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Research Summary

for

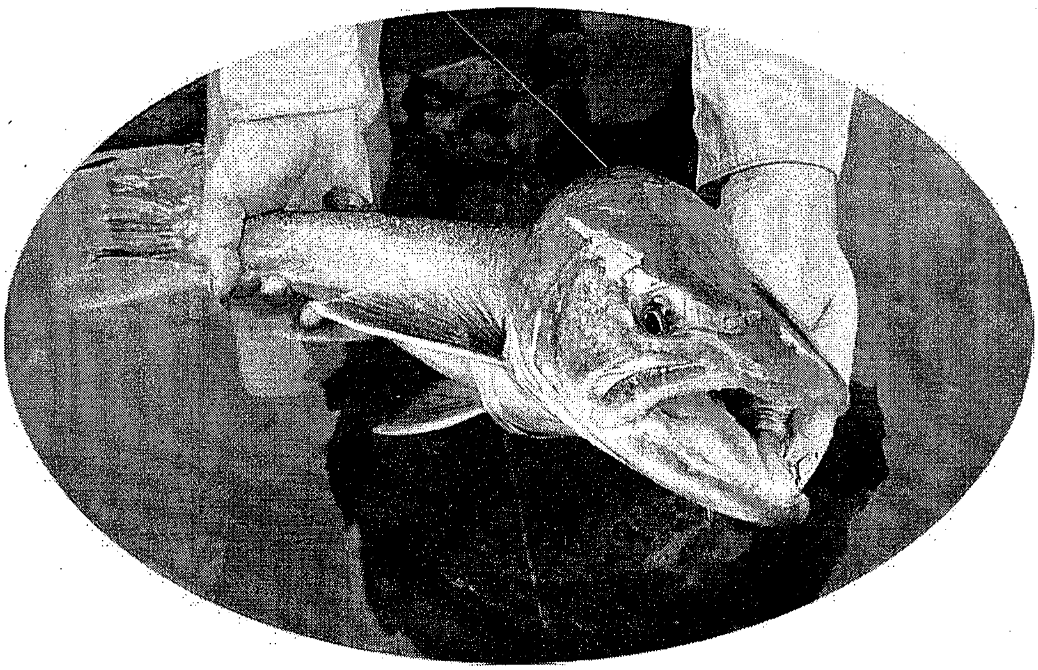
Action Plan to Conserve Bull Trout in Glacier National Park, Montana

Michael H. Meeuwig and Christopher S. Guy

US Geological Survey, Montana Cooperative Fishery Research Unit,
Department of Ecology, Montana State University, Bozeman, MT 59717

Wade A. Fredenberg

US Fish and Wildlife Service, Creston Fish and Wildlife Center
780 Creston Hatchery Road, Kalispell, MT 59901



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Abstract

This document provides a summary of research activities conducted during the period of June 2004 through October 2006 associated with the document "Action Plan to Conserve Bull Trout in Glacier National Park, Montana." Information presented in this research summary represent data directly associated with comments and suggested conservation actions outlined in the action plan. This document provides a general description of the study area, field and laboratory methodologies, data analytic techniques, brief interpretation of data analyses, and general conclusions of research results. For a comprehensive description of research activities conducted by the US Geological Survey, Montana Cooperative Fishery Research Unit, see Meeuwig and Guy (2007).

Study Area

Glacier National Park, Montana, is geographically divided by three major drainages; the Columbia Drainage, the Hudson Drainage, and the Missouri Drainage. Bull trout are native in the Columbia and Hudson drainages. The action plan focuses on 17 lakes within Glacier National Park west of the Continental Divide (Figure 1), which are part of the North Fork Flathead (USGS Cataloging Unit: 17010206) and the Middle Fork Flathead (USGS Cataloging Unit: 17010207) watersheds (USEPA 2006) in the Columbia Drainage. Situated in glaciated valleys, lakes within Glacier National Park can generally be classified as cirque and moraine lakes (Gallagher 1999). 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).

The study lakes vary in size and elevation (Table 1) and fish assemblages (Appendix 1). Fish assemblages within the study system vary from monospecific (e.g., Upper Kintla Lake), to lakes containing intact native species assemblages (e.g., Cerulean Lake), to lakes containing complex fish assemblages with multiple nonnative introductions and invasions (e.g., Lake McDonald). The study lakes represent the known distribution of adfluvial bull trout *Salvelinus confluentus* in Glacier National Park west of the Continental Divide, a species of char listed as Threatened under the US Endangered Species Act of 1973. Eight of the study lakes are inhabited by lake trout *Salvelinus namaycush*, a nonnative char species.

