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Suppression of invasive lake trout in an isolated backcountry lake in Glacier National Park

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Abstract Fisheries managers have implemented suppression programmes to control non-native lake trout, *Salvelinus namaycush* (Walbaum), in several lakes throughout the western United States. This study determined the feasibility of experimentally suppressing lake trout using gillnets in an isolated backcountry lake in Glacier National Park, Montana, USA, for the conservation of threatened bull trout, *Salvelinus confluentus* (Suckley). The demographics of the lake trout population during suppression (2009–2013) were described, and those data were used to assess the effects of suppression scenarios on population growth rate (λ) using an age-structured population model. Model simulations indicated that the population was growing exponentially ($\lambda = 1.23$, 95% CI: 1.16–1.28) prior to suppression. However, suppression resulted in declining λ (0.61–0.79) for lake trout, which was concomitant with stable bull trout adult abundances. Continued suppression at or above observed exploitation levels is needed to ensure continued population declines.

KEYWORDS: demographics, introduced species, invasive species, matrix model, *Salvelinus confluentus*, *Salvelinus namaycush*.

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Introduction

Introductions of non-native fishes threaten many native fishes (Vitousek *et al.* 1997) and are a major cause of freshwater fish extinctions throughout North America (Miller *et al.* 1989; Wilcove *et al.* 1998; Rahel 2000; Clavero & Garcia-Berthou 2005). Lake trout, *Salvelinus namaycush* (Walbaum), are relatively large, long-lived piscivores native to deep, cold, oligotrophic lakes of Canada and the northern United States, including the Great Lakes (Crossman 1995; Behnke 2002). However, lake trout were widely introduced into lakes and reservoirs outside their native range in the western United States during the late 19th and early 20th centuries (Crossman 1995). Since their wide introduction, lake trout have expanded to more than 200 waters through dispersal and unauthorised translocations (Martinez *et al.* 2009). Although lake trout occupy an important ecological niche as a top-level predator in lakes where they are native, they have become problematic in many lakes where they are introduced because they prey on and compete with native fishes, including popular sport fishes (Martinez *et al.* 2009; Ferguson *et al.* 2012), and can negatively affect both aquatic and terrestrial communities (Spencer *et al.* 1991; Baril *et al.* 2013; Middleton *et al.* 2013).

Fisheries managers have implemented various strategies to control or reduce lake trout abundance in several lakes throughout the western United States (Hansen *et al.* 2008; Martinez *et al.* 2009; Syslo *et al.* 2011; Cox *et al.* 2013; Ng *et al.* 2016). Lake trout populations are vulnerable to overexploitation because their life history is characterised by slow growth, late maturity, low reproductive potential and a slow adult replacement rate (Healey 1978; Shuter *et al.* 1998). Lake trout population collapse from commercial harvest prior to the appearance of sea lamprey *Petromyzon marinus* L., in the Laurentian Great Lakes (Hansen 1999) provides evidence that lake trout can be suppressed using mechanical methods.

Populations of bull trout, *Salvelinus confluentus* (Suckley), a federally listed threatened species (USFWS 1998), have declined in most lentic situations where lake trout have been introduced or invaded in western North America (Donald & 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 and creating a strong potential for competitive interactions (Donald & Alger 1993; Guy *et al.* 2011).

Glacier National Park (GNP) supports approximately one-third of the remaining natural lake core areas for bull trout in the United States (Fredenberg *et al.* 2007). However, the majority of adfluvial bull trout populations in western GNP have declined 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* (Audzijonytë & Väinölä), 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 abundance increased, lake trout emigrated upstream from Flathead Lake and established self-sustaining populations in several connected lakes in GNP in <30 years (Fredenberg 2002; Muhlfeld *et al.* 2011).

Of the five largest lakes west of the Continental Divide in GNP, Quartz Lake supports the most robust bull trout population and was considered a high priority for bull trout conservation (Fredenberg *et al.* 2007). The discovery of lake trout in Lower Quartz Lake in 2003 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, and fisheries managers were concerned that without immediate intervention the Quartz Lake bull trout population would experience a decline similar to those observed in other GNP lakes (Fredenberg 2002) and elsewhere (Donald & Alger 1993; Martinez *et al.* 2009). In response, the National Park Service (NPS) partnered with researchers from the U. S. Geological Survey (USGS) to assess the feasibility of suppressing lake trout in Quartz Lake.

Quartz Lake is distinctive among lakes targeted for lake trout suppression in the western United States where adfluvial populations of bull trout occur (e.g. Lake Pend Oreille and Upper Priest Lake, Idaho; Swan Lake and Flathead Lake, Montana) because (1) it is relatively small (352 ha); (2) it is isolated from future lake trout immigration by a fish passage barrier; (3) the lake trout invasion was believed to be in its early stages; and (4) biological productivity is relatively low and *Mysis* shrimp are not present. Fisheries managers believed that this combination of attributes would increase the probability of successfully suppressing the lake trout population in Quartz Lake to conserve the native bull trout population.

From 2009 to 2013, an intensive gillnetting programme was implemented in Quartz Lake to assess whether invasive lake trout suppression was feasible in an isolated backcountry lake. Data gathered during the suppression period were used to describe the baseline demographic characteristics of the lake trout population and to identify suppression scenarios that would suppress the population. The objectives of this study were to (1) identify the timing and location of spawning by lake trout to inform the suppression programme; (2) describe the demographics of the lake trout population in Quartz Lake; (3) assess the effectiveness of 5 years (2009–2013) of control measures on population growth rate; and (4) use this information to predict the effects of lake trout suppression scenarios.

Materials and methods

Study site

Quartz Lake (surface area = 352 ha; maximum depth = 83 m; elevation = 1346 m) is a glacially formed lake in the headwaters of the Columbia River Basin, Montana (Fredenberg *et al.* 2007). Quartz Lake is an oligotrophic, dimictic lake with stratification occurring in late June and destratification in early October. The native fish assemblage in the Quartz drainage consists of bull trout, westslope cutthroat trout, *Oncorhynchus clarkii lewisi* (Girard), mountain whitefish, *Prosopium williamsoni* (Girard), longnose sucker, *Catostomus catostomus* (Forster), largescale sucker, *Catostomus macrocheilus* Girard, slimy sculpin, *Cottus cognatus* Richardson, and redside shiner, *Richardsonius balteatus* (Richardson). 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). Due to limited access (i.e. 3.7 km into the backcountry) and boating restrictions (i.e. no motorised boats), fishing exploitation for all fish species occupying Quartz Lake is minimal, particularly for lake trout that occupy deep areas of the lake (C. Downs, unpublished data; Fredenberg 2014).

