

EFFICACY OF SUPPRESSING NON-NATIVE LAKE TROUT IN AN ISOLATED
BACKCOUNTRY LAKE IN GLACIER NATIONAL PARK

by

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

of

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in

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DEDICATION

This thesis is dedicated to my beautiful wife, Amy Fredenberg, for her unending patience and encouragement to persevere throughout my graduate research, and to my parents, Mark and Susie Fredenberg, who challenged me to pursue my dreams and supported me through my failures. I would not be where I am today without the support and guidance provided by you.

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ABSTRACT

Prior to the recent invasion of non-native lake trout *Salvelinus namaycush*, Glacier National Park (GNP) supported approximately one-third of the remaining natural lake habitat supporting threatened bull trout *Salvelinus confluentus*. However, bull trout populations have recently declined and are at high risk of extirpation in several lakes in western GNP due to the establishment of lake trout. In 2009, the U.S. Geological Survey and the National Park Service began suppressing lake trout in Quartz Lake (352 ha) to reduce impacts to native bull trout. The objectives of this study were to: (1) describe the demography of the lake trout population during the suppression program (2009-2013); (2) identify the timing and location of lake trout spawning; (3) determine the most efficient combination of gill net mesh color and twine diameter to capture juvenile lake trout (age 2 to age 4); (4) assess the effects of suppression on the growth rate of the lake trout population and use this information to model harvest scenarios; and (5) determine whether suppression negatively impacted bull trout. Lake trout exhibited slower growth, lower condition, and lower fecundity relative to other populations. Spawning locations were identified on cobble and boulder substrates (depths 2-20 m) near the base of two avalanche chutes where adults began aggregating between 1 and 9 October prior to thermal destratification (11-12 C°). Catch rates of spawning (ripe) adults were highest 12-25 October when temperatures declined to below 10 C°. Gill nets with 0.1 mm twine thickness and green color increased catchability of juvenile lake trout. Although density dependent parameters were not included, population simulation models indicated the population was growing exponentially and would likely reach carrying capacity within ten years without suppression. Suppression resulted in declining population growth rates (λ) from 1.23 prior to suppression to 0.61-0.79 during suppression. Bull trout redd abundances remained stable throughout the suppression period. My results indicate targeted suppression successfully reduced lake trout abundance and that continued suppression at or above observed exploitation levels is needed to ensure continued population declines and to avoid impacts to the bull trout population.

CHAPTER 1

USING DEMOGRAPHIC CHARACTERISTICS AND POPULATION GROWTH
MODELS TO ASSESS SUPPRESSION OF NON-NATIVE LAKE TROUT IN AN
ISOLATED BACKCOUNTRY LAKE IN GLACIER NATIONAL PARKIntroduction

Non-native species are one of the most serious threats to global biodiversity (Vitousek et al. 1997), and are a leading cause of freshwater fish extinctions in western North America (Wilcove et al. 1998; Clavero and Garcia-Berthou 2005). Forty species of freshwater fish were known to be extirpated in North America between 1889 and 1989, and introductions of non-native species contributed to 68% of those extinctions (Miller and Williams 1989). Over the past century, non-native fish species have been widely introduced throughout the United States for aquaculture and recreational fisheries, and in many cases have eliminated native fish species, homogenized freshwater fish faunas, and reduced regional biodiversity (Miller and Williams 1989; Rahel 2000). Non-native fishes have impacted many species and populations of native fishes through competition, predation, and hybridization (Miller and Williams 1989; Rahel 2000).

Lake trout *Salvelinus namaycush* are large, long-lived, piscivores native to deep, cold, oligotrophic lakes of Canada and northern parts of the United States (Crossman 1995; Behnke 2002). Their life history is characterized by slow growth, late maturity, low reproductive potential, and a slow adult replacement rate (Shuter et al. 1998), making the species highly vulnerable to overexploitation (Healy 1978b; Shuter et al. 1998).

Population collapses of lake trout from commercial harvest and sea lamprey *Petromyzon marinus* predation occurred in the Laurentian Great Lakes (Lake Erie, Lake Ontario, Lake Superior, Lake Huron, and Lake Michigan) during the 1940s and 1950s (Wells and McLain 1972; Coble et al. 1990; Hansen et al. 1995). However, the collapse of the lake trout populations in Lake Superior and Lake Erie were believed to be a result imparted by overharvest by commercial fisherman (Hartman 1972).

Although lake trout populations have dramatically declined within their native range in the Great Lakes (Wells and McLain 1972; Hartman 1972; Hansen et al. 1995), introduced lake trout have expanded their range throughout the western United States (Martinez et al. 2009). Beginning in the late 19th and early 20th century, lake trout were widely introduced outside of their native range into lakes and reservoirs in the western United States (Crossman 1995), and have since colonized new waters via translocation or natural dispersal (Martinez et al. 2009; Kalinowski et al. 2010). Currently, lake trout are widespread in the western United States, occurring in over 200 waters (Martinez et al. 2009). Although lake trout occupy an important ecological niche as a top-level predator throughout their native range, they have become problematic in the western United States because they prey on and compete with native and sport fishes (Ruzycki et al. 2003; Koel et al. 2005; Martinez et al. 2009). In many cases, the introduction and subsequent proliferation of non-native lake trout has resulted in negative impacts throughout both aquatic and terrestrial communities (Baril et al. 2013; Middleton et al. 2013).

To mitigate lake trout impacts, natural resource agencies have implemented several control programs to reduce their abundance in the western United States (Hansen

et al. 2008; Martinez et al. 2009; Cox 2010; Syslo 2010). However, eradication and control program effectiveness is often correlated with spatial and temporal scale (Britton et al. 2011), and the few successful non-native fish eradication programs using mechanical removal methods have generally focused on small alpine or subalpine lakes (Knapp and Matthews 1998; Vredenberg 2004). However, the overexploitation of the lake trout populations in Lake Superior and Lake Erie provide supporting evidence that lake trout populations can be suppressed in larger systems using mechanical removal methods. Therefore, it is reasonable to believe that manual removal methods could be used to eradicate or control a non-native fish species, such as the lake trout, for the benefit of native fish in other relatively small systems.

Bull trout *Salvelinus confluentus* populations have dramatically declined throughout their historic range primarily due to habitat loss, invasive species, and climate change (Rieman and Myers 1997; Rieman et al. 2007). Consequently, the bull trout was listed as a threatened species within the U.S. Endangered Species Act in 1998 (USFWS 1999). Where introduced, non-native lake trout consistently displace native bull trout through predation and competition (Donald and Alger 1993; Fredenberg 2002; Martinez et al. 2009). Lake trout and bull trout share similar feeding strategies, morphology, growth rates, and diets, indicating similar trophic positions as top-level piscivores, creating a strong potential for competitive interactions (Donald and Alger 1993; Guy et al. 2011).

The vast majority of native bull trout populations in western Glacier National Park (GNP) have declined precipitously in the last 25-30 years, owing to the invasion and

establishment of non-native lake trout from Flathead Lake (Fredenberg 2002; Meeuwig et al. 2008; Muhlfeld et al. 2012). The introduction of lake trout into Flathead Lake in 1905 and the establishment of the opossum shrimp *Mysis diluviana* in 1981 (Spencer et al. 1991) led to the proliferation and subsequent replacement of the bull trout as the dominant top-level piscivore (Fredenberg 2002; Ellis et al. 2011). As lake trout abundances increased, lake trout emigrated upstream from Flathead Lake and established self-sustaining populations in several connected lakes in GNP (Muhlfeld et al. 2011). Lake trout have largely replaced bull trout as the dominant top-level predator in these systems in less than 30 years (Fredenberg 2002). Lake trout have invaded and become established in nine of the 12 connected lakes west of the Continental Divide where bull trout are native in GNP (Fredenberg et al. 2007). In eight of these lakes, bull trout populations have declined to the point that they are functionally extirpated (Fredenberg et al. 2007).

Of the approximately 100 lakes in the contiguous United States with native adfluvial (lake-dwelling) bull trout populations, about half are in undammed ecosystems. Glacier National Park supports approximately one-third of the remaining natural lake habitat for bull trout in the United States (Fredenberg et al. 2007). Of the five largest lakes west of the Continental Divide in GNP, Quartz Lake supports the most robust bull trout population (Fredenberg et al. 2007). Therefore, Quartz Lake was given highest priority for bull trout conservation within GNP (Fredenberg et al. 2007). In 2005, lake trout were discovered in Quartz Lake. The inaccessibility and lack of historical data citing lake trout introduction into the system (Morton 1968a, 1968b) suggest that lake

trout colonized Quartz Lake from downstream populations (Fredenberg et al. 2007). Unless suppression-based management was implemented, these ecologically unique populations would likely have declined and the few interconnected bull trout populations remaining would be at risk of extirpation. In response, the National Park Service (NPS) partnered with researchers from the U. S. Geological Survey (USGS) Northern Rocky Mountain Science Center (NOROCK) to evaluate non-native lake trout control options in the Quartz Lake system to protect one of the most robust bull trout populations west of the Continental Divide in GNP.

Quartz Lake is unique among lakes targeted for lake trout suppression in the western United States because (1) it is relatively small (352 ha), shallow (maximum depth = 83 m), and lacks habitat complexity; (2) it is isolated from future lake trout immigration by the completion of the barrier falls downstream of Middle Quartz Lake; (3) it was believed to be in the early stages of invasion by non-native lake trout; and (4) biological productivity is low and *Mysis* shrimp are not present. It was believed that the combination of these attributes would increase the probability of successfully suppressing the lake trout population in Quartz Lake.

However, the demographic characteristics of the lake trout population in Quartz Lake were unknown prior to this study. Data gathered during the last four years (2009-2013) of lake trout suppression were used to describe the baseline demographic characteristics (survival, growth, condition, abundance, fecundity, length and age structure, and age at maturity) of the lake trout population in Quartz Lake, and were used to identify harvest scenarios that would suppress the lake trout population. The

objectives of this study were to: (1) describe the demography of the non-native lake trout population in Quartz Lake; (2) identify the timing and location of spawning by lake trout; (3) assess the effectiveness of four years (2009-2013) of control measures on the population growth rate; (4) use this information to model lake trout harvest scenarios; and (5) determine whether four years of suppression has negatively impacted the spawning population of bull trout in Quartz Lake.

Study Location

Quartz Lake is a glacially formed lake located in the headwaters of the Columbia River Basin, Montana (Figure 1.0). Quartz Lake is the fifth largest lake west of the Continental Divide in GNP (Fredenberg et al. 2007), with a surface area of 352 ha and a maximum depth of 83 m. The lake is at an elevation of 1,346 m and is positioned in a narrow glaciated valley that is supplied by perennial flow from snow and glacial runoff from the Lewis Range. The limnetic zone substrate is dominated by a mixture of cobble and boulder. Quartz is an oligotrophic, dimictic lake with stratification occurring in late June and destratification in early October. Three avalanche chutes along the northern shore line have deposited large angular cobble substrates during the spring and winter months.

The native fish assemblage in the Quartz drainage consists of bull trout, westslope cutthroat trout *Oncorhynchus clarkii lewisi*, mountain whitefish *Prosopium williamsoni*, longnose sucker *Catostomus catostomus*, largescale sucker *Catostomus macrocheilus*, slimy sculpin *Cottus cognatus*, and reidside shiner *Richardsonius balteatus*. The lake

trout is the only non-native fish species in the drainage and was first detected in Lower Quartz Lake in 2003 and in Quartz Lake in 2005 (Fredenberg et al. 2007).

There are no natural putative fish barriers in the Quartz drainage, although several high gradient cascades serve as potential intermittent barriers between Lower Quartz and Middle Quartz lakes. The discovery of lake trout in Lower Quartz Lake prompted construction of an artificial barrier approximately 100 m downstream of Middle Quartz Lake in 2004 to conserve the upstream native fish assemblages in Middle Quartz, Quartz, and Cerulean lakes. Unfortunately, lake trout were detected in Quartz Lake in 2005 before the barrier was completed. The NPS completed the barrier in 2012 to deter further invasions.

Methods

Timing and Location of Spawning

The timing and location of spawning by lake trout were assessed using acoustic telemetry, similar to Dux (2005) and Cox (2010). Lake trout ≥ 550 mm were captured by angling and surgically implanted with acoustic transmitters (Model CTT-83-3-1, Sonotronics Inc.) during June of each year (2009-2013). Transmitters were 62 mm in length, 16 mm in diameter, and weighed 22 g in air. The expected battery life for each transmitter was approximately 36 months. Lake trout were anesthetized with tricane methanesulfonate (MS-222), and transmitters were inserted into the abdominal cavity via a small incision (< 20 mm) along the mid-ventral line anterior to the pelvic girdle (Winter 1996; Dux 2005). The incision was closed with 3-4 non-absorbable synthetic sutures

(Ethicon Inc.). Fish were relocated daily to identify potential spawning concentrations and to inform netting efforts (see below). Tagged individuals were relocated beginning in late September through the beginning of November.

A kernel density surface was created in ArcGIS 10.1 (ESRI 2012) to identify areas where mature lake trout occurred in the highest concentrations during spawning (Cox 2010). Kernel density was calculated by pooling the relocation points for all individuals from 2009 to 2013. A relative relocation density surface of Quartz Lake was created using the ArcGIS raster calculator (ESRI 2012) and the maximum kernel-density was scaled to one to identify the highest relocation densities. The areas of highest relocation densities were subsequently targeted for spawner netting to increase exploitation of adult lake trout (Cox 2010). All recaptured fish were euthanized.

Water temperatures were collected along a vertical profile of the lake from 29 May 2012 to 30 October 2012 using HOBO water temperature data loggers (Model U22-001, Onset Inc.). A rope was anchored in approximately 55 m of water and a water temperature logger was attached at 5-m increments. The data loggers recorded lake temperatures every hour with an estimated battery life of 5 years. The temperature profile data, telemetry data, and adult netting results were used to define the spawning period (see below).

Gillnetting

Adult lake trout were removed from potential spawning areas from early October through early November using sinking monofilament gill nets. Each net was 91-m long by 3-m deep, with a mesh size of 51-, 57-, or 65-mm bar measure containing 0.2 mm

twine diameter and white mesh. A minimum of two nets and maximum of five nets were connected to form gangs that were deployed at potential spawning locations between 5 m and 45 m in depth. Nets were retrieved every hour to reduce bycatch of bull trout, westslope cutthroat trout, and other native fish species. Total length, weight, sex, maturity (mature or immature based on field observation of the gonads), and the mesh size the fish was captured in were recorded for all captured lake trout.

Juvenile netting occurred for five weeks beginning in June and ending the first week of July from 2010 through 2013. Sinking gill nets were used in a random sampling design to sample juvenile lake trout up to 400 mm total length (TL). The sampling stratum was defined as all areas of the lake at or below 30 m to avoid incidental bycatch of non-target species. Netting did not occur in the smaller, shallower east basin known to contain a greater proportion of bull trout. Sampling locations were randomly assigned using 200 m² locations developed from satellite imagery of Quartz Lake in ArcGIS 10.1 (ESRI 2012). Each location was assigned a random number between 1 and 74, and each location was sampled at least one time per year. Gill nets were deployed at depths varying from 30 m to 83 m between 0400 and 2400 h and were retrieved within 3-6 h. Juvenile gill nets were 91-m long by 2-m deep monofilament nets containing 0.2 mm twine diameter and white mesh, which were joined together to form gangs of three nets having mesh sizes of 26-, 28-, and 32-mm bar measure. Total length (to the nearest mm) and mesh size the fish was captured in was recorded for all captured lake trout. All captured lake trout were euthanized.

Length and Age Structure

Gill nets are highly length specific in their capture and thus may not represent the true length structure of the targeted fish population (Hamley 1975). Therefore, I used the mesh sizes of captured fish to model gill-net selectivity. The program Select in R was used to model gill-net selectivity curves (Millar and Holst 1997; Millar 2000; R Core Team 2013). A log-normal distribution of net selectivity was chosen because it had the lowest model deviance. Selectivity curves for juvenile netting were used to examine the length distribution of fish captured in each mesh size, and to determine the overall length range of fish being selected for in the population. Selectivity analysis could not be modeled for spawners because the sample size was small and the lengths of fish in the varying gill-net meshes were uniform. Annual cumulative length-frequencies were used to describe the temporal change in the length structure of juvenile and adult lake trout from 2009 through 2013.

Sagittal otoliths were removed for age estimation from 10 individuals per centimeter length interval when present ($N = 491$). Otoliths are more reliable than scales for ageing fish due to the inconsistencies of scale annulus development and deterioration of the outer scale edge that commonly occurs with slow growing long-lived species (Dubois and Lagueux 1968; Healey 1978a; Sharp and Bernard 1988). Sagittal otoliths were cleaned, dried, and mounted in clear epoxy, and a thin section was cut perpendicular to the sulcal groove through the nucleus of the otolith (DeVries and Frie 1996; Dux 2005; Cox 2010). Each section was mounted on a slide and sanded until all annuli were discernible. Mineral oil was applied if needed to aid in discerning annuli (Syslo 2010).

An experienced technician counted the number of annuli using a compound light microscope at 40x magnification to estimate fish age (Campana 1992; Dux 2005). A subsample of otoliths ($N = 66$) were aged by an independent reader for age comparisons (Campana et al. 1995). Prior knowledge of fish lengths was avoided to reduce aging bias (Sharp and Bernard 1988).

Growth and Condition

Growth was modeled with the von Bertalanffy (VBF) growth model:

$$L_t = L_{\infty} * (1 - e^{-K(t-t_0)}),$$

where L_t is the length at time t , L_{∞} is the asymptotic length, K is the growth coefficient, and t_0 is the theoretical age at which length is equal to zero (Ricker 1975). To determine whether growth varied by sex, a pooled model was compared to a model with sex-specific parameters, L_{∞} , K , and t_0 . Akaike's Information Criterion adjusted for small sample sizes (AIC_c) was used as a model selection criterion (Hurvich and Tsai 1989; Burnham and Anderson 2002). The model with the lowest AIC_c value was used to model fish growth. Using the `nls` function in R 3.0.1 (R Core Team 2013), a nonlinear least squares regression was used to estimate the growth model parameters. Ninety-five percent confidence intervals were constructed using 5,000 bootstrap data sets randomly selected with replacement from the original data set. Age and length data were also used to calculate the mean length-at-age and to develop an age-length key to assign ages to all sampled lake trout (DeVries and Frie 1996; Isely and Grabowski 2007; Cox 2010).

All lake trout weighed (to the nearest g) throughout the suppression program were used to assess body condition. The lake trout standard weight equation (Piccolo et al.

