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ARTICLE

Managing for Coexistence of Kokanee and Trophy Lake Trout in a Montane Reservoir

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Abstract
Kokanee *Oncorhynchus nerka* and Lake Trout *Salvelinus namaycush* are stocked for sportfishing in lakes and reservoirs throughout the western United States and Canada. However, where the two species co-occur, unsustainable levels of predation by Lake Trout can lead to declines in kokanee abundance and declines in Lake Trout growth and body condition. Such declines occurred in Blue Mesa Reservoir, Colorado. In 2009, managers began removing Lake Trout (<740 mm TL) in an attempt to sustain the hatchery-dependent kokanee population while still providing a trophy Lake Trout fishery. To evaluate this and other strategies for achieving the dual management goals, we developed age-structured kokanee and Lake Trout population models and linked them to a bioenergetics model of Lake Trout predation. We found that the existing level of Lake Trout removal (0.23; ages 4–9) is insufficient to prevent further decline and ultimately the extirpation of the kokanee population. If removal of age-4–9 Lake Trout is intensified to 0.38, the kokanee population would persist; however, removal would have to be increased to 0.63 to allow a return to historic kokanee abundance. Focusing removal on age-4 Lake Trout (0.78) would allow for persistence of kokanee and would leave more trophy Lake Trout for anglers, suggesting that the two goals are compatible under some circumstances. However, management costs of balancing kokanee with trophy Lake Trout are high and put both fisheries at risk unless Lake Trout abundance is controlled.

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

Lake Trout are widely distributed outside of their native range as 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 sizes than are typical for the species (Martinez et al. 2009). The potential for Lake Trout to reach large sizes has created a devoted angler clientele in many waters where Lake Trout have been introduced, and protective fishing regulations were implemented in the 1980s and early 1990s to foster production of trophy-sized Lake Trout (Martinez et al. 2009). Many

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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 have thrived in western lakes and reservoirs, protected from harvest and consuming energy-rich salmonid prey over longer growing seasons than occur in their native range.

Many waters have the potential to produce relatively large Lake Trout, but sustaining suitable prey populations 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). However, Lake Trout growth and condition declined after Lake Trout depleted the reservoir's populations of Utah Chub *Gila atraria* and kokanee *Oncorhynchus nerka* (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 (Ellis et al. 2011; Schoen et al. 2012).

Lake Pend Oreille (Idaho) also supported large Lake Trout in the past, but the forage base was not sustainable. Lake Trout were introduced in 1925 and became abundant in the mid-1990s (Martinez et al. 2009). Kokanee were also introduced into Lake Pend Oreille, became self-sustaining by the mid-1930s, and were abundant enough to support a commercial fishery. However, by 2000, the kokanee population in the lake was nearly extirpated by Lake Trout (Hansen et al. 2008). During 2006, intensive Lake Trout removal began in Lake Pend Oreille in an attempt to induce mortality rates exceeding 50% per year (Hansen et al. 2008), a threshold that Healey (1978) stated would produce a decline in abundance in most North American Lake Trout populations. Trap nets and gill nets were used by managers, a commercial Lake Trout fishery was initiated, and cash incentives ($10–15 per fish) were offered to encourage Lake Trout harvest by anglers.

Blue Mesa Reservoir (BMR; Colorado) has a food web similar to those in the systems described above. However, individual Lake Trout in BMR exhibit some of the fastest growth rates on the continent (Martinez et al. 2009). Due to the abundant supply of stocked kokanee prey, four consecutive state-record-sized Lake Trout were taken by anglers, 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 indicate that the primary species of interest to BMR anglers is kokanee, with 45% of anglers traveling to BMR specifically to target that species, while 7% of anglers target Lake Trout (D. Brauch, unpublished data). The value of the BMR kokanee fishery to the local economy has been estimated at more than $5 million per year (Johnson et al. 2009).

Lake Trout were sporadically stocked in BMR during 1968–1992, with no evidence of natural recruitment. However, beginning in 1993, angler creel surveys showed a Lake Trout size structure that was indicative of natural recruitment despite removal of size regulations and an increase in the daily bag limit to eight fish. This apparent onset of wild recruitment corresponded with new dam operations implemented in 1992, which kept the reservoir level more stable during fall and winter, when Lake Trout eggs are incubating. Relative weight (W_r) of large fish (>1,000 mm TL) decreased in recent years from over 154 in 2000 to 108 in 2009, suggesting a decrease in prey availability. This decrease in prey was corroborated by annual hydroacoustics and creel surveys, which demonstrated a significant decrease in kokanee abundance (Brauch, unpublished data). Annual hydroacoustics surveys estimated that the abundance of pelagic fish (mostly kokanee) decreased by 90% from over 1 million fish in 2002 to less than 100,000 fish in 2009, and angler effort and catch per effort also declined. Creel surveys showed a decrease in angler harvest from 130,000 kokanee in 2002 to less than 20,000 in 2009. The kokanee decline occurred despite efforts to boost abundance through increased annual fry stocking—from 1.4 million in 1994 to 3.1 million fish in 2009. Because BMR is hatchery sustained and the reservoir has also supplied up to 90% of the hatchery kokanee eggs used to stock 26 waters in the state annually, the decline in the BMR kokanee population is of concern to CPW. In 2009, CPW began a Lake Trout removal program in an attempt to suppress Lake Trout and prevent the extirpation of the kokanee population in BMR. The purpose of the present investigation was to inform managers about management strategies that could allow for an abundant kokanee population and egg supply while secondarily maintaining anglers' opportunities to catch 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). Blue Mesa Dam was completed on the Gunnison River in 1965 with the intention of capturing high spring runoff for summer irrigation while also supporting power generation and flat-water recreation. The 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, drawing anglers from all 48 of the contiguous United States (Brauch, unpublished data). The fish community consists primarily of stocked kokanee and Rainbow Trout *O. mykiss* and naturally reproducing Lake Trout, Brown Trout *Salmo trutta*, Yellow Perch *Perca flavescens*, White Suckers *Catostomus commersonii*, and Longnose Suckers *C. 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, and then migrate back upstream to ROJ, where the eggs are stripped, fertilized, and hatched. Natural reproduction of kokanee is negligible in BMR and in 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 the Fishery Analysis and Modeling Simulator (FAMS, version 1.0; Slipke and Maceina 2010) to predict potential changes in Lake Trout abundance and size structure under different management scenarios, including selective gillnetting. 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 (years) to recruit to the fishery ($t_r - t_0$; where t_r = time at recruitment and t_0 = theoretical time at which fish length is zero); W_∞ = maximum theoretical weight from predicting L_∞ and the weight–length regression; K = growth coefficient from the von Bertalanffy growth equation; β = beta coefficient computed by FAMS, adjusting yield for input weight–length relationship; $X = e^{-Kr}$; $X_1 = e^{-K(MaxAge - t_0)}$, where MaxAge is the maximum age observed in the sampled population; $P = Z/K$; and Q = slope of the weight–length regression + 1.

Simulations were of a 40-year duration, which allowed the Lake Trout population to reach a stable age distribution. Other parameters included the intercept (a) and slope (b) of the $\log_e$ transformed weight–length relationship; conditional fishing mortality by age (cf_{age}); conditional natural mortality by age (cm_{age}); annual recruitment; and minimum TL at recruitment. Table 1 contains a complete list of parameter values that were obtained from BMR Lake Trout by using the following methods.

