Purifying a Yellowstone Cutthroat Trout Stream by Removing Rainbow Trout and Hybrids via Electrofishing

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Abstract—Long-term persistence of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in the South Fork Snake River drainage in Idaho is threatened by hybridization with introduced Rainbow Trout *O. mykiss.* We completed eight backpack electrofishing removals from 2010 to 2015 to remove Rainbow Trout and hybrids from a 9.3-km isolated reach of Palisades Creek (a South Fork tributary) to improve the purity of the population. For two removals, a subsample of *Oncorhynchus* were genetically screened at seven diagnostic nuclear DNA loci. A total of 14,092 fish were captured across all removals, of which 3,446 were putative Rainbow Trout or hybrids which were culled from the population. The proportion of the total catch comprised of Yellowstone Cutthroat Trout increased from 67% in 2010 to 86% by the second removal of 2015, whereas the proportion of Cutthroat Trout alleles increased from 80% to 90%. Considering the capture efficiencies achieved, initial hybridization levels observed, and number of removals conducted, ending phenotypic purity should have been 94% rather than 86%; this discrepancy was likely due to low capture efficiency for fish <150 mm TL, extremely high flows throughout 2011 that prevented electrofishing removals that year, and perhaps a competitive or survival advantage for Rainbow Trout and hybrids over Cutthroat Trout.

Introduction

The Rainbow Trout *Oncorhynchus mykiss* is globally one of most widely introduced species of fish outside their native range (Fausch et al. 2001), and have established self-sustaining populations on every continent but Antarctica. When they have been stocked where native salmonids exist, they often competitively displace or hybridize with the native stock of fish. For example, in the South Fork Snake River drainage in Idaho, the long-term persistence of Yellowstone Cutthroat Trout *O. clarkii bouvieri* is threatened by an increasing abundance of and hybridization with Rainbow Trout (High 2010).

Once hybridization between a native population of Cutthroat Trout and nonnative Rainbow Trout occurs, it has been argued that the process will usually lead to genomic extinction of the Cutthroat Trout parental form (Allendorf and Leary 1988). An alternate viewpoint argues that longitudinal gradients in introgression are more common in hybridized populations of Cutthroat Trout, with hybrid zones being mediated by environmental conditions and ecological differences between taxa that interact to help segregate the parental forms and provide resistance to genomic extinction (McKelvey et al. 2016). Under either scenario, manually removing *O. mykiss* alleles will theoretically reduce both the rate and spread of hybridization and introgression in Cutthroat Trout populations (e.g., Al-Chokhachy et al. 2014).

Attempts to eradicate nonnative salmonids in streams have produced mixed results. The use of fish toxicants has sometimes been successful (e.g., Gresswell 1991), but often results in incomplete removal of target populations (reviewed in Meronek et al. 1996). Moreover, piscicides kill nontarget species as well, and biologists must consider the negative perception that application of piscicides sometimes evokes from the public (Finlayson et al. 2010). Like piscicides, electrofishing removals are also successful at reducing the abundance of nonnative species but typically do not lead to complete eradication (e.g., Thompson and Rahel 1996) unless the treatment reaches are very short (<3 km), the streams are very small (<3 m wide), and multiple electrofishing removals per year for many consecutive years are conducted (e.g., Shepard et al. 2014).

However, complete eradication of Rainbow Trout is not necessary when the goal of a project is not to completely purify a stream but rather to transform a moderate to heavily hybridized Cutthroat Trout population into a minimally hybridized population. While the value of hybridized populations of Cutthroat Trout has been intensively debated (Allendorf et al. 2004; Campton and Kaeding 2005), representatives from most fish and wildlife agencies in the western U.S. have collectively developed a Cutthroat Trout conservation strategy that includes three categories for classifying populations (UDWR 2000), including core (<1% introgressed), conservation (1-10% introgressed), and sport fish (>10% introgressed) populations. The goal of our project was to transform a heavily hybridized Cutthroat Trout population (>25% introgressed) into a minimally hybridized population (i.e., <10% introgressed).

