

DEMOGRAPHY OF LAKE TROUT IN RELATION TO POPULATION
SUPPRESSION IN YELLOWSTONE LAKE, YELLOWSTONE NATIONAL PARK

by

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of

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ABSTRACT

Introduced lake trout *Salvelinus namaycush* threaten to extirpate native Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* in Yellowstone Lake, Yellowstone National Park. Suppression of the lake trout population is deemed necessary for the conservation of Yellowstone cutthroat trout. A National Park Service gill netting program removed nearly 273,000 lake trout from Yellowstone Lake between 1995 and 2007. Lake trout population size has not been estimated; therefore, it is difficult to determine the efficacy of the program (i.e., proportion of the population that has been removed). My objectives were to (1) examine catch per unit effort (C/f) through time and catch as a function of effort to determine if the suppression program has caused lake trout abundance to decline, (2) determine if length structure, age structure, individual growth, mortality, body condition, length at maturity, age at maturity, and fecundity have changed as a function of harvest, and (3) develop age-structured models to determine the level of mortality required to cause population growth rate to decline below 1.0 (replacement). An increase in lake trout abundance was indicated by increasing C/f over time. Additionally, catch has continued to increase as a function of effort, indicating lake trout abundance is increasing. Population metrics were not clearly indicative of a response to harvest. However, metrics were comparable to North American lake trout populations where harvest has occurred, indicating that lake trout have not reached carrying capacity in Yellowstone Lake. Results from an age-structured matrix model determined the rate of population growth was 1.1 given the current rate of fishing mortality and that population growth rate would be 1.3 in the absence of fishing mortality. The current rate of population growth is positive; however, it is slower than it would be in the absence of lake trout suppression. Fishing mortality needs to increase from the rate of 0.22 estimated in 2007 to at least 0.32 to reduce population growth rate below replacement. Lake trout suppression is becoming an increasingly common management practice throughout the Intermountain West. Thus, Yellowstone Lake provides a case study for evaluating a strategy to remove the apex predator from a large lake.

CHAPTER 1

ANALYSIS OF CATCH PER UNIT EFFORT AND POPULATION METRICS TO
ASSESS THE EFFICACY OF LAKE TROUT SUPPRESSION IN YELLOWSTONE
LAKEIntroduction

Introduced fish species have been implicated in the decline of many native freshwater fishes throughout the western United States (Miller et al. 1989; Rahel 2000). Various sport fishes were introduced throughout the western U.S. during the westward expansion of the late 19th and 20th centuries to improve angling opportunities (Li and Moyle 1999; Nico and Fuller 1999). The species introduced were often large piscivores that filled the niche of top predator in their native ecosystems (Li and Moyle 1999).

The desirability of lake trout *Salvelinus namaycush* as a sport fish led to its wide introduction outside its native range (Crossman 1995). Lake trout have been introduced into lakes and reservoirs in eight western U.S. states (Martinez et al. 2009) and their presence has led to declines in native salmonid populations (Donald and Alger 1993; 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 (Spencer et al. 1991; Vander Zanden et al. 2003; Koel et al 2005; Tronstad 2008).

Lake trout were discovered in Yellowstone Lake in 1994 (Kaeding et al. 1995) after being introduced from nearby Lewis Lake in the mid-to-late 1980s (Munro et al. 2005). In 1996, it was estimated that the lake trout population in Yellowstone Lake consumed 522,000 Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* per year

and the consumption of Yellowstone cutthroat trout biomass by an uncontrolled lake trout population would eventually exceed the amount produced (Ruzycki et al. 2003). The level of predation exerted by lake trout was expected to cause the Yellowstone cutthroat trout population to decrease by as much as 60% within 100 years (Stapp and Hayward 2002). Abundance of Yellowstone cutthroat trout has declined noticeably since the discovery of lake trout (Koel et al. 2005). In addition to the direct effects within the lake, the reduced numbers of Yellowstone cutthroat trout reduce the flux of nutrients to the terrestrial ecosystem surrounding the lake (Crait and Ben-David 2006; Tronstad 2008). Further, Yellowstone cutthroat trout are an important species because they have a high socioeconomic value with Yellowstone Park anglers (Varley and Schullery 1995) and Yellowstone Lake contains the largest population of genetically pure Yellowstone cutthroat trout in the world (Gresswell and Varley 1988).

Suppression of the lake trout population in Yellowstone Lake was considered necessary to conserve the Yellowstone cutthroat trout population (McIntyre 1995). Thus, a lake trout removal program was initiated in 1998 (Ruzycki 2004), with the purpose of reducing lake trout abundance and decreasing predation on Yellowstone cutthroat trout (McIntyre 1995). Lake trout suppression has since been implemented or considered for the purpose of conserving native salmonids in several lakes in the western U.S. (Martinez et al. 2009). As the longest ongoing lake trout removal project in the West, the suppression program on Yellowstone Lake provides a case study to evaluate the effectiveness of strategies for removing the apex predator from a large lake.

Lake trout have been exploited throughout their native range, and the collapse of commercial lake trout fisheries in the Laurentian Great Lakes indicates that overexploitation is possible (Hansen 1999). 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 (Healy 1978a). However, lake trout population metrics are strongly influenced by lake size, lake productivity, and diet (Healy 1978a; Trippel 1993; Shuter et al. 1998; Pazzia et al. 2002). Sustainable yields of lake trout are positively related to lake area and productivity (Shuter et al. 1998), and lake trout populations can be overexploited when harvest exceeds 0.25 to 0.75 kg/ha (Martin and Olver 1980).

Exploitation can cause changes in population metrics and an eventual decline in abundance. A high level of harvest causes length- and age-frequency distributions to shift toward smaller and younger fish, and total annual mortality rates to increase (Van Den Avyle and Hayward 1999). Additionally, compensatory responses may be evident in population metrics if a reduction in abundance reduces the effects of density dependence (Rose et al. 2001). Lake trout have exhibited compensatory responses to increased fishing effort. Growth rates in exploited populations from lakes Michigan, Superior, and Huron were near the maximum observed for lake trout populations throughout North America (Healy 1978a). Lake trout in Lake Superior had faster growth and higher fecundity during a period of low abundance caused by exploitation when compared to periods of higher abundance (Ferrerri and Taylor 1996). Growth rates for lake trout in Lake Superior decreased due to an increase in abundance when the population recovered

from overexploitation (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 compensatory responses in age at first maturity and fecundity when harvested (Healy 1978a; Healy 1978b). Compensatory responses 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 (Healy 1978b; Trippel 1995).

The goal of this study was to assess whether the suppression program has caused changes in the lake trout population (e.g., relative abundance, individual growth rate, body condition) that are indicative of overharvest. The National Park Service (NPS) collects demographic data as a part of the suppression program; however, lake trout abundance has not been estimated. Therefore, data obtained from removed lake trout were used to conduct several analyses that indirectly assessed the efficacy of the suppression program relative to overharvesting the lake trout population. The objectives of this study were: i) examine temporal patterns in catch per unit effort (C/f) and determine if it has declined over time, ii) determine whether catch has declined relative to increased fishing effort, and iii) determine whether population metrics such as length structure, age structure, individual growth, mortality, body condition, length at maturity, age at maturity, and fecundity exhibit temporal patterns that are related to increases in fishing effort. Any changes in population metrics were deemed to be indicative of compensatory responses caused by changes in density. Lake trout suppression is likely to be successful in Yellowstone Lake because the species is vulnerable to overexploitation

throughout its native range (Healy 1978a). If the lake trout suppression program is succeeding, catch will decline relative to increased effort and C/f will decline over time. Additionally, changes in population metrics will indicate a decrease in density and metrics will become more characteristic of an exploited fish population as effort increases.

Study Area

Yellowstone Lake (Figure 1.1) was formed by a series of volcanic eruptions and magma chamber collapses creating two major basins, the West Thumb and Main Basin (Morgan et al. 2003). The lake is at an elevation of 2,357 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), with diatoms dominating the phytoplankton assemblage throughout the year (Benson 1961). The zooplankton community consists primarily of the rotifer *Conochilus unicornis*, Copepoda (*Diaptomus* spp., *Cyclops* spp.) and Cladocera (*Daphnia* spp.). Zooplankton and amphipods (*Gammarus* spp.) are important food sources for native Yellowstone cutthroat

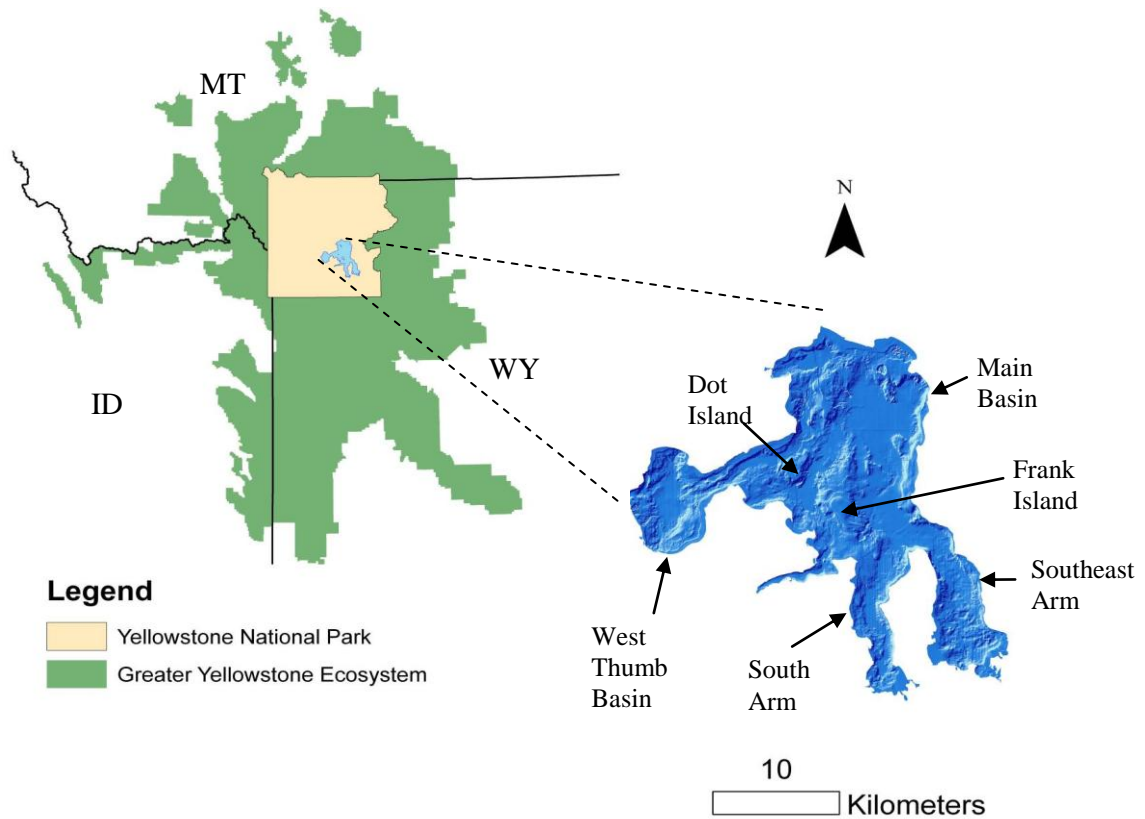


Figure 1.1. Location of Yellowstone Lake within Yellowstone National Park and the Greater Yellowstone Ecosystem. The map of the lake indicates the locations of major basins and islands.

trout (Benson 1961) and introduced lake trout (Ruzycki et al. 2003).

The fish assemblage in the lake consists of two native species, Yellowstone cutthroat trout and longnose dace *Rhinichthys cataractae*, and three introduced species in addition to lake trout, longnose sucker *Catostomus catostomus*, redbside shiner *Richardsonius balteatus*, and lake chub *Couesius plumbeus* (Gresswell and Varley 1988).

Methods

Data Collection

Sampling. The removal of lake trout began when they were first caught in gill nets used to assess the Yellowstone cutthroat trout population 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 (Kaeding and Boltz 1997; Ruzycki 2004). The lake is divided into 30 gill-netting areas for reference by NPS fisheries personnel (Figure 1.2). Gill nets were first set for the purpose of maximizing lake trout catch in 1998 and were used primarily for this purpose through 2007. Three different netting strategies were used to remove lake trout from Yellowstone Lake: control netting, spawner netting, and distribution netting.

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 netting methods varied as the program developed, but the same mesh sizes were used from 1998 through 2007 and net lengths were similar from 2002 through 2007. Control nets were sinking gill nets 100-m long and 3.3-m deep with bar-mesh sizes of 25, 32, or 38 mm. From 2002 through 2007, six nets of the same mesh size were combined to form a gang that was set along a depth contour varying from 40 to 65 m. The number of control gangs fished annually from 1998 through 2007 varied from 317 to 671. Control gangs were fished from late May through early October and lifted weekly, or as weather conditions permitted. Total length (mm), weight (nearest g), sex, and maturity code (0

for immature, 1 for mature) were recorded and otoliths were obtained from a subsample of the control netting catch over the duration of the suppression program (Table 1.1).

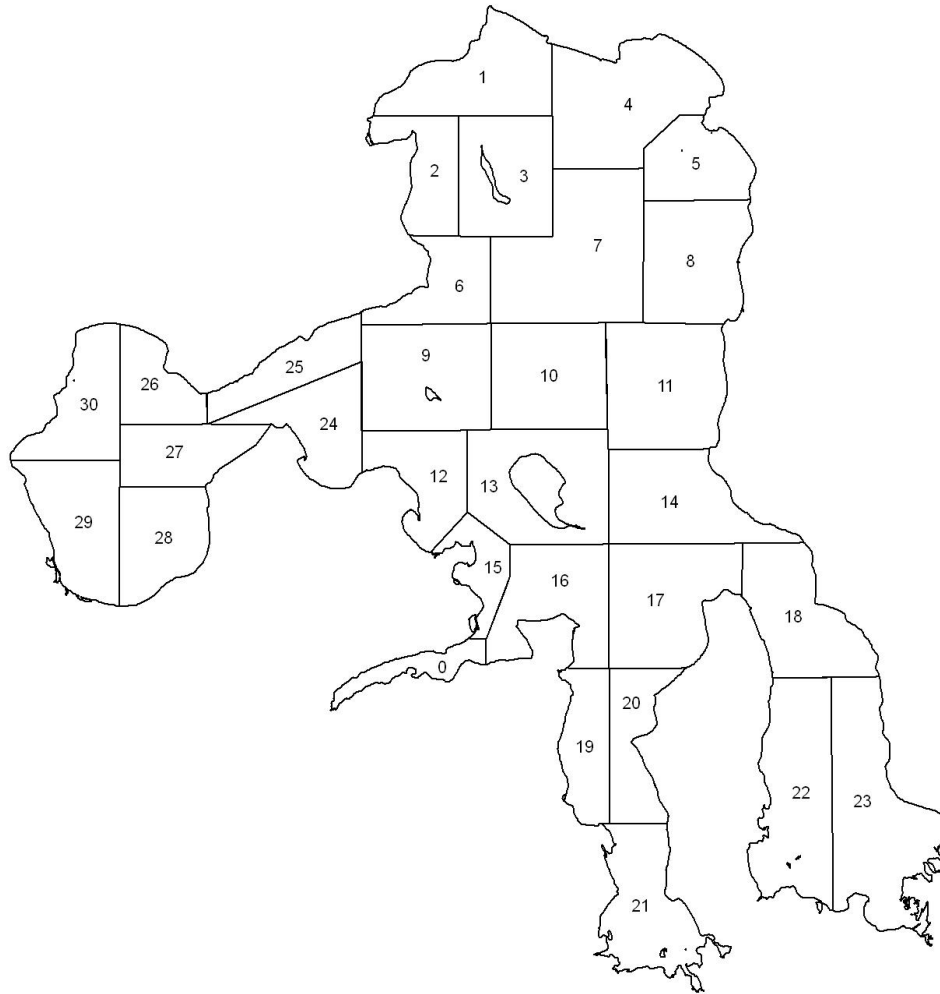


Figure 1.2. Gill netting areas in Yellowstone Lake, Yellowstone National Park.

Table 1.1. Total effort, number of lake trout caught, and number of lake trout sampled for population metrics by removal method and year in Yellowstone Lake, Yellowstone National Park. Symbols in the netting type column are as follows: D represents distribution netting, C represents control netting, S represents spawner netting, and E represents electrofishing. Netting effort was computed as the sum of 100-m net nights and electrofishing effort was computed as the sum time in hours.

Year	Removal method	Effort	Number of fish	Population metric				
				Length	Weight	Otoliths	Maturity	Fecundity
1995	D	250	155	154	154			
1996	D	676	256	255	155	20	250	
	C	805	173	173	165	50	171	
	S	143	153	153	126	1	153	11
1997	D	137	166	162	160	15	125	
	C	140	216	212	208	27	181	
	S	22	486	486	472	30	484	
1998	D	46	83	82	75	3	70	
	C	1,145	7,322	7,263	7,252		556	
	S	303	397	397	380	34	391	
1999	D	48	98	98	98		67	
	C	1,112	4,678	3,035	410	10	208	
	S	486	910	910	909	61	907	
2000	D	37	82	82	14		37	
	C	2,795	11,928	11,924	1,099	88	377	
	S	768	861	856	1		795	
2001	C	10,470	14,797	14,780	3	68	491	
	S	850	940	940			901	
2002	D	43	56	56		20		
	C	14,385	11,708	11,648		36	32	
	S	425	794	794		187	757	
2003	D	39	74	59		20	37	
	C	17,468	15,546	15,546		1	5	
2004	S	474	2,373	2,373	2	292	2,369	
	D	45	56	56		16	51	
	C	15,471	19,351	19,351		37	34	
	S	766	7,283	7,280		147	7,261	
	E	8.67	1,063	1,063			1,063	

Table 1.1. Continued.

Year	Removal method	Effort	Number of fish	Population metric				
				Length	Weight	Otoliths	Maturity	Fecundity
2005	D	45	71	71	47	70	64	
	C	18,347	30,449	26,036		77	244	
	S	983	4,568	4,568		218	4,532	
	E	23.78	1,344	1,338		8	1,338	
2006	C	24,010	52,593	4,433		212	1,049	
	S	1061	6,442	6,437		394	6,422	119
	E	26.25	1,075	1,075		123	1,075	
2007	D	47	177	177	177	177	177	
	C	26,947	63,766	4,234	303	299	690	
	S	1,413	9,543	9,531	348	347	9,449	130
	E	14.10	533	533	2	2	533	2

Spawner netting targeted adult lake trout (> 400 mm total length). Spawner-netting gill nets were similar in length from 1998 through 2007; however, mesh sizes varied by year. Sinking gillnets were 100-m long and 3.3-m deep with bar-mesh sizes of 38, 44, 51, 57, 64, 70, or 76 mm. Two nets of the same mesh size were combined to form a gang that was fished at known spawning or staging locations. The number of spawner gangs fished annually from 1998 through 2007 varied from 161 to 498. Spawner gangs were fished from late August through October and were lifted daily to minimize gear saturation and bycatch of Yellowstone cutthroat trout (Ruzycki 2004). Night electrofishing was conducted from 2004-2007 at shallow spawning areas (primarily in the West Thumb Basin) during peak spawning activity. The amount of annual electrofishing effort varied from 8.67 hours in 2004 to 26.25 hours in 2006, accounting for 5-20% of all spawning fish removed (i.e., gill netting and electrofishing pooled). Total length, sex, and maturity were recorded for most spawning lake trout caught (Table 1.1). Lake trout

caught in spawner netting were subsampled for weight in intermittent years and otoliths in most years. Ovaries were removed from pre-spawning females caught in 1996, 2006, and 2007 for fecundity estimation.

Distribution netting consisted of lake-wide sampling of multiple depth strata to collect data on lake trout population demographics and spatial distribution (Ruzycki 2004). Distribution netting occurred at 16 fixed sites throughout the lake. Each site originally consisted of three depth strata: an epilimnetic stratum (<15 m), a shallow stratum (15-30 m), and a deep stratum (30-50 m). The epilimnetic stratum was not sampled after 1997 to minimize bycatch of Yellowstone cutthroat trout (Ruzycki 2004). 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 that were each 3.3-m deep and consisted of mesh panels 8-17 m long were combined to form a gang. A gang was set over night at each depth stratum by site. Distribution netting occurred in intermittent years between 1997 and 2007 (Table 1.1). Total length, sex, and maturity were recorded for nearly all fish caught in distribution netting (Table 1.1). Otoliths were removed and weights were recorded in intermittent years from lake trout caught in distribution netting.

Age. Sagittal otoliths were used to estimate lake trout ages. Each otolith was sanded to create a section perpendicular to the sulcal groove, halfway through the long axis. Sectioned otoliths were burnt over an alcohol flame until they turned dark brown (Barber and McFarlane 1987). Darkened otoliths were mounted on slides and mineral oil was applied to the sectioned side to improve clarity. Ages were determined by counting

annuli under a compound microscope at 40-100 power magnification. Otoliths were aged without knowledge of fish length.

