

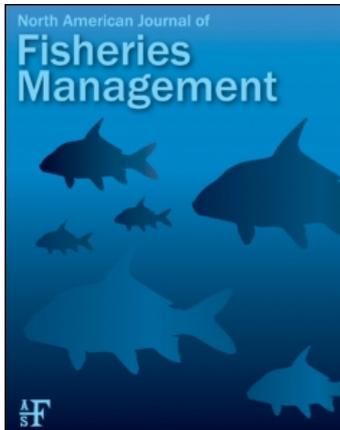
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ARTICLE

Spatiotemporal Distribution and Population Characteristics of a Nonnative Lake Trout Population, with Implications for Suppression

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Abstract

We evaluated the distribution and population characteristics of nonnative lake trout *Salvelinus namaycush* in Lake McDonald, Glacier National Park, Montana, to provide biological data in support of a potential suppression program. Using ultrasonic telemetry, we identified spatial and temporal distribution patterns by tracking 36 adult lake trout (1,137 relocations). Lake trout rarely occupied depths greater than 30 m and were commonly located in the upper hypolimnion directly below the metalimnion during thermal stratification. After breakdown of the metalimnion in the fall, lake trout primarily aggregated at two spawning sites. Lake trout population characteristics were similar to those of populations within the species' native range. However, lake trout in Lake McDonald exhibited lower total annual mortality (13.2%), later maturity (age 12 for males, age 15 for females), lower body condition, and slower growth than are typically observed in the southern extent of their range. These results will be useful in determining where to target suppression activities (e.g., gillnetting, trap-netting, or electrofishing) and in evaluating responses to suppression efforts. Similar evaluations of lake trout distribution patterns and population characteristics are recommended to increase the likelihood that suppression programs will succeed.

Nonnative lake trout *Salvelinus namaycush* are widely distributed across the western USA as a result of numerous introductions (Martinez et al. 2009). Stocking has been the primary introduction mechanism (Crossman 1995), but subsequent natural reproduction and dispersal have contributed to additional range expansion (Fredenberg 2002; Martinez et al. 2009). Nonnative lake trout populations are often problematic because they have negative impacts on native or desired sport fish populations

(Behnke 1992; Crossman 1995; Ruzycki et al. 2003; Martinez et al. 2009). To address this problem, several natural resource agencies are using suppression as a management strategy for controlling nonnative lake trout populations (Martinez et al. 2009). Suppression is being tested in several locations, but the two most aggressive programs occur in Yellowstone Lake, Yellowstone National Park (Koel et al. 2005; Syslo 2010), and Lake Pend Oreille, Idaho (Hansen et al. 2008).

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Lake trout are vulnerable to overexploitation because they are often characterized by slow growth, late maturity, and low reproductive potential (Shuter et al. 1998). Overharvest has been one of the greatest threats to lake trout populations in their native range (Keleher 1972; Healey 1978b; Martin and Olver 1980; Olver et al. 2004). Exceeding thresholds of 50% total annual mortality and 0.5 kg/ha in yield has been suggested as unsustainable (Healey 1978b; Hansen et al. 2008). The vulnerability to exploitation observed for lake trout in other systems has provided the impetus for exploring suppression as a management tool for controlling nonnative populations.

Lake trout were introduced into Flathead Lake, Montana, a century ago (Spencer et al. 1991) and are now found throughout much of the Flathead River drainage (Muhlfeld et al. 2000; Fredenberg 2002). In 1959, nonnative lake trout were first documented in Lake McDonald, Glacier National Park, Montana (Fredenberg 2002), and have since established a self-sustaining population. Natural dispersal of nonnative lake trout from Flathead Lake, which is located 93 river kilometers downstream of Lake McDonald, is the likely source of the Lake McDonald population (Fredenberg 2002).

Native species, particularly the bull trout *S. confluentus*, have declined in abundance since the colonization of lake trout in Lake McDonald and other Glacier National Park lakes (Fredenberg 2002). This response is not surprising because adfluvial bull trout populations generally cannot be sustained after lake trout introductions (Donald and Alger 1993; Fredenberg 2002). Concerns about the status of bull trout in Lake McDonald were heightened in 1998, when bull trout were listed as threatened under the U.S. Endangered Species Act. Lake trout suppression is considered a management option to prevent further decline of the bull trout populations in Lake McDonald and other lakes in Glacier National Park.

Attempts to suppress lake trout in other waters, such as Yellowstone Lake and Lake Pend Oreille, provide insight for developing suppression strategies elsewhere (Koel et al. 2005; Hansen et al. 2008). These programs have used multiple methods (e.g., gill nets, trap nets, anglers, and electrofishing) to remove lake trout (Koel et al. 2005; Hansen et al. 2008). Thus, understanding the spatial and temporal distribution of lake trout is helpful for most effectively targeting lake trout in each water body (P. E. Bigelow, U.S. National Park Service, personal communication). If distinct spatial and temporal distribution patterns exist in a population and can be targeted, there is a greater likelihood that benchmark exploitation rates resulting in recruitment overfishing can be achieved. For example, lake trout aggregate during spawning in fall (Martin and Olver 1980), and the identification and targeting of spawning sites could be an effective approach to increase exploitation and reduce recruitment. In addition to seasonal distribution patterns, the influence of diel period on lake trout distribution is poorly understood and may have finer-scale implications for where and when suppression activities should occur.

