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Patrick Allen Kennedy
State of Idaho

Kevin Meyer
Government of the State of Idaho

Daniel J. Schill
Government of the State of Idaho

Matthew R. Campbell
Idaho Department of Fish and Game

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Survival and Reproductive Success of Hatchery YY Male Brook Trout Stocked in Idaho Streams

Patrick A. Kennedy,* Kevin A. Meyer, and Daniel J. Schill
Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

Matthew R. Campbell and Ninh V. Vu
Idaho Department of Fish and Game, 1800 Trout Road, Eagle, Idaho 83616, USA

Abstract
Nonnative Brook Trout *Salvelinus fontinalis* were introduced throughout western North America in the early and mid 1900s, resulting in populations that are difficult to eradicate and that often threaten native salmonids. Male YY Brook Trout (M_{YY}), created in the hatchery by feminizing XY males and then crossing them with normal XY males, comprise a novel approach to eradicating undesirable Brook Trout populations. If stocked M_{YY} Brook Trout survive and reproduce with wild females, it could eventually drive the wild population sex ratio to 100% males, at which point the population would be unable to reproduce and would be eradicated after stocking ceased. In this study, we stocked the limited number of catchable-size (mean TL = 229 mm) M_{YY} hatchery Brook Trout available from an established M_{YY} broodstock into four streams. In two streams, the wild Brook Trout population was suppressed via electrofishing prior to stocking to determine whether diminished competition with wild fish would increase the survival of hatchery M_{YY} fish. We used genetic assignment testing to identify the successful reproduction of stocked M_{YY} fish. Apparent survival of M_{YY} Brook Trout averaged 18% in streams with wild population suppression (mean suppression, 17%) and 9% in streams without suppression, suggesting that suppression of the wild population before stocking increased M_{YY} survival poststocking. Hatchery M_{YY} Brook Trout comprised an estimated 3.1% of all adult Brook Trout during spawning. Genetic assignment tests identified successful reproduction of M_{YY} fish in all streams in which they were stocked, with an average of 3.7% of fry being the progeny of M_{YY} fish. Our results confirm that hatchery M_{YY} fish stocked in streams can survive and spawn successfully with wild fish and produce all-male progeny. Despite the slightly reduced fitness of M_{YY} Brook Trout, this technology may be a viable method for eradicating undesirable nonnative Brook Trout populations.

Brook Trout *Salvelinus fontinalis* were originally introduced in western U.S. waters, which are outside their native range, by the U.S. Fish Commission in the early 1900s (MacCrimmon and Campbell 1969; MacCrimmon et al. 1971) and continue to colonize new habitats in western North America (Dunham et al. 2002). Nonnative Brook Trout populations have negatively impacted native fish populations through hybridization, competition, and predation (reviewed in Dunham et al. 2004). Consequently, fisheries managers have worked to suppress or eliminate nonnative Brook Trout populations using a variety of methods. For example, piscicides have been used with some success (Gresswell 1991; Lee 2001; Lentsch et al. 2001; Hepworth et al. 2002), but they have the drawback of negatively affecting native fish populations (Britton et al. 2011) and other aquatic fauna (Hamilton et al. 2009; Billman et al. 2012) and are increasingly being restricted in some U.S. states (J. Carter, Arizona Game and Fish, personal communication). Multiple-pass electrofishing has also been used to physically remove Brook

*Corresponding author: pat.kennedy@idfg.idaho.gov
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Trout from streams (e.g., Thompson and Rahel 1996; Meyer et al. 2006; Shepard et al. 2014); the results have been mixed, however, and it has been questioned whether stream electrofishing removal by itself can make meaningful progress in Brook Trout eradication at the landscape scale (Schill et al. 2017). Most recently, tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*) have been introduced into alpine lakes and have successfully eradicated Brook Trout in some (but not most) of them (Koenig et al. 2015). The mixed success of these methods identifies the need for additional methods for nonnative fish eradication.

One method, suggested decades ago for eradicating undesirable fish populations, is shifting the population sex ratio toward all males (Hamilton 1967). In this scenario, shifting the sex ratio over time could be accomplished by annual introductions of hatchery-produced male fish with a YY genotype (M_{YY}) to eliminate females, eventually resulting in population eradication (Gutierrez and Teem 2006; Teem and Gutierrez 2010). To create an M_{YY} broodstock, XY males are feminized by exposing them to estrogen. After being reared to maturity, the resulting XY neo-females are crossed with normal XY males and, on average, one-quarter of the subsequent progeny will be M_{YY}. Then, by exposing half of the M_{YY} fish to estrogen at an early age, an M_{YY} and F_{YY} broodstock can be created, and all their progeny are M_{YY}. These M_{YY} progeny can then be stocked into wild fish populations and theoretically drive the sex ratio to 100% males (Parshad 2011). Although YY fish culture is occasionally used in commercial hatcheries (e.g., Mair et al. 1997; Liu et al. 2013), a stocking program utilizing YY fish has not yet been tested in the wild to eradicate a nonnative fish species (Wedekind 2012, in press).

