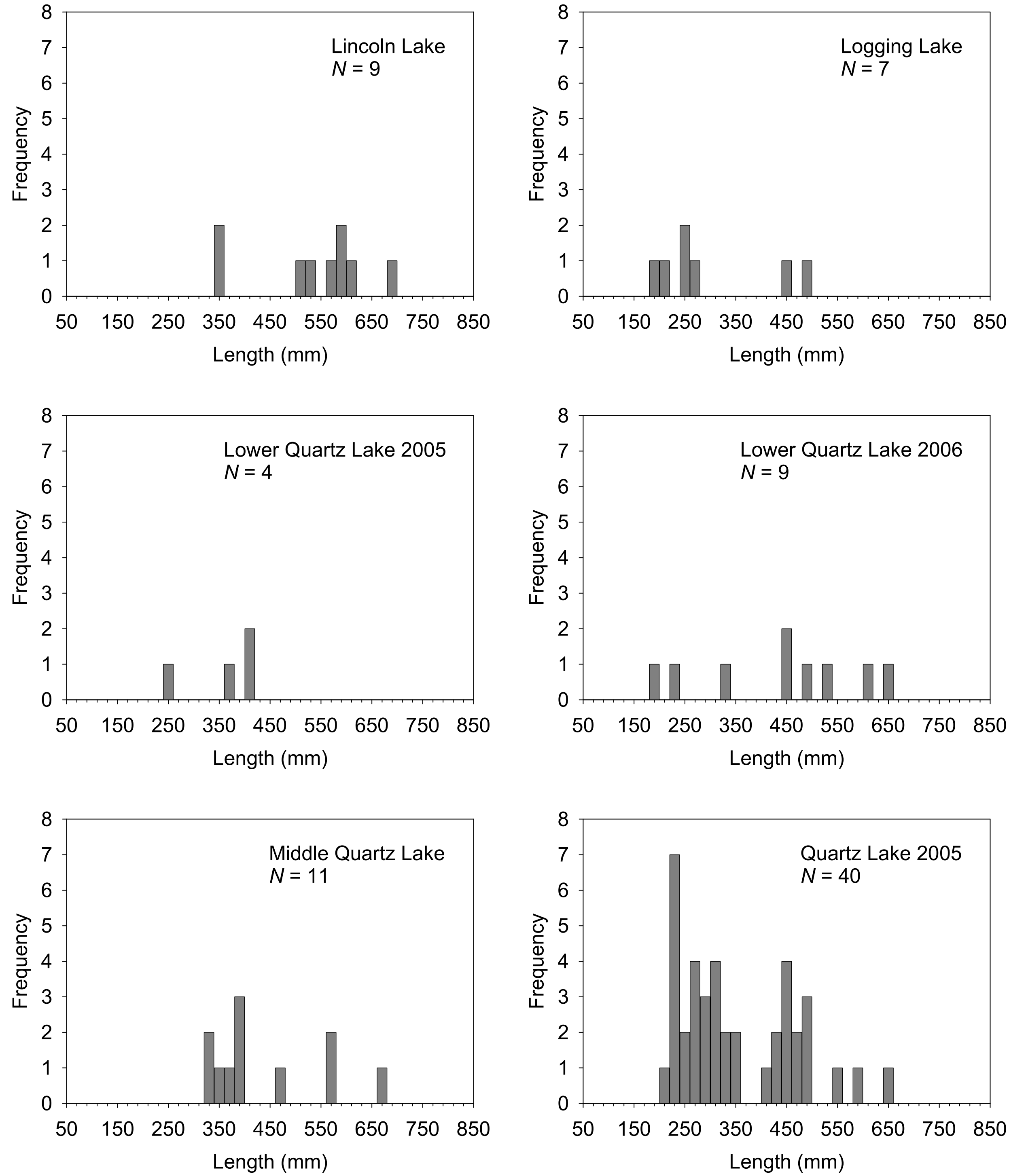

Figure 5c. Length-frequency histograms for bull trout sampled in Lincoln Lake, Logging Lake, Lower Quartz Lake (2005), Lower Quartz Lake (2006), Middle Quartz Lake, and Quartz Lake (2005) Glacier National Park, using experimental gill nets. Length categories binned over 20 mm intervals.

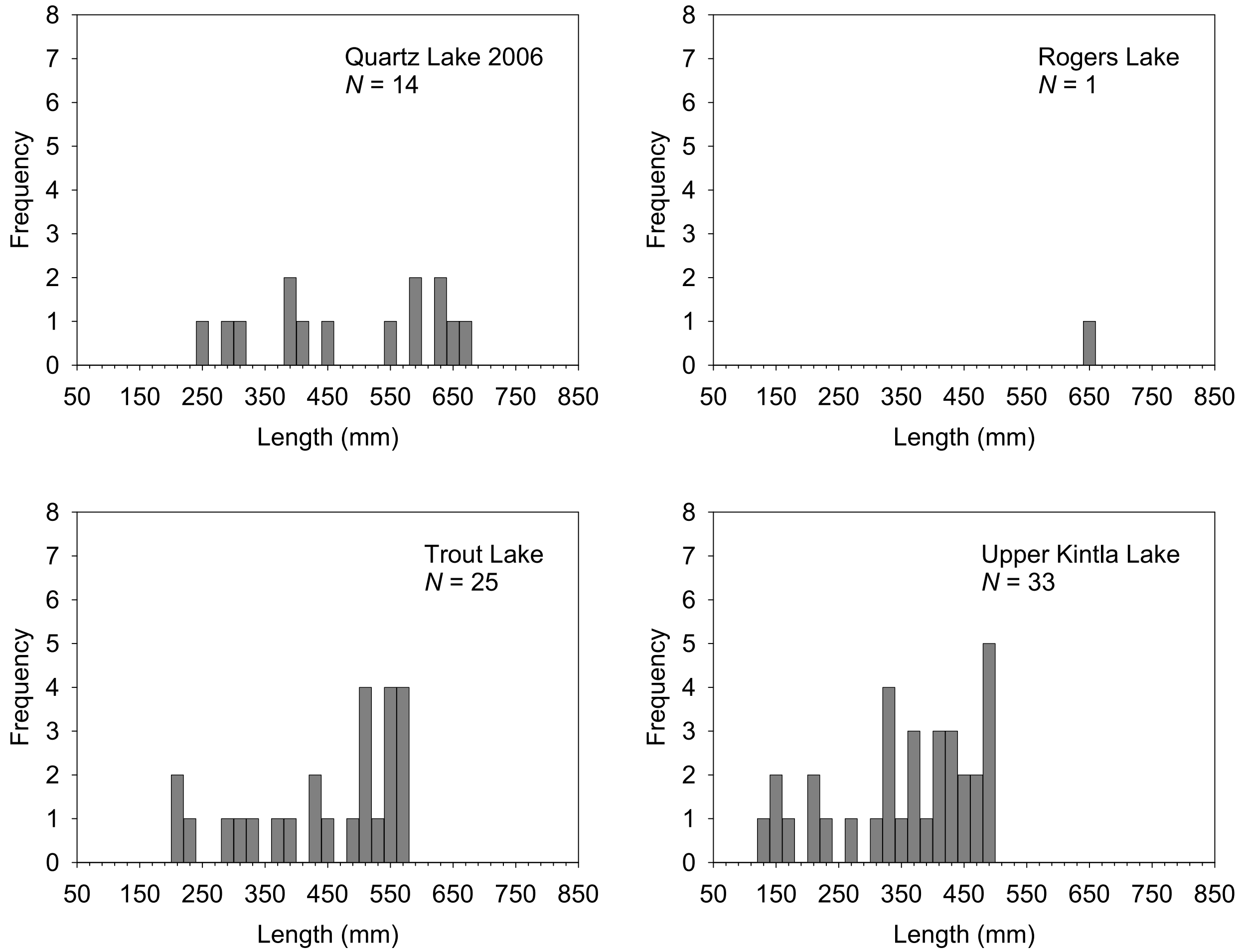

Figure 5d. Length-frequency histograms for bull trout sampled in Quartz Lake (2006), Rogers Lake, Trout Lake, and Upper Kintla Lake, Glacier National Park, using experimental gill nets. Length categories binned over 20 mm intervals.

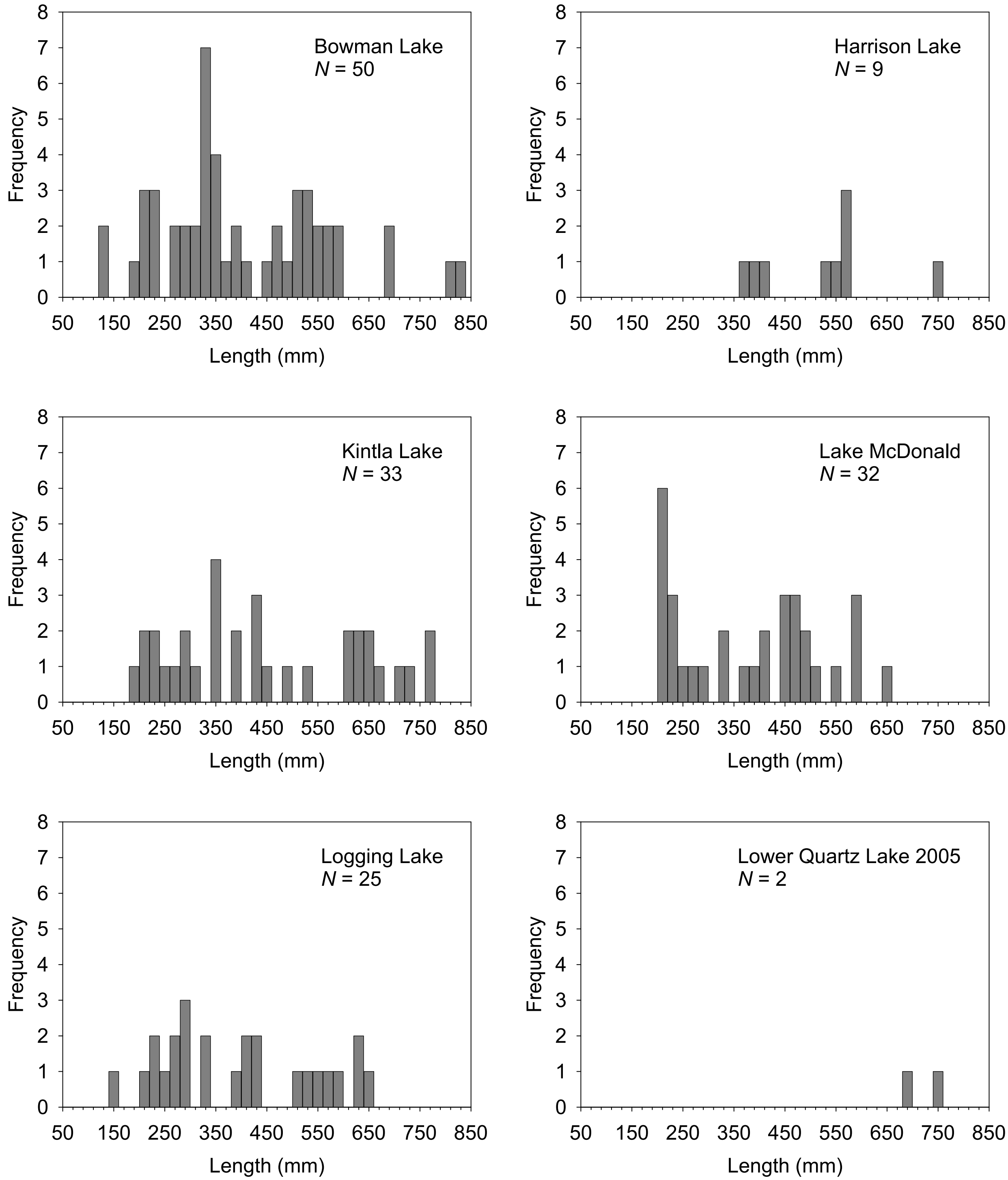

Figure 6a. Length-frequency histograms for lake trout sampled in Bowman Lake, Harrison Lake, Kintla Lake, Lake McDonald, Logging Lake, and Lower Quartz Lake (2005), Glacier National Park, using experimental gill nets. Length categories binned over 20 mm intervals.

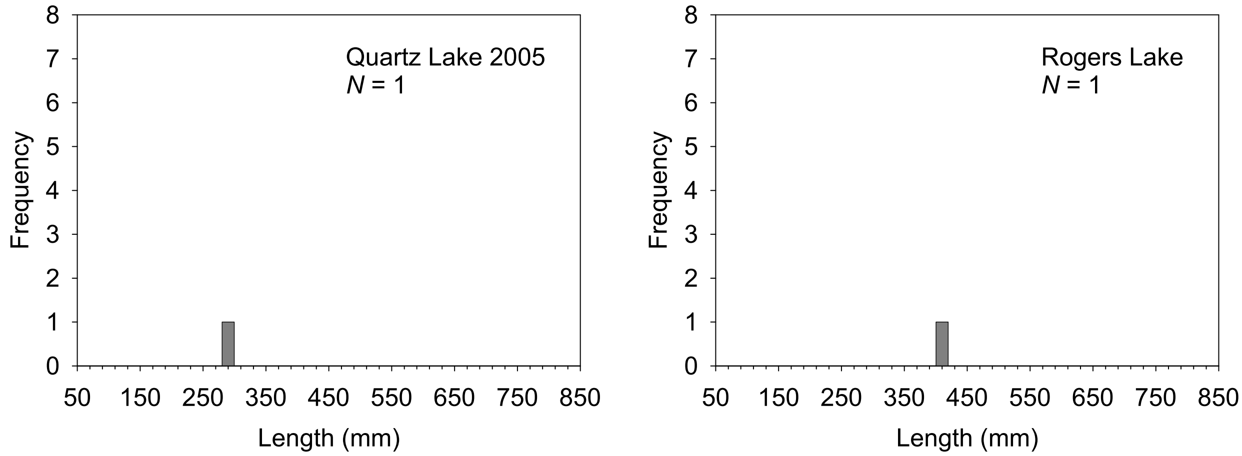

Figure 6b. Length-frequency histograms for lake trout sampled in Quartz Lake (2005) and Rogers Lake, Glacier National Park, using experimental gill nets. Length categories binned over 20 mm intervals.

Mean C/*f* varied from 0.025 to 1.081 bull trout per net·hour (Figure 7). For lakes inhabited by nonnative lake trout, mean C/*f* was less than 0.075 bull trout per net·hour, except for Quartz Lake in 2005 and 2006 and Lower Quartz Lake in 2006 (Table 3). Invasion of Quartz Lake by lake trout was documented in the summer of 2005; therefore, lake trout may be only beginning to increase in this lake and the response by bull trout populations observed in other lakes (Figure 1) may not have occurred yet. Mean C/*f* was less than 0.075 bull trout per net·hour in Lincoln Lake. Although lake trout have not been documented in Lincoln Lake, an abundance of brook trout *Salvelinus fontinalis*, a nonnative char, were sampled from this lake (Appendix 3).

For lakes inhabited by lake trout, mean C/*f* varied from 0.009 to 0.192 lake trout per net·hour (Figure 7). Lake trout C/*f* was greater than bull trout C/*f* in Bowman Lake, Kintla Lake, Lake McDonald, and Logging Lake (Table 3). Mean C/*f* was similar for lake trout and bull trout in Harrison Lake (Table 3), where lake trout invasion was documented in 2000. Mean C/*f* was similar for lake trout and bull trout in Rogers Lake and lake trout C/*f* was less than bull trout C/*f* in Lower Quartz Lake (Figure 7; Table 3). Mean C/*f* values for lake trout and bull trout from these lakes are based on a limited sample size (Appendix 3); additionally, lake trout have only recently been documented in Lower Quartz Lake (2003) and were first documented in Rogers Lake in 2005.

