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ARTICLE

Simulated Effects of YY-Male Stocking and Manual Suppression for Eradicating Nonnative Brook Trout Populations

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Abstract
Eradication of nonnative Brook Trout *Salvelinus fontinalis* populations is difficult to achieve with standard techniques, such as electrofishing removal or piscicides; new approaches are needed. A novel concept is to stock "supermale" hatchery fish with wild conspecifics. Supermales (M_{YY}) have two Y-chromosomes, resulting in offspring that are all males; over time, successful supermale reproduction could eradicate the wild population. We constructed an age-structured stochastic model to investigate the effects of manually suppressing wild fish and stocking M_{YY} fingerlings on the long-term viability of hypothetical nonnative Brook Trout populations. In streams, an annual stocking rate of supermales equivalent to 50% of wild age-0 Brook Trout density combined with an annual selective suppression rate equivalent to 50% of wild Brook Trout density resulted in a time to extirpation of only 2–4 years if supermale fitness was equivalent to wild male fitness. However, time to extirpation in streams was 5–15 years if supermale fitness was 80% lower than wild male fitness. In alpine lakes, higher supermale stocking rates and nonselective gillnetting were required to eradicate Brook Trout populations. If supermales were assumed to be as fit as wild males, however, any supermale stocking rate greater than 49% in alpine lakes or 60% in streams achieved eradication in 10 years or less, regardless of the suppression rate. Because manual suppression and the stocking of M_{YY} fingerlings can readily be conducted at the levels assumed in our simulations, use of such an integrated pest management (IPM) approach could extirpate undesirable Brook Trout populations within reasonably short periods of time. Given the recent successful development of an M_{YY} Brook Trout broodstock capable of producing large numbers of M_{YY} fingerlings and given the positive results of the present simulations for both streams and alpine lakes, field testing of M_{YY} stocking is warranted within an IPM program that includes manual suppression for eradicating undesirable Brook Trout populations.

The historical and ongoing spread of nonnative species across the landscape poses mounting challenges for fishery managers, and perhaps no other taxa exhibit these challenges better than salmonids. The Brook Trout *Salvelinus fontinalis* was originally introduced into western U.S. waters by the U.S. Fish Commission in the late 19th century and is now common outside of its native range (MacCrimmon and Campbell 1969; Dunham et al. 2002). However, the tendency of Brook Trout to mature early and attain high densities often results in stunted populations with a high proportion of small adult fish that are undesirable to anglers (Rabe 1970; Donald and Alger 1989; Hall 1991). Furthermore, Brook Trout in western North America have been linked to the declines or extirpation of native salmonids in streams (reviewed by Dunham et al. 2004) and of native amphibians in alpine lakes (Pilliod and Peterson 2001; Knapp et al. 2007).

Brook Trout are thus increasingly targeted for removal from streams and alpine lakes across western North

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America, although eradication of established populations is difficult and rarely achieved. Chemical piscicides, such as rotenone and antimycin-A, have been used to eradicate Brook Trout in a few small streams, including Arnica Creek in Yellowstone National Park (Gresswell 1991) and Sun Creek in Crater Lake National Park (Buktenica et al. 2013). However, piscicides also kill nontarget species (Britton et al. 2011), and their use often results in incomplete removal of target populations (reviewed by Meronek et al. 1996). Similarly, electrofishing has been used to eradicate nonnative Brook Trout from short reaches of small streams (Shepard et al. 2002, 2014) but has been unsuccessful in larger streams (Thompson and Rahel 1996; Meyer et al. 2006). Moreover, the amount of effort and expense necessary to eradicate a population solely via electrofishing is usually exorbitant (Buktenica et al. 2013; Shepard et al. 2014; Pacas and Taylor 2015). This is likely due to the Brook Trout's tendency to mature early and display reduced natural mortality when subject to high exploitation—a response that diminishes the effect of removal on the population (McFadden 1961; Meyer et al. 2006). Intensive gillnetting has eradicated Brook Trout populations in a few alpine lakes (e.g., Knapp and Matthews 1998; Parker et al. 2001), although this technique may be effective only in lakes smaller than 3 ha in size (Knapp and Matthews 1998). More recently, tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*) have been used to eradicate Brook Trout in some alpine lakes, but the technique appears to be ineffective in lakes with inlets or outlets because Brook Trout continue to reside in flowing-water areas not inhabited by tiger muskellunge (Koenig et al. 2015). In the most comprehensive study to date on population effects of Brook Trout removal in alpine lakes, Hall (1991) concluded that methods designed to reduce recruitment should be evaluated because massive density reductions alone were not effective in suppressing larger populations. Collectively, these and other studies suggest that manual or chemical eradication of undesirable nonnative populations is often impractical (Britton et al. 2011) or is feasible only in small waters because in larger populations, a few individuals often survive to repopulate the system (Franssen et al. 2014; Makhrov et al. 2014). Effective management of large, complex systems requires development of alternative approaches for eliminating nonnative Brook Trout and other undesirable exotics.

One such approach could be sex-skewing methods in which anthropogenic shifting of the sex ratio toward males would reduce long-term population viability and theoretically cause extirpation of undesired populations (Hamilton 1967). Several possible variants of this concept are currently being considered for nonnative fish control, but two have been particularly well studied from a mathematical perspective (Parshad et al. 2013). The "daughterless" approach was conceived in Australia as a method for eliminating Common Carp *Cyprinus carpio* populations (Thresher 2008). This approach involves the use of a transgenic construct, and the release of such fish into the wild is highly controversial because release of a genetically modified organism (GMO) is irreversible and could result in severe negative population effects if spread to native populations (Muir and Howard 1999, 2004). A second method, the Trojan Y-chromosome (TYC) approach (Gutierrez and Teem 2006), does not rely on genetic engineering but instead involves development of a YY-male hatchery broodstock via sex reversal techniques that are already commonly used in commercial aquaculture.