Fecundity. Fecundity was estimated volumetrically in 1998 (Ruzycki et al. 2003) and gravimetrically in 2006 (P. Doepke, National Park Service, personal communication). In 2007, fecundity was estimated gravimetrically for pre-spawning mature females. Each ovary was weighed to the nearest 0.1 g. A cross-section of 5-15% ovary weight was removed from the anterior, middle, and posterior sections of each ovary (Murua et al. 2003), and weighed to the nearest 0.1 g. Eggs were counted in each section and the sum was divided by the section weight to estimate eggs/g. The measurements of eggs/g from each section were averaged and multiplied by total ovary weight to obtain an estimate of eggs per ovary (Trippel 1993). Ten percent of ovaries were randomly selected for full counts of eggs to validate gravimetric estimates.

Data Analysis

Catch and Effort. The spatial and temporal distributions of fishing effort were examined by netting type to determine whether the sampling design represented the entire lake trout population in Yellowstone Lake and whether fishing pressure varied by location and year. The spatial distribution of fishing effort was examined by calculating the sum of 100-m net nights from 1995 through 2007 for each gill-netting area. The temporal distribution of effort was examined by plotting annual values of total lake-wide effort (the sum of 100-m net nights) through time.

Catch per unit effort (C/f , calculated as the number of fish per 100 m of net) was used as an index of relative abundance for the suppression program. The use of C/f as an index of relative abundance requires catchability to remain constant through time; however, catchability often changes after the establishment of a fishery (Hilborn and Walters 1992). The lake trout suppression program may have become increasingly efficient over time as the locations that produced high lake trout catches were fished with increased effort (P. E. Bigelow, Yellowstone National Park, personal communication). Thus, C/f tends to be higher than the actual abundance, defined as hyperstability (Hilborn and Walters 1992). Therefore, estimates of C/f from unstandardized control and spawner netting were not reliable.

Distribution netting produced the least biased C/f data because it occurred at fixed locations determined by a random stratified design; however, the sample size from distribution netting was not large enough to detect temporal trends in C/f . A post hoc power analysis was used to determine the number of sites needed to detect a change in C/f of 1.9, which is equal to the greatest observed difference among years. Probabilities used for Type I (α) and Type II (β) error were 0.1 and 0.2, respectively. Using a two-sample t-test, the sample size required to detect a difference among years was 46 nets, whereas the actual sample size was 32 nets.

Sample sizes (i.e., numbers of gangs) for C/f obtained from control and spawner netting from 1998 through 2007 were larger than sample sizes from distribution netting. Therefore, C/f was analyzed using data obtained only from control and spawner netting after the data were standardized to avoid hyperstability. Standardized locations were

determined by establishing a 500-m square grid over a spatially referenced polygon of Yellowstone Lake in ArcGIS 9.2 (ESRI 2006). Cells that contained at least five years of C/f data, from 1998 through 2007, by mesh size were used as standardized locations to evaluate temporal variation in C/f . Catch per unit effort was analyzed by mesh because meshes are selective for lengths and ages of fish (Hamley 1975). Effort by mesh varied by year; therefore, age classes targeted varied by year. Analysis of C/f in control netting was restricted to data obtained from 2002 through 2007 because gang lengths were consistent. Catch per unit effort was analyzed from 1998 through 2007 in spawner netting. Catch per unit effort data met the requirement of at least five years of data at standardized locations within 25-, 32-, 38-mm mesh sizes in control netting and 51- and 64-mm mesh sizes in spawner netting. All standardized locations for examining C/f occurred within the West Thumb Basin, where fishing effort was the highest.

Gear saturation reduces gill net efficiency with increasing set duration, affecting C/f indices if set durations are not standardized (Hansen et al. 1998). Gill net set durations were variable in Yellowstone Lake, requiring C/f data standardizations for saturation before making temporal comparisons. Catch per unit effort data were standardized by examining catch as an asymptotic function of set duration (Hansen et al. 1998). Asymptotic models were estimated by mesh, within year, because the rate of saturation was expected to vary by mesh size and the abundance of fish vulnerable to a mesh size (Hansen et al. 1998). Catch per unit effort was modeled as a function of the set duration, in nights:

$$C / f = \alpha(1 - e^{-\beta \cdot \text{nights}}), \quad (1)$$

where α is the maximum C/f observed by mesh size and year, and β is the rate at which C/f approaches α . Catch per unit effort data were normalized with the $\log_e(C/f+1)$ transformation prior to model estimation and the right side of the equation was \log_e -transformed during estimation. Models were fit using the nonlinear least squares (NLS) procedure in the program R 2.9.2 (R Development Core Team 2009). Catch per unit effort was corrected by rearranging the asymptotic equation to solve for β for each gang:

$$\beta = \frac{-\log_e\left(1 - \frac{C/f}{\alpha}\right)}{\text{nights}}. \quad (2)$$

The estimate of β was used in equation (1) with $\text{nights} = 1$ to standardize C/f for variation in duration (Hansen et al. 1998).

Corrected C/f data were pooled across standardized locations. Although standardized locations occurred throughout the West Thumb Basin, observations that were closer together in space and time were more likely to be similar than observations that were farther apart. In addition, C/f was observed to consistently change among seasons within years. Therefore, generalized additive mixed models (GAMMs) that incorporated temporal and spatial correlations between observations were used to model the within-year temporal and among-year temporal trends in C/f . Within-year dates were transformed to values varying from 0.0 to 0.99, with zero representing the first fishing day of the year and 0.99 representing the last fishing day of the year (Wood 2006). Among-year dates were calculated as the year followed by the decimal within-year date (e.g., 2007.5 represents the middle of the 2007 fishing season). The within-year temporal trend was estimated with cyclic cubic regression splines and the among-year temporal

trend was estimated with cubic regression splines (Wood 2006). A separable exponential spatial-temporal correlation structure was used, where the spatial correlation was multiplied by the temporal correlation (Greenwood et al. *in press*). The correlation provided the same temporal correlation within locations and the same spatial correlation within time steps (Greenwood et al. *in press*). Generalized additive mixed models were estimated using the multiple smoothing parameter estimation (MGCV, Wood 2006) and nonlinear mixed effects (NLME, Pinheiro et al. 2009) packages in R 2.9.2. Catch per unit effort observations were \log_e transformed prior to model estimation to homogenize variances.

A model selection approach was used to assess whether trends in C/f were supported by the data because P -values are unreliable for GAMMs (Zuur et al. 2009). Several progressively complex models were estimated within each mesh size: y -intercept (β_0) only model, model with among-year temporal trend, model with within-year temporal trend, and full model with among-year and within-year temporal trends. Models were estimated with and without correlated errors to determine if accounting for correlations was supported. Models estimated within each mesh size were ranked according to Akaike's Information Criterion (AIC) values, and the model with the lowest AIC value was determined to have the most support (Burnham and Anderson 2002). Models within 2 AIC units were considered to have equal support (Burnham and Anderson 2002).

The relationship between annual catch and annual effort was used to determine if fishing effort caused population abundance to decline. Total annual catch increases as a

function of total annual effort until the population is overexploited, then total annual catch will decrease with further increases in effort resulting in a dome-shaped relationship (Ricker 1975). Catch and effort data were standardized by calculating annual totals at the same areas used for C/f analyses previously described. Total annual effort was standardized for gill-net saturation because set durations increased through the duration of the suppression program and as duration increases the amount of effective effort decreases because of net saturation. Effort was standardized for each gang using values of β from equation 1 to model the rate at which the amount of effective effort decreased as set duration increased. The effective effort ($effort_s$) for a gang was calculated using the coefficient β as a rate of exponential decay, which decreased the amount of effort by β as the net set increased. $Effort_s$ was calculated for each gang as the sum of nightly units of effort (E_i), which were reduced by the coefficient β each night (i):

$$effort_s = \sum_{i=1}^k E_i = effort \cdot e^{-\beta \cdot (i-1)}, \quad (3)$$

where k = the duration of the net set in nights. The term $i-1$ was included so that effort was not reduced in a one-night set. Total annual catch and total annual $effort_s$ were examined within each mesh size for dome-shaped (i.e., negative quadratic) or linear relationships. Regressions were fit using R 2.9.2 and $\alpha = 0.1$ was used for statistical significance to reduce the likelihood of making a Type II error.

Biomass Harvested. Annual biomass of lake trout harvested was estimated by year. Year specific length-weight regressions were used to predict the weight of individual fish from total length. The length-weight regression from the nearest year was

used to estimate fish weights for years without weight data. Weights of individual fish were summed within the West Thumb Basin, Main Basin, and lake-wide by year. Biomass was divided by the surface area of the respective basin or the entire lake for estimates of biomass removed per unit area (kg/ha).

Cumulative Effort. I assumed that changes in the metrics of an exploited population are caused by the cumulative effects of fishing effort. Therefore, annual values of population metrics in the following sections were examined as a function of cumulative effort (effort_s). The amount of cumulative effort_s targeting each age class was calculated over the time the age class was vulnerable to the fishery. Cumulative effort_s was calculated using the following steps. First, selectivity by mesh size and age class was determined from a sample of aged fish caught in all mesh sizes throughout the suppression program. For each mesh size, the number of lake trout in each age class was divided by the number of lake trout in the age class with the highest abundance; thus scaling the selectivity of the mesh size for each age class relative to one. Second, the amount of total effort_s for each mesh size by year was calculated by summing the amount of effort_s for individual gangs. Third, total effort_s for each mesh size by year was multiplied by the relative selectivity of the mesh size by age class; thus the product being the amount of effort_s targeting each age class by mesh size. Fourth, the amount of effort_s targeting each age class was summed among mesh sizes for an estimate of the total effort_s targeting each age class by year. Finally, cumulative effort_s targeting each age class was computed by summing the effort_s targeting the age class by the years it was vulnerable to the gear.

Population Metrics and Fishing Effort. Annual values of mean length and body condition were calculated by age whereas length structure, age structure and mortality were calculated by age group and netting type. Population metrics calculated by age were regressed as a function of cumulative effort_s targeting age-classes through time. Metrics estimated by netting type were regressed as a function of cumulative effort_s targeting all age classes caught in the netting type. An $\alpha = 0.1$ was used for statistical significance.

Length and Age Structure. 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 (Hamley 1975). Therefore, length-frequency data were standardized to account for unequal selectivity and effort among mesh sizes (Hansen et al. 1997). Standardizations for mesh selectivity are commonly made by comparing the length-frequency of the catch to the true length-frequency of the population; however, methods exist for indirectly estimating selectivity when the true length-frequency of the population is unknown (Hansen et al. 1997; Millar and Holst 1997).

Indirect estimates of retention probabilities of mesh sizes for 5-mm length classes of lake trout were estimated using log-linear models in program SELECT in R 2.9.2 (Millar and Holst 1997). The analysis was performed on length data by netting type (control, spawner, or distribution) within year. Differences in effort among mesh sizes were corrected by scaling the peaks of each mesh selectivity curve relative to the peak for the mesh with the greatest amount of effort. Selectivity curves obtained by mesh were

summed for an estimate of overall selectivity of the complement of gill net meshes for lake trout lengths. The estimate of overall selectivity was used to scale the catch of lake trout in each length class relative to the catch of the length class most likely to be caught by the gear, which was determined by the peak of the overall selectivity curve (Millar 2000).

Temporal comparisons of length frequencies were restricted to years in which netting types used the same mesh sizes. I used boxplots to examine temporal variation in length frequencies by netting type. Annual median length was regressed against cumulative effort_s by netting type to determine if median length varied as a function of the lake trout fishery.

Standardized annual length frequencies were converted to age frequencies using year-specific age-length keys (Isley and Grabowski 2007). Age frequencies were computed for years without age data using the age-length key for the nearest year. Boxplots were used to examine temporal variation in age frequencies by netting type. Annual median age was regressed against cumulative effort_s to determine if median age varied as a function of the lake trout fishery.

Growth and Body Condition. Growth was analyzed by year using von Bertalanffy growth models (VBF). The Galucci-Quinn parameterization of the von Bertalanffy growth equation was used to describe growth because it avoids the correlation of model parameters k and L_{∞} inherent in the VBF model (Galucci and Quinn 1979). The NLS procedure in R 2.9.2 was used to estimate annual values of model parameters using the following equation:

$$L_t = L_\infty \cdot (1 - e^{-(\omega/L_\infty)t}) \quad (\text{Shuter et al. 1998}), \quad (4)$$

where L_t = length at time t , L_∞ = the theoretical maximum length of lake trout in the population, ω = the rate of growth near the origin, and t = age (Gallucci and Quinn 1979). A set of nested models were estimated for years with age data by sex (i.e., 2002 through 2007) to determine if estimating parameters by sex improved model fit. Four VBF models were fit within each year: no parameter by sex interactions, L_∞ by sex interaction, model with ω by sex interaction, and L_∞ by sex and ω by sex interactions. The VBF model with the lowest AIC score was considered to have the most support. Annual estimates of ω and L_∞ by sex were regressed against cumulative effort_s. Annual estimates of ω and L_∞ for models with sexes pooled were regressed against cumulative effort_s to increase the time series to 1998 through 2007.

Mean length at age was estimated by early season (fish caught earlier than 1 August) and late season (fish 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 class and season combinations had fewer than five fish in order to avoid possible influences of outliers. Regressions of mean length at age on cumulative effort_s were estimated for age class and season combinations with at least five annual mean length values, resulting in regressions for 12 age-class and season combinations.

Relative weight (W_r) was calculated as an index of body condition for lake trout using the equation:

$$W_r = (W/W_S) \cdot 100 \quad (\text{Anderson and Neumann 1996}), \quad (5)$$

where W is the observed fish weight (in grams) and W_s is the weight predicted by the standard weight equation for lake trout:

$$\log_{10}(W_s) = -5.681 + 3.246 \cdot \log_{10}(L) \quad (\text{Piccolo et al. 1993}), \quad (6)$$

where L is length in mm.

Body condition values can be affected by sampling season and sex (Pope and Kruse 2007). Therefore, I tested for effects of season and sex on lake trout W_r using a pooled sample of weight data from 1997, 1998, 1999, and 2007. Lake trout were assigned to early season and late season (see definition above). Season and sex effects were analyzed for juvenile lake trout (caught in control netting) using two-way analysis of variance (ANOVA). Season had a significant effect on juvenile W_r ($F = 82.83$; $df = 1, 1717$; $P < 0.01$), but sex did not ($F = 0.10$; $df = 1, 1717$; $P = 0.75$). Seasonal effects were not tested for adult lake trout because they are caught in spawner netting, which occurs only in the late season. Sex effects were tested for adult fish using a two sample t-test. Sex had a significant effect on adult lake trout W_r ($t = 14.04$; $df = 2946$; $P < 0.01$). Thus, median W_r was calculated by age within season for juvenile lake trout and by age within sex for adult lake trout. Median W_r at age was regressed against cumulative effort_s. In addition, age-specific W_r values computed in 2007 were compared to the cumulative distribution of W_r for lake trout populations across the range of the species (Hubert et al. 1994).

Maturity and Fecundity. Annual probabilities of 50% maturity at length were estimated by sex using logistic regression for binary response data (Heibo and Vollestad 2002). Annual values of length at 50% probability of maturity were converted to ages

using year-specific VBF growth equations. Lengths and ages at 50% probability of maturity were regressed against cumulative effort_s by sex.

Length-fecundity relationships were constructed for fecundity estimates obtained in 2007 by gravimetric estimates and full counts. Fecundity did not vary by count method (ANCOVA; $F = 0.19$; $df = 1, 74$; $P = 0.67$). Length-fecundity relationships were compared using ANCOVA by year to determine if fecundity changed over the duration of the suppression program. Estimates of mean relative fecundity (eggs/kg body mass) were compared over time and to lake trout populations throughout North America.

Mortality. Annual age frequencies were used to estimate mortality by netting type. Total instantaneous mortality rate (Z) was estimated using catch curve regressions of the natural logarithm of catch at age on age (Ricker 1975). Total instantaneous mortality rate was converted to total annual mortality (A) using the equation: $A = 1 - e^{-Z}$. Ages that were included in annual catch curves were consistent among years in control netting (ages 3-6) and distribution netting (ages 2+), but were variable among years in spawner netting. Ages included in catch curve mortality estimates for spawner netting varied from 6-11 in 1999 to 10-17 in 2007. Mortality was not estimated for distribution netting from 1999 through 2004 because age frequencies did not conform to a type three survivorship curve. Although mortality estimates from control and spawner netting were not representative of the entire population, inter-annual comparisons were useful for assessing the effects of lake trout suppression. Annual estimates of total annual mortality by netting type were regressed against cumulative effort_s.

Mortality estimates obtained with traditional catch curve regressions require the assumption of constant recruitment because they are computed across multiple cohorts. However, recruitment is often variable in fish populations (Miranda and Betolli 2007). Catch curves for single cohorts provide a method to estimate mortality when recruitment is variable (Miranda and Betolli 2007). Therefore, I estimated mortality in 2007 with a cohort catch curve for the 1999 year class. The 1999 cohort was chosen because it was the year class with the most catch- at-age observations that were collected from standardized control and spawner netting. Estimates of total annual mortality obtained from the cohort catch curve and the traditional catch curve from distribution netting were compared to assess the effects of variable recruitment on linear catch curve mortality estimates.

Results

Catch and Effort

Fishing effort was not evenly distributed throughout Yellowstone Lake (Figures 1.3 and 1.4). Sixty-four percent of control netting occurred in the West Thumb Basin from 1995 through 2007. Of the control netting that occurred in the Main Basin, 27% occurred near Frank Island and 19% occurred near Dot Island. The Southeast Arm and northeast portions of the lake had the least fishing effort. Eighty-one percent of spawner-netting effort occurred in the West Thumb Basin from 1995 through 2007. Total annual effort increased steeply from 1999 to 2007 in control netting, reaching 28,000 100-m net nights in 2007 (Figure 1.5). Total annual effort increased gradually over time within spawner netting, but has remained below 1,500 100-m net nights.

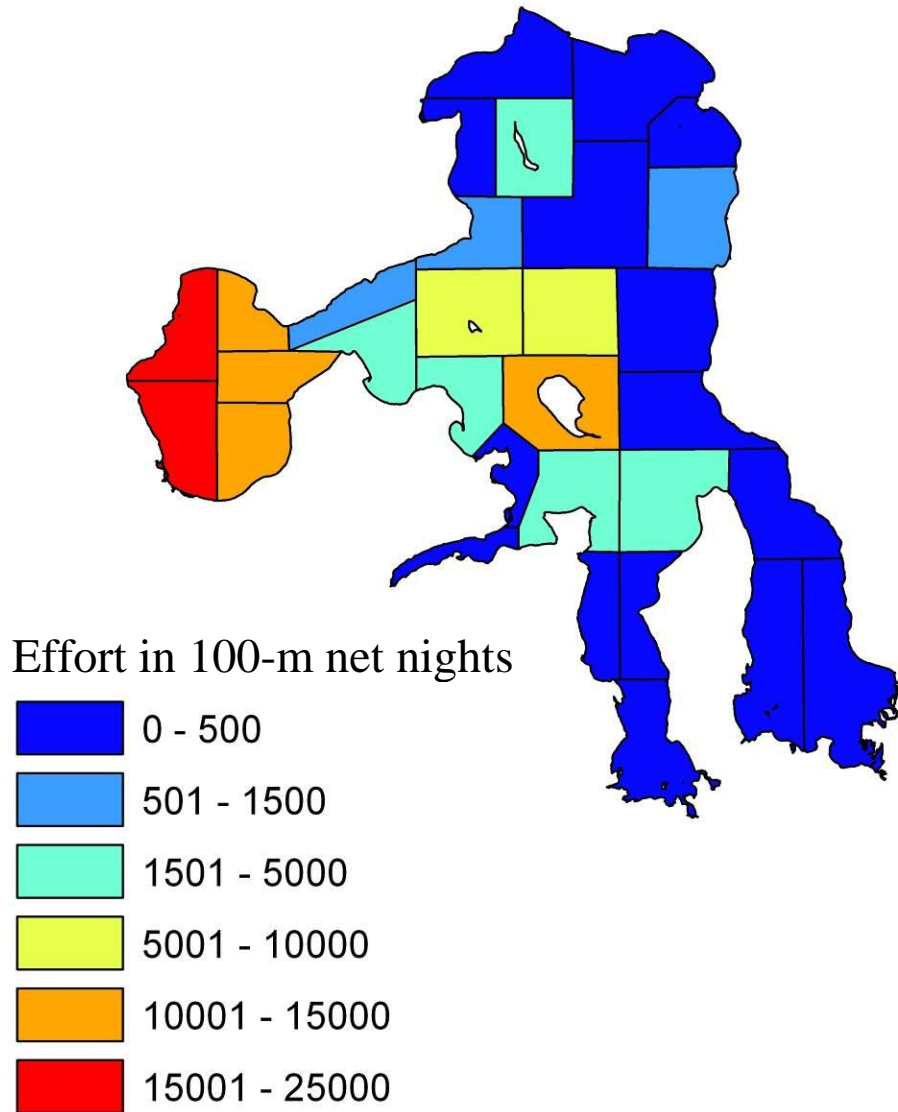


Figure 1.3. Gill-netting effort (sum of 100-m net nights) targeting juvenile lake trout using control netting (see text for definition of control netting) by lake area from 1995 through 2007 in Yellowstone Lake, Yellowstone National Park.

