THESIS

# MANAGEMENT STRATEGIES FOR MULTI-USE RECREATIONAL FISHERIES: COEXISTENCE OF KOKANEE AND TROPHY LAKE TROUT IN WESTERN WATERS


Submitted by

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## ABSTRACT


MANAGEMENT STRATEGIES FOR MULTIUSE RECREATIONAL FISHERIES: COEXISTENCE OF KOKANEE AND TROPHY LAKE TROUT IN WESTERN WATERS

Kokanee *Oncorhynchus nerka* are stocked in coldwater reservoirs throughout the western United States for sport fishing and they are a popular fish for both managers and anglers alike. Lake trout *Salvelinus namaycush* have also been introduced to many western reservoirs, partly because they can attain relatively large sizes (> 30 kg). These piscivores require a large, high quality forage base to sustain high growth rates, and kokanee can fulfill this requirement. However, where lake trout and kokanee co-occur, lake trout often grow in size and numbers and their consumptive demand increases beyond the capacity of the kokanee population to support. Consequently, kokanee abundance declines followed by precipitous declines in lake trout growth and body condition. My work focused on finding a management strategy that could produce sustainable fisheries for both in Blue Mesa Reservoir, Colorado, where lake trout appear to have diminished kokanee abundance. In 2009, managers began a lake trout removal program in an attempt to achieve the primary management goal of a sustainable, hatchery-dependent kokanee population and the secondary goal to provide a trophy lake trout fishery. I developed an age-structured kokanee population model using estimates of natural mortality, harvest, and predation from lake trout with a fixed annual stocking quota of kokanee fry. Age-specific estimates of natural and fishing mortality were estimated using an allometric model and creel survey, respectively. I then determined lake trout consumptive demand on the kokanee population with a bioenergetics model by estimating lake trout abundance, growth rates, diet, and energy densities of predator and prey species. Then alternative management scenarios to reduce lake trout consumptive demand were evaluated using the Fishery Analysis and Modeling Simulator parameterized for the Blue Mesa Reservoir lake trout population. After estimating the current level of lake trout removal ($\mu$ = 0.231 for age-4 through age-9), it was incrementally increased to determine the level that allowed for a stable kokanee population ($\mu$ = 0.381). The simulations suggested that removal of lake trout must be intensified if kokanee and fast-growing lake trout are to persist in Blue Mesa Reservoir, Colorado.

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## Introduction

Within their native range (Canada, Alaska, the Great Lakes region and New England) lake trout *Salvelinus namaycush* are one of the largest apical predators and can attain sizes of over 45 kg (Scott and Crossman 1973). Even in systems with relatively low productivity, lake trout can attain sizes of ~18 kg (Donald and Alger 1986). Native lake trout are usually relatively slow growing, reaching sexual maturity at about 10 years of age, with long population doubling times (Healey 1978, Ferreri and Taylor 1996). Lake trout may live more than 50 years, but a typical maximum age is between 35-40 years (Power 1978, Dux 2005).

Lake trout are widely distributed outside their native range, a result of human introductions followed by natural movement to reservoirs and lakes across northern and western North America (Crossman 1995, Hansen et al. 2008, Martinez et al. 2009). Some introduced populations grow faster and attain larger size than is typical for the species (Martinez et al. 2009). Their potential to reach large size has created a devoted angler clientele in many waters where lake trout have been introduced, and protective fishing regulations were put in place on lake trout in the 1980s and early 1990s to foster production of trophy sized fish (Martinez et al. 2009). Many agencies still manage lake trout as a trophy fish, with regulations usually including protective slot limits (Johnson and Martinez 2000, Martinez et al. 2009). Lake trout thrived in western lakes and reservoirs, protected from harvest and enjoying energy-rich salmonid prey and longer growing seasons than occur in their native range.

There are many western U.S. lakes and reservoirs with the potential to produce relatively large lake trout, but sustaining suitable forage bases has been problematic. For example, Flaming Gorge Reservoir (Utah, Wyoming) historically produced trophy lake trout (> 20 kg) starting in the 1980s (Luecke et al. 1999, Martinez et al. 2009). But, lake trout predation depleted native Utah chub *Gila atraria* and introduced kokanee *Oncorhynchus nerka* and growth and condition of lake trout declined (Yule and Luecke 1993, Luecke et al. 1999). In Flathead Lake (Montana) and Lake Chelan (Washington) lake trout became abundant and were detrimental to populations of kokanee and native trout species (BIA 2012; Schoen et al. 2012).

Lake Pend Oreille (Idaho) is another example of a system that supported large lake trout in the past, but the forage base was not sustainable. Lake trout were introduced into this system in 1925, and became abundant in the mid-1990s (Martinez et al. 2009). Kokanee were also introduced into the system, became self-sustaining by the mid-1930s, and were abundant enough to support a commercial fishery. But, by 2000 the kokanee population in Lake Pend Oreille was nearly extirpated by predation from lake trout and the lake trout population had the capacity to reach an abundance of 400,000 fish by 2010 without management intervention (Hansen et al. 2008). In 2006, intensive lake trout removal began in Lake Pend Oreille in an attempt to induce mortality rates > 50% per year (Hansen et al. 2008), a threshold that Healey (1978) stated would induce a decline in lake trout abundance in most populations in North America. Trap nets and gill nets were used by the management agency for lake trout removal and a commercial fishery was also initiated. Further, cash incentives ($10-$15 per fish) were offered as a means to encourage lake trout harvest.

Blue Mesa Reservoir (BMR), Colorado, has a similar food web as the systems described above. However, individual lake trout in BMR exhibit some of the fastest growth rates on the continent (Martinez et al. 2009). An abundant supply of stocked kokanee prey led to four consecutive state record size lake trout being taken, beginning with a 17 kg fish in 1998. Two record sized lake trout were harvested in 2003, and the latest (22.8 kg) was caught in 2007. Although large lake trout are sought by specialized anglers, Colorado Parks and Wildlife (CPW) creel surveys showed the primary species of interest in BMR is kokanee, with 45% of anglers traveling to the location to specifically target that species while 7% targeted lake trout (D. Brauch, unpublished). The kokanee fishery has been valued at more than $5 million per year to the local economy (Johnson et al. 2009).

Lake trout were stocked in BMR during 1973-1992, and by 1993 gill net surveys showed a size structure indicative of natural recruitment, despite removal of size regulations and an increase in the daily bag limit to 8 fish. This apparent change in wild recruitment corresponded with new dam operations implemented in 1992 that kept the reservoir level more stable during fall and winter, when lake trout eggs are incubating. Relative weight ($W_r$) of large individuals (> 1,000 mm TL) decreased in recent years from $W_r$ > 154 in 2000 to 108 in 2009, suggesting a decrease in prey availability. This decrease in prey was corroborated by SONAR and creel surveys that demonstrated a significant decrease in kokanee abundance (Brauch, unpublished). Annual SONAR surveys estimated that pelagic fish (mostly kokanee) abundance decreased 90% from > 1,000,000 in 2002 to < 100,000 in 2009. Similarly, creel survey data showed a decrease in angler harvest from 130,000 kokanee in 2002 to < 20,000 in 2009. This decline in the kokanee population occurred despite efforts to boost abundance through increased annual fry stocking from 1.4 million per year in 1994 to 3.1 million per year in 2009. Because BMR has supplied up to 90% of the state's hatchery supply of kokanee eggs used to stock 26 waters annually, the current state of the kokanee population has caused tremendous concern for CPW. In 2009 CPW began a lake trout removal program in an attempt to save the kokanee population from extirpation. The purpose of this investigation was to inform managers about management strategies that could allow for an abundant kokanee population and egg supply while secondarily maintaining angling opportunity for large lake trout.

## Methods

*Study area*

Located near Gunnison, Colorado, BMR is the state's largest reservoir with a surface area of 3,793 ha (Johnson and Martinez 2000). Blue Mesa Reservoir is a mesotrophic system that is thermally stratified from early May through late October (Johnson and Koski 2005). The dam was completed in 1965 with the intent to capture high spring runoff for summer irrigation, but also for power generation, and flat water recreation. Blue Mesa Reservoir is contained within the Curecanti National Recreation Area but the fishery in BMR is managed by CPW.

Blue Mesa Reservoir is a destination fishery, and since completion of the recreation area has received anglers from all contiguous 48 states of the U.S. (Brauch, unpublished). The fish community consists primarily of stocked kokanee and rainbow trout *Oncorhynchus mykiss* and wild lake trout, brown trout *Salmo trutta*, yellow perch *Perca flavescens*, white sucker *Catostomus commersonii*, and longnose sucker *Catostomus catostomus*. Kokanee are released every spring from the Roaring Judy Fish Hatchery (ROJ) into the East River, a tributary to BMR. Kokanee fry are imprinted to this location, rear in BMR until mature then migrate back upstream to ROJ where eggs are stripped, fertilized, and hatched. Natural reproduction of kokanee is negligible in BMR, and most other Colorado reservoirs (Johnson and Martinez 2000), emphasizing the importance of a stable egg supply for sustaining the State's kokanee fisheries.

*Lake trout population modeling*

We used Fishery Analysis and Modeling Simulator (FAMS; Slipke and Maceina 2010) to predict potential changes in lake trout abundance and size structure under different management scenarios including gill netting and water level manipulation. We used the Dynamic Pool Model within FAMS to simulate the effect of age-specific exploitation and natural mortality rates. The application uses a modified Beverton-Holt equilibrium yield model (Ricker 1975; Slipke and Maceina 2010):

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

where F = instantaneous rate of fishing mortality (exploitation),

$N_t$ = number of recruits entering the fishery at some minimum length at time (t),

Z = instantaneous rate of total mortality;

r = time in years to recruit to the fishery ($t_r - t_0$);

$t_r$ = time at recruitment;

$t_0$ = theoretical time when fish length is zero;

$W_\infty$ = maximum theoretical weight from predicting $L_\infty$ and the weight-length regression;

K = growth coefficient from the von Bertalanffy growth equation;

β = Beta coefficient computed by FAMS adjusting yield for input W-L relation;

$X = e^{-Kr}$;

$X_1 = e^{-K(\text{Maxage} - \text{to})}$ where Maxage is the maximum age observed in the sampled population;

P = Z/K;

Q = slope of the weight-length regression + 1.

Required parameters included: the species; $L_\infty$, K, and $t_0$ from the von Bertalanffy growth function (VBGF; Isely and Grabowski 2007); the intercept (a) and slope (b) of the $\log_e$ transformed weight-length relation; conditional fishing mortality and conditional natural mortality by age ($cf_{age}$ and $cm_{age}$, respectively); annual recruitment; and minimum total length at recruitment. Table 1 contains a complete list of parameter values that were obtained from BMR lake trout using the following methods.

*Lake trout abundance, age and growth, mortality, and recruitment.*– Lake trout abundance was estimated from a reservoir-wide population estimate using the Summer Profundal Index Netting protocol (SPIN; Sandstrom and Lester 2009) from 8 to 12 August 2011. Briefly, SPIN is a stratified-random gill netting method that allows for relatively rapid estimation of lake trout density, and subsequent estimation of abundance. The SPIN method has been calibrated using hundreds of systems with independent lake trout abundance estimates and known lake trout population sizes. See Sandstrom and Lester (2009) for further details.

Left sagittal otoliths (arbitrarily chosen to maintain consistency) were extracted from 545 lake trout culled in fall 2010 for age interpretation. Otoliths were sectioned perpendicular to the sulcus using an Isomet™ low speed saw with diamond wafering blades. Thin sections were sanded to a thickness of 0.8-1.0 mm and then polished. An image of the otolith thin section was digitally captured at 32× magnification to be used for age estimation. Two experienced readers estimated the age of all lake trout independently from each other without prior knowledge of fish length or weight. Lake trout age was estimated by assigning ages to checks assumed to be annuli on the digital images of sectioned otoliths. If there was disagreement between the estimated ages, then both readers would discuss the image until there was agreement.

Growth of lake trout was computed by fitting a VBGF (Isely and Grabowski 2007) to size at age data using the nonlinear models procedure (Proc NLIN) in SAS version 9.2 (SAS 2008). An age-length key was constructed to compute unbiased mean size at age (Devries and Frie 1996). The proportion of fish of each age in 50 mm size increments was computed and multiplied by an estimated unbiased size distribution of the population from SPIN, resulting in the age distribution of the population.

The age distribution of the population was then $\log_e$ transformed and total instantaneous mortality (Z) was calculated using the slope of the catch curve for lake trout ages 4-9. This age group comprised the descending limb of the catch curve (Miranda and Bettoli 2007); younger lake trout were not considered fully recruited to the sampling gear. Abundance of age 10-20 lake trout was low and consisted of an unknown mix of wild and stocked fish; thus, this age group was not used in mortality estimation. Creel harvest estimates from 2009 and 2010 surveys were used to determine angling exploitation (Brauch, unpublished) and combined with actual numbers of lake trout removed with gill nets to find the total instantaneous fishing mortality (F). Then, instantaneous natural mortality (M) for the population could be obtained by M = Z – F. Exploitation was set at zero in FAMS scenarios for ages 0-3 and age-10 and over due to negligible harvest by anglers and because CPW released lake trout over 765 mm (age-10) to preserve large fish for anglers. Abundance of young of year lake trout was back-calculated using M and applied to the age-4 abundance estimated from SPIN.

We used results from a mark-recapture and hydroacoustics study completed in 2002 (Crockett et al. 2006) and CPW creel surveys (Brauch, unpublished) to corroborate trends in lake trout population abundance. Colorado Parks and Wildlife conducted an intensive creel survey on BMR from May 1 through October 31 and has taken place annually from 1993-2012. The survey used a stratified random design with instantaneous counts of all anglers, and access point interviews. Counts were conducted at 4 hour intervals three times per day and about 10% of the anglers counted were interviewed either on boat ramps or along the shoreline. Catch, harvest, and size of harvested fish were recorded for each species. Lake trout catch per angler hour was computed from the total catch estimate and total angling effort (shore and boat anglers combined).

*Consumptive demand of lake trout on kokanee*

Stable carbon and nitrogen isotope analyses were conducted on various organisms collected from BMR to characterize the food web structure. A 1 $cm^3$ muscle plug was collected during CPW gill net sampling (spring and fall 2010) from lake trout, kokanee, brown trout, rainbow trout, white sucker, longnose sucker, and yellow perch. Epaxial muscle tissue with skin removed was taken from between the dorsal fin and lateral line then each sample was stored at -20 °C. Zooplankton, crayfish, amphipods and chironomids were also collected from the reservoir or fish stomachs during gill net sampling periods and stored at -20 °C. In the laboratory, samples (n = 306) were dried at 60 °C for 48-72 hours then ground to a fine powder with a mortar and pestle. Each sample was then analyzed for $\delta^{13}C$, $\delta^{15}N$, and carbon-to-nitrogen (C:N) ratio in a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer. Isotopic signatures were expressed as δ values, in parts per thousand (‰) differences from C and N standards:

$$\delta_{sample} = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

where R is the isotopic ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) of the sample or standard (Fry 2006). Standards used for normalization correction were brown trout (n = 22, $\delta^{13}C$ = -25.58‰, $\delta^{15}N$ = 17.31‰, 49.74% C, 12.95% N) and corn (n = 24, $\delta^{13}C$ = -11.66‰, $\delta^{15}N$ = 0.93‰, 45.97% C, 2.09% N). Standards used to determine isotopic precision were mink (n = 40, $\delta^{13}C$ = -25.21‰, $\delta^{15}N$ = 11.30‰, 49.99% C, 13.40% N) and rice (n = 9, $\delta^{13}C$ = -29.02‰, $\delta^{15}N$ = 0.93‰). Methionine (n = 26, $\delta^{13}C$ = -27.68‰, $\delta^{15}N$ = -4.71‰, 40.75% C, 9.41% N) was the chemical standard used to determine instrument linearity. The standard error from the mean of each standard used in analysis never exceeded 0.07‰.

Lipids are known to be depleted in $^{13}C$ when compared to muscle tissues, and lipid content can vary greatly among individual fish within a species as well as when comparing across species (Gearing 1991; Johnson et al. 2002). To avoid potential bias from differing lipid concentrations among samples and species, mathematical corrections for lipid content from Post et al. (2007) were applied to $\delta^{13}C$ values:

$$\delta^{13}C_{normalized} = \delta^{13}C_{measured} - 3.32 + 0.99 \times C{:}N$$

where C:N is the carbon-to-nitrogen ratio.