The inspiration, mathematical underpinnings, and techniques required for development of a TYC program were first discussed in regard to elimination of undesirable Nile Tilapia *Oreochromis niloticus* and Asian carp populations (Gutierrez and Teem 2006; Teem and Gutierrez 2010). The methodology originally suggested was to use endogenous hormone exposure methods, which are well established in commercial aquaculture (Bye and Lincoln 1986; Piferrer 2001), to culture egg-producing YY males (feminized F_{YY} males) and subsequently release them in target waters to breed with wild XY males (Gutierrez and Teem 2006; Teem and Gutierrez 2010). Over time, this process would theoretically skew the undesirable exotic population's sex ratio to all males, with the use of F_{YY} fish speeding the process because all of their progeny in the wild would be males, half of which would be "supermales" (non-feminized M_{YY} males) that could produce even more male offspring. Modeling results have suggested that a TYC program releasing F_{YY} fish over time and ending with stocking cessation could drive an undesirable population to extirpation (Gutierrez and Teem 2006; Teem and Gutierrez 2010). More recently, a TYC program using only M_{YY} supermales has been mathematically modeled and could also theoretically cause population eradication (Parshad 2011; Parshad et al. 2013). One advantage of an M_{YY} program relative to an F_{YY} program is that it does not involve the release of hormone-treated fish; instead, the offspring of treated fish are released, which may be less concerning to the public (Bye and Lincoln 1986). Recently, a YY broodstock of Brook Trout was successfully developed with the capability of producing large numbers of M_{YY} fish for release, which could be used to potentially eradicate exotic Brook Trout populations (Schill et al. 2016).

Before a TYC stocking program with this broodstock can be implemented in the field, population simulations are needed to identify the likely range of program results and to guide field experiments. The most urgent uncertainties pertaining to the utility of TYC methods include the number of Trojan fish to be released and the duration over which they must be released into a system to eradicate the target populations (Gutierrez and Teem 2006; Stelkens and Wedekind 2010). Existing simulations suggest that use of the technique would require many decades to attain the collapse of nonnative populations (e.g., Teem and Gutierrez 2010). However, published TYC modeling studies have not included concurrent manual removal (hereafter, suppression) of the wild population as part of an integrated pest management (IPM) program (Kogan 1998). In the modeling of Common Carp eradication, an IPM approach has been predicted to be far more effective than the use of daughterless sex-skewing alone (Brown and Gilligan 2014; Thresher et al. 2014).

In general, stocked hatchery salmonids do not survive as well after release as wild fish, especially in streams (Wiley et al. 1993; High and Meyer 2009). Even if survival of stocked YY males is similar to that of wild males, the stocked males might not be as reproductively fit. For example, although stocked and wild male salmonids may display similar courtship behavior, wild males may be more aggressive and hence more likely to produce progeny (e.g., Venditti et al. 2013). Either reduced survival or poor reproductive fitness would extend the time to eradication of nonnative populations when a TYC strategy is used (Senior et al. 2013).

Our goal was to predict whether stocked supermale (M_{YY}) Brook Trout could be used in conjunction with manual suppression of wild fish to efficiently eradicate undesirable Brook Trout populations from streams and lakes in western North America. To achieve this end, we used stochastic simulation models to (1) estimate how long it would take to eradicate hypothetical wild Brook Trout populations from both streams and lakes by using only M_{YY} fish stocked at multiple rates; (2) determine how much concurrent suppression of the wild population would influence the time to extirpation; and (3) quantify how reduced fitness of stocked M_{YY} Brook Trout (in terms of survival or reproductive effectiveness) would influence the time to extirpation.

METHODS

We constructed an age-structured stochastic model to simulate the effects of a range of fishing mortality rates (imposed via manual suppression) and supermale stocking rates on the long-term viability of hypothetical wild Brook Trout populations. For stream evaluations, we parameterized the model to mimic the Brook Trout population in Hunt Creek, Michigan, during 1949–1962 (McFadden et al. 1967) because population demographics were similar to those of introduced Brook Trout in western North America (e.g., Meyer et al. 2006). In addition, population parameters for the Brook Trout in Hunt Creek were estimated over a sufficiently long period to enable estimation of interannual variation for purposes of simulating stochastic environmental variation.

Age-specific starting abundance and annual survival were estimated from age- and year-specific abundance of Brook Trout in Hunt Creek during 1949–1962 (McFadden et al. 1967: their Table 3). First, starting abundance ($n_{i=0,j}$) was set to the age-specific abundance present in Hunt Creek in 1962 (Table 1). Second, age- and year-specific annual survival ($S_{i,j}$) was estimated as the ratio of estimated abundance (n) during adjacent years (i) and ages (j) in Hunt Creek during

TABLE 1. Parameters of age-structured simulation models for nonnative Brook Trout in hypothetical 10-km streams and alpine lakes in Idaho (n_0 = age-specific starting abundance; S_j = age-specific survival; SD_S = age-specific SD of survival; f_j = age-specific fecundity; SD_f = age-specific SD of fecundity; Sel_j = age-specific relative selectivity; K = age-specific carrying capacity).

Age (years)	n_0	S_j	SD_S	f_j	SD_f	Sel_j	K
Stream model							
0	5,052	0.425	0.072	0.000	0.000	0.495	6,641
1	1,589	0.175	0.042	1.497	0.508	0.909	2,822
2	448	0.086	0.043	5.110	1.956	0.948	493
3	52	0.023	0.032	11.710	4.955	0.975	43
4	2			11.743	19.655	0.984	1
Alpine lake model							
0	1,885	0.300	0.050	0.000	0.000	0.043	1,885
1	566	0.650	0.050	1.497	0.508	0.608	566
2	368	0.650	0.050	5.110	1.956	0.831	368
3	239	0.650	0.050	11.710	4.955	0.955	239
4+	443	0.650	0.050	11.743	19.655	0.988	443

1949–1962 ($S_{i,j} = n_{i+1,j+1}/n_{i,j}$). Third, the average annual age-specific survival (S_i) and its associated interannual variation (SD_S) were estimated as the mean and SD among annual estimates of age-specific survival (Table 1).

Age-specific per capita production of age-0 Brook Trout was estimated from age- and year-specific abundance and egg production of Brook Trout in Hunt Creek during 1949–1962 (McFadden et al. 1967: their Tables 3 and 10). First, per capita age- and year-specific production of age-0 Brook Trout ($f_{i,j} = [n_{i,j}/egg_{i,j}] \times [n_{i,j=0}/egg_i]$) was estimated from age- and year-specific abundance ($n_{i,j}$), age- and year-specific egg production ($egg_{i,j}$), annual age-0 abundance ($n_{i,j=0}$), and annual total egg production (egg_i). Second, average annual and interannual variation in per capita age- and year-specific production of age-0 Brook Trout was estimated as the mean and SD among annual estimates of per capita age- and year-specific production of age-0 Brook Trout (Table 1).

