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Comparing growth and body condition of wild and hatchery M_{YY} brook trout in streams and alpine lakes

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Abstract

Biologists have theorized that stocking YY males (created via in-hatchery hormonal sex-reversal and selective breeding; hereafter M_{YY} fish) could be used to eradicate unwanted non-native vertebrate populations, but little is known about the fitness of M_{YY} individuals once released into the wild. We compared growth and body condition of stocked hatchery-reared M_{YY} brook trout (*Salvelinus fontinalis* Mitchell) to wild conspecifics in two streams and two alpine lakes. Maximum age for wild fish was age 6 at one stream and age 4 or 5 at the remaining waters, whereas for hatchery M_{YY} fish, maximum age was age 5 at one stream and age 4 at the remaining waters. Total length ranged from 103 to 359 mm for wild brook trout and 115 to 353 mm for hatchery M_{YY} brook trout. Growth rates and body condition of stocked M_{YY} brook trout did not differ from wild fish in the same waters. Given that the success of M_{YY} eradication programs is primarily contingent upon M_{YY} individuals having fitness characteristics similar to wild conspecifics, our results provide further evidence that the stocking of hatchery-reared M_{YY} fish may be a viable tool for eradicating unwanted non-native fish populations.

KEYWORDS
fitness, hatchery trout, integrated pest management, nonnative, stream salmonids, supermales

1 | INTRODUCTION

Non-native fishes are considered one of the greatest threats to native freshwater fish populations worldwide (Gozlan et al., 2010). Negative effects of exotic fish on native fish populations include hybridization, predation, competition, habitat modification, and disease transmission (Fausch, 2007; McMahon et al., 2007; Rhymer & Simberloff, 1996; Vander Zanden et al., 1999; Zaret & Paine, 1973). While the introduction of non-native fish species outside their original distributional range includes myriad taxonomic groups, perhaps no taxa exemplify this problem more than salmonids (Buoro et al., 2016). The brook trout (*Salvelinus fontinalis* Mitchell) is a paradoxical example of a species that has been extirpated from much of its native range in eastern North America (Hudy et al., 2008) due in part to displacement by non-native rainbow trout (*Oncorhynchus mykiss* Walbaum; Habera & Moore, 2005), yet in western North America (Dunham et al., 2002) and northern Europe (Korsu et al., 2010; Spens et al., 2007), brook trout are an invasive species that threatens the long-term viability of countless populations of various native salmonids.

To diminish negative effects of non-native freshwater fishes on native taxa, fisheries managers, and conservation biologists often implement mechanical (e.g., Knapp & Matthews, 1998; Meyer et al., 2006), chemical (e.g., Gresswell, 1991; Treanor et al., 2017), or biological (e.g., Koenig et al., 2015) eradication programs, which are often unsuccessful (reviewed in Meronek et al., 1996, and Rytwinski et al., 2019). The fact that conventional eradication programs often fail to remove the undesirable species highlights the need for novel conservation methods for eradicating non-native vertebrate populations.

One eradication method that has been considered is to shift the sex ratio of an unwanted population to all males, theoretically causing the population to collapse (Gutierrez & Teem, 2006; Hamilton, 1967).

In fisheries, this could potentially be accomplished by hatchery rearing and subsequent stocking of individuals with two Y chromosomes (i.e., males with a genotype of YY rather than XY—hereafter $M_{YY;}$ e.g., Schill et al., 2016). Population models considering possible eradication of non-native brook trout populations have indicated that eradication is theoretically feasible if the fitness of hatchery M_{YY} individuals approaches that of individuals in the wild population (Day et al., 2020; Schill et al., 2017). Due to the novelty of using M_{YY} vertebrates as an eradication method, almost nothing is known about the fitness of hatchery M_{YY} fish once released into the wild. In the only such study ever conducted, hatchery M_{YY} brook trout that were reared to about 225 mm total length and stocked in four North American mountain streams survived, spawned successfully with wild conspecifics, and produced all-male progeny, though reproductive success was lower for M_{YY} fish than for their wild counterparts (Kennedy et al., 2018b). While those preliminary results were insightful, additional evaluations of M_{YY} fitness are clearly needed.

