The use of M_{YY} fish to eradicate non-native Brook Trout populations in Idaho

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Abstract - Brook Trout *Salvelinus fontinalis* (BKT) in the west have established self-sustaining populations that threaten native salmonids and are difficult to eradicate. One novel eradication approach uses hatchery-produced, genetically YY male fish (M_{YY}) created by feminizing XY males and crossing with normal XY males. All progeny of M_{YY} × wild female crosses are male, thus successful stocking and reproduction by M_{YY} fish could potentially shift sex ratios of wild populations to 100% male, causing extirpation of undesirable populations. The Idaho Department of Fish and Game is evaluating such an approach in streams and alpine lakes, which previously has included: 1) M_{YY} BKT hatchery broodstock development; 2) demonstration of successful M_{YY} post-release survival and reproduction in streams; and, 3) population simulations predicting that, with realistic rates of wild fish suppression and M_{YY} stocking, survival, and reproductive success, complete eradication of wild BKT populations could occur in reasonable management timelines. Here we present results to date from the culminating M_{YY} BKT stocking field trial ongoing in several streams and alpine lakes. In one stream, the sex ratio has shifted from 28% males in 2016 to 77% male in 2021. Growth rates and body condition appear to be equivalent between M_{YY} and wild BKT. Preliminary findings indicate that M_{YY} offspring production has been higher in streams than in lakes, when stocking fingerlings instead of catchables, and when wild fish are suppressed annually. Whether complete eradication occurs in any waters remains to be seen.

Introduction

Brook Trout *Salvelinus fontinalis* (BKT) in the west have established self-sustaining populations in streams and alpine lakes that threaten myriad native salmonid populations via hybridization and competition for space and resources (reviewed in Dunham et al. 2004). Once established, eradication of non-native BKT populations is difficult with standard techniques such as electrofishing, gill netting, chemicals (such as rotenone), and biological control (such as predator stocking).

A novel eradication approach introduced by Gutierrez and Teem (2006) suggested the use of hatchery produced male fish with an YY genotype (known as "supermales", herein referred to as M_{YY} fish) to shift the sex ratio of the wild population. A M_{YY} broodstock must first be created using the following steps: converting normal M_{XY} males to F_{XY} fish by exposing them to estrogen; crossing F_{XY} fish with normal M_{XY} males and retaining all YY offspring, using genetic sex markers to differentiate fish (see below); and, converting ½ of the M_{YY} offspring from M_{YY} to F_{YY} by exposing them to estrogen (Teem and Gutierrez 2010). Annual stocking of the offspring of this M_{YY} and F_{YY} broodstock theoretically could shift the sex ratio of the wild population to 100% male, thus collapsing the population.

The Idaho Department of Fish and Game (IDFG) developed a "recipe" to successfully create a M_{YY} and F_{YY} BKT broodstock in 2012 (Schill et al. 2016), which annually produces 20,000 – 30,000 M_{YY} BKT for stocking needs.

Population models considering possible eradication of BKT populations indicated that eradication is theoretically feasible if the fitness of hatchery M_{YY} individuals approaches that of individuals in the wild population (Schill et al. 2017). A detailed review of past IDFG M_{YY} studies is provided by Kennedy et al. (2017).

Due to the novelty of using M_{YY} vertebrates as an eradication method, almost nothing is known about the fitness of M_{YY} individuals once released into the wild. In the only such study ever conducted, hatchery M_{YY} BKT were reared to about 225 mm total length and stocked in four Idaho mountain streams; these fish survived and 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. 2018). While those preliminary results were insightful, additional evaluations of M_{YY} fitness are clearly needed.

To more thoroughly evaluate the practical use of M_{YY} BKT as an eradication tool, a broad-scale field study was initiated in 2015 in several Idaho streams and alpine lakes containing wild BKT. The objectives for this paper are to: 1) further evaluate M_{YY} BKT fitness relative to wild fish by comparing growth rates and body condition; and, 2) present preliminary sex ratio changes and M_{YY} BKT offspring production at study waters being annually stocked with M_{YY} BKT.