The population growth rate in each year was treated as a function of year-specific total abundance and assumed carrying capacity (K; Ricker 1975). Carrying capacity for the population was set at 10,000 total fish of all ages based on a reasonable density of 1,000 total Brook Trout per stream kilometer (Peterson et al. 2004; Meyer et al. 2006) and a hypothetical stream length of 10 km (Table 1). However, it should be noted that the stream length is immaterial in study result interpretation for managers considering other stream sizes as long as the rates of manual suppression of wild fish and M_{YY} stocking are maintained at the simulated levels. The maximum population growth rate (R_{max}) for simulated populations was set at the highest net reproduction rate estimated for the Brook Trout population in Hunt Creek (R_0 = 1.878; McFadden et al. 1967: their Table 12). Population growth in each year was treated as a density-dependent function of total year-specific abundance (n_j) in relation to K (Ricker 1975):

$$n_{j+1} = n_j \times R_{max}^{\left(1-\frac{n_j}{K}\right)}.$$

Simulated fishery management actions included a range of suppression rates (via electrofishing removals) and supermale stocking rates. In practice, fish stocked in streams would be adipose fin-clipped so that they could be distinguished from wild fish during electrofishing and released. Wild fish suppression was first simulated for three rates (25, 50, and 75% of the population) in conjunction with relative age-specific selectivity (Sel_j) to electrofishing gear, as derived from typical recapture rates of marked fish during pulsed-DC mark–recapture studies in Idaho streams (Table 1; Meyer and High 2011). Next, stocking of supermale fingerlings was incorporated into the same models at three proportions (10, 25, and 50%) of the expected number of age-0 Brook Trout ($n_{j=0}$ = 6,640 fish) present at the simulated K (n = 10,000 fish) and average age-specific survival rates (S_i) of the simulated population (Table 1). Fitness (survival and reproductive success) was initially assumed to be the same for stocked M_{YY} Brook Trout as for their wild counterparts. To evaluate less-than-optimal fitness of stocked supermales relative to wild fish (Senior et al. 2013), we also simulated incremental stocking rates under an assumption that stocked fish were only 20% as fit as wild fish. For example, a stocking rate of 50% low-fitness YY males equated to a stocking rate of 10% full-fitness YY males.

Modeling of alpine lake populations was the same as for streams except that parameter values were set to mimic the abundance and survival of Brook Trout in alpine lakes (Table 1). Age-specific starting abundance and annual survival were estimated from age- and year-specific abundance of Brook Trout typical for Idaho alpine lakes. Age-specific per capita production of age-0 Brook Trout and the R_{max} for the simulated population were assumed to be the same as those in Hunt Creek during 1949–1962 (see above; McFadden et al. 1967) because no suitable time series data were available for alpine lakes. The K for the population was set at 3,500 total fish of all ages (Table 1). Levels of suppression and supermale stocking in alpine lakes were the same as for streams, but suppression in alpine lakes would require the use of lethal overnight gillnetting. Therefore, in alpine lake simulations, stocked YY males were subjected to the same suppression rates as wild fish during the years after stocking.

Model uncertainty and parameter influence were evaluated using local sensitivity analysis (Cross and Beissinger 2001; Ellner and Fieberg 2003). Each parameter was subject to deviations of ±10% while all other parameters were held at base values, as summarized in Table 1 (McCarthy et al. 1996; Essington 2003). Sensitivity of the model was expressed as the percentage difference between the mean total abundance associated with each parameter deviation and the mean total abundance associated with all parameters at base values. A parameter deviation that caused a 10% difference in simulated total abundance was considered linearly sensitive to the parameter; a parameter deviation that caused less than a 10% difference in total abundance was insensitive to the parameter; and a parameter deviation that caused greater than a 10% difference in total abundance was highly sensitive to the parameter. For each parameter deviation, the model was run for 1,000 iterations for a 50-year period.

For each water body type and each combination of suppression and supermale stocking rates, 1,000 iterations of the model were run for a 50-year period. The distribution of simulated abundance in each year over 1,000 iterations was summarized as a mean and SD. The expected abundance in each simulated year was represented as the mean, and the 95% confidence limits (CL) of uncertainty in expected abundance during each simulated year were represented as 1.96 units of the SD (lower CL = mean − [1.96 × SD]; upper CL = mean + [1.96 × SD]). Time to extirpation for each combination of removal rate and stocking rate was represented as the year in which total abundance of all age-groups declined to zero for all simulations.

To more fully evaluate the effect of stocking rate on the eradication of hypothetical Brook Trout populations, we subsequently modeled the number of years to extirpation in both streams and alpine lakes across a wider range of stocking rates than established above. For these simulations, we modeled suppression rates of 0, 25, and 50% assuming that supermales were as fit as wild fish; and then varied stocking rates from 0% to 100% in 10% increments. Assuming that supermales are only one-fifth as fit as wild fish, results from these simulations would equate to stocking rates of 0% to 500% in the poor-fitness scenario.

RESULTS

Simulated total abundance was insensitive to all model parameters except for K, which was linearly related to simulated abundance. A ±10% deviation in K induced an approximately 10% difference in total abundance, thereby indicating linear sensitivity of simulated total abundance to K (Table 2). Simulated total abundance was insensitive to perturbations in all other parameters, as ±10% deviations in those parameters caused simulated total abundance to differ by less than 3.5% from the base model.

Under the assumption that stocked supermales survived and reproduced as effectively as wild males in streams, Brook Trout could be eradicated using several combinations of supermale stocking and electrofishing suppression rates. For example, time to extirpation was 12–13 years for 10%

TABLE 2. Results of a sensitivity analysis of an age-structured simulation model for nonnative Brook Trout in a hypothetical 10-km stream in Idaho. Each parameter of the model was subject to deviations ±10% of the base value shown in Table 1, while all other parameters were held at their base values. Simulations were run for 50 years and 1,000 iterations. Results are expressed as total simulated abundance of all ages of Brook Trout in year 50 (Min = minimum; Mean = mean; Max = maximum). Mean difference is the percent difference in simulated abundance between the base and each parameter deviation. See Table 1 for parameter definitions.