Once δ values were determined we used "MixSIR" software to estimate proportions of prey species being consumed. MixSIR is a Bayesian mixing model developed by Semmens and Moore (2008) that determines probability distributions for proportional source contributions to a predator's diet from prey types included in the model. Inputs for MixSIR are individual predator isotopic signatures and mean and standard deviations of prey isotopic signatures. Amount of isotopic fractionation with standard deviation for both $\delta^{13}C$ and $\delta^{15}N$ must also be included. We used default mean and standard deviations of fractionation previously determined by McCutchan et al. (2003) and validated in the model by Moore and Semmens (2008). We used $25 \times 10^6$ iterations in all runs of MixSIR which amply satisfied quality assurances (Semmens and Moore 2008).

The lake trout population was divided into four size/age classes corresponding to dietary and energetic differences related to trophic ontogeny (Table 2). The smallest size class was lake trout < age-3 (< 332 mm TL) and these fish consumed only invertebrates. The second group was age-3 fish ($332 \leq TL < 409$ mm) and corresponded to lake trout transitioning to piscivory. Fish in the third group were $4 \leq age \leq 10$ ($409 \leq TL < 740$ mm) and were 94.9% piscivorous. The last group consisted of fish ≥ age-10 (≥ 740 mm) and they were 98.1% piscivorous. This pattern of trophic ontogeny was virtually the same as that found for BMR lake trout by Johnson and Martinez (2000) and Johnson et al. (2002). Prey categories included 1) small invertebrates (chironomid larvae and pupae, amphipods, and daphnia), 2) crayfish, 3) yellow perch < 160 mm TL, 4) rainbow trout < 300 mm TL, and 5) kokanee. Catostomids did not appear in any lake trout guts or in the stable isotope mixing models. Median values from the probability distribution for each prey category generated by MixSIR were used to estimate diet composition (Table 2) used in the following bioenergetics modeling.

*Consumption.*– Because of the unusually rapid growth of lake trout in BMR, we wanted to estimate lake trout consumptive demand as accurately as possible. To accomplish this, we measured energy density of lake trout and all prey species found in lake trout diets. Fish collected from BMR (n = 73) for calorimetry were measured to the nearest mm, weighed to the nearest gram, and then frozen whole at -20 °C. Whole fish were then cut into ~1.5 cm cubes while still frozen and dried to constant weight at 60 °C to determine water content. Then the entire fish was ground to a fine powder and homogenized. Three subsamples of each fish were analyzed in a Parr 1261 isoperibol bomb calorimeter for energy density. Energy content of each dry sample was then converted back to energy on a wet-weight basis using water content determined for each sample.

Consumptive demand of lake trout was estimated using Fish Bioenergetics 3.0 (Hanson et al. 1997). Average energy density of four age groups of lake trout and their prey (Table 2) were determined from measured values, by taxon (rainbow trout, yellow perch, crayfish and small invertebrates) or in size-classes consumed by lake trout (kokanee). Lake trout diet composition was determined for size classes identical to those listed in the stable isotope mixing models. Age classes of lake trout were converted to weights at age using the VBGF. Other parameters required for Fish Bioenergetics 3.0 include water temperature, prey digestibility, first age and timing of spawning, and fraction of body mass lost to spawning. We used observed thermal profiles and assumed lake trout sought temperature closest to their optimum (10°C; Stewart et al. 1983) to develop the thermal history in simulations: day 1 through 89: 4°C, day 90 through 119; 5°C, day 120 through 143: at 8°C, day 144 through 303; 10°C, day 304 through 333: 8°C, and day 334 through 365: 4°C. Day 1 coincides with January 1, and temperatures are mean measured values from BMR below the thermocline if stratified and mean temperature if isothermal. Prey fish, crayfish, and small invertebrates were 3.3%, 25%, and 10% indigestible, respectively (Yule and Luecke 1993). First age at spawning was set to age-6 to coincide with observed age at 50% maturity, and occurred on day 300 of simulations with 9.1% of fish mass lost to spawning. Day 300 was chosen to coincide with the height of observed lake trout spawning in late October. Fish mass spawned was a mean value associated with measured ripe skein weight (14.8% body weight) from female lake trout from BMR and the average value for males (3.3%) from Ruzycki et al. (2003). Sex ratio used was 50% as observed in BMR, and spawning occurred every year of the simulation.

Because we were most interested in population level impacts to kokanee, we converted the mass of kokanee consumed into numbers of kokanee. From stomach content analyses we found that the mean total length of kokanee consumed was equivalent to 33% of lake trout total length, a value corroborated by Johnson and Martinez (2000), Ruzycki et al. (2003), and Yule and Luecke (1993). Length of kokanee consumed based on lake trout length was converted to wet weight with a weight-length relationship for kokanee from BMR (below). Per capita biomass consumed by each age group of lake trout was divided by kokanee weight to yield number of kokanee consumed per fish. This value was then scaled up to the population level using the number of lake trout predicted in the FAMS simulations. Kokanee age class partitioning was accomplished using an age-at-length key specific to BMR (Brauch, unpublished) for use in the following age structured population dynamics model.

*Kokanee population modeling*

We created an age-structured model of kokanee population dynamics to evaluate effects of various sources of mortality, including lake trout predation on kokanee abundance and egg production (Figure 1). In particular, the model was used to evaluate how various lake trout management scenarios affected the kokanee population, hatchery production, and fishery. Each simulation began when a number of kokanee fry (FRY) were released from ROJ and traveled downstream to the reservoir. Mortality at this stage included losses from river resident brown trout (P(BRN)) which were measured in the system (below). In the reservoir age-0 and age-1 fish experienced losses due to entrainment through the dam's outlet works (P(dam)), unspecified sources of natural mortality (P(nm)) (e.g., non-lake trout predation, disease), and lake trout predation (P(LKT)). Age-2 through age-5 fish experienced natural mortality and lake trout predation, but it was assumed that these kokanee were large enough to avoid entrainment in dam releases (Johnson and Koski 2005). Fishing mortality (P(fm)) was included for all age classes, based on findings from creel surveys. Number of eggs available at ROJ was determined from maturity schedules ((P(mat)), sex ratio (P(fem)), the proportion returning to the hatchery (P(ROJ)), and fecundity (FEC). Target egg production was set by CPW at $\geq 4.135 \times 10^6$ (to produce $3.100 \times 10^6$ fry, with surplus eggs used in other hatchery facilities.

Kokanee mortality from brown trout predation during river transit was estimated by a study in 2010; we determined that the brown trout population in the river above BMR was capable of consuming about 10% of stocked fry, up to a maximum of 300,000 fry (Brauch, unpublished). Losses to irrigation diversions were negligible because CPW began screening or closing diversion outlets on the day kokanee are stocked. Kokanee are known to be susceptible to entrainment in dam releases (Johnson and Koski 2005, Johnson and Dauble 2006). Likelihood of entrainment through the dam in age-0 (P(dam) = 0.037) and age-1 (P(dam) = 0.018) kokanee was determined from Johnson and Koski (2005). Natural mortality in the reservoir (P(nm)) was estimated from McGurk (1999) using kokanee weight at age ($W_t$) in grams:

$$\mathrm{P(nm)} = 1.38 \times \mathrm{W}_t{}^{-0.19}$$

Weight of the kokanee was obtained using a weight-length regression from captured BMR fish:

$$\log_e(\mathrm{W}) = 2.7889 \times \log_e(\mathrm{TL}) - 10.414$$

Total rate of instantaneous mortality ($Z_{age}$) was calculated for each age class by combining all sources of mortality:

$$\mathrm{Z}_{0,1} = \log_e[\mathrm{P(nm)}] + \log_e[\mathrm{P(fm)}] + \log_e[\mathrm{P(LKT)}] + \log_e[\mathrm{P(dam)}] \text{ for age-0 and age-1}$$

$$Z_{2,3,4,5} = \log_e[\mathrm{P(nm)}] + \log_e[\mathrm{P(fm)}] + \log_e[\mathrm{P(LKT)}] \text{ for age-2 through age-5}$$

Proportion of age-classes (ages 2-5) that were mature (P(mat)), sex ratio (P(fem)), and mean length at age (Table 3) were calculated from data obtained during spawn takes at ROJ. Fecundity (FEC) was estimated from Martinez (1996):

$$\mathrm{FEC} = 7.1 \times 10^{-5} \times \mathrm{TL}^{2.8}$$

We assumed that 75% of the mature fish migrating from Blue Mesa Reservoir were able to complete the journey back to the hatchery (Brauch, personal observation).

We developed a baseline simulation in which the natural mortality rate computed from McGurk (1999) was assumed to be the only source of non-harvest mortality (representing a modest piscivore population) and exploitation rate was assumed to be $P(fm)_0 = 3.6 \times 10^{-5}$, $P(fm)_1 = 1.2 \times 10^{-3}$, $P(fm)_2 = 0.1325$, $P(fm)_3 = 0.7175$, $P(fm)_4 = 0.125$, and $P(fm)_5 = 0.01$. These exploitation rates were calculated by fitting the baseline simulation to total harvest estimates from the 1993 BMR creel survey. Results of this simulation were used to compare the kokanee population expected under historic fishing pressure and low predation mortality (as was the case in 1993) to simulations with higher predation by lake trout. The three primary functions used in the model predict the number of age-0 kokanee arriving at the reservoir:

$$\mathrm{N_0 = FRY \times [1 - P(BRN)]},$$

and the number of kokanee in each age-class at the end of year t:

$$\mathrm{N_{t+1} = N_t \times e^{-Z_i}} \text{ for age-0 and age-1}$$

$$\mathrm{N_{t+1} = (N_t \times e^{-Z_i}) - [N_t \times P(mat)]} \text{ for age-2 through age-5}$$

where $Z_i$ is the age specific instantaneous mortality rate. The number of eggs produced during the ROJ spawn-take (EGGS) was computed as:

$$\mathrm{EGGS = \sum_2^5 [\left(N_i \times P(mat) \times P(ROJ) \times P(fem)\right) \times \left(a \times TL_i^b\right)]}.$$

If EGGS > $4.135 \times 10^6$ then the surplus was recorded and assumed to be used at other kokanee hatcheries to stock other waters. Further, we assumed that ROJ would have a full supply of kokanee eggs for the first five years supplemented by egg takes in other systems if necessary because of BMR's importance to the statewide fishery, but after that no additional eggs from other systems would be available for stocking BMR. See Table 3 for a complete list of parameters.

*Lake trout suppression.*– Initial suppression by CPW employed 61 m long by 2 m tall, 44-mm bar mesh gill nets. Nets were set for 45 min to minimize mortality of large (> 765 mm) lake trout which were released. All lake trout < 765 mm that were captured were removed. Two or three 4-person boat crews worked 15 days in fall 2010. We estimated daily costs by summing per capita wages, lodging and meal costs, and boat fuel expense.

After completing baseline simulations of contemporary kokanee population dynamics under the existing removal plan, we adjusted the level of lake trout predation (P(LKT)) by simulating effects of lake trout exploitation levels (angling + mechanical removal) in FAMS to represent differing suppression strategies. Lake trout exploitation was increased by increments of 0.05 to determine the level of suppression needed to stabilize the kokanee population at the CPW target abundance. We compared effects of removal of three size classes of lake trout: age-4 through age-9 (the current removal strategy), age-4 only (most abundant age-class in current gill netting), and age $\geq$ 10 (large fish desirable to anglers). We determined the number of lake trout that needed to be removed for kokanee sustainability and the number of trophy lake trout left in the population after each scenario. Because labor for mechanical removal might become limiting, we also evaluated potential effects of reduced lake trout recruitment (e.g., with fall drawdown of the reservoir to expose lake trout eggs to drying) on kokanee abundance and the number of large lake trout. We reduced lake trout recruitment by 5% increments until we reached a recruitment level resulting in a stable kokanee population and at CPW's target abundance. In all scenarios we tracked the number of trophy lake trout (> 965 mm TL) produced because the agency was interested in tradeoffs in the lake trout fishery required to sustain the kokanee population and fishery. In all simulations, we assumed that angler harvest rate of both species was constant.

After we determined the number and sizes of lake trout that would need to be removed to reach CPW kokanee targets, we considered how best to accomplish suppression with gill nets while minimizing kokanee bycatch. We used catch data from experimental horizontal gill nets (targeting substrate-oriented fish; SPIN) and experimental vertical gill nets (targeting pelagic fish) to evaluate how mesh size (12.7 – 63.5 mm bar) and net depth (in 10-m intervals) could be used to optimize lake trout suppression and minimize kokanee bycatch.

**Results**

The existing suppression program at BMR utilized 40 boat-days or 1,280 person-hours of labor to remove 1,242 lake trout (2.84 fish/net-hour) in 326 gill net sets over the 15 day removal effort. Daily costs totaled $940 per boat-day in 2010, for a total of about $38,000 or about $30 per lake trout removed.

*Lake trout population modeling*

Using 81 SPIN net sets, we captured 129 lake trout ranging in size from 230 mm to 996 mm TL. The area-weighted catch per unit effort was 2.29, yielding a lake trout density estimate of 11.14/ha. The area sampled was 3059.5 ha. The resulting abundance estimate for lake trout > 230 mm TL was 34,071 with 68% confidence limits of 27,144 (LCL) and 41,929 (UCL). The slope of the $\log_e$ transformed age distribution for age classes 4 through 9 was 0.707 (instantaneous total mortality). Aging supported that catch curve's relatively high total mortality in BMR: of 780 lake trout otoliths aged since 1993, no fish > age-20 have been observed. Natural mortality of lake trout was estimated to be 0.444 by subtracting the mean creel harvest estimate, and known numbers removed. Back calculated abundance from age-4 lake trout using estimates of natural mortality yielded the number of young of year (58,500).

Creel survey and historic abundance estimates together corroborated our lake trout abundance estimate from SPIN. Mark-recapture and hydroacoustic survey lake trout abundance estimates were computed in 2002 (Crockett et al. 2006). Data from SPIN (2011) and creel survey data (obtained concurrently with the 2002 estimates) indicated that abundance of lake trout ≥ 425 mm TL nearly doubled in the nine years between 2002 and this study (Figure 2).

Specifically, the SPIN estimate indicated that abundance of lake trout in this size class increased from approximately 8,114 (2002 estimate) to approximately 19,612 fish. Over this same time period lake trout catch per angler hour doubled from about 0.02 fish per hour to 0.04 fish per hour.

*Baseline simulation*

Per capita and cohort consumption by age-4 lake trout were at 34 and 335,868 kokanee per year, respectively. Cohort consumption declined with lake trout size/age because as they grew larger, lake trout were less numerous and they consumed fewer, larger, more energy dense kokanee (Table 2). Total consumptive demand of the lake trout population was estimated at $1.47 \times 10^6$ kokanee per year. The kokanee population was not sustainable under baseline conditions and persisted less than three years beyond the five year stocking subsidy from other waters. The baseline scenario predicted the highest number of trophy lake trout (11; Table 4) in the population at the end of the simulation. But, this scenario would not be sustainable because lake trout condition would likely decline very soon after kokanee extirpation, and no trophy length lake trout would be available for anglers.

*Increased exploitation of age-4 through age-9 lake trout*

When removal of age-4 through age-9 lake trout was increased by 0.10 ($cf_{4\text{-}9} = 0.331$) in addition to the contemporary removal of 1,250 fish, the kokanee population was extirpated, although it lasted eight years longer than in the baseline simulation (Figure 3). The kokanee population became sustainable at 600,000 fish and $4.74 \times 10^6$ eggs per year if removal of age-4 through age-9 lake trout was increased by 0.15 ($cf_{4\text{-}9} = 0.381$) in addition to the contemporary removal of 1,250 fish. This required the removal of 2,894 more lake trout. The predicted number of trophy lake trout at the end of the simulation was 3.

To approach CPW's kokanee population target of 700,000 fish, removal of age-4 through age-9 lake trout had to be increased by 0.40 ($cf_{4\text{-}9} = 0.681$). This resulted in a kokanee population size of 689,000, and $7.27 \times 10^6$ eggs for hatcheries. To reach this level, over 7,500 lake trout must be removed by managers and there would be no trophy lake trout available for anglers.

*Increased exploitation of age-4 lake trout*

When exploitation of just age-4 lake trout is increased by 0.25 above the contemporary level of removal the kokanee population stabilized at 594,000 fish with $4.59 \times 10^6$ million eggs returned to the hatchery every year (Figure 3). To achieve this, an additional 1,583 age-4 lake trout would need to be removed annually (total = 2,830 lake trout). This would reduce total consumptive demand to 1.37 million, about 7% below the consumption in the baseline simulation. The number of trophy lake trout at the end of this scenario was 7. To approach CPW's kokanee target, exploitation on age-4 fish would need to be increased to $cf_4 = 0.731$, by removing an additional 3,167 age-4 lake trout. Kokanee abundance was predicted to increase to 675,000 fish and consumptive demand was reduced to $1.26 \times 10^6$ kokanee per year. Four trophy lake trout would be available for anglers.

*Increased exploitation of age-10 and older lake trout*

Raising exploitation of large lake trout (≥ age-10) had no effect on kokanee sustainability, even if all large lake trout in BMR were removed (Figure 3). The kokanee population was extirpated within three years of the end of stocking from other sources, just as in the baseline simulation. Consumption of kokanee by this group was reduced from 13,805 to 5,665 fish but this had a negligible effect on the kokanee population and no trophy lake trout were available for anglers.

*Reduced lake trout recruitment*

When abundance of young of year lake trout was reduced by 10% the kokanee population persisted four years longer than in the baseline simulation, but the population was still extirpated (Figure 3). When it was reduced by 15% the kokanee population stabilized at 633,000 fish with just over $4.35 \times 10^6$ eggs available for collection at the hatchery. Total consumptive demand was reduced to $1.25 \times 10^6$ kokanee per year. This scenario resulted in 9 trophy lake trout remaining in BMR. To meet CPW's kokanee population target, lake trout recruitment had to be reduced by 25%, yielding $5.72 \times 10^6$ kokanee eggs annually. Total annual consumption of kokanee was reduced to $1.10 \times 10^6$ and there were 8 trophy lake trout remaining in BMR for anglers.

*Optimal lake trout suppression by gill netting*

Our modeling showed that specifically targeting age-4 lake trout would yield the greatest reduction in number of kokanee consumed per lake trout, and netting effort showed that it was possible to focus gill net catch on this age-class. By using gill nets of 28.6 to 38.1 mm bar mesh, catch of age-4 lake trout could be maximized while reducing bycatch of older fish; thus, longer duration sets could be used. About 79% of the catch of age-4 lake trout came in this mesh range, while 30% of older lake trout were caught in these nets (Figure 4). Unfortunately, kokanee bycatch was high in these meshes with 48% of all kokanee caught in gill nets coming from these sizes. However, there was spatial segregation between lake trout and kokanee. We found that 87% of kokanee were captured above the thermocline (< 30 m) and 77% of lake trout were captured below the thermocline in the combination of daytime SPIN netting and overnight vertical gill netting during August (Figure 5). Kokanee bycatch could be reduced while still capturing large numbers of lake trout by setting gill nets below 30 m.

## Discussion

Our modeling suggests that the BMR kokanee population will continue to decline without intensified lake trout suppression. While the most palatable management tool available to CPW may be the angling public, liberalized harvest regulations have not been sufficient to reduce lake trout predation and allow for kokanee recovery. Funding for economic incentives to harvest lake trout (e.g., bounties) used in other systems (e.g., Lake Pend Oreille and Flathead Lake) was not available. Until such funding becomes available, mechanical removal by managers or some other management intervention appears to be required.

Modeling scenarios suggested that a sustainable and abundant kokanee population can coexist with a trophy lake trout population, and this can be accomplished using several of the suppression methods we evaluated. The most effective and least labor-intensive method would be reducing lake trout recruitment by at least 15% through water level manipulation. Simply reducing recruitment of lake trout also resulted in the highest number of trophy lake trout available for anglers. Lake trout exhibit a variety of spawning depths, ranging from < 2 m in smaller lakes within their native range (Gunn 1995) to more than 91 m in Lake Huron (Nester and Poe 1987). If lake trout do spawn in shallow depths in BMR, then the surface elevation of the reservoir could be lowered after spawning ends in November to dewater eggs and reduce recruitment, as appeared to be the case prior to new dam operations that began in 1992. While water level management to reduce lake trout recruitment is technically possible in reservoirs, higher priority uses for the water (e.g., hydropower, irrigation, endangered fish flows downstream) can trump fishery management objectives, particularly in the arid Western U.S. For this reason, we did not consider water level manipulation a feasible strategy at BMR.

Intensifying the current suppression program by gill netting more age-4 through 9 lake trout would allow for a sustainable kokanee population while still providing some trophy lake trout angling opportunity. Achieving this balance would require removing an additional 2,900 lake trout per year over and above the 1,250 currently being culled, assuming angler harvest remained constant. Alternatively, simulations showed if gill netting focused entirely on age-4 lake trout, then the additional number of lake trout that would need to be removed is reduced substantially to approximately 1,600 fish. The sensitivity of the kokanee population to abundance of relatively young piscivores illustrates a generalization of managing fish predator-prey interactions that can be applied to BMR. Because many piscivores, including lake trout, consume prey fish in proportion to their own length (Mittelbach and Persson 1998), small lake trout consume more kokanee per capita than larger lake trout (albeit less biomass). Further, the population level effect of a cohort of small predators is greater than for an older, typically less abundant predator cohort. This effect is amplified when prey energy density increases with size, as was observed for kokanee in BMR. Small lake trout would require a greater biomass of lower energy prey to produce a given amount of growth than would large lake trout feeding on more energy-rich prey. In BMR, the age-4 cohort of lake trout consumed mostly age-1 kokanee, requiring about 336,000 kokanee to satisfy their observed growth, due to the small size and lower energy density of age-1 kokanee compared to older kokanee.

Interestingly, our simulations showed that despite the rapid growth and relatively large size of age-10 and older lake trout in BMR, removing these fish had a negligible effect on sustainability of the kokanee population. Consumptive demand of these larger lake trout at the current abundance was just 13,800 kokanee/year which could potentially be reduced to < 5,600 kokanee/year. While this could impact the number of mature kokanee returning to the hatchery, the overall effect on kokanee of removing large lake trout was predicted to be minimal but resulted in no trophy sized lake trout for anglers. Thus, removing large lake trout is not considered a viable management option to serve BMR's dual goals of sustaining the kokanee fishery while maintaining some trophy lake trout for anglers. This result should be interpreted cautiously with respect to other systems because the longevity of BMR lake trout is lower than in many other populations, with few fish living beyond 20 years of age.

A caveat to the intensive exploitation of lake trout is the possibility of a compensatory response. It has been shown for many species, including lake trout, that intensive fishing can induce increased fecundity, earlier age at maturation, and increased growth (Ricker 1975; Healey 1978, Ferreri and Taylor 1996). However, we found that in BMR, removing large lake trout would have a negligible effect on the kokanee population and small lake trout should be exploited. This fishing regime could still influence recruitment if preserving large, old fish increased reproductive success through maternal effects (Berkeley et al. 2004; Birkland and Dayton 2005) but such effects are not anticipated based on the low longevity of the population.

Managing for a strong kokanee fishery while preserving large lake trout for trophy anglers appears to be a sustainable strategy for BMR based on the simulations presented here. However, this strategy may not be advisable in larger systems or those with different demographic characteristics. Blue Mesa Reservoir is approximately one tenth the surface area of other lake trout waters in the West where suppression is occurring, such as Yellowstone Lake, Lake Pend Oreille, and Flathead Lake (Martinez et al. 2009). Of these waters, Yellowstone Lake has had the most intensive removal program using gill nets. The removal program began there in 1995 when lake trout were discovered but they continue to be problematic even though almost 450,000 were removed by 2009 (Syslo et al. 2011). Netting occurs from ice-off through October every year with overnight and multi-night sets, but lake trout CPUE continues to increase. In Flathead Lake angler harvest incentives have been ineffective and there is currently a draft Environmental Impact Statement assessing the need for intensified removal of lake trout to restore native species (BIA 2012). The assessment will look at four alternatives that range from no action to reducing lake trout abundance of all age classes by 90% (188,000 fish) using a combination of fishing contests and mechanical removal.

Alternatively, lake trout suppression at Lake Pend Oreille (Hansen et al. 2008; Hansen et al. 2010) appears to be having an impact with increased kokanee spawning and abundance (IDFG 2012). Removal by incentivized anglers and commercial-scale netting was concurrent with an increase in survival of age-1 to age-2 kokanee from 10% to 30% and an increase in survival of age-2 and age-3 kokanee from 4% to 51% from 2007 to 2008, respectively (Martinez et al. 2009). Recently, Idaho Department of Fish and Game reopened the kokanee fishery allowing a six fish daily bag limit (IDFG 2013). This example suggests that with an intensive removal and cooperation between the fishing public and agencies, lake trout populations can be managed to reduce abundance to a level that allows for recovery of their prey resources.

In BMR, we believe a smaller netting program would be sufficient to sustain the management objectives. If past netting CPUE and associated costs continued, the target number of age-4 lake trout (n = 2,830 fish) could be removed for about $85,400. Changing to smaller mesh and longer nets set in deep water overnight during August (when lake trout would be confined to the hypolimnion) could focus the catch on age-4 lake trout and make the process more efficient, but regardless, mechanical removal is an expensive undertaking. Encouraging anglers to harvest the additional 2,830 fish (total ~7,000 fish per year) could be less expensive if a bounty of $12 per fish was sufficient for anglers to achieve the removal target, disregarding costs of administering the bounty program.

Conducting a large scale, intensive suppression program is challenging in large water bodies (Kolar et al. 2010). If controlling the consumption of a piscivore is the primary goal, then it may behoove managers to examine whether focusing removal on younger age classes would be feasible because they are typically the most numerous in a population and consume the largest number of individual prey. Such a strategy may control overall abundance of the piscivore, reduce the likelihood of compensatory responses, and simultaneously reduce consumptive demand on the species of conservation concern.

**Management Recommendations**

Intensified suppression of lake trout is required to ensure perpetuation of the BMR kokanee population and desirable growth and body condition of lake trout. If mechanical removal by gill netting is to be continued, costs may be reduced and large lake trout preserved if longer nets with smaller meshes are used. To minimize kokanee bycatch, nets should be placed below the thermocline during the peak of thermal stratification. Changing to overnight sets could increase the encounter probability of crepuscular or nocturnally active lake trout. Such a netting scheme could also reduce conflict with lake trout anglers, who typically target the fish in the spring and fall when the reservoir is isothermal, and in the same locations that netting is most effective. Because anglers already harvest more small lake trout than were captured by a relatively expensive netting program, reconsidering an angler incentive program, as is in place in other western lake trout waters, could be worthwhile. Even if funds for a bounty were not available, offering prizes for catching select PIT tagged fish could encourage anglers to harvest more fish.  Minimizing administrative costs for such a lottery could make it a more cost-effective approach than removing fish with gill nets.

Table 1. Input parameter values used in Fishery Analysis and Modeling Simulator 1.0 to predict lake trout abundance by age class in Blue Mesa Reservoir, Colorado. Results of these model runs were used to estimate consumptive demand of kokanee. Values were obtained from the existing lake trout population in Blue Mesa Reservoir.

| Name | Meaning | Value |
|---|---|---|
| b | Weight-Length parameter | 3.3354 |
| a | Weight-Length parameter | -6.0084 |
| $L_\infty$ (mm) | Theoretical maximum length | 1150.71 |
| Num years | Length of model run (years) | 30 |
| k | VBGF growth coefficient | 0.0986 |
| $t_0$ (years) | Theoretical time when TL = 0 | -0.4492 |
| $W_\infty$ (g) | Theoretical maximum weight | 15890.85 |
| MaxAge | Maximum age of fish | 20 |
| Recruitment | Abundance of young of year | 58,500 |
| cm | Probability of natural mortality, age 0-20 | 0.3589 |
| | Probability of fishing mortality, age 0-3 | 0.0000 |
| fm | age 4-9 | 0.2307 |
| | age 10-20 | 0.0000 |

Table 2. Diet composition used in bioenergetics simulations to estimate consumptive demand of four age-classes of lake trout (LKT) preying on kokanee (KOK), rainbow trout (RBT), yellow perch (YPE), crayfish *Orconectes* spp. (CFI), and other small invertebrates (SMI) in Blue Mesa Reservoir , Colorado. Diet proportions were obtained from stable isotope measurements and energy density was determined by calorimetry of taxa from BMR. Lake trout and kokanee energy density reported are averages of measured values of lake trout age groups and kokanee sizes consumed by each age group of lake trout.

| Parameter | LKT TL (mm) | LKT Age (yrs) | KOK | RBT | YPE | CFI | SMI | LKT |
|---|---|---|---|---|---|---|---|---|
| Diet | < 332 | < 3 | -- | -- | -- | 0.500 | 0.500 | -- |
| | 332 < 409 | 3 | 0.576 | 0.034 | 0.266 | 0.058 | 0.066 | -- |
| | 409 < 478 | 4 | 0.478 | 0.053 | 0.307 | 0.091 | 0.072 | |
| | 409 < 740 | 4-9 | 0.458 | 0.110 | 0.381 | 0.039 | 0.012 | -- |
| | ≥ 740 | ≥ 10 | 0.937 | 0.012 | 0.031 | 0.019 | -- | -- |
| Energy density (J/g) | | < 3 | -- | -- | -- | 3,706 | 2,107 | 2,358 |
| | | 3 | 7,063 | 6,451 | 4,182 | 3,706 | 2,107 | 4,707 |
| | | 4 | 7,580 | 6,451 | 4,182 | 3,706 | 2,107 | 5,701 |
| | | 4-9 | 8,615 | 6,451 | 4,182 | 3,706 | 2,107 | 7,689 |
| | | ≥ 10 | 10,801 | 6,451 | 4,182 | 3,706 | -- | 11,889 |

Table 3. Parameters of the age-structured population model for kokanee (KOK) in Blue Mesa Reservoir. Brown trout is BRN, LKT is lake trout, ROJ is Roaring Judy Fish Hatchery.

| Name | Meaning | Value | Source |
|---|---|---|---|
| FRY | Fry released into East River | -- | Initial, computed |
| P(BRN) | Loss of migrating fry to brown trout predation in river | 0.10, ≤ 300,000 | Brauch, CPW, unpub. data |
| P(dam) | Dam entrainment of kokanee, age-0 | 0.037 | Johnson and Koski (2005) |
| | Dam entrainment of kokanee, age-1 | 0.018 | |
| P(nm) | Non-LKT mortality, parameter, a | 1.38 | McGurk (1999) |
| | Non-LKT mortality, parameter, b | -0.19 | |
| W-L | Weight-Length parameter, a | $9 \times 10^{-6}$ | Johnson and Koski (2005) |
| | Weight-Length parameter, b | 3.024 | |
| P(fm) | Probability of fishing mortality, Age-0 | $3.6 \times 10^{-5}$ | Brauch, CPW, pers. comm. |
| | Age-1 | $1.2 \times 10^{-3}$ | |
| | Age-2 | 0.1325 | |
| | Age-3 | 0.7163 | |
| | Age-4 | 0.125 | |
| | Age-5 | 0.01 | |
| $KOK_n$ | Kokanee abundance, age-n cohort | -- | Computed |
| SONAR | Number of kokanee | ≥ 700,000 | Target |
| P(LKT) | Kokanee lost to lake trout predation | -- | Varied |
| P(mat) | Proportion of cohort mature, Age-2 | 0.021 | Brauch, CPW, pers. comm. |
| | Age-3 | 0.361 | |
| | Age-4 | 0.9 | |
| | Age-5 | 1 | |
| P(ROJ) | Proportion of mature fish reaching ROJ | 0.75 | Brauch, CPW, pers. comm. |
| P(fem) | Proportion of mature fish that are female | 0.45 | Brauch, CPW, pers. comm. |
| TL | Total length (mm) of mature fish, Age-2 | 306 | Brauch, CPW, pers. comm. |
| | Age-3 | 404 | |
| | Age-4 | 465 | |
| | Age-5 | 503 | |
| FEC | Kokanee fecundity parameter, a | $7.1 \times 10^{-5}$ | Martinez (1996) |
| | Kokanee fecundity parameter, b | 2.8 | |
| EGGS | Eggs obtained from spawn-take | $\geq 4.135 \times 10^{6}$ | Target |
| HATCH | Proportion of eggs that produce fry | 0.75 | Brauch, CPW, pers. comm. |

Table 4. Effects of differing lake trout suppression strategies on the lake trout fishery and predation pressure on kokanee at equilibrium in Blue Mesa Reservoir. The baseline model included relaxed angling limits and gill net removals in effect during the study and no eggs available for collection at the Roaring Judy Fish Hatchery (ROJ). Trophies are lake trout ≥ 965 mm total length.

| | | Lake trout | | Kokanee | | |
|---|---|---|---|---|---|---|
| Manipulation | | Trophies available | Additional fish removed | Final abundance | Number of eggs at ROJ | Consumed (fish per year) |
| Baseline | ----- | 11 | 0 | 0 | 0 | 1,472,042 |
| Increased exploitation age-4 to 9 | 0.10 | 5 | 2,017 | 0 | 0 | 1,392,755 |
| | 0.15 | 3 | 2,894 | 599,236 | 4,740,681 | 1,360,057 |
| | 0.40 | 0 | 6,273 | 688,944 | 7,270,984 | 1,243,419 |
| Increased exploitation age-4 | 0.20 | 8 | 1,267 | 0 | 0 | 1,387,855 |
| | 0.25 | 7 | 1,583 | 594,065 | 4,589,504 | 1,366,809 |
| | 0.50 | 4 | 3,167 | 674,997 | 6,873,518 | 1,261,575 |
| Increased exploitation age-10 and up | 1.00 | 0 | 243 | 0 | 0 | 1,463,906 |
| Reduced recruitment | 0.10 | 10 | 0 | 0 | 0 | 1,324,837 |
| | 0.15 | 9 | 0 | 631,483 | 4,351,636 | 1,251,236 |
| | 0.20 | 9 | 0 | 670,933 | 5,033,669 | 1,177,634 |
| | 0.25 | 8 | 0 | 710,382 | 5,715,695 | 1,104,032 |

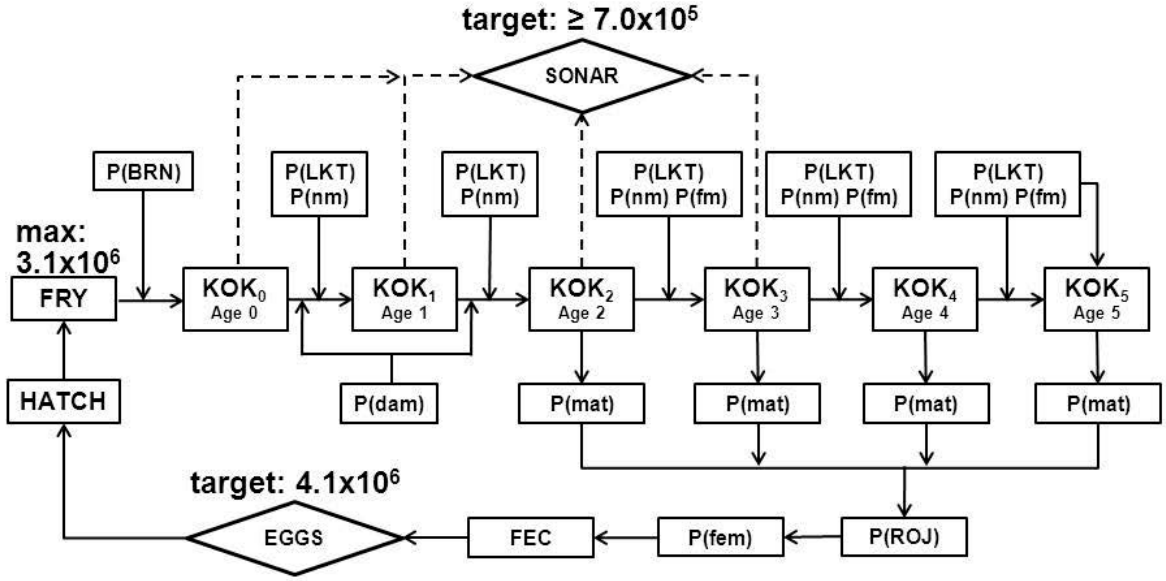


Figure 1. Age structured model of kokanee population dynamics at Blue Mesa Reservoir, Colorado. See Table 3 for variable names and values. Up to $3.1 \times 10^6$ kokanee (KOK) fry are stocked every April. Kokanee suffer mortality during river transit, from lake trout (LKT) predation, other sources of natural mortality, and exploitation. A fraction of female KOK surviving to adulthood return to their natal hatchery where they are stripped and the eggs are reared for stocking the next generation. Managers set a target population size of $7.0 \times 10^5$ KOK, estimated by SONAR surveys in August, to obtain the eggs required to sustain the population.

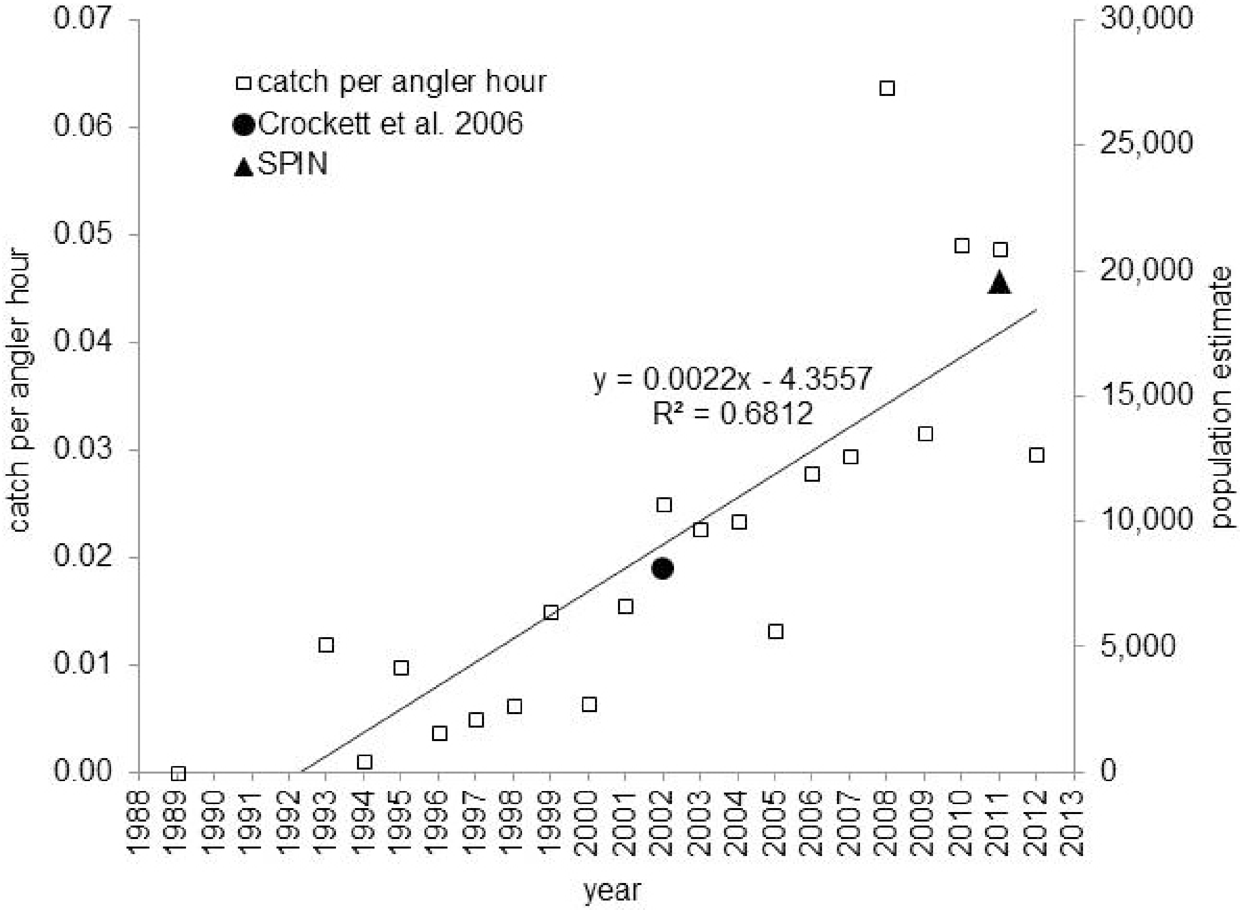


Figure 2. A comparison of lake trout population trends in Blue Mesa Reservoir, Colorado. Lake trout catch per angler hour (open squares) has increased dramatically since creel surveys began in 1989. Population estimates (solid) for lake trout ≥ 425 mm total length have also increased by a similar proportion from 2002 (hydroacoustics and mark-recapture; Crockett et al. 2006) to 2011 (Summer Profundal Index Netting; present study) .

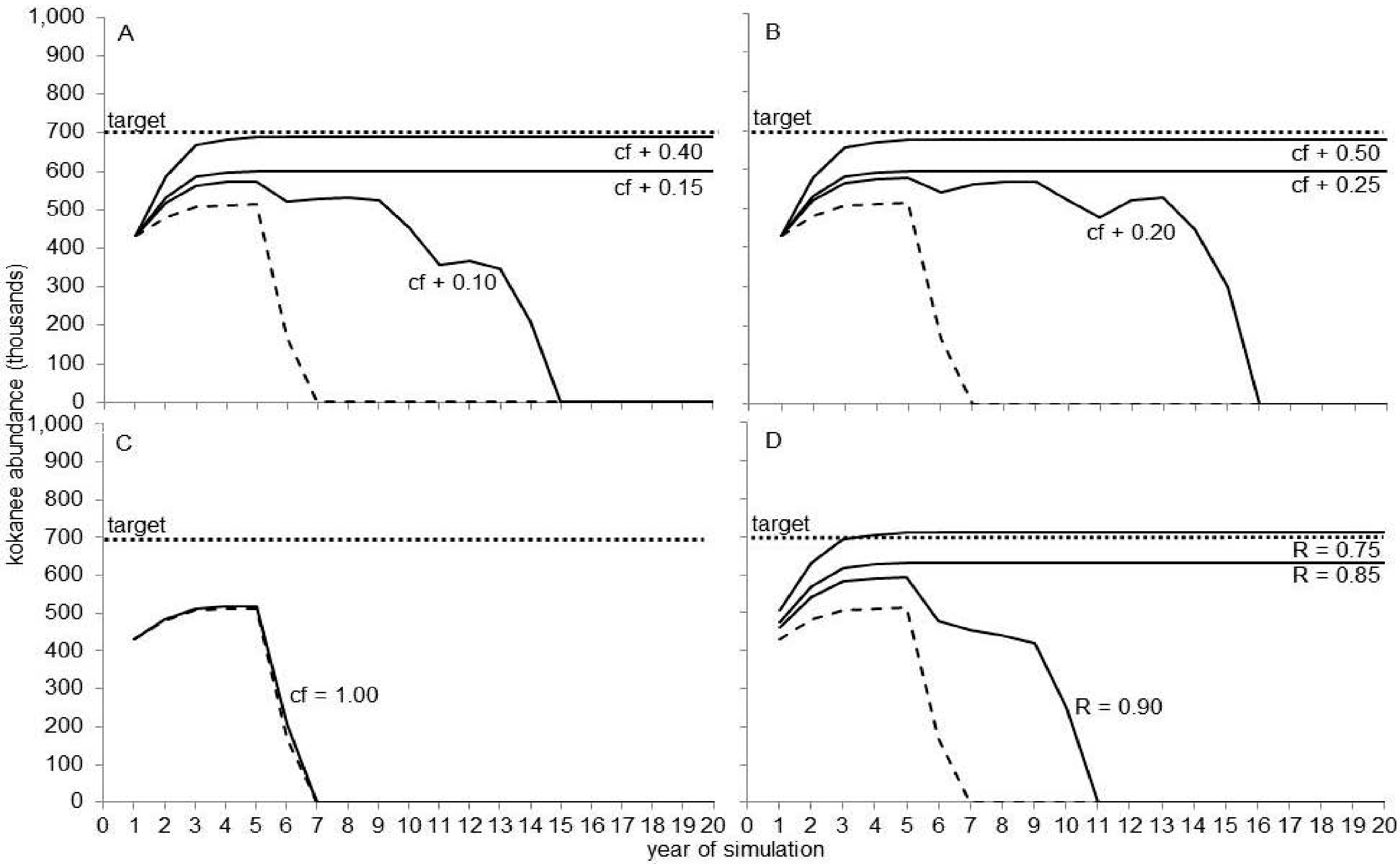


Figure 3. Results from the age structured model of kokanee population dynamics at Blue Mesa Reservoir, Colorado. The dotted line represents Colorado Parks and Wildlife (CPW) target kokanee abundance. The dashed line represents the model baseline scenario with lake trout exploitation (cf) at 0.2307. Simulations of increased lake trout exploitation for age 4-9 (A) showed a stable kokanee population when cf was increased by 0.15, and approached CPW target abundance when increased by 0.40. When only age-4 (B) exploitation was increased, stability occurred when cf increased by 0.25 and target value approached when increased by 0.50. If age 4-9 exploitation was left at current levels and increased for lake trout ≥ age-10 (C), kokanee were eliminated even if all lake trout were removed. Recruitment (R) had to be reduced to 0.85 of baseline to stabilize kokanee abundance (D), and further reduced to 0.75 to meet target kokanee abundance levels.

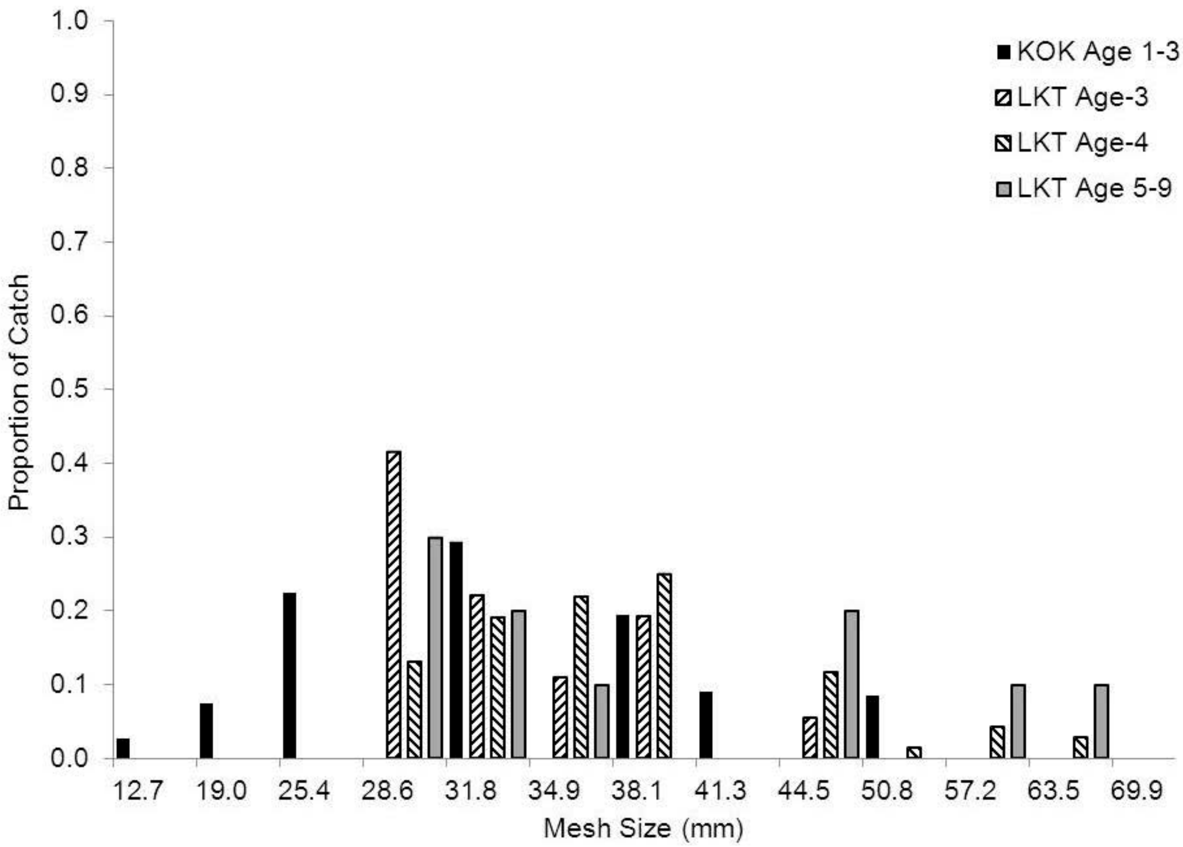


Figure 4. Proportion of total catch of kokanee (KOK) and lake trout (LKT) captured from gill nets with a range of mesh sizes (bar) in Blue Mesa Reservoir. Bycatch of kokanee is only avoidable with ≥ 57.2 mm gill nets (dashed line) but only age-5 and older lake trout would be vulnerable to these mesh sizes.

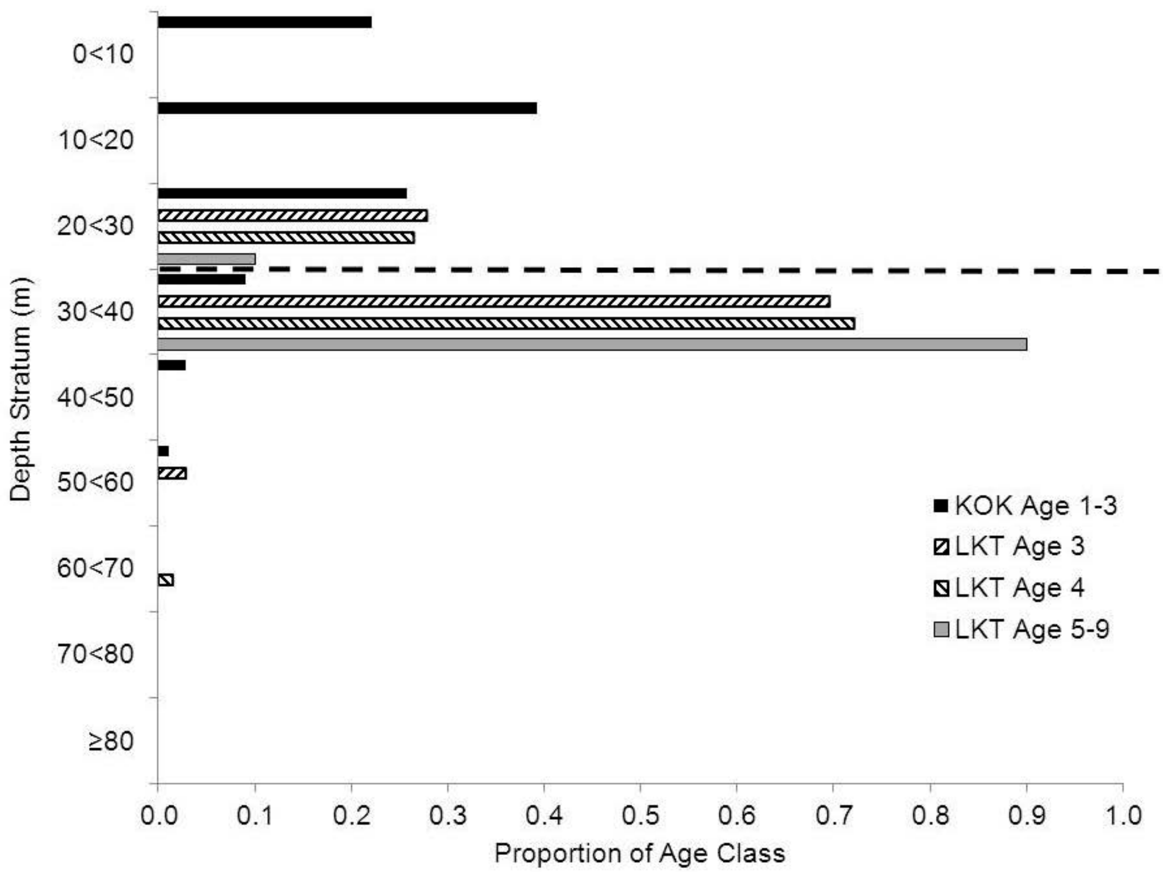


Figure 5. Proportions of age classes of kokanee (KOK) and lake trout (LKT) by capture depth in Blue Mesa Reservoir. Lake trout were captured during Summer Profundal Index Netting in August 2011 and kokanee proportions were compiled from vertical gill net data. Dashed line represents the minimum net depth to optimize LKT removal and minimize KOK bycatch.

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## Appendix A

## Methods

To determine potential spawning locations of lake trout *Salvelinus namaycush* in Blue Mesa Reservoir (BMR) we surgically implanted sonic telemetry transmitters in 29 individuals for tracking during the fall spawning season. Lake trout > 760 mm had Sonotronics model CT-05-48 series transmitters (measuring 80 by 15.6 mm) surgically implanted inside the peritoneal cavity. Weight of tags in water was 12 g, which is < 1% of fish weight resulting in negligible effects to mobility and function of the fish post-surgery (Jepsen et al. 2005). Lake trout have shown no behavioral changes in response to sonic telemetry tracking, either by boat or shore (Blanchfield et al. 2005). Battery life of the transmitters was 48 months once activated, which allowed for multiple spawning seasons to be monitored.

### *Surgical Procedure*

Lake trout > 760 mm captured in horizontal gill nets during standard Colorado Parks and Wildlife (CPW) mark-recapture sampling in May 2010 were held in net pens at the Elk Creek Marina prior to surgery. Length and weight of the fish was recorded and each was scanned for a previously implanted passive integrated transponder (PIT) tag. Fish remained under observation for at least 24 hours to ensure only healthy (maintained good equilibrium and mobility) subjects were used for the implantation procedure. Each transmitter was activated and verified functional immediately prior to the surgical procedure. Lake trout were anesthetized by being placed into a 500 L tank containing $CO_2$ saturated water and held there until equilibrium was lost. Immediately after loss of equilibrium the fish was placed on the operating table in a v-shaped foam pad soaked in Stress Coat™ and gills were irrigated with $O_2$ saturated water using a small 12V electric recirculating pump. Using a #15 scalpel blade, a 20 mm incision was made adjacent to the ventral midline anterior to the pelvic girdle. An activated transmitter was inserted into the peritoneal cavity in an anterior direction from the incision. The incision was then closed using three simple interrupted sutures (Maxon™ 3-0 non-absorbable monofilament with cutting needle) and sealed with Vetbond™ cyanoacrylate adhesive. Non-absorbable monofilament suture material was used as it has been shown to result in the least amount of post-surgical inflammation and faster healing times (Wagner et al. 2000). Surgical procedures were advised during a training session by Terry W. Campbell, DVM at the Colorado State University Veterinary Teaching Hospital. Duration of each procedure was about two minutes. After the adhesive had cured (about 10 seconds) the fish were placed into a tank containing $O_2$ saturated water and revived. During the revival period, if no PIT tag was detected during previous scanning, a Biomark BIO12.BPL 134.2 kHz PIT tag preloaded in a single use needle was implanted within the vertical septum of the epaxial myomeres using a Biomark MK-25 rapid implant gun. Tags were scanned using a Biomark Pocket Reader-EX and tag number recorded. The lake trout were then placed back into the holding pens for an observation period not less than 24 hours to ensure recovery, then released back into the respective location where captured. No mortalities occurred during the surgical procedure, and all fish were released in excellent condition. See Table 1A for a complete list of sonic tag pulse codes, PIT tag numbers, and weight-length of each respective lake trout receiving the implants.

*Tracking*

Tracking occurred during the October-November spawning season of 2010 and 2011 using a Sonotronics USR-96 receiver with DH-4 directional hydrophone. The hydrophone was extended about one meter under water to reduce wind and wave noise to a minimal level. Tracking lake trout occurred from 40 predetermined listening points throughout BMR, each approximately 800 m apart (Table 2A). The manufacturer of the transmitter states there is a 1,000 m range, thus the 800 m listening radius. All frequencies were scanned (70-83 kHz) and a 360 rotation of the hydrophone was used at each frequency. Gain on the receiver was turned to maximum to facilitate the highest detection likelihood for each transmitter. When a transmitter was detected, the gain was turned down until barely discernible but still clearly heard. This allowed for the most directional signal reception and compass bearing of the hydrophone was recorded along with the individual tag number. The process was repeated at the next listening point and, if the same fish was detected, triangulation used to determine the approximate location. It required 8-10 hours to complete tracking through the entire reservoir in all three basins as long as weather conditions permitted. See Figure 1A for a description of the different BMR basins. Tracking occurred on four days in 2010 (8 and 20 October, 2 and 10 November) beginning at sunrise. All 40 stations were successfully surveyed each day. In 2011, tracking began at sunset to determine if lake trout would be closer to the shoreline after dusk and occurred on19-20 October in Sapinero and Cebolla basins, respectively. The Iola basin was omitted due to time constraints and only one basin was completed each night due to the requisite slow travel after dark on BMR.

**Results and Discussion**

All but three fish (numbers 20, 25, and 30) were detected at some point during the tracking periods. I was unable to activate one of the tags during the surgical procedures, so there is a possibility of a few other malfunctioning tags which could have defaulted to an off mode or had premature battery failure. Another possible scenario is that the fish were harvested by anglers, but no tags were returned even though contact information was on all of them. There was one known tag expulsion from fish number 8. The tag was detected at the release location in the west end of Cebolla basin, but the lake trout was recaptured in a CPW gill net two weeks after release in the Sapinero basin. There were seven lake trout detected on all tracking occasions in both years (tag numbers 3, 9, 10, 11, 22, 29, and 33). All tags but #33 were located in a different area of the reservoir at each detection, indicating movement of the lake trout and successful transmitter retention. Tag number 33 was located in virtually the same spot in Sapinero at all times and could be another expulsion (Figure 2A). It is known that fish number 33 was released at the far eastern end of the Sapinero basin approximately 4,000 m east of the last known location. All other tags were located in different parts of the reservoir every time they were detected, even though they were not detected during every tracking event. Possible reasons for not detecting a specific lake trout could be the individual was in one of the arms where I ceased tracking after two attempts due to excessive noise and echo from canyon walls leading to triangulation error, or the signal could have been blocked by some underwater obstruction.

There were 19 of 29 lake trout located on 8 October 2010, primarily in the Sapinero basin (Figure 2A) and three in Cebolla (Figure 3A). Although this does include tag number 8 that is the aforementioned known expelled tag. Lake trout were evenly scattered throughout Sapinero and on the western side of Cebolla with no specific site fidelity for the detected groups. The following listening period on 20 October 2010 did show slightly more site fidelity for some groups of lake trout (Figure 4A). Fish numbers 10, 14, 22, and 24 were clustered next to the dam while another grouping of four lake trout (fish numbers 3, 4, 18, and 21) were near the mouth of the West Elk arm. Another loose grouping (9, 11, 12, and 19) was located just west of Middle Bridge. No lake trout were detected in the Cebolla or Iola basins during the 20 October 2010 tracking session, all 16 were in the Sapinero basin.

There were 14 lake trout located during the 2 November 2010 tracking session with 11 found in Sapinero (Figure 5A), one in Cebolla (Figure 6A), and two in Iola (Figure 7A). The single lake trout detected in Cebolla was in the canyon just west of the Elk Creek Marina. Fish number 10 was found the furthest east near the mouth of the Gunnison River and showed the most movement of any lake trout. Just 13 days prior it was the closest fish to the dam and had traversed the length of the reservoir. A tight grouping of four lake trout (fish numbers 2, 9, 19, and 21) were located just west of Middle Bridge along the northern side of the channel. Fish were most scattered during the last tracking period of the 2010 season (10 November) with 17 fish being located, 10 of which were in Sapinero (Figure 8A). There were four found in Cebolla and three in Iola (Figures 9A and 10A, respectively). Only one small grouping of three fish (numbers 9, 15, and 19) was observed in the usual area just west of Middle Bridge.

The largest group of lake trout was observed during the evening tracking on 19 October 2011 (Figure 11A). Of the 15 triangulated, seven were located on the eastern edge of a gently sloping ridge approximately 1,600 m west of Middle Bridge (circled in figure). Two were on the northern side of the channel in a similar location to the previous year, and the rest were scattered around the western portion of the basin. Four lake trout were also scattered along the length of the channel in Cebolla when tracking was completed on 20 October 2011 (Figure 12A).

Lake trout tend to form localized groups during the spawning season (Esteve et al. 2008). Two larger aggregations of lake trout were observed in the Sapinero basin, with the largest occurring during the evening tracking session of 2011. The two most likely spawning grounds observed are the two areas at the eastern edge of the basin as circled in Figures 5A and 11A. Spawning areas with cobble substrates to provide adequate interstitial space to protect young are preferred (Nester and Poe 1987; Marsden et al. 1995). Both of these locations consist of gravel and cobble substrates and are on the margin from gently sloping to steep substrate. Access to deep water from spawning areas to provide further protection to the young is also a known trait of preferred spawning grounds (Nester and Poe 1987). Other than basin preference, this trait could not be used in evaluating potential spawning sites at BMR due to the nature of the underwater topography.

Although there are no firm conclusions resulting from this tracking study (i.e. the direct observation of spawning), use of the two potential spawning sites can be verified by further study such as using eggs nets as in Fitzsimons (1995). Egg deposition densities can be a very strong indicator of heavy site use, and lake trout tend to return to the same site time after time (Esteve et al. 2008). It is highly likely that these are not the only two sites being used in BMR, but merely coincidental that high numbers of tagged fish were observed there. The long distance traveled by fish numbers 5, 10, and 21, going from the Sapinero basin to virtually the same spot at the northeast end of the Iola basin, could indicate that another site exists.

Table 1A. Transmitting frequencies and coded beep series for sonic tags implanted in 29 lake trout (*Salvelinus namaycush*) in Blue Mesa Reservoir, Colorado from 18 to 25 May 2010. Total length (mm) and weight (g) for each corresponding fish is given with PIT tag number. Pulse code is a series of tones transmitted followed by a pause, for example 3-3-4 is three tones, short pause, three tones, short pause, then four tones followed by an 860 millisecond interval between each series.

| Sonic Tag Number | Frequency (kHz) | Pulse Code | Interval (ms) | Sample Number | PIT Tag Number | Length (mm) | Weight (g) |
|---|---|---|---|---|---|---|---|
| 2 | 70 | 3-3-4 | 860 | BMR051910004 | 985121020103922 | 833 | 6,000 |
| 3 | 71 | 3-6-5 | 890 | BMR051910266 | 985121020112822 | 865 | 10,500 |
| 4 | 72 | 3-6-6 | 880 | BMR051810021 | 985121020114519 | 886 | 8,200 |
| 5 | 73 | 4-4-7 | 910 | BMR051810017 | 985121020121196 | 804 | 6,180 |
| 6 | 74 | 4-4-8 | 900 | BMR052010007 | 985121020116359 | 852 | 7,500 |
| 7 | 75 | 4-8-8 | 930 | BMR051910263 | 985121020109803 | 773 | 5,500 |
| 8 | 76 | 5-5-5 | 920 | BMR051810010 | 985121020102666 | 845 | 6,850 |
| 9 | 77 | 6-7-7 | 950 | BMR051810022 | 985121010113514 | 852 | 8,200 |
| 10 | 78 | 6-7-8 | 940 | BMR051810251 | 985121020109760 | 867 | 9,250 |
| 11 | 79 | 3-3-5-4 | 970 | BMR051910005 | 985121020112682 | 778 | 5,800 |
| 12 | 80 | 3-3-5-5 | 960 | BMR052010257 | 985121020102475 | 865 | 7,500 |
| 13 | 81 | 3-3-8-6 | 990 | BMR051810018 | 985121020120584 | 784 | 6,050 |
| 14 | 82 | 3-3-8-7 | 980 | BMR052010254 | 985121020117880 | 848 | 10,250 |
| 15 | 83 | 3-4-5-8 | 1010 | BMR052010012 | 985121020110572 | 1,030 | 14,750 |
| 17 | 70 | 3-5-4-5 | 1040 | BMR052410254 | 985121020112024 | 770 | 5,000 |
| 18 | 71 | 3-5-4-6 | 1050 | BMR051910003 | 985121020117439 | 793 | 6,750 |
| 19 | 72 | 3-5-7-8 | 1060 | BMR052010005 | 985121020110422 | 943 | 10,000 |
| 20 | 73 | 3-5-8-4 | 1070 | BMR052010010 | 985121020112572 | 919 | 9,300 |
| 21 | 74 | 3-6-6-6 | 1080 | BMR051910264 | 985121020104565 | 810 | 8,500 |
| 22 | 75 | 3-6-6-7 | 1090 | BMR052510252 | 985121020112727 | 784 | 6,900 |
| 23 | 76 | 3-7-7-4 | 1100 | BMR052010008 | 985121020113971 | 809 | 6,550 |
| 24 | 77 | 3-7-7-5 | 1110 | BMR052510006 | 985121020109535 | 825 | 6,400 |
| 25 | 78 | 4-4-6-7 | 1120 | BMR052010009 | 985121020113687 | 798 | 7,000 |
| 27 | 80 | 4-5-6-8 | 1140 | BMR052010253 | 985121020103543 | 790 | 5,750 |
| 28 | 81 | 4-5-7-7 | 1150 | BMR052010006 | 985121020112496 | 993 | 15,200 |
| 29 | 82 | 4-7-4-7 | 1160 | BMR052010011 | 985121020113490 | 913 | 9,250 |
| 30 | 83 | 4-7-4-8 | 1170 | BMR051910265 | 985121020112060 | 824 | 7,000 |
| 32 | 70 | 5-5-7-8 | 1200 | BMR052410260 | 985121020108387 | 1,040 | 16,125 |
| 33 | 71 | 5-7-6-7 | 1230 | BMR051910262 | 985121020113622 | 896 | 9,500 |

Table 2A. Listening station coordinates used for Blue Mesa Reservoir, Colorado sonic telemetry in the fall of 2010 and 2011. Coordinates are in UTM (NAD 83 Datum) and are approximately 800 meters apart, thus making each listening radius 800 meters to allow for triangulation of received signals. Maximum range reported by the sonic tag manufacturer (Sonotronics model CT-05-48) is 1,000 meters.

| Station | Easting | Northing | Station | Easting | Northing |
|---|---|---|---|---|---|
| 01 | 296550 | 4258905 | 21 | 307197 | 4260412 |
| 02 | 297263 | 4259359 | 22 | 307498 | 4259611 |
| 03 | 297935 | 4259687 | 23 | 308001 | 4260538 |
| 04 | 298117 | 4258898 | 24 | 308825 | 4260628 |
| 05 | 298697 | 4258371 | 25 | 309574 | 4260325 |
| 06 | 298720 | 4259034 | 26 | 309932 | 4259593 |
| 07 | 298694 | 4259840 | 27 | 310524 | 4258906 |
| 08 | 298806 | 4260655 | 28 | 311241 | 4259044 |
| 09 | 298497 | 4260984 | 29 | 311600 | 4259319 |
| 10 | 299009 | 4261861 | 30 | 312410 | 4259285 |
| 11 | 299525 | 4261061 | 31 | 313047 | 4259388 |
| 12 | 300294 | 4261129 | 32 | 313793 | 4259551 |
| 13 | 301099 | 4261104 | 33 | 314629 | 4259468 |
| 14 | 301804 | 4260757 | 34 | 315411 | 4259704 |
| 15 | 302520 | 4260429 | 35 | 315973 | 4260326 |
| 16 | 303291 | 4260147 | 36 | 316626 | 4260789 |
| 17 | 304110 | 4260188 | 37 | 317386 | 4261049 |
| 18 | 304876 | 4259916 | 38 | 318188 | 4261159 |
| 19 | 305687 | 4259806 | 39 | 319029 | 4261080 |
| 20 | 306442 | 4260150 | 40 | 319681 | 4261421 |

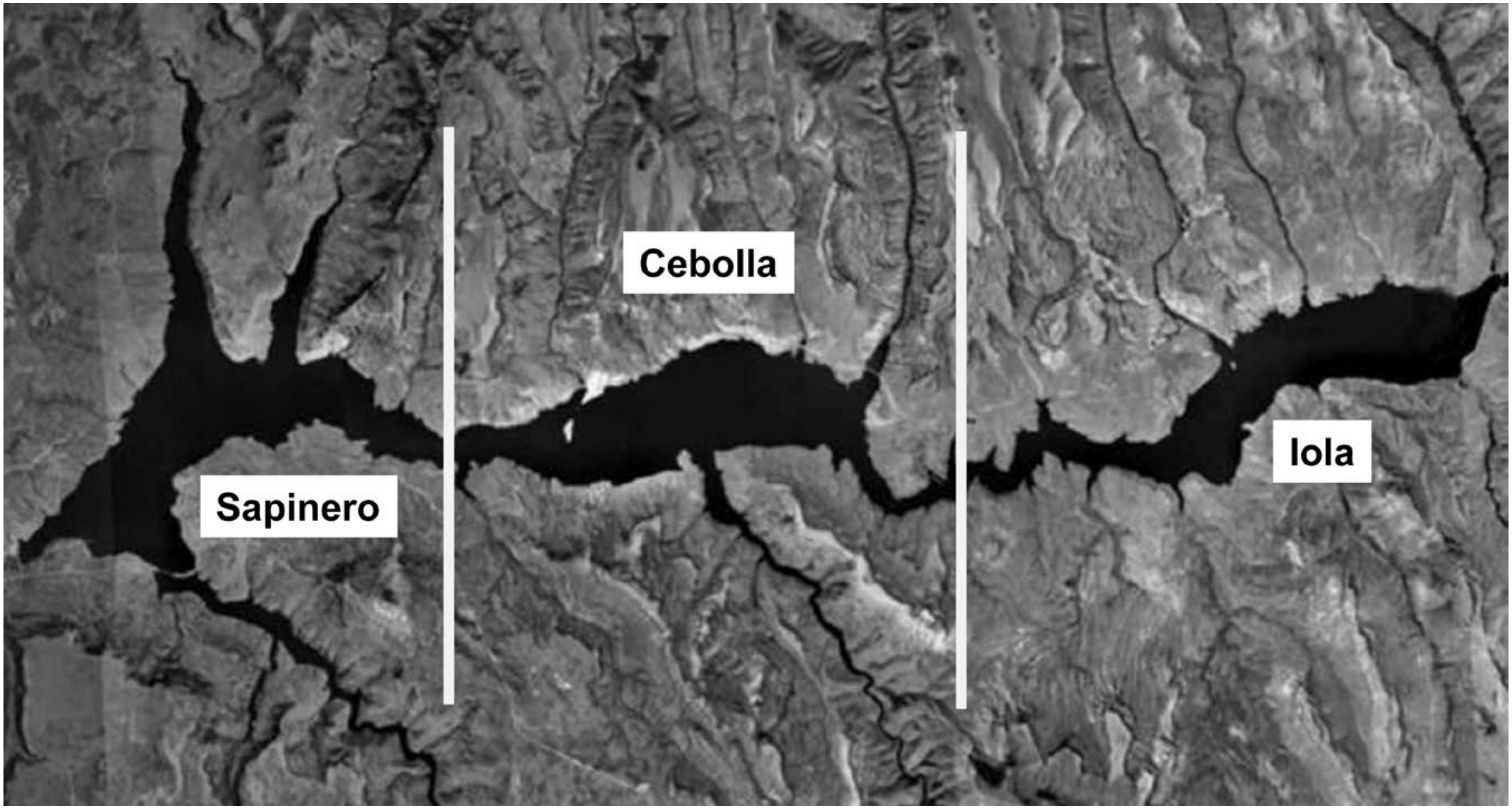


Figure 1A. Overview of Blue Mesa Reservoir, Colorado showing relative locations of the three basins. The dam is located at the far western edge (left) of the Sapinero basin. Within Sapinero are the three main arms including the Lake Fork (bottom), Soap Creek (upper left), and West Elk (second from upper left). Sapinero and Cebolla are separated by Middle Bridge while Cebolla and Iola are separated by the Elk Creek Marina. The satellite image is from Google Earth (2012).

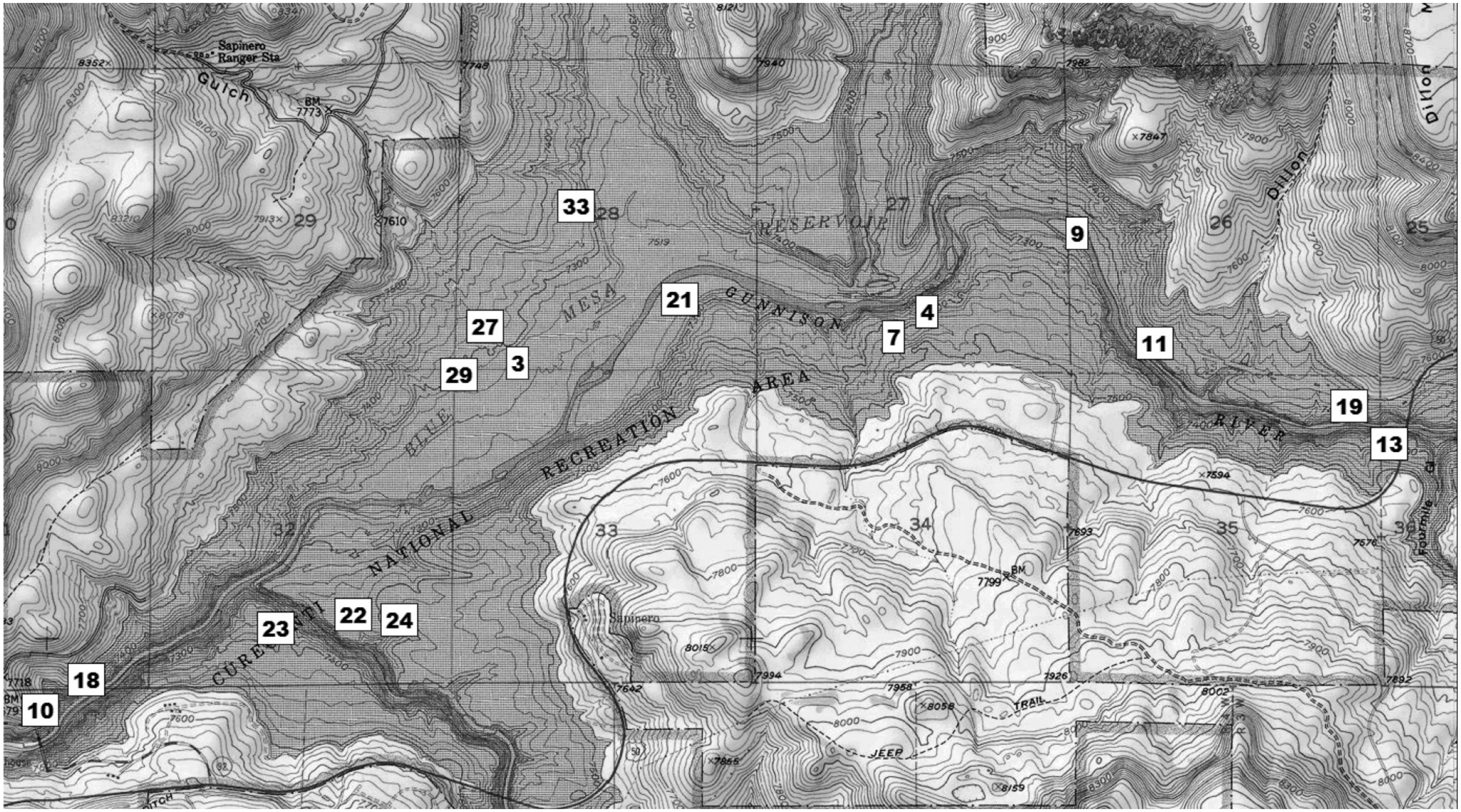


Figure 2A. Locations of lake trout (*Salvelinus namaycush*) in the Sapinero basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 8 October 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

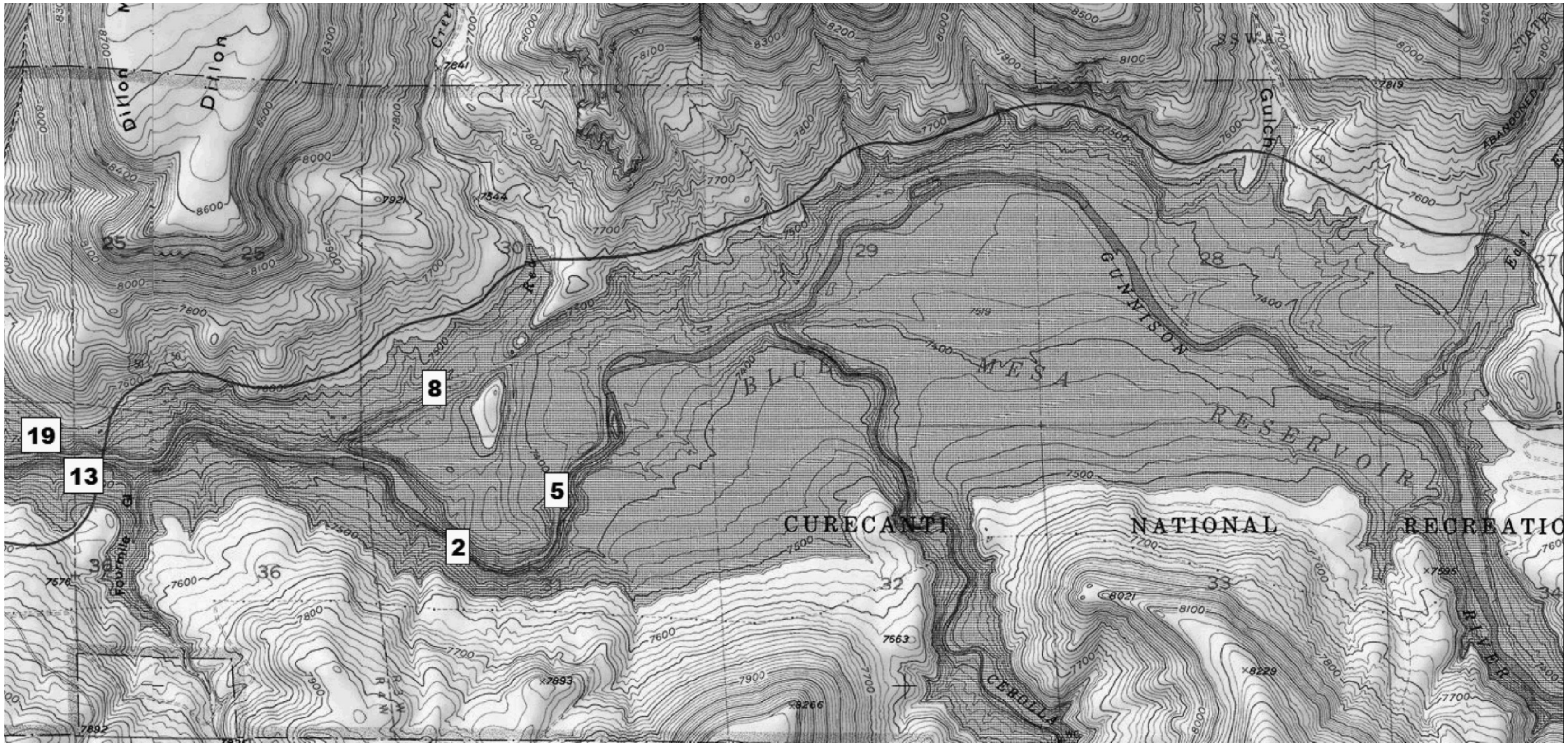


Figure 3A. Locations of lake trout (*Salvelinus namaycush*) in the Cebolla basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 8 October 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

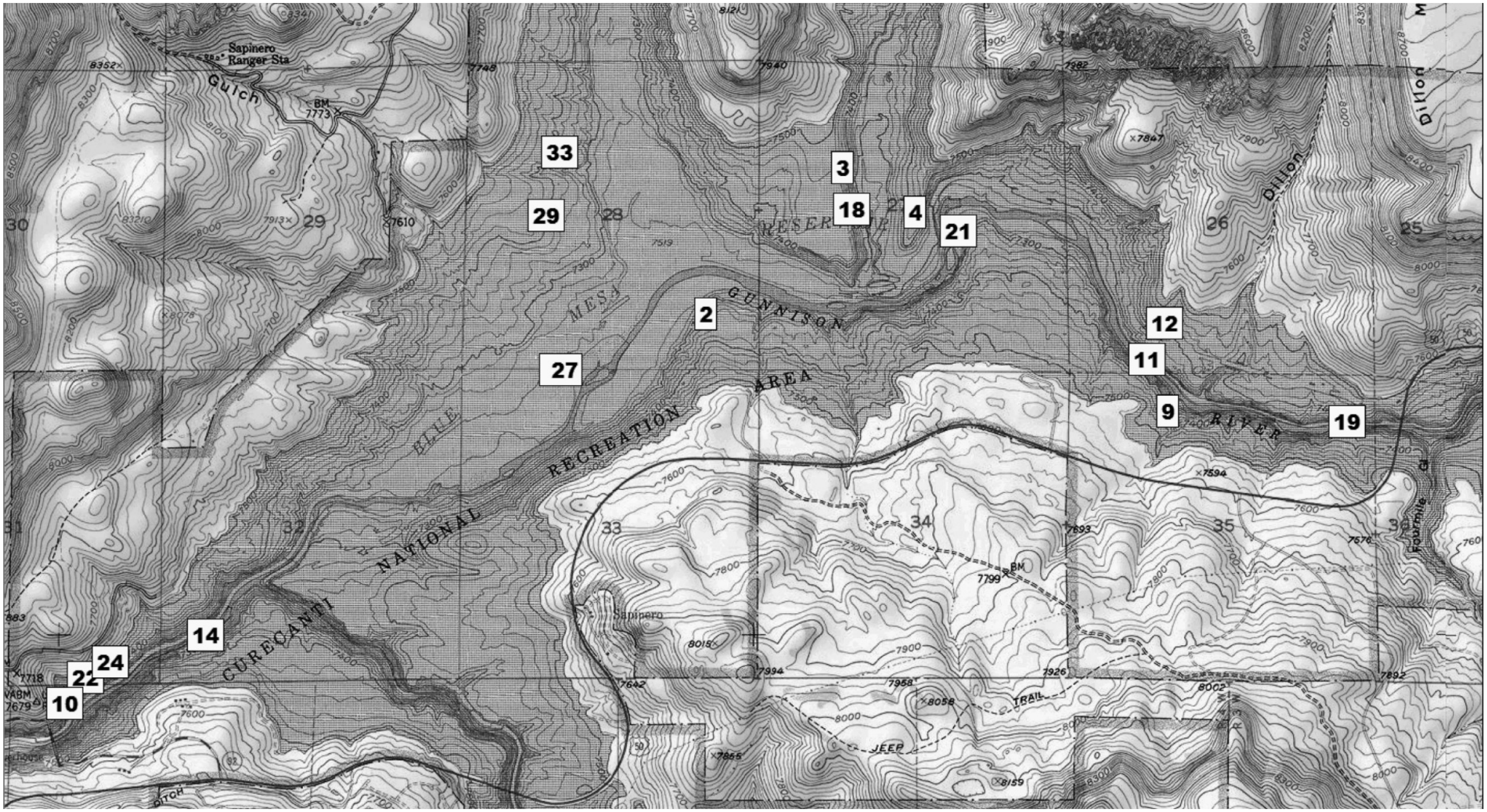


Figure 4A. Locations of lake trout (*Salvelinus namaycush*) in the Sapinero basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 20 October 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

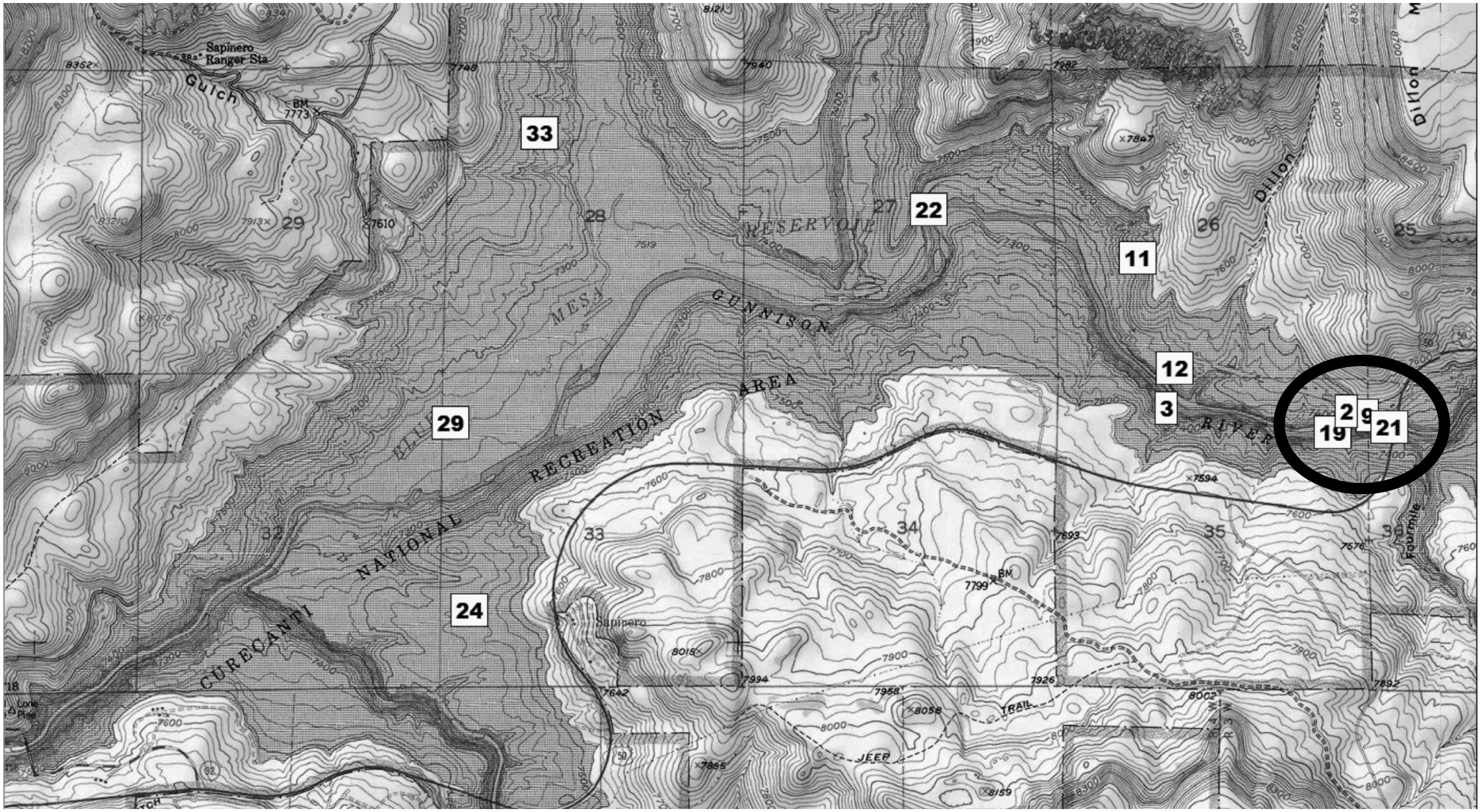


Figure 5A. Locations of lake trout (*Salvelinus namaycush*) in the Sapinero basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 2 November 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. Note the circled grouping of tagged lake trout at the east end of the basin. The map was created using National Geographic TOPO software (2008).

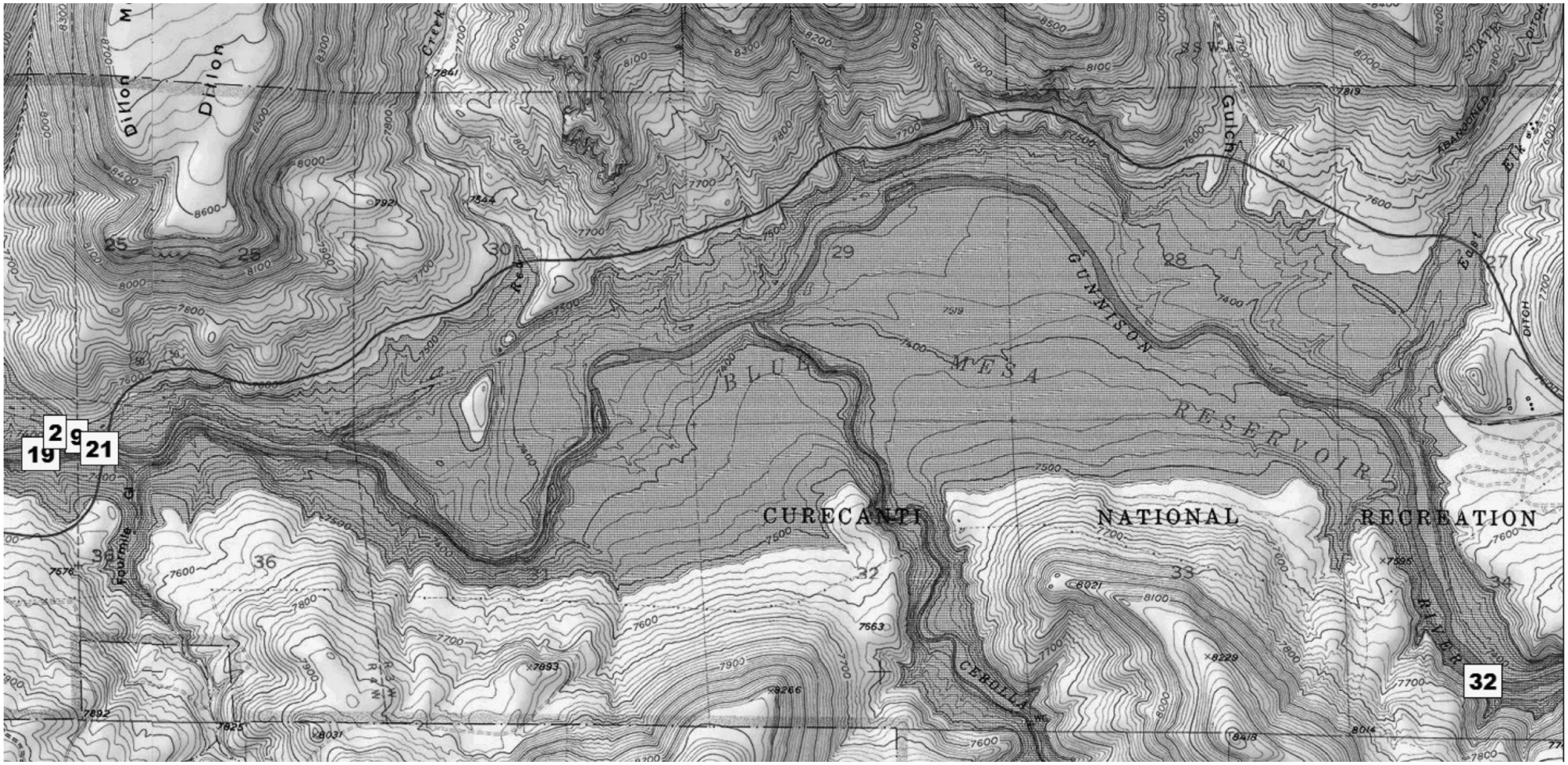


Figure 6A. Locations of lake trout (*Salvelinus namaycush*) in the Cebolla basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 2 November 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

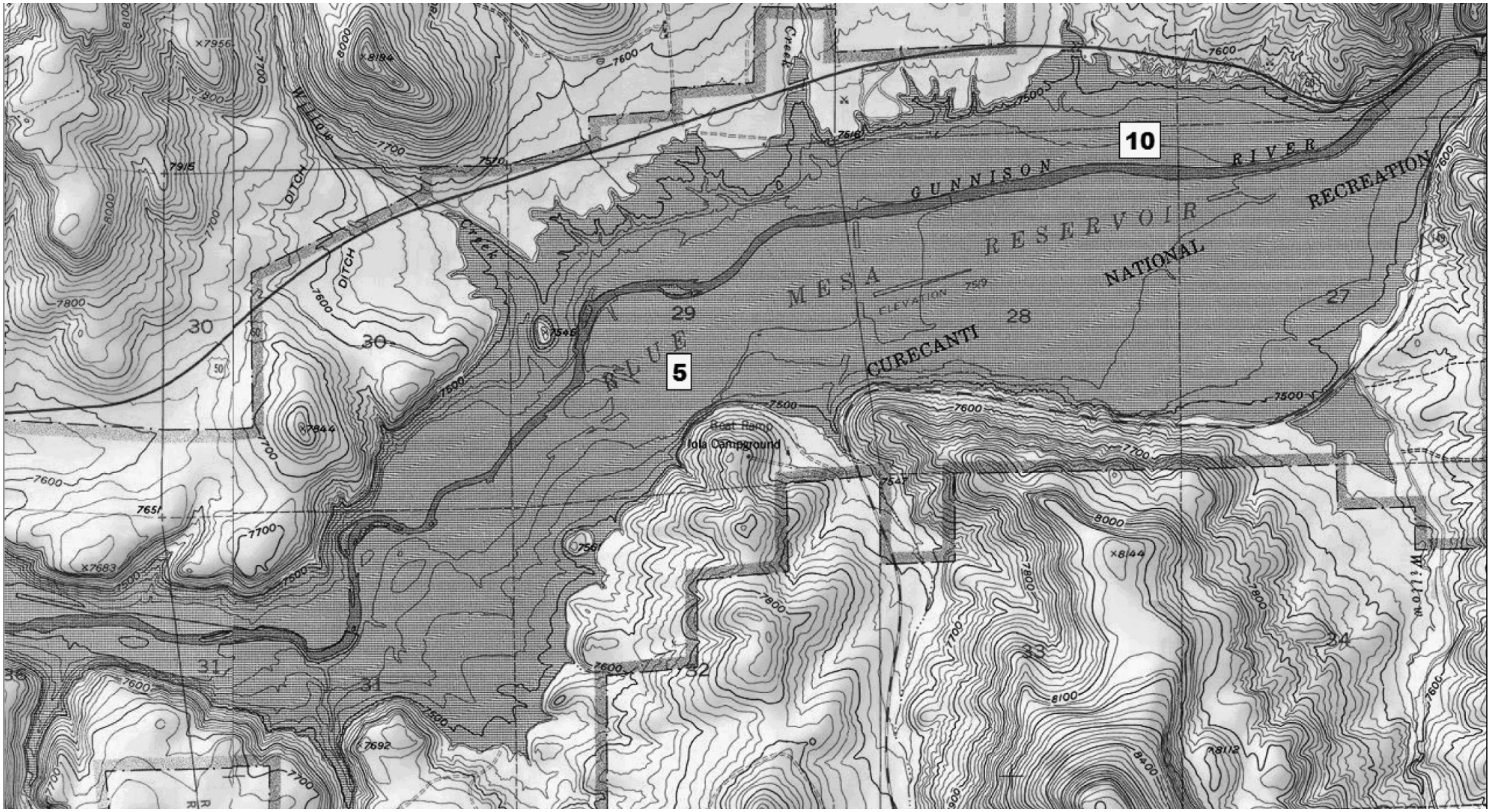

Figure 7A. Locations of lake trout (*Salvelinus namaycush*) in the Iola basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 2 November 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

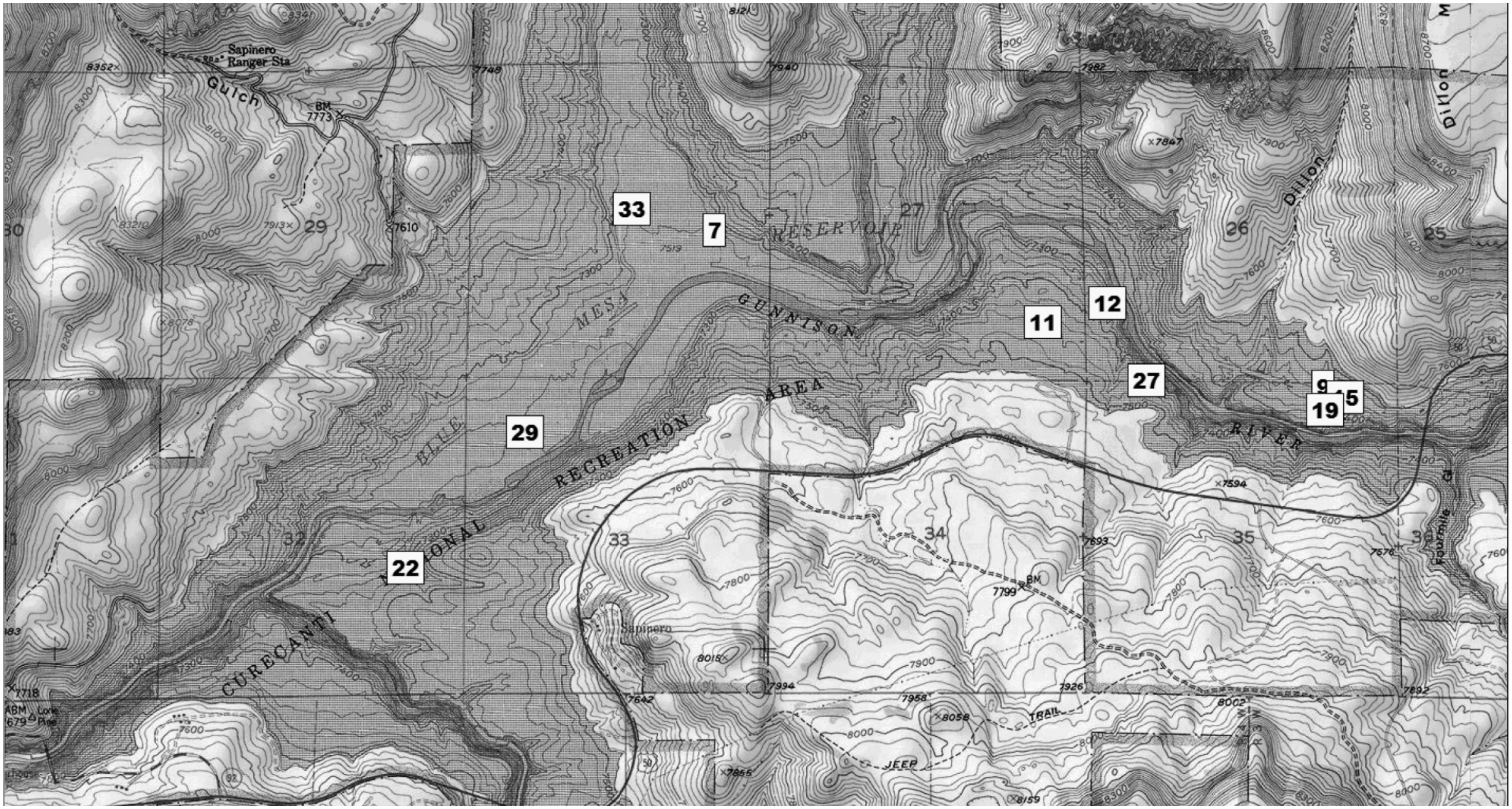


Figure 8A. Locations of lake trout (*Salvelinus namaycush*) in the Sapinero basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 10 November 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

