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ARTICLE

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

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

Brett High
Idaho Department of Fish and Game, 4279 Commerce Circle, Idaho Falls, Idaho 83401, USA

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

Abstract
The South Fork of the Snake River in Idaho supports one of the few remaining fluvial populations of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, but long-term persistence of Cutthroat Trout in the drainage is threatened by introgression with introduced Rainbow Trout *O. mykiss*. We completed eight backpack electrofishing removals from 2010 to 2015 to remove Rainbow Trout and Rainbow Trout × Cutthroat Trout hybrids from a 9.3-km isolated reach of Palisades Creek (a tributary of the South Fork) in an attempt to improve the purity of the population. For two removals, fish from 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 removed from the stream. The proportion of the total catch that Yellowstone Cutthroat Trout comprised (across all size-classes combined) increased slowly over time, from 67% in 2010 to 86% for the second removal in 2015. By the end of the study, an estimated 90% of the alleles at the loci we screened were Cutthroat Trout compared with 80% at the beginning. Capture efficiency across all years and size-classes averaged 38%, ranged from 23% to 52%, and was much higher for larger fish (i.e., ≥250 mm TL) than for smaller fish. Considering the capture efficiencies achieved, initial hybridization levels observed, and number of removals conducted, ending phenotypic purity should have been 94% rather than the 86% we observed. This discrepancy was at least partly due to low capture efficiency for fish < 150 mm and extremely high flows throughout 2011 that prevented electrofishing removals that year, but also suggests that Rainbow Trout and hybrids somehow might have been recolonizing the stream or had a competitive or survival advantage over Cutthroat Trout.

Rainbow Trout *Oncorhynchus mykiss* is globally one of most widely introduced species of fish outside their native range (MacCrimmon 1971; Fausch et al. 2001). Rainbow Trout are often (but not always) well adapted to these new environments and have consequently 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. In western North America, hybridization between native Cutthroat Trout *O. clarkii* and introduced Rainbow Trout has been a leading cause in the decline of many subspecies of Cutthroat Trout (Young 1995; Behnke 2002). As an example, the South Fork of the Snake River in Idaho supports one of the few remaining fluvial populations of Yellowstone Cutthroat Trout *O. clarkii bouvieri* (Thurow et al. 1988; Gresswell 2011), but their long-term persistence is threatened by the presence and possible expansion of Rainbow Trout and Rainbow Trout × Cutthroat Trout hybrids (High 2010). Controlling the abundance and spread of Rainbow Trout and hybrids in the South Fork drainage is a high priority for many

*Corresponding author: kevin.meyer@idfg.idaho.gov
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governmental and nongovernmental organizations, including the Idaho Department of Fish and Game (IDFG 2007), which manages the fishery.

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; Leary et al. 1995; Allendorf et al. 2001; Muhlfeld et al., in press). An alternate viewpoint argues that longitudinal gradients in introgression are more common in hybridized populations of Cutthroat Trout, and hybrid zones are 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; Young et al. 2016, in press). While resolving these dichotomous views is crucial for long-term, broad-scale Cutthroat Trout conservation, removing Rainbow Trout and hybrids within any given isolated Cutthroat Trout population should theoretically reduce both the rate and spread of hybridization in that population (e.g., Host 2003; Al-Chokhachy et al. 2014). While the value of hybridized populations of Cutthroat Trout has been intensively debated (Allendorf et al. 2004, 2005; Campton and Kaeding 2005), representatives from most fish and wildlife management agencies in the western United States have collectively developed a Cutthroat Trout conservation strategy that includes three categories for classifying populations (UDWR 2000): core (<1% introgressed), conservation (1–10% introgressed), and sport fish (>10% introgressed) populations. The goal of conserving as many populations in core and conservation categories as possible implies that shifting populations from a lower to a higher purity level would also be beneficial.

