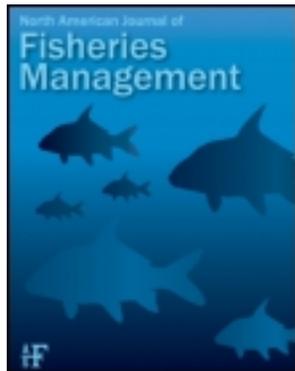


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ARTICLE

## Comparison of Harvest Scenarios for the Cost-Effective Suppression of Lake Trout in Swan Lake, Montana

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### Abstract

Given the large amount of resources required for long-term control or eradication projects, it is important to assess strategies and associated costs and outcomes before a particular plan is implemented. We developed a population model to assess the cost-effectiveness of mechanical removal strategies for suppressing long-term abundance of nonnative Lake Trout *Salvelinus namaycush* in Swan Lake, Montana. We examined the efficacy of targeting life stages (i.e., juveniles or adults) using temporally pulsed fishing effort for reducing abundance and program cost. Exploitation rates were high (0.80 for juveniles and 0.68 for adults) compared with other lakes in the western USA with Lake Trout suppression programs. Harvesting juveniles every year caused the population to decline, whereas harvesting only adults caused the population to increase above carrying capacity. Simultaneous harvest of juveniles and adults was required to cause the population to collapse (i.e., 95% reduction relative to unharvested abundance) with 95% confidence. The population could collapse within 15 years for a total program cost of US\$1,578,480 using the most aggressive scenario. Substantial variation in cost existed among harvest scenarios for a given reduction in abundance; however, total program cost was minimized when collapse was rapid. Our approach provides a useful case study for evaluating long-term mechanical removal options for fish populations that are not likely to be eradicated.

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Eradication or long-term control of nonnative species are common management endeavors. Early detection and rapid response may increase the probability of successfully eradicating or controlling nonnative populations (Simberloff 2003); however, it is important to assess all possible strategies and their outcomes before enacting a particular plan given the large amount of resources often required (Simberloff 2009). Before implementing a management plan for nonnative species, managers should determine whether eradication is a realistic objective. If eradication is not feasible, managers can determine the reduction required to reduce detrimental effects on native biota

through long-term control (Basse et al. 2003; Pine et al. 2007; Baxter et al. 2008; Peterson et al. 2008).

The efficacy of eradication projects for fishes appears to be limited compared with other taxa and decreases with increasing spatial scale (Britton et al. 2011). For example, the few published management successes that exist indicate that nonnative fishes have been eradicated in small alpine lakes using mechanical removal (Knapp et al. 2007) and in streams and small impoundments using chemical treatments (Gresswell 1991; Britton and Brazier 2006). The rarity of published studies reporting successful fish eradication using mechanical removal

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in large ecosystems (Donkers et al. 2012) indicates nonnative fish populations are less likely to be eradicated at larger spatial scales, where chemical treatment is unrealistic and mechanical removal remains the only viable alternative (Britton et al. 2011). Density-dependent compensation can further reduce the probability that established nonnative fish populations will be eradicated (Zipkin et al. 2008). Nevertheless, the use of mechanical removal for long-term control of nonnative fishes may increase in the future as managers attempt to avert the negative effects of nonnative fishes on native species in large and open ecosystems (Koehn 2004; Mueller et al. 2005; DeGrandchamp 2008; Jiao et al. 2009; Martinez et al. 2009).

Demographic models can be used to set realistic expectations and determine the most cost-effective management strategy if the goal for nonnative species removal is long-term control of abundance. For example, the cost of mechanical removal projects can be minimized by reducing the intensity and frequency of removal events (Basse et al. 2003; Baxter et al. 2008; Peterson et al. 2008). Additional increases in cost-effectiveness can be achieved by targeting life stages that are most vulnerable to suppression or that make the largest contribution to population growth rate (Govindarajulu et al. 2005; Martin et al. 2010) and by synchronizing intra-annual removal periods with important life cycle events (e.g., spawning or dispersal; Jiao et al. 2009). The aforementioned findings highlight the importance of collecting baseline demographic data for the target population and determining the efficacy of management actions before committing to long-term population suppression.

Lake Trout *Salvelinus namaycush* is an apex piscivore native to northern North America that has been extensively introduced outside of its native range, including 15 countries (Crossman 1995). Lake Trout have been introduced to large lakes and reservoirs in eight western U.S. states (Martinez et al. 2009), where they have had detrimental effects on native salmonid populations (Donald and Alger 1993; Fredenberg et al. 2002; Koel et al. 2005) and subsequently altered ecosystem structure and function (Tronstad et al. 2010; Ellis et al. 2011). The negative effects demonstrated by nonnative Lake Trout led to the initiation of several mechanical removal projects for the species in the western USA (Martinez et al. 2009). Individual large-scale mechanical removal projects for Lake Trout may cost nearly US\$1 million annually and compete with other agency priorities (Martinez et al. 2009). The large size (541–49,854 ha surface area) of lakes where Lake Trout removal is ongoing or being considered (Martinez et al. 2009) reduces the likelihood of eradication using current technologies (i.e., gill nets, trap nets, and angling). Therefore, the goal of Lake Trout suppression programs is often to reduce the negative effects on native salmonids or sport fish by reducing competition and predation (Koel et al. 2005; Hansen et al. 2010). However, when the magnitude of Lake Trout population decline required to reduce negative interactions with native species is unknown, the goal of Lake Trout control may best be stated as achieving the greatest reduction in abundance given a time frame and cost.

Lake Trout were introduced into Flathead Lake, Montana, in 1905 and subsequently colonized lakes throughout the Flathead River system (Spencer et al. 1991; Fredenberg 2002). Lake Trout were discovered in the Swan River drainage in 1998, and the population is predicted to increase exponentially without population suppression (Cox et al. 2013). The Swan River drainage contains a population of native Bull Trout *Salvelinus confluentus*, listed as threatened under the U.S. Endangered Species Act (USFWS 1998). Lake Trout have consistently displaced populations of Bull Trout throughout the Intermountain West (Donald and Alger 1993; Fredenberg 2002). Thus, an experimental Lake Trout suppression program was initiated in Swan Lake in 2008 to determine whether the Lake Trout population could be reduced to avoid negative effects on populations of native species and sport fish.