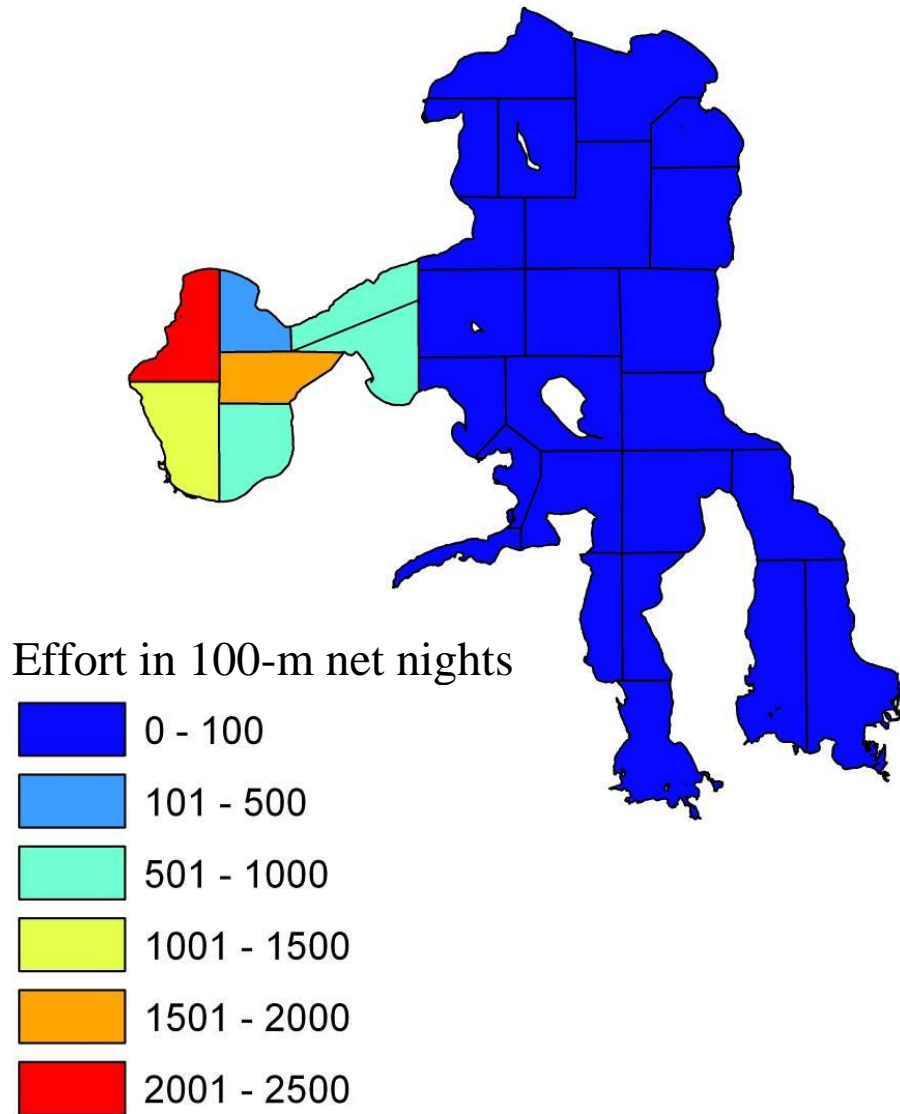


Figure 1.4. Gill-netting effort (sum of 100-m net nights) targeting spawning adult lake trout using spawner netting (see text for definition of spawner netting) by lake area from 1995 through 2007 in Yellowstone Lake, Yellowstone National Park.

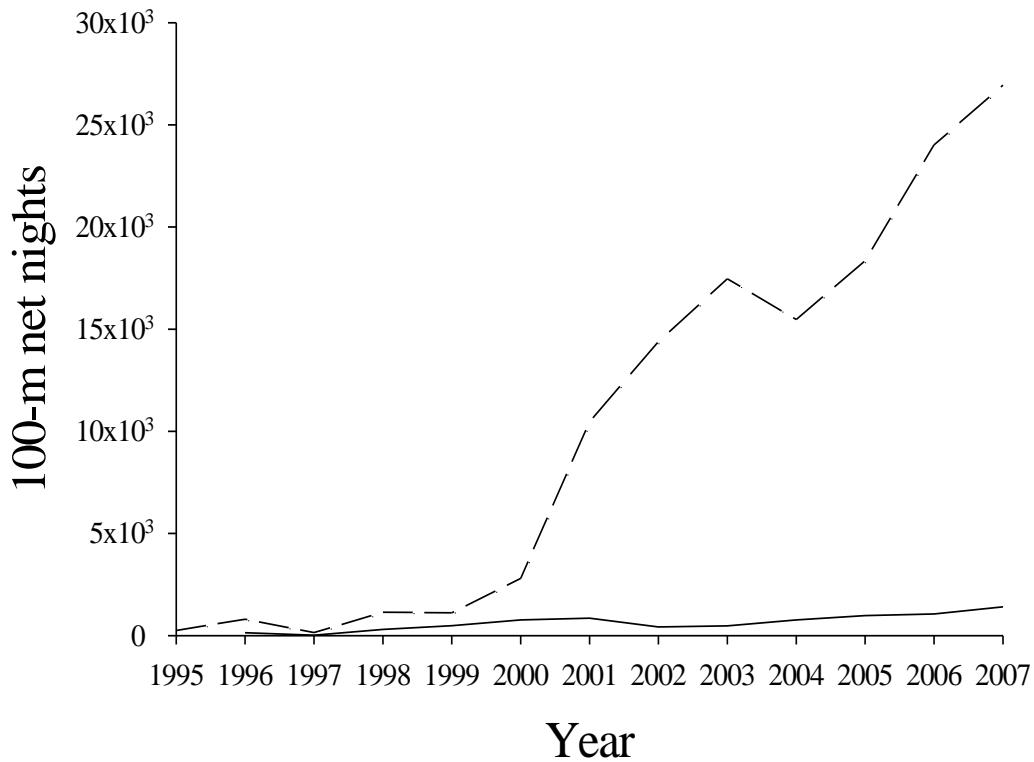


Figure 1.5. Gill-netting effort (sum of 100-m net nights) targeting juvenile lake trout in control netting (dashed line) and spawning adult lake trout in spawner netting (solid line) from 1995 through 2007 in Yellowstone Lake, Yellowstone National Park.

Catch per unit effort varied among years and the best supported model for C/f with the 25-mm mesh had an among-year temporal effect and no within-year temporal effect (Table 1.2). The trend within the 25-mm mesh was sigmoidal where C/f increased from 2004-2006, but C/f in 2007 was similar to 2003 (Figure 1.6). The largest difference in C/f with the 25-mm mesh occurred between 2004 (2.06 fish per 100 m of net) and 2007 (2.76 fish per 100 m of net). The best supported model for C/f with the 32-mm mesh included among-year and within-year temporal effects (Table 1.2). Catch per unit effort increased each year and was highest in June and lowest in August (Figure 1.6).

Catch per unit effort in the 32-mm mesh was 1.23 in 2002 and 1.70 in 2007; an increase of 38%. The best model for C/f with the 38-mm mesh included a within-year temporal effect and an among-year temporal effect was nearly supported. However, the among-year temporal effect with the 38-mm mesh indicated a decrease in C/f of only 6%. The within-year temporal effect indicated C/f was highest in June and lowest in August (Table 1.2 and Figure 1.6). Variation in C/f was best described by models containing both among-year and within-year temporal effects for the 51- and 64-mm meshes. Catch per unit effort peaked in late September and early October, corresponding with peak in spawning. Catch per unit effort with the 51-mm mesh was lowest in 1998 at 2.75 and peaked at 10.70 in 2007; an increase of 328%. Similarly, C/f with the 64-mm mesh increased from 2.82 in 1998 to 9.11 in 2007; an increase of 223%.

Table 1.2. Models for lake trout C/f by year at standardized locations (see Methods for standardized location description) in Yellowstone Lake, Yellowstone National Park. Models are for 2002 through 2007 in 25-, 32-, and 38-mm bar meshes and 1998 through 2007 in 51- and 64-mm bar meshes. Models are ranked by ascending AIC values within mesh size. The model term “Year” is the among-year temporal effect and “Season” is the within-year temporal effect. A “Y” in the “Correlation” column indicates the model included an exponential correlation structure.

Mesh	Model	Correlation	Likelihood	df	AIC
25 mm	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$	Y	-69.97	6.98	153.91
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$	Y	-69.97	6.98	153.91
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$	Y	-75.74	4.00	159.48
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$		-75.34	5.45	161.59
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$		-75.34	5.45	161.59
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$		-85.07	2.00	174.14
	$\text{Log}_e(C/f+1) = \beta_0$		-85.07	2.00	174.14
32 mm	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$	Y	-53.96	9.16	126.24
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$	Y	-60.57	7.44	136.04
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$	Y	-70.88	5.00	151.78
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$		-67.34	10.06	154.82
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$		-79.06	8.15	174.43
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$		-104.93	5.47	220.80
	$\text{Log}_e(C/f+1) = \beta_0$		-116.08	2.00	236.16
38 mm	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$	Y	-37.61	8.82	92.86
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$	Y	-37.10	9.84	93.88
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$		-44.42	10.16	109.16
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$	Y	-52.11	5.00	114.23
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$		-50.45	7.47	115.84
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$		-76.26	3.76	160.03
	$\text{Log}_e(C/f+1) = \beta_0$		-78.76	2.00	161.51

Table 1.2. Continued

Mesh	Model	Correlation	Likelihood	df	AIC
51 mm	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$		-271.01	11.96	565.94
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$	Y	-270.89	12.94	567.65
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$		-289.94	8.79	597.44
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$	Y	-289.90	10.72	601.24
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$	Y	-388.03	7.76	791.57
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$		-387.28	7.14	788.83
	$\text{Log}_e(C/f+1) = \beta_0$		-414.53	2.00	833.07
64 mm	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$	Y	-505.46	12.16	1035.24
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year}) + s(\text{Season})$		-517.82	10.59	1056.80
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$	Y	-532.84	7.69	1081.07
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Year})$		-551.25	5.75	1114.00
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$	Y	-608.69	8.41	1234.22
	$\text{Log}_e(C/f+1) = \beta_0 + s(\text{Season})$		-621.79	6.63	1256.85
	$\text{Log}_e(C/f+1) = \beta_0$			2.00	1344.00

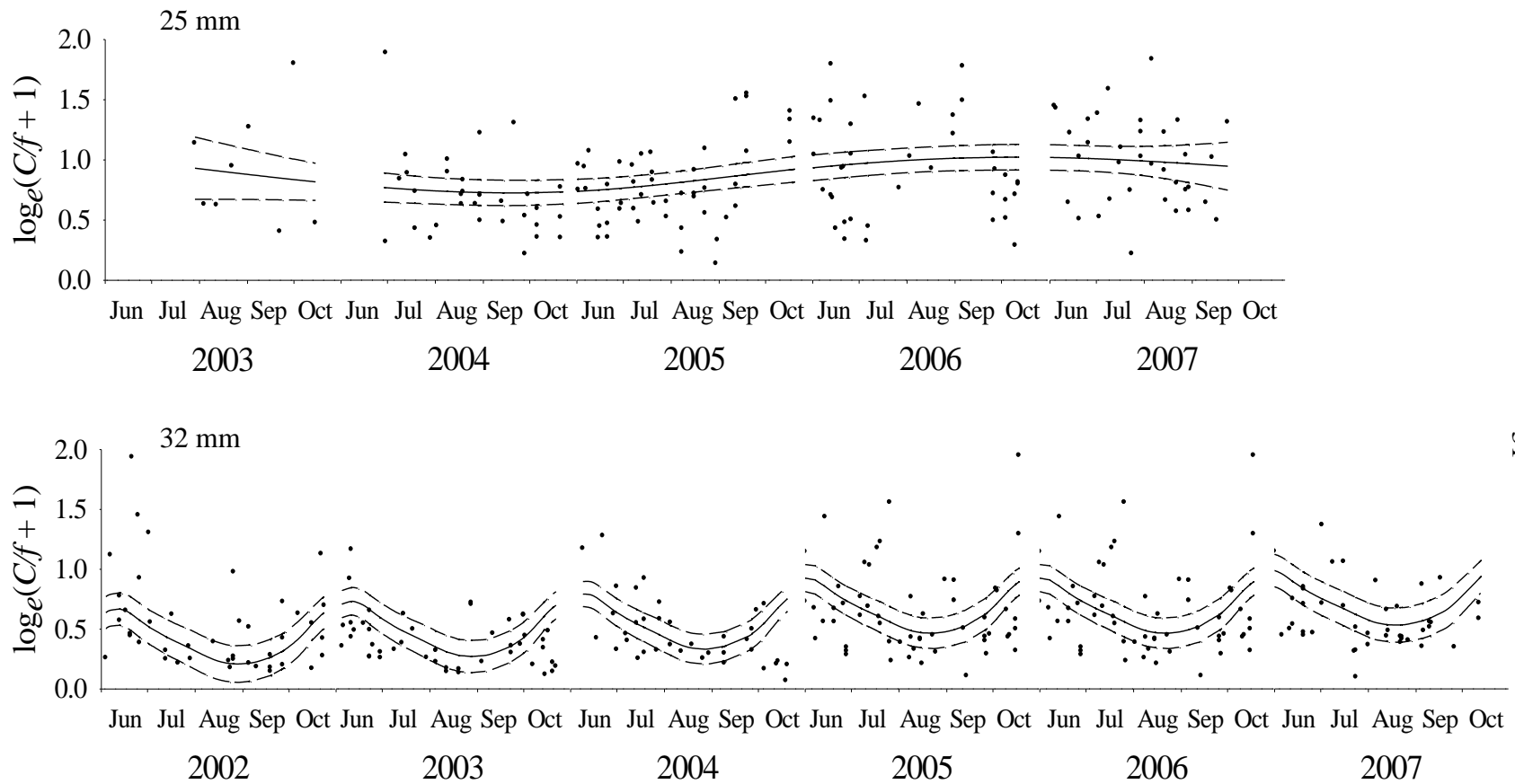


Figure 1.6. Catch per unit effort ($\log_e[C/f+1]$) for lake trout in Yellowstone Lake, Yellowstone National Park. Data are for 2002 through 2007 for 25-, 32-, and 38-mm bar mesh sizes and 1998 through 2007 for 51- and 64-mm bar mesh sizes. The solid line delineates mean C/f predicted by generalized additive mixed models and the dashed lines delineate 90% confidence intervals.

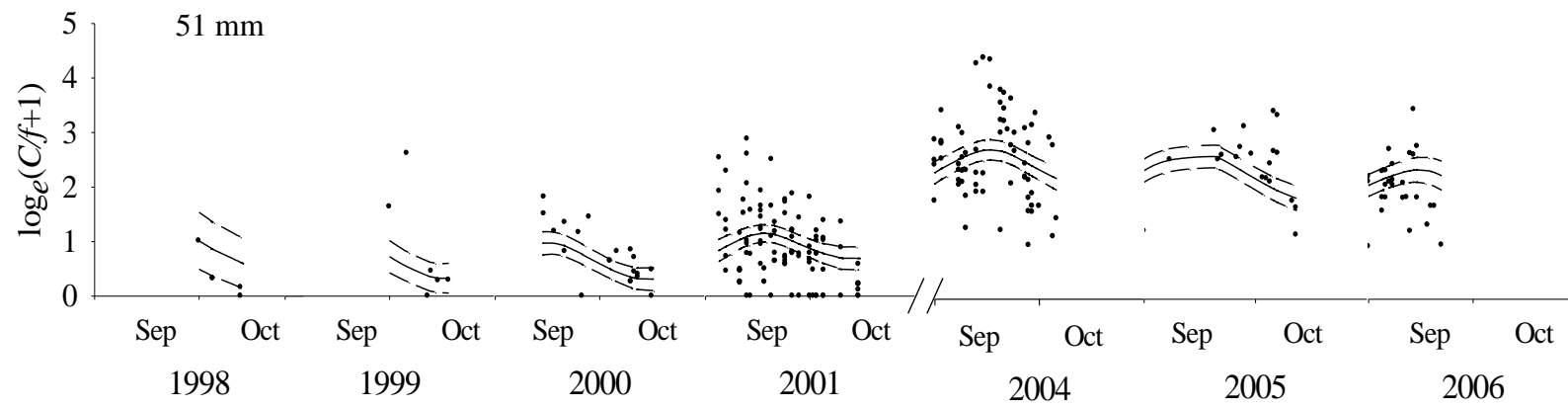
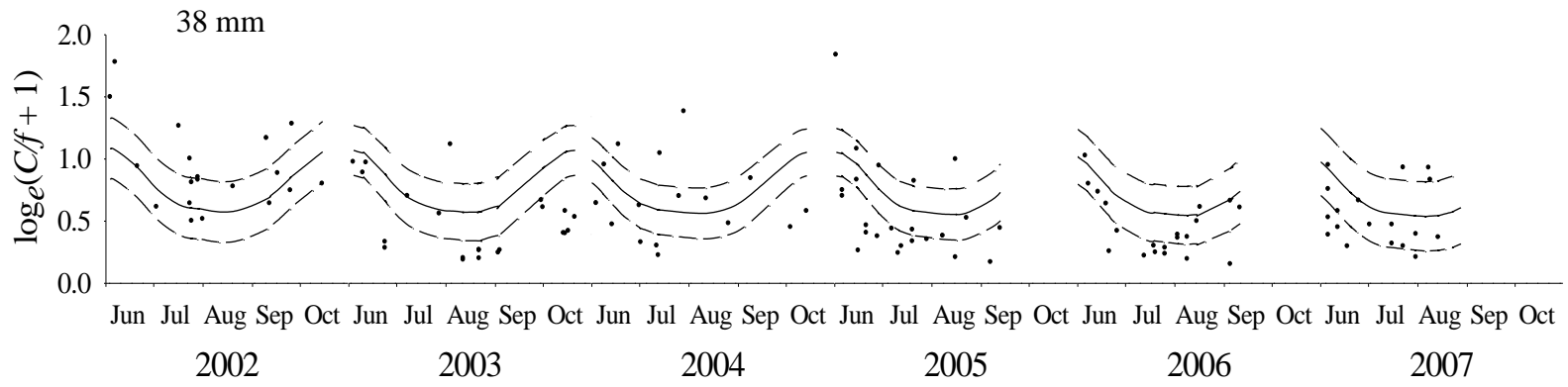


Figure 1.6. Continued.

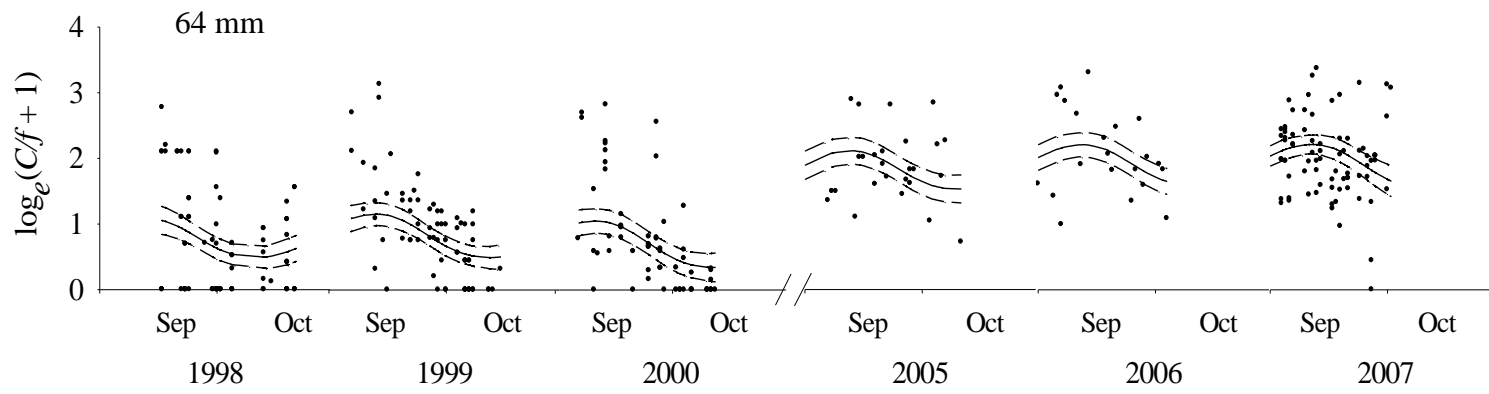


Figure 1.6. Continued.

Catch was not quadratically related to effort_s for any mesh size (Figure 1.7). Catch varied from 16 to 6,951 lake trout and effort_s varied from 0.5 to 1,548 100-m net nights in the 25- and 32-mm mesh. Catch was linearly related to annual effort_s in the 25-mm and 32-mm meshes (Figure 1.7). Within the 38-mm mesh, effort_s varied from 49 to 738 100-m net nights and catch varied from 304 to 1,197 lake trout. Catch and effort_s were not related in the 38-mm mesh (Figure 1.7). Effort_s varied from 5 to 258 100-m net nights in the 51- and 64-mm meshes, and catch varied from 11 to 3,610 lake trout. Catch was linearly related with effort_s in the 51- and 64-mm meshes (Figure 1.7).