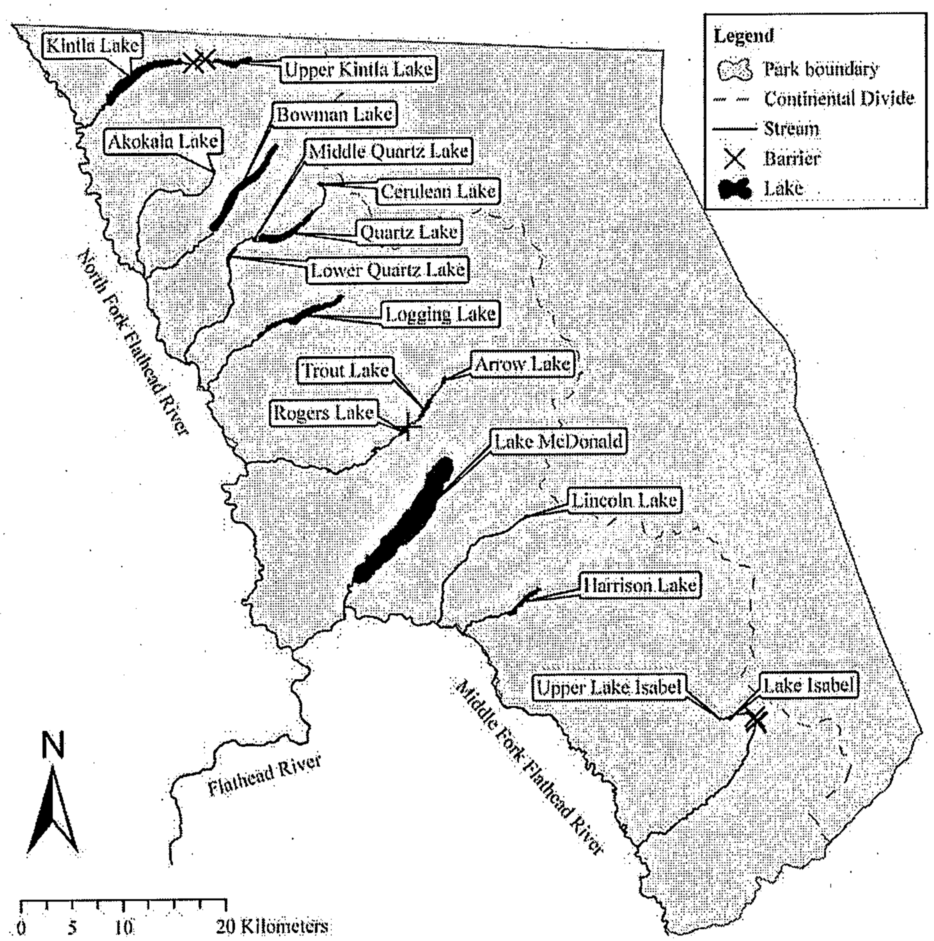

Figure 1. Seventeen lakes sampled in Glacier National Park west of the Continental Divide during 2004, 2005, and 2006, and the locations of six barriers to upstream fish movement (**X**). Barriers consisted of waterfalls with a vertical drop of 6 feet or greater. Two barriers were located in Kintla Creek downstream of Upper Kintla Lake, one barrier was located in Camas Creek downstream of Trout Lake, and three barriers were located in Park Creek downstream of Lake Isabel.

Table 1. Surface area, maximum depth, maximum length, and elevation for 17 lakes in Glacier National Park, Montana. Maximum depth for Upper Lake Isabel was not measured.

Lake	Surface area (acres)	Maximum depth (feet)	Maximum length (miles)	Elevation (feet)
Akokala Lake	22	23	0.4	4,733
Arrow Lake	59	54	0.5	4,070
Bowman Lake	1,724	253	6.5	4,028
Cerulean Lake	49	118	0.4	4,667
Harrison Lake	403	135	1.4	3,693
Kintla Lake	1,714	390	4.2	4,008
Lake Isabel	44	52	0.4	5,714
Lake McDonald	6,872	464	9.4	3,152
Lincoln Lake	35	74	0.4	4,595
Logging Lake	1,114	198	4.9	3,808
Lower Quartz Lake	168	62	1.2	4,189
Middle Quartz Lake	47	41	0.4	4,395
Quartz Lake	869	273	3.0	4,415
Rogers Lake	84	14	0.6	3,792
Trout Lake	215	163	1.7	3,903
Upper Kintla Lake	467	183	2.3	4,369
Upper Lake Isabel	12		0.2	5,989

Methods

Sampling methodology

All sampling was conducted during the summer and fall of 2004, 2005, and 2006. For comprehensive sampling methodology see Meeuwig and Guy (2007). Gill net surveys were conducted in all study lakes with the exception of Upper Lake Isabel. Surveys were conducted with sinking experimental gill nets that were 125-ft long and 6-ft deep and that were constructed of multifilament nylon with five panels; 0.75-, 1.00-, 1.25-, 1.50-, and 2.00-inch bar mesh. Gill nets were configured as either single (one 125-ft net) or double (two 125-ft nets tied end-to-end). Gill nets were set during the late afternoon and evening, allowed to soak overnight, and pulled the following morning beginning at sunrise. All fish encountered were enumerated by species, measured for length (total length) and weight (wet weight), and returned to the lake. A non-lethal fin clip (≈ 0.04 inch^2) was removed from bull trout encountered for genetic analysis; additionally, otoliths, for age analysis, were removed from bull trout that died as a result of sampling.

Hook and line surveys were conducted opportunistically at study lakes in an effort to increase sample size for genetic analysis of bull trout. Shoreline electrofishing surveys were conducted in sites located in wadeable portions of the littoral zone of all study lakes with the exceptions of Cerulean Lake and Rogers Lake. Stream electrofishing surveys were conducted in the primary inlet and outlet of most study lakes. 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 0.25 miles). Fish encountered during hook and line, shoreline electrofishing, and stream electrofishing surveys were sampled as above.

Surveys were conducted to detect the presence of putative barriers to upstream fish movement (hereafter referred to as barriers) within streams of the study system. Waterfalls with a vertical drop of greater than or equal to 6 ft (Evans and Johnston 1980) were considered barriers. Stream reaches between each study lake and the nearest major stream (i.e., Middle Fork Flathead River or North Fork Flathead River) were surveyed by walking along the stream channel. Barriers encountered were measured for height, photographed, and their location recorded using a handheld global positioning system (GPS) receiver.

Bull trout redd surveys were conducted in the inlet streams of Bowman Lake, Harrison Lake, Logging Lake, Lower Quartz Lake, Middle Quartz Lake, and Quartz Lake. Redd surveys were conducted in an upstream direction starting at the mouth of each stream and continuing until a barrier was reached (e.g., Logging Creek), another lake was reached (e.g., Quartz Creek from Lower Quartz Lake to Middle Quartz Lake and Middle Quartz Lake to Quartz Lake), or until habitat no longer appeared suitable for spawning based on a qualitative assessment of substrate type, water availability, and stream gradient (e.g., Bowman Creek, Harrison Creek, and Quartz Creek). The number of redds observed was recorded and their locations were recorded using a handheld GPS receiver.

Laboratory and data analysis

Laboratory procedures and data analyses reported here represent information directly relevant to the action plan (for additional data and analyses see Meeuwig and Guy 2007). Bull trout length data were summarized by lake as minimum, mean, and maximum length of individuals sampled during gill-net, hook and line, and shoreline electrofishing surveys (i.e., lake samples excluding stream electrofishing surveys).

Otoliths removed from bull trout were embedded in epoxy resin and sectioned in the transverse plane to a thickness of 0.023 inches using a low speed saw. Sectioned otoliths were mounted to a standard microslide, sanded, and polished. The sectioned otolith was examined under a compound microscope and annuli were counted to determine fish age. Fish age was determined without knowledge of fish size (length or weight). Maximum age of bull trout sampled was summarized by lake.

Mean relative abundance (measured as catch per unit effort) was calculated separately for bull trout and lake trout sampled during gill-net surveys. Relative abundance was calculated for each gill net as the number of individuals of a species sampled per hour the net was set (for nets set as double, i.e., two 125-ft nets tied end-to-end, the number of hours was multiplied by two). The mean relative abundance per lake was calculated as the sum of the individual relative abundance estimates for all nets set at a given lake divided by the number of nets set.

Bull trout genetic samples were analyzed from 16 lakes in Glacier National Park; samples were not analyzed from Rogers Lake as only one individual was sampled from this lake. Additionally, genetic samples were analyzed from juvenile bull trout sampled in Hallowat Creek, Trail Creek, and Whale Creek (samples provided by Montana Fish, Wildlife and Parks; C. Muhlfeld). These streams are tributaries to the North Fork Flathead River and samples represent offspring of migratory bull trout from Flathead Lake (Fraley and Shepard 1989). These samples were treated as a composite sample of Flathead Lake bull trout. Nuclear DNA was extracted from tissue samples (see above) and was genotyped at 11 polymorphic microsatellite loci (Dehaan and Ardren 2005). Genetic diversity, measured as expected heterozygosity (H_e) averaged across loci, was calculated for each lake. Genetic similarity was calculated between all pairs of lakes, measured as pairwise F_{st} values (Weir and Cockerham 1984).

