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ARTICLE

Population Dynamics and Evaluation of Alternative Management Strategies for Nonnative Lake Trout in Priest Lake, Idaho

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Abstract

Lake Trout *Salvelinus namaycush* have been introduced widely throughout the western USA to enhance recreational fisheries, but high predatory demand can create challenges for management of yield and trophy fisheries alike. Lake Trout were introduced to Priest Lake, Idaho, during the 1920s, but few fishery-independent data are available to guide current or future management actions. We collected fishery-independent data to describe population dynamics and evaluate potential management scenarios using an age-structured population model. Lake Trout in Priest Lake were characterized by fast growth at young ages, which resulted in young age at maturity. However, adult growth rates and body condition were lower than for other Lake Trout populations. High rates of skipped spawning (>50%) were also observed. Model projections indicated that the population was growing ($\lambda = 1.03$). Eradication could be achieved by increasing annual mortality to 0.32, approximately twice the current rate. A protected slot length limit could increase population length-structure, but few fish grew fast enough to exit the slot. In contrast, a juvenile removal scenario targeting age-2 to age-5 Lake Trout maintained short-term harvest of trophy-length individuals while reducing overall population abundance.

Lake Trout *Salvelinus namaycush* are recognized throughout their native and introduced distributions for the ability to attain trophy sizes (>45 kg) and provide valuable recreational and commercial fisheries (Martin and Olver 1980; Shuter et al. 1998). In their native distribution, desirability as a commercial species has often resulted in overfishing and population collapse (Healey 1978; Richards et al. 2004; Tsehaye et al. 2014). Beyond the native distribution, this desirability has led to widespread introduction of Lake Trout, where populations are sustained by natural reproduction or stocking (Crossman 1995; Martinez et al. 2009). However, like many other nonnative species, Lake Trout introduction has ecological consequences (Quist and Hubert 2004).

Lake Trout often exhibit fast growth, and as a top-level consumer, their demand for prey is high. Supporting nonnative Lake Trout populations can therefore have high economic,

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ecological, and social consequences. In an evaluation of the costs associated with stocking prey fishes in Colorado reservoirs, Johnson and Martinez (2000) found that supplying such prey cost US$200 per Lake Trout supported. For species of conservation concern, such as Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Yellowstone Lake, Wyoming, predation by Lake Trout is immeasurable in economic terms (Ruzycki et al. 2003). In addition to their high demand for prey fishes, Lake Trout also exhibit predatory inertia and resistance to starvation (Eby et al. 1995; Schoen et al. 2012). These long-lived predators can subsist on suboptimal prey for prolonged periods and quickly respond to increased prey availability (Martinez et al. 2009). However, as prey resources decline, the quality of Lake Trout fisheries also declines.

Lake Trout can also destabilize ecological interactions, potentially creating trophic cascades, which further complicate the ability to achieve management goals (Eby et al. 2006). For example, in Flathead Lake, Montana, the interaction of introduced Lake Trout with introduced opossum shrimp *Mysis diluviana* created both top-down and bottom-up pressures that ultimately extirpated lacustrine Sockeye Salmon (kokanee) *O. nerka* (Ellis et al. 2011). The lack of coevolutionary history between nonnative Lake Trout and other members of the fish assemblage can produce unstable food-web interactions (Eby et al. 2006). The combination of long life, vulnerability to overharvest, piscivory, predatory inertia, and food-web instability makes managing Lake Trout fisheries challenging.

Nonnative Lake Trout management has centered around three primary goals in the western USA: eradication, trophy, and balance (Martinez et al. 2009). Eradication efforts seek to exploit vulnerabilities in Lake Trout life history (i.e., slow growth, late maturation) to collapse populations (Martinez et al. 2009) and frequently involve high-effort gill netting (Hansen et al. 2008; Syslo et al. 2011). Elsewhere, fisheries for nonnative Lake Trout are managed to produce trophy-length individuals (Johnson and Martinez 2000; Martinez et al. 2009; Janssen et al. 2012; Idaho Department of Fish and Game 2013). Restrictive harvest regulations, such as bag limits and protected slot length limits, are used to reduce mortality and facilitate the production of trophy individuals (Dextrase and Ball 1991). Finally, some managers seek a compromise between the trophy and eradication management goals. By targeting specific Lake Trout size-classes for harvest or removal, their goal is to minimize the overall abundance and negative side-effects of Lake Trout while still retaining a fishery (Luecke et al. 1994; Pate et al. 2014). Since young (e.g., age-4 to age-9) Lake Trout can be the most numerous class of these predators, targeted mechanical removal of small fish can reduce undesirable interactions with other fishes and still allow for sufficient Lake Trout abundance and size structure to provide a desirable fishery (Pate et al. 2014).

Lake Trout were introduced to Priest Lake, Idaho, in 1925, but initially remained at low abundance (Crossman 1995; Martinez et al. 2009). Kokanee were introduced in the mid-1940s and became established quickly (Bjornn 1961; Rieman et al. 1979). Although Lake Trout abundance remained low, the new prey base allowed Lake Trout to reach trophy sizes (Rieman et al. 1979). In the late-1960s, opossum shrimp were introduced to increase kokanee production (Leusink 1968; Bowles et al. 1991). After introduction of the shrimp, both kokanee and Lake Trout growth increased. In 1971, Priest Lake produced the largest Lake Trout caught by an angler outside the Great Lakes, a 125-cm-long fish weighing 26.1 kg (Martinez et al. 2009). Although subsequent downward shifts in the maximum length attained by Lake Trout indicated that opossum shrimp had altered the food web, neither kokanee nor Lake Trout harvest deviated much from preintroduction rates for nearly 10 years postintroduction (Davis et al. 2000). However, in 1976, the kokanee fishery collapsed (Rieman et al. 1979; Fredericks et al. 2009), and Lake Trout harvest began to increase, more than doubling from 1978 to 1994 (Davis and Horner 1995).

Although Lake Trout continue to dominate the recreational fishery in Priest Lake, recent increases in kokanee harvest in nearby Lake Pend Oreille after Lake Trout suppression have raised questions about the feasibility of alternative management goals for Priest Lake. Therefore, the objectives of this study were to assess current population dynamics of Lake Trout in Priest Lake and to evaluate potential management scenarios. Using an age-structured population model, we evaluated three different harvest scenarios that represent three general strategies for Lake Trout populations: an eradication-type effort with constant age-specific fishing mortality, a protected slot limit to promote trophy fish production, and a juvenile removal effort to balance predation with yield and size structure.

STUDY AREA

Priest Lake is a 9,461-ha dimictic lake located in the Columbia River basin of northern Idaho (Figure 1). The roughly 1,554 km^2 watershed is granitic and dominated by coniferous forest cover (Bjornn 1957; Maiolie et al. 2013). Approximately 19% of the lake is less than 12 m deep (Rieman et al. 1979). Thermal stratification generally occurs mid-July through the end of October, with a thermocline at a depth of about 35–50 m, and summer surface water temperatures reach 26°C in shallow areas (Kemmerer et al. 1924; Bjornn 1957; Rieman et al. 1979).