Fitness generally refers to reproductive success, but can be quantified using metrics that are correlated with growth and body condition. For instance, fish body length and body condition were positively correlated with milt potency (Wedekind et al., 2007), mate choice (de Gaudemar et al., 2000), post-spawning survival (Cunjak et al., 1987), and fry production (Blanchfield et al., 2003; Hargrove et al., 2021). In addition, dominance hierarchies, which regulate the use of optimal feeding and resting habitats, and thus overall energy budget, were largely related to body length and condition in salmonids (Fausch & White, 1981; Nakano, 1995). Because growth rates and body condition data are easily obtained and are correlated with fitness, we sought to determine whether growth and condition of hatchery M_{YY} brook trout were similar to wild brook trout in high-elevation streams and alpine lakes, which encompass the habitats where they commonly displace native salmonids in western North America.

2 | METHODS

Wild and hatchery M_{YY} brook trout were sampled from two streams (i.e., Dry Creek and Tripod Creek) and two alpine lakes (i.e., Seafoam Lake #4 and Lloyds Lake) in central Idaho (Table 1). Waters included in the present study are a subset of several streams and alpine lakes currently being stocked with M_{YY} brook trout to evaluate their ability to eradicate unwanted wild brook trout populations (Kennedy et al., 2017). Streams varied from 1.4 to 5.2 m in average width and 1625 to 2279 m in elevation. Lakes varied from 2.7 to 2.9 ha in surface area and 2092 to 2426 m in elevation.

M_{YY} brook trout were developed and reared either at Mackay or Hayspur fish hatcheries following procedures described by Schill et al. (2016). Fish were stocked annually as age 0 fingerlings (mean = 131 mm SD = 18.83; TL), and were adipose-clipped prior to release to differentiate them from wild fish. They were stocked at levels (Table 1) equal to approximately 50% of the wild brook trout population abundance at the time the study began, which was determined from abundance estimates obtained for each population (Kennedy et al., 2017, 2018a). Stocking of M_{YY} fish occurred for several years prior to field sampling, to estimate fish growth for multiple age classes.

Fish were sampled in streams via backpack electrofishing in July of 2020 and 2021. Electrofisher settings were 60 Hz and 25% duty cycle, and voltage was adjusted until the electrofishing unit produced approximately 100 watts of average power output, to optimize capture of salmonids in small streams (Meyer et al., 2021).

Seafoam Lake #4 was accessible by vehicle, so sampling was conducted using raft electrofishing and gill netting in September 2020 and September 2021. Raft electrofisher settings were 60 Hz, 25% duty cycle, and 300–400 volts, which produced 7–10 amps of peak current. Three pairs of gill nets were set in locations evenly dispersed around the lake. Nets were set each afternoon and pulled the following morning in the same order in which they were set. Gill net pairs consisted of one floating and one sinking experimental gill net (46 m long and 2 m deep; consisting of nylon mesh panels of 19-, 25-, 32-, 38-, 51-, and 64-mm bar mesh). All net sets were set perpendicular to the shoreline with the smaller mesh toward the shore.

Lloyds Lake could not be accessed by vehicle so raft electrofishing was not possible. Instead, sampling was in June 2021 with gill nets and hook-and-line angling. Three floating gill nets (36-m long 1.8 m deep; consisting of nylon mesh panels of 10-, 13-, 19-, 25-,

TABLE 1 Physical characteristics, treatment type, and initial stocking dates of four Idaho waters in which hatchery M_{YY} (i.e., males with two Y chromosomes) and wild brook trout were sampled in July of 2020 and 2021 for growth and body condition comparisons

Parameter	Seafoam Lake #4	Lloyd Lake	Dry Creek	Tripod Creek
Latitude	44.508	45.193	44.127	44.318
Longitude	−115.126	−116.164	−113.568	−112.076
Initial M_{YY} stocking year	2017	2015	2016	2016
Annual M_{YY} stocking number	1176	1194	4326	6938
Wild fish suppression	Yes	No	Yes	No
Surface area (ha)	2.7	2.9	-	-
Reach length (km)	-	-	6.5	9.1
Average wetted width (m)	-	-	5.2	1.4
Gradient (%)	-	-	1.5	1
Elevation (m)	2423	2092	2377	2146

32-, and 38-mm bar mesh) were evenly distributed around the lake and oriented perpendicular to the shoreline, with the smaller mesh toward the shore. Nets were set in the afternoon and pulled the following morning in the same order in which they were set.