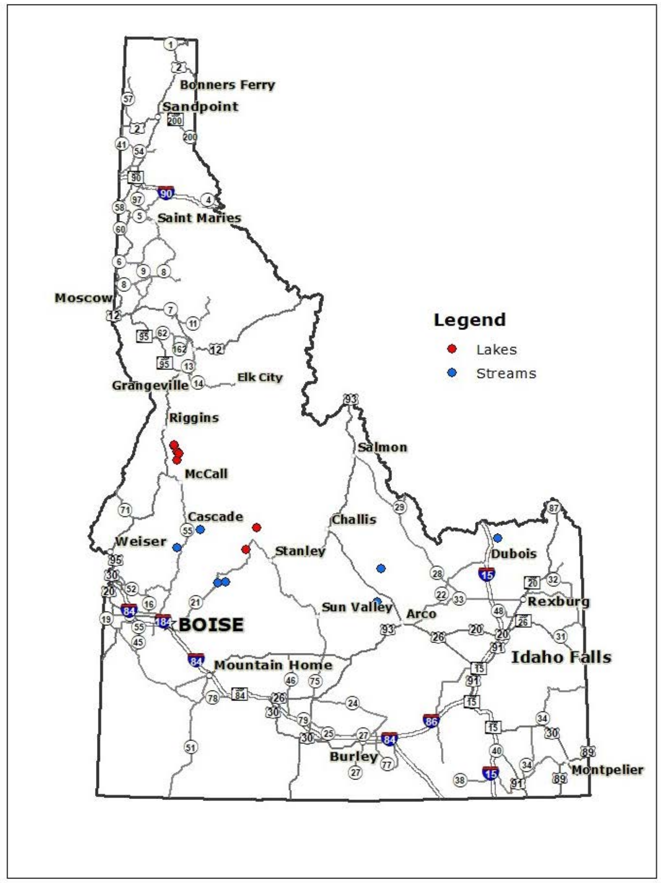

Figure 1. Location of M_{YY} Brook Trout study waters in Idaho.

Methods

For complete details on YY broodstock production see Schill et al. (2016). Offspring are annually produced by crossing F_{YY} and M_{YY} broodstock at the IDFG Hayspur Hatchery. All M_{YY} BKT are adipose fin clipped prior to stocking to differentiate between wild and M_{YY} BKT in the field. Offspring are reared to either fingerling-size (~120 mm total length, at eight months of age) or catchable-size (~225 mm, at 20 months of age) for stocking purposes.

This study was initiated in 2015, but not all waters were sampled or stocked in the first year, and some waters were not included in the study until 2017. A total of 15 waterbodies comprise the entire study, most of which receive annual stocking of either fingerling- or catchable-sized M_{YY} BKT (Figure 1; Table 1). All study waters have self-sustaining wild BKT populations which comprise > 80% of the original fish species composition.

At several study waters, wild BKT are suppressed annually, prior to stocking, to evaluate whether suppression of wild fish improves the post-release performance of M_{YY} BKT. Suppression streams undergo annual suppression of the wild BKT population using backpack electrofishing, whereas suppression of wild fish in lakes relies on boat electrofishing and gill netting. All study stream treatment reaches have both a downstream and upstream passage barrier with a total stream length not exceeding 10 km between the barriers. Study lakes also have passage barriers. Passage barriers provide isolation from potential recolonization by wild BKT. To assess barrier passage, fish are marked with double maxillary clips below each downstream barrier in every stream and alpine lake; to date no recolonizing fish have been observed above passage barriers. Two streams and two lakes receive no stocking or wild suppression and serve as controls.

Stocking Rates

Fingerling and catchable M_{YY} BKT are stocked annually in a single event. Fish are stocked by hand using buckets and in backpacks for streams and via helicopter and bucket (90–100 gal capacity SEI Industries Bambi bucket or 208 L barrel) for alpine lakes, except Martin and Seafoam Lake #4 which are stocked directly by hatchery truck.