The native fish assemblage includes Bull Trout *S. confluentus*, Westslope Cutthroat Trout, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *P. coulterii*, Largescale Sucker *Catostomus macrocheilus*, Longnose Sucker *C. catostomus*, Northern Pikeminnow *Ptychocheilus oregonensis*, Redside Shiner *Richardsonius balteatus*, Peamouth *Mylocheilus caurinus*, and Slimy Sculpin *Cottus cognatus* (Bjornn 1957; Rieman et al. 1979; Maiolie et al. 2011). In addition to Lake Trout and kokanee, at least seven other fish species have been introduced: Brook Trout *S. fontinalis*, Tench *Tinca tinca*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass

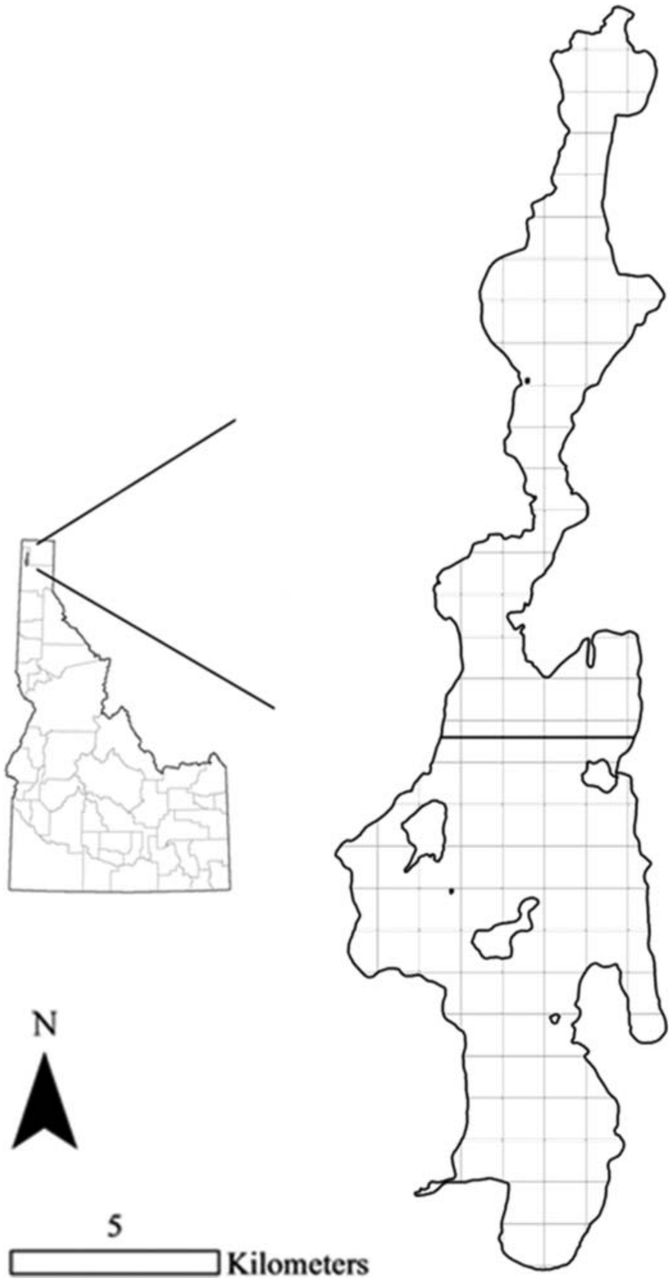

FIGURE 1. Location of Priest Lake in the northern Idaho panhandle, with strata (horizontal black line) and sampling grid (gray lines).

Micropterus dolomieu, Northern Pike *Esox lucius*, Green Sunfish *Lepomis cyanellus*, and Yellow Perch *Perca flavescens* (Fredericks et al. 2009), although most are in low abundance and unlikely to be significant ecological drivers.

METHODS

Field sampling and laboratory processing.—A mark–recapture study using a stratified random sampling design (Thompson 2012) was conducted from March to May 2013 to estimate Lake Trout abundance. The lake was divided into north and south strata of equal area, which were sampled systematically on alternate days. The lake was then divided by a 1 km^2 grid. One to seven locations were selected randomly each day for sampling. Lake Trout were captured using bottom-set monofilament gill nets (1.8 m deep × 91.4 m long) in one of eight mesh sizes (50.8-, 63.5-, 76.2-, 88.9-, 101.6-, 114.3-, 127.0-, or 139.7-mm stretch mesh). Twelve nets were combined to form a 1,097-m-long gang where each mesh size was represented at least once but no more than twice. Gangs were set during daylight hours in a serpentine pattern along an isobath (mean maximum depth, 37 m), soaked for 1 h, and lifted slowly with a hydraulic lifter.

Eight large nylon multimesh trap nets were also used to capture Lake Trout: six larger trap nets and two smaller "juvenile" trap nets (Hansen et al. 2008). Locations in each stratum with suitable bathymetry and substrate type were identified, and trap-net locations were randomly selected. Four trap nets were placed in the north stratum and four were placed in the south stratum. In mid-April, two trap nets from each stratum were moved to new locations. Trap nets were allowed to soak for two to three nights and then lifted.

Lake Trout captured in both gill nets and trap nets were measured (mm, total length) and tagged in the dorsal musculature with a uniquely numbered T-bar tag (Floy Tag, Seattle). Approximately every fifth Lake Trout was also tagged with a uniquely numbered spaghetti tag (Floy Tag) to evaluate tag loss (Pine et al. 2003). In addition to the identification number, tags included a toll-free telephone number, which anglers could use to report their catch to the Idaho Department of Fish and Game tag-reporting program (Meyer et al. 2012). Two hundred spaghetti tags (38% of spaghetti tags) were marked as US$50 reward tags.

Because trauma from handling can result in postrelease mortality, each Lake Trout was assessed for gill-net trauma and barotrauma using three condition ratings (mild, moderate, or severe; Ng et al. 2015). Gill-net captured Lake Trout in mild condition (i.e., able to orient and swim) were released alongside the boat after they were processed. Trap-net–captured fish were retained in a holding tank and released away from the leads and pot once the trap net was lowered. Fish experiencing barotrauma or exhaustion were allowed to recuperate and then released directly into the open lake or by using a weighted deep-release cage (0.9 m × 0.6 m × 1.2 m). The cage was lowered to approximately 30 m and held at depth to allow fish to swim out of the open bottom. After 10 min, the cage was lifted. If fish remained inside the cage, it was lowered to 30 m for an additional 10 min.

Sagittal otoliths were collected from all handling mortalities during the mark–recapture study. Sex was also recorded. Additionally, five gill-net gangs (three north stratum, two south stratum) were randomly selected to collect age and growth information from all fish captured. Age structures were collected, and length, weight (nearest g), and sex were recorded. Sagittal otoliths from 10 Lake Trout per 10-mm length-group were used to determine fish age, preferentially from fish collected during random sampling. Structures from handling mortalities were then used to sample additional length classes. Otoliths were mounted in epoxy, thin-sectioned with a low-speed saw (Beuhler, Lake Bluff, Illinois), and viewed under a dissecting scope using transmitted light (Quist et al. 2012). Body condition for spring-captured Lake Trout was evaluated using relative weight (W_r; Piccolo et al. 1993; Hubert et al. 1994; Neumann et al. 2012) for each of the standard length categories for Lake Trout: stock ($\geq$280 mm), quality ($\geq$500 mm), preferred ($\geq$700 mm), memorable ($\geq$850 mm), and trophy ($\geq$1,000 mm; Piccolo et al. 1993).

No reproductive (i.e., ripe) Lake Trout have been observed in Priest Lake other than in the autumn; hence, because Lake Trout gonadal maturation does not occur until autumn (Goetz et al. 2011), a separate netting effort was conducted in October 2013 prior to peak spawning to evaluate maturity schedule and fecundity. Lake Trout were collected using gill nets in the same manner as in spring 2013. Two sites in the north stratum and three sites in the south stratum were randomly selected for sampling. Length, weight, and sex were recorded for each fish, and otoliths were collected as in the spring. Maturity status of female Lake Trout was assessed macroscopically in the field during autumn sampling (Sitar et al. 2014). Small, translucent ovaries that had granular, undersized eggs ($\leq$1 mm diameter) were categorized as immature. Ovaries that were large and contained well-developed or loose eggs (>3 mm diameter) were categorized as mature. Sexually mature female Lake Trout may not spawn every year (Sitar et al. 2014); skipped spawners were identified by their thinner, less developed ovaries and smaller eggs (1–2 mm diameter). The presence of atretic follicles was also used to distinguish skip-spawners from immature fish.

Intact ovaries from mature females were preserved in a 150 mL/L formaldehyde solution. Fecundity (f) was estimated gravimetrically (Murua et al. 2003). Each ovary was weighed to the nearest 0.01 g; three cross-sectional subsamples were taken from each ovary (anterior, medial, and posterior sections) and weighed to the nearest 0.01 g. Vitellogenic eggs ($\geq$3 mm in diameter) were counted. Mean egg density was estimated for each ovary and multiplied by total ovary mass.

