DISTRIBUTION AND POPULATION CHARACTERISTICS OF LAKE TROUT IN LAKE MCDONALD, GLACIER NATIONAL PARK: IMPLICATIONS FOR SUPPRESSION

by

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APPROVAL

of a thesis submitted by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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STATEMENT OF PERMISSION TO USE

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November, 2005

DEDICATION

This thesis is dedicated to my wife, Andylyn Dux, for her endless support and many sacrifices and to my parents, Richard and Linda Dux, for always encouraging my education. I especially thank my father for finding time to take me fishing, which started me down the path towards a fisheries career.

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ABSTRACT

Bull trout *Salvelinus confluentus* have declined since the establishment of nonnative lake trout *Salvelinus namaycush* in Lake McDonald, Glacier National Park (GNP). In an attempt to prevent further decline of this population, GNP is considering implementing a lake trout suppression program. I used ultrasonic telemetry to examine the spatial and temporal distribution of lake trout and gill nets to evaluate population characteristics and diet. Model simulations were used to predict lake trout responses to varying levels of suppression. I relocated 36 lake trout (508-859 mm total length) 1,137 times from June through November 2003 and March through November 2004. Lake trout had a narrow vertical distribution during all seasons in both 2003 and 2004, rarely occupying depths >30 m. During thermal stratification, lake trout occupied depths in the upper hypolimnion where mean temperature varied from 8-9˚C and dissolved oxygen was highest. Lake trout typically were suspended in the water column during all seasons except autumn. When spawning commenced in late-October, lake trout were associated with littoral habitats containing clean cobble and boulder substrates. The lake trout population had a broad age structure and a maximum age of 37 years. Males reached maturity earlier (12 years) than females (15 years), and total annual mortality rate for lake trout ages 8-27 was 13.2%. Growth rates were slow and relative weight values were among the lowest observed for lake trout throughout their range. Food habits were sampled from 254 lake trout, and 95% of the diet by weight consisted of fish prey. Model simulations indicated that substantial population reduction could be achieved with moderate exploitation (20-50%); however, this was more easily achieved as the size at which lake trout could effectively be captured was reduced. Simulations suggested that recruitment could be reduced to a level where adults are not being replaced at low exploitation (10-30%). These data will allow suppression efforts to be focused at times and places that will maximize efficiency, and population simulations suggest that substantial reduction of the lake trout population is feasible. Ultimately, results from this study should promote recovery of bull trout in Lake McDonald.

INTRODUCTION

The intentional introduction (stocking) of nonnative fishes has been a common fisheries management practice for many years (Li and Moyle 1999). Additionally, illegal and unintentional fish introductions have been, and continue to be, prevalent throughout the United States, with nearly 400 illegal introductions documented in Montana alone (Vashro 1995). While introductions can produce benefits, such as increased fishing opportunities, they frequently are not sustained because of instability of disturbed food webs (Spencer et al. 1991; McMahon and Bennett 1996). The disturbances introduced fishes create in aquatic systems are problematic for resource managers (Holcik 1991; Rahel 1997), as nonnative fishes are likely the greatest cause for decline and extirpation of native fishes in North America (Miller et al. 1989).

The desirability of many predatory fishes as sport fish has resulted in widespread introductions of these species (e.g., McMahon and Bennett 1996). Predatory fishes have a propensity to disperse, by natural or artificial means, to waters beyond the introduction site (Li and Moyle 1999). For example, construction of reservoirs in the Columbia River basin, and the subsequent reduction of riverine salmonid fisheries, spurred introductions of predatory fishes that have since expanded their range to unimpounded waters (Li and Moyle 1999). Now, in addition to loss of riverine habitat, native salmonids are subjected to high levels of predation by introduced fishes (Rieman et al. 1991; Vigg et al. 1991; Tabor et al. 1993).

Lake trout *Salvelinus namaycush* exemplify the ability of a predatory species to establish populations beyond the introduction site if suitable conditions exist (Crossman

1995). Lake trout introduced into Flathead Lake, Montana a century ago (Spencer et al. 1991) are now found throughout much of the Flathead River drainage (Zollweg 1998; Muhlfeld et al. 2000; Fredenberg 2002), thus demonstrating the ability of this species to widely disperse from the introduction site. Lake trout can also spread from illegal introductions, as illustrated by the discovery of lake trout in 1994 in Yellowstone Lake, Yellowstone National Park (YNP), the largest lacustrine habitat for native Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (Kaeding et al. 1996). The probable source of this illegal introduction was nearby Lewis Lake, YNP, which also supports an introduced population of lake trout (Munro et al. 2005). Regardless of the mechanism for establishment, nonnative lake trout populations are of particular concern because they often have negative impacts on native fish populations (Behnke 1992; Crossman 1995; Ruzycki and Beauchamp 1997).

Bull trout *Salvelinus confluentus* are particularly susceptible to negative interactions with lake trout. Lake trout displace bull trout and bull trout populations generally cannot be sustained in mountain lakes after lake trout introduction (Donald and Alger 1993). Three sources of evidence that bull trout are negatively influenced by lake trout include: i) displacement of native bull trout populations by introduced lake trout, ii) failure of bull trout to colonize suitable low-elevation lakes containing lake trout, and iii) relatively high mortality rates within bull trout populations in sympatry with lake trout (Donald and Alger 1993).

In 1959, nonnative lake trout were first documented in Lake McDonald, Glacier National Park (GNP, Fredenberg 2002) and have since established a reproducing population. Natural dispersal of introduced lake trout from Flathead Lake (located 93 river-kilometers downstream) is the likely source of this population (Fredenberg 2002). Lake trout have invaded other lakes in the Flathead River drainage of GNP since the Lake McDonald population was established. Native species, particularly bull trout, have declined in abundance since the introduction of lake trout in Lake McDonald and other GNP lakes (Fredenberg 2002).

In 2000, Lake McDonald and three other GNP lakes supporting nonnative lake trout populations exhibited declines in bull trout abundance from similar sampling conducted in 1969 (Fredenberg 2002). These studies indicated lake trout abundance increased in each of the lakes, while they were documented for the first time in another lake, suggesting continuing range expansion (Fredenberg 2002). Additionally, bull trout abundance remained stable in a lake that did not contain lake trout (Fredenberg 2002). Lake McDonald exemplifies the magnitude of this shift in species abundance, as bull trout abundance declined by 82% and lake trout abundance increased by 300% from 1969 to 2000 (Fredenberg 2002). These data support the hypothesis that introduced lake trout displace or replace native bull trout as the dominant top predator in mountain lakes.

National Park Service (NPS) policy requires the restoration, to the extent possible, of impaired native animal populations (B. Michels, National Park Service, personal communication). This includes the restoration of native fish populations, such as bull trout populations. Concerns about the status of bull trout in Lake McDonald were heightened in 1998, when bull trout were listed as a threatened species under the Endangered Species Act (ESA). To prevent further decline of the bull trout population in

Lake McDonald, GNP is considering implementing a lake trout suppression program (B. Michels, National Park Service, personal communication), similar to the suppression effort currently underway in Yellowstone Lake, YNP to minimize the impact nonnative lake trout have on native Yellowstone cutthroat trout (Mahony and Ruzycki 1997; Koel et al. in press).

Lake trout suppression in Yellowstone Lake provides insight for developing lake trout suppression programs elsewhere (Koel et al. in press). One of the primary challenges to suppressing lake trout in Yellowstone Lake has been understanding their distribution (P. Bigelow, National Park Service, personal communication). Thus, the success of suppression efforts in Lake McDonald will largely depend upon identifying patterns in the spatial and temporal distribution of lake trout. This knowledge will allow suppression efforts to target frequently occupied habitats at times that will maximize catch. Additionally, understanding lake trout population characteristics is critical for evaluating lake trout population responses to suppression.

Most lake trout studies have been conducted within the native range of the species. Thus, more limited information exists for introduced lake trout populations. Understanding similarities between introduced and native lake trout populations may facilitate development of suppression and management strategies for introduced populations. Further, population modeling to assess the feasibility of suppressing a lake trout population has never been done. Suppression may be an effective management tool for mitigating threats that introduced lake trout pose to native fish populations, but knowledge regarding the level of exploitation required to suppress a lake trout population to a desired level is lacking. Thus, the objectives of this study were to i) document the seasonal and diel distribution of lake trout, ii) identify potential lake trout spawning areas and document spawning timing, iii) evaluate lake trout population characteristics, including age structure, growth rate, and survival rate, iv) incorporate population data into model simulations to predict the effects varying levels of exploitation may have on the lake trout population, and v) describe the diet of lake trout in Lake McDonald.

STUDY AREA

Lake McDonald is situated in a narrow glacial valley at an elevation of 961 m in the Flathead River drainage of GNP, northwestern Montana (Latitude 48° 32′ 15″ Longitude 113° 59′ 45″, Figure 1). It is the largest and deepest lake in GNP, with a total surface area of 2,763 ha and maximum depth of 142 m. The limnetic zone of Lake McDonald generally exceeds 60 m in depth and is dominated by glacial silt substrate, while nearshore waters are steep sloping with a mixture of glacial silt, cobble, and boulder substrates. Lake McDonald is an oligotrophic lake, and thermal stratification typically occurs from July through September. McDonald Creek is the primary tributary to Lake McDonald and receives its water mainly from seasonal melting of headwater snowfields. Maximum surface water temperature generally does not exceed 18° C and mean Secchi depth is 14.8 m (Ellis et al. 1992). Phytoplankton biomass is low with a mean total standing crop of 0.233 ml/m^3 (Ellis et al. 1992). Despite having a cold winter climate, Lake McDonald freezes only occasionally. Lake McDonald experiences few anthropogenic disturbances and angling pressure is low.

Native fishes in Lake McDonald include bull trout, westslope cutthroat trout *Oncorhynchus clarki lewisi*, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coulteri*, longnose sucker *Catostomus catostomus*, largescale sucker *Catostomus macrocheilus*, peamouth chub *Mylocheilus caurinus*, northern pikeminnow *Ptychocheilus oregonensis*, redside shiner *Richardsonius balteatus*, mottled sculpin *Cottus bairdi*, and slimy sculpin *Cottus cognatus.* Common nonnative species are lake trout and lake whitefish *Coregonus clupeiformes,* but kokanee *Oncorhynchus nerka,* rainbow trout *Oncorhynchus mykiss*, and brook trout *Salvelinus fontinalis* are also present.

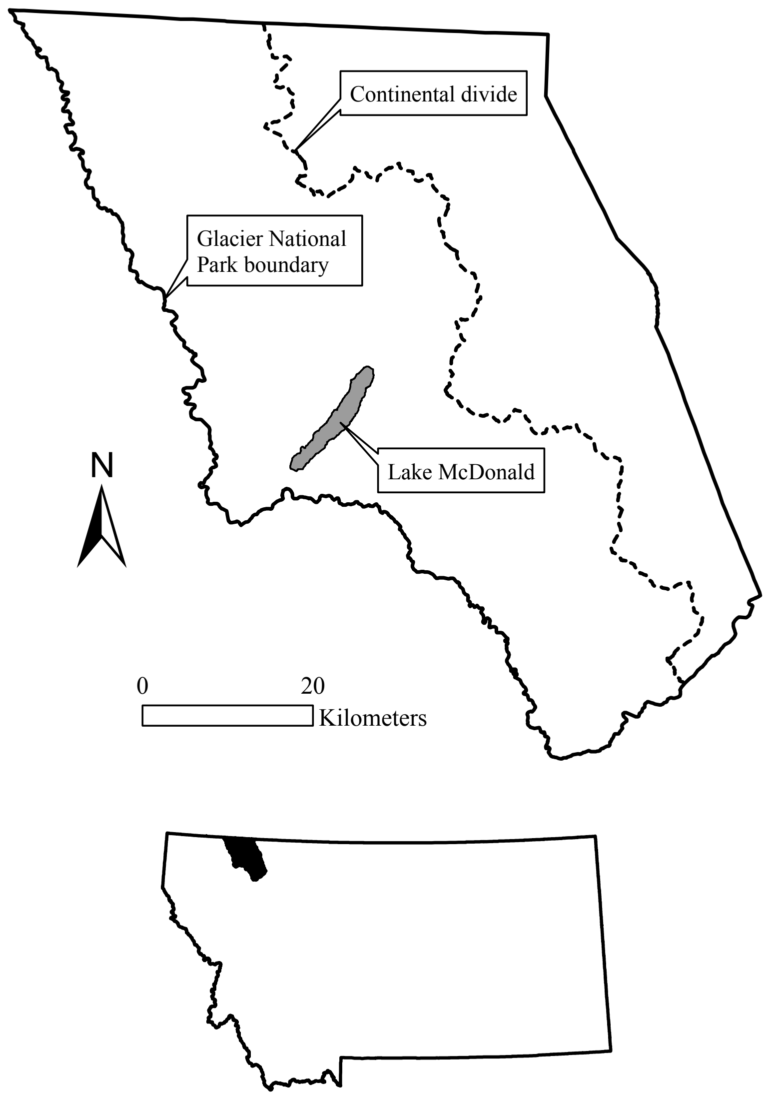


Figure 1. Location of Lake McDonald and the continental divide (Great Divide) in Glacier National Park, Montana.

METHODS

Data Collection

Abiotic Factors

Water temperature, dissolved oxygen, and water transparency were measured to examine their relationship to lake trout distribution. Vertical temperature profiles were measured 1-2 times monthly from March through May (2004 only), 2-3 times monthly from June through August, and 1-2 times monthly from September through November. Vertical dissolved oxygen profiles were measured from May through November 2004 and at the same time as temperature profiles. Two profile stations were selected to represent nearshore and offshore habitats. An additional nearshore and offshore station were sampled during thermal stratification in 2004. Measurements were taken with a Yellow Springs Institute (YSI) 600XL sonde at 1-m intervals from 1-58 m. Minimal temperature and dissolved oxygen variation occurs at depths greater than 58 m (Ellis et al. 1992), so I did not take measurements beyond this depth. The YSI sonde was calibrated before measuring each profile. Water transparency was measured weekly with a 20-cm Secchi disk at a station on the south end of Lake McDonald.

Temperature profile data were used to delineate seasons during each year. Two seasons were identified (stratified, post-stratified) in 2003, but four seasons (isothermal, pre-stratified, stratified, post-stratified) were present in 2004 because of a longer field season. The isothermal season started on the first day of tracking in 2004 and lasted until water temperatures were no longer completely isothermal in the upper 58 m of the water column. The date of the first temperature profile measurement when temperatures were no longer isothermal constituted the beginning of the pre-stratified season. The stratified season started on the date that a thermocline was first detected. A thermocline was defined as a 1.0˚C temperature change in any 1-m interval of a temperature profile (Horne and Goldman 1994). The post-stratified season began on the date when a thermocline was no longer present and continued until the last day of tracking each year.

Temperature and dissolved oxygen data were displayed using contour plots. Temperature contours followed 1.0˚C intervals and dissolved oxygen contours were in 0.1 mg/L intervals. Contours were interpolated for dates when actual measurements were not recorded.

Population Characteristics and Diet

Lake trout were sampled from May through October in 2003 (Figure 2). In 2004, sampling occurred from March through June and September through November (Figure 2). Lake trout were sampled with 38.1-m x 1.8-m sinking, experimental gill nets consisted of 7.6-m panels of 12, 24, 36, 48 and 65 mm bar-measure mesh. Additionally, some fish were sampled by angling and hoop nets. Angling was conducted by trolling in depths <10 m with artificial lures and single hooks, typically in early morning. Hoop nets were 3.7 m long x 0.8 m diameter and constructed with 25-mm knotless nylon mesh. Gill nets were set during low-light or dark hours, typically in early morning, and pulled after 2-3 hours to minimize stress and mortality to native fish (e.g., bull trout). Nets were set perpendicular to shore, with the nearshore end typically in <10 m of water and the offshore end usually in 20-60 m of water. Sampling locations were spread throughout the entire lake to obtain a representative sample of lake trout.

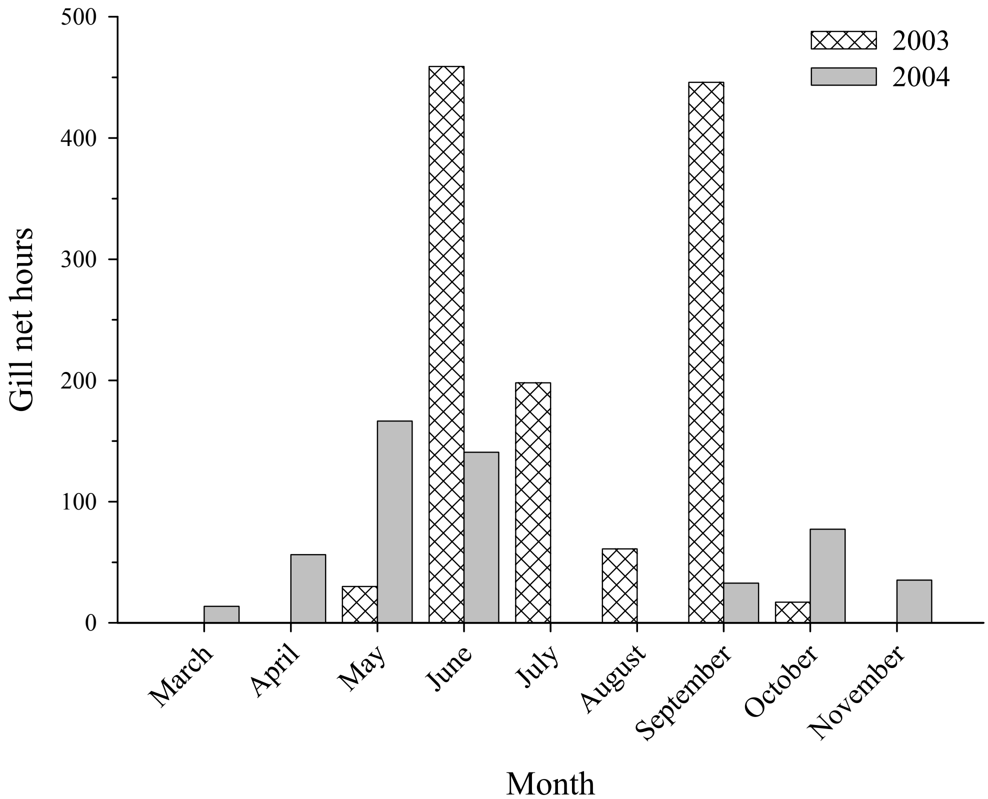


Figure 2. Monthly gill netting effort on Lake McDonald, Glacier National Park in 2003 and 2004. Each gill net hour represents one hour of fishing time for a 38.1-m x 1.8-m sinking, experimental mesh gill net (7.6-m panels of 12, 24, 36, 48, and 65 mm bar-measure mesh). Netting was not conducted in March-April and November 2003, or from July through August 2004.

All lake trout were enumerated, measured (total length; nearest 1 mm), weighed (nearest 1 g), and sex was determined when possible. During spawning, stage of sexual maturity and ripeness were recorded. Maturity of each fish was classified as either immature (undeveloped gonads) or mature (enlarged gonads and, for females, well developed eggs or flaccid, vascularized ovaries and occasionally residual eggs from a previous spawning). Fish that expelled gametes when pressure was applied to the abdomen were considered to be ripe. Lake trout not receiving transmitters were sacrificed and sagittal otoliths and stomachs were removed. Stomach contents were preserved in 15% formalin.

Sagittal otoliths were used to estimate ages for lake trout. Otolith preparation generally followed the methods of Secor et al. (1992). Each otolith was mounted in epoxy resin and a transverse section capturing the core was removed with a low-speed Isomet (Beuhler Inc.) saw. Sectioned otoliths were mounted on glass slides with thermoplastic cement and polished using sandpaper varying from 600-1500 grit. Clove oil was used to improve clarity of prepared otoliths. Ages were determined by counting the number of annuli with a compound light microscope (Campana 1992) at 40-100 power magnification. I estimated ages twice for all 2003 samples and a subsample of 28 otoliths from fish >486 mm in 2004 to evaluate precision of age estimates.

