ASSESSMENT OF AN INVASIVE LAKE TROUT POPULATION IN SWAN LAKE, MONTANA

by

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APPROVAL

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

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STATEMENT OF PERMISSION TO USE

DEDICATION

I dedicate this thesis to my family, and thank them for supporting me in most of my wildest dreams. I would also like to dedicate this thesis to my beloved friends and colleagues at Montana State University and the Swan Valley Bull Trout Working Group. Without them, this research would not have been possible.

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ABSTRACT

The recent invasion of lake trout into the Swan River drainage in Northwest Montana threatens one of the last remaining recreational bull trout fisheries in the USA. An inter-agency group is implementing an experimental lake trout suppression program on Swan Lake. The objectives of this study were to establish a baseline data set on the lake trout population in Swan Lake concurrently with the experimental removal effort, simulate alternative management scenarios using matrix models and identify spawning locations of lake trout to target adult fish and embryos. A commercial gill-net sampling effort provided data to estimate abundance, size structure, age structure, growth, condition, maturity, fecundity, and mortality of lake trout in Swan Lake. Lake trout in Swan Lake grew rapidly, attained large sizes, and were in high condition. The size and age structure of lake trout sampled was skewed towards juvenile lake trout, indicating the population was growing rapidly. Matrix-model simulations also indicated the lake trout population would continue to grow with no suppression efforts, but suppression efforts could reduce the population growth rate. Population growth was particularly sensitive to changes in age-0 survival in population models. Elasticity analysis of matrix simulations indicated survival from birth to sexual maturity, followed by survival of adult fish contributed most to population growth. Lake trout spawning locations were identified using ultrasonic telemetry, short-set gill nets, and in-situ egg nets. Spawning locations identified with acoustic telemetry were confirmed by capturing gravid lake trout in gill nets and lake trout eggs in the substrate. These results suggest that the inter-agency group should focus removal efforts on sub-adult and adult lake trout at if extirpation of the population is the goal. Given the uncertainty in the vital rates and the potential bias in exploitation rates used to model suppression scenarios, annual suppression efforts should be increased from the 2008 level to ensure a decline in the lake trout population.

CHAPTER 1

POPULATION CHARACTERISTICS AND MODEL MANAGEMENT SCENARIOS OF INVASIVE LAKE TROUT IN SWAN LAKE, MONTANA

Introduction

Nonnative species (introduced and invasive) are the second leading cause of anthropogenic environmental change and biodiversity loss worldwide (Vitousek et al. 1997; Wilcove et al. 1998). Forty-two percent of threatened or endangered species in the USA are at risk because of nonnative species (Wilcove et al. 1998), and 68% of fish extinctions in the USA have been attributed in part to negative interactions with nonnative species (Miller et al. 1989). Aquatic ecosystems in the USA have also become more similar due to the introduction of popular fish species to enhance subsistence and sport fisheries (Rahel 2000). Most biological introductions have little effect on recipient ecosystems and only a few introduced species have negative impacts (Gozlan 2008). In some cases, introductions can be beneficial to biodiversity (Gozlan 2008). However, when introduced species cause the extirpation of regional biota, biotic homogenization and biodiversity loss occur simultaneously (Rahel 2002). The evolutionary consequences of global biotic homogenization and biodiversity loss remain uncertain (Olden et al. 2004).

Lake trout *Salvelinus namaycush* have had detrimental effects on native fishes where they have been introduced in the western USA (Martinez et al. 2009). Lake trout were widely distributed outside their native range beginning in the late 19th century (Crossman 1995). At this time, the intentional introduction of fish species was viewed as

beneficial to society (Rahel 1997). Lake trout are well adapted for deep oligotrophic lakes in the western USA and were a desirable sport fish because of their propensity to grow to trophy sizes (Crossman 1995; Martinez et al. 2009). Lake trout are problematic as both predators and competitors of native species (Martinez et al. 2009). Introduced lake trout have altered linkages between terrestrial and aquatic food webs where they have reduced populations of migratory fish species including kokanee salmon *Oncorhynchus nerka* (Spencer et al. 1991) and Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (Koel et al. 2005).

In 1998, bull trout *Salvelinus confluentus* in the upper Columbia and Klamath River basins were listed as threatened under the U.S. Endangered Species Act (USFWS 1998). After habitat loss and degradation, introduced species represent the greatest threat to bull trout in the upper Columbia River basin (Leary et al. 1993; USFWS 1998). The US Fish and Wildlife Service identified two "stronghold" bull trout populations in the upper Columbia River Basin (USFWS 1998). These strongholds, Hungry Horse Reservoir and Swan Lake, occur within the Flathead River system in northwest Montana. Swan Lake and Hungry Horse Reservoir support two of the last recreational fisheries in the USA where anglers can legally harvest bull trout. Bull trout populations have consistently been displaced by lake trout in the Intermountain West (Donald and Alger 1993; Fredenberg 2002), especially where introduced opossum shrimp *Mysis relicta* have given lake trout an ecological advantage (Bowles et al. 1991; Spencer et al. 1991; Stafford et al. 2002). Lake trout were first introduced into Flathead Lake in 1905 and subsequently colonized lakes throughout the Flathead River system (Spencer et al. 1991; Fredenberg 2002). Lake trout were discovered in the Swan River drainage in 1998. In

2003, Montana Fish, Wildlife and Parks (MTFWP) recorded the first juvenile lake trout in annual gill net sampling (L.R. Rosenthal, MTFWP, unpublished data). To date, bull trout and kokanee redd counts in the Swan River drainage have been stable.

Management agencies of the Swan Valley Bull Trout Working Group (SVBTWG) are implementing an experimental lake trout suppression program to conserve the bull trout population in Swan Lake. Suppressing an invasive lake trout population in a relatively small freshwater lake should be feasible, given that overexploitation has precipitated the collapse of fisheries in marine systems and the Great Lakes (Hansen 1999; Hutchings 2000). In Lake Superior, lake trout populations were in decline from overexploitation prior to the introduction of sea lamprey (Hansen 1999; Wilberg 2004). The collapse of the lake trout population in Lake Erie was related exclusively to exploitation because sea lamprey never became abundant (Hartman 1972). Lake trout exhibit a relatively long lived, late maturing life-history strategy (Healey 1978a; Martin and Olver 1980) that makes populations vulnerable to overharvest (Musick 1999).

The objectives of this study were to gather baseline biological information on an invasive lake trout population in Swan Lake concurrently with an experimental suppression program and model potential management scenarios using the biological data gathered in this study. Population characteristics including abundance, size and age structure, growth, condition, maturity, and fecundity were quantified. Abundance estimates will allow biologists to estimate exploitation from suppression efforts and track changes in lake trout abundance through time. Lake trout populations have exhibited compensatory responses in growth, maturation, and fecundity as a function of changes in

density (Healy 1978a, 1978b; Ferreri and Taylor 1996; Sitar and He 2006). Monitoring these biological metrics will provide alternative analyses to corroborate trends in abundance and evaluate the efficacy of suppression efforts. It is likely the lake trout population in Swan Lake is still growing; therefore, somatic growth, condition, size at maturity, and age-specific fecundity should be high when compared with other lake trout populations.

Age-stage structured matrices were used to model population growth for "no suppression" and "suppression" scenarios. Sensitivity-elasticity analyses were used to determine the relative contribution of each age class to population growth and identify age or stage classes on which to focus suppression efforts (Caswell 2001; Benton and Grant 1999). I predict the population will continue to grow towards carrying capacity with no suppression efforts, but if exploitation on Swan Lake approaches 50%, the population will be overharvested (Healey 1978a; Hansen 2008).

Study Area

Swan Lake (47.9628° N, 113.9033° W) is a glacially formed lake in the Flathead drainage in northwest Montana at an elevation of 940 m with a surface area of 1,335 ha (Figure 1.1). The Swan River is the primary tributary and outlet of the lake, entering in the southwest and exiting to the north. The Swan River flows 22 km out of Swan Lake, entering Flathead Lake in the town of Bigfork. In 1902, the Swan River was dammed approximately 1.6 km upstream of the confluence with Flathead Lake (Baxter et al. 1999).

A fish ladder was constructed around Bigfork Dam in the 1950s. Lake trout would have had access to Swan Lake by migrating upstream from Flathead Lake until the fish ladder at Bigfork Dam was removed in 1992. It is uncertain whether lake trout populated Swan Lake by illegal introduction(s) or by natural colonization events. Two lakes in the upper Swan River drainage approximately 50 km upstream from Swan Lake, Holland Lake and Lindbergh Lake, also contain bull trout populations. Lake trout were discovered in Lindbergh Lake in 2009 by MTFWP (L.R. Rosenthal, unpublished data).

The morphometry of Swan Lake is characterized by two deep (>30m) basins at the north and south ends and a shallower mid-lake section (Figure 1.2). Mean depth is 16 m and maximum depth is 43 m. Bottom substrate is dominated by fine sand and silt in depositional zones, with several reefs consisting of larger substrates scattered throughout the lake, particularly in the mid-lake region. Shoreline substrate is dominated by glacial till, with a section of large angular cobble and boulders along Montana Highway 83 on the southeast edge of the lake.

Dissolved nutrient levels (TDS=112 mg/l) in Swan Lake are relatively high among lakes containing lake trout populations (Shuter et al. 1998; McDermid et al. 2010). Swan Lake is dimictic and stratifies during summer months, with the thermocline at approximately 18 m in late summer. Hypolimnetic oxygen deficiencies have been recorded in the deep basins with the highest deficits (e.g., <0.1% O_2 saturation) in the south basin (Butler et al. 1995). Oxygen deficiencies in the hypolimnion are attributed to nutrient inputs from the Swan River from historical logging and road construction within the drainage (Butler et al. 1995).

Swan Lake contains a diverse fish assemblage with several native and nonnative species. Native fish species include westslope cutthroat trout *Oncorhynchus clarkii lewisi*, bull trout, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coulterii*, northern pikeminnow *Ptychocheilus oregonensis*, peamouth *Mylocheilus caurinus*, redside shiner *Richardsonius balteatus*, longnose sucker *Catostomus catostomus*, largescale sucker *Catostomus macrocheilus*, and slimy sculpin *Cottus cognatus*. Introduced species include lake trout, kokanee, rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis*, northern pike *Esox lucius*, brook stickleback *Culaea inconstans*, and central mudminnow *Umbra limi*. Introduced *M. relicta* are also part of the food web in Swan Lake.

Methods

A stratified random sampling design was developed to sample the lake trout population in 2007 and 2008. The sampling stratum was designated as all of the lake at or below thermocline depth (~18 m), where lake trout were expected to occur during lake stratification (Figure 1.2; Martin and Olver 1980). Sampling occurred from 19 September to 4 October in 2007 and from 9 September to 25 September in 2008. Professional harvest consultants from Harbor Fisheries (Bailey's Harbor, Wisconsin) were contracted to deploy sampling gears in 2007 and 2008. Random starting locations for net sets were generated in a polygon of the lake area deeper than 18 m using Hawth's Analysis Tools in ArcGIS 9.2 (Beyer 2004; ESRI 2006). The gang was set from a

random starting location within the sampling stratum during morning and evening crepuscular hours in 2007 and 2008.

Three 91.4 m-panels of 2.5, 3.2, 3.8, 4.5, and 5.1-cm bar mesh sinking monofilament gill net were combined to form a 1,371 m-long gang in 2007. In 2008, the length of the gang was doubled, and an additional six 91.4-m panels of 1.9-cm bar mesh were added, forming a gang 3,290 m long. The gang fished for an average of 2.4 h per set in 2007 and 3.5 h per set in 2008. Short sets were conducted to minimize bycatch mortality of bull trout.

In 2007, two deep-water trap nets were deployed in the northern and southern portions of the sampling stratum (see Peterson and Maiolie [2005] for trap net diagram). Trap-net leads were 274.3-m long by 9.1-m deep with a 9.1-m^3 box at the cod end. The trap nets fished for 23 nights, but captured only 40 lake trout. Trap nets were not deployed in 2008.

All lake trout captured were measured to the nearest millimeter (TL). Size structure of the lake trout population was described using relative length-frequency histograms. The mesh size in which each fish was captured was recorded to model selectivity of the gill nets used. Gill-net selectivity curves were modeled using the SELECT program in R (Millar and Holst 1997; Millar 2000; R Core Development team 2009). The log-normal distribution produced the lowest model deviance among the four distributions available in program SELECT. Log-normal relative selectivity curves were estimated for each mesh size in the gang. An overall relative selectivity curve for the entire gang was calculated by summing individual mesh size selectivity curves and

scaling the peak to one. Selectivity curves were modeled to examine the size distribution of fish captured in each mesh size and determine the overall range of fish being sampled.

A mark-recapture study was conducted to estimate lake trout abundance in 2007; but extremely low recapture numbers precluded a reliable abundance estimate. Thus, a depletion method was used to estimate lake trout abundance in Swan Lake in 2008. Three five-day sampling periods were conducted from 9 September to 25 September in 2008. The gill-net gang was set twice daily within each sampling period. Effort in each sampling period consisted of ten sets of the gill-net gang. The lake trout population was assumed to be closed during sampling. All lake trout captured were euthanized and enumerated.

Depletion estimates for fish fully recruited to the sampling gear in 2008 were calculated using a conditional maximum likelihood approach in program MARK (Huggins 1989, 1991; Alho 1990; White and Burnham 1999; White 2008). The conditional likelihood approach allowed for the use of individual covariates in models of capture probability *p* (Huggins 1989). Depletion estimates were behavioral models (M_b) with recapture probability (*c*) fixed at zero (Otis et al. 1978; Lukacs 2009). Differences in diet and sexual maturity among lake trout could have influenced movement behavior and therefore capture probability. Diet analyses indicated that lake trout in Swan Lake up to approximately 450 mm fed almost exclusively on *M. relicta* and fish greater than 450 mm were piscivorous (C.S. Guy, Montana State University, unpublished data). Approximately 95% of lake trout captured larger than 700 mm were sexually mature. Thus, lake trout encounter histories were grouped into three ontogenetic stages delineated by length: 1) sexually immature fish feeding on *M. relicta* (270-449 mm); 2) sexually

immature, piscivorous fish (450-699 mm); and 3) sexually mature, piscivorous fish ($\geq$ 700 mm).

Capture probabilities were modeled with linear logistic models (Huggins 1989, 1991; Huggins and Yip 1997). Group effects (betas) based on diet (β_{mys} or β_{pisc}), maturity (β_{imm} , β_{mat}), and diet-maturity ($\beta_{imm\text{-}mys}$, $\beta_{imm\text{-}pisc}$, $\beta_{mat\text{-}pisc}$) were used to model capture probability differently by ontogenetic stage (Table 1.1). Total length was used as an individual covariate to model capture probability because gill net selectivity could influence capture probability continuously as a function of length. Continuous length effects were also modeled for maturity, diet, and maturity-diet groupings (e.g., $\beta_{length(imm)}$, $\beta_{length(pisc)}$, $\beta_{length(imm\text{-}mys)}$) to allow the effect of length on capture probability differ among ontogenetic stages. Models with common continuous length effects (β_{length}) and intercepts (β_0) were also constructed. The simplest model of capture probability (*p.*) estimated one capture probability for all individuals. Models of capture probability assumed that all individuals within a group had equal capture probabilities. Models with continuous length effects assumed that all individuals of a given length within each ontogenetic stage had equal capture probabilities.

Thirteen models were constructed to estimate capture probability for the three ontogenetic groups. Models were ranked using AIC_c as a model selection criterion (Burnham and Anderson 2002). Abundance and 95% confidence limits for each ontogenetic stage was calculated using estimated capture probabilities in a Horvitz-Thompson estimator (Horvitz and Thompson 1952; Huggins 1989; Lukacs 2009). Abundance and associated confidence limits for each ontogenetic group were model-averaged estimates from the suite of 13 models, weighted by AIC_c. Catch per unit effort

(i.e, lake trout $\bullet m^{-1} \bullet h^{-1}$) was also calculated for each ontogenetic stage as an index of abundance in 2007 and 2008.

Saggital otoliths were collected from lake trout for age determination. Otoliths provide better estimates of age than scales, especially for older lake trout (Dubois and Lageux 1968; Casselman 1990; Burnham-Curtis and Bronte 1996; Schram and Fabrizio 1998). Ten otoliths per centimeter length group were collected from lake trout captured in 2007 and 2008 (N=611). Saggital otoliths were mounted in clear epoxy and a thin section was cut perpendicular to the sulcal grove through the nucleus of the otolith (Dux 2005). Thin sections were polished with a sequence of fine (600-1200 grit) sand paper until annuli were discernible at 40x magnification. An age-length key was constructed to estimate the age-frequency distribution of lake trout captured in 2007 and 2008 (DeVries and Frie 1996).