Data summarization.—Lake Trout abundance was estimated using a robust-design Huggins closed-population model with two periods and weekly sampling intervals, performed with Program MARK (Huggins 1991; White and Burnham 1999). Detection probability and survival were specified as constant across sampling events. Estimated abundance was corrected for postrelease mortality by using postrelease mortality rates from a separate survival study (see below).

The subsample of aged Lake Trout was used to create an age–length key. Because of missing age-classes, multinomial logistic regression of age on length was used to estimate length-specific age frequency (Gerritsen et al. 2006). Population length-frequency was estimated from gill-net catch rates using relative retention probability estimated for 97 length-classes determined with the SELECT method (Millar and Fryer 1999). All combinations of five parametric forms for selectivity, three specifications for fishing power, and a correction for entangling were evaluated. The model with the lowest mean model deviance was chosen as the top model (Jonsson et al. 2013). Population age-frequency distribution was then approximated by applying the age–length key to gill-net selectivity–corrected length frequencies (Millar 1992). A von Bertalanffy growth model was fit to observed length-at-age data to obtain parameters used to estimate natural mortality (Gallucci and Quinn II 1979).

Instantaneous total annual mortality (Z) was estimated from gill-net selectivity–corrected catch-at-age for age-3 to age-35 fish. The Chapman–Robson estimator was used with peak-plus criterion and corrected for overdispersion (Chapman and Robson 1960; Smith et al. 2012). Because catch of age-1 and age-2 Lake Trout was low and because no data on survival of age-0 Lake Trout were available for Priest Lake, survival rates of age-0, age-1, and age-2 Lake Trout were obtained from the literature (Shuter et al. 1998; Sitar et al. 1999).

Exploitation (μ) for age-3 and older Lake Trout was estimated using tags reported during the 1-year period after tagging. The number of tags returned was corrected for nonreporting, using average reporting rates developed by Meyer et al. (2012) for Idaho fisheries. Meyer et al. (2012) found that 54.2% of nonreward tags were reported and 91.7% of US$50 reward tags were reported. The number of fish available for harvest was corrected for postrelease mortality (Ng et al. 2015). After excluding fish that had been reported as harvested during the tagging period ($n = 3$), the total number of tagged fish available was estimated. The predicted probability of mortality was calculated for each released fish using previously developed relationships between Lake Trout condition, size, and postrelease mortality (Ng et al. 2015). The estimated number of mortalities was subtracted from the total number of available fish for harvest to obtain a corrected number of available fish. Exploitation was estimated by dividing the number of reported tags by the respective reporting rate (i.e., for US$0 and US$50 tags), then dividing by the corrected number of fish available for harvest. Exploitation was converted to instantaneous fishing mortality (F) using the relationship for a Type 2 fishery: $F = \mu Z / A$ (Ricker 1975).

Instantaneous natural mortality (M) was obtained by $M = Z - F$ (Ricker 1975). Additionally, to account for uncertainty in estimates of natural mortality, M was also estimated by using equations from Quinn and Deriso (1999), Hoenig (1983), and Shuter et al. (1998). Quinn and Deriso (1999) used the relationship between survival and maximum observed age ($t_{\max}$):

$$M = \frac{-\ln 0.01}{t_{\max}}.$$

Hoenig (1983) used a regression estimator based on data for fishes, mollusks, and cetaceans to develop the following relationship between M and $t_{\max}$:

$$\ln(M) = 1.44 - 0.982 \cdot \ln(t_{\max}).$$

Using information on Lake Trout populations in Ontario, Shuter et al. (1998) developed an estimator for M:

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

where $\omega = K \cdot L_{\infty}$, and K and L_{∞} are parameters of the von Bertalanffy growth model. The average of these four estimates was used as the final estimate of M in population models.

Maturity and reproduction ogives (i.e., age-specific probability of maturity or spawning) were modeled using logistic regression (Sitar et al. 2014). For the maturity ogive, all mature females, including skipped spawners, were considered mature. However, because of the presence of skipped spawners, this approach can overestimate the number of spawners in a given year. Therefore, we also evaluated reproduction ogives, where female Lake Trout that were immature or skipped spawning were pooled and considered nonreproductive. Mean fecundity at age was estimated using linear regression.

Population modeling.—An age-structured, female-based matrix (i.e., Leslie matrix) model was used to evaluate Lake Trout population growth trajectory and dynamics (Caswell 2001; Morris and Doak 2002). Analyses were conducted in R using functions from the Popbio package (Stubben and Milligan 2007; R Core Team 2014). The matrix model included 35 age-classes (i.e., maximum age observed) and a prebreeding census. The observed age of first maturity was 6 years. The proportion of female offspring produced was specified as 0.5 since the observed sex ratio did not differ significantly from 0.5 (0.45 female; 95% confidence interval [CI]: 0.39–0.51). We evaluated asymptotic population growth rate and transient dynamics, which provide more realistic estimates of population growth over the short-term (Morris and Doak 2002). The population was projected over a period of 5, 10, or 20 years, and average population growth rate (λ) was calculated as the geometric mean of the population growth rate between each time step (i.e., 1 year) over the projection period. We varied F from 0 to 1.5 in 0.01 increments to evaluate effects of different harvest levels.

In addition to λ, we estimated average population size, number of Lake Trout harvested, biomass, biomass harvested, and abundance and number of Lake Trout harvested by incremental standardized length category over a 10-year period. Biomass was calculated by multiplying age-specific abundance by observed mean weight at age. We used a multinomial regression of length on age to convert harvest by age-class to harvest by incremental size-class. The number of Lake Trout harvested per age-class for a given value of F was calculated using

$$C_i = \frac{F_i}{F_i + M_i} N_{i\bullet},$$

where C_i is the harvest for age-class i, F_i is the fishing mortality for age-class i, M_i is the natural mortality for age-class i, and $N_{i\bullet}$ is 10-year average abundance for age-class i (Quinn and Deriso 1999).

Parametric bootstrap was used to incorporate uncertainty in all of the vital rate estimates and to obtain 95% CI values for estimates of abundance, biomass, and harvest (Morris and Doak 2002). Age-specific survival rates and probability of spawning were modeled as beta distributions, setting the mean to the observed value and setting the variance to the observed standard error. Beta distributions are flexible distributions bounded by 0 and 1 and are therefore appropriate for generating survival probabilities. For literature values of survival where no standard errors were available, we specified the variance of the beta distribution as equal to 20% of the mean (Syslo et al. 2011; Cox et al. 2013). Fecundity at age was modeled using a stretch-beta distribution, with the maximum number of eggs set to three times the mean number of eggs, since variation in fecundity is not uncommon in fishes (Healey 1978). Stretch-beta distributions are also flexible and can be scaled across a specified range to provide appropriate values for fecundity. Confidence intervals were estimated as the 97.5th and 2.5th percentiles of 1,000 bootstrap samples.

We evaluated the outcome of each management goal (i.e., eradication, trophy, and balance) at various fishing intensities. The eradication goal assumed constant F across age-classes ≥age 3 (Dux et al. 2011). The trophy goal modeled the implementation of a protected slot length limit that was based on a historical regulation for Priest Lake (Davis et al. 2000) that protected fish 660–813 mm long. Based on mean length–age data, the regulation would protect age-23 to age-35 Lake Trout. The balance goal incorporated targeted mechanical removal and recreational angling. We modeled a mechanical removal effort that targeted juvenile Lake Trout and sought to compromise between maintaining a Lake Trout fishery and reducing the abundance of Lake Trout. Asymptotic sensitivity analysis (Caswell 1988) indicated that population growth rate was most sensitive to changes in survival of Lake Trout at age 2 to age 5. Therefore, these age-classes were targeted in simulations to maximize the effect of a removal effort, while minimizing the effects on recreationally desirable fish (i.e., greater than quality length [500 mm]). In addition to the mechanical removal of juvenile fish, we assumed that angler exploitation would remain constant at the observed rate for age-3 and older Lake Trout.