A minimum of two hatchery M_{YY} brook trout and two wild brook trout were collected from every 10-mm length bin, when present in the sample. The number of fish sacrificed was limited to not interfere with the ongoing M_{YY} hatchery brook trout study (Kennedy et al., 2017, 2018a). As part of that overarching M_{YY} evaluation, wild brook trout were suppressed annually in Dry Creek and Seafoam Lake #4 (Table 1), with an annual population suppression rate of about 50% (as determined from mark-recapture data). Wild brook trout were not removed from the remaining two waters.

Each fish sampled was measured in total length (mm) and weight (g). Fish were euthanized with a lethal dose of anesthetic and sagittal otoliths were removed (Schneidervin & Hubert, 1986). Fish were either processed on shore or placed in individually labeled plastic bags, preserved using ice, and later processed in a laboratory. One otolith from each fish was randomly selected and embedded in epoxy. Using a low-speed saw (Buehler Inc.), a 0.55-mm section of each otolith was cut through the transverse plane of the otolith to expose a cross-section of the nucleus. Sectioned otoliths were polished and then photographed in immersion oil using reflected light at 40x magnification with a Leica (model DFC450 C) digital camera and a Leica (model DM 4000 B) compound light microscope. Photographs were reviewed by two independent readers who were unaware of fish length, and age was estimated by enumerating presumptive annuli. In cases where readers did not agree on the age of the fish, fish length was considered to determine a consensus age.

Length, weight, and age were used to compare growth rates and body condition (i.e., linear regression of log[length] on log[weight]) between hatchery M_{YY} and wild brook trout. Growth rate and body condition were compared between groups (hereafter we refer to them as wild and hatchery "strains") using linear regression and von Bertalanffy growth models (von Bertalanffy, 1938) in statistical software R (R Development Core Team, 2020). Growth was modeled using either linear regression or a von Bertalanffy growth model because preliminary analysis indicated that growth was asymptotic in one water (i.e., Dry Creek) but linear in other waters.

Asymptotic growth was estimated by fitting a von Bertalanffy growth function (von Bertalanffy, 1938), and linear growth was estimated by fitting a linear regression model (Ogle et al., 2017). Within the asymptotic growth model, the effect of strain on growth was evaluated by estimating the theoretical maximum average length the population could achieve (L_∞), the Brody growth coefficient (K), and the theoretical age when length equals zero (t_0) for each strain. Ninety-five percent confidence intervals (CIs) were estimated for all

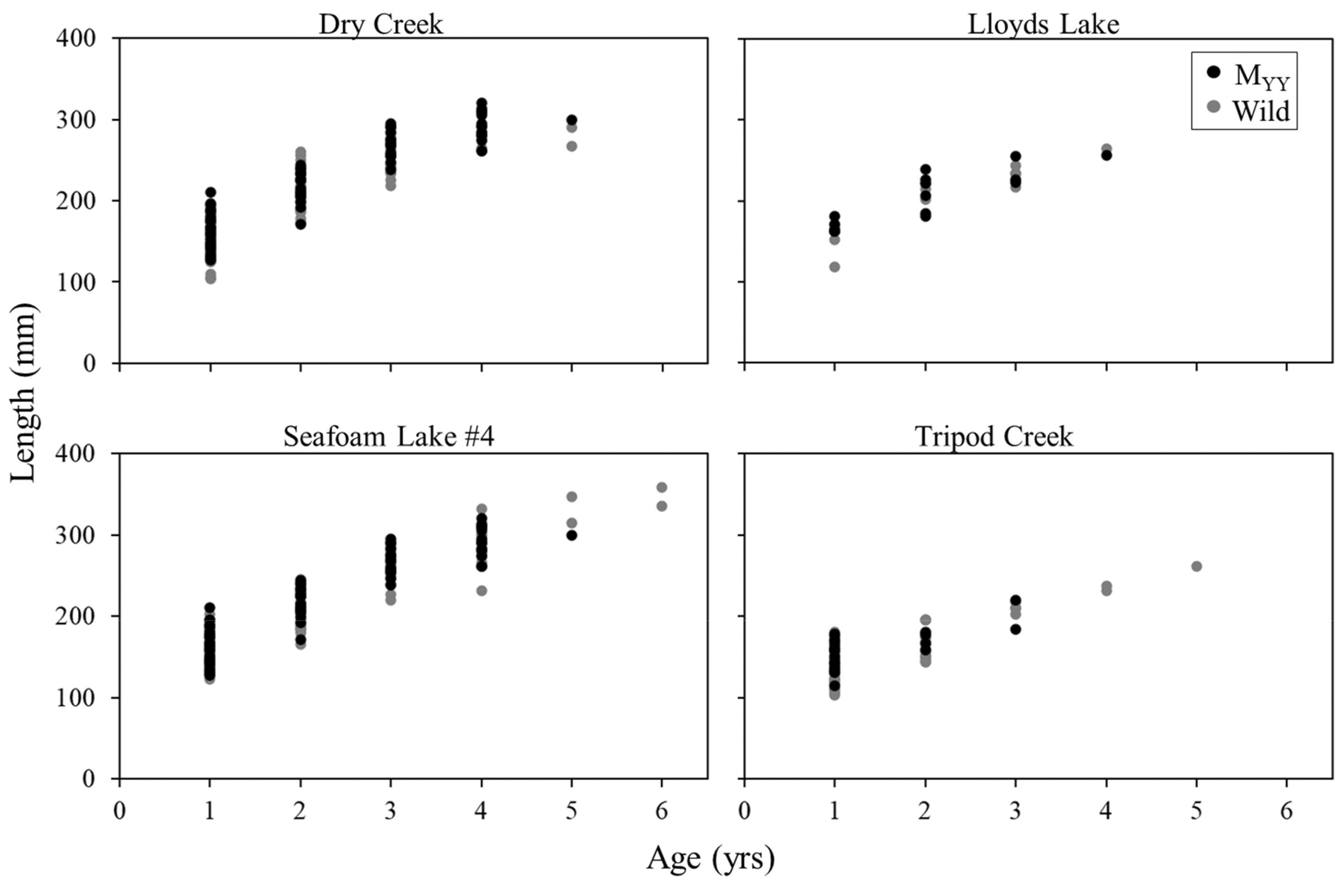

FIGURE 1 Back-calculated length at age for hatchery M_{YY} and wild brook trout sampled in July of 2020 and 2021 at four Idaho waters. Each data point represents an individual fish at its age when captured

parameters, and parameter estimates were considered statistically different between wild and hatchery strains if the CIs did not overlap (Ogle et al., 2017).

Linear growth models were developed with length at capture as the response variable, and predictor variables for the estimated age of the fish at capture (age), a categorical variable that designated the fish as either M_{YY} or wild (strain), and an age × strain interaction term. By constructing models in this manner, the slope was the estimated growth rate for wild fish (which were the reference strain in the model), and the interaction term was the estimated difference in growth rate between hatchery M_{YY} fish and wild fish. Ninety-five percent CIs were constructed for each parameter estimate, and growth was considered significantly different between wild and hatchery M_{YY} brook trout if the interaction term in the model produced 95% CIs that did not overlap zero (Johnson, 1999).

Body condition models were linearized with $\log_e$ transformed weight as the response variable, $\log_e$ transformed length as the predictor variable, and a length × strain interaction term (Quinn & Deriso, 1999). As with linear growth models, the interaction term was the estimated difference in condition between hatchery M_{YY} fish and wild fish, and the condition was considered significantly different if the interaction term in the model produced 95% CIs that did not overlap zero (Johnson, 1999).