Age information was also used to describe the somatic growth of the lake trout captured in 2007 and 2008. Length-at-age data were used to model growth for both sexes (N=611) with the von Bertalanffy growth model (Ricker 1975):

$$\mathrm{TL} = L_{\infty} \cdot (1 - e^{-K \cdot (\mathrm{Age} - t_0)}),$$

where L_{∞} is the maximum theoretical length, K is the growth coefficient, and t_0 is the theoretical length at age 0. Growth model parameters were estimated by fitting the above model in nonlinear least squares regression using the nls function in R (R Core Development Team 2009). To test for differences in growth between male and female lake trout, two von Bertalanffy growth models were fit to length at age data for fish with age, length, and sex information (N_{males}=168, $N_{females}$= 111). A model with sex-specific

L_{∞}, K, and t_0 parameters was compared to a sexes pooled model using AIC_c as a model selection criterion (Burnham and Anderson 2002). Mean length at age was predicted from von Bertalanffy growth model in R 2.9.2. Mean size at age (length and weight) and annual growth increments were calculated from size-at-age data for age classes with more than five samples. Annual growth increments (length) were observed for a small sample of lake trout marked in 2007 and recaptured in 2008. Observed annual growth increments from recaptured fish were pooled within each of the three ontogenetic groups: immature planktivorous (<450 mm, N=19), immature-piscivorous (450-699 mm, N=7), mature-piscivorous (700+ mm, N=8). Mean maximum length was calculated as the average TL of the ten largest fish sampled for comparison with a meta-analysis of lake trout growth across North America by McDermid et al. (2010).

Weight data were collected to quantify body condition, estimate yield (kg/ha), and estimate total standing crop (kg/ha) in 2008. Ten lake trout per centimeter length group were weighed (nearest 1.0 g) in 2007 and 2008 (N=580). Inter-annual trends in W_r were not of direct interest, thus weight data from 2007 and 2008 were pooled. Relative weight (W_r) was calculated as an index of condition for lake trout (Piccolo et al. 1993; Anderson and Neumann 1996) and analyzed by sex and ontogenetic stage. A $\log_{10}$ length-$\log_{10}$ weight regression was created to predict weights for lake trout that were not weighed to estimate harvest (kg/yr) and total yield (kg/ha). Total yield in 2008 was estimated with a sexes pooled $\log_{10}$length-$\log_{10}$weight regression because regression parameters did not differ significantly between male and female lake trout (ANCOVA: $F_{1,278}$=2.51, P=0.11). Total yield (kg/ha) from exploitation was estimated as the sum of empirical and predicted weights for all lake trout captured in 2008 divided by lake surface area.

Standing crop was estimated by determining the abundance of each age class and the mean weight of a fish in each age class. Abundance of each age class was calculated by multiplying the abundance estimate for each ontogenetic stage by the relative age-frequency distribution of each stage. Mean weight at age was predicted from the length-weight regression with the mean length at age predicted from the von Bertalanffy growth model. Standing crop of each age class was calculated by multiplying the abundance of each age class by the average weight. Total standing crop of lake trout age 4 and greater was estimated as the sum of standing crop estimates for all age classes divided by the surface area of Swan Lake.

Length and age at 50% and 90% maturity (Lm_{50}, Lm_{90}; A_{50} ,A_{90}) were estimated to describe the maturity schedule of lake trout in Swan Lake. Sex, stage of maturity, length, and age were recorded for a random sample (N= 280) of lake trout in 2007 and 2008. Maturity was considered a binary response variable (i.e., fish were either mature or immature) and fish were designated mature only if fully developed gonads were present. Logistic models were fitted for both sexes with length and age as predictors. Models were constructed for both sexes, because male lake trout generally mature at younger ages than females (Martin and Olver 1980). The length and age at which 50% and 90% of the sample were mature was predicted from logistic models. Confidence limits for length and age at 50% and 90% maturity were calculated using a bootstrap procedure (Wang et al. 2008). Maturity data were randomly sampled with replacement to generate one thousand bootstrap data sets. Bootstrap data sets were the same sample size as the original data sets. Length and age at 50% and 90% maturity were calculated from a logistic regression for each bootstrap data set. Confidence limits for length and age at

50% and 90% maturity were the 2.5th and 97.5th percentiles of the 1,000 lengths and ages at 50% and 90% maturity predicted from bootstrapped data sets (Wang et al. 2008). The probability of maturity at age (pm_t) predicted from the logistic regression for females was used to model fertility in matrix population models (see below).

Fecundity was estimated gravimetrically for all gravid female lake trout (N=26) captured in 2008 (Murua et al. 2003). Female lake trout were measured for length, otoliths were removed for age determination, and ovaries were preserved in a 5% buffered formalin solution. Approximately 10% of the preserved ovary weight was sampled from the posterior, medial, and anterior sections of both ovaries. Sections were weighed (nearest 1.0 g) and developed eggs were counted. Mean egg density was determined for each ovary. Fecundity was estimated as the product of mean egg density and ovary weight. Total fecundity was calculated by summing the fecundity of left and right ovaries. The fecundity-length relationship was modeled with a linear regression in R 2.9.2 (R Core Development Team 2009). Mean fecundity at age (f_t) was calculated from fecundity-at-age data for age classes with greater than one observation. Fecundity for lake trout age 11+ was calculated as the mean of fecundity estimates for fish age 11+ because age classes beyond age 10 had only one observation. Mean fecundity at age (f_t) was used to model fertility in matrix models (see below).

Information on natural mortality was needed for population models, but no direct estimates of age-specific natural mortality were possible with sample data. The lake trout population was assumed to follow a type-III survivorship curve, reaching an asymptotic survival rate at age 3 (Sitar et al. 1999). Age specific survival rates for lake trout age 0-3 were obtained from the literature. Survival from age 0 to age 1 (S_0) was the mean of five

separate studies reported in Shuter et al. (1998). Survival rates for lake trout age 1-2 were obtained from Sitar et al. (1999). An instantaneous natural mortality (*M*) was predicted using von Bertalanffy growth parameters L_∞ and *K* (described above) in a model to predict *M* for lake trout populations in Ontario lakes (equation 5 in Shuter et al. 1998):

$$M=2.064\cdot\omega^{0.655}\cdot L_\infty^{-0.933}, \quad (1)$$

where ω is the product of von Bertalanffy parameters L_∞ and *K* (Galucci and Quinn 1979; Shuter et al. 1998). To quantify uncertainty in *M*, the von Bertalanffy growth parameters ω and L_∞ were generated 5,000 times from normal distributions with mean and SD equal to the parameter estimates and predicted SEs. Instantaneous natural mortality (*M*) was then calculated for the 5,000 simulations of ω and L_∞ in equation (1) and converted to annual survival (*S*) as $S=e^{-M}$ (Miranda and Bettoli 2007). The mean and SD of the 5,000 simulated survival rates were used to model natural survival for lake trout age 3 and greater in projection matrices (see below).

Exploitation (i.e., fishing mortality) for each ontogenetic stage in 2008 (E_{stage}) was calculated as:

$$E_{stage}= R_{stage} / \hat{N}_{stage}, \quad (2)$$

where R_{stage} is the number of lake trout removed from an ontogenetic stage and $\hat{N}_{stage}$ is the 2008 abundance estimate for the corresponding ontogenetic stage. Exploitation rates were used to simulate fishing mortality in projection matrices.

Matrix population models were used to evaluate two alternative management scenarios (i.e., “no suppression” or “suppression”) of the lake trout population in Swan

Lake. Sensitivity-elasticity analyses were conducted to evaluate how survival and fertility rates (i.e., matrix elements) contribute to population growth. Matrices were female based and structured after a post-breeding census to consider age-0 survival explicitly in sensitivity-elasticity analyses. Data were available for lake trout up to age 16 in Swan Lake; however it is not uncommon for lake trout lake trout to live longer than 20 years (Martin and Olver 1980). An age 16+ stage was included so that the life span of lake trout in the model was not limited to 16 years. Projection matrices were of the form:

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

where F_0-F_{16+} are fertility rates for lake trout age 0-16+, S_0-S_{15} are annual survival rates for lake trout ages 0-15, and S_{16+} is annual survival in the 16+ stage. Fertility elements (F_1-F_{16+}) for each age t were modeled as:

$$F_t = f_t \cdot pm_t \cdot p_f, \tag{3}$$

where f_t is mean fecundity at age t, p_{m} is the probability of maturity for females age t, and p_{f} is the proportion of offspring that are female (Table 1.2). The per-capita annual population growth rate (λ) was calculated as the dominant eigenvalue of matrix **A** (Caswell 2001).

The no suppression scenario used natural survival rates as transition elements in matrix **A** (Table 1.3). Survival rates in the suppression scenario were adjusted to include both natural mortality and exploitation (Table 1.3). Natural annual mortality and exploitation were considered additive in the suppression scenario because the lake trout

population was assumed to be below carrying capacity (i.e., no density dependence limiting natural survival) and the period of exploitation was short (i.e., exploitation does not compete with natural mortality for the entire year).

A simulation approach was used to account for uncertainty in fertility and survival rates used to parameterize matrices. Fertility elements were calculated (equation 3) from randomly generated fertility vital rates in each simulation of both scenarios. The probability of maturity at age (pm_t) was generated from a beta distribution with mean and SD equal to the predicted pm_t and SE from the logistic regression of maturity at age (see above). A beta distribution was used to constrain probabilities of maturity between 0-1 (Morris and Doak 2002). Fecundity at age (f_t) was generated in each simulation from a stretched beta distribution with mean and SD calculated from fecundity-at-age data (Morris and Doak 2002). Stretched beta distributions were used to constrain simulated fecundity values to a realistic range (i.e., non-negative values). The minimum and maximum fecundity values from sample data were used as to specify the range of stretched beta distributions. The proportion of offspring that are female (p_f) was assumed to be a constant 0.5.

Uncertainty in natural survival rates was incorporated in population matrices by generating random age-specific survival rates for each simulation. A beta distribution was used to constrain survival rates to values from zero to one. Age-0 survival (S_0) was generated with the mean and standard deviation calculated from data in Shuter et al. (1998). No measure of variation for age-1 and 2 survival rates was available for Lake Huron data (Sitar et al. 1999). Thus, annual survival rates for age 1 and 2 (S_1, S_2) were generated from a beta distributions with mean equal to the rates in Sitar et al. (1999) and

SD equal to 20% of the estimates. Natural survival rates for lake trout age 3 and greater were generated using mean and SD of the simulated annual *S* rates (see above).

For simulations in the suppression scenario, survival rates were adjusted to include the estimated exploitation rates of in age classes fully recruited to the sampling gear. Exploitation rates for the three ontogenetic groups were used to adjust survival rates in the following age classes: immature-planktivorous = age 4-5, immature-piscivorous = age 6-7, mature-piscivorous =age 8+. Uncertainty in exploitation rates was modeled by generating the denominator in equation (2) from a normal distribution with mean and standard deviation equal to the 2008 abundance estimates and SE in each suppression matrix.

Five thousand matrices were generated for each of the no suppression and suppression management scenarios. The per-capita population growth rate (λ) was calculated for each matrix simulated in the two management scenarios. Population growth in the two management scenarios was compared with histograms of the simulated population growth rates. Approximate 95% confidence limits of the mean population growth rate for both scenarios were calculated as the 2.5 and 97.5 percentiles of the 5,000 simulations.

Sensitivity and elasticity values were calculated for matrix elements in the no suppression simulations, as these matrices represented the population in a natural state. Sensitivity represents the effect of an absolute change in matrix element a_{ij} on λ, relative to equal absolute changes in other elements (de Kroon et al. 1986):

$$s_{ij} = \partial\lambda / \partial a_{ij} .$$

Using the analytical solution of Caswell (1978), sensitivity was calculated as:

$$s_{ij} = v_i \cdot w_j \ / <\mathbf{w},\mathbf{v}>,$$

where v_i is the ith element of the left eigenvector of matrix **A** , w_j is the jth element of the right eigenvector of matrix **A**, and <**w,v**> is the scalar product of the left and right eigenvectors of matrix **A**, respectively**.**

Elasticity (e_{ij}) is the proportional change in λ resulting from a proportional change in a matrix element a_{ij} (Caswell 1984; deKroon et al. 1986):

$$e_{ij} = \partial \log\lambda / \partial \log a_{ij}$$

$$= (a_{ij} / \lambda) \cdot (\partial\lambda / \partial a_{ij}).$$

Elasticity represents the proportional contribution of matrix elements to the population growth rate λ (de Kroon et al. 1986). Confidence limits (95%) on sensitivity and elasticity values were calculated as the 2.5th and 97.5th percentiles of the sensitivity and elasticity of each element for the 5,000 simulations. Matrix simulations were programmed in R using functions from the popbio package (Stubben and Milligan 2007; R Core Development Team 2009). Vital rates from the beta and stretched beta distributions were generated using the betaval and strechbetaval functions in the popbio package. Population growth rates and sensitivity-elasticity matrices were calculated using the eigen.analysis function in the popbio package (Stubben and Milligan 2007).

Results

Lake trout sampled in Swan Lake were mostly immature-planktivorous fish in 2007 and 2008 (Figures 1.3 and 1.4). Lake trout varied in length from 166 (age 2) to 945 mm TL (age 16), but fish 220 to 400 mm (ages 3, 4, and 5) composed 94% the sample

(Figures 1.3 and 1.4). Less than 5% of the lake trout captured in 2007 and 2008 were greater than 500 mm (age 6) and less than 1% were greater than 700 mm (age 8). In 2007, 2,156 lake trout were captured and 3,785 were captured in 2008.

The gill-net gang used captured a wide range of lake trout size classes (166-945 mm). Overall, the gill-net gang was most selective for lake trout from 300 to 450 mm (Figure 1.5). The gill-net gang was less selective for individuals greater than 600 mm. Adding 1.91-cm bar mesh to the gang in 2008 allowed for the capture of lake trout below 220 mm (age 2). In 2007, the greatest number of fish were captured in the 2.5 cm bar mesh (N=937), followed by the 3.2 cm bar mesh (N=788). In 2008, the 3.2 cm bar mesh captured the greatest number of fish (N=1,555) followed by the 2.5 cm bar mesh (N=1,123). The 2.5 and 3.2 cm bar mesh captured 82% of all lake trout in 2007 and 71% in 2008.

The sampling design employed in 2008 resulted in a decline in catch of immature-planktivorous lake trout over the three-week sampling period (Table 1.4). Catch of immature-piscivorous and mature-piscivorous lake trout did not decline across sampling periods. Models of capture probability with continuous individual length effects ranked higher than models with only categorical effects (Table 1.5). The four highest ranked depletion models composed 84% of the AICc weight (Table 1.5). Each of these models contained a continuous individual length effect based on diet (Table 1.5). The top model (lowest AIC_c) had two capture probabilities for planktivorous and piscivorous fish, modeled with a common intercept and a continuous length effect for the two diet groupings (Tables 1.5 and 1.6). For the top model, capture probability varied from 0.18 (0.11-0.30, 95% CL) for immature-piscivorous fish of median length (575 mm) to 0.50

(0.34-0.67, 95% CL) for mature- piscivorous fish of median length (823 mm; Table 1.7). Models with continuous length effects for sexual maturity groupings (i.e., no diet groupings) ranked low among the suite of models considered. A common capture probability for all fish ranked among the lowest of the models considered.

The model averaged estimate of lake trout abundance was 7,067 (5,762-8,823, 95% CL) fish greater than 270 mm prior to sampling in 2008 (Table 1.8). Immature-planktivorous fish composed 93% of the population estimate. Immature-piscivorous fish composed 6% of the population estimate and only 1% of the population estimate was mature-piscivorous fish. Relative uncertainty (i.e., the coefficient of variation of the mean, CV_{mean}) among abundance estimates was greatest for immature-piscivorous fish, followed by mature-piscivorous fish (Table 1.8). Exploitation was estimated to be 44% (35-53%, 95 % CL) for immature-planktivorous fish, 44% (33-80%, 95% CL) for immature-piscivorous fish and 76% (66-91%, 95% CL) for mature-piscivorous fish (Table 1.9). Catch-per-unit effort was greatest for immature-planktivorous fish in both years and catch per unit effort decreased from 2007 to 2008 for all ontogenetic stages (Figure 1.6). Density of lake trout ≥ 270 mm was 5.3 fish/ha in 2008 (4.3-6.6, 95% CL). Standing crop of lake trout was 4.6 kg/ha of fish ≥ 270 mm before sampling in 2008. Total harvest of lake trout was 1,714 kg and yield was 1.28 kg/ha in 2008. Sampling in 2008 removed 28% of the total lake trout (≥270 mm) biomass.