1993) was used to calculate relative weight (W_r ; Anderson and Neumann 1996; Pope and Kruse 2007). Relative weight was calculated and analyzed using five length categories described by Hubert et al. (1994) by sex. Temporal changes in W_r were not of interest, thus all W_r data were pooled from 2009 through 2013 ($N = 453$).

In addition, weight data were used to estimate annual yield (kg/ha). All lake trout measured for length and weight were used to form a length-weight regression equation that was used to predict the weights of lake trout that were not weighed. Observed and predicted weights of fish harvested yearly were summed and divided by the Quartz Lake surface area (352 ha) to estimate annual yield (Syslo 2010).

Abundance

The abundance of juvenile lake trout (age 5 to age 7) was estimated using a Leslie depletion regression model that incorporated both catch and effort. Standard error of the population abundance estimate was computed using the formula described by Seber (2002). Lower and upper exploitation (μ) rates were estimated annually for lake trout age 5 to age 7. The annual lower and upper exploitation confidence intervals were estimated by dividing the number of lake trout harvested by the lower and upper confidence limits from the population estimate.

Abundance was estimated for fish $\geq$ age 10 using a Jolly-Seber mark-recapture model of the acoustically tagged adult lake trout. Standard error was calculated for parameter estimates using the methodology described by Pollock et al. (1990). The Jolly-Seber open population abundance estimator was used because this was a continuous mark-recapture effort for an open population over several years. The annual lower and

upper exploitation confidence intervals were estimated by dividing the number of adult lake trout harvested by the lower and upper confidence limits from the population estimate. An estimate of exploitation was calculated in 2012 but deemed unreliable because all tagged individuals were recaptured and removed from the population.

Exploitation rates (μ) for spawners and juveniles were converted to total conditional interval mortality by substituting μ for m . The mean of the upper and lower confidence limits for the annual total conditional interval mortality rates were used in population modeling (see below).

Maturity and Fecundity

Maturity schedules for fish are often defined as the age or length where 50% of the population is mature (Heibo and Vollestad 2002; Syslo 2010). Using age, length, and maturity data collected from lake trout ($N = 292$), sex-specific length and age at 50% maturity were estimated using a logistic regression model for the binary response data (Heibo and Vollestad 2002; Syslo 2010). Ninety-five percent confidence intervals for the estimated length and age at 50% maturity were calculated using 5,000 bootstrap data sets randomly sampled with replacement. I used sex-specific models because male lake trout often mature at younger ages and smaller sizes than females (Cox 2010). Predicted female probability at maturity (p_i) was used to model fertility in matrix population models (below).

Fecundity was estimated gravimetrically for females with intact skeins sampled in 2011 ($N = 10$) and 2012 ($N = 17$). A 10% cross-section of the ovary weight was sampled from the posterior, medial, and anterior section of the left and right ovary, and cross-

sections were weighed to the nearest 1.0 g and eggs were enumerated (Murua et al. 2003; Syslo 2010). The number of eggs in each cross-section was divided by the weight of the cross-section to estimate the average number of eggs per gram (egg/g) and then averaged and multiplied by the total ovary weight to estimate the number of eggs per ovary (Trippel 1993; Syslo 2010). The sum of the number of eggs in the left and right ovaries was the fecundity for each fish. Mean fecundity at age (f_i) was calculated for ages where $N > 1$ (Cox 2010). Fecundity estimates for age 8 and age 9 where only one individual was sampled were pooled and the mean was used to estimate fecundity for those ages. The mean fecundity of fish $\geq$ age 16 was used to estimate fecundity for fish $\geq$ age 16 because age classes beyond age 16 only consisted of two observations. Mean fecundity at age (f_i) estimates were used in the matrix-population models. Linear regression analysis was used to describe the fecundity-length relationship and to compare the relationship with other lake trout populations.

Mortality

Total instantaneous mortality rates (Z) for juveniles and spawners were estimated using Hoenig et al. (1983) version of the Chapman-Robson catch-curve model (Smith et al. 2012). Total instantaneous mortality was estimated annually for age-5 to age-7 juvenile lake trout. Total instantaneous mortality for spawners $\geq$ age 10 was estimated by pooling spawner catch data for years 2009-2013.

Recruitment is often variable in fish populations (Miranda and Bettoli 2007), and Chapman-Robson catch-curves assume recruitment is constant among cohorts (Syslo 2010). Because this assumption may be unrealistic for lake trout in Quartz Lake, I used a

cohort catch-curve to estimate Z . Total instantaneous mortality was estimated for the 1998 cohort using spawner catch data from 2009 to 2013. The 1998 cohort was selected because it had the longest catch history.

Natural mortality estimates for age-0 to age-2 lake trout could not be directly estimated using empirical data and were therefore obtained from the literature (Cox 2010; Syslo et al. 2013). I used the mean survival rates for age 0 lake trout (0.0043) based on five studies reported in Shuter et al. (1998), and age 1 (0.449) and age 2 (0.78) were estimated from Sitar et al. (1999). Randomly generated age-specific survival rates for fish that were not fully selected by the gear were included in population matrices to incorporate uncertainty in the natural survival rates used in each simulation. Beta distributions were used to constrain survival rates between zero and one, and survival was generated using the mean and SD values for each age-class (Morris and Doak 2002; Cox 2010). The mean and SD for age-0 survival was calculated from data in Shuter et al. (1998). The mean and SD for age-1 and age-2 survival rates provided by Sitar et al. (1999) had no measure of variation; therefore, I followed the Cox (2010) methodology and assumed SD = 20%. Lake trout $\geq$ age 3 were assumed to have a constant rate of instantaneous natural mortality (M) and von Bertalanffy growth parameters L_∞ and K (previously described) were used in a model developed to predict M for Ontario Lakes lake trout populations (Galucci and Quinn 1979; Shuter et al. 1998). Uncertainty of M was incorporated by randomly generating parameters ω (the product of VBF parameters L_∞ and K) and L_∞ 5,000 times from normal distributions where the mean was equal to parameter estimates and the SD was equal to predicted standard (Cox 2010).

Instantaneous natural mortality was calculated for each of the 5,000 simulated parameters of ω and L_∞ . Finally, each of the 5,000 simulated M rates were converted to natural conditional interval survival (S) as $S_i = e^{-M}$ (Miranda and Bettoli 2007) and the mean and SD of the survival rates were used in the projection matrices to represent natural survival rates for lake trout $\geq$ age 3 (Cox 2010).

Total instantaneous mortality rate estimates from the catch-curves were converted to instantaneous fishing mortality (F) by subtracting instantaneous natural mortality (M) from Z ($F = Z - M$; Miranda and Bettoli 2007; Syslo 2010). Instantaneous natural mortality and F rates were converted to conditional interval fishing (m) and conditional interval natural (n) mortality using the equations $m = 1 - e^{-F}$ and $n = 1 - e^{-M}$ (Miranda and Bettoli 2007; Syslo 2010). Age-specific total conditional interval mortality (A_i) for ages where natural and fishing mortality occurred simultaneously were computed with the equation $A = m + n - mn$ (Miranda and Bettoli 2007). Age specific total conditional interval mortality was converted to survival (S_i) using $S_i = 1 - A_i$ (Miranda and Bettoli 2007). Total conditional interval fishing mortality was assumed to affect age 5 to age 7 and $\geq$ age 10 lake trout because they were fully vulnerable to the mesh sizes used. Age-0 to age-4 and age-8 to age-9 lake trout were not fully selected with the sampling gears, so fishing mortality was set at zero; this is a conservative approach because some lake trout age 2 to age 4 and ages 8 to age 9 were sampled.

Population Modeling

Prospective perturbation analysis is a common tool in population modeling to evaluate potential changes in the population growth rate (λ) in response to changes in

vital rates (Caswell 2000). Perturbation analyses are often used to model alternative management scenarios prior to implementation (Caswell 2000). The age-specific vital rates and population characteristics collected and estimated (described previously) were used to construct a female-based post-breeding age-structured Leslie matrix. The population vital rates collected from harvested lake trout were used to construct an age-structured model as follows:

$$Q = \begin{bmatrix} F_0 & F_1 & \cdots & F_{16+} \\ S_0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & S_{15} & S_{16+} \end{bmatrix},$$

where F_x is the fertility value for age x , and S_x is the annual survival rate for age x . An age 16+ element was added to the matrices because a small sample of fish were greater than 20 years of age and lake trout often live to be over 25 years of age (Schram and Fabrizio 1998; Dux 2005). Age-specific fertility (F_x) was calculated with the equation:

$$F_x = f_i * p_i * 0.5,$$

where f_i is the mean fecundity at age i , and p_i is the probability of maturity for females age i (Cox 2010). Fecundity was multiplied by 0.5 because half of the offspring were assumed female. Population growth was projected by multiplying matrix Q by a population size vector to estimate the abundance of fish through time for each suppression scenario. The 2009 population abundance of all ages was estimated by projecting a population size of one female forward through time until abundances closely matched estimates from the depletion and Jolly-Seber models for age 5 to age 7 and $\geq$ age

10 (see above). The abundance of each year class was used to form the population vector.

Uncertainty in fertility rates was incorporated in population matrices by randomly generating age-specific fertility vital rates for each simulation (Cox 2010). A beta distribution with mean and SD equal to the predicted p_i and SE from the maturity-at-age logistic regression was used to constrain probabilities of maturity between zero and one (Cox 2010). The probability of maturity-at-age was generated using the beta distribution (Cox 2010). A stretched beta distribution with mean and SD calculated from the fecundity-at-age data were used to generate f_i values (Morris and Doak 2002; Cox 2010). The range of the stretched beta distributions was defined as all values within the minimum and maximum fecundity values from the empirical data (Cox 2010).

I estimated the population growth rate for seven management scenarios. Each of the seven models projected lake trout abundance ($\geq$ age 1) for a 20-year period to predict the effects of suppression levels on lake trout abundance in Quartz Lake. The no suppression and suppression management scenarios were each simulated with 5,000 generated population matrices. The population growth rate was calculated for each matrix and the mean λ was estimated. The 2.5 and 97.5 percentiles of the simulated distributions were used to approximate 95% confidence limits for mean λ (Cox 2010).

The no suppression model was used to simulate the population in the absence of fishing mortality using natural survival rates as the transitional survival elements in the matrix. The no suppression model was used for elasticity and sensitivity analyses to determine how the age class(es) vital rates (survival and fertility) contribute to population

growth rate (Caswell 2000). The transitional survival elements for the age classes fully selected by sampling gears were manipulated in the suppression population projection models to predict the population trajectory given specific A rates. Suppression scenarios included three models where $A = 0.25, 0.50, \text{ and } 0.75$. Three additional population models included estimates of A for juveniles and adults from the four years of suppression to estimate population trajectories. The lower (A_{lj}), mid (A_{mj}), and upper (A_{uj}) values of the total conditional interval mortality for age-5 to age-7 lake trout (juvenile) were calculated from the confidence interval values of total conditional interval mortality derived from the Chapman-Robson and depletion models (see above). For A_{lj} , A_{mj} , and A_{uj} , I used the average of the lower confidence, point estimate, and upper confidence values from the annual Chapman-Robson and depletion models, respectively. Similarly, the lower (A_{la}), mid (A_{ma}), and upper (A_{ua}) values of the total conditional interval mortality for lake trout $\geq$ age 10 (adult) were calculated from the Chapman-Robson, cohort catch-curves, and Jolly-Seber estimates. For A_{la} , A_{ma} , A_{ua} , I used the average of the lower confidence, point estimate, and upper confidence values from the Chapman-Robson, cohort catch-curves, and Jolly-Seber estimates (see above).

The carrying capacity (K) of the lake trout population in Quartz Lake was estimated by scaling the carrying capacity of nearby Flathead Lake to the surface area (ha) of Quartz Lake (Hansen et al. 2010; Syslo et al. 2013). The surface area of Quartz Lake (352 ha) was divided by the surface area of Flathead Lake (49,450 ha) to establish the surface area ratio. The population estimate of 1,480,280 lake trout $\geq$ age 1 in Flathead Lake (Syslo et al. 2013) was multiplied by the surface area ratio of 0.007119 to

estimate the K of Quartz Lake (10,538 lake trout $\geq$ age 1). This estimate likely represents the theoretical upper limit of K for Quartz Lake due to the lack of *Mysis* shrimp.

Bull Trout Monitoring

Redd count data (Downs et al. 2013) were used to monitor trends in the bull trout populations from 2003 to 2013 (Rieman and Myers 1997; Dunham et al. 2001; Al-Chokhachy et al. 2005; Muhlfeld et al. 2006; Downs et al. 2011). I used a nonparametric rank-correlation procedure (Daniel 1990) to test for significant trends in the annual redd count data (Rieman and Myers 1997). Specifically, Kendall's tau-b coefficient was used to account for potential bias induced by ties in the data set, and statistical significance was determined at the $\alpha = 0.05$ level (Rieman and Myers 1997; Downs et al. 2013).

Results

Timing and Location of Spawning

Thirty adult lake trout (14 males and 16 females; mean length = 620 mm, SD = 68) were implanted with acoustic transmitters from 2009 through 2013. Tagged adults were widely distributed throughout Quartz Lake during September and began to congregate near two avalanche chutes in early October (Figure 1.1). Mature adults were most densely concentrated near the base of two avalanche chutes along the northeastern shore (Figure 1.1), where recurring avalanches have deposited large substrate particle sizes (i.e., cobble and boulder), creating underwater colluvial fans that vary in depth from 2-20 m. Mature lake trout typically began congregating near the base of the avalanche chutes between the first and second weeks of October when surface temperatures were

between 11-12 C° and the lake was beginning to destratify. Diel tracking surveys revealed that adult lake trout moved from deep areas along the colluvial fans during the day to shallow areas on the colluvial fans at night. Twenty-eight (93%) of the tagged lake trout were recaptured during spawner gillnetting in one of the two avalanche chutes described previously. Spawner gillnetting focused on the two colluvial depositional areas identified by the telemetry data as the primary spawning locations for lake trout in Quartz Lake (below).

Gillnetting

Spawner gillnetting for years 2009 through 2013 resulted in the removal of 352 lake trout. The mean length of fish captured during spawner netting was 630 mm TL (95% CI = 609-632 mm), with 96% of the catch comprised of fish > 400 mm TL (Figure 1.3). In 2012, the thermocline began to descend and Quartz Lake destratified by the second week of October (Figure 1.2). Gill net catches of ripe lake trout were highest from 12 October through 25 October each year.

Juvenile gillnetting during spring 2010 through 2013 resulted in the removal of 1,457 lake trout. Juvenile lake trout varied in length from 113 mm to 665 mm TL (mean = 269 mm, 95% CI = 266-271 mm), with 98% of the catch comprised of fish varying in length from 170 mm to 380 mm (Figure 1.4). The gill net gang used for juvenile lake trout was fully selective for lengths between 290 and 400 mm TL.

Length and Age Structure

The length structure of lake trout caught in gill nets shifted during the four years (2009-2013) of suppression efforts. Annual cumulative length-frequency distributions reflected a decrease in lake trout length for juvenile and adult lake trout (Figure 1.5), indicating a larger percent of the cumulative catch was comprised of smaller individuals.

Four hundred and ninety one lake trout varying in length from 113 mm to 861 mm (mean = 468, SD = 190) were aged. Lake trout ages varied from 2 to 24 years (mean = 8, SD = 4). Eighty-two percent of the subsampled otoliths aged by two independent readers were within two years of age and the mean coefficient of variation (SD/mean) was 9.8%.

Growth and Condition

Growth did not vary between male and female lake trout. The sex-pooled VBF model had a lower AIC_c value than the model with sex specific growth parameters (Table 1.0). Thus, the sex-pooled model was used to describe male and female growth (Figure 1.6). Lake trout $\leq$ age 10 grew slowly when compared to growth rates from nearby lake trout populations in Swan (Cox 2010) and Flathead (Beauchamp 1996) lakes in Montana, and Yellowstone Lake, Yellowstone National Park, Wyoming (Ruzycki and Beauchamp 1997; Figure 1.7).

Lake trout weight was highly correlated with length ($r^2 = 0.99$; d.f. = 1,201; $P < 0.001$; Figure 1.8). Lake trout in Quartz Lake were in lower relative condition, and W_r values in all length categories were below the 50th percentile of the mean cumulative frequency distribution for 58 lake trout populations throughout North America (Hubert et

al. 1994). Mean relative weight varied from 80 (95% CI = 71-88) for *S-Q*, to 93 (95% CI = 89-97) for the *P-M* length category (Table 1.1). Among the five length categories, mean W_r for females in the *P-M* length category was highest when compared to the mean cumulative frequency distribution (Hubert et al. 1994).

Total annual yield declined from 1.01 kg/ha in 2009 to 0.37-0.55 kg/ha in 2010-2013. Juvenile yield estimates increased over the duration of the project from 0.14 kg/ha in 2009 to 0.18 kg/ha in 2013 (Table 1.2). Spawner annual yield varied from 0.24 kg/ha in 2010 to 1.01 kg/ha in 2009 to (Table 1.2).

Abundance

Juvenile and adult abundance estimates declined following the first year of suppression. Adult abundance estimates varied from 146 in 2009 to 60 in 2011 (Table 1.3). The estimated abundance of age-5 to age-7 lake trout declined from 326 in 2010 to between 159 and 279 for the following three years (Table 1.4). The age structure was dominated by juvenile lake trout, indicating the lake trout population had expanded in recent years.

Maturity and Fecundity

Age and length at maturity differed between male and female lake trout. Fifty percent of male lake trout reached sexual maturity at 453 mm TL (95% CI = 413-478) and age 7 (95% CI = 7-8), whereas 50 percent of female lake trout reached sexual maturity at 556 mm TL (95% CI = 502-586) and age 9 (95% CI = 8-9). Mature male

lake trout varied from 430 to 851 mm TL (mean = 610 mm; SD = 82) and mature female lake trout varied from 428 to 861 mm TL (mean = 676 mm; SD = 64; Figure 1.9).

Female length was positively related to fecundity ($r^2 = 0.75$, d.f. = 27, $P < 0.001$) (Figure 1.10). Mean female lake trout fecundity was 4,337 eggs (95% CI = 3,455-5,219) for individuals varying in length from 582 mm (age 8) to 820 mm (age 18) (mean TL = 679; SD = 63). Relative mean fecundity was 1,277 (95% CI = 1,116-1,439) eggs/kg.

Mortality

Instantaneous natural mortality for lake trout $\geq$ age 3 was estimated at 0.06 (95% CI = 0.05-0.07). Total conditional interval mortality rates derived from annual Chapman-Robson catch-curve estimates for age-5 to age-7 lake trout increased annually from 0.68 in 2010 to 0.98 in 2013 (Table 1.5). Total conditional interval mortality rates derived from depletion estimates of abundance varied from 0.51 in 2010 to 0.95 in 2011 (Table 1.5). The mean total conditional interval mortality values (A_{lj} , A_{mj} , A_{uj}) varied from 0.71 to 0.87 (Table 1.8).