For all regression models examining the influence of lake morphometry on bull trout relative abundance (C/*f*) in the absence of lake trout, Lake Isabel was determined to be a influential outlier and was removed from the models. Upper Kintla Lake was determined to be an influential outlier for the regression models examining maximum length and shoreline development, and Trout Lake was determined to be an influential outlier for the regression model examining maximum length. In the absence of lake trout, bull trout relative abundance was significantly influenced by lake surface area, maximum depth, and shoreline development ($P < 0.05$; Table 4), but bull trout relative abundance was not influenced by the maximum length of the lake ($P = 0.23$; Table 4) or available spawning habitat ($P = 0.61$; Table 4).

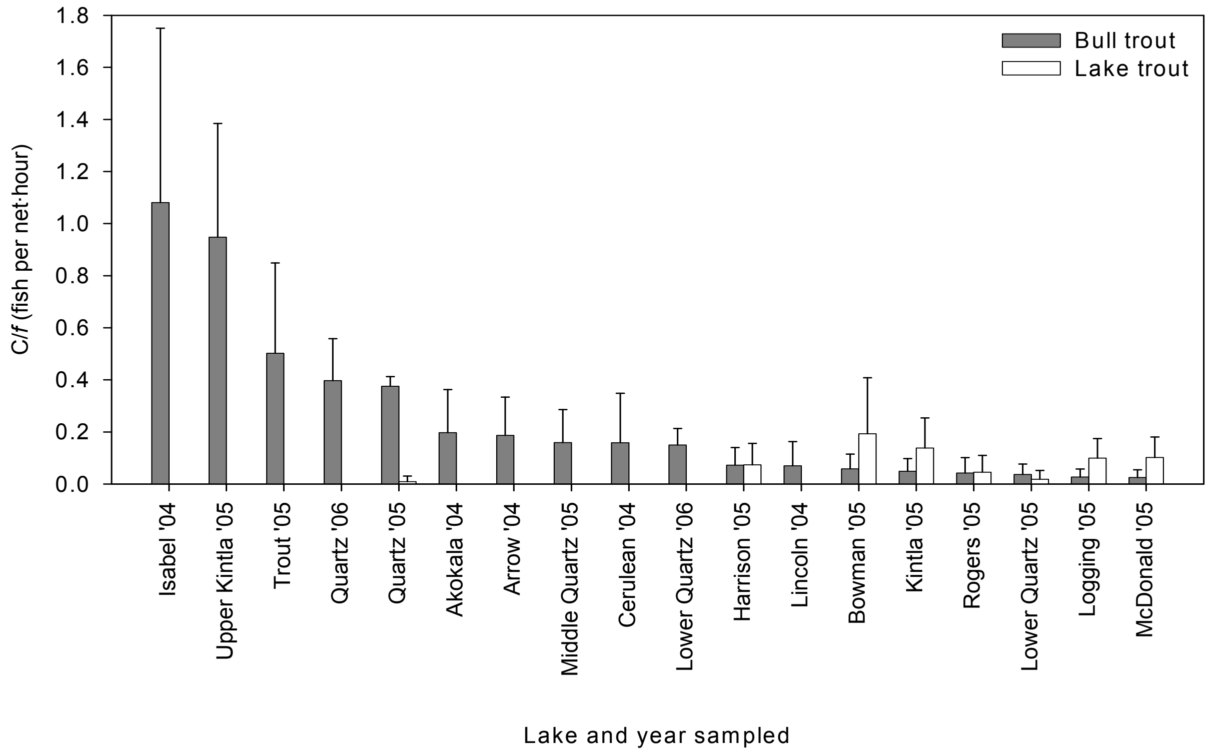

Figure 7. Mean bull trout (filled bars) and lake trout (open bars) C/*f* (fish per net·hour + standard deviation) for gill net surveys conducted in Glacier National Park.

Table 3. Mean gill net catch per unit effort (± standard deviation) for bull trout and lake trout in Glacier National Park lakes where lake trout are present.

	Catch per unit effort ± standard deviation	
Lake	Bull trout	Lake trout
Bowman Lake	0.0581 ± 0.0562	0.1924 ± 0.2154
Harrison Lake	0.0722 ± 0.0682	0.0738 ± 0.0822
Kintla Lake	0.0484 ± 0.0492	0.1379 ± 0.1159
Lake McDonald	0.0250 ± 0.0290	0.1017 ± 0.0786
Logging Lake	0.0270 ± 0.0306	0.0995 ± 0.0748
Lower Quartz Lake 2005	0.0367 ± 0.0399	0.0181 ± 0.0339
Lower Quartz Lake 2006	0.1497 ± 0.0633	0.0000 ± 0.0000
Quartz Lake 2005	0.3753 ± 0.0370	0.0088 ± 0.0216
Quartz Lake 2006	0.3967 ± 0.1608	0.0000 ± 0.0000
Rogers Lake	0.0420 ± 0.0593	0.0454 ± 0.0642

Increases in lake surface area and maximum depth result in an overall increase in habitat availability, and increases in shoreline development likely results in increased variability in microhabitat types. These increases may result in increased habitat partitioning and decreased niche overlap among fishes, reduced competition among prey fishes, and increased primary productivity. Under this scenario, there may be a greater prey base for bull trout resulting in increased abundance. Based on the *a priori* criteria for removal of influential outliers, Lake Isabel, Upper Kintla Lake, and Trout Lake were removed from the model examining the effects of lake maximum length on bull trout relative abundance in the absence of lake trout. The remaining lakes in the model (Akokala Lake, Arrow Lake, Cerulean Lake, Lincoln Lake, and Middle Quartz Lake) are all of similar length (Table 1) and all had similar relative abundance of bull trout (Figure 9), which likely resulted in the insignificant effect observed.

Available spawning habitat, as measured for this analysis, also did not have a significant effect on bull trout relative abundance. The metric used to quantify available spawning habitat (km of stream with a gradient less than 2%) may not accurately represent the realized spawning habitat. Variable such as substrate type, substrate embeddedness, cover habitat, and groundwater influence have been shown to have an influence on bull trout spawning behavior (Fraley and Shepard 1989). Substrate type and embeddedness were measured at a small scale for most of the streams examined during stream electrofishing surveys (Appendix 7); however, these data may not represent substrate type and embeddedness beyond the stream reaches examined during electrofishing surveys.

Table 4. Predictor variable, sample size (*N*), parameter estimates (β_0 = y intercept; β_1 = slope), coefficient of determination (r^2), and probability value for significance test (*P*) for regression models examining the influence of lake morphometry on the relative abundance of bull trout in lakes where lake trout were absent.

		Parameter estimates			
Predictor variable	*N*	β_0	β_1	r^2	*P*
Log_{10}(surface area)	7	-0.5959	0.6205	0.8687	0.0022
Maximum depth	7	-0.0558	0.0131	0.6376	0.0313
Log_{10}(maximum length)	5	0.3088	1.0249	0.4329	0.2274
Shoreline development	6	-0.3260	0.3613	0.7841	0.0189
Log_{10}(spawning habitat)	8	0.4590	0.0939	0.0463	0.6089

For lakes where lake trout were present, none of the predictor variables examined had a significant influence on bull trout relative abundance (Table 5). Variability in bull trout relative abundance was poorly explained by the variables examined, and the slope parameters for the models examined were near zero (Table 5).

Table 5. Predictor variable, sample size (*N*), parameter estimates (β_0 = y intercept; β_1 = slope), coefficient of determination (r^2), and probability value for significance test (*P*) for regression models examining the influence of lake morphometry on the relative abundance of bull trout in lakes where lake trout were present.

Predictor variable	*N*	Parameter estimates β_0	β_1	r^2	*P*
Log_{10}(surface area)	10	0.1215	0.0007	0.0000	0.9940
Maximum depth	10	0.0993	0.0004	0.0133	0.7507
Log_{10}(maximum length)	10	0.1293	-0.0099	0.0007	0.9439
Shoreline development	10	0.1257	-0.0013	0.0000	0.9917
Log_{10}(spawning habitat)	10	0.1053	0.1192	0.1648	0.2444

The interaction between lake trout presence and lake surface area had a significant effect on bull trout relative abundance ($F_{1,\ 12.4}$ = 19.41, P = 0.0008). Similarly, the interaction between lake trout presence and lake maximum depth had a significant effect on bull trout relative abundance ($F_{1,\ 12.6}$ = 10.84, P = 0.0061). The interaction between lake trout presence and shoreline development had a marginally insignificant effect on bull trout relative abundance ($F_{1,\ 11.4}$ = 4.07, P = 0.0679); examination of main effects for this model indicated that neither lake trout presence ($F_{1,\ 12.9}$ = 2.68, P = 0.1259) nor shoreline development ($F_{1,\ 12.5}$ = 1.09, P = 0.3153) had a significant effect on bull trout relative abundance (non-significant interaction term removed). Based on Akaike's information criterion values, adjusted for small sample size, the model that included lake trout presence and surface area provided the best fit to the data (Burnham and Anderson 1998).

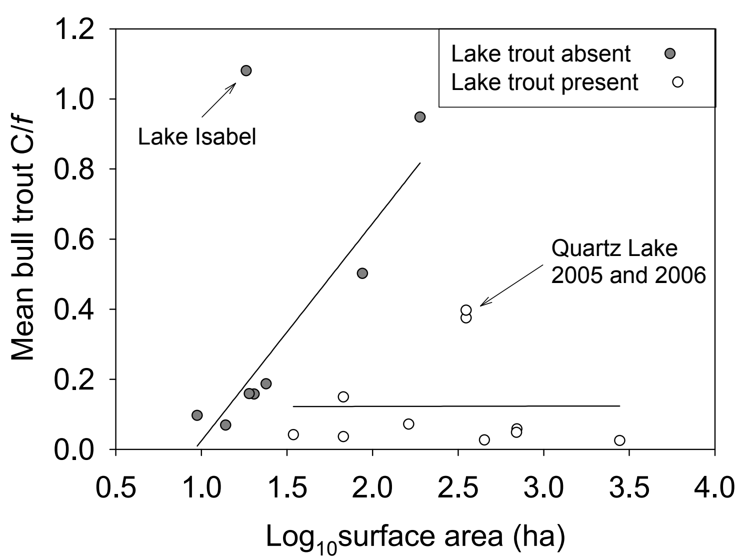

Figure 8. Interaction between lake trout presence and lake surface area on bull trout relative abundance for lakes in Glacier National Park.

Bull trout C/*f* remained relatively low and consistent among lakes invaded by lake trout; however, bull trout C/*f* increased with increasing lake surface area among lakes not invaded by lake trout (Figure 8). Bull trout relative abundance from Lake Isabel was not included in this analysis as it was shown to be an influential outlier; however, it is included in Figure 8 to illustrate the magnitude of its difference from other lakes. Samples from Quartz Lake (2005 and 2006) are also highlighted in Figure 8 to illustrate their intermediate values between lakes invaded and not invaded by lake trout. Lake trout were only recently documented in Quartz Lake and this invasion may not have had enough time to produce significant declines in bull trout abundance.

These data suggest that bull trout relative abundance is influenced by habitat availability and possibly niche availability (see above) when lake trout are absent. Invasion by nonnative lake trout may result in suppression of bull trout populations to levels below that which may be naturally present in the absence of lake trout.

Hook and Line Surveys

Hook and line sampling was conducted at 14 of the 17 study lakes (Appendix 3). Individuals sampled using hook and line accounted for a large proportion of bull trout sampled at some lakes (e.g., Cerulean Lake: 14 of the 20 bull trout sampled). Effort related to hook and line sampling was not documented; therefore, it is difficult to describe the relative contribution of this method to the total sample. However, hook and line sampling generally appears to be a viable and simple sampling method for trout and char in the remote lakes examined in this study, and was efficient in increasing sample sizes of target species.

Shoreline Electrofishing Surveys

Shoreline electrofishing resulted in the sampling of small (e.g., < 150 mm) bull trout from four of the 15 lakes sampled. Bull trout length varied from 37 to 148 mm among lakes (Table 6). Length at age for bull trout in the Saint Mary River Drainage, Montana and Alberta, is 103.2 ± 5.2 mm (age-1), 155.4 ± 3.8 mm (age-2), and 191.5 ± 3.9 mm (age-3) (mean length ± 95% confidence interval; Mogen and Kaeding 2004). Assuming that growth rates of bull trout in the Saint Mary River Drainage are similar to those in the lakes sampled at similar latitudes, bull trout observed inhabiting shoreline habitat were within their juvenile life stage and possibly age-1 fish. Additionally, length-at-age data from this study indicates that age-2 bull trout varied from 120 to 266 mm (see below); although, these data are not comprehensive and represent a small sample size. Therefore, the presence of these individuals within lake littoral zone habitats offers an exception to the general “rule” that juvenile bull trout (age 1 to 3) occupy fluvial systems regardless of adult life history strategy (McPhail and Baxter 1996).

Bull trout were not detected in shoreline habitat for 11 of the 15 lakes examined; however, water temperatures of shoreline habitat were often greater than that preferred by bull trout (e.g., 15° C; McPhail and Baxter 1996; Selong et al. 2001) and exceeded 20.0° C at some sites (Appendix 5). Additionally, bull trout were detected in shoreline habitat for lakes that had among the greatest gill net C/*f* for bull trout with the exceptions of Trout Lake and Quartz Lake, both of which are large lakes resulting in limited representation of total available habitat in shoreline electrofishing samples.

Table 6. Lake, site code, date sampled, temperature, electrofishing time (Fishing time), number of bull trout sampled (*N*), catch per unit effort (C/*f*; fish per minute), and minimum (Min.) and maximum (Max.) length for bull trout sampled during shoreline electrofishing surveys in Glacier National Park.