Parameter	Deviation (%)	Min	−1 × SD	Mean	+1 × SD	Max	Mean difference (%)
Base	–	2,159	6,136	9,447	12,758	39,065	
R_{max}	−10	1,320	6,089	9,402	12,714	30,309	−0.5
	+10	579	6,573	9,576	12,580	21,760	1.4
K	−10	3,030	5,617	8,479	11,340	21,889	−10.3
	+10	789	7,146	10,525	13,905	33,214	11.4
n_0	−10	2,602	6,298	9,378	12,458	32,320	−0.7
	+10	2,944	6,052	9,407	12,763	42,045	−0.4
S_0	−10	3,240	6,529	9,427	12,324	24,238	−0.2
	+10	3,059	6,274	9,647	13,021	24,724	2.1
S_1	−10	2,459	6,315	9,420	12,525	26,540	−0.3
	+10	2,520	6,200	9,635	13,070	28,654	2.0
S_2	−10	659	6,227	9,462	12,697	27,789	0.2
	+10	2,339	6,159	9,483	12,807	43,757	0.4
S_3	−10	2,254	5,883	9,348	12,813	63,298	−1.0
	+10	2,107	6,312	9,386	12,460	32,933	−0.6
SD (S_0)	−10	789	6,094	9,396	12,699	33,431	−0.5
	+10	4	6,269	9,114	11,960	23,160	−3.5
SD (S_1)	−10	1,626	6,333	9,550	12,767	32,011	1.1
	+10	3,211	6,097	9,329	12,560	28,280	−1.3
SD (S_2)	−10	3,229	6,347	9,520	12,693	29,677	0.8
	+10	3,422	6,328	9,370	12,413	28,361	−0.8
SD (S_3)	−10	2,917	6,334	9,428	12,523	26,280	−0.2
	+10	2,796	6,298	9,574	12,850	27,620	1.3
f_1	−10	2,977	6,076	9,277	12,479	30,452	−1.8
	+10	2,518	6,348	9,401	12,454	26,606	−0.5
f_2	−10	0	6,199	9,500	12,801	35,731	0.6
	+10	0	6,164	9,433	12,701	38,096	−0.2
f_3	−10	360	6,310	9,510	12,709	25,084	0.7
	+10	3,109	6,309	9,283	12,256	28,745	−1.7
f_4	−10	1,298	5,902	9,570	13,238	43,978	1.3
	+10	1,786	6,177	9,186	12,196	24,524	−2.8
SD (f_1)	−10	3,212	6,387	9,521	12,656	29,461	0.8
	+10	0	5,778	9,321	12,864	45,828	−1.3
SD (f_2)	−10	2,639	6,253	9,284	12,315	24,028	−1.7
	+10	2,819	6,182	9,550	12,917	39,121	1.1
SD (f_3)	−10	2,509	6,006	9,412	12,819	41,595	−0.4
	+10	3,327	6,160	9,596	13,033	37,697	1.6
SD (f_4)	−10	3,191	6,287	9,409	12,531	28,076	−0.4
	+10	0	6,042	9,304	12,566	46,040	−1.5

supermale stocking and 50% electrofishing suppression; 25% stocking and 25% suppression; or 50% stocking and 0% suppression (Table 3). Similarly, time to extirpation was as little as 6 years for 10% supermale stocking and 75% electrofishing suppression; 25% stocking and 50% suppression; or 50% stocking and 25% suppression (Table 3). Some combinations of supermale stocking and electrofishing did not result in extirpation within 50 years, although such predictions were highly uncertain (Table 3). However, a positive aspect of the simulation findings was that uncertainty shrank to relative insignificance for scenarios in which the predicted time to Brook Trout extirpation approached

TABLE 3. Predicted number of years to extirpation and 95% confidence limits (LCL = lower confidence limit; UCL = upper confidence limit) for Brook Trout in hypothetical 10-km streams and alpine lakes in Idaho subjected to a range of selective electrofishing (streams) and nonselective gillnetting (lakes) suppression rates and supermale (M_{YY}) Brook Trout stocking rates. Predictions assumed that supermale fitness (survival and reproductive success) was equivalent to wild male fitness (good survival) or was 20% of wild male fitness (poor survival).

		Good survival			Poor survival		
Suppression rate (%)	Stocking rate (%)	Years	LCL	UCL	Years	LCL	UCL
Streams							
0	10	>50	>50	>50	>50	>50	>50
	25	>50	9	>50	>50	>50	>50
	50	12	3	12	>50	>50	>50
25	10	>50	13	>50	>50	>50	>50
	25	13	4	14	>50	>50	>50
	50	6	3	7	>50	14	>50
50	10	13	5	14	>50	15	>50
	25	6	3	7	26	8	28
	50	4	2	4	12	5	15
75	10	6	4	6	10	6	11
	25	4	2	4	7	4	8
	50	4	2	4	6	4	6
Alpine lakes							
0	10	>50	1	>50	>50	1	>50
	25	23	1	25	>50	1	>50
	50	8	1	8	>50	1	>50
25	10	>50	1	>50	>50	1	>50
	25	14	1	15	>50	1	>50
	50	8	1	8	>50	1	>50
50	10	20	1	23	>50	1	>50
	25	10	1	10	>50	1	>50
	50	7	1	8	18	1	21
75	10	11	1	13	25	1	30
	25	7	1	8	16	1	19
	50	6	1	7	11	1	12

the shorter time durations of interest to management (Figure 1).

When stocked supermales were assumed to be only one-fifth as fit as wild males in streams, Brook Trout could be eradicated only by using high rates of supermale stocking with or without concurrent electrofishing suppression. For example, wild Brook Trout were not eradicated by (1) any supermale stocking rate when used with a 25% or lower electrofishing suppression rate or (2) a 25% or lower supermale stocking rate combined with a 50% suppression rate in poor-fitness scenarios (Figure 2). Eradication was only achieved in 10 years or less by annually removing 75% of the wild population through electrofishing and by stocking supermales at a rate of 10% or higher, although a stocking rate of 50% and a suppression rate of 50% eradicated the population in 12 years (Table 3).

For alpine lakes, when supermales were assumed to survive and reproduce as effectively as wild males, Brook Trout could be eradicated using several combinations of supermale stocking and gill-net suppression, although the time to extirpation was longer than that in streams. For example, time to extirpation was 8–11 years at 10% supermale stocking and 75% gillnetting suppression; 25% stocking and 50% suppression; and 50% stocking and 25% suppression (Table 3). Population eradication was achievable in 10 years or less only at (1) a supermale stocking rate of 50% or greater (regardless of the suppression rate) or (2) a supermale stocking rate of 25% and a suppression rate of 50% or greater (Figure 2; Table 3).