In addition to distribution patterns, population metrics (e.g., age, growth, survival, age at maturity, and fecundity) can indicate how vulnerable a population is to exploitation. Although lake trout are susceptible to overexploitation, they exhibit plasticity in population characteristics throughout their native range and little is known about their population characteristics in systems where they are nonnative (Martinez et al. 2009). Additionally, the documentation of population characteristics prior to initiating suppression activities provides a baseline for evaluating suppression efficacy. Thus, the objectives of our study were to describe lake trout spatial and temporal distribution and population characteristics in a glacial lake outside the species' native range. The results from this study will be used to determine whether suppression of lake trout is feasible in Lake McDonald. If so, these data will also be used to help develop the most effective suppression program. Given the popularity of lake trout suppression programs in the Intermountain West (Martinez et al. 2009) and the lack of peer-reviewed publications that describe such programs, this study provides a useful case history to assist natural resource agencies in planning nonnative eradication programs.

METHODS

Study area.—Lake McDonald is in a narrow glacial valley at an elevation of 961 m in the Flathead River drainage of northwestern Montana. It is the largest and deepest lake in Glacier National Park, having a surface area of 2,763 ha and a maximum depth of 142 m. The limnetic zone of Lake McDonald seldom exceeds 60 m in depth and is dominated by glacial silt substrate; shorelines slope steeply and are characterized by a mixture of glacial silt, cobble, and boulder substrates. Lake McDonald is an ultraoligotrophic lake, and thermal stratification typically occurs during July through September. Maximum surface water temperature generally does not exceed 18°C, and phytoplankton biomass is low (mean total standing crop = 0.23 mL/m³; Ellis et al. 1992). Despite a cold winter climate, Lake McDonald freezes only occasionally. The lake experiences few anthropogenic disturbances, and angling pressure is low.

Native fishes in Lake McDonald include the bull trout, west-slope cutthroat trout *Oncorhynchus clarkii lewisi*, mountain whitefish *Prosopium williamsoni*, and pygmy whitefish *P. coulterii*. Additionally, there are native catostomid, cyprinid, and cottid species. Common nonnative species are the lake trout and lake whitefish *Coregonus clupeaformis*; other nonnative species are less abundant.

Sampling.—Vertical temperature profiles were measured to examine their relationship to lake trout distribution (Dux 2005). Vertical temperature profiles were measured one to two times monthly during March–May and September–November and two to three times monthly during June–August. Pelagic profile sites were established on each half of the lake, and two nearshore sites (adjacent to the pelagic sites) were added during stratified conditions (see Dux 2005 for more details). Temperature profile data

were used to delineate seasons during each year. Two seasons were identified (stratified and poststratified) in 2003, and four seasons (isothermal, prestratified, stratified, and poststratified) were present in 2004 because of a longer sampling duration (Dux 2005).

Lake trout were sampled during May–October 2003, March–June 2004, and September–November 2004. Sampling was primarily conducted by use of sinking gill nets (38.1×1.8 m) that consisted of five 7.6-m panels (bar mesh = 12, 24, 36, 48, and 65 mm). Gillnetting occurred primarily during May and June and to a lesser extent in September–November. Gill nets were set during the morning crepuscular period and were pulled after 2–3 h to minimize stress to lake trout (intended for tagging) and to bycatch species (primarily bull trout). Gillnetting locations were subjectively selected in an attempt to maximize catch; however, sampling did occur throughout the lake (i.e., no single area was targeted).

All lake trout were measured for total length and weighed; sex was also determined when possible. Lake trout that did not receive transmitters were sacrificed, and their sagittal otoliths were removed for age estimation. The methods of Secor et al. (1992) were generally followed for otolith preparation (Dux 2005). A single reader estimated age by counting the number of annuli with a compound light microscope (Campana 1992) at 40–100 \times magnification. A single reader estimated age twice for a subsample of 181 otoliths, and the mean coefficient of variation (calculated as $100 \times [SD/mean]$) was 6.9%.

Two transmitter sizes were used to minimize the transmitter weight: body weight ratios while maximizing battery longevity. We used 39 transmitters that were 102 mm long and 18 mm in diameter, weighed 39 g in air, and had an 18-month battery life; five smaller transmitters were 85 mm long and 18 mm in diameter, weighed 32 g in air, and had a 12-month battery life (Model DT-97; Sonotronics, Inc.). Surgical procedures were adapted from Summerfelt and Smith (1990) and Winter (1996; see Dux 2005 for more details).

A systematic tracking schedule ensured that lake trout relocations were obtained at all times of day during a 24-h period. Four diel tracking periods were delineated (dawn, day, dusk, and night). The dawn and dusk periods represented the crepuscular hours and were 4-h periods centered on sunrise and sunset. The daylight hours between the dawn and dusk periods constituted the day period, and the night period consisted of all dark hours between dusk and dawn periods.