Somatic growth did not vary between male and female lake trout. A common von Bertalanffy model had a lower AIC_c than a model with separate growth parameters for male and female lake trout (Table 1.10). Therefore, one von Bertalanffy growth model was fit for both male and female lake trout (Figure 1.7). Natural annual mortality was

estimated at 8.1% (7.5-8.7, 95% CL) using the von Bertalanffy growth parameters (see methods). Somatic growth varied among the ontogenetic stages. Growth in length and weight among the ontogenetic groups was highest for immature-piscivorous lake trout (age 5-7). Annual growth increments in length peaked at age 5 and annual increments in weight reached a maximum at age 7 (Figure 1.8). Observed growth increments from fish marked in 2007 and recaptured in 2008 reflected as similar pattern in lifetime growth, with an increasing growth rate as lake trout became piscivorous and a reduced growth rate after becoming sexually mature (Figure 1.9).

Relative weight (W_r) of lake trout increased with increasing size (Figure 1.10). Although mean W_r was similar between immature males and females, sexually mature females were in better condition than males (Figure 1.10). Among the three ontogenetic groups, W_r for immature-planktivorous (280-449) and immature-piscivorous (450-699) lake trout were between the 50th and 60th percentiles of the cumulative frequency distribution of mean W_r among lake trout populations (Hubert et al. 1994). Mean W_r for mature-piscivorous lake trout in Swan Lake was above 110, which corresponded to the 92nd percentile among lake trout populations (Hubert et al. 1994).

Male lake trout were sexually mature at smaller sizes and younger ages than females. Mature male lake trout varied from 385 to 945 mm TL and mature female lake varied from 665 to 899 mm TL (Figure 1.11). Fifty percent of male lake trout were mature at 590 mm (547-604, 95% CL) and 90% were sexually mature at 712 mm (670-727, 95% CI), whereas 50% of females were mature at 708 mm (697-727, 95% CL) and 90% were mature at 753 mm (731-780, 95% CL). Age at 50% and 90% maturity for males was predicted to be 6.1 (5.7-6.3, 95% CL) and 7.6 (7.0-8.0, 95% CL), respectively

(Table 1.11). Age at 50% and 90% maturity for females maturity was predicted to be 7.4 (7.0-7.8, 95% CL) and 8.1 (7.1-8.6, 95% CL), respectively (Table 1.11).

Fecundity varied from 1,390 to 14,717 eggs for female lake trout sampled from 680 to 900 mm (age 7-15). Mean fecundity was 8,464 (7,124-9,804, 95% CL) eggs per fish. Fecundity was positively related to length and length explained 68% of the variation in fecundity (Figure 1.12). Mean relative fecundity was 1,396 (1,241-1,551, 95% CL) eggs/kg body mass.

In the no-suppression modeling scenario, the per-capita annual population growth rate (λ) of the lake trout population in Swan Lake was 1.35 (1.25-1.43, 95% CL). At this rate, lake trout abundance in Swan Lake would double every 2.3 years (1.9-2.9, 95% CL). In the suppression scenario, the mean population growth rate was 0.94 (0.44-1.14, 95% CL). Suppression scenario simulations reduced population growth by 30% (16-67, 95% CL) of the no suppression growth rate. It was uncertain whether the population would grow, decline, or remain stable at the estimated exploitation rates because the confidence limits of λ in the suppression scenario overlapped one (Figure 1.13).

Sensitivity analysis indicated that population growth was most sensitive to changes in survival rates. The population growth rate was highly sensitive to changes in the survival of age-0 lake trout (Table 1.12). Population growth was less sensitive to changes in survival rates with increasing age. The relative contribution of survival rates to λ (i.e., elasticity) was constant for juvenile fish age 0 to age 6, but decreased with age for reproductive age classes age 7 and older (Table 1.13). Summed elasticities were greatest for juvenile survival rates (0.602), followed by survival rates of reproductive age classes (0.311). Thus, survival rates from birth to sexual maturity made the largest

relative contribution to λ, followed by survival of reproductive age classes. Fertility rates had the lowest summed elasticity (0.087) and made the smallest relative contribution to λ.

Discussion

Understanding lake trout population dynamics has been necessary for the management and conservation of native lake trout populations throughout North America (Healey 1978a; Shuter et al. 1998). Knowledge of lake trout life history and management is now being re-examined in the context of controlling lake trout as a non-native species. The detrimental impacts of introduced lake trout to aquatic ecosystems in the western USA have prompted natural resource management agencies to implement lake trout suppression programs (Martinez et al. 2009).

The size and age structure observed in this study indicated lake trout had been reproducing in Swan Lake since 1992, but juvenile recruitment had increased in recent years. When nonnative species colonize novel systems, there is an inherent time lag between the initial establishment of the population and onset of exponential growth (Crooks and Soulé 1999; Sakai et al. 2001). Lake trout were first documented in the Swan River system in 1998, but juvenile lake trout did not appear in MFWP annual gill-net surveys until 2003. By 2008, lake trout abundance was estimated to be between 5,800 and 8,800 lake trout greater than 270 mm in Swan Lake, with 94% being juveniles age 3 to 5. Populations with high intrinsic growth rates, such as an invasive species in a favorable environment (e.g., Deering and Vankat 1999), have an age structure dominated by juveniles (Caswell 1984; Charlesworth 1994).

Size-selectivity of the gill nets used was a potential source for bias in describing the size and age structure of the lake trout population (Hansen et al. 1997). The mesh sizes used were selective for a wide size range, but the selectivity of the nets was reduced for adult lake trout. Although the peak selectivity of the largest mesh size was for fish 590 mm, gill nets captured lake trout as large as 945 mm. Including larger mesh sizes in future netting efforts would reduce uncertainty due to gear selectivity for describing the size and age structure of the lake trout population in Swan Lake.

Abundance estimates for piscivorous fish were likely biased low, as the total number of mature-piscivorous lake trout captured in 2008 during lake-wide sampling (this study) and at spawning locations (see chapter 2) was greater than the abundance estimate for the mature-piscivorous ontogenetic stage. Furthermore, catch of piscivorous fish did not decline through each of the three sampling periods, which is necessary for a depletion estimate (Zippin 1958). Individual heterogeneity in capture probability was a potential source for the bias in abundance estimates for piscivorous fish because all individuals of a given length within an ontogenetic group were assumed to have an equal capture probability. Piscivorous lake trout may occur suspended in the water column to pursue pelagic prey species such as cisco *Coregonus artedi* or kokanee (Dux 2005; Dunlop et al. 2010). Sinking gill nets used in this study would not have sampled lake trout swimming more than several meters off the bottom. Thus, individuals suspended in the water column would have been effectively uncatchable. If some piscivorous individuals were suspended in the water column more than others, the most catchable individuals would be removed first resulting in a decline in catchability of piscivorous fish through time. This would result in an overestimate of capture probability and an

underestimate of abundance (Williams et al. 2001). Underestimating abundance would in turn cause exploitation to be overestimated. Under conditions of decreasing capture probability through time, bias in depletion estimates can be reduced by conducting additional sampling periods (Riley and Fausch 1992). Incorporating individual heterogeneity into models of capture probability for piscivorous lake trout could also help reduce bias in depletion estimates (Williams et al. 2001).

Growth and condition within lake trout populations are dependent on food availability, which can be limited at high densities (Matuszek et al. 1990; Johnson and Martinez 2000). Growth and condition of juvenile lake trout in Swan Lake were similar to populations throughout North America (Martin and Olver 1980; Hubert et al. 1994). The moderate size at age and condition of juvenile lake trout in Swan Lake may reflect increased intraspecific competition among the large cohorts produced in recent years. Adult lake trout attained large maximum sizes and were in high condition in Swan Lake (Hubert et al. 1994; Shuter et al. 1998; McDermid et al. 2010). The increasing trend in W_r from juvenile to adult was likely influenced by the ontogenetic shift to piscivory (Hubert et al. 1994) and gonad maturation. The large size at age and high condition of adult lake trout reflected abundant food resources in Swan Lake (Matuszek et al. 1990; Johnson and Martinez 2000).

Somatic growth rates also influence the maturity schedule of lake trout populations (Matuszek et al. 1990; Ferreri and Taylor 1996). Fast-growing, piscivorous lake trout populations mature at younger ages and larger sizes than slow-growing planktivorous populations (Martin and Olver 1980). Although age at maturity in Swan Lake was similar to lake trout populations across North America (Healey 1978a; Martin

and Olver 1980; McDermid et al. 2010), the size at which female lake trout reached maturity was larger than any population reported in the literature. Length at 50% maturity was greater than populations in the Great Lakes (Madenjian et al.1998), inland lakes in Ontario (Trippel 1993), and inland lakes in Alaska (Burr 1991). The maturity schedule further reflected favorable growth conditions for adult lake trout during this study.

Lake trout in Swan Lake had relatively high length and age-specific fecundity in comparison with other lake trout populations. A 790 mm lake trout in Swan Lake was as fecund as an 830-900 mm lake trout in Lake Superior (Ferreri and Taylor 1996). Relative fecundity in Swan Lake was similar to the average relative fecundity reported for lake trout populations in the Great Lakes (Martin and Olver 1980), inland lakes in Ontario (Shuter et al. 1998), and other populations throughout North America (Martin and Olver 1980). The consistency in relative fecundity (eggs/kg body weight) among lake trout populations indicate fecundity may be relatively fixed for lake trout of a given weight (Ferreri and Taylor 1996; Shuter et al. 1998). Population density has been shown to affect age-specific fecundity through changes in growth (Ferreri and Taylor 1996). Fecundity at length may be more variable for lake trout due to differences in condition among populations (i.e., weight varies among populations for fish of a given length). The relatively high length and age-specific fecundity in Swan Lake further indicated that resources were not limiting adult lake trout.

Somatic growth varies widely among lake trout populations throughout their geographic range in relation to lake productivity and food web structure (Trippel 1993; Shuter et al. 1998; Johnson and Martinez 2000; Lienesch 2005; McDermid et al. 2010).

Lake trout generally grow faster and attain larger sizes in lakes with high productivity and pelagic forage species (Martin and Olver 1980; Shuter et al. 1998, McDermid et al. 2010). Swan Lake is relatively productive among lakes supporting lake trout populations (Shuter 1998; McDermid et al. 2010) and the food web contains several forage species including kokanee and pygmy whitefish. Given the productivity and food web structure of Swan Lake, lake trout should be expected to have relatively high growth rates. In comparison with other lake trout populations, somatic growth rates, condition, and size at maturity of lake trout in Swan Lake were near the upper limit for the species.

The no-suppression modeling scenario illustrated that the lake trout population in Swan Lake is growing at an exponential rate, despite the uncertainty in the vital rates used to parameterize the models. That is, the population growth rate was never below one in no-suppression simulations. The mean per-capita population growth rate and doubling time in the no-suppression scenario was similar to the growth rate estimated for lake trout in Lake Pend Oreille, Idaho prior to implementing a suppression program (Hansen et al. 2008). The skewed size and age structure of lake trout captured corroborated the relatively high growth rate of the population in the no-suppression scenario (Caswell et al. 1984; Charlesworth 1994). The mean population growth rate of the no-suppression scenario represented a ‘snap shot’ of the population growth rate at the current survival and fertility rates. If survival and fertility rates vary from year to year, the true population growth rate would be less than that estimated with deterministic matrices (Case 2000). Furthermore, density dependence will eventually affect the vital rates as the population approaches carrying capacity. The relatively high somatic growth, condition, and size at maturity of lake trout in Swan Lake suggest that density

dependence had minimal effects on the population; however, the population growth rate estimated in this study should not be assumed constant.

Survival rates from birth to sexual maturity contributed most to population growth followed by survival rates of reproductive adults. Lake trout populations may be particularly susceptible to overexploitation because individuals are vulnerable to harvest before reaching sexual maturity (Trippel 1995). The population growth rate was highly sensitive to changes in the survival of age-0 lake trout. Targeting age-0 lake trout (i.e., incubating embryos) may be an effective complement to mechanical removal efforts focused on capturing juvenile and adult lake trout.

Although the juvenile survival rates that contribute most to population growth in matrix models were from the literature (i.e., Sitar et al. 1999), uncertainty in these rates was accounted for by simulation. Juvenile survival rates in Swan Lake are likely higher than in Lake Superior. Lake trout populations in Lake Superior are likely closer to equilibrium densities than the population in Swan Lake, thus density dependence may affect juvenile survival (Corradin et al. 2008). Juvenile lake trout in Lake Superior may be further affected by early mortality syndrome (Honeyfield et al. 2005) and introduced egg predators (Chotkowski and Marsden 1995). Furthermore, introduced *M. relicta* in Swan Lake likely provide conditions for high juvenile lake trout survival (Bowles et al. 1991; Stafford et al. 2002). Population models could be improved with estimates of juvenile lake trout survival rates from Swan Lake.

The estimated exploitation rates decreased population growth from the no-suppression scenario, but not all suppression simulations produced population growth rates below one. Exploitation among the immature-piscivorous and mature-piscivorous

ontogenetic stages may have been overestimated because abundance estimates were likely underestimated for these ontogenetic groups. If true exploitation rates are lower than the estimated values, the population growth rate would be higher than estimated in the suppression scenario. Given the uncertainty in the vital rates and the potential bias in exploitation rates for piscivorous fish used to model suppression scenarios, annual suppression efforts should be increased from the 2008 level to ensure a decline in the lake trout population.

Total annual mortality exceeding 50% and yield greater than 0.5 kg/ha has been suggested as the threshold for overharvest in lake trout populations (Healey 1978a). However, there is a negative relationship between lake area and yield for lake trout populations (Goddard et al. 1987; Payne et al. 1990; Marshall 1996). Populations in small lakes (< 1000 ha) can sustain yields as high as 1.69 kg/ha (Marshall 1996). Yield for lake trout in Swan Lake was predicted to be 1.0 kg/ha given its surface area and 0.86 kg/ha given the number of species present using the models of Marshall (1996). Maintaining total annual mortality of 50% and annual yields greater than 1.0 kg/ha will help ensure a decline in the lake trout population in Swan Lake. Population metrics (i.e., size at age, maturity schedule, condition, fecundity) may not exhibit compensatory responses if density was not limiting the lake trout population at the start of the experimental suppression program. However, changes in population metrics will reflect increased density in the future if suppression efforts do not reduce lake trout abundance in Swan Lake.

Control programs for invasive species have been implemented worldwide to reduce the impacts of nonnative species on regional biota (Myers et al. 2000). The

efficacy of suppression efforts can be evaluated in an adaptive management framework by tracking population metrics through time and utilizing models to simulate management actions. Matrix population models are a flexible theoretical framework to evaluate success benchmarks for the control of nonnative species. As new information becomes available, models can be updated to determine if success benchmarks are being met. The experimental lake trout suppression program on Swan Lake will provide a case study to quantify the effects of suppression on the dynamics of a growing lake trout population that may be useful for lake trout suppression programs in the Intermountain West.

Table 1.1. Models of capture probability *p* used to estimate abundance of lake trout greater than age 4 in Swan Lake, Montana in 2008. Subscript mys = planktivorous diet, pisc = piscivorous diet, imm = sexually immature, and mat = sexually mature. Recapture probability (*c*) was fixed at zero for each model.