Telemetry, netting and demographic data

Acoustic telemetry was used to improve the efficiency of gillnetting adult lake trout. The timing and location of lake trout spawning were assessed following the methods described by Dux *et al.* (2011). Lake trout ≥550 mm were captured throughout the lake by angling during spring (2009–2013) and surgically implanted with acoustic transmitters (Model CTT-83-3-1, Sonotronics, Inc., Tucson, AZ, USA). Transmitters were 62 mm long, 16 mm diameter and weighed 22 g. The expected battery life for each transmitter was approximately 36 months. Surgical procedures were adapted from Winter (1996) (see Fredenberg 2014 for further details). Fish were tracked daily (day and night) beginning in late September through the beginning of November from a boat equipped with a directional hydrophone (DH-4, Sonotronics) and a portable scanning receiver (USR-96, Sonotronics, Inc.) to identify potential spawning concentrations and to inform netting efforts. Transmitter code, date and time, global positioning system coordinates and water depth were recorded at each location.

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 detection points for all individuals from 2009 to 2013. A relative relocation density surface of Quartz Lake was created using the ArcGIS raster calculator [ESRI (Environmental Systems Research Institute) 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 gillnetting to increase exploitation of adult lake trout. Substrate type and size of spawning patches with suitable spawning habitat were visually estimated from the boat or using divers. All recaptured fish were euthanised.

Water temperature, along with telemetry data and adult netting results, was used to define the spawning period. Hourly water temperatures were recorded in the middle of the lake along a vertical profile from 29 May 2012 to 30 October 2012 using HOBO water temperature data loggers (Model U22-001, Onset, Inc., Bourne, MA, USA). A rope was anchored in approximately 55 m of water, and water temperature loggers were attached at 5-m increments.

Adult lake trout were removed from potential spawning areas from early October through early November using sinking monofilament gillnets. Each net was 91 m long by 3 m deep, with a mesh size of 51-, 57- or 65-mm bar measure constructed from 0.2-mm-diameter clear monofilament mesh. A minimum of two nets and maximum of five nets were connected to form gangs that were deployed in a serpentine pattern at putative spawning locations between 5 m and 45 m in depth. Nets were retrieved every 1–2 h to reduce bycatch mortality of bull trout. Total length (mm), weight (g), sex, maturity (mature or immature based on field necropsy) and the mesh sizes in which fish were captured were recorded for all lake trout.

Bottom-set gillnets were fished to sample juvenile lake trout up to 400 mm total length (*TL*) beginning in June and ending the first week of July from 2010 through 2013. The sampling frame was defined as all areas of the lake 30 m and deeper, a depth selected to reduce bycatch of non-target species. Sampling areas were 200 m^2 [developed from satellite imagery of Quartz Lake in ArcGIS 10.1 (ESRI (Environmental Systems

Research Institute) 2012)]; areas were sampled in random order, and each area was sampled at least once per year. Gillnets were deployed at depths varying from 30 m to 83 m between 0400 and 2400 h and were retrieved within 3–6 h. Gillnets that targeted juvenile lake trout were 91 m long by 2 m deep made of 0.2-mm-diameter clear monofilament joined together to form gangs of three nets having mesh sizes of 26-, 28-, and 32-mm bar measure. Total length (mm) and mesh size in which each fish was captured were recorded for all lake trout to estimate gillnet selectivity. All captured lake trout were euthanised.

Gillnets are highly selective for certain sizes of fish and thus may not represent the true length structure of the targeted fish population (Hamley 1975). Therefore, the mesh sizes of captured fish were used to model gillnet selectivity. Gillnet selectivity was estimated following methods described by Syslo *et al.* (2013). Selectivity could not be modelled for spawners because the sample size was small and fish lengths were uniform among gillnet mesh sizes, and thus, models would not converge. 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 from lake trout throughout the study for age estimation from 10 individuals per centimetre length interval when present. Standard methods were used to prepare the otoliths for sectioning and mounting (see Fredenberg 2014 for details). An experienced technician counted the number of annuli using a compound light microscope at 40× magnification to estimate fish age (Campana 1992; Dux *et al.* 2011). 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 ageing bias (Sharp & Bernard 1988). Ages were assigned to all fish by applying an age–length key to length–frequencies corrected for selectivity. A von Bertalanffy (VBF) growth model was fit to observed length-at-age data for both sexes combined because growth rate did not differ between male and female lake trout (see Fredenberg 2014).

Lake trout collected throughout the suppression programme were weighed to the nearest gram to estimate annual yield (kg ha^{-1}) from suppression netting. A weight–length model was used to predict the weight for lake trout that only had a length measurement. Observed and predicted weights of fish harvested were summed by year and divided by the Quartz Lake surface area to estimate annual yield.

Maturity schedules for fish are often defined as the age or length where 50% of the population is mature and is used in age-structured matrix model (Heibo & Vollestad 2002; Syslo *et al.* 2011). 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 & Vollestad 2002; Cox *et al.* 2013). Ninety-five percent confidence intervals for the estimated length and age at 50% maturity were calculated using 5000 bootstrap data sets randomly sampled with replacement. Sex-specific models were used because male lake trout may mature at younger ages and smaller sizes than females (Cox *et al.* 2013). Predicted female probability at maturity (p_i) was used to model fertility in matrix population models (below).

Fecundity (eggs female^{-1}) was estimated gravimetrically for all gravid female lake trout captured in 2011 (n = 10) and 2012 (n = 17) (Trippel 1993; Murua *et al.* 2003; Syslo 2010). Mean fecundity at age (f_i) was calculated for age classes with more than one observation (Cox *et al.* 2013) and used in the fertility elements in the matrix models. Linear regression analysis was used to describe the fecundity–length relationship and to compare the observed relationship with other lake trout populations.

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

Abundance was estimated for age-10 and older fish using a Jolly–Seber mark–recapture model of adult lake trout captured in gillnets. Adults were marked with acoustic tags in the spring and recaptured in the autumn from 2009 through 2013 (see Materials and methods above). Standard error was calculated 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 population assumed every marked fish had the same probability of being recaptured, every marked fish had the same probability of survival, acoustic tags were neither lost or overlooked, all emigration was permanent, and the survival probability of each fish was independent of other fish.