Tracking was conducted in June–November 2003 and March–November 2004 by using a USR-96 scanning receiver and a DH-4 directional hydrophone (Sonotronics). We sampled two diel periods on each day of tracking, the goal being to relocate as many different fish as possible during a sampling day. Tracking followed a transect that bisected the lake longitudinally. The narrow shape of Lake McDonald and detection ranges of the equipment (>1 km) allowed fish to be detected between this transect and either shoreline. When a fish was detected, we departed from the transect to locate the fish and then

returned to the transect and proceeded with tracking. We varied our starting point between each end of the lake to ensure that the fish were not always relocated at the same time of day. Relocating all tagged fish in a single day usually was not possible; however, because of the tracking design and movement by lake trout, no single fish or groups of fish were overrepresented in the data. Transmitter code, Global Positioning System coordinates, fish depth (from transmitter sensor), date, and time were recorded at each location. From blind tests, mean accuracy for relocating transmitters was $11.1 \text{ m} \pm 9.6 \text{ m}$ (95% confidence interval [CI]). Depth sensors were tested at known depths from 1 to 45 m at 1-m intervals, and accuracy was 1.5 m (95% CI $\pm 0.8 \text{ m}$).

A multi-tiered approach was used to identify and characterize potential lake trout spawning sites and to estimate when spawning was initiated. Tracking was conducted throughout the fall and ended on 7 November. When relocations of two or more lake trout were observed at a site, subsequent gill-net sampling (as previously described) and underwater video observation (via Aqua-Vu DT camera) were conducted to evaluate the presence of additional mature lake trout at the site. Four additional sites were selected subjectively (spread throughout the lake) to represent areas where mature lake trout were caught during other seasons but where spawning was not suspected. Gill nets were set at these sites, and catch rates of mature fish were compared with catch rates at potential spawning sites. Ripeness of lake trout captured in all gill nets was evaluated to estimate when spawning was initiated. The underwater video camera was also used to examine substrate type and size at each site (Dux 2005). Spawning evaluations were only conducted during 2004.

Data analysis.—Lake trout spatial distribution was examined by season (i.e., isothermal, prestratified, stratified, and poststratified) to identify when lake trout could most effectively be targeted. Further, distribution was evaluated by diel period (i.e., dawn, day, dusk, and night) to determine whether suppression activities could be more effective during a particular time of day. Means for each distribution variable (fish depth and distance to shore) were calculated for individual fish during each diel period within each season, and individual fish were the experimental units for all analyses. Differences in means for each distribution variable among seasons and diel periods were tested by using repeated-measures analysis of variance. These analyses were conducted with the mixed-model (MIXED) procedure in the Statistical Analysis System version 9.0 (Littell et al. 1998). Two factors (season and diel period), the first-order autoregressive covariance structure, and the Satterthwaite degrees of freedom approximation were specified in the model. Differences in distribution variable means between years were tested separately by using the same repeated-measures analysis of variance procedure. We specified an α of 0.05 for all analyses and used the Bonferroni correction when multiple pairwise comparisons were conducted (Sokal and Rohlf 1995).

Total annual mortality was estimated by use of the catch curve regression method (Ricker 1975) and Fishery Analyses

and Simulation Tools version 2.0 (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 (Miranda and Bettoli 2007). Also, an age-length key was applied to convert the age and length distributions for the subsample of aged fish to represent the age and length distributions for all sampled fish (DeVries and Frie 1996). Lake trout sampled after 30 September were not included in the mortality estimate or sex ratio because gillnetting targeted adults at potential spawning sites.

We used a von Bertalanffy growth model to describe individual growth (Isely and Grabowski 2007). The model was fitted to length-at-age data by using the nonlinear model (NLIN) procedure in the Statistical Analysis System. Relative weight (W_r) was used as an index of body condition (Anderson and Neumann 1996). We used the standard weight equation from Piccolo et al. (1993). During the spawning season, stage of sexual maturity was recorded (Dux 2005). Age and total length at which 50% of male and female lake trout were sexually mature were estimated with logistic regression (Heibo and Vollestad 2002). Parameter estimates for the weight-length relationship were calculated based on all sampled fish via linear regression on \log_{10} transformed data (Pope and Kruse 2007).

RESULTS

Tagged lake trout varied from 508 to 859 mm in total length (mean = 619 mm; ± 24 mm 95% CI) and from 940 to 5,950 g in weight (mean = 2,082 g; ± 330 g 95% CI). Nineteen lake trout were captured from the north half of the lake (six different areas), and 25 fish were captured from the south half (seven different areas). From 26 June to 7 November 2003, 242 telemetry relocations were obtained from 16 lake trout (mean = 15.1 relocations/fish); from 26 March to 7 November 2004, 34 lake trout were relocated 893 times (mean = 26.3 relocations/fish). Seven lake trout died within 7 d of release, one died 9 months after release, seven were harvested by anglers in Lake McDonald, and three disappeared. Another fish was harvested in 2005 by an angler in Flathead Lake (93 river kilometers downstream).

Vertical distribution of lake trout was highly influenced by water temperature (Figure 1). During the stratified season in both years, lake trout had the narrowest vertical distribution, were predominately found in the upper hypolimnion immediately below the metalimnion, and avoided warm ($>12^\circ\text{C}$) 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. The maximum observed temperature used by a lake trout was 15.7°C during the 2003 stratified season. In 2004, the greatest mean depth of lake trout was observed during the stratified season, when the epilimnion was deeper. In 2003, seasonal and diel differences in fish depth were not tested because of a significant interaction between season and diel period ($F = 2.99$, $df = 3, 53$, $P = 0.04$; Table 1). However,

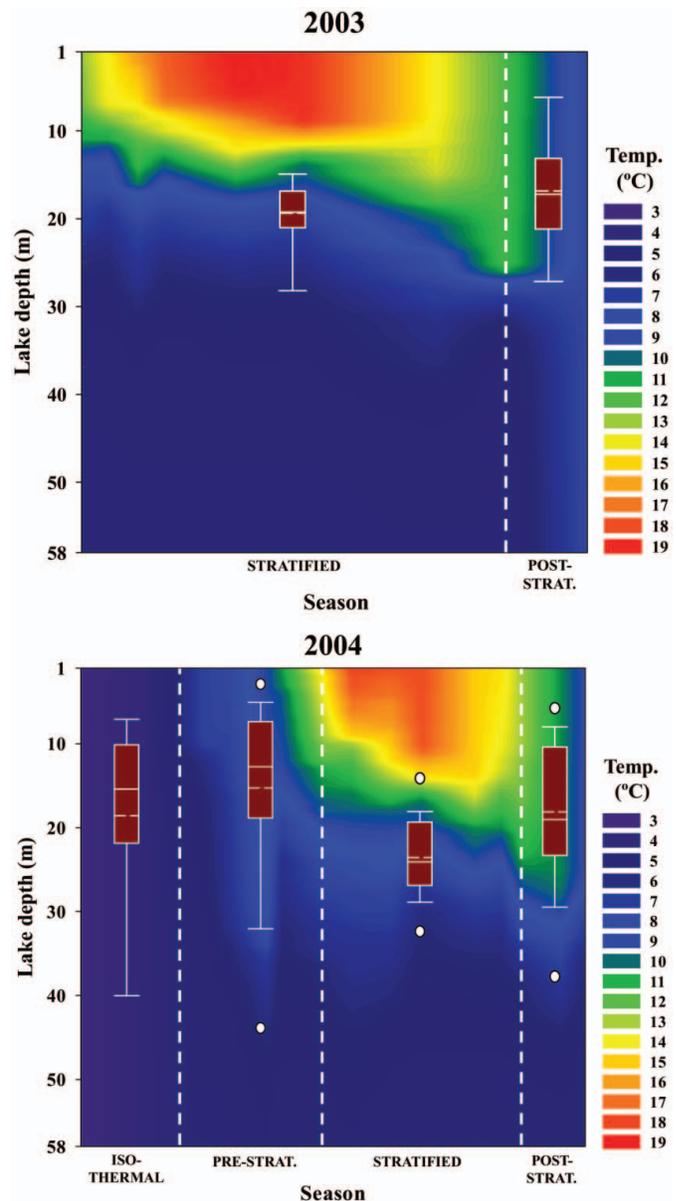


FIGURE 1. Box-and-whisker plots of lake trout depth in Lake McDonald, Glacier National Park, Montana, overlaid on temperature isopleths for each season (delineated based on thermal profiles) in 2003 and 2004: isothermal, prestratified (pre-strat.), stratified, and poststratified (post-strat.). Within each box, median depth is indicated by a solid line, 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. Note that sampling duration was shorter in 2003 than in 2004, resulting in the different seasonal scaling between years.

fish occupied shallower water during the poststratified season in all periods except the day period. Mean fish depth differed significantly among seasons in 2004, but there were no significant differences among diel periods ($F = 0.48$; $df = 3, 196$; $P = 0.70$). Lake trout occupied significantly shallower depths during the stratified season in 2003 than in 2004 ($F = 5.86$, $df = 3, 196$; $P = 0.002$).

TABLE 1. Means ($\pm 95\%$ confidence intervals) for lake trout depth, distance to shore, occupied temperature (Temp.), and dissolved oxygen (DO) by year, season, and diel period for tagged individuals that were relocated in Lake McDonald, 2003 and 2004. Means are not reported for sample size less than 3. Seasonal differences within each year that were not statistically significant ($P > 0.05$) share the same letter (x-z).