Under such a program, sex ratios in wild Brook Trout populations would only shift if the M_{YY} Brook Trout survive and successfully reproduce after stocking. Hatchery trout encounter many challenges upon their release into the wild, and due to several factors often exhibit low survival, especially in streams (e.g., Miller 1952; Bettinger and Bettoli 2002; High and Meyer 2009). Low survival in streams is largely attributed to the stress of adjusting to natural stream flows, coupled with starvation and competition with resident fish (Schuck 1948; Miller 1958; Hochachka and Sinclair 1962). Competition with wild resident fish has been identified as a major factor contributing to the low survival of hatchery trout in streams (Miller 1954). Though rarely evaluated, past studies suggest manual removal (hereafter, "suppression") of wild fish prior to stocking hatchery M_{YY} fish could markedly improve survival of the stocked hatchery trout (Miller 1958; Horner 1978). In addition, the success of an M_{YY} stocking program requires that the M_{YY} fish mature at a high rate and spawn at a similar time as wild fish, and that the testes and milt of M_{YY} fish perform similarly to those of their wild counterparts. Existing research suggests that sex-reversed fish have reduced reproductive abilities relative to wild males (e.g., Senior et al. 2014), but for the progeny of sex-reversed fish no such reduction has been identified (e.g., Salirrosas et al. 2017). Currently, the physiological performance of stocked M_{YY} Brook Trout relative to wild males (as determined by sperm quality) is uncertain.

The Idaho Department of Fish and Game (IDFG) developed an M_{YY} Brook Trout broodstock for experimental use in eradicating undesirable wild Brook Trout populations (Schill et al. 2016). However, before broad-scale stocking evaluations are undertaken, a preliminary evaluation of postrelease survival and reproductive success in the wild was desired. During 2014, a limited number (n = 2,000) of catchable-size M_{YY} Brook Trout were available for stocking. The objectives of this study were to (1) evaluate the postrelease survival and reproductive success of M_{YY} Brook Trout, (2) assess whether reducing competition with wild Brook Trout would improve the survival and reproductive success of M_{YY} Brook Trout, and (3) evaluate the spawn timing, maturity, and sperm motility of M_{YY} Brook Trout in the hatchery and in the wild and compare them with those of wild Brook Trout.

METHODS

Study area.— This study was conducted in the Big Lost River basin in south-central Idaho, where trout are not native but where wild Rainbow Trout *Oncorhynchus mykiss* and Brook Trout are well established (Gamett 2003). The four study streams were Wildhorse, Bear, Iron Bog, and Cherry creeks. These study streams were selected because they were known to contain wild Brook Trout populations.

Two treatments were implemented in this study: (1) at suppression stream reaches (Wildhorse and Bear creeks), wild Brook Trout were removed via electrofishing before stocking to create vacant habitat for M_{YY} fish; and (2) at nonsuppression stream reaches (Iron Bog and Cherry creeks), M_{YY} fish were stocked without first suppressing the wild population.

Hatchery M_{YY} production and rearing.— At the Ashton Fish Hatchery, IDFG staff feminized male Brook Trout fry with estrogen (in the form of 17β-estradiol) to create an adult broodstock of M_{YY} Brook Trout (for complete details, see Schill et al. 2016). The M_{YY} Brook Trout evaluated in this study were produced by crossing F_{YY} and M_{YY} broodstocks in November 2013. Subsequent fry were reared to catchable size (203–254 mm total length) at the Mackay Hatchery in outdoor concrete raceways in 10–12°C single-use spring water until the time of release. On June 17, 2014, lengths and weights from 100 M_{YY} Brook

Trout were recorded at Mackay Hatchery prior to stocking; fish averaged 229 mm (range, 148–300 mm; Figure 1) and 130 g in weight (35–295 g), and had an average relative weight of 92.9 (69.8–136.9). All M_{YY} fish were adipose fin–clipped prior to stocking so they could be differentiated from wild Brook Trout during subsequent stream sampling.

Stream evaluations.— Just prior to stocking, the abundance of wild Brook Trout was suppressed in the treatment reaches in Bear and Wildhorse creeks using single-pass backpack electrofishing over an average reach length of 2.3 km (Table 1). Electrofishing crews consisted of 2–3 people with electrofishers, depending on stream flow and habitat (e.g., beaver dams) and 2–3 people with nets and buckets. We used a pulsed-DC waveform operated at 40–60 Hz, 350–900 V, and a 1–6-ms pulse width. During suppression efforts, individuals with electrofishers covered all available habitats throughout the treatment reach, moving methodically upstream. All captured salmonids were measured to the nearest millimeter. Wild Brook Trout captured in the suppression streams were euthanized with a lethal dose of anesthetic. Salmonids other than Brook Trout comprised less than 1% of the total catch among all treatment reaches; they were released alive and not included in any of our analyses. During suppression, dissections were conducted to phenotypically estimate the sex ratios of 145 and 82 wild Brook Trout ≥150 mm in Bear and Wildhorse creeks, respectively.

TABLE 1. Treatment and physical details of the 2-km treatment reaches established in four study streams.