Under the assumption that supermales were one-fifth as fit as wild males in alpine lakes, Brook Trout could only be eradicated by using very high rates of supermale stocking and gill-net suppression. For example, Brook Trout were

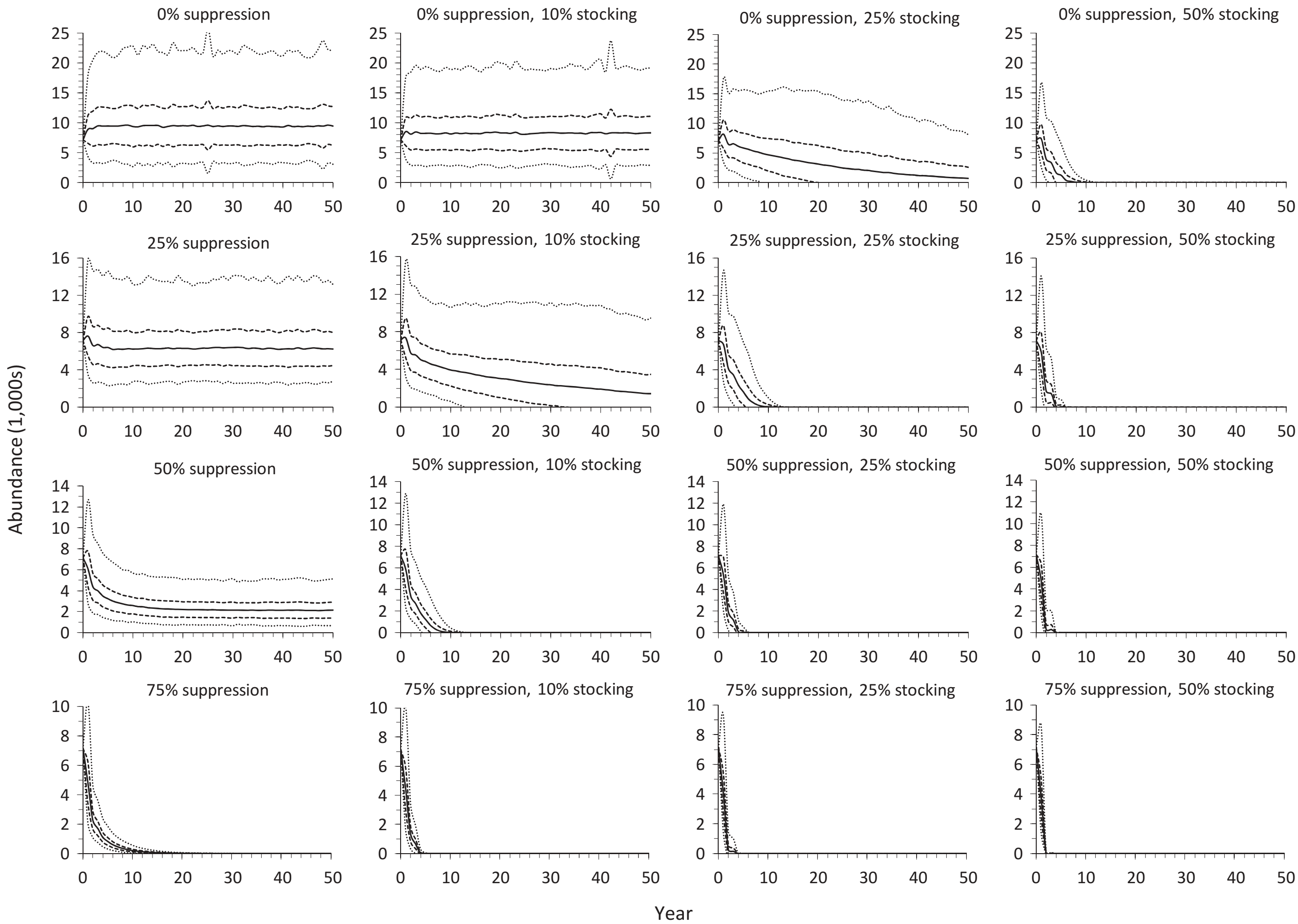

FIGURE 1. Simulated abundance of Brook Trout (mean [solid line]; ±1 SD [dashed lines]; ±1.96 SD [dotted lines]) in a hypothetical 10-km Idaho stream subjected to a range of electrofishing suppression rates (first row of panels = 0%; second row = 25%; third row = 50%; fourth row = 75%) and supermale (M_{YY}) Brook Trout stocking rates (first column of panels = 0%; second column = 10%; third column = 25%; fourth column = 50%). Simulations assumed that supermale fitness (survival and reproductive success) was equivalent to that of wild males (good survival).

only eradicated by a suppression rate of 75% (regardless of stocking rate) or when both the stocking rate and the suppression rate were at least 50% (Table 3). Eradication was not achievable within 10 years in alpine lakes at any of the initial combinations of suppression and stocking rates when we assumed that stocked supermales were 80% less fit than wild fish (Table 3).

Across a broader range of potential stocking rates, the suppression rate influenced the number of years to extirpation for hypothetical Brook Trout populations more dramatically in streams than in alpine lakes. For example, reducing suppression in streams from 50% to 25% would require more than a doubling of the supermale stocking rate to maintain a 10-year eradication time frame, whereas in alpine lakes, the same reduction in suppression would require only a 40% increase in supermale stocking rate to maintain a 10-year eradication time frame (Figure 3). When supermales were presumed to be as fit as wild males, any stocking rate greater than 50% in alpine lakes or greater than 60% in streams achieved eradication in 10 years or less, regardless of the suppression rate.