Total instantaneous mortality rates (Z) for juveniles and spawners were estimated using the Hoenig *et al.* (1983) version of the Chapman–Robson catch-curve model (Smith *et al.* 2012). Total instantaneous mortality was estimated each year for age-5 to age-7 lake trout by truncating the catch curve to those ages. Total instantaneous mortality for spawners ages 10 and older was estimated by pooling spawner catch data for years 2009–2013.

Given that recruitment is often variable in fish populations and the Chapman–Robson catch-curve method assumes recruitment is constant among cohorts (Miranda & Bettoli 2007), a cohort catch curve was also used 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 for age-0 to age-2 lake trout could not be directly estimated using empirical data and was therefore obtained from the literature (Corradin *et al.* 2008; Cox *et al.* 2013; Syslo *et al.* 2013). We used the methods described by Cox *et al.* (2013) to estimate natural mortality for age-0 to age-2 lake trout (i.e. used values from Shuter *et al.* 1998 and Sitar *et al.* 1999) and to randomly generate age-specific survival rates for fish that were not fully selected by the gear. Age-3 and older lake trout were assumed to have a constant rate of instantaneous natural mortality (M), and von Bertalanffy growth parameters L_∞ and K from Quartz Lake were used in a model developed to predict M for Ontario lakes lake trout populations (Galucci & 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_∞ 5000 times from normal distributions where the mean was equal to parameter estimates and the SD was equal to predicted standard deviation (Cox *et al.* 2013). Instantaneous natural mortality was calculated for each of the 5000 simulated parameters of ω and L_∞. Finally, each of the 5000 simulated M rates was converted to natural conditional interval survival (S_M) as $S_M = e^{-M}$ (Miranda & Bettoli 2007), and the mean and SD of the survival rates were used in the projection matrices described below to represent natural survival rates for lake trout ≥age 3 (Cox *et al.* 2013).

Instantaneous fishing mortality rate (F) was estimated by $F = Z - M$ (Miranda & Bettoli 2007). Instantaneous natural mortality and F were converted to conditional interval fishing (m) and natural mortality rates (n) using the equations $m = 1 - e^{-F}$ and $n = 1 - e^{-M}$ (Miranda & Bettoli 2007). Age-specific total conditional interval mortality (A_i) for ages where natural and fishing mortality occurred simultaneously was computed with the equation $A = m + n - mn$ (Miranda & Bettoli 2007). Age-specific total conditional interval mortality was converted to survival (S_i) using $S_i = 1 - A_i$ (Miranda & Bettoli 2007). Total conditional interval fishing mortality was assumed to affect age-5 to age-7 and age-10 and older lake trout because they were vulnerable to the mesh sizes used. Age-0 to age-4 and age-8 to age-9 lake trout were not effectively sampled with the nets fished, so fishing mortality was set at zero. This is a conservative approach because some lake trout ages 2–4 and ages 8–9 were sampled.

Exploitation rates (μ) for spawners and juveniles from abundance estimates were converted to total conditional interval mortality by substituting μ for m (Miranda & Bettoli 2007). The mean total conditional interval mortality rate and confidence interval were calculated for each year, and the upper and lower confidence intervals were averaged to obtain a mean upper and lower confidence interval for use in the population models. 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.

Population modelling

The age-specific vital rates from this study and literature values were used to construct a female-based, post-breeding age-structured Leslie matrix. This modelling approach has been used to assess population dynamics and evaluate lake trout suppression programmes elsewhere (e.g. Hansen *et al.* 2008; Cox 2010; Ng *et al.* 2016). The population vital rates estimated from gillnet-harvested lake trout were used to construct an age-structured model as follows:

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

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 >16 years of age and lake trout often live to be over 25 years of age (Schram & Fabrizio 1998; Dux *et al.* 2011). Age-specific fertility (F_x) was calculated with the equation:

$$F_x = f_i \times p_i \times 0.5,$$

where f_i is the mean fecundity at age i, and p_i is the probability of maturity for females age i (Cox *et al.* 2013). Fecundity was multiplied by 0.5 because half of the offspring were assumed female. Population growth was projected by multiplying matrix $\mathbf{Q}$ 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 ages 5–7 and ages 10 and older. 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, and a beta distribution with mean and SD equal to the bootstrapped estimates of p_i and SE from the maturity-at-age logistic regression was used to constrain probabilities of maturity between zero and one (Cox *et al.* 2013). The probability of maturity at age was generated using the beta distribution (Cox *et al.* 2013). Alternate-year spawning could not be assessed because the majority of acoustically tagged females were recaptured and killed each year. A stretched beta distribution with mean and SD calculated from the fecundity-at-age data was used to generate f_i values (Morris & Doak 2002; Cox *et al.* 2013). The range of the stretched beta distributions was defined as all values within the minimum and maximum fecundity values from the empirical data (Cox *et al.* 2013).

The lake trout population growth rate was estimated for seven management scenarios. Each of the seven models projected lake trout abundance (≥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 5000 generated population matrices. The dominant eigenvalue for each matrix was used to calculate the population growth rate, and the mean of population growth rate (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 *et al.* 2013).

A scenario without suppression was used to model 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) contributed to population growth rate (Caswell 2000; see Fredenberg 2014 for detailed methods). 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 and 0.75. Three additional population models included estimates of A for juveniles and adults from the 5 years of suppression to estimate population trajectories. The lower (A_{lj}), middle (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. For A_{lj}, A_{mj} and A_{uj}, the average of the lower confidence, point estimate and upper confidence values was used from the annual Chapman–Robson and depletion models. Similarly, the lower (A_{la}), middle (A_{ma}) and upper (A_{ua}) values of the total conditional interval mortality for age-10 and older lake trout (adult) were calculated from the Chapman–Robson, cohort catch curves and Jolly–Seber estimates. For $A_{la,}$ A_{ma} and $A_{ua,}$ the average of the lower confidence, point estimate and upper confidence values was used from the Chapman–Robson, cohort catch curves and Jolly–Seber estimates. R (R Core Development Team 2013) was used for all analyses and modelling.

Results

Thirty adult lake trout (14 males and 16 females; mean length = 620 mm, SD = 68) were captured throughout the lake and implanted with acoustic transmitters from 2009 through 2013. Tagged adults were widely distributed throughout Quartz Lake during summer and early autumn (September) and then began to congregate in early October near two avalanche chutes along the north-eastern shore (Fig. 1) where recurring avalanches had deposited cobble and boulder, creating underwater colluvial fans that varied in depth from 2 to 20 m. These congregations of mature lake trout coincided with surface temperatures of 11–12 °C and the beginning of lake destratification. 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.