Stream	Treatment	Reach slope (%)	Mean elevation (m)	Reach length (km)
Bear Creek	Suppression	3.4	2,067	1.9
Cherry Creek	Nonsuppression	1.5	1,969	2.4
Wildhorse Creek	Suppression	2.4	2,296	2.6
Iron Bog Creek	Nonsuppression	3.6	2,280	2.4

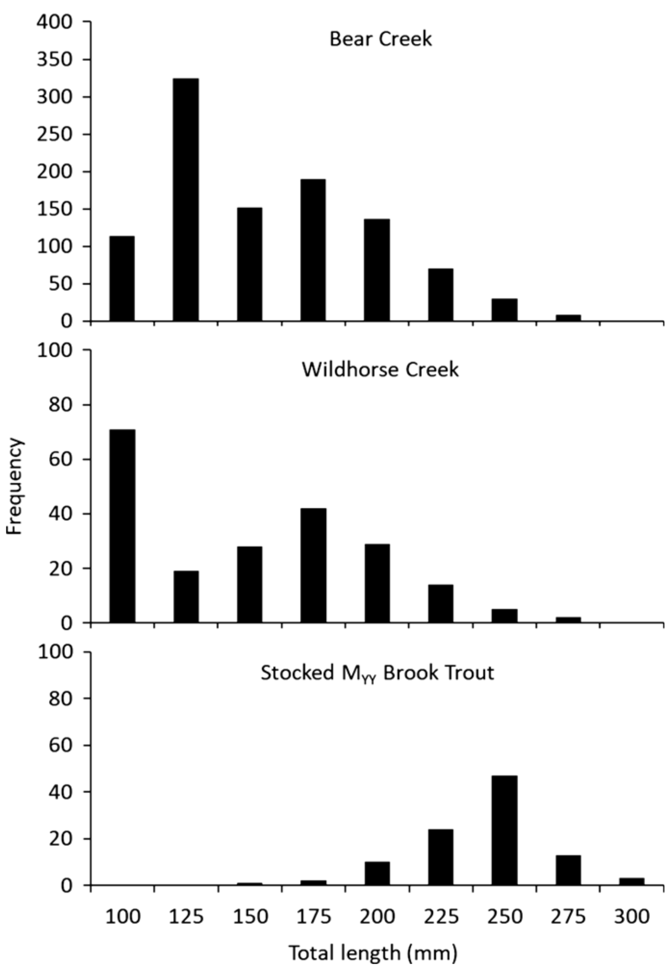

FIGURE 1. Length-frequency histograms of wild Brook Trout removed from Wildhorse and Bear creeks in June 2014, and catchable-size M_{YY} Brook Trout stocked into the four study streams immediately afterwards.

On June 26–27, 2014, approximately 500 (range, 492–512) M_{YY} Brook Trout were evenly dispersed throughout the treatment reach of each study stream (Table 2). During October 6–15, 2014, mark–recapture electrofishing surveys were conducted within each treatment reach to estimate the abundance of wild (≥100 mm only) and M_{YY} Brook Trout. Two separate 300-m survey sites were randomly selected within each treatment reach. One to seven days prior to the recapture effort, wild and M_{YY} Brook Trout were captured using electrofishing within the survey sites in each stream, anesthetized, measured to the nearest millimeter, marked using a hole-punch in the caudal fin, and released back into the stream after recovery from the anesthesia.

The Fisheries Analysis+ software package (Montana Fish, Wildlife and Parks 2004) was used to estimate wild and M_{YY} Brook Trout abundance separately, using the modified Peterson estimator. For wild Brook Trout, separate abundance estimates were calculated for the smallest length groups possible (usually 25 mm), having at least three recaptured fish per length group in order to satisfy model assumptions; since the M_{YY} fish were all very similar in length and the sample size was low, they were not broken down into length groups prior to population estimation. We assumed that there was (1) no mortality of marked fish between the marking and recapture passes and (2) no movement of marked or unmarked fish out of the survey site between the marking and recapture runs.

TABLE 2. Stocking rates and estimates of angler exploitation, emigration, and apparent survival of M_{YY} Brook Trout stocked in 2-km treatment reaches in four study streams. Dashes indicate that confidence intervals (CIs) could not be estimated.

		Angler exploitation		Emigration		Apparent survival	
Stream	M_{YY} Brook Trout stocked	Rate (%)	90% CI	Rate (%)	90% CI	Rate (%)	90% CI
Bear Creek	492	0.0	0.0	2.4	2.3	24.8	23.6
Cherry Creek	500	0.0	0.0	0.5	0.6	9.6	–
Wildhorse Creek	506	27.5	16.0	0.2	–	10.3	4.9
Iron Bog Creek	512	22.0	14.4	2.0	1.3	8.6	8.0

We used the simple random sampling formulas in Scheaffer et al. (1996) to estimate population totals (with associated 90% confidence intervals [CIs]) for each stream.

During the October mark–recapture surveys, single-pass electrofishing was also conducted 300 m above and below each treatment reach in each study stream to characterize the poststocking emigration of M_{YY} Brook Trout out of the treatment reaches. Unadjusted emigration rates were calculated as the number of M_{YY} Brook Trout emigrants captured outside the treatment reach, divided by the number of M_{YY} Brook Trout stocked into the treatment reach. This estimate was adjusted by dividing it by the single-pass capture efficiency (number of marked fish recaptured divided by the number of fish marked) for M_{YY} Brook Trout in the mark–recapture surveys. Variances for the proportions in the individual streams were calculated following the formulas in Fleiss (1981:13–17). Since computing adjusted emigration rates involved dividing a proportion by another proportion, variance estimates for adjusted emigration were computed using the approximate formula for the variance of a ratio in Yates (1980). Because emigrants clearly may have moved more than 300 m outside of the stocking reach, our estimates of emigration should be regarded as minimum values.