Ultimately, the efficacy of Lake Trout removal is a function of total monetary amount expended and the reduction in population size that can be achieved per monetary amount. Our objective was to evaluate the effects of temporally varying netting effort and targeting different life stages (i.e., prereproductive or reproductive) on the reduction that could be achieved given removal program cost. We predicted that strategies using pulsed fishing effort targeting specific life stages would result in similar population reductions for a reduced cost relative to the currently used strategy of targeting all life stages every year.

## METHODS

**Study Area.**—Swan Lake is located in the Flathead River drainage in northwestern Montana (Figure 1). The Swan River is the primary tributary and outlet of Swan Lake. The lake is at an elevation of 940 m, has a surface area of 1,335 ha, and a mean depth of 16 m. However, the lake has two deep (>30 m) basins at the north and south ends. Swan Lake thermally stratifies in the summer, with a thermocline at about 18 m. Swan Lake contains several native and nonnative species (Cox et al. 2013). The native fishes are Bull Trout, Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *Prosopium coulterii*, Slimy Sculpin *Cottus cognatus*, Northern Pikeminnow *Ptychocheilus oregonensis*, Peamouth *Mylocheilus caurinus*, Redside Shiner *Richardsonius balteatus*, Largescale Sucker *Catostomus macrocheilus*, and Longnose Sucker *Catostomus catostomus*. The nonnative fish species are Lake Trout, Rainbow Trout *Oncorhynchus mykiss*, Brook Trout *Salvelinus fontinalis*, kokanee *Oncorhynchus nerka*, Northern Pike *Esox lucius*, Yellow Perch *Perca flavescens*, Pumpkinseed *Lepomis gibbosus*, Central Mudminnow *Umbra limi*, and Brook Stickleback *Culaea inconstans*. Opossum shrimp *Mysis diluviana* were also introduced into the lake.

**Netting.**—Two types of gill netting were conducted by contract harvesters: juvenile netting and spawner netting. Juvenile netting occurred each year from 2008 to 2011 and spawner netting occurred in 2010 and 2011. Juvenile netting occurred for

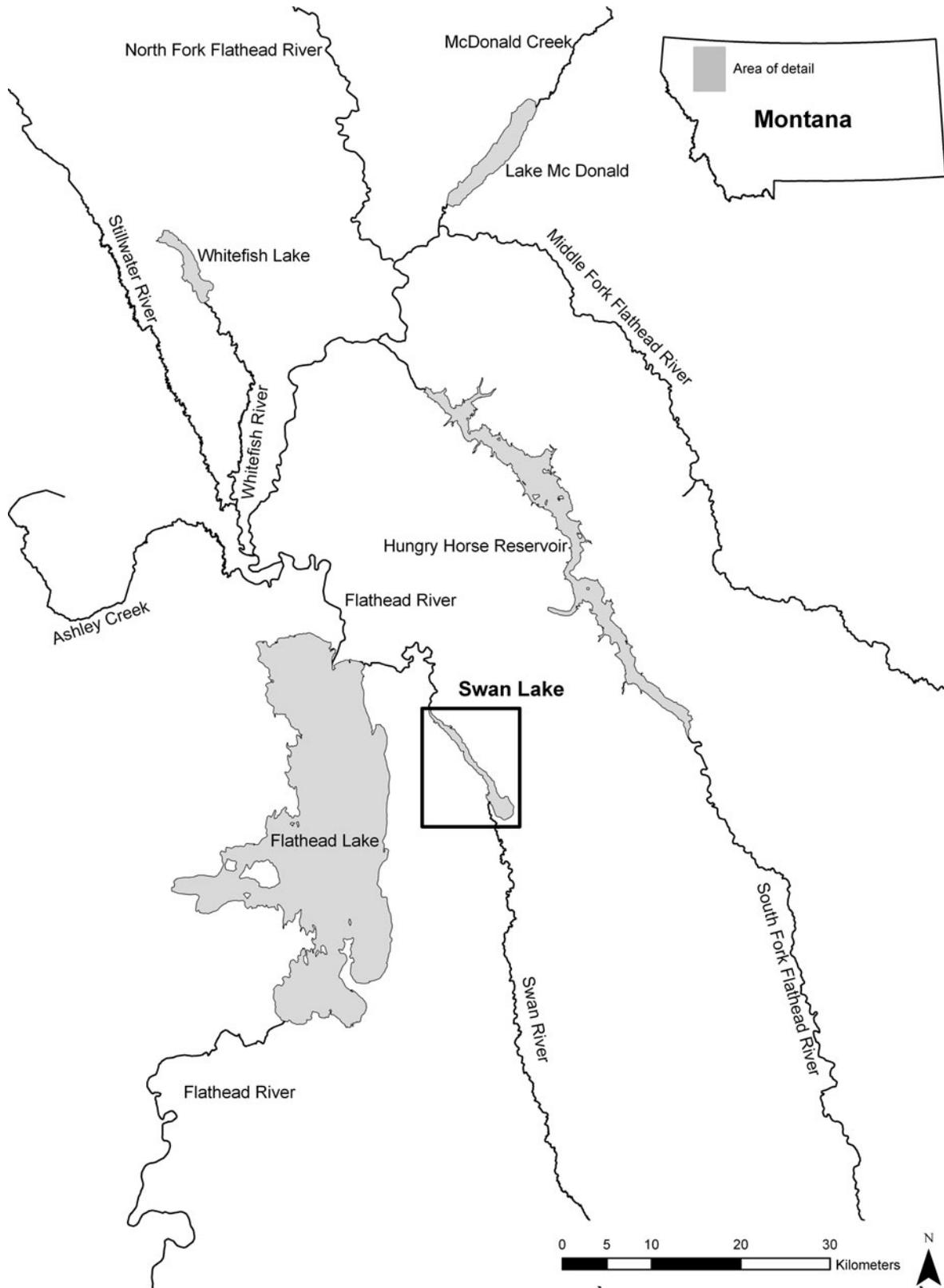


FIGURE 1. Location of Swan Lake in the Flathead River drainage, northwestern Montana.