For each scenario, outcomes were evaluated for values of F from 0 to 1.5 in 0.01 increments on the targeted age-classes for each scenario (i.e., ≥age 3 [eradication], age 3–age 22 [trophy], and age 2–age 5 [balance]). In the eradication scenario, we evaluated λ over 5, 10, and 20 years. In the scenarios that maintained a fishery (i.e., trophy and balance), we estimated λ and median population size, number of fish harvested, biomass, biomass harvested, and abundance and number of Lake Trout harvested by incremental standard length category over a 10-year period. For the balance scenario, harvest was calculated for the portion of fishing effort that was due to angling, excluding mechanical removal harvest. Bootstrap confidence intervals were calculated as above. For all bootstrap simulations, age-specific standard errors from the observed survival rates (i.e., Chapman–Robson estimator) were used.

We performed a sensitivity analysis for λ to provide insight into potential effects of density-dependent responses of Lake Trout to increased F. We evaluated the effect of a 20% increase in probability of spawning to reflect a potential increase in food resources for adult Lake Trout following increases in F. We also evaluated the effect of a 20% increase in mean fecundity at age, representing a potential increase in growth rate since fecundity is most closely correlated with body size. Reproductive rates were increased across all ages, and average population growth was estimated over a 10-year period for both vital rates.

RESULTS

In spring 2013, 4,392 individual Lake Trout were captured from gill nets and trap nets, of which 2,959 were marked and released. Of these, 104 individuals were recaptured during the spring netting, and 1 individual was recaptured three times. No tag loss was observed. After correcting for postrelease mortality, the estimated population size was 43,210 (95% CI: 31,569–59,451) or 4.6 fish/ha (95% CI: 3.3–6.3 fish/ha). Trap nets were fished for a total of 550 net nights, for which the mean catch rate was 1.26 fish/net night (SD = 2.11 fish/net night). For the 130 gill-net gangs set, the average hourly catch rate was 24.70 fish/gang (SD = 27.23 fish/gang). Catch rates were not significantly different between strata for gill nets ($t = -0.58$, df = 126, $P = 0.57$) or trap nets ($t = 0.30$, df = 121, $P = 0.77$).

Lake Trout varied in length from 174 to 1,130 mm (mean ± SD; 549 ± 114 mm). The majority of Lake Trout captured were quality length (proportional stock density [PSD] = 71, PSD-preferred = 7, PSD-memorable = 2, PSD-trophy = 0). On average, Lake Trout in Priest Lake were in good condition (mean $W_r = 90 \pm 13$ SD). However, there was a slight but statistically significant negative relationship between W_r and length ($\beta_1 = -0.072$, $P < 0.0001$). Stock-length fish had an average W_r of 95 (±10 SD). Quality-length fish had an average W_r of 83 (±12 SD). Both preferred- and memorable-length fish had mean W_r of 76 (±10 SD). Lake Trout ($n = 628$) varied in age from 2 to 35 years (Figures 2 and 3; Table 1). After correcting for gill-net selectivity, peak abundance in the catch occurred at age 3. Total instantaneous mortality for age-3 and older fish was 0.108 (95% CI: 0.084–0.133) and survival was 89.7% (95% CI: 87.5–91.9%).

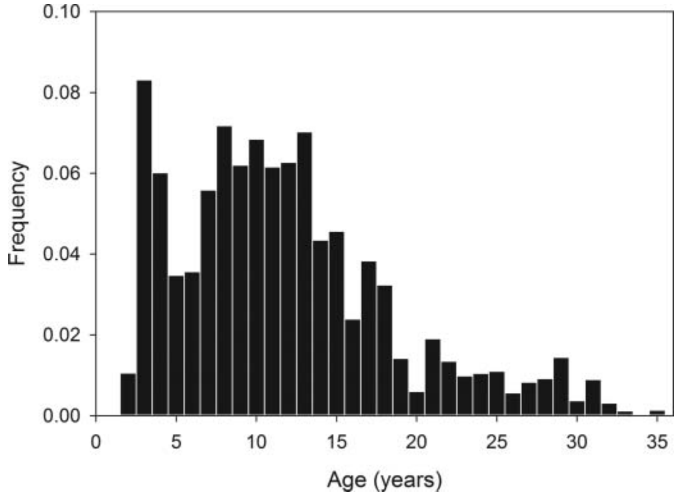

FIGURE 2. Age-frequency distribution of Lake Trout sampled in spring 2013 from Priest Lake, Idaho. Data are for gill-net–captured fish, corrected for selectivity.

Between May 10, 2013, and May 10, 2014, 23 reward-tagged and 164 nonreward-tagged Lake Trout were reported harvested. After correcting for nonreporting, we estimated that 25 reward-tagged Lake Trout and 303 nonreward-tagged Lake Trout were harvested during the period. Although 2,959 Lake Trout were released during the tagging period, we estimated that 554 died after release. Estimated postrelease mortality rate was 22% (95% CI: 20–24%) for gill-net–captured fish and 3% (95% CI: 2–4%) for trap-net–captured fish. Thus, after correcting for nonreporting and postrelease mortality, μ was estimated to be 0.136 and F was 0.143. Based on observed F and Z, M was 0. The estimate of M was 0.132 using Quinn and Deriso (1999), 0.054 using Shuter et al. (1998), and 0.129 using Hoenig (1983). The average of the three estimates of M was 0.079, and Z used in the simulations was 0.222.

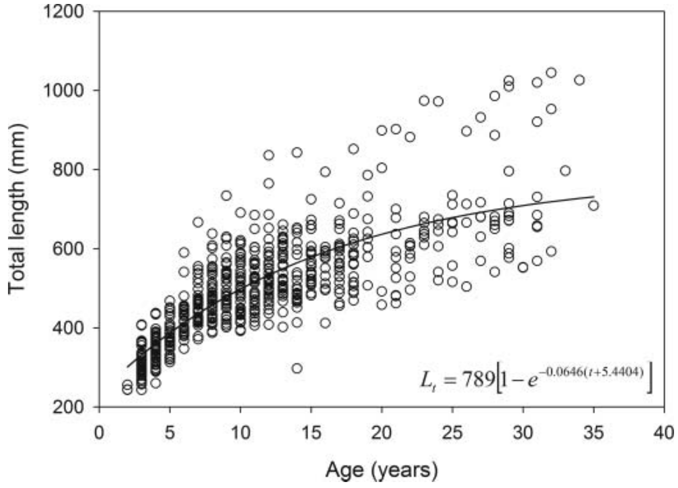

FIGURE 3. Von Bertalanffy growth model fit to length-at-age data for Lake Trout sampled in 2013 from Priest Lake, Idaho.

TABLE 1. Mean and standard deviation (in parentheses) of characteristics and vital rates used in population simulations for Lake Trout in Priest Lake, Idaho; female abundance (*N*), survival (*S*), probability of spawning (*P*), and fecundity (*f*, number of eggs) for the *i*th age class.