The unadjusted survival of M_{YY} Brook Trout was estimated by dividing the abundance of M_{YY} Brook Trout within the treatment reach in October by the number stocked in June 2014. Apparent survival was calculated by subtracting the emigration rate from the unadjusted survival estimate.

To evaluate angler exploitation of M_{YY} trout after stocking, approximately 10% (n = 50) were tagged (prior to stocking) using 70-mm (51 mm of tubing) fluorescent orange–green T-bar anchor tags (Dell 1968). The tags were labeled with "IDFG" and the tag reporting phone number on one side, with the unique tag number on the reverse side. Anglers could report tags using the IDFG "Tag!You're-It!" phone system and Web site, as well as at regional IDFG offices or by mail (for details, see Meyer et al. 2012). We assumed that anglers reported 41% of these tags (K. A. Meyer, unpublished data) to calculate angler exploitation through 4 months after stocking. We followed the methods in Meyer and Schill (2014) to estimate 90% CIs around the estimates of exploitation.

Genetic analyses.— In 2014, tissue samples were collected from M_{YY} Brook Trout at the hatchery and from wild Brook Trout at each study stream to assess the magnitude of genetic differences and the associated ability to genetically differentiate the two groups. To determine whether M_{YY} Brook Trout successfully reproduced in the wild, approximately 100 tissue samples were collected from Brook Trout fry (<90 mm) at each treatment reach in October 2015. Fry were sampled at multiple locations over the entire treatment reach to minimize family effects (Whiteley et al. 2012). These fry had to be the progeny of either wild M_{XY} or hatchery M_{YY} males that had spawned the prior fall, and we sought to identify paternity using the methods described below.

Tissue samples were clipped from the caudal fins and preserved in vials filled with 100% ethyl alcohol; all tissue samples were genotyped. DNA was extracted from all samples using the Nexttec Genomic DNA Isolation Kit from XpressBio (Thurmont, Maryland). All samples were screened with a 240–single nucleotide polymorphic (SNP) locus panel. The panel included loci described in Sauvage et al. (2012) and loci identified and developed from restriction site–associated DNA sequencing (Columbia River Inter-Tribal Fish Commission, unpublished data; and IDFG, unpublished data). Primer and allelic information for all of the loci used in this study are available at FishGen.net (Marker Set = IDFG Salvelinus fontinalis GTseq v1.0_240). Genotyping followed Genotyping in Thousands Sequencing (GTseq) protocols developed by Campbell et al. (2015). The power of genetic assignment tests depends largely on the level of genetic differentiation between populations, with high statistical certainty observed (99.9%) with $F_{ST} \geq 0.15$ (Manel et al. 2002).

Putative first-generation (F_1) progeny from M_{YY} Brook Trout were identified using STRUCTURE version 2.3.3 (Pritchard et al. 2000). STRUCTURE was used to estimate individual membership coefficients assuming an admixture model, uncorrelated allele frequencies, and no population priors. Under the admixture model, STRUCTURE estimates a membership coefficient (Q) that represents the proportion of an individual's genome that is assigned to a predetermined number of clusters (K). We assumed that $K = 2$, corresponding to progeny from either wild or M_{YY} Brook Trout. A total of 50,000 Markov chain–Monte Carlo samples were drawn after discarding the first 10,000 iterations. For comparison purposes, we created simulated F_1 progeny between known M_{YY} Brook Trout and wild individuals and used their admixture proportions as criteria for assigning juveniles as F_1 progeny between M_{YY} and wild females. Confidence intervals (90%) were estimated around the proportion of M_{YY} progeny in each population and for all fry samples combined, following the small-proportion formula in Fleiss (1981).

M_{YY} spawn timing and maturity rates.— At Mackay Hatchery in 2014, we retained 100 M_{YY} Brook Trout through November 6 in an outdoor uncovered circular tank, in 10–12°C single-use spring water, to estimate peak ripeness timing and the maturation rate. From October 9 through November 6, 20 M_{YY} Brook Trout were randomly selected each week and examined for ripeness by attempting to express milt. Males were classified as ripe if milt was expressed from the vent as the abdomen was depressed. After examination for ripeness, fish were placed in a lethal bath of anesthetic. Necropsies were conducted to determine whether each fish was mature. Fish were identified as mature by the presence of enlarged white testes. In 2016, we again evaluated maturity rates and ripeness ($n = 113$) under the same conditions as in 2014, except that necropsies for maturity were not conducted until October 26.

To evaluate whether the M_{YY} maturity rates previously estimated in the hatchery (in the absence of females) differed from those in the wild, in August 2016 we released 598 M_{YY} fish in the East Fork Big Lost River. This river is near the other study streams (mean distance, 18.9 km) and Mackay Hatchery (16.4 km) and was known to contain wild Brook Trout. On October 18, 2016, M_{YY} and wild Brook Trout were captured from the stream via electrofishing and examined for ripeness and maturity as described above. Sperm motility was also investigated from M_{YY} and wild Brook Trout captured from the stream. Milt was extracted from live fish into a 10-mL beaker by gently squeezing the abdomen. Milt (0.5–1.0 mL) was transferred to a microscope slide with a clean, disposable pipette. A cover slip was placed over the milt, then a 0.25-mL drop of saline solution was added at the side of the cover slip to activate the milt (Billard et al. 1995). Within 15 s of the time the milt was extracted from the live fish, it was examined under a 40× compound microscope and motility was characterized as either motile or not motile by the observation of active sperm movement under magnification.