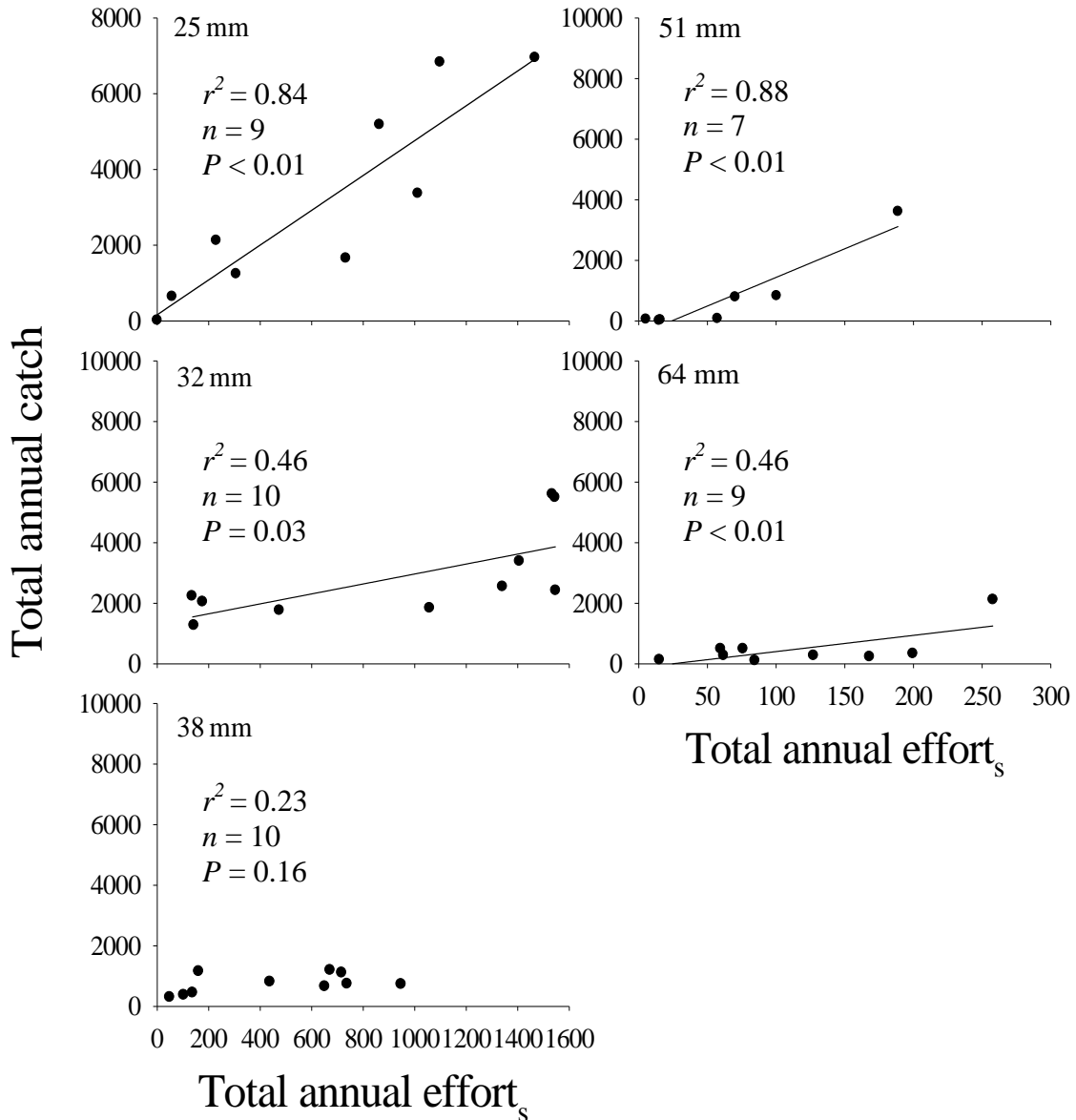


Figure 1.7. Catch as a function of effort_s (100-m net nights, see text for definition of effort_s) at standardized locations by mesh from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park.

Biomass Harvested

Biomass harvested increased over the duration of the suppression program (Table 1.3). The lake-wide estimate of biomass harvested increased from 0.001 kg/ha in 1995 to 0.744 kg/ha in 2007. Annual estimates of harvested biomass in the West Thumb Basin were often more than 10 times higher than biomass harvested in the Main Basin. For example, harvest varied from 0.000 kg/ha to 0.334 kg/ha the Main Basin and from 0.007 kg/ha to 4.906 kg/ha in the West Thumb Basin.

Table 1.3. Estimated biomass harvested (kg/ha) by basin and lake-wide from 1995 through 2007 for Yellowstone Lake, Yellowstone National Park.

Year	Basin		
	Main Basin	West Thumb	Lake-wide
1995	0.000	0.007	0.001
1996	0.025	0.010	0.034
1997	0.010	0.339	0.050
1998	0.025	0.408	0.125
1999	0.019	0.797	0.117
2000	0.072	0.674	0.196
2001 ^a	0.066	0.671	0.202
2002 ^a	0.088	0.488	0.187
2003 ^a	0.067	1.503	0.269
2004 ^a	0.035	4.906	0.537
2005	0.091	3.390	0.473
2006 ^a	0.297	3.785	0.733
2007	0.334	3.602	0.744

^a Weight of fish estimated using weight-length relationship from the nearest year.

Population Metrics

Length and Age Structure. In control netting, the peak selectivity of the 25-mm mesh size was 255 mm total length, the 32-mm mesh size selected lake trout 320 mm total length, and the 38-mm mesh size selected for lake trout 385 mm total length. For

spawner netting, the peak selectivities of the 51-, 57-, 64-, 70-, and 76-mm meshes were 525, 590, 655, 720, 785 mm total length, respectively. Median and quartile lake trout lengths decreased from 1998 through 2007 for control and spawner netting (Figures 1.8 and 1.9). For control netting, median total length decreased 25 mm from 1998 to 2007. The interquartile range of lake trout lengths for control netting varied from 35 to 65 mm. For spawner netting, the median total length was 615 mm in 1998 and decreased to 565 mm in 2006, but increased to 575 mm in 2007. The interquartile range for spawning lake trout varied from 115 mm in 1998 to 60 mm in 2005. For distribution netting, no fish >600 mm have been caught since 2000 (Figure 1.10). The median length was 315 mm (mean = 373) in 1998 and increased to 415 mm (mean = 404) in 2003 and subsequently decreased to 308 mm (mean = 343 mm) in 2007 for distribution netting. Length-frequency distributions from distribution netting were variable, with the interquartile range varying from 280 mm in 1997 to 60 mm in 1999. Median length decreased as a function of cumulative effort_s for control netting ($r^2 = 0.52$, $P = 0.02$) and spawner netting ($r^2 = 0.73$, $P = 0.06$), but not for distribution netting ($r^2=0.04$, $P = 0.6$) (Figure 1.11).

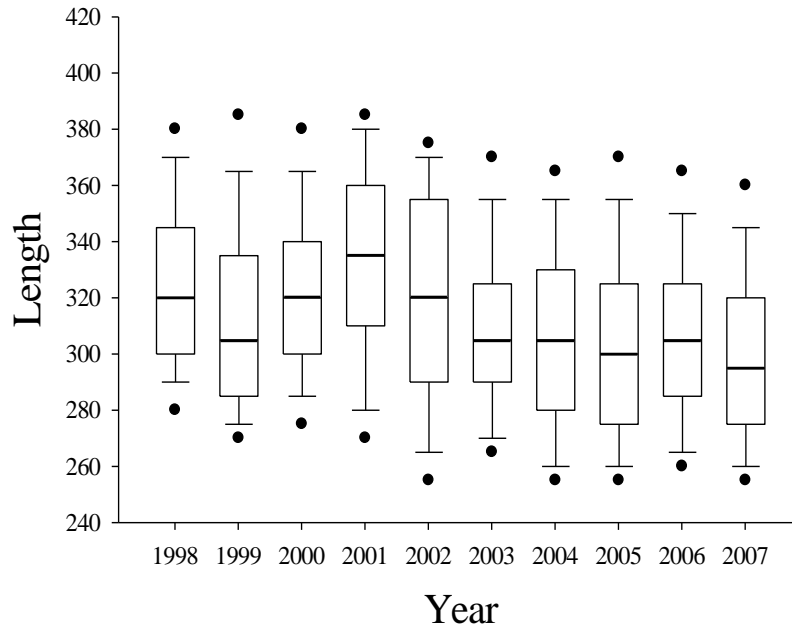


Figure 1.8. Quartile box plots for length of juvenile lake trout from control netting (see text for definition of control netting) from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park. Boxes indicate interquartile range (25th and 75th percentiles), bold lines delineate the median, and dots delineate 5th and 95th percentiles.

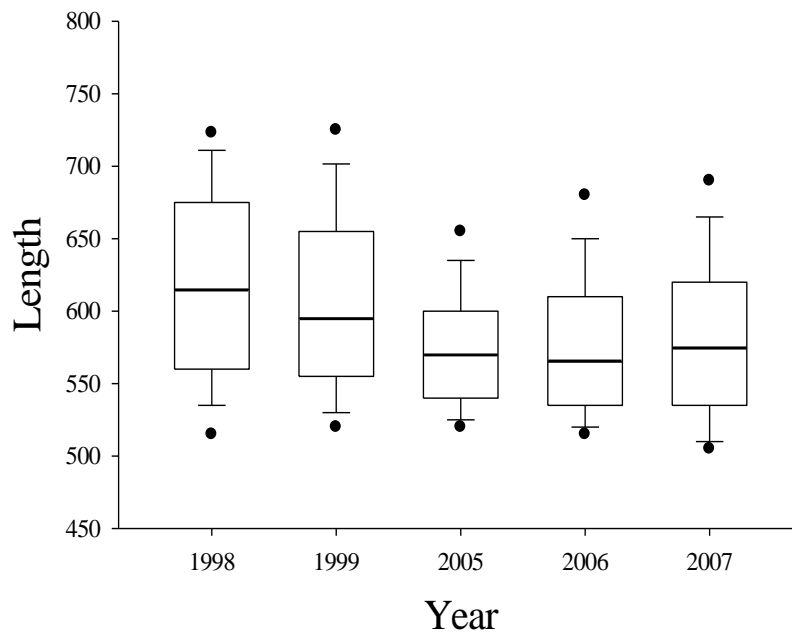


Figure 1.9. Quartile box plots for length of spawning adult lake trout from spawner netting (see text for definition of spawner netting) from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park. Boxes indicate interquartile range (25th and 75th percentiles), bold lines delineate the median, and dots delineate 5th and 95th percentiles.

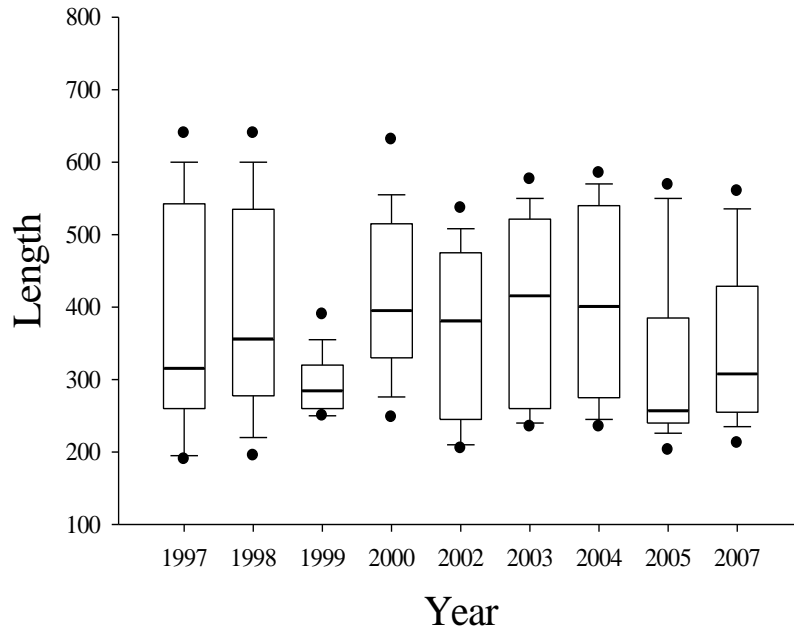


Figure 1.10. Quartile box plots for length of lake trout from distribution netting (see text for definition of distribution netting) from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park. Boxes indicate interquartile range (25th and 75th percentiles), bold lines delineate the median, and dots delineate 5th and 95th percentiles.

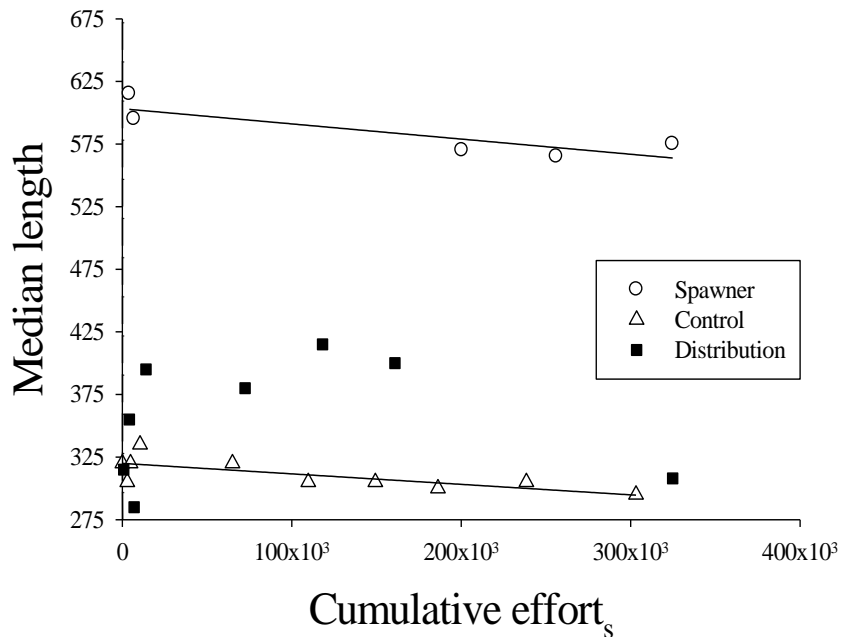


Figure 1.11. Median length as a function of cumulative effort_s (see text for definition of effort_s) by netting type from 1997 through 2007 for lake trout in Yellowstone Lake, Yellowstone National Park. Regression functions are displayed for significant ($p \leq 0.1$) regression models.

Median and quartile ages for control, spawner, and distribution netting did not decrease from 1998 through 2007 (Figures 1.12, 1.13, and 1.14). Median age within control netting varied from 2 to 4, but was 3 in seven of the ten years. Age distributions for spawner netting were skewed toward larger fish in 1998 and 2007; however, the median age was 8 in four of the five years. Median age for distribution netting varied from 2 to 5. Median age was 4 (mean = 4.7) in 1997 and 3 (mean = 3.8) in 2007. Median age did not change as a function of cumulative effort_s for control netting ($r^2 = 0.02$, $P = 0.68$) or spawner netting ($r^2 = 0.33$, $P = 0.3$). Median age was not a significant negative quadratic function of cumulative effort_s distribution netting ($r^2 = 0.32$, $P=0.14$) (Figure 1.15).

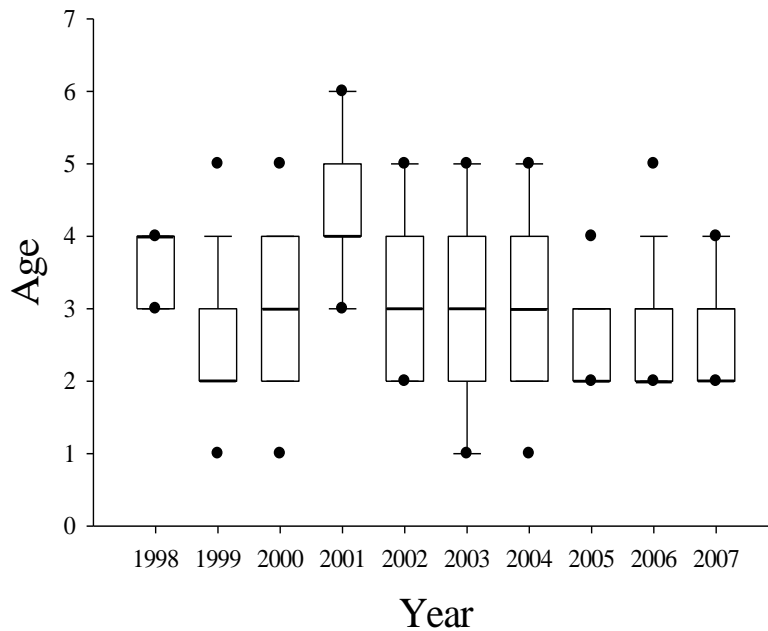


Figure 1.12. Quartile box plots for age of juvenile lake trout from control netting (see text for definition of control netting) from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park. Boxes indicate interquartile range (25th and 75th percentiles), bold lines delineate the median, and dots delineate 5th and 95th percentiles.

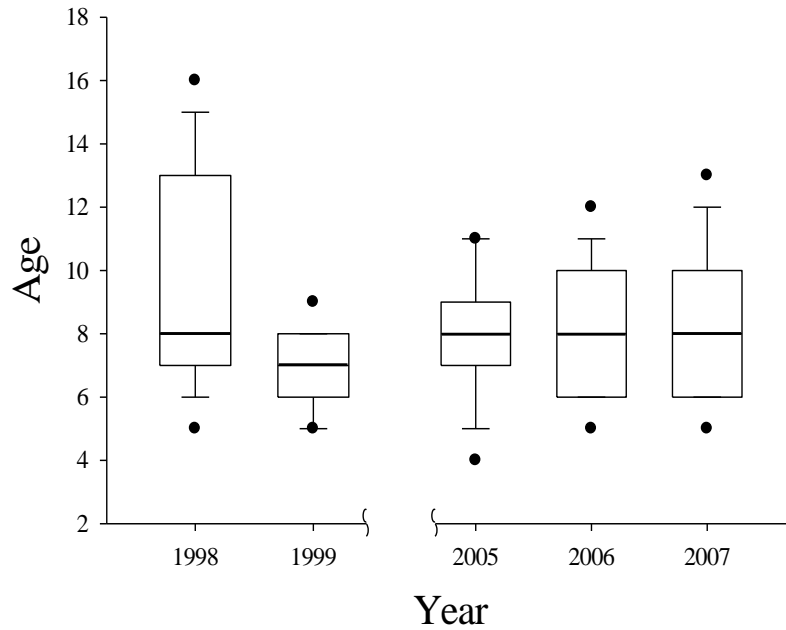


Figure 1.13. Quartile box plots for age of spawning adult lake trout in spawner netting (see text for definition of spawner netting) from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park. Boxes indicate interquartile range (25th and 75th percentiles), bold lines delineate the median, and dots delineate 5th and 95th percentiles.

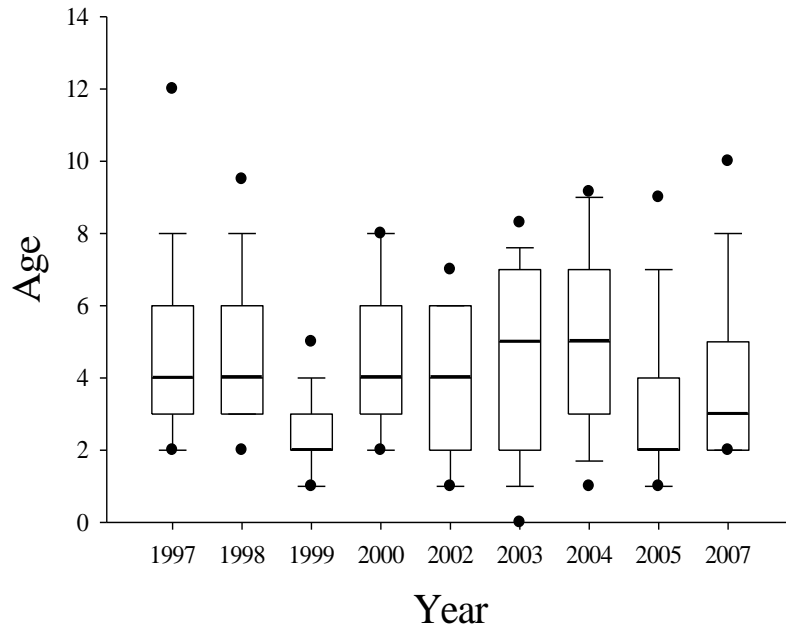


Figure 1.14. Quartile box plots for age of lake trout from distribution netting (see text for definition of distribution netting) from 1998 through 2007 in Yellowstone Lake, Yellowstone National Park. Boxes indicate interquartile range (25th and 75th percentiles), bold lines delineate the median, and dots delineate 5th and 95th percentiles.