Age (years)	TL (mm)	Mass (g)	N_i	S_i	P_i	f_i
0				0.0043 (0.001)[a]	0.00 (0.00)	0 (0)
1			2241	0.450 (0.090)[b]	0.00 (0.00)	0 (0)
2	301	258	1996	0.780 (0.156)[b]	0.00 (0.00)	0 (0)
3	332	338	1556	0.825 (0.012)	0.00 (0.00)	0 (0)
4	360	425	1125	0.825 (0.012)	0.00 (0.00)	0 (0)
5	387	519	649	0.825 (0.012)	0.00 (0.00)	0 (0)
6	412	618	666	0.825 (0.012)	0.15 (0.04)	2097 (235)
7	436	721	1045	0.825 (0.012)	0.17 (0.04)	2137 (218)
8	458	827	1342	0.825 (0.012)	0.19 (0.04)	2177 (202)
9	479	935	1160	0.825 (0.012)	0.21 (0.04)	2217 (188)
10	498	1044	1280	0.825 (0.012)	0.23 (0.04)	2257 (175)
11	516	1153	1152	0.825 (0.012)	0.25 (0.04)	2297 (164)
12	533	1262	1173	0.825 (0.012)	0.28 (0.04)	2337 (154)
13	549	1369	1314	0.825 (0.012)	0.30 (0.05)	2377 (148)
14	564	1476	813	0.825 (0.012)	0.33 (0.05)	2417 (144)
15	579	1580	854	0.825 (0.012)	0.36 (0.05)	2457 (144)
16	592	1682	447	0.825 (0.012)	0.38 (0.06)	2497 (146)
17	604	1781	716	0.825 (0.012)	0.41 (0.06)	2537 (152)
18	616	1877	605	0.825 (0.012)	0.44 (0.07)	2577 (160)
19	627	1971	265	0.825 (0.012)	0.47 (0.07)	2617 (171)
20	637	2061	112	0.825 (0.012)	0.50 (0.08)	2657 (184)
21	646	2148	356	0.825 (0.012)	0.53 (0.08)	2697 (198)
22	655	2231	252	0.825 (0.012)	0.56 (0.09)	2737 (213)
23	664	2311	184	0.825 (0.012)	0.59 (0.09)	2777 (229)
24	671	2388	196	0.825 (0.012)	0.62 (0.10)	2817 (247)
25	679	2461	205	0.825 (0.012)	0.65 (0.10)	2857 (264)
26	686	2531	105	0.825 (0.012)	0.68 (0.10)	2897 (283)
27	692	2598	154	0.825 (0.012)	0.70 (0.10)	2937 (301)
28	698	2662	171	0.825 (0.012)	0.73 (0.10)	2976 (320)
29	704	2723	270	0.825 (0.012)	0.75 (0.10)	3016 (340)
30	709	2780	69	0.825 (0.012)	0.78 (0.10)	3056 (359)
31	714	2835	167	0.825 (0.012)	0.80 (0.10)	3096 (379)
32	719	2887	58	0.825 (0.012)	0.81 (0.10)	3136 (399)
33	723	2936	22	0.825 (0.012)	0.83 (0.09)	3176 (419)
34	728	2983	3	0.825 (0.012)	0.85 (0.09)	3216 (439)
35	731	3027	25		0.86 (0.08)	3256 (459)

[a] Vital rate estimate from Shuter et al. (1998) with standard deviation equal to 20% of the mean.

[b] Vital rate estimate from Sitar et al. (1999) with standard deviation equal to 20% of the mean.

During the 2013 autumn netting, 133 female Lake Trout were captured. Minimum observed age of maturity was 6 years. Age at 50% maturity was 7.5 years (95% CI: 6.7–8.3 years; Figure 4). However, age at 50% reproductivity (i.e., excluding nonspawning fish) was 19.9 years (14.8–24.9 years; Figure 5). The reproductive schedule (i.e., reproduction ogive) of female Lake Trout was described by the following logistic regression equation:

$$P_{\text{reproductive}} = \frac{e^{0.12\text{age} - 2.43}}{1 + e^{0.12\text{age} - 2.43}} .$$

Fecundity tended to increase with age (Figure 5). Mean fecundity was 2,443 eggs ($n = 32$; 2,150–2,735 eggs) and

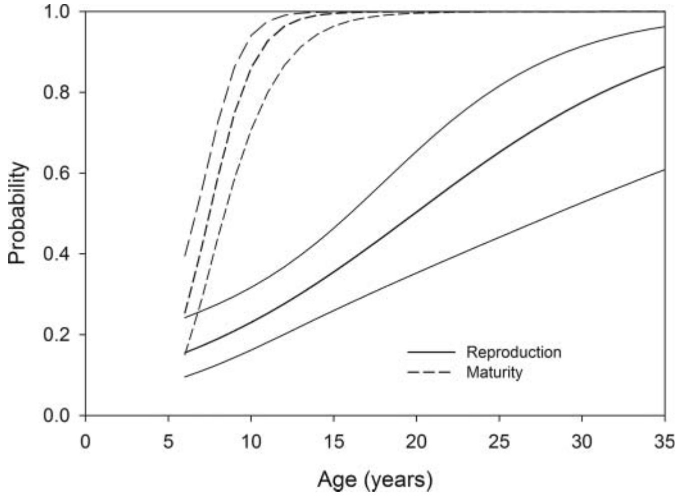

FIGURE 4. Maturity and reproductive ogives for Lake Trout sampled in autumn 2013 from Priest Lake, Idaho. Maturity ogive indicates the probability of maturity for Lake Trout at age. Reproductive ogive represents the probability of spawning at a given age. Lines are predicted probability bounded with respective 95% CI values.

varied from 1,206 to 5,847 eggs per female. Mean relative fecundity was 1,392 (1,304–1,482) eggs/kg body mass.

Asymptotic population growth rate for the observed population matrix was 1.01, but mean population growth rate from transient dynamics analysis indicated more rapid average growth in the short term. At current levels of exploitation, the simulated 5-year λ was 1.42 (95% CI: 1.11–1.38), the 10-year λ was 1.10 (95% CI: 1.03–1.18), and the 20-year λ was 1.05 (95% CI: 0.98–1.12). Average annual abundance projected over 10 years was 93,250 Lake Trout (95% CI: 61,647–134,698), with an average annual harvest of 33,225 Lake Trout (95% CI: 21,020–49,724). Projected average biomass was 41,626 kg (95% CI: 32,496–53,864 kg), with a harvest of 25,556 (95% CI: 20,072–32,819). The number of stock-quality–length fish was projected to be 30,049 (95% CI: 15,868–48,804), with 19,209 (95% CI: 10,144–31,199) in the harvest. The number of quality-preferred–length fish was projected to be 10,809 (95% CI: 9,796–12,113), with 6,910 (95% CI: 6,262–7,743) in the harvest. Simulated abundance of memorable-trophy–length (463, 95% CI: 451–475) and trophy-length Lake Trout (215, 95% CI: 207–223) was much lower than for the other length categories. Harvest of memorable-trophy–length (296, 95% CI: 289–303) and trophy-length Lake Trout (137, 95% CI: 132–142) was also low.

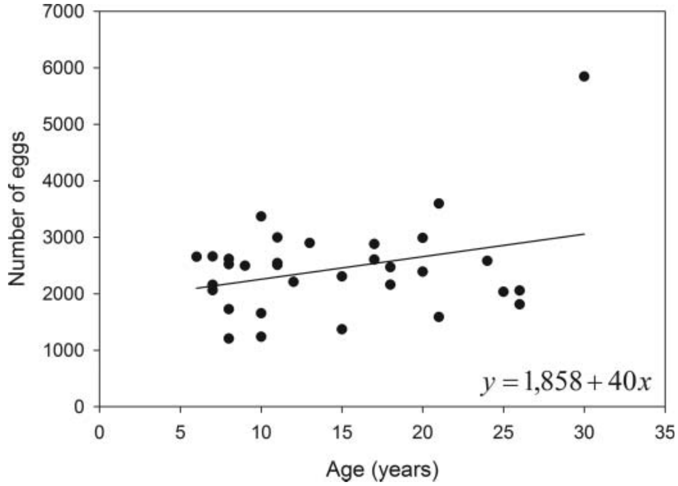

FIGURE 5. Observed fecundity at age for female Lake Trout sampled in autumn 2013 from Priest Lake, Idaho.

Population projections for the eradication scenario indicated that causing the population to decline would be possible (Figure 6). The level of F associated with replacement rate (i.e., $\lambda = 1$) decreased as the duration of fishing increased. To achieve $\lambda < 1$, on average, over a period of 5 years, F would need to be maintained at nearly five times the current level of fishing mortality ($F = 0.65$, $A = 0.52$). Over a 10-year period, F would need to be maintained at 0.31 ($A = 0.32$). Finally, over a 20-year period, F would need to be maintained at 0.27 ($A = 0.27$), less than twice the current exploitation rate.

In contrast to the eradication scenario, the scenarios that maintained a Lake Trout fishery exhibited slower declines in λ with increasing F because fishing mortality was applied to fewer age-classes in the latter two scenarios (Figure 7). Mean λ did not reach replacement until $F = 0.32$ ($A = 0.33$) for the trophy scenario and $F = 0.45$ ($A = 0.41$) for the balance scenario. Trends in abundance and biomass at various levels of F for the trophy and balance scenarios corresponded to trends in λ. In the trophy scenario, peak number of fish harvested (37,091 fish/year, 20,367–53,816) and peak biomass harvested (24,159 kg/year, 16,676–31,642) occurred at $F = 0.12$. In the balance scenario, peak harvest by anglers occurred in the scenario without any removal effort (i.e., observed conditions).