Spawner gillnetting during 2009 through 2013 removed 352 mature lake trout. The mean length of these fish was 630 mm *TL* (95% CI = 609–632 mm), with 96% of the catch comprised of fish > 400 mm *TL*. In 2012, the thermocline began to descend and Quartz Lake destratified by the second week of October. Gillnet 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 1457 lake trout. Lake trout captured during juvenile gillnetting varied from 113 to 665 mm *TL* (mean = 269 mm, 95% CI = 266–271 mm), with 98% of the catch comprised of fish varying from 170 to 380 mm *TL*. The gillnet gang used for juvenile lake trout was fully selective for lengths between 290 and 400 mm *TL*. Bull trout bycatch

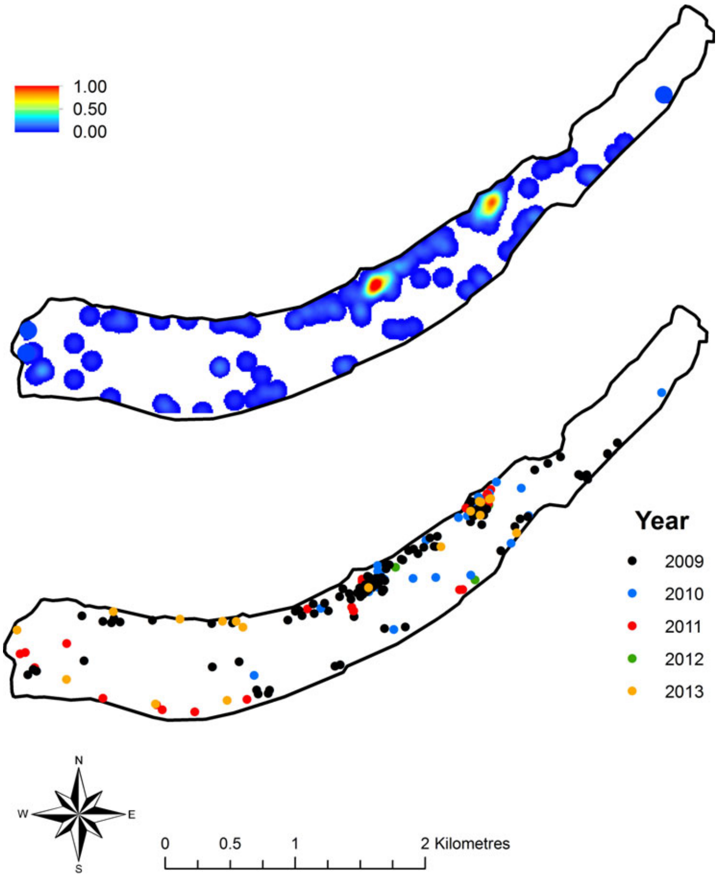

Figure 1. Relative detection density (top image) used to identify potential spawning locations and individual detection by year (bottom image) for acoustic-tagged adult lake trout from 28 September through 29 October for years 2009 through 2013 in Quartz Lake, Montana. Spawning areas were identified at the base of the two largest avalanche chutes (AV). [Colour figure can be viewed at wileyonlinelibrary.com]

declined after 2009 (n = 146) and was lowest in 2011 (n = 56). Adult bull trout (> 400 mm) bycatch mortality varied from 29 (31%) in 2010 to 6 (18%) in 2013; only 33 juvenile bull trout were incidentally killed during the study.

The length structure of lake trout caught in gillnets shifted during the 5 years (2009–2013) of suppression efforts. Annual cumulative length–frequency distributions reflected a decrease in lake trout length for juvenile and adult lake trout (Fig. 2), indicating that the length structure of these groups shifted to younger, smaller fish.

Four hundred and ninety-one lake trout varying in length from 113 to 861 mm TL (mean = 468, SD = 190) were aged. Eighty-two percent of 66 subsampled otoliths aged by two independent readers were within 2 years of age, and the mean coefficient of variation (SD/mean) was 9.8%. Lake trout ages varied from 2 to 24 years. The estimated VBF was:

$$TL = 1033\left(1 - e^{-0.092\times(\text{Age}-1.0)}\right)$$

(Fig. 3).

Lake trout weight was correlated with length ($r^2 = 0.99$; d.f. = 1201; $P < 0.001$), and the weight–length relationship for lake trout in Quartz Lake was $\log_{10}(W) = -5.99 + 3.23{*}\log_{10}(TL)$. Total annual yield declined from 1.01 kg ha^{-1} in 2009 to 0.37–0.55 kg ha^{-1} in 2010–2013. Juvenile yield estimates increased over the duration of the project from 0.14 kg ha^{-1} in 2010 to 0.18 kg ha^{-1} in 2013. Spawner annual yield varied from 0.24 kg ha^{-1} in 2010 to 1.01 kg ha^{-1} in 2009.

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). The estimated abundance of age-5 to age-7 lake trout varied from 326 in 2010 to 159-279 in the following 3 years (Table 1). The age structure was dominated by juvenile lake trout, indicating successful recruitment of lake trout since 2005.

Age and length at maturity differed between male and female lake trout. Mature male lake trout varied from 430 to 851 mm TL (mean = 610 mm; SD = 82). The maturity schedule of male lake trout was described

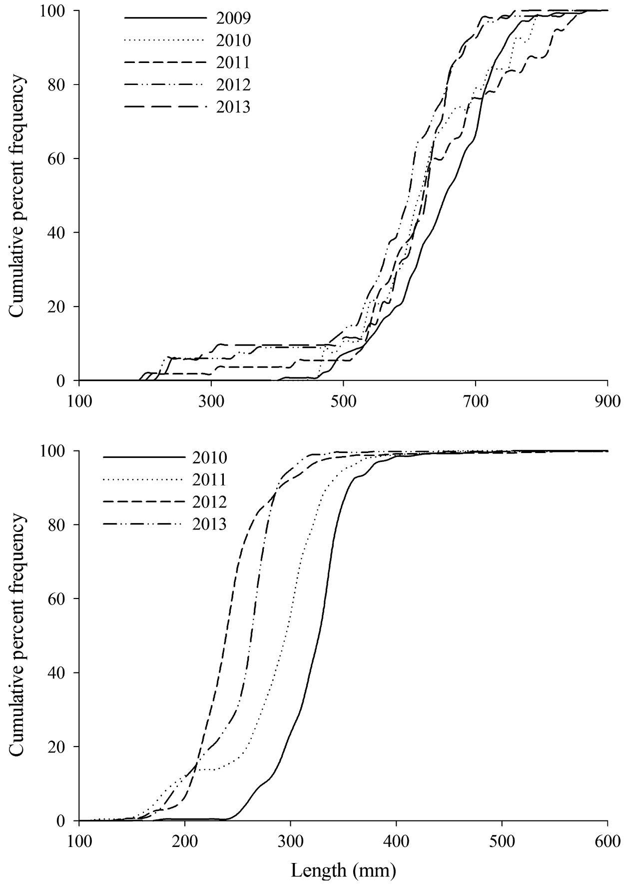

Figure 2. Annual cumulative length–frequency for lake trout caught during spawner (top panel) and juvenile (bottom panel) gillnetting in Quartz Lake, Montana.

Table 1. Annual abundance $\hat{N}$ (SE) estimated using Leslie depletion regression model for juvenile (ages 5–7) and Jolly–Seber annual abundance estimates for adult (age ≥ 10) lake trout sampled in years 2009 through 2013 in Quartz Lake, Glacier National Park, Montana. The annual abundance estimate for adults in year 2012 reflects the number of adults caught because all marked fish were recaptured

Year	$\hat{N}_{\text{Juveniles}}$	$\hat{N}_{\text{Adults}}$
2009	–	146 (6.8)
2010	326 (193)	81 (21.2)
2011	167 (5)	60 (5.8)
2012	159 (18)	63 (0.0)
2013	279 (53)	–

by the logistic regression $p_i = e^{0.031\times TL-14.234}/(1+e^{0.031\times TL-14.234})$. Fifty percent of male lake trout reached sexual maturity at 453 mm *TL* (95% CI = 413–478) and age 7 (95% CI = 7–8). Mature female lake trout varied from 428 to 861 mm *TL* (mean = 676 mm; SD = 64), and 50% of female lake trout reached sexual maturity at 556 mm *TL* (95% CI = 502–586) and age 9 (95% CI = 8–9). The maturity schedule for females was described by the logistic regression $p_i = e^{0.046\times TL-25.92}/(1+e^{0.0461\times TL-25.92})$.

Mean female lake trout fecundity was 4337 eggs (95% CI = 3455–5219) for individuals varying in length from 582 mm (age 8) to 820 mm (age 18) (mean *TL* = 679; SD = 63). Mean fecundity was positively associated with age for the age classes sampled (Table 2). Mean relative fecundity was 1277 (95%

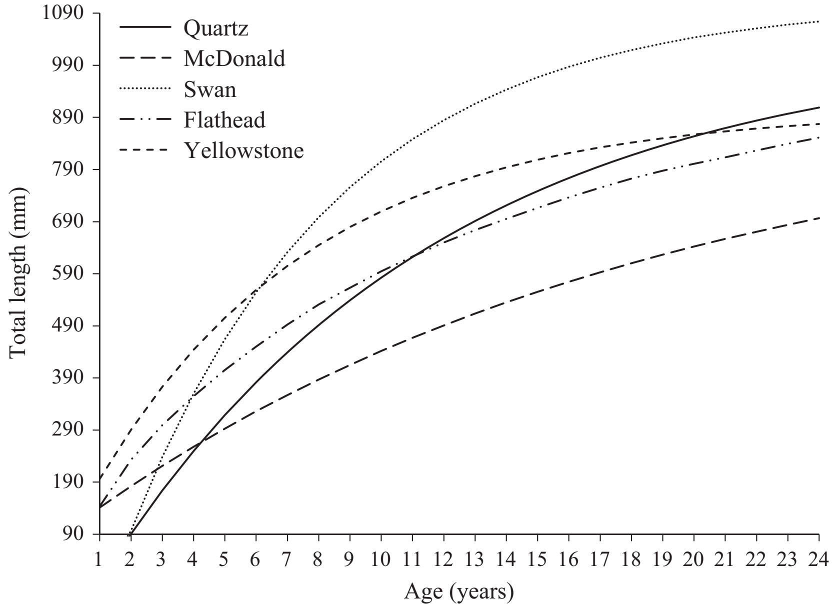

Figure 3. Mean length at age produced from the von Bertalanffy growth curve for lake trout in Quartz Lake (this study), Lake McDonald (Dux 2005), Swan (Cox 2010) and Flathead lakes (Beauchamp 1996), Montana; and Yellowstone Lake, Wyoming (Ruzycki & Beauchamp 1997).

CI = 1116–1439) eggs kg^{-1}. Female length was positively related to fecundity ($r^2 = 0.75$, d.f. = 27, $P < 0.001$) and was described with fecundity–length relationship: fecundity = $-18121 + TL*33.07$.

Instantaneous natural mortality for lake trout ≥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 3). Total conditional interval mortality rates derived from depletion estimates of abundance varied from 0.51 in 2010 to 0.95 in 2011 (Table 3). The mean total conditional interval mortality values (A_{lj}, A_{mj}, A_{uj}) varied from 0.71 to 0.87 (Table 4).

Total conditional interval mortality rates derived from the Chapman–Robson and cohort catch curves for lake trout ages 10 and older were similar, but the total conditional interval mortality rates derived from the Jolly–Seber model were disparate. Total conditional interval mortality rates derived from the Chapman–Robson and cohort catch curves were 0.34 and 0.32 (Table 5), respectively. Estimates of total conditional interval mortality derived from the Jolly–Seber varied from 0.61 to 0.94 and exceeded estimates derived from the catch curves (Tables 5 and 6). Mean total conditional interval mortality values used in population modelling (A_{la}, A_{ma}, A_{ua}) varied from 0.41 to 0.57 (Table 4).

Mean population growth rate (λ) of the lake trout population in the no-suppression scenario was 1.23 (95% CI = 1.16–1.28; Fig. 4). 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). Sensitivity analysis indicated that λ was most sensitive to changes in age-0 survival.