Lake	Site	Date	Temperature (° C)	Fishing time (min)	*N*	C/*f*	Length (mm) Min.	Length (mm) Max.
Akokala Lake	03	07/11/2004	9.2	14.63	1	0.07		37
	04	07/11/2004	8.6	25.45	1	0.04		44
	05	07/12/2004	11.3	15.90	0	0.00		
	06	07/12/2004	10.2	22.23	0	0.00		
Arrow Lake	02	06/25/2004		29.17	15	0.51	73	142
	04	06/26/2004		16.73	3	0.18	82	92
Bowman Lake	01	06/23/2005	9.9	19.95	0	0.00		
	02	06/23/2005	10.3	25.10	0	0.00		
	03	06/24/2005	11.2	31.17	0	0.00		
	04	06/24/2005	11.9	12.57	0	0.00		
	05	07/01/2005	10.8	21.63	0	0.00		
	06	07/01/2005	11.1	28.55	0	0.00		
	01	06/02/2006	12.6	20.92	0	0.00		
	02	06/02/2006	12.0	29.20	0	0.00		
	03	06/03/2006	10.5	20.42	0	0.00		
	04	06/03/2006	10.2	18.78	0	0.00		
Harrison Lake	01	08/25/2005	18.0	14.25	0	0.00		
	02	08/25/2005	16.7	14.62	0	0.00		
	03	08/25/2005	16.5	10.58	0	0.00		
Kintla Lake	01	06/20/2005	19.8	40.12	0	0.00		
	02	06/20/2005	20.1	36.03	0	0.00		
	03	06/21/2005	12.1	27.73	0	0.00		
	04	06/21/2005	11.4	33.57	0	0.00		
	05	06/30/2005	12.5	23.32	0	0.00		
	06	06/30/2005	12.6	24.78	0	0.00		
	01	06/06/2006	14.5	29.43	0	0.00		
	02	06/06/2006	12.2	24.33	0	0.00		
	03	06/06/2006	11.9	22.30	0	0.00		
Lake Isabel	03	09/05/2004	10.3	11.67	1	0.09		135
	04	09/05/2004	8.2	24.20	8	0.33	101	121
Lake McDonald	01	05/31/2006	13.0	17.75	0	0.00		
	02	05/31/2006	10.5	26.65	0	0.00		
	03	05/31/2006	10.5	18.02	0	0.00		
	04	06/01/2006	11.7	17.97	0	0.00		
	05	06/01/2006	11.7	21.13	0	0.00		
Lincoln Lake	02	08/07/2004	14.0	16.75	0	0.00		
	03	08/07/2004	14.2	16.00	0	0.00		
	05	08/09/2004	12.9	11.82	0	0.00		
	06	08/09/2004	12.8	15.80	0	0.00		

Table 5: continued on next page

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Logging Lake	02	08/16/2005	18.7	19.33	0	0.00		
	03	08/16/2005	18.7	14.00	0	0.00		
	04	08/16/2005	18.6	18.72	0	0.00		
	06	08/17/2005	17.7	16.92	0	0.00		
	07	08/17/2005	17.1	12.00	0	0.00		
	08	08/17/2005	17.1	9.33	0	0.00		
Lower Quartz Lake	01	08/01/2005	18.9	21.08	0	0.00		
	02	08/01/2005	19.6	10.85	0	0.00		
	03	08/02/2005	19.7	15.85	0	0.00		
	04	08/02/2005	19.7	13.68	0	0.00		
	07	08/03/2005	18.8	19.80	0	0.00		
	08	08/03/2005	19.9	11.32	0	0.00		
Middle Quartz Lake	03	08/05/2005	19.5	13.10	0	0.00		
	04	08/05/2005	19.6	11.42	0	0.00		
	05	08/05/2005	19.6	13.23	0	0.00		
	06	08/06/2005	21.4	8.75	0	0.00		
	07	08/06/2005	22.0	7.35	0	0.00		
	08	08/06/2005	20.7	10.60	0	0.00		
Quartz Lake	01	06/28/2006	13.9	19.97	0	0.00		
	02	06/28/2006	13.6	16.65	0	0.00		
	03	06/29/2006	13.5	20.97	0	0.00		
	05	06/30/2006	16.7	15.58	0	0.00		
	06	07/01/2006	16.8	20.98	0	0.00		
	07	07/01/2006	16.2	16.07	0	0.00		
Rogers Lake	01	08/02/2006	21.0	8.62	0	0.00		
	02	08/02/2006	21.0	7.57	0	0.00		
Trout Lake	01	07/22/2005	19.3	14.30	0	0.00		
	02	07/22/2005	19.2	16.22	0	0.00		
	04	07/23/2005	19.1	13.10	0	0.00		
	05	07/23/2005	19.2	12.67	0	0.00		
	06	07/24/2005	17.8	11.43	0	0.00		
	07	07/24/2005	17.8	14.47	0	0.00		
Upper Kintla Lake	01	07/12/2005	12.8	14.85	0	0.00		
	02	07/12/2005	12.8	14.83	1	0.07		134
	06	07/13/2005	10.7	20.88	6	0.29	49	141
	07	07/13/2005	10.6	22.20	0	0.00		
	08	07/15/2005	12.5	14.28	0	0.00		
	09	07/15/2005	13.0	19.15	2	0.10	134	148

Table 5: continued on next page

Stream Electrofishing Surveys

Electrofishing surveys of lake inlet and outlet streams yielded low numbers of bull trout (Table 7; Appendix 3). This coupled with the observation of small bull trout inhabiting lake shoreline habitat (see above) suggests that bull trout in GNP may be moving out of stream habitat at an early age. Recent research suggests that in Lake Pend Oreille, Idaho, bull trout move out of stream habitat at an early age (as young as age 0);

however, the majority of bull trout returning to spawning grounds had emigrated at age 3 or 4 suggesting low survival for individuals emigrating at an early age (Downs et al. 2006). The outlet of Upper Kintla Lake was the only stream electrofishing site where large numbers of age-0 bull trout were observed (Table 7). This stream section was larger (approximately 30 m wide) than inlet and outlet streams of other lakes examined (Appendix 6) and a small unnamed lake is present immediately downstream from the short reach. Other species present in inlet and outlet streams surveyed include cutthroat trout, brook trout, longnose sucker *Catostomus catostomus*, northern pikeminnow *Ptychocheilus oregonensis*, redside shiner *Richardsonius balteatus*, and sculpin sp. *Cottus spp.* (Appendix 3).

Physical habitat was not quantified for the outlet of Upper Kintla Lake, the outlet of Lower Quartz Lake or the inlet or outlet of Arrow Lake. Stream electrofishing sites varied in length from 87 to 156 m, and were generally less than 1.00-m deep Appendix 6), with the exceptions of the inlet of Akokala Lake, the outlet of Bowman Lake, the Inlet of Quartz Lake, and Aggassiz Creek (inlet of Upper Lake Isabel), each with maximum depths greater than 1.00 m. Stream electrofishing sites varied in mean wetted width from 3.58 to 18.57 m, with most sites less than 15-m wide, and varied in mean depth from 0.11 to 0.31 m (Appendix 6). Dominant substrate varied from gravel to boulder with average substrate embeddedness varying from less than 5% embedded to 50 to 75% embedded (Appendix 6).

Table 7. Lake, site (inlet or outlet), date sampled, temperature, electrofishing time (Fishing time), number of bull trout sampled (*N*), catch per unit effort (C/*f*; fish per minute), and minimum (Min.) and maximum (Max.) length for bull trout sampled during stream electrofishing surveys in Glacier National Park.

Lake	Site	Date	Temperature (° C)	Fishing time (min)	N	C/f	Length (mm) Min.	Length (mm) Max.
Akokala Lake	Inlet	07/11/2004	6.4	26.40	3	0.11	32	93
	Outlet	07/11/2004	9.5	27.35	1	0.04		206
Arrow Lake	Inlet	06/25/2004	8.9	20.20	0	0.00		
	Outlet	06/25/2004			0	0.00		
Bowman Lake	Inlet	08/01/2006	9.8	28.28	2	0.07	135	136
	Outlet	08/14/2006	18.2	17.73	0	0.00		
Kintla Lake	Inlet	08/16/2006	11.7	7.08	0	0.00		
Lake Isabel	Inlet	09/02/2004	8.2	20.73	4	0.19	96	255
	Outlet	09/02/2004	10.3	16.08	0	0.00		
Lincoln Lake	Inlet	08/09/2004	13.5	23.67	3	0.13	57	104
	Outlet	08/06/2004	16.8	39.28	0	0.00		
Logging Lake	Inlet	08/17/2005	14.0	14.97	0	0.00		
	Outlet	08/15/2005	20.1	20.67	0	0.00		
Lower Quartz Lake	Inlet	08/03/2005	17.2	11.45	0	0.00		
	Outlet	08/03/2005	20.3	15.45	0	0.00		
Middle Quartz Lake	Inlet	08/04/2005	19.6	18.47	0	0.00		
	Outlet	08/04/2005	20.0	11.38	0	0.00		
Quartz Lake	Inlet	06/30/2006	9.4	22.03	1	0.05		86
Trout Lake	Inlet	07/23/2005	18.6	27.42	0	0.00		
	Outlet	07/26/2005	18.6	25.77	0	0.00		
Upper Kintla Lake	Inlet	07/13/2005	7.7	9.97	1	0.10		129
	Outlet	07/13/2005	10.5	37.90	20	0.53	39	65
	Agassiz	07/13/2005	9.3	14.97	2	0.13	202	244

Electrofishing efficiency may have been low in GNP streams during sampling. Water conductivity, which is directly related to the transfer of energy from water to fish (Reynolds 1996), was generally low in sampled streams (< 100 µS/cm; Appendix 8). Additionally, water velocity was often high and dominance of boulder and cobble substrate coupled with low embeddedness (Appendix 7) resulting in decreased electrofishing efficiency.

Barrier Surveys

Potential dispersal barriers (vertical drop greater than 1.8 m) were observed in Camas Creek downstream of Trout Lake (between Rogers Lake and Trout Lake), Kintla Creek downstream of Upper Kintla Lake (between Kintla Lake and Upper Kintla Lake), and Park Creek downstream of Lake Isabel (between the Middle Fork Flathead River and Lake Isabel). Additional barriers to future colonization into habitat currently unoccupied by bull trout were observed in Camas Creek upstream of Arrow Lake (between Arrow Lake and Camas Lake) and in Logging Creek upstream of Logging Lake (between Logging Lake and Grace Lake). Although not measured, a known barrier to migration exists 0.90 km upstream of Lake McDonald in McDonald Creek. Potential barriers in the form of vertical waterfalls, such as those observed in Kintla Creek and Park Creek, were easily measured. However, many potential barriers were in the form of large vertical falls, or complex, high-gradient, and high-velocity cascades that were not easily measured; therefore, digital images of certain barriers were captured with a size reference (i.e., a stadia rod) and quantified based on the image (Table 8; Figure 9).

Table 8. Stream, barrier location description, method of measurement (image analysis or on site), height, and width of potential dispersal barriers observed in Glacier National Park.

Stream	Barrier location description	Measurement	Height (m)	Width (m)
Camas Creek	Downstream of Trout Lake	Image	7.2	23.2
Kintla Creek	Downstream of Upper Kintla Lake	Image	6.7	14.3
	Downstream of Upper Kintla Lake	On site	2.8	2.7
Logging Lake	Downstream of Grace Lake	Image	6.9	9.5
Park Creek	Downstream of Lake Isabel	On Site	1.8	2.9
	Downstream of Lake Isabel	On Site	2.4	3.4
	Downstream of Lake Isabel	On Site	2.7	3.0

Figure 9. Dispersal barriers observed in Camas Creek downstream of Trout Lake (upper left panel), Kintla Creek downstream of Upper Kintla Lake (upper right panel), Kintla Creek downstream of Upper Kintla Lake (lower left panel), and Park Creek downstream of Lake Isabel (lower right panel).

The cascades and waterfalls observed in Kintla Creek between Kintla Lake and Upper Kintla Lake (Table 8) and the observation of bull trout as the only species of fish occupying Upper Kintla Lake (Appendix 3) suggest that Upper Kintla Lake has been historically isolated from immigration following the establishment of bull trout. A large waterfall between Logging Lake and Grace Lake has the potential to isolate Grace Lake from immigration. Grace Lake was historically fishless, but was stocked and now contains a population of nonnative Yellowstone cutthroat trout. The detection of lake trout, rainbow trout *Oncorhynchus mykiss*, mountain whitefish, longnose sucker, and northern pikeminnow in Rogers Lake, which were not detected in Trout Lake, indicates that the large waterfall observed between Trout Lake and Rogers Lake is acting as a barrier to upstream migration. A large cascade was observed between Arrow Lake and Camas Lake. Fish sampling was not conducted in Camas Lake (but was historically stocked with Yellowstone cutthroat trout). A series of waterfalls were observed in Park Creek between the Middle Fork Flathead River and Lake Isabel. The presence of bull trout and cutthroat trout as the only fish species detected in Lake Isabel suggests that these waterfalls (or other potential barriers not observed) are acting as a barrier to upstream migration by other fishes and have blocked immigration into this lake following colonization by bull trout and cutthroat trout.

The observed structures classified as migratory barriers appear to have minimized colonization. It is important to note that these structures are considered to be contemporary barriers. The presence of bull trout and other fishes in water bodies upstream of these barriers suggests that these structures have not been active barriers at some point in the past. Temporary breaches as a result of hydrologic events (e.g., log jams, stream channel migration) or geologic events that minimized the barriers or created them likely occurred in the past. However, current trends in species richness suggest that these barriers have been active for a relatively long time and have played a significant role in distribution of fishes in GNP. Additionally, these structures appear to play a role in current invasion dynamics of lake trout in GNP and their function should be monitored as a natural method of minimizing further invasion.

No potential barriers were observed in Kintla Creek between the North Fork Flathead River and Kintla Lake or in Bowman Creek between the North Fork Flathead River and Bowman Lake. Akokala Creek is highly braided with an abundance of beaver activity, log jams, and large woody debris, making it potentially difficult to navigate; however, no permanent barriers (i.e., waterfalls or cascades) were observed between the North Fork Flathead River and Akokala Lake. Barriers were not observed between the Middle Fork Flathead River and Lake McDonald. A 2001 survey of Quartz Creek, between the North Fork Flathead River and Lower Quartz Lake (W. A. Fredenberg, US Fish and Wildlife Service, unpublished data), found log jams, braided channels, and debris jams were common but no potential fish passage barriers were found.

Redd Surveys

The number of bull trout redds observed was low (Table 9). The highest number of bull trout redds observed was in Quartz Creek, upstream of Quartz Lake, in 2004 (N = 55) followed by Quartz Creek, upstream of Quartz Lake, in 2006 (N = 36) and Logging Creek, upstream of Logging Lake, in 2005 (N = 20). The remaining stream sections observed had fewer than 10 redds each; with many sections having no observed redds (Table 9). The number of bull trout redds observed among streams and between years was highly variable (Table 9; Figures 10-13). Redd survey sections varied in length from 0.39 to 3.55 km, and temperatures were generally low enough for bull trout to have initiated spawning (9° C; McPhail and Baxter 1996); except upstream of Logging Lake in 2006, between Middle Quartz and Quartz Lake in 2004 and between Lower Quartz Lake and Middle Quartz Lake in 2004 and 2006 (although one redds were observed in this section; Table 9). See Appendix 11 for a comprehensive list of redd locations.

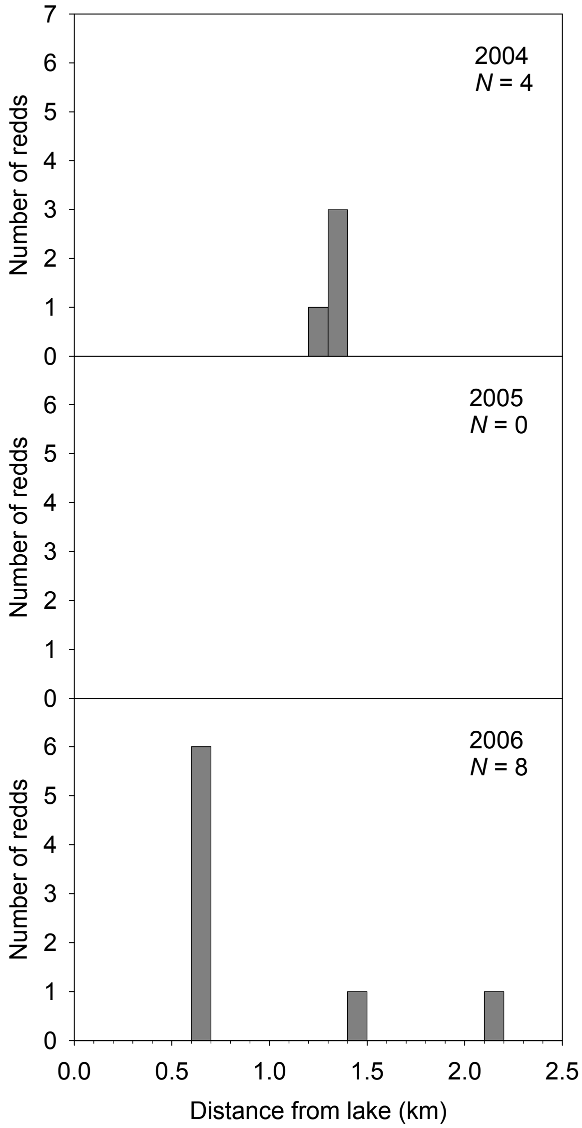
High flow and corresponding high sediment loads in Harrison Creek during 2004 redd surveys may have decreased the ability to detect bull trout redds. A large number of spawning kokanee were present in Harrison Creek during 2005 redd surveys. The spawning kokanee had produced many small redds in substrate that was likely suitable for bull trout spawning. Therefore, it would have been difficult to accurately identify any bull trout redds that had been superimposed by kokanee redds. High flow in 2005, immediately prior to redd surveys, may have also obscured bull trout redds in Quartz Creek, upstream of Quartz Lake, and Bowman Creek, upstream of Bowman Lake. In both of these sections, there was evidence of high flow events (e.g., disturbed riparian vegetations, lack of periphyton on stream substrate). Additionally, there were shallow depressions that appeared to be the correct size and shape to be bull trout redds; however, they had been filled in with sand and pebbles and their tail-outs had been obscured, making positive identification difficult.

Environmental stochasticity in Glacier National Park may limit bull trout spawning. A previous debris flow resulted in Bowman Creek running subsurface up to the point where it enters Bowman Lake for many years (W. A. Fredenberg, US Fish and Wildlife Service, personal communication) and 2006 was the first year that any bull trout redds were observed in the stream reach. Similarly, Camas Creek appears to have experienced a debris flow within the last year that has resulted in this stream reach being eliminated for potential spawning until natural events create an active stream channel. Additionally, inlet streams to Cerulean Lake and Lincoln Lake were observed to go subsurface before entering these lakes during summer months. If this type of stream flow occurs during the spawning season it would likely limit the ability for bull trout to use these sites as spawning areas. Alternatively, high redd counts, such as Logging Lake in 2005, may indicate unusually favorable flow conditions.

The longitudinal distribution of bull trout redds within the stream sections examined (Figures 10 – 13) will aid in determining appropriate reference sites for future bull trout redd surveys. In general, temperatures in stream reaches were appropriate for bull trout spawning; however, continued sampling will help determine the appropriate dates to perform redd surveys in order to maximize the likelihood of observing redds.

Table 9. Population, date sampled, section length, temperature, and number of redds observed during redd surveys in Glacier National Park.

Population	Date sampled	Section length (km)	Temperature (° C)	Number of redds
Bowman Lake	10/10/2004	3.55	6	0
	10/19/2005	2.88	6	0
	10/16/2006	2.88	6	2
Harrison Lake	10/6-7/2004	2.37	8	4
	10/19/2005	2.37	7	0
	10/13/2006	2.36	8	8
Logging Lake	10/05/2004	1.90	8	3
	10/22/2005	1.23	7	20
	10/14/2006	1.23	10	0
Lower Quartz Lake	10/12/2004	1.52	11	1
	10/21/2005	0.54	9	3
	10/15/2006	0.54	11	2
Middle Quartz Lake	10/12/2004	0.39	12	0
	10/21/2005	0.39	9	0
	10/15/2006	0.32	10	0
Quartz Lake	10/13/2004	1.50	6	55
	10/22/2005	0.93	5	4
	10/15/2006	1.01	7	36



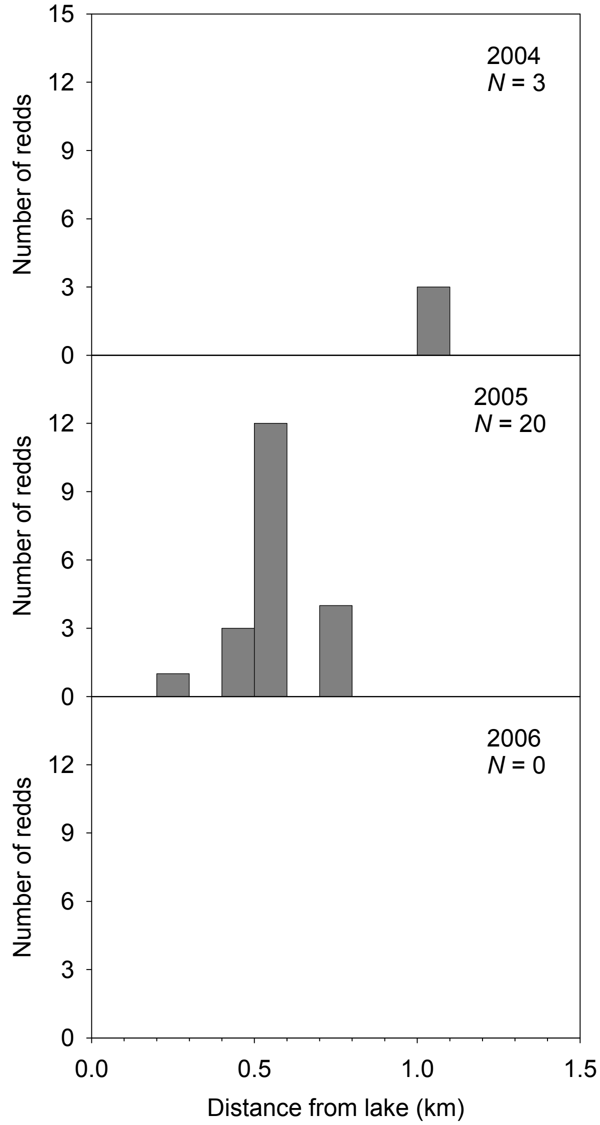


Figure 10. Distribution and number of bull trout redds observed in Harrison Creek sampled in an upstream direction from the inlet of Harrison Lake (0.0 km) for 2004, 2005, and 2006.

Figure 11. Distribution and number of bull trout redds observed in Logging Creek sampled in an upstream direction from the inlet of Logging Lake (0.0 km) for 2004, 2005, and 2006.

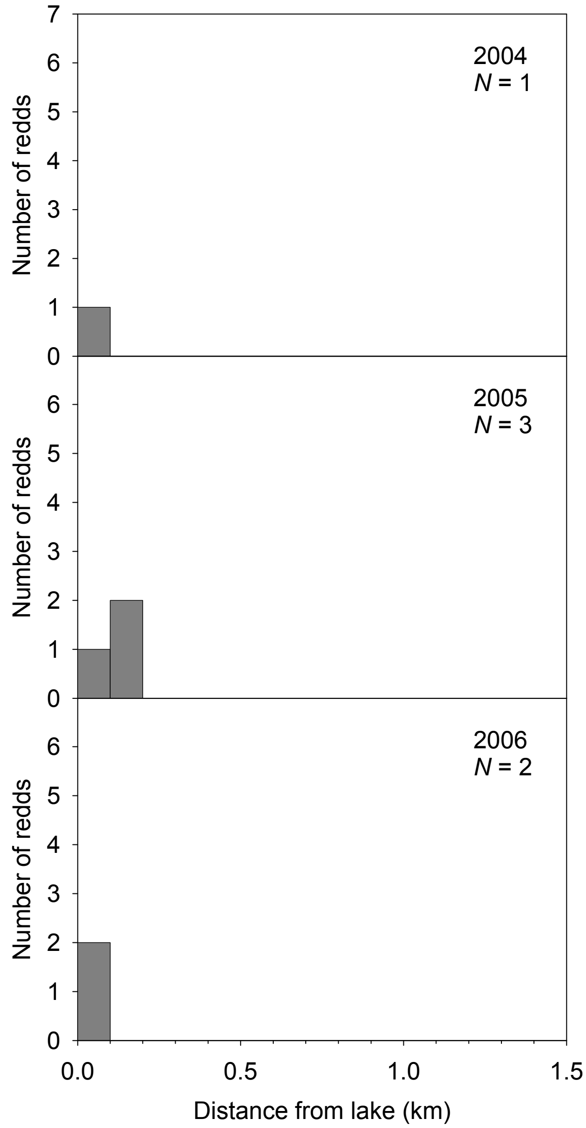


Figure 12. Distribution and number of bull trout redds observed in Quartz Creek sampled in an upstream direction from the inlet of Lower Quartz Lake (0.0 km) for 2004, 2005, and 2006.

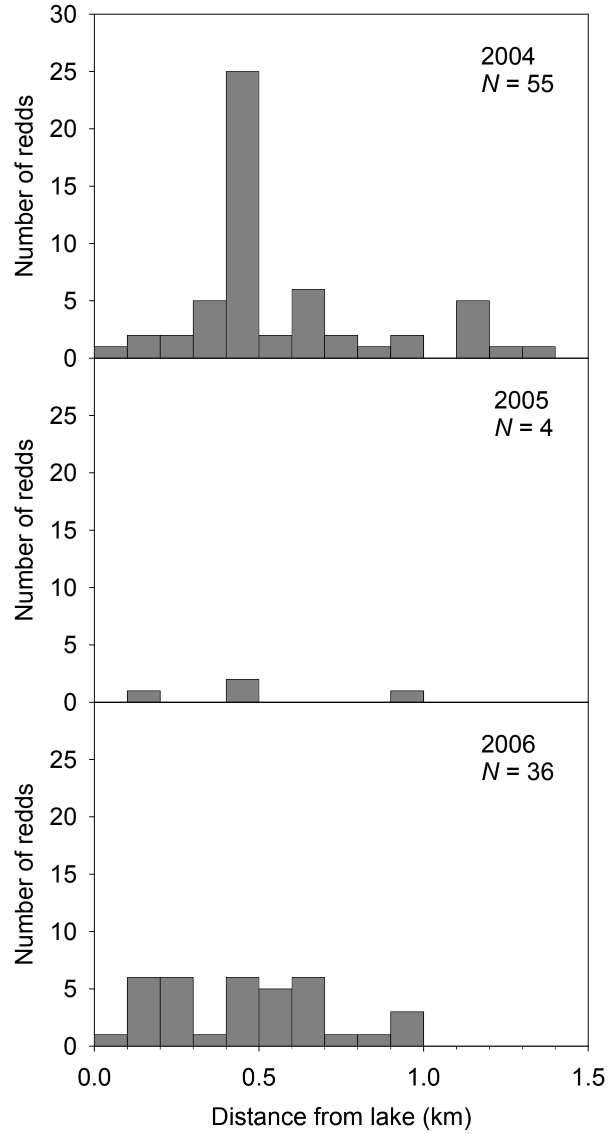


Figure 13. Distribution and number of bull trout redds observed in Quartz Creek sampled in an upstream direction from the inlet of Quartz Lake (0.0 km) for 2004, 2005, and 2006

Age Estimates

One hundred eighty-five bull trout were aged and comprised individuals from 16 lakes. Samples sizes varied among lakes from 1 to 35. Bull trout were between 120 and 704 mm in length and from 2 to 16 years of age (Table 10). Average coefficient of variation between age reading one and two varied from 2.43% to 10.10% among lakes; overall, coefficient of variation between age reading one and two varied from 0.00% to 32.64% with a mean (± SD) of 5.60 ± 8.23% (Table 10). Where otoliths were available from a broad range of length classes a linear trend was observed between bull trout length and age (Figures 14a-14c). Low sample sizes within and among age classes precludes meaningful analysis of mortality rates and length-at-age estimates for most populations. However, these data provide general information on the age classes present in some of the lakes within GNP. Future analyses will include providing age estimates for lake trout sampled in GNP for comparison among lakes and between bull trout and lake trout.

Table 10. Lake, sample size (*N*), minimum and maximum length of bull trout, minimum and maximum estimated ages from age reading one and two, and mean coefficient of variation (CV ± SD) based on otoliths sampled from bull trout in Glacier National Park.

		Length (mm)		Reading 1 (years)		Reading 2 (years)		
Lake	N	Min.	Max.	Min.	Max.	Min.	Max.	CV (%)
Akokala Lake	5	296	314	5	6	6	8	6.61 ± 9.42
Arrow Lake	9	470	590	8	12	8	12	2.43 ± 5.38
Bowman Lake	9	194	599	3	9	3	8	4.92 ± 7.96
Cerulean Lake	5	275	675	6	10	7	11	4.87 ± 4.76
Harrison Lake	7	266	704	5	12	5	12	7.22 ± 9.62
Kintla Lake	8	181	468	3	5	4	7	7.44 ± 10.48
Lake Isabel	35	198	290	4	12	4	12	5.80 ± 9.39
Lake McDonald	7	302	570	4	8	5	8	7.43 ± 10.78
Lincoln Lake	6	348	688	4	14	6	14	7.04 ± 10.99
Logging Lake	6	196	454	3	7	3	5	7.30 ± 11.35
Lower Quartz Lake	8	198	651	4	14	4	14	7.79 ± 10.10
Middle Quartz Lake	8	351	667	8	7	5	8	4.75 ± 6.77
Quartz Lake	35	207	643	3	13	3	13	4.37 ± 7.03
Rogers Lake	1	642	642	13	13	15	15	10.10
Trout Lake	16	205	580	4	16	4	15	4.52 ± 4.78
Upper Kintla Lake	20	120	495	2	10	3	9	6.29 ± 9.18

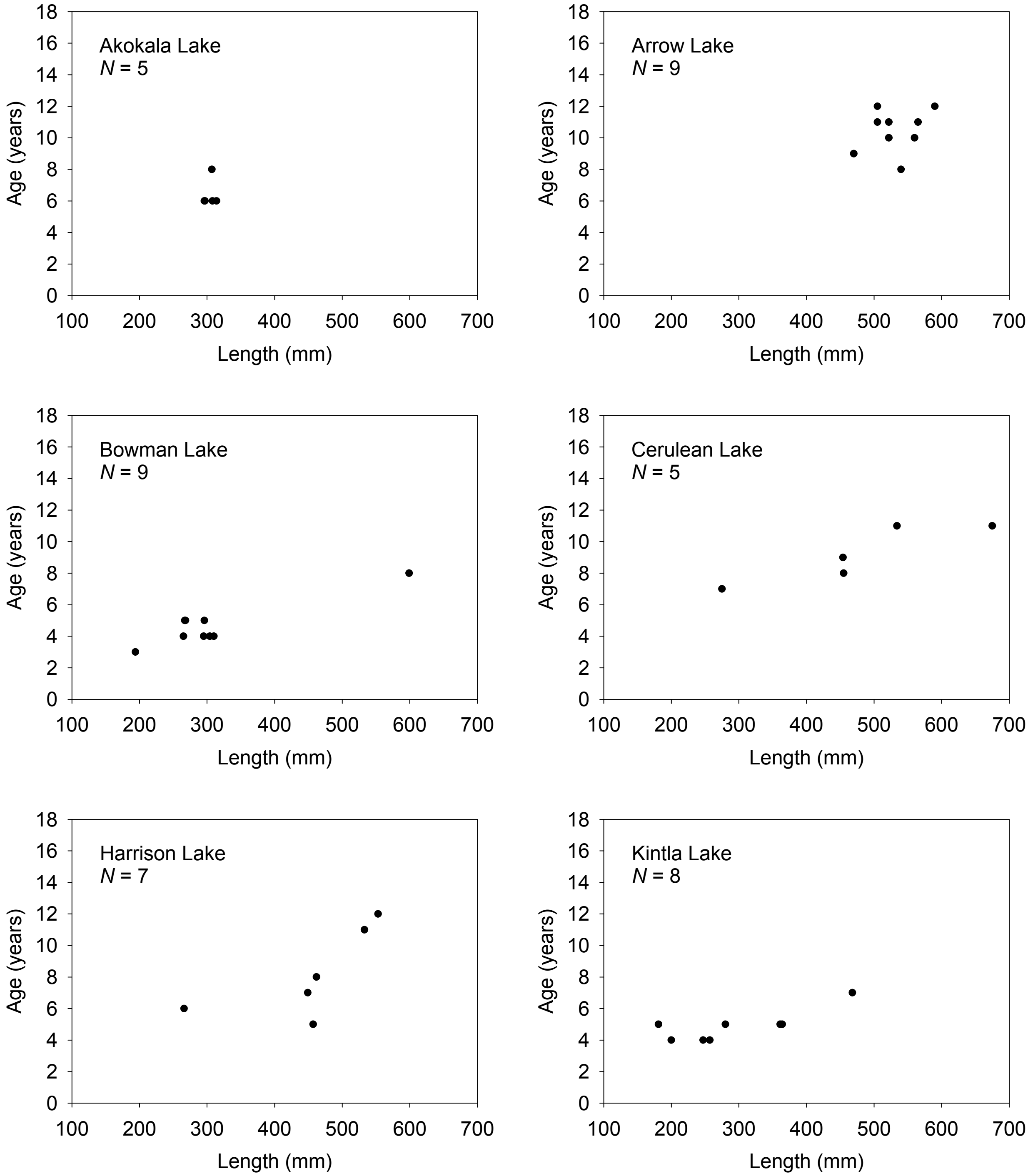


Figure 14a. Estimated age based on otoliths as a function of length for bull trout from Akokala Lake, Arrow Lake, Bowman Lake, Cerulean Lake, Harrison Lake, and Kintla Lake, Glacier National.

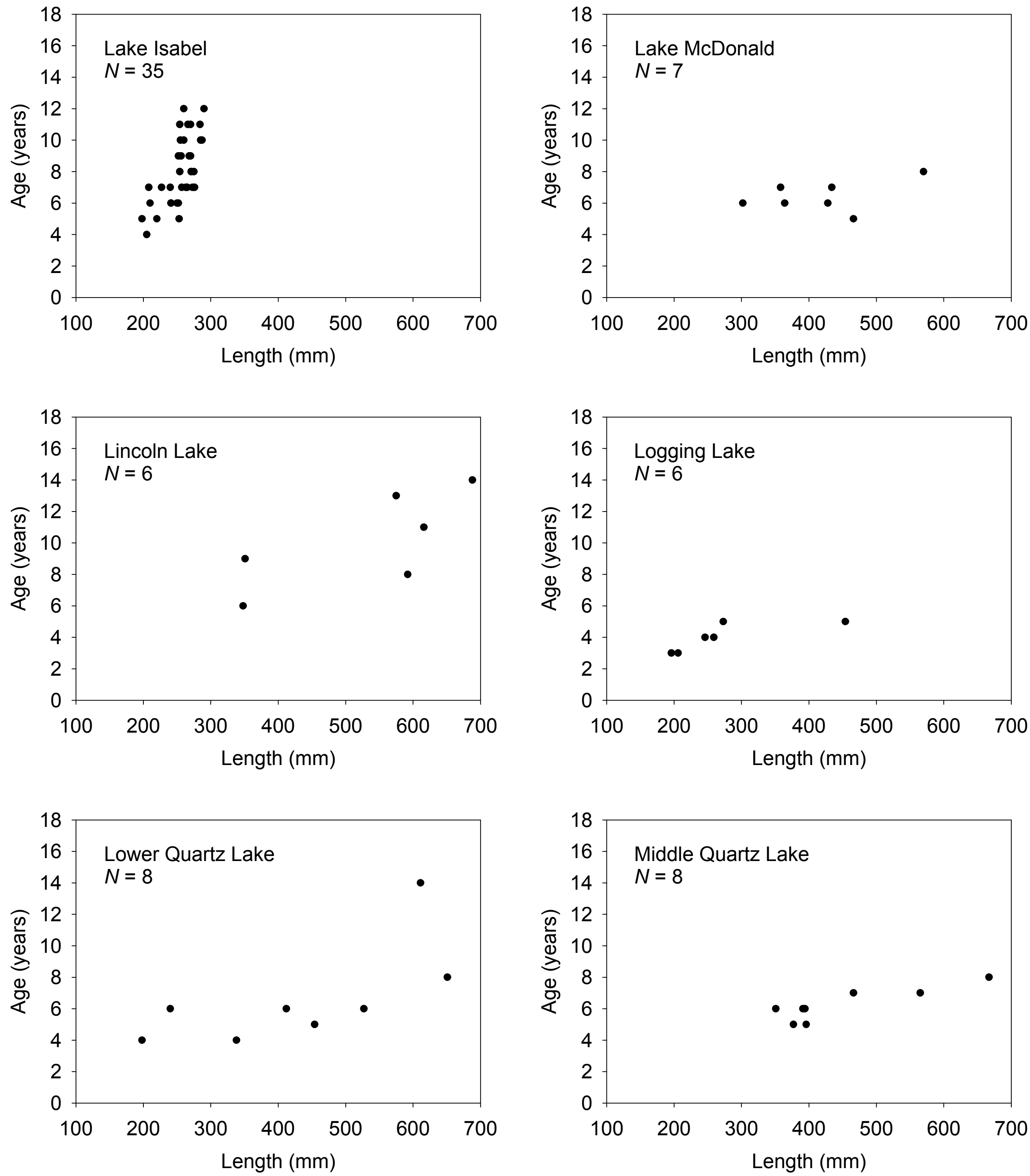


Figure 14b. Estimated age based on otoliths as a function of length for bull trout from Lake Isabel, Lake McDonald, Lincoln Lake, Logging Lake, Lower Quartz Lake, and Middle Quartz Lake, Glacier National Park.

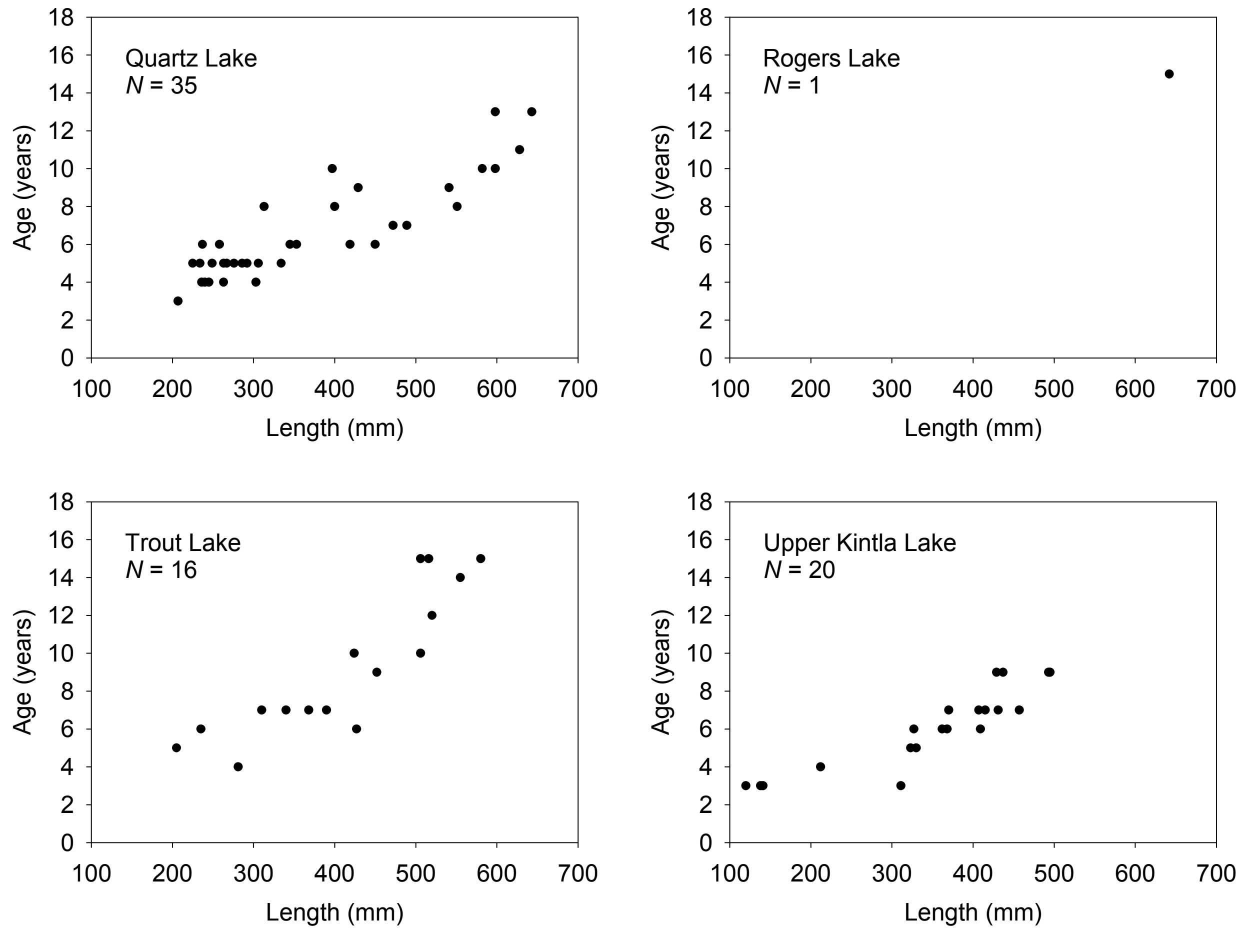


Figure 14c. Estimated age based on otoliths as a function of length for bull trout from Quartz Lake, Rogers Lake, Trout Lake, and Upper Kintla Lake, Glacier National Park.

Population Genetics

Sample sizes for genetic analysis varied from 4 to 18 individuals among lakes (Table 11). Observed heterozygosity was generally high and patterns of allelic diversity were similar to that of observed heterozygosity (Table 11). In general, bull trout from lakes in GNP conformed to Hardy-Weinberg equilibrium. Significant deviation from Hardy-Weinberg equilibrium was observed for Harrison Lake and marginal deviations were observed for Lincoln Lake and Quartz Lake (Table 11). These deviations may result if lakes are influenced by immigration, selection, or non-random mating (Frankham et al. 2002).

Table 11. Lake, sample size (*N*), observed heterozygosity, expected heterozygosity, Hardy-Weinberg *P*-value, and allelic diversity for bull trout sampled in Glacier National Park.

Lake	*N*	Observed heterozygosity	Expected heterozygosity	Hardy-Weinberg *P*-value	Allelic diversity
Akokala Lake	15	0.5733	0.6033	0.6411	3.9
Arrow Lake	16	0.2063	0.1719	0.5092	1.8
Bowman Lake	17	0.5871	0.6253	0.6908	5.4
Cerulean Lake	16	0.5688	0.5605	0.4468	4.5
Harrison Lake	8	0.3345	0.4288	0.0453	3.6
Kintla Lake	12	0.6955	0.7003	0.4578	5.9
Lake Isabel	18	0.3833	0.4046	0.8587	4.3
Lake McDonald	8	0.6875	0.6406	0.9956	5.3
Lincoln Lake	9	0.5302	0.6143	0.0645	4.6
Logging Lake	7	0.6667	0.5757	0.9993	3.8
Lower Quartz Lake	4	0.4417	0.4653	0.6298	3.0
Middle Quartz Lake	11	0.5841	0.5156	0.9731	4.3
Quartz Lake	15	0.5607	0.6005	0.0566	5.2
Trout Lake	17	0.2059	0.2026	0.6304	2.2
Upper Kintla Lake	16	0.2875	0.2586	0.6884	2.7
Upper Lake Isabel	7	0.3357	0.2732	0.8097	2.1

Pairwise F_{st} values varied from 0.0000 to 0.6904 among lakes (Appendix 10) with values greater than 0.15 often considered an indication of significant differentiation among lakes (Frankham et al. 2002). Pairwise comparisons between lakes isolated above barriers and other lakes within GNP resulted in high F_{st} values (e.g., comparisons between Upper Kintla Lake and other lakes; Appendix 10). This suggests that these lakes have been isolated for a considerable amount of time and that the barriers that we mapped during the course of this study have been effective at maintaining reproductive isolation. Also of note, are comparisons among lakes within the Quartz Drainage. Pairwise F_{st} values for Middle Quartz Lake, Quartz Lake, and Cerulean Lake (located with the Rainbow Creek Drainage tributary to Quartz Creek) are extremely low suggesting that these lakes may be acting as one population. Similarly, the value comparing Arrow Lake and Trout Lake is very low. Interestingly, pairwise F_{st} values show genetic similarity between Kintla Lake and Lake McDonald suggesting that gene flow may be occurring between these lakes. Alternatively, these observations may be the result of random chance associated with low sample sizes (see below: Future Activities).

The visual representation provided by the neighbor-joining tree corroborates results based on pairwise F_{st} values. Lakes isolated above barriers are often grouped separately from other lakes (e.g., Upper Kintla Lake, the grouping of Lake Isabel and Upper Lake Isabel, and the grouping of Trout Lake and Arrow Lake; Figure 15). Also, lakes in the Quartz Basin (including Cerulean Lake) group together. Kintla Lake and Lake McDonald also grouped together, both of which are easily accessible from mainstem Flathead River habitat (low gradient and close proximity to mainstem habitat). Overall, no large-scale grouping was observed based on geographic locations. For example, lakes tributary to the North Fork Flathead River often grouped together with lakes tributary to the Middle Fork Flathead River.

Additional bull trout samples are available and will be analyzed to provide a larger sample size for all lakes with a target sample size of 20 individuals per lake, and two additional microsatellite loci will be examined.

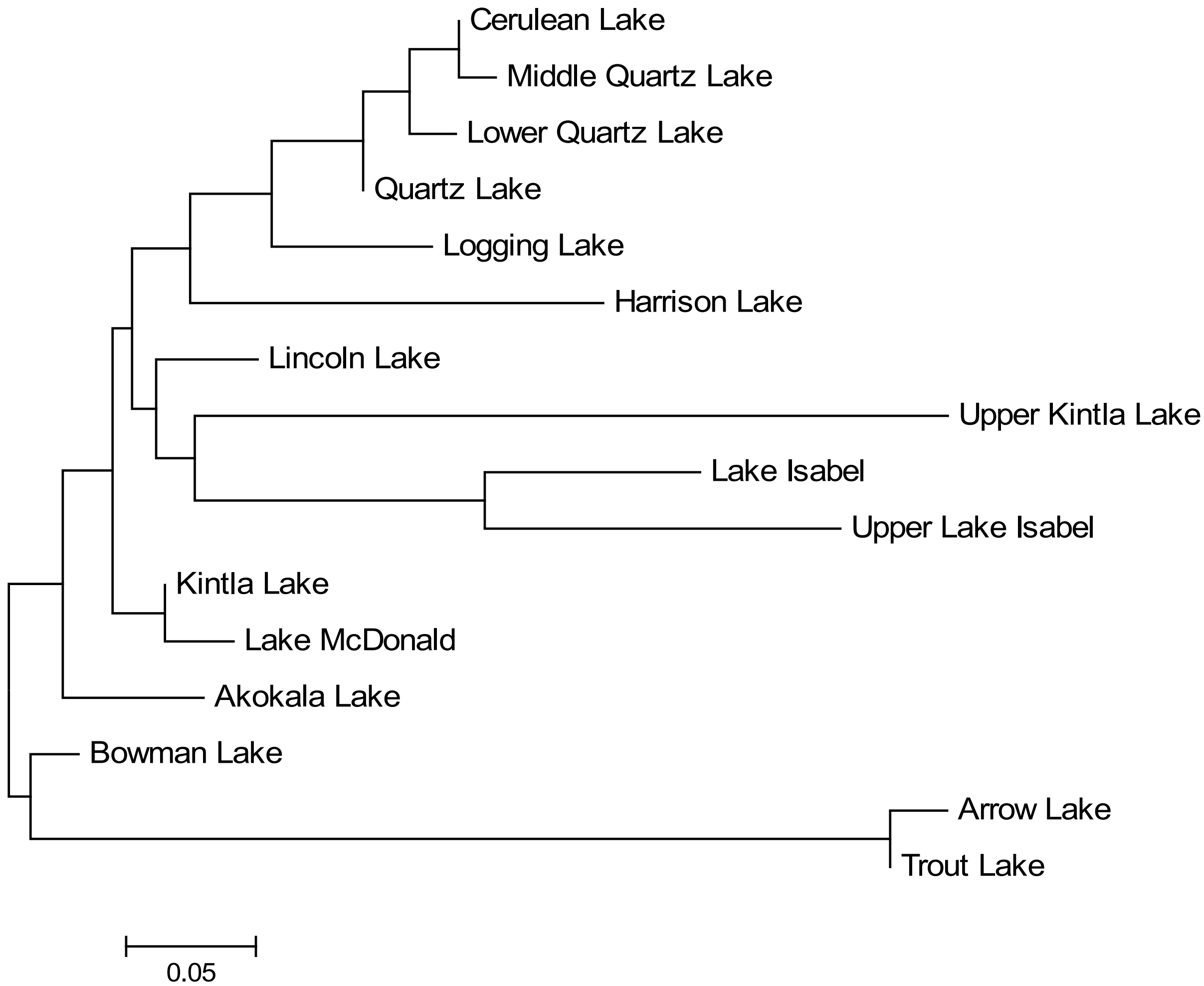


Figure 15. Bull trout neighbor-joining tree based on pairwise F_{st} values for 16 lakes in Glacier National Park.