3 weeks in late August and early September. To minimize by-catch of Bull Trout, juvenile nets were set at depths >20 m and soak times averaged 7.8 h. Sinking gill nets were 91.4 m long with 0.28-mm monofilament nylon twine. Juvenile netting used mesh sizes of 19, 25, 32, 38, 44, or 51 mm (bar measure) in 2008 and 2009. Mesh sizes of 22 and 29 mm were added to the gill-net complement in 2010 and 2011. In 2008, six nets of each mesh were attached to form a 3,290-m gang and nets were set randomly to collect demographic data and obtain a population estimate using depletion methods (see below). In contrast to 2008, meshes were fished with unequal effort from 2009 to 2011 and were set in locations that maximized Lake Trout catch. Juvenile netting effort (1 unit = 100 m of net set for 1 h) was 3,467 units in 2008, 1,779 units in 2009, 2,257 units in 2010, and 2,726 units in 2011. All Lake Trout captured were measured for TL (mm). Lake Trout captured in 2008 were subsampled for sex and stage of maturity (Cox et al. 2013). Ovaries and otoliths were removed from a subsample of fish for fecundity and age determination (Cox et al. 2013). Spawner netting occurred for 3 weeks during peak spawning season (October) and consisted of large-mesh (51-, 57-, and 64-mm bar measure) gill nets set at known spawning sites. The amount of effort used to target spawning fish was 1,278 units in 2010 and 813 units in 2011. Contract harvesters were paid \$64,375 for 3 weeks of juvenile netting and an additional \$22,500 for 3 weeks of spawner netting. In-kind contributions from Montana Fish, Wildlife and Parks (FWP) and the U.S. Fish and Wildlife Service totaled \$9,335 for juvenile netting and \$9,022 for spawner netting.

**Exploitation.**—Exploitation for juvenile netting ( $\mu_{juv}$ ) was calculated annually as the catch divided by abundance ( $\hat{N}$ ) of Lake Trout targeted by juvenile netting. Abundance was estimated using a multiple sampling period depletion estimator (see below). Netting did not occur on weekends; therefore, each of the 3 weeks of netting was considered a separate sampling period. The population estimate was restricted to Lake Trout in length-classes that were selected for every sampling period and year. Therefore, we estimated the abundance of Lake Trout vulnerable to the 19-, 25-, and 32-mm meshes in 2008 and 2009 and the 19-, 22-, 25-, 29-, and 32-mm meshes in 2010 and 2011. Gill-net selectivity was estimated for 5-mm length-classes by mesh, sampling period, and year using log-linear models with the SELECT method in R 2.15.2 (Millar and Holst 1997; R Development Core Team 2012). Within sampling period, differences in effort among mesh sizes were corrected by scaling the peak of each mesh selectivity curve relative to the peak for the mesh with the greatest effort. Selectivity curves by mesh were summed for an estimate of overall selectivity of the complement of gill-net meshes for Lake Trout lengths. Relative selectivity for each length-class was estimated by dividing the overall selectivity for the length-class by the overall selectivity for the length-class with the maximum value. Within each length-class, the observed catch was divided by the relative selectivity to produce the corrected catch for the sampling period. Inference was

restricted to length-classes between the peaks of the selectivity curves for the 19-mm and 32-mm meshes (i.e., 206–350 mm). A Leslie depletion estimator in the R package FSA (Ogle 2013) was used to estimate abundance of 206–350 mm Lake Trout in each year from the corrected total catch and total effort by sampling period. Confidence intervals for exploitation were calculated by dividing the catch by the 95% CIs for  $\hat{N}$ . Mean exploitation rate among years 2009–2011 was used in model simulations (see below). The mean coefficient of variation (CV) for population estimates was used as the coefficient of variation for  $\mu_{juv}$ .

Abundance was not estimable for adult Lake Trout targeted by spawner netting because decreases in catch over sampling periods could be attributed to fish leaving the spawning sites rather than depletion. Survival of spawning Lake Trout was estimated from the ratio of CPUE for individual cohorts in successive years of spawner netting (Ricker 1975). Survival was estimated for Lake Trout from age 6 through age 10 because Lake Trout were fully recruited to spawner netting at age 6 and there were fewer than five observations beyond age 10 (Ricker 1975). Survival of spawning Lake Trout ( $S_{sp}$ ) was calculated as the geometric mean of cohort-specific survival rates (Ricker 1975). Survival was converted to total instantaneous mortality [ $Z_{sp} = -\log_e(S_{sp})$ ]. Instantaneous fishing mortality for spawner netting ( $F_{sp}$ ) was estimated by partitioning total instantaneous mortality into natural ( $M = 0.085$ ; Cox et al. 2013) and fishing components ( $Z_{sp} = F_{sp} + M$ ; Miranda and Bettoli 2007). Total annual mortality ( $A_{sp}$ ) was estimated as  $1 - S_{sp}$  and exploitation was estimated as  $\mu_{sp} = F_{sp} \cdot A_{sp} / Z_{sp}$  (Miranda and Bettoli 2007). For simulations, we assumed that natural mortality was known without error and variation in  $S_{sp}$  represented variation in  $\mu_{sp}$  (see below).

**Selectivity.**—Selectivity for juvenile netting was modeled as the average relative selectivity among 2009 through 2011. For each year, relative selectivity for 10-mm length-classes was estimated for the entire complement of gill nets (i.e., 19-mm through 51-mm meshes). Within each year, differences in effort among mesh sizes were accounted for by scaling the peak of each mesh selectivity curve relative to the peak for the mesh with the greatest effort. The average length selectivity among 2009–2011 was converted to age-specific selectivity ( $sel_{juv_i}$ ) using age-length data (Cox et al. 2013). First, the proportion of fish in each 10-mm length category was calculated by age. Second, the proportion of fish in the length category was multiplied by selectivity for the length category. Third, the product among length categories was summed by age. We assumed that female Lake Trout are only caught if they spawn and used the age-specific probability of maturity (Table 1) as a surrogate for spawner selectivity ( $sel_{sp_i}$ ).