Lake trout stomach contents were examined with a dissecting microscope and identified to the lowest taxonomic level possible depending on the extent of digestion. Prey fish typically were identified to species or family and invertebrates generally were identified to family or order. Diet items were classified as unidentified fish or unidentified invertebrates when digestion prevented further classification. A reference collection containing all fish species known to inhabit Lake McDonald aided in identification of partially digested fish. Prey items were enumerated, wet weight (nearest 0.001 g) was recorded for each taxonomic group, and standard length (nearest 1 mm) was measured for each fish prey item when possible. When invertebrates in a single taxonomic group were abundant, 200 individuals were subsampled and total number was determined by extrapolation. Frequency of occurrence and percent composition by weight of prey items were determined for each taxonomic group (Bowen 1996).

Distribution

Ultrasonic, depth-sensing transmitters were implanted in adult lake trout to assess their seasonal and diel distribution. Two sizes of transmitters were used to minimize transmitter to body weight ratios while maximizing battery longevity. I used 39 transmitters that were 102 mm long, 18 mm diameter, weighed 39 g in air, and had a minimum battery life of 18 months; five smaller transmitters were 85 mm long, 18 mm diameter, weighed 32 g in air, and had a minimum battery life of 12 months (Model DT-97, Sonotronics Inc.). In 2003, the first 19 lake trout >550 mm were implanted with 18-month transmitters, and all fish that survived were tracked until the end of the 2004 field season. In 2004, an additional 25 transmitters (twenty 18-month and five 12-month) were deployed, but fish were selectively chosen by size to provide a more representative sample of adult-size lake trout. Difficulty capturing fish in 2003 resulted in fish being implanted during two time periods (6 June-18 July and 17-27 September). In 2004, 19 fish were implanted from 29 March to 16 June; however, six transmitters were returned by anglers during the summer and were re-deployed from 30 September to 26 October.

Surgical procedures were modified from Winter (1996) and Summerfelt and Smith (1990). Fish were anesthetized with tricaine methanesulfonate (MS-222) and transferred to a portable operating table. During surgery, a water pitcher was used to irrigate the gills with additional MS-222 water or lake water to keep the fish at a desired level of anesthesia (Muhlfeld et al. 2003). An incision large enough to insert the transmitter was made about 10 mm lateral of the mid-ventral line and posterior of the pelvic girdle. When possible, sex was determined by internal examination of the gonads via the incision opening. A transmitter was inserted into the abdominal cavity and the incision was closed with several simple interrupted sutures using a size 3-0 swaged cutting needle and nonabsorbable nylon monofilament suture material (Ethicon Inc.). Surgery time averaged 6.4 minutes (SE = 0.2), and afterwards, fish were briefly placed in a recovery tub of 0.5% fine-stock salt solution to restore electrolytes and the mucous membrane (R. Hunt, Montana Fish, Wildlife and Parks, personal communication). After surgery, fish were held in a net pen for recovery, which typically lasted <60 minutes. Fish were released in the vicinity of capture and were allowed an acclimation period of at least seven days before tracking commenced (Guy et al. 1992).

A systematic tracking schedule assured lake trout relocations were obtained at all times of day during a 24-h period. Four diel tracking periods were delineated (dawn, day, dusk, night). The dawn and dusk periods represented the crepuscular hours and were 4-h periods centered on sunrise and sunset, respectively (Paukert et al. 2004). For example, a 4-h dawn tracking period began 2 h before sunrise and ended 2 h after sunrise, as determined from a regional sunrise-sunset table. The daylight hours between the dawn and dusk periods constituted the day period, and the night period consisted of all dark hours between the dusk and dawn periods.

Tracking was conducted from June through November 2003 and from March through November 2004. I sampled two diel periods each day of tracking, with the goal of relocating as many different fish as possible during a sampling day. Relocating all fish usually was not possible because of a combination of factors, such as the large number of ultrasonic-tagged fish, lake size, variable weather conditions, slower boat navigation at night, and reduced detection range during lake stratification. Fish not relocated during one day were generally relocated the following day of tracking, although I did not specifically target previously missed fish for relocation. It was rare for fish not to be relocated for more than three consecutive tracking days. Starting points for tracking were varied daily to avoid repeatedly relocating fish at the same time of day. The same fish were commonly relocated during multiple diel periods, seasons, and years.

Tracking was conducted with a USR-96 scanning receiver and DH-4 directional hydrophone (Sonotronics Inc.). For each relocation, the boat was navigated over the fish until equal signal strength in every direction was achieved (Guy et al. 1994). When a final fix was determined, I recorded Universal Transverse Mercator (UTM) coordinates from a global positioning system (GPS, accuracy <9 m), transmitter code, transmitter ping interval (later translated to fish depth), lake depth (measured using a depth finder), date, time, and weather conditions.

The data collected for each fish relocation were used to examine several continuous variables (fish depth, relative depth, water temperature, dissolved oxygen, and distance to shore) that described lake trout distribution. Fish depth was the depth occupied by fish as determined from transmitter depth sensors. Relative depth described the vertical position of the fish in the water column relative to the lake depth at that location. For example, a fish suspended in 20 m of water where the lake depth was 50 m would have a relative depth value of 0.4. Temperature and dissolved oxygen values at the depth occupied by fish at each relocation were estimated by extrapolating from the profile measured closest in time and nearest to the relocation. Distance from each relocation to the nearest profile site and to the nearest shore was calculated using ArcGIS version 9.0 software.

I performed blind tests to estimate accuracy and precision for relocating transmitters. This involved suspending an 18-month transmitter 20 m beneath an anchored buoy, and a blindfolded observer relocated the transmitter without previous knowledge of its location. When the final location was determined, a laser rangefinder was used to measure the distance from the hydrophone to the buoy. This exercise was repeated twice by three different observers (without moving the transmitter) to assess precision. Mean accuracy for relocating these transmitters was 11.1 m and precision was ±9.6 m (95% confidence interval). To assure proper function of transmitter depth sensors, all transmitters were tested at known depths by lowering transmitters on a downrigger cable to 7.5 m, 15 m, and 30.5 m prior to deployment. Additionally, a subsample of 9 transmitters was tested at known depths from 1-45 m at 1-m intervals to more thoroughly check accuracy of depth sensors. These depth sensors had a mean accuracy of 1.5 m (±0.8).

Spawning Evaluation

A multi-tiered approach was used to identify and characterize likely lake trout spawning sites and estimate when spawning was initiated. Tracking was continued into the spawning period to identify likely spawning sites because lake trout aggregate during spawning (Gunn 1995). When relocations of $\geq$2 lake trout were observed at a site, subsequent gill net sampling (using previously described sampling gears and techniques) was conducted to confirm presence and evaluate abundance of mature lake trout at the site. Also, evaluating the ripeness of lake trout captured in gill nets provided an estimate of when spawning was initiated. To further evaluate likely spawning sites, an Aqua-Vu DT series underwater video camera was used to document presence of mature lake trout and evaluate substrate. Video footage was recorded to a VHS tape and later converted to digital format. A 400 mm polyvinylchloride (PVC) pipe with labeled length increments was suspended below the camera lens using a chain to provide a frame of reference for estimating substrate sizes (Nester and Poe 1987). The camera was subsequently drifted throughout each spawning site and the most frequently occurring substrate size categories were determined subjectively. Substrate size categories followed the modified Wentworth scale (McMahon et al. 1996). Spawning evaluations were only conducted during 2004 because of limited sampling time in 2003.

Data Analysis

Distribution

Lake trout distribution was examined at seasonal (isothermal, pre-stratified, stratified, post-stratified), and diel (dawn, day, dusk, night) scales. Means for each distribution variable (fish depth, relative depth, water temperature, dissolved oxygen, distance to shore) were calculated for individual fish during each diel period within each season, and individual fish were the experimental unit for all analyses. Differences in means for each distribution variable among seasons and diel periods were tested using repeated measures ANOVA. These analyses were conducted using the mixed model procedure in SAS version 9.0 (Proc MIXED; Littell 1998). Two factors (season, diel period) were included in the model, and the first-order autoregressive covariance structure and Satterthwaite degrees of freedom approximation were specified in the model. Differences in distribution variable means between years were tested separately using the same repeated measures ANOVA procedure.

Home range was estimated for all lake trout relocated at least 25 times during 2004. Home range was not estimated in 2003 because wildfires prevented sampling parts of the lake throughout much of the summer, which could bias estimates. The criteria of 25 relocations was determined subjectively to maximize the number of relocations used to construct the estimate, while minimizing the number of fish excluded from the analysis. The minimum convex polygon (MCP) method, which calculates the area of a convex polygon encompassing a specified percentage of relocations (e.g., 100%, 50%), was used to estimate home range. All MCP home range estimates were calculated using the Animal Movement extension (Hooge and Eichenlaub 1997) for ArcView version 3.3 software. Estimates using the MCP method can be a function of the number of relocations, with home range size increasing as the number of relocations increases (White and Garrott 1990). Thus, simple linear regression was used to examine the relationship between home range size and the number of relocations used in the estimate. To evaluate annual core home range, 50% of the extreme observations from the relocations for each fish were eliminated, and home range was estimated using the remaining relocations. Extreme observations were removed using Animal Movement, which removes the selected percentage of relocations based on their largest harmonic mean value while recalculating harmonic mean values after removing each relocation (Hooge and Eichenlaub 1997). In addition to representing a core occupation area, this restricted home range estimate reduces the influence of extreme values that can affect the estimate (White and Garrott 1990). Because of the irregular shoreline shape of Lake McDonald, the MCP sometimes extended outside the boundary of the lake. I corrected for this by removing the portions of each polygon lying outside the shoreline boundary and recalculating the area of the modified polygon using ArcGIS version 9.0 software. The relationship between home range size (100% MCP and 50% MCP) and fish length was evaluated using simple linear regression.

I specified an alpha level of 0.05 for all analyses, and the Bonferroni correction was used when multiple pairwise comparisons were conducted (Sokal and Rohlf 1995). Diagnostic plots were used to test the assumptions of normality and homogeneity of variance for models used in the analyses.

Population Characteristics

Total annual mortality was estimated using the catch-curve regression method (Ricker 1975) with Fishery Analyses and Simulation Tools (FAST) version 2.0 software (Slipke and Maceina 2001). Mortality was only estimated for age classes on the descending limb of the catch-curve to account for potential sampling bias for younger age classes (Van Den Avyle and Hayward 1999). Also, an age-length key was applied to convert the distribution of ages and lengths from the subsample of aged fish to represent the age and length distribution of all sampled fish (DeVries and Frie 1996). Lake trout sampled after 30 September were not included in the mortality estimate because gill netting targeted adults at potential spawning sites.

To describe lake trout growth rate, I applied the von Bertalanffy growth model:

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

where L_t = the length at time t, L_∞ = the theoretical maximum length, K = the growth coefficient, and t_0 = the time when length theoretically equals 0 mm. The model was fit to length-at-age data using the nonlinear model procedure (Proc NLIN) in SAS version 9.0. This growth model can be used to predict mean length-at-age or inverted to predict time required to reach a given length. The standard weight equation for lake trout was used to calculate relative weight as an index of body condition for lake trout (Piccolo et al. 1993; Anderson and Neumann 1996). Age and total length at which 50% of male and female lake trout were sexually mature was estimated using logistic regression (Heibo and Vollestad 2002), and parameter estimates for the weight-length relationship were estimated from all sampled fish using linear regression on $\log_{10}$ transformed data. The coefficient of variation (CV = SD/mean) was calculated for ages estimated twice for the same sample to measure precision (Campana et al. 1995).

Population Simulations

Modeling simulations were conducted using FAST software (Slipke and Maceina 2001) to assess the effects of varying levels of exploitation on the lake trout population. This software uses the Jones modification of the Beverton-Holt equilibrium yield model (Ricker 1975), similar to other population modeling programs (e.g., MOCPOP; Beamesderfer 1991). Previously, FAST has been used to model fish population responses to varying levels of exploitation (Slipke and Maceina 2001; Quist et al. 2002; Slipke et al. 2002). Despite using the model for the same purpose, my interpretation of model results was unconventional. I was interested in predicting how much exploitation is necessary to suppress or extirpate lake trout in Lake McDonald, rather than preventing overharvest of an exploited population.

I used the yield-per-recruit (YPR) modeling option in FAST to simulate yield and population size at varying levels of exploitation. The model required input parameters describing growth, mortality, the weight-length relationship, longevity, and maturity (Table 1) and estimates yield (Y) using the following equation:

$$Y = (F \cdot N_t \cdot e^{Zr} \cdot W_\infty) \cdot K^{-1} \cdot [\beta(X, P, Q)] - [\beta(X_1, P, Q)],$$

where F = instantaneous fishing mortality rate; $N_t = N_0 \cdot e^{-M(t_r - t_n)}$, the number of recruits entering the fishery at some minimum length at time (t); N_0 = initial population size; M = instantaneous natural mortality rate; t_r = age of recruitment to the fishery; $r = (t_r - t_o)$, time to recruit to the fishery; t_o = time when length theoretically equals 0 mm as estimated by the von Bertalanffy model; Z = instantaneous total mortality rate ($F + M$); W_∞ = maximum theoretical weight derived from L_∞ and the weight-length relationship; K = the growth coefficient from the von Bertalanffy model; β = the incomplete beta function; $X = e^{-Kr}$; $P = Z/K$; Q = slope of the weight-length relationship + 1; $X_1 = e^{-K(Age_{\max} - t_0)}$; and Age_{max} = the maximum age sampled (Slipke and Maceina 2001). Varying rates of conditional natural mortality (cm; natural mortality rate in the absence of fishing mortality) and conditional fishing mortality (cf; exploitation rate in the absence of natural mortality) were input to model different rates of exploitation. Rates of cm and cf were used to estimate F (= -log$_e$[1 – cf]) and M (= -log$_e$[1-cm]) in the equilibrium yield model (Slipke and Maceina 2001). The catch-curve estimate of total annual mortality for lake trout was used to approximate one level of cm because fishing mortality in Lake McDonald is believed to be minimal. Additionally, a higher cm of 20% was selected for comparison purposes. Various rates of cf from 0-90% at 5% intervals were modeled. Longevity was estimated based on the oldest lake trout sampled.

The YPR simulations were conducted for two different minimum length limits (hereafter referred to as minimum effective capture size; MEC). One MEC (373 mm) represented the mean total length of the youngest age class on the descending limb of the catch-curve. Thus, this was the mean length when lake trout fully recruited to the gill nets used in this study. The other MEC was set lower (250 mm) to evaluate benefits that may be associated with developing sampling techniques to effectively capture smaller lake trout. Population size simulations estimated abundance of fish >473 mm and fish

>300 mm total length. The 473 mm limit was selected to represent the population of mature fish, as this was the estimated mean length-at-maturity for males (females matured at a longer length). The 300 mm limit was chosen to represent a larger portion of the population for comparison purposes. All YPR simulations assumed an initial population size of 20,000 recruits, as this seemed to be a plausible population size for Lake McDonald given lake trout density estimates for lakes of similar size (Healey 1978b). However, the actual population size is not critical as it only changes the scale and not the trajectory of model predictions.

Table 1. Parameters used to model the effects of exploitation on the lake trout population in Lake McDonald. Abbreviations are as follows: L_∞= theoretical maximum length, K = the growth coefficient, t_0 = time when length would theoretically be equal to 0 years, and TL = total length.

Parameter	Value
Initial population size	20,000
von Bertalanffy growth coefficients	L_∞ = 922 mm; K = 0.054; t_0 = -2.075 years
Conditional natural mortality (cm)	13% and 20%
Conditional fishing mortality (cf)	0% to 95% (5% intervals)
Log_{10}(weight):log_{10}(length) coefficients	Intercept = -5.61; slope = 3.18
Maximum age	37
Female age at sexual maturity	15 years
Fecundity-to-length relation	Fecundity = -19,019 + 34.26(TL); Peck (1988)
Percent of fish that are females	56%
Percent of females spawning annually	100%
Minimum length limits (MEC)	250 mm and 373 mm TL

In addition to YPR modeling, I simulated the effects of exploitation on the spawning potential ratio (SPR). The SPR was developed to assess recruitment overfishing and is derived by estimating the number of mature eggs produced by an average recruit in its lifetime (potential recruit fecundity; *P*) at an equilibrium population density where density-dependent growth and survival does not occur (Goodyear 1993). Potential recruit fecundity is expressed as:

$$P = \sum_{i=1}^{n} E_i \prod_{j=0}^{i=1} S_{ij} \ ,$$

where n = the number of ages in the unfished population; E_i = mean fecundity of females of age i in the absence of density dependent growth; $S_{ij} = e^{-(F_{ij}+M_{ij})}$, the density-independent annual survival probabilities of females of age i when age j; F_{ij} = the instantaneous fishing mortality rate of females of age i when age j; and M_{ij} = the instantaneous natural mortality rate of females of age i when age j.

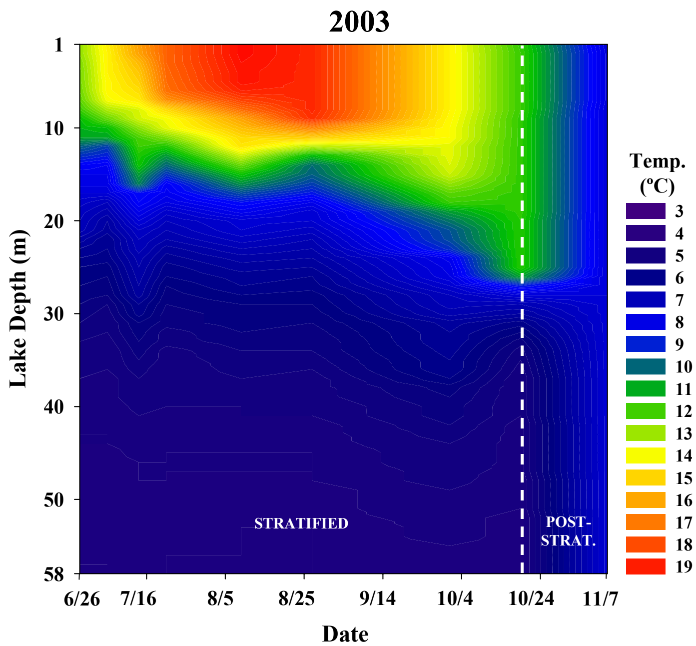
The SPR ($P_{\text{fished}}/P_{\text{unfished}}$) has a maximum value of 1.00 (no exploitation) and declines towards a potential minimum of 0 as exploitation increases. A fecundity-length relationship is necessary to estimate SPR, but limited fecundity data precluded developing a relationship specific to Lake McDonald. Thus, I used a linear fecundity-length relationship for lake trout in Lake Superior (Peck 1988). Sex ratio was estimated from gill netting data, and the percentage of mature females spawning annually was assumed to be 100%. I used the same MECs (250 mm and 373 mm) for SPR simulations that were included in the YPR models.

RESULTS

Abiotic Factors

Within years, considerable temperature variation existed among seasons (Figure 3). The thermal regime was similar during the stratified and post-stratified seasons in both 2003 and 2004 (Figure 3), but comparisons between years could not be made for the isothermal and pre-stratified seasons because of a shorter field season in 2003. The highest surface temperature recorded was 19.4 ˚C on 21 July 2003. Dissolved oxygen levels (2004 data only) varied from 7.8 to 12.3 mg/L, remaining high during all seasons at all depths (Figure 4). The lowest dissolved oxygen measurement of 7.8 mg/L was recorded at a depth of 1 m on 11 August 2004. A positive heterograde dissolved oxygen distribution was present during the stratified season, but other seasons exhibited a fairly uniform orthograde distribution (Figure 4).