Abundance and number of fish harvested for each length category were generally lower for the trophy scenario than for the balance scenario (Figure 8). The exception was that the protected slot limit in the trophy scenario maintained higher abundances of trophy-length fish in the population for all values of F, though fewer trophy-length fish were harvested. In contrast, the balance scenario maintained nearly constant numbers of preferred-length fish in the population across a wide range of F and also allowed for harvest. Harvest rate of trophy-length fish in the balance scenario was unchanged from the current conditions in Priest Lake.

Transient sensitivity analysis of the Lake Trout population was consistent with the asymptotic sensitivity analysis, which indicated that λ was less sensitive to reproductive rates than to juvenile survival rates. On average, increasing fecundity or probability of spawning by 20% resulted in a 2.2% increase in λ over a 10-year period.

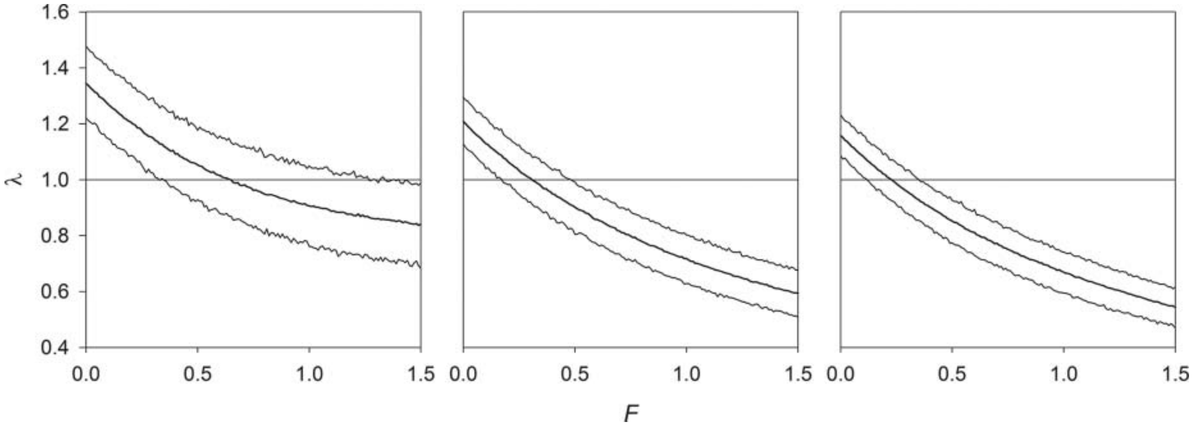

FIGURE 6. Median population growth rate (λ) with 95% CIs for the eradication scenario at various levels of fishing mortality (F) over 5- (left), 10- (center), or 20-year (right) periods for Lake Trout in Priest Lake, Idaho. The horizontal reference line indicates $\lambda = 1$ (replacement).

DISCUSSION

In this study, we coupled a biological evaluation of the nonnative Lake Trout population in Priest Lake with a demographic model to evaluate trade-offs in implementation of three potential management scenarios. Length at age indicated that individual Lake Trout grew rapidly at young ages but growth rates declined with age. Slow adult growth rates combined with declining body condition with length and high rates of skipped spawning may be caused by low prey availability for piscivorous age-classes. These types of density-dependent restrictions in adult growth rate and reproductive rate have implications for the success of eradication, trophy, and balance management scenarios.

Population length structure is a useful indicator of growth rates and growth potential. Fish populations with ample prey resources, low densities, and hence low competition, generally grow faster and larger. Lake Trout can reach lengths up to 1,570 mm (Martin and Olver 1980). Although the largest fish captured during sampling was 1,130 mm, few fish captured were longer than memorable length. Furthermore, L_∞ was only 789 mm, which was lower than for many nonnative Lake Trout populations, including Yellowstone Lake ($L_\infty = 812$ mm; Syslo et al. 2011); Lake McDonald, Montana ($L_\infty = 922$ mm; Dux et al. 2011); Quartz Lake, Montana ($L_\infty = 1{,}033$ mm; Fredenberg 2014); Swan Lake, Montana ($L_\infty = 1{,}112$ mm; Cox et al. 2013); and Blue Mesa Reservoir, Colorado ($L_\infty = 1{,}151$ mm; Pate et al. 2014). Reductions in growth rates can occur in Lake Trout populations where prey resources are limited, due to either high Lake Trout density or low density of prey fishes (Pazzia et al. 2002). Further evidence for the low prey abundance in Priest Lake is the high variability in individual growth rates; age-specific length varied by 34% on average. Variability in individual growth rates is another indication of prey limitations for Lake Trout (Eby et al. 1995).

In Priest Lake, opossum shrimp probably provide an abundant food source for juvenile Lake Trout, whereas kokanee and other fishes are important for larger Lake Trout (Bowles et al. 1991). The body condition of adult Lake Trout showed several signs that current prey resources are inadequate. Furthermore, prey density alone may not be sufficient to maintain good condition of larger Lake Trout; prey size is also an important consideration (Kerr 1971; Johnson and Martinez 2000; Pazzia et al. 2002). Given these biological factors, we found evidence of a mismatch between carrying capacity for juvenile versus adult Lake Trout.

Patterns in body condition of Lake Trout in Priest Lake also provided evidence of a mismatch between adult and juvenile prey availability. The average body condition of Lake Trout in Priest Lake was in the 50th percentile for 58 North American stocks (Hubert et al. 1994), and W_r decreased with length. Furthermore, catch of preferred- and memorable-length fish was rare, and for those captured, their relative weights were below the 5th percentile for those classes (Hubert et al. 1994). Food supply is a major factor influencing Lake Trout body condition (Martin and Olver 1980). For example, generally poor (1st–5th percentile) Lake Trout body condition in Lake McDonald, Glacier National Park, was attributed to limited food resources (Dux et al. 2011). In contrast, in Blue Mesa Reservoir, high kokanee availability has historically allowed Lake Trout to reach trophy sizes and excellent body condition (mean $W_r >$ 150; Pate et al. 2014). However, recent declines of kokanee in Blue Mesa Reservoir by as much as 90% have coincided with decreases in W_r to 108 for trophy-length fish. Lake Trout in Yellowstone Lake were also in better condition (median $W_r \geq$ 100) than Lake Trout in Priest Lake. The good condition of Lake Trout in Yellowstone Lake is probably representative of superior prey resources due to higher productivity (Syslo 2010). Thus, reduced prey fish abundance can lead to declines in body condition such as those observed in Priest Lake.