**Vital rates.**—Age-specific survival of Lake Trout  $\geq$  age 1 ( $S_i$ ), probability of maturity ( $P_i$ ), and fecundity at age ( $Fec_i$ ) were estimated in a previous study (Cox et al. 2013; Table 1). Survival of age-0 Lake Trout was estimated by converting a stock-recruitment model to a density-dependent survival

TABLE 1. Mean (standard deviation in parentheses) age-specific survival ( $S_i$ ), probability of maturity ( $P_i$ ), fecundity ( $Fec_i$ ), and selectivity to juvenile netting ( $sel_{juv_i}$ ) for Lake Trout in Swan Lake, Montana. Values of  $S_i$ ,  $P_i$ , and  $Fec_i$  are from Cox et al. (2013).

Age	Natural survival ( $S_i$ )	Probability of maturity ( $P_i$ )	Fecundity ( $Fec_i$ )	Juvenile netting selectivity ( $sel_{juv_i}$ )
1	0.45 (0.09)	0	0	0
2	0.78 (0.16)	0	0	0.41
3	0.92 (0.0035)	0	0	0.69
4	0.92 (0.0035)	0	0	0.80
5	0.92 (0.0035)	0	0	0.49
6	0.92 (0.0035)	0	0	0.24
7	0.92 (0.0035)	0.19 (0.073)	5,571 (2,371)	0.15
8	0.92 (0.0035)	0.84 (0.099)	6,182 (3,388)	0.09
9	0.92 (0.0035)	1.0	10,367 (2,703)	0.06
10	0.92 (0.0035)	1.0	9,789 (665)	0.05
11	0.92 (0.0035)	1.0	12,793 (951)	0.04
12	0.92 (0.0035)	1.0	12,793 (951)	0.03
13 +	0.92 (0.0035)	1.0	12,793 (951)	0.02

function (see below). Although the Lake Trout population in Swan Lake has not reached carrying capacity, the Lake Trout population in nearby Flathead Lake is likely at carrying capacity. Therefore, we scaled the abundance estimate for Lake Trout in Flathead Lake by surface area to estimate the abundance of Lake Trout in Swan Lake at carrying capacity (Hansen et al. 2010). The population estimate of 1,480,280 Lake Trout  $\geq$  age 1 in Flathead Lake (B. Hansen, Confederated Salish Kootenai Tribes, personal communication) was multiplied by 0.027 to scale for surface area, resulting in 39,968 Lake Trout  $\geq$  1 in Swan Lake at carrying capacity. Lake Trout recruitment likely follows the Ricker stock–recruitment function (Richards et al. 2004):

$$R = \alpha \cdot S_p \cdot e^{-\beta \cdot S_p} \cdot e^\varepsilon,$$

where  $R$  = abundance of age-1 recruits,  $S_p$  = spawning-stock abundance the previous year (i.e., the abundance of mature females),  $\alpha$  = the rate of recruitment at low spawning-stock abundance,  $\beta$  = the density-dependent decrease in recruitment, and  $\varepsilon$  = multiplicative process error (Ricker 1954). We used estimates of  $\alpha$  and  $\varepsilon$  for Lake Trout in Lake Superior ( $\alpha = 5.698$  and  $\varepsilon = 0.19$ ; Hansen et al. 2010) because  $\alpha$  and  $\varepsilon$  are generally similar among populations of the same species (Myers et al. 1999). The parameter  $\beta$  was adjusted until the carrying capacity produced by the model equaled 19,984 female Lake Trout  $\geq$  age 1 (i.e., 39,968/2), resulting in  $\beta = 0.000262$ .

**Model structure.**—A female-based Leslie matrix was used to model the Lake Trout population (Caswell 2001). Although the oldest Lake Trout observed in Swan Lake was 16 years old, Lake Trout commonly live longer than 20 years (Martin and Olver 1980). Therefore, the matrix model included age-classes 0–19 and a category for Lake Trout age 20 and greater. The matrix model included a postbreeding census (Caswell 2001)

and fertility was calculated as  $Fec_i \cdot P_i \cdot 0.5$ , where 0.5 accounts for half of the offspring being female. The stock recruitment relationship was converted to density-dependent age-0 survival ( $S_0$ ) by  $R/Fec_{sp}$ , where  $Fec_{sp}$  = the number of eggs produced by the spawning stock the previous year. Exploitation rates (i.e.,  $\mu_{juv}$  and  $\mu_{sp}$ ) were converted to instantaneous fishing mortality,  $F = -\log_e(1-\mu)$ . Instantaneous fishing mortality was multiplied by age-specific selectivity to determine age-specific instantaneous fishing mortality (Quinn and Deriso 1999). Thus, age-specific survival including fishing mortality was calculated as  $e^{(\log_e[S_i] + sel_{sp_i} \cdot -F_{sp} + sel_{juv_i} \cdot -F_{juv})}$ .

**Scenarios.**—The suppression program could adopt one of four annual netting schemes: no harvest (indicated by 0), juvenile netting only (indicated by 1), spawner netting only (indicated by 2), or both juvenile and spawner netting (indicated by 3). We evaluated 53 temporal combinations of annual netting schemes (management scenarios; Table 2) to determine the management scenarios that resulted in the greatest reductions in population size for a given cost. For each netting scheme (1, 2, and 3), we evaluated the effects of implementing suppression every year and alternating 1 year on with 1 year off, 2 years on with 2 years off, 3 years on with 3 years off, 4 years on and 4 years off, and 5 years on with 5 years off (Basse et al. 2003). We also evaluated the effectiveness of scenarios with off periods twice as long as on periods (e.g., 1 year on with 2 years off, 2 years on with 4 years off, etc.; Basse et al. 2003). For scenarios where harvest (on) periods consisted of netting scheme 3, we also evaluated the effects of implementing netting schemes 1 or 2 instead of off periods.

**Simulations.**—For each management scenario, we simulated 1,000 matrix replicates to account for uncertainty in Lake Trout vital rates (Caswell 2001) using R 2.15.2. Vital rates for each matrix replicate were generated from predicted values of age-specific survival, probability of maturity, and fecundity with associated standard deviations (Table 1) using the Popbio

TABLE 2. Scenarios for annual harvest strategies, where 0 = no harvest, 1 = juvenile netting only, 2 = spawner netting only, and 3 = both juvenile and spawner netting occurring within a year. Each number represents 1 year (e.g., scenario 3 consists of 2 years of juvenile netting followed by 2 years of no harvest). Annual costs are as follows: 1 = \$73,710; 2 = \$31,522; and 3 = \$105,232.