Total conditional interval mortality rates derived from the Chapman-Robson and cohort catch-curves for lake trout $\geq$ age 10 were similar; however, the total conditional interval mortality rates derived from the Jolly-Seber model were disparate. Total conditional interval mortality derived from the Chapman-Robson and cohort catch-curves were 0.34 and 0.32 (Table 1.6), respectively. Interestingly, estimates of total conditional interval mortality derived from the Jolly-Seber exceeded estimates derived from the catch-curves (Tables 1.6 and 1.7). Total conditional interval mortality derived from the Jolly-Seber model varied from 0.61 to 0.94 (Table 1.7). Mean total conditional interval

mortality values used in population modeling (A_{la} , A_{ma} , A_{ua}) varied from 0.41 to 0.57 (Table 1.8).

Population Modeling

Mean population growth rate (λ) of the lake trout population in the no suppression scenario was 1.23 (95% CI = 1.16-1.28; Figure 1.11). If the population growth rate remained constant under this scenario, the population would have doubled approximately every 3.3 years (95% CI = 2.8 - 4.6 years) and carrying capacity for lake trout $\geq$ age 1 would be exceeded by 2015 (Figure 1.12).

Lake trout population growth rate (λ) was most sensitive to changes in age 0 survival (Table 1.9) and became less sensitive as age increased. The relative contribution of survival rates to λ was constant for age-0 to age-7 lake trout and decreased thereafter (Table 1.9), suggesting that λ is most sensitive to changes in juvenile survival rates.

All harvest suppression scenarios, with the exception of the low suppression alternative ($A = 0.25$), produced population growth rates less than one (Table 1.10). The six suppression scenarios produced a wide array of mean population growth rates varying from 0.61 (95% CI = 0.63-0.70) to 1.10 (95% CI = 1.04-1.16; Table 1.10). The suppression models incorporating the mean A_{xj} and A_{xa} estimates resulted in mean population growth rates between 0.79 (95% CI = 0.81-0.90) and 0.61 (95% CI = 0.63-0.70). Population abundance estimates following 20 years of suppression varied from $\hat{N} = 3$ where $A = A_{uj}$, and A_{ua} to $> K$ for the no suppression and the suppression scenario where $A = 0.25$ (Figures 1.12 and 1.13).

Bull Trout Monitoring

Bull trout bycatch declined after 2009 ($N = 146$) and was lowest in 2011 ($N = 56$; Table 1.11). Adult bull trout (> 400 mm) bycatch mortality varied from 29 in 2010 to 6 in 2013 (Table 1.11). The bull trout bycatch did not appear to influence adult bull trout abundance. Mean redd count for Quartz Creek from 2003 through 2008 was 30 redds ($SD = 17$). Similarly, the mean redd count during suppression from 2009 through 2013 was 30 redds ($SD = 5$; Figure 1.14). Moreover, bull trout redd counts did not exhibit a statistically significant trend ($\tau\text{-}b = -0.09$, $P = 0.76$) from 2003 through 2013. High flows in 2005 obscured redds (Meeuwig and Guy 2007); therefore, the 2005 redd count was removed and the data was reanalyzed. After removing the 2005 redd count, there was no significant trend in redd numbers from 2003 through 2013 ($\tau\text{-}b = -0.24$, $P = 0.37$).

Discussion

Although lake trout populations within their native range have declined due to over-exploitation and the introduction of a non-native fish species (Hansen 1999; Hutchings 2000; Wildberg et al. 2004), lake trout populations introduced throughout the western United States have expanded and have produced long lasting negative ecological consequences (Martinez et al 2009). As such, natural resource agencies have implemented lake trout suppression programs (e.g., Swan, Pend Oreille, Yellowstone, Upper Priest and Flathead lakes) to reduce the negative impacts on native and recreational fish species and aquatic ecosystems (Martinez et al. 2009). My results

indicate that the lake trout population in Quartz Lake was characterized by slow growth, poor relative condition, late maturity and low reproductive potential, making it vulnerable to overexploitation (Shuter et al. 1998). Results of four years (2009-2013) of suppression indicate the abundance of lake trout population has declined and that suppression has negatively influenced the lake trout population growth rate in Quartz Lake. Several lines of evidence suggest that experimental suppression of non-native lake trout resulted in declining length and age structure, adult abundances, adult annual yield, and survival. My results indicate the early detection of the lake trout population within Quartz Lake and the rapid management response decreased the population growth rate to below replacement, likely increasing the probability of successfully suppressing the lake trout population within Quartz Lake.

Although lake trout were first documented in Quartz Lake in 2005, several lake trout $\geq$ age 15 ($N = 6$) were removed during 2009 spawner netting, indicating lake trout were within Quartz Lake and likely reproducing for a number of years prior to 2005. Further, the length and age structure of the lake trout population in 2010 indicated that juvenile recruitment had increased in recent years resulting in larger cohorts recruiting to the mesh sizes used for juvenile netting. If left unabated, my analysis indicates that the population would likely have reached carrying capacity ($\sim 10,500$ individuals) by 2015. Nevertheless, my results indicate that four years of suppression has reduced the population to between 3,854 and 2,584 individuals.

Spawning habitats identified using telemetry were characteristic of lake trout spawning habitat throughout their native and introduced ranges (Gunn 1995; Marsden et

al. 1995; Dux 2005; Cox 2010). Spawning likely occurred in two relatively shallow areas varying in depth from 2 to 20 m at the base of two avalanche chutes along the northeastern shore in areas characterized by unembedded cobble and boulder substrates. Similarly, Dux et al. (2011) found that lake trout spawned at a mean depth of 18 m on cobble and boulder substrates containing deep interstitial spaces free of fine sediments in Lake McDonald, GNP. In Swan Lake, Montana, Cox (2010) identified two locations consisting of coarse, angular substrates where lake trout spawned in depths varying from 1.2 to 12.8 m. The lack of suitable spawning habitat and the high recapture rates of acoustic-tagged adults on the two colluvial fans suggest spawning was limited to these locations. Although sensitivity analysis indicated that the lake trout population growth rate was most sensitive to changes in juvenile survival rates, removal of spawning adults decreases survival of mature fish and reduces the probability of successful spawning and thus juvenile recruitment. Therefore, using a combination of telemetry and targeted gillnetting of spawning adults appears to be an efficient way to reduce the population growth rate and to increase fishing mortality on the adult component of the lake trout population. Thus, to ensure the decline of abundance and population growth rate, targeted gillnetting of the spawning adults should be continued.

Lake trout in Quartz Lake began aggregating near the potential spawning locations in early October prior to lake destratification, when surface temperatures were between 11° and 12° C. These results are consistent with other studies that reported lake trout spawning behavior was initiated following lake destratification and declining water temperatures between 8° and 14° C (Gunn 1995; Dux 2005). Similarly, lake trout began

aggregating near the potential spawning locations in Lake McDonald shortly before destratification when the surface water temperature was 12° C (Dux et al. 2011). The first ripe lake trout caught in Lake McDonald (Dux et al. 2011) and Quartz Lake in 2012 occurred when surface temperature declined to 10° C. Although the first ripe lake trout were caught at the same surface temperature, Quartz Lake surface temperature declined to 10° C (15 October) approximately 10 days prior to Lake McDonald (25 October; Dux et al. 2011). Spawning aggregations in Quartz Lake disbanded the last week of October.

The length structure of the lake trout population decreased during the suppression program, suggesting selective harvest removed large proportions of the targeted length classes. Truncation of size and age distributions in fish populations is a common response to size selective harvest (Coleman et al. 2000; Kocovsky and Carline 2001; Hutchings and Reynolds 2004). For example, Atlantic cod *Gadus mohua* populations in the Northwest Atlantic declined by more than 90% over a 40 year period, and during the decline the age and length structure shifted to smaller individuals that were younger in age (Hutchings 2005). Similarly, the length and age structure of the lake trout population in Swan Lake, Montana, declined in response to three years of selective harvest (Rosenthal et al. 2012). The cumulative frequencies for juvenile lake trout shifted to lengths that were newly recruited to the mesh sizes used. Therefore, the addition of gill nets having smaller mesh sizes (e.g., 19 mm bar) should be considered to broaden the length and age range of lake trout vulnerable to harvest (see Chapter 2). Specifically, the use of 19.1 mm bar measure nets is recommended to target younger age classes (age 3 and age 4) that were not fully selected by the mesh sizes in this study. The length of

adult lake trout also decreased, and a larger proportion of the catch was made up of individuals that recently matured and congregated at the spawning locations.

Growth rate and body condition of lake trout in Quartz Lake were low relative to other populations throughout North America (Hubert et al. 1994; Cox 2010; Syslo 2010). Lake trout up to age 10 in Quartz Lake grew slowly when compared to other lake trout populations throughout North America (Hubert et al. 1994). Age at maturity is often linked to individual growth rates (Ferrerri and Tayler 1996); therefore, the slow individual growth in Quartz Lake may aid suppression efforts by increasing the amount of time resource agencies have to remove individuals prior to their maturation. The low W_r of lake trout in the stock-quality and quality-preferred length categories are typical for less productive systems such as Quartz Lake (Hubert et al. 1994). Similarly, the W_r of preferred-memorable and memorable-trophy length categories remained low, which is indicative of systems with low densities of prey fish (Hubert et al. 1994). The wider associated 95% confidence intervals for the mean W_r of lake trout in *M-T* length category is likely explained by the small sample size. However, the condition factors of lake trout in Quartz Lake were comparable to lake trout in a similar oligotrophic system in nearby Lake McDonald, GNP (Dux et al. 2011). Both Lake McDonald and Quartz Lake are glacially formed and supplied by perennial snow melt and glacial runoff, resulting in systems characterized by low productivity.

Total annual yield of 0.5 kg/ha has been suggested as the maximum sustainable yield threshold for lake trout populations (Healy 1978a). Annual yield in Quartz Lake exceeded the 0.5 kg/ha threshold for all years with the exception of 2010 and 2013.

Although effort increased from 2009, spawner yield decreased to between 0.24 and 0.39 kg/ha for the following four years. Thus, it is reasonable to assume the abundance of mature lake trout has decreased since 2009, which is corroborated by the Jolly-Seber abundance estimates. Furthermore, juvenile yield increased from 2011 to 2013.

Although this could partially be due to an increased effectiveness of the gillnetting crew, it is unlikely to fully account for changes because gill nets were randomly placed. Thus, the increase in juvenile yield can most likely be explained by the increasing strength of cohorts recruiting to the mesh sizes used to capture juveniles. The increasing strength in cohorts further exemplifies a growing population with an age structure that is dominated by young individuals.

Adult lake trout reached maturity at older ages as compared to most lake trout populations throughout western North America (Healey 1978b; Cox 2010). For example, male and female lake trout in Quartz Lake matured at older ages (males = 7.2, females = 8.7) and smaller lengths (males = 453 mm, females = 556 mm) than males and females in Swan Lake, which matured at ages 6.1 and 7.4 and lengths at 590 mm and 708 mm for males and females, respectively (Cox 2010). Additionally, length at maturity was relatively low when compared to other populations (Hansen et al. 2008; Madenjian et al. 1998; Cox 2010; Syslo 2010). Typically, piscivorous lake trout populations have high individual growth and mature at younger ages and larger sizes than slow-growing planktivorous populations (Martin and Olver 1980). Although lake trout in Quartz Lake appeared to be mainly piscivorous (observations of stomach contents), they matured at older ages and shorter lengths when compared to other piscivorous populations (Hansen

et al. 2008; Madenjian et al. 1998; Cox 2010; Syslo 2010). This can likely be attributed to the relatively slow growth and lower condition factors of lake trout within this oligotrophic system. The time it takes for a fish to mature is often related to growth rate (Ferrerri and Tayler 1996); thus, a population of slow growing fish will often mature at older ages. Fish populations exhibiting slow individual growth and late age-at-maturity are often susceptible to overexploitation (Shuter et al. 1998). Lake trout in Quartz Lake possess these characteristics, further supporting the notion that suppression of the lake trout population in Quartz Lake is an achievable goal given the current suppression effort.

Lake trout fecundity in Quartz Lake was relatively low when compared to fecundity estimates elsewhere (Trippel 1993). For example, the estimated mean fecundity of a 600 mm fish in Quartz Lake (1,721 eggs) was less than a 600 mm fish in six lake trout populations in Ontario (1,828-3,210 eggs; Trippel 1993) and Yellowstone Lake (3,823 eggs; Syslo 2010). The relative mean fecundity in Quartz Lake (1,277 eggs/kg) was well below values reported in the literature (Shuter et al. 1998; Syslo 2010). For instance, Shuter (et. al 1998) reported a mean of 1,506 eggs/kg for 13 lake trout populations throughout inland lakes in Ontario, and Syslo (2010) reported a mean relative fecundity of approximately 1,550 eggs/ kg in Yellowstone Lake. The below average length-specific and relative fecundity values observed in Quartz Lake suggest that the population exhibits a lower reproductive potential and a slower replacement rate. These demographic characteristics are typical of populations that are prone to overexploitation (Shuter et al. 1998).

The no suppression model used to determine the growth rate of the lake trout population in Quartz Lake prior to suppression in 2009 revealed that the population was exponentially growing and approaching the maximum growth rate. Although this population growth rate can only be considered a glimpse of the population's growth rate at the current fecundity and survival rates, it clearly depicts a population that is exponentially growing. The population abundance in 2009 was estimated near 4,200 lake trout ($\geq$ age 1). In comparison to the estimated carrying capacity ($N = 10,538$), this value is near $K/2$, the maximum population growth rate. The carrying capacity for lake trout $\geq$ age 1 in Quartz Lake was considerably lower when compared to nearby Swan (39,968) and Flathead lakes (1,480,280; Syslo et al. 2013). This is to be expected because the surface area of Quartz Lake is approximately 26% of Swan Lake and 0.7% of Flathead Lake surface areas. The small surface area and carrying capacity of Quartz Lake relative to other lakes targeted for lake trout suppression should allow natural resource agencies to reach a suppression target with less effort. Further, the current population growth rate for the no suppression scenario in Quartz Lake was lower than the population growth rates estimated for expanding lake trout populations in Swan Lake, Montana (Cox 2010), and Lake Pend Oreille, Idaho (Hansen et al. 2008). Similarly, the time it would take the lake trout population in Quartz Lake to double was greater than the predicted doubling time for Swan Lake and Lake Pend Orielle (Hansen et al. 2008; Cox 2010). This was most likely a function of Quartz Lake being less productive and not having *Mysis* shrimp, which are known to accelerate lake trout population growth rates (Stafford et al. 2002).

Eventually, if left unabated, density dependence would affect the vital rates of the population as the population neared carrying capacity.

When compared to the no suppression alternative, each of the six suppression scenarios resulted in lower mean population growth rates. However, when total conditional interval mortality was 0.25 the mean population growth rate was greater than one (i.e., replacement) and the population would continue to grow. Total annual mortality exceeding 50% has been suggested as the threshold for overharvest in lake trout populations (Healy 1978a). In Yellowstone Lake, an exploitation rate between 0.31 and 0.43 would cause a decline in the lake trout population (Syslo et al. 2011). Similarly, in Lake McDonald, GNP, models indicated recruitment overfishing could be achieved with an exploitation rate as low as 0.36 (Dux 2005). When these exploitation rates are converted to total annual mortality rates, they vary from 0.39 to 0.51 (Syslo et al. 2013). Here, suppression scenarios where total conditional interval mortality was ≥ 0.50 resulted in population growth rates below one. Although the mean population growth rate was less than one when $A = 0.50$, the upper confidence limit of the estimate was 0.99, which is very close to a stable population growth rate of one. Therefore, increasing the total conditional interval mortality rate or increasing the age range of fish subjected to this total conditional interval mortality rate is recommended to decrease the time to reach a suppression target. It may be beneficial for future suppression efforts to extend the mesh sizes used to increase total annual mortality rates for smaller individuals (age 3 and age 4) that were not recruited to the mesh sizes used in this study, or to increase total annual

mortality rates to ≥ 0.70 for age 5 to age 7 and $\geq$ age 10 to reduce population abundance in the shortest time interval.

Total conditional interval mortality rates during the Quartz Lake suppression program exceeded rates needed to cause declines in the lake trout population. However, the time it took to reach future suppression targets differed when the upper and lower total conditional interval mortality limits were used in population abundance simulations. For example, in population simulations where total conditional interval mortality was simulated at the lower limit for juveniles ($A_{lj} = 0.71$) and adults ($A_{la} = 0.41$), lake trout abundance declined to below $N = 500$ by the year 2029 but failed to fall below $N = 50$ within 20 years. In contrast, when total conditional interval mortality was simulated at the upper limit for juveniles ($A_{lj} = 0.87$) and adults ($A_{ua} = 0.57$), lake trout abundance was reduced over a much shorter time period and declined below $N = 500$ by the year 2018 and $N = 50$ by the year 2022. Total conditional interval mortality rates estimated for lake trout in Quartz Lake were high relative to ongoing suppression programs elsewhere in the Rocky Mountains. For instance, in Yellowstone Lake total annual mortality rates varied from 0.23 to 0.30 and total annual mortality rates for spawning lake trout varied from 0.35 to 0.59 (Syslo 2010). In Lake Pend Oreille, Idaho, the total annual mortality rate estimated in 2006 was 0.58, and it was determined that this mortality rate could cause the population to decrease (Hansen et al. 2008). However, it is important to note that the length and ages of the lake trout used to estimate fishing mortality differ among suppression programs. For example, total conditional interval mortality rate estimates for

lake trout in Quartz Lake affect age 5-7 and $\geq$ age 10 lake trout, whereas in Yellowstone Lake total annual mortality rates affected age 2-17 lake trout (Syslo 2010).

My analysis suggests that the observed lake trout suppression levels are negatively impacting the population growth rate. At the current suppression levels, the mean population growth rate is estimated to be between 0.61 and 0.79. However, the suppression effort during the last four years is probably near the maximum attainable exploitation rate given the constraints of the boat size and manual method of net retrieval. Therefore, I recommend that managers consider increasing the boat size and using a mechanical net puller to more effectively and efficiently reduce the lake trout population size.