Methods

Rainbow Trout and Hybrid Removal

Palisades Creek is a primary spawning tributary for Cutthroat Trout in the South Fork Snake River drainage in eastern Idaho. The main stem of Palisades Creek is about 30 km in length. However, about 10 km upstream from its confluence with the South Fork, there is a high-gradient, cascading section that serves as a natural barrier to fish movement, and Rainbow Trout and hybrids are absent above this barrier. In 2009, a permanent electric weir was installed on Palisades Creek about 0.7 km upstream from its confluence (High 2010), which is 90-100% efficient at stopping upstream migrating Rainbow Trout (B. High, unpublished data). The downstream electric weir and upstream natural barrier formed the boundaries of our study.

We used backpack electrofishers to capture and remove Rainbow Trout and hybrids in late summer or autumn when flows were at their annual low point. One removal was conducted in 2010 and in 2012, whereas two removals (separated by about one month) were conducted annually from 2013 to 2015. Removal efforts were not possible during 2011 because of unusually high flow conditions that rendered electrofishing inefficient and dangerous all summer and autumn. Also, high flows damaged the electric weir in 2011 early in the spawning run and it had to be shut down for the rest of the spawning period. The weir was repaired in the winter of 2011-2012 and has been fully operational since.

Electrofishing teams consisted of 3 to 4 people operating backpack electrofishers and two or more additional people with nets and buckets. All captured trout were identified to species (hybrids were classified as a separate taxa) and measured for total length. Trout <100 mm comprised <5% of the total catch, were too small to effectively capture, and are difficult to phenotypically differentiate for these taxa, thus they were not included in our analyses, though when captured they were culled.

Taxa were separated based on previous studies (e.g., Meyer et al. 2006) which identified that, in contrast to Rainbow Trout and hybrids, Yellowstone Cutthroat Trout have (1) no white on the leading tips of the anal, dorsal, or pelvic fins, (2) fewer spots on the top of the head, (3) a bright red-orange throat slash, and (4) spots on the side of the body clustered dorsally and posteriorly. With regard to head spots, we counted spots on the head that were above the eyes, starting from just anterior of the nares and extending posterior to the point of scale formation; there is often one spot next to each nares on pure Yellowstone Cutthroat Trout, and if present these were not counted.

For six of the eight removals, we marked fish before the removal in order to estimate trout abundance using the modified Peterson mark-recapture estimator. Capture efficiency in each size group in each year was calculated as the number of marked fish caught in the recapture run divided by the total number marked.

Genetic Analyses

In 2012 and the first removal of 2015, we collected genetic samples to (1) estimate allelic purity of the population early in the project and at the end of the study, and (2) confirm the accuracy of phenotypic-based fish identification. Small fin clips were randomly collected from fish throughout the stream. We screened all samples for Rainbow Trout hybridization/introgression with seven diagnostic nuclear DNA (nDNA) markers (Occ34, Occ35, Occ36, Occ37, Occ38, Occ42 and OM55; Ostberg and Rodriquez 2002). We classified fish as Yellowstone Cutthroat Trout if they were homozygous for *O. c. bouvieri* alleles at all loci, Rainbow Trout if they were homozygous for *O. mykiss* alleles at all loci, and hybrids if they possessed alleles from both parental species. For each individual fish, using seven codominant nDNA loci gave us a 90% probability of detecting introgression at 15% or greater.

Phenotypic introgression was calculated as the number of non-Cutthroat Trout caught in each removal divided by all *Oncorhynchus* captured. Observed levels of phenotypic introgression were compared to expectations that were approximated based on estimates of species composition and removal efficiency. For these approximations we assumed that (1) fish did not grow between removals in the same year (usually removals were separated by no more than one month), and (2) fish grew approximately 50 mm between years, up to 350 mm in length. The latter assumption is equivalent to growth rates typical for these taxa in inland Rocky Mountain streams. As an example, for the 150-200 mm size group in 2012, Rainbow Trout and hybrids comprised 28% of the catch, and capture efficiency (i.e., removal efficiency) was an estimated 38%. Based on these results and our assumed growth rates, we expected that for the next removal (i.e., the first removal in 2013), Rainbow Trout and hybrid composition would have declined to 18% of the catch in the 200-250 mm size group, instead of the 21% we observed. Expected phenotypic introgression levels could not be approximated for the smallest size group (100-150 mm) because capture efficiency for fish <100 mm was not available (i.e., we did not mark fish <100 mm).