Scenario	Annual harvest strategy
1	1
2	10
3	1100
4	111000
5	11110000
6	1111100000
7	100
8	110000
9	111000000
10	111100000000
11	111110000000000
12	2
13	20
14	2200
15	222000
16	22220000
17	2222200000
18	200
19	220000
20	222000000
21	222200000000
22	222220000000000
23	3
24	30
25	3300
26	333000
27	33330000
28	3333300000
29	300
30	330000
31	333000000
32	333300000000
33	333330000000000
34	32
35	3322
36	333222
37	33332222
38	3333322222
39	322
40	332222
41	33322222
42	333322222222
43	33333222222222
44	31
45	3311
46	333111

TABLE 2. Continued.

Scenario	Annual harvest strategy
47	33331111
48	3333311111
49	311
50	331111
51	3331111111
52	333311111111
53	3333311111111111

package in R (Stubben and Milligan 2007). Age-specific rates of survival and probabilities of maturity were generated from beta distributions (Morris and Doak 2002). Age-specific fecundity values were generated from stretched beta distributions (Morris and Doak 2002). Recruitment process error was simulated by generating a value for  $\epsilon$  from a normal distribution for each simulation. Uncertainty in  $\mu_{juv}$  and  $\mu_{sp}$  was included using beta distributions with estimated standard deviations.

Paired simulations were projected for each matrix replicate. The first simulation included natural mortality as the only source of mortality and the second included age-specific mortality rates imposed by the management scenario. Both projections were seeded with two age-8 Lake Trout (Kalinowski et al. 2010) and were projected for 221 years to evaluate long-term population dynamics (i.e., equilibrium). The starting point for management scenarios was year 46 because the mean abundance of 206–350 mm Lake Trout in year 46 from 1,000 simulations closely matched the population estimate for females in 2008 (i.e.,  $\hat{N}/2$ ). For each matrix projection, abundance of Lake Trout  $\geq$  age 1 was recorded at 5, 10, 20, and 175 years after year 46. Year 175 represents long-term abundance after oscillations have dampened. To account for population cycles caused by periodic harvest, the long-term abundance was estimated as the predicted population size from a lowess smoother (span = 0.1) fit to population abundance as a function of time. For each matrix replicate, we calculated the difference in abundance at 5, 10, 20, and 175 years. Differences were expressed as percent reduction achieved by the management scenario relative to no harvest. A population was considered to have collapsed (i.e., declined below the quasi-extinction threshold; Morris and Doak 2002) when the abundance of Lake Trout  $\geq$  age 1 declined 95%, which was the reduction in yield when the Lake Michigan Lake Trout fishery collapsed (Hansen 1999). The cumulative probability of quasi extinction for each scenario was calculated at each time step as the proportion of the 1,000 simulations that declined to 994 female individuals (5% of mean unharvested carrying capacity) during or before year  $t$  (Morris and Doak 2002). The time to collapse was plotted as a function of cumulative program cost for scenarios causing collapse within 30 years to determine whether the program cost could be minimized by causing the collapse to occur rapidly.

TABLE 3. Estimated abundance of 206–350-mm Lake Trout ( $\hat{N}$ ; SE in parentheses) and exploitation rate ( $\mu$ ; 95% CI in parentheses) from 2008 through 2011 in Swan Lake, Montana.

Year	$\hat{N}$	$\mu$
2008	6,953 (530)	0.41 (0.35–0.48)
2009	3,640 (502)	0.80 (0.63–1.00)
2010	10,423 (166)	0.89 (0.86–0.92)
2011	7,191 (710)	0.69 (0.58–0.87)

**RESULTS**

The abundance of 206–350-mm Lake Trout varied from 3,640 to 10,423 (Table 3). Exploitation from juvenile netting varied from 0.41 to 0.89 and was substantially lower in 2008 than 2009–2011 (Table 3). The mean exploitation rate in juvenile netting from 2009 to 2011 was 0.80 (CV = 0.08). Exploitation from spawner netting was 0.68 (SD = 0.07).

Harvesting juveniles every year (scenario 1) resulted in population decline but over a longer time frame than the scenario

where both juveniles and spawners were harvested every year (scenario 23; Figure 2). Harvesting spawners every year (scenario 12) resulted in a population increase to 138% of carrying capacity through density-dependent compensation (Figure 2C). Most scenarios that alternated harvest of juveniles only with years off resulted in population increases to carrying capacity (scenarios 4–11). However, scenarios 2 and 3 resulted in sustained abundance at 70% of carrying capacity. Scenarios alternating harvest of spawners only with years off (scenarios 13–22) resulted in population increases to 117–145% of carrying capacity.

The scenario that included both juvenile and spawner netting every year (scenario 23; Table 2) caused the greatest population decline in the shortest time frame (Figure 3). Scenarios alternating 3 and 0 for equal time periods resulted in median reductions of 98–100% (Figure 3A). Scenarios alternating 3 and 0 with off periods twice the length of on periods (scenarios 29–33; Figure 3B) resulted in sustained reductions of 30–88%.

Scenarios harvesting both juveniles and spawners during on periods and harvesting spawners during off periods resulted in