Results

Barriers were observed in three drainages potentially isolating five lakes from future natural colonization by fishes; Camas Creek drainage isolating Arrow Lake and Trout Lake, Kintla Creek drainage isolating Upper Kintla Lake, and Park Creek drainage isolating Lake Isabel and Upper Lake Isabel (Table 2; Figure 1). In addition to the barriers measured in Kintla Creek drainage, numerous other cascades and high gradient reaches were observed in Kintla Creek between Kintla Lake and Upper Kintla Lake.

Table 2. Height and geographic location of barriers to upstream fish movement located in Camas Creek downstream of Arrow Lake and Trout Lake, Kintla Creek downstream of Upper Kintla Lake, and Park Creek downstream of Upper Lake Isabel and Lake Isabel.

		Location [Universal Transverse Mercator (UTM)]		
Drainage	Height (ft)	Zone	Easting (m)	Northing (m)
Camas Creek drainage	24	12	284138	5394448
Kintla Creek drainage	9	11	703692	5428725
	22	11	702566	5428317
Park Creek drainage	6	12	317984	5365850
	8	12	317977	5365859
	9	12	317780	5366304

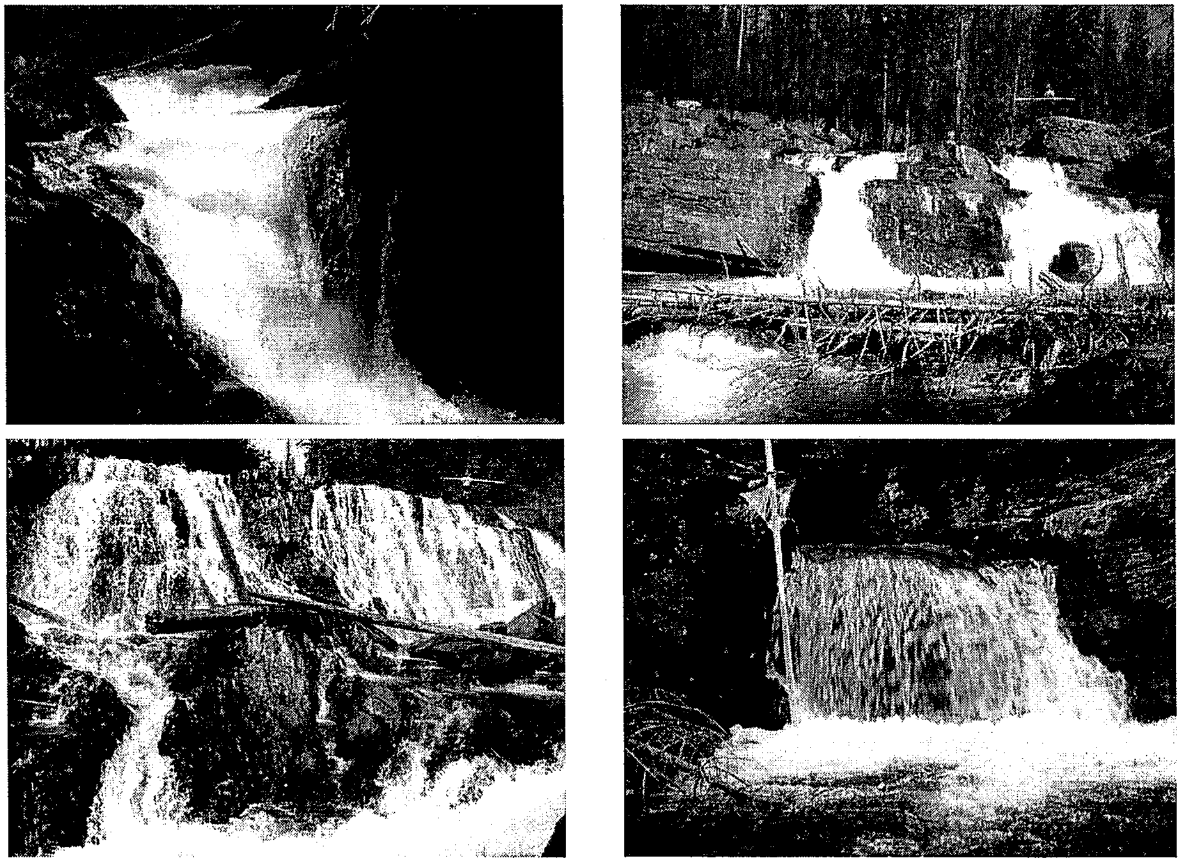

Figure 2. Barriers to upstream fish movement observed in Kintla Creek downstream of Upper Kintla Lake (upper left panel and upper right panel), Camas Creek downstream of Trout Lake (lower left panel), and Park Creek downstream of Lake Isabel (lower right panel).

The barriers observed in Kintla Creek between Kintla Lake and Upper Kintla Lake (Table 2; Figures 1 and 2) and the observation of bull trout as the only species of fish occupying Upper Kintla Lake (Appendix 1) suggest that Upper Kintla Lake has been historically isolated from immigration following the establishment of bull trout. Rainbow trout *Oncorhynchus mykiss*, mountain whitefish *Prosopium williamsoni*, longnose sucker *Catostomus catostomus*, and northern pikeminnow *Ptychocheilus oregonensis* were observed in Rogers Lake (Appendix 1), but were not observed in Trout Lake (0.68 miles upstream of Rogers Lake; Figure 1; Appendix 1) or in Arrow Lake (1.49 miles upstream of Trout Lake; Figure 1; Appendix 1). This pattern suggests that the large waterfall observed between Trout Lake and Rogers Lake is acting as a barrier to upstream fish movement. A series of waterfalls was observed in Park Creek between the Middle Fork Flathead River and Lake Isabel and Upper Lake Isabel. The presence of bull trout and cutthroat trout as the only fish species detected in Lake Isabel and Upper Lake Isabel suggests that these waterfalls are acting as a barrier to upstream movement by other fishes and have blocked immigration into these lakes following colonization by bull trout and cutthroat trout.

The observed barriers appear to have affected fish colonization patterns among the study lakes. However, 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 may not have 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. Alternatively, the structures identified as barriers may not be true barriers, but may have allowed limited, sporadic, or seasonal passage during some past colonization. However, the current distribution of species richness suggests that these barriers have been active for a relatively long time and have played a significant role in distribution of fishes in the study system. Additionally, the barriers documented during this study appear to play a role in current invasion dynamics of lake trout in Glacier National Park, as lake trout were not detected in any lake located upstream of the observed barriers (Figure 3).