3 | RESULTS

For 381 brook trout sampled across four waters, maximum age was age 6 at Dry Creek and age 4 or 5 at other waters for wild brook trout, and age 5 at Dry Creek and age 4 at other waters for hatchery M_{YY} brook trout. Total length ranged from 103 to 359 mm for wild brook trout and 115 to 353 mm for hatchery M_{YY} brook trout.

Growth did not differ between wild and hatchery-reared MYY brook trout in any stream or lake we sampled. In Dry Creek, where growth was asymptotic, K was 0.37/year (95% CI = 0.17–0.59/year), and L_∞ was 357 mm (311–500 mm) for hatchery M_{YY} brook trout, and 0.51/year (0.28–0.81/year) and 306 mm (273–378 mm) for wild brook trout. In other waters, where growth was linear, hatchery M_{YY} brook trout grew an estimated 24–43 mm per year, whereas wild brook trout grew an estimated 36–42 mm per year, although differences in growth rate were not significant (Figure 1; Table 2). In two waters where growth was linear (i.e., Seafoam Lake #4 and Tripod Creek), age 0 M_{YY} fish were significantly larger than their wild counterparts, but this did not translate into different growth rates (Table 2). Body condition also did not differ significantly between wild and hatchery M_{YY} brook trout (Figure 2; Table 3).

TABLE 2 Parameter estimates from von Bertalanffy (VBGF) and linear regression growth models for hatchery M_{YY} and wild brook trout sampled in July of 2020 and 2021 at four Idaho waters

Parameter	Estimate	LCI	UCI
Dry Creek (VBGF)			
$L\infty$ (Wild)	306	273	378
$L\infty$ (M_{YY})	357	311	500
K (Wild)	0.51	0.28	0.81
K (M_{YY})	0.37	0.17	0.59
t_0 (Wild)	−0.31	−0.92	0.06
t_0 (M_{YY})	−0.63	−1.40	−0.19
Lloyd Lake (Linear)			
Intercept	118.74	90.06	147.42
Age	38.63	27.01	50.25
Strain (M_{YY})	20.93	−15.23	57.09
Age × Strain	−6.75	−22.29	8.78
Seafoam Lake #4 (Linear)			
Intercept	124.28	115.29	133.27
Age	41.71	38.46	44.96
Strain (M_{YY})	10.98	2.31	34.53
Age × Strain	1.15	−5.31	7.60
Tripod Creek (Linear)			
Intercept	95.77	83.98	107.56
Age	35.66	29.95	41.37
Strain (M_{YY})	30.21	9.59	50.83
Age × Strain	−11.55	−24.39	1.29

Note: Lower (LCI) and upper (UCI) bounds for 95% confidence intervals are also included.

4 | DISCUSSION

We found that hatchery M_{YY} brook trout stocked into mountain streams and alpine lakes as age 0 fingerlings grew at a similar rate and maintained a similar body condition as wild brook trout, unlike other studies that generally demonstrated poorer performance of hatchery salmonids than wild counterparts (reviewed in Araki et al., 2008). For example, hatchery salmonids generally suffer higher mortality (Jonsson et al., 2003; Miller, 1954), slower growth (Bohlin et al., 2002; Finstad & Heggberget, 1993), and lower reproductive fitness (reviewed in Christie et al., 2014) than wild salmonids in the same environment. Reproductive fitness was also slightly lower for catchable-sized (not fingerling) hatchery M_{YY} brook trout than wild conspecifics in several mountain streams (Kennedy et al., 2018b). Taken together, results of Kennedy et al. (2018b) and our study suggest that hatchery M_{YY} fish stocked into lentic and lotic waters may survive and grow similarly to wild fish, but once they reach maturity, they may have lower reproductive fitness. However, these are the first studies to evaluate M_{YY} vertebrates in the wild, so more research is needed on all aspects of their post-release performance.