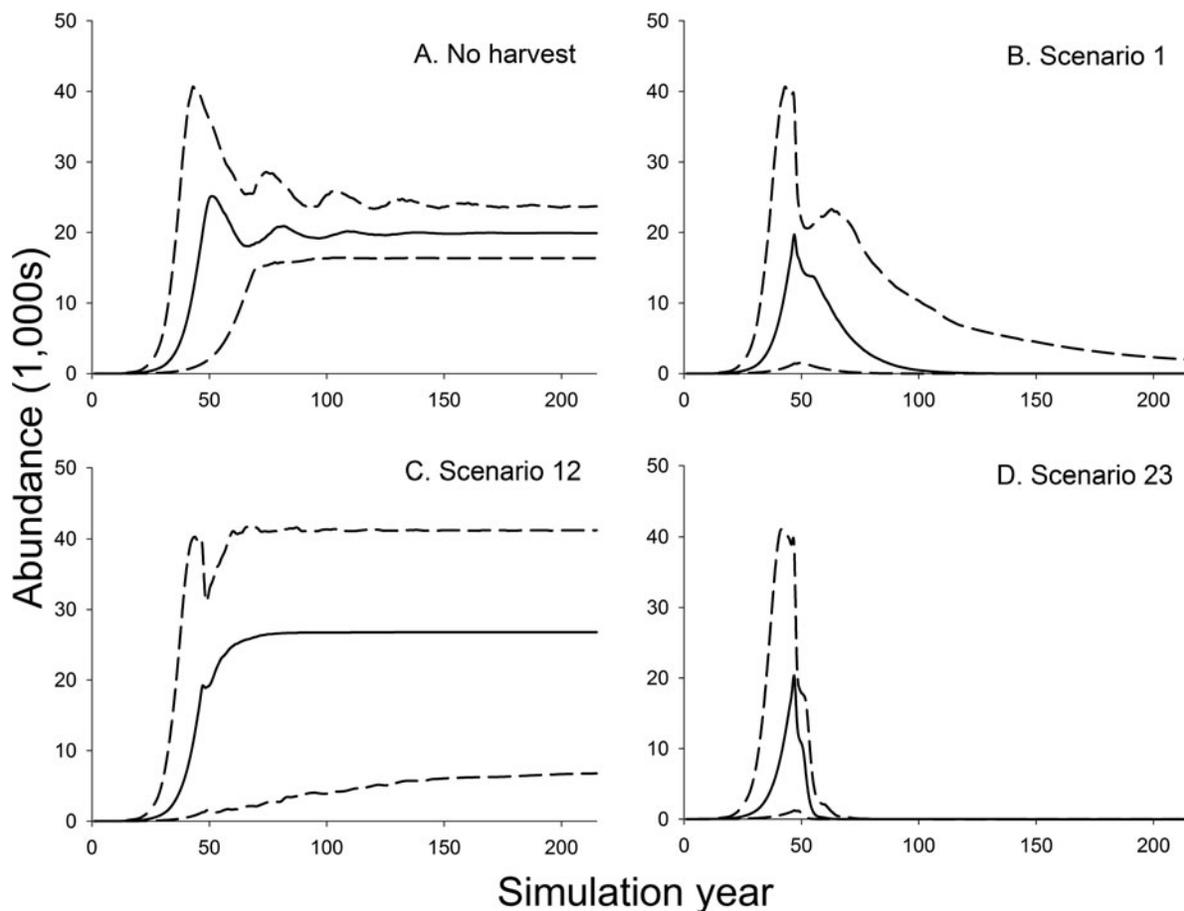


FIGURE 2. Population trajectories for Lake Trout in Swan Lake, Montana, for scenarios where (A) no harvest occurred, (B) juveniles were harvested every year (scenario 1), (C) spawners were harvested every year (scenario 12), and (D) both juveniles and spawners were harvested every year (scenario 23). Dashed lines delineate 95% CIs.

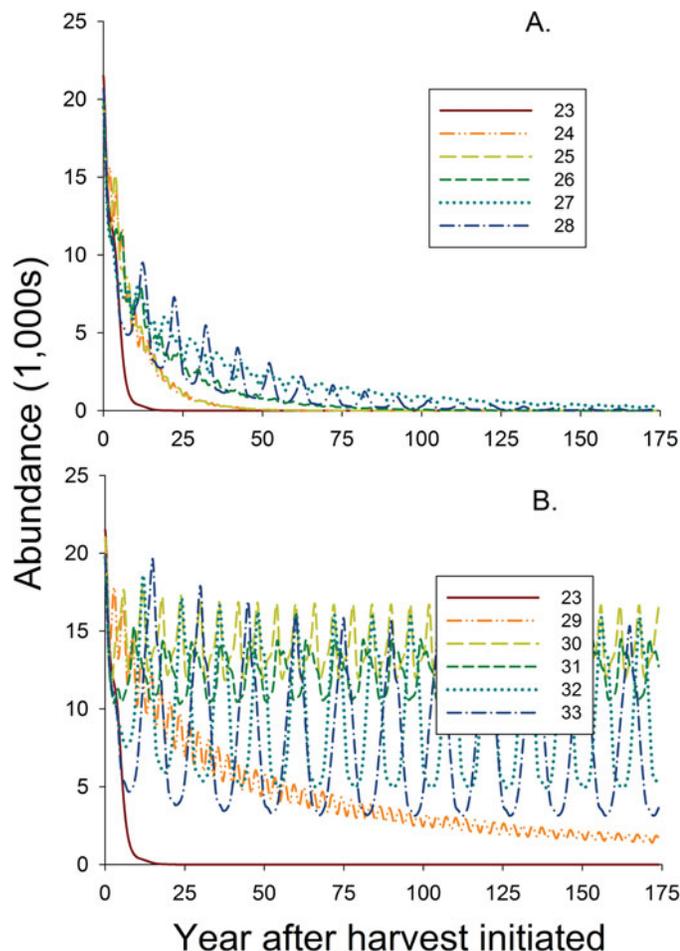


FIGURE 3. Population trajectories for Lake Trout in Swan Lake, Montana, for scenarios where juveniles and adults were harvested with (A) on and off periods of equal length and (B) off periods twice as long as on periods. Legends indicate management scenarios (Table 2). [Figure available in color online.]

population declines with time to collapse varying from 51 to 53 years (scenarios 34–36) or reductions varying from 47% (Scenario 41) to 100% (scenarios 37–40 and 42–43). Although median reductions were large for scenarios 37–40 and 42–43, lower confidence limits for reductions varied from 2% to 45%. Scenarios harvesting both juveniles and spawners during on periods and harvesting juveniles during off periods (scenarios 44–53) caused population declines with the time to collapse varying from 15 to 27 years.

Large variability existed among scenarios in the cost for a given reduction in abundance (Figure 4). For example, in 10 years the population could be reduced 69% using scenario 27 or 68% using scenario 29; the average annual cost for scenario 27 was \$63,139 versus \$42,092 for scenario 29. For most scenarios, variability in the reduction achieved (i.e., CI width) increased through the first 20 years and then decreased as time progressed (Figure 4). Scenarios that alternated harvest of juveniles only or

adults only with off periods (scenarios 2–11 and 13–22) had the highest variability.