Capture probability (Model Structure)	Model Description
$p_{mys}(\beta_0 + \beta_{length(mys)})$, $p_{pisc}(\beta_0 + \beta_{length(pisc)})$	Common intercept with length effects based on diet
$p_{mys}(\beta_{mys} + \beta_{length(mys)})$, $p_{pisc}(\beta_{pisc} + \beta_{length(pisc)})$	Categorical effects and continuous length effects based on diet
$p_{imm\text{-}mys}(\beta_{imm} + \beta_{length(mys)})$, $p_{imm\text{-}pisc}(\beta_{imm} + \beta_{length(pisc)})$, $p_{mat\text{-}pisc}(\beta_{mat} + \beta_{length(pisc)})$	Categorical maturity effects, continuous length effects based on diet
$p_{imm\text{-}mys}(\beta_{imm\text{-}mys} + \beta_{length(imm\text{-}mys)})$, $p_{imm\text{-}pisc}(\beta_{imm\text{-}pisc} + \beta_{length(imm\text{-}pisc)})$, $p_{mat\text{-}pisc}(\beta_{mat\text{-}pisc} + \beta_{length(mat\text{-}pisc)})$	Categorical effects and continuous length effects based on diet and maturity
$p_{mys}(\beta_{mys} + \beta_{length})$, $p_{pisc}(\beta_{pisc} + \beta_{length})$	Categorical diet effects, common length effect
$p_{imm\text{-}mys}(\beta_{mys} + \beta_{length(imm)})$, $p_{imm\text{-}pisc}(\beta_{pisc} + \beta_{(length(imm)})$, $p_{mat\text{-}pisc}(\beta_{pisc} + \beta_{length(mat)})$	Categorical diet effects, continuous length effects based on maturity
$p_{imm\text{-}mys}(\beta_{imm\text{-}mys} + \beta_{length})$, $p_{imm\text{-}pisc}(\beta_{imm\text{-}pisc} + \beta_{length})$, $p_{mat\text{-}pisc}(\beta_{mat\text{-}pisc} + \beta_{length})$	Categorical diet-maturity effects, common continuous length effect
$p_{imm}(\beta_{imm} + \beta_{length})$, $p_{mat}(\beta_{mat} + \beta_{length})$	Categorical maturity effects, common continuous length effect
$p_{imm}(\beta_0 + \beta_{length(imm)})$, $p_{mat}(\beta_0 + \beta_{length(mat)})$	Common intercept, continuous length effects based on maturity
$p_{imm}(\beta_{imm} + \beta_{length(imm)})$, $p_{mat}(\beta_{mat} + \beta_{length(mat)})$	Categorical and length effects based on maturity
$p_{mys}(\beta_{mys})$, $p_{pisc}(\beta_{pisc})$	Categorical diet effect
$p.(\beta_0)$	Common *p*
$p_{imm\text{-}mys}(\beta_{imm\text{-}mys})$, $p_{imm\text{-}pisc}(\beta_{imm\text{-}pisc})$, $p_{mat\text{-}pisc}(\beta_{mat\text{-}pisc})$	Categorical diet-maturity effects

Table 1.2. Vital rates used to model fertility (F_1-F_{16+}) rates in population matrices for the lake trout population in Swan Lake, Montana. Errors for vital rates are SD for sample data and SE for model predictions.

Symbol	Definition	Age(t)	Value	Error	Source
f_t	Fecundity at age t	7	5,571	2,371	This study, fecundity-age Data
		8	6,182	3,388	
		9	10,367	2,703	
		10	9,789	665	
		11+	12,793	951	
pm_t	Probability of maturity at age t	1-6	0	N/A	This study, predicted maturity at age from logistic regression for females
		7	0.19	0.073	
		8	0.84	0.099	
		9-16+	1	N/A	
p_f	Proportion of offspring that are female	8-16+	0.5	N/A	Martin and Olver (1980)

Table 1.3. Natural survival rates (S) used as transition elements (S_0-S_{16+}) in population matrices of lake trout in Swan Lake, Montana.

Element(s)	Age(s)	S	Error	Source
S_0	0	0.0043	0.00084	Shuter et al. (1998), error is SD of observations in Shuter et al. (1998)
S_1	1	0.45	0.09	Sitar et al. (1999), error assumed to be 20% of value
S_2	2	0.78	0.16	
$S_{3\text{-}16+}$	3-16+	0.92	0.0035	Equation (1), value is mean predicted by equation (1) for 5000 simulations of von Bertalanffy growth parameters. Error is SD of S calculated in 5000 simulations

Table 1.4. Number of lake trout in each ontogenetic stage collected in three sampling periods from 9 September 2008 to 25 September 2008 in Swan Lake, Montana.

Ontogenetic stage	Length (mm TL)	Sampling period 1	2	3
Immature-planktivorous	270-449	1176	917	770
Immature-piscivorous	450-699	79	72	41
Sexually mature-piscivorous	700 +	29	31	8

Table 1.5. Model selection results for capture probabilities (p) in depletion estimates of lake trout abundance in Swan Lake, Montana in 2008. Subscripts identify ontogenetic groupings: mys = *Mysis* diet, pisc = piscivorous diet, imm = sexually immature, and mat = sexually mature. Recapture probability (c) was fixed at zero for each model.

Capture probability (Model Structure)	AIC_c	ΔAIC_c	AIC_c weight	Number parameters	Model likelihood
$p_{mys}(\beta_0 + \beta_{length(mys)}), p_{pisc}(\beta_0 + \beta_{length(pisc)})$	6746.116	0.000	0.31557	3	1.0000
$p_{mys}(\beta_{mys} + \beta_{length(mys)}), p_{pisc}(\beta_{pisc} + \beta_{length(pisc)})$	6746.230	0.114	0.29812	4	0.9447
$p_{imm\text{-}mys}(\beta_{imm} + \beta_{length(mys)}), p_{imm\text{-}pisc}(\beta_{imm} + \beta_{length(pisc)}),$ $p_{mat\text{-}pisc}(\beta_{mat} + \beta_{length(pisc)})$	6747.780	1.664	0.13734	4	0.4352
$p_{imm\text{-}mys}(\beta_{imm\text{-}mys} + \beta_{length(imm\text{-}mys)}), p_{imm\text{-}pisc}(\beta_{imm\text{-}pisc} + \beta_{length(imm\text{-}pisc)}),$ $p_{mat\text{-}pisc}(\beta_{mat\text{-}pisc} + \beta_{length(mat\text{-}pisc)})$	6748.684	2.568	0.08737	6	0.2769
$p_{mys}(\beta_{mys} + \beta_{length}), p_{pisc}(\beta_{pisc} + \beta_{length})$	6749.428	3.312	0.06024	3	0.1909
$p_{imm\text{-}mys}(\beta_{mys} + \beta_{length(imm)}), p_{imm\text{-}pisc}(\beta_{pisc} + \beta_{(length(imm)}),$ $p_{mat\text{-}pisc}(\beta_{pisc} + \beta_{length(mat)})$	6749.932	3.816	0.04682	4	0.1484
$p_{imm\text{-}mys}(\beta_{imm\text{-}mys} + \beta_{length}), p_{imm\text{-}pisc}(\beta_{imm\text{-}pisc} + \beta_{length}),$ $p_{mat\text{-}pisc}(\beta_{mat\text{-}pisc} + \beta_{length})$	6750.073	3.957	0.04364	4	0.1383
$p_{imm}(\beta_{imm} + \beta_{length}), p_{mat}(\beta_{mat} + \beta_{length})$	6754.919	8.803	0.00387	3	0.0123
$p_{imm}(\beta_0 + \beta_{length(imm)}), p_{mat}(\beta_0 + \beta_{length(mat)})$	6754.992	8.876	0.00373	3	0.0118
$p_{imm}(\beta_{imm} + \beta_{length(imm)}), p_{mat}(\beta_{mat} + \beta_{length(mat)})$	6756.463	10.347	0.00179	4	0.0057
$p_{mys}(\beta_{mys}), p_{pisc}(\beta_{pisc})$	6758.962	12.846	0.00051	2	0.0016
$p.(\beta_0)$	6759.643	13.526	0.00036	1	0.0011
$p_{imm\text{-}mys}(\beta_{imm\text{-}mys}), p_{imm\text{-}pisc}(\beta_{imm\text{-}pisc}), p_{mat\text{-}pisc}(\beta_{mat\text{-}pisc})$	6759.970	13.854	0.00031	3	0.0010

Table 1.6. Parameter estimates from top model of capture probability estimated from lake trout capture data in Swan Lake, Montana 2008.

			95 % CL	
Parameter (β)	Estimate	SE	Lower	Upper
β_0	-4.98	0.959	-6.86	-3.10
$\beta_{length(mys)}$	0.010	0.003	0.005	0.016
$\beta_{length(pisc)}$	0.006	0.001	0.003	0.008

Table 1.7. Estimated capture probability (*p*) for fish of median length within each ontogenetic stage in Swan Lake, Montana 2008. Capture probabilities are from top model.

	Median	Capture probability			95% CL	
Ontogenetic stage	length	(model structure)	*p*	SE	Lower	Upper
Immature-planktivorous	360	$p_{mys}(\beta_0 + \beta_{length(mys)})$	0.23	0.020	0.194	0.274
Immature-piscivorous	575	$p_{pisc}(\beta_0 + \beta_{length(pisc)})$	0.18	0.049	0.106	0.300
Mature-piscivorous	823	$p_{pisc}(\beta_0 + \beta_{length(pisc)})$	0.50	0.089	0.336	0.672

Table 1.8. Model averaged estimates of abundance ($\hat{N}_{stage}$), model standard error (SE), coefficient of variation of the mean (CV_{mean}), and 95% confidence limits by ontogenetic stage for lake trout in Swan Lake, Montana 2008.

	Length					95% CL	
Ontogenetic stage	(mm TL)	Age	$\hat{N}_{stage}$	SE	CV_{mean}	Lower	Upper
Immature-planktivorous	270-449	4-5	6,541	669	0.102	5,446	8,105
Immature-piscivorous	450-699	5-7	436	141	0.323	240	581
Mature-piscivorous	700 +	7+	90	13	0.144	76	137
Total	270 +	4+	7,067			5,762	8,823

Table 1.9. Lake trout removed (R_{stage}), population estimate ($\widehat{N}_{stage}$), and exploitation estimates (E_{stage}) by ontogenetic stage for lake trout collected in Swan Lake, Montana in 2008. Equation (2) was used to calculate E_{stage}. Confidence limits (CL) of exploitation rates were calculated from confidence limits for abundance estimates.

Ontogenetic stage	Length (mm TL)	R_{stage}	$\widehat{N}_{stage}$	E_{stage}	95% CL Lower	95% CL Upper
Immature-planktivorous	270-449	2,863	6,541	0.44	0.35	0.53
Immature-piscivorous	450-699	192	436	0.44	0.33	0.80
Mature-piscivorous	700 +	68	90	0.76	0.66	0.91

Table 1.10. Model selection results for effects of sex on von Bertalanffy growth parameters from Swan Lake, Montana in 2007 and 2008. Models are ranked by AIC_c values from lowest to highest.

Model	AIC_c	AIC_c weight	Model Likelihood
Common model	2963.316	0.927	1.00
Separate sex models	2968.409	0.072	0.08

Table 1.11. Logistic regression models of maturity at age for lake trout collected in Swan Lake, Montana in 2007 and 2008.

Sex	Parameter	Estimate	SE	Logistic model
Male	β_0	-9.22	1.79	$pm_t = e^{1.53 \cdot Age - 9.22} / (1 + e^{1.53 \cdot Age - 9.22})$
	β_1	1.53	0.28	
Female	β_0	-23.48	5.58	$pm_t = e^{3.15 \cdot Age - 23.48} / (1 + e^{3.15 \cdot Age - 23.48})$
	β_1	3.15	0.77	

Table 1.12. Sensitivity of population growth to matrix elements from 5,000 simulations of the no suppression scenario for lake trout in Swan Lake, Montana. Matrix elements are survival (S_t) and fertility rates (F_t) at age t.

Matrix element	Mean sensitivity	95% CL	
		Lower	Upper
S_0	27.799	19.804	38.753
S_1	0.267	0.189	0.396
S_2	0.156	0.115	0.262
S_3	0.126	0.109	0.143
S_4	0.126	0.109	0.143
S_5	0.126	0.109	0.143
S_6	0.126	0.109	0.143
S_7	0.120	0.103	0.135
S_8	0.099	0.084	0.114
S_9	0.071	0.058	0.084
S_{10}	0.052	0.041	0.063
S_{11}	0.036	0.027	0.044
S_{12}	0.024	0.017	0.032
S_{13}	0.017	0.011	0.023
S_{14}	0.014	0.007	0.017
S_{15}	0.008	0.005	0.012
S_{16+}	0.018	0.009	0.033
F_7	$1.11 \cdot 10^{-5}$	$7.30 \cdot 10^{-6}$	$1.49 \cdot 10^{-5}$
F_8	$7.52 \cdot 10^{-6}$	$5.33 \cdot 10^{-6}$	$9.75 \cdot 10^{-6}$
F_9	$5.10 \cdot 10^{-6}$	$3.86 \cdot 10^{-6}$	$6.42 \cdot 10^{-6}$
F_{10}	$3.47 \cdot 10^{-6}$	$2.78 \cdot 10^{-6}$	$4.27 \cdot 10^{-6}$
F_{11}	$2.36 \cdot 10^{-6}$	$1.95 \cdot 10^{-6}$	$2.87 \cdot 10^{-6}$
F_{12}	$1.61 \cdot 10^{-6}$	$1.32 \cdot 10^{-6}$	$1.96 \cdot 10^{-6}$
F_{13}	$1.10 \cdot 10^{-6}$	$8.74 \cdot 10^{-7}$	$1.36 \cdot 10^{-6}$
F_{14}	$7.53 \cdot 10^{-7}$	$5.71 \cdot 10^{-7}$	$9.56 \cdot 10^{-7}$
F_{15}	$5.15 \cdot 10^{-7}$	$3.70 \cdot 10^{-7}$	$6.78 \cdot 10^{-7}$
F_{16+}	$1.13 \cdot 10^{-6}$	$6.73 \cdot 10^{-7}$	$1.78 \cdot 10^{-6}$

Table 1.13. Elasticity of population growth rate to matrix elements in no suppression scenario for lake trout in Swan Lake, Montana. Matrix elements are survival (S_t) and fertility rates (F_t) at age t.

Matrix element	Mean elasticity	95% CL	
		Lower	Upper
S_0	0.086	0.080	0.092
S_1	0.086	0.080	0.092
S_2	0.086	0.080	0.092
S_3	0.086	0.080	0.092
S_4	0.086	0.080	0.092
S_5	0.086	0.080	0.092
S_6	0.086	0.080	0.092
S_7	0.082	0.075	0.088
S_8	0.068	0.056	0.076
S_9	0.048	0.038	0.058
S_{10}	0.036	0.027	0.044
S_{11}	0.024	0.017	0.032
S_{12}	0.017	0.011	0.023
S_{13}	0.011	0.007	0.017
S_{14}	0.008	0.005	0.012
S_{15}	0.005	0.003	0.009
S_{16+}	0.012	0.006	0.024
F_7	0.004	0.0009	0.011
F_8	0.014	0.003	0.030
F_9	0.020	0.009	0.027
F_{10}	0.013	0.010	0.016
F_{11}	0.011	0.009	0.013
F_{12}	0.008	0.006	0.009
F_{13}	0.005	0.004	0.006
F_{14}	0.004	0.003	0.005
F_{15}	0.003	0.002	0.003
F_{16+}	0.005	0.003	0.009

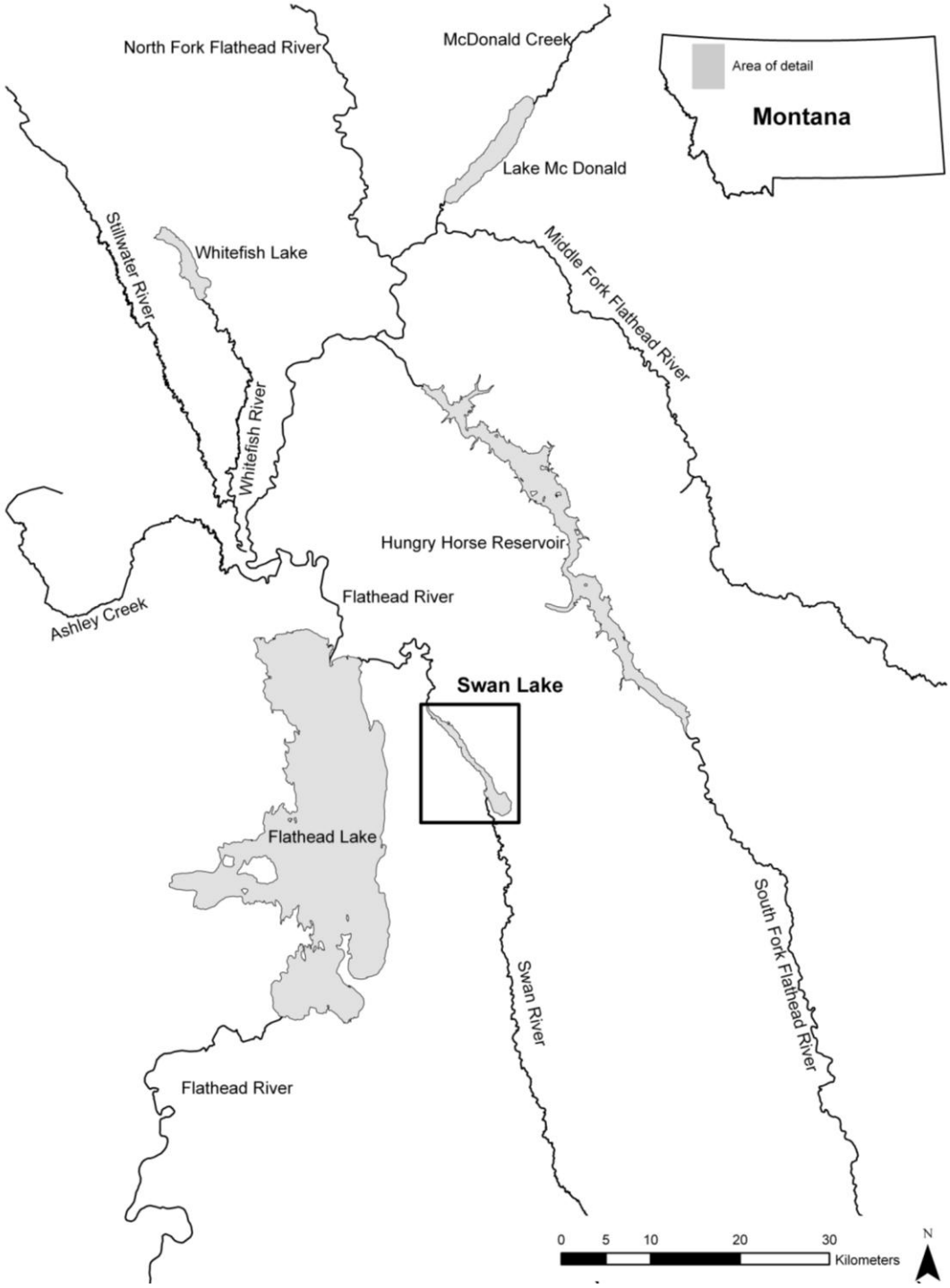

Figure 1.1. Location of Swan Lake in the Flathead River drainage, northwest Montana.