The primary source of uncertainty in the vital rates used in the model was the survival rate estimates for age-0 to age-2 lake trout. Because the juvenile survival rates that contribute most to population growth in the matrix models (age-0) were from the literature, I attempted to address this uncertainty by incorporating randomly generated age-specific survival rates in simulation models. However, the survival rates are likely biased low, because the Lake Superior lake trout population was likely affected by density dependence, which may affect juvenile survival (Corradin et al. 2008). Furthermore, juvenile lake trout in Lake Superior may be limited by egg predation from species such as burbot *Lota lota* and crayfish *Orconectes* spp. (Chotkowski and Marsden 1999) that are not present in Quartz Lake. Although uncertainty was incorporated in the vital rate estimates, future population models could be improved with estimates of age-0 to age-2 survival rates from lake trout in Quartz Lake.

The bull trout redd count analysis suggests that suppression efforts did not influence the bull trout spawning population. Annual redd counts and trend analysis suggested the bull trout population in Quartz Lake remained stable during the suppression period. However, increasing the suppression effort could have potential negative effects on the bull trout population within Quartz Lake, and should be viewed in an adaptive management framework. Bull trout abundance monitoring via redd counts should continue to ensure suppression efforts are not negatively affecting the bull trout population.

Conclusions

Non-native lake trout suppression programs are increasing in frequency and magnitude throughout the Intermountain West (Martinez et al. 2009). To my knowledge, experimental suppression of non-native lake trout in Quartz Lake is the first project to assess the feasibility of suppressing lake trout in a relatively small, isolated backcountry lake. My results indicate that suppression efforts from 2009-2013 negatively impacted the population growth, length and age structure, survival, and abundance of lake trout in Quartz Lake. Moreover, the population is characterized by relatively slow growth, poor condition, late maturity, and low reproductive potential. Together, these results suggest that the population is extremely vulnerable to overexploitation (Shuter et al. 1998), thereby increasing the likelihood of reaching a targeted management suppression level. To ensure lake trout abundance continues to decline, I recommend: (1) suppression be continued at or above current levels, (2) juvenile and targeted spawner gillnetting be continued, (3) increasing the boat size and incorporating a mechanical net puller, and (4)

the integration of smaller bar measure nets to increase the targeted length range.

Furthermore, I conclude that the use of manual methods to suppress a non-native lake trout population for the conservation of threatened bull trout is feasible within Quartz Lake and other similar backcountry lakes in GNP and elsewhere. The results of this project will aid future management of lake trout within Quartz Lake and other potential suppression efforts within GNP and regionally.

Tables

Table 1.0. von Bertalanffy growth model selection results to determine if growth was dependent on sex for lake trout in Quartz Lake, Glacier National Park, Montana.

Model	AIC _c	AIC _c Weight	Model Likelihood
Sexes pooled	3179.397	0.999	1.000
Separate sex	3194.925	0.004	0.0004

Table 1.1. Mean (95% CI), minimum, maximum, and sample size (N) of relative weight for male (M) and female (F) lake trout by length category in Quartz Lake, Glacier National Park, Montana. Length categories are defined as: stock-quality (300-499 mm), quality-preferred (500-649 mm), preferred-memorable (650-799 mm) and memorable-trophy (800-999 mm; Hubert et al. 1994). Percentile was a comparison of the empirical data with the cumulative frequency distribution of W_r values for 48 lake trout populations throughout North America (Hubert et al. 1994).

Length Category	Mean	Min-Max	N	Sex	Percentile
Stock-Quality	82 (69-94)	54-97	34	M	< 5
	80 (71-88)	57-102	35	F	< 50
Quality-Preferred	87 (85-89)	46-136	125	M	< 25
	86 (81-90)	64-117	60	F	< 25
Preferred-Memorable	86 (80-92)	51-132	48	M	< 25
	93 (89-97)	67-141	65	F	< 50
Memorable-Trophy	87 (81-93)	81-97	4	M	< 25
	88 (83-94)	76-101	7	F	< 25

Table 1.2. Estimated annual yield (kg/ha) for spawner and juvenile lake trout in Quartz Lake, Glacier National Park, Montana.

Year	Spawner Yield	Juvenile Yield	Total Yield
2009	1.01	--	1.01
2010	0.24	0.14	0.38
2011	0.39	0.13	0.52
2012	0.39	0.16	0.55
2013	0.30	0.18	0.48

Table 1.3. Jolly-Seber mark recapture estimates from empirical data; where m_i is the number of marked fish in the i^{th} sample, n_i is the number of fish captured in the i^{th} sample, R_i is the number of marked fish returned to the population after the i^{th} sample, r_i is the number of the R_i fished released in the i^{th} sample that were subsequently caught, z_i is the number of fish captured before the i^{th} sample, $\hat{M}_i$ (SE) is the estimated number of marked fish in the population just prior to the i^{th} sample, $\hat{N}_i$ (SE) is the estimated population size prior to the i^{th} sample, and $\hat{B}_i$ (SE) is the estimated number of fish added to the population between the i^{th} to the $(i + 1)^{\text{th}}$ sample in Quartz Lake, Glacier National Park, Montana.

Year	m_i	n_i	R_i	r_i	z_i	$\hat{M}_i$	$\hat{N}_i$	$\hat{B}_i$
2009	0	11	11	11	--	--	--	--
2009	10	143	7	6	1	11.1(0.5)	146(6.8)	73(22.3)
2010	4	57	3	3	3	7.0(0.0)	81(21.2)	32(22.5)
2011	5	57	6	5	1	6.2(0.5)	60(5.8)	56(5.5)
2012	6	63	4	4	0	6.0(0.0)	63(0.0)	--
2013	4	42	0	--	--	--	--	--

Table 1.4. Annual abundance $\hat{N}$ (SE) and upper and lower annual exploitation rates for juvenile lake trout age 5 to age 7 sampled during five weeks in the spring for years 2009 through 2013 in Quartz Lake, Glacier National Park, Montana.

Year	$\hat{N}$	$\hat{N}$ Upper	Captured	Upper Exploitation	Lower Exploitation
2010	326(193)	938	233	0.71	0.25
2011	167(5)	184	166	0.99	0.90
2012	159(18)	217	156	0.98	0.72
2013	279(53)	449	200	0.72	0.45

Table 1.5. Total conditional interval (A), instantaneous fishing (F), and conditional fishing (m) mortality derived from annual Chapman-Robson catch-curve estimates of instantaneous mortality (Z) for juvenile lake trout age 5 to age 7 in Quartz Lake, Glacier National Park, Montana. In addition, A and m rates derived from estimates of interval fishing mortality (μ) from the Leslie Depletion estimates of abundance. Conditional natural mortality (n) was converted from instantaneous natural mortality using the von Bertalanffy estimate of instantaneous natural mortality (M). Upper and lower 95% CI are in parentheses.

Mortality Estimated for Age-5 to Age-7 Juveniles					
	Mortality Estimate	2010	2011	2012	2013
Chapman-Robson Catch Curve	M	0.06 (0.06-0.07)	0.06 (0.06-0.07)	0.06 (0.06-0.07)	0.06 (0.06-0.07)
	A	0.68 (0.63-0.73)	0.80 (0.75-0.86)	0.91 (0.87-0.95)	0.98 (0.97-1.00)
	Z	1.15 (1.00-1.31)	1.62 (1.34-1.89)	2.37 (1.91-2.84)	3.97 (2.98-4.95)
	F	1.09 (0.94-1.25)	1.56 (1.28-1.83)	2.31 (1.85-2.78)	3.91 (2.92-4.89)
	m	0.66 (0.61-0.71)	0.79 (0.72-0.84)	0.90 (0.84-0.94)	0.98 (0.95-0.99)
	n	0.06 (0.05-0.07)	0.06 (0.05-0.07)	0.06 (0.05-0.07)	0.06 (0.05-0.07)
	μ	0.65 (0.51-0.79)	0.77 (0.59-0.86)	0.89 (0.84-0.93)	0.97 (0.95-0.99)
Derived from Leslie Depletion Estimates of Abundance	A	0.51 (0.30-0.73)	0.95 (0.91-0.99)	0.86 (0.74-0.98)	0.61 (0.48-0.74)
	m	0.48 (0.25-0.71)	0.95 (0.90-0.99)	0.85 (0.72-0.98)	0.59 (0.45-0.72)
	n	0.06 (0.05-0.07)	0.06 (0.05-0.07)	0.06 (0.05-0.07)	0.06 (0.05-0.07)

Table 1.6. Total conditional interval (A), instantaneous fishing (F), interval fishing (μ) and conditional fishing (m) mortality estimates derived from the 2009-2013 pooled Chapman-Robson catch-curve, and the 1998 cohort catch-curve estimates of total instantaneous mortality (Z) for adults $\geq$ age-10 lake trout in Quartz Lake, Glacier National Park, Montana (see methods for details). Conditional natural mortality (n) was converted from the von Bertalanffy estimate of instantaneous natural mortality (M). Upper and lower 95% CI are in parentheses.

Mortality Estimates for Age-10 and Greater		
Mortality Estimate	Chapman-Robson Catch-Curve	Cohort Catch-Curve
M	0.06 (0.06-0.07)	0.06 (0.06-0.07)
A	0.34 (0.31-0.38)	0.32 (0.19-0.44)
Z	0.42 (0.37-0.47)	0.39 (0.21-0.58)
F	0.36 (0.31-0.41)	0.33 (0.15-0.52)
m	0.30 (0.27-0.34)	0.28 (0.14-0.41)
n	0.06 (0.05-0.07)	0.06 (0.05-0.07)
μ	0.29 (0.26-0.33)	0.27 (0.14-0.39)

Table 1.7. Total conditional interval (A) and conditional fishing (n) mortality rates derived from interval fishing mortality rates (μ) derived from the Jolly-Seber population abundance estimates for mature lake trout in Quartz Lake, Glacier National Park, Montana for years 2009-2012. Conditional natural mortality (n) was converted from the von Bertalanffy estimate of instantaneous natural mortality (M). Upper and lower 95% CI are in parentheses.

Computed From Jolly-Seber Estimates of Abundance			
Mortality Estimate	2009	2010	2011
M	0.06 (0.06-0.07)	0.06 (0.06-0.07)	0.06 (0.06-0.07)
A	0.94 (0.91-0.98)	0.61 (0.49-0.72)	0.89 (0.81-0.95)
m	0.94 (0.90-0.98)	0.58 (0.46-0.70)	0.88 (0.80-0.95)
n	0.06 (0.05-0.07)	0.06 (0.05-0.07)	0.06 (0.05-0.07)

Table 1.8. Mean total conditional interval mortality rates (A) used for population abundance projections following 20 years ($\hat{N}_{20}$) of suppression for simulations where A is set at the mean lower (A_{lx}), mid (A_{mx}) and upper (A_{ux}) total conditional interval mortality rate estimates for juveniles age 5 to age 7 (A_{xj}) and adults $\geq$ Age 10 (A_{xa}) calculated from Table 1.5, Table 1.6, and Table 1.7 for lake trout in Quartz Lake, Glacier National Park, Montana. 95% CI are noted in parentheses.

Suppression Scenario	Mean Total Conditional Interval Mortality (A)	
	A_{xj}	A_{xa}
No Suppression	0.06 (0.05-0.07)	0.06 (0.05-0.07)
A_{lx}	0.71 (0.56-0.85)	0.41 (0.15-0.68)
A_{mx}	0.79 (0.68-0.90)	0.49 (0.23-0.75)
A_{ux}	0.87 (0.79-0.95)	0.57 (0.31-0.82)

Table 1.9. Mean sensitivity and elasticity (95% CI) of the population growth rate to survival (S_i) and fertility (F_i) matrix elements from 5,000 simulations of the no suppression scenario for lake trout in Quartz Lake, Glacier National Park, Montana.

Matrix element	Mean sensitivity	Mean Elasticity
S_0	18.692 (13.219-26.302)	0.063 (0.059-0.067)
S_1	0.179 (0.127-0.262)	0.063 (0.059-0.067)
S_2	0.105 (0.079-0.185)	0.063 (0.059-0.067)
S_3	0.083 (0.073-0.091)	0.063 (0.059-0.067)
S_4	0.083 (0.073-0.091)	0.063 (0.059-0.067)
S_5	0.083 (0.073-0.091)	0.063 (0.059-0.067)
S_6	0.083 (0.073-0.091)	0.063 (0.059-0.067)
S_7	0.083 (0.073-0.091)	0.063 (0.059-0.067)
S_8	0.083 (0.072-0.089)	0.062 (0.058-0.066)
S_9	0.079 (0.070-0.086)	0.060 (0.056-0.064)
S_{10}	0.072 (0.065-0.078)	0.055 (0.047-0.058)
S_{11}	0.064 (0.059-0.069)	0.049 (0.039-0.052)
S_{12}	0.054 (0.049-0.059)	0.042 (0.032-0.046)
S_{13}	0.046 (0.040-0.051)	0.035 (0.026-0.040)
S_{14}	0.037 (0.031-0.042)	0.029 (0.020-0.034)
S_{15}	0.030 (0.024-0.035)	0.023 (0.015-0.028)
S_{16+}	0.099 (0.069-0.142)	0.076 (0.051-0.114)
F_8	$1.30 \cdot 10^{-5}$ ($7.62 \cdot 10^{-6}$ - $1.83 \cdot 10^{-5}$)	0.001 (0.0003-0.003)
F_9	$9.94 \cdot 10^{-6}$ ($6.16 \cdot 10^{-6}$ - $1.35 \cdot 10^{-5}$)	0.002 (0.004-0.004)
F_{10}	$7.58 \cdot 10^{-6}$ ($4.95 \cdot 10^{-6}$ - $9.95 \cdot 10^{-6}$)	0.005 (0.004-0.009)
F_{11}	$5.79 \cdot 10^{-6}$ ($4.00 \cdot 10^{-6}$ - $7.36 \cdot 10^{-6}$)	0.006 (0.004-0.008)
F_{12}	$4.42 \cdot 10^{-6}$ ($3.22 \cdot 10^{-6}$ - $5.48 \cdot 10^{-6}$)	0.008 (0.003-0.014)
F_{13}	$3.38 \cdot 10^{-6}$ ($2.60 \cdot 10^{-6}$ - $4.09 \cdot 10^{-6}$)	0.006 (0.005-0.008)
F_{14}	$2.59 \cdot 10^{-6}$ ($2.09 \cdot 10^{-6}$ - $3.08 \cdot 10^{-6}$)	0.007 (0.005-0.008)
F_{15}	$1.98 \cdot 10^{-6}$ ($1.67 \cdot 10^{-6}$ - $2.33 \cdot 10^{-6}$)	0.006 (0.001-0.008)
F_{16+}	$6.51 \cdot 10^{-6}$ ($5.38 \cdot 10^{-6}$ - $7.95 \cdot 10^{-6}$)	0.023 (0.018-0.028)

Table 1.10. Mean population growth rate (λ), 95% CI, and population abundance estimates estimate ($\hat{N}_{20}$) (lake trout $\geq$ age 1) following twenty years for six suppression scenario simulations and a no suppression scenario simulation in Quartz Lake, Glacier National Park, Montana. For definitions of total conditional interval mortality refer to methods.

Suppression Scenario	λ	95% CI	$\hat{N}_{20}$
No Suppression	1.23	1.16-1.28	$> K$
$A=0.25$	1.10	1.04-1.16	$> K$
$A=0.50$	0.94	0.87-0.99	2,538
$A=0.75$	0.73	0.68-0.78	6
A_{lx}	0.79	0.75-0.84	404
A_{mx}	0.72	0.68-0.76	59
A_{ux}	0.61	0.57-0.64	3

Table 1.11. Total annual bull trout (BLT) bycatch and subsequent juvenile and adult (≥ 400 mm TL) BLT removed during suppression years 2009-2013 in Quartz Lake, Glacier National Park, Montana. The lake trout (LKT) to BLT ratio removed represents the number of LKT removed per BLT removed.

Year	BLT Caught	Juvenile BLT Removed	Adult BLT Removed	Total BLT Removed	LKT: BLT Removed
2009	146	14	13	27	19:1
2010	122	14	29	43	16:1
2011	56	3	8	11	35:1
2012	60	4	8	12	58:1
2013	90	21	6	27	90:1

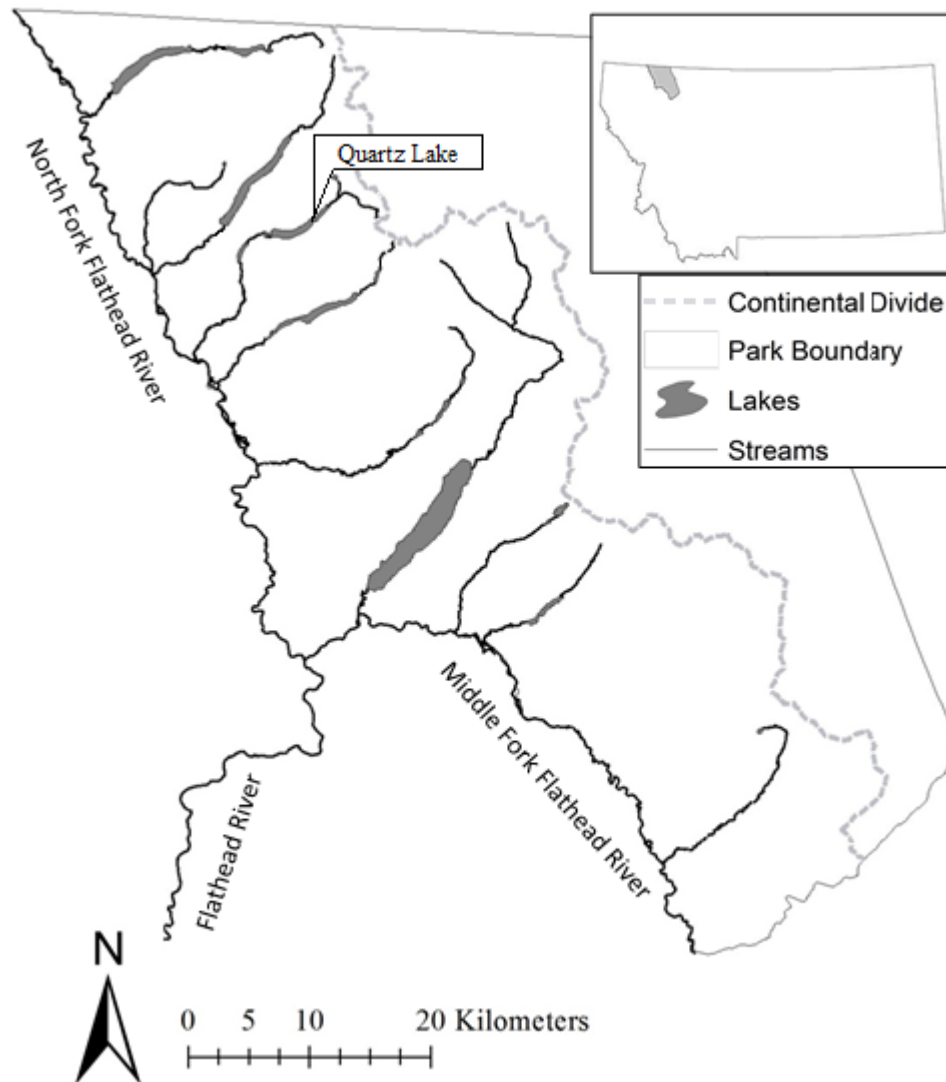
Figures

Figure 1.0. Location of Glacier National Park and Quartz Lake in northwestern Montana.