Prior attempts to eradicate nonnative salmonids from streams have produced mixed results. The use of fish toxicants such as antimycin and rotenone have been successful at removing nonnative salmonids from streams (e.g., Gresswell 1991), but the use of such piscicides often results in incomplete removal of target populations (reviewed in Meronek et al. 1996). Moreover, piscicides kill nontarget species as well (such as remnant Cutthroat Trout that biologists are often attempting to conserve), and biologists must consider the negative perception that application of piscicides sometimes evokes from the public (Finlayson et al. 2010; Billman et al. 2012). 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; Meyer et al. 2006a; Peterson et al. 2008; Carmona-Catot et al. 2010) 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 (Kulp and Moore 2000; Shepard et al. 2014).

While removal of undesirable nonnative fish taxa has proven difficult, most of the aforementioned electrofishing removal attempts have targeted nonnative Brook Trout *Salvelinus fontinalis*. Relative to most other salmonids, Brook Trout mature at an early age and are often able to withstand intense removal pressure with little impact on their abundance or survival (e.g., Meyer et al. 2006a). Rainbow Trout may not be as resilient as Brook Trout to sustained intensive removal pressure because they typically mature later in life (Meyer et al. 2014). Our objective was to transform a Cutthroat Trout population known to be heavily hybridized (>25% introgressed) into a minimally hybridized population (i.e., <10% introgressed).

STUDY AREA

Palisades Creek is a fourth-order stream (1:24,000 hydrologic scale) with a mean width of approximately 10 m and an average gradient of approximately 2.0%. The fish community is predominantly Yellowstone Cutthroat Trout, nonnative Rainbow Trout, and their hybrids. Although a few wild Brown Trout *Salmo trutta* and Mountain Whitefish *Prosopium williamsoni* are also present, they comprise <1% of the salmonid population and were not included in any aspects of our study. Paiute Sculpin *Cottus beldingi* are the only known nongame fish present.

The main stem of Palisades Creek is about 30 km in length. However, about 10 km upstream from the confluence with the South Fork of the Snake River, there is a high-gradient, cascading section that fish surveys have identified as a natural velocity barrier to fish (K. A. Meyer, unpublished data); Rainbow Trout and hybrids have not been observed upstream from this barrier (Meyer et al. 2006b), although Yellowstone Cutthroat Trout and Paiute Sculpin are present above the barrier. Consequently, removal of Rainbow Trout and hybrids from Palisades Creek occurred only in the lower portion of the stream.

In an attempt to prevent upstream migration of Rainbow Trout and hybrids into Palisades Creek, various weirs have been operated in the lower end of the creek by Idaho Department of Fish and Game since the year 2000. Most of these weirs were not highly efficient or could not be operated during high spring flows, when Rainbow Trout migrate into spawning tributaries in this system (High 2010). In 2009, a permanent electric weir was installed on Palisades Creek about 0.7 km upstream from the confluence with the main stem (High 2010; Larson et al. 2014); when in operation the electric weir is 90–100% efficient at stopping upstream-migrating Rainbow Trout (B. High, unpublished data).

METHODS

Rainbow Trout and hybrid removal.—We used backpack electrofishers to conduct removals of Rainbow Trout and hybrids from the electric weir upstream about 9.3 km to the natural velocity barrier noted above. Removals were conducted 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 1 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, because of damaging high flows, the electric weir failed in 2011 early in the spawning run and 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.

During removals, teams with backpack electrofishers and nets fished sequential stream sections of about 800 m. Electrofishing teams consisted of three or four people operating backpack electrofishers and two or more additional people with nets and buckets, and crew size depended on stream flow and staff availability. We used a pulsed-DC waveform operated at 60 Hz, 200–600 V, and a 2–5-ms pulse width. During sampling, crew members with backpack electrofishers sampled all available habitats. Where gradient was too steep to effectively net fish, one electrofisher was used to chase trout downstream out of the steep section and into an area with slower water velocity where fish could be more easily immobilized and netted, while the remaining electrofishers were used to block the downstream end of the slower water.