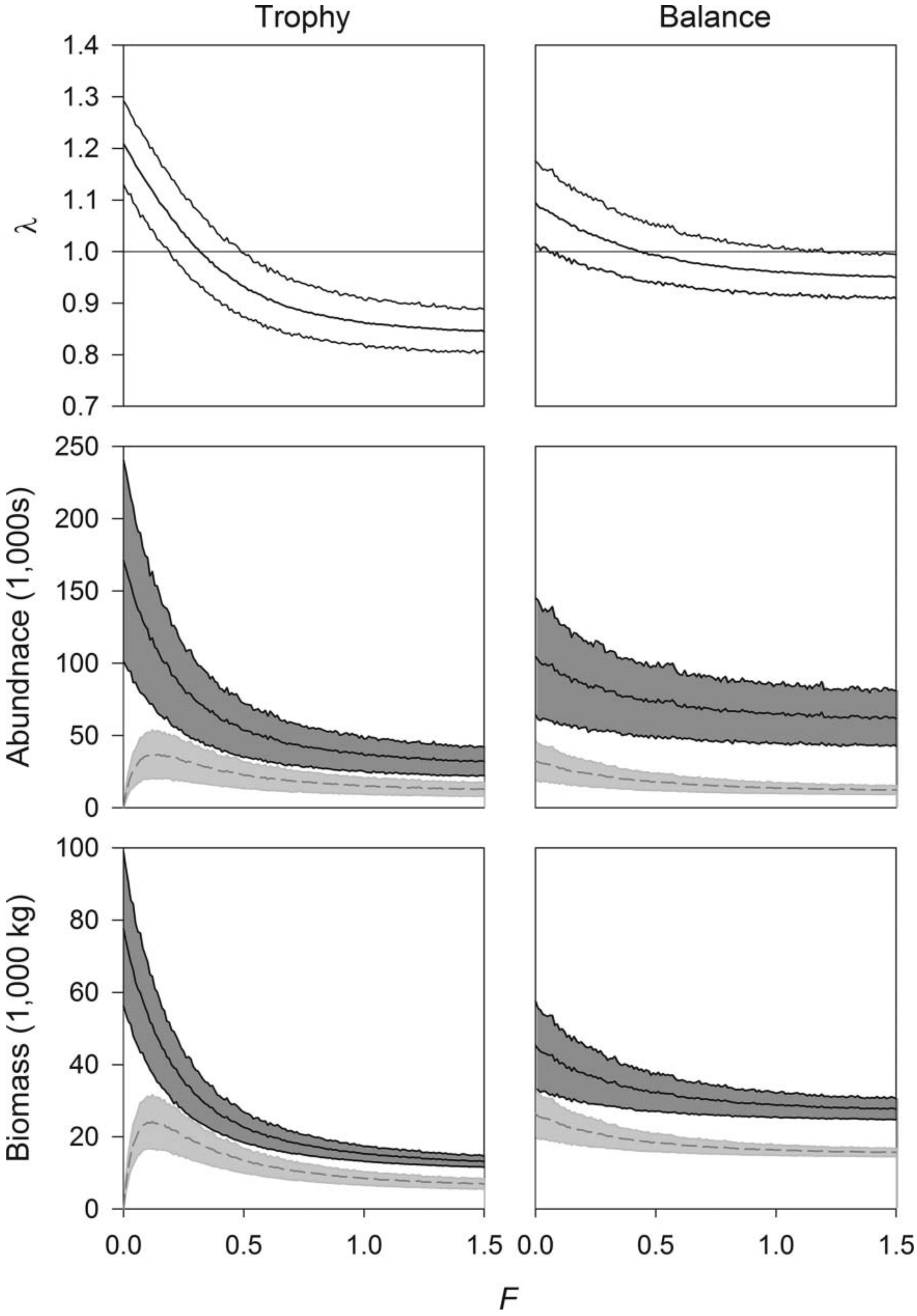

FIGURE 7. Population growth rate (λ), abundance, and biomass under two management scenarios at various levels of fishing mortality (*F*) over a period of 10 years for Lake Trout in Priest Lake, Idaho. Mean population growth is shown with a reference line indicating $\lambda = 1$ (replacement). Median population abundance (solid line) and median number of fish harvested (dashed line) are in the second row. Median population biomass (kg; solid lines) and median biomass harvested (dashed line) are in the bottom row. Ninety-five percent CIs are shown. Management scenarios are trophy (left), a protected slot limit for fish age 23 and above (i.e., 660–813 mm); and balance (right), a mechanical juvenile removal scenario for age-2 to age-5 Lake Trout.

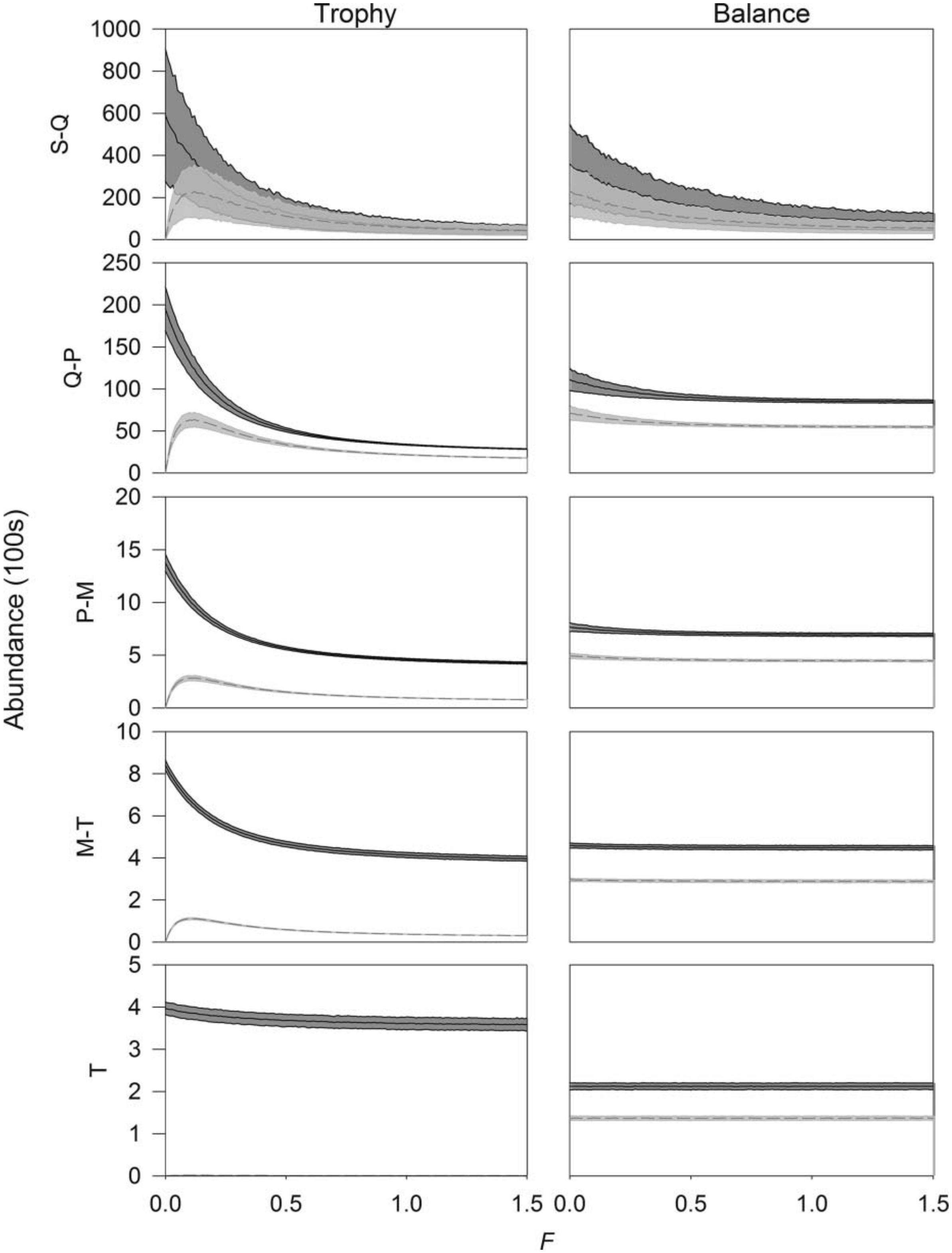

FIGURE 8. Abundance of Lake Trout by incremental standard-length categories under two management scenarios at various levels of fishing mortality (*F*) in Priest Lake, Idaho. The length categories, from top to bottom row, are stock-quality (280–500 mm), quality-preferred (501–700), preferred-memorable (701–850 mm), memorable-trophy (851–1,000 mm), and trophy (>1,000 mm). Median abundance (solid lines) and median number harvested (dashed lines) are shown with 95% CIs. Management scenarios are trophy (left), a protected slot limit (660–813 mm, age 23 and above); and balance (right), where age-2 to age-5 Lake Trout were removed.

Reproductive rates can also be used to evaluate population status (Trippel 1995). Age at first maturity in Lake Trout populations varies from 4 to 13 years for female Lake Trout (Martin and Olver 1980) and is closely tied to lake productivity and individual growth rates (Trippel 1993). Female Lake Trout in Priest Lake matured at relatively young ages; we first observed maturity at age 6, and by age 8, more than 50% of the population was mature. Although age at maturation was indicative of high individual growth rates, the high rate of skipped spawning (0.54) suggests energetic limitations later in life. For example, skipped spawning was linked to high Lake Trout density and reduced availability of the prey fish Cisco *Coregonus artedii* in Greenwich Lake, Ontario (Trippel 1993). Furthermore, previous studies of Canadian populations noted that skip-spawning is more frequent at northern latitudes, where rates may be as high as 87% (Healey 1978; Sitar et al. 2014). Skip-spawning is also known to occur at lower latitudes, where high rates are related to restriction in food supply (Martin and Olver 1980; Sitar et al. 2014). Reproductive parameters in Priest Lake further suggest energetic mismatches between juvenile and adult Lake Trout.