Stable Isotope Analysis

Muscle samples were collected from 475 fish and sent to South Dakota State University – Plant Science Department for stable isotope analysis. Appendix 12 provides a summary of the species and numbers of individuals being analyzed to examine food-web structure in GNP lakes. These data will help elucidate potential mechanisms of bull trout displacement by lake trout.

Future Activities

- Examine otoliths from lake trout sampled during the years 2004, 2005, and 2006.
- Genotype additional bull trout samples collected from lakes in GNP to increase sample sizes. Perform a comprehensive population genetic analysis for GNP bull trout.
- Examine food-web structure of lakes within GNP based on stable isotope analysis to elucidate potential mechanisms of bull trout displacement.
- Estimate extent and potential productivity of spawning and rearing habitat for bull trout.
- Synthesize available and forthcoming data to develop a comprehensive action plan for the long-term monitoring, management, and recovery of bull trout resources in GNP.
    - Prepare an additional scientific report to act as a data analysis supplement for inclusion with the comprehensive action plan.

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Appendix 1. Lake, year sampled, net code, net configuration (Conf.; Single represents one 38 m gill net; Double represents two 38 m gill nets tied end-to-end and set as one), large mesh in (near shore) or out (offshore), net set time (Set), net pull time (Pull), net soak time, near shore depth (D1), and offshore depth (D2) for gill nets set in 16 lakes in Glacier National Park. Gill nets were set in the late afternoon and evening and pulled starting at sunrise on the following day.

				Large	Time (h)		Soak	Depth (m)	
Lake	Year	Net	Conf.	mesh	Set	Pull	time (h)	D1	D2
Akokala Lake	2004	01	Single	In	20:43	06:15	9.53	1.9	3.2
		02	Single	Out	21:03	06:36	9.55	1.7	4.4
		03	Single	In	21:20	06:55	9.58	1.3	1.9
		04	Single	Out	21:18	06:32	9.23	1.1	3.9
		05	Single	Out	21:35	06:50	9.25	2.2	5.6
		06	Single	In	21:47	07:03	9.27	2.3	6.5
		07	Single	Out	22:00	07:20	9.33	2.0	6.3
Arrow Lake	2004	05	Single	In	21:00	05:53	8.88	1.2	13.8
		06	Single	Out	21:15	06:30	9.25	1.1	10.1
		07	Single	In	21:34	06:49	9.25	1.1	14.1
		08	Single	In	21:49	07:05	9.27	2.1	16.1
		09	Single	In	21:13	06:34	9.35	0.2	8.6
		10	Single	Out	21:25	06:47	9.37	1.2	8.9
		11	Single	In	21:49	07:13	9.40	2.4	10.0
		12	Single	Out	22:00	07:30	9.50	0.6	3.9
Bowman Lake	2005	01	Double	Out	20:00	08:39	12.65	3.7	40.7
		02	Double	Out	21:02	09:55	12.88	4.0	35.6
		03	Double	Out	20:43	09:57	13.23	5.1	40.5
		04	Double	Out	17:15	08:13	14.97	2.5	36.6
		05	Double	Out	16:45	09:02	16.28	2.0	39.6
		06	Double	Out	16:30	08:30	16.00	0.8	16.8
		07	Double	Out	17:00	09:15	16.25	1.5	22.6
		08	Double	Out	17:34	06:15	12.68	5.5	27.3
		09	Double	Out	18:00	06:51	12.85	1.6	33.6
		10	Double	Out	18:26	07:41	13.25	5.2	51.1
Cerulean Lake	2004	01	Single	Out	21:09	06:29	9.33	0.9	9.2
		02	Single	Out	21:29	07:55	10.43	0.5	23.4
		04	Single	In	22:26	06:29	8.05	1.1	20.4
		05	Single	In	22:27	60:49	8.37	0.7	18.0
Harrison Lake	2005	01	Single	Out	21:40	11:22	13.70	8.0	16.4
		02	Single	Out	21:09	10.42	13.55	3.8	16.1
		03	Single	Out	20:33	09:36	13.05	4.2	28.4
		04	Single	Out	20:03	08:03	12.00	4.5	30.1
		05	Single	Out	20:22	07:42	11.33	4.1	13.3
		06	Single	Out	20:45	08:33	11.80	5.2	20.7
		07	Single	Out	21:20	09:33	12.22	2.4	14.2
		08	Single	Out	21:53	10:47	12.90	7.9	11.6
		09	Single	Out	20:24	07:52	11.47	4.6	14.7
		10	Single	Out	20:42	08:23	11.68	5.1	23.0
Kintla Lake	2005	01	Double	Out	22:30	11:57	13.45	1.3	4.7
		02	Double	Out	22:10	11:20	13.17	1.0	14.2
		03	Double	Out	21:43	10:05	12.37	1.2	12.9
		04	Double	Out	21:37	11:00	13.38	4.3	48.1
		05	Double	Out	22:46	08:32	9.77	1.8	16.2

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Lake	Year	Net	Conf.	Large mesh	Time (h) Set	Pull	Soak time (h)	Depth (m) D1	D2
Kintla Lake	2005	06	Double	Out	22:17	09:58	11.68	5.4	39.5
		07	Double	Out	20:30	12:47	16.28	1.4	23.0
		08	Double	Out	21:03	09:27	12.40	2.3	33.0
		09	Double	Out	20:26	08:35	12.15	1.1	46.3
		10	Double	Out	20:55	11:47	14.87	1.6	16.3
Lake Isabel	2004	01	Single	Out	17:18	11:40	18.37	2.1	8.0
		02	Single	Out	17:38	10:48	17.17	3.0	10.0
		03	Single	In	17:58	09:58	16.00	2.8	8.8
Lake McDonald	2005	01	Double	Out	18:10	09:07	14.95	2.5	15.7
		02	Double	Out	19:08	11:30	16.37	8.8	28.9
		03	Double	Out	18:36	10:35	15.98	15.3	27.0
		04	Double	Out	18:15	10:25	16.17	3.2	16.0
		05	Double	Out	17:54	10:15	16.35	15.1	31.0
		06	Double	Out	17:37	10:02	16.42	6.6	28.6
		07	Double	Out	17:20	09:35	16.25	4.2	41.6
		08	Double	Out	16:59	09:16	16.28	3.6	26.1
		09	Double	Out	18:26	10:10	15.73	5.2	32.6
		10	Double	Out	18:57	11:16	16.32	56.8	65.9
Lincoln Lake	2004	01	Single	Out	21:14	07:05	9.85	1.0	9.3
		02	Single	In	21:23	07:20	9.95	0.9	13.8
		03	Single	Out	21:45	07:40	9.92	1.5	16.8
		04	Single	In	21:53	07:58	10.08	0.5	19.5
		05	Single	Out	20:23	07:30	11.12	4.2	10.7
		06	Single	Out	20:45	07:53	11.13	1.3	16.3
		07	Single	In	20:53	08:09	11.27	1.1	18.8
		08	Single	Out	21:22	08:26	11.07	0.7	18.0
		09	Single	In	20:47	07:38	10.85	2.1	5.6
		10	Single	Out	21:00	08:13	11.22	2.6	6.1
		11	Single	In	21:13	08:42	11.48	2.4	6.1
		12	Single	Out	21:30	09:19	11.82	3.0	6.7
Logging Lake	2005	01	Double	Out	21:33	08:43	11.17	0.5	4.0
		02	Double	Out	21:53	09:14	11.35	2.0	5.9
		03	Double	Out	22:13	10:09	11.93	3.1	7.9
		04	Double	Out	20:59	07:25	10.43	2.0	19.2
		05	Double	Out	20:37	07:40	11.05	0.7	21.2
		06	Double	Out	21:22	08:15	10.88	2.0	27.2
		07	Double	Out	20:53	08:50	11.95	1.5	18.7
		08	Double	Out	20:24	09:30	13.10	3.2	37.2
		09	Double	Out	19:13	10:16	15.05	6.5	37.8
		10	Double	Out	18:28	09:36	15.13	5.5	25.7
Lower Quartz Lake	2005	01	Single	Out	20:39	08:54	12.25	1.6	5.6
		02	Single	Out	20:52	09:47	12.92	1.7	5.6
		03	Single	Out	21:54	13:20	15.43	3.0	16.3
		04	Single	Out	22:14	14:22	16.13	0.5	16.3
		05	Single	Out	21:43	08:20	10.62	4.5	17.0
		06	Single	Out	21:58	08:39	10.68	6.1	17.0
		07	Single	Out	20:46	08:40	11.90	4.5	14.5
		08	Single	Out	21:07	09:13	12.10	4.5	15.9

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Lake	Year	Net	Conf.	Large mesh	Time (h) Set	Time (h) Pull	Soak time (h)	Depth (m) D1	Depth (m) D2
Lower Quartz Lake	2006	01	Single	Out	17:31	08:29	14.97	3.9	6.3
		02	Single	In	17:55	09:05	15.17	3.0	5.8
		03	Single	In	18:31	09:27	14.93	2.9	5.7
		04	Single	In	18:56	09:55	14.98	8.0	8.6
Middle Quartz Lake	2005	01	Single	Out	21:29	08:39	11.17	1.1	8.4
		02	Single	Out	21:54	09:37	11.72	7.0	10.0
		03	Single	Out	22:22	10:04	11.70	5.1	9.8
		04	Single	Out	21:05	08:16	11.18	2.5	8.5
		05	Single	Out	21:27	08:52	11.42	4.5	10.9
		06	Single	Out	21:44	09:19	11.58	6.0	10.3
Quartz Lake	2005	01	Single	Out	17:32	09:20	15.80	3.4	22.7
		02	Single	Out	17:59	10:35	16.60	4.4	21.6
		03	Single	Out	18:30	12:28	17.97	0.9	13.3
		04	Single	Out	19:01	13:23	18.37	0.5	15.0
		05	Single	Out	19:23	14:15	18.87	1.7	17.5
		06	Single	Out	19:49	15:15	19.43	1.6	10.7
	2006	01	Double	Out	21:20	06:10	8.83	7.2	10.4
		02	Double	Out	21:45	06:34	8.82	2.2	18.0
Rogers Lake	2005	01	Single	Out	20:14	07:15	11.02	2.3	2.7
		02	Single	Out	20:32	08:27	11.92	3.1	4.3
Trout Lake	2005	01	Single	Out	21:32	08:55	11.38	2.4	10.3
		02	Single	Out	21:56	09:32	11.60	1.8	10.0
		03	Single	Out	22:53	12:17	13.40	0.6	15.9
		04	Single	Out	23:07	12:56	13.82	1.1	12.8
Upper Kintla Lake	2005	01	Single	Out	21:31	06:26	8.92	1.2	15.6
		02	Single	Out	22:03	07:02	8.98	1.7	26.3
		03	Single	Out	22:20	07:22	9.03	0.1	15.8
		04	Single	Out	22:38	07:38	9.00	0.1	15.4

Appendix 2. Lake, year sampled, site code, site length, site width, number of transects used to quantify habitat (*N*), and mean depth (± standard deviation) for shoreline electrofishing sites in 15 lakes in Glacier National Park.

Lake	Year	Site	Length (m)	Width (m)	*N*	Mean depth ± SD (m)
Akokala Lake	2004	03	100	2.00	11	0.11 ± 0.04
		04	100	2.00	11	0.14 ± 0.02
		05	100	2.00	11	0.11 ± 0.05
		06	100	2.00	11	0.23 ± 0.09
Arrow Lake	2004	02	173	3.00		
		04	106	3.00		
Bowman Lake	2005	01	100	3.00	11	0.35 ± 0.05
		02	100	3.00	11	0.30 ± 0.04
		03	100	3.00	11	0.40 ± 0.05
		04	100	3.00	11	0.42 ± 0.07
		05	100	3.00	11	0.23 ± 0.06
		06	100	3.00	11	0.12 ± 0.04
	2006	01	100	3.00	11	0.31 ± 0.06
		02	100	3.00	11	0.34 ± 0.06
		03	100	3.00	11	0.39 ± 0.05
		04	100	3.00	11	0.29 ± 0.07
Harrison Lake	2005	01	100	3.00	11	0.29 ± 0.05
		02	100	3.00	11	0.28 ± 0.06
		03	100	3.00	11	0.33 ± 0.05
Kintla Lake	2005	01	100	3.00	11	0.23 ± 0.03
		02	100	3.00	11	0.34 ± 0.09
		03	100	3.00	11	0.34 ± 0.06
		04	100	3.00	11	0.39 ± 0.06
		05	100	3.00	11	0.20 ± 0.07
		06	100	3.00	11	0.28 ± 0.08
	2006	01	100	3.00	11	0.33 ± 0.05
		02	100	3.00	11	0.36 ± 0.05
		03	100	3.00	11	0.30 ± 0.06
Lake Isabel	2004	03	100	3.00		
		04	100	3.00		
Lake McDonald	2006	01	100	3.00	11	0.52 ± 0.11
		02	100	3.00	11	0.61 ± 0.11
		03	100	3.00	11	0.41 ± 0.10
		04	100	3.00	11	0.28 ± 0.12
		05	100	3.00	11	0.24 ± 0.06
Lincoln Lake	2004	02	100	3.00	11	0.13 ± 0.07
		03	100	3.00	11	0.10 ± 0.04
		05	100	3.00	11	0.38 ± 0.16
		06	100	3.00	11	0.31 ± 0.10
Logging Lake	2005	02	100	3.00	11	0.23 ± 0.04
		03	100	3.00	11	0.39 ± 0.09
		04	100	3.00	11	0.19 ± 0.03
		06	100	3.00	11	0.26 ± 0.03
		07	100	3.00	11	0.26 ± 0.03
		08	100	3.00	11	0.25 ± 0.04
Lower Quartz Lake	2005	01	100	3.00	11	0.24 ± 0.05
		02	100	3.00	11	0.14 ± 0.06

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Lake	Year	Site	Length (m)	Width (m)	*N*	Mean depth ± SD (m)
Lower Quartz Lake	2005	03	100	3.00	11	0.25 ± 0.04
		04	100	3.00	11	0.33 ± 0.04
		07	100	3.00	11	0.27 ± 0.07
		08	100	3.00	11	0.22 ± 0.05
Middle Quartz Lake	2005	03	100	3.00	11	0.23 ± 0.08
		04	100	3.00	11	0.20 ± 0.10
		05	100	3.00	11	0.30 ± 0.07
		06	100	3.00	11	0.24 ± 0.02
		07	100	3.00	11	0.22 ± 0.06
		08	100	3.00	11	0.26 ± 0.05
Quartz Lake	2006	01	100	3.00	11	0.31 ± 0.08
		02	100	3.00	11	0.27 ± 0.09
		03	100	3.00	11	0.44 ± 0.05
		05	100	3.00	11	0.32 ± 0.04
		06	100	3.00	11	0.31 ± 0.06
		07	100	3.00	11	0.28 ± 0.09
Rogers Lake	2006	01	100	3.00	11	0.09 ± 0.02
		02	100	3.00	11	0.08 ± 0.03
Trout Lake	2005	01	100	3.00	11	0.22 ± 0.12
		02	100	3.00	11	0.39 ± 0.17
		04	100	3.00	11	0.41 ± 0.16
		05	100	3.00	11	0.25 ± 0.03
		06	100	3.00	11	0.20 ± 0.06
		07	100	3.00	11	0.19 ± 0.03
Upper Kintla Lake	2005	01	100	3.00	11	0.22 ± 0.06
		02	100	3.00	11	0.26 ± 0.02
		06	100	3.00	11	0.28 ± 0.08
		07	100	3.00	11	0.45 ± 0.05
		08	100	3.00	11	0.35 ± 0.03
		09	100	3.00	11	0.36 ± 0.07

Appendix 3. Lake, year sampled, species sampled, and number sampled by gill nets, hook and line, shoreline electrofishing, and stream electrofishing for lakes sampled in Glacier National Park.