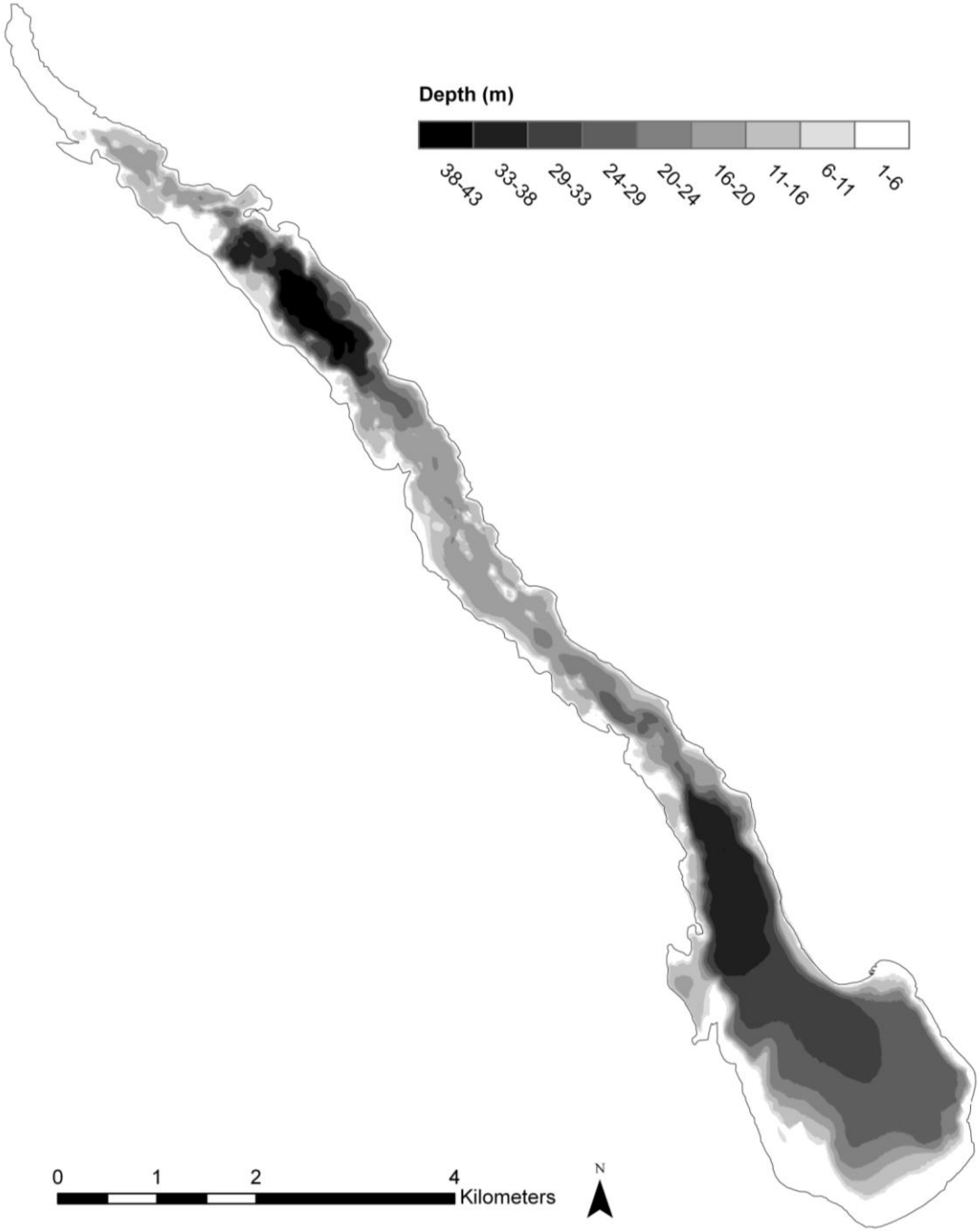

Figure 1.2. Bathymetric map of Swan Lake, Montana from June 2005.

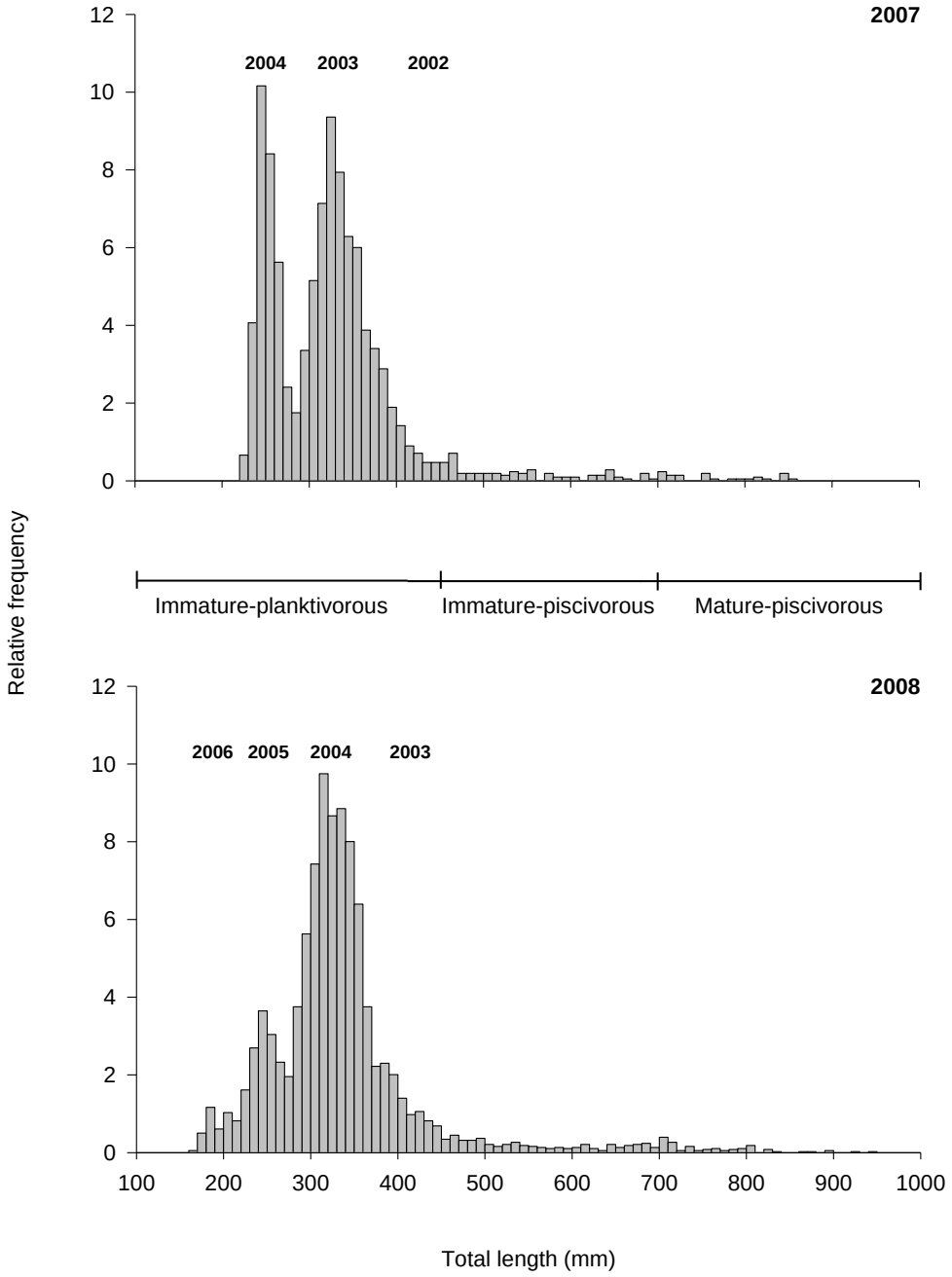

Figure 1.3. Relative length-frequency distributions of lake trout collected with gill nets in Swan Lake in September and October in 2007 and 2008. Sampling year is noted in bold in upper right. Years above bars delineate the mode of the year class. Center axis delineates length classes in each of the three ontogenetic groups.

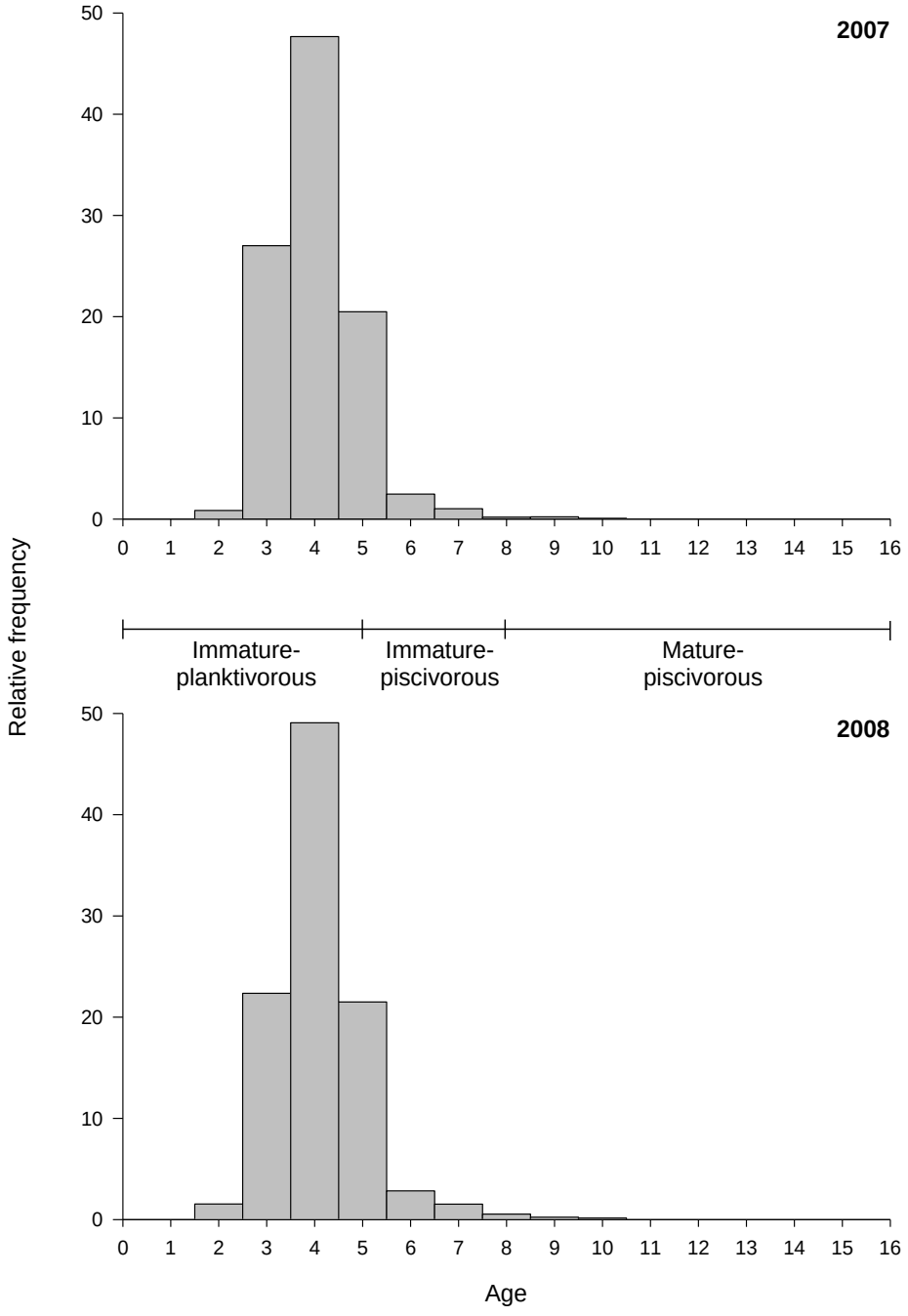

Figure 1.4. Age-frequency distribution of lake trout captured with gill nets in Swan Lake from September through October in 2007 and 2008. Center axis delineates age classes in each of the three ontogenetic groups.

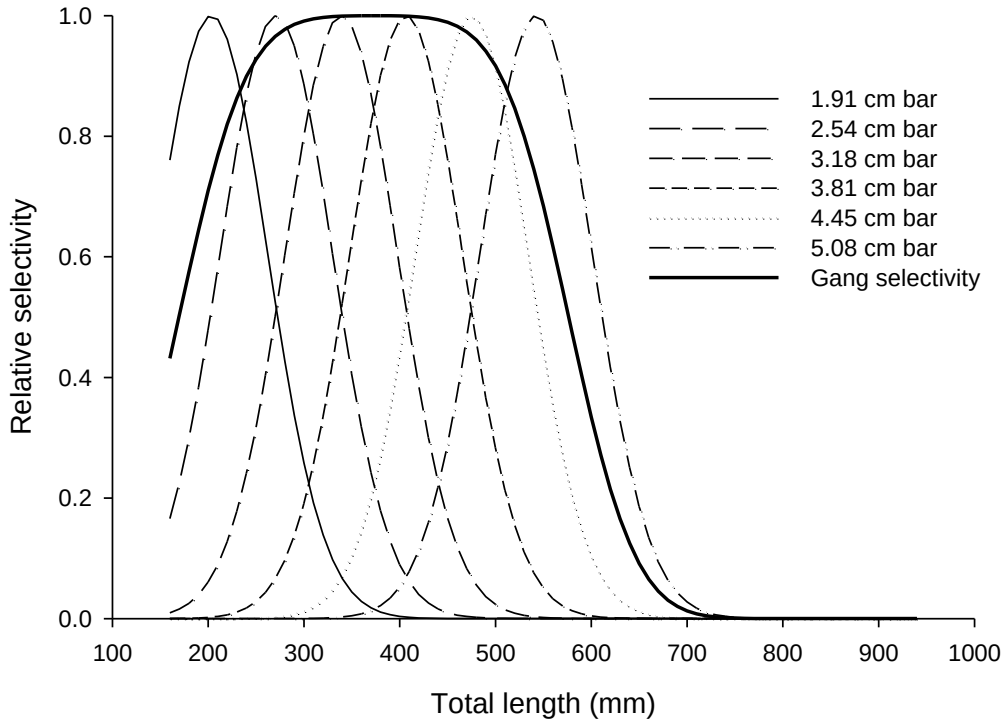

Figure 1.5. Relative selectivity curves for mesh sizes used to sample lake trout in Swan Lake, Montana in September and October 2007 and 2008.

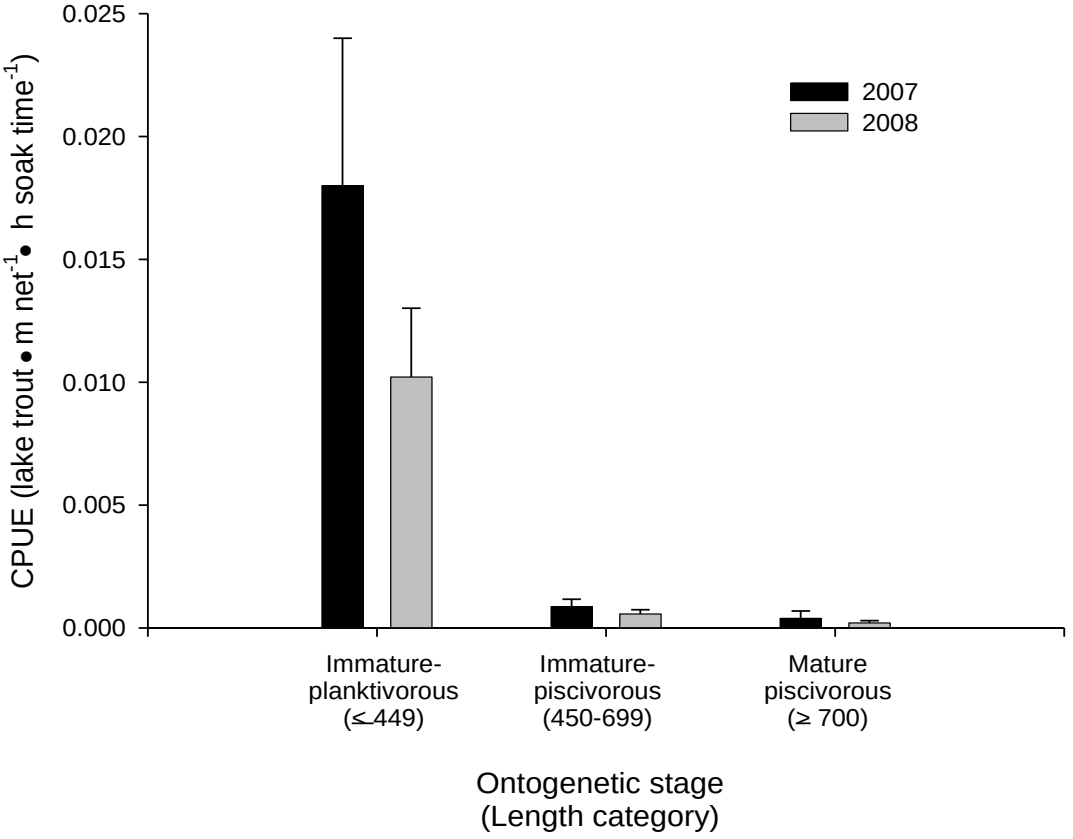

Figure 1.6. Mean catch-per-unit effort of lake trout captured in Swan Lake, Montana in gill nets during 2007 and 2008. Error bars represent 95% confidence interval.

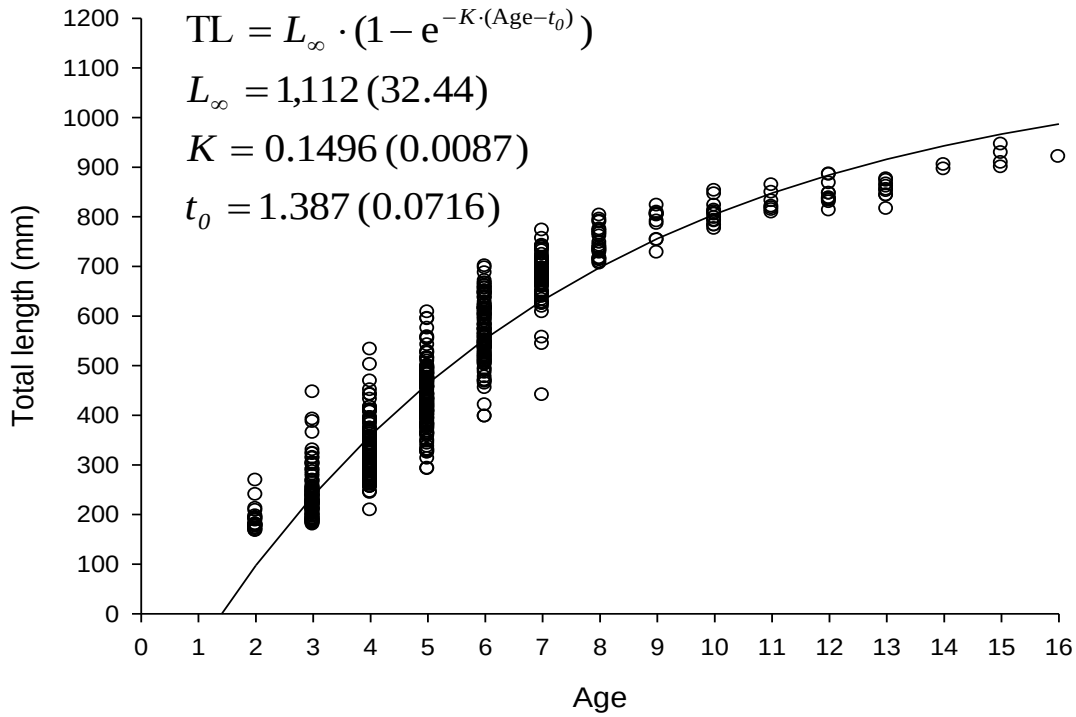

Figure 1.7. Length at age and von Bertalanffy growth model for lake trout collected with gill nets in Swan Lake, Montana in September and October 2007 and 2008 (N=611). Parameter estimates are shown with SE in parenthesis.

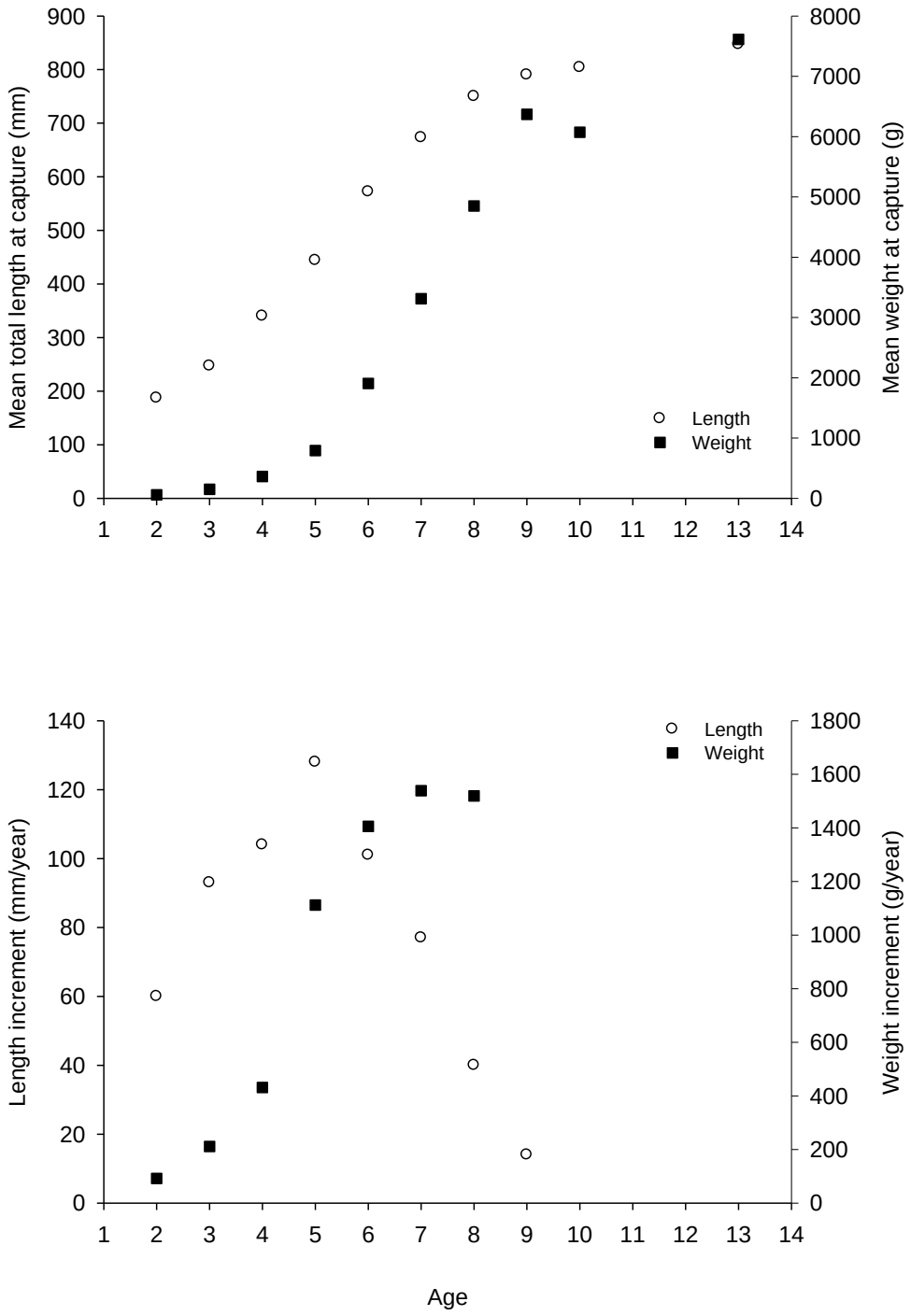

Figure 1.8. Mean length and weight at age for lake trout (top panel) and annual growth increments from mean length and weight at age data (bottom panel) captured in September and October 2007 and 2008 in Swan Lake, Montana.

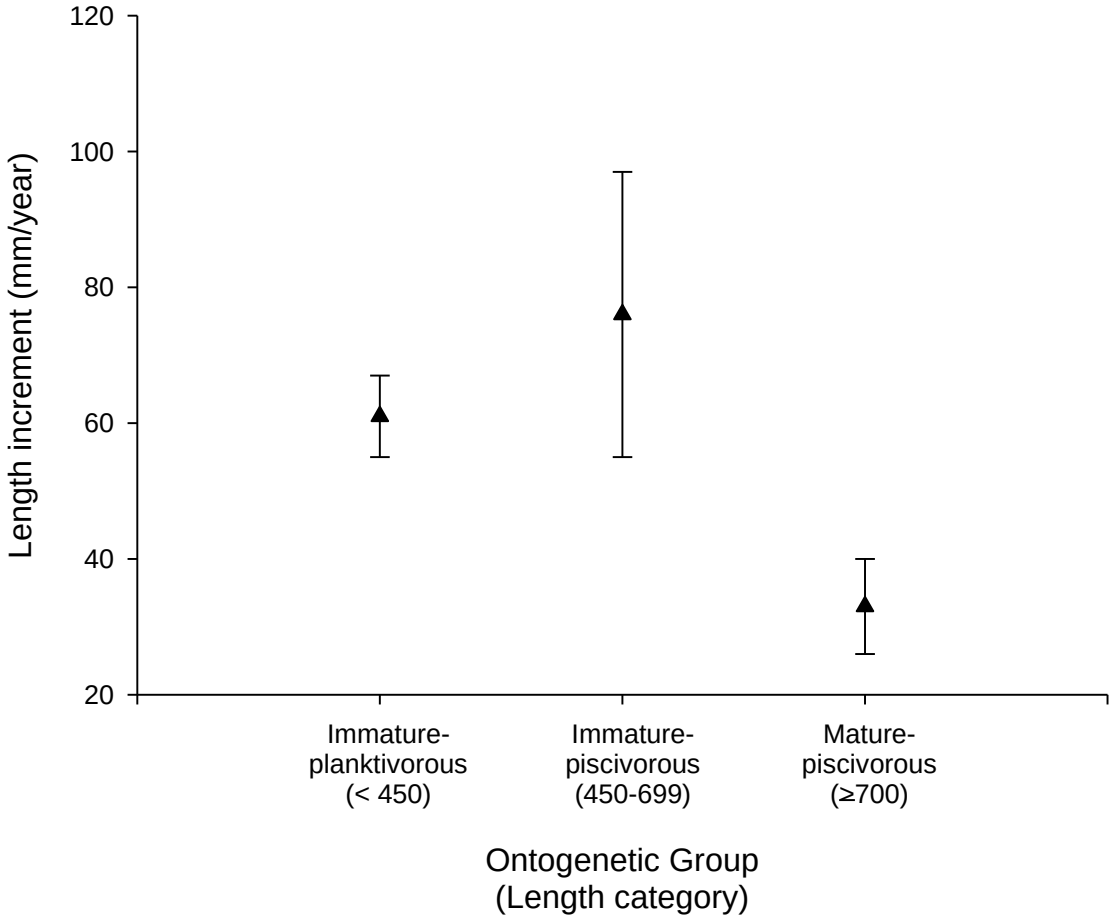

Figure 1.9. Mean annual growth increments (length) for lake trout marked in 2007 and recaptured in 2008 in Swan Lake, Montana. Error bars are 95% confidence interval.

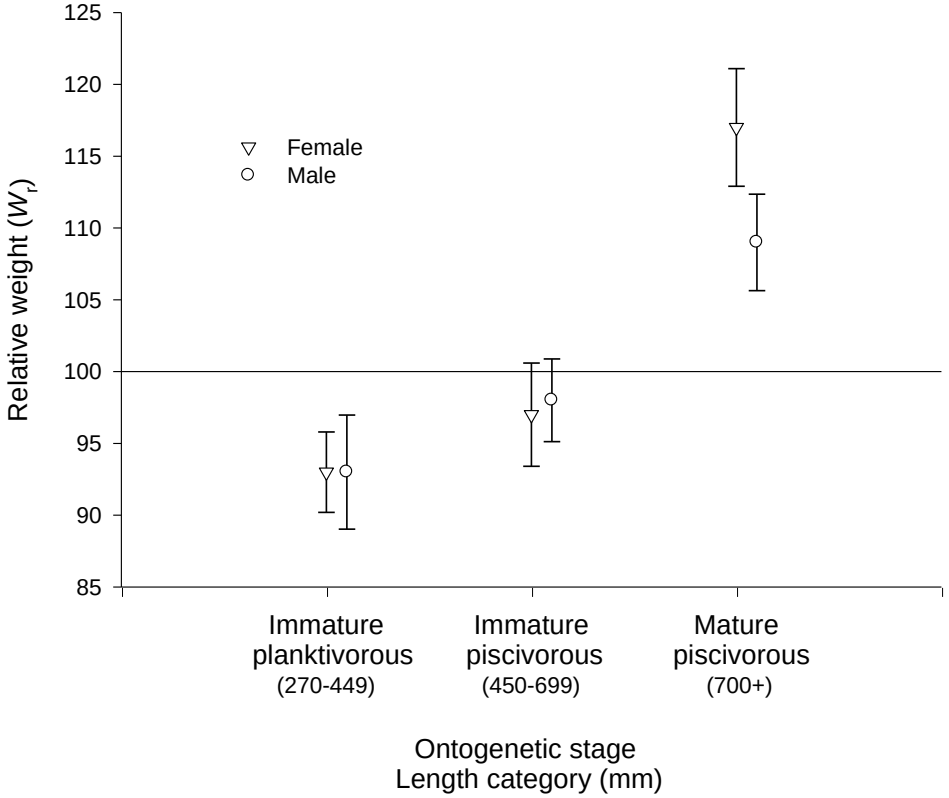

Figure 1.10. Relative weight (W_r) by ontogenetic stage and sex for lake trout collected in Swan Lake during September and October in 2007 and 2008. Error bars represent 95% confidence limits.

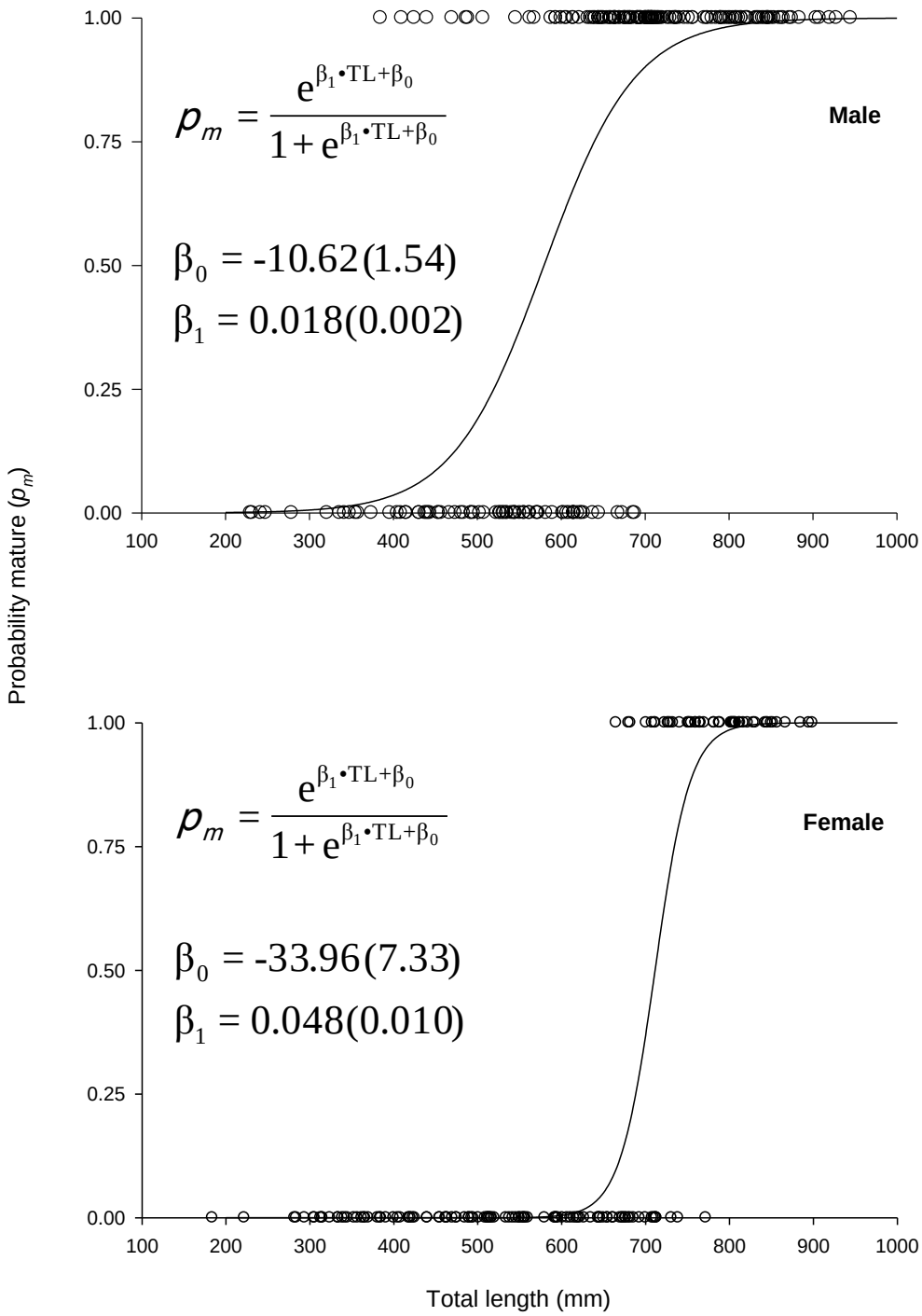

Figure 1.11. Logistic regression models to predict length at 50% and 90% maturity for lake trout in Swan Lake, Montana collected during September-October 2007 and 2008. Model parameter estimates are shown with SE in parenthesis.

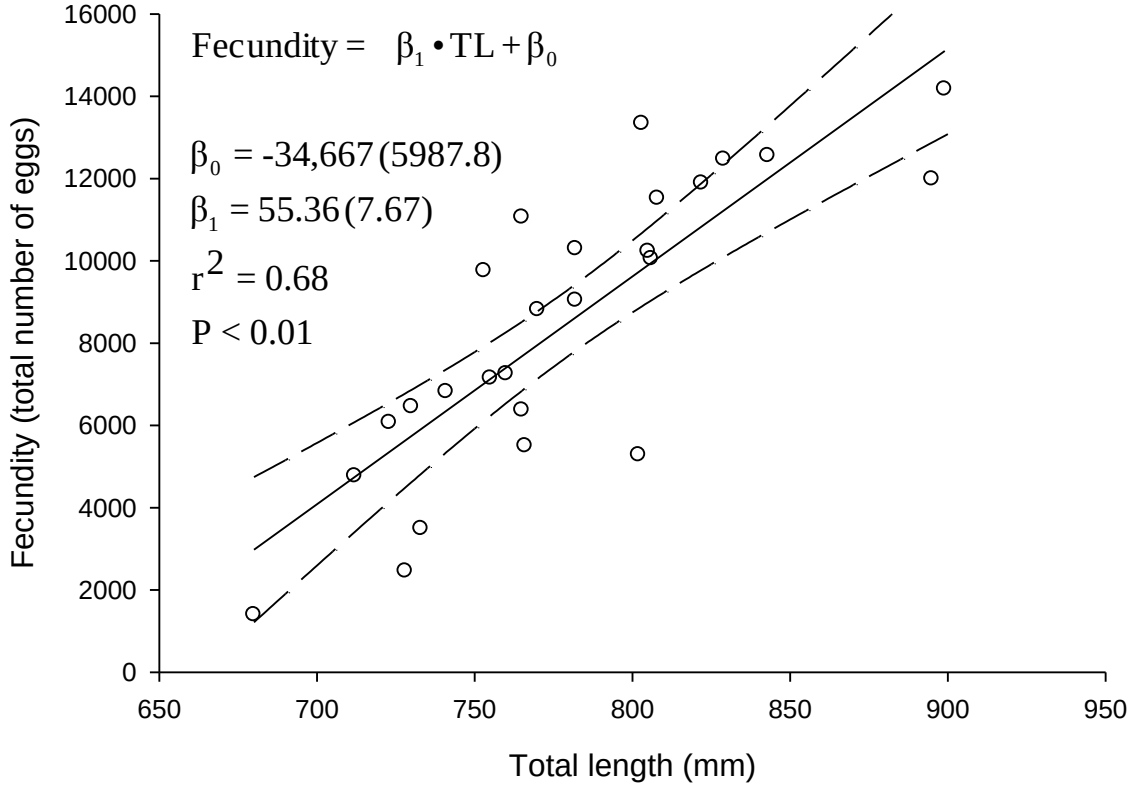

Figure 1.12. Fecundity-length relationship for lake trout in Swan Lake, Montana collected in 2008. Solid line represents the predicted regression model and dashed lines delineate the 95% confidence interval. Model parameter estimates are shown with SE in parenthesis.

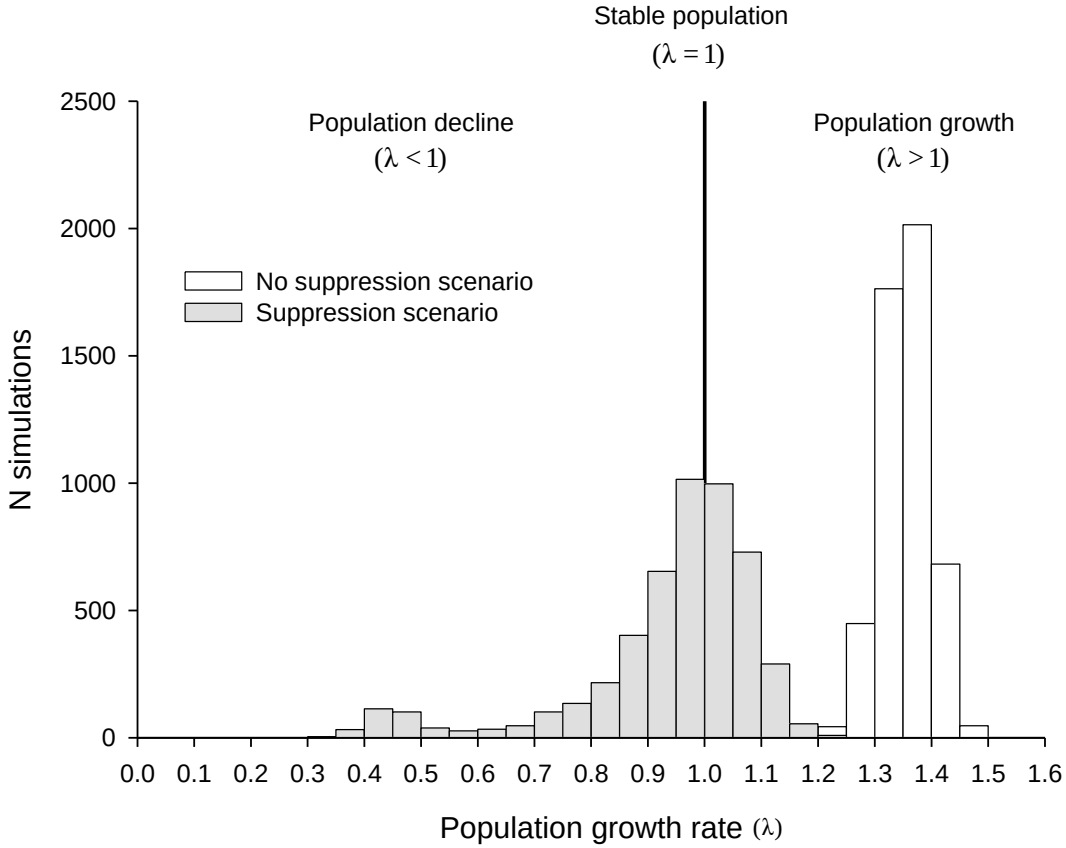

Figure 1.13. Distributions of population growth rates from simulations of no suppression and suppression management scenarios for lake trout in Swan Lake, Montana.

CHAPTER 2

IDENTIFICATION OF LAKE TROUT SPAWNING LOCATIONS IN SWAN LAKE, MONTANA

Introduction

The reproductive behavior of lake trout *Salvelinus namaycush* has been studied extensively for conservation and restoration of native lake trout populations (Marsden et al. 1995). Targeting lake trout during the spawning season has recently been considered for suppressing introduced lake trout populations where they threaten native species and recreational fisheries in the western USA (Dux 2005; Martinez et al. 2009). Lake trout are vulnerable to over exploitation because of their long-lived, late-maturing life history (Trippel 1993; but see Musick 1999). Lake trout suppression programs must achieve recruitment overfishing by minimizing survival of juveniles to reproductive ages and maintaining a low density of spawning adults. Agencies of the Swan Valley Bull Trout Working Group (SVBTWG) in northwest Montana are implementing an experimental lake trout suppression program to evaluate the potential for mechanical removal to suppress an invasive lake trout population in Swan Lake.

Identifying spawning locations of this population will allow the SVBTWG to target high densities of adult fish during the spawning period. Sensitivity-elasticity analyses have shown that long-lived, late-maturing species are sensitive to changes in survival rates of juveniles and adults (Heppel et al. 1999, 2000; see chapter 1). Targeting spawning locations with gill nets or other gears may be a cost-effective method to maximize catch of adult fish with minimal effort. The objectives of this study were to

identify the spawning locations of an invasive lake trout population. Introduced lake trout should exhibit similar reproductive behavior outside their natural range. I predict lake trout will be found spawning over coarse angular substrates in Swan Lake. Knowledge of spawning locations will allow management agencies to target incubating lake trout embryos with alternative suppression techniques, and provide opportunities to study early life history and recruitment of nonnative lake trout in the Intermountain West.

Methods

Lake trout spawning locations were identified in Swan Lake using three complementary sampling methods. Ultrasonic telemetry was used in 2007 and 2008 to locate areas where mature lake trout occurred from mid-October to mid-November. In 2008, short-set gill nets and mesh in-situ egg nets were deployed in areas where density of telemetry relocations was highest to confirm spawning by lake trout.

Nineteen adult lake trout were implanted with depth-sensitive ultrasonic transmitters (Model custom DT, Sonotronics Inc.) during gill net sampling in 2007 (see chapter 1, Table 2.1). Fish were anesthetized with tricane methanesulfonate (MS-222), and an incision was made left of the mid-ventral line. Transmitters were inserted in the body cavity and incisions were closed using Ethicon Vicryl 3-0 braided nylon sutures. I anticipated implanting twelve additional lake trout with transmitters in 2008, however due to technical difficulties only four additional transmitters were deployed. Four transmitters from 2007 were relocated in 2008 as well. Transmitters were implanted only in male lake trout in 2008 because male lake trout spend more time at spawning locations

than females (Martin and Olver 1980, Gunn 1995) and ovary samples were needed for fecundity estimates (see chapter 1).

Fish were relocated manually with a directional hydrophone (Model DH-4) and ultrasonic receiver (Sonotronics Inc, Tucson AZ). Tracking was conducted after dark in 2007 and 2008. A north south oriented transect of eleven points was used to select a random starting point for each tracking event in 2007 to minimize any geographic bias in tracking (i.e., repeatedly tracking where fish were known to be located). The entire lake was scanned on tracking nights in 2008. Tag frequencies were scanned along the transect by moving the hydrophone 90 degrees east and 90 degrees west until a transmitter was detected. Locations were recorded when the acoustic signal was equal in all directions (Guy et al. 1994; Dux 2005). Fish positions were recorded using a hand-held GPS unit with an external antenna in 2007 (Garmin GPSMap76s) and a boat mounted GPS unit (Garmin GPSMap460s) in 2008. Error in GPS positions was generally less than 3.6 m. Tag number, tag pulse interval (to determine fish depth), and lake depth were recorded for each relocation. Error in relocations was not directly estimated. However, relocation error from manual tracking with similar ultrasonic transmitters has been reported between 8.5 and 11.6 m in lake trout (Flavelle et al. 2002; Dux 2005; Morbey et al. 2006).

A kernel density surface was created to identify areas where adult lake trout occurred in the highest concentration from mid-October to mid-November in 2007 and 2008. The kernel density of relocations throughout the lake was calculated in each year by pooling relocations of all individuals. Kernel-density surfaces for 2007 and 2008 were generated in ArcGIS 9.2 (ESRI 2006). A relative relocation density (RRD) surface of

Swan Lake was created to identify the areas of highest relocation density by scaling the maximum kernel-density in each year to one using the ArcGIS raster calculator (ESRI 2006). Mean slope (%) and SD was calculated at spawning sites using the slope surface analysis tool in ArcGIS 9.2 (ESRI 2006) with a 1m bathymetric grid of Swan Lake (M. Reller, Constellation Services, unpublished data).

In 2008, short-set gill nets were deployed locations identified with kernel density surfaces to confirm the presence of gravid lake trout. A 274.3-m long gill net with 5.08-cm bar mesh was set at each site once weekly from 20 October 2008 to 9 November 2008. The net fished for an average of 2.16 h per set. All lake trout captured were euthanized, measured to the nearest mm TL, and otoliths removed for age determination (see chapter 1). Sex was determined for all fish by dissection if gametes were not readily expressed during handling.

Egg nets were buried in the substrate in 2008 to collect lake trout eggs at spawning locations identified with 2007 telemetry data. Sixty egg nets were constructed following Perkins and Krueger (1994). Egg net bags had circular openings (33 cm diameter) and each sampled an area of 0.08 m^2. Egg nets were buried by SCUBA divers in mid-to-late September, before any lake trout with ultrasonic transmitters had arrived at the alleged spawning locations. Three rows of 10 egg nets spaced approximately 1.5 m apart were buried in the substrate at water depths of 3.05, 4.57, and 6.10 m at the two alleged spawning locations. Nets were retrieved by SCUBA divers from 20 November 2008 to 23 November 2008, approximately two weeks after the last telemetry relocations were recorded at either site. Samples from egg nets were sorted immediately after

retrieval and all eggs were preserved in 95% ethanol. Mean egg density (eggs/m^2) was calculated by depth contour and site (Perkins and Krueger 1994). Overall mean egg density was calculated for each site as the average density of all nets (Perkins and Krueger 1994).

Eleven eggs were genotyped at six microsattelite loci to determine their species of origin. For comparison, three known bull trout and three known lake trout samples were also genotyped. Alleles at these six microsatellite loci are either fixed or have disparate range for lake trout or bull trout (e.g., locus *Sfo12* is fixed at 224 for bull trout and is either 254 or 283 for lake trout; Angers 1997). In addition, several of these microsatellite loci are present in either lake trout or bull trout, but not both. For example, locus *Sco216* is amplified using PCR in bull trout but not lake trout (Dehaan 2005) and locus *Sna-MSU11* is amplified in lake trout but not bull trout (Rollins 2008). The species identity of eggs captured at spawning locations were determined by comparing the microsatellite alleles found at these six loci to the samples of known origin.

Results

Fifteen adult lake trout (12 male, 3 female) were relocated 125 times from 11 October 2007 to 13 November 2007 and six male lake trout and one female lake trout were relocated 35 times from 16 October to 9 November 2008. Relocations were most densely concentrated at two sites in the southern end of Swan Lake (Figure 2.1). These sites were along Montana Highway 83 on the southeast shore, where coarse, angular substrates descend into the lake (Figures 2.2). Mean slope was 72% (SD= 44%) at the

northern site and 39% (SD= 39%) at the southern site. On one evening (22 October 2007), six of 17 fish were observed at the two sites. Two large males (809 and 815 mm) were observed only at these locations throughout the sampling period in 2007. One female lake trout was observed at each site on two consecutive nights (22 and 23 October 2007). Four of seven telemetered fish were observed at the spawning sites on 20 October 2008. Fish depth varied from 1.5 to 12.8 m and averaged 6.7 m (SD = 2.4) at both sites in 2007. Fish depth varied from 1.2 to 8.8 m and averaged 6.6 m (SD = 2.3) at both sites in 2008.

Gravid lake trout were captured in gill nets at the north and south spawning sites (Figure 2.1). Sixty-nine adult lake trout were captured in six gill-net sets from 22 October to 5 November 2008. Catch per unit effort (0.095 fish $\cdot$ $m^{-1}\cdot$ h soak $time^{-1}$) of sexually mature fish was approximately 10 times greater at spawning locations than during lake-wide removal netting in 2008 (Table 2.2; see Figure 1.6). Length of spawning males varied from 605 to 928 mm and spawning female lake trout varied in length from 788 to 885 mm (Figure 2.3). The sex ratio (M: F) of fish captured at spawning sites in 2008 was 4.3:1.

Three-hundred and fifty-six eggs were collected in 58 egg nets buried at the two spawning sites (Figure 2.1). Eggs collected were identified as lake trout based on DNA sequencing (Table 2.3). Of these, 80% were eyed embryos, 10% were chorions, 6% had no visible embryo, and 4% were covered in white fungus. Egg density varied from zero to 1,113 eggs/m^2. Mean egg density was 113 eggs/m^2 at the north site and 38 eggs/ m^2 at the south site (Table 2.4). At the north site, egg density was lowest in nets set at the 4.57

m contour and was similar between the 3.05 and 6.10 m depth contours (Table 2.4). At the south site, egg density varied little among depth contours (Table 2.4).

Discussion

Using three complementary sampling methods, lake trout spawning locations were successfully identified in Swan Lake. Two primary spawning sites were identified with telemetry relocations in 2007. In 2008, short-set gill nets confirmed the presence of gravid adult lake trout at spawning locations. Egg nets buried in the substrate confirmed that spawning had occurred at these two sites.

Spawning sites in Swan Lake were characteristic of lake trout spawning habitat, with coarse angular substrate on a steep slope (Marsden et al. 1995). Lake trout rely on interstitial space for secure egg deposition and protection from predators (DeRoche 1969; Gunn 1995; Marsden et al. 1995; Sly and Evans 1996; Claramunt et al. 2005). Lake trout generally use cobble (26-100 cm) and rubble (0.65-25 cm) substrates for egg deposition in their native range (Marsden et al. 1995). Substrates at these locations were angular tailings along Montana Highway 83.

Lake trout commonly use habitat created by humans for spawning (Marsden et al. 1995). Prevost (1957) found lake trout eggs in angular fill used to elevate a railroad bed in Lake Massawippi, Quebec. Lake trout used remnant mine tailings and marina breakwalls for egg deposition in Lake Champlain (Elrott and Marsden 2004). In Lake McDonald, Glacier National Park, lake trout were found congregating during the autumn on a steep shoreline where tailings from construction of the Going to the Sun Road

descend into the lake (Dux 2005). Historic road construction may facilitate the colonization of lakes in the western USA by creating high-quality spawning habitat for lake trout.

Lake trout exhibit spawning site fidelity (Gunn 1995; Elrott and Marsden 2004) and generally use fewer sites in smaller lakes (Marshall 1996; Melville 2005). Lake trout in Swan Lake were found at the same two locations during the autumn in 2007 and 2008. Individual male lake trout also exhibited site fidelity in 2007 and 2008. Males typically arrive at spawning locations earlier and remain longer than females (DeRoche 1969; Martin and Olver 1980; McLean et al. 1981; Gunn 1995). In 2007, multiple male lake trout remained at spawning locations for several consecutive nights and the final telemetry relocation recorded at the spawning sites was of a large male lake trout. Female lake trout have been shown to move greater distances during the spawning season (McLean et al. 1981). Relocations of the three telemetered female lake trout in 2007 were more widely distributed than for males. Although three telemetered females were relocated around shoals in the mid-lake region in 2007, telemetry relocations of lake trout of either sex were not consistently oriented around any of the rocky shoals in the mid-lake region. In 2008, fewer relocations were made in the mid-lake region suggesting that this is not a high-use area. Care was taken to tag adult lake trout over a wide spatial scale during lake-wide gill net sampling in both years. Given the size and shape of Swan Lake, it is unlikely aggregations of telemetered lake trout would have been missed during the tracking periods in 2007 and 2008. Although the highest densities of telemetered lake

trout occurred at the same locations in 2007 and 2008, alternative spawning sites may exist.

Egg nets confirmed that spawning had occurred at the locations identified with acoustic telemetry. Female lake trout broadcast several clutches of eggs in patches of suitable habitat across spawning areas (DeRoche 1969; Esteve 2008). Estimates of egg density vary at spawning locations due to patchy egg deposition by females (Gunn 1995; Kelso 1995; Marsden et al. 1995). Egg density at spawning locations in Swan Lake was low when compared to estimates of egg density in lakes where lake trout are native. Mean egg density was 538 eggs/m^2 for lake trout populations in Ontario (Martin and Olver 1980). Estimates of mean egg density varied from six to 6,178 eggs/m^2 at eight sites in Lake Ontario (Fitzsimmons 1995). At fifteen spawning sites in Lake Champlain, egg density varied from 0.001 to 9,623 eggs/m^2 (Elrott and Marsden 2004). In Parry Sound, Lake Huron mean lake trout egg density was 454.7 eggs/m^2 (Jonas et al. 2005). Low egg density in Lake Michigan (7.5 eggs/m^2) was thought to be due to a low abundance of broodstock (Jonas et al. 2005).

The relatively low egg density observed at spawning locations in Swan Lake may reflect a relatively low abundance of spawning adults (see chapter 1). Although predation on lake trout eggs by predators including sculpins *Cottus* spp. and crayfish can inflict mortality up to 80% during the first several weeks after spawning, eggs that survive this early period are likely to survive through the winter (Claramunt et al. 2005). Egg samplers in Swan Lake were retrieved approximately two weeks after the last

telemetered male lake trout was relocated at the spawning locations. Thus, egg density estimates from nets in Swan Lake should reflect successful egg deposition. However, the removal of gravid female lake trout with gill nets at spawning locations could have indirectly reduced egg density.

Spawning locations of an invasive lake trout population were successfully identified in a relatively small lake using ultrasonic telemetry, egg nets, and short-set gill nets. Matrix model simulations have shown that long lived, late maturing species are sensitive to changes in juvenile and adult survival rates (see chapter 1; Heppel et al. 1999, 2000). Targeting spawning locations is an efficient means to reduce survival rates of both adult and age-0 lake trout. Management agencies in the Intermountain West can exploit the site fidelity of spawning lake trout and maximize CPUE of adult lake trout by netting these areas through the spawning period. Knowledge of spawning locations may also facilitate the application of in-situ embryo reduction techniques in the future (e.g., using electricity; Bohl et al. 2010).

Table 2.1. Biological data for lake trout implanted with ultrasonic transmitters in Swan Lake in 2007 and 2008. U=unknown sex.

Year tagged	TL (mm)	Weight (g)	Sex	Number of Relocations 2007	2008
2007	857	10104	F	*	
	847	7821	M	*	
	760	5613	F	9	3
	622	2815	M	5	4
	840	9188	M	15	
	594	2365	M	5	1
	701	3983	M	2	
	711	4512	F	10	
	809	6540	M	16	
	594	2211	M	6	
	815	7011	M	10	10
	822	6098	M	5	
	721	4356	M	7	
	640	2749	M	5	
	602	2355	U	2	
	708	3354	F	10	
	757	4946	M	12	
	651	3066	M	8	
2008	705	3740	M		3
	706	3815	M		4
	800	6228	M		10
	757	4915	M		*

*Transmitter stationary and fish either died or shed transmitter. Data from these fish were not included in analyses

Table.2.2. Summary of lake trout catch data using short-set gill nets at spawning locations in Swan Lake, 2008.

Date	Site	Catch per unit effort (lake trout·m net^{-1}·h^{-1})	Sex ratio (M:F)
10/22/2008	N	0.12	2.5:1
10/28/2008	N	0.12	3.7:1
11/6/2008	N	0.07	9:1
10/23/2008	S	0.10	6:1
10/30/2008	S	0.13	6:1
11/5/2008	S	0.03	5:0

Table 2.3. Species identification genetic results for samples of known origin and egg samples collected in Swan Lake, November 2008. NA = no amplification.

		Locus					
Sample name	Species	*Sfo12*	*Sna_MSU12*	*Sna_MSU10*	*Sna_MSU08*	*Sna_MSU11*	*Sco216*
Bull Trout GSC_017	Bull trout	224224	NA	NA	129129	NA	231231
Bull Trout GSC_1077	Bull trout	224224	NA	NA	129129	NA	231231
Bull Trout GSC_995	Bull trout	224224	NA	NA	129129	NA	231231
Swan Lake Sna 1	Lake trout	254254	200200	235239	156177	229245	NA
Swan Lake Sna 2	Lake trout	254254	200200	235239	177177	229245	NA
Swan Lake Sna 3	Lake trout	254254	198200	235239	156177	245251	NA
Egg sample 01	Unknown	254254	200216	196235	156156	245251	NA
Egg sample 02	Unknown	254254	200200	201235	156177	251251	NA
Egg sample 03	Unknown	254254	198200	196239	177177	229251	NA
Egg sample 04	Unknown	254254	198216	196239	156177	245245	NA
Egg sample 05	Unknown	254254	200216	239239	156177	245251	NA
Egg sample 06	Unknown	254254	200216	235235	156177	245245	NA
Egg sample 07	Unknown	254254	200200	235239	177177	245251	NA
Egg sample 08	Unknown	254254	200200	235235	156177	251251	NA
Egg sample 09	Unknown	254254	198216	196235	156177	229251	NA
Egg sample 10	Unknown	254254	200200	196235	156177	245245	NA
Egg sample 11	Unknown	254254	200200	196196	177177	245245	NA

Table 2.4. Summary of egg-net data collected at lake trout spawning locations in Swan Lake, from September through November 2008.

Site	Depth (m)	Number of samples	Samples with eggs	Total eggs	Mean egg density ±SD	Egg density min-max
North	3.05	10	6	109	136 ± 109	0-1,113
	4.57	10	6	55	69 ± 28	0-238
	6.10	10	7	107	134 ± 71	0-638
South	3.05	10	1	38	48 ± 47	0-475
	4.57	10	2	27	34 ± 30	0-313
	6.10	8	4	20	31 ± 14	0-100

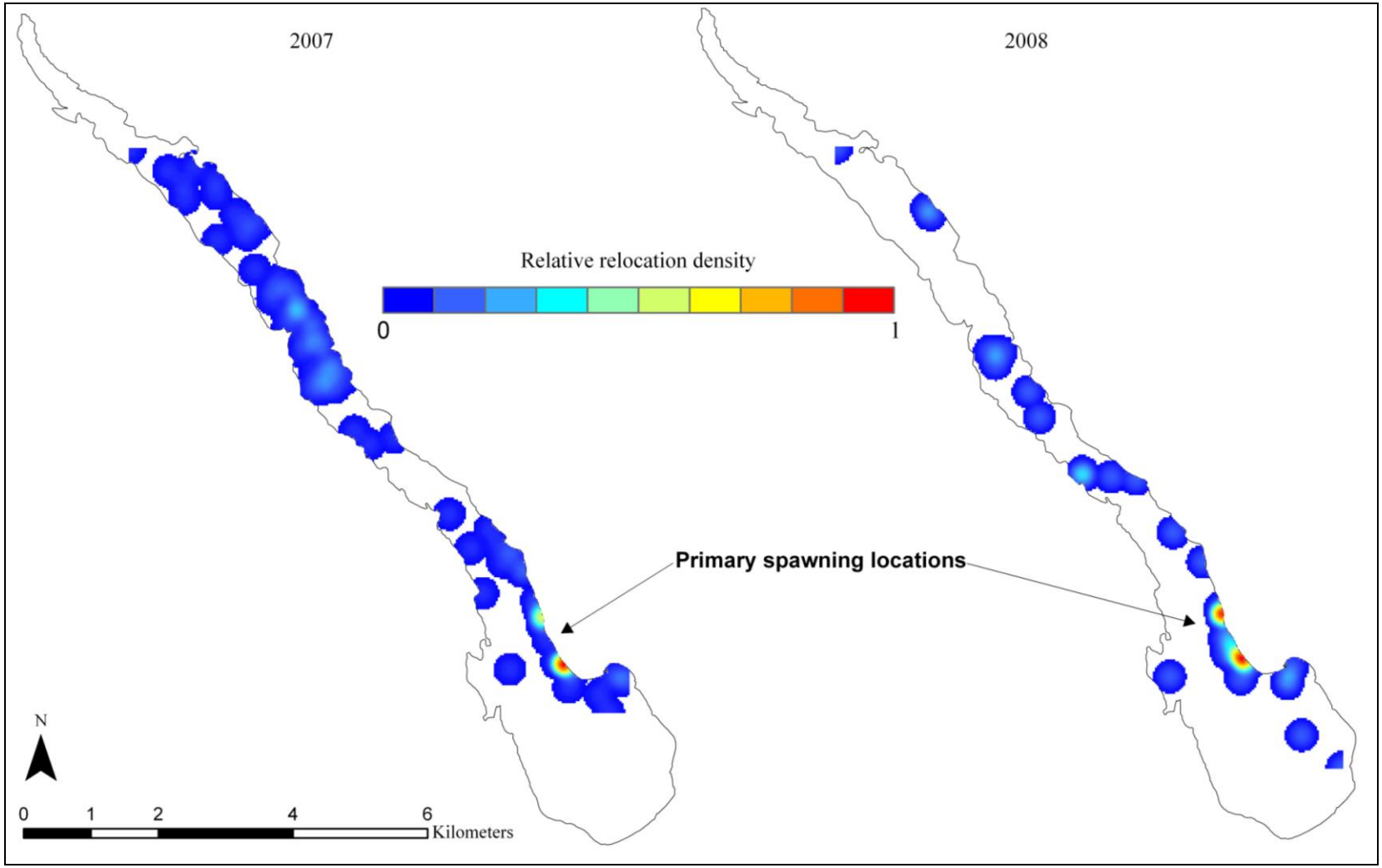

Figure 2.1. Relative relocation density surfaces generated from telemetry relocations of adult lake trout in Swan Lake, Montana from October through November in 2007 and 2008.

5 cm

Figure 2.2. Example of substrate used for egg deposition by lake trout in Swan Lake, Montana. In the center is an egg net in-situ immediately prior to retrieval in late November 2008.

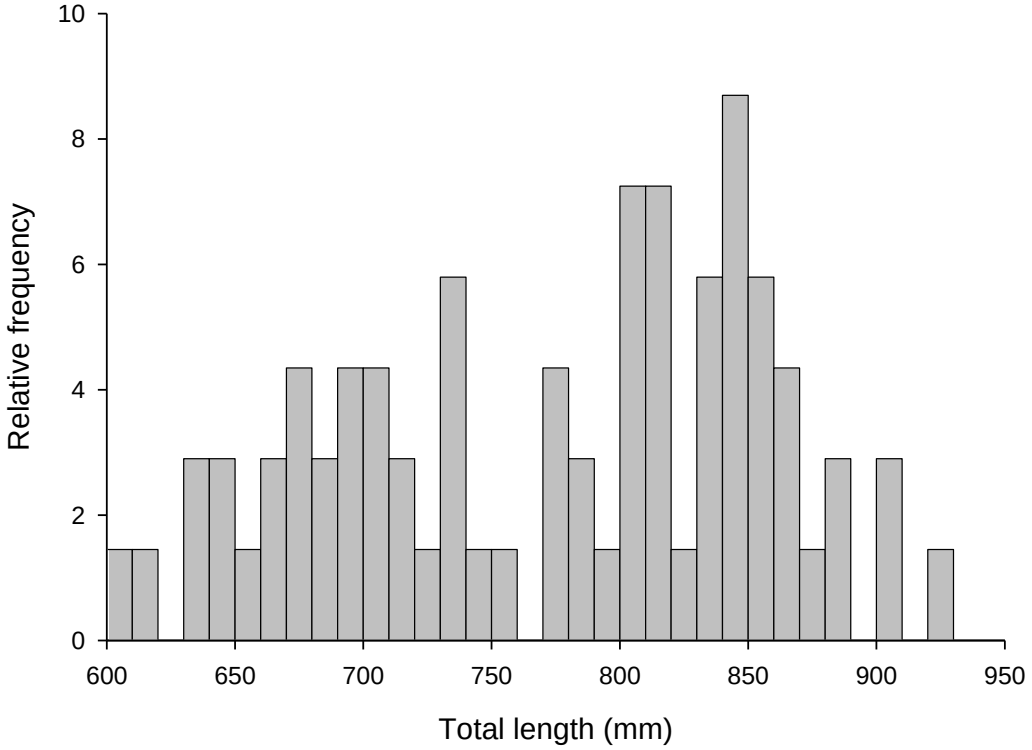

Figure 2.3. Relative length-frequency distribution of lake trout captured at spawning locations in Swan Lake, from 22 October to 5 November 2008.

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