Compared with faster growing Lake Trout populations, the population in Priest Lake had higher density, lower average body condition, and lower reproductive output. Although the density of Lake Trout (>age 5) in Priest Lake (3.2 fish/ha) is close to the average for North American populations (mean adult density = 4.4 fish/ha, range = 0.9–14.2 fish/ha; Hansen et al. 2008), it is higher than for fast-growing nonnative Lake Trout popualtions, such as in Lake Pend Oreille. Total density of Lake Trout in Priest Lake (4.8 fish/ha) was over 10 times the density in Lake Pend Oreille (0.9 fish/ha) prior to removal efforts, when λ was 1.63 (Hansen et al. 2008). Compared with Lake Trout in Priest Lake, individuals in Swan Lake, Montana, were in better condition, had five times the age-specific fecundity, and did not appear to skip spawning (Cox et al. 2013), probably reflecting higher productivity in Swan Lake (total dissolved solids = 112 mg/L) than Priest Lake (8.36 mg/L; Bowles et al. 1991). As a result, the population in Swan Lake grew about 30% faster than in Priest Lake ($\lambda = 1.35$; Cox et al. 2013). More similar to Lake Trout in Priest Lake, those in Quartz Lake, Montana, were below the 50th percentile in mean W_r and experienced similar levels of natural mortality ($M = 0.06$; Fredenberg 2014). Twenty-year average population growth rate for Lake Trout in Quartz Lake was 1.23, whereas λ was 1.05 for Priest Lake. Although Quartz Lake lacks opossum shrimp, the main difference between populations appears to the high rate of skipped spawning among Lake Trout in Priest Lake. Thus, relatively high densities of Lake Trout and low productivity in Priest Lake appear to manifest as low body condition and low reproductive output, which ultimately lead to slower population growth.

Due to their slow growth and late maturity, Lake Trout populations are thought to be susceptible to overexploitation (Healey 1978; Martin and Olver 1980). The reduced reproductive rate of female Lake Trout in Priest Lake suggests that less effort would be required to collapse the population there than in other western lakes. We found that total annual mortality rates as low as 27% could cause the population to decline, lower than the frequently cited assertion that Lake Trout populations cannot sustain total annual mortality rates greater than 50% (Healey 1978). For example, the young and rapidly growing Lake Trout population in Yellowstone Lake required an estimated total annual mortality greater than 39% over a 20-year period to reduce their population (Syslo et al. 2011). Similarly, in Lake McDonald, simulations indicated that the Lake Trout population would decline if total annual mortality was between 44% and 49% (Dux 2005). Therefore, removal of Lake Trout in Priest Lake apparently is possible and would require lower levels of mortality than in other lakes, though we caution that compensatory mechanisms could ultimately necessitate additional effort at low population densities (Ferreri and Taylor 1996; Sitar and He 2006).

Protected slot length limits are designed to promote the growth and survival of trophy individuals, and our simulation indicated that such a limit would successfully maintain the number of trophy individuals across a wide range of fishing intensities. However, increasing abundance of trophy-length individuals could further exacerbate prey limitations in Priest Lake. In Flaming Gorge Reservoir, Wyoming–Utah population models indicated that regulations maximizing catch of trophy Lake Trout also maximized prey consumption (Luecke et al. 1994). Furthermore, although we designated trophy status by length, somatic weight is often the determining factor for recreational angler satisfaction (Johnson and Martinez 2000). Fish in low-productivity systems may require more prey resources to attain the same growth rates as fish in more productive waters because prey density affects foraging efficiency (Mason et al. 1998). Large Lake Trout in Priest Lake are already in poor condition, and increasing their abundance through protective limits would probably exacerbate the problem and eventually result in angler dissatisfaction.

Removing juvenile Lake Trout (i.e., ages 2–5) has the potential to decrease population density and increase individual growth rates but would not guarantee reduction in consumption rates. If juvenile removal reduces Lake Trout abundance such that the overall predatory pressure of Lake Trout in Priest Lake is reduced, sport fishes (e.g., kokanee) may increase in abundance. However, management with this goal in mind should be pursued cautiously because of the foraging efficiency and predatory inertia of Lake Trout (Eby et al. 1995; Schoen et al. 2012). Even if Lake Trout density is decreased, remaining individuals may increase consumption of prey fish. If maintaining a Lake Trout fishery with more ideal length composition is desirable, the juvenile removal scenario may provide the best option to increase effort without risk of collapsing the population. Another benefit of the juvenile removal scenario is that it does not assume any changes in angler effort or exploitation. In this scenario, a limited mechanical removal of juvenile fish could be conducted, but there is no dependence on angler effort, which can be difficult to manipulate (Radomski et al. 2001).

We used a deterministic exponential growth model, which does not incorporate density-dependent dynamics. Although these types of matrix models have previously been used to evaluate population growth of Lake Trout populations (Syslo et al. 2011; Cox et al. 2013; Fredenberg 2014), slow growth and poor condition of Lake Trout in Priest Lake are indicators that density-dependent forces are already governing this population. Indeed, density-dependent responses are not only possible but also potentially desirable consequences of increasing exploitation in Priest Lake. Lake Trout populations have demonstrated density-dependent responses to harvest and prey abundance, including compensatory responses in growth and age-at-maturity (Sitar et al. 1999; Syslo et al. 2013). For example, individual Lake Trout growth rates increased in response to increasing exploitation in Ontario (Healey 1978). This response indicated that increased body growth may be an important compensating mechanism in exploited Lake Trout populations (Healey 1978). Since Lake Trout generally appear to mature at a fixed size rather than a fixed age, increased individual growth rates under high exploitation can lead to earlier age of maturation (Healey 1978; Ferreri and Taylor 1996). Maternal effects, such as egg size and quality, may also be density-dependent (Trippel 1993), as is skipped spawning (Sitar et al. 2014). We evaluated the potential short-term consequences of such density-dependent responses in length-at-age and probability of spawning, using sensitivity analysis. Interestingly, the effect was smaller than expected; a 20% change in either vital rate resulted in less than 20% change in population growth rate.

Another potential density-dependent response is increased survival. Consistent with other studies of Lake Trout population dynamics, we found that population growth rate was most sensitive to age-0 (and juvenile) survival rates (Cox et al. 2013). Because juvenile survival rates were unavailable for Priest Lake, we used literature values corresponding to the Lake Superior (age-0 survival; Shuter et al. 1998) and Ontario lakes (age-1 and age-2 survival; Sitar et al. 2014), where different factors, such as predation by Sea Lamprey *Petromyzon marinus* and low population density, influence survival rates. However, as discussed above, density-dependent responses in adult Lake Trout growth rates are common. In a simulation study using an age-structured population model, Rose (2005) demonstrated that when adult and juvenile density-dependence occurred simultaneously, they dampened each other. Therefore, although density-dependent effects across multiple age-classes may be present, such forces may ultimately cancel each other. In the absence of data for Priest Lake, we chose to omit from the model any density-dependent effects on recruitment and adult growth.

Fisheries management is an iterative process because fish populations are highly dynamic (Parrish et al. 1995). The present study provides insight on the short-term (10-year) population dynamics under three management scenarios representing alternative management scenarios for Lake Trout populations. As with any study using population models, projections are uncertain because variation in vital rates depends on intrinsic, biotic, and abiotic factors (Shuter et al. 1998) as well as stochastic environmental processes (Morris and Doak 2002). Despite these limitations, population models are useful for synthesizing information and comparing management actions. Our research provides a foundation for assessing biological feasibility of potential management actions and serves as a baseline for future monitoring and assessment (Johnson and Martinez 2000). More broadly, these types of models help advance understanding of the intrinsic factors that regulate fish populations and provide a basis for formulating hypotheses about the drivers of population growth and decline. Moving forward, management "experiments" and monitoring will allow us to test hypotheses about fish population dynamics.

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