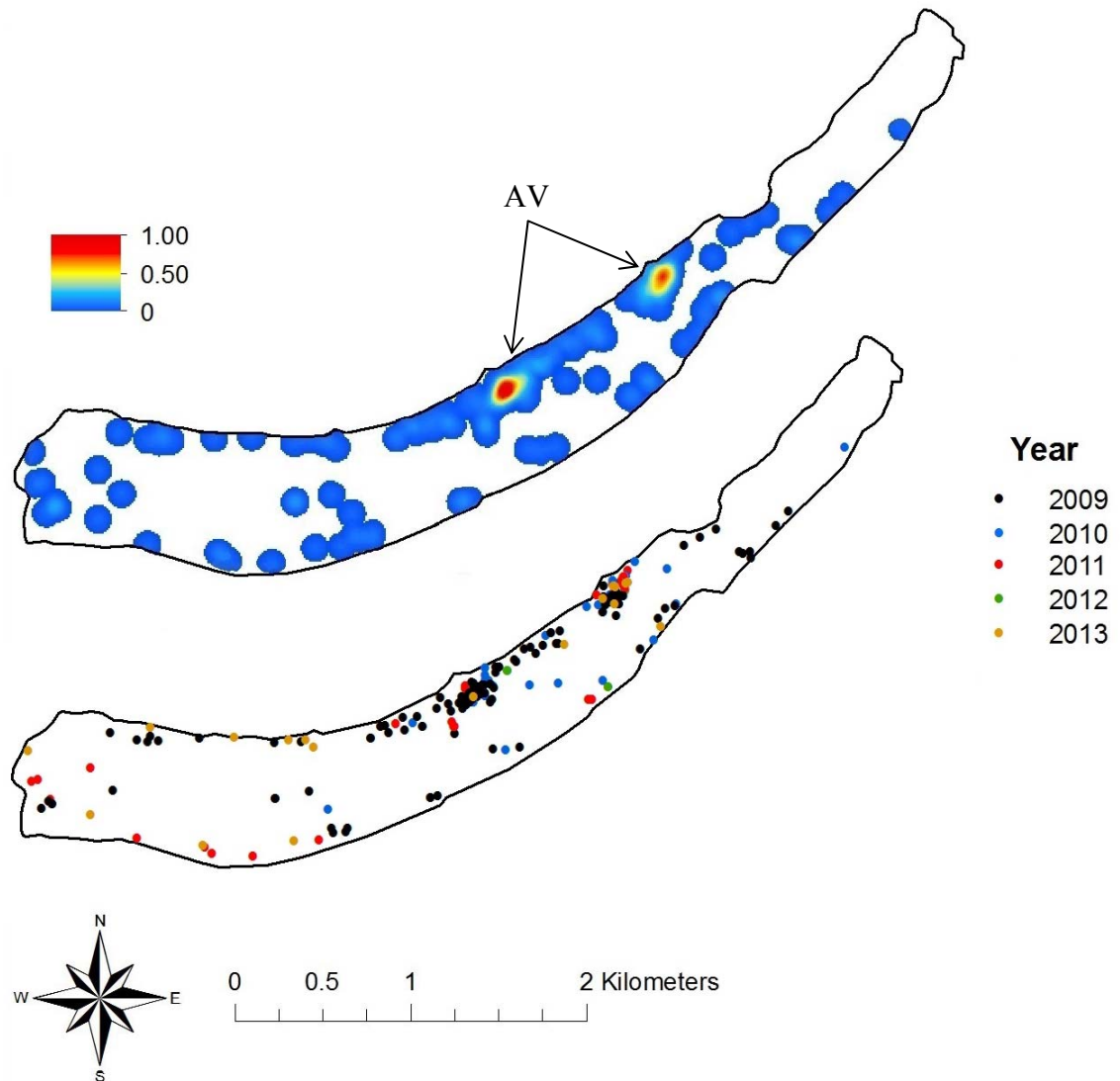


Figure 1.1. Relative relocation density (top image) used to identify potential spawning locations, and individual relocations by year (bottom image) for acoustic-tagged adult lake trout from 28 September through 29 October for years 2009 through 2013 in Quartz Lake, Glacier National Park, Montana. Spawning areas were identified at the base of the two largest avalanche chutes (AV).

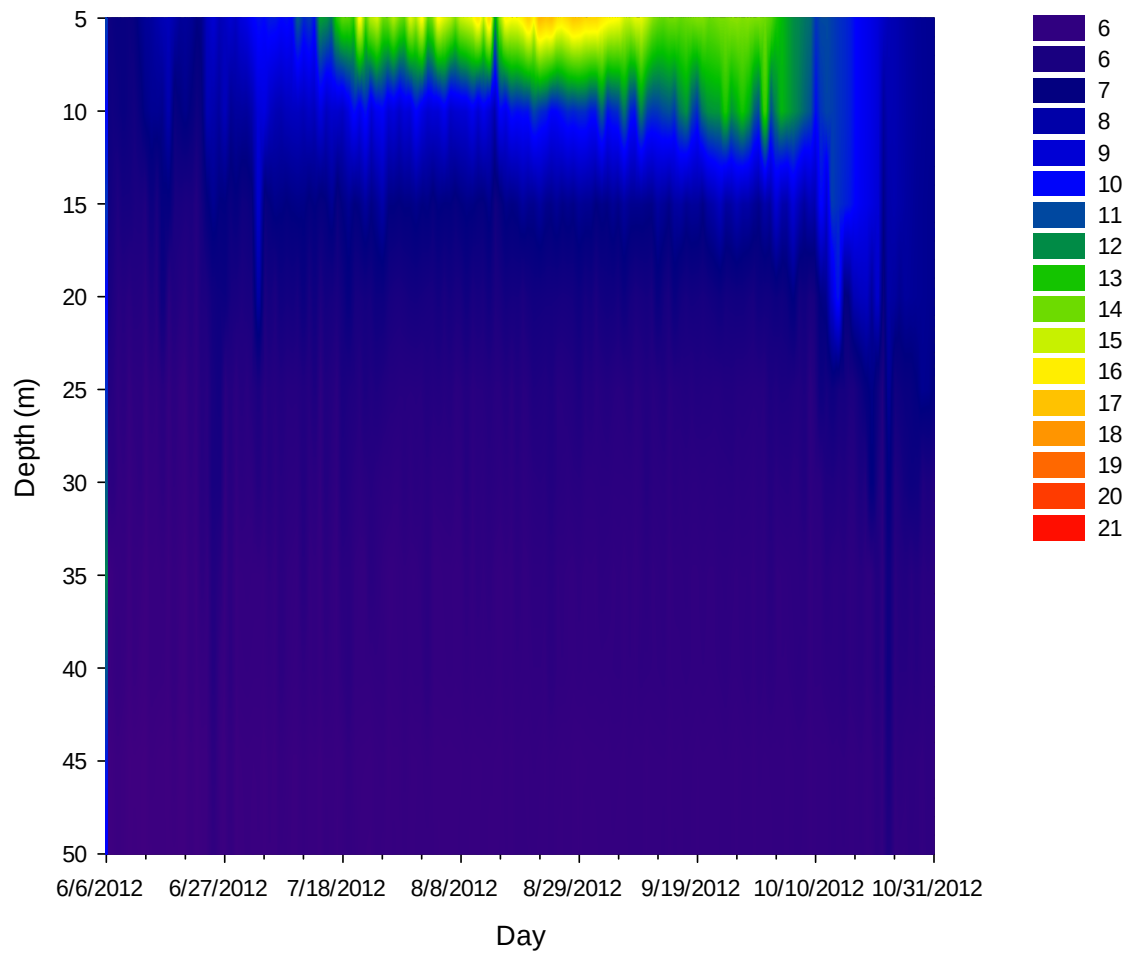


Figure 1.2. Water temperature profile of Quartz Lake, Glacier National Park, Montana, 6 June through 31 October, 2012.

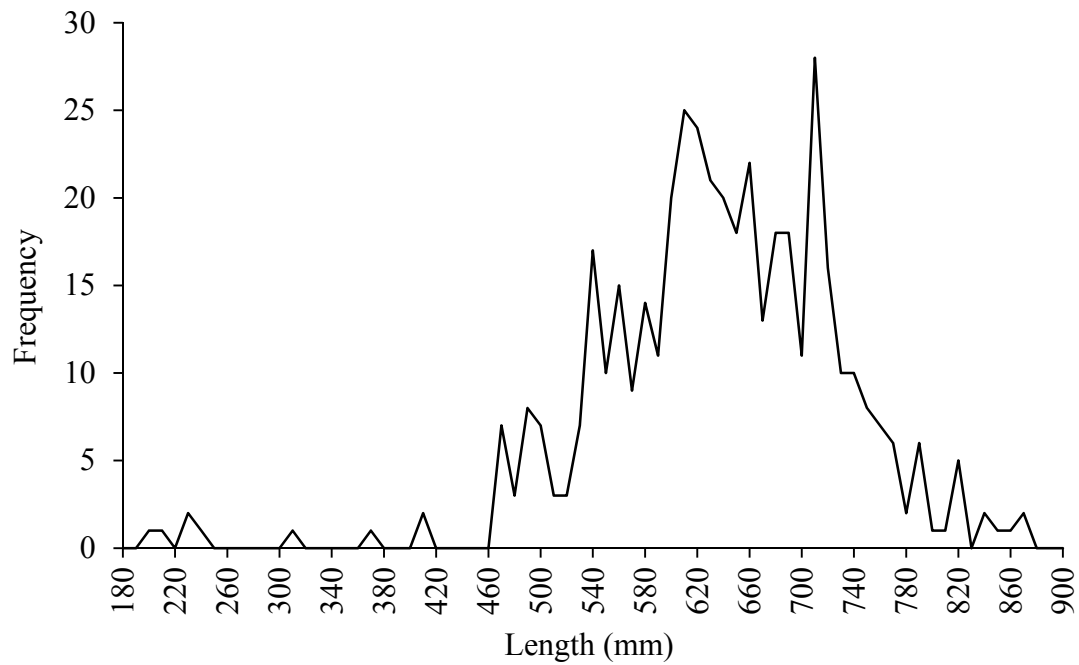


Figure 1.3. Length-frequency distribution of lake trout captured with gill nets during spawner netting in Quartz Lake, Glacier National Park, Montana (2010-2013).

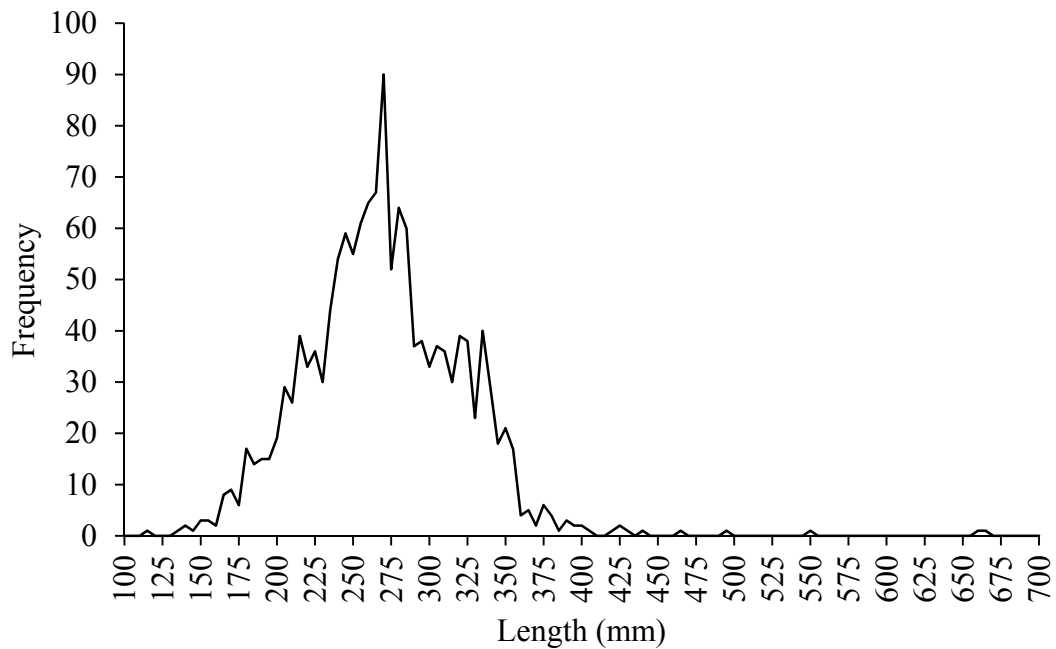


Figure 1.4. Length-frequency distribution of lake trout captured with gill nets during juvenile netting in Quartz Lake, Glacier National Park, Montana (2009-2013).

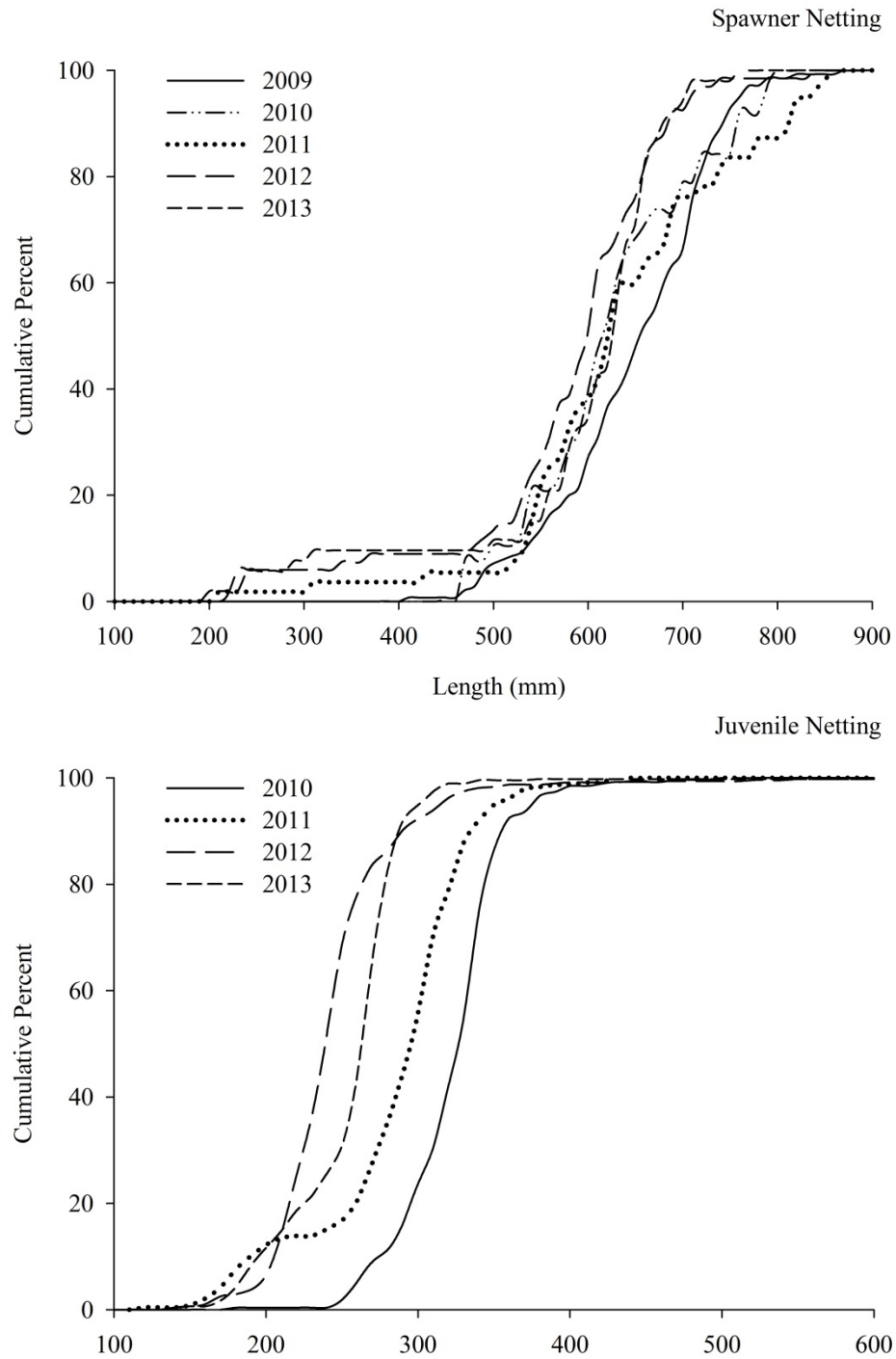


Figure 1.5. Annual cumulative length-frequency distributions for lake trout caught during spawner (top panel) and juvenile (bottom panel) gillnetting in Quartz Lake, Glacier National Park, Montana.