In one alpine lake and one stream, size at age 0 was significantly larger for hatchery M_{YY} brook trout than for wild fish, likely because age 0 M_{YY} fingerlings were stocked in summer at a larger size (~130 mm) than wild counterparts (~55 mm in their first summer; Kennedy et al., 2017 and Kennedy et al., 2018b). The lack of a difference in growth rate between the two strains we measured later indicates that the size advantage of age 0 hatchery M_{YY}

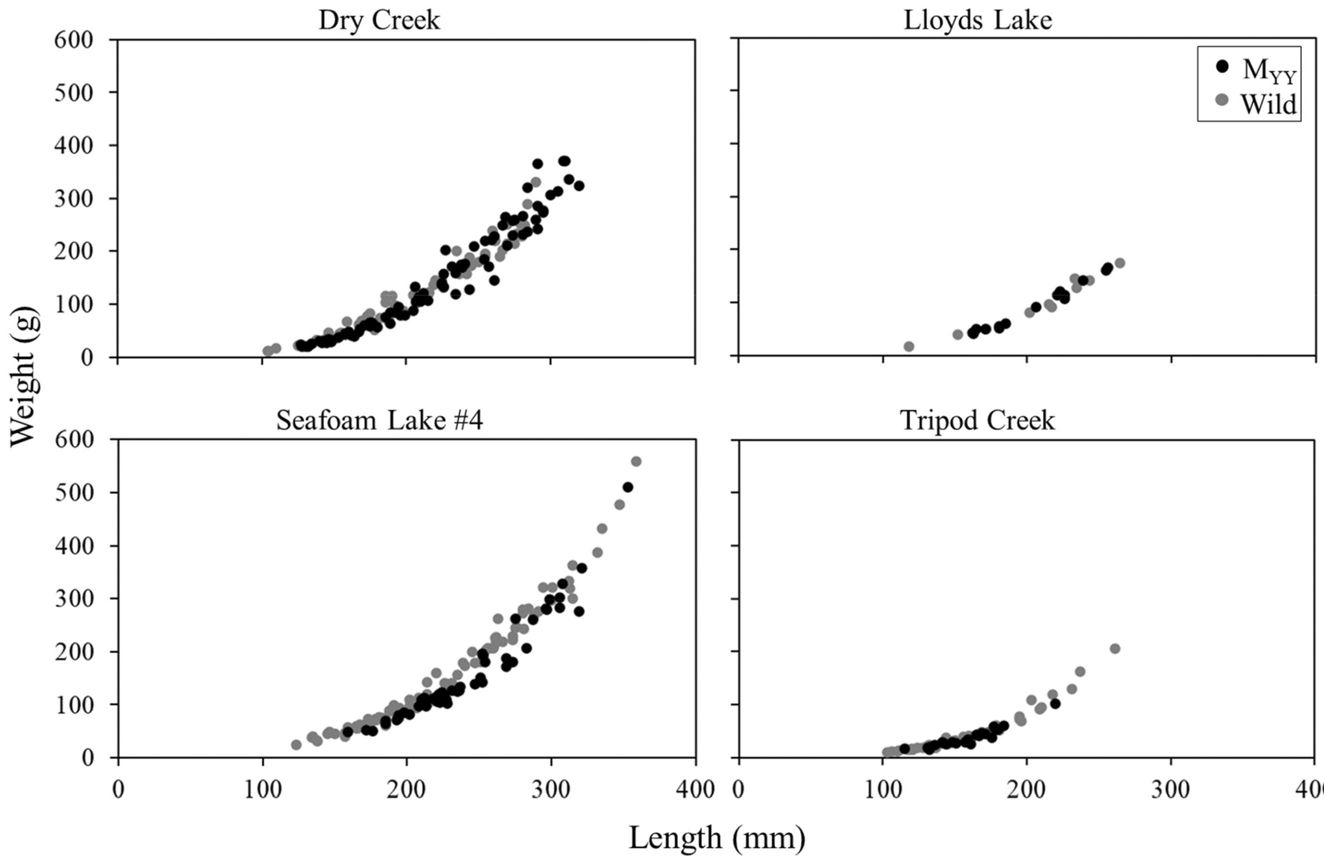

FIGURE 2 Length–weight relationships for hatchery M_{YY} and wild brook trout sampled in July of 2020 and 2021 at four Idaho waters. Each data point represents an individual fish

fish at the time of stocking did not affect their growth rate or that of wild fish. Although wild fish are generally superior in overall fitness to hatchery fish, a size advantage at stocking may allow hatchery fish to overcome their inferior fitness (reviewed in Tatara & Berejikian, 2012). Additional research is needed to compare growth and condition of wild and stocked M_{YY} fish to elucidate if a particular size or age at stocking results in optimal post-release performance of M_{YY} fish.