Lake Trout abundance, age, growth, mortality, and recruitment.—Lake Trout abundance was obtained from a reservoir-wide population estimate using the Summer Profundal Index Netting (SPIN) protocol (Sandstrom and Lester 2009) on August 8–12, 2011. Briefly, SPIN is a stratified-random gillnetting method that allows for relatively rapid estimation of Lake Trout density and abundance. The SPIN method has been calibrated using hundreds of systems with independent Lake Trout abundance estimates and known Lake Trout population sizes. The equation (from Sandstrom and Lester 2009) used to calculate density using CPUE is

$$\text{density (Lake Trout/ha)} = \sum_h W_h \times \frac{\sum V_{hi}}{n\, sets_h} \times 4.86,$$

where W_h = proportion of stratum h of the total area sampled; V_{hi} = gill-net selectivity score for fish caught in stratum h of net set i; n = number of fish caught; and $sets_h$ = number of net sets in stratum h.

We corroborated our SPIN estimate by using information from a mark–recapture study in 2002 (Crockett et al. 2006) and by using the trend in angler catch rate observed in annual CPW creel surveys (Brauch, unpublished data). Colorado Parks and Wildlife conducted an intensive creel survey on BMR during May 1–October 31 annually in 1993–2012. The survey used a stratified random design, with instantaneous counts of all anglers and access point interviews. Counts were conducted at 3–5-h intervals three times per day, and about 10% of the counted anglers 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).

Left sagittal otoliths (arbitrarily chosen to maintain consistency) for age interpretation were extracted from 545 Lake Trout culled in fall 2010. Otoliths were sectioned perpendicular to the sulcus by using an Isomet low-speed saw with diamond wafering blades. Thin sections were sanded to a thickness of 0.8–1.0 mm and were then polished. An image of the otolith thin section was digitally captured at 32 × magnification to be used for age estimation. The ages of all Lake Trout were independently estimated by two experienced readers 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. A subsample of 25 images was sent to Cornell University for outside age verification.

Growth of Lake Trout was computed by fitting a von Bertalanffy growth function (VBGF; Isely and Grabowski 2007) to length-at-age data collected during 2010–2012. The VBGF was fitted by using the nonlinear models procedure (PROC NLIN) in the Statistical Analysis System version 9.2 (SAS Institute 2009). We did not include Lake Trout growth compensation in our simulations, partly because even at existing low levels of kokanee abundance, Lake Trout growth was higher in BMR than in most other populations. An age–length key was constructed using 50-mm size categories to compute unbiased mean size at age (Quist et al. 2012). The age–length key was then applied to the number of Lake Trout in each 50-mm size category estimated by SPIN, resulting in the age distribution of the population.

The population's age distribution was $\log_e$ transformed, and Z was calculated using the slope of the catch curve for Lake Trout of ages 4–9. This age-group comprised the descending limb of the catch curve (Miranda and Bettoli 2007); younger Lake Trout were not considered to be fully recruited to the sampling gear. Abundance of age-10–30 Lake Trout was low and consisted of an unknown mix of wild and stocked fish; therefore, 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 data) and were combined with actual numbers of Lake Trout removed by gillnetting to find F. Instantaneous natural mortality (M) for

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

Symbol	Definition	Value
b	Weight–length parameter	3.335
a	Weight–length parameter	−6.008
L_∞ (mm)	Theoretical maximum TL	1,151
Num years	Length of model run (years)	40
k	von Bertalanffy growth coefficient	0.099
t_0 (years)	Theoretical time when TL = 0	−0.449
W_∞ (g)	Theoretical maximum weight	15,891
MaxAge (years)	Maximum age of fish	30
Recruitment	Abundance of age-0 fish	58,500
cm	Probability of natural mortality, catch curve, ages 0–30	0.359
	Estimated natural mortality, literature, ages 0–30	0.130
fm	Probability of fishing mortality	
	Ages 0–3	0.000
	Ages 4–9	0.231
	Ages 10–30	0.000

the population could then be obtained by $M = Z - F$. In addition to the catch curve mortality estimate, we estimated M by using equations from Quinn and Deriso (1999), Shuter et al. (1998), and Pauly (1980). Quinn and Deriso (1999) described natural mortality as

$$M = \frac{-\log_e(0.01)}{t_{max}},$$

where t_{max} = maximum age. The equation from Shuter et al. (1998) is

$$M = 2.064 \times (K \times L_\infty)^{0.655} \times L_\infty^{-0.933}.$$

Pauly (1980) described natural mortality as

$$\log_{10} M = -0.0066 - (0.279 \times \log_{10} L_\infty) + (0.643 \times \log_{10} K) + [0.4634 \times \log_{10}(\text{temp})],$$

where temp is the average annual water temperature. An average of these three estimators was used in place of the catch curve estimate in an alternate series of FAMS modeling scenarios.

Exploitation was set at zero in FAMS scenarios for ages less than 4 and for ages 10 and older because harvest by anglers was negligible and because CPW released Lake Trout over 740 mm (age 10) to preserve large fish for anglers. We tracked the abundance of memorable-sized (800–999-mm) and trophy-sized (≥1,000-mm) Lake Trout (Neumann et al. 2012) in our simulations. Colorado Parks and Wildlife awards a master angler certificate to any angler that catches a fish over the specified length for that species. The threshold size for Lake Trout is 813 mm; thus, the number of fish larger than this size is similar to the sum of memorable- and trophy-sized fish.

Lake Trout consumptive demand for kokanee.—To characterize the food web structure, carbon and nitrogen stable isotope analyses were conducted on Lake Trout (307–1,015 mm TL), kokanee (147–456 mm TL), Brown Trout (384–620 mm TL), Rainbow Trout (223–412 mm TL), White Suckers (153–402 mm TL), Longnose Suckers (168–275 mm TL), and Yellow Perch (103–321 mm TL) collected from BMR. A 1-cm^3 muscle plug was collected during CPW gill-net sampling in May, June, October, and November 2010. Epaxial muscle tissue with skin removed was sampled between the dorsal fin and lateral line; each sample was stored at −20°C. Zooplankton, crayfish, amphipods, and chironomids were also collected in bulk from the reservoir or from fish stomachs during the same gill-net sampling periods and were stored at −20°C. In the laboratory, samples (n = 306) were dried at 60°C for 48–72 h, after which they were ground to a fine powder with a mortar and pestle. Each sample was then analyzed for δ^{13}C, δ^{15}N, and carbon : nitrogen (C:N) ratio in a Thermo Delta V isotope ratio mass spectrometer interfaced to a CE Instruments NC2500 elemental analyzer. Isotopic signatures were expressed as δ values in parts per thousand (‰) differences from C and N standards:

$$\delta_{sample} = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000,$$

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; δ^{13}C = −25.58‰, δ^{15}N = 17.31‰; 49.74% C, 12.95% N) and corn (n = 24; δ^{13}C = −11.66‰, δ^{15}N = 0.93‰; 45.97% C, 2.09% N). Standards used to determine isotopic precision were American mink *Neovison vison* (n = 40; δ^{13}C = −25.21‰, δ^{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 SE from the mean of each standard used in analysis never exceeded 0.07‰.

Lipids are known to be depleted in ^{13}C relative to muscle tissues, and lipid content can vary greatly among individual fish within a species as well as 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:

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

Once the δ values were determined, we used MixSIR software to estimate the proportions of prey species consumed by Lake Trout. MixSIR, a Bayesian mixing model developed by Semmens and Moore (2008), 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 the means and SDs of prey isotopic signatures. Amount of isotopic fractionation with SD for both $\delta^{13}C$ and $\delta^{15}N$ must also be included. We used default means and SDs of fractionation that were previously determined by McCutchan et al. (2003) and validated in the model by Moore and Semmens (2008). We used 25×10^6 iterations in all runs of MixSIR, which amply satisfied quality assurance requirements (Semmens and Moore 2008).

The Lake Trout population was divided into five size-/age-classes corresponding to dietary and energetic differences related to trophic ontogeny (Table 2). The smallest size-class consisted of Lake Trout less than 332 mm TL (age < 3), and these fish consumed only invertebrates. The second size-class included fish ranging from 332 mm TL to less than 409 mm TL (age 3) and corresponded to individuals transitioning to piscivory. The third size-class included Lake Trout from 409 mm TL to less than 478 mm TL and corresponded to age-4 fish. Fish in the fourth size-class ranged from 409 mm TL to less than 740 mm TL (ages 4 to <10) and were 94.9% piscivorous. The last size-class consisted of 740-mm TL and larger fish (age ≥ 10), which 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, chironomid pupae, amphipods, and daphnia), (2) crayfish, (3) Yellow Perch smaller than 160 mm TL, (4) Rainbow Trout smaller than 300 mm TL, and (5) kokanee. Catostomids did not appear in any Lake Trout gut contents 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), which was used in the following bioenergetics modeling.

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 millimeter, weighed to the nearest gram, and then frozen whole at −20°C. Whole fish were cut into approximately 1.5-cm cubes while still frozen and were dried to constant weight at 60°C to determine water content. The entire fish was then ground to a fine powder and homogenized. Three subsamples of each fish were analyzed for energy density in a Parr 1261 isoperibol bomb calorimeter. Energy content of each dry sample was then converted to energy on a wet weight basis using water content determined for each sample.

Consumptive demand by Lake Trout was estimated using Fish Bioenergetics version 3.0 (Hanson et al. 1997). Average energy densities of five age-groups of Lake Trout and their prey (Table 2) were determined from measured values either by prey taxon (Rainbow Trout, Yellow Perch, crayfish, and small invertebrates) or in the size-classes consumed by Lake Trout (kokanee). Lake Trout diet composition was determined for size-classes identical to those used in the stable isotope mixing models. Age-classes of Lake Trout were converted to weights at age by using the VBGF. Other parameters required for Fish Bioenergetics 3.0 included water temperature, prey digestibility, age at first spawning, timing of spawning, and fraction of body mass lost to spawning. Under the assumption that Lake Trout sought temperatures closest to their optimum (10°C; Stewart et al. 1983), we used observed thermal profiles to develop the thermal history in simulations: 4°C on days 1–89; 5°C on days 90–119; 8°C on days 120–143; 10°C on days 144–303; 8°C on days 304–333; and 4°C on days 334–365. Day 1 coincided with January 1, and temperatures were the 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).

In all culled Lake Trout, the peritoneal cavity was exposed and examined to assess gender and maturity. Age at first spawning was set to age 6 to coincide with observed age at 50% maturity; spawning occurred on day 300 of simulations, and 9.1% of fish mass was 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 (1) measured ripe skein weight (14.8% of body weight) from female Lake Trout collected in BMR and (2) the average value for male Lake Trout (3.3%; from Ruzycki et al. 2003). Sex ratio was 50% (as observed in BMR), and spawning occurred in every year of the simulation.

Because we were most interested in population-level impacts on kokanee, we converted the mass of kokanee consumed into numbers of kokanee consumed. From stomach content analyses, we found that the mean TL of kokanee consumed by Lake Trout was equivalent to 33% of predator TL, a value corroborated

TABLE 2. Diet composition used in bioenergetics simulations to estimate consumptive demand by five Lake Trout (LKT) age-classes preying on kokanee (KOK), Rainbow Trout (RBT), Yellow Perch (YPE), crayfish *Orconectes* spp. (CFI), and other small invertebrates (SMI) in Blue Mesa Reservoir. Diet proportions were obtained from stable isotope measurements; energy density was determined by calorimetry of taxa from the reservoir. Lake Trout and kokanee energy densities are averages of measured values for Lake Trout age-groups and for the kokanee sizes consumed by each Lake Trout age-group.

		Prey type					
LKT TL (mm)	LKT age (years)	KOK	RBT	YPE	CFI	SMI	LKT energy density
		Diet proportions					
<332	<3				0.500	0.500	
332 to <409	3	0.576	0.034	0.266	0.058	0.066	
409 to <478	4	0.478	0.053	0.307	0.091	0.072	
409 to <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

by Yule and Luecke (1993), Johnson and Martinez (2000), and Ruzycki et al. (2003). The length of kokanee consumed based on Lake Trout length was converted to wet weight by using a weight–length relationship for BMR kokanee (below). Per capita kokanee biomass consumed by each Lake Trout age-group was divided by kokanee weight to yield the number of kokanee consumed per fish. This value was then scaled up to the population level by using the number of Lake Trout predicted in the FAMS simulations. Kokanee age-class partitioning was accomplished with an age–length key specific to BMR (Brauch, unpublished data) and was used in the age-structured population dynamics model described below.

Kokanee population modeling.—We created an age-structured model of kokanee population dynamics to evaluate the 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 BMR. Mortality at this stage included losses from river-resident Brown Trout (P[BRN]); these losses were measured in the system (see below). In the reservoir, age-0 and age-1 kokanee experienced losses due to entrainment through the dam's outlet works (P[dam]), unspecified sources of natural mortality (P[nm]; e.g., predation by species other than Lake Trout; disease), and Lake Trout predation (P[LKT]). Age-2–5 kokanee experienced natural mortality and Lake Trout predation, but we assumed that they 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 kokanee eggs available at ROJ was determined from maturity schedules (P[mat]), sex ratio (proportion of mature fish that were female, P[fem]), the proportion returning to the hatchery (P[ROJ]), and fecundity (FEC). Target egg production was set by CPW at a minimum of 4.135×10^6 eggs to produce 3.100×10^6 fry, with surplus eggs used in other hatchery facilities.

Kokanee mortality from Brown Trout predation during river transit was estimated by a study conducted in 2010 (Brauch, unpublished data); the Brown Trout population in the river above BMR was found to be capable of consuming 261,000 ± 59,000 stocked kokanee fry (mean ± 95% confidence interval [CI]). Losses to irrigation diversions are negligible because CPW begins screening or closing diversion outlets on the day of kokanee stocking. Kokanee are known to be susceptible to entrainment in dam releases (Johnson and Koski 2005; Johnson and Dauble 2006). Likelihood of entrainment through Blue Mesa Dam for age-0 ($P[\text{dam}] = 0.037$) and age-1 ($P[\text{dam}] = 0.018$) kokanee was determined based on Johnson and Koski (2005). Natural mortality in the reservoir (P[nm]) was estimated from McGurk (1999) by using kokanee weight at age (W_t) in grams,

$$P\,(\text{nm}) = 1.380 \times W_t^{-0.19}.$$

Kokanee weight was obtained using a weight–length regression from fish captured in BMR:

$$\log_e W = (2.789 \times \log_e \text{TL}) - 10.414.$$

The Z for each age-class (Z_{age}) was calculated by combining all sources of mortality:

$$Z_{0,1} = \log_e P(\text{nm}) + \log_e P(\text{fm}) + \log_e P(\text{LKT}) + \log_e P(\text{dam}) \text{ for ages 0 and 1;}$$

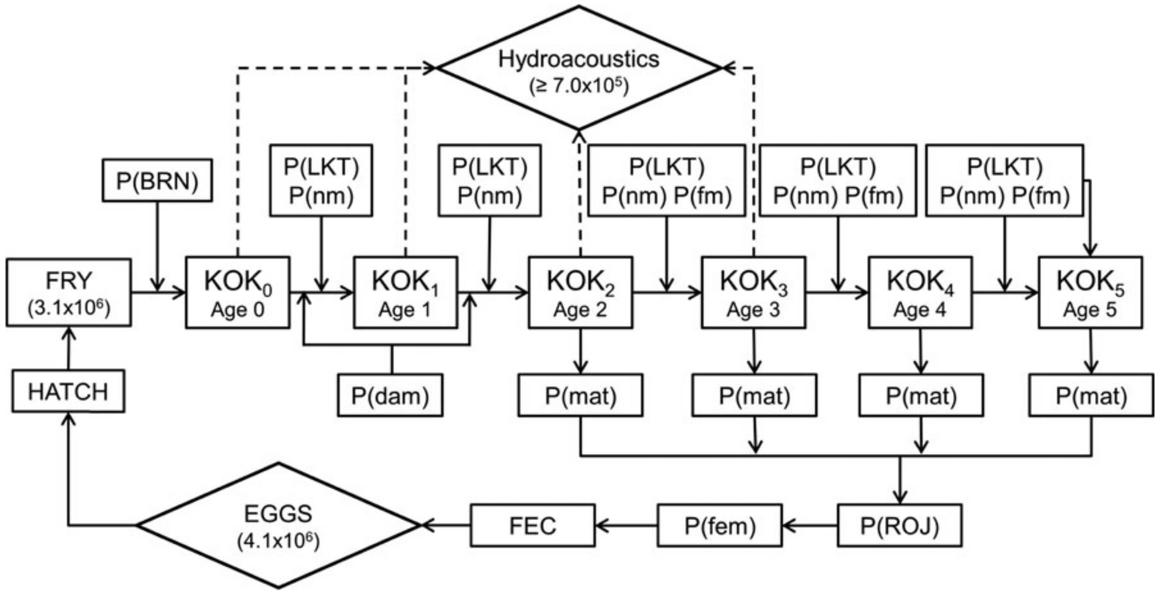

FIGURE 1. Age-structured model of kokanee population dynamics in Blue Mesa Reservoir, Colorado. See Table 3 for variable definitions and values. Up to 3.1×10^6 kokanee (KOK) fry are stocked every April. Kokanee suffer mortality during river transit and due to Lake Trout (LKT) predation, other sources of natural mortality, and exploitation. A fraction of female KOK surviving to adulthood return to their natal hatchery (Roaring Judy Fish Hatchery [ROJ]), where they are stripped and the eggs are reared for stocking the next generation. Managers set a target population size of 700,000 KOK (estimated by hydroacoustics surveys in August) to obtain the number of eggs required to sustain the population.

and

$$Z_{2,3,4,5} = \log_e P(\mathrm{nm}) + \log_e P(\mathrm{fm}) + \log_e P(\mathrm{LKT}) \text{ for ages } 2-5.$$

The proportion of age-2–5 kokanee that were mature (P[mat]), the proportion female (P[fem]), and the mean length at age (Table 3) were calculated from data obtained during spawn takes at ROJ. Fecundity (FEC) was estimated as (Martinez 1996):

$$\mathrm{FEC} = (7.100 \times 10^{-5}) \times \mathrm{TL}^{2.8}.$$

We assumed that 75% of the mature fish migrating from BMR were able to complete the journey back to ROJ (D. Brauch, personal observation).

We developed a baseline simulation in which (1) the natural mortality rate computed from McGurk (1999) was assumed to be the only source of non-harvest mortality (representing a modest piscivore population) for kokanee; and (2) the exploitation rate P(fm) was assumed to be 3.600×10^{-5} for age 0, 1.200×10^{-3} for age 1, 0.132 for age 2, 0.718 for age 3, 0.125 for age 4, and 0.010 for age 5. 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 that would be expected under historic fishing pressure and low predation mortality (as was the case in 1993) to the population obtained in simulations with higher predation by Lake Trout. The primary functions used in the model predicted (1) the number of age-0 kokanee arriving at the reservoir:

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

(2) the number of age-0 and age-1 kokanee at the end of year t:

$$N_{t+1} = N_t \times e^{-Z_i} \text{ for ages 0 and 1;} \tag{2}$$

(3) the number of kokanee of ages 2–5 at the end of year t:

$$N_{t+1} = (N_t \times e^{-Z_i}) - [N_t \times P(\mathrm{mat})] \text{ for ages } 2-5, \tag{3}$$

where Z_i is the age-specific instantaneous mortality rate; and (4) the number of eggs produced during the ROJ spawn take (EGGS):

$$\mathrm{EGGS} = \sum_{2}^{5} \left\{ [N_i \times P\,(\mathrm{mat}) \times P(\mathrm{ROJ}) \times P\,(\mathrm{fem})] \times \left(a \times \mathrm{TL}_i^b\right) \right\}. \tag{4}$$

If EGGS exceeded 4.135×10^6, then the surplus was recorded and assumed to be used at other kokanee hatcheries

TABLE 3. Parameters of the age-structured population model for kokanee (KOK) in Blue Mesa Reservoir (BRN = Brown Trout; LKT = Lake Trout; ROJ = Roaring Judy Fish Hatchery; CPW = Colorado Parks and Wildlife).

Symbol	Definition	Value	Source
FRY	Number of KOK fry released into the East River		Initial, computed
P(BRN)	Loss of migrating KOK fry to BRN predation in the river	0.084 ± 0.02[a]	Brauch, unpublished data
P(dam)	Entrainment of age-0 KOK in Blue Mesa Dam	0.037	Johnson and Koski 2005
	Entrainment of age-1 KOK in Blue Mesa Dam	0.018	
P(nm)	Non-LKT mortality parameter *a*	1.380	McGurk 1999
	Non-LKT mortality parameter *b*	−0.190	
W–L	Weight–length parameter *a*	9×10^{-6}	Johnson and Koski 2005
	Weight–length parameter *b*	3.024	
P(fm)	Probability of fishing mortality		
	Age 0	3.6×10^{-5}	Brauch, unpublished data
	Age 1	1.2×10^{-3}	
	Age 2	0.132	
	Age 3	0.716	
	Age 4	0.125	
	Age 5	0.010	
KOK_n	KOK abundance, age-*n* cohort		Computed
Hydroacoustics	Number of KOK	≥700,000	CPW target
P(LKT)	KOK lost to LKT predation		Varied
P(mat)	Proportion of KOK cohort mature		
	Age 2	0.021	Brauch, unpublished data
	Age 3	0.361	
	Age 4	0.900	
	Age 5	1.000	
P(ROJ)	Proportion of mature KOK reaching ROJ	0.750	Brauch, unpublished data
P(fem)	Proportion of mature KOK that are female	0.450	Brauch, unpublished data
TL	Total length (mm) of mature KOK		
	Age 2	306	Brauch, unpublished data
	Age 3	404	
	Age 4	465	
	Age 5	503	
FEC	KOK fecundity parameter *a*	7.1×10^{-5}	Martinez 1996
	KOK fecundity parameter *b*	2.800	
EGGS	Number of KOK eggs obtained from spawn take	$\geq 4.135 \times 10^{6}$	CPW target
HATCH	Proportion of KOK eggs that produce fry	0.750	Brauch, unpublished data

[a]Mean ± 95% CI.

for stocking other waters. Furthermore, we assumed that ROJ would have a full supply of kokanee eggs for the first 5 years supplemented by egg takes in other systems if necessary because of BMR's importance to the statewide fishery, but after those 5 years no additional eggs from other systems would be available for stocking BMR. See Table 3 for a complete list of parameters used in the kokanee model.

Lake Trout suppression.—Suppression by CPW employed 61-m-long × 2-m-tall, 44-mm bar-mesh gill nets. Nets were set for 45 min to minimize mortality of large (≥740-mm) Lake Trout, which were released. All captured Lake Trout less than 740 mm were removed. Two or three boat crews (four persons in each crew) worked for 15 d in fall 2010. Although Lake Trout suppression started in 2009, it was considered a trial removal period. We estimated daily costs based on 2010 data (the first intensive removal effort) by summing per capita wages, lodging and meal costs, and boat fuel expenses.

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 the 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 the effects of removing three age-classes of Lake Trout: ages 4–9 (the current removal strategy); age 4 only (the most abundant age-class in current gillnetting); and ages 10 and older (large fish that are desirable to anglers). We determined the number of Lake Trout that had to be removed to achieve kokanee sustainability and the number of large Lake Trout remaining in the population after each scenario. The upper and lower confidence limits (UCL and LCL, respectively) for kokanee abundance were the result of using the upper and lower bounds in both the Brown Trout (95% CI) and Lake Trout (68% CI) population estimates. The LCL results from the highest level of predation by both species; likewise, the UCL is from the lowest predation level. In all scenarios, we tracked the number of memorable- and trophy-sized Lake Trout produced, as CPW was interested in Lake Trout fishery tradeoffs that would be required to sustain the kokanee population and fishery. In all simulations, we assumed that the angler harvest rates of both species were constant.

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

RESULTS

The existing suppression program employed 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-d removal effort. Daily costs totaled $940 per boat-day in 2010, for an overall cost of about $38,000 (or about $30 per Lake Trout removed).

Lake Trout Population Modeling

Using 81 SPIN sets, we captured 129 Lake Trout ranging in size from 230 to 996 mm TL. The area-weighted CPUE was 2.29 Lake Trout/net set (corrected for gear selectivity and strata area), yielding a Lake Trout density estimate of 11.14 fish/ha. The area sampled was 3,059.5 ha. The resulting estimated abundance of Lake Trout larger than 409 mm TL was 23,907 (68% CI: LCL = 19,249, UCL = 28,565). The slope of the $\log_e$ transformed age distribution for ages 4–9 (i.e., Z) was 0.71. There were 4,000 Lake Trout in the creel harvest estimate (Brauch, unpublished data). Combining this with the known number of Lake Trout removed by managers yielded an F-value of 0.27. The M of Lake Trout was estimated at 0.44 by subtracting F from Z. Alternatively, M was estimated at 0.14 from averaging the values obtained with the equations of Quinn and Deriso (1999), Shuter et al. (1998), and Pauly (1980).

Creel survey data and a historic abundance estimate together lent support to our Lake Trout abundance estimate from SPIN. Angler catch rate of Lake Trout increased linearly from about 0.025 fish/angler-hour in 2002 to about 0.048 fish/angler-hour in 2011 (Figure 2). Assuming that the angler catch rate is proportional to abundance (Hansen et al. 1995), this trend suggests that the Lake Trout population almost tripled in size over that time period. We found a similar rate of increase in Lake Trout abundance estimated by mark–recapture in 2002 (Crockett et al. 2006) and by SPIN in 2011. Mark–recapture and hydroacoustic survey estimates of Lake Trout abundance were computed in 2002 (Crockett et al. 2006). Specifically, the SPIN estimate indicated that the abundance of 409-mm and larger Lake Trout increased from a mean of 7,828 fish (2002 mark–recapture estimate) to a mean of 23,907 fish (68% CI = $\pm$4,658).

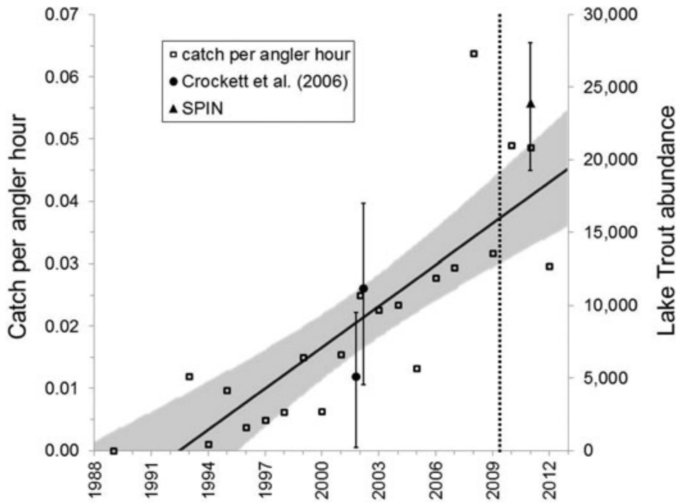

FIGURE 2. Comparison of Lake Trout population trends in Blue Mesa Reservoir. Lake Trout (all size-classes) catch per angler-hour (open squares) has increased since creel surveys began in 1989. Population estimates (solid symbols) for 425-mm TL and larger Lake Trout have also increased by a similar proportion from 2002 (hydroacoustics and mark–recapture; Crockett et al. 2006) to 2011 (Summer Profundal Index Netting [SPIN] protocol; present study). The vertical dotted line represents the start of Lake Trout suppression in 2009.

Baseline Simulation

When using the catch curve estimate of Lake Trout mortality (M = 0.44), the per capita consumption of kokanee by age-4 Lake Trout was 34 fish/year, and the cohort consumption of kokanee by age-4 Lake Trout was 336,000 fish/year. Cohort consumption declined with Lake Trout size (age) because as they grew larger, Lake Trout were less numerous and consumed fewer, larger, more energy-dense kokanee (Table 2). The Lake Trout population's total consumptive demand was estimated at $1.47 \times 10^6 \pm 280{,}000$ kokanee/year. The kokanee population was not sustainable under baseline conditions and persisted less than 2 years beyond the 5-year stocking subsidy from other waters. The baseline scenario predicted the highest number of memorable-sized (160 $\pm$ 30) and trophy-sized (3 $\pm$ 1) Lake Trout in the population at the end of the simulation. Similar results occurred when Lake Trout M was 0.14. The kokanee population lasted less than 2 years from the start of the model run, and total consumptive demand by the Lake Trout population was $1.75 \times 10^6 \pm 330{,}000$ kokanee/year. This scenario predicted 4,500 ± 850 memorable-sized Lake Trout and 1,200 ± 200 trophy-sized Lake Trout.

Increased Exploitation of Age-4–9 Lake Trout

When an *M* of 0.44 for Lake Trout was used and when removal of age-4–9 Lake Trout was increased by 0.10 ($cf_{4–9}$ = 0.33) in addition to the contemporary removal of 1,250 fish, the kokanee population was again extirpated, although kokanee persisted 8 years longer in this scenario than in the baseline simulation. The kokanee population became sustainable at 617,000 ± 107,000 fish if removal of age-4–9 Lake Trout was increased by 0.15 ($cf_{4–9}$ = 0.38) in addition to the contemporary removal. This required the removal of 3,000 more Lake Trout, and 44 ± 9 memorable-sized and 1 ± 1 trophy-sized Lake Trout remained at the end of the simulation. When the alternate Lake Trout *M*-value of 0.14 was used, the kokanee population became sustainable when exploitation was increased by 0.25 ($cf_{4–9}$ = 0.48). The resulting kokanee abundance was 663,000 ± 97,000 fish, and there were 127 ± 25 trophy-sized Lake Trout and 457 ± 90 memorable-sized Lake Trout available.

To match CPW's target of 700,000 kokanee when Lake Trout *M* was 0.44 (Figure 3), removal of age-4–9 Lake Trout had to be increased by 0.40 ($cf_{4–9}$ = 0.68). This resulted in a kokanee population size of 707,000 ± 107,000 fish. To reach this level, over 6,400 Lake Trout must be removed, and there would be only two memorable-sized Lake Trout and no trophy-sized Lake Trout available for anglers. To reach the target kokanee abundance when the alternate Lake Trout *M* of 0.14 was used, the exploitation level had to be increased by 0.30 ($cf_{4–9}$ = 0.53). Ending kokanee abundance was 703,000 ± 90,000 fish, and there were 69 ± 14 trophy-sized and 249 ± 49 memorable-sized Lake Trout available. An additional 10,600 Lake Trout had to be removed above the contemporary level, totaling almost 12,000 fish.

Increased Exploitation of Age-4 Lake Trout

When exploitation of only age-4 Lake Trout was increased by 0.20 above the contemporary level of removal and when *M* was 0.44, the kokanee population stabilized at 596,000 ± 111,000 fish. To achieve this, an additional 1,300 age-4 Lake Trout would have to be removed each year (total = 2,550 Lake Trout). This would reduce the Lake Trout population's total consumptive demand to $1.39 \times 10^6 \pm 270{,}000$ kokanee, which is about 5% below the consumption in the baseline simulation. The numbers of memorable- and trophy-sized Lake Trout at the end of this scenario were 121 ± 24 and 3 ± 1, respectively. Results from using the alternative Lake Trout *M*-value of 0.14 were identical when both sustainable and target kokanee abundances were reached (Table 4). Exploitation had to be increased by 0.55 (cf_4 = 0.78) through removal of 4,700 additional Lake Trout. Final kokanee abundance was 703,000 ± 90,000 fish, with consumptive demand by Lake Trout reduced to $1.17 \times 10^6 \pm 220{,}000$ kokanee. There were 383 ± 76 trophy-sized Lake Trout and 1,384 ± 272 memorable-sized Lake Trout available.

To approach CPW's kokanee target when Lake Trout *M* is equal to 0.44, exploitation on age-4 Lake Trout would have to be increased to 0.73 by removing an additional 3,500 age-4 Lake Trout. Kokanee abundance was predicted to increase to 709,000 ± 89,000 fish, and consumptive demand was reduced to $1.24 \times 10^6 \pm 240{,}000$ kokanee/year. The number of large Lake Trout available to anglers was 47 ± 9 memorable-sized fish and 1 ± 1 trophy-sized fish.

Increased Exploitation of Age-10 and Older Lake Trout

Increasing the exploitation of large Lake Trout (age ≥ 10) had no effect on kokanee sustainability, even if all large Lake Trout in BMR were removed under both *M*-estimates. Similar to the baseline simulation results, the kokanee population was extirpated within 3 years after cessation of stocking from other sources. Consumption of kokanee by this group of Lake Trout was reduced, but the effect on the kokanee population was negligible, and no memorable- or trophy-sized Lake Trout were available for anglers.

Optimal Lake Trout Suppression by Gillnetting

Our modeling showed that specifically targeting age-4 Lake Trout would yield the greatest reduction in the number of kokanee consumed per Lake Trout, and netting experience demonstrated that it was possible to intensify the gill-net catch of this age-class. By using gill nets with 28.6–38.1-mm bar mesh, the catch of age-4 Lake Trout could be increased while potentially reducing the bycatch of older fish; thus, longer-duration sets could be used. About 79% of the age-4 Lake Trout catch was obtained in this mesh range, and 60% of age-5–9 Lake Trout were caught in these nets (Figure 4). Unfortunately, kokanee bycatch in these meshes was high: 48% of all kokanee caught in gill nets were obtained from these mesh 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 and overnight vertical gillnetting during August (Figure 5). By setting the gill nets below 30 m, kokanee bycatch could be reduced while still allowing for the capture of large numbers of Lake Trout.

DISCUSSION

Our modeling suggests that the BMR kokanee population would continue to decline without intensified Lake Trout suppression. Although the most palatable management tool available to CPW may be Lake Trout harvest by the angling public, to date the liberalized harvest regulations have not resulted in reduced Lake Trout predation or in kokanee recovery. Economic incentives to harvest Lake Trout, including bounties and contests, have been used in other systems (e.g., Lake Pend Oreille and Flathead Lake), but funding for such efforts was not available in the present case. Until funding becomes available,

TABLE 4. Effects of suppression strategies on trophy-sized (≥1,000-mm TL) and memorable-sized (≥800-mm TL) Lake Trout (LKT) in Blue Mesa Reservoir under two natural mortality (M) scenarios. Values are remaining trophy- and memorable-sized Lake Trout at the end of simulations with means, lower, and upper confidence limits (LCL and UCL, respectively). Age 4 and ages 4–9 represent the LKT age-classes targeted for removal; Δ represents the increase in exploitation above 2010 values. Shaded rows indicate a stable kokanee population, and boxed rows indicate that the target abundance of 700,000 kokanee was met.

	Age-4 LKT			Age-4–9 LKT		
Δ	LCL	Mean	UCL	LCL	Mean	UCL
			M = 0.44, trophy size			
0.10	3	4	5	2	2	2
0.15	3	4	4	1	1	2
0.20	3	3	4	1	1	1
0.25	3	3	4	0	0	1
0.30	2	3	3	0	0	0
0.35	2	3	3	0	0	0
0.40	2	2	3	0	0	0
0.45	2	2	2	0	0	0
0.50	1	2	2	0	0	0
0.55	1	1	2	0	0	0
			M = 0.44, memorable size			
0.10	115	142	170	57	71	85
0.15	106	131	157	36	44	53
0.20	98	121	145	22	27	32
0.25	89	110	132	12	15	19
0.30	81	100	119	7	8	10
0.35	72	89	107	3	4	5
0.40	63	79	94	2	2	2
0.45	55	68	81	1	1	1
0.50	46	57	69	0	0	0
0.55	38	47	56	0	0	0
			M = 0.14, trophy size			
0.10	941	1,163	1,392	469	580	694
0.15	871	1,077	1,288	295	364	436
0.20	801	990	1,185	178	220	263
0.25	731	904	1,081	102	127	152
0.30	661	817	978	56	69	83
0.35	591	730	874	28	35	42
0.40	521	644	770	13	16	20
0.45	451	557	666	6	7	8
0.50	380	470	563	2	2	3
0.55	310	383	459	1	1	1
			M = 0.14, memorable size			
0.10	3,399	4,201	5,026	1,694	2,094	2,505
0.15	3,147	3,888	4,653	1,064	1,315	1,573
0.20	2,894	3,576	4,279	642	794	950
0.25	2,641	3,263	3,905	370	457	547
0.30	2,388	2,951	3,530	202	249	298
0.35	2,135	2,638	3,156	103	127	152
0.40	1,881	2,325	2,781	48	59	71
0.45	1,628	2,011	2,407	20	25	30
0.50	1,374	1,698	2,031	7	9	11
0.55	1,120	1,384	1,656	2	3	3

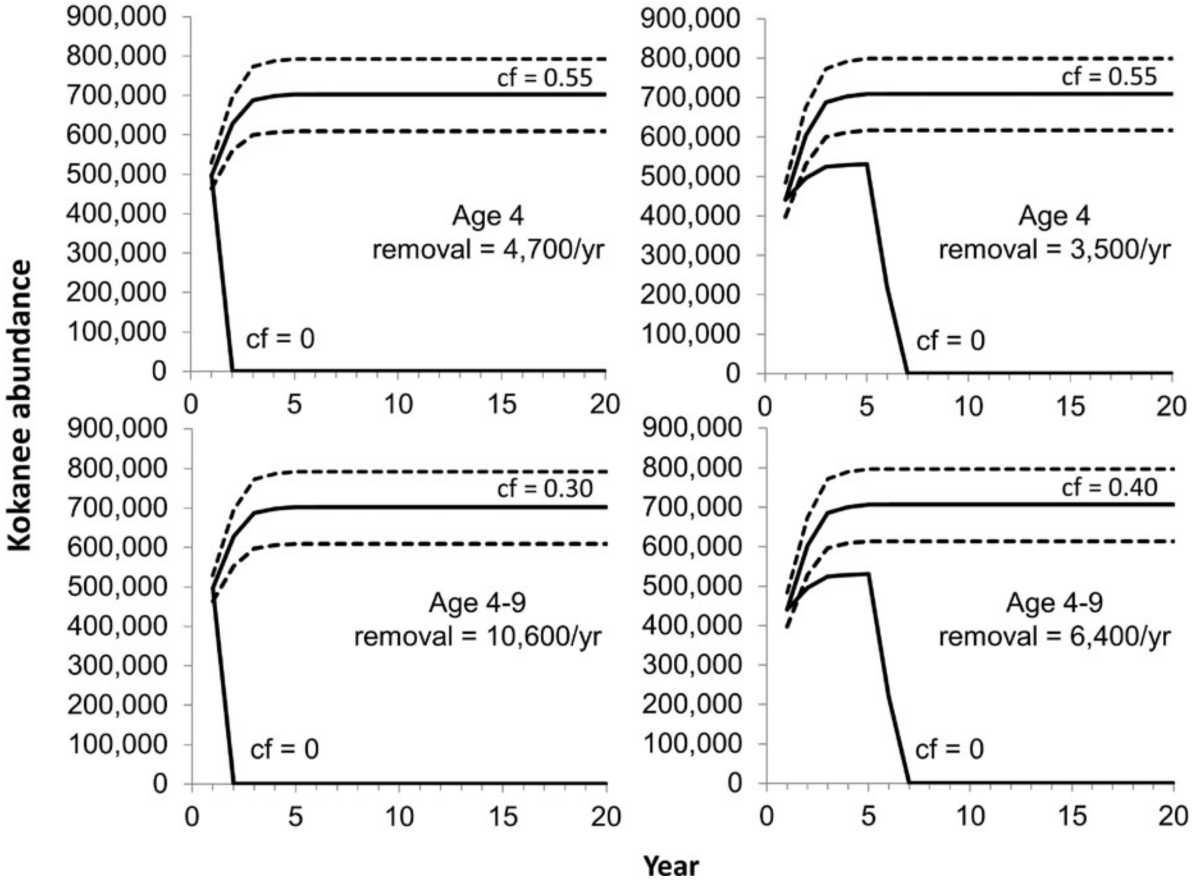

FIGURE 3. Results from the age-structured model of kokanee population dynamics in Blue Mesa Reservoir, Colorado, under two instantaneous rates of natural mortality (M) for Lake Trout ($M = 0.14$, left panels; $M = 0.44$, right panels). The baseline scenario of no additional Lake Trout removal (conditional fishing mortality [cf] = 0) caused the kokanee population to decline to zero within the first few years. Simulations of increased exploitation for age-4 Lake Trout reached CPW's target kokanee abundance (700,000 fish) when exploitation was increased by 0.55 under both values of M. For age-4–9 Lake Trout and an M-value of 0.14, exploitation had to be increased by 0.30 to reach the target kokanee abundance. When M was 0.44 for ages 4–9, exploitation had to be increased by 0.40 to reach the target kokanee abundance.

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 limited number of large Lake Trout (almost 400 Lake Trout $\geq$ 1,000 mm under the best-case scenario); this can be accomplished via several of the suppression methods we evaluated. Intensifying the current suppression program by gillnetting more age-4–9 Lake Trout would allow for a sustainable kokanee fishery while still providing some opportunity for angling large Lake Trout under the lower-M scenarios, although focusing effort on age-4 Lake Trout would be a more efficient alternative. Achieving this balance would require removal of over five times the number of age-4–9 Lake Trout currently being culled, assuming that angler harvest would remain constant. Alternatively, simulations indicated that if gillnetting focuses on age-4 Lake Trout, then the additional number of Lake Trout that would have to be removed is substantially reduced because per capita consumption of kokanee is higher for this age-class than for older Lake Trout. The sensitivity of the kokanee population to the 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 (albeit less biomass) per capita than larger Lake Trout. Furthermore, the population-level effect of a cohort of small predators is greater than that of an older, typically less abundant cohort of predators. 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 Lake Trout cohort consumed mostly age-1 kokanee, requiring about 336,000 kokanee to satisfy their observed growth due to the smaller size and lower energy density of age-1 kokanee in comparison with older kokanee. As was shown by Johnson and Martinez (2000) and by the present study, the growth of large Lake Trout relies

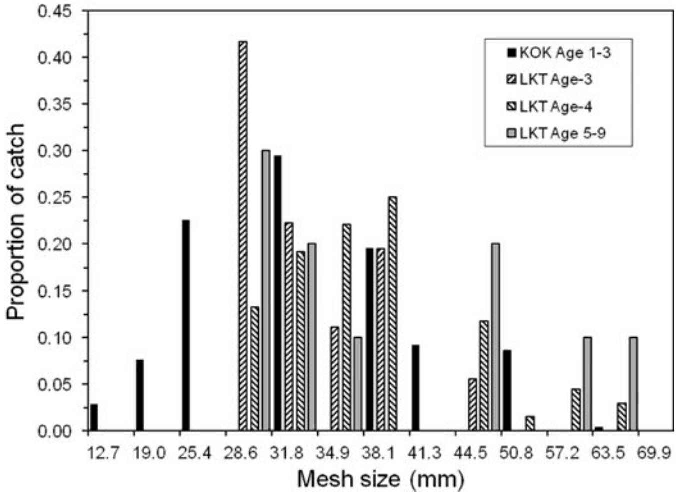

FIGURE 4. Proportions of total kokanee (KOK) catch and total Lake Trout (LKT) catch in gill nets with a range of mesh sizes (bars) in Blue Mesa Reservoir. Bycatch of KOK is only avoidable when gill nets with 57.2-mm or larger mesh are used (dashed line), but only age-5 and older LKT would be vulnerable to those larger mesh sizes.

heavily on stocked prey and represents a substantial financial cost to the managing agency.

Interestingly, our simulations showed that despite the rapid growth and relatively large size of age-10 and older Lake Trout in BMR, removal of these fish had a negligible effect on sustainability of the kokanee population. Consumptive demand by these larger Lake Trout at the current abundance was less than 1% of the annual stocking quota. Although kokanee losses to large Lake Trout could impact the number of mature kokanee

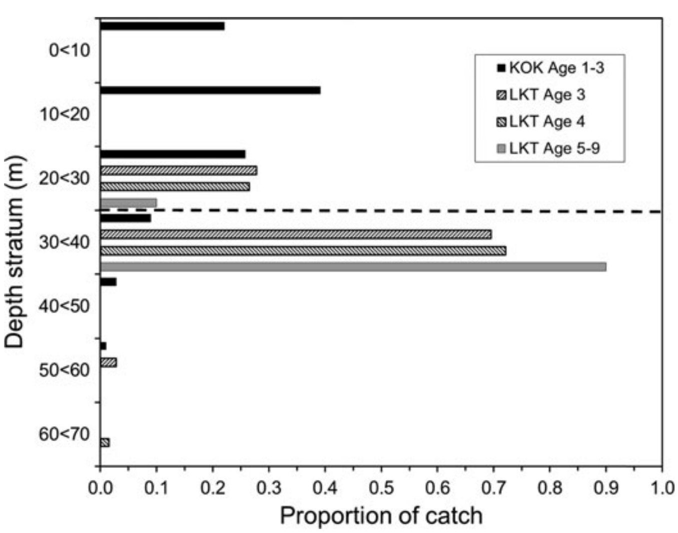

FIGURE 5. Proportions of kokanee (KOK) age-classes and Lake Trout (LKT) age-classes obtained at various capture depths in Blue Mesa Reservoir. Lake Trout were captured during Summer Profundal Index Netting (August 2011), and KOK proportions were compiled from vertical gill-net data. The horizontal dashed line represents the minimum net depth at which LKT removal is optimized and KOK bycatch is minimized.

returning to ROJ, removal of large Lake Trout would be inconsequential to kokanee abundance in the reservoir and would result in an absence of memorable- or trophy-sized Lake Trout for anglers. Thus, removal of large Lake Trout was not considered a sensible management option for serving the dual goals of sustaining the BMR kokanee fishery while maintaining some large 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 that of many other populations, with few fish living beyond age 30 based on the observed age structure.

A caveat to the intensive exploitation of Lake Trout is the possibility of a compensatory response. It has been shown that for many species, including Lake Trout, intensive, size-selective fishing can induce greater fecundity, earlier age at maturation, and higher growth (Ricker 1975; Healey 1978; Ferreri and Taylor 1996). However, we found that in BMR, removal of large Lake Trout would have a negligible effect on the kokanee population; instead, small Lake Trout should be exploited. This fishing regime could still influence recruitment if preserving large, old Lake Trout increases the reproductive success through maternal effects (Berkeley et al. 2004; Birkeland and Dayton 2005), but such effects are not anticipated based on the already relatively short life span and young age at maturity of Lake Trout in BMR. In addition, we found that BMR Lake Trout have exceptional growth rates and W_r values ranging from 120 to 150 in 800-mm TL and larger fish; this is indicative of a population approaching maximum prey consumption rates even at a time when kokanee abundance is at a 10-year low (Brauch, unpublished data). A compensatory response in consumption or growth should not occur with this Lake Trout 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 depends on strict control of Lake Trout abundance and may not be advisable in larger systems or in populations with different demographic characteristics. Blue Mesa Reservoir has approximately one-tenth the surface area of many other western U.S. waters where Lake Trout suppression is occurring (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 Lake Trout continue to be problematic even though almost 450,000 fish were removed by 2009 (Syslo et al. 2011). Netting in Yellowstone Lake occurs from ice-off through October every year, with overnight and multi-night sets; due to intensive effort, the growth of the Lake Trout population has slowed. In Flathead Lake, angler harvest incentives have been ineffective, and there is currently a draft environmental impact statement assessing the need for intensified Lake Trout removal to restore native species (BIA 2012). The assessment will look at four alternatives that range from no action to reducing Lake Trout abundance in all age-classes by 90% (188,000 fish) via a combination of fishing contests and mechanical removal.

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

We believe a smaller removal program in BMR would be sufficient to sustain the management objectives. If netting CPUE and associated costs continue at their previous levels, removal of the required additional number of age-4 Lake Trout could be accomplished for about $85,400 per year. Changing to smaller mesh sizes and longer gill nets set in deep water overnight during August (when Lake Trout are confined to the hypolimnion) could focus the catch on age-4 Lake Trout and could make the process more efficient; regardless, mechanical removal is an expensive undertaking. Encouraging anglers to harvest the necessary number of additional Lake Trout (~7,000 fish/year) could be less expensive if a bounty of $12 per fish is 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 consumption by a piscivore is the primary goal, then it may behoove managers to examine whether focusing removal on younger age-classes would be feasible since 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 sustain the BMR kokanee population and to achieve desirable growth and body condition of Lake Trout. If mechanical removal by gillnetting is to continue, the costs may be reduced and large Lake Trout may be preserved if longer nets with smaller mesh sizes 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 probability of encountering crepuscular or nocturnally active Lake Trout. This type of netting scheme could also reduce conflict with Lake Trout anglers, who typically target the fish during the spring and fall (when the reservoir is isothermal) in the same locations where netting is most effective. Because anglers already harvest more small Lake Trout than are captured by a relatively expensive netting program, reconsidering an angler incentive program like those used in some other western Lake Trout waters could be worthwhile. Even if funds for a bounty are not available, options such as offering prizes for catching select PIT-tagged Lake Trout could encourage anglers to harvest more fish. Minimizing administrative costs for such a lottery could make it a more cost-effective approach than the removal of Lake Trout via gillnetting.

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