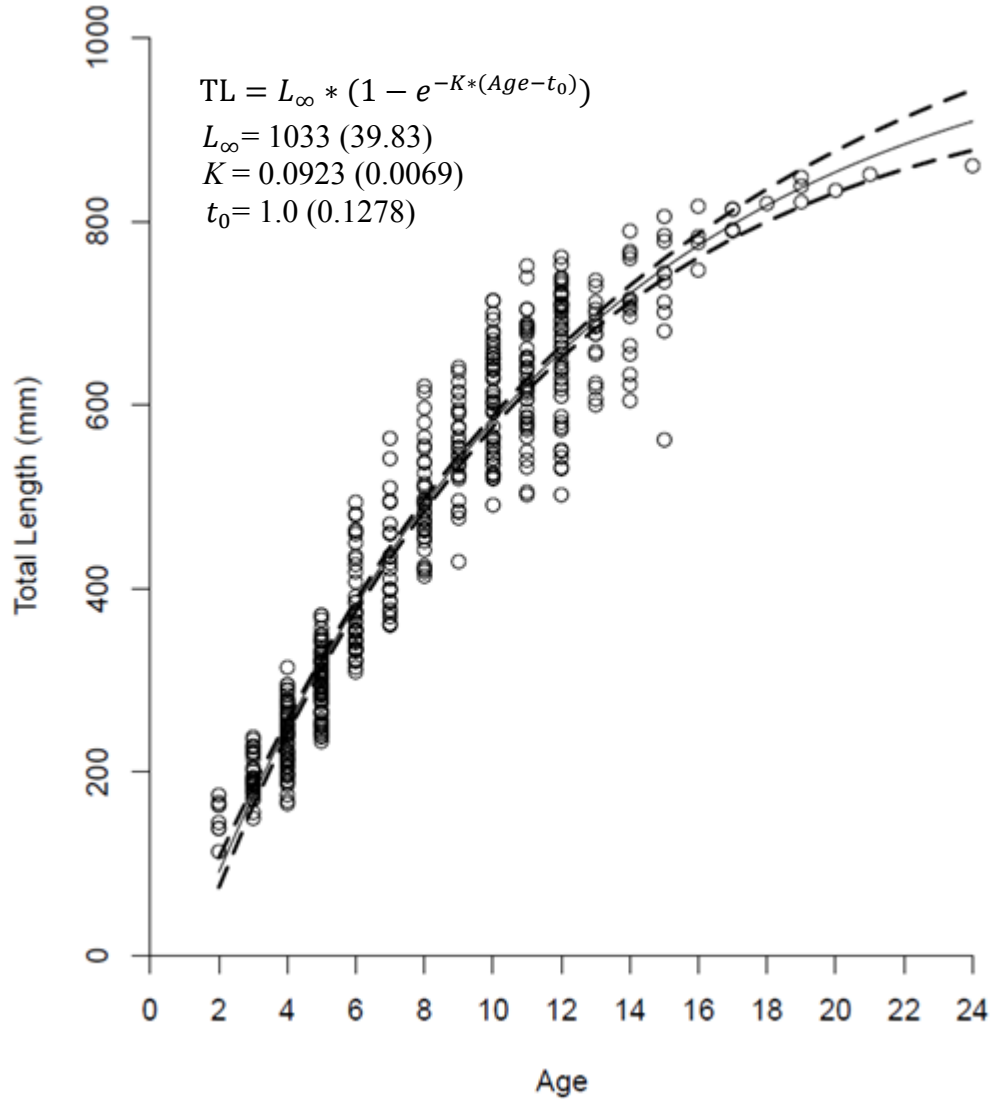


Figure 1.6. von Bertalanffy growth model and length-at-age for lake trout sampled 2009-2013 in Quartz Lake, Glacier National Park, Montana. Dashed lines represent 95% confidence and standard error for parameter estimates are in parentheses.

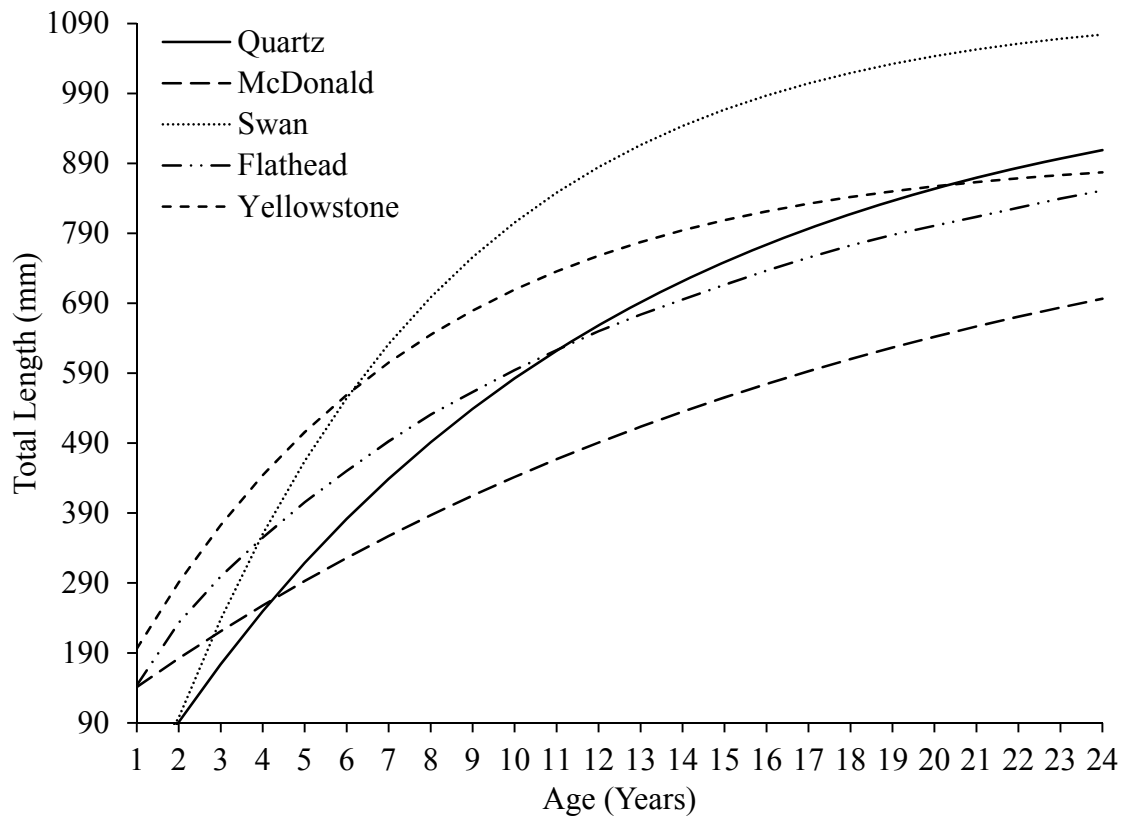


Figure 1.7. Mean length-at-age produced from the von Bertalanffy growth curve for lake trout in Quartz Lake and Lake McDonald, Glacier National Park (Dux 2005); Swan (Cox 2010) and Flathead lakes (Beauchamp 1996) in Montana; and Yellowstone Lake (Ruzycki and Beauchamp 1997), Yellowstone National Park, Wyoming.

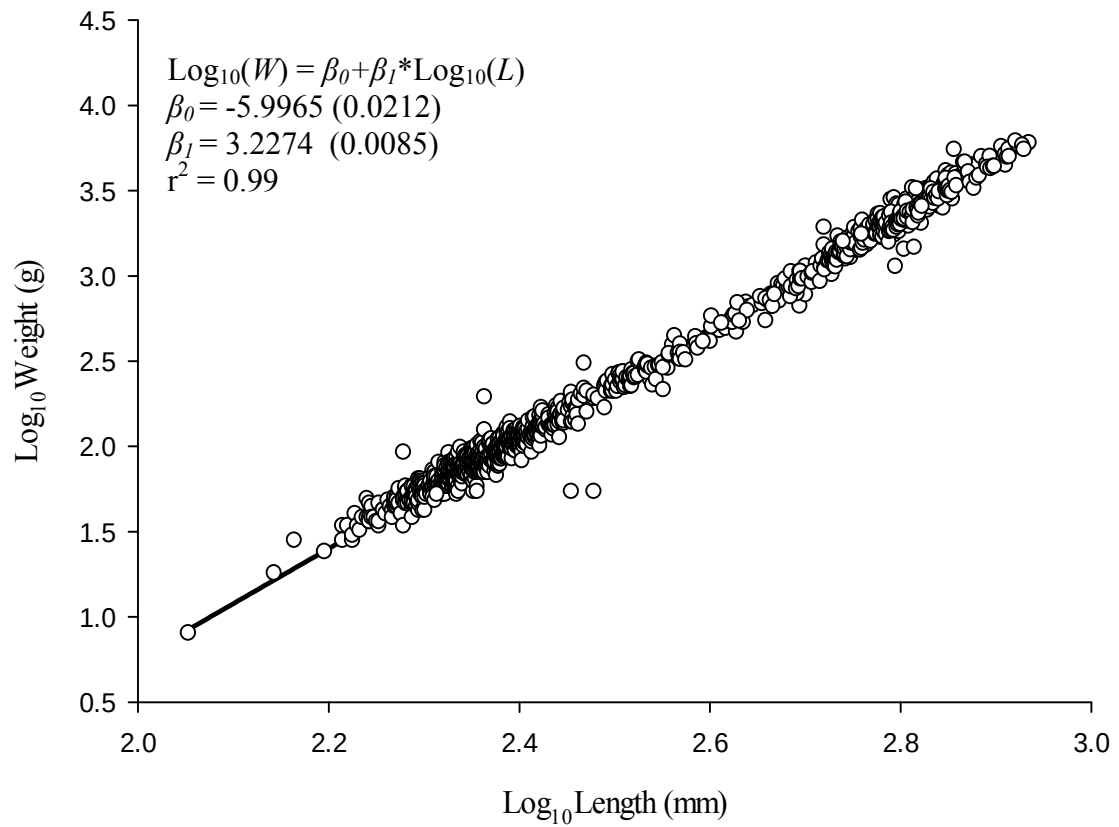


Figure 1.8. Length-weight regression model to predict weight at length for lake trout in Quartz Lake, Glacier National Park, Montana. Standard error for model parameters are in parentheses.

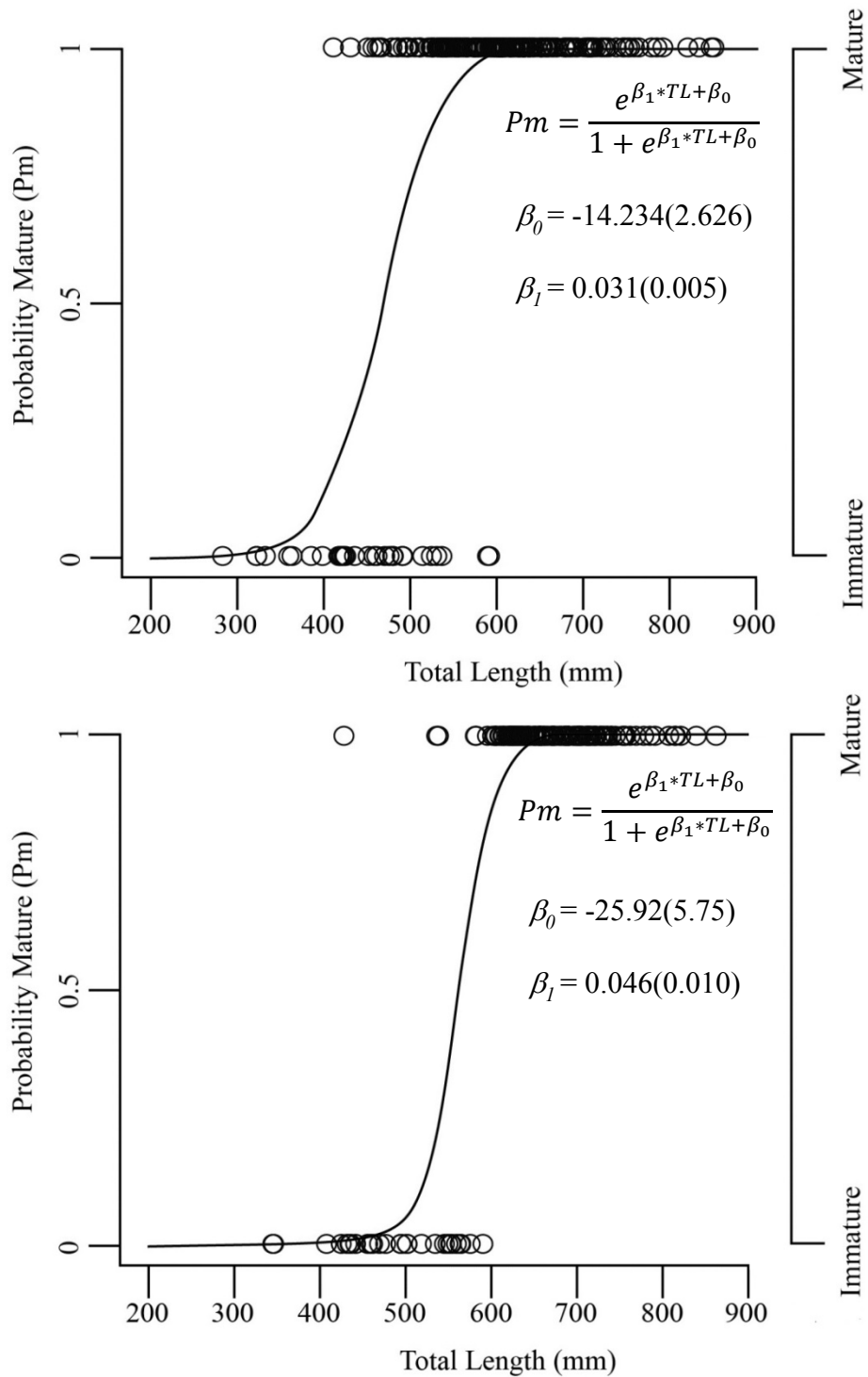


Figure 1.9. Logistic regression models used to predict length at 50% maturity for male (top panel) and female (bottom panel) lake trout in Quartz Lake, Glacier National Park, Montana. Standard error for model parameters are in parentheses.

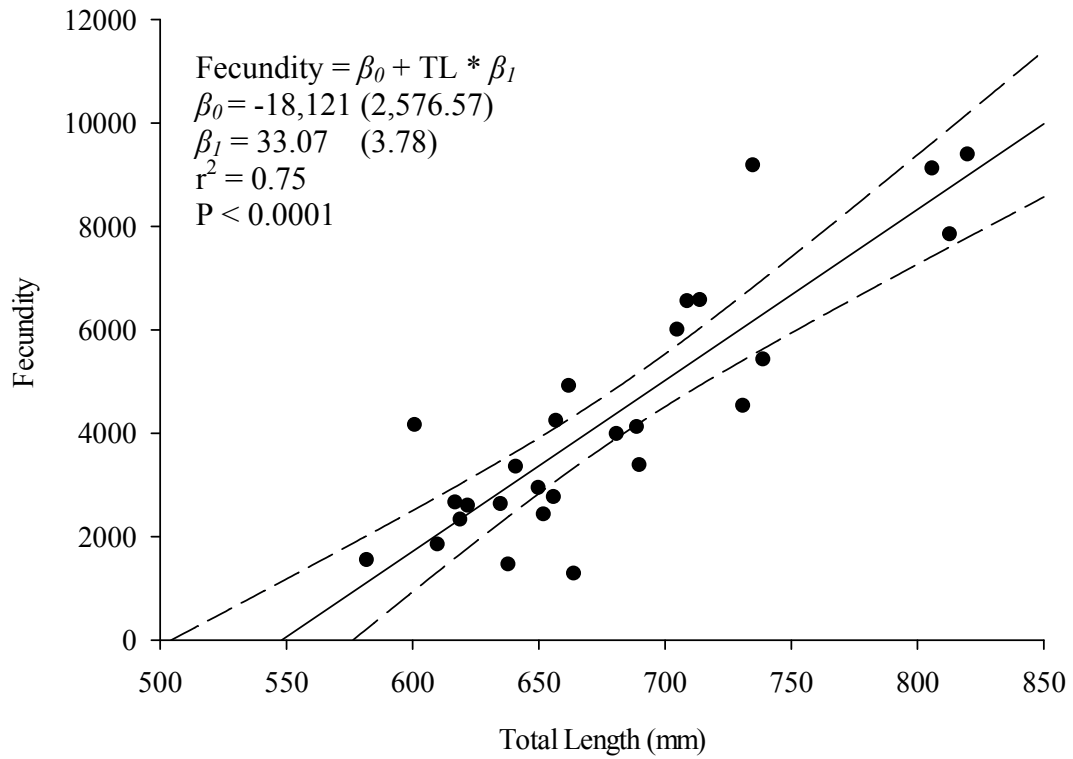


Figure 1.10. Fecundity-length relationship and parameter estimates (SE) for lake trout ($N = 27$) in Quartz Lake, Glacier National Park, Montana. The solid line represents the linear regression model and the dashed lines represent the 95% CI.

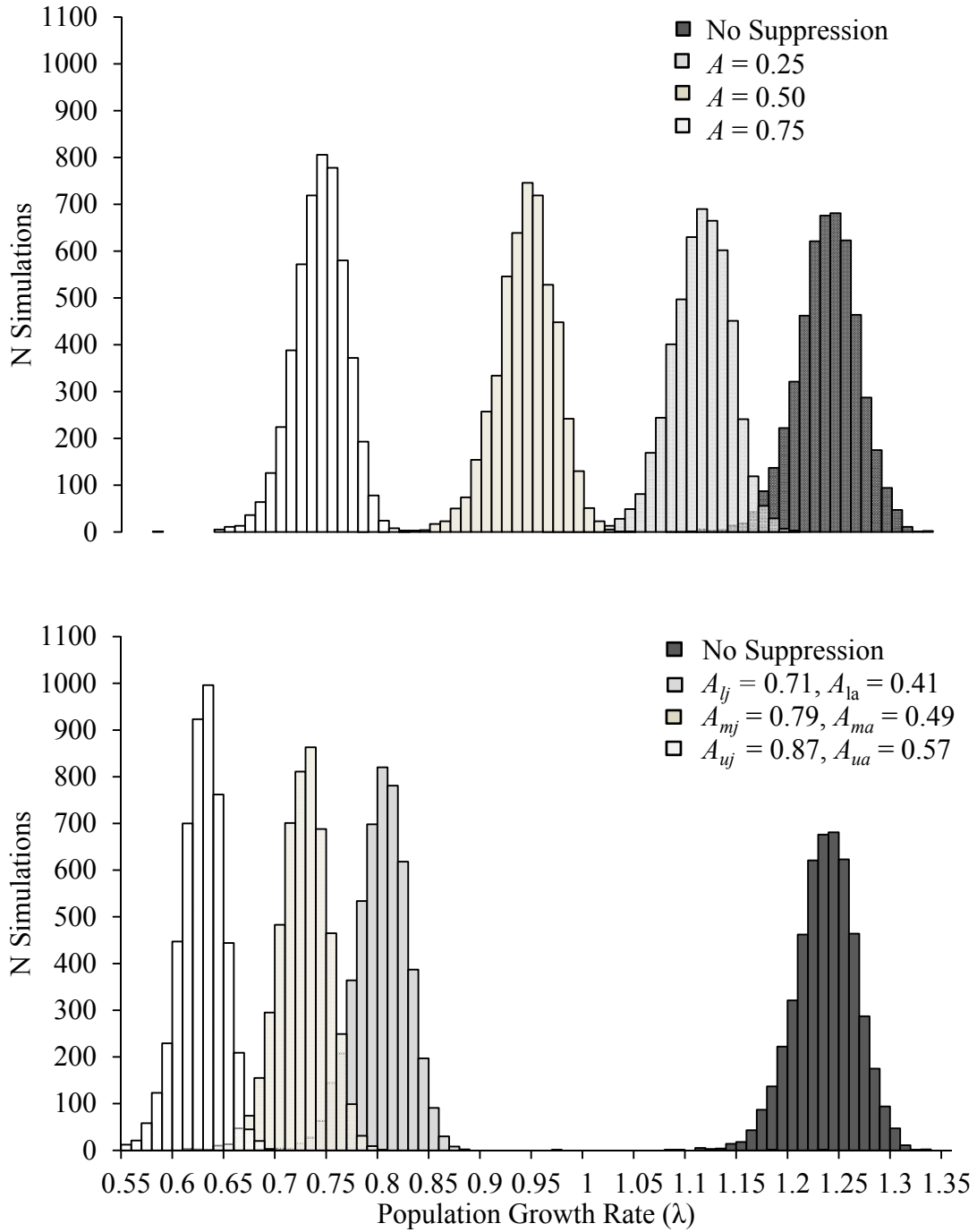


Figure 1.11. Mean population growth rate (λ) distributions from simulations of lake trout harvest in Quartz Lake, Glacier National Park, Montana. Total conditional interval mortality rates (A) for lake trout age 5 to age 7 and $\geq$ age 10 are 0.25, 0.50 and 0.75 (top panel), and mean population growth rate distributions for simulations incorporating mean lower (A_{lx}), mid (A_{mx}) and upper (A_{ux}) total conditional interval mortality rate estimates for juveniles (A_{xj}) and adults (A_{xa}) (bottom panel).

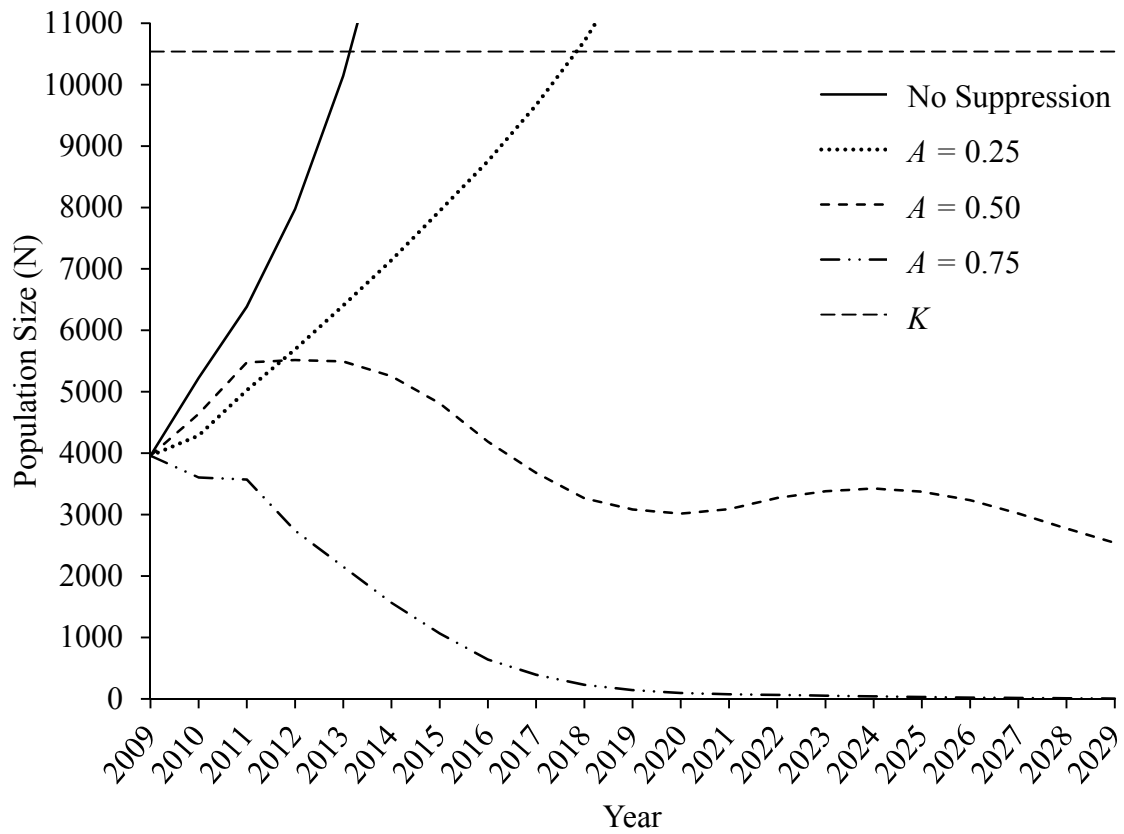


Figure 1.12. Population abundance projections compared to carrying capacity (K) (10,538) following 20 years ($\hat{N}_{20}$) of no suppression and suppression where total conditional interval mortality (A) rates are set at 0.25, 0.50 and 0.75 for age-5 to age-7 and $\geq$ age-10 lake trout in Quartz Lake, Glacier National Park, Montana.

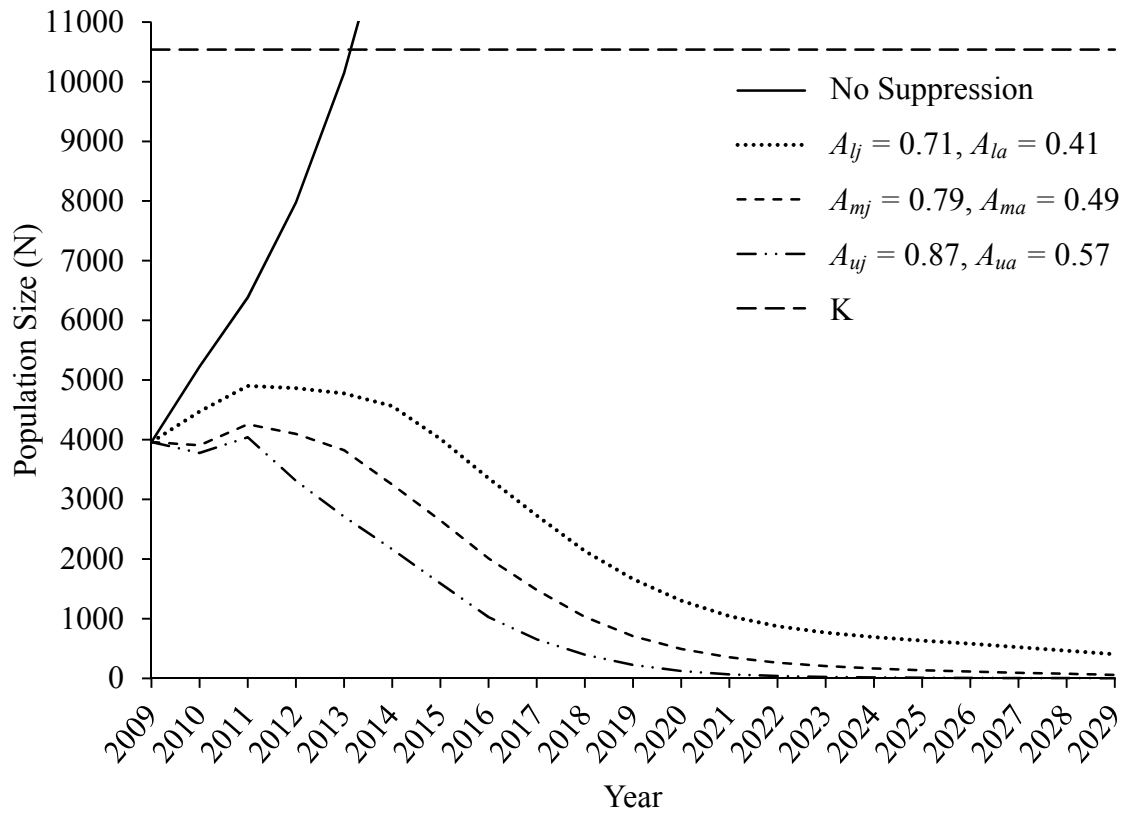


Figure 1.13. Lake trout population abundance projections compared to carrying capacity (K) following 20 years ($\hat{N}_{20}$) of no suppression, and suppression simulations incorporating mean lower (A_{lx}), mid (A_{mx}) and upper (A_{ux}) total conditional interval mortality rate estimates for juveniles age 5 to age 7 (A_{xj}) and adults $\geq$ age 10 (A_{xa}) in Quartz Lake, Glacier National Park, Montana.

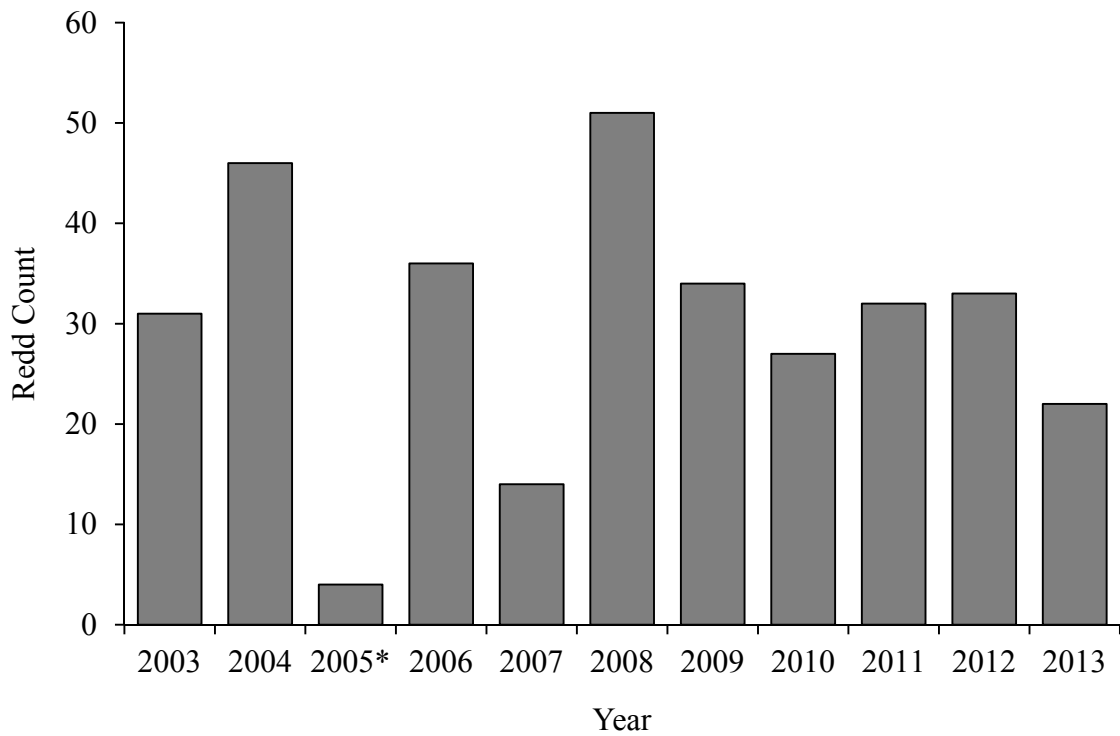


Figure 1.14. Bull trout redd counts from 2003 through 2013 in Quartz Creek upstream of Quartz Lake, Glacier National Park, Montana. *Redds were obscured by high flows in 2005 (Meeuwig and Guy 2007).

CHAPTER 2

GILL NET TWINE THICKNESS AND COLOR INFLUENCE CATCHABILITY OF
JUVENILE LAKE TROUT IN A GLACIAL LAKEIntroduction

Introduced species are one of the leading threats to aquatic biodiversity (Vitousek et al. 1997; Clavero and Garcia-Berthou 2005), and are a leading cause of freshwater fish extinctions throughout western North America (Miller and Williams 1989; Wilcove 1998). Over the past century, the introduction of fish species for aquaculture and recreation have resulted in declines of many species and populations of native fishes in the United States through competition, predation, and introgressive hybridization (Rahel 2000). As such, non-native species suppression programs have been widely implemented to reduce or eliminate invasive species that pose a threat to native and recreational fisheries. Understanding the effectiveness of suppression techniques is needed to inform and enhance management strategies for controlling invasive fish species in aquatic ecosystems.

In the western United States, the proliferation of non-native lake trout *Salvelinus namaycush* has become one of the predominant threats to native fish species (Martinez et al. 2009). Lake trout are top-level predators that are expanding their range within the western United States through unauthorized translocations and natural dispersal (Kalinowski et al. 2010; Muhlfeld et al. 2012). Although lake trout are an important species within their native range (Crossman 1995), they often predate on and compete

with native fishes in lakes where they have been introduced (Donald and Alger 1993; Fredenberg 2002; Koel et al. 2005; Martinez et al. 2009). Consequently, natural resource agencies have implemented several lake trout gillnetting suppression programs to reduce the spread and abundance of non-native lake trout for the conservation of native and recreational fish populations in lentic ecosystems throughout the Intermountain West (Hansen et al. 2008; Martinez et al. 2009; Cox 2010; Syslo 2010; Syslo et al. 2013).

Gill nets are highly size specific in their capture (Hansen et al. 1997), yet research focusing on the removal of small lake trout (< 250 mm; typically age-2-4 fish) (hereafter referred to as juveniles) using gill nets is limited. This is surprising because the lake trout is a long-lived, late maturing species, and population growth rates are sensitive to changes in survival rates during the juvenile phase of their life history (Crouse et al. 1987; Heppell et al. 2000; Gerber and Heppell 2004; Cox 2010). The efficacy of removing juvenile lake trout has been limited because the twine diameter (0.20 mm) typically used in large mesh gill nets (≥ 26 mm bar) to capture larger individuals (≥ 250 mm) is likely too thick for gill-net mesh sizes that are fully selective for 200-250 mm lake trout (19.1 mm bar). When twine diameter is not scaled properly to the mesh sizes being used, gill nets become less efficient due to their visibility and lack of flexibility (Hamley 1975; Jensen 1995; Hovgard 1996; Gray et al. 2005). Gill-net color has also been shown to influence the capture efficiency of some fish species or specific size classes of fish (Jester 1973). Visual feeding fish often exhibit avoidance behavior when confronted with a gill net within their visual spectrum (Stewart 1984, cited by Balik and Cubuk 2001). Lake trout are visual predators (Confer et al. 1978), and likely have keen

eyesight that enables them to avoid capture by gill nets. By properly identifying and matching gill-net color to the distinct properties of the aqueous environment, natural resource agencies may be able to increase gill-net efficiency for juvenile lake trout. However, no studies have assessed whether gill-net twine diameter and color influence the capture of juvenile lake trout. Extending the length and age range of harvestable juvenile lake trout using the most effective gill net types will enable natural resource agencies to remove a greater proportion of lake trout prior to reaching maturity, thus increasing the potential success of conserving fish species threatened by non-native lake trout.

Determining the most effective combination of net color and mesh twine diameter to harvest juvenile lake trout will provide useful information for natural resource agencies tasked with controlling non-native lake trout in Glacier National Park (GNP) and elsewhere. Here, I conducted an in situ experiment to assess whether gill net twine diameter and color influences the catch of juvenile lake trout in a glacial lake.

Study Location

Quartz Lake is a glacially formed lake located in the headwaters of the Columbia River Basin, GNP, Montana. Quartz Lake is the fifth largest lake west of the Continental Divide in GNP (Fredenberg et al. 2007), with a surface area of 352 ha and a maximum depth of 83 m. The lake is at an elevation of 1,346 m and is positioned in a narrow glaciated valley that is supplied by perennial flow from snow and glacial runoff from the Lewis Range. Quartz Lake is an oligotrophic, dimictic lake with stratification occurring

in late June and destratification in early October. The limnetic zone substrate is dominated by a mixture of cobble and boulder.

The native fish assemblage in the Quartz drainage consists of bull trout, westslope cutthroat trout *Oncorhynchus clarkii lewisi*, mountain whitefish *Prosopium williamsoni*, longnose sucker *Catostomus catostomus*, largescale sucker *Catostomus macrocheilus*, slimy sculpin *Cottus cognatus*, and redbelt shiner *Richardsonius balteatus*. The lake trout is the only non-native fish species in the drainage.

There are no natural putative fish barriers in the Quartz drainage, although several high gradient cascades serve as potential intermittent barriers between Lower Quartz and Middle Quartz lakes. The discovery of lake trout in Lower Quartz Lake prompted the initiation of a project in 2004 to construct an artificial barrier approximately 100 m downstream of Middle Quartz Lake to conserve the upstream native fish assemblages in Quartz and Cerulean lakes. Unfortunately, lake trout were detected in Lower Quartz Lake in 2003 and in Quartz Lake in 2005 before the barrier was completed (Fredenberg et al. 2007). The NPS completed the barrier in 2012 to deter further invasions.

Methods

I conducted an in situ experiment to assess whether twine diameter (0.10 and 0.20 mm) and color (blue, green, and white) of sinking gill nets influenced the capture efficiency of juvenile lake trout in Quartz Lake from 1 – 11 October 2012. I used a random sampling design to distribute gill nets in depths greater than 30 m to avoid incidental capture of bull trout and westslope cutthroat trout. Random sampling locations

($N = 74$) were assigned using a 200 m² grid developed from satellite imagery of Quartz Lake in ArcGIS 10.1 (ESRI 2012). I randomly sampled 14 individual locations by setting two gangs of nets within each 200 m² location to avoid potential bias associated with differing habitats, concentrations of fish, turbidity, and water clarity (Jester 1973). Each gang consisted of three monofilament gill net panels (blue, green, and white) that were 30.5 m long by 2 m deep with mesh sizes of 19.1 mm bar attached in sequence with approximately 2 m of line attached between each panel to ensure the capture of each net was independent (Balik and Cubuk 2001). One gang consisted of the 0.10 mm twine diameter gill nets of each color, while the second gang consisted of 0.20 mm twine diameter gill nets of each color. Gangs of nets were set approximately 100 m apart to ensure independence. Total length (TL; mm) and weight (g) was recorded for each captured fish by net category (twine diameter and net color).

I used a split-plot design to account for the hierarchical nesting of the sampling. A split-plot experiment is a blocked experiment where the blocks are referred to as “whole plots” and the experimental units within blocks are referred to as “split plots” (Jones and Nachtsheim 2009). Therefore, I treated the two gangs at each randomly sampled location as the whole-plot experimental unit, with the factor being the twine diameter, and the individual nets within each gang as the split-plot with the factor being net color.