Mean Secchi disk transparency was 12.6 m (±2.6) in 2003 and 13.7 m (±1.0) in 2004. The lowest Secchi disk reading each year was 7.3 m on 25 June 2003 and 11.3 m on 15 May 2004, each occurring during months when Lake McDonald was influenced by spring runoff. Secchi disk measurements reached a high of 17.7 m on 26 August 2003 and 16.5 m on 20 August 2004.



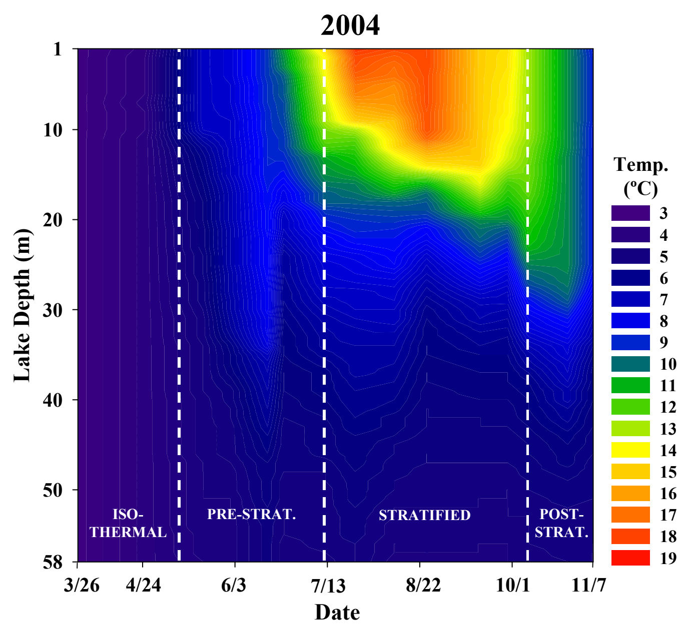


Figure 3. Temperature isopleths for 2003 and 2004 from Lake McDonald, Glacier National Park. Four seasons were identified: isothermal (no temperature gradient), pre-stratified (pre-strat.; temperature gradient without thermocline), stratified (thermocline present as determined by a 1.0º C temperature change in any 1-m interval of the temperature profile), and post-stratified (post-strat.; thermocline no longer present). In 2003, only two seasons were present because of a shorter sampling period.

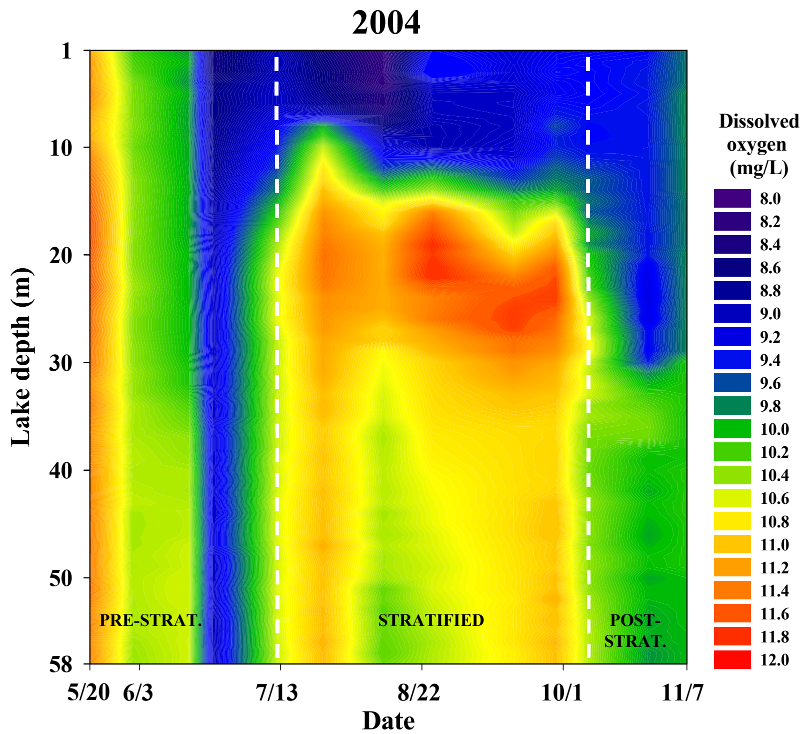


Figure 4. Dissolved oxygen isopleth for Lake McDonald, Glacier National Park in 2004. Seasons were delineated based on temperature criteria (see Figure 3).

Distribution

Ultrasonic, depth-sensing transmitters were implanted in 44 adult lake trout (Table 2) varying from 508 to 859 mm total length (mean = 619 ±24) and 940 to 5,950 g (mean = 2,082 ±330). From 26 June 2003 to 7 November 2003, 242 telemetry relocations were obtained from 16 lake trout, and 34 lake trout were relocated 893 times from 26 March to 7 November 2004 (Table 2). Seven lake trout died within 7 d of release, one died nine months after release, nine were harvested by anglers (based on transmitters returned), two were reported caught and released by anglers, and three fish disappeared (e.g., harvested, transmitters failed, emigrated). One of the harvested fish was caught in 2005 by an angler in Flathead Lake, 93 river-kilometers downstream from Lake McDonald and connected by the Flathead River.

Table 2. Size, sex, tracking period, number of annual relocations, and survival status for all lake trout implanted with ultrasonic transmitters during 2003 and 2004 in Lake McDonald, Glacier National Park (U=unknown; M=male; F=female).

Fish	Length (mm)	Weight (g)	Sex	Tracking period	2003 locations	2004 locations	Survival status
LT1	669	2246	U	21 June-7 Nov 2003 26 Mar-7 Nov 2004	32	44	Survived
LT2	652	2742	U	17 June-7 Nov 2003 26 Mar-7 Nov 2004	28	40	Survived
LT3	603	1462	U	Did not track			Died
LT4	629	2080	U	27 Jun-7 Nov 2003 26 Mar-23 Jul 2004	32	28	Harvested
LT5	603	1812	U	1 Jul-7 Nov 2003 26 Mar-7 Nov 2004	24	47	Survived
LT6	814	5950	U	2 Jul-7 Nov 2003 26 Mar-7 Nov 2004	29	38	Survived
LT7	565	1374	U	1 Jul-7 Nov 2003 27 Mar-2 June 2004	27	15	Harvested
LT8	704	2805	U	3 Jul-7 Nov 2003 27 Mar-5 Nov 2004	20	39	Survived
LT9	570	1295	U	3 Jul-17 Oct 2003	17		Harvested
LT10	716	3846	U	22 Jul-7 Nov 2003 26 Mar-5 Nov 2004	16	40	Survived
LT11	740	3655	U	Did not track			Died
LT12	635	2256	U	7 Aug-7 Nov 2003 26 Mar-5 Aug 2004	12	24	Missing
LT13	702	3025	U	6 Nov-7 Nov 2003	2		Harvested
LT14	735	3100	U	27 Sep-7 Nov 2003 26 Mar-24 Aug 2004	6	32	Harvested
LT15	601	1948	M	17 Oct-7 Nov 2003 26 Mar-25 June 2004	2	17	Died
LT16	703	2852	M	17 Oct-7 Nov 2003 27 Mar-25 Apr 2004	3	6	Harvested
LT17	585	1371	U	Did not track			Missing
LT18	664	2390	M	17 Oct-7 Nov 2003 26 Mar-5 Nov 2004	3	42	Survived
LT19	608	1636	F	5 Nov-7 Nov 2003 26 Mar-7 Nov 2004	2	44	Survived
LT20	569	1365	U	23 Apr-24 Apr 2004		3	Harvested

Table 2 continued.

LT21	527	1135	U	23 Apr-9 Jul 2004	19	Harvested
LT22	572	1581	U	25 Apr-4 Nov 2004	32	Survived
LT23	573	1368	U	17 May-5 Nov 2004	30	Survived
LT24	619	1829	U	17 May-7 Nov 2004	41	Survived
LT25	508	940	U	24 May-7 June 2004	6	Missing
LT26	665	2392	U	24 May-5 Nov 2004	39	Survived
LT27	539	1209	U	Did not track		Died
LT28	524	1085	U	Did not track		Died
LT29	595	1650	U	17 May-5 Nov 2004	45	Survived
LT30	519	975	U	Did not track		Died
LT31	590	1615	F	24 May-5 Nov 2004	34	Survived
LT32	578	1560	U	24 May-7 Nov 2004	36	Survived
LT33	544	1230	U	26 May-7 Nov 2004	36	Survived
LT34	579	1498	F	27 May-25 Oct 2004	26	Recaptured (died)
LT35	590	1890	F	27 May-5 Nov 2004	31	Survived
LT36	557	1325	U	Did not track		Died
LT37	529	1259	F	24 June-7 Nov 2004	25	Survived
LT38	523	1025	F	Did not track		Died
LT39	665	2557	M	7 Oct-7 Nov 2004	9	Survived
LT40	639	2305	M	7 Oct-5 Nov 2004	6	Survived
LT41	685	2707	M	7 Oct-4 Nov 2004	6	Survived
LT42	859	5518	M	25 Oct-7 Nov 2004	6	Survived
LT43	663	2550	M	1 Nov-7 Nov 2004	3	Survived
LT44	515	1179	M	2 Nov-5 Nov 2004	2	Survived

Lake trout rarely (9% of all relocations) occupied depths >30 m during all seasons in 2003 and 2004 (Figure 5), despite an abundance of deeper waters. In 2003, seasonal and diel differences in fish depth were not tested because of an interaction between season and diel period ($F_{3, 53}$= 2.99, P = 0.04). Mean fish depth differed significantly among seasons in 2004 (Figure 5), but there were no differences among diel periods ($F_{3, 196}$ = 0.48, P = 0.70; Table 3). Lake trout occupied shallower depths during the stratified season in 2003 (mean = 19.4 m ±3.6) than in 2004 (mean = 23.3 m ±2.0, $F_{1, 60}$ = 5.86, P = 0.02). Annual depth differences were not tested for the post-stratified season because of an interaction between year and diel period ($F_{3, 59}$ = 2.78, P = 0.05); however, mean depth only varied by 1.1 m between years (2003 = 16.9 m ±3.6, 2004 = 18.0 m ±3.5). Despite significant differences in mean depth among seasons and between years, the means never differed by more than 8.2 meters. However, the biological significance of these differences becomes evident when depth distribution is overlaid on temperature isopleths for each year (Figure 5). In 2004, lake trout had the greatest mean depth (23.3 m ±2.0) during the stratified season when the epilimnion was well-defined. During the stratified season in both years, lake trout had the narrowest vertical distribution, were predominantly found in the upper hypolimnion immediately below the thermocline, and avoided warm (>12˚C) surface waters. During all other seasons (when surface waters were cooler), lake trout frequently occupied shallower depths. The most variable vertical distribution was observed during the isothermal season in 2004. Mean temperature used by lake trout during the stratified season differed between years ($F_{1, 78}$ = 7.04, P = 0.01) and was 8.5˚C (±1.0) in 2003 and 9.1˚C (±0.6) in 2004. The maximum observed temperature used by a lake trout was 15.7˚C during the 2003 stratified season. Further, mean temperature did not differ by diel period during any season in 2003 ($F_{3, 56}$ = 0.25, P = 0.86) or 2004 ($F_{3, 231}$ = 0.65, P = 0.58).

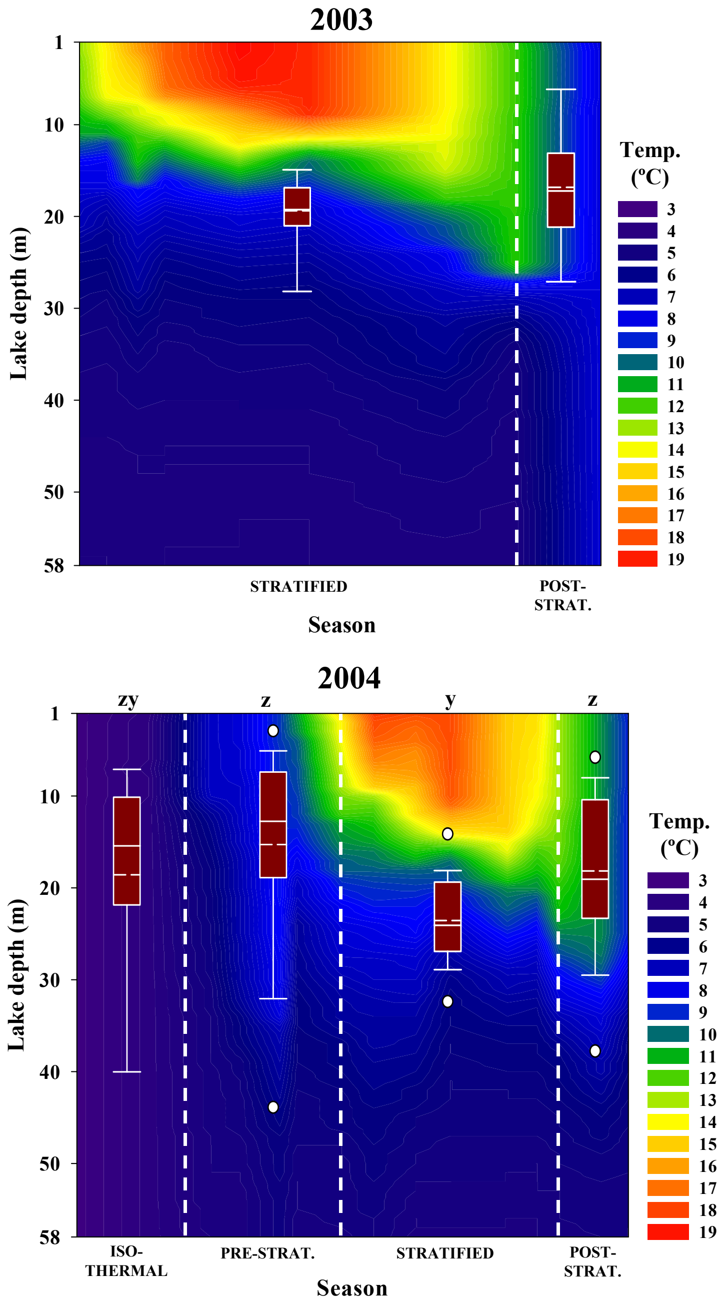


Figure 5. Lake trout depth by season in Lake McDonald, Glacier National Park overlaid on temperature isopleths for 2003 and 2004. Within each box, median depth is indicated by a solid line and mean depth is shown by a dashed line, boxes represent the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles, and circles represent outliers within the 5th and 95th percentiles. Lake trout depths not significantly different ($P > 0.05$) between seasons are indicated by the same letter above each season. Seasonal differences could not be tested in 2003 because of a significant season by diel period interaction.

Table 3. Means and 95% confidence intervals for distribution variables by year, season, and diel period for lake trout tracked in Lake McDonald, Glacier National Park in 2003 and 2004. Confidence intervals were not reported when sample size was <3. Seasonal differences within each year that were not statistically significant ($P > 0.05$) are indicated by the same letter preceding the mean. Seasonal distribution variable means that are not preceded by letters could not be tested because of a significant interaction. There were no diel differences for any distribution variable, thus letters are not shown. Dissolved oxygen (D.O.) was not measured during 2003 or the 2004 isothermal season.

Temporal scale	Mean depth (m)	Mean temp. (˚C)	Mean D.O. (mg/L)	Mean relative depth	Mean distance to shore (m)
2003					
Stratified	19.4 ± 3.6	z8.5 ± 1.0		z0.44 ± 0.13	z327.6 ± 90.5
Dawn	19.0 ± 3.4	8.8 ± 1.4		0.44 ± 0.13	324.9 ± 114.3
Day	19.8 ± 2.9	8.5 ± 1.3		0.44 ± 0.12	335.6 ± 104.8
Dusk	19.4 ± 4.9	8.1 ± 1.1		0.40 ± 0.20	338.9 ± 112.2
Night	19.5 ± 7.7	8.1 ± 1.3		0.52 ± 0.27	381.8 ± 163.4
Post-stratified	16.9 ± 3.6	z7.9 ± 0.6		y0.78 ± 0.12	y95.1 ± 72.0
Dawn	15.7 ± 4.6	7.6 ± 0.1		0.88 ± 0.11	58.8 ± 19.6
Day	22.5 ± 6.4	7.9 ± 1.3		0.70 ± 0.18	113.4 ± 97.5
Dusk	13.4 ± 4.4	7.6 ± 0.1		0.82 ± 0.13	60.7 ± 29.5
Night	14.3	7.6		1.0	11.7
2004					
Isothermal	zy18.3 ± 6.9	z3.5 ± 0.1		zy0.56 ± 0.15	zy271.9 ± 100.5
Dawn	31.2±47.9	3.6 ± 1.1		0.65 ± 0.49	246.9 ± 463.3
Day	18.9 ± 7.5	3.5 ± 0.1		0.58 ± 0.16	272.2 ± 99.6
Dusk	36.1	3.1		0.96	164.4
Night	1.2	3.9		0.44	51.3
Pre-stratified	z15.1 ± 4.4	y7.6 ± 0.4	z10.2 ± 0.1	z0.56 ± 0.09	y180.4 ± 45.5
Dawn	15.3 ± 4.8	7.8 ± 0.4	10.1 ± 0.1	0.56 ± 0.12	157.4 ± 60.5
Day	15.4 ± 4.2	7.6 ± 0.3	10.2 ± 0.2	0.59 ± 0.08	205.6 ± 47.8
Dusk	15.3 ± 4.8	7.6 ± 0.5	10.4 ± 0.3	0.62 ± 0.12	132.3 ± 47.6
Night	15.3 ± 5.7	7.4 ± 0.5	10.3 ± 0.2	0.55 ± 0.13	190.4 ± 72.3
Stratified	y23.3 ± 2.0	x9.1 ± 0.6	y10.9 ± 0.2	z0.60 ± 0.07	z240.2 ± 41.5
Dawn	24.6 ± 3.2	8.6 ± 0.7	11.1 ± 0.2	0.57 ± 0.10	287.0 ± 64.2
Day	24.1 ± 1.9	9.0 ± 0.6	10.9 ± 0.2	0.61 ± 0.08	241.5 ± 55.1
Dusk	22.0 ± 2.6	9.3 ± 0.7	11.0 ± 0.3	0.54 ± 0.08	258.7 ± 56.4
Night	22.2 ± 2.9	8.9 ± 0.8	10.9 ± 0.2	0.66 ± 0.11	193.1 ± 44.9
Post-stratified	z18.0 ± 3.5	x9.1 ± 0.3	x9.7 ± 0.1	y0.77 ± 0.06	x77.5 ± 24.0
Dawn	14.4 ± 8.1	10.1 ± 0.4	9.5 ± 0.3	0.73 ± 0.18	92.8 ± 59.0
Day	17.2 ± 6.6	9.1 ± 0.4	9.6 ± 0.1	0.70 ± 0.08	89.7 ± 36.5
Dusk	18.6 ± 5.4	9.4 ± 0.6	9.6 ± 0.2	0.82 ± 0.12	62.3 ± 31.1
Night	18.9 ± 3.5	8.5 ± 0.3	9.8 ± 0.1	0.85 ± 0.05	65.2 ± 18.9

Mean dissolved oxygen level used by lake trout differed between each season in 2004 ($P < 0.001$); however, seasonal means varied little (9.7-10.9 mg/L). There were no diel period differences in mean dissolved oxygen among seasons in 2004 ($F_{3, 192} = 0.86$, $P = 0.46$; Table 3). Despite high dissolved oxygen levels throughout the water column, lake trout were most commonly located in depths with the highest dissolved oxygen levels during the stratified season (Figure 6).

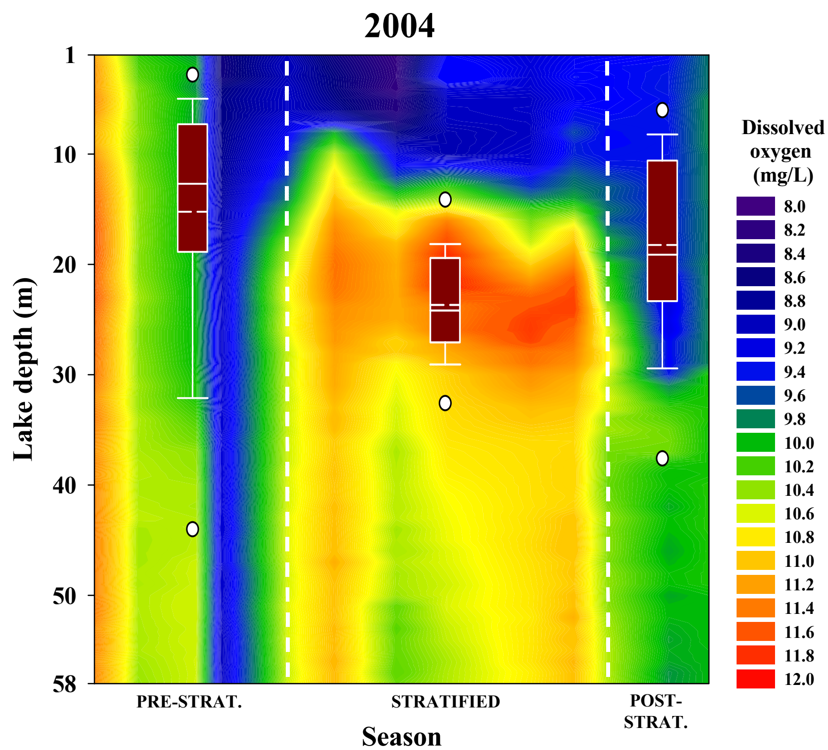


Figure 6. Lake trout depth by season in Lake McDonald Glacier National Park overlaid on a dissolved oxygen isopleth for 2004. Within each box, median depth is indicated by a solid line and mean depth is shown by a dashed line, boxes represent the 25th and 75th percentiles, and circles represent outliers within the 5th and 95th percentiles.

Lake trout were typically suspended in the water column in all but the post-stratified season, when they were more closely associated with the lake bottom (Table 3). Relative depth differed among seasons during both years (Table 3), but not among diel periods in 2003 ($F_{3, 51} = 1.15$, $P = 0.34$) or 2004 ($F_{3, 210} = 1.11$, $P = 0.35$). Also, relative depth during the 2003 stratified season (mean = 0.44 ±0.13) was shallower ($F_{1, 52} = 9.53$, $P = 0.003$) than in the 2004 stratified season (mean = 0.60 ±0.07), but there was no difference between years during the post-stratified season ($F_{1, 88} = 0.99$, $P = 0.32$).

Mean distance to shore varied seasonally during both years, with lake trout typically occupying nearshore habitats in the post-stratified season and pelagic habitats during all other seasons (Table 3). In 2004, lake trout moved farther from shore after thermal stratification developed (Table 3). Additionally, lake trout distance to shore was greater ($F_{1, 52} = 9.96$, $P = 0.003$) during the stratified season in 2003 (mean = 327.6 ±90.5) than in 2004 (mean = 240.2, ±41.5). In contrast, there was no difference ($F_{1, 94} = 0.43$, $P = 0.52$) between years during the post-stratified season. Similar to other distribution variables, distance to shore did not differ among diel periods in 2003 ($F_{3, 50} = 0.14$, $P = 0.94$) or 2004 ($F_{3, 211} =$, $P = 0.11$).

Home range size was estimated based on 25-44 relocations for each of 21 lake trout tracked during the 2004 field season. The relationship between home range size and number of relocations per individual was not significant for both 100% ($P = 0.863$, $r^2 = 0.002$, n = 21) and 50% MCP ($P = 0.703$, $r^2 = 0.008$, n = 21) estimates, thus using varying numbers of relocations for each fish did not bias home range estimates. The mean 100% MCP was 1,600 ha (±247) an area equivalent to 58% of the surface area of

Lake McDonald. While lake trout had tendencies to move throughout large portions of the lake on an annual basis, the mean 50% MCP was 199 ha (±99) and indicated that they used much smaller core areas. There was no relationship between home range size and fish length for 100% ($P = 0.744$, $r^2 = 0.006$, n = 21) or 50% ($P = 0.490$, $r^2 = 0.025$, n = 21) MCP estimates.

Spawning Evaluation

Lake trout began to arrive at likely spawning sites during late-September 2004, shortly before thermal destratification (about 8 October) when surface water temperature was about 12˚C. Lake trout were most abundant at likely spawning sites from late-October to early-November. The first ripe lake trout was captured on 25 October when surface water temperature was 10˚C, and gill net catches of ripe lake trout were highest from 28 October through 8 November. This suggests that spawning was initiated during the last week of October.

Yellow Rocks and Rocky Point were identified as likely spawning sites based on high abundance of lake trout relative to other areas of Lake McDonald during the 2004 post-stratified season (Figure 7). Lake trout were most abundant at Yellow Rocks, with 8 of 19 (42%) tracked lake trout relocated at this site at least once during the post-stratified season. Further, 37% of all relocations during the post-stratified season were located at this site. In comparison, Rocky Point was used by 4 of 19 (21%) lake trout, accounting for 7% of all telemetry relocations during the post-stratified season. Both sites were used fairly infrequently by lake trout during all other seasons in 2004 (Figures 8 and 9).

Moreover, many of the relocations at these sites during the 2004 stratified season occurred immediately prior to the start of the post-stratified season and may have been related to spawning.

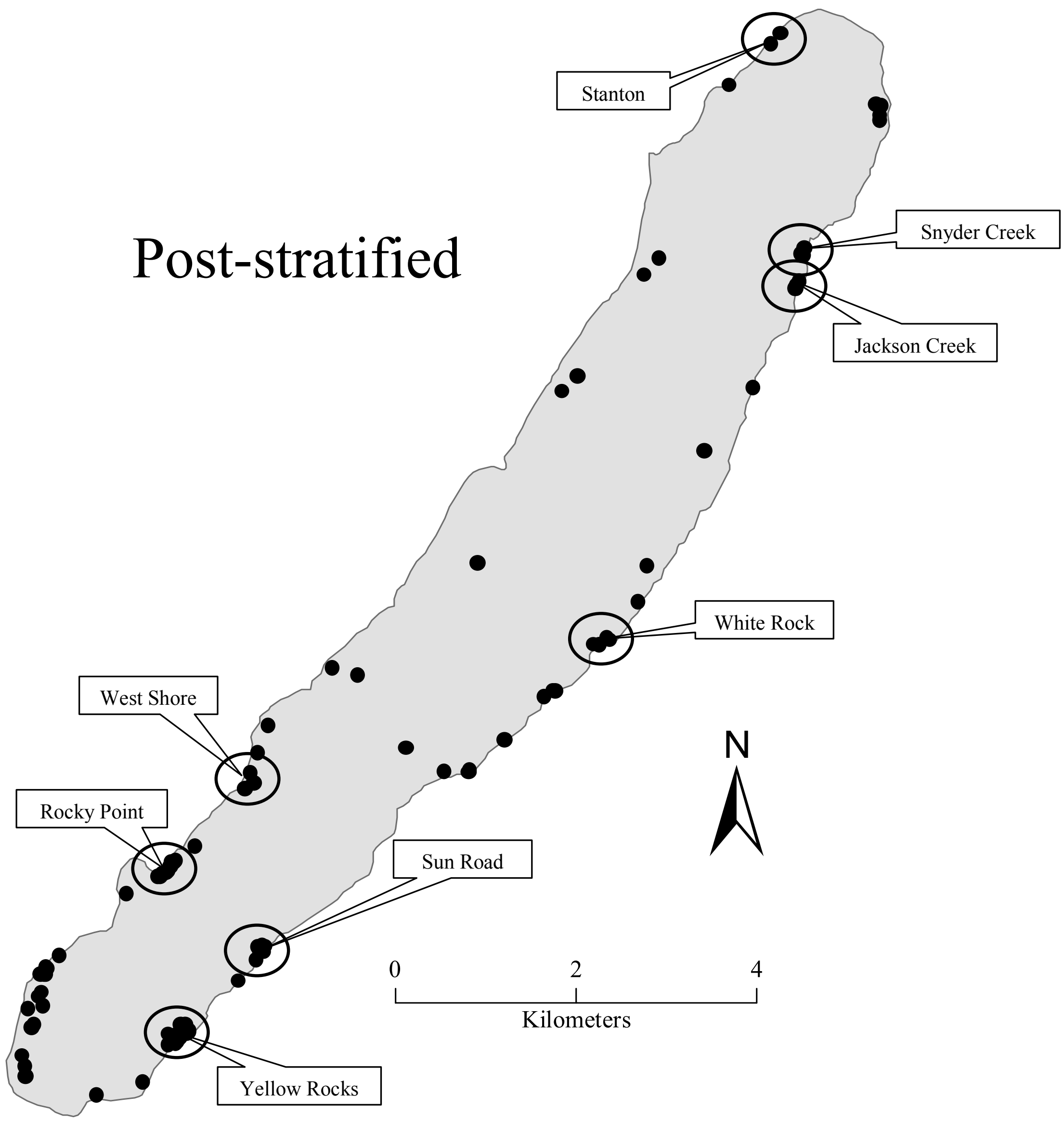


Figure 7. Lake trout telemetry relocations for the 2004 post-stratified season in Lake McDonald, Glacier National Park. Yellow Rocks and Rocky Point are probable spawning sites and other labeled sites are potential spawning areas.

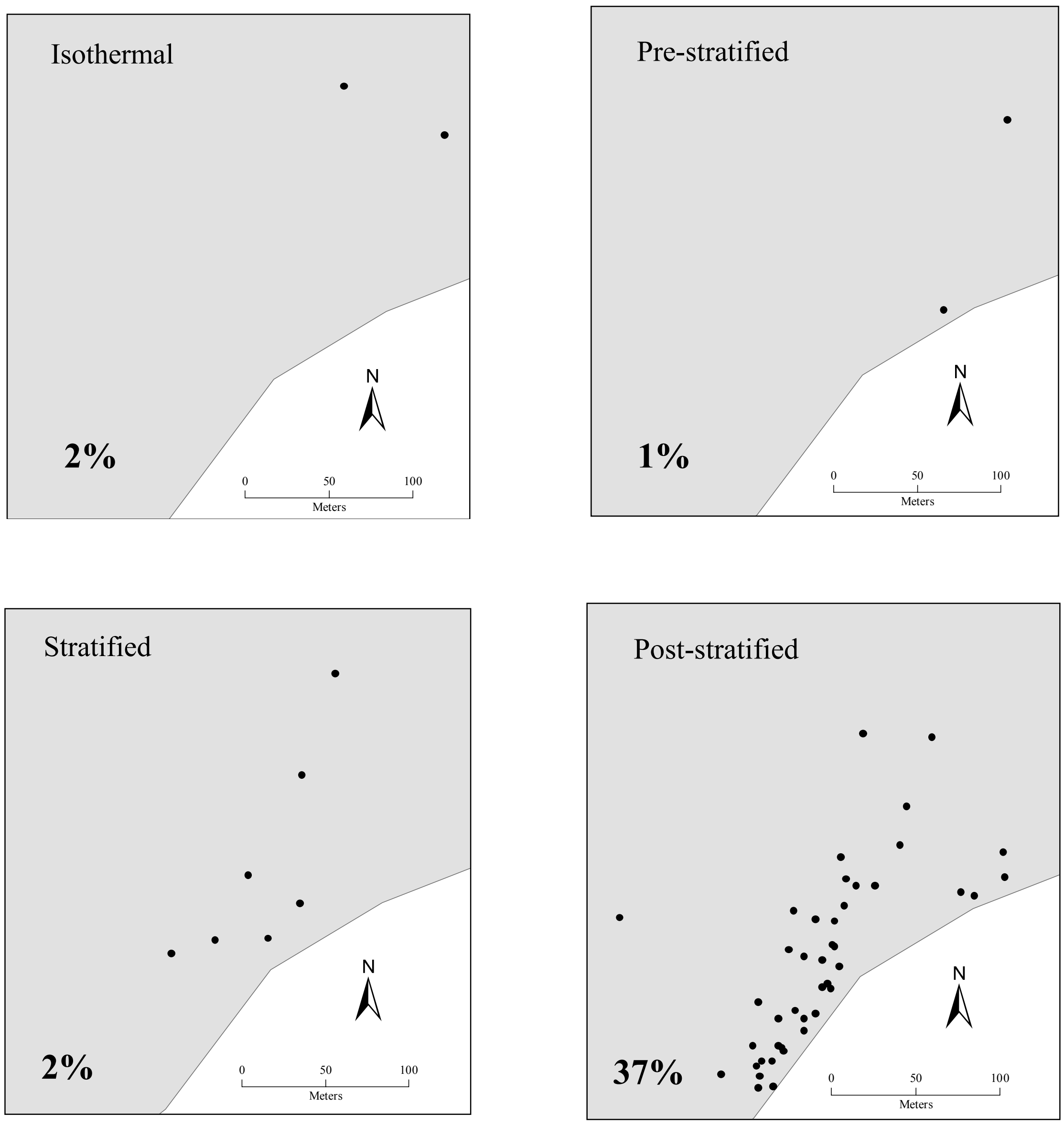


Figure 8. Lake trout telemetry relocations during each season in 2004 at the Yellow Rocks spawning site in Lake McDonald, Glacier National Park. The gray shaded areas represent Lake McDonald and white areas represent land. Percentages indicate the proportion of relocations at the site relative to the total number of relocations throughout Lake McDonald during each season.

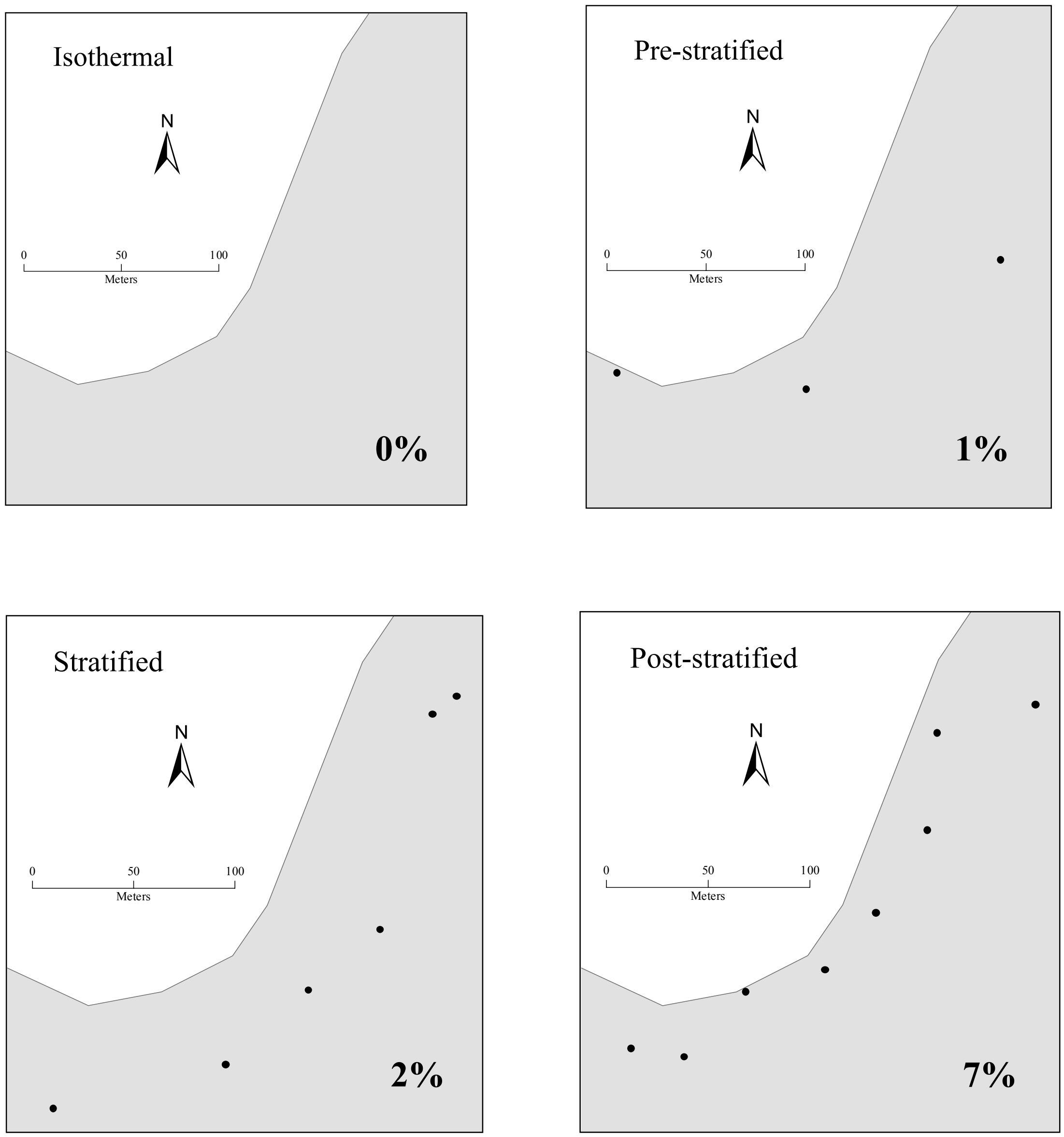


Figure 9. Lake trout telemetry relocations during each season in 2004 at the Rocky Point spawning site in Lake McDonald, Glacier National Park. The gray shaded areas represent Lake McDonald and the white areas represent land. Percentages indicate the proportion of relocations at the site relative to the total number of relocations throughout Lake McDonald during each season.

Gill netting and underwater video observations supported telemetry observations at Yellow Rocks and Rocky Point. During the post-stratified season, gill net catch-per-unit-effort (C/*f*) for mature lake trout was 4.4 lake trout per hour at Yellow Rocks and 11.6 lake trout per hour at Rocky Point (Table 4). In comparison, C/*f* for mature lake trout at sites where spawning activity was not suspected was 0.4 lake trout per hour (Table 4). The sex ratio for mature lake trout was highly skewed, with 92% males at Yellow Rocks and 94% males at Rocky Point. Adult-sized lake trout were observed at both sites using underwater video and were viewed at depths similar to those occupied by tracked lake trout.

Substrate at the Yellow Rocks and Rocky Point spawning sites was dominated by cobble (64-256 mm) and boulder (>256 mm). Typically, these substrates had deep interstitial spaces that were relatively free of fine sediments. Cobble and boulder substrates free of fine sediments were never observed on camera at ten random sites in Lake McDonald, suggesting that these substrates may be fairly limited.

In addition to the two likely spawning sites, six additional sites were identified that had similar characteristics to Yellow Rocks and Rocky Point (Figure 7). Lake trout abundance was lower at these sites, but each was used by $\geq$2 tracked lake trout, gill net C/*f* was higher than for sites where spawning was not suspected (Table 4), and adult-sized lake trout were observed with underwater video. Cobble and boulder substrate was present at each of these sites, although the abundance of these substrates relative to Yellow Rocks and Rocky Point could not be quantified.

Table 4. Catch-per-unit-effort (C/*f*) data for mature lake trout sampled at potential spawning sites and non-spawning sites in Lake McDonald, Glacier National Park during 2004. Each gill net hour represents one hour of fishing time for a 38.1-m x 1.8-m sinking, experimental mesh gill net (7.6-m panels of 12, 24, 36, 48, and 65 mm bar-measure mesh).