Maturity and ripeness were summarized as percent mature and ripe, respectively. Confidence bounds were calculated following the small-proportion formula in Fleiss (1981).

RESULTS

During suppression efforts, we removed a total of 1,026 wild Brook Trout from the Bear Creek study reach and 210 from the Wildhorse Creek reach (Table 3). The removed fish were of similar size in the two reaches (Bear Creek: mean = 145 mm, range = 33–290 mm; Wildhorse Creek: mean = 140 mm, range = 68–254). Dissections of wild Brook Trout ≥150 mm to estimate phenotypic sex ratios for the wild population identified that 57% (90% CI, 49–64%) of the fish in Bear Creek were males and that 38% (29–47%) in Wildhorse Creek were males.

In October there were an estimated 266 M_{YY} Brook Trout and 8,361 wild Brook Trout (≥100 mm) in all treatment reaches combined, so that M_{YY} fish comprised approximately 3.1% of the Brook Trout ≥100 mm (wild males and females and hatchery M_{YY} fish) present in the treatment reaches (Table 3). The estimated abundance of wild Brook Trout in October was much higher in the Bear Creek treatment reach (3,064) than in the treatment reaches of the other three study streams (mean = 1,766). The estimated abundance of M_{YY} Brook Trout was also considerably higher in Bear Creek (122) than in the other three study streams (mean = 48).

Using these abundance estimates and assuming that there was no mortality of wild fish from June to October, M_{YY} fish were stocked at an average rate of about 26% (range = 16–39%) of the wild Brook Trout population abundance across all study reaches (Table 3). Moreover, the removals in June constituted an estimated 25% and 9% suppression of the wild populations in the Bear and Wildhorse Creek study reaches, respectively.

Emigration and angler exploitation appeared to have only a limited effect on M_{YY} Brook Trout abundance in the treatment reaches. Emigration was rare, averaging only 1.3% and ranging from 0.2% in Wildhorse Creek to 2.4% in Bear Creek (Table 2). Angler exploitation rates varied across the study streams. Bear and Cherry creeks had zero estimated angler exploitation of M_{YY} fish, whereas M_{YY} exploitation was an estimated 27.5% in Wildhorse Creek and 22.0% in Iron Bog Creek. No catch and release of M_{YY} fish was reported via angler tag returns.

The apparent survival of M_{YY} fish averaged 13.3%, ranging from a high of 24.8% in Bear Creek to a low of 8.6% in Iron Bog Creek (Table 2). Survival averaged 17.5% at suppression streams and 9.1% at nonsuppression streams, suggesting that the suppression of wild Brook Trout improved the survival of M_{YY} Brook Trout.

TABLE 3. Summary of Brook Trout suppression and October abundance estimates within the 2-km treatment reaches at four study streams. Dashes indicate that confidence intervals (CIs) could not be estimated.

	Wild Brook Trout			M_{YY} Brook Trout		
	June removal	October abundance		June stocking	October abundance	
Stream	Number	Estimate (>100 mm)	90% CI	Number	Estimate	90% CI
Bear Creek	1,026	3,064	553	492	122	116
Cherry Creek	0	1,847	216	500	48	–
Wildhorse Creek	210	2,146	301	506	52	25
Iron Bog Creek	0	1,304	233	512	44	41

TABLE 4. Summary of examinations of M_{YY} Brook Trout at Mackay Hatchery in 2014 and 2016 to estimate peak spawn timing.

Date	Number examined	Percent ripe
2014		
Oct 9	20	25
Oct 16	20	60
Oct 23	20	85
Oct 30	20	80
Nov 6	20	75
2016		
Sep 28	113	28
Oct 5	113	35
Oct 12	112	87
Oct 19	104	87
Oct 26	79	77

In 2014, the peak spawn timing of hatchery-held M_{YY} fish (n = 100) was estimated to be about October 23 (Table 4). A strong majority (84%; 90% CI, 77–92%) of M_{YY} Brook Trout retained at the hatchery matured by late October or early November. In 2016, weekly examinations of an additional subset of fish at the hatchery (n = 113) identified peak ripeness between October 12 and 19. Necropsies (n = 113) showed that 96% (92–99%) matured over the duration of the study in 2016. Evaluations of wild (n = 15) and M_{YY} Brook Trout (n = 71) captured by electrofishing from the wild on October 18 identified that 96% (91–100%) of M_{YY} and 47% (22–71%) of wild Brook Trout were mature. Motile sperm were identified in 99% and 100% of mature M_{YY} and wild male Brook Trout, respectively.

In 2015, we collected tissue samples from an average of 96 (range, 93–100) Brook Trout fry from each of the four study streams for genetic assignment tests (Table 5). Expected heterozygosity (H_E) using the 100 SNP loci was generally high for wild Brook Trout, averaging 0.38 (range, 0.36–0.40) across all study populations. The sample of M_{YY} Brook Trout exhibited lower H_E (0.21). Genetic differentiation as measured by F_{ST} among wild and M_{YY} Brook Trout was large, averaging 0.31 (range, 0.23–0.34).

Altogether, 382 tissue samples were obtained from Brook Trout fry from the four study streams combined. Tissue samples from M_{YY} Brook Trout and wild individuals collected prior to stocking were classified into their respective clusters with high membership coefficients (Q > 0.95; Table 5). Simulated F_1 progeny assigned similarly to both clusters, with an average membership coefficient ranging from 0.49 to 0.53. Stocked M_{YY} Brook Trout successfully reproduced with wild females in each of the study streams, with 14 of the 382 fry tissue samples being assigned as F_1 M_{YY} progeny; all 14 individuals identified as F_1 progeny were also identified as genetic XY males. Therefore, M_{YY} progeny comprised 3.7% (90% CI, 2.3–5.8%) of the combined age-0 Brook Trout year-class across all study streams. The progeny of M_{YY} Brook Trout comprised 3.2% (1.0–8.4%), 4.3% (1.6–9.9%), 2.1% (0.5–7.0%), and 5.0% (2.1–10.6%) of all fry at Bear, Cherry, Iron Bog, and Wildhorse creeks, respectively.

DISCUSSION

Across all of the study streams, the M_{YY} Brook Trout that were stocked comprised an estimated 3.1% of all fish ≥100 mm that were present in the study reaches in 2014, and M_{YY} fish produced an estimated 3.7% of the progeny in those reaches that year. While these findings demonstrate that hatchery M_{YY} Brook Trout can successfully compete reproductively with wild male conspecifics in streams, they do not indicate that M_{YY} fish were more successful reproductively, since only a portion of the wild Brook Trout were males. In the Bear and Wildhorse Creek study reaches, where phenotypic sex ratios were determined for wild fish, M_{YY} fish comprised an estimated 6.3% of the Brook Trout males ≥100 mm and they produced 4.1% of the progeny that year, suggesting that M_{YY} fish were slightly less reproductively successful than their wild conspecifics. Because wild adult abundance was estimated for all fish larger than 100 mm, even this characterization of M_{YY} reproductive success would be inflated if a

TABLE 5. Proportional membership of five sample groups of Brook Trout used to identify successful M_{YY} progeny over two treatment levels in four study streams. For each sample group, the life stage, sample year, sample size, and expected heterozygosity (H_E) are given.

Stream	Treatment	Sample group	Life stage	Sample year	Sample size	H_E	Proportional membership		
							Min	Max	Avg
Bear Creek	Suppression	Pretreatment	Fry	2014	44	0.40	0.001	0.101	0.012
		M_{YY} Brook Trout	Adult	2015	69	0.21	0.984	0.999	0.998
		Simulated F_1 progeny	–	–	10	–	0.423	0.600	0.521
		Not detected as M_{YY} progeny	Fry	2015	92	0.42	0.001	0.110	0.011
		Detected as M_{YY} progeny	Fry	2015	3	–	0.456	0.554	0.509
Cherry Creek	Nonsuppression	Pretreatment	Fry	2014	33	0.40	0.002	0.054	0.010
		M_{YY} Brook Trout	Adult	2015	69	0.21	0.989	0.999	0.997
		Simulated F_1 progeny	–	–	10	–	0.412	0.602	0.513
		Not detected as M_{YY} progeny	Fry	2015	89	0.40	0.002	0.326	0.014
		Detected as M_{YY} progeny	Fry	2015	4	–	0.417	0.552	0.500
Iron Bog Creek	Nonsuppression	Pretreatment	Fry	2014	43	0.39	0.001	0.058	0.008
		M_{YY} Brook Trout	Adult	2015	69	0.21	0.987	0.999	0.997
		Simulated F_1 progeny	–	–	10	–	0.285	0.523	0.423
		Not detected as M_{YY} progeny	Fry	2015	92	0.39	0.001	0.243	0.014
		Detected as M_{YY} progeny	Fry	2015	2	–	0.405	0.644	0.525
Wildhorse Creek	Suppression	Pretreatment	Fry	2014	123	0.36	0.002	0.230	0.013
		M_{YY} Brook Trout	Adult	2015	69	0.21	0.986	0.999	0.996
		Simulated F_1 progeny	–	–	10	–	0.251	0.606	0.421
		Not detected as M_{YY} progeny	Fry	2015	95	0.36	0.002	0.175	0.011
		Detected as M_{YY} progeny	Fry	2015	5	–	0.359	0.606	0.480

low proportion of the male Brook Trout between 100 and 149 mm were mature (Meyer et al. 2006). We did not estimate size at maturity for wild Brook Trout, but if we assume that males become sexually mature at 150 mm (Meyer et al. 2006) and limit the abundance estimate to fish greater than 150 mm, then M_{YY} fish comprised 9.6% of all spawning male Brook Trout at the Bear and Wildhorse study reaches combined, and produced 4.1% of the progeny. Regardless of their exact reproductive success, our results suggest that M_{YY} Brook Trout were not as reproductively fit as their wild conspecifics, which is not surprising since hatchery trout generally exhibit lower reproductive fitness than wild trout (Araki et al. 2008). This has largely been attributed to the lower survival of hatchery fish (Wiley et al. 1993), but agonistic competition with wild males and lower reproductive success (Schroder et al. 2010; Venditti et al. 2013) may also be important factors.

Uncertainty regarding the reproductive performance of stocked M_{YY} Brook Trout relative to wild Brook Trout led us to directly examine their spawn timing, maturity, and sperm motility in both the hatchery and the wild. Our findings indicate that M_{YY} Brook Trout raised to catchable size had maturity, ripeness, and sperm motility rates comparable to, if not higher than, those of wild fish. This suggests that the deficiencies in reproduction that we observed for M_{YY} Brook Trout are attributable to some behavioral factor rather than to reproductive physiology.

Schill et al. (2017) simulated eradication times for unwanted wild Brook Trout populations under various M_{YY} stocking, wild suppression, and M_{YY} fitness scenarios, and their results suggest that under a number of reasonable scenarios eradication might occur as quickly as 10 years or less. In our study, (1) the M_{YY} stocking rate averaged 27% and the suppression of the wild Brook Trout populations averaged 17%; (2) M_{YY} survival averaged 9% in nonsuppressed streams and 18% in suppressed streams; and (3) M_{YY} reproductive fitness was apparently slightly reduced (perhaps by 50%) relative to that of wild fish. While it is tempting to use the results in Schill et al. (2017) to predict how long eradication would take in our study streams, we avoid that for several reasons. Most importantly, Schill et al. (2017) simulated eradication times using fingerling hatchery fish rather than catchable-size fish, and survival, size at maturity, reproductive fitness, and other important population metrics are obviously not equivalent between the two size-classes. Second, the results from Schill et al. (2017) stem from simulated populations for which the entire population was treated, whereas our streams were not isolated and only a small portion of each stream was stocked with M_{YY} fish. Moreover, wild Brook Trout from outside our study reaches may have recolonized the vacated habitat in our suppression streams, diminishing any positive benefit to the stocked M_{YY} fish. Thus, eradication times predicted from our results would likely be very misleading. However, the purpose of this study was not to eradicate wild Brook Trout but rather to evaluate the survival and reproductive success of hatchery M_{YY} fish released into the wild. Studies are under way to empirically evaluate Brook Trout eradication times in Idaho streams and alpine lakes and to determine how size at stocking, stocking rate, and suppression rate affect eradication (e.g., Kennedy et al. 2018).

Although rarely evaluated, the survival of hatchery trout can be improved through the suppression of wild fish (Miller 1958; Horner 1978). In these two studies, hatchery survival was improved by 66–150% when wild trout were removed. In our study, M_{YY} survival averaged 9% in nonsuppression streams but 18% in suppression streams, which is concurrent with the results of the above-noted studies. However, even in nonsuppression streams M_{YY} Brook Trout survival was comparable to that of wild Brook Trout in Rocky Mountain streams (Meyer et al. 2006) and higher than is often reported for stream-stocked hatchery catchable-size Rainbow Trout (e.g., Miller 1952; Dillon et al. 2000; High and Meyer 2009).

The survival of M_{YY} Brook Trout was reduced only slightly by emigration, but was reduced to a greater degree by exploitation, though only for two of the four study streams. As mentioned above, our estimates of M_{YY} emigration should be considered minimum estimates because we did not search the entire stream for migrants. The majority of studies on movement by hatchery trout in small streams suggest, however, that poststocking movement tends to be minimal. For example, 88% of the stocked Rainbow Trout in a Michigan stream exhibited little movement (<1.2 km) from the stocking location (Cooper 1953); 75% of reported catches of hatchery Rainbow Trout, Brook Trout, and Brown Trout *Salmo trutta* in a Virginia stream were within 1 km of their stocking locations (Helfrich and Kendall 1982); and 66% of stocked catchable Rainbow Trout were captured within a few hundred meters of their stocking location in an Idaho stream (Heimer et al. 1985). As all of our study streams are located on public property with well-developed roads and in two cases there are campgrounds near the study reach, we anticipated some angler exploitation of the stocked M_{YY} fish. Nevertheless, our results suggest that most of the postrelease loss of hatchery M_{YY} Brook Trout was due to natural mortality.

When considering an M_{YY} stocking program to eradicate undesirable fish, a key question is the size of hatchery fish that will be most effective. Rearing fish to fry or fingerling size is much less expensive than rearing them to catchable size and requires less hatchery space, but postrelease survival is typically much lower (Wiley et al. 1993). For our study, there were several advantages to stocking catchable-size M_{YY} Brook Trout. First, nearly all of the M_{YY} fish that we stocked were ready to spawn in the first year, and their spawn timing was in synchrony with the wild Brook Trout at our study streams. Thus, the hatchery fish only had to survive a few months in the stream before they could potentially produce progeny. Second, the catchable-size fish had a competitive size advantage over most of the wild trout, which may have increased their survival (Hochachka and Sinclair 1962; Xu et al. 2010). Third, size has been identified as an advantage during agonistic behavior between hatchery and wild trout (Petrosky and Bjornn 1988), so stocking catchable-size M_{YY} Brook Trout may have increased their spawning success. As noted, the primary disadvantages to raising fish to catchable size are the expense and rearing space required, which could reduce the number of populations that an M_{YY} stocking program could treat. Furthermore, if the undesirable fish population were in a remote lake, catchable-size fish would require helicopter stocking, which is more expensive than stocking from fixed-wing aircraft or packing fish in backpacks.