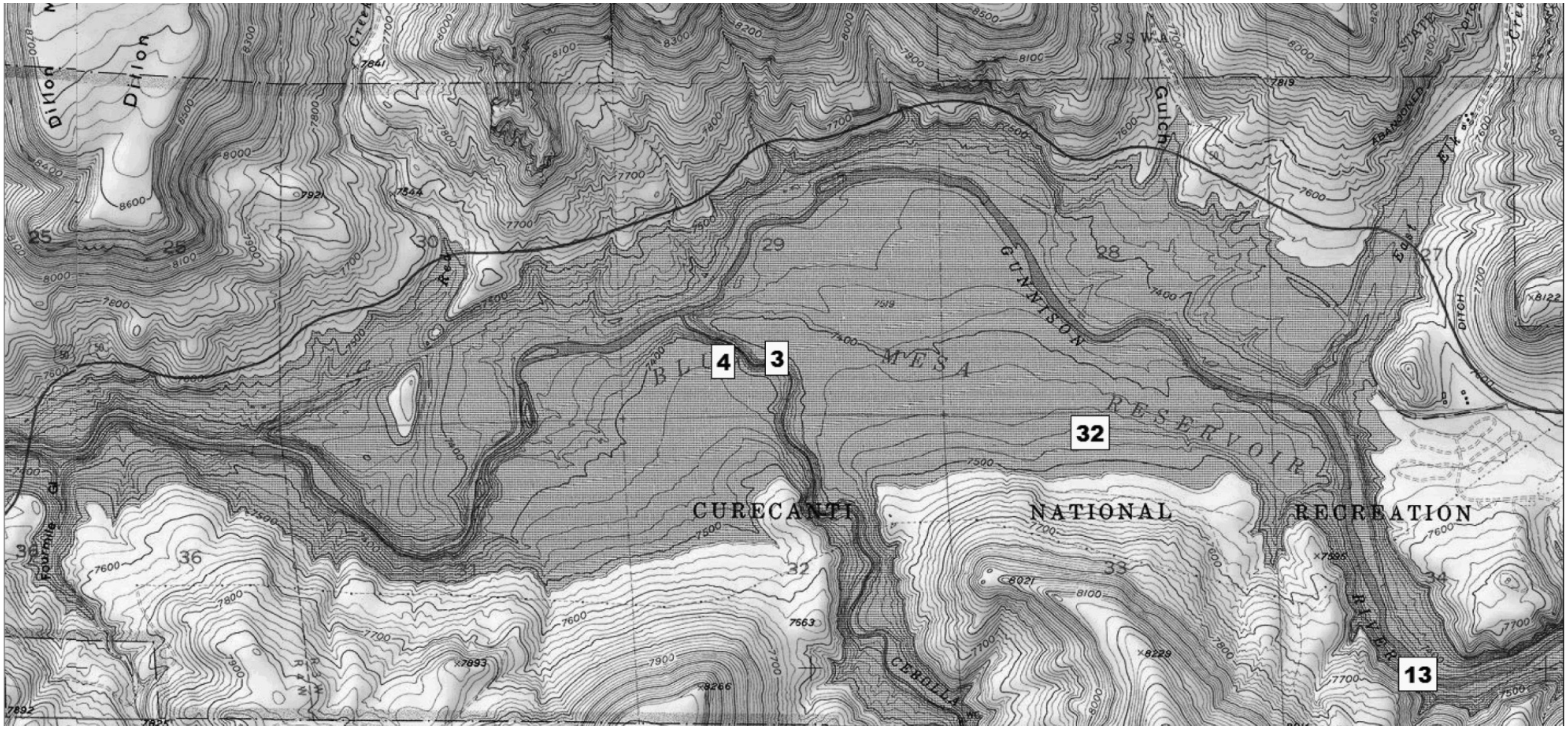


Figure 9A.  Locations of lake trout (*Salvelinus namaycush*) in the Cebolla basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 10 November 2010.  Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points.  Numbers correspond to individual fish tag identification numbers.  The map was created using National Geographic TOPO software (2008).

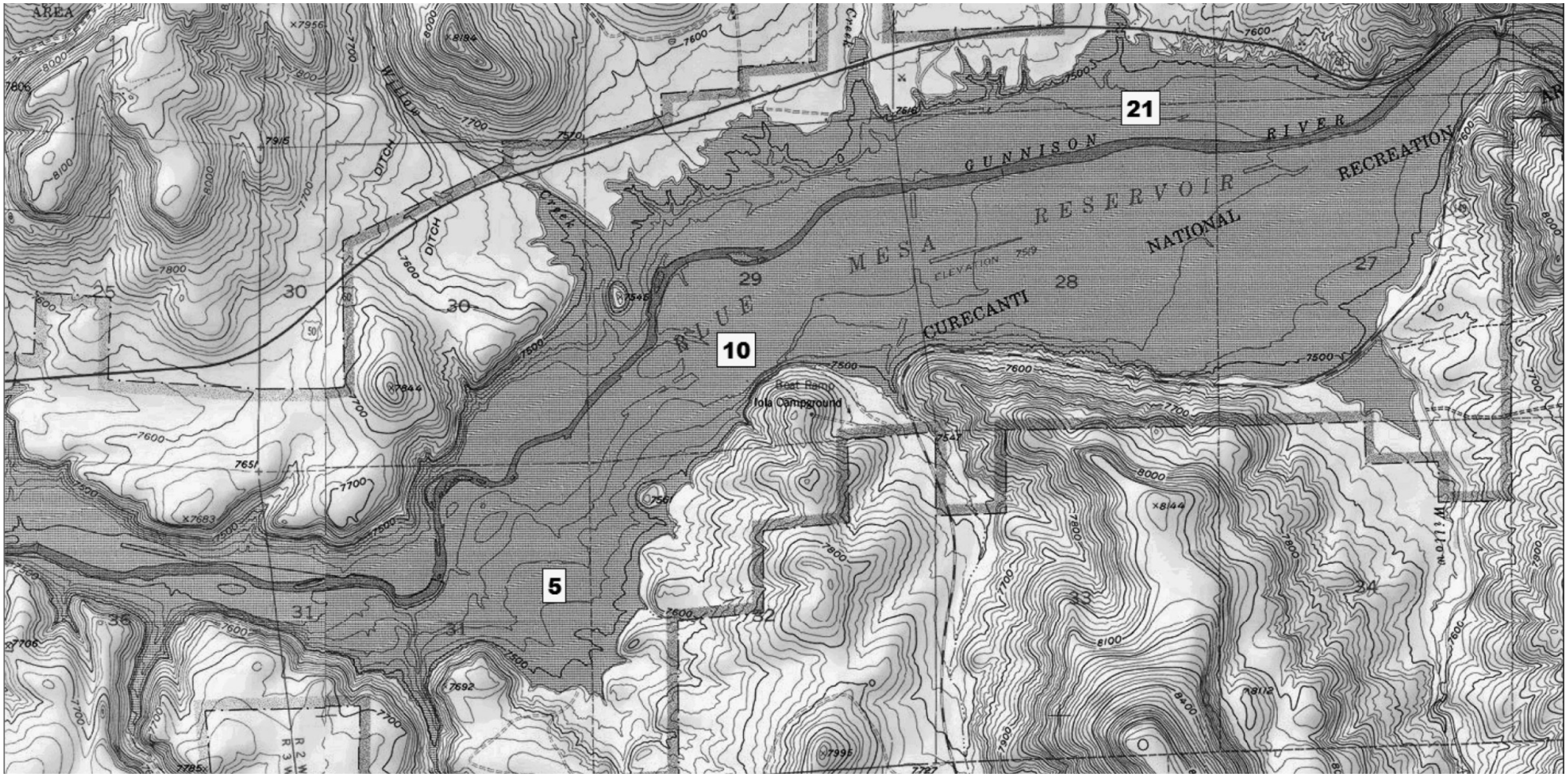


Figure 10A. Locations of lake trout (*Salvelinus namaycush*) in the Iola basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 10 November 2010. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

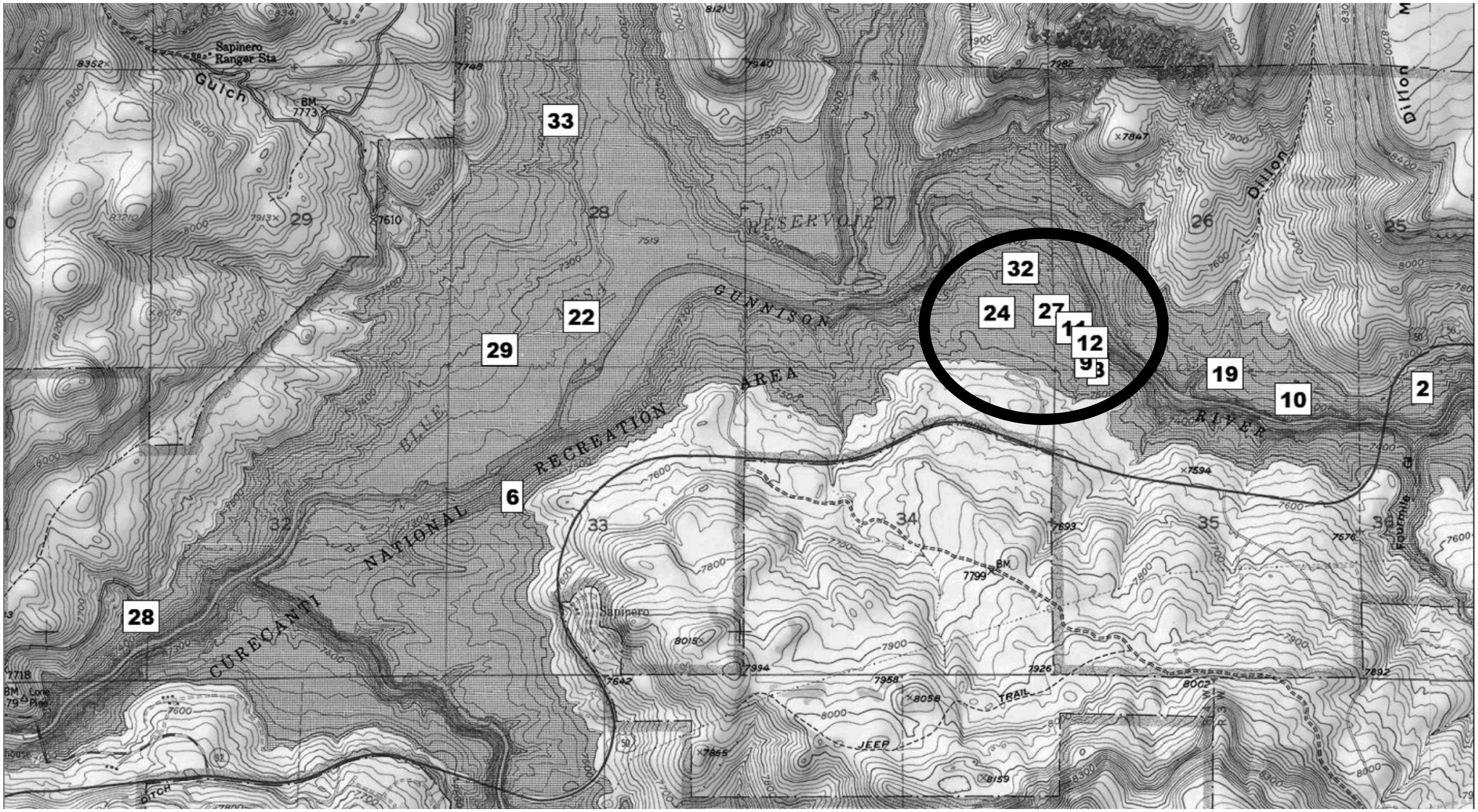


Figure 11A. Locations of lake trout (*Salvelinus namaycush*) in the Sapinero basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 19 October 2011. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. Note the circled congregation of tagged lake trout at the east end of the basin. The map was created using National Geographic TOPO software (2008).

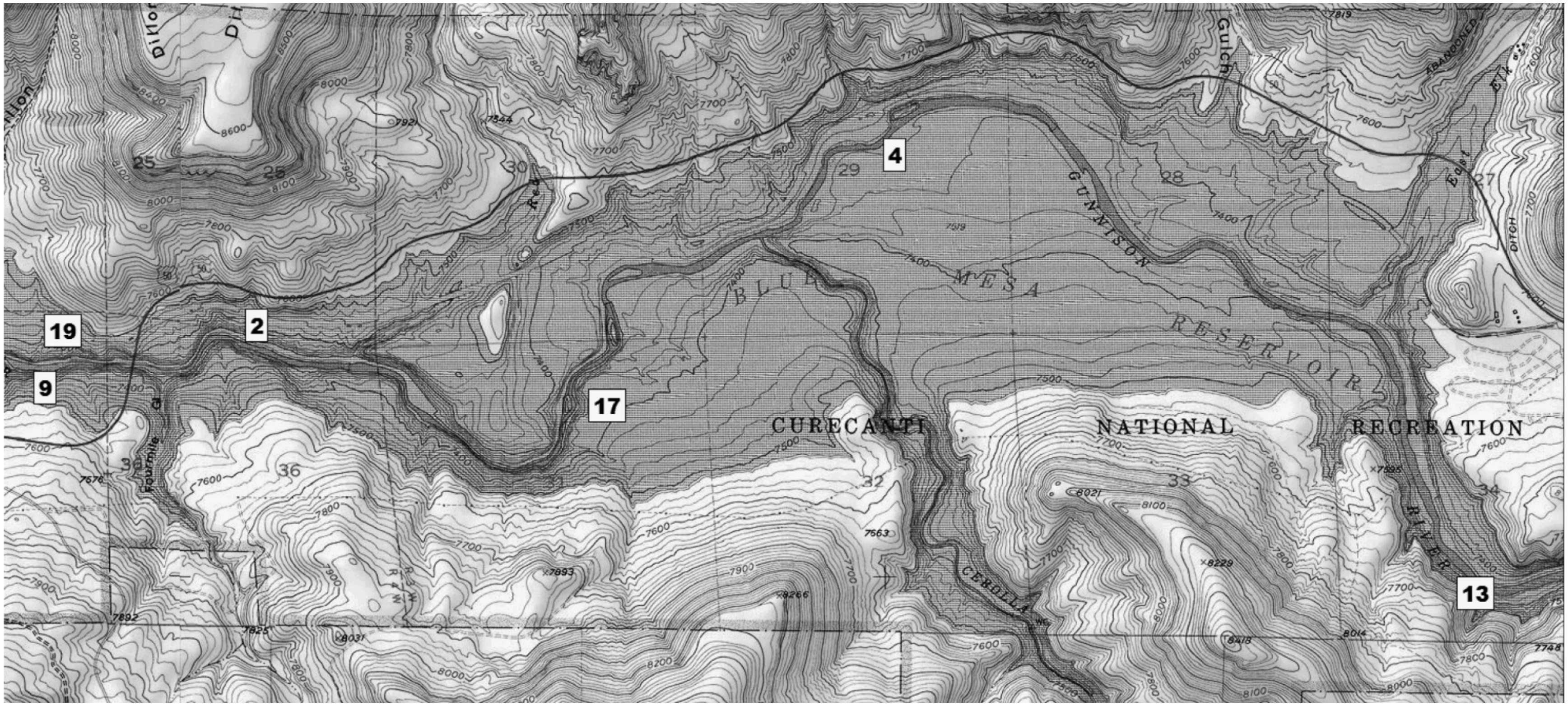


Figure 12A. Locations of lake trout (*Salvelinus namaycush*) in the Cebolla basin of Blue Mesa Reservoir, Colorado implanted with Sonotronics model CT-05-48 series transmitters on 20 October 2011. Lake trout were triangulated from a boat using a Sonotronics USR-96 receiver with DH-4 directional hydrophone at standardized listening points. Numbers correspond to individual fish tag identification numbers. The map was created using National Geographic TOPO software (2008).

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