Of the study lakes not located upstream of a putative barrier, lake trout were not documented in Middle Quartz Lake or Cerulean Lake (Figure 3). Lake trout have been documented in both Lower Quartz Lake and Quartz Lake; therefore, lake trout must have moved through Middle Quartz Lake at some time to colonize Quartz Lake. Middle Quartz Lake may represent less preferred habitat or lake trout are present in this lake at levels below which were detectable.

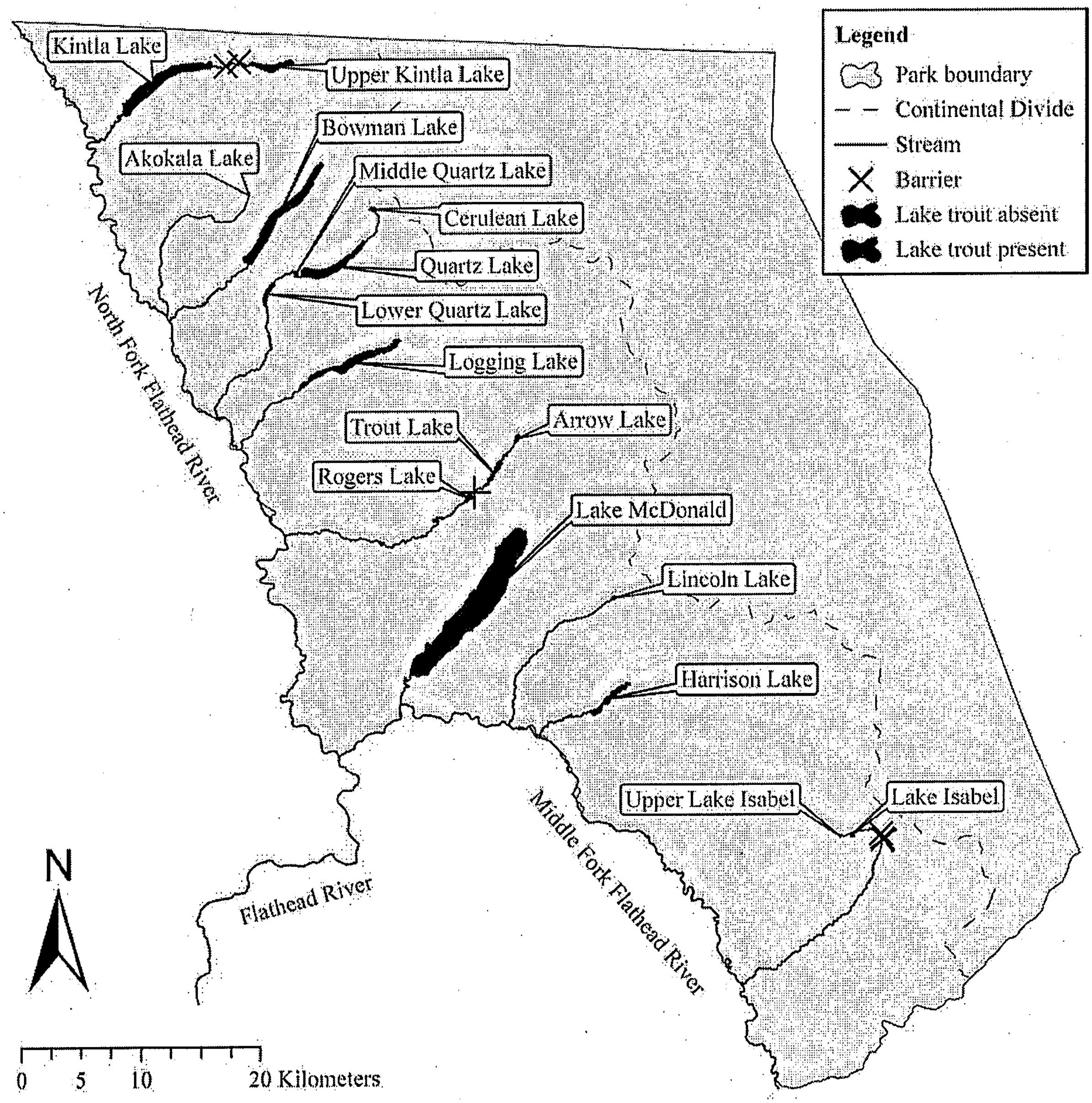

Figure 3. Absence (•) and presence (•) of lake trout in gill-net, hook and line, and shoreline electrofishing samples from 17 lakes in Glacier National Park, Montana.

The proximity of Middle Quartz Lake to Quartz Lake, separated by only 0.25 miles of low gradient stream, would make passage of fish between the two a relatively simple, and perhaps regular, event. It is believed that Cerulean Lake is also accessible by lake trout as no putative barriers were detected in the stream reach between Quartz Lake and Cerulean Lake. Therefore, lake trout may already occupy Cerulean Lake at low levels, or Cerulean Lake is at threat of invasion and establishment by lake trout.

Lake trout were also not documented in Akokala Lake or Lincoln Lake (Figure 3). As above, lake trout may already be present in these lakes at levels below which were detectable based on sampling methodology. Alternatively the distance of these lakes from major sources of colonization (i.e., the Middle Fork Flathead River and North Fork Flathead River) may represent an impediment to colonization by lake trout. These lakes, which are generally shallow and small (Table 1), may also represent less preferred habitat for lake trout. However, based on the current known distribution of lake trout and trends in lake trout presence and the locations of putative barriers, it is believed that these lakes are at threat of invasion and establishment by lake trout.

The average number of bull trout sampled during gill-net, hook and line, and shoreline electrofishing among study lakes was 20 individuals. The greatest number of bull trout sampled was 66 from Lake Isabel and the smallest sample size of bull trout was 1 from Rogers Lake (Table 3). Bull trout length varied from 1.5 to 30.7 inches among all lakes sampled (Table 3). For the majority of lakes, bull trout length varied from approximately 4 inches to approximately 24 inches (Table 3). Maximum age of bull trout sampled varied from 5 to 15 years among study lakes (Table 3). The majority of lakes sampled had age-11 and older bull trout.

The smallest bull trout observed in lake habitats were sampled from Akokala Lake, Arrow Lake, Lake Isabel, and Upper Kintla Lake, where shoreline electrofishing surveys were effective at sampling small length-class (i.e., less than 6 inches) bull trout. Based on trends in age estimates from the study lakes discussed in this document (see Meeuwig and Guy 2007 for complete bull trout age and length data) and studies of bull trout in the Saint Mary Drainage, Glacier National Park (Mogen and Kaeding 2004), these small length-class bull trout were likely age 2 or younger.