DISCUSSION

Our simulation results mimic those of many field studies in which the use of manual suppression alone often failed to eradicate Brook Trout in stream segments longer than 5 km. In both alpine lakes and stream simulations, only 2 of 16 initial simulation scenarios relying solely on manual suppression (i.e., no supermale stocking) resulted in population extirpation; both of those scenarios required 75% suppression rates sustained for more than a decade—a level of effort that would be difficult to maintain. Electrofishing removal in even

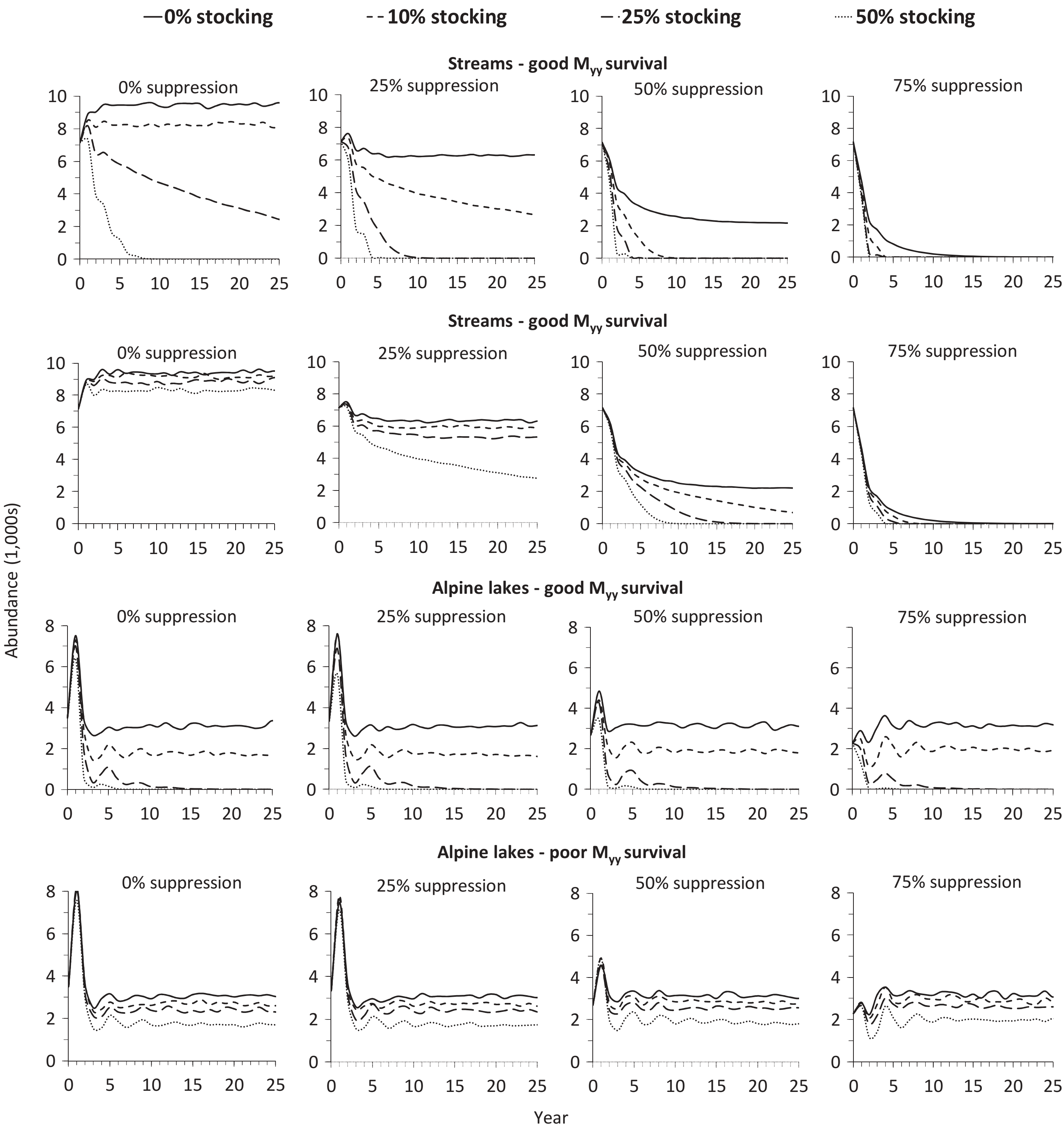

FIGURE 2. Simulated abundance of Brook Trout in hypothetical 10-km streams and alpine lakes in Idaho subjected to a range of selective electrofishing (streams) and nonselective gillnetting (lakes) suppression rates and a range of supermale (M_{YY}) Brook Trout stocking rates. Simulations assumed that supermale fitness (survival and reproductive success) was equivalent to wild male fitness (good survival) or was 20% of wild male fitness (poor survival).

moderate-sized streams is often unsuccessful (Thompson and Rahel 1996; Meyer et al. 2006), and intensive gillnetting removal is usually unsuccessful in all but small alpine lakes (Hall 1991; Knapp and Matthews 1998; Parker et al. 2001). Manual suppression of Brook Trout populations could be sustained indefinitely to protect sympatric native species,

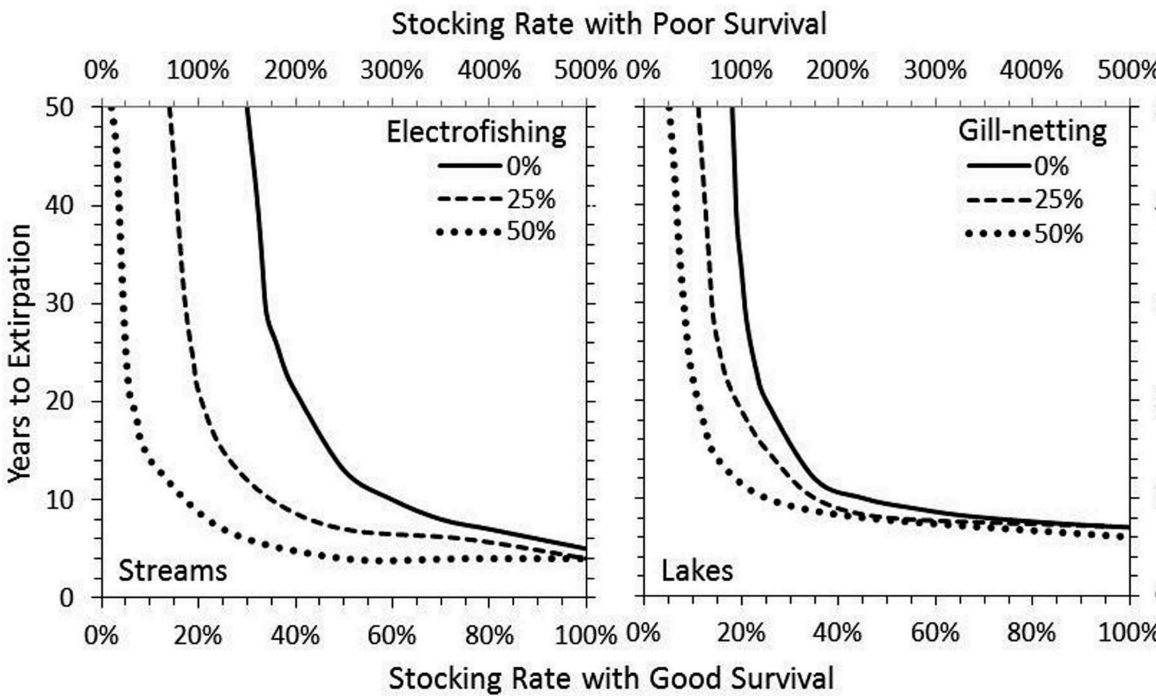

FIGURE 3. Predicted number of years to extirpation in all simulations for Brook Trout in hypothetical 10-km streams (left panel) and hypothetical alpine lakes (right panel) subjected to a range of selective electrofishing (streams) and nonselective gillnetting (lakes) suppression rates and a range of supermale (M_{YY}) Brook Trout stocking rates. Simulations assumed that supermale fitness (survival and reproductive success) was equivalent to wild male fitness (good survival; lower *x*-axis) or was 20% of wild male fitness (poor survival; upper *x*-axis).