Cumulative suppression program cost was positively associated with time to population collapse (Figure 5), indicating the most cost-effective strategy for causing collapse is to exert more effort during the first several years of the program. Collapse could not be attained in less than 15 years. Scenario 23 was the most cost-effective strategy for causing population collapse and caused collapse after 15 years of harvest for a total cost of \$1,578,480.

## DISCUSSION

Scenarios with substantially different annual costs caused similar long-term reductions in Lake Trout abundance. However, it was possible to cause the population to collapse and the total program cost was minimized when collapse occurred rapidly. We recommend that managers continue to target juveniles and spawning adults every year to cause population collapse in the shortest time frame. Had collapse not been attainable, the large amount of variation in population reductions for management scenarios (i.e., 95% CIs) would have complicated the choice of a cost-effective strategy for a long-term reduction in abundance. Nevertheless, our results indicated that certain scenarios would likely be counterproductive for reducing Lake Trout abundance in Swan Lake. The comparison of multiple competing strategies for cost-effective, long-term Lake Trout control should be useful in larger ecosystems with lower exploitation rates.

Unintended increases in abundance of harvested populations through overcompensation have been demonstrated using population models (Zipkin et al. 2009) and empirically. For example, a 7-year suppression program for Smallmouth Bass *Micropterus dolomieu* in Little Moose Lake, New York, reduced the biomass of Smallmouth Bass; however, the total abundance increased through increased recruitment (Weidel et al. 2007). When the objective is to reduce total abundance in populations with overcompensation, it may not be beneficial to remove individuals unless most of the population can be removed (Zipkin et al. 2008). Our results indicated that targeting only spawning Lake Trout is likely to be counterproductive for reducing abundance in Swan Lake. Similarly, trap-netting and angling were less effective than gill netting for suppressing Lake Trout in Lake Pend Oreille, Idaho, because they did not remove a large enough proportion of subadult fish from the population (Hansen et al. 2010). The aforementioned findings highlight the necessity of targeting the broadest range of age-classes possible with high levels of fishing mortality to cause a decrease in total Lake Trout abundance.

Exploitation rates for the Lake Trout fishery in Swan Lake were higher than levels required for gill-net fisheries in other lakes in the western USA, where the objective was to suppress Lake Trout. Model results indicated that an exploitation rate of 0.36 would cause recruitment overfishing in Lake McDonald,

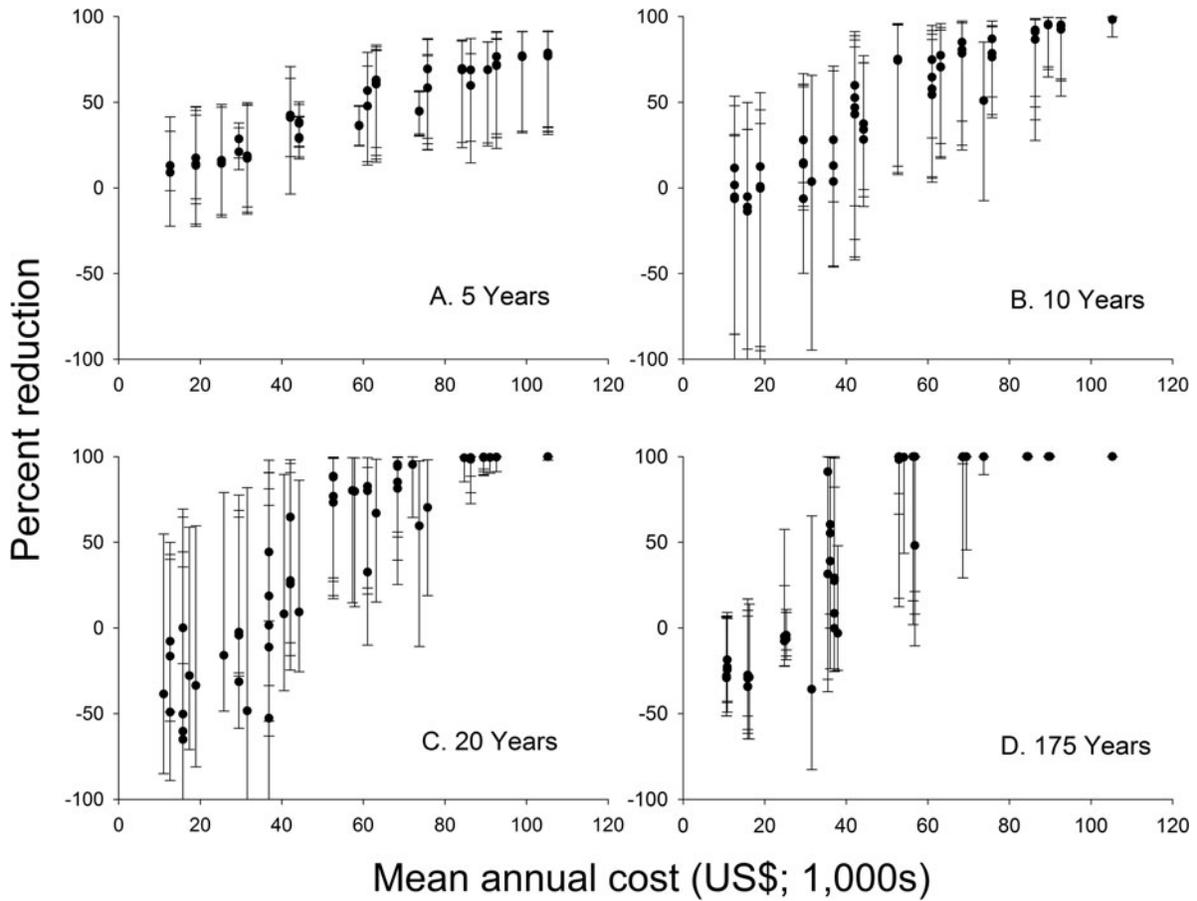


FIGURE 4. Median percent reduction in abundance of Lake Trout  $\geq$  age 1 at various time frames ([A] 5 years, [B] 10 years, [C] 20 years, and [D] 175 years) as a function of the mean annual cost for the 53 management scenarios (see Table 2). Bars delineate 95% CIs.

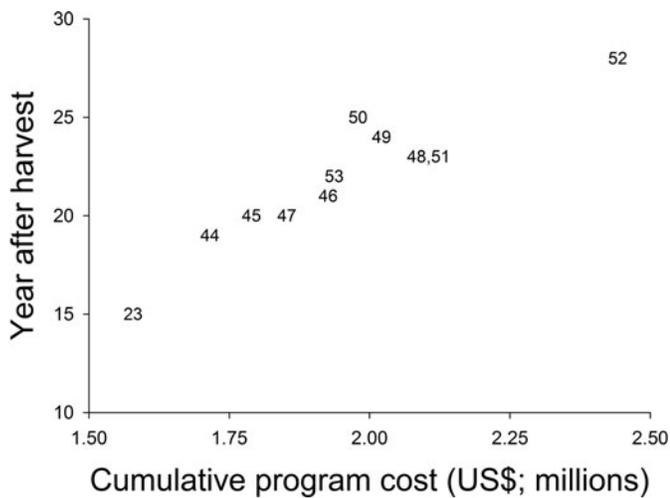


FIGURE 5. Time until 95% probability of collapse as a function of cumulative program cost for harvest scenarios (indicated by number; see Table 2) causing Lake Trout population collapse (i.e., 95% reduction relative to unharvested abundance) within 30 years in Swan Lake, Montana.

Glacier National Park (Dux 2005). Similarly, an exploitation rate between 0.31 and 0.43 was necessary to cause the decline of Lake Trout in Yellowstone Lake, Yellowstone National Park (Syslo et al. 2011), and an exploitation rate between 0.30 and 0.36 could cause a Lake Trout population collapse in Lake Pend Oreille (exploitation rates converted from  $F$  and  $M$ ; Hansen et al. 2010). Exploitation rates in this range correspond to total annual mortality rates varying from 0.39 to 0.51. Lake Trout populations throughout the native range of the species collapsed when total annual mortality was near 0.50 (Healey 1978).

A demographic model indicated that a nonnative Lake Trout population in Lake Pend Oreille could be suppressed within 24 years (20–29 years; 95% CI) using a combination of gill netting, trap-netting, and angling with observed instantaneous fishing mortality rates (0.02 for gill nets, 0.5 for trap nets, and 0.75 for angling; Hansen et al. 2010). However, gill netting alone could suppress the Lake Pend Oreille Lake Trout population in a time frame similar to Swan Lake as instantaneous fishing mortality approached 1.0 ( $\mu = 0.58$ ; Hansen et al. 2010). The level of instantaneous fishing mortality that

suppressed the population in Lake Pend Oreille was less than the level required to suppress the population in Swan Lake, likely because natural mortality in Lake Pend Oreille ( $M = 0.208$ ) was more than twice that of Swan Lake and age-specific fishery selectivity was higher for several age-classes in Lake Pend Oreille.

The small size of Swan Lake relative to other lakes in the western USA with Lake Trout suppression programs resulted in higher exploitation rates given less fishing pressure. For example, at least 25,000 100-m net-nights would result in an exploitation rate of 0.31 in 34,000-ha Yellowstone Lake (Syslo et al. 2011). In Swan Lake, a mean exploitation rate of 0.80 on juvenile Lake Trout from 2009 to 2011 resulted from an average annual effort of 289 100-m net-nights of juvenile netting. The reduced effort required relative to other lakes corresponds to a reduced cost for suppressing Lake Trout abundance. For example, the annual cost of Lake Trout suppression in Lake Pend Oreille is about \$480,000 for gill netting and trap-netting and as high as \$265,000 for angler incentives (A. M. Dux, Idaho Fish and Game, personal communication). The annual cost of using gill nets and trap nets for Lake Trout suppression in Yellowstone Lake has increased through time as annual effort has increased to comply with harvest benchmarks, and \$1.6 million will be spent on Lake Trout suppression in 2013 (T. M. Koel, National Park Service, personal communication). The total cost to suppress Lake Trout through 15 years in Swan Lake is nearly equal to 1 year of suppression in Yellowstone Lake or 2 years in Lake Pend Oreille.

Collapse is not synonymous with eradication and effectively reset the density of Lake Trout to the level present in Swan Lake 14–15 years before harvest was initiated. Therefore, suppression would have to be reinitiated unless harvest can reduce Lake Trout abundance below our collapse threshold of 1,988. Catchability may increase if fish aggregate and fishing effort is concentrated in areas where fish are most abundant (Hilborn and Walters 1992). Thus, exploitation rates may increase as Lake Trout abundance declines, particularly when targeting spawning aggregations (Erisman et al. 2011). If exploitation increases as the population declines, the actual minimum population threshold may be less than 1,988 fish. If catchability decreases with decreasing abundance (Pierce and Tomcko 2003), our minimum population threshold may be greater than 1,988 Lake Trout and the reduced efficiency may indicate that a more cost-effective strategy is to harvest when abundance exceeds a certain threshold (i.e., upper-trigger harvest; Baxter et al. 2008). Additional years of abundance and exploitation estimates may elucidate the relationship between density and catchability, allowing for estimation of the minimum Lake Trout population size attainable.

Spawner exploitation in the model may have been conservative because probability of maturity was used as a surrogate for selectivity. We assumed that female Lake Trout are only vulnerable if they spawn; however, female Lake Trout smaller than minimum length at maturity have been caught in spawner netting. We recommend the continuation of spawner netting to

refine the exploitation estimate while achieving the most rapid reduction possible.

Initiating population suppression programs in rapid response to the detection of nonnative species is likely to increase the probability of eradication; however, an understanding of the biology of the nonnative species is likely to increase the effectiveness of long-term control when immediate eradication cannot be achieved (Simberloff 2003). For populations with limited data, managers should build preliminary models to evaluate the likelihood of suppression achieving desired results (Starfield et al. 1997). Data collected through initial removal efforts can then be used to refine the model. Lake Trout removal was initiated relatively quickly after the discovery of the species in Swan Lake without sacrificing the study of Lake Trout population biology (Cox et al. 2013). Thus, we were able to evaluate the efficacy of the program to meet realistic targets for Lake Trout removal and evaluate the cost-effectiveness of removal scenarios. Our approach provides a useful case study for evaluating long-term mechanical removal options for fish populations that are not likely to be eradicated.

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