Table 3. Number of bull trout measured for length (N_L) and their minimum, mean, and maximum length (inches), and number of bull trout aged (N_A) and their maximum age (years) for 17 lakes in Glacier National Park, Montana. Only one bull trout was sampled from Rogers Lake so no minimum and maximum lengths are provided, and no fish were aged from Upper Lake Isabel.

	Length (inches)				Maximum age (years)	
Lake	N_L	Minimum	Mean	Maximum	N_A	Age
Akokala Lake	18	1.5	13.7	30.7	5	8
Arrow Lake	37	2.9	12.1	27.4	9	12
Bowman Lake	17	4.9	12.0	28.1	9	8
Cerulean Lake	20	10.0	19.0	28.1	5	11
Harrison Lake	9	10.5	18.4	27.7	7	12
Kintla Lake	13	7.1	13.4	20.5	9	7
Lake Isabel	66	3.8	9.2	11.7	35	12
Lake McDonald	8	11.9	16.4	22.4	7	8
Lincoln Lake	9	13.7	21.0	27.1	6	14
Logging Lake	7	7.7	12.0	19.4	6	5
Lower Quartz Lake	14	7.8	16.4	25.6	8	14
Middle Quartz Lake	11	12.6	17.3	26.3	8	8
Quartz Lake	59	8.1	15.5	26.1	35	13
Rogers Lake	1		25.3		1	15
Trout Lake	28	8.1	17.7	22.8	17	15
Upper Kintla Lake	50	1.9	13.0	19.6	20	9
Upper Lake Isabel	5	12.1	13.3	15.6		

Table 4. Site length, number of bull trout sampled (*N*), and the mean length of bull trout sampled during stream electrofishing surveys of inlet and outlet (Reach) streams for 12 study lakes in Glacier National Park, Montana.

Lake	Reach	Site length (feet)	*N*	Mean length (inches)
Akokala Lake	Inlet	512	3	2.6
	Outlet	364	1	8.1
Arrow Lake	Inlet	≈ 328	0	
	Outlet	≈ 328	0	
Bowman Lake	Inlet	328	2	5.3
	Outlet	328	0	
Kintla Lake	Inlet	≈ 328	0	
Lake Isabel	Inlet	285	4	5.5
	Outlet	364	0	
Lincoln Lake	Inlet	328	2	3.2
	Outlet	328	0	
Logging Lake	Inlet	410	0	
	Outlet	328	0	
Lower Quartz Lake	Inlet	328	0	
	Outlet	≈ 328	0	
Middle Quartz Lake	Inlet	361	0	
	Outlet	361	0	
Quartz Lake	Inlet	328	1	3.4
Trout Lake	Inlet	394	0	
	Outlet	328	0	
Upper Kintla Lake	Inlet	328	1	5.1
	Agassiz (inlet)	≈ 328	2	8.8
	Outlet	328	20	1.9

Few juvenile bull trout were observed during stream electrofishing surveys (*N* = 37 over all stream electrofishing sites; Table 4). It has generally been accepted that juvenile bull trout (age 1 to 3) occupy stream habitats regardless of adult life history strategy (McPhail and Baxter 1996); although recent studies have documented early emigration of juvenile bull trout from stream to lake habitat with corresponding low survival (Downs et al. 2006). The observations of small size-class bull trout in littoral habitat and few bull trout in the inlet and outlet streams of the study lakes provides evidence that adfluvial bull trout in Glacier National Park may be emigrating from spawning streams at an earlier age than in many systems. This finding warrants further investigation as early emigration by bull trout may represent a life history strategy used by adfluvial bull trout in Glacier National Park. Early emigration may also result in juvenile bull trout experiencing predation pressure by native and nonnative piscivores.

Bull trout relative abundance varied from 0.03 to 1.08 fish per net·hour among study lakes. Bull trout were most abundant in Lake Isabel and Upper Kintla Lake (Figure 4). Bull trout abundance was lowest in lakes where lake trout were present (Figures 3 and 4) with the exception of Quartz Lake. If bull trout abundance decreases as a function of lake trout establishment, the trend observed in other lakes colonized by lake trout may not be exhibited yet in Quartz Lake. Lake trout were first documented in Quartz Lake in 2005, whereas they have been established in other lakes for a greater amount of time. The population size of lake trout in Quartz Lake may just be beginning to increase, with a potential decrease in abundance of bull trout.

For lakes where lake trout are not established, bull trout abundance appears to be partially affected by lake size (a possible surrogate for available habitat). With the exception of Lake Isabel, bull trout abundance was positively associated with lake surface area (Meeuwig and Guy 2007). Bull trout in Lake Isabel appear to have adopted an alternative life history. A high abundance of bull trout was observed in Lake Isabel (Figure 4); however, these bull trout do not appear to attain the large sizes observed in all other study lakes (Table 3). For example, the largest bull trout observed in Lake Isabel was 11.7 inches, whereas bull trout from all other lakes reach a maximum length of at least 15.6 inches with most lakes represented by bull trout reaching lengths of approximately 24 inches and greater (Table 3). The alternative life history strategy adopted by bull trout in Lake Isabel may allow them to occur at a greater abundance.