Table 2. Age-specific natural survival (S_i), probability of maturity (p_i) and fecundity (f_i) used in population simulations for lake trout in Quartz Lake, Montana. Values in parentheses are SE

Age	S_i	p_i	f_i
0	0.0043 (0.00084)*	0	0
1	0.45 (0.09)*	0	0
2	0.78 (0.16)†	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)	1498 (42)
9	0.94 (0.0036)	0.59 (0.08)	1498 (42)
10	0.94 (0.0036)	0.81 (0.05)	2731 (812)
11	0.94 (0.0036)	0.92 (0.04)	3189 (399)
12	0.94 (0.0036)	1	4230 (1808)
13	0.94 (0.0036)	1	4509 (396)
14	0.94 (0.0036)	1	6285 (288)
15	0.94 (0.0036)	1	7422 (2436)
16+	0.94 (0.0036)	1	8614 (773)

*From Shuter *et al.* (1998), with SE equal to SD of the observations.
†From Sitar *et al.* (1999), with SE equal to 20% of the value.

All harvest suppression scenarios, with the exception of the low suppression alternative ($A = 0.25$), produced population growth rates <1 (Fig. 4 and Table 7). The six suppression scenarios produced mean population growth rates varying from 0.61 (95% CI = 0.57–0.64) to 1.10 (95% CI = 1.04–1.16; Table 7). 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 $\hat{N} = 0$ (highest suppression scenario) to 449 962 with the no-suppression scenario (Fig. 5 and Table 7).

Discussion

Management agencies have implemented suppression programmes to control non-native lake trout for conservation of native fishes and recreational fisheries in several states in the western United States. This study was implemented to describe the demographics of a lake trout population during suppression in an isolated back-country lake and to use this information to assess the population growth rate under various suppression scenarios. Suppression resulted in declining λ from 1.23 prior to suppression to 0.61–0.79 during suppression. These results indicate that suppression efforts successfully reduced lake trout abundance and that continued suppression at or above observed exploitation levels is needed to ensure continued population declines.

Spawning habitats identified using telemetry were characteristic of lake trout spawning habitat throughout their native and introduced ranges (Gunn 1995; Marsden *et al.* 1995; Cox 2010; Dux *et al.* 2011). Spawning likely occurred in two relatively shallow areas varying in depth from 2 to 20 m at the base of two avalanche chutes in areas characterised by unembedded cobble and boulder substrates. Similarly, Cox (2010) identified two locations consisting of coarse, angular rock substrates where lake trout spawned in depths from 1.2 to 12.8 m in Swan Lake, Montana; and Dux *et al.* (2011) reported that lake trout spawned at a mean depth of 18 m on cobble and boulder substrates in Lake McDonald, Montana. The concentration of detections of acoustic-tagged adults on the two colluvial fans and the limited availability of these habitats elsewhere in the lake (Fredenberg 2014) suggest lake trout spawning was limited to these locations in Quartz Lake. Furthermore, lake trout in Quartz

Table 3. 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 ages 5–7 in Quartz Lake, Montana. Values in parentheses are upper and lower 95% CI

	Mortality estimate	2010	2011	2012	2013
From 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)
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 4. Mean total conditional interval mortality rates (A) used for population abundance projections after 20 years of suppression ($\hat{N}_{20}$) for simulations where A is set at the mean lower (A_{lx}), mean middle (A_{mx}) and mean upper (A_{ux}) total conditional interval mortality rate estimates for juveniles ages 5 to 7 (A_{xj}) and adults age ≥ 10 (A_{xa}) calculated from Table 3, Table 5 and Table 6 for lake trout in Quartz Lake, Glacier National Park, Montana. Values in parentheses are upper and lower 95% CI

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

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 6. Total conditional interval (A) and conditional fishing (m) mortality rates derived from interval fishing mortality rates (μ) 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). Values in parentheses are the upper and lower 95% CI

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)

Lake began aggregating near the putative spawning locations in early October prior to lake destratification, when surface temperatures were between 11 and 12 °C, and ripe adults were caught when surface temperatures declined below 10 °C. These results are consistent with other studies that reported lake trout initiated spawning behaviour following lake destratification and when water temperatures declined to 8–14 °C (Gunn 1995; Dux *et al.* 2011). These results suggest that lake trout spawn over a short period of time (~2 weeks) in habitat that was limited in area and consistent with other lake trout studies. Given this predictable behaviour, telemetry is a critical tool for identifying areas for efficient removal of lake trout.

The size structure of juvenile and adult lake trout shifted to younger, smaller fish during the suppression programme. Truncation of size and age distributions in fish populations is a common response to size-selective harvest (Coleman *et al.* 2000; Kocovsky & Carline 2001; Hutchings & Reynolds 2004). For example, Atlantic cod, *Gadus mohua* (L.), populations in the Northwest Atlantic declined by more than 90% over a 40-year period due to targeted harvest of large individuals, and during the decline, the length structure shifted to smaller and younger individuals (Hutchings 2000). Similarly, the length and age structure of the non-native lake trout population in Swan Lake, Montana, shifted to smaller and

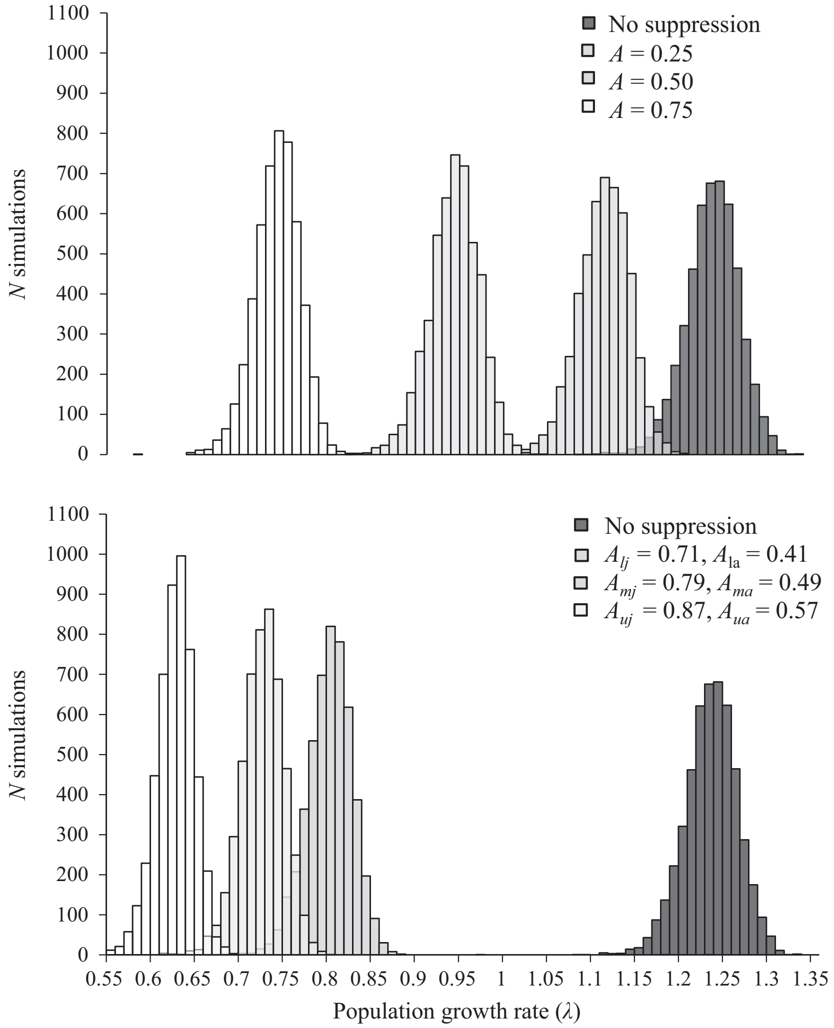

Figure 4. Mean population growth rate distributions from simulations of lake trout harvest in Quartz Lake, Montana. Total conditional interval mortality rates (A) for lake trout ages 5–7 and ages 10 and older are 0.25, 0.50 and 0.75 (top panel), and mean population growth rate distributions for simulations incorporating mean lower (A_{lx}), middle (A_{mx}) and upper (A_{ux}) total conditional interval mortality rate estimates for juveniles (A_{xj}) and adults (A_{xa}) (bottom panel).

Table 7. Mean population growth rate (λ), 95% CI and population abundance estimates for lake trout age ≥ 1 ($\hat{N}_{20}$) after 20 years for six suppression scenario simulations and a no-suppression scenario simulation in Quartz Lake, Montana

Suppression scenario	λ	95% CI	$\hat{N}_{20}$
No Suppression	1.23	1.16–1.28	449 962
A = 0.25	1.10	1.04–1.16	40 788
A = 0.50	0.94	0.87–0.99	2538
A = 0.75	0.73	0.68–0.78	6
A_{lx}	0.79	0.75–0.84	89
A_{mx}	0.72	0.68–0.76	18
A_{ux}	0.61	0.57–0.64	0

younger individuals in response to 3 years of targeted removal of juvenile and adult fish (Rosenthal *et al.* 2012).

Growth rate of lake trout in Quartz Lake was low relative to other populations throughout North America (Hubert *et al.* 1994; Martinez *et al.* 2009; Syslo 2010; Cox *et al.* 2013). Lake trout up to age 10 in Quartz Lake grew slowly when compared to nearby lake trout populations in Swan (Cox *et al.* 2013) and Flathead lakes (Beauchamp 1996) in Montana and Yellowstone Lake, Wyoming (Ruzycki & Beauchamp 1997). Adult lake trout also reached maturity at older ages as compared to most lake trout populations throughout western North America (Healey 1978; Cox *et al.* 2013). For example, male and female lake trout in Quartz Lake matured at older ages (males = 7.2 years, females = 8.7 years) 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 years and mean

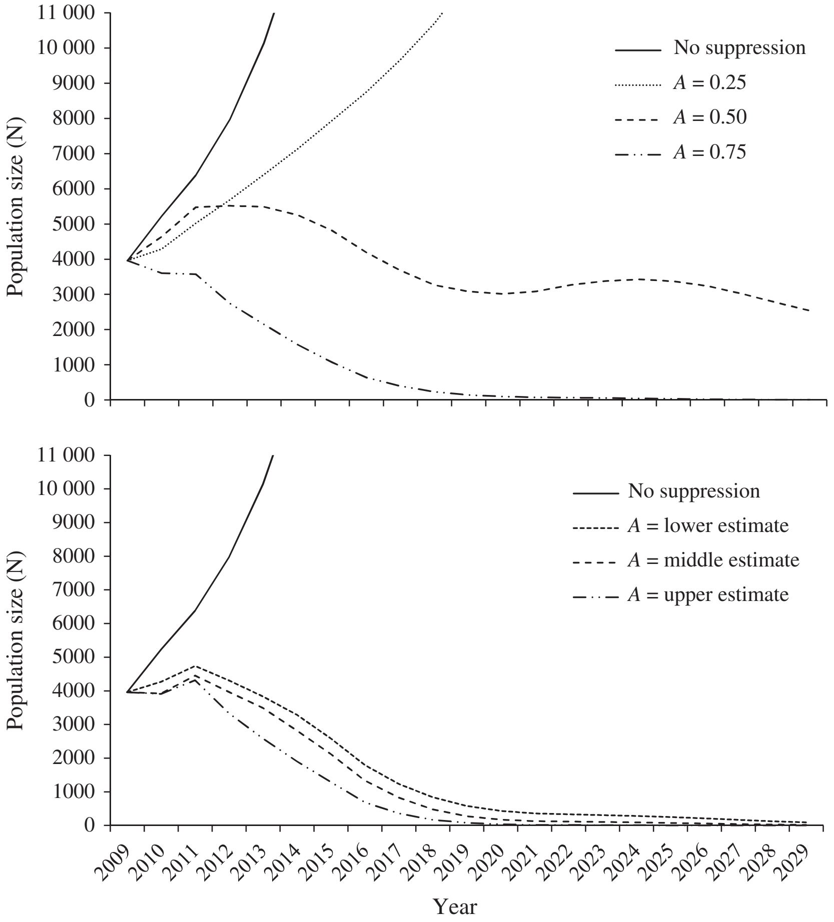

Figure 5. Mean population abundance projections ($\hat{N}_{20}$) following 20 years of no suppression and suppression where total conditional interval mortality (A) rates are set at 0.25, 0.50 and 0.75 for age-5 to age-7 and age 10 and older lake trout (top panel) and suppression simulations incorporating mean lower (A_{lj} = 0.71, A_{la} = 0.41), middle (A_{mj} = 0.79, A_{ma} = 0.49) and upper (A_{uj} = 0.87, A_{ua} = 0.57) total conditional interval mortality rate estimates for juveniles ages 5–7 (A_{xj}) and adults ages 10 and older (A_{xa}; bottom panel) in Quartz Lake, Glacier National Park, Montana.

lengths of 590 and 708 mm for males and females, respectively (Cox *et al.* 2013). Additionally, length at maturity was relatively low when compared to other populations (Madenjian *et al.* 1998; Hansen *et al.* 2008; Syslo *et al.* 2011; Cox *et al.* 2013). Fish populations exhibiting slow individual growth and late age at maturity are often susceptible to overexploitation (Shuter *et al.* 1998), suggesting that the lake trout population in Quartz Lake is particularly vulnerable to overexploitation.