					Electrofishing	
Lake	Year	Species	Gill net	Hook and line	Shoreline	Stream
Akokala Lake	2004	Bull trout	13	3	2	4
		Cutthroat trout	4	10		11
		Mountain whitefish	86			
		Sculpin			74	10
Arrow Lake	2004	Bull trout	17	7	18	
		Cutthroat trout	62	5	21	13
Bowman Lake	2005	Bull trout	17			
		Cutthroat trout	23			
		Lake trout	52			
		Longnose sucker	37		15	
		Mountain whitefish	406			
		Redside shiner	5		22	
		Sculpin	3		124	
	2006	Bull trout				2
		Longnose sucker			3	
		Sculpin			48	43
Cerulean Lake	2004	Bull trout	6	14		
		Cutthroat trout		61		
		Mountain whitefish	56			
Harrison Lake	2005	Bull trout	9			
		Brook trout	1			
		Cutthroat trout	12	9	1	
		Kokanee	4	1		
		Lake trout	9	1		
		Longnose sucker	51		2	
		Mountain whitefish	338			
		Sculpin			3	
Kintla Lake	2005	Bull trout	12			
		Cutthroat trout	47		1	
		Lake trout	34	1		
		Longnose sucker	111		128	
		Mountain whitefish	379			
		Peamouth	35		11	
		Redside shiner	8			
		Sculpin			58	
	2006	Bull trout		2		
		Cutthroat trout		2		2
		Lake trout		1		
		Longnose sucker			24	
		Peamouth			2	
		Sculpin			35	2
Lake Isabel	2004	Bull trout	57		9	4
		Cutthroat trout	93		3	67
Lake McDonald	2005	Bull trout	8			
		Cutthroat trout	2			
		Kokanee	8			
		Lake trout	33			

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Lake	Year	Species	Gill net	Hook and line	Electrofishing Shoreline	Electrofishing Stream
Lake McDonald	2005	Lake whitefish	73			
		Largescale sucker	23			
		Longnose sucker	41			
		Mountain whitefish	68			
		Northern pikeminnow	115			
		Peamouth	90			
		Pygmy whitefish	10			
		Redside shiner	7			
	2006	Cutthroat trout			2	
		Longnose sucker			3	
		Mountain whitefish			1	
		Northern pikeminnow			20	
		Peamouth			13	
		Redside shiner			16	
		Sculpin			21	
Lincoln Lake	2004	Bull trout	9			3
		Brook trout	10	2		17
		Cutthroat trout	7	27		7
		Longnose sucker	187	1		
		Mountain whitefish	65			
		Sculpin			20	12
Logging Lake	2005	Bull trout	7			
		Cutthroat trout	41			3
		Lake trout	25	2		
		Longnose sucker	175			1
		Mountain whitefish	492			
		Northern pikeminnow	239		21	8
		Redside shiner	5		10	4
		Sculpin			15	25
	2006	Lake trout		1		
Lower Quartz Lake	2005	Bull trout	4			
		Cutthroat trout	45			1
		Lake trout	2			
		Longnose sucker	105		20	3
		Mountain whitefish	190			
		Redside shiner	3		33	
		Sculpin			23	14
	2006	Bull trout	9	1		
		Cutthroat trout	13	4		
		Lake trout		1		
		Longnose sucker	25			
		Mountain whitefish	45			
Middle Quartz Lake	2005	Bull trout	11			
		Cutthroat trout	12	4		8
		Longnose sucker	42		1	4
		Mountain whitefish	140			
		Redside shiner	5		10	1
		Sculpin				17

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Lake	Year	Species	Gill net	Hook and line	Electrofishing Shoreline	Electrofishing Stream
Quartz Lake	2005	Bull trout	40			
		Cutthroat trout	23			
		Lake trout	1			
		Largescale sucker	9			
		Longnose sucker	45			
		Mountain whitefish	254			
		Redside shiner	1			
	2006	Bull trout	14	5		1
		Cutthroat trout	5	1		
		Lake trout		3		
		Longnose sucker	17		59	
		Mountain whitefish	78			
		Redside shiner	6		20	
		Sculpin			18	
Rogers Lake	2005	Bull trout	1			
		Cutthroat trout	9	5		
		Lake trout	1			
		Longnose sucker	37			
		Mountain whitefish	77			
		Northern pikeminnow	5			
		Rainbow trout		1		
	2006	Mountain whitefish			1	
Trout Lake	2005	Bull trout	26	3		
		Cutthroat trout	98			9
		Sculpin	1		7	79
Upper Kintla Lake	2005	Bull trout	34	9	9	23
Upper Lake Isabel	2004	Bull trout		7		

Appendix 4. Lake, year sampled, site code, the number of observations used to quantify substrate (*N*), mean substrate type calculated from substrate type codes (± standard deviation), dominant substrate type, and mean substrate embeddedness calculated from substrate embeddedness codes (± standard deviation) for shoreline electrofishing sites in 15 lakes in Glacier National Park. Three substrate measurements were made at each of 11 transects for each site; however, bedrock and other (e.g., woody debris and bryopsids) substrate types were not included in the analysis. Therefore, *N* is less than 33 for some sites.

				Substrate		
Lake	Year	Site	*N*	Type (mean ± SD)	Dominant type	Embeddedness (mean ± SD)
Akokala Lake	2004	03	33	0.94 ± 0.97	Silt and clay	4.67 ± 0.48
		04	33	3.00 ± 1.46	Cobble	3.15 ± 1.06
		05	33	1.67 ± 1.45	Silt and clay, Gravel	4.06 ± 0.86
		06	33	1.18 ± 1.61	Silt and clay	4.45 ± 0.83
Arrow Lake	2004	02				
		04				
Bowman Lake	2005	01	33	3.21 ± 0.48	Pebble	0.82 ± 0.81
		02	33	3.91 ± 0.72	Cobble	0.27 ± 0.45
		03	33	3.21 ± 0.65	Pebble	0.97 ± 1.05
		04	33	3.00 ± 1.27	Gravel, Cobble	2.03 ± 1.24
		05	33	3.70 ± 0.68	Cobble	0.27 ± 0.45
		06	33	3.09 ± 0.77	Pebble	1.30 ± 1.10
	2006	01	33	3.06 ± 1.46	Cobble	2.61 ± 1.41
		02	33	4.06 ± 0.70	Cobble	1.21 ± 1.17
		03	33	4.42 ± 0.83	Boulder	1.15 ± 1.18
		04	33	3.91 ± 0.58	Cobble	1.27 ± 1.01
Harrison Lake	2005	01	33	3.45 ± 1.03	Cobble	2.33 ± 1.31
		02	33	3.67 ± 1.31	Cobble, Boulder	1.27 ± 1.28
		03	33	3.88 ± 0.99	Cobble	2.03 ± 1.10
Kintla Lake	2005	01	33	3.52 ± 0.57	Pebble	0.39 ± 0.66
		02	33	3.94 ± 0.66	Cobble	0.79 ± 0.65
		03	33	3.73 ± 0.63	Cobble	0.73 ± 0.98
		04	33	4.09 ± 0.84	Cobble	0.61 ± 0.93
		05	33	3.88 ± 0.74	Cobble	0.61 ± 0.66
		06	33	4.52 ± 0.57	Boulder	1.00 ± 0.75
	2006	01	31	4.23 ± 0.62	Cobble	1.71 ± 1.01
		02	33	3.73 ± 0.72	Cobble	1.12 ± 1.14
		03	33	4.09 ± 0.68	Cobble	0.79 ± 0.99
Lake Isabel	2004	03				
		04				
Lake McDonald	2006	01	33	3.70 ± 1.16	Boulder	2.00 ± 1.00
		02	33	4.58 ± 0.61	Boulder	0.85 ± 0.80
		03	30	3.57 ± 0.94	Pebble	1.53 ± 1.31
		04	25	3.20 ± 0.65	Pebble	1.36 ± 0.57
		05	33	3.70 ± 0.81	Cobble	1.33 ± 0.78
Lincoln Lake	2004	02	33	2.70 ± 1.42	Pebble	2.73 ± 1.42
		03	33	2.61 ± 1.78	Pebble	3.24 ± 1.30

Appendix 4: continued on next page

Lake	Year	Site	*N*	Substrate Type (mean ± SD)	Substrate Dominant Type	Substrate Embeddedness (mean ± SD)
Lincoln Lake	2004	05	33	3.09 ± 0.80	Pebble	1.42 ± 1.48
		06	33	3.67 ± 0.60	Cobble	0.33 ± 0.54
Logging Lake	2005	02	33	3.21 ± 0.99	Pebble	2.67 ± 0.99
		03	33	3.15 ± 1.09	Pebble	3.00 ± 0.94
		04	33	3.18 ± 0.58	Pebble	1.94 ± 1.39
		06	33	3.27 ± 0.63	Pebble	1.88 ± 0.60
		07	33	3.97 ± 1.07	Boulder	2.67 ± 1.19
		08	33	3.79 ± 1.32	Boulder	2.88 ± 1.17
Lower Quartz Lake	2005	01	31	4.00 ± 1.06	Boulder	2.58 ± 1.09
		02	33	2.45 ± 0.51	Gravel	2.82 ± 1.18
		03	33	3.30 ± 1.49	Boulder	2.67 ± 1.41
		04	33	4.27 ± 0.88	Boulder	2.97 ± 1.13
		07	32	3.59 ± 1.32	Pebble	2.88 ± 1.10
		08	33	2.82 ± 0.58	Pebble	3.24 ± 0.75
Middle Quartz Lake	2005	03	32	3.22 ± 1.34	Pebble	2.66 ± 1.23
		04	31	3.26 ± 1.15	Pebble	2.61 ± 1.26
		05	33	3.55 ± 0.83	Pebble	1.94 ± 1.06
		06	31	2.55 ± 1.46	Gravel	3.58 ± 0.72
		07	22	2.95 ± 1.33	Gravel	2.95 ± 1.21
		08	33	2.64 ± 0.86	Gravel	3.45 ± 0.79
Quartz Lake	2006	01	33	4.42 ± 0.56	Cobble	0.67 ± 0.69
		02	33	4.30 ± 0.88	Boulder	1.52 ± 1.18
		03	33	3.03 ± 1.38	Cobble	2.33 ± 1.73
		05	32	4.28 ± 0.68	Cobble	0.91 ± 1.25
		06	33	4.64 ± 0.49	Boulder	0.82 ± 0.88
		07	33	4.45 ± 0.56	Cobble, Boulder	0.58 ± 0.71
Rogers Lake	2006	01	33	3.24 ± 0.61	Pebble	1.85 ± 0.97
		02	33	2.91 ± 0.77	Pebble	2.79 ± 1.11
Trout Lake	2005	01	18	3.67 ± 0.77	Pebble	1.67 ± 0.69
		02	33	4.76 ± 0.61	Boulder	1.42 ± 1.37
		04	32	3.97 ± 0.74	Cobble	3.00 ± 1.30
		05	33	3.88 ± 1.34	Boulder	2.82 ± 1.38
		06	33	3.21 ± 0.60	Pebble	1.88 ± 1.39
		07	33	4.12 ± 0.96	Boulder	2.36 ± 1.14
Upper Kintla Lake	2005	01	33	3.70 ± 0.95	Cobble	1.39 ± 1.14
		02	33	3.97 ± 0.81	Cobble	1.06 ± 0.97
		06	33	3.67 ± 0.99	Pebble, Cobble	1.52 ± 1.28
		07	33	3.42 ± 1.37	Boulder	1.94 ± 1.54
		08	33	3.45 ± 0.71	Pebble	1.30 ± 1.24
		09	33	4.21 ± 0.82	Boulder	1.36 ± 1.17

Appendix 5. Lake, year sampled, site code, temperature, dissolved oxygen, conductivity, and salinity for shoreline electrofishing sites in 15 lakes in Glacier National Park.

Lake	Year	Site	Temperature (° C)	Dissolved oxygen (mg/L)	Conductivity (µS/cm)	Salinity (ppt)
Akokala Lake	2004	03	9.2	8.34	5.1	0.0
		04	8.6	9.66	0.0	0.0
		05	11.3	9.93	21.7	0.0
		06	10.2	9.98	0.6	0.0
Arrow Lake	2004	02				
		04				
Bowman Lake	2005	01	9.9	10.18	85.9	0.1
		02	10.3	10.10	86.5	0.1
		03	11.2	10.22	53.6	0.0
		04	11.9	9.65	88.8	0.1
		05	10.8	9.80	86.3	0.0
		06	11.1	9.85	87.3	0.1
	2006	01	12.6	11.14	85.2	0.1
		02	12.0	11.75	22.0	0.0
		03	10.5	11.93	58.8	0.1
		04	10.2	13.10	36.6	0.0
Harrison Lake	2005	01	18.0	8.05	18.7	0.0
		02	16.7	8.43	53.2	0.0
		03	16.5	8.44	11.5	0.0
Kintla Lake	2005	01	19.8	8.76	110.3	0.1
		02	20.1	8.21	117.6	0.1
		03	12.1	10.51	91.4	0.1
		04	11.4	10.27	88.5	0.1
		05	12.5	9.68	59.9	0.1
		06	12.6	10.01	78.3	0.1
	2006	01	14.5	10.28	30.1	0.0
		02	12.2	10.81	3.2	0.0
		03	11.9	10.82	54.6	0.0
Lake Isabel	2004	03	10.3	8.76	20.6	0.0
		04	8.2	9.43	22.2	0.0
Lake McDonald	2006	01	13.0	11.50	65.3	0.0
		02	10.5	12.74	76.0	0.1
		03	10.5	12.74	76.0	0.1
		04	11.7	12.28	77.4	0.1
		05	11.7	12.28	77.4	0.1
Lincoln Lake	2004	02	14.0	13.03	20.3	0.0
		03	14.2	12.80	10.2	0.0
		05	12.9	8.51	11.9	0.0
		06	12.8	9.09	18.8	0.0
Logging Lake	2005	02	18.7	7.55	0.6	0.0
		03	18.7	7.51	47.4	0.0
		04	18.6	7.14	19.9	0.0
		06	17.7	7.65	29.4	0.0
		07	17.1	7.86	42.1	0.0
		08	17.1	7.86	42.1	0.0
Lower Quartz Lake	2005	01	18.9	6.50	45.7	0.0
		02	19.6	6.76	21.5	0.0

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Lower Quartz Lake	2005	03	19.7	7.15	7.2	0.0
		04	19.7	7.47	57.7	0.0
		07	18.8	7.61	0.5	0.0
		08	19.9	7.31	57.9	0.0
Middle Quartz Lake	2005	03	19.5	7.05	54.2	0.0
		04	19.6	7.02	52.8	0.0
		05	19.6	6.89	5.2	0.0
		06	21.4	7.13	32.3	0.0
		07	22.0	7.24	15.0	0.0
		08	20.7	7.39	19.0	0.0
Quartz Lake	2006	01	13.9	10.13	45.3	0.0
		02	13.6	10.36	24.7	0.0
		03	13.5	12.26	10.5	0.0
		05	16.7	9.41	27.4	0.0
		06	16.8	8.89	43.9	0.0
		07	16.2	9.37	33.3	0.0
Rogers Lake	2006	01	21.0			
		02	21.0			
Trout Lake	2005	01	19.3	7.85	18.9	0.0
		02	19.2	7.37	23.0	0.0
		04	19.1	7.83	49.9	0.0
		05	19.2	7.63	50.2	0.0
		06	17.8	7.97	49.2	0.0
		07	17.8	7.97	49.2	0.0
Upper Kintla Lake	2005	01	12.8	8.93	54.1	0.0
		02	12.8	9.28	9.5	0.0
		06	10.7	9.83	78.8	0.0
		07	10.6	9.43	78.6	0.1
		08	12.5	9.38	82.3	0.1
		09	13.0	9.33	55.1	0.1

Appendix 6. Lake, year sampled, stream site (lake inlet or outlet), site length, number of transects used to quantify habitat (*N*), mean wetted width (± standard deviation), mean depth (± standard deviation), and maximum depth for stream electrofishing sites associated with 12 lakes in Glacier National Park.