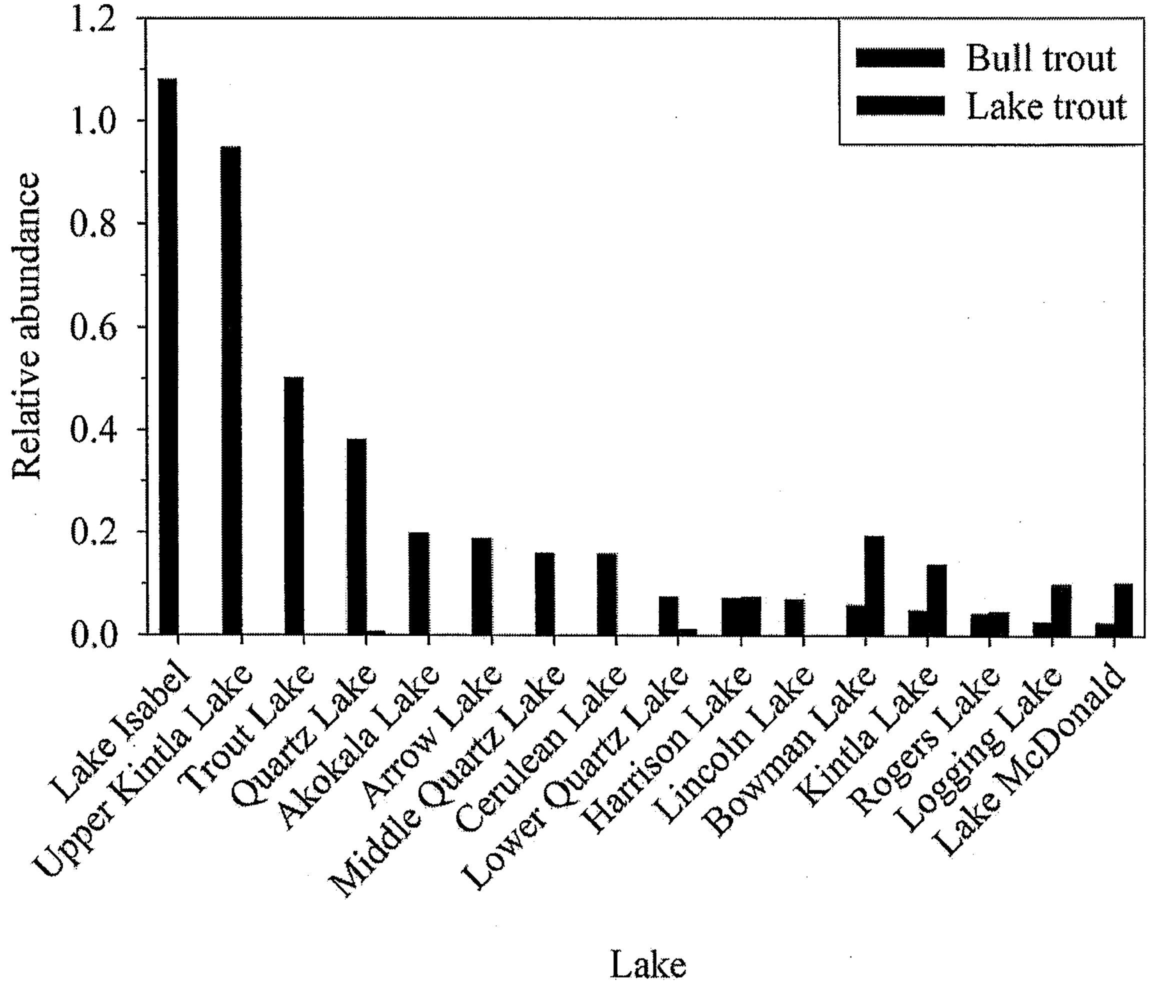

Figure 4. Relative abundance (fish per net·hour) of bull trout and lake trout sampled during gill-net surveys for 16 lakes in Glacier National Park, Montana. Lakes arranged in order of decreasing bull trout relative abundance.

For lakes where lake trout are present a similar relationship between bull trout relative abundance and lake size was not observed (Meeuwig and Guy 2007). In these lakes, bull trout relative abundance was relatively constant and low (Figure 4) regardless of lake size, which varied greatly from 84 to 6,872 acres. The only lake where lake trout were documented that had a high abundance of bull trout was Quartz Lake; however, if the lake trout population is only beginning to increase (as above) the trend in bull trout abundance may decrease over time resulting in a situation more similar to other lakes where lake trout are present.

Lake trout relative abundance varied from 0.01 to 0.19 fish per net·hour among study lakes where lake trout were present. Lake trout abundance was greatest in Bowman Lake, Kintla Lake, Lake McDonald, and Logging Lake, moderate in Harrison Lake and Rogers Lake, and lowest in Lower Quartz Lake and Quartz Lake (Figure 4). Where lake trout were present, lake trout abundance was greater than bull trout abundance, with the exceptions of Lower Quartz Lake and Quartz Lake. It is difficult to explain the mechanistic basis for the observed trends between bull trout and lake trout abundance when both species are present; however, both species are generally top-level predators. Therefore, resource limitation may result if these species are sharing or partitioning resources. Alternatively, one species may eventually be displaced as a result of competitive exclusion (Donald and Alger 1993).

Genetic diversity of bull trout varied from a low of 0.22 to a high of 0.74 among lakes. In general, lakes located upstream of barriers had low genetic diversity (e.g., Arrow Lake, Trout Lake, and Upper Kintla Lake; Figure 5). Genetic diversity was greater in Lake Isabel and Upper Lake Isabel, also located upstream of a barrier, but still less than other lakes within the study system (Figure 5). Loss of genetic diversity is common in isolated populations (Frankham et al. 2002), providing supporting evidence that the structures identified as barriers have minimized gene flow throughout the study system over an ecological time-scale. Harrison Lake also exhibited relatively low genetic diversity compared to other lakes located within Glacier National Park (Figure 5). Genetic diversity was moderate and similar among Middle Quartz Lake, Quartz Lake, and Cerulean Lake, all located within the same drainage (Figure 5). Genetic diversity was greatest in Kintla Lake and Lake McDonald (Figure 5), both large lakes in close proximity to the North Fork Flathead River and Middle Fork Flathead River. These rivers may act as corridors for fish dispersal and resultant gene flow.

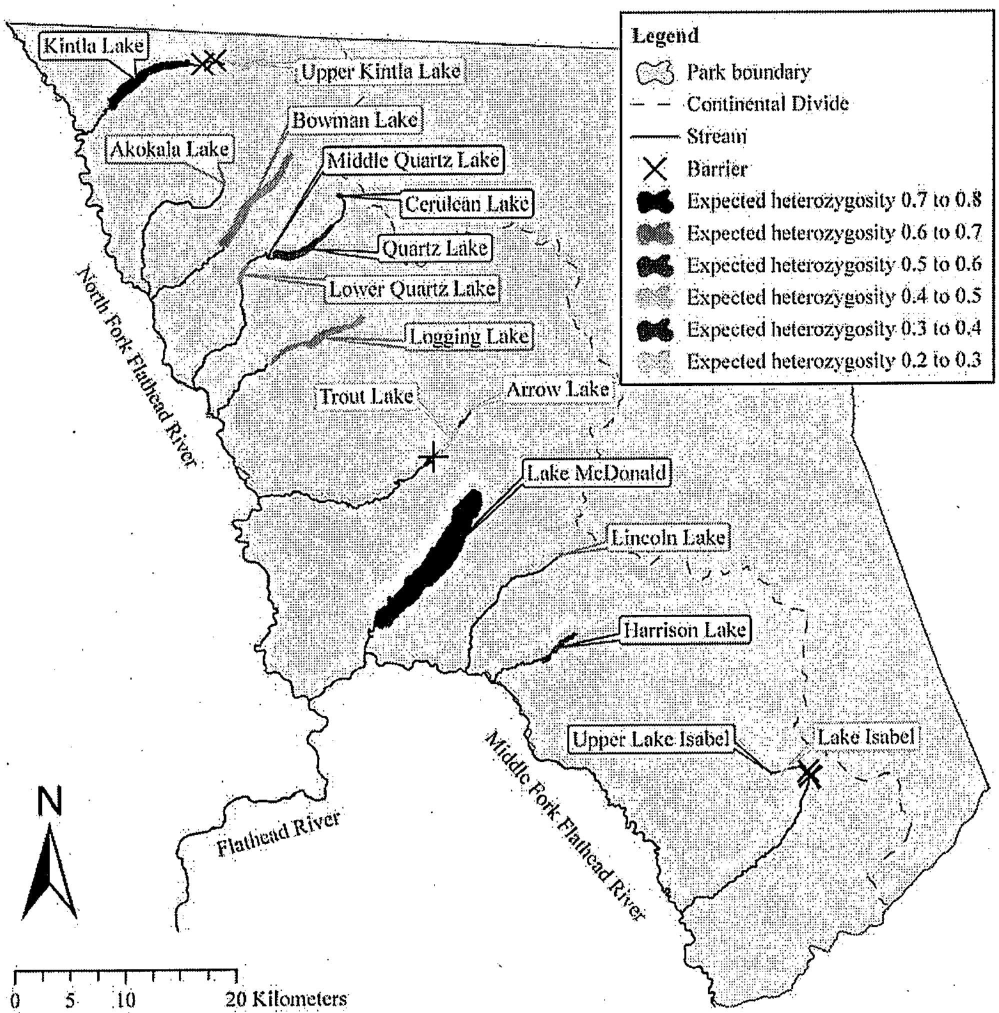

Figure 5. Genetic diversity for bull trout from 16 lakes in Glacier National Park, Montana. Genetic diversity was quantified as expected heterozygosity and categorized as 0.7 to 0.8 (•), 0.6 to 0.7 (•), 0.5 to 0.6 (•), 0.4 to 0.5 (•), 0.3 to 0.4 (•), and 0.2 to 0.3 (•). Larger expected heterozygosity values represent lakes with greater genetic diversity.

Table 5. Lakes sampled for genetic analysis (Lake) and their top three most genetically similar lakes based on pairwise F_{st} values.

Lake	Order of genetic similarity		
	1st most similar lake	2nd most similar lake	3rd most similar lake
Akokala Lake	Kintla Lake	Flathead Lake*	Lake McDonald
Arrow Lake	Trout Lake	Bowman Lake	Flathead Lake*
Bowman Lake	Kintla Lake	Lake McDonald	Flathead Lake*
Cerulean Lake	Middle Quartz Lake	Quartz Lake	Lower Quartz Lake
Harrison Lake	Flathead Lake*	Kintla Lake	Lincoln Lake
Kintla Lake	Lake McDonald	Flathead Lake*	Lincoln Lake
Lake Isabel	Kintla Lake	Upper Lake Isabel	Lake McDonald
Lake McDonald	Kintla Lake	Flathead Lake*	Bowman Lake
Lincoln Lake	Kintla Lake	Lake McDonald	Flathead Lake*
Logging Lake	Kintla Lake	Lake McDonald	Flathead Lake*
Lower Quartz Lake	Quartz Lake	Cerulean Lake	Middle Quartz Lake
Middle Quartz Lake	Cerulean Lake	Quartz Lake	Lower Quartz Lake
Quartz Lake	Cerulean Lake	Middle Quartz Lake	Lower Quartz Lake
Trout Lake	Arrow Lake	Bowman Lake	Kintla Lake
Upper Kintla Lake	Kintla Lake	Lake McDonald	Flathead Lake*
Upper Lake Isabel	Lake Isabel	Kintla Lake	Lake McDonald
Flathead Lake*	Lake McDonald	Kintla Lake	Bowman Lake

*Flathead Lake is represented by a composite sample of juvenile bull trout sampled from Hallowat Creek, Trail Creek, and Whale Creek; spawning and rearing streams tributary to the North Fork Flathead River for migratory bull trout from Flathead Lake.

Genetic similarity was highly variable among lakes (Appendix 2), varying from < 0.01 (highly similar) to 0.66 (highly differentiated). In general, lakes located within close proximity to one another had bull trout that were more genetically similar. For example, bull trout were similar among lakes within the Quartz Creek drainage (including Cerulean Lake), with slightly less similarity associated with Lower Quartz Lake (Table 5; Appendix 2). However, the presence of a barrier between lakes in close proximity to one another appears to result in decreased genetic similarity. For example, although Upper Kintla Lake is geographically the closest lake to Kintla Lake, bull trout from Kintla Lake are more genetically similar to bull trout from Lake McDonald than they are to bull trout from Upper Kintla Lake (Table 5; Appendix 2) suggesting decreased gene flow associated with the barriers.

The high degree of genetic similarity observed between bull trout in Kintla Lake and Lake McDonald (Table 5; Appendix 2), along with high genetic diversity within Lake McDonald and Kintla Lake (Figure 5), suggests that there may be a high degree of gene flow between these lakes or these lakes are acting together in a larger interconnected Flathead Drainage bull trout metapopulation. In addition to the genetic similarity between Lake McDonald and Kintla Lake, the composite Flathead Lake sample was the second most genetically similar sample to both Kintla Lake and Lake McDonald (Table 7). Further research is warranted to determine the degree of genetic connectivity between these lakes, other lakes within Glacier National Park, and other parts of the Flathead River system, as documentation and understanding of potential metapopulation dynamics in this system may have conservation implications within and outside of Glacier National Park.

The number of bull trout redds observed was generally low and variable among years sampled (Table 6). Temperatures were generally low enough for bull trout to have initiated spawning (i.e., ≤ 48° F; 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 redds were observed in this section; Table 6). The greatest number (Table 6) and density (Figure 7) of bull trout redds observed among years was in Quartz Creek upstream of Quartz Lake, followed by Logging Creek upstream of Logging Lake. Although redd density was greater for Lower Quartz Lake than for Harrison Lake (Figure 7), the stream reach surveyed for Lower Quartz Lake was short (0.31 miles) and the number of redds observed among years for Lower Quartz Lake (N = 6) was less than that observed for Harrison Lake (N = 12). No redds were observed in any years for Middle Quartz Lake and only two redds were observed among years for Bowman Lake (Table 6).

Table 6. Number of bull trout redds observed in 2004, 2005, and 2006 in stream reaches sampled.

Stream reach	Number of bull trout redds observed		
	2004	2005	2006
Bowman Creek upstream of Bowman Lake	0	0	2
Harrison Creek upstream of Harrison Lake	4	0	8
Logging Creek upstream of Logging Lake	3	20	0
Quartz Creek upstream of Lower Quartz Lake	1	3	2
Quartz Creek upstream of Middle Quartz Lake	0	0	0
Quartz Creek upstream of Quartz Lake	55	4	36

Some of the variability in redd counts may be the result of variable biotic and abiotic conditions. High redd counts, such as those observed for Logging Lake in 2005 (Table 6), may indicate highly favorable flow conditions. However, factors such as high sediment loads and superimposition of bull trout redds by spawning kokanee *Oncorhynchus nerka* (e.g., Harrison Lake) may limit sampling efficiency. Additionally, high flow events prior to redd counts may obscure bull trout redds by moving substrate and filling in depressions left by bull trout spawning activity.