To calculate genotypic introgression, we combined phenotypic catch data with genetic findings, because not all captured fish were genetically analyzed in the years that genetic samples were processed, and in only two of the eight removals were genetic data analyzed. All captured fish phenotypically designated as pure Yellowstone Cutthroat Trout and pure Rainbow Trout were assigned to have 0 and 14 *O. mykiss* alleles, respectively. For fish phenotypically designated as hybrids, we calculated the mean number of *O. mykiss* alleles in the hybrids that were genetically sampled, and assumed that all the remaining hybrids not genetically sampled had the same number of *O. mykiss* alleles.

Results

We captured a total of 14,654 trout in Palisades Creek across all removals, of which 3,446 (24%) were putatively Rainbow Trout or hybrids that were removed from the stream (Table 1). An additional 200 Rainbow Trout and hybrids were caught and removed during the fish marking runs conducted during the week prior to the removals.

The phenotype matched the genotype of individual fish with a high degree of accuracy (Figure 1), especially if Rainbow Trout and hybrids were combined into one taxa (phenotypic accuracy = 94%). All phenotyping mistakes were between hybrids and parental taxa. Hybrids were mistaken for parental taxa most often when almost none or almost all of their alleles were Rainbow Trout alleles (Figure 1). Phenotypic characteristics that best distinguished Yellowstone Cutthroat Trout from hybrids were fish having (1) no white on the leading tip of the anal,

Table 1. Mark-recapture population abundance estimates and the number of Rainbow Trout and hybrids removed during each removal effort at Palisades Creek, Idaho. Population estimates were not conducted for the first and last removals. Two removals were completed in 2013-2015.

	Rainbow Trout and hybrid abundance						Yellowstone Cutthroat Trout abundance		
	<20 cm		20-29 cm		≥30 cm				
Year	Estimate	Removed	Estimate	Removed	Estimate	Removed	<20 cm	20-29 cm	≥30 cm
2010	-	260	-	426	-	148	-	-	-
2012	467	136	461	231	57	48	1,993	925	235
2013-1	1,766	294	476	56	26	13	1,953	1,820	333
2013-2	1,435	446	460	140	16	5	2,457	1,514	566
2014-1	752	148	535	169	53	24	2,322	1,054	325
2014-2	1,026	194	401	201	23	17	4,956	1,195	229
2015-1	426	97	276	163	43	23	3,554	884	215
2015-2	-	109	-	89	-	9	-	-	-

dorsal, or pelvic fins, (2) fewer than five spots on the top of the head, (3) a bright red-orange throat slash, and (4) spots on the side of the body clustered dorsally and posteriorly (Table 2).

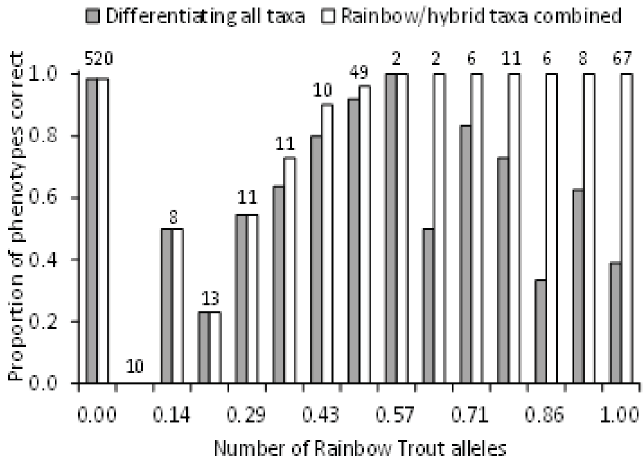

Figure 1. Accuracy of using phenotype to delineate the genotype of Yellowstone Cutthroat Trout, Rainbow Trout, and Cutthroat × Rainbow hybrids with varying proportions of Rainbow Trout alleles in individual fish in Palisades Creek, Idaho. Number of fish examined given above each set of bars.