In streams, stocking rate was set at 125 catchables/km because that is a typical stocking rate for Idaho streams. However, once abundance estimates could be made at each water, stocking rate was adjusted to be 50% of the original adult wild BKT population size. This rate was selected because earlier research indicated that a 50% stocking rate could skew the sex ratio of wild BKT populations in a reasonable amount of time (Schill et al. 2017). This adjustment resulted in a 46% reduction in East Threemile Creek and 27% reduction in Pikes Fork Creek from the original catchable stocking rate. The fingerling stocking rate in streams was set at four times the catchable stocking rate (500 fingerlings/km) based on the ratio of juvenile to adult fish presented by McFadden (1961) for a stream in Wisconsin, but at narrow study streams (East Fork Clear and Tripod Creeks; Table 1), we reduced stocking densities to 250 fingerlings/km. Stocking rates in fingerling streams were also adjusted once abundance estimates were available which resulted in an increase of 34% in Dry Creek and 116% in Tripod Creek while East Fork Clear Creek was reduced by 92%.

In alpine lakes, stocking rate was set at 175 fingerlings/ha because that is a typical stocking rate for such waters in Idaho. Because the weight of catchables is five times heavier than fingerlings, we stocked 1/5 as many catchables (35/ha) in alpine lakes receiving catchable fish. Since abundance estimates were not available for most alpine lakes, no adjustment to the original stocking rate was made for any lakes.

Abundance Estimates

Mark-recapture abundance estimates of wild and M_{YY} BKT ≥ 100 mm TL have been conducted annually at each suppression stream and alpine lake once incorporated into the study. All data are pooled over the entire study reach by year and total BKT abundance is estimated using the modified Peterson estimator from the FSA package in statistical package R (R Core Team 2022). At non-suppression streams, we complete multiple-pass depletion abundance surveys every 3 years and estimate abundance with the maximum-likelihood model in the MicroFish software package (Van Deventer and Platts 1989). No such estimates are possible at non-suppression alpine lakes.

Sex Ratio Monitoring and Genetic Assignment

Prior to the first stocking event, sex ratios were obtained for the wild BKT population at each study water to obtain baseline sex ratios. In subsequent years, genetic samples have been obtained annually from all suppression waters and tri-annually from non-suppression and control waters. Tissue samples were collected from approximately 100 BKT fry (≤ 100 mm) and 100 BKT adults (≥ 100 mm) from each waterbody during July–September to estimate sex ratios and reproductive success. Tissue samples are caudal fin clips preserved on Whatman™ 3MM chromatography paper (Thermo Fisher Scientific, Inc., Pittsburgh, Pennsylvania). Samples are screened by the IDFG Eagle Genetics Lab using two genetic markers that differentiate sex in BKT: SexY_Brook1 (Schill et al. 2016) and the master sex-determining gene sdY (Yano et al. 2013). For detailed information on primer sequencing, amplification, and sex markers, see Roth et al. (2021). We calculate 95% confidence intervals (CIs) around the estimated male proportions, following Fleiss (1981).

Growth and Body Condition

To assess whether growth and body condition was comparable between hatchery M_{YY} and wild BKT, some fish were collected from two study streams (Dry and Tripod Creeks; Table 1) using backpack electrofishing and from two lakes (Seafoam Lake #4 and Lloyds Lake; Table 2) using either raft electrofishing or gillnetting. A minimum of two hatchery M_{YY} BKT and two wild BKT were selected from every 10 mm length-bin, when present. Each selected fish was euthanized, measured for length and weight, and had the sagittal otoliths removed. One otolith from each fish was embedded in epoxy and, using a low-speed saw, 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 the readers did not agree on the age of the fish, fish length was considered to determine a consensus age.

Comparisons of growth rate and body condition between hatchery M_{YY} and wild fish were conducted using linear regression and von Bertalanffy growth models (von Bertalanffy 1938) in statistical software R (R Core Team 2021) because preliminary analysis indicated that growth was asymptotic in one water (i.e., Dry Creek) but linear in the remaining three waters. Within the asymptotic growth model, the effect of hatchery M_{YY} and wild BKT strain on growth was evaluated by estimating the theoretical maximum average length fish in the population could achieve (L_∞), the Brody growth coefficient (K), and the theoretical age when length equals zero (t_0) for each strain. We estimated 95% CIs for all parameters, and estimates were considered statistically different between hatchery M_{YY} and wild BKT strains if the CIs did not overlap (Ogle et al., 2017).