Temporal scale	Fish depth (m)	Distance to shore (m)	Temp. ($^{\circ}\text{C}$)	DO (mg/L)
Year: 2003				
Stratified season	19.4 \pm 3.6	327.6 \pm 90.5 z	8.5 \pm 1.0 z	
Dawn	19.0 \pm 3.4	324.9 \pm 114.3	8.8 \pm 1.4	
Day	19.8 \pm 2.9	335.6 \pm 104.8	8.5 \pm 1.3	
Dusk	19.4 \pm 4.9	338.9 \pm 112.2	8.1 \pm 1.1	
Night	19.5 \pm 7.7	381.8 \pm 163.4	8.1 \pm 1.3	
Poststratified season	16.9 \pm 3.6	95.1 \pm 72.0 y	7.9 \pm 0.6 z	
Dawn	15.7 \pm 4.6	58.8 \pm 19.6	7.6 \pm 0.1	
Day	22.5 \pm 6.4	113.4 \pm 97.5	7.9 \pm 1.3	
Dusk	13.4 \pm 4.4	60.7 \pm 29.5	7.6 \pm 0.1	
Night				
Year: 2004				
Isothermal season	18.3 \pm 6.9 zy	271.9 \pm 100.5 zy	3.5 \pm 0.1 z	
Dawn	31.2 \pm 47.9	246.9 \pm 463.3	3.6 \pm 1.1	
Day	18.9 \pm 7.5	272.2 \pm 99.6	3.5 \pm 0.1	
Dusk				
Night				
Prestratified season	15.1 \pm 4.4 z	180.4 \pm 45.5 y	7.6 \pm 0.4 y	10.2 \pm 0.1 z
Dawn	15.3 \pm 4.8	157.4 \pm 60.5	7.8 \pm 0.4	10.1 \pm 0.1
Day	15.4 \pm 4.2	205.6 \pm 47.8	7.6 \pm 0.3	10.2 \pm 0.2
Dusk	15.3 \pm 4.8	132.3 \pm 47.6	7.6 \pm 0.5	10.4 \pm 0.3
Night	15.3 \pm 5.7	190.4 \pm 72.3	7.4 \pm 0.5	10.3 \pm 0.2
Stratified season	23.3 \pm 2.0 y	240.2 \pm 41.5 z	9.1 \pm 0.6 x	10.9 \pm 0.2 y
Dawn	24.6 \pm 3.2	287.0 \pm 64.2	8.6 \pm 0.7	11.1 \pm 0.2
Day	24.1 \pm 1.9	241.5 \pm 55.1	9.0 \pm 0.6	10.9 \pm 0.2
Dusk	22.0 \pm 2.6	258.7 \pm 56.4	9.3 \pm 0.7	11.0 \pm 0.3
Night	22.2 \pm 2.9	193.1 \pm 44.9	8.9 \pm 0.8	10.9 \pm 0.2
Poststratified season	18.0 \pm 3.5 z	77.5 \pm 24.0 x	9.1 \pm 0.3 x	9.7 \pm 0.1 x
Dawn	14.4 \pm 8.1	92.8 \pm 59.0	10.1 \pm 0.4	9.5 \pm 0.3
Day	17.2 \pm 6.6	89.7 \pm 36.5	9.1 \pm 0.4	9.6 \pm 0.1
Dusk	18.6 \pm 5.4	62.3 \pm 31.1	9.4 \pm 0.6	9.6 \pm 0.2
Night	18.9 \pm 3.5	65.2 \pm 18.9	8.5 \pm 0.3	9.8 \pm 0.1

= 1, 60, $P = 0.02$; Table 1; Figure 1). Annual depth differences were not tested for the poststratified season because there was a significant interaction between year and diel period ($F = 2.78$; $df = 3, 59$; $P = 0.05$); however, mean depth only varied by 1.1 m between years. The interaction occurred because fish depth in 2004 was shallower during the dawn and day periods and deeper during the dusk and night periods (Table 1). Mean temperature did not differ significantly by diel period during any season in 2003 ($F = 0.25$; $df = 3, 56$; $P = 0.86$) or 2004 ($F = 0.65$; $df = 3, 231$; $P = 0.58$). For all seasons in 2003 and 2004, lake trout rarely (9% of all relocations) occupied depths greater than 30 m (Figure 1), despite an abundance of deepwater habitat.

Lake trout horizontal distribution was related to water temperature and spawning location. Mean distance to shore varied

seasonally during both years; lake trout predominately occupied nearshore habitats in the poststratified season and displayed a more pelagic distribution during all other seasons (Table 1; Figure 2). Lake trout distance to shore was significantly greater ($F = 9.96$; $df = 1, 52$; $P = 0.003$) during the stratified season in 2003 than in 2004. In 2004, lake trout moved farther from shore after thermal stratification developed (Table 1). In contrast, there was no significant difference ($F = 0.43$; $df = 1, 94$; $P = 0.52$) between years in distance to shore during the poststratified season. Distance to shore did not significantly differ among diel periods in 2003 ($F = 0.14$; $df = 3, 50$; $P = 0.94$) or 2004 ($F = 2.02$; $df = 3, 211$; $P = 0.11$).

Spawning began during the last week of October, and lake trout aggregated at two primary sites (Yellow Rocks and Rocky