An inherent limitation of our study was that wild brook trout populations in two study waters, Dry Creek and Seafoam Lake #4, were subjected to manual population suppression for several years, which could have affected growth and condition of fish in our study. However, growth and condition did not differ between suppression and non-suppression waters for either wild or hatchery M_{YY} fish in our study. By contrast, suppressing wild brook trout populations in two Rocky Mountain streams improved post-stocking survival of hatchery M_{YY} brook trout compared to their survival in two streams without suppression of wild fish (Kennedy et al., 2018b). Brook trout are capable of compensatory responses to population reductions, such as improved growth, reduced natural mortality, and increased recruitment (Hall, 1991; McFadden, 1961; Messner, 2017; Meyer et al., 2006). In our study, manually suppressing wild brook trout may have caused a compensatory response in both wild and hatchery fish via some mechanism that we did not monitor, such as reduced natural mortality that masked suppression-related changes in growth or condition.

Our study was also limited by a need to sacrifice few fish for sampling and a need to include males and females in the sample of wild fish. First, we were constrained by an ongoing long-term M_{YY} study that limited the number of fish we could sacrifice, which limited the sample size of brook trout from each water and the number of study waters. Second, the sample of wild brook trout included both males and females, whereas the sample of hatchery M_{YY} brook trout included only males. In wild brook trout populations, male brook trout often grow faster than females (e.g., Hoover, 1939; McFadden, 1961; Toetz et al., 1991), so we would have needed to determine sex of all fish sampled to compare growth of hatchery males to wild males. However, male brook trout do not always grow faster than females (e.g., Curry et al., 2003), and even when they do, the growth difference between sexes for brook trout is usually only a few millimeters at each age, so we consider this limitation minor.

Despite these limitations, our results indicate that hatchery M_{YY} brook trout survived for several years, grew at an equivalent rate, and maintained an equivalent body condition as wild fish in alpine lakes and mountain streams. Although our results are encouraging, factors other than growth and condition could determine the success of using M_{YY} technology as a biological control for invasive fishes. Indeed, hatchery M_{YY} fish liberated in the

TABLE 3 Parameter estimates for simple linear regression models of $\log_e$(weight) against $\log_e$(length) for hatchery M_{YY} and wild brook trout sampled in July of 2020 and 2021 at four Idaho waters

Parameter	Estimate	LCI	UCI
Dry Creek			
Intercept	−11.49	−12.55	−10.42
$\log_e$ (Length)	3.03	2.83	3.23
Strain (M_{YY})	−0.39	−1.86	1.07
$\log_e$ (Length) × Strain	0.05	−0.22	0.33
Lloyd Lake			
Intercept	−11.05	−12.03	−10.07
$\log_e$ (Length)	2.91	2.73	3.10
Strain (M_{YY})	−0.73	−2.23	0.76
$\log_e$ (Length) × Strain	0.13	−0.15	0.42
Seafoam Lake #4			
Intercept	−10.23	−10.76	−9.70
$\log_e$ (Length)	2.80	2.70	2.90
Strain (M_{YY})	−1.08	−2.20	0.04
$\log_e$ (Length) × Strain	0.17	−0.04	0.37
Tripod Creek			
Intercept	−12.93	−13.75	−12.11
$\log_e$ (Length)	3.27	3.11	3.43
Strain (M_{YY})	0.71	−1.29	2.70
$\log_e$ (Length) × Strain	−0.16	−0.56	0.23

Note: Lower (LCI) and upper (UCI) bounds for 95% confidence intervals are also included.

wild must also reproduce at adequate rates (not equivalent rates) to steadily skew the sex ratio of the entire invasive population. Although they appear capable of doing so (Kennedy et al., 2018b), a lack of information comparing M_{YY} vertebrates to wild counterparts highlights the need for additional research before concluding that hatchery-reared M_{YY} fish can eradicate unwanted non-native fish populations.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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