Site name	GPS coordinates	Gill net sets	Gill net hours	C/*f* for mature lake trout	Mature lake trout captured	Mature males (%)
Yellow Rocks	280708 N 5380115 E	8	5.4	4.4	24	91.6
Rocky Point	280599 N 5381972 E	4	2.6	11.6	30	94.1
West Shore	281457 N 5382880 E	2	1.4	4.3	6	100.0
Stanton	287015 N 5390761 E	6	3.9	5.4	21	85.7
Snyder Creek	287648 N 5388795 E	2	1.3	1.6	2	100.0
Jackson Creek	287570 N 5388434 E	2	1.0	2.9	3	100.0
White Rock	285389 N 5384478 E	2	1.5	3.3	5	80.0
Sun Road	281641 N 5381103 E	2	1.2	0.9	1	100.0
Non-spawning sites		18	14.8	0.4	6	83.3

Population Characteristics

Four hundred and fifteen lake trout were sampled (401 gill net, 8 angling, 6 hoop net), and lengths varied from 134 to 978 mm (Figure 10). Lake trout varied in age from 1 to 37 years (n = 273; Figure 11) and had a mean age of 11.2 (±0.8) years. I estimated age twice for a subsample of 181 otoliths, and the mean coefficient of variation was 6.9%. The same age was assigned for 32% of samples, 74% were within 1 year, and 94% were within 2 years. Length-at-age was highly variable, particularly for fish >15 years (Figure 12). For example, the oldest lake trout was 37 years and 589 mm, and the largest lake trout was 978 mm and 29 years. Growth rate for lake trout in Lake McDonald was slow (Figure 12), especially compared to growth rates for two other regional lake trout populations (Flathead Lake, MT and Yellowstone Lake, WY; Figure 13). Lake trout condition was poor, as all length categories had extremely low mean W_r values (Table 5). These W_r values were below the 11th percentile when compared to the cumulative frequency distribution of mean W_r values for lake trout throughout North America (Hubert et al. 1994; Table 5). Sexual maturity was reached at 12 years (473 mm) for males and 15 years (555 mm) for females. The youngest mature lake trout sampled was 11 years (male), and the shortest mature fish was a 433 mm male. Total annual mortality for lake trout ages 8-27 was 13.2% (P <0.001, r^2 = 0.63, β_0 = 4.22, β_1 = -1.41, n = 20). Lake trout younger than age-8 were on the ascending limb of the catch-curve, thus were not included in the mortality estimate (Figure 14). The proportion of female lake trout sampled relative to males was 0.56. Fish sampled after 30 September each year were not included in the sex ratio estimate because gill netting targeted adults at potential spawning sites. The weight-length relationship for lake trout was highly significant (P <0.001, r^2 = 0.99, n = 415; Figure 15).

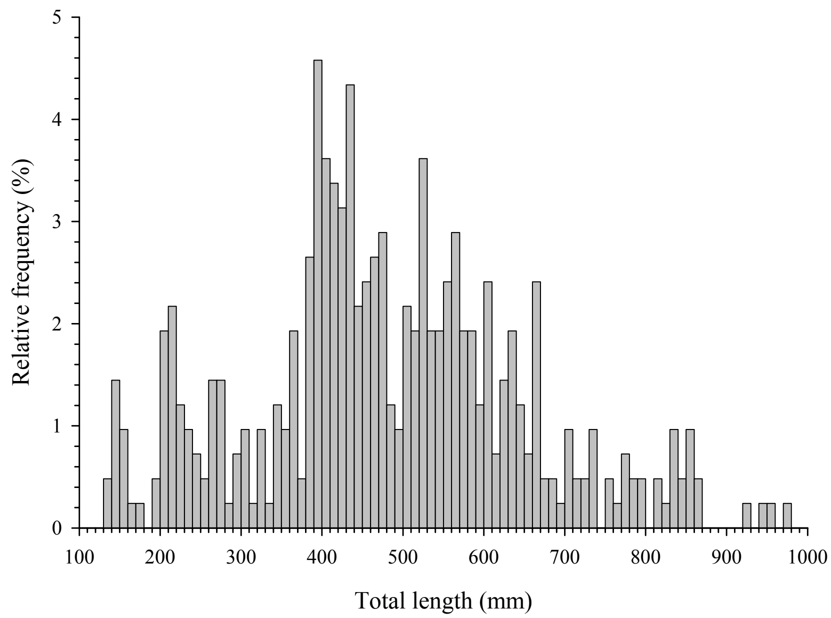


Figure 10. Length frequency for 415 lake trout sampled from Lake McDonald, Glacier National Park in 2003 and 2004 (years pooled).

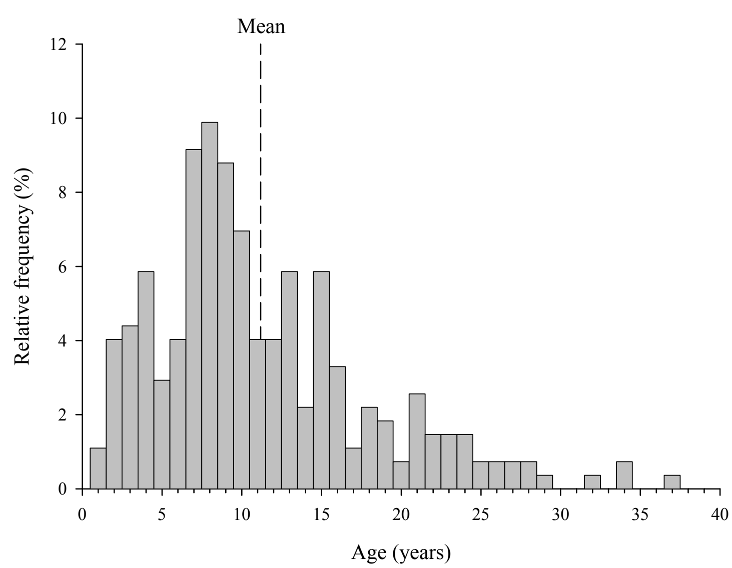


Figure 11. Age frequency for 273 lake trout sampled in Lake McDonald, Glacier National Park in 2003 and 2004 (years pooled).

Table 5. Mean relative weight (W_r) and 95% confidence intervals by length category for lake trout in Lake McDonald, Glacier National Park during 2003 and 2004 (years pooled). Mean W_r for each length category was compared to percentiles from a cumulative frequency distribution of mean W_r for lake trout throughout their North American range (Hubert et al. 1994).

Length category	N	Mean W_r	Percentile of cumulative frequency distribution
Stock-quality	164	75 (±1.0)	< 1st
Quality-preferred	122	78 (±1.4)	< 1st
Preferred-memorable	40	85 (±3.2)	9th
Memorable-trophy	19	86 (±4.6)	10th

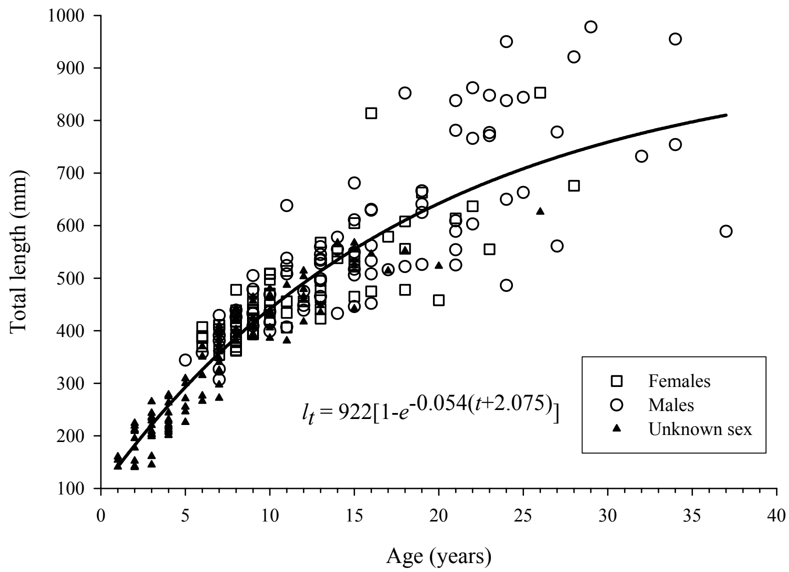


Figure 12. Length-at-age and von Bertalanffy growth model for lake trout sampled from Lake McDonald, Glacier National Park in 2003 and 2004 (n=273). Growth is described by the fitted von Bertalanffy growth model, where l_t = total length at time t and t = age in years.

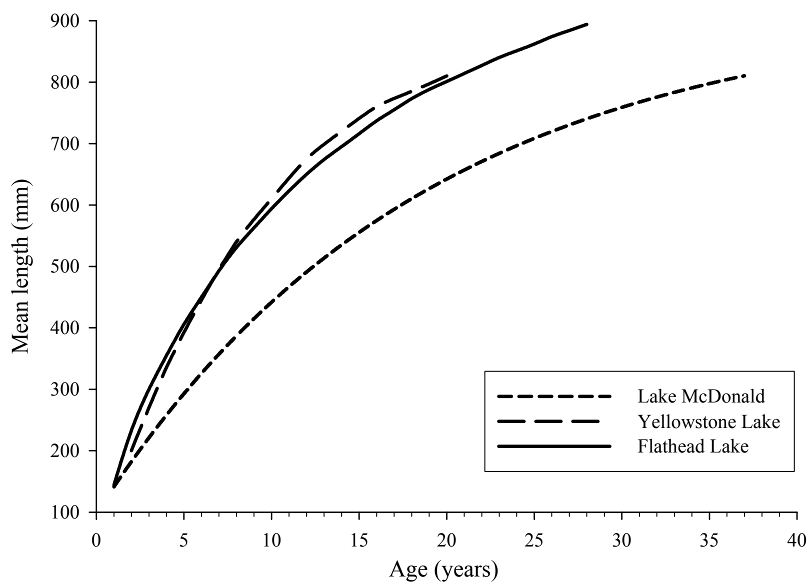


Figure 13. Growth rate for lake trout in Lake McDonald, Glacier National Park compared to two regional lake trout populations (Flathead Lake, MT and Yellowstone Lake, WY). Growth rate was determined by fitting the von Bertalanffy growth model to mean length-at-age data for each population. Growth rates were reported by Ruzycki and Beauchamp (1997) for Yellowstone Lake and by Beauchamp (1996) for Flathead Lake.

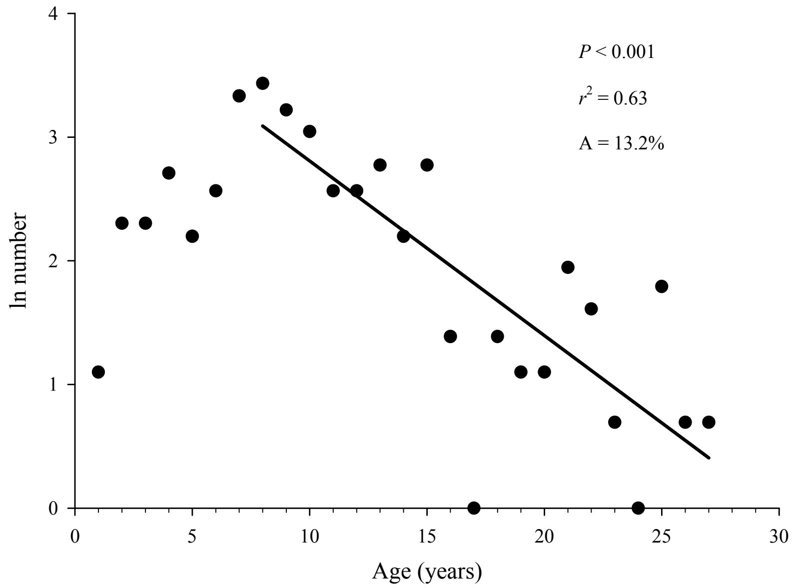


Figure 14. Catch-curve for lake trout (n = 273) sampled from Lake McDonald, Glacier National Park in 2003 and 2004. Total annual mortality (A) was 13.2%.

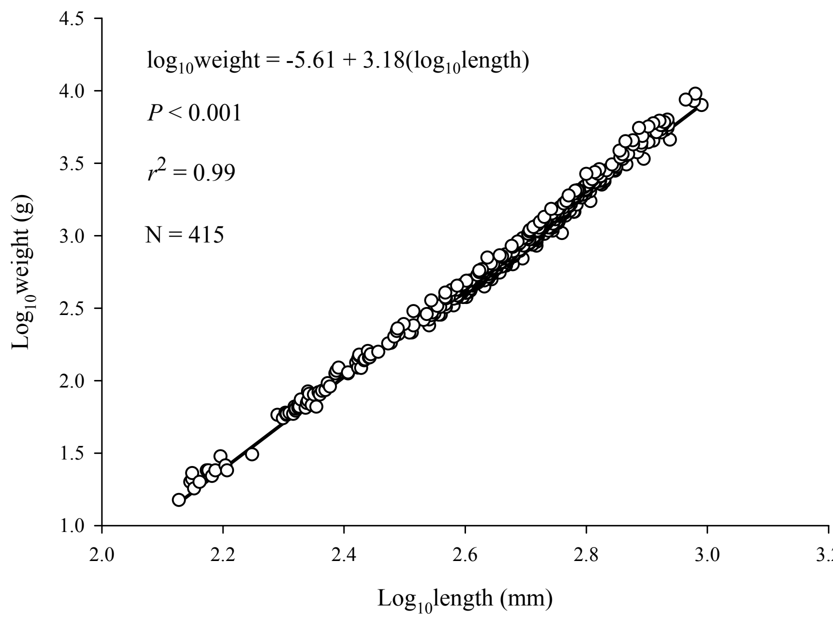


Figure 15. Weight-length relationship for lake trout sampled from Lake McDonald, Glacier National Park in 2003 and 2004 (years pooled). Weight and length data were $\log_{10}$ transformed.

Population Simulations

Growth overfishing (the point beyond which yield declines as exploitation increases) was more easily reached at a lower conditional natural mortality rate (cm = 13%) and lower minimum effective capture size (MEC = 250 mm; Figure 16). At a higher MEC (373 mm), growth overfishing was minimal even at high exploitation rates given cm = 13%, and at cm = 20% yield reached a plateau, but growth overfishing never occurred. Yield was lower at the higher cm (20%) because of lower survival, but growth overfishing was more easily achieved at cm = 13%.

Similar to yield, the effect of exploitation on population size was influenced by MEC and cm rate (Figure 17). Population reductions were possible at lower exploitation rates for the 250 mm MEC because smaller fish could be harvested, thus leaving fewer fish to recruit to larger sizes. Further, the higher cm of 20% allowed for greater population reductions at a given exploitation rate because of lower natural survival. Despite the effects of MEC and cm rate, simulations predicted population declines of about 30-95% at moderate exploitation rates of 20-50%. Declines were highest for mature lake trout (>473 mm), but even these larger lake trout could not be completely eliminated unless exploitation rate exceeded 80%.

In contrast to yield and population size, SPR simulations were not highly influenced by MEC and cm (Figure 18). At all levels of MEC and cm, potential lifetime egg production was reduced by >90% at exploitation rates <20%. Moreover, SPR was 0 at exploitation of 38% for 250 mm MEC, and 47% for 373 mm MEC (all for cm = 13%), and these values change by <3% when cm =20%.

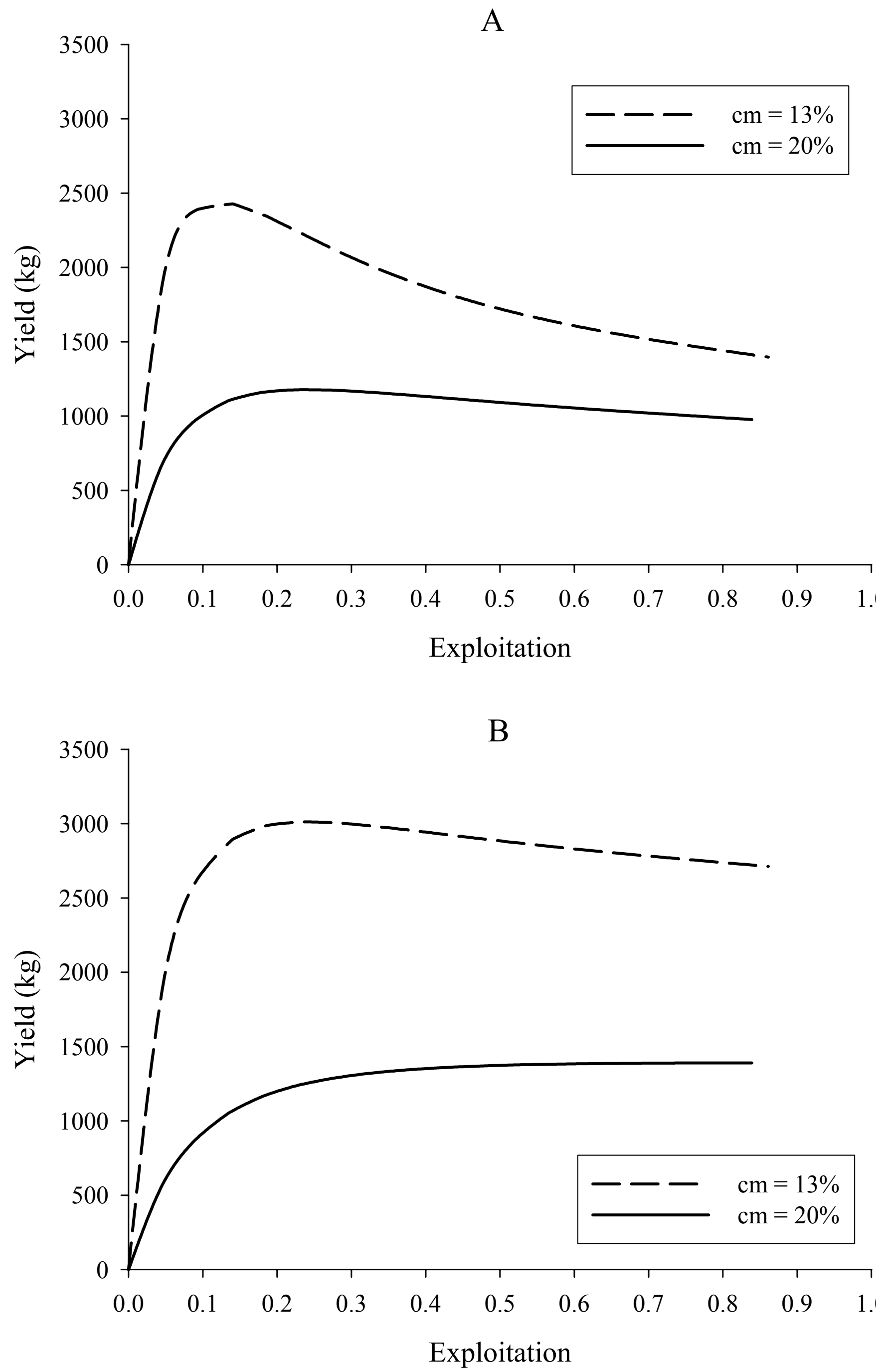
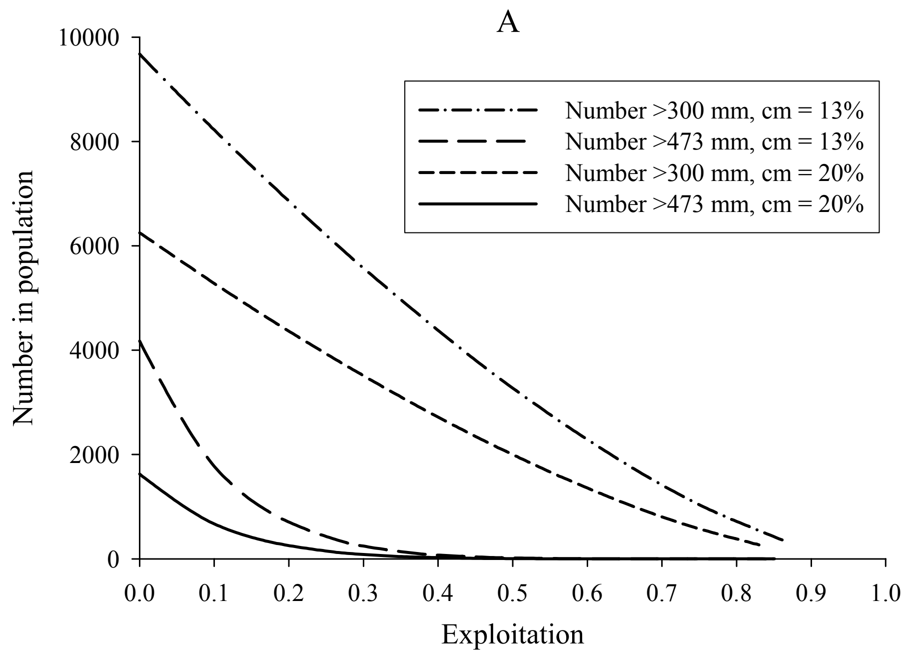


Figure 16. Simulated yields for the lake trout population in Lake McDonald, Glacier National Park with conditional natural mortality (cm) rates of 13% and 20%. Yield was simulated for minimum effective capture sizes of 250 mm total length (A) and 373 mm total length (B).



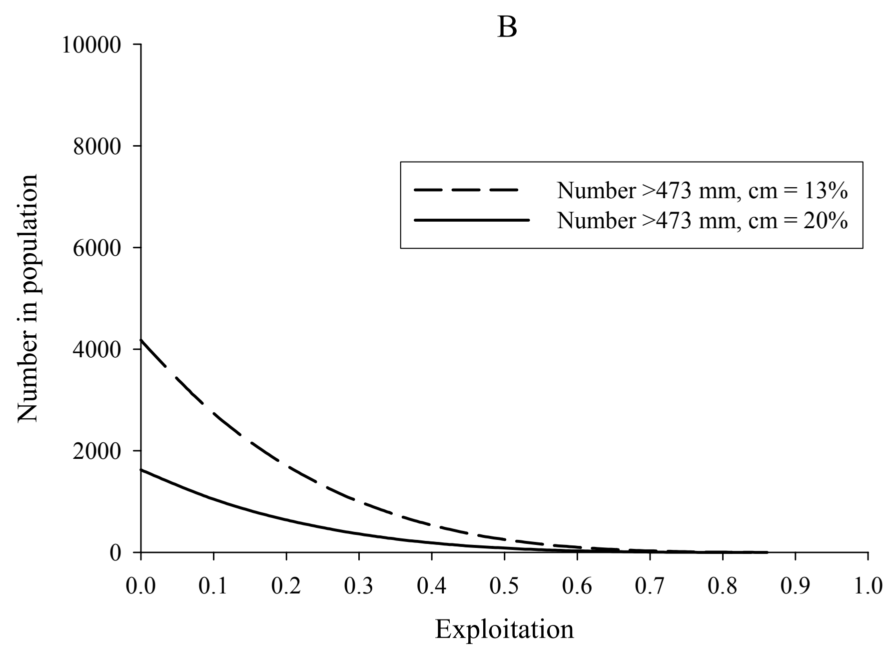


Figure 17. Simulated population sizes for lake trout in Lake McDonald, Glacier National Park with conditional natural mortality (cm) rates of 13% and 20%. Population size was simulated for fish >300 mm and >473 mm total length given a minimum effective capture size (MEC) of 250 mm (A) and 373 mm (B). All simulations assumed an initial population size of 20,000 recruits. Note that fish >300 mm were not included in the second simulation because they were below the 373 mm MEC.

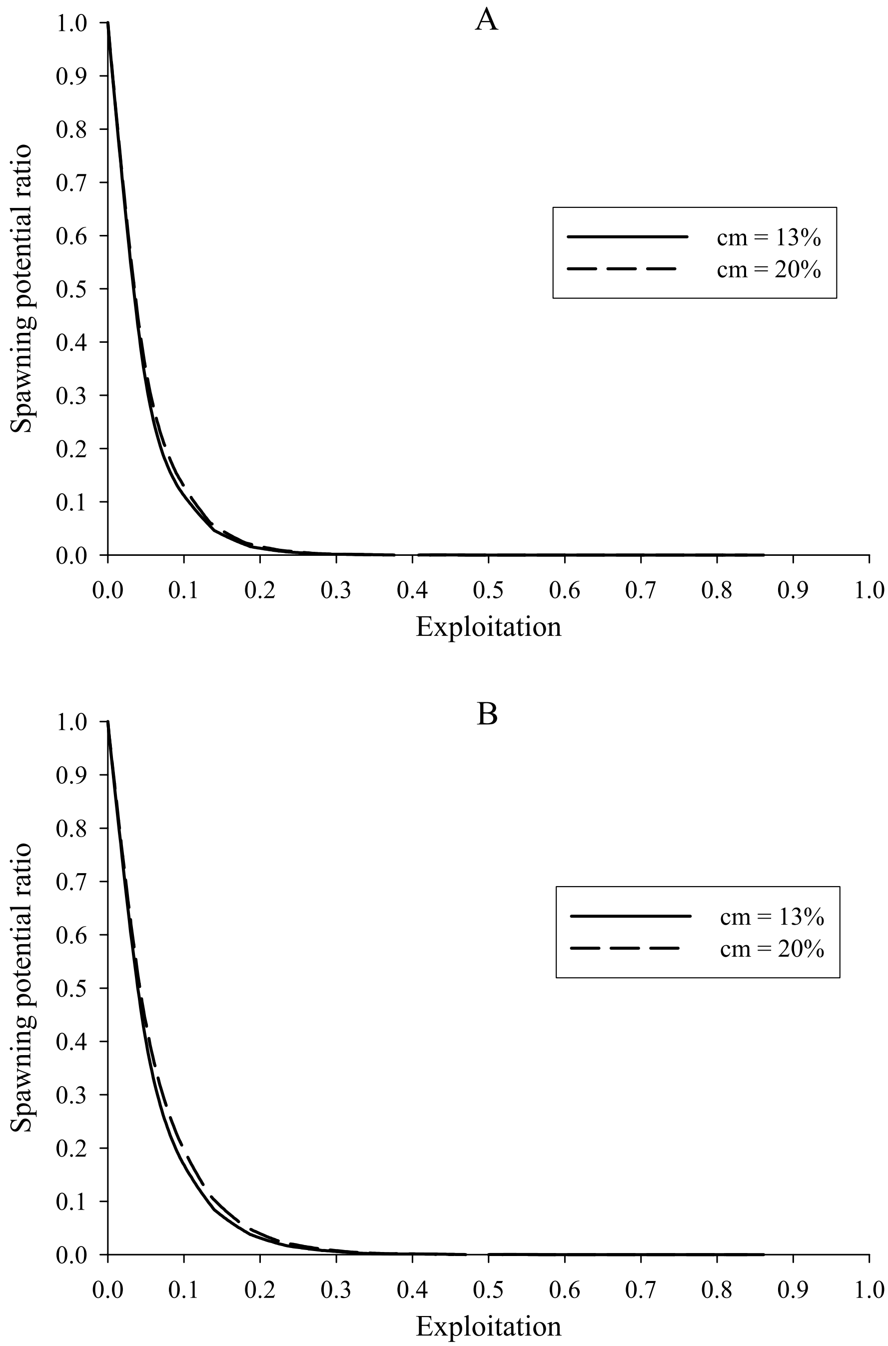


Figure 18. Simulated spawning potential ratios (SPR) for lake trout in Lake McDonald, Glacier National Park with conditional natural mortality (cm) rates of 13% and 20%. Simulations were conducted assuming a minimum effective capture size of 250 mm (A) and 373 mm total length (B).

Diet

Stomach contents were sampled from 254 lake trout (140-978 mm) from May through November 2003 and 2004 (years pooled; Appendix A). The proportion of empty stomachs was 18.6% in the pre-stratified season and 24.6% in the stratified season; however, this total increased to 70.0% during the post-stratified season. The mean weight of total prey consumed per lake trout (empty stomachs excluded) was 4.2 g (±2.0). Fish and invertebrates were important prey items numerically (Figure 19), but fish composed the majority of the diet items by weight (Figure 20). Fish prey made up 95.1% of the total weight of prey consumed by lake trout. Lake whitefish, mountain whitefish, and pygmy whitefish (classified as whitefish species) were the most abundant prey items by weight during the pre-stratified and stratified seasons, but were absent from lake trout diets in the post-stratified season (Figure 20). Unidentified fish were most abundant in the post-stratified season, with no other prey item constituting >11% of the diet by weight (Figure 20). Salmonids (*Oncorhynchus spp.* and *Salvelinus spp.*) were consumed infrequently, although cannibalism of lake trout contributed 9.1% by weight to the diet during the stratified season (Figure 20). There were no identifiable westslope cutthroat trout or bull trout found in lake trout stomach samples.

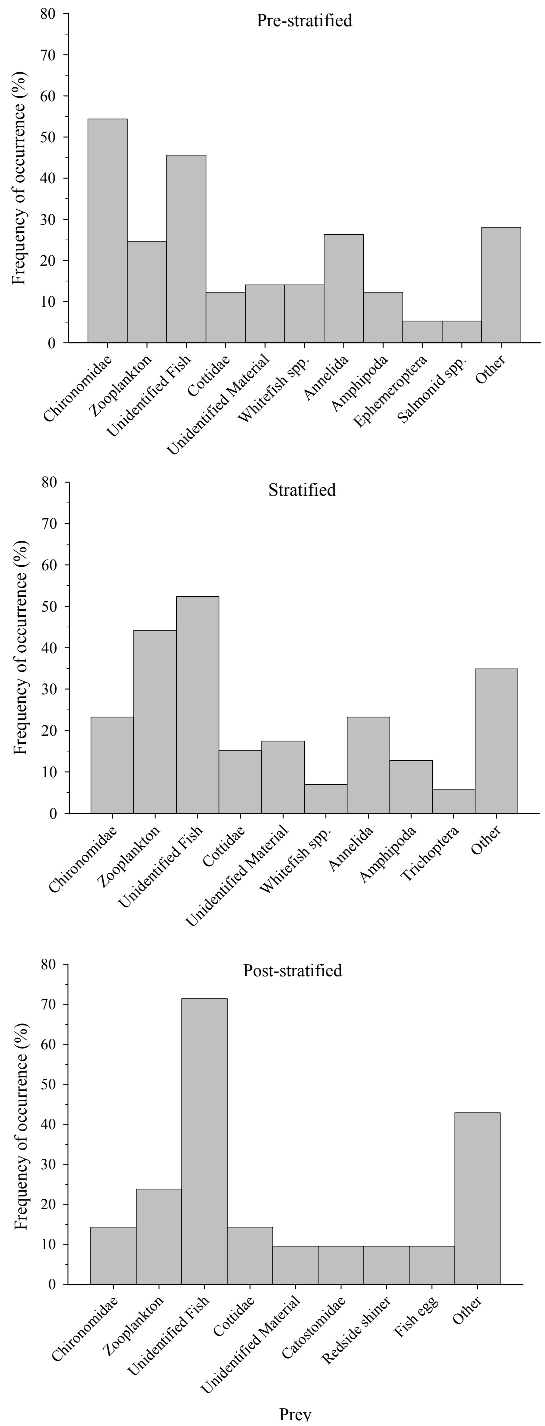


Figure 19. Frequency of occurrence by season (see text for season delineation) of prey items for lake trout sampled from Lake McDonald, Glacier National Park from May through November 2003 and 2004 (years pooled). Prey items occurring in <5% of lake trout diets were classified as Other.

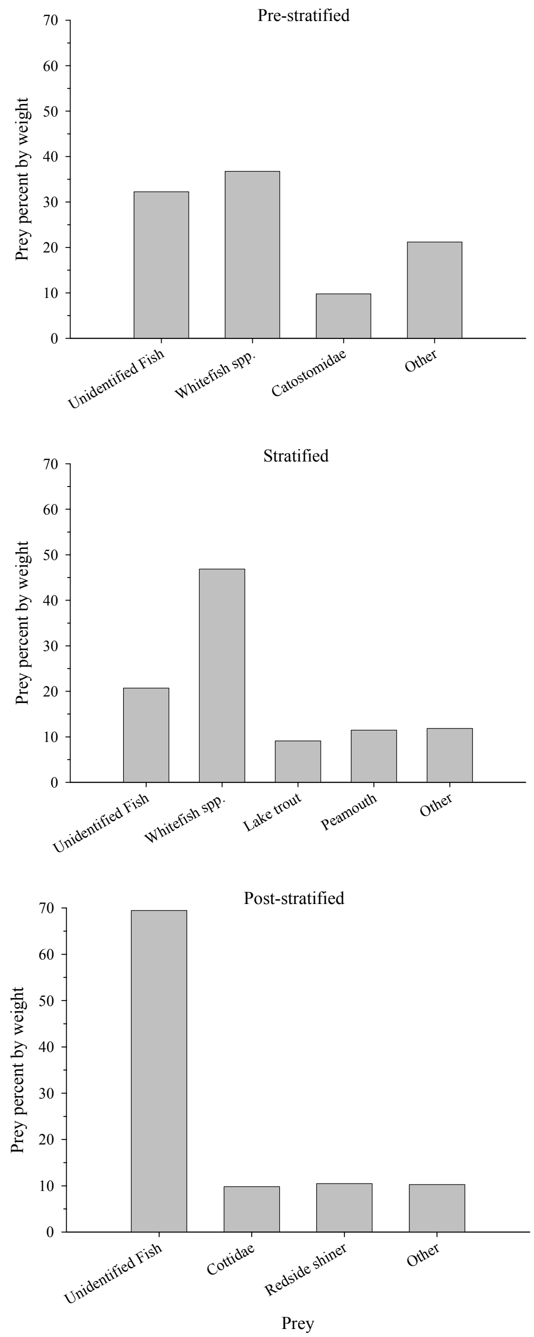


Figure 20. Percent by weight of prey items by season (see text for season delineation) for lake trout sampled from Lake McDonald, Glacier National Park from May through November 2003 and 2004 (years pooled). Prey items making up <5% by weight of lake trout diets were classified as Other.

DISCUSSION

Distribution

The rare use of depths >30 m by lake trout is fairly consistent with the vertical distribution described for lake trout in other deep lakes (Johnson 1975; Eck and Wells 1986). This is not surprising since fish densities in oligotrophic lakes typically support the largest fish biomass in the upper portion of the water column because of more abundant food resources (Johnson 1975; Sandlund et al. 1985).

Temperature appeared to have the greatest influence on vertical distribution. Lake trout had the most variable vertical distribution during isothermal conditions, and constricted their distribution considerably as water temperatures warmed. When warmer temperatures were available during stratification, lake trout occupied the upper hypolimnion where temperatures were within the fundamental thermal niche (10 ± 2°C) for the species (Magnuson et al. 1990). Lake trout depth during the stratified season was greater in 2004 than in 2003, corresponding to a deeper thermocline in 2004. This further demonstrates the affinity lake trout have for the interface between the metalimnion and hypolimnion.

In pelagic systems, such as Lake McDonald, stratification provides habitat structure in an otherwise homogeneous environment and a mechanism for species to partition thermal habitat (Brandt et al. 1980). Thus, lake trout may be isolated from prey species that inhabit the epilimnion (e.g., westslope cutthroat trout). The epilimnion appeared to be a thermal barrier, as lake trout were rarely located in this region and the maximum observed temperature occupied (15.7°C) was well below maximum surface temperatures. Further, lake trout occupied shallower depths immediately prior to and immediately after thermal stratification, suggesting that temperature was restricting their use of shallower waters. These observations are consistent with other studies that suggest lake trout are infrequently found at temperatures >15°C (Johnson 1975; Martin and Olver 1980).

Lake trout distribution may not be influenced entirely by temperature preference and lake thermal structure, but also by prey distribution (Sellers et al. 1998). The high dissolved oxygen levels present at depths occupied by lake trout during stratification provide insight into the influence of prey on vertical distribution of lake trout. Despite dissolved oxygen levels throughout the water column that were well above the lower limit of 5-6 mg/L for lake trout (Sellers et al. 1998), depths with the highest dissolved oxygen were used by lake trout during stratification. In contrast, lake trout did not occupy depths with the highest dissolved oxygen during other seasons. Thus, dissolved oxygen itself did not appear to influence lake trout distribution. Instead, elevated dissolved oxygen resulted from a concentration of phytoplankton near the thermocline, which is common in deep, oligotrophic lakes (Horne and Goldman 1994; Wetzel 2001). A previous study in Lake McDonald documented elevated levels of dissolved oxygen in depths with high algal biomass during stratification (Ellis et al. 1992), which closely matched my observations. The concentration of phytoplankton likely attracted zooplankton and various fishes. Whitefish species (lake whitefish, mountain whitefish, pygmy whitefish), which prey on zooplankton in Flathead Lake (Leathe and Graham

1982), dominated the lake trout diet during stratification. Thus, prey abundance likely influenced the vertical distribution of lake trout during stratification. Lake trout in Canadian Shield lakes had a similar vertical distribution during stratification in response to elevated dissolved oxygen levels (Sellers et al. 1998).

The consumption of prey that often occupy pelagic habitats (e.g., whitefish species) suggests that prey location contributed to the vertical position (relative depth) of lake trout in the water column. Also, vertical position of lake trout may be related to the steep bathymetry of Lake McDonald, which results in a relatively small amount of benthic habitat at depths frequently used by lake trout. Vertical position of lake trout is rarely documented; however, lake trout were frequently suspended in the hypolimnion in a small Canadian Shield lake during thermal stratification (Snucins and Gunn 1995).

Distance to shore and depth distribution illustrated a shift to pelagic habitats as water temperatures warmed in summer, followed by a shift back to littoral habitats after thermal destratification. Similar depth distribution patterns have been reported (Snucins and Gunn 1995; Sellers et al. 1998); however, I am unaware of any studies that have quantified seasonal changes in distance to shore for lake trout.

The lack of diel differences in distribution of lake trout in Lake McDonald was unexpected since diel variation in distribution has been reported for lake trout. For example, lake trout in small Canadian Shield lakes vertically migrated into the epilimnion at night during stratification (Sellers et al. 1998). Lake trout in another Canadian Shield lake moved closer to shore at night to occupy a groundwater site that provided thermal refuge (Snucins and Gunn 1995). Similarity in diel distribution within seasons indicates that lake trout in Lake McDonald have narrow diel habitat requirements.

Lake trout are a mobile species and have been reported to occupy areas >57 km from tagging sites in Lake Michigan (Schmalz et al. 2002). In this study, lake trout also displayed the ability to move long distances. However, they often occupied relatively small areas of Lake McDonald. Walch and Bergersen (1982) reported lake trout home ranges that encompassed <20% of the surface area of small Colorado lakes and suggested that restricted home ranges are established when habitat requirements can be met in a limited area. Similarly, Charnov et al. (1976) suggested that fish increase home range size when prey is limited. Based on these explanations and considering the slow growth rate and poor condition for lake trout in Lake McDonald, I would expect lake trout to establish larger core home ranges to obtain sufficient resources. An alternative explanation is that smaller home range results from social interactions among fish (Fish and Savitz 1983). Home ranges may be relocated during different seasons to meet changing habitat needs (e.g., spawning sites; Walch and Bergersen 1982). Sample sizes were not large enough in my study to estimate home range for each season; however, this would have been useful for determining if seasonal changes in location or size of home ranges occurred.

Spawning Evaluation

The combined methods of telemetry, gill netting, and underwater video observation were effective for identifying likely spawning sites for lake trout. Marsden et al. (1995) caution the use of methods from which spawning evidence can only be inferred; however, each individual method corroborated the others and added confidence to inferences about location of spawning sites. Other studies have also had success identifying lake trout spawning sites using a multiple-method approach (Beauchamp et al. 1992; Gunn and Sein 2000).

Lake trout behavior observed during the spawning period was comparable to behavior of populations in their native range. Departure of lake trout from a pelagic distribution to a more littoral and benthic distribution during post-stratification is explained by spawning behavior, since lake trout broadcast their eggs over bottom substrates (Gunn 1995). Lake trout spawn when water temperature declines to 14˚-8˚C in autumn, which usually coincides with thermal destratification (Gunn 1995). In Lake McDonald, disruption of thermal stratification appeared to trigger arrival of lake trout at spawning sites, but spawning was not initiated until the last week of October. Spawning likely ended in mid-November based on an average spawning duration for lake trout of about 2-3 weeks (MacLean et al. 1981). Lake trout most commonly spawn in shallow water (Sly and Evans 1996). For example, lake trout spawn <10 m from shore in depths <2 m in small Ontario lakes (Gunn 1995), and all confirmed spawning sites in the Great Lakes occur in littoral waters <18 m deep (Marsden et al. 1995). Lake trout in Lake McDonald also used littoral areas during spawning, but mean depth (18.0 m) was greater than typically reported. Lack of spawning in shallow depths might be attributed to the presence of suitable spawning substrate in deeper waters than would be expected in lakes with more gradual sloping shorelines. Lake trout are exclusively nocturnal spawners

(Gunn 1995), but fish occupied similar habitats during all times of day, indicating they remain at spawning sites even when not in the physical act of spawning.

The sex ratio was highly skewed towards males at Yellow Rocks and Rocky Point during spawning, which is a common occurrence at lake trout spawning sites (Martin and Olver 1980). Earlier maturity, earlier arrival at spawning sites, and longer duration of time spent at spawning sites by males leads to the skewed sex ratio (Martin and Olver 1980). This could present problems for suppressing mature females during the spawning season. Further, this problem may be compounded if a portion of the females in the population do not spawn annually because some females may not visit any of the spawning sites in a given year. Intermittent spawning is common in native lake trout populations (Adams 1997), and females may spawn every other year (Kennedy 1954) or as infrequently as every 4 years (Donald and Alger 1986). Limited capture of mature females during spawning precluded accurate assessment of spawning frequency, but two mature females with developing ovaries and residual eggs from spawning in a previous year were sampled. Thus, some level of intermittent spawning may be occurring.

Lake trout were abundant in localized habitats (e.g., Yellow Rocks, Rocky Point) during spawning, but this was not surprising since density of spawning lake trout as high as 20 fish/m^3 has been reported (Gunn 1995). A common feature shared by these sites was an abundance of cobble and boulder substrate where fine sediments were absent. It is widely accepted that lake trout usually spawn over rubble, cobble, and boulder substrates having deep interstitial spaces and lacking fine sediments (Martin and Olver 1980; Nester and Poe 1987; Marsden and Krueger 1991). The presence of similar substrate at each of the potential spawning sites further suggests that substrate may be an important characteristic of lake trout spawning sites in Lake McDonald. The Yellow Rocks site is unique because it is an artificially created habitat. A large amount of angular cobble and boulder substrate was deposited into the lake at this site during construction of the Going-to-the-Sun Road. The large size and angular shape of this substrate provides deeper interstitial spaces than observed for substrates at other spawning sites, possibly contributing to the high abundance of lake trout that used this site.

Yellow Rocks and Rocky Point appear to be sites where a large percentage of spawning takes place in Lake McDonald, but the number of other sites where spawning occurs is less certain. Future research to further evaluate spawning sites, spawning behavior, and substrate availability would be valuable since the spawning period appears to be the most advantageous time for suppressing lake trout. Benefits of suppressing lake trout during spawning have been realized in Yellowstone Lake, where much of the success of the suppression program comes from targeting lake trout spawning sites (Koel et al., in press).

Population Characteristics

The age and size structure of the lake trout population in Lake McDonald were characteristic of lake trout populations in their native range (Johnson 1976; Healey 1978b). An abundance of older fish in the population and a low total annual mortality rate (13.2%) suggest that angling exploitation is low in Lake McDonald. Natural mortality of 10-20% is typical in unexploited native lake trout populations (Shuter et al. 1998; Mills et al. 2002).

Considerable variation exists in age- and length-at-maturity for lake trout populations (Healey 1978b; Trippel 1993; Madenjian et al. 1998). While lake trout in some populations may mature as early as 3-4 years (Madenjian et al. 1998), the later maturity of lake trout in Lake McDonald (12-15 years) was typical of populations in northern portions of their native range (Healey 1978b; Adams 1997). A commonality between Lake McDonald and northern lakes is low productivity, resulting in slow lake trout growth. This slow growth likely accounts for late maturity because maturity is related to growth (Ferreri and Taylor 1996; Madenjian et al. 1998).

Lake trout length-at-age was highly variable, but similar variability occurs in other populations (Johnson 1976; Burnham-Curtis and Bronte 1996; Burr 1997). The observed variability likely is not a function of age estimation given the precision of estimates and the close agreement of estimates with those of Stafford et al. (2002) for lake trout in Lake McDonald. Vander Zanden et al. (2000) suggested that variation in growth rate for same-aged fish may result from individual-level diet differences. For example, lake trout that successfully exhibit an ontogenetic diet shift to larger prey or different prey types may experience faster growth than same-aged fish that do not make this transition (Burr 1997). This behavior may be necessary to minimize intraspecific competition if certain prey items are limited in Lake McDonald. Lake trout were in very poor condition and exhibited slow growth compared to other populations, so food resources may be limiting growth.

Movement of lake trout between Lake McDonald and Flathead Lake may also contribute to the variability in growth. Faster growing individuals in the population may be immigrants from Flathead Lake, a more productive system. However, based on the amount of variability in growth there would be substantial immigration, which seems unlikely. Moreover, there was no noticeable evidence of wider otolith growth increments at earlier ages followed by narrower increments that would suggest this type of population interchange.

Population Simulations

Growth overfishing was achieved, but only at lower MEC (250 mm) and cm (13%) levels. This is the first time that these simulations have been applied to a lake trout population, but other studies have shown that decreasing minimum length limits (e.g., lowering MEC) can result in growth overfishing (Slipke and Maceina 2001; Quist et al. 2002). For example, lower yield was predicted for the sauger fishery in the Tennessee River at a 254 mm minimum length limit than for a 356 mm limit (Slipke and Maceina 2001). Population reduction was achieved at both MEC and cm levels, but greater reductions were possible at lower MEC and higher cm levels. These simulations suggest that yield and population size can be reduced, but extirpating the lake trout population is likely not feasible.

Recruitment overfishing was more easily achieved than growth overfishing, regardless of the MEC and cm level. Not only was lifetime egg production reduced dramatically at low (<20%) exploitation, but it was eliminated at moderate (36-61%)

exploitation. This strongly suggests that low to moderate exploitation of mature lake trout could reduce recruitment to a level where adults are not being replaced. Further, substantial population reduction could be achieved by targeting only mature fish in the population. This would be easier than trying to harvest adults and smaller fish, especially given the vulnerability of mature fish during the spawning period. The SPR simulation has been applied to populations of other long-lived inland species, including shovelnose sturgeon *Scaphirhynchus platorynchus* (Quist et al. 2002) and channel catfish *Ictalurus punctatus* (Slipke et al. 2002). Shovelnose sturgeon are susceptible to recruitment overfishing at low exploitation rates ($\leq$20%; Quist et al. 2002), but channel catfish did not reach a critical minimum SPR until exploitation exceeded 45% (Slipke et al. 2002). Neither of these species were as vulnerable to recruitment overfishing as lake trout. The earlier maturity of channel catfish and shovelnose sturgeon relative to lake trout in Lake McDonald may explain this increased susceptibility of lake trout to recruitment overfishing. Channel catfish mature at about 3 years (Helms 1975) and shovelnose sturgeon generally mature at age 5 (Moos 1978). In comparison, lake trout took about 10 years longer to mature. Exploitation can have a greater effect on lifetime egg production when fish are later to mature because there is more opportunity to remove fish from the population before they begin producing eggs.

It is important to note that model simulations assume that sampling gears do not capture any fish below the MEC. This is unrealistic because some small fish will inevitably be captured even if not fully recruited to the gear, thus making simulation predictions conservative. More importantly, all simulations assume that lake trout do not exhibit a compensatory response to exploitation, which would result in underestimation of exploitation rates required to influence the population. This is probably an unrealistic assumption because lake trout often exhibit compensatory responses to exploitation, such as increased growth rate and fecundity, decreased age- and length-at-maturity, and decreased natural mortality rate (Healey 1978a; Healey 1978b; Ferreri and Taylor 1996). The types and magnitude of compensatory responses are difficult to predict, especially without knowing the level of exploitation that might be exerted on the population. If lake trout suppression is conducted, compensatory responses should be monitored for and incorporated into new model simulations. Further, a fecundity-length relationship specific to Lake McDonald would strengthen predictions made from SPR simulations.

Diet

Lake trout growth is largely a function of prey fish availability (Martin 1966). When prey fishes are available lake trout are highly piscivorous (Martin 1977; Eck and Wells 1986; Ruzycki et al. 2001). However, lake trout consume mostly invertebrates and growth rate is slower when prey fish are limited (Martin 1966; Donald and Alger 1986). Despite deriving most of their caloric content from fish prey, lake trout growth in Lake McDonald was slow. Although lake trout grew faster in Flathead Lake, both populations consumed primarily whitefish and a diversity of fish species and invertebrates (Kershner and Beauchamp 2001; this study). Faster growth of lake trout in Lake McDonald might be expected given their high level of piscivory and similar diet to the Flathead Lake population, but the mean weight of prey in stomach samples was extremely low (4.2 g).

Low prey weight is not attributed to rapid digestion because fish were sampled from short duration gill net sets and digestion is slow in cold water temperatures (Finstad 2005). If prey was more abundant, lake trout stomachs would likely contain more food. Thus, prey appears to be limited, which is further supported by the poor condition of lake trout in Lake McDonald. Given the similarities in diet between lake trout and bull trout (Donald and Alger 1993), limited prey resources also may be negatively influencing bull trout growth in Lake McDonald. Suppressing lake trout may increase prey abundance, thus benefiting bull trout.

A gradual increase in the number of empty lake trout stomachs from spring through summer, followed by a sharp increase in empty stomachs during autumn was also observed by Martin (1977) for lake trout in Lake Opeongo, Ontario. Lake trout rarely feed during spawning (Martin 1977), which accounts for the increase in empty stomachs during the post-stratified season. The percentage of unidentified fish in the diet increased during the post-stratified season. Since few lake trout were actively feeding during spawning, it is possible that more time elapsed between feeding events and led to more digested prey items. Whitefish species were absent from the diet during the post-stratified season, after being the most abundant prey item by weight in previous seasons. If whitefish species occupied pelagic habitats while lake trout shifted their distribution to littoral areas during post-stratification, whitefish species may not have been a readily available prey source. Alternatively, the large percentage of unidentified fish in the diet during post-stratification may have masked the presence of whitefish species in the diet of lake trout.

Management Recommendations

My research indicates that substantial reduction of the lake trout population in Lake McDonald is feasible. Distinct patterns in the spatial and temporal distribution of lake trout were described that will allow suppression efforts to be focused at times and places that will maximize efficiency. Lake trout are particularly vulnerable during spawning when they concentrate in localized habitats. In contrast, suppression would be inefficient during seasons when lake trout occupy pelagic habitats and are dispersed throughout the lake. The lake trout population was characterized by slow growth, late maturity, and low reproductive potential, which are attributes common to lake trout populations that make the species vulnerable to overexploitation (Shuter et al. 1998). Population simulations indicated that the population is extremely susceptible to recruitment overfishing at low to moderate exploitation rates. This suggests that a suppression program might only need to target the adult portion of the population during spawning to be successful. Focusing efforts during this short time period would reduce expenses and potential impacts to native fish species.

Many gear types have been considered for suppressing lake trout (Varley and Schullery 1995), but the effective use of gill nets to suppress lake trout in Yellowstone Lake (Koel et al. in press) suggests this gear would also be appropriate for Lake McDonald. Minimizing bycatch of native species has been challenging in Yellowstone Lake, but gill net deployment strategies have been developed to reduce bycatch (Koel et al. in press). In Lake McDonald, bycatch of bull trout was low (12.6 lake trout for every bull trout); however, if bull trout abundance increases as suppression activities progress then bycatch may become more prevalent. Deepwater trap nets used in commercial fisheries are another gear with high potential for suppressing lake trout, but require greater effort and expense to operate.

Suppression efforts of greater intensity and shorter duration are generally more successful than less intense, longer duration efforts because they dampen compensatory responses (Brodeur et al. 2001). Thus, this type of suppression approach would likely be optimal to mitigate for any compensatory responses. Standardized assessments should be conducted periodically to evaluate compensatory responses and population trends that will be critical for determining the effectiveness of suppression. As new population data are collected, model simulations can be updated to aid in the suppression evaluation process.

In addition to compensatory responses, immigration of lake trout could make suppression more difficult. I documented lake trout movement out of Lake McDonald; however, it is likely that lake trout also enter the lake. Future research is necessary to better understand lake trout movement in the Lake McDonald drainage. Unless lake trout immigration occurs at low levels, it will need to be controlled in order for suppression to be successful.

Information learned to date from the active lake trout suppression program on Yellowstone Lake further supports my conclusion that suppression can be effective. Suppression efforts on Yellowstone Lake have resulted in reduced catch rates and decreased average length-at-maturity for lake trout, both indicating that suppression is negatively influencing the population (Koel et al. in press). Further, the much smaller size and lower productivity of Lake McDonald relative to Yellowstone Lake would make suppression easier.

Many of the suppression techniques currently used on Yellowstone Lake are similar to those recommended for Lake McDonald. Identifying and targeting areas where lake trout occur in high density, particularly spawning sites, has been critical to increasing suppression efficiency in Yellowstone Lake (Bigelow et al. 2003). Also, examining population characteristics (e.g., average length-at-maturity) and trend data (e.g., gill net C/*f*) has been important for assessing the response of lake trout to suppression (Koel et al. in press).

While Yellowstone Lake is a valuable test case for development of lake trout suppression strategies, this study provides guidance for assessing the response lake trout exhibit to suppression. Evidence from Yellowstone Lake suggests that suppression is negatively influencing the lake trout population, but the level of exploitation required to reduce the population to a desired level is unknown. The modeling approach I used can be applied to predict the effect various exploitation rates will have on the population. Additionally, the lake trout distribution patterns in Lake McDonald may be similar in other lakes where lake trout have been introduced. If so, this information will be useful for more efficiently targeting lake trout for suppression.

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APPENDICES

APPENDIX A

LAKE TROUT DIET

Table 6. Season, number of lake trout sampled (N), number of stomachs containing food, prey frequency of occurrence (FO, percent), and prey percent by weight sampled in 2003 and 2004 (years pooled) in Lake McDonald.

Season	N	Number with food	Prey	FO	Percent by weight
Pre-stratified	70	57	Amphipoda	12.28	0.51
			Araneae	1.75	0.01
			Bird	1.75	0.05
			Catostomidae	3.51	9.80
			Chironomidae	54.39	3.16
			Coleoptera	1.75	0.29
			Cottidae	12.28	4.00
			Ephemeroptera	5.26	0.11
			Annelida	26.32	2.41
			Peamouth chub	1.75	3.00
			Plecoptera	1.75	0.00
			Redside shiner	3.51	3.98
			Salmonid species	5.26	2.69
			Trichoptera	1.75	0.05
			Unidentified fish	45.61	32.25
			Unidentified material	14.04	0.41
			Whitefish species	14.04	36.75
			Zooplankton	24.56	0.53
Stratified	114	86	Amphipoda	12.79	0.13
			Catostomidae	2.33	0.35
			Chironomidae	23.26	0.41
			Coleoptera	1.16	0.00
			Cottidae	15.12	4.60
			Ephemeroptera	2.33	0.01
			Hemiptera	3.49	0.02
			Annelida	23.26	1.26
			Kokanee	1.16	2.62
			Lake trout	2.33	9.11
			Megaloptera	1.16	0.04
			Mollusca	1.16	0.02
			Peamouth chub	2.33	11.45
			Plecoptera	1.16	0.01
			Redside shiner	3.49	0.79
			Trichoptera	5.81	0.03
			Unidentified fish	52.33	20.71
			Unidentified material	17.44	0.64
			Whitefish species	6.98	46.88
			Zooplankton	44.19	0.91

Table 6. Continued

Post-stratified	70	21	Catostomidae	9.52	4.39
			Chironomidae	14.29	0.04
			Cottidae	14.29	9.81
			Fish egg	9.52	2.11
			Annelida	4.76	0.13
			Redside shiner	9.52	10.47
			Unidentified fish	71.43	69.47
			Unidentified material	9.52	3.01
			Zooplankton	23.81	0.58

APPENDIX B

LAKE TROUT SEASONAL TELMETRY RELOCATIONS

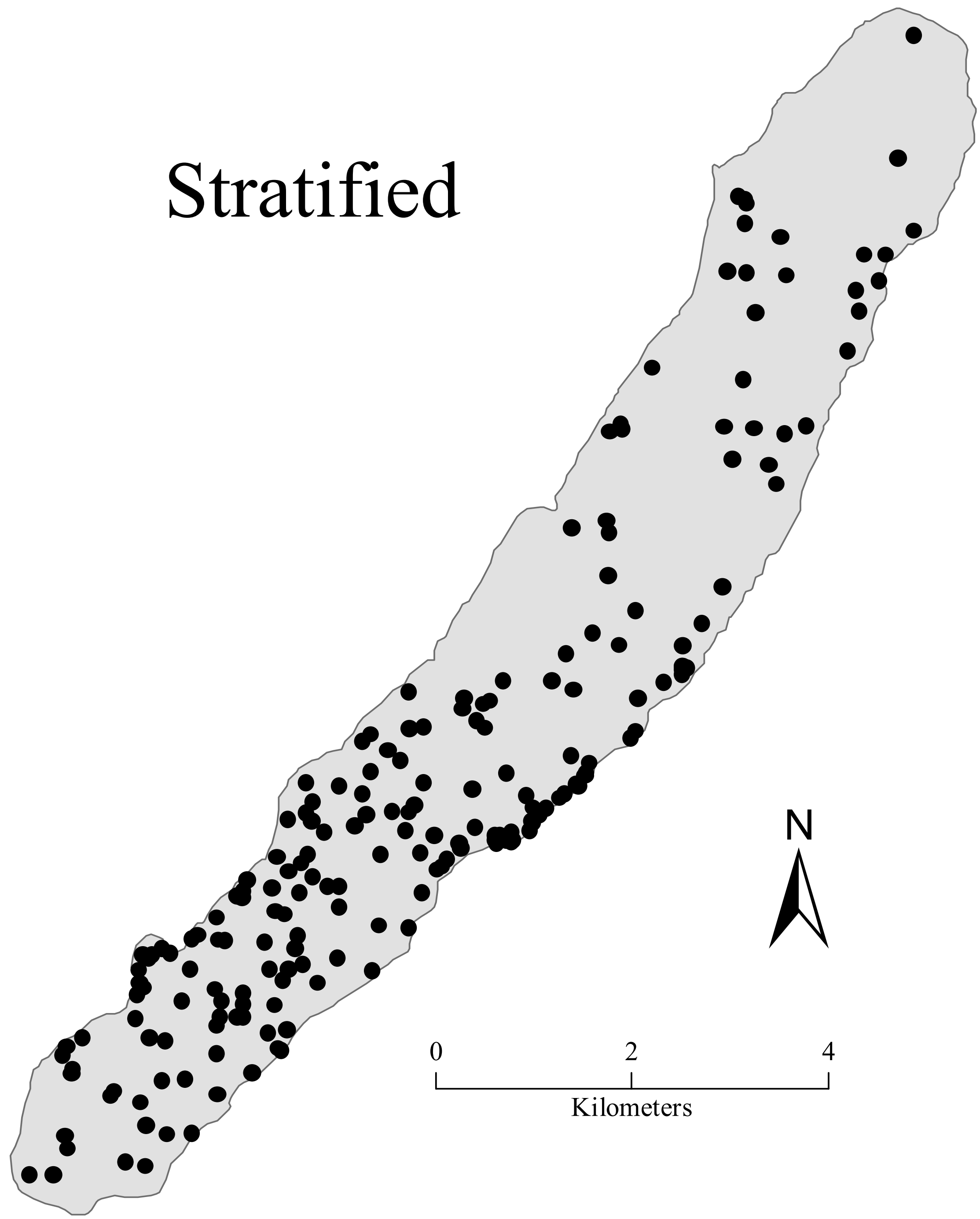

Figure 21. Lake trout telemetry relocations for the 2003 stratified season in Lake McDonald, Glacier National Park.

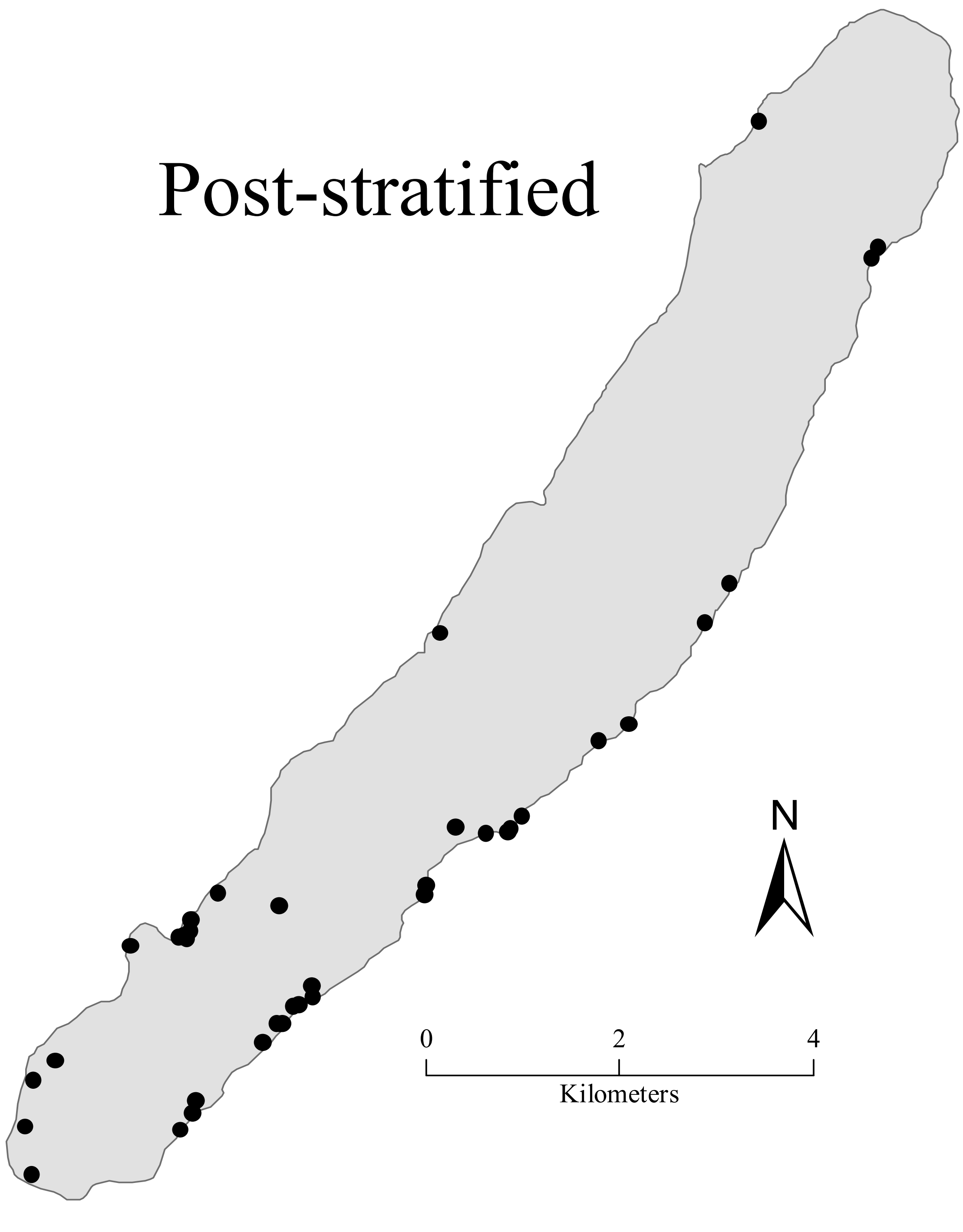

Figure 22. Lake trout telemetry relocations for the 2003 post-stratified season in Lake McDonald, Glacier National Park.

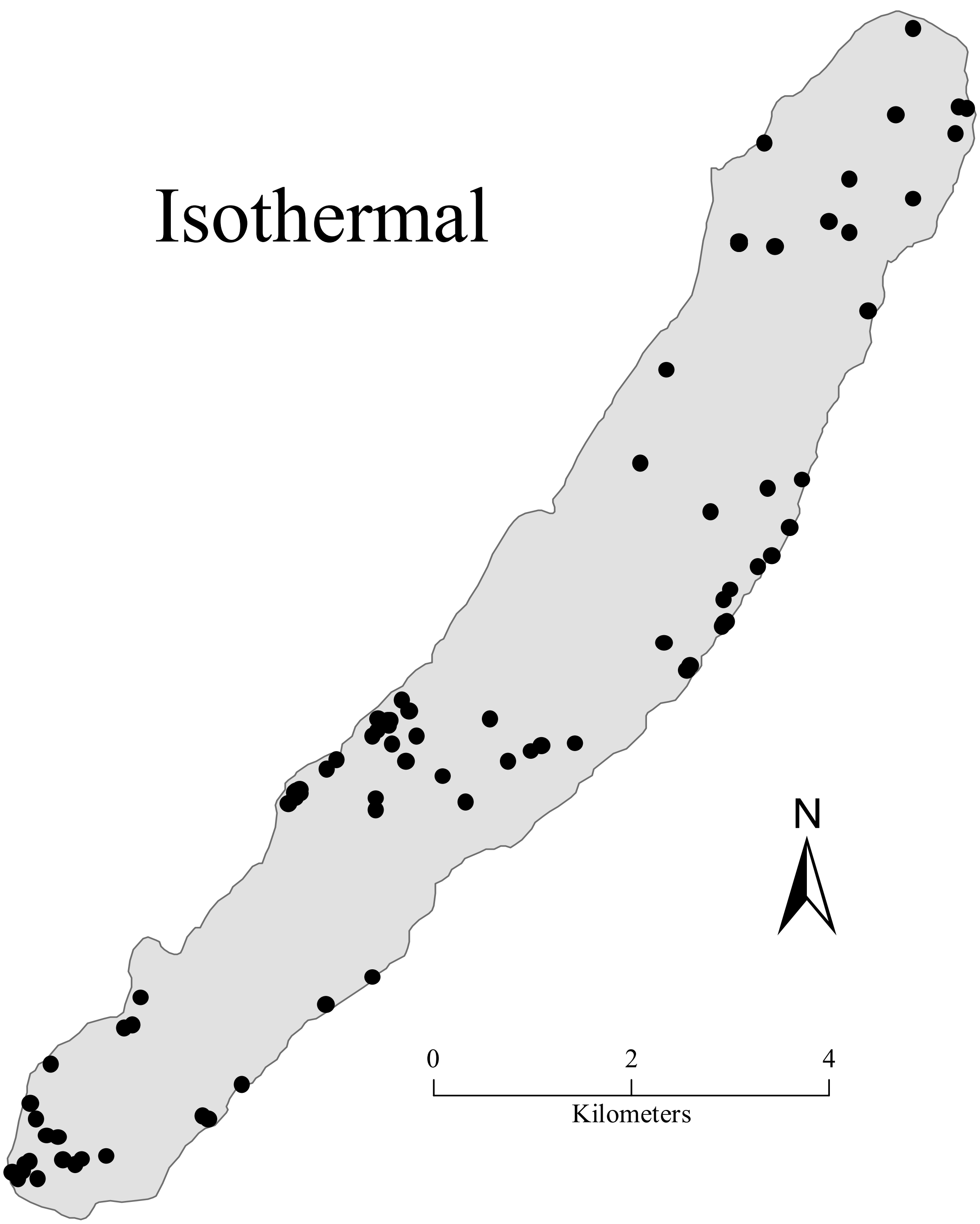

Figure 23. Lake trout telemetry relocations for the 2004 isothermal season in Lake McDonald, Glacier National Park.

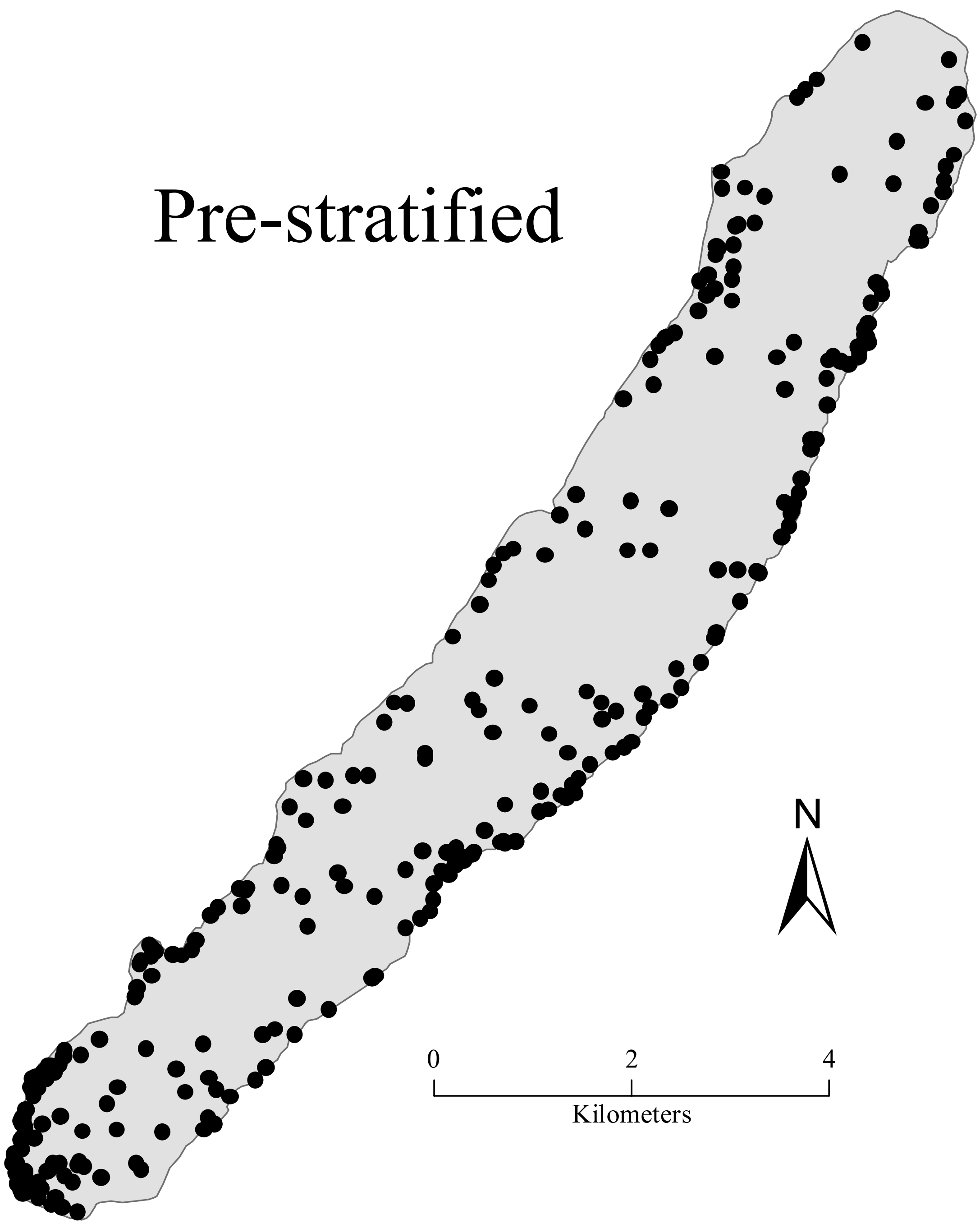

Figure 24. Lake trout telemetry relocations for the 2004 pre-stratified season in Lake McDonald, Glacier National Park.

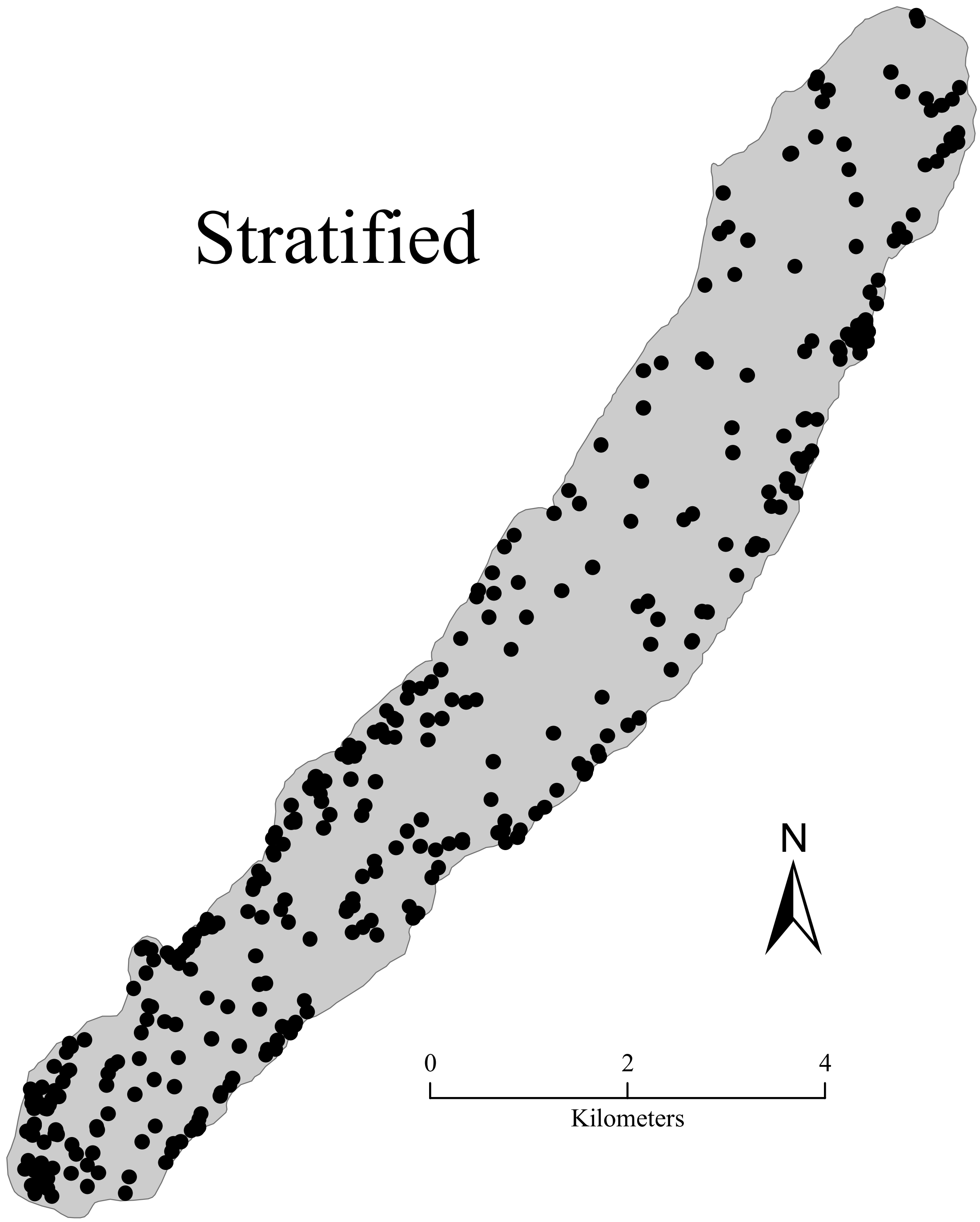

Figure 25. Lake trout telemetry relocations for the 2004 stratified season in Lake McDonald, Glacier National Park.

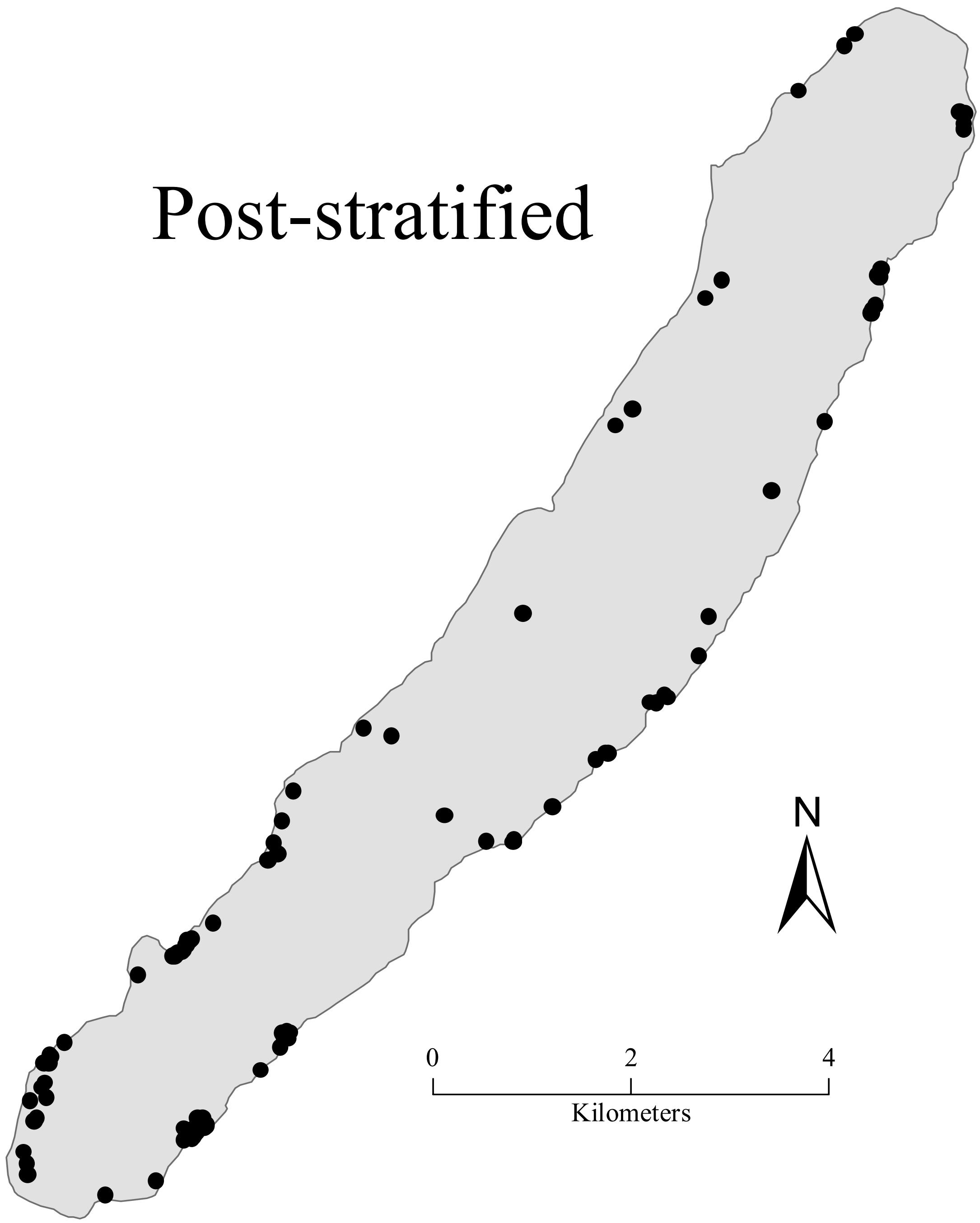

Figure 26. Lake trout telemetry relocations for the 2004 post-stratified season in Lake McDonald, Glacier National Park.