despite little or no chance of nonnative population eradication (Peterson et al. 2004, 2008). However, such efforts have been described as quixotic enterprises (Meyer et al. 2006), and we believe that the manpower and high fiscal costs required to merely suppress undesirable exotic Brook Trout populations in perpetuity would hinder meaningful progress in native fish restoration across a larger landscape.

The present findings also agree with past simulation studies predicting that the stocking of M_{YY} fish in a TYC program could eradicate wild nonnative fish populations. However, in contrast to our findings, others have consistently found that many decades would be required to eradicate populations (Gutierrez and Teem 2006; Teem and Gutierrez 2010; Parshad et al. 2013). For example, in a simulation study evaluating the release of F_{YY} Asian carp, 50–170 years were needed to eradicate a population, depending on the stocking rate (Teem and Gutierrez 2010). A more recent study reported that a TYC approach was slightly more efficient than a "daughterless" transgenic construct for eradicating Common Carp, but it still found that extirpation using either method would take decades (Teem et al. 2014). Such slow responses are unlikely to be acceptable to fishery managers or the public (Thresher 2007) and may partly explain why management interest in the TYC approach has been limited to date.

Responses predicted by previous studies were slower than our predictions for several reasons. First, previous studies generally modeled low (4–7%) stocking rates of reproductively competent adults (Gutierrez and Teem 2006; Teem and Gutierrez 2010; Parshad 2011; Teem et al. 2014), whereas we modeled fingerling stocking rates as high as 100% of the existing wild fish while assuming that the stocked supermales were as fit as wild males. Such stocking rates are feasible for many undesirable Brook Trout populations in western North America, and our results demonstrate the importance of stocking at higher rates to quickly eradicate populations. Second, Brook Trout have a shorter generation time than most other nonnative fish species, thereby making them more vulnerable to sex-skewing eradication methods (Cotton and Wedekind 2007; Thresher et al. 2014). Third, no prior TYC simulation studies have included concurrent manual suppression as part of an IPM program. Although TYC and daughterless approaches are quite different in their design and ecological implications, both involve skewing the wild population's sex ratio. Simulation studies of the daughterless eradication method have predicted that the stocking of fish with sex-skewing characteristics, if conducted in concert with suppression of a wild population at even a low to moderate intensity, would markedly shorten the time to eradication (Bax and Thresher 2009; Thresher et al. 2014).

From a management perspective, Brook Trout extirpation in our study was possible within reasonable time frames for hypothetical populations in both streams and alpine lakes. For example, in streams, when supermale fitness was assumed equal to wild male fitness, a 50% supermale stocking rate in conjunction with a 50% suppression rate resulted in a time to extirpation of only 4 years. A single electrofishing run removes about 50% of the Brook Trout in small streams (Meyer and High 2011), and 5,000 stocked supermale fingerlings would meet the targeted 50% stocking rate for our hypothetical 10-km stream. Stocking of more costly, larger catchable-sized trout (~250 mm TL) at such levels is relatively common in Idaho streams and other western streams. Therefore, our results suggest that sufficient suppression and fingerling stocking levels can be readily imposed on wild stream-dwelling Brook Trout populations at the 10-km scale to eradicate undesirable populations. If the above predictions are accurate, Brook Trout eradication in shorter stream lengths would be considerably easier to accomplish. For example, an equivalent IPM effort for a 5-km reach would require half as much electrofishing effort and half as many M_{YY} fish (2,500) for stocking annually. Eradication in larger stream drainages may be feasible with such a program as long as wild fish suppression rates and M_{YY} stocking rates are maintained at the levels we simulated. Managers desiring to attempt an IPM eradication in longer streams need only use the same scaling approach as described above while considering electrofishing manpower constraints and hatchery production capacity and costs.

In the past, successful eradication has either relied on piscicides (e.g., Gresswell 1991), which are increasingly scrutinized in many states, or on electrofishing short stream reaches (<4 km) requiring numerous removal passes each year for several years (Kulp and Moore 2000; Shepard et al. 2002, 2014). We are unaware of any successful salmonid eradication effort in a stream longer than 5 km that has relied solely on electrofishing. If Brook Trout eradication is possible using the IPM approach simulated here, then the development and use of stocked YY fish could represent a meaningful step forward in the eradication of undesired nonnative Brook Trout.

Our simulations suggest that longer times to extirpation and higher stocking rates would be needed to eradicate Brook Trout from alpine lakes compared to streams, in part because Brook Trout mature later and live longer in lakes than in streams, which slows the demographic input of successful M_{YY} spawning in the wild population. Additionally, lethal overnight gillnetting removes some supermales from lakes, whereas supermales are not killed with selective electrofishing removals in streams. In an IPM program, manual suppression substantially reduces the time to extirpation, but the targeted harvesting of only wild fish results in a much shorter response (Bax and Thresher 2009). A likely reason for the relative insensitivity of our alpine lake results to suppression rates above 40% was the use of nonselective gill nets, as stocked YY males would also be killed at the same high rates as wild males. If early field trials indicate that stocked YY males experience adequate survival and effectively reproduce, future workers could compare simulation results from nonlethal netting approaches (e.g., modified trap nets) that would allow for selective wild fish removal.

While our results indicate that the stocking of supermales in lakes is likely to be successful, other methods, such as piscicides, may be faster and thus more desirable, although the downside is the risk to nontarget species. Use of piscicides (e.g., rotenone) can be risky in alpine lakes because of the long time required for adequate detoxification of low-flow outlet streams with potassium permanganate.

Our predictions of Brook Trout population response to M_{YY} stocking could be overly optimistic, particularly if the fitness of stocked YY males is lower than we simulated. Incorporating poor M_{YY} fitness into the simulations resulted in predicted times to extirpation that might not be practical for management. Hatchery-reared trout stocked into wild trout populations experience higher mortality than their wild counterparts (Needham and Slater 1944; Miller 1954), and it is conceivable that the survival rates of stocked M_{YY} fish could be well below those we assumed at the highest stocking densities evaluated, particularly those in the low-fitness simulations for alpine lakes. However, hatchery trout survival, though poor, is typically much higher when trout are stocked in lakes than in streams, regardless of fish size at stocking (Wiley et al. 1993). Most previous TYC simulation studies have generally assumed that stocked YY fish persist and mate with equal efficiency as wild fish (Gutierrez and Teem 2006; Teem and Gutierrez 2010; Parshad 2011), whereas we modeled both equivalent and much poorer fitness of hatchery supermales. Fecundity of stocked F_{YY} was more important than the probability of mating or relative offspring survival for eradicating nonnative mosquitofish *Gambusia* spp. populations (Senior et al. 2013). However, our proposed TYC approach relies on the release of only sperm-producing M_{YY} fish, so that result regarding the importance of fecundity is not applicable. The limitation of any TYC strategy could be poorer survival of stocked supermale fish compared to that of wild fish (Cotton and Wedekind 2007), but this may vary greatly among species and stocking environments. Field evaluations of supermale survival relative to their wild counterparts would provide invaluable information for future studies of the efficiency of any TYC program.

Although survival or reproductive effectiveness of stocked fingerling M_{YY} Brook Trout may be lower than that of wild fish, such an outcome is not a certainty. Suppression of wild Brook Trout could lead to increased survival of stocked supermales. For example, survival of stocked Rainbow Trout *Oncorhynchus mykiss* fry increased 2.5-fold when 30% of potential predators were manually removed from an Idaho stream (Horner 1978). Similarly, fingerling and larger hatchery Cutthroat Trout *O. clarkii* survived poorly when stocked into stream reaches already populated by wild trout, but survival was about two-thirds greater when resident wild trout were removed (Miller 1955). In alpine lakes, stocked Brook Trout M_{YY} fingerlings may benefit from increased age-0 survival and an associated recruitment pulse like those consistently found in California alpine lakes after sustained wild Brook Trout removal via gillnetting (Hall 1991). The twofold to fivefold recruitment increase following multiyear gill-net exploitation rates of 40–60% in California alpine lakes was attributed to less cannibalism and reduced competition (Hall 1991). Furthermore, in many streams and nearly all alpine lakes, stocked fingerling Brook Trout will far exceed wild fish in size at age, which should be beneficial in agonistic encounters with wild conspecifics (Petrosky and Bjornn 1984).

Several important assumptions are inherent in our simulation approach. First, we assumed that the long-term Hunt Creek data set from the midwestern USA suitably represented stochasticity in western Brook Trout waters; this assumption was necessary because no similar data exist for streams or alpine lakes in western North America. Second, we assumed that population growth was a density-dependent function of abundance and K in a logistic population growth model (Ricker 1975). More specifically, we assumed that the progeny: parent ratio was equal among spawners for both M_{YY} and wild fish when incorporating YY genetic material. Third, as in all other TYC simulation studies, we assumed that genetic sex always determined phenotypic sex and that all phenotypes were stable after sexual maturation (e.g., Parshad et al. 2013). Environmental factors, including water temperature and water chemistry, or social factors (e.g., population density) can influence phenotypic sex in some species during sexual differentiation (e.g., Luckenbach et al. 2009). However, Brook Trout, like other salmonids, are determinate gonophores with primary germ cells that transition directly to one sex or the other (Sacobie and Benfey 2005). The species should therefore be reasonably refractory to phenotypic sex change (Yamamoto 1969), although we are not aware of any study that has directly evaluated the stability of phenotypic sex in Brook Trout. Last, we assumed that each spawning pair only mated with each other and that a given pairing produced all the progeny from a given female—in other words, a YY male spawning with an XX female would produce 100% XY Brook Trout. Although such exclusive mating behavior is unlikely, our results would be robust to violation of this assumption if the behavior of less-successful males, such as "sneaker" males (Morita et al. 2009), is similar between supermales and wild fish.

Study assumptions aside, an M_{YY} release program has several advantages over other technological approaches to nonnative fish control. First, the M_{YY} approach does not involve genetic engineering to produce a GMO (Senior et al. 2015), as GMOs are typically viewed with suspicion by the general public (Cotton and Wedekind 2007). Sex reversal and associated manipulations inherent in a TYC approach are species specific and involve a simple reassortment of pre-existing sex chromosomes among individuals; therefore, the manipulations can be readily halted or reversed with the cessation of M_{YY} stocking (Cotton and Wedekind 2007; Senior et al. 2015). These features influence the degree of public acceptability and presumably explain why the TYC approach, among the various "genetic" eradication approaches, is considered the least likely to generate public controversy (Thresher et al. 2014). Although not an advantage of this approach relative to other genetic approaches, it is worth noting that the amount of hormone released into the aquatic environment for development of the existing YY Brook Trout broodstock is inconsequential and is exceeded by the natural release of the same natural hormone into a stream by a single pregnant woman in 7–21 d, depending on the levels removed by secondary sewage treatment (Schill et al. 2016). For an additional perspective, a single domestic cow releases 0.7 g of estrogenic compounds annually into the environment (Lange et al. 2002), which is nearly 50 times more than that required to create the entire existing broodstock of YY Brook Trout.

To date, the TYC approach for any species has been entirely theoretical, and an empirical field test of the approach has yet to be conducted (Wedekind 2012; Makhrov et al. 2014). Given the successful production of a YY Brook Trout broodstock that can be used to generate large numbers of M_{YY} fish for stocking (Schill et al. 2016) and given the results of the present simulations, field testing is needed to determine whether M_{YY} stocking can be used to eradicate undesirable Brook Trout populations. The first step in such a program should seek to determine whether stocked M_{YY} Brook Trout initially survive to spawn and successfully reproduce (Cotton and Wedekind 2007; Wedekind 2012). Such an effort began during August 2014, when M_{YY} Brook Trout were released in segments of four central Idaho streams containing exotic Brook Trout as part of a TYC pilot study.

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