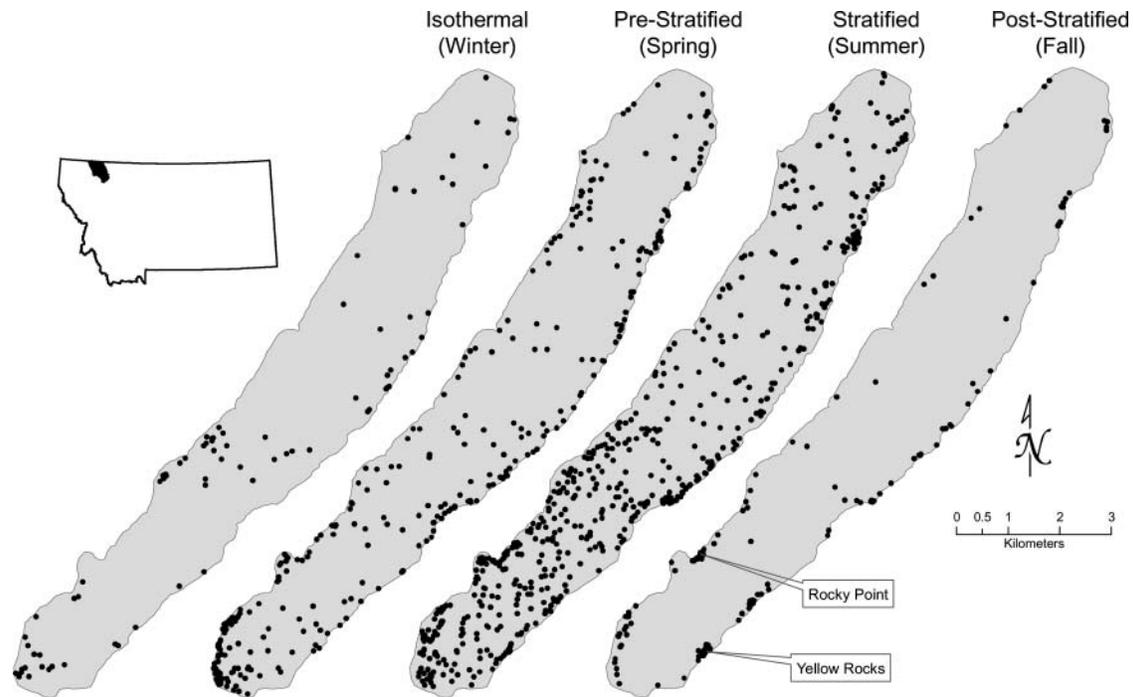


FIGURE 2. Map of lake trout locations (2003 and 2004 pooled) for each season (delineated based on thermal profiles; see Methods) in Lake McDonald. Yellow Rocks and Rocky Point were identified as potential lake trout spawning sites.

Point; Figure 2). Aggregations started to form at potential spawning sites during late September, shortly before poststratification (approximately 8 October), when surface water temperature was 12°C. Lake trout were most abundant at potential 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 during 28 October through 8 November. Tagged lake trout were most abundant at Yellow Rocks; 42% of the tagged individuals were relocated at this site at least once during the poststratified season. Rocky Point was the next most highly used location; 21% of the tagged lake trout were relocated there. During all other seasons, neither site was frequently used by lake trout. Moreover, many of the relocations at these sites during the 2004 stratified season occurred immediately prior to the start of the poststratified season and may have been related to spawning (e.g., staging behavior). Gillnetting and underwater video observations supported telemetry observations at Yellow Rocks and Rocky Point. During the poststratified season, gill-net catch per unit effort for mature lake trout was 2.4 fish/h (SE = 0.9 fish/h; total effort = 10.8 h) at Yellow Rocks and 6.1 fish/h (SE = 1.8 fish/h; total effort = 5.2 h) at Rocky Point. In contrast, the catch per unit effort for mature lake trout at four sites where spawning activity was not suspected was 0.2 fish/h (SE = 0.1 fish/h; total effort = 13.0 h). The sex ratio for mature lake trout was highly skewed: 92% males at Yellow Rocks and 94% males at Rocky Point. Substrate at the Yellow Rocks and Rocky Point sites was predominately cobble (64–256 mm) and boulder (>256 mm).

Typically, these substrates had deep interstitial spaces that were relatively free of fine sediments.

The 415 sampled lake trout had lengths that varied from 134 to 978 mm; their subsampled ($N = 273$) ages varied from 1 to 37 years (Table 2). Length at age was highly variable,

TABLE 2. Summary of population metrics for lake trout in Lake McDonald. Relative weight (W_r) was calculated as an index of condition, which was assessed for fish in four size categories: stock-quality (S-Q; 300–499 mm), quality-preferred (Q-P; 500–649 mm), preferred-memorable (P-M; 650–799 mm), and memorable-trophy (M-T; 800–999 mm); no trophy ($\geq 1,000$ mm) size fish were captured.

Metric	Median	Minimum	Maximum
Length (mm)	465	134	978
Age (years)	9	1	37
Condition (W_r)			
S-Q	75	60	99
Q-P	78	55	104
P-M	84	65	113
M-T	88	64	102
Length or age at maturity			
Males			
Length (mm)	638	433	978
Age (years)	20	11	37
Females			
Length (mm)	637	575	853
Age (years)	19	16	28

particularly for fish older than 15 years. For example, the oldest lake trout was age 37 and 589 mm, whereas the largest lake trout was 978 mm and age 29. Individual growth rate for lake trout in Lake McDonald was slow ($l_t = 922\{1 - e^{-0.054(t + 2.075)}\}$, where l_t is length at time t and e is the base of natural logarithms). The weight-length relationship for lake trout ($r^2 = 0.99$, $P < 0.001$, $N = 415$) was $\log_{10}(\text{weight}) = -5.61 + 3.18 \cdot \log_{10}(\text{length})$. Median W_r of lake trout was below 90 for all length categories (Table 2). Thus, lake trout were below the 11th percentile compared with the cumulative frequency distribution of mean W_r values for lake trout throughout North America (Hubert et al. 1994). Age and length at 50% maturity were 12 years and 473 mm, respectively, for males and 15 years and 555 mm, respectively, for females. The youngest mature lake trout sampled was 11 years old (male), and the shortest mature fish was a 433-mm male. The proportion of female lake trout sampled relative to males was 0.56. Total annual mortality for lake trout of ages 8–27 was 13.2% ($r^2 = 0.63$, $P < 0.001$, $\beta_0 = 4.22$, $\beta_1 = -0.141$, $N = 20$), where β_0 is the intercept and β_1 is the slope.

DISCUSSION

The large-scale spatial and temporal distribution of lake trout was a function of water temperature and spawning behavior. A warm epilimnion during stratification forced lake trout into the upper hypolimnion, where temperatures were within the fundamental thermal niche of this species ($10 \pm 2^\circ\text{C}$; Magnuson et al. 1990). In response to a deeper metalimnion in 2004, lake trout used greater depths and further demonstrated their affinity for the interface between the metalimnion and hypolimnion. Depths greater than 30 m had cold temperatures that were relatively constant; these depths were apparently avoided by lake trout, similar to populations in other deep lakes (Johnson 1975; Eck and Wells 1986). In lakes that, like Lake McDonald, are dominated by pelagic habitat, stratification provides habitat structure in an otherwise homogeneous environment and is a mechanism by which species can partition thermal habitat (Brandt et al. 1980). Lake trout may be isolated from prey species that inhabit the epilimnion (e.g., westslope cutthroat trout). However, lake trout are probably using the upper hypolimnion because of prey availability. As is common in many deep oligotrophic lakes, Lake McDonald has high densities of phytoplankton near the metalimnion (Ellis et al. 1992), which attracts zooplankton (Wetzel 2001). Whitefishes, which prey on zooplankton in nearby Flathead Lake (Tohtz 1993), were predominant in the lake trout diet during stratification in Lake McDonald (Dux 2005). This suggests that lake trout selected depths in the upper hypolimnion to be in close proximity to prey in addition to seeking suitable water temperatures. Lake trout occupied habitats farther offshore during stratification than during the prestratified or poststratified season. The steep bathymetry of Lake McDonald provides abundant hypolimnetic habitat close to shore, but lake trout spent more time in the pelagic zone. This spatial pattern suggests a response to prey distribution. Studies of

lake trout distribution relative to their prey are limited, but prey distribution has been suggested to structure lake trout habitat use—sometimes more strongly than water temperature (Sellers et al. 1998). Thus, we suspect that distribution might vary among nonnative lake trout populations because prey communities are often quite different (Johnson and Martinez 2000; Ruzycki et al. 2001, 2003; Stafford et al. 2002; Hansen et al. 2008).

Lake trout exhibited distribution patterns that will influence their vulnerability to suppression efforts. Their frequent use of pelagic habitats during all but the poststratified season would make them difficult to target with most traditional sampling gears (e.g., gill nets, trap nets, or electrofishing) throughout much of the year. During the poststratified season, they occurred closer to shore and had a more benthic distribution, which would make traditional gears more effective. The lack of diel differences in lake trout distribution suggests that suppression can be conducted irrespective of time of day; however, fish activity levels and gear avoidance during daylight may still make it necessary to target fish during crepuscular periods.

Lake trout spawning behavior in Lake McDonald was similar to that of populations in the species' native range. The shift from a pelagic distribution to a littoral distribution during poststratification is explained by spawning behavior since lake trout broadcast their eggs over bottom substrates (Gunn 1995). Lake trout spawn when water temperature declines to 8–14°C in fall, which usually coincides with thermal destratification (Gunn 1995). In Lake McDonald, disruption of thermal stratification appeared to trigger arrival of lake trout at potential spawning sites, but spawning was not initiated until late October. Lake trout most commonly spawn in depths of less than 12 m (Scott and Crossman 1973). For example, lake trout in small Ontario lakes spawned less than 10 m from shore in depths less than 2 m (Gunn 1995). Lake trout spawned deeper in Lake McDonald (mean depth = 18.0 m) than has typically been reported for lake trout in other areas. It is unlikely that we failed to detect the use of shallower depths for spawning because diel depth differences were not observed during the spawning period. Shorelines in Lake McDonald slope steeply, so spawning depth may be attributable to the presence of suitable spawning substrate in deeper waters than would be expected for lakes with gradually sloping shorelines.

The localized distribution of lake trout during spawning was not surprising because aggregated spawning behavior is typical (Martin and Olver 1980; Gunn 1995). A common feature shared by these sites was large substrate and a lack of fine sediments. It is widely accepted that lake trout prefer to spawn over rubble, cobble, and boulder substrates with deep interstitial spaces and a lack of fine sediments (Martin and Olver 1980; Nester and Poe 1987; Marsden and Krueger 1991). Thus, substrate appears to be an important characteristic of lake trout spawning sites in Lake McDonald. The Yellow Rocks site is unique because it was artificially created. A large amount of angular cobble and boulder substrate was deposited into the lake at this site during road construction. The large size and angular shape of

this substrate provide deeper interstitial spaces than observed for substrates at other potential spawning sites, possibly making Yellow Rocks preferable to sites with natural substrate.