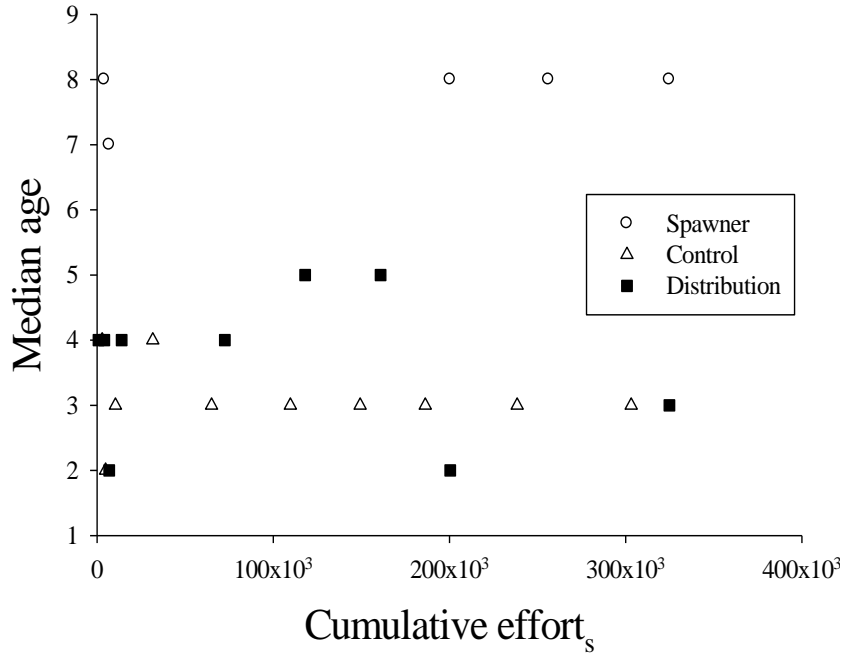


Figure 1.15. Median age as a function of cumulative effort_s (see text for definition of effort_s) by netting type from 1997 through 2007 for lake trout in Yellowstone Lake, Yellowstone National Park. Regression functions are not displayed because regressions were not significant ($p \leq 0.1$).

Growth and Body Condition. Mean length at capture for lake trout caught in 2007 varied from 203 mm for age 1 to 734 mm for age 17 (Table 1.4). Von Bertalanffy growth models with sex interactions for at least one parameter were supported over models without sex interactions each year from 2002 through 2007; however, the parameters interacting with sex in the best supported model varied by year (Table 1.5). Akaike Information Criterion values for all models in 2004 and 2006 were within 2 units (Table 1.5), indicating models were equally supported (Burnham and Anderson 2002). Estimates of L_{∞} were higher for females than males in five of six years and estimates of ω were higher for males than females in four of six years (Figure 1.16). Parameters L_{∞} and ω from the growth models for males varied from 632 to 854 mm and 125 to 208 mm/year, respectively (Figure 1.16). Parameters L_{∞} and ω from annual growth models for females varied from 765 to 919 mm and 122 to 154 mm/year, respectively (Figure

1.16). Regressions of L_{∞} as a function of cumulative effort_s were also non-significant for males ($P = 0.84$, $r^2 = 0.01$, $n = 6$) and females ($P = 0.32$, $r^2 = 0.23$, $n = 6$). Regressions of ω as a function of cumulative effort_s were not significant for males ($P = 0.32$, $r^2 = 0.24$, $n = 6$) or females ($P = 0.67$, $r^2 = 0.05$, $n = 6$). For VBF growth models for sexes combined, L_{∞} varied from 719 to 887 mm and ω varied from 120 to 157 mm/year. The parameter L_{∞} from growth models for sexes combined did not decrease as a function of cumulative effort_s ($P = 0.16$, $r^2 = 0.16$, $n = 8$) and ω was not related to cumulative effort_s ($P = 0.98$, $r^2 = 0.00$, $n = 8$). Mean length at age was positively related to cumulative effort_s for age 4, and negatively related to cumulative effort_s for ages 2, 8, 10, and 12 (Table 1.6).

Table 1.4. Sample size, mean total length at capture (mm), standard deviation (SD), and minimum-maximum values by age for lake trout sampled in 2007 in Yellowstone Lake, Yellowstone National Park.

Age	<i>N</i>	Mean	SD	Min-max
1	4	203	60	123-262
2	90	251	40	170-370
3	84	314	48	199-415
4	66	388	57	254-497
5	56	444	71	304-612
6	65	529	96	340-724
7	47	570	84	380-762
8	42	589	84	429-757
9	25	627	98	426-788
10	38	632	90	461-804
11	34	658	100	447-847
12	30	666	121	395-912
13	21	696	95	572-921
14	13	707	108	509-873
15	3	845	61	795-913
16	6	767	94	638-907
17	3	734	58	669-775

Table 1.5. Sample size (N), coefficient of determination (r^2), and Akaike's Information Criterion (AIC) values for von Bertalanffy growth models with parameter by sex interactions estimated by year for lake trout in Yellowstone Lake, Yellowstone National Park. The model was: $L_t = L_\infty \cdot (1 - e^{-(\omega/L_\infty)t})$, where L_t = length at time t , L_∞ = the theoretical maximum length of lake trout in the population, ω = the rate of growth near the origin, and t = age. The column labeled "Interactions" displays the parameter by sex interactions included in the model. Models are ranked by ascending AIC values by Year.

Year	Interactions	N	r^2	AIC
2002	L_∞ *Sex, ω *Sex	73	0.49	768.509
	L_∞ *Sex	73	0.47	770.559
	ω *Sex	73	0.43	775.931
	none	73	0.40	779.217
2003	ω *Sex	288	0.61	3249.417
	L_∞ *Sex, ω *Sex	288	0.61	3251.393
	L_∞ *Sex	288	0.60	3253.938
	none	288	0.56	3281.518
2004	L_∞ *Sex	268	0.65	3158.338
	ω *Sex	268	0.65	3159.238
	none	268	0.65	3160.184
	L_∞ *Sex, ω *Sex	268	0.65	3160.273
2005	L_∞ *Sex, ω *Sex	411	0.79	4696.054
	L_∞ *Sex	411	0.79	4697.690
	none	411	0.79	4697.846
	ω *Sex	411	0.79	4699.824
2006	L_∞ *Sex	589	0.77	6713.066
	L_∞ *Sex, ω *Sex	589	0.77	6713.829
	none	589	0.77	6714.886
	ω *Sex	589	0.77	6715.889
2007	ω *Sex	621	0.79	7190.757
	L_∞ *Sex, ω *Sex	621	0.79	7192.734
	L_∞ *Sex	621	0.79	7193.367
	none	621	0.79	7194.679

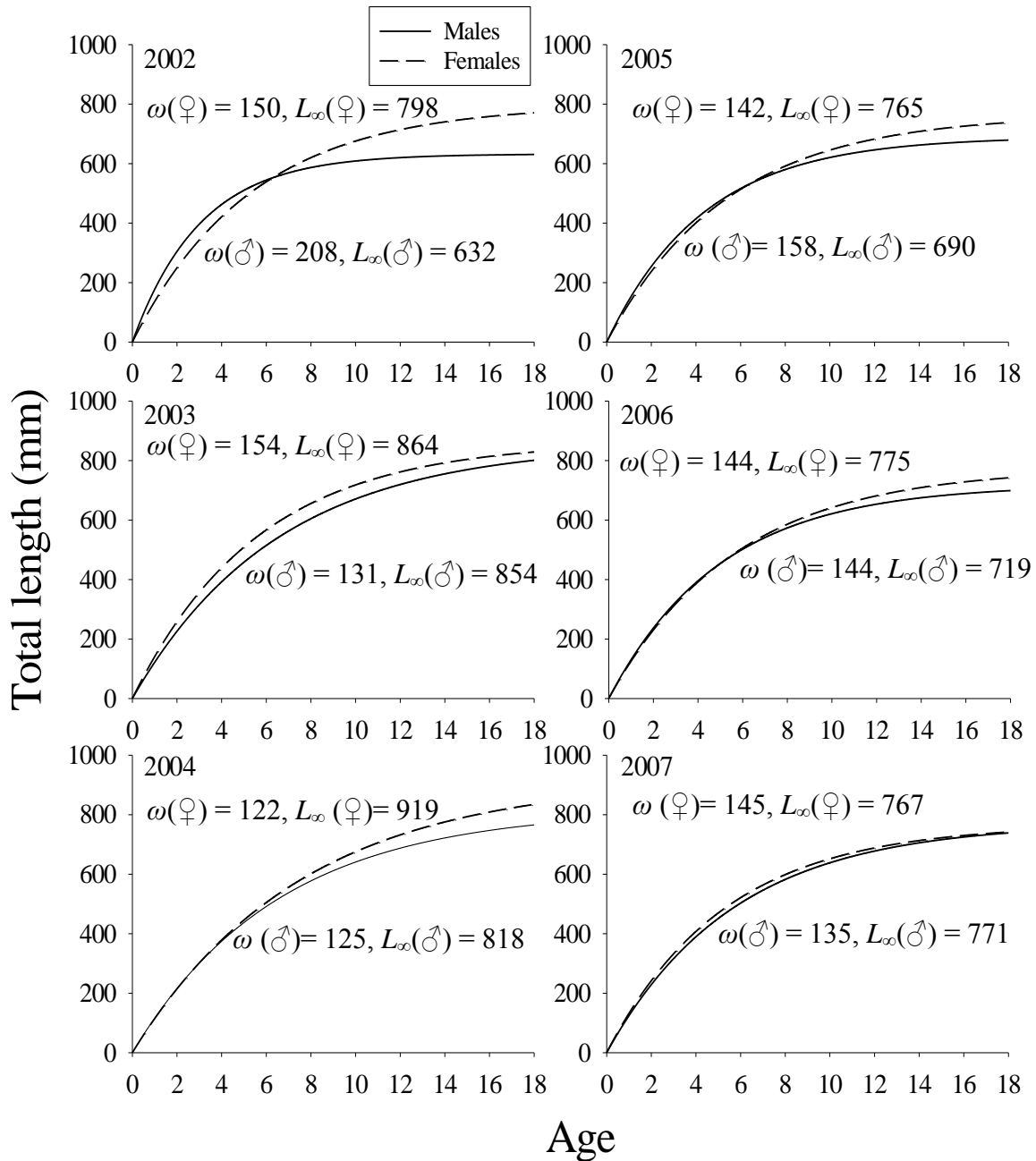


Figure 1.16. Von Bertalanffy growth models by sex for lake trout in Yellowstone Lake, Yellowstone National Park. The equation is: $L_t = L_\infty \cdot (1 - e^{-(\omega/L_\infty)t})$, where L_t = length at time t , L_∞ = the theoretical maximum length of lake trout in the population, ω = the rate of growth near the origin, and t = age. Sex-specific parameter estimates are displayed in graph panels. Parameter estimates for females are displayed above regression lines and estimates for males are displayed below.

Table 1.6. Regression statistics for mean length at capture and cumulative effort_s (see text for definition of effort_s) for lake trout in Yellowstone Lake, Yellowstone National Park by age, season and netting type from 1998 through 2007. Season represents whether lake trout were sampled in the early season (from the start of fishing in May through 31 July) or late season (from 1 August through the end of the season in October). Netting types are as follows: C represents control netting (netting targeting juvenile lake trout), and S represents spawner netting (netting targeting spawning adult lake trout).

Age	Season	Netting type	<i>N</i>	β_1	r^2	<i>P</i> -value
2	Early	C	5	-0.0031	0.69	0.08
3	Early	C	7	-0.0006	0.24	0.26
4	Early	C	7	-0.0003	0.07	0.57
4	Late	C	7	0.0023	0.57	0.05
5	Late	C,S	8	-0.0001	0.00	0.88
6	Late	C,S	8	-0.0005	0.05	0.59
7	Late	S	7	0.0000	0.01	0.82
8	Late	S	7	-0.0016	0.79	0.01
9	Late	S	5	-0.0027	0.51	0.18
10	Late	S	6	-0.0077	0.92	<0.01
11	Late	S	5	-0.0085	0.32	0.32
12	Late	S	5	-0.0304	0.84	0.03

Lake trout body condition was high in 2007. Median W_r for ages one through four was greater than the 95th percentile value for lake trout populations throughout North America (Table 1.7; Hubert et al. 1994). Median W_r for ages 5-17 was greater than or equal to 100. Median W_r at age was positively related to cumulative effort_s for age-2 lake trout (Table 1.8); however median W_r was not related to cumulative effort_s for lake trout ages 3 through 11 (Tables 1.8 and 1.9).

Table 1.7. Sample size (N), median, minimum-maximum, and percentile relative weight (W_r) by age for lake trout sampled in 2007 in Yellowstone Lake, Yellowstone National Park. Percentile was determined by comparing the observed median with the cumulative frequency distribution of W_r values for lake trout populations across North America (Hubert et al. 1994).

Age	N	Median	Min-max	Percentile
1	15	123	104-150	>95
2	200	121	98-146	>95
3	136	119	91-150	>95
4	86	122	88-148	>95
5	75	110	90-148	>90
6	64	109	86-138	>90
7	50	104	88-139	>75
8	40	107	81-137	>90
9	30	110	86-148	>90
10	31	109	90-136	>90
11	27	110	90-138	>90
12	19	109	88-126	>90
13	16	102	87-123	>75
14	12	105	81-120	>75
15	8	100	92-111	>75
16	10	104	88-126	>75
17	4	106	100-118	= 90

Table 1.8. Regression statistics for median relative weight (W_r) and cumulative effort_s (see text for definition of effort_s) for netting targeting juvenile lake trout in Yellowstone Lake, Yellowstone National Park by age and season from 1998 through 2007. Season represents whether lake trout were sampled in the early season (from the start of fishing in May through 31 July) or late season (from 1 August through the end of the season in October).

Age	Season	N	β_1	r^2	P -value
2	Late	7	0.0010	0.72	0.02
3	Early	6	0.0002	0.28	0.28
3	Late	6	0.0002	0.33	0.23
4	Late	6	0.0002	0.16	0.44

Table 1.9. Regression statistics for median relative weight (W_r) at age from 1998 through 2007 as a function of cumulative effort_s (see text for definition of effort_s) for netting targeting adult lake trout in Yellowstone Lake, Yellowstone National Park by age and season. Season represents whether lake trout were sampled in the early season (from the start of fishing in May through 31 July) or late season (from 1 August through the end of the season in October).

Age	Sex	<i>N</i>	β_1	r^2	<i>P</i> -value
5	Male	6	0.0002	0.23	0.34
6	Male	6	0.0001	0.34	0.23
7	Male	6	-0.0001	0.13	0.48
7	Female	6	0.0000	0.00	0.99
8	Male	6	-0.0000	0.06	0.62
8	Female	6	-0.0000	0.03	0.72
9	Male	6	0.0000	0.00	0.90
9	Female	6	0.0000	0.10	0.53
10	Female	5	-0.0002	0.06	0.68
11	Female	5	0.0001	0.04	0.75

Maturity and Fecundity. Length at 50% maturity for males varied from 481 mm in 1997 to 422 mm in 2007. Age at 50% maturity for males in 1997 was 5.9 and in 2007 was 4.4. Length at 50% maturity for females was 655 mm in 1997 and 541 mm in 2007. Age at 50% maturity for females in 1997 was 10.3 and in 2007 was 6.7. Length and age at 50% maturity declined as a function of cumulative effort_s for males and females (Figures 1.17 and 1.18).

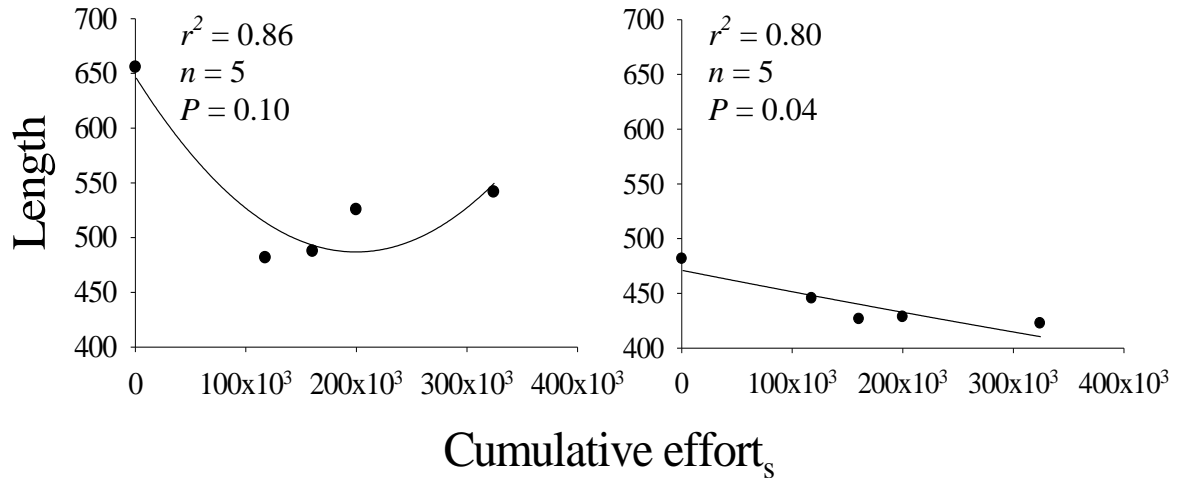


Figure 1.17. Length at 50% probability of maturity as a function of cumulative effort_s (see text for definition of effort_s) for female (left panel) and male (right panel) lake trout in Yellowstone Lake, Yellowstone National Park from 1997 through 2007. Regression functions are displayed for significant ($p \leq 0.1$) regression models.

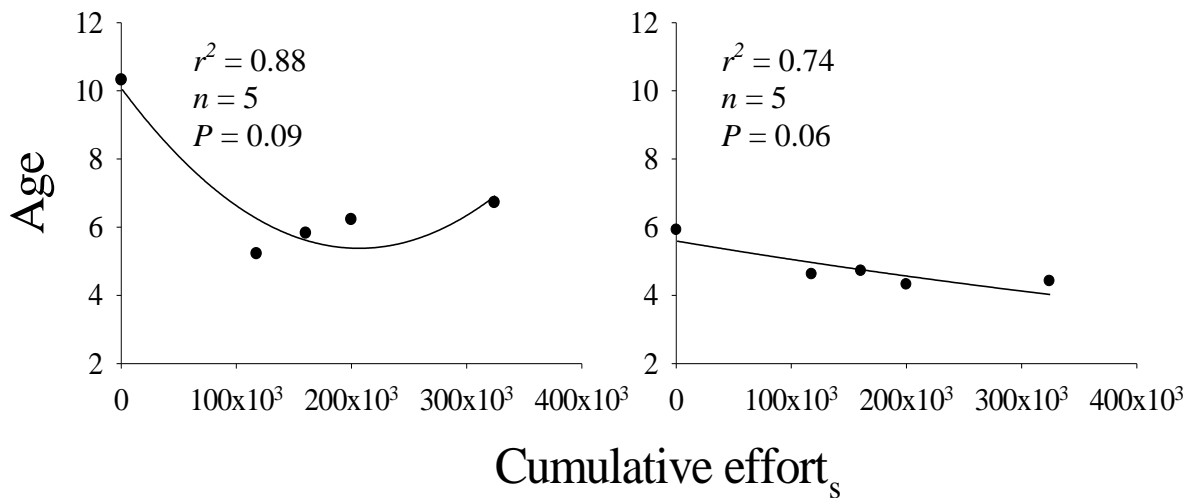


Figure 1.18. Age at 50% probability of maturity as a function of cumulative effort_s (see text for definition of effort_s) for female (left panel) and male (right panel) lake trout in Yellowstone Lake, Yellowstone National Park from 1997 through 2007. Regression functions are displayed for significant ($p \leq 0.1$) regression models.

Number of eggs per female varied from 798 for a 468-mm lake trout to 16,834 for a 906-mm lake trout (Figure 1.19). Mean relative fecundity increased from 718 ± 167 (95% CI) eggs in 1996 to 1551 ± 101 (95% CI) eggs in 2006 and $1,556 \pm 779$ (95% CI)

eggs in 2007. Differences among length-fecundity slopes for 1998, 2006, and 2007 (Figure 1.19 and Table 1.10) were not significant ($F = 1.8$, $df = 2, 201$, $P = 0.17$).

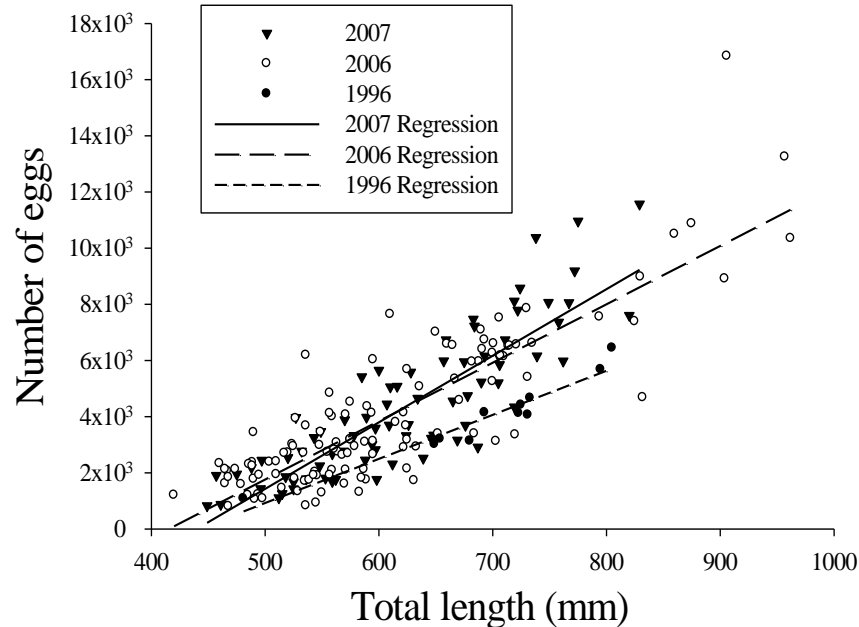


Figure 1.19. Length-fecundity regressions for 1996, 2006, and 2007 for lake trout in Yellowstone Lake, Yellowstone National Park.