Environmental stochasticity in Glacier National Park may limit bull trout spawning. A previous debris flow resulted in Bowman Creek running subsurface during the fall up to the point where it enters Bowman Lake for many years and 2006 was the first year that any bull trout redds were observed in this stream reach. Similarly, Camas Creek directly upstream of Arrow Lake appears to have experienced a debris flow sometime during the period of summer 2005 to summer 2006. This debris flow has resulted in Camas Creek entering Arrow Lake subsurface, eliminating the potential for spawning migrations into this stream reach 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.

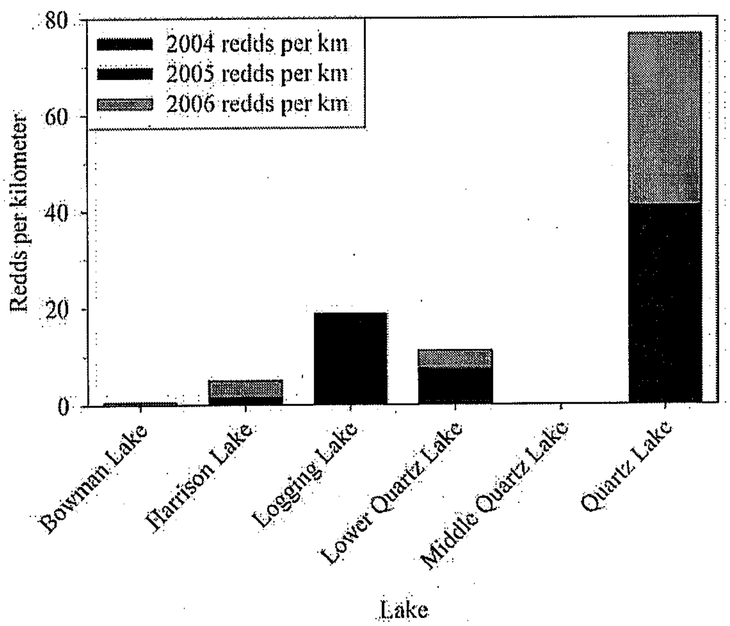

Figure 7. Number of bull trout redds per kilometer observed during redd surveys conducted in 2004, 2005, and 2006 for lakes in Glacier National Park, Montana.

Conclusions

- Bull trout abundance is highly variable among Glacier National Park lakes, but generally higher for lakes where lake trout are not present.
- Lake trout abundance is generally greater than bull trout abundance in lakes where lake trout are present.
- Alternative life history strategies for bull trout may exist in Glacier National Park, which warrant further investigation.
    - Early emigration of juveniles from spawning and rearing sites.
- Barriers to fish movement appear to have had a strong influence on past fish colonization patterns as well as contemporary species invasion dynamics.
    - Species richness is generally lower for lakes located upstream of identified barriers.
    - Lake trout are not present in any lake located upstream of identified barriers.
- Genetic diversity and similarity of bull trout in Glacier National Park is influenced by geography of the study system and the presence of barriers to fish movement.
    - Genetic diversity is lower for bull trout located upstream of identified barriers.
    - Trends in genetic similarity among lakes are affected by geographic proximity of lakes, the presence of barriers, and potential metapopulation dynamics of the greater Flathead Drainage.
- Bull trout redd counts were variable among sites and years.
    - Environmental stochasticity and factors affecting sampling efficiency should be considered when interpreting or planning redd surveys.

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Appendix 1. Species sampled at 17 lakes in Glacier National Park during gill-net, electrofishing, and hook and line surveys during the summers of 2004, 2005, and 2006. A blue dash (—) represents native species, a red dash (—) represents nonnative species, and potential hybrid cutthroat trout (westslope cutthroat trout X Yellowstone cutthroat trout) based on historic stocking records are represented by a gray dash (—).

	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	Rogers Lake	Trout Lake	Upper Kintla Lake	Upper Lake Isabel
Bull trout	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brook trout					—				—								
Lake trout			—		—	—		—		—	—		—	—			
Cutthroat trout	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
Kokanee					—			—									
Rainbow trout														—			
Lake whitefish								—									
Mountain whitefish	—		—	—	—	—		—	—	—	—	—	—	—			
Pygmy whitefish								—									
Largescale sucker								—					—				
Longnose sucker			—		—	—		—	—	—	—	—	—	—			
Northern pikeminnow								—		—				—			
Peamouth						—		—									
Redside shiner			—			—		—		—	—	—	—				
Sculpin	—		—		—	—		—	—	—	—	—	—		—		

Appendix 2. Pairwise F_{st} values based on analysis of 11 microsatellite loci for bull trout from 16 lakes in Glacier National Park, Montana, and a composite sample representing Flathead Lake bull trout.

Lake	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	Upper Lake Isabel
Arrow Lake	0.37															
Bowman Lake	0.14	0.34														
Cerulean Lake	0.24	0.52	0.21													
Harrison Lake	0.35	0.64	0.32	0.40												
Kintla Lake	0.08	0.36	0.07	0.17	0.30											
Lake Isabel	0.27	0.56	0.32	0.34	0.43	0.21										
Lake McDonald	0.11	0.39	0.07	0.19	0.32	< 0.01	0.22									
Lincoln Lake	0.13	0.45	0.16	0.23	0.31	0.06	0.23	0.08								
Logging Lake	0.17	0.45	0.15	0.15	0.33	0.09	0.28	0.12	0.16							
Lower Quartz Lake	0.17	0.41	0.13	0.06	0.34	0.10	0.28	0.12	0.17	0.12						
Middle Quartz Lake	0.24	0.57	0.21	< 0.01	0.43	0.18	0.37	0.20	0.25	0.17	0.06					
Quartz Lake	0.20	0.48	0.16	< 0.01	0.35	0.15	0.31	0.16	0.20	0.12	0.05	0.01				
Trout Lake	0.35	0.02	0.31	0.50	0.62	0.33	0.54	0.36	0.43	0.43	0.39	0.54	0.46			
Upper Kintla Lake	0.39	0.62	0.38	0.48	0.55	0.24	0.42	0.30	0.35	0.40	0.41	0.51	0.45	0.59		
Upper Lake Isabel	0.33	0.66	0.36	0.37	0.52	0.27	0.22	0.30	0.31	0.33	0.32	0.41	0.34	0.63	0.56	
Flathead Lake	0.10	0.35	0.09	0.16	0.29	0.03	0.23	0.01	0.12	0.12	0.09	0.16	0.13	0.34	0.31	0.30