We sedated all captured trout with peppermint oil, identified them to species (hybrids were classified as a separate taxa), and measured their TL. Taxa were separated based on previous studies (Campbell et al. 2002; Meyer et al. 2006b, 2017), which have 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 than five spots on the top of the head (excluding one spot by each naris, which are common on pure Yellowstone Cutthroat Trout), (3) a bright red-orange throat slash, and (4) spots on the side of the body clustered dorsally and posteriorly; for more details on characteristics used to separate these three taxa, see Meyer et al. (2017). Trout < 100 mm comprised <5% of the total catch, were too small to effectively capture in this stream, and are difficult to accurately differentiate (based on phenotype) for these taxa (Miller 1950; Martinez 1984; Seiler et al. 2009). For these reasons trout < 100 mm were not included in our analyses or summaries of data, although fish of this size that were captured and identified to be Rainbow Trout or hybrids were removed from the stream.

In the lower 4 km of Palisades Creek, a road paralleled the stream, and we removed Rainbow Trout and hybrids in this section and transported them with hatchery trucks to nearby community fishing waters. In the roadless section of stream we euthanized Rainbow Trout and hybrids after capture. We released all Yellowstone Cutthroat Trout after they recovered from sedation.

For six of the eight removals we conducted mark–recapture abundance estimates. To do this, we collected, measured, and marked fish with an upper or lower caudal fin clip several days before the removals. Only Yellowstone Cutthroat Trout ≥ 100 mm TL were marked, whereas all Rainbow Trout and hybrids that were encountered during the marking runs (including those < 100 mm) were removed from the stream. We used the Fisheries Analysis + software package (MFWP 2004) to estimate trout abundance using the modified Peterson estimator. Separate abundance estimates were made for the smallest size-groups possible (usually 50 mm) having at least three recaptured, marked fish per group in order to satisfy model assumptions. We assumed that there was (1) no mortality of marked fish, (2) no movement of marked or unmarked fish out of Palisades Creek between the marking and recapture run, and (3) no difference in capture efficiency between Cutthroat Trout, Rainbow Trout, and hybrids. This last assumption allowed us to remove Rainbow Trout and hybrids during the marking run rather than marking and releasing them. This assumption seemed justified because these taxa have similar behavioral characteristics (Griffith 1988; Behnke 2002) and because previous mark–recapture electrofishing surveys of these taxa in eastern Idaho have produced similar capture efficiencies (High, unpublished data). We pooled all trout together for an overall estimate of trout abundance (cf., Mullner et al. 1998; Isaak and Hubert 2004) and estimated abundance for each species (hybrids were grouped with Rainbow Trout for abundance estimates) based on the proportion of catch comprised by each species in each size-group during the recapture run (cf., Meyer et al. 2014). 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 of fish marked.

Genetic analyses.—In 2012 and the first removal of 2015, we collected genetic samples to (1) estimate the proportion of Rainbow Trout genetic admixture in the population early in the project and at the end of the study and (2) confirm the accuracy of phenotypic-based fish identification (also see Meyer et al. 2017). Genetic samples (i.e., small fin clips) were generally collected from the first 30 fish captured from each 800-m section during these two removals.

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 Rodriguez 2002). We classified fish as Yellowstone Cutthroat Trout if they were homozygous for *O. clarkii bouvieri* alleles at all loci, Rainbow Trout if they were homozygous for *O. mykiss* alleles at all loci, and hybrids if they possessed a mixture of alleles from the two parental species. For each individual fish, using seven codominant nDNA loci gave us a 90% probability of detecting introgression at 15% or greater.

A change in the proportion of parentals, F_1 generation fish, and backcrosses from 2012 to 2015 was assessed by comparing cumulative length frequencies with the Kolmogorov–Smirnov goodness-of-fit procedure. The level of introgression was calculated two ways: (1) the proportion of non-Cutthroat

Trout fish captured in the population (herein termed phenotypic introgression) and (2) the proportion of non-Cutthroat Trout alleles in the population (herein termed genotypic introgression).