Table 1.10. Coefficients and statistics for length-fecundity relationships for lake trout in Yellowstone Lake, Yellowstone National Park.

Year	N	β_0	β_1	r^2	P -value
1996	11	-6,926	15.7	0.92	<0.01
2006	119	-8,640	20.8	0.73	<0.01
2007	77	-10,421	23.7	0.74	<0.01

Mortality. Total annual mortality was not significantly related to cumulative effort, for control netting ($r^2 = 0.42$, $P = 0.12$) or spawner netting ($r^2 = 0.56$, $P = 0.25$) (Figure 1.20). Estimates of total annual mortality were consistently higher for spawner and control netting than for distribution netting. Total annual mortality varied from 0.33

± 0.35 (95% CI) to 0.69 ± 0.10 (95% CI) for control netting and from 0.35 ± 0.64 (95% CI) to 0.59 ± 0.11 (95% CI) for spawner netting. Total annual mortality for distribution netting increased as a function of cumulative effort_s ($r^2 = 0.93$, $P = 0.04$). Total annual mortality for distribution netting increased from 0.23 ± 0.11 (95% CI) in 1998 to 0.30 ± 0.04 (95% CI) in 2007. Total annual mortality from the cohort catch curve for the 1999 year-class was 0.30 ± 0.17 (95% CI) in 2007, similar to the total annual mortality estimate from 2007 distribution netting.

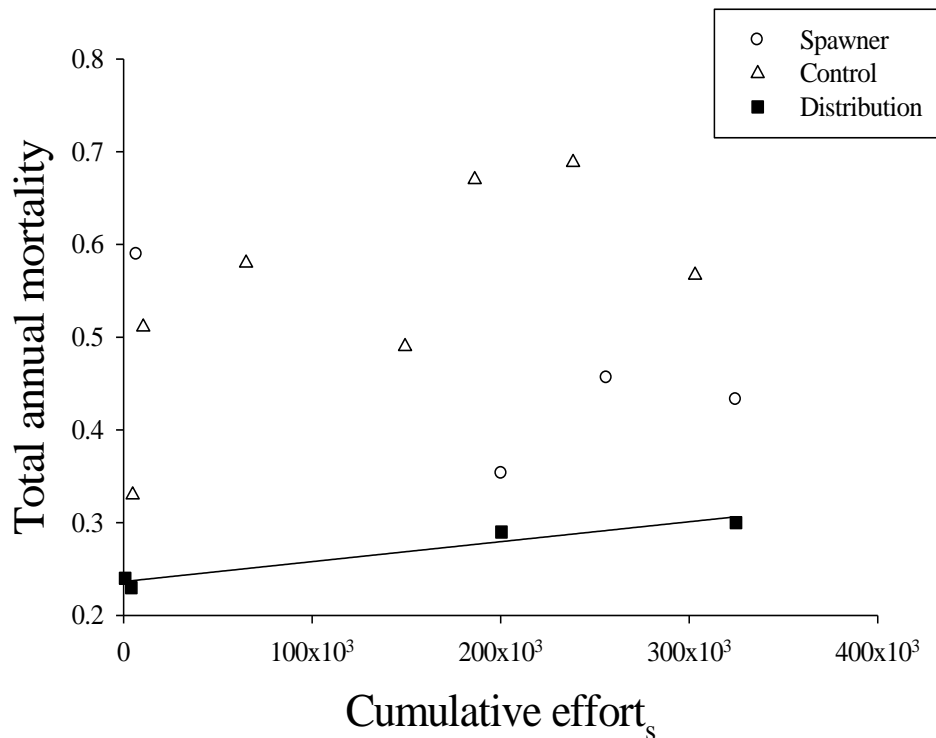


Figure 1.20. Total annual mortality as a function of cumulative effort_s (see text for definition of effort_s) by netting type from 1997 through 2007 for lake trout in Yellowstone Lake, Yellowstone National Park. Regression functions are displayed for significant ($p \leq 0.1$) regression models.

Discussion

Catch of lake trout in Yellowstone Lake has not declined since the suppression program started despite increased effort. The relationship between catch and effort is typically used to determine levels of sustainable harvest (Ricker 1975; Hilborn and Walters 1992). However, in the case of Yellowstone Lake the relationship can be used to determine the amount of effort needed to cause the lake trout population to collapse. The effort needed to cause a population to collapse is likely any point beyond the peak of the dome-shaped relationship between catch and effort (Ricker 1975; Hilborn and Walters 1992; Haddon 2001). Unfortunately, the relationships between catch and effort for lake trout in Yellowstone Lake were either linear or asymptotic, not quadratic. It is possible that the highest observed catch and effort data represent the peak of the dome-shaped relationship. However, additional effort will be needed to fully express the peak of the relationship and estimate the effort needed to collapse the lake trout fishery in Yellowstone Lake. The use of the relationship between harvest and effort to estimate maximum sustained yield has been problematic because overharvest must occur to find the peak of the relationship (Hilborn and Walters 1992).

Unsurprisingly, the temporal variation in C/f corroborates the catch and effort data. In general, C/f continued to increase throughout the duration of the suppression program. I surmise that observed patterns in catch and C/f are a function of the lake trout population abundance increasing. The use of catch rates as an index of abundance requires the assumption of a linear relationship between C/f and stock density (i.e., catchability remains constant; Hilborn and Walters 1992). Hyperstability (i.e., catchability increases or remains high as density declines) was of particular concern in

Yellowstone Lake because netting efficiency likely increased as NPS personnel learned where to set nets to maximize lake trout catch. Catchability can be assumed to remain constant if sampling effort is randomly distributed (i.e., non-random search does not occur; Hilborn and Walters 1992). Although locations for lake trout C/f in Yellowstone Lake were not randomly selected, my analysis of C/f at fixed locations through time avoided the effects of non-random search as NPS personnel learned where to set nets to maximize catch. Additionally, C/f data were standardized to avoid gear saturation caused by inconsistent set durations through time. Variation in catchability is commonly observed across seasons (Schoenbeck et al. 2005; van Poorten and Post 2005; McNery and Cross 2006); however, seasonal variation in C/f was explicitly modeled by a within-year temporal trend in the generalized additive models used for C/f . Therefore, seasonal changes in catchability were not likely to affect the analysis of C/f .

The lake trout suppression program in Yellowstone Lake uses an adaptive management strategy where nets are set in areas where catch rates are expected to be high (Koel et al. 2005). Although this strategy can maximize lake trout catch, it restricted analyses of catch and effort to the West Thumb Basin, which represents about 14% of lake surface area. However, it is unlikely that only 14% of the population is exposed to fishing effort. The temporal patterns observed in C/f and the lack of decreasing catch with increased effort may be a function of immigration by lake trout from the Main Basin to West Thumb Basin. The West Thumb Basin contains the highest percentage of known spawning habitat relative to the rest of the lake (Koel et al. 2007). Fish are likely being replaced in the West Thumb Basin faster than they can be removed, thus densities in the Main Basin may be relatively high and merit attention. Lake trout movement has been

positively associated with density in Lake Michigan (Schmalz et al. 2002). However, it is not clear where density is highest in Yellowstone Lake and low catch rates in the Main Basin do not indicate that density is high enough to cause emigration. Therefore, emigration from the Main Basin may be caused by higher quality habitat or greater food abundance in the West Thumb Basin.

The biomass harvested further corroborates the hypothesis that immigration is occurring from the Main Basin to the West Thumb Basin. The last four year estimates for biomass harvested in the West Thumb Basin are unsustainable for any lake trout population (Martin and Oliver 1980). The West Thumb Basin harvest of 3.6 kg/ha exceeded most literature values (see Appendix B for detailed comparisons), but the harvest of 0.33 kg/ha for the Main Basin was similar to populations that have provided a sustainable harvest (Healy 1978a; Martin and Oliver 1980). Lake trout in Lac La Ronge, Ontario, provided a sustainable harvest of 0.45 kg/ha, while harvest varying from 0.37 to 0.67 kg/ha over 10 years reduced lake trout abundance in Great Slave Lake, Northwest Territories (Keleher 1972; Healy 1978a). Lake trout harvests in the Laurentian Great Lakes varied annually from 0.24 kg/ha in Lake Superior to 0.58 kg/ha in Lake Michigan (Healy 1978a), and these populations collapsed from overexploitation (Hansen 1999).

Sustainable yield of lake trout is positively related to lake size and productivity (Trippel 1993; Marshall 1996; Shuter et al. 1998). Sustainable yield increases for populations at lower latitudes (Healy 1978a) and populations with fish assemblages that allow lake trout to be piscivorous (Matuszek et al. 1990). Therefore, the biomass harvested and the number of years harvest must occur to cause a population decline likely vary by ecosystem. Even in low productivity waters sustained annual harvest of lake

trout have been suggested to occur at levels up to 0.75 kg/ha (Martin and Oliver 1980). Although productivity for Yellowstone Lake (i.e., total dissolved solids [TDS]; 63 mg/l) ranks in the 76th percentile compared to 54 lakes containing lake trout across Ontario (Shuter et al. 1998), the productivity of Yellowstone Lake ranks only in the 31st percentile compared to 16 lake trout lakes throughout North America varying from 32,000 ha to 8.2 million ha (Matuszek 1978; Marshall 1996). Productivity is highly correlated with maximum sustained yield (MSY) at the regional scale (e.g., within Ontario; Shuter et al. 1998); however, lake area appears to be a better predictor of MSY for lake trout range-wide (Marshall 1996). Maximum annual sustainable lake trout harvest (kg/yr) over 12- to 17-year periods from 14 lakes throughout North America was positively related to lake area (Marshall 1996). However, maximum sustained yield of lake trout per unit area (kg/ha/yr) declined as lake area increased (Marshall 1996). The average annual lake-wide yield (0.28 kg/ha/yr) over the duration of the lake trout suppression program in Yellowstone Lake is well below the maximum sustained yield (0.61 kg/ha/yr) predicted by the surface area of Yellowstone Lake using the model in Marshall (1996). However, the harvest observed in 2007 (0.77 kg/ha) was greater than the maximum sustainable yield predicted by the surface area of Yellowstone Lake. It is likely that harvest benchmarks for Yellowstone Lake will need to exceed 0.61 kg/ha given that the population is expanding and there is a lack of interspecific competitors given the low diversity of fish species.

Compensatory responses to fishing effort were not consistent among population metrics. It is likely that any decreases in lake trout abundance from fishing were slightly offset by recruitment to the fishery. In addition, the population metrics did not clearly

support the catch data with regard to a growing lake trout population. This may be a function of the population being well below carrying capacity and the subsequent lack of density dependent responses. Finally, the inconsistency in population metrics related to fishing effort could be related to the natural variation in population metrics masking relationships. Quantifying compensatory responses to harvest with field data is often difficult because of variability in field measurements and compensation results from multiple processes involving multiple life stages (Rose et al. 2001). Compensatory responses to a decrease in density are most easily observed when the population is at carrying capacity (Rose et al. 2001). Given the recent introduction of lake trout in Yellowstone Lake (Munro et al. 2005), it is likely that the population was not at carrying capacity when the suppression program was initiated.

Unexploited fish populations typically have a high proportion of large and old fish (Johnson 1976; Kocovsky and Carline 2001; Dux 2005), and size and age structures decrease as populations are harvested (Goedde and Coble 1981; McDonald and Hershey 1989; Haedrich and Barnes 2001). In Yellowstone Lake, length was correlated with cumulative fishing effort, but median age remained constant. Thus, individual growth rate must have declined throughout the suppression program. Declines in individual growth rates were most evident for age 2 and ages greater than age 8. Interestingly, individual growth rates for age 4 fish increased throughout the suppression program. This may be a function of the large amount of effort from the control netting on age-4 fish. Thus, the netting program is operating much like a reverse slot-length limit, where much of the fishing pressure is on fish 250-500 mm. Inverse slot-length limits impose harvest on an intermediate size-range of fish to protect small fish to recruitment and large

fish for reproduction (Noble and Jones 1999). Additionally, inverse slot length limits decrease intraspecific competition within the harvested length range, resulting in increased growth and the attainment of trophy sizes (Noble and Jones 1999). Therefore, as lake trout enter the 250-500 mm length range competitive interactions are minimized and growth rates are elevated. Mean length at age decreased for lake trout over age 8. It is likely that a precipitous decline in the Yellowstone cutthroat trout population (Koel et al. 2005) contributed to the decline in growth rates for age 8 and older lake trout because 90% of the diet for lake trout age 9 and older is Yellowstone cutthroat trout (Ruzycki et al. 2003). The differences in growth among age classes is likely why the parameters from the von Bertalanffy growth model did not change as a function of fishing effort. Annual von Bertalanffy growth models were estimated with length-at-age data pooled from different seasons to incorporate all age-classes, which may have caused a loss of sensitivity when evaluating trends in growth. Regressions of mean length at age likely provided more sensitive comparison of growth through time because the analyses were stratified by season and age. Growth rates were high for the segment of the lake trout population in Yellowstone Lake that is targeted by control netting. Mean lengths at age computed for 2007 indicate high lake trout growth rates for ages 1 through 5 and average growth rates for ages 8 and older in comparison to mean length at age from native lake trout populations across North America with varying levels of harvest (Healy 1978a; Martin and Olver 1980). Estimates of L_{∞} and ω obtained in 2007 rank in the 88th percentile when compared to 54 lake trout populations in across Ontario; however, productivity (TDS) ranks in the 76th percentile (Shuter et al. 1998). Low lake trout density likely explains high lake trout growth rates because Yellowstone Lake is not

particularly productive compared to lakes containing lake trout throughout North America (Matuszek 1978).

Body condition is often negatively related to density (Muth and Wolfert 1986; McDonald and Hershey 1989; Schindler et al. 1997) and has declined in introduced lake trout populations that depleted their prey resource (Martinez et al. 2009). Conversely, lake trout body condition has increased in populations where exploitation caused a decline in density (Martin and Olver 1980; McDonald and Hershey 1989). In general, relative weight was high for lake trout in Yellowstone Lake, but was only positively correlated with fishing effort for age-2 lake trout.

Decreases in length and age at maturity as a function of fishing effort were clearly observed for males, whereas decreases for females were less conclusive. Declines in length or age at maturity can be caused by genetic selection or compensatory responses that indicate a population has declined in size (Trippel 1995). It is unlikely that the observed shift was caused by genetic selection because only two or three generations of lake trout have been exposed to fishing pressure. Decreases in age at maturity for lake trout in the Laurentian Great Lakes have been attributed to increased individual growth rates, which decrease the number of years for individuals to reach a size at which they mature (Madenjian et al 1998; Sitar and He 2006). A shift toward larger size at maturity was reported for lake trout in Lake Superior when abundance was reduced (Sitar and He 2006). The shift toward larger size at maturity was attributed to increased growth rates caused by increased food availability (Sitar and He 2006). However, size and age at maturity have decreased in populations of marine species that have been overharvested (Trippel 1995). The onset of maturity is controlled by growth or energy intake in early

life stages; thus, a smaller size at maturity could occur if fish obtain necessary nutrition early in life (Trippel 1995). Age at 50% maturity increased from age 6 in 1997 to age 11 in 2005 for females in an introduced lake trout population in Flathead Lake as the population approached carrying capacity as indicated by relatively constant C/f over a 10-year period (CSKT and MFWP 2006). The change in age at 50% maturity for females in Flathead Lake occurred with a change in length at maturity from about 500 mm in 1997 to about 580 mm in 2005. The patterns in age and length at maturity in Flathead Lake indicate that similar shifts can be observed in both metrics in response to changing density.

Fifty percent maturity for males in Yellowstone Lake occurred at a small size and a young age when compared to North American lake trout populations with varying levels of harvest (Healy 1978a; Trippel 1993; Sitar and He 2006). Age at 50% maturity for males in Yellowstone Lake in 2007 was similar to estimates for the lake trout population in Lake Michigan (Madenjian et al. 1998), which had not recovered from overharvest. However, length at maturity was much smaller in Yellowstone Lake than in Lake Michigan. Males in Lake Michigan mature at ages of 4.3 to 6.3 years and lengths of 563 to 600 mm (Madenjian et al 1998). Lengths and ages at 50% maturity reported for Lake Michigan were similar to values reported for the other Laurentian Great Lakes (Madenjian et al. 1998). Maturity for males in Yellowstone Lake occurred at a smaller size and earlier age than in Lake Pend Oreille, where 50% maturity for male lake trout occurred at a length of 632 mm and an age of 6.5 years (Hansen 2007).

Length and age at 50% maturity for females in Yellowstone Lake in 2007 was comparable to lakes of similar productivity with varying levels of harvest in Ontario and

large lakes at low latitudes throughout North America (Healy 1978a; Trippel 1993; Madenjian et al. 1998; Sitar and He 2006). Female lake trout in Yellowstone Lake matured at a similar age and smaller size than females in Lake Michigan, which matured at ages of 5.5 to 7.4 and lengths of 628 to 654 (Madenjian et al. 1998). Age at 50% maturity for females in Yellowstone Lake is similar to the estimate of 7.3 for Lake Pend Oreille; however, length at maturity is much smaller for females in Yellowstone Lake (Hansen et al. 2008). Age and length at 50% maturity for female lake trout in Yellowstone Lake occurred at a younger age and smaller size than in Flathead Lake in 2005, when the population was approaching carrying capacity (CSKT and MFWP 2006). Fifty percent maturity for females in Yellowstone Lake occurred at a similar length and age to females in Flathead Lake in 1997, before carrying capacity was reached.

Interestingly, a decrease in lake trout density in Yellowstone Lake was not supported by C/f data. An alternative explanation for the observed decrease in length and age at maturity is that samples from 1997 may have included fish from the source population, Lewis Lake. The lake trout population in Lewis Lake is characterized by poor growth and body condition caused by low food availability (P. E. Bigelow, Yellowstone National Park, personal communication). Introductions of lake trout likely occurred in the mid-to-late 1980s and as recent as 1996 (Munroe et al 2005). Maturity models including those fish may reflect biological conditions in Lewis Lake rather than Yellowstone Lake.

Fecundity was higher in 2006 and 2007 than in 1996; however, comparisons were complicated by a small sample in 1996 that may have included lake trout from Lewis Lake. Relative fecundity in 1996 was well below values reported in the literature,

whereas relative fecundity in 2006 and 2007 were similar to the mean value of 1,506 eggs/kg reported for 13 lake trout populations across Ontario (Shuter et al. 1998) and 1,592 eggs/kg reported for Lake Ontario (Fitzsimons and O’Gormon 1996). Length-specific fecundity for lake trout in Yellowstone Lake in 2007 was high compared to other lake trout populations. For example, a 600-mm lake trout in Yellowstone Lake in 2007 averaged 3,799 eggs whereas lake trout of the same size averaged 2,768 – 2,930 eggs in five moderately exploited lakes in Ontario (Trippel 1993) and 1,537 eggs in Lake Superior (Peck 1988, cited by Dux 2005). The above-average length-specific fecundity combined with average weight-specific fecundity indicates that high body condition explains high fecundity in Yellowstone Lake.

The rate of total annual mortality estimated for lake trout in Yellowstone Lake was within those reported for sustainable harvested populations. Lake trout populations throughout North America can typically sustain total annual mortality rates of up to 0.5 (Healy 1978a). Increasing rates of mortality have been observed for lake trout populations in Lake Opeongo, Ontario, and Great Slave Lake after the initiation of harvest that caused these populations to decline (Healy 1978b). However, the increases in mortality resulting in lake trout declines in Lake Opeongo and Great Slave Lake were greater than observed in Yellowstone Lake and mortality was near 0.5 when the populations declined (Healy 1978b). The rate of total annual mortality for lake trout in Yellowstone Lake is similar to natural mortality rates for some native lake trout populations, which typically have natural mortality rates from 0.1 to 0.3 (Healy 1978a; Martin and Olver 1980; Shuter et al. 1998; Sitar et al. 1999). The relationship between total annual mortality and fishing effort indicates that fishing effort needs to increase over

the amount expended in 2007 to cause total annual mortality to increase to 0.5 (see Chapter 2).

Is the suppression program working in Yellowstone Lake? The answer to that question is complicated. The high individual growth rate, high body condition, low age and size at maturity, and high fecundity indicate that lake trout density in Yellowstone Lake has not reached carrying capacity. The catch and C/f data suggest that the lake trout population is continuing to grow, but obviously at a lower rate than if the suppression program was not in place. The reduced rate of population increase in conjunction with the decline of the Yellowstone cutthroat trout population is likely increasing food availability for the lake trout juveniles. The effects of increased food availability on juvenile growth and maturity schedule likely increases the resistance of the population to overharvest by increasing reproductive capacity (Trippel 1995). It appears that the lake trout population in Yellowstone Lake is increasing despite more than a decade of gill netting. However, the removal of nearly 273,000 lake trout between 1995 and 2007 prevented millions of Yellowstone cutthroat trout from being consumed. Fishing effort needs to increase in Yellowstone Lake for the suppression program to cause the lake trout population to decline. Additional removal methods may increase the efficacy of lake trout suppression in Yellowstone Lake (see Discussion section in Chapter 2).

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. Additionally, the eradication of introduced species has been more successful when reintroduction or reinvasion was prevented (Bomford and O'Brien 1995; Myers et al. 2000). Isolated islands offer many examples of successful eradications of introduced or invasive mammals, plants, and insects (Veitch and Clout 2002; Howald et al. 2007). Similar to islands, lakes provide isolation from source populations, thereby increasing the probability of successful eradication.

The removal of individuals needs to be maintained continuously or until the population is eradicated for population suppression to succeed (Myers et al. 2000). For example, an eradication effort for grey squirrels in Italy was initially effective at reducing squirrel density; however, when the eradication program was suspended for three years the population increased in size and spatial extent and eradication was no longer feasible (Bertolino and Genovesi 2003). A continuous control or eradication program is particularly important if the population exhibits compensatory responses to removal and a subsequent resilience to population reduction (Rieman and Beamesderfer 1990), which may be occurring for lake trout in Yellowstone Lake. Compensatory responses to population reduction have been observed for many species in addition to fish. For example, populations of snowshoe hares *Lepus americanus* and introduced rats *Rattus* spp. have responded to control efforts by increasing recruitment through increased juvenile survival (Brown and Tuan 2005) and recolonization of areas where mortality was highest (Sullivan and Sullivan 1986; Brown and Tuan 2005). Additionally, invasive yellow starthistle *Centaurea solstitialis* may respond to population reduction by increasing

per-capita reproduction (Garren and Strauss 2009). By increasing resilience to eradication, populations require control to be exerted continuously (Rieman and Beamesderfer 1990) or across increased spatial and temporal scales (Sullivan and Sullivan 1986; Brown and Tuan 2005).

Eradication or control of introduced populations is ubiquitous because introduced species rank second to habitat destruction among threats to world-wide biodiversity (Simberloff 2001). Lake trout have been introduced extensively throughout the western United States where the species has negatively affected numerous salmonid populations (Donald and Alger 1993; Fredenberg 2002; Vander Zanden et al. 2003; Koel et al. 2005) and ecosystems (Spencer et al. 1991; Vander Zanden et al. 2003; Koel et al 2005; Tronstad 2008). Consequently, lake trout suppression has become an increasingly common management practice for the conservation of native fishes and ecosystems throughout the western U.S. (Martinez et al. 2009). As the longest ongoing lake trout removal project, the lake trout suppression program on Yellowstone Lake provides a case study for the evaluation of a lake trout suppression strategy. Lake trout suppression in Yellowstone Lake highlights the necessity for long-term planning that incorporates a large amount of fishing pressure to eradicate a species from a large natural lake.

CHAPTER 2

LAKE TROUT POPULATION GROWTH IN YELLOWSTONE LAKE: A
MODELING APPROACHIntroduction

Lake trout populations have declined or collapsed in many lakes where overharvest has occurred (Keleher 1972; Healy 1978a; Hansen 1999; Hansen et al. 2008). Most notably, overharvest caused the collapse of the largest lake trout populations in the world, which existed in the Laurentian Great Lakes (Hansen 1999). The vulnerability of lake trout populations to overharvest is attributed to the species' slow growth and late age at sexual maturity (Healy 1978a). Overharvest of lake trout populations is likely to occur when total annual mortality exceeds 0.5 (Healy 1978a). However, the response of lake trout populations to exploitation is influenced by lake size, latitude, productivity, fish assemblage, and diet (Healy 1978a; Trippel 1993; Marshall 1996; Shuter et al. 1998).

The goal of the lake trout suppression program in Yellowstone Lake is to cause the lake trout population to decline (Bigelow et al. 2003). Lake trout removal began when gill netting was initiated in 1995 and gill-netting effort has increased through the duration of the program (Koel et al. 2005). However, analyses of catch per unit effort and population metrics indicate the population is increasing and an increase in fishing effort is required to cause the lake trout population to decline (Chapter 1).

Estimating the level of mortality needed to cause recruitment overfishing of the lake trout population in Yellowstone Lake requires integrating the population characteristics obtained in Chapter 1 into a population model. Matrix models provide a

method for integrating age- or stage- specific values of fecundity and survival to predict population growth rate (Caswell 2001), and have been used extensively to conduct population viability analyses (PVAs) for the conservation of wildlife species (Morris and Doak 2002). Simulation approaches allow for the incorporation of stochasticity and uncertainty in vital rate estimates to provide probabilistic estimates of a population growth trajectory (Morris and Doak 2002).

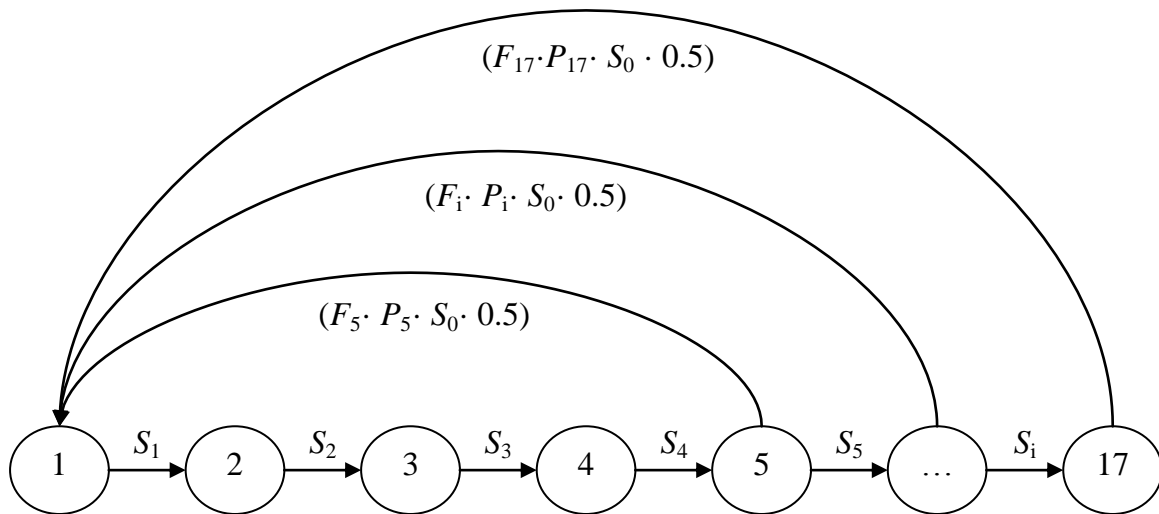
Unlike traditional applications of PVAs, the goal of this study was to determine the amount of harvest that will cause the lake trout population to collapse. Specifically, the objectives of this study were to use an age-structured matrix simulation model to i) estimate the rate of population growth (λ) given population characteristics obtained in Chapter 1 and ii) predict the level of mortality and fishing effort needed to cause recruitment overfishing.

Methods

Model Formulation

A female-based Leslie matrix was used to model the lake trout population. An age-structured model was selected because reproductive rates (i.e., fecundity and probability of maturity) increase with age. Age-specific vital rates were estimated for 2007, which was the most recent year with complete demographic data. The life cycle for female lake trout in Yellowstone Lake included ages 0-17 (Figure 2.1) because 17 was the maximum lake trout age observed in 2007. I assumed that females produced offspring at age 5, which is the minimum observed age of sexual maturity, and females spawned every year. A sex ratio of 1:1 was observed in distribution netting (see Chapter 1 for description of netting).

a)



b)

$$\begin{bmatrix} 0 & 0 & 0 & 0 & (F_5 \cdot P_5 \cdot S_0 \cdot 0.5) & \dots & (F_{17} \cdot P_{17} \cdot S_0 \cdot 0.5) \\ S_1 & & & & & & \\ & S_2 & & & & & \\ & & S_3 & & & & \\ & & & S_4 & & & \\ & & & & S_5 & & \\ & & & & & \dots & \\ & & & & & & S_{17} \end{bmatrix}$$

Figure 2.1. Life cycle diagram (a) and age-structured Leslie matrix (b) for lake trout in Yellowstone Lake, Yellowstone National Park. The symbols F_i , P_i , and S_i represent age-specific fecundity, probability of maturity, and survival.

The basic model was:

$$\mathbf{n}_{t+1} = \mathbf{A} \cdot \mathbf{n}_t,$$

where \mathbf{n}_t is a vector containing the abundance of females in each age-class at time t and \mathbf{A} is the projection matrix (Caswell 2001). Each time step is one year. The matrix \mathbf{A} consists of survival probabilities and fecundity rates (Figure 2.1). The age-specific

survival probabilities (S_i) are contained in the subdiagonal of the matrix. The age-specific fecundity rates (contained in the top row of \mathbf{A}) are the number of age-1 fish at time $t + 1$ per spawning female at time t . Age-specific fecundity per female was calculated as:

$$F_i \cdot P_i \cdot S_0 \cdot 0.5,$$

where F_i is the number of eggs produced and P_i is the probability of maturity for females age i . The matrix model included a pre-breeding census, which requires the fecundity term to include survival of age-0 fish (S_0) to be counted as age-1 fish the following year. Fecundity was multiplied by 0.5 to account for half of the offspring being female.

Model Parameterization

Fecundity. Length at age was used to predict age-specific values of fecundity (F_i) and probability of maturity (P_i). Length at age for females was determined using the von Bertalanffy growth model:

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

where L_t = length at time t , L_∞ = theoretical maximum length of lake trout in the population, K = growth coefficient, t = age, and t_0 = age when length theoretically equals 0 mm. Length-fecundity and length-maturity models (Table 2.1; Chapter 1) were used to predict the mean and standard deviation for F_i and P_i given length at age i .

Table 2.1. Equations used to predict length at age, fecundity at length, and probability of maturity at length for lake trout in 2007 in Yellowstone Lake, Yellowstone National Park (Chapter 1).

Predicted variable	Equation
Length at age	$\text{Length} = 793 \cdot (1 - e^{(-0.18(\text{Age}+0.46)}))$
Fecundity (F_i)	$F_i = -10,421 + 23.74 (\text{Length}_i)$
Probability of maturity (P_i)	$P_i = e^{-17.35+0.03(\text{Length}_i)} / 1 + e^{-17.35+0.03(\text{Length}_i)}$

Survival. Natural mortality was estimated as an instantaneous rate (M) and converted to annual survival rate for the matrix model with the equation: $S_i = e^{-M}$. Ages 2-17 were assumed to have a constant rate of natural mortality estimated with the formula provided by Pauly (1980):

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

where M is the instantaneous rate of natural mortality, L_{∞} and K are coefficients estimated from the von Bertalanffy growth equation, and T is mean annual environmental water temperature. Mean annual environmental water temperature was 5.1° C for Yellowstone Lake (Ruzycski 2003). Natural survival rates have not been estimated for age-0 and age-1 lake trout in Yellowstone Lake; therefore, I 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).

Fishing mortality was estimated from the catch curve regression model for distribution netting in 2007 (Chapter 1). Instantaneous fishing mortality (F) was estimated by partitioning total instantaneous mortality (Z) into natural (M) and fishing components with the equation: $Z = M + F$ (Miranda and Bettolli 2007). Instantaneous fishing and natural mortality rates were converted to annual fishing (m) and natural (n)

mortality rates with the equations: $m = 1 - e^{-F}$ and $n = 1 - e^{-M}$. 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). Total conditional interval mortality was used instead of total annual mortality because m and n occurred in the same interval and competed for the same fish (Miranda and Bettoli 2007). I assumed conditional interval fishing mortality affected lake trout ages 3 through 17. Age-2 lake trout were not fully vulnerable to the gear, thus fishing mortality was zero. This provides a conservative estimate of the level of fishing mortality required to decrease the lake trout population because some age-2 lake trout are caught.

Initial Population Vector. The starting population size was determined by dividing the number of lake trout harvested in 2007 by the observed m for a crude estimate of population abundance: $74,000 / 0.22 \approx 340,000$ fish. The observed sex ratio was 1:1. Therefore, the abundance estimate was multiplied by 0.5, resulting in 170,000 female lake trout. The 170,000 female lake trout were distributed among age classes based on the observed age frequency from the 2007 distribution netting (Chapter 1).

Management Scenarios

Conditional interval fishing mortality varied from 0 to 0.7 in increments of 0.05. The scenario with 0 fishing mortality represents population growth in the absence of m . Each level of m was maintained for 5, 10, and 20 years. In addition, a model with the observed m in 2007 was developed to determine the current population growth rate (λ). It is likely that juvenile survival in Yellowstone Lake is higher than values reported in

literature throughout their native range given predation is lower (Claramunt et al. 2005) and competition is minimal (Carl 2008). Therefore, additional management scenarios were simulated with survival of age-0 and age-1 lake trout doubled from the values reported in the literature (Shuter et al. 1998; Sitar et al. 1999).

Model Simulations

Each management scenario was simulated 1,000 times using R 2.9.2 (R Development Core Team 2009) to incorporate variation in vital rate estimates. The first step of each simulation run was to create a Leslie projection matrix replicate (\mathbf{A}_i ; Figure 2.1). Vital rates for the matrix were estimated from predicted values of age-specific survival, fecundity, and probabilities of maturity and associated standard deviations (Table 2.2). 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 stretch beta distributions, which have central tendencies and tails that are restricted to logical parameter values instead of approaching infinity (Morris and Doak 2002). Rates of survival and probabilities of maturity were generated from beta distributions, which have tails restricted between 0 and 1. Fecundity values were generated from stretched beta distributions, which have tails restricted to specified minimum and maximum values (Morris and Doak 2002). The minimum and maximum fecundity values used for the distribution were 300 and 15,000 eggs. Each matrix replicate (\mathbf{A}_i) was iterated with the population vector (\mathbf{n}_t) for 5, 10, or 20 years. The abundance at each time step (\mathbf{N}_t) and λ_t

Table 2.2. 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-specific vital rates are survival (S_i), fecundity (F_i), and probability of maturity (P_i). Survival rates and standard deviations displayed for ages 2-17 in 2007 were computed using catch curve regression. Mean total length (mm) at age was predicted from the von Bertalanffy growth curve for females. Values of fecundity and probabilities of maturity were estimated from mean length at age with length-fecundity and length-maturity relationships.

Age	S_i in absence of fishing mortality		Total length (mm)	F_i	P_i
	S_i in 2007				
0	0.0043 ^a	-	22	0	0
1	0.449 ^b	-	145	0	0
2	0.898	-	249	0	0
3	0.898	0.7(0.12)	335	0	0
4	0.898	0.7(0.12)	407	0	0
5	0.898	0.7(0.12)	468	689(292)	0.040(0.044)
6	0.898	0.7(0.12)	519	1899(224)	0.165(0.091)
7	0.898	0.7(0.12)	561	2896(179)	0.413(0.147)
8	0.898	0.7(0.12)	597	3751(153)	0.677(0.192)
9	0.898	0.7(0.12)	627	4463(148)	0.839(0.162)
10	0.898	0.7(0.12)	652	5057(155)	0.917(0.113)
11	0.898	0.7(0.12)	673	5555(168)	0.954(0.053)
12	0.898	0.7(0.12)	690	5959(183)	0.973(0.053)
13	0.898	0.7(0.12)	705	6315(199)	0.982(0.037)
14	0.898	0.7(0.12)	717	6600(213)	0.988(0.028)
15	0.898	0.7(0.12)	728	6861(226)	0.991(0.022)
16	0.898	0.7(0.12)	736	7051(236)	0.993(0.017)
17	0	0	743	7217(245)	0.994(0.014)

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

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

at each time step was computed: $\lambda_t = N_t/N_{t-1}$. Mean λ_t and final population abundance were computed for each simulation.

Summary Statistics

The geometric mean was used as the summary statistic for mean λ_t s and final abundances because the values are typically log-normally distributed (Morris and Doak 2002). Geometric mean λ and percent reduction in population size were examined as

functions of m for the 5-, 10-, and 20-year time frames. The rate of mortality at which λ was equal to one was noted as the rate of mortality at which λ was at replacement. The population would decline from recruitment overfishing if mortality increased beyond the rate that caused replacement. Annual estimates of m from Chapter 1 were regressed as a function of annual gill-netting effort (sum of 100-m net nights) to develop a model for predicting the amount of effort that would cause desired rates of mortality in the future.

Results

In the absence of fishing mortality, the 20-year estimate of λ was 1.31 when juvenile survival was equal to literature values and 1.54 when juvenile survival was double literature values. The rate of m in 2007 was 0.22. Estimates of geometric mean λ at $m = 0.22$ were 1.20 for the 5-year time frame, 1.14 for the 10-year time frame, and 1.10 for the 20-year time frame for the scenario with juvenile survival equal to literature values (Figure 2.2). When juvenile survival was double literature values, geometric mean λ at $m = 0.22$ increased to 1.59 for the 5-year time frame, 1.39 for the 10-year time frame, and 1.32 for the 20-year time frame (Figure 2.2).

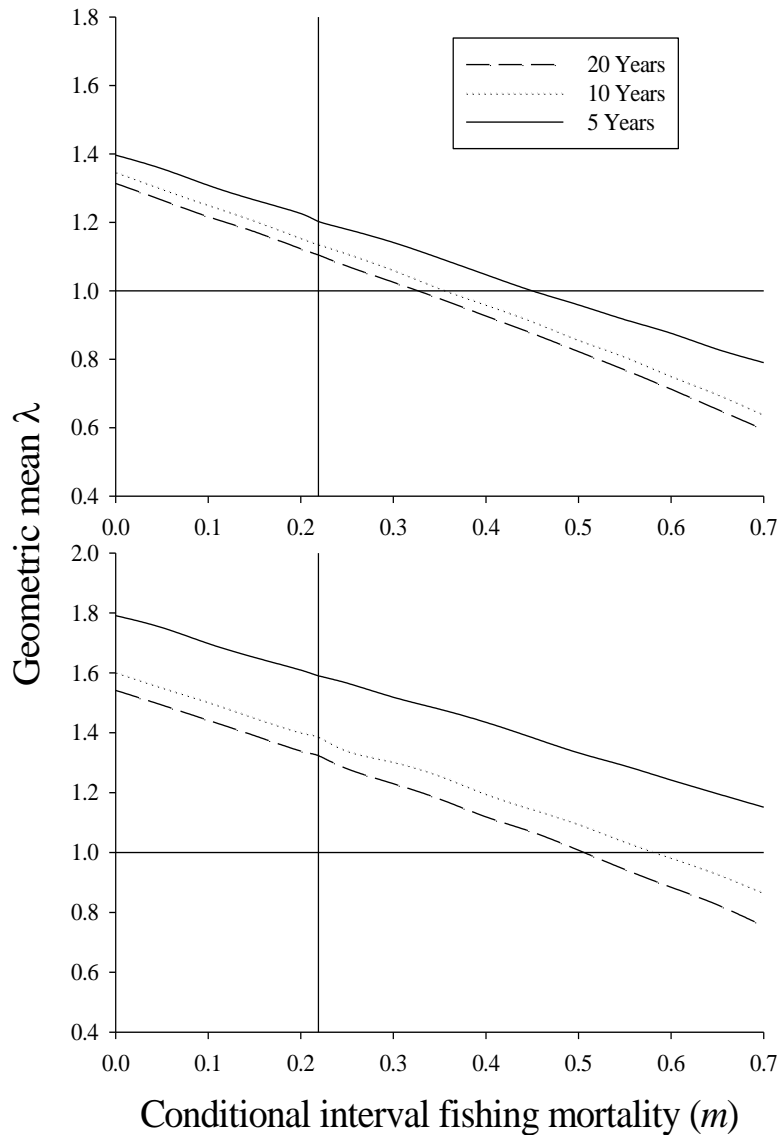


Figure 2.2. Geometric mean λ at given levels of conditional interval fishing mortality (m) over 5-, 10-, and 20-year time frames for lake trout in Yellowstone Lake, Yellowstone National Park. The top panel shows simulated population growth rates with estimates of juvenile survival equal to literature values from the native range of lake trout. The bottom panel shows population growth rates when literature estimates of juvenile survival are doubled. The horizontal reference line indicates λ equal to one (replacement). The vertical reference line indicates the level of m observed in 2007.

Population growth rate was reduced to one when m was 0.32 ($A=0.39$) over a 20-year time frame when juvenile survival rates were equal to literature values. However,

rates of m that caused λ to equal one increased by 1.5-2 times when juvenile survival rates were doubled (Table 2.3).

Table 2.3. Estimates of conditional interval fishing mortality (m) and corresponding values of total interval mortality rate (A) resulting in λ equal to one over three timeframe scenarios for lake trout in Yellowstone Lake, Yellowstone National Park. Estimates of m and A are displayed for the scenario where juvenile survival equals literature values and the scenario where juvenile survival is double literature values.

Juvenile S_i scenario	Time frame (years)	m	A
Literature values	5	0.46	0.51
	10	0.35	0.42
	20	0.32	0.39
Double	5	0.87	0.88
	10	0.58	0.63
	20	0.50	0.55

Rates of m were more effective at reducing λ when maintained for longer time frames (Figure 2.2). Similarly, the percent reduction in population size at a given value of m was greater for longer time frames (Figure 2.3). For example, a rate of m equal to 0.4 reduced initial lake trout abundance by 23% when m was maintained for 5 years and 86% when m was maintained for 20 years, assuming juvenile survival was equal to literature values.

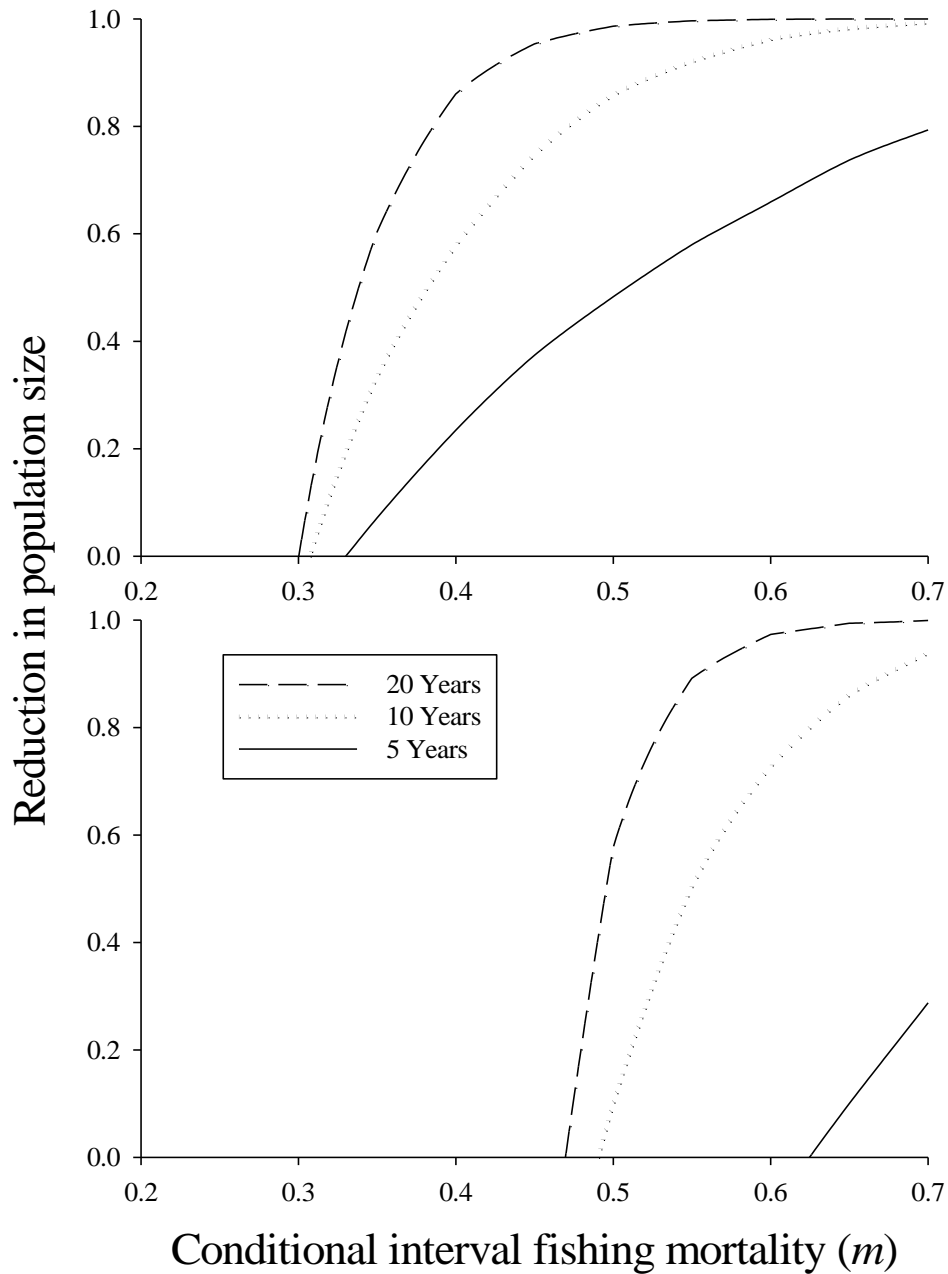


Figure 2.3. Proportion reduction in population size given levels of conditional interval fishing mortality (m) for lake trout in Yellowstone Lake, Yellowstone National Park. Levels of m varied from 0 to 0.7 in increments of 0.05 and were maintained for 5-, 10-, and 20- year time frames. The top panel displays population reductions with estimates of juvenile survival equal to literature values from the native range of lake trout. The bottom panel displays population reductions with literature estimates of juvenile survival doubled. The population was not reduced when m was less than 0.30 (top panel) or 0.46 (bottom panel).

Conditional interval fishing mortality increased as a function of annual fishing effort (Figure 2.4). Fishing effort needs to increase to 56,666 100-m net nights to cause m to equal 0.32, which would cause λ to decline to one over a 20-year time frame if juvenile survival is assumed to equal literature values. If juvenile survival is double literature values, annual fishing effort would have to increase to 110,000 100-m net nights to cause λ to decline to one over a 20-year time frame. These increases in fishing effort are 2.0 and 3.9 times the amount of total annual fishing effort in 2007. The increase in fishing effort required to decrease λ to one is greater over shorter time frames.

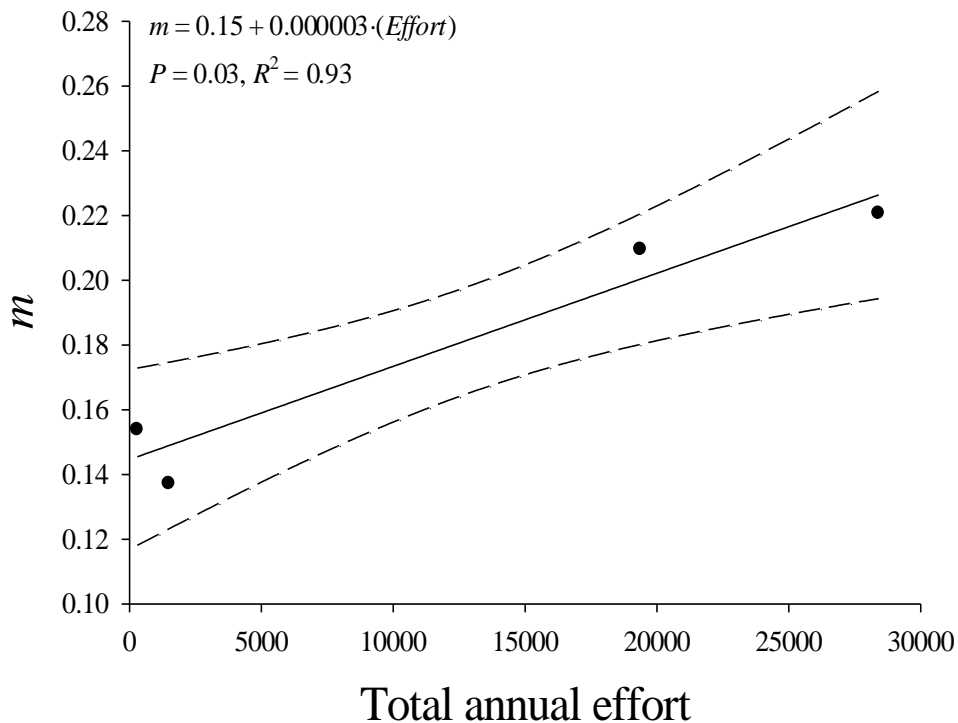


Figure 2.4. Annual estimates of conditional interval fishing mortality (m) as a function of total annual effort (sum of 100-m net nights) for lake trout in Yellowstone Lake, Yellowstone National Park. Annual values of m were estimated from catch curve regressions for distribution netting (Chapter 1) and an estimate of natural mortality from a meta-analysis (Pauly 1980). Dashed lines delineate the 95% confidence interval.

Discussion

The rate of population growth was greater than one for both juvenile survival scenarios at the level of m observed in 2007. Although the population is increasing, the suppression program reduced the rate of increase. At λ observed in the absence of fishing mortality the population would double every 2.5 years whereas doubling would occur every 7.3 years at the level of m estimated for 2007. The positive rate of population growth estimated from model simulations corroborates catch and effort results from Chapter 1, which indicated an increase in lake trout abundance.

The Leslie matrix model indicated a definitive increase in lake trout abundance; however, more accurate estimates of the level of fishing mortality required to cause a decline in the population could be provided with additional data and more realistic modeling approaches. Model results were sensitive to changes in survival rates for age-0 and age-1 lake trout, which were obtained from the literature. Additionally, high sensitivity of λ to age-0 survival occurred in matrix models for lake trout populations in Lake Superior (Ferreri et al. 1995). Further investigation is needed to determine juvenile survival rates or stock-recruitment relationships for lake trout in Yellowstone Lake. A more realistic modeling approach would incorporate density dependence, which is likely to reduce λ at high lake trout abundance. Survival of age-0 lake trout is negatively related to adult density in Lake Superior (Ferreri et al. 1995). In Yellowstone Lake, an increase in the number of spawning adults may reduce age-0 survival and cause λ to decrease. 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 cause population characteristics to shift towards higher growth, earlier ages at maturity, and higher fecundity rates (Chapter 1) and λ to increase. The evaluation of age-specific contributions to λ (i.e., sensitivity and elasticity analyses) could improve the efficiency of the suppression program by indicating which age classes could be targeted for the greatest decline in λ (Caswell 2001; Fefferman and Reed 2006). More realistic models will be developed to estimate age-specific contributions to λ within a simulation framework that includes varying levels of density dependence.

A total annual mortality of 0.5 has been hypothesized as the level which causes overharvest in lake trout populations within their native range (Healy 1978a); however, the duration of harvest was not considered. The rate of total annual mortality that would cause recruitment overfishing over a 20-year time frame was between 0.39 and 0.5 in Yellowstone Lake, depending on which juvenile survival scenario was used. The rate of total annual mortality required to cause a decline in lake trout abundance in Yellowstone Lake increased when mortality was maintained for shorter time frames. Similarly, simulations evaluating the potential for removal of a northern pikeminnow *Ptychocheilus oregonensis* population indicated that the time required to reduce the population declined with increasing levels of exploitation (Rieman and Beamesderfer 1990).

The level of 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 0.45-0.50 (Hansen 2007). 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 ($A=0.44-0.49$; Dux 2005). Similarly, an exploitation rate of 0.44 ($A=0.51$) resulting from gill netting in Swan Lake, Montana, caused a decrease in the abundance of introduced lake trout (B. Cox, Montana State University, unpublished data). The above studies support the assertion that lake trout populations are likely to decline when A is near 0.5 (Healy 1978b).

Fishing intensity must increase to reduce the lake trout population in Yellowstone Lake. For example, if NPS desired to decrease abundance by 50% a minimum conditional interval fishing mortality rate of 0.38 would have to be maintained for 10 years. A 2.7-fold increase in gill-netting effort must be sustained to keep conditional interval fishing mortality at 0.38, assuming the observed relationship between effort and mortality is linear at levels of fishing effort higher than observed in 2007.

The use of multiple removal techniques may lead to a higher rate of lake trout mortality. For example, modeling indicated that lake trout suppression would be effective in Lake Pend Oreille if a combination of trap netting, gill netting, and angler incentives were used, but would be far less effective if any of these methods were used alone (Hansen 2007). Fishing effort needs to increase more than two-fold in Yellowstone Lake if gill nets are the only gear used in the future. Therefore, the possibility for implementing trap netting should be investigated. Increases in lake trout harvest may also be possible by hiring commercial contract fishers. Radio telemetry and habitat mapping (Bigelow 2009) may be useful for identifying additional lake trout spawning areas. Spawning areas have the highest catch per unit effort (P. E. Bigelow, personal

communication) and could be targeted with gill nets to increase mortality of spawning adults and reduce recruitment. Methods for interrupting spawning, reducing embryo survival, and genetic techniques for reducing fitness should be investigated, as these management practices are being applied for controlling other invasive fishes (Kapuscinski and Patronski 2005; Wagner et al. 2006; Thresher 2008; Bohl et al. 2010).

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APPENDICES

APPENDIX A

POPULATION METRICS BY YEAR

Table A.1. Median and mean (in parentheses) length and age by netting method by year for lake trout in Yellowstone Lake, Yellowstone National Park. Netting methods are distribution (D), control (C), and spawner (S, see Chapter 1 for description of netting methods).

Year	Netting method					
	D	C	S	D	C	S
	Median Length (Mean)			Median Age (Mean)		
1997	315 (373)			4 (4.7)		
1998	355 (386)	320 (325)	615 (618)	4 (4.6)	4 (3.8)	8 (9.9)
1999	285 (300)	305 (314)	595 (606)	2 (2.5)	2 (3.1)	7 (6.9)
2000	395 (416)	320 (321)		4 (4.5)	3 (3.1)	
2001		335 (333)			4 (4.4)	
2002	380 (367)	320 (320)		4 (3.7)	3 (3.3)	
2003	415 (404)	305 (309)		5 (4.6)	3 (3.1)	
2004	400 (414)	305 (307)		5 (5.1)	3 (3.1)	
2005	258 (324)	300 (304)	570 (575)	2 (3.4)	3 (2.7)	8 (8.0)
2006		305 (306)	565 (578)		3 (2.9)	8 (8.5)
2007	308 (343)	295 (299)	575 (582)	3 (3.9)	3 (2.8)	8 (8.4)

Table A.2. Total annual mortality (A), 95% confidence interval for A , and ages included for catch curve mortality estimates by netting type by year for lake trout in Yellowstone Lake, Yellowstone National Park (see Chapter 1 for description of netting methods).

Year	Netting method					
	Distribution		Control		Spawner	
	A (95% CI)	Ages	A (95% CI)	Ages	A (95% CI)	Ages
1997	0.24 (0.18-0.35)	2-15				
1998	0.23 (0.06-0.37)	3-8	0.75 (0.00-0.96) ^a	4-7		
1999			0.33 (0.00-0.68)	3-6	0.59 (0.00-0.63)	6-11
2000			0.51 (0.09-0.73)	3-6		
2001			0.65 (0.37-0.81) ^a	4-7		
2002			0.58 (0.46-0.67)	3-6		
2003			0.49 (0.08-0.72) ^a	3-7		
2004			0.49 (0.16-0.69)	3-6		
2005	0.29 (0.13-0.35)	2-9	0.67 (0.00-0.90)	3-6	0.35 (0.00-0.99)	10-14
2006			0.69 (0.54-0.79)	3-6	0.46 (0.23-0.62)	10-16
2007	0.30 (0.25-0.32)	2-12	0.56 (0.39-0.69)	3-6	0.43 (0.33-0.52)	10-17

^aMortality estimates were excluded from regression of A as a function of cumulative fishing effort.

Table A.3. Parameters ω and L_{∞} from von Bertalanffy growth models by year for lake trout in Yellowstone Lake, Yellowstone National Park. Males and females were pooled for model estimation.

Year	ω	L_{∞}
1996	120	863
2000	156	858
2002	157	723
2003	133	887
2004	127	826
2005	151	719
2006	140	741
2007	140	768

Table A.4. Median relative weight values for age 2-4 lake trout by season and year in Yellowstone Lake, Yellowstone National Park.

Age	Season	Year						
		1996	1997	1998	1999	2000	2005	2007
2	Late	109	108	109	107	112	128	118
3	Early	116	108	119	116	121		122
	Late	104	106	110	99	111		113
4	Late		96	112	104	116	113	112

Table A.5. Median relative weight values for age 5-11 lake trout by season and year in Yellowstone Lake, Yellowstone National Park.

Age	Sex	Year					
		1996	1997	1998	1999	2000	2007
5	M	96	99	104	93	110	108
6	M	104	103	99	98	96	106
7	M	112	102	100	98	103	99
	F	109	111	106	102	104	106
8	M	110	105	102	102	107	103
	F	117	111	104	107	110	108
9	M	114	104	98	102	106	106
	F	114	108	109	106	110	112
10	F	120	111	109	106		109
11	F	114	111	106	108		112

Table A.6. Mean length at age for lake trout ages 5-11 by season and year in Yellowstone Lake, Yellowstone National Park.

Age	Season	Year								
		1998	2000	2001	2002	2003	2004	2005	2006	2007
2	Early		299		296			272	279	252
3	Early		334	319	330	307		338	314	314
4	Early		382	356	354	345		384	340	365
	Late	371		305		422	380	383	388	450
5	Late	462		381	528	472	425	456	453	473
6	Late	484		444	556	534	477	504	508	528
7	Late	541			557	574	541	575	553	553
8	Late	593			606	614	583	597	556	545
9	Late				621	659	616	605	597	657
10	Late				663	702	664	637	609	553
11	Late					748	726	610	643	653
12	Late					758	717	644	679	540

Table A.7. Length (L_{m50}) and age (A_{m50}) at 50% maturity for males (M) and females (F) by year for lake trout in Yellowstone Lake, Yellowstone National Park.

Year	Sex			
	M		F	
	L_{m50}		A_{m50}	
1997	481	655	5.9	10.3
2003	445	481	4.6	5.2
2004	426	487	4.7	5.8
2005	428	525	4.3	6.2
2007	422	541	4.4	6.7

APPENDIX B

COMPARISON OF LAKE TROUT POPULATION METRICS IN
YELLOWSTONE LAKE TO POPULATIONS THOUGHOUT NORTH
AMERICA

Table B.1. Biomass of lake trout harvested from the West Thumb Basin (WT) and Main Basin (MB) of Yellowstone Lake in 2007 compared to several lakes in North America.

Lake	Area (ha)	Harvest (kg/ha)	Result	Source
Yellowstone - WT	4,258	3.6		
Athapuskow	25,413	0.85	stable	Martin and Olver 1980
Nipigon	448,260	0.62	decline	Martin and Olver 1980
Michigan	5,800,000	0.58	decline	Healy 1978a
La Ronge	142,452	0.45	stable	Martin and Olver 1980
Huron	5,960,000	0.43	decline	Martin and Olver 1980
Great Slave	2,700,000	0.37-0.67	decline	Healy 1978
Yellowstone - MB	29,850	0.33		
Opeongo	5,860	0.33	stable	Martin and Olver 1980
Superior	8,240,000	0.24	decline	Martin and Olver 1980

Table B.2. Mean length at age (nearest cm) for lake trout in Yellowstone Lake in 2007 compared to several lake trout populations in North America.

Lake	Age												Source
	1	2	3	4	5	6	7	8	9	10	11	12	
Opeongo		20	24	28	34	37	44	50	55	58	62	66	Martin and Olver 1980
Little Bear		20	28	34	39	44	48	53	57	61	64	68	Healy 1978a
Superior	10	16	22	29	36	43	52	60	69	78	87		Martin and Olver 1980
Michigan	18	25	33	41	48	55	61	67	73				Martin and Olver 1980
Great Slave					41	37	48	49	49	51	54	55	Martin and Olver 1980
La Ronge		27	38	43	51	54	59	61	64	66	69	71	Martin and Olver 1980
Great Bear							38	39	27	50	41	51	Martin and Olver 1980
Hottah	20	26	31	44	48	53	56	58	60	62	65	68	Healy 1978a
Yellowstone	20	25	31	39	44	53	57	59	63	63	66	67	

Table B.3. Age and length at 50% maturity for female and male lake trout in Yellowstone Lake in 2007 compared to several lake trout populations in North America.

Lake	Age		Length		Source
	Female	Male	Female	Male	
Hottah	5		504		Healy 1978a
Michigan	5.5-7.4	4.3-6.3	628-654	563-600	Madenjian et al. 1998
Swan (Canada)	6		519		Healy 1978a
Yellowstone	6.7	4.4	541	422	
La Ronge	7		607		Healy 1978a
Pend Orielle	7.3	6.5	673	632	Hansen 2007
Opeongo	7-8		496-542		Healy 1978a
Great Slave	7-10		488-542		Healy 1978a
Superior	8		715		Healy 1978a
Flathead	11		580		CSKT and MFWP 2006
McDonald	15	12	555	473	Dux 2005
Great Bear	14-15		528-607		Healy 1978a

Table B.4. Fecundity for a 600 mm lake trout in Yellowstone Lake in 2007 compared to several lake trout populations in North America.

Lake	Fecundity	Source
Superior	1,537	Peck 1988
Greenwich	1,828	Trippel 1993
Little Joe	2,871	Trippel 1993
Loch Erne	3,013	Trippel 1993
Islets	3,014	Trippel 1993
South Otterskin	3,054	Trippel 1993
Burnt Island	3,210	Trippel 1993
Yellowstone	3,799	

Table B.5. Total annual mortality for lake trout in Yellowstone Lake in 2007 compared to several lake trout populations in North America.

Lake	Total annual mortality	Ages	Source
Pend Orielle	0.58		Hansen 2007
Opeongo	0.48-0.56	8 to 9	Healy 1978a
Superior ^a	0.50	10 to 16	Healy 1978a
Michigan ^a	0.50		Healy 1978a
Swan (CAN)	0.49	5 to 11	Healy 1978a
Hottah	0.32	10 to 23	Healy 1978a
Great Slave-East	0.30	11 to 22	Healy 1978a
La Ronge	0.28-0.32	8 to 16	Healy 1978a
Yellowstone	0.30	2 to 12	
Manitou	0.25	7 to 16	Healy 1978a
Great Slave-West	0.23	9 to 21	Healy 1978a
McDonald	0.13	8 to 27	Dux 2005

^aTotal annual mortality in the presence of sea lamprey.