Total annual yield of 0.5 kg ha^{-1} has been suggested as the maximum sustainable yield threshold for lake trout populations (Healey 1978). Annual yield in Quartz Lake exceeded the 0.5 kg ha^{-1} threshold for years 2009, 2011 and 2012. However, this benchmark may not be appropriate given that many of the lakes Healey (1978) studied were probably less productive and considerably larger (in area and volume) than Quartz Lake. The validity of Healey's (1978) threshold for lake trout populations outside their native range will be better understood as more scientific knowledge accumulates on lake trout suppression efforts.

Although fishing effort increased from 2009, spawner yield decreased to 0.24–0.39 kg ha^{-1} during the following 4 years. Thus, the abundance of mature lake trout has likely decreased since suppression commenced in 2009, which is corroborated by the Jolly–Seber abundance estimates. Conversely, juvenile yield increased from 2011 to 2013. The increasing strength in cohorts is further evidence of a growing population with an age structure dominated by younger individuals. Although the increase in juvenile yield could partially be due to an increased effectiveness of the gillnetting crew, it is unlikely to fully account for changes because gillnets were randomly placed. Thus, the increase in juvenile yield is most likely explained by the increasing strength of cohorts recruiting to the mesh sizes used to capture juveniles or compensatory responses associated with harvest of larger individuals. However, compensatory responses to fishing effort were not observed in Yellowstone Lake, which was likely below carrying capacity prior to suppression of the lake trout population (Syslo 2010). Nonetheless, this study represents a limited time frame (5 years), and more data are needed to address these uncertainties. Monitoring these metrics through time will provide further insight into the compensatory responses of the lake trout population to continued suppression efforts in Quartz Lake.

Mean relative fecundity in Quartz Lake (1277 eggs kg^{-1}) was below values reported in the literature (Shuter *et al.* 1998; Syslo 2010). For instance, Shuter *et al.* (1998) reported a mean of 1506 eggs kg^{-1} for 13 lake trout populations throughout inland lakes in Ontario, and Syslo (2010) reported a mean relative fecundity of approximately 1550 eggs kg^{-1} 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.

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 growing exponentially. As expected, compared with the no-suppression alternative, each of the six suppression scenarios resulted in lower mean population growth rates, but the population continued to grow at $A = 0.25$. Total annual mortality exceeding 50% has been suggested as the threshold for overharvest in lake trout populations (Healey 1978). In Yellowstone Lake, Wyoming, it was determined that 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, Montana, 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). In Quartz Lake, suppression scenarios where total conditional interval mortality was ≥ 0.50 resulted in population growth rates below replacement; however, at $A = 0.50$ we caution that the upper confidence interval for population growth rate approached 1. 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.

Total conditional interval mortality rates during the Quartz Lake suppression programme 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 equal to the lower limit for juveniles ($A_{lj} = 0.71$) and adults ($A_{la} = 0.41$), lake trout abundance declined to below $N = 500$ within 20 years but failed to fall below $N = 50$ within the same period. In contrast, when total conditional interval mortality was simulated at the upper limit for juveniles ($A_{uj} = 0.87$) 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 below $N = 50$ by the year 2022.

Total conditional interval mortality rates estimated for lake trout in Quartz Lake were high relative to ongoing suppression programmes elsewhere for lake trout. For instance, in Yellowstone Lake, total annual mortality rates varied from 0.26 to 0.41 (Syslo *et al.* 2011). 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 ages of the lake trout used to estimate fishing mortality differed among suppression programmes. For example, total conditional interval mortality rate estimates for lake trout in Quartz Lake affect age-5 to age-7 and ages ≥10 lake trout, whereas in Yellowstone Lake total annual mortality rates affected age-2 to age-17 lake trout (Syslo 2010).

The primary source of uncertainty in the vital rates used in the model was the survival rate estimates used from the literature for age-0 to age-2 lake trout. These survival rates were potentially biased low because the Lake Superior lake trout population was likely density limited, which may affect juvenile survival (Corradin *et al.* 2008). Therefore, randomly generated age-specific survival rates were incorporated in the simulation models to address this uncertainty. Although uncertainty was incorporated in the vital rate estimates, future population models could be improved with estimates of age-0 to age-2 lake trout survival rates in Quartz Lake.

While 5 years of gillnetting successfully suppressed the lake trout population, these suppression efforts did not appear to influence the bull trout spawning population. The mean bull trout redd count for Quartz Creek from 2003 through 2008 and during the suppression (2009–2013) was 30 redds (SD = 17; Downs *et al.* 2013); thus, bull trout redd counts did not exhibit a statistically significant trend from 2003 through 2013 (Downs *et al.* 2013). Further, although comparison points presently are few, bull trout redd abundance (estimated approximately one generation after suppression commenced) was above the long-term average (2003-2015; $n = 33$) in 2014 ($n = 66$) and 2015 ($n = 39$), suggesting that removal of lake trout may be having a positive effect on the bull trout population growth rate.

This analysis suggests that the lake trout suppression levels are negatively influencing the population growth rate. At the present suppression levels, the mean population growth rate was estimated to be between 0.61 and 0.79. However, the suppression effort during the 5-year suppression programme is probably near the maximum attainable exploitation rate given the constraints of working in the backcountry. These results indicate that targeted suppression successfully reduced lake trout abundance within an isolated backcountry lake and that continued suppression at or above observed exploitation levels is needed to ensure continued population declines. To ensure that the lake trout abundance continues to decline in Quartz Lake, the following actions are recommended: (1) continuing suppression at or above current exploitation levels, which could be accomplished more efficiently by increasing the boat size (boat used in this study was 5.5-m long) and incorporating a mechanical (hydraulic) net puller; (2) continuing juvenile and targeted spawner gillnetting and adult telemetry efforts; (3) integrating smaller bar measure nets (i.e. 19 mm) to increase the removal of smaller juvenile lake trout; and (4) periodically updating these data and population models to track changes in lake trout population dynamics over time. Additionally, continued monitoring of the bull trout population is needed to ensure that suppression efforts do not negatively influence the population.

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