Phenotypic introgression was calculated simply as the number of non-Cutthroat Trout caught in each removal divided by all *Oncorhynchus* captured. Observed levels of phenotypic introgression were compared with 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 1 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 (Carlander 1969). 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 our genetic findings, because not all captured fish were genetically analyzed in the years genetic samples were processed, and genetic samples were analyzed in only two of the eight removals. All captured fish that were 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. Because the average number of *O. mykiss* alleles in hybrids were equivalent in genetic samples from 2012 (mean = 6.4 out of 14) and 2015 (mean = 6.6), we assumed that hybrids had, on average, 6.5 *O. mykiss* alleles for all removals for which genetic samples were not collected.

Characterizing Rainbow Trout introgression at the levels of both individual fish and alleles in the population was considered important because they can potentially lead to markedly different conclusions. As an example, suppose hypothetically that in a hybridized Cutthroat Trout population of 100 total fish, 80 fish were pure Cutthroat Trout and the remainder were either Rainbow Trout or hybrids. We would phenotypically characterize such an *Oncorhynchus* population as 20% non-Yellowstone Cutthroat Trout. However, if only five fish were pure Rainbow Trout, and for the 15 hybrids the percentage of alleles that were *O. mykiss* were the same as our average above (i.e., 46%), then genotypic introgression in the entire *Oncorhynchus* population would be 12% non-Yellowstone Cutthroat Trout.

Both characterizations of introgression assumed that all phenotypic designations were accurate and that the entire *Oncorhynchus* population formed a randomly mating population. Regarding the first assumption, our phenotypic designations agreed with the genotype of the fish with a high degree of accuracy (see Results), thus mistakes in phenotyping individual fish likely had a negligible effect on our findings and conclusions. Regarding the assumption that all *Oncorhynchus* formed a randomly mating population, results from a Hardy–Weinberg exact test (with the software program Genepop; http://genepop.curtin.edu.au/) suggested there was some level of assortative reproduction in Palisades Creek; however, the presence of large numbers of hybrids each year in this isolated stream clearly indicated that hybridization between parental species was common and recurrent.

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 consequently removed from the stream (Table 1). An additional 200 Rainbow Trout and hybrids were caught and removed during the fish marking runs (across all years) 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).

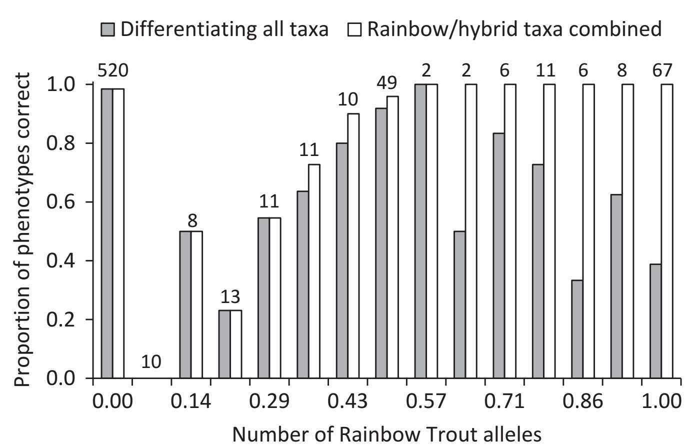

FIGURE 1. Accuracy of using phenotype to delineate the genotype of Yellowstone Cutthroat Trout, Rainbow Trout, and Cutthroat Trout × Rainbow Trout hybrids with varying proportions of Rainbow Trout alleles in individual fish in Palisades Creek, Idaho.

TABLE 1. Mark–recapture population abundance estimates by year (and removal effort) 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.

	Rainbow Trout and hybrid abundance						Yellowstone Cutthroat Trout abundance		
	<20 cm		20–29 cm		≥30 cm				
Year (removal effort)	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			

Total trout abundance (all *Oncorhynchus* combined) averaged 5,872 fish (631 trout/km) and ranged from 4,138 to 7,830 fish during the study (Table 1). Abundance increased initially for both Yellowstone Cutthroat Trout and Rainbow Trout and hybrids, but by the final population estimate in 2015, abundance since 2010 had increased by 48% for Cutