

Response of non-native lake trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park

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Abstract: Introduced lake trout (*Salvelinus namaycush*) threaten to extirpate native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in the 34 000 ha Yellowstone Lake in Yellowstone National Park, USA. Suppression (and eventual eradication) of the lake trout population is deemed necessary for the conservation of Yellowstone cutthroat trout. A US National Park Service gill-netting program removed nearly 450 000 lake trout from Yellowstone Lake from 1995 through 2009. We examined temporal variation in individual growth, body condition, length and age at maturity, fecundity, mortality, and population models to assess the efficacy of the lake trout suppression program. Population metrics did not indicate over-harvest despite more than a decade of fish removal. The current rate of population growth is positive; however, it is lower than it would be in the absence of lake trout suppression. Fishing effort needs to increase above observed levels to reduce population growth rate below replacement. Additionally, high sensitivity of population growth rate to reproductive vital rates indicates that increasing fishing mortality for sexually mature lake trout may increase the effectiveness of suppression. Lake trout suppression in Yellowstone Lake illustrates the complexities of trying to remove an apex predator to restore a relatively large remote lentic ecosystem with a simple fish assemblage.

Résumé : Les touladis (*Salvelinus namaycush*) introduits dans le lac Yellowstone de 34 000 ha dans le parc national de Yellowstone, É.-U., menacent d'en extirper la truite fardée de Yellowstone (*Oncorhynchus clarkii bouvieri*) indigène. On croit que la réduction (et éventuellement l'éradication) de la population de touladis est nécessaire à la conservation des truites fardées de Yellowstone. Un programme de pêche au filet maillant mené par le service des parcs nationaux des É.-U. a retiré presque 450 000 touladis du lac Yellowstone de 1995 jusqu'à la fin de 2009. Nous examinons la variation temporelle de la croissance individuelle, de la condition corporelle, de la longueur et de l'âge à la maturité, de la fécondité, de la mortalité et des modèles démographiques afin d'évaluer l'efficacité du programme d'élimination des touladis. Les métriques de la population n'indiquent pas de récolte excessive malgré le retrait de poissons pendant plus d'une décennie. Le taux actuel de croissance de la population est positif; cependant, il est plus bas qu'il ne le serait en absence du programme d'élimination des touladis. L'effort de pêche devra être accru au-delà des niveaux observés afin de réduire le taux de croissance de la population sous le seuil de remplacement. De plus, la forte sensibilité du taux de croissance de la population aux taux vitaux reproductifs indique que l'augmentation de la mortalité due à la pêche chez les touladis à maturité sexuelle pourrait améliorer l'efficacité de l'élimination. L'élimination des touladis dans le lac de Yellowstone illustre les difficultés reliées aux efforts pour retirer un prédateur de sommet de réseau trophique afin de restaurer un écosystème léntique relativement grand avec un peuplement simple de poissons.

[Traduit par la Rédaction]

Introduction

Non-native species have long been recognized as a driver of the global decline in biodiversity (Vitousek et al. 1997; Simberloff 2001) and are often ranked second to habitat loss and degradation as the most prevalent threat to freshwater biodiversity (Miller et al. 1989; Cambray 2003; Dextrase and Mandrak 2006). Non-native fishes have been implicated in

the decline of many native freshwater fish species worldwide (Holčik 1991; Ogutu-Ohwayo and Hecky 1991; Jelks et al. 2008). Eradication projects have been implemented for populations of non-native fishes; however, peer-reviewed articles assessing the efficacy of eradication projects are sparse, and most of these projects have occurred on small spatial scales such as high mountain streams, alpine lakes, and small impoundments (Thompson and Rahel 1996; Knapp and Mat-

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thews 1998; Britton and Brazier 2006). Information on suppression or eradication of populations of non-native fishes in larger water bodies is becoming increasingly important. For example, the invasion of several carp species (*Hypophthalmichthys* and *Cyprinus* spp.) throughout large river systems in North America and Australia may shift the management focus for these species from containment to removal (Kolar and Lodge 2002; Koehn 2004; DeGrandchamp et al. 2008).

The objective of many fish removal projects is to reverse native fish population declines caused by non-native predators (Mueller 2004; Louette and Declerck 2006; Martinez et al. 2009). The lake trout (*Salvelinus namaycush*) is an apex predator native to northern North America that has been introduced to 15 countries around the world and extensively within the United States (Crossman 1995). Lake trout have negatively affected native fish species in ecosystems where they have been successfully introduced (Crossman 1995), including large lakes and reservoirs in eight western US states (Martinez et al. 2009), where their presence has led to declines in native salmonid populations (Fredenberg 2002; Vander Zanden et al. 2003; Koel et al. 2005). Introductions of lake trout have also altered trophic dynamics in lakes and surrounding terrestrial ecosystems (Vander Zanden et al. 2003; Tronstad et al. 2010; Ellis et al. 2011).

Lake trout were discovered in Yellowstone Lake, Yellowstone National Park, in 1994 (Kaeding et al. 1995) after being illegally introduced in the mid- to late 1980s (Munro et al. 2005). Yellowstone Lake is the largest lake above 2000 m elevation in North America and contains the largest population of nonhybridized Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in the world (Gresswell and Varley 1988). The Yellowstone cutthroat trout is considered a “sensitive species” by the US Forest Service and Bureau of Land Management and an imperiled species by state agencies in Idaho, Montana, Nevada, Utah, and Wyoming (Gresswell 2009). Yellowstone Lake represents nearly 80% of the remaining lacustrine habitat for Yellowstone cutthroat trout (Gresswell et al. 1994), which is a keystone species in the Greater Yellowstone Ecosystem. Spawning migrations of Yellowstone cutthroat trout have been documented in 68 of Yellowstone Lake’s 124 tributaries (Gresswell et al. 1994), representing a substantial source of nutrients for the terrestrial ecosystem (Crait and Ben-David 2006). Thirteen mammal species and 15 bird species have been documented feeding on Yellowstone cutthroat trout (Schullery and Varley 1995).

The level of predation exerted by lake trout is expected to cause the Yellowstone cutthroat trout population to decrease by as much as 60% within 100 years (Stapp and Hayward 2002; Ruzycski et al. 2003). Relative abundance of Yellowstone cutthroat trout in netting assessments declined 11% per year after the discovery of lake trout (Koel et al. 2005). A lake trout removal program was initiated in 1995 with the purpose of reducing lake trout abundance and decreasing predation on Yellowstone cutthroat trout (McIntyre 1995). Lake trout suppression has been implemented or considered for the purpose of conserving native salmonids in several lakes in the Intermountain West of the USA (Martinez et al. 2009). As the longest ongoing lake trout removal project in the Intermountain West, the suppression program on Yellowstone Lake provides a unique case study to evaluate the effectiveness of removing a non-native predator from a large lake.

Lake trout have been exploited throughout their native range where the collapse of several lake trout fisheries indicates that overexploitation is possible (Martin and Olver 1980). The vulnerability of lake trout populations to overharvest is attributed to the species’ life-history strategy, which is characterized by relatively slow growth and late age at maturity (Healey 1978a). However, lake trout population metrics are strongly influenced by lake size, lake productivity, and diet (Trippel 1993; Shuter et al. 1998; Pazzia et al. 2002).

Exploitation can cause changes in population metrics and an eventual decline in abundance. A high level of harvest causes mortality rates to increase, with compensatory responses becoming evident in population metrics if a reduction in abundance reduces the effects of density dependence (Rose et al. 2001). Individual growth rates typically increase in exploited lake trout populations (Healey 1978a; Ferreri and Taylor 1996; Sitar and He 2006). Similarly, lake trout body condition increased in populations where exploitation caused a decline in density (Martin and Olver 1980; McDonald and Hershey 1989). Lake trout have also exhibited reductions in age at first maturity and increases in fecundity when harvested (Healey 1978a, 1978b; Ferreri and Taylor 1996). Although compensatory responses indicate a decrease in abundance, they can increase the resilience of populations to overharvest (Rose et al. 2001). For example, reduced age at maturity and elevated fecundity can increase the reproductive output of an exploited population (Healey 1978b; Trippel 1995).

Suppression was implemented by the National Park Service (NPS) in rapid response to the detection of lake trout (McIntyre 1995), with the goal of removing as many lake trout as possible given limited resources. Abundance was not estimated when suppression was initiated; therefore, harvest rates cannot be used to evaluate the effectiveness of the suppression program. We used available data from 1996 through 2009 to assess whether the suppression program has been successful at overharvesting the lake trout population (i.e., recruitment overfishing). We hypothesized that population metrics such as individual growth, body condition, fecundity, length at maturity, age at maturity, and mortality could be used to determine the efficacy of the suppression program given previous research on exploited lake trout populations (see paragraph above). We then used an age-structured matrix demographic model to simulate several scenarios of fishing mortality and the subsequent effects on population growth. These results provide guidance for the NPS and other natural resource agencies with regard to establishing harvest benchmarks to increase suppression program efficacy and highlight the need for baseline data when initiating non-native species removal.

Materials and methods

Study area

Yellowstone Lake is at an elevation of 2357 m, has a surface area of 34 020 ha, 239 km of shoreline, a mean depth of 48.5 m (Kaplinski 1991), and a maximum depth of 133 m (Morgan et al. 2003). The lake is typically ice-covered from mid-December until late May or early June. Thermal stratification occurs through July and early August, with summer surface water temperature reaching 17 °C and a thermocline

at about 15 m (Koel et al. 2007). Hydrothermal activity occurs throughout the lake, but is concentrated in the West Thumb Basin (Kaplinski 1991) where hydrothermal vents create warmer than lake-average water temperatures.

The lake is categorized as oligo-mesotrophic (Theriot et al. 1997), and the fish assemblage consists of two native species, Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*). Three fish species have been introduced in addition to lake trout: longnose sucker (*Catostomus catostomus*), reidside shiner (*Richardsonius balteatus*), and lake chub (*Couesius plumbeus*; Gresswell and Varley 1988).

Data collection

The removal of lake trout began when they were first caught in gill nets in 1994 (Kaeding et al. 1995). Removal intensified as gill nets were used to determine the distribution and population characteristics of lake trout from 1995 through 1998 (Ruzycki 2004). Gill nets were first set for the purpose of maximizing lake trout catch in 1998 and were used primarily for this purpose through 2009. Netting methods (i.e., mesh sizes and locations fished) were most similar from 2001 through 2008. Three different netting strategies were used to remove lake trout from Yellowstone Lake: control netting, spawner netting, and distribution netting (see Ruzycki (2004) for a detailed description of netting methods). Control netting targeted juvenile lake trout (250 to 400 mm total length) and constituted the majority of effort exerted in the suppression program since 1998. Control nets were sinking gill nets with bar-mesh sizes of 25, 32, or 38 mm. Annual effort (1 unit = 100 m of net set for 1 night) in control netting increased from 1145 to 16 725 units from 1998 through 2009, peaking at 28 500 units in 2007. Control nets were fished from ice-off in late May or early June through October.

Spawner netting targeted adult lake trout (>400 mm total length) at known spawning or staging locations. Sinking gill nets had bar-mesh sizes of 38, 44, 51, 57, 64, 70, or 76 mm. Effort increased from 142 to 2600 units from 1996 to 2009. Spawner nets were fished from late August through October and were lifted every 1–3 days to minimize gear saturation and bycatch of Yellowstone cutthroat trout. Night electrofishing was conducted from 2004 to 2007 at shallow spawning areas (primarily in the West Thumb Basin) during peak spawning activity. The amount of annual electrofishing effort varied from 8.67 to 26.25 h total electrofishing time (occurring over 5–14 nights per year) and accounted for 5%–20% of all spawning fish removed (i.e., gill-netting and electrofishing pooled).

Distribution netting consisted of lake-wide sampling of multiple depth strata to collect data on lake trout population demographics and spatial distribution. Distribution netting typically occurred at 16 fixed sites throughout the lake. Each site consisted of two depth strata: a shallow stratum (15–30 m) and a deep stratum (30–50 m). A small-mesh (consisting of 19, 25, 32, 38, 44, and 51 mm bar mesh) and a large-mesh (consisting of 57, 64, 70, 76, and 89 mm bar mesh) experimental gill net were combined to form a gang. A gang was set overnight at each depth stratum by site.

Age, growth, and body condition

Sagittal otoliths were used to estimate lake trout ages

through the suppression program (Ruzycki et al. 2003; Syslo 2010). Regressions of annual mean length at age values through time were used to assess changes in individual growth rate because of highly variable sample sizes among years. Mean length at age was estimated for lake trout caught on or later than 1 August to avoid possible biases caused by seasonal growth. Mean length at age was not estimated for years where age classes had fewer than five observations to avoid possible influences of outliers. Regressions of mean length at age through time were estimated for age classes with at least five annual mean length values. The von Bertalanffy (VBF) equation was used to describe growth in length and provided parameters to estimate natural mortality (see below). The NLS procedure in R 2.9.2 was used to estimate values of model parameters using the following equation:

$$(1) \quad L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$$

where L_t is length at time t , L_∞ is theoretical maximum length of lake trout in the population, K is the growth coefficient, t is age, and t_0 is age when length theoretically equals 0 mm (Isely and Grabowski 2007).

Body condition was compared between 1998 and 2007 because these years had adequate mass data and represent conditions before and after 10 years of removal. Analysis of covariance (ANCOVA) was used to compare mass–length regression models from 1998 and 2007. Gonadal development over the course of the year can influence mass measurements, especially for female fish (Pope and Kruse 2007). Therefore, the ANCOVA model for mass as a function of total length included categorical predictors for year (1998 or 2007), whether fish were mature (>401 mm) or immature (<400 mm), and sex. Mass and length observations were \log_e -transformed prior to model estimation for linearity.

Fecundity and maturity

Fecundity was estimated volumetrically in 1998 (Ruzycki et al. 2003) and gravimetrically in 2006 and 2007 (Syslo 2010). Mass–fecundity relationships were compared by year with ANCOVA to determine whether fecundity changed over the duration of the suppression program.

Maturity was estimated for fish caught in distribution netting to avoid biases caused by netting methods that target immature or spawning mature lake trout. Annual probabilities of 50% maturity at length were estimated by sex using logistic regression for binary response data. Logistic regression models included total length and year as continuous variables. Annual values of length at maturity were converted to ages using year-specific VBF growth models.

Mortality and harvest

Recruitment likely increased through time given the relatively recent date of lake trout introduction. Therefore, mortality was estimated for lake trout caught in control and spawner netting using a statistical catch at age analysis (SCAA). The SCAA model was estimated using catch at age observations for age 2–17 lake trout and gill-netting effort from combined control and spawner netting from 2001 through 2008. Methods followed Haddon (2001) except age-specific fishery selectivity was estimated using a double logistic function (Linton et al. 2007). Natural mortality was es-

estimated as an instantaneous rate (M) with the formula provided by Pauly (1980):

$$(2) \quad \log(M) = -0.0066 - 0.279 \cdot \log_{10}(L_{\infty}) + 0.6543 \cdot \log_{10}(K) + 0.4634 \cdot \log_{10}(T)$$

where M is the instantaneous rate of natural mortality, L_{∞} and K are coefficients estimated from the VBF growth equation, and T is mean annual environmental water temperature. Mean annual environmental water temperature was 5.1 °C for Yellowstone Lake (Ruzycki et al. 2003).

Estimates of lake trout mortality were obtained using catch curve regressions for lake trout caught in distribution netting in addition to the SCAA for catch data. Although increasing recruitment may bias catch curve estimates of mortality, the distribution netting data were considered most representative of the population, and general agreement between separate data sets would strengthen conclusions. Length structure of fish caught in gill nets may not represent the length structure of the population because gill nets are selective for certain sizes of fish; therefore, length–frequency data were standardized to account for unequal selectivity and effort among mesh sizes (Syslo 2010). Standardized annual length frequencies were converted to age frequencies using year-specific age–length keys (Isely and Grabowski 2007). Age frequencies were computed for years without age data using the age–length key for the nearest year. Total instantaneous mortality rate (Z) was estimated as the slope of catch curve regressions of the natural logarithm of catch at age on age (Miranda and Bettoli 2007). Total instantaneous mortality (Z) was evaluated through time with an ANCOVA model that included year as a continuous variable. Instantaneous mortality rates were converted to total annual mortality (A) and exploitation (μ ; Miranda and Bettoli 2007). Exploitation represents the proportion of the population removed over an interval; therefore, by dividing the annual harvest by μ we recreated estimates of annual lake trout abundances. An extremely small lower 95% confidence interval (CI) for μ resulted from a large standard error estimated for Z in 1998 and created an unrealistic upper 95% CI for reconstructed abundance in 1998. Therefore, the CI for μ used to back-calculate abundance in 1998 was estimated using the standard error for Z from the 1997 catch curve regression. Annual abundances after harvest were computed by subtracting the harvest from the back-calculated abundance, and a model was fit to the abundances for an estimate of population growth rate (λ).

Age-structured population model

Model structure

A female-based Leslie matrix was used to model the lake trout population (Caswell 2001). Age-specific reproductive rates were estimated using the most recent estimates of demographic parameters (Table 1). Although the oldest lake trout observed in Yellowstone Lake was 17 years, maximum age estimates in native populations vary from 20 to 62 years (Martin and Olver 1980). Therefore, the matrix model included age classes 0 to 30 because length at age reached an asymptote at age 30. An age 30+ stage was included so that the life span was not limited to 30 years. We assumed that females produced offspring at age 5 (the minimum observed

age of sexual maturity) and also assumed females spawned every year. The matrix model included a prebreeding census, which requires the fertility term to include survival of age-0 fish (S_0) to be counted as age-1 fish the following year (Caswell 2001). Fertility was multiplied by 0.5 to account for half of the offspring being female.

Model parameterization

Length at age was used to predict age-specific values of fecundity (Fec_i) and probability of maturity (P_i). Length at age for females was determined using the VBF growth model for females (where $t_0 = -0.16$, $K = 0.18$, and $L_{\infty} = 781$). The mean and standard deviation for Fec_i and P_i given length at age i were determined from models of length–fecundity ($\log(Fec_i) = -15.08 + 3.626 \times \log(\text{length}_i)$) and length–maturity:

$$(3) \quad P_i = \frac{\exp(-21.0 + 0.04 \cdot \text{length}_i)}{1 + \exp(-21.0 + 0.04 \cdot \text{length}_i)}$$

Natural mortality was estimated as an instantaneous rate (M) using VBF parameters for females and converted to annual survival rate for ages 2–30+ in the matrix model with the following equation: $S_i = \exp(-M)$ (Miranda and Bettoli 2007). Natural survival rates have not been estimated for age-0 and age-1 lake trout in Yellowstone Lake; therefore, we used estimates from the native range of the species. Annual natural survival rate was assumed to be 0.0043 for age-0 lake trout (Shuter et al. 1998) and 0.449 for age-1 lake trout (Sitar et al. 1999).

Age-specific instantaneous fishing (F) mortality was modeled as the product of fully selected fishing mortality and age-specific selectivity (Haddon 2001). Instantaneous fishing and natural (M) mortality rates were converted to conditional interval fishing (m) and natural (n) mortality rates with the following equations: $m = 1 - \exp(-F)$ and $n = 1 - \exp(-M)$ (Miranda and Bettoli 2007). Estimates of age-specific survival (S_i) that included both natural and fishing mortality were computed as the complement of total conditional interval mortality ($A = m + n - mn$; Miranda and Bettoli 2007).

The matrix model was not sensitive to starting population size because it did not include density dependence. However, short-term results were sensitive to the starting age frequency. We considered the age frequency from distribution netting to be the most representative of the population in any given year. The starting population size was the SCAA abundance estimate for 2008 distributed among age classes using the age frequency for distribution netting in 2009. The abundance of age-1 lake trout was extrapolated from an exponential decay function fit to the age frequency for ages 2–17. The observed sex ratio was 1:1. Therefore, the abundance estimate was multiplied by 0.5, resulting in 231 481 female lake trout ages 1–17.

Model simulations

Fully selected fishing mortality (F) varied from 0 to 1.5 in increments of 0.1. Each level of F was maintained for 5, 10, and 20 years. Each management scenario was simulated 1000 times using R 2.9.2 (R Development Core Team 2009) to incorporate variation in selectivity and vital rate estimates. The first step of each simulation run was to create a Leslie projection matrix replicate. Vital rates for the matrix were estimated from predicted values of age-specific survival, fecundity, and

Table 1. Mean and standard deviation (in parentheses) of age-specific vital rates used in population simulations for lake trout in Yellowstone Lake, Yellowstone National Park.

Age	S_i in absence of fishing mortality	Sel_i	Total length (mm)	Fec_i	P_i
0	0.0043 ^a	0	—	0	0
1	0.449 ^b	0	145	0	0
2	0.898	1.000 (0.000)	249	0	0
3	0.898	0.995 (0.016)	335	0	0
4	0.898	0.990 (0.034)	407	0	0
5	0.898	0.984 (0.051)	468	822 (289)	0.097 (0.058)
6	0.898	0.977 (0.068)	519	1373 (221)	0.391 (0.107)
7	0.898	0.969 (0.084)	561	2009 (176)	0.732 (0.116)
8	0.898	0.960 (0.010)	597	2660 (152)	0.901 (0.075)
9	0.898	0.950 (0.114)	627	3309 (148)	0.961 (0.040)
10	0.898	0.940 (0.130)	652	3927 (155)	0.983 (0.022)
11	0.898	0.927 (0.143)	673	4499 (168)	0.991 (0.013)
12	0.898	0.914 (0.157)	690	5020 (182)	0.995 (0.008)
13	0.898	0.900 (0.171)	705	5467 (196)	0.997 (0.005)
14	0.898	0.884 (0.185)	717	5882 (208)	0.998 (0.004)
15	0.898	0.868 (0.200)	728	6223 (218)	0.998 (0.003)
16	0.898	0.851 (0.212)	736	6512 (228)	0.999 (0.002)
17	0.898	0.832 (0.224)	743	6778 (236)	0.999 (0.002)
18	0.898	0.832 (0.224)	749	6982 (242)	0.999 (0.002)
19	0.898	0.832 (0.224)	755	7156 (249)	0.999 (0.002)
20	0.898	0.832 (0.224)	759	7332 (253)	0.999 (0.002)
21	0.898	0.832 (0.224)	762	7440 (257)	0.999 (0.002)
22	0.898	0.832 (0.224)	795	7548 (259)	0.999 (0.002)
23	0.898	0.832 (0.224)	768	7621 (262)	0.999 (0.002)
24	0.898	0.832 (0.224)	770	7694 (265)	0.999 (0.002)
25	0.898	0.832 (0.224)	772	7769 (266)	0.999 (0.002)
26	0.898	0.832 (0.224)	773	7806 (269)	0.999 (0.002)
27	0.898	0.832 (0.224)	774	7881 (270)	0.999 (0.002)
28	0.898	0.832 (0.224)	775	7919 (272)	0.999 (0.002)
29	0.898	0.832 (0.224)	776	7956 (272)	0.999 (0.002)
30	0.898	0.832 (0.224)	777	7956 (272)	0.999 (0.002)

Note: Age-specific vital rates are survival (S_i), relative selectivity (Sel_i), fecundity (Fec_i), and probability of maturity (P_i).

^aVital rate estimate from Shuter et al. (1998), with standard deviation (SD) equal to 15% of the mean.

^bVital rate estimate from Sitar et al. (1999), with SD equal to 15% of the mean.

probabilities of maturity and associated standard deviations (Table 1). The popbio package (Stubben and Milligan 2007) was used to generate vital rate values for each matrix replicate. Vital rate values were generated from beta and stretched beta distributions, which have central tendencies and tails that are restricted to logical parameter values instead of approaching infinity (Morris and Doak 2002). Age-specific rates of survival and probabilities of maturity were generated from beta distributions, which had tails restricted between 0 and 1. Age-specific selectivity and fecundity values were log-normally distributed and generated from stretched beta distributions, which had tails restricted to specified minimum and maximum values (Morris and Doak 2002). Each matrix replicate (\mathbf{A}_i) was iterated with the population vector (\mathbf{n}_i) for 5, 10, or 20 years. For each simulation, λ at each time step (λ_t) was computed from the abundance (N_t): $\lambda_t = N_t/N_{t-1}$, and the mean of λ_t was calculated over all time steps.

Summary statistics

The geometric mean ($\pm 95\%$ CI) was used as the summary statistic for mean λ_t (Morris and Doak 2002). Geometric

mean λ (λ_G) was examined as a function of F for the 5-, 10-, and 20-year time frames. The rate of mortality at which λ_G was equal to one was noted as the rate of mortality at which λ_G was at replacement. The population would decline from recruitment overfishing if mortality increased beyond the rate that caused replacement.

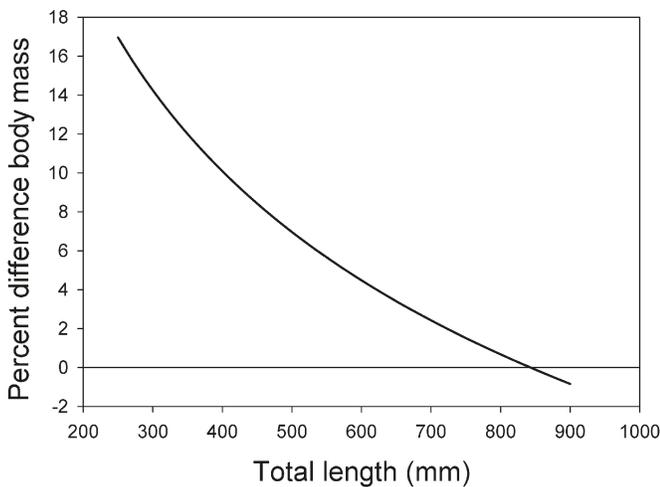
Sensitivity analysis

A sensitivity analysis was conducted to examine which parameters influenced our model the most (Nicolson et al. 2002) and which age classes of lake trout had the largest effect on population growth rate (Caswell 2001). Commonly used analytical sensitivity and elasticity analyses based on matrix eigenvalues assume the population is at stable age distribution and are based on long-term population dynamics (Morris and Doak 2002). However, harvested populations or populations changing in abundance are not likely at stable age distribution (Fefferman and Reed 2006), and we were interested in sensitivity over the short term. Therefore, we used a conventional simulation approach to evaluate sensitivity (Cross and Beissinger 2001). The sensitivity value for each

Table 2. Regression statistics for mean length at capture through time (years; N = the number of years) from 1998 through 2007.

Age	β_0	β_1	r^2	F	P	N
4	-16 572	8.46	0.34	2.55	0.17	7
5	-2 096	1.27	0.01	0.05	0.84	8
6	-7 891	4.19	0.12	0.79	0.41	8
7	-2 240	1.40	0.09	0.52	0.50	7
8	11 203	-5.30	0.39	3.16	0.14	7
9	20 910	-10.13	0.45	2.43	0.22	5
10	49 587	-24.42	0.77	13.69	0.02	6
11	55 489	-27.34	0.55	3.62	0.15	5
12	95 960	-47.53	0.81	13.11	0.04	5

Fig. 1. Percent change in mass at length between 1998 and 2007 for lake trout in Yellowstone Lake, Yellowstone National Park. The horizontal reference line indicates no change from 1998.



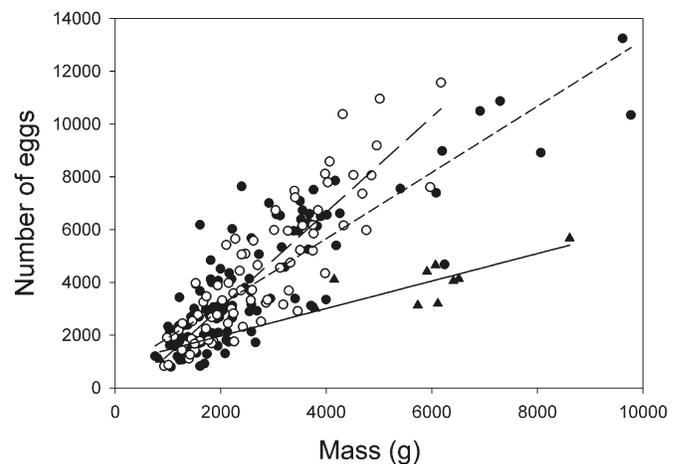
vital rate was calculated as the percent reduction in λ_G at 5, 10, and 20 years given a 10% reduction in the vital rate. Sensitivities were calculated with F equal to the rate observed in 2005. For each matrix replicate in 1000 simulations, each vital rate was reduced by 10% while holding all other vital rates constant. The reduction in λ_G given each altered vital rate relative to λ_G produced by the unaltered matrix was calculated at 5, 10, and 20 time steps. The reductions in λ_G were averaged across the 1000 matrix replicates for a mean estimate of sensitivity of λ_G to each vital rate through each time frame. The sensitivity of population growth rate to total annual reproduction was estimated by summing age-specific sensitivities to fecundity across all age classes.

Results

Temporal analyses of population metrics yielded mixed results regarding the trend in lake trout density. Compensatory increases in growth were not detected with regressions of mean length at age through time, and mean length decreased through time for age 10 and 12 lake trout (Table 2). Mass-length regression slopes ($F_{[1,1924]} = 7.23, P < 0.01$) and intercepts ($F_{[1,1924]} = 71.09, P < 0.01$) differed between 1998 and 2007. Lake trout smaller than 840 mm weighed up to 17% more in 2007, and the difference in body mass between 1998 and 2007 decreased with increasing length (Fig. 1).

Slopes for the mass-fecundity models differed between

Fig. 2. Mass-fecundity regressions for 1996 (triangles), 2006 (solid circles), and 2007 (open circles) for lake trout in Yellowstone Lake, Yellowstone National Park.

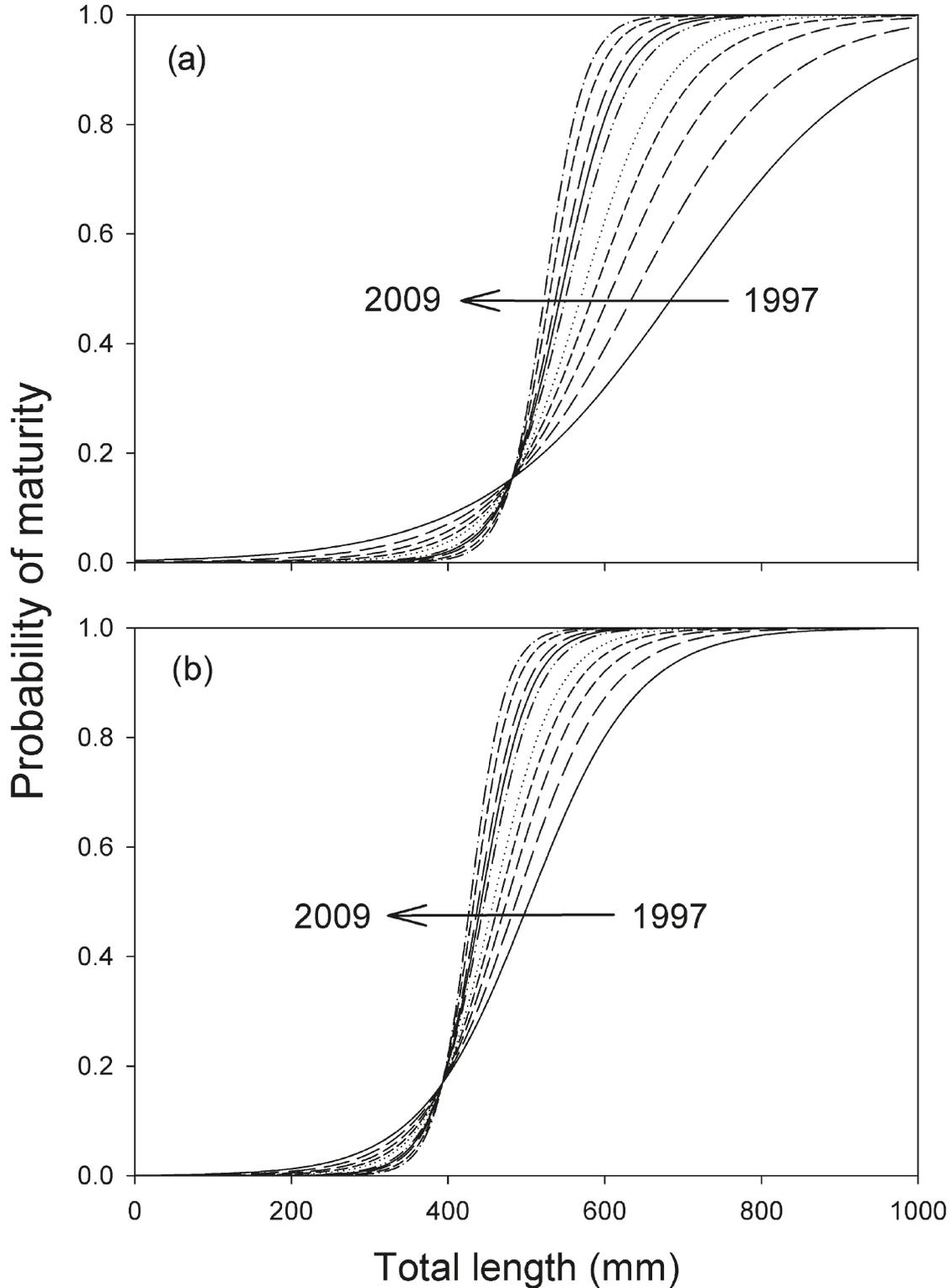


1996 and 2006 ($F_{[1,201]} = 6.57, P = 0.01$) and between 1996 and 2007 ($F_{[1,201]} = 16.75, P < 0.01$; Fig. 2). However, intercepts for mass-fecundity models were similar between 1996 and 2006 ($F_{[1,201]} = 0.21, P = 0.65$) and between 1996 and 2007 ($F_{[1,201]} = 0.056, P = 0.28$). Length at maturity decreased from 1997 through 2009 for males and females ($P < 0.01$). Length at probability of 50% maturity for females decreased from 694 mm in 1997 to 524 mm in 2009 (Fig. 3a), corresponding to a decrease in age at 50% maturity from 11.8 to 6.3 (Table 3). For males, the length at probability of 50% maturity decreased from 503 mm in 1997 to 428 mm in 2009 (Fig. 3b), corresponding in a decrease in age of 6.3 to 4.5 (Table 3).

Annual harvest estimated by the SCAA model closely matched the observed harvest from 2001 through 2006 (Fig. 4a). However, a paucity of data for recently recruited cohorts resulted in a poor fit for 2007 and 2008. Fully selected fishing mortality was likely overestimated in 2007, and variability increased through time for estimates of abundance (Figs. 4a-4c). Abundance increased from 87 042 (67 093-100 477; 95% CI) lake trout in 2001 to 305 101 (150 986-770 365; 95% CI) in 2008 (Fig. 4c), and mean λ calculated from annual abundance estimates was 1.21. Estimated F increased from 0.22 (0.15-0.30; 95% CI) in 2001 to 0.56 (0.38-0.76; 95% CI) in 2007 before declining to 0.18 (0.12-0.26; 95% CI) in 2008 (Fig. 4b). Recruitment of age-2 lake trout increased from 20 931 (12 875-30 569; 95% CI) to 129 430 (33 476-614 513; 95% CI) lake

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Fig. 3. Probability of maturity at length by year for female (a) and male (b) lake trout in Yellowstone Lake, Yellowstone National Park.



trout from 2001 through 2008. The catchability coefficient, indicating the increase in F given a 1-unit increase in gill-netting effort (1 unit = 100 m of net set for 1 night), was 1.35×10^{-5} (1.03×10^{-5} to 1.69×10^{-5} ; 95% CI). Selectivity was one for age-2 lake trout and gradually declined to 0.83 for age-17 lake trout (Fig. 4d).

Total annual mortality (A) from catch curve regressions in-

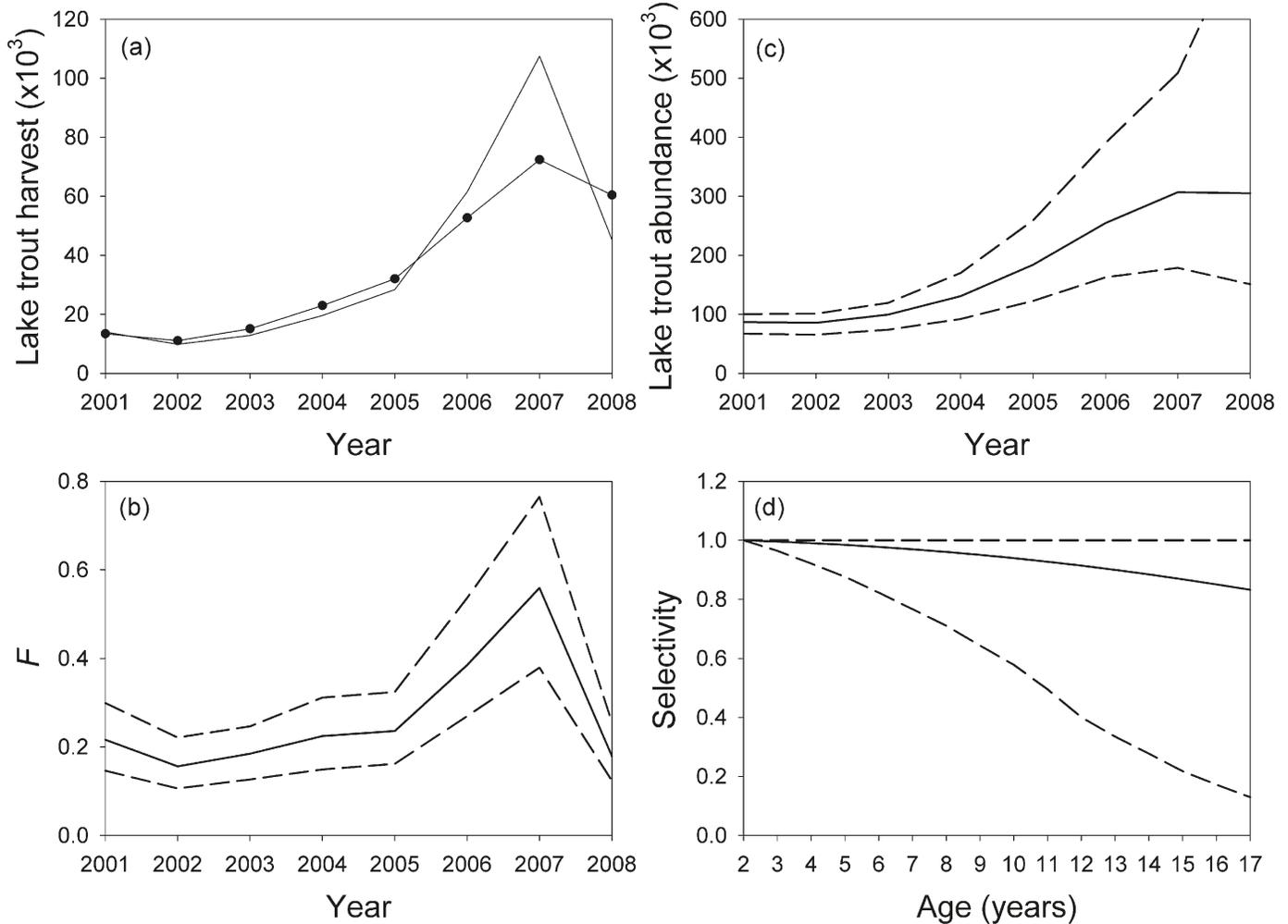
creased from 0.24 (95% CI = 0.14–0.36) in 1997 to 0.34 (95% CI = 0.26–0.40) in 2009 (Table 4). Estimates of natural mortality were near 0.1 through the duration of the program (Table 4), with small deviations from this value caused by slightly varying VBF growth parameters (Table 3). Consequently, μ increased from 0.14 (95% CI = 0.003–0.263) in 1998 to 0.26 (95% CI = 0.19–0.32) in 2009. Estimates of Z

Table 3. Population metrics (95% confidence interval) by year for lake trout in Yellowstone Lake, Yellowstone National Park.

Year	Metric						
	t_0	K	L_∞	L_{m50}		A_{m50}	
				Female	Male	Female	Male
1997	—	—	—	694 (602–1172)	503 (456–559)	11.8 (8.6–15.0)	6.3 (5.4–7.5)
1998	0.66 (0.37–0.95)	0.18 (0.15–0.21)	807 (768–846)	641 (587–762)	487 (452–521)	9.8 (8.2–15.5)	6.0 (5.4–6.7)
1999	—	—	—	609 (572–667)	474 (448–498)	6.8 (6.0–8.2)	4.4 (4.0–4.8)
2000	-1.11 (-2.46–0.25)	0.09 (0.01–0.17)	1163 (514–1812)	588 (560–624)	465 (444–483)	6.3 (5.8–7.1)	4.3 (4.0–4.5)
2002	-0.57 (-1.26–0.12)	0.18 (0.12–0.24)	764 (678–850)	—	—	—	—
2003	-1.23 (-2.15 – -0.31)	0.10 (0.06–0.14)	1004 (853–1155)	553 (534–573)	447 (432–461)	6.5 (6.1–6.9)	4.7 (4.4–4.9)
2004	-2.73 (-4.55 – -0.91)	0.04 (0.00–0.08)	1684 (200–3170)	546 (528–565)	442 (427–457)	7.0 (6.6–7.5)	5.0 (4.7–5.3)
2005	-0.86 (-1.36 – -0.36)	0.14 (0.11–0.18)	810 (730–890)	540 (523–560)	439 (423–455)	6.6 (6.2–7.2)	4.5 (4.2–4.8)
2006	-1.91 (-2.54 – -1.28)	0.09 (0.07–0.11)	983 (850–1116)	—	—	—	—
2007	-0.47 (-0.80 – -0.13)	0.15 (0.13–0.17)	812 (765–860)	531 (514–549)	433 (416–449)	6.4 (6.0–6.9)	4.5 (4.3–4.8)
2009	—	—	—	524 (506–544)	428 (410–447)	6.3 (5.9–6.7)	4.5 (4.2–4.8)

Note: The table includes parameters t_0 , K , and L_∞ from von Bertalanffy growth models (see text for definition), length (mm) at 50% maturity (L_{m50}), and age (years) at 50% maturity (A_{m50}).

Fig. 4. Statistical catch-at-age results from 1998 through 2007 for lake trout in Yellowstone Lake, Yellowstone National Park. (a) Observed harvest by year (connected dots) and estimated harvest (solid line). (b) Mean (solid line) fully selected fishing mortality (F) and 95% confidence intervals (dashed lines). (c) Mean lake trout abundance (solid line) and 95% confidence interval (dashed lines). (d) Mean selectivity (solid line) and 95% confidence intervals (dashed lines).



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Table 4. Annual estimates of total instantaneous mortality (Z), instantaneous natural mortality (M), instantaneous fishing mortality (F), and total annual mortality (A) from catch curve regressions for lake trout in Yellowstone Lake, Yellowstone National Park.

Year	Z (SE)	M	F	A
1997	0.276 (0.049)	0.108	0.168	0.24
1998	0.262 (0.078)	0.108	0.154	0.23
2005	0.342 (0.058)	0.092	0.251	0.29
2007	0.352 (0.030)	0.095	0.257	0.30
2009	0.410 (0.048)	0.095	0.315	0.34

Note: SE, standard error.

increased through time (Table 4); however, the year effect was not significant ($F_{[1,43]} = 2.289$, $P = 0.138$). Back-calculated annual abundances of ages 2–17 lake trout increased from 49 798 (95% CI = 29 405–136 873) lake trout in 1998 to 290 038 (95% CI = 213 464–432 514) in 2009 and represent a λ of 1.2. Estimates of fishing mortality from catch curves were lesser than estimates from the SCAA, but only differed by 0.01 in 2005 (Table 4; Fig. 4b).

In the absence of fishing mortality, the 20-year estimate of λ_G from the matrix model was 1.29 (95% CI = 1.14–1.39). Estimates of λ_G at observed selectivity and fishing mortality ($F = 0.25$) in 2005 were 1.09 (95% CI = 0.96–1.2) for the 5-year time frame, 1.07 (95% CI = 0.94–1.19) for the 10-year time frame, and 1.07 (95% CI = 0.94–1.18) for the 20-year time frame (Fig. 5). Rates of F were more effective at reducing λ_G when maintained for longer time frames (Fig. 5). Geometric mean λ was reduced to one when F was 0.34 ($A = 0.36$) over a 20-year time frame and when F was 0.39 ($A = 0.39$) over a 5-year time frame. The upper 95% CI for λ_G was reduced to one when F was 0.52 ($A = 0.46$) over a 20-year time frame and when F was 0.59 ($A = 0.50$) over a 5-year time frame.

Population growth rate was most sensitive to S_0 (Figs. 6a–6b). A 10% reduction in S_0 caused a 1.86% reduction in λ_G over 5 years, a 1.38% reduction over 10 years, and a 1.23% reduction over 20 years. Population growth rate was also highly sensitive to survival for ages 1 through 6, and sensitivity to survival decreased after age 6 (Figs. 6a–6b). Sensitivity of λ_G to S_1 – S_5 increased relative to the sensitivity to S_0 as time frames increased. Ten percent reductions in age-specific fecundities (accomplished by reducing P_i or Fec_i) never caused λ_G to decrease more than 0.25%. However, the sum of sensitivities across all P or Fec equaled the sensitivity to S_0 .

Discussion

Population abundances estimated from the SCAA model and reconstructed from catch curve mortality estimates corroborated the matrix model, indicating the lake trout population was increasing despite more than a decade of removal. However, analyses of body condition, maturity, and fecundity appeared to indicate decreasing abundance. Given the increase in the lake trout population over the duration of the suppression program, apparent compensatory responses were likely caused by changing trophic dynamics. It is likely that a precipitous decline in the Yellowstone cutthroat trout population (Koel et al. 2005) increased resource availability for juvenile

lake trout, which prey on similar items (Benson 1961; Ruzycki et al. 2003). Additionally, the declining Yellowstone cutthroat trout population may have contributed to the decline in body condition and growth for older lake trout because 90% of the diet for lake trout age 9 and older is Yellowstone cutthroat trout (Ruzycki et al. 2003). Future research should address temporal shifts in lake trout diets and diet overlap between Yellowstone cutthroat trout and lake trout. An alternative explanation for apparent compensatory responses is that lake trout sampled in the 1990s may have included fish from the source population, Lewis Lake (Munro et al. 2005). The lake trout population in Lewis Lake is at carrying capacity and is characterized by poor growth and body condition caused by low food availability. Lake trout were likely introduced into Yellowstone Lake as recently as the mid-1990s (Munro et al. 2005), and mass, maturity, and fecundity samples collected early in the suppression program may include those fish and reflect biological conditions in Lewis Lake rather than Yellowstone Lake.

Several population metrics indicated that lake trout have not reached carrying capacity in Yellowstone Lake. The most recent estimates of VBF growth model parameters L_∞ and ω (a measure of pre-reproductive growth calculated as the product of t_0 and K) rank in the 88th percentile when compared with 54 lake trout populations across Ontario (Shuter et al. 1998). Additionally, 50% maturity for males in Yellowstone Lake occurred at a small size and young age when compared with North American lake trout populations with varying levels of harvest (Healey 1978a; Trippel 1993; Sitar and He 2006). Age at 50% maturity for males in Yellowstone Lake in 2009 was similar to estimates for lake trout in Lake Michigan (Madenjian et al. 1998), where density had not recovered from collapse. Female lake trout in Yellowstone Lake matured at a similar age and smaller size than females in Lake Michigan, which matured at ages 5.5 to 7.4 and lengths of 628 to 654 mm (Madenjian et al. 1998). However, declining body condition for larger lake trout may indicate that piscivorous lake trout are approaching carrying capacity. Given ontogenetic shifts in lake trout diet (Ruzycki et al. 2003), carrying capacities likely vary for juvenile and adult lake trout and are likely to change as the forage base changes. Future population modeling may require density dependence, which is likely to reduce population growth rate (λ) at high lake trout abundance (Ferreri et al. 1995). Density-dependent reductions in growth are expected if lake trout abundance increases (Sitar and He 2006). Reductions in growth may result in later ages at maturity and reductions in fecundity (Ferreri and Taylor 1996; Madenjian et al. 1998). Conversely, reductions in lake trout density would increase the resilience of the population to reduction through shifts towards higher growth, earlier maturity, and higher fecundity rates (Zipkin et al. 2008; Johnston and Post 2009). Population metrics should be monitored into the future to determine whether density-dependent patterns are expressed.

The amount of fishing effort required to reduce mean λ to one over a 20-year time frame is 25 262 units per year, and effort must increase to 28 977 units per year to reduce λ to one over a 5-year time frame. Thus, the amount of effort expended each year should be at least the amount expended in 2007, when effort peaked at 28 500 units. Fishing effort must increase beyond these levels when considering variability in

Fig. 5. Geometric mean population growth rate (λ_G ; black lines) with 95% confidence intervals (gray lines) at given levels of fully selected fishing mortality (F) over 5- (solid line), 10- (dashed line), and 20-year (dotted line) time frames for lake trout in Yellowstone Lake, Yellowstone National Park. The horizontal reference line indicates $\lambda_G = 1$ (replacement).

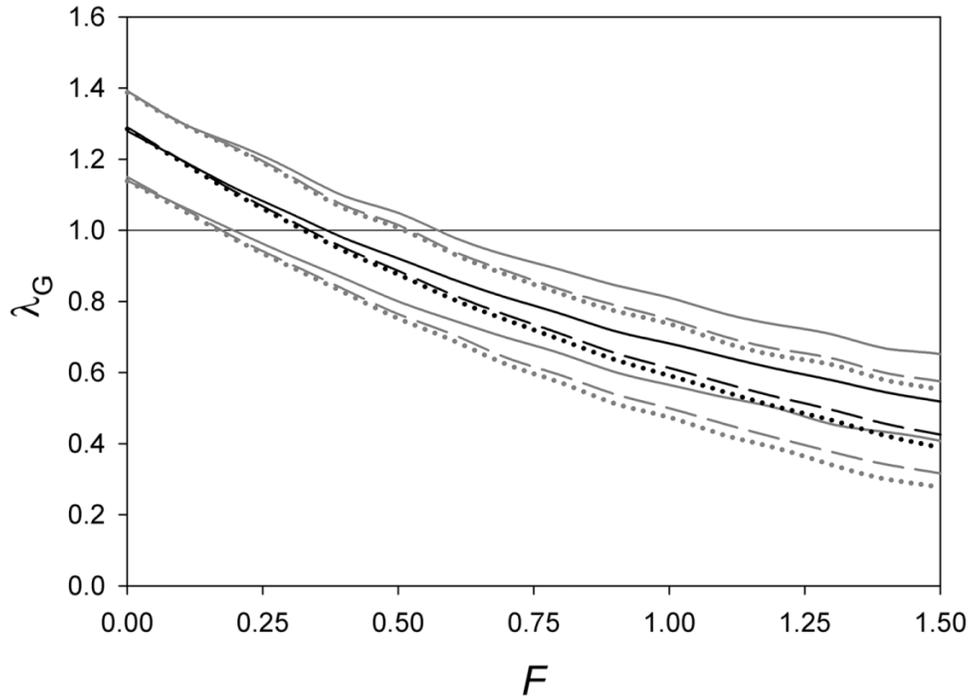
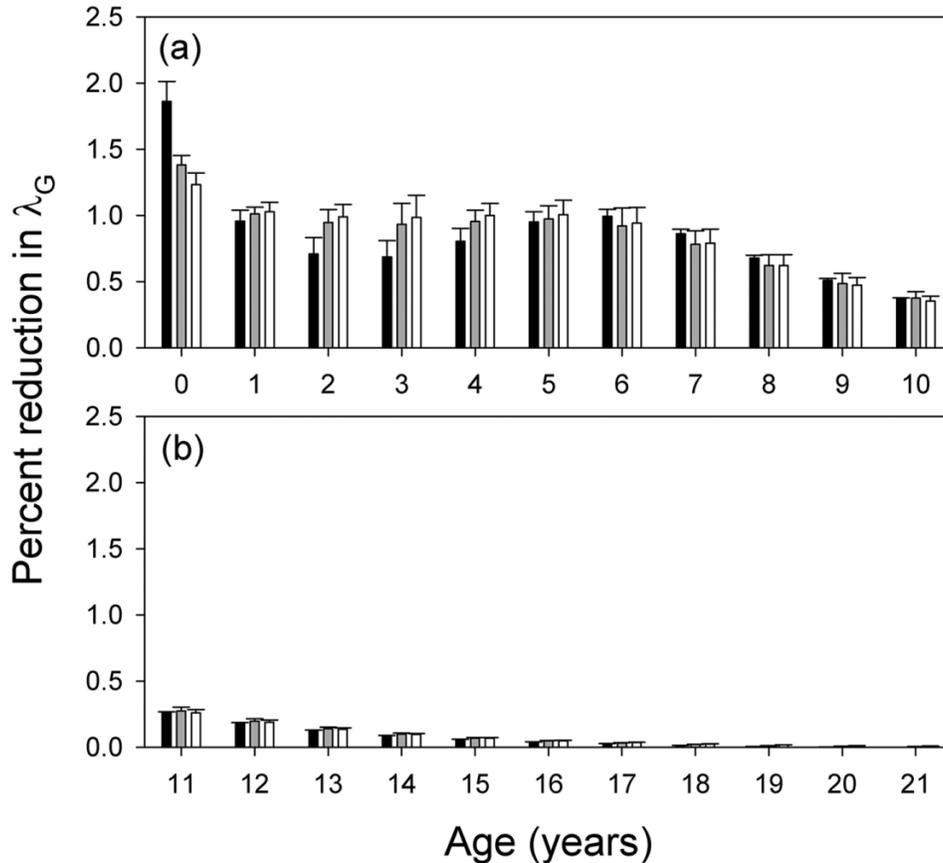


Fig. 6. Percent reduction in geometric mean population growth rate (λ_G) over 5- (black bars), 10- (gray bars), and 20-year (open bars) time frames given 10% reductions in age-specific survival for ages 0–10 (a) and 11–21 (b). Error bars delineate standard errors. Reductions in population growth rate for ages 21–30+ were less than 0.006% and are not displayed.



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estimates of λ and catchability (q). For example, the lower confidence interval for q indicates that effort must be 50 315 units to reduce the upper CI of λ to one over a 20-year time frame.

Population growth rate (λ) was most sensitive to reproduction (through fecundity or S_0), indicating that increasing fishery selectivity for mature lake trout or targeting developing lake trout embryos may increase the effectiveness of lake trout suppression. Increased selectivity for mature lake trout will require increased fishing effort with large-mesh gill nets or the implementation of trap nets. A telemetry study would be useful for identifying additional spawning sites where gill net catch per unit effort is high. Although electrofishing at spawning sites produced a high catch per unit effort, depth at the majority of sites limits effectiveness (Koel et al. 2007). The current netting strategy was developed to maximize lake trout harvest while reducing bycatch of Yellowstone cutthroat trout (Koel et al. 2005). Bycatch is currently less than 0.1 Yellowstone cutthroat trout per lake trout (Koel et al. 2005); however, it may increase if mature lake trout are targeted with increased gill-netting effort, as these fish are likely to occupy depths in the upper hypolimnion in close proximity to Yellowstone cutthroat trout prey (Ruzycki et al. 2003; Dux et al. 2011). Future studies should address the effect of bycatch mortality on Yellowstone cutthroat trout population growth rate relative to predation rate and the efficiency of trap-netting versus gill-netting for lake trout suppression (Hansen et al. 2010).

The level of total annual mortality required to cause a decline in lake trout abundance in Yellowstone Lake was similar to the level of mortality required to suppress other introduced lake trout populations. A population model indicated the lake trout population in Lake Pend Oreille was likely to decline when total annual mortality (A) was between 0.45 and 0.50 (Hansen et al. 2010). Spawning potential ratio simulations for an introduced lake trout population in Lake McDonald, Glacier National Park, indicated that recruitment overfishing was likely to occur when exploitation exceeded 0.36 ($A = 0.44\text{--}0.49$; Dux 2005). The above studies support the assertion that lake trout populations are likely to decline when A is near 0.5 (Healey 1978b).

We evaluated the increase in fishing mortality required to reduce λ to 1.0 as a minimal target for management in the future; however, the goal for lake trout suppression in Yellowstone Lake is not to decrease λ to replacement, but to decrease lake trout abundance as much as possible. The few existing examples of suppression projects eliciting recovery of native fish populations indicate that reductions in predator abundance of greater than 80%–90% were required (Dudley and Matter 2000; Lepak et al. 2006). Clearly, a multiple species assessment would be useful for determining the reduction in lake trout required to elicit recovery of the Yellowstone cutthroat trout population.

For a population eradication program to succeed, the number of individuals removed must exceed the number of individuals being produced (Bomford and O'Brien 1995). Although this statement seems obvious, it highlights the importance of inflicting mortality on the population before population growth reaches the steep section of the logistic growth curve. Rapid detection and response increase the effectiveness of population eradication programs (Simberloff

2003), and the implementation of population suppression in Yellowstone Lake soon after the discovery of lake trout may have increased the probability of success. However, the lake trout suppression program also highlights the potential drawbacks of such an approach. Lake trout suppression was initiated without knowledge of population size, and harvest benchmarks that would lead to successful population decline were not determined. Consequently, the program proceeded for several years with inadequate resources, and the lake trout population continued to increase.

Eradication or suppression of introduced populations is ubiquitous because introduced species rank second to habitat destruction among threats to world-wide biodiversity (Simberloff 2001). However, the results of such projects are often not reported in the peer-reviewed literature (Simberloff 2009). Lake trout suppression has become an increasingly common management practice for the conservation of native fishes and ecosystems throughout the western USA (Martinez et al. 2009), and large-scale removals of other fish species are likely to be considered in the future (Kolar and Lodge 2002; Koehn 2004; DeGrandchamp et al. 2008). As the longest ongoing lake trout removal project, the lake trout suppression program in Yellowstone Lake provides a case study for the evaluation of a large-scale suppression effort for a non-native fish species. Lake trout suppression in Yellowstone Lake highlights the necessity for baseline data, long-term planning, and a large amount of fishing pressure to substantially reduce a non-native predator from a large, natural water body.

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