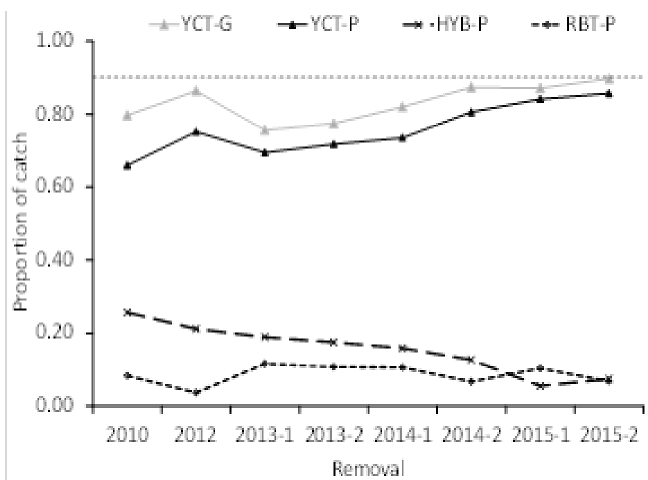

Figure 2. Proportion of the catch during eight backpack electrofishing removals of Yellowstone Cutthroat Trout (YCT), Rainbow Trout (RBT), and hybrids (HYB) in Palisades Creek, Idaho. Shown for Cutthroat Trout are phenotypic (P) and genotypic (G) proportions of the catch, whereas only phenotype is depicted for Rainbow Trout and hybrids. Horizontal line (small dashes) represents the goal of at least 90% of the trout being comprised of Cutthroat Trout.

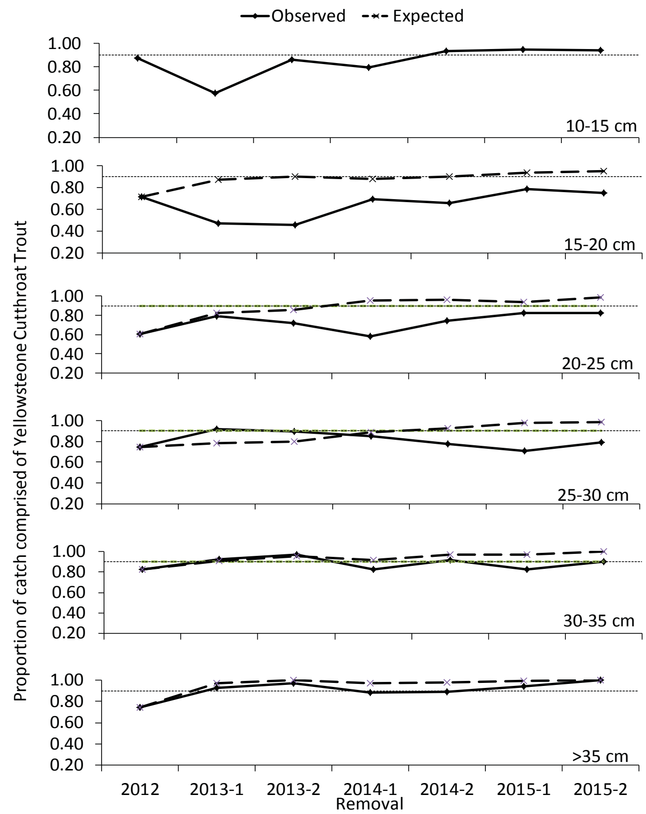

Figure 3. Observed (solid line) and expected (dashed line) proportions of captured fish by 50 mm size groups that were Yellowstone Cutthroat Trout during eight backpack electrofishing removals from 2010 to 2015 in Palisades Creek, Idaho. Horizontal lines (small dashes) represent the goal of at least 90% Cutthroat Trout.

Total trout abundance averaged 5,872 fish (range 4,138-7,830), or 631 trout/km (Table 1). Abundance increased initially for both Yellowstone Cutthroat Trout and Rainbow Trout and hybrids, but by the end of 2015, abundance since 2010 had increased by 48% for Cutthroat Trout and declined by 24% for Rainbow Trout and hybrids.