I used Poisson log-linear regression to test the null hypothesis that twine diameter and net color did not influence the number of captured lake trout. The response variable was the mean number of fish caught per hour. I tested for differences in the mean

number of fish caught by twine diameter and netting location, and for differences in mean number of fish caught by net color after accounting for location and twine diameter. Assumptions of independence were met by using a paired design at the whole-plot and split-plot levels. A goodness of fit test (GOF) was conducted for the whole-plot and split-plot levels to determine whether the Poisson log-linear model was adequate for these data. The p-values from the GOF test for the whole-plot level (deviance statistic = 31.56, d.f. = 13, $P < 0.0001$) and the split-plot level (deviance statistic = 144.4, d.f. = 56, $P < 0.0001$) suggested that the Poisson log-linear model might be inadequate for these data. As a result, deviance residuals were examined and many large residuals were found. Models believed to be adequately rich in explanatory variables were fit for both levels; therefore, the analysis proceeded in both cases using the quasi-likelihood estimation to account for extra-Poisson variation (Quinn and Keough 2002). Normality and equal variance were assessed using residual and normal probability plots. All statistical analyses were conducted with R 3.1.0 (R Core Team 2013) and the statistical significance was defined as $\alpha = 0.05$ for all analyses.

Results

A total of 416 juvenile lake trout were captured during the study. Lake trout varied in length from 168 to 364 mm and the mean length was 227 mm (SD = 20 mm). Lake trout weight varied from 168 to 364 g and the mean weight was 82.6 g (SD = 26.7 g). Gill nets with twine diameters of 0.10 mm accounted for 69% of the total lake trout captured, while gill nets with twine diameters of 0.20 mm accounted for 31% of the total

lake trout captured during the study (Figure 2.0). Green gill nets accounted for about 41%; blue 33%; and white 26% of the total juvenile lake trout catch (Figure 2.0).

Twine diameter strongly influenced the mean number of fish caught per gang ($T = 4.854$, d.f. = 13, $P = 0.0003$); the small twine diameter (0.10 mm) caught significantly more juvenile lake trout per hour than 0.20 mm twine diameter after accounting for location. The mean number of fish caught per hour in 0.10 mm twine diameter gangs was 2.36 times greater than the mean number of fish caught in 0.20 mm twine diameter gangs after accounting for location (Approximate Wald's 95% CI = 1.61 to 3.46 times).

Gill-net color also influenced juvenile lake trout catch after accounting for location and twine diameter. Green nets caught significantly more fish than white nets ($T = 2.412$, d.f. = 56, $P = 0.019$). Green nets also caught more fish than blue nets ($T = 1.826$, d.f. = 56, $P = 0.068$) and blue nets caught more fish than white nets ($T = 1.715$, d.f. = 56, $P = 0.086$; Figure 2.1), but these differences were not significantly different ($\alpha = 0.05$). After accounting for location and diameter, the mean number of fish caught in green nets was about 1.5 times (Approximate Wald's 95% CI = 1.08-2.19) greater than the mean number caught in white nets, 1.2 times (Approximate Wald's 95% CI = 0.97-1.55) greater than the mean number of fish caught in blue nets. Furthermore, the mean number of fish caught in blue nets was 1.2 times greater than the mean number of fish caught in white nets (Approximate Wald's 95% CI = 0.96-1.61).

Discussion

I found that 0.10 mm twine diameter gill nets caught on average more than two times as many juvenile lake trout as compared to 0.20 mm twine diameter gill nets. My results are consistent with other studies that have found a strong effect of twine diameter on catch efficiency for other freshwater fish species (Hansen 1974; Hamley 1975; Jensen 1995; Turunen 1996; Yokota et al. 2001). For example, Jensen (1995) reported that a decrease in twine diameter from 0.17 mm to 0.10 mm increased the capture rate of Arctic char *Salvelinus alpinus* by 2.2 times. Similarly, 0.15 mm diameter gill nets caught nearly twice as many pikeperch *Stizostedion lucioperca* than 0.20 mm diameter gill nets (Turunen 1996). Although 0.20 mm twine diameter gill nets are commonly used in suppression efforts to remove juvenile lake trout throughout the Intermountain West (Todd Stuth, Hickey Brothers Fisheries LLC, personal communication), my results suggest that using a smaller twine diameter (0.10 mm) may increase gill-net efficiency in other lakes where suppression is occurring. However, the 0.10 mm twine diameter nets were less durable and nets generally needed to be replaced after a week or two of fishing. Therefore, I recommend when determining the appropriate twine diameter for gill netting, a catch rate to cost benefit analysis is needed to determine whether catch rates are high enough to offset the increasing cost of net repair.

Gill-net color influenced the capture efficiency of juvenile lake trout. Green gill nets caught significantly more lake trout per hour than white nets. Although the difference in catch between green and blue, and blue and white nets were not statistically significant, the borderline p-values indicate green nets caught more fish than blue and

blue caught more than white. These results contradict those reported by Wanner et al. (2010) who suggested the capture efficiency of visual predators (walleye *Sander vitreus*, sauger *Sander canadensis*, smallmouth bass *Micropterus dolomieu*, goldeye *Hiodon alosoides*, and freshwater drum *Aplodinotus grunniens*) was higher for white gill nets as compared to green gill nets. However, Wanner et al.'s (2010) study was conducted in a turbid environment in the Missouri River, suggesting that gill-net color capture efficiency is location and species-specific. Turbidity in Quartz Lake is generally low and varies seasonally. Perennial flow supplied by snow and glacial runoff from the Lewis Range contribute fine glacial silt to Quartz Lake, which is likely responsible for Quartz Lake's green coloration. The increase in capture efficiency of green gill nets, therefore, is likely a function of the nets more closely matching the water color. These results are consistent with Jester (1973) who reported that orange and yellow net colors increased the capture efficiency of small sunfish and larger largemouth bass *Micropterus salmoides*, and brown nets were most effective at capturing river carpsucker *Carpiodes carpio*, but less effective at capturing gizzard shad *Dorosoma cepedianum*, channel catfish *Ictalurus punctatus*, and white bass *Morone chrysops*. Matching gill-net color to specific water properties, such as turbidity, or the visual spectrum of the target species may be an effective way of limiting the nets visibility (Matsuda et al. 2009) and potentially increasing juvenile lake trout capture rates.

Suppression of non-native lake trout to conserve native or recreational fish species is a common goal among resource managers in the western United States (Martinez et al. 2009). Gill nets are currently the primary method for removing non-

native lake trout (Koel et al. 2005; Cox 2010; Hansen et al. 2010; Syslo 2010; Syslo et al. 2013; see Chapter 1), yet research identifying the optimal gill-net color and twine diameter for the capture of juvenile lake trout was lacking prior to my study. Of the gill net twine diameters and colors assessed in this study, green gill nets with 0.10 mm twine diameter maximized the catch of juvenile lake trout in Quartz Lake. However, future applications of this work should be assessed on a case-by-case basis, as fish visual spectrums differ among species and physical characteristics of the water. For visual predators such as the lake trout (Confer et al. 1978), net visibility likely depends on how well the net color matches the background color of the water (Tsuda and Inoue 1973, cited by Hamley 1975). Identification of the appropriate mesh size to twine diameter ratio should be determined prior to the implementation of suppression programs.

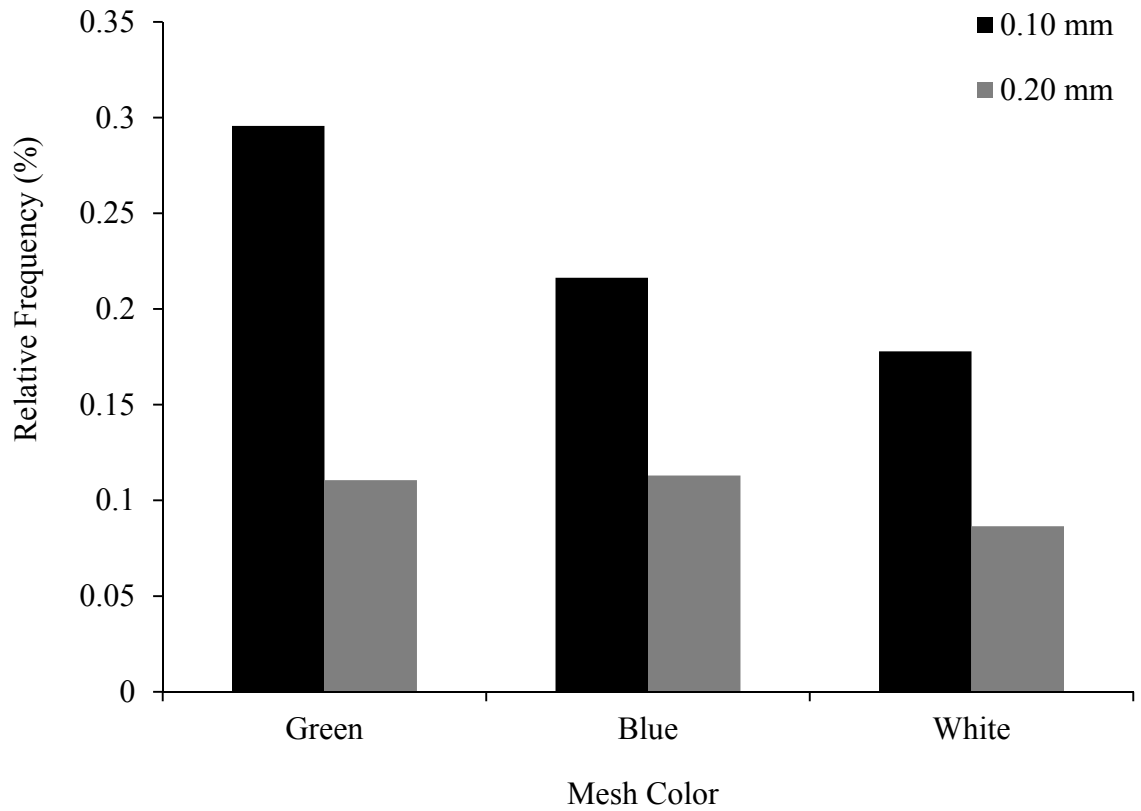
Figures

Figure 2.0. Relative-frequency of lake trout caught by twine diameter and net color from 1-11 October 2012 in Quartz Lake, Glacier National Park, Montana.

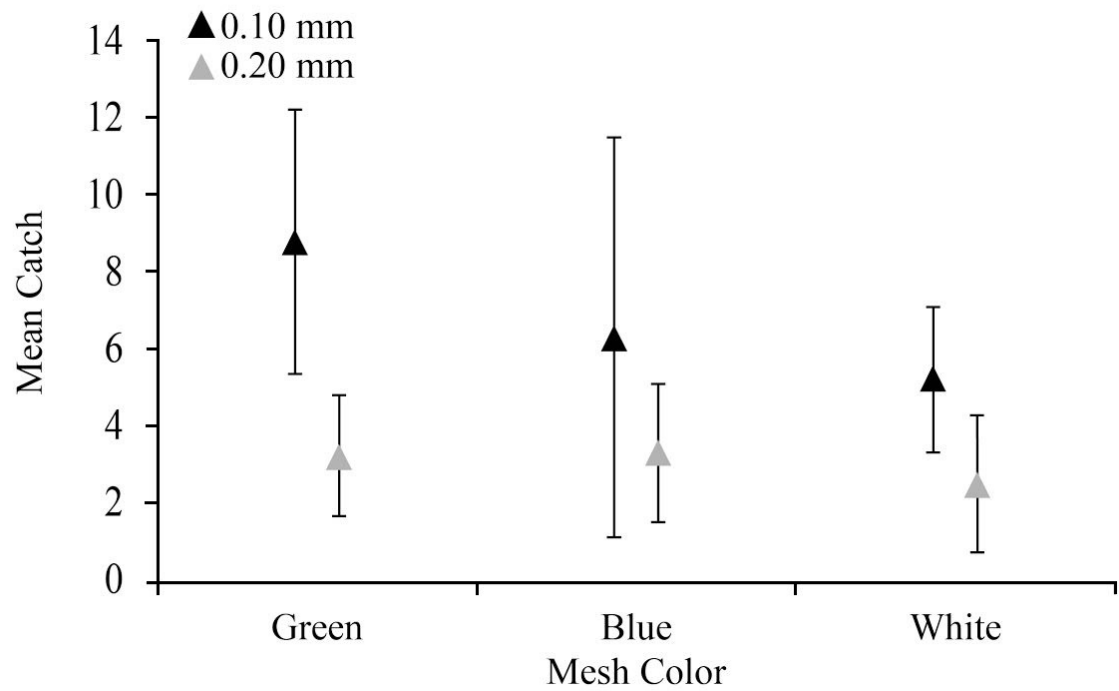


Figure 2.1. Mean number of lake trout caught in gill nets by net color and twine diameter from 1-11 October 2012 in Quartz Lake, Glacier National Park, Montana. The bars delineate 95% confidence intervals.

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APPENDICES

APPENDIX A

POPULATION METRICS BY AGE

Table A.1. Age-specific natural survival (S_i), probability of maturity (p_i), and fecundity (f_i) vital rates used in population simulations for lake trout in Quartz Lake, Glacier National Park, Montana. Standard error for vital rate estimates are in parentheses.

Age	S_i	p_i	f_i
0	0.0043(0.00084) ^a	0	0
1	0.45(0.09) ^a	0	0
2	0.78(0.16) ^b	0	0
3	0.94(0.0036)	0	0
4	0.94(0.0036)	0	0
5	0.94(0.0036)	0	0
6	0.94(0.0036)	0	0
7	0.94(0.0036)	0	0
8	0.94(0.0036)	0.15(0.09)	1,498(42)
9	0.94(0.0036)	0.59(0.08)	1,498(42)
10	0.94(0.0036)	0.81(0.05)	2,731(812)
11	0.94(0.0036)	0.92(0.04)	3,189(399)
12	0.94(0.0036)	1	4,230(1,808)
13	0.94(0.0036)	1	4,509(396)
14	0.94(0.0036)	1	6,285(288)
15	0.94(0.0036)	1	7,422(2,436)
16+	0.94(0.0036)	1	8614(773)

^a Vital rate estimate from Shuter et al. (1998), with SE equal to SD of the observations.

^b Vital rate estimation from Sitar et al. (1999), with SE equal to 20% of the value.

APPENDIX B

CATCH PER UNIT EFFORT BY NETTING TYPE

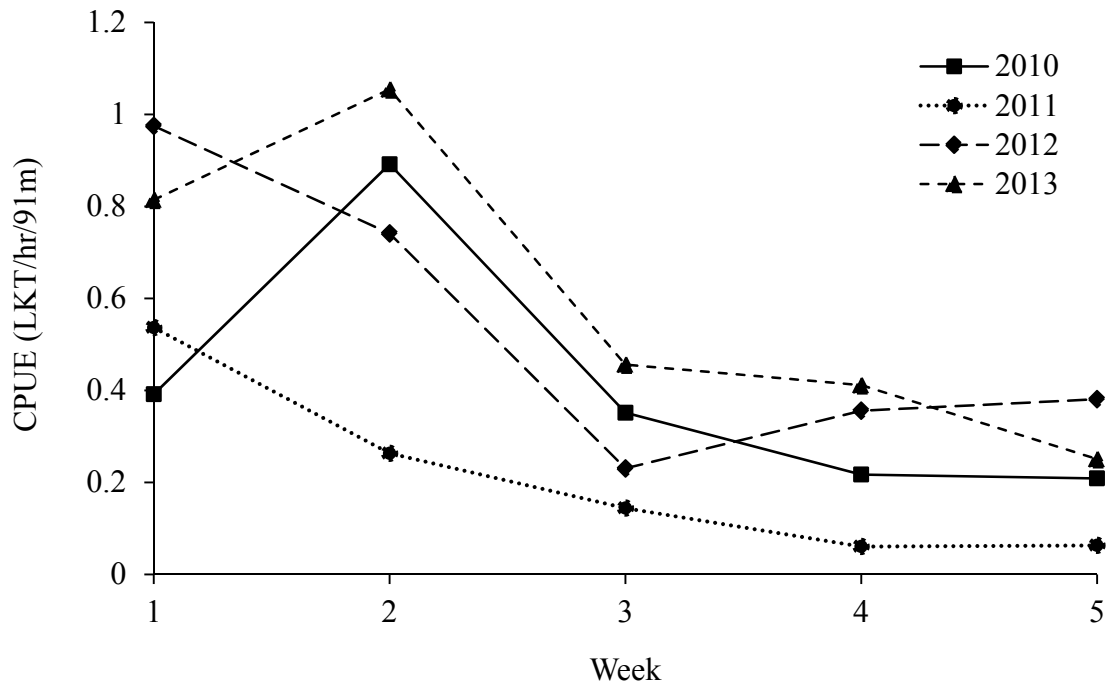


Figure B.1. Juvenile lake trout (LKT) catch per unit effort (CPUE) from the last week in May through the last week in June 2010-2013 in Quartz Lake, Montana.

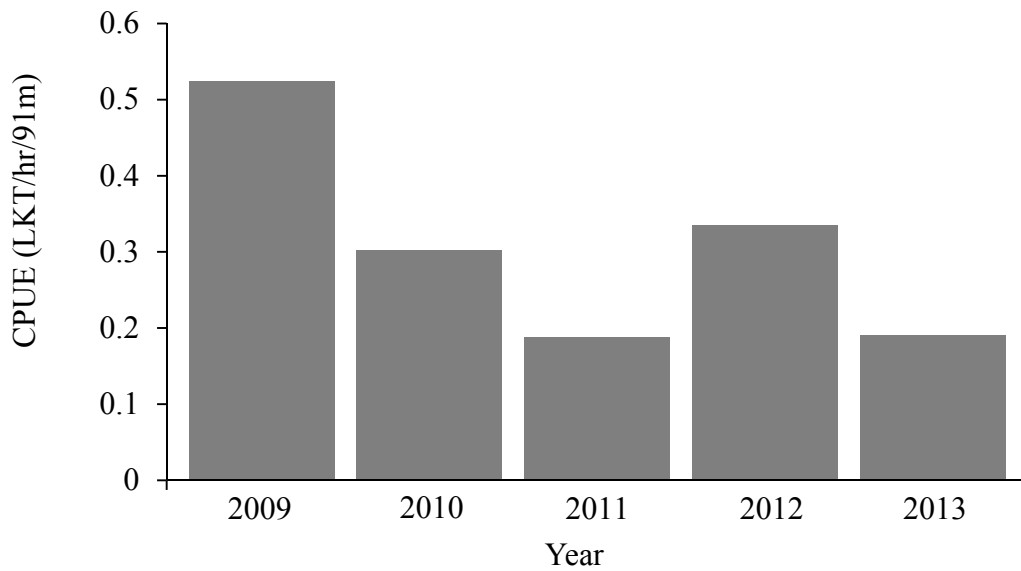


Figure B. 2. Adult lake trout (LKT) catch per unit effort (CPUE) during October 2009-2013 in Quartz Lake, Montana.