The age structure and size structure of the lake trout population in Lake McDonald were characteristic of unexploited populations in the species' native range (Johnson 1976; Healey 1978b). Individual growth was much slower in Lake McDonald than in Yellowstone Lake or Flathead Lake (Beauchamp 1996; Ruzycski et al. 2003). The observed variability is probably not a function of age estimation, given the precision of estimates and their close agreement with estimates reported by Stafford et al. (2002). Variation in growth rate for fish of the same age may result from individual diet differences (Vander Zanden et al. 2000). The slow growth of lake trout was corroborated by the low body condition and suggests that food resources may be limiting because Lake McDonald is an unproductive glacial lake. Variation in growth was also expressed 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 age 3–4 (Madenjian et al. 1998), the later maturity of lake trout in Lake McDonald was typical of populations in northern portions of the native range (Healey 1978b; Adams 1997). A commonality between Lake McDonald and northern lakes is low productivity, resulting in slow growth of lake trout. The slow growth probably accounts for late maturity (Ferreri and Taylor 1996; Madenjian et al. 1998). Total annual mortality was within the range reported for natural mortality in unexploited lake trout populations (Shuter et al. 1998; Mills et al. 2002). Interestingly, we observed a mean annual fishing mortality rate of 16% for our tagged fish, which was 3% higher than our total annual mortality estimate. This inconsistency is perplexing; nevertheless, we believe that the lake trout population in Lake McDonald is relatively unexploited.

Unfortunately, fecundity of mature females in this population is unknown, and we did not have estimates of survival for lake trout younger than age 8. Thus, we were unable to reliably develop age-structured models with which to analyze various harvest scenarios that would reflect the lake trout population in Lake McDonald. Regardless, this lake trout population appears to be particularly susceptible to exploitation given their late maturity and slow growth. Lake trout often exhibit compensatory responses to harvest mortality, such as increased growth rate and fecundity, decreased age and length at maturity, and decreased natural mortality rate (Healey 1978a, 1978b; Ferreri and Taylor 1996). Although compensatory mechanisms would functionally reduce suppression effects, there is a threshold mortality rate beyond which population decline occurs regardless of compensation. It is believed that lake trout populations are not sustainable when total annual mortality exceeds 50% (Healey 1978b). Thus, suppression programs need to exert enough effort to exceed this threshold mortality rate and overcome compensatory responses. Establishment of baseline population characteristic data is important for monitoring changes to these variables dur-

ing the course of suppression efforts, such as occurred on Lake Pend Oreille (Hansen et al. 2008).

The aggregation of lake trout at two primary spawning sites emerged as the most important distribution pattern that could be exploited if suppression is initiated. Presumably, high mortality on the reproductive segment of the population could be achieved with minimal effort relative to other times of year. Lake trout have been vulnerable to capture at spawning sites in Yellowstone Lake (Koel et al. 2005) and Lake Pend Oreille (J. P. Fredericks, Idaho Department of Fish and Game, personal communication). Telemetry research has not been conducted in Yellowstone Lake, but suppression of adult lake trout improved markedly once a telemetry study was conducted in Lake Pend Oreille. The vulnerability of adult lake trout during spawning—combined with late maturity and unproductive growth conditions—increases the likelihood that recruitment overfishing can be achieved in Lake McDonald. Ideally, multiple life stages of lake trout should be targeted to most effectively reduce population growth; thus, knowledge of the spawning areas in Lake McDonald also provides a venue for attempts at reducing juvenile survival.

Lake trout are rapidly expanding their distribution in the western United States, thus requiring increasing management to minimize threats to existing fisheries. Although suppression is still unproven as an effective management strategy, perceived successes have been reported, and the popularity of suppression as a management tool is growing. Managers are often compelled to take quick action when new nonnative populations are discovered, assuming that suppression is likely to be easier at lower population density. The reactionary nature of quick action can lead to a less effective suppression approach. In contrast, numerous lake trout populations are well established, and managers struggle to decide whether suppression can be effective. We recommend that managers dealing with either scenario adopt an approach similar to ours, wherein lake trout distribution patterns and population characteristics are better understood before action is taken. Although additional time is required to gather information, the benefit of improved efficiency and maximized exploitation is likely to offset the delay. Similarly, increased knowledge may indicate that suppression is likely to be more or less difficult or resource intensive than originally thought. In either case, more informed management decisions can be made and responses can be better evaluated.

Ultimately, the full testing of suppression techniques on populations over time will determine whether this strategy has merit for long-term management of introduced lake trout. However, if poor candidate populations are selected for suppression or if exploitation thresholds are not reached because distribution patterns are not clearly identified, then the viability of suppression for managing introduced lake trout could be masked. We believe Lake McDonald is a strong candidate system in which to test the suppression of lake trout. More importantly, an approach similar to the one described here should be used by managers prior to implementing suppression efforts or can be used to improve existing suppression programs.

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