Lake	Year	Site	Length (m)	*N*	Mean wetted width ± SD (m)	Mean depth ± SD (m)	Maximum depth (m)
Akokala Lake	2004	Inlet	156	17	9.37 ± 2.95	0.27 ± 0.13	2.29
		Outlet	111	12	12.86 ± 5.08	0.24 ± 0.08	0.79
Arrow Lake	2004	Inlet					
		Outlet					
Bowman Lake	2006	Inlet	100	11	9.60 ± 3.75	0.26 ± 0.14	0.88
		Outlet	100	11	17.04 ± 4.61	0.29 ± 0.12	1.11
Kintla Lake	2006	Inlet					
Lake Isabel	2004	Inlet	87	10	3.68 ± 1.98	0.11 ± 0.05	0.41
		Outlet	111	12	6.50 ± 1.81	0.17 ± 0.10	0.77
Lincoln Lake	2004	Inlet	100	11	3.58 ± 1.43	0.11 ± 0.04	0.48
		Outlet	100	10	7.03 ± 2.78	0.19 ± 0.06	0.58
Logging Lake	2005	Inlet	125	14	14.28 ± 2.35	0.24 ± 0.14	0.94
		Outlet	100	11	14.72 ± 2.68	0.15 ± 0.03	0.43
Lower Quartz Lake	2005	Inlet	100	11	11.26 ± 2.38	0.22 ± 0.07	0.72
		Outlet					
Middle Quartz Lake	2005	Inlet	110	12	18.57 ± 5.55	0.21 ± 0.07	0.87
		Outlet	110	12	10.79 ± 1.96	0.31 ± 0.07	0.88
Quartz Lake	2006	Inlet	100	11	11.62 ± 3.44	0.30 ± 0.06	1.15
Trout Lake	2005	Inlet	120	13	12.21 ± 3.70	0.29 ± 0.17	0.96
		Outlet	100	11	10.84 ± 1.25	0.17 ± 0.03	0.51
Upper Kintla Lake	2005	Inlet	100	11	6.52 ± 1.65	0.26 ± 0.10	0.91
		Outlet					
		Agassiz	120	13	10.41 ± 2.68	0.31 ± 0.09	1.14

Appendix 7. Lake, year sampled, stream site (lake inlet or outlet), the number of observations used to quantify substrate (*N*), mean substrate type calculated from substrate type codes (± standard deviation), dominant substrate type, and mean substrate embeddedness calculated from substrate embeddedness codes (± standard deviation) for stream electrofishing sites associated with 12 lakes in Glacier National Park.

				Substrate		
Lake	Year	Site	*N*	Type (mean ± SD)	Dominant type	Embeddedness (mean ± SD)
Akokala Lake	2004	Inlet	51	2.51 ± 0.58	Pebble	1.25 ± 1.25
		Outlet	36	3.83 ± 0.65	Cobble	0.17 ± 0.51
Arrow Lake	2004	Inlet				
		Outlet				
Bowman Lake	2006	Inlet	33	2.76 ± 0.87	Pebble	3.27 ± 0.94
		Outlet	33	3.64 ± 0.55	Cobble	1.09 ± 1.04
Kintla Lake	2006	Inlet				
Lake Isabel	2004	Inlet	29	3.24 ± 0.91	Cobble	1.07 ± 1.25
		Outlet	36	3.44 ± 1.30	Pebble	0.92 ± 1.66
Lincoln Lake	2004	Inlet	33	3.58 ± 0.56	Cobble	
		Outlet	30	4.20 ± 1.03	Boulder	
Logging Lake	2005	Inlet	42	2.43 ± 0.77	Pebble	3.02 ± 0.81
		Outlet	33	4.67 ± 0.65	Boulder	1.97 ± 1.24
Lower Quartz Lake	2005	Inlet	33	3.64 ± 0.55	Cobble	0.58 ± 0.71
		Outlet				
Middle Quartz Lake	2005	Inlet	36	4.00 ± 0.83	Pebble, Cobble, Boulder	1.31 ± 0.89
		Outlet	36	4.47 ± 0.70	Boulder	1.14 ± 0.96
Quartz Lake	2006	Inlet	33	3.06 ± 0.70	Pebble	2.73 ± 0.94
Trout Lake	2005	Inlet	39	4.10 ± 0.79	Cobble	1.38 ± 1.16
		Outlet	27	4.78 ± 0.42	Boulder	1.52 ± 0.89
Upper Kintla Lake	2005	Inlet	33	2.76 ± 0.90	Pebble	2.97 ± 1.02
		Outlet				
		Agassiz	39	3.00 ± 0.00	Pebble	2.77 ± 0.93

Appendix 8. Lake, year sampled, stream site (lake inlet or outlet), temperature, dissolved oxygen, conductivity, and salinity for stream electrofishing sites associated with 12 lakes in Glacier National Park.

Lake	Year	Site	Temperature (° C)	Dissolved oxygen (mg/L)	Conductivity (μS/cm)	Salinity (ppt)
Akokala Lake	2004	Inlet	6.4	11.79	25.2	0.0
		Outlet	9.5	11.68	46.1	0.0
Arrow Lake	2004	Inlet				
		Outlet				
Bowman Lake	2006	Inlet	9.8	9.53	91.6	0.1
		Outlet	18.2	8.60	104.9	0.1
Kintla Lake	2006	Inlet	11.7	10.30	75.0	0.0
Lake Isabel	2004	Inlet	8.2	9.43	22.2	0.0
		Outlet	10.3	8.76	20.6	0.0
Lincoln Lake	2004	Inlet	13.5	19.58	19.1	0.0
		Outlet	16.8	11.74	19.6	0.0
Logging Lake	2005	Inlet	14.0	8.01	31.6	0.0
		Outlet	20.1	7.70	42.6	0.0
Lower Quartz Lake	2005	Inlet	17.2	7.47	55.1	0.0
		Outlet	20.3	7.33	58.0	0.0
Middle Quartz Lake	2005	Inlet	19.6	7.81	57.7	0.0
		Outlet	20.0	7.50	57.9	0.0
Quartz Lake	2006	Inlet	9.4	10.70	49.3	0.0
Trout Lake	2005	Inlet	18.6	7.51	37.4	0.0
		Outlet	18.6	7.75	11.3	0.0
Upper Kintla Lake	2005	Inlet	7.7	10.99	62.7	0.0
		Outlet	10.5	8.96	82.0	0.1
		Agassiz	9.3	10.12	46.6	0.0

Appendix 9. Lake, year sampled, stream site (lake inlet or outlet), length and width (± standard deviation) of undercut banks, and numbers of woody debris (single, aggregate, or root wad) for stream electrofishing sites associated with 12 lakes in Glacier National Park.

			Undercut banks (m)		Woody debris (*N*)		
Lake	Year	Site	Length	Width	Single	Aggregate	Root wad
Akokala Lake	2004	Inlet	2.74	0.51 ± 0.25	8		
			3.17	0.68 ± 0.08			
		Outlet			24	2	1
Arrow Lake	2004	Inlet					
		Outlet					
Bowman Lake	2006	Inlet	2.65	0.64 ± 0.40	18	7	2
			4.27	0.61 ± 0.16			
			1.68	0.66 ± 0.54			
			1.86	0.41 ± 0.24			
		Outlet	3.35	1.27 ± 0.41	11	2	
Kintla Lake	2006	Inlet					
Lake Isabel	2004	Inlet	2.12	0.29 ± 0.06	24	2	
			2.27	0.30 ± 0.10			
		Outlet			27	8	3
Lincoln Lake	2004	Inlet	4.48	0.49 ± 0.10	20	2	8
			1.40	0.38 ± 0.15			
			1.43	0.46 ± 0.11			
			2.59	0.39 ± 0.05			
		Outlet			19	5	1
Logging Lake	2005	Inlet			37	10	1
		Outlet			22	4	
Lower Quartz Lake	2005	Inlet			18	6	2
		Outlet					
Middle Quartz Lake	2005	Inlet			16	9	6
		Outlet			25	5	10
Quartz Lake	2006	Inlet			29	7	3
Trout Lake	2005	Inlet	1.68	0.82 ± 0.36	6		1
		Outlet			10		
Upper Kintla Lake	2005	Inlet	3.35	0.40 ± 0.14	15	14	14
		Outlet					
		Agassiz	2.26	0.65 ± 0.23	15	3	4
			0.85	1.06 ± 0.16			
			3.05	0.72 ± 0.10			
			1.89	0.77 ± 0.21			

Appendix 10. Pairwise F_{st} values based on 10 microsatellite loci for 16 bull trout populations in Glacier National Park.

Population	Akokala Lake	Arrow Lake	Bowman Lake	Cerulean Lake	Harrison Lake	Kintla Lake	Lake Isabel	Lake McDonald	Lincoln Lake	Logging Lake	Lower Quartz Lake	Middle Quartz Lake	Quartz Lake	Trout Lake	Upper Kintla Lake
Arrow Lake	0.3904														
Bowman Lake	0.1423	0.3692													
Cerulean Lake	0.2019	0.5062	0.1716												
Harrison Lake	0.2611	0.6431	0.2229	0.2552											
Kintla Lake	0.0890	0.3852	0.0524	0.1270	0.2115										
Lake Isabel	0.2905	0.6059	0.3494	0.3050	0.3712	0.2510									
Lake McDonald	0.1211	0.4786	0.0746	0.1746	0.2432	0.0053	0.2778								
Lincoln Lake	0.1152	0.4782	0.1538	0.1809	0.1933	0.0600	0.2331	0.0994							
Logging Lake	0.1789	0.5519	0.1566	0.1143	0.2432	0.0993	0.3273	0.1632	0.1879						
Lower Quartz Lake	0.1893	0.6074	0.1472	0.0322	0.2519	0.1006	0.3192	0.1278	0.1656	0.1685					
Middle Quartz Lake	0.2189	0.5599	0.1799	0.0000	0.2988	0.1377	0.3557	0.2075	0.2200	0.1419	0.0415				
Quartz Lake	0.1689	0.4783	0.1213	0.0078	0.2376	0.0979	0.2938	0.1443	0.1628	0.0788	0.0549	0.0152			
Trout Lake	0.3779	0.0198	0.3500	0.4841	0.6189	0.3652	0.5855	0.4533	0.4538	0.5237	0.5705	0.5346	0.4541		
Upper Kintla Lake	0.4053	0.6650	0.3983	0.4505	0.5169	0.2754	0.4510	0.3436	0.3525	0.4715	0.4996	0.4900	0.4438	0.6430	
Upper Lake Isabel	0.3487	0.6904	0.3769	0.3118	0.4471	0.2997	0.2197	0.3583	0.2999	0.3841	0.3775	0.3674	0.3069	0.6563	0.5717

Appendix 11. Population (lake), year sampled, number of redds observed, and georeferenced location (UTM coordinates) for redds observed during redd surveys.

			Location (UTM coordinates)		
Population	Year sampled	Number of redds	Zone	Easting (m)	Northing (m)
Bowman Lake	2004	0			
	2005	0			
	2006	1	11	0711286	5421155
		1	11	0711304	5421154
Harrison Lake	2004	1	12	0297952	5379450
		1	12	0297984	5379480
		1	12	0298011	5379503
		1	12	0298017	5379527
	2005	0			
	2006	6	12	0297385	5379173
		1	12	0298055	5379566
		1	12	0298532	5380170
Logging Lake	2004	1	11	0719446	5407482
		2	11	0719492	5407479
	2005	1	11	0718992	5406898
		3	11	0719002	5407093
		5	11	0719129	5407094
		7	11	0719192	5407073
		1	11	0719307	5407167
		3	11	0719311	5407166
	2006	0			
Lower Quartz Lake	2004	1	11	0708024	5410788
	2005	1	11	0708048	5410787
		1	11	0708081	5410850
		1	11	0708121	5410832
	2006	1	11	0708029	5410770
		1	11	0708047	5410795
Middle Quartz Lake	2004	0			
	2005	0			
	2006	0			
Quartz Lake	2004	1	11	0715453	5414742
		1	11	0715492	5414790
		1	11	0715500	5414803
		1	11	0715536	5414938
		1	11	0715542	5414967
		1	11	0715584	5415025
		1	11	0715586	5415027
		1	11	0715585	5415034
		2	11	0715582	5415032
		9	11	0715626	5415057
		6	11	0715649	5415067
		4	11	0715667	5415068
		2	11	0715699	5415079
		2	11	0715705	5415092
		2	11	0715702	5415108
		1	11	0715705	5415125

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Quartz Lake	2004	1	11	0715739	5415158
		2	11	0715772	5415199
		1	11	0715796	5415251
		1	11	0715804	5415257
		2	11	0715833	5415254
		1	11	0715927	5415250
		1	11	0715935	5415244
		1	11	0716018	5415291
		1	11	0716058	5415363
		1	11	0716053	5415361
		2	11	0716171	5415496
		1	11	0716185	5415495
		1	11	0716194	5415497
		1	11	0716224	5415512
		1	11	0716277	5415662
		1	11	0716331	5415720
	2005	1	11	0715503	5414797
		1	11	0715632	5415062
		1	11	0715667	5415071
		1	11	0716061	5415368
	2006	1	11	0715466	5414745
		1	11	0715487	5414771
		1	11	0715488	5414781
		1	11	0715498	5414809
		1	11	0715515	5414838
		1	11	0715502	5414837
		1	11	0715501	5414853
		2	11	0715509	5414887
		1	11	0715523	5414906
		1	11	0715517	5414925
		2	11	0715543	5414942
		1	11	0715573	5415023
		1	11	0715614	5415054
		1	11	0715644	5415061
		4	11	0715666	5415073
		1	11	0715713	5415107
		1	11	0715726	5415121
		2	11	0715739	5415152
		1	11	0715763	5415180
		1	11	0715772	5415191
		1	11	0715772	5415198
		1	11	0715768	5415230
		1	11	0715783	5415241
		1	11	0715837	5415245
		1	11	0715860	5415232
		1	11	0715907	5415256
		1	11	0716021	5415297
		2	11	0716054	5415353
		1	11	0716065	5415378

Appendix 12. Number of muscle samples collected in Glacier National Park and prepared for stable isotope analysis. BLT = Bull trout; LKT = Lake trout; WCT = Westslope cutthroat trout; KOK = Kokanee; BRK = Brook trout; MWF = Mountain whitefish; PWF = Pigmy whitefish; LWF = Lake whitefish; LNS = Longnose sucker; LSS = Largescale sucker; NPM = Norther pikeminnow; PEM = Peamount; RSS = Redside shiner.

Lake	BLT	LKT	WCT	KOK	BRK	MWF	PWF	LWF	LNS	LSS	NPM	PEM	RSS
Akokala Lake	10		5			5							
Arrow Lake	10		5										
Bowman Lake	10	10	5			5			5				4
Cerulean Lake	10		5			5							
Harrison Lake	8	10	5	4	1	5			5				
Kintla Lake	10	10	5			5			5			5	4
Lake Isabel	10		5										
Lake McDonald	8	10	2	5		5	5	4	5	5	5	5	4
Lincoln Lake	9		5		5	5			5				
Logging Lake	6	10	5			5			5		5		5
Lower Quartz Lake	10	3	5			5			5				4
Middle Quartz Lake	10		5			5			5				5
Quartz Lake	20	3	10			10			10	5			5
Trout Lake	10		5										
Upper Kintla Lake	10												