Other, less understood genetic processes, such as the stability of phenotypic sex, could thwart the ability of M_{YY} fish to eradicate invasive species. As sex ratios in a population become more skewed toward males, individuals that are able to produce female progeny could be strongly selected for (Thresher 2007). For example, density-dependent or growth-induced sex changes have been reported in exploited Lake Herring *Coregonus artedii* populations in Lake Superior (Bowen et al. 1991)—though it should be noted that this study is not without limitations and provided no genetic evidence. The ability to avoid mating with individuals with specific genotypes has been demonstrated in other vertebrates (e.g., Manser et al. 2015) and other mechanisms for favoring a particular genetic trait also have been reported (Moen et al. 2007). In fact, some birds can directly influence the sex ratio of a population by producing biased sex ratios in progeny (Komdeur et al. 1997). Whether such genetic processes could emerge in a Brook Trout population with a highly skewed sex ratio is currently unknown and can only be determined empirically. If such genetic processes occur in invasive fish species, the application of multiple methods for eradication (i.e., integrated pest management; Kogan 1998), including extensive electrofishing, may be necessary to overcome such counter-selective pressures (Thresher 2007).

Management Implications

To our knowledge, this experiment represents the first time that hatchery-produced M_{YY} fish of any species have been released into the wild. The study documents that catchable-size M_{YY} Brook Trout persisted long enough after stocking to spawn successfully with wild fish and that all of their progeny were XY males. Thus, this study represents an important advance toward the use of M_{YY} Brook Trout for the eradication of undesirable nonnative Brook Trout populations where they threaten native species or provide unsatisfactory fisheries for anglers.

Despite these encouraging results, biologists should consider a number of factors before implementing an M_{YY} stocking program to eradicate undesirable Brook Trout populations, assuming that an M_{YY} broodstock or their hatchery progeny can be produced or obtained. Assuming that the purpose of such a program will most often target native species conservation, we first recommend that the treated population (either in a stream or in a lake) be isolated, because Brook Trout are known to readily invade upstream and downstream habitat (Adams et al. 2000, 2001). While long-term maintenance stocking of M_{YY} fish could suppress the abundance of wild Brook Trout in a connected population (similar to maintenance electrofishing; see Peterson et al. 2008), such a program could be indefinite and might provide little to no conservation benefit to the native species. However, this is not to suggest that an M_{YY} stocking program be limited to isolated headwater streams, and it has been demonstrated mathematically that such a program could work in a larger, dendritic riverine system (Gutierrez et al. 2011).

Second, consideration must be given to stocking M_{YY} fish in waters where Brook Trout are sympatric with native salmonids. For example, it has been well documented that Brook Trout competitively displace native Cutthroat Trout *O. clarkii* when the two species are in sympatry (reviewed in Dunham et al. 2002). Brook Trout also negatively impact native Bull Trout *S. confluentus* populations via direct competition (McMahon et al. 2007) or by reproducing with them, creating sterile hybrids (Leary et al. 1993). Since stocking M_{YY} Brook Trout would inherently result in short-term increases in the total Brook Trout abundance, and likely the abundance of wild Brook Trout as well, this could intensify (at least in the short term) any negative ecological impacts that a sympatric Cutthroat or Bull Trout population was already experiencing. Nevertheless, we do not believe that these examples should discourage biologists from considering an M_{YY} stocking program where nonnative Brook Trout are sympatric with native salmonids. On the contrary, we feel that this is a question that needs direct investigation because such a program may still be more feasible, cost-effective, and (in the long term) beneficial than other Brook Trout eradication efforts, such as the use of piscicides or mechanical removal.

In streams, we suggest that at least one pass of electrofishing be conducted to suppress the wild Brook Trout population before annual M_{YY} Brook Trout stocking is done. One pass will often remove ~50% of the wild population (Meyer and High 2011), creating (at least temporarily) unoccupied habitat that will likely improve the survival of the stocked M_{YY} hatchery fish. However, many existing Brook Trout stream removal projects employ three or more electrofishing passes annually without achieving complete eradication. The efficacy of an M_{YY} program may be enhanced where these large efforts are in-progress.

While higher M_{YY} stocking rates are associated with faster eradication of the wild population (Schill et al. 2017), excessive stocking may reduce poststocking M_{YY} survival via density dependence. We thus recommend that stocking rates be commensurate with suppression rates, but we also encourage additional research on wild suppression and M_{YY} stocking rates. By marking M_{YY} Brook Trout before stocking (e.g., with adipose fin clips), all of the M_{YY} fish stocked in previous years can be selectively released during suppression efforts. Finally, as mentioned above, the most cost-effective target release size for M_{YY} Brook Trout (or other species, for that matter) is not known, and we consider this an important question needing direct evaluation. Considering that most of the factors we have addressed focus on stream stocking scenarios, consideration of alpine lake treatment strategies is ripe for further research regarding the use of M_{YY} fish, including investigations of suppression strategies, stocking rates, and poststocking M_{YY} survival.

Finally, for workers considering M_{YY} programs in the United States, it is important to note that development of an M_{YY} broodstock involves the use of hormones and is thus overseen and permitted by the U.S. Food and Drug Administration. The U.S. Food and Drug Administration approved the release of M_{YY} broodstock progeny into the wild for this study.

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