Linear growth models were developed with length at capture as the response variable; predictor variables included the estimated age of the fish at capture (age), a categorical variable that designated the fish as either hatchery M_{YY} or wild (strain), and an age × strain interaction term. By constructing the models in this manner, the slope of the line 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 hatchery M_{YY} and wild BKT 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 and Deriso, 1999). As with linear growth models, the interaction term was the estimated difference in condition for hatchery M_{YY} fish compared to wild

Table 1. Physical description of M_{YY} Brook Trout study streams and controls where NS = non-suppression treatment, S = suppression treatment, C = catchables, and F = fingerlings.

						% Male offspring				
						Start		Current		
Stream	Treatment	M_{YY} BKT size stocked	Reach length (km)	Avg. wetted width	Avg. annual # stocked	Year	% (n)	Year	% (n)	% M_{YY}
Alder Creek	Control	-	2.4	4.9	-	2014	42% (100)	2019	58% (100)	0%[1]
Beaver Creek	Control	-	4.0	2.4	-	2016	45% (99)	2019	57% (99)	0%[1]
Dry Creek	S	F	6.5	5	3,886	2016	28% (105)	2021	77% (105)	78%[2]
East Fork Clear Creek	NS	F	3.9	2.1	535	2016	57% (98)	2019	60% (89)	26%[1]
East Threemile Creek	NS	C	6.5	2.7	1,079	2017	51% (97)	2019	48% (110)	4%[1]
Pike's Fork Creek	S	C	7.5	3.7	792	2017	51% (97)	2021	49% (98)	13%[2]
Tripod Creek	NS	F	9.1	1.4	5,691	2016	27% (100)	2019	58% (77)	2%[1]

[1]Estimates from the 2019 sampling; samples will be taken again in 2022.

[2]Estimates from the 2021 sampling.

Table 2. Physical description of M_{YY} Brook Trout study lakes and controls where NS = non-suppression treatment, S = suppression treatment, C = catchables, and F = fingerlings.

						% Male offspring				
						Start		Current		
Stream	Treatment	M_{YY} BKT size stocked	Lake size (ha)	Elevation (m)	Avg. annual # stocked	Year	% (n)	Year	% (n)	% M_{YY}[1]
Black Lake	NS	C	2.6	2,177	207	2016	0% (1)	2021	35% (34)	8%
Duck Lake	NS	F	4.96	2,177	2,180	2015	45% (109)	2021	52% (52)	0%
Lloyds Lake	NS	F	2.91	2,092	1,290	2015	50% (8)	2021	100% (1)	0%
Martin Lake	S	F	2.50	2,107	865	2017	100% (1)	2021	0% (1)	0%
Rainbow Lake	NS	C	8.78	2,150	705	2016	25% (4)	2021	50% (162)	3%
Seafoam Lake #4	S	F	2.72	2,423	1,098	2017	54% (26)	2021	50% (8)	0%
Snowslide Lake #1	Control	-	4.86	2,188	-	2015	0% (1)	2021	0% (5)	0%
Upper Hazard Lake	Control	-	15.84	2,265	-	2015	48% (109)	2021	54% (46)	0%

[1]Estimates from the 2021 sampling.

fish, and condition was considered significantly different if the interaction term in the model produced 95% CIs that did not overlap zero (Johnson, 1999).

Results

Annual stocking has occurred at all waterbodies from inception of the study (2015–2017; Table 1 and 2) and is scheduled to continue until 10 years of stocking M_{YY} BKT has been completed at each waterbody. On average we annually stock between 535 and 5,691 fingerling M_{YY} and 792 to 1,079 catchable M_{YY} BKT into streams and 865 to 2,180 fingerling and 207 to 705 catchable M_{YY} BKT into lakes.

The proportion of adult (≥ 100 mm) BKT ranged from 0 to 67% M_{YY} BKT across all streams and suppression lakes following M_{YY} stocking. We were unable to estimate abundance in non-suppression lakes due to limitations of lethal sampling methods for alpine lakes (i.e. gillnets). The proportion of M_{YY} BKT was highest in streams stocked with fingerlings (19% to 67%) compared to streams stocked with catchables (0% – 10%) and suppression lakes (3% – 39%).