Capture efficiency for each removal averaged 38% and ranged from a low of 23% for the first removal of 2014 (the removal with the highest stream flow) to a high of 52% for the 2012 removal (when flow was the lowest of any removals). Capture efficiency generally increased as fish size increased.

The proportion of the total catch that Yellowstone Cutthroat Trout comprised increased from 67% in 2010 to 86% by the second removal in 2015 (Figure 2). Within each size class, the proportion of the total

Table 2. Frequency of occurrence of the variations in phenotypic characteristics used to distinguish Yellowstone Cutthroat Trout from Rainbow Trout and hybrids in Palisades Creek, Idaho.

		Genotypic composition (%)			
		Yellowstone Cutthroat	Hybrids		Rainbow
Meristic	Characteristic	Trout	$>F_1$	F_1	Trout
Head spots	Five or more	4.6	68.2	91.2	96.3
	Fewer than five	95.4	31.8	8.8	3.7
Belly	Orange hue	26.1	9.1	5.9	0.0
	White hue	73.9	90.9	94.1	100.0
Pelvic fins	White tips present	0.5	52.3	58.8	100.0
	White tips absent	99.5	47.7	41.2	0.0
Anal fin	White tips present	0.9	56.8	79.4	100.0
	White tips absent	99.1	43.2	20.6	0.0
Dorsal fin	White tips present	0.0	38.6	70.6	88.9
	White tips absent	100.0	61.4	29.4	11.1
Throat slash	Bright red-orange and prominent	89.9	34.1	17.6	0.0
	Dull but continuous	4.1	11.4	17.6	0.0
	Faint and barely visible	6.0	43.2	64.7	59.3
	Absent	0.0	11.4	0.0	40.7
Body spots	Smaller; distributed evenly on sides	3.7	70.5	76.5	100.0
	Larger; clustered dorsally and posteriorly	96.3	29.5	23.5	0.0
Side coloration	Presence of reddish hue	5.5	61.4	85.3	96.3
	Absence of reddish hue	94.5	38.6	14.7	3.7

catch comprised of Yellowstone Cutthroat Trout varied through time (Figure 3). For the smallest size classes (100-200 mm), Cutthroat Trout comprised 75% of the total catch in 2010 and 88% by the second removal of 2015, constituting a 17% increase. In comparison, for intermediate-sized fish (200-299 mm) Cutthroat Trout comprised 60% of the catch in 2010 and 81% by the second removal of 2015 (a 35% increase), and for spawning-sized fish (≥300 mm), Cutthroat Trout comprised 60% of the catch in 2010 and 91% by the second removal of 2015 (a 52% increase).

For small and medium size classes of fish, the decline in the proportion of the total catch comprised of Rainbow Trout and hybrids did not keep pace with expectations, whereas for the largest size classes, expectations more closely matched the observed reduction in Rainbow Trout and hybrid composition in the population (Figure 3). A large group of Rainbow Trout and hybrids 100-200 mm in length (mostly age-1 and age-2 fish) was apparent in both 2013 removals (Table 1; Figure 3), which in subsequent years was also apparent in larger size classes, suggesting that 2011 was a successful spawning year for Rainbow Trout and hybrids. By the end of the study, based on initial fish composition and our estimated capture efficiency for each size class during each removal, phenotypic purity for the entire Cutthroat Trout population should have reached 94%, rather than the 86% we observed.

In 2010, across all size classes, genetic analyses indicated that 80% of the alleles were Cutthroat Trout alleles, compared to 67% of the fish being phenotypically classified as Cutthroat Trout. By the final removal effort of 2015, an estimated 90% of the alleles were Cutthroat Trout compared to 86% of the fish. The gap between the number of Cutthroat Trout alleles and fish in Palisades Creek narrowed from the start to the end of the study because the overall abundance of hybrids declined to a greater extent (83% reduction) than did Rainbow Trout abundance (51%; Figure 2).

Purification of the stream worked better in the upper reaches of the stream relative to the lower reaches (Figure 4). In fact, for the smallest size class in the lowest reach, the proportion of the total catch that Yellowstone Cutthroat Trout comprised actually declined through time.

Discussion

The capture efficiencies we achieved and the number of removals we conducted should have reduced the number of non-Cutthroat Trout fish in Palisades Creek to 6% instead of the 14% level that we observed. We believe that one or more of the following issues may have diminished the observed success of the removals relative to expectations. First, this was partly an artifact of our inability to capture small fish, with capture efficiency for fish 100-150 mm in length averaging only 0.11, and for fry being inherently even lower (though we did not empirically measure it). Moreover, extremely high flows throughout 2011 prevented weir operation, and precluded electrofishing removals that year, so that age-0 and age-1 Rainbow Trout and hybrids at the start of the study were not appreciably vulnerable to removal for the first several years of the study. Unusually high flows in 2011 theoretically should have diminished spawning success of Rainbow Trout and hybrids (Fausch et al. 2001) because they spawn in later winter to early spring and fry would have emerged during the height of the spring flooding, but catch data in later years indicated that 2011 was in fact a productive year for *O. mykiss* recruitment.

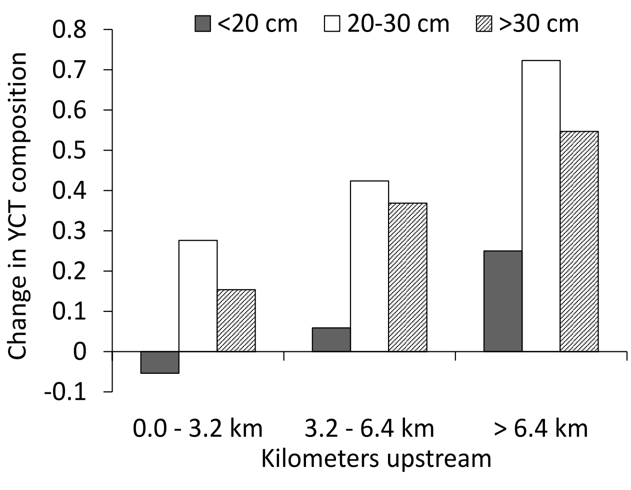

Figure 4. Longitudinal differences in the change (from the first to the last removal effort) in the proportion of the trout population comprised of Yellowstone Cutthroat Trout in Palisades Creek, Idaho.

Another explanation for why expectations lagged behind observed reductions in *O. mykiss* alleles is that the weir on Palisades Creek may not completely block upstream migrating Rainbow Trout and hybrids during operation, or may not be operated long enough each year to block all Rainbow Trout and hybrid spawners attempting to access Palisades Creek. The fact that purification was least effective at the bottom of the study area supports the reinvasion supposition, but the following observations do not: (1) weir efficiency is monitored annually and is usually 90-100% during operation (B. High, unpublished data); (2) the proportion of the catch at the weir comprised of Rainbow Trout and hybrids is already very low in most years (about 6% on average; B. High, unpublished data); (3) the gap in time between the start and end dates of weir operation, and the first and last Rainbow Trout or hybrid caught in the trap each year, indicates that the weir is annually being operated well before and after the spawning run of Rainbow Trout and hybrids occurs; and (4) although the electrical component of the weir is annually deactivated in mid-July, the fish trap is closed when the weir is not being operated, and there is little to no pool for jumping over the waterfall at the weir, so even during the off-season the weir is largely if not completely a barrier to upstream movement. Another potential source of stream recolonization (besides fish getting past the weir) is the few man-made ponds on private property adjacent to the lower 3 km of the treatment reach. In Idaho, IDFG oversees private pond fish stocking regulations and enforcement, and in our study area, any Rainbow Trout stocked on private property must by sterile, though such regulations may be violated by landowners. Private ponds are also required to be screened to prevent fish escapement, and in order to create immediate fisheries, they are usually stocked with catchable-sized fish, which are readily apparent at capture (based on the condition of their fins) but were never encountered during our study. Taken collectively, we deem it unlikely that stream recolonization by any of these means was occurring at a sufficient rate to explain much of the lag in *O. mykiss* allele reduction in Palisades Creek.

One final possibility is that Rainbow Trout and hybrids may have an interspecific competitive or selective advantage over Yellowstone Cutthroat

Trout. For Cutthroat Trout, a competitive disadvantage with nonnative Brook Trout *Salvelinus fontinalis* is fundamentally acknowledged (see review in Dunham et al. 2002), but with Rainbow Trout, competition is considered less important in the extirpation of Cutthroat Trout populations than introgression (Young 1995). Nevertheless, Rainbow Trout and hybrids tend to spawn earlier than Yellowstone Cutthroat Trout (Henderson et al. 2000), giving juvenile fish the additional advantage of larger size stemming from earlier emergence. Results from stochastic Lotka–Volterra modeling applied to long-term population monitoring in the South Fork Snake River suggest that hybridization has been the primary mechanism for reductions in Yellowstone Cutthroat Trout abundance in the river, but direct competition was supported by the models as well (Van Kirk et al. 2010). While some studies suggest that hybrids have reduced fitness compared to parental Westslope Cutthroat Trout *O. c. clarkii* (Muhlfeld et al. 2009), this may not hold true for Yellowstone Cutthroat Trout. Regardless of which of these explanations contributed to the slight lag in purification we observed, we found that after eight removals over five years, the goal of reducing Rainbow Trout and hybrids to ≤ 10% in Palisades Creek, at least at the level of *O. mykiss* alleles in the entire Oncorhynchus population, was nevertheless achieved.

We observed a stronger response to removal of Rainbow Trout and hybrids in upstream reaches of the study area compared to downstream reaches. Since the weir prevents reinvasion of Rainbow Trout and hybrids downstream of the study area, the most likely explanation for the longitudinal gradient we observed in removal response is immigration by Yellowstone Cutthroat Trout from upstream of the natural velocity barrier. Since Rainbow Trout and hybrids are absent upstream of the barrier, any influx of Cutthroat Trout at the upper end of our study area would have biased the computed rate of Rainbow Trout reduction relative to lower reaches of the stream.

Conclusions

While others have shown that removing Rainbow Trout and hybrids from portions of hybridized Cutthroat Trout populations has led to reduced levels of introgression in the population (Al-Chokhachy et al. 2014), our study is the first we are aware of attempting to reduce O. mykiss alleles throughout an entire Cutthroat Trout population. For the Yellowstone Cutthroat Trout population in Palisades Creek, eight electrofishing removals were needed to reduce the percentage of fish with *O. mykiss* alleles from 33% to 14% and the percentage of *O. mykis*s alleles in the population from 20% to 10%. Completely purifying a hybridized Yellowstone Cutthroat Trout population using electrofishing suppression will be difficult, but not impossible if fitness selects against Rainbow Trout alleles (Muhlfeld et al. 2009).

A number of factors should be considered by biologists attempting such a project. Of utmost importance is that the target Cutthroat Trout population be isolated from future Rainbow Trout reinvasion by a downstream barrier. Target populations would ideally reside in streams where high electrofishing capture efficiency (i.e., at least 25-30%) can be achieved so that a meaningful percentage of Rainbow Trout and hybrids can be removed with each electrofishing pass. Biologists must be able to differentiate Cutthroat Trout, Rainbow Trout, and their hybrids with a high degree of accuracy to avoid inadvertently culling Cutthroat Trout or releasing captured hybrids; in our study only 0.5% of the Yellowstone Cutthroat Trout that were captured were mistakenly identified as hybrids, and only 41 of the 897 Rainbow Trout alleles detected in the fish we analyzed genetically were accidentally released due to mistaken identification. If the goal is not complete purification, biologists should recognize that hybridization within Cutthroat Trout populations is a dynamic process influenced by demography, zoogeography, and climate, and is rarely at equilibrium (McKelvey et al. 2016). As such, maintaining the proportion of *O. mykiss* alleles in the treated population below the targeted level may require periodic maintenance electrofishing removals, as has been recommended for nonnative Brook Trout when their complete eradication from Cutthroat Trout streams is not possible (Peterson et al. 2008). Finally, periodic monitoring of genotypic introgression levels in the population should be undertaken to confirm any assessments based on phenotypic characterization.

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