On average there has been a 16% increase in male sex ratio across all study streams with the highest increase at Dry Creek (49%) and lowest at East Threemile Creek (-3%, Table 1). Genetic assignment analyses indicate the proportion of offspring produced by M_{YY} BKT stocked into study streams has varied from 0% to 78% (Table 1). Although sample sizes have been low for some lakes, results show that sex ratios have changed very little (Table 2), and M_{YY} BKT offspring have only been detected at two of the six study lakes in 2021.

Growth and Body Condition

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

Growth did not differ between hatchery-reared M_{YY} and wild BKT 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} BKT, while K was 0.51/year (0.28 – 0.81/year) and L∞ was 306 mm (273 – 378 mm) for wild BKT. In other waters, where growth was linear, hatchery M_{YY} BKT grew an estimated 24 – 43 mm per year, whereas wild BKT grew an estimated 36 – 42 mm per year, although differences in growth rate were not significant (Figure 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. Body condition also did not differ significantly between wild and hatchery M_{YY} BKT (Figure 3).

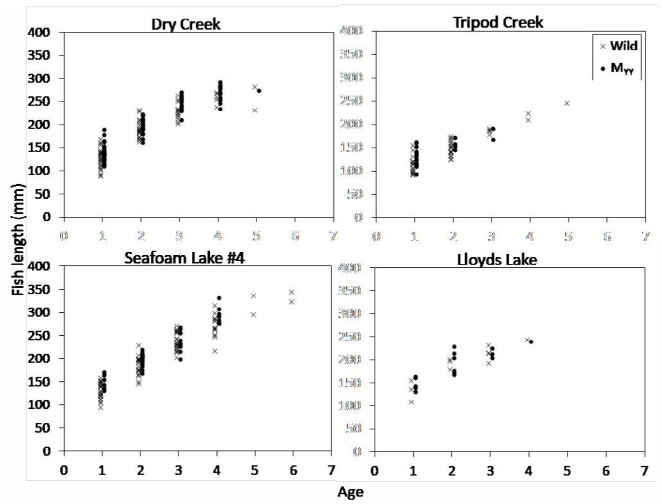

Figure 2. Back-calculated length-at-age for hatchery M_{YY} and wild brook trout sampled in four Idaho waters. Each data point represents an individual fish at its age when captured.

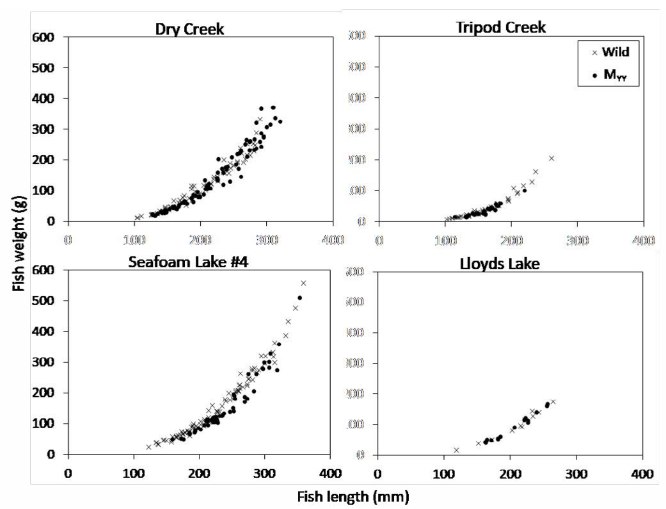

Figure 3. Length-weight relationships for hatchery M_{YY} and wild brook trout sampled in four Idaho waters. Each data point represents an individual fish.

Discussion

This study is now in its 7th survey year for some waters, and clearly there are greater shifts in sex ratio and M_{YY} BKT offspring (fry production) in streams compared to lakes, and in streams stocked with fingerlings compared to streams stocked with catchables. It is not surprising to see streams exhibiting faster and more promising results over lakes as prior simulations suggested the need for much longer time frames to reach eradication in lakes (Schill et al. 2017). This is likely due in part to later maturity and longer life spans in lakes compared to streams. Moreover, the use of lethal gillnet sampling methods in lakes removes both M_{YY} and wild BKT from the system, whereas stream electrofishing allows the release of M_{YY} fish (Schill et al. 2017). The superior performance of M_{YY} fingerlings compared to catchables is likely due to greater longevity of fingerlings. Indeed, catchable trout rarely survive more than a year after being released in Idaho waters (High and Meyer 2009; Cassinelli and Meyer 2018), and while fingerlings are also known to generally have poor survival, our results have documented M_{YY} fingerlings surviving for many years (Figure 2), providing numerous opportunities to spawn. Stocking rates are also inherently much higher for fingerlings than catchables, so even if survival of fingerlings is lower than survival for catchables, the total number of spawning M_{YY} fish could be higher for fingerlings.

Dry Creek currently exhibits the most promising results, with the highest increase in sex ratio towards males and highest proportion of M_{YY} offspring. Tripod Creek also exhibited an increase in male sex ratio by 31%, but unlike Dry Creek, only a small proportion of the sampled males were M_{YY} offspring. The main treatment difference between these two streams is the use of manual suppression of the wild BKT population at Dry Creek and no suppression in Tripod Creek. Manual suppression through electrofishing has been used for decades to reduce the density of non-native trout and lead to an increase in native salmonids (Moore et al. 1983) and more specifically to reduce non-native BKT populations (Shepard et al. 2014). Suppression of wild trout populations has contributed to increased survival of both stocked Rainbow trout *Oncorhynchus mykiss* (Horner 1987) and fingerling Cutthroat Trout *Oncorhynchus clarkii* (Miller 1955). As such, manual suppression has likely increased survival of our stocked M_{YY} BKT in this study.

Results of this study indicate that hatchery M_{YY} BKT stocked into mountain streams and alpine lakes as age-0 fingerlings grew at a similar rate and maintained a similar body condition as wild BKT. Our growth results are contrary to much of the existing literature demonstrating poorer performance for hatchery salmonids relative to their wild counterparts (reviewed in Araki et al. 2008). For example, hatchery salmonids generally demonstrate poorer survival (Miller 1954; Jonsson et al. 2003), slower growth (Finstad and Heggberget 1993; Bohlin et al. 2002), and reduced reproductive fitness (reviewed in Christie et al., 2014) compared to wild salmonids in the same environments. Kennedy et al. (2018) reported slightly reduced reproductive fitness for hatchery M_{YY} BKT relative to wild conspecifics in several mountain streams, though their study was conducted on catchable-sized fish (as compared to fingerlings in the present study), and they did not compare growth or condition between M_{YY} and wild fish. Taken together, the results of Kennedy et al. (2018) and the present study suggest that hatchery M_{YY} fish stocked in lentic and lotic waters may survive and grow similarly to wild fish, but once they reach maturity, they may have comparatively lower reproductive fitness. However, since these are the first studies ever to evaluate M_{YY} vertebrates liberated into the wild, more research is clearly needed on all aspects of their post-release performance.

There was no evidence that growth or condition differed in suppression and non-suppression waters for either wild or hatchery fish. The lack of a suppression effect on fish growth and condition in our study may be related to the well documented ability of BKT to undergo compensatory responses to population changes (McFadden 1961; Meyer et al. 2006). Additionally, the wild components of the BKT populations were composed of both male and female individuals, whereas the hatchery M_{YY} components of the populations were inherently composed of only males. In wild BKT populations, male BKT often grow faster than females (McFadden 1961), so had we assessed fish sex, we could have compared the growth of hatchery males to wild males. However, male BKT do not always grow faster than females (Curry et al. 2003), and even when they do, the growth difference between sexes for BKT is usually only a few millimeters at each age, so we consider this limitation minor.

Our results clearly indicate that hatchery M_{YY} fingerling BKT can survive for several years, grow at an equivalent rate, maintain an equivalent body condition relative to wild BKT in both alpine lakes and mountain streams, and can successfully reproduce with wild BKT. In contrast, survival and successful reproduction by catchable M_{YY} BKT appears to be diminished, and thus they are failing to shift the sex ratio of wild BKT toward 100% male. Whether the use of M_{YY} BKT stocking can be used to successfully eradicate any wild BKT populations remains to be seen, but promising results are apparent when fingerling M_{YY} BKT are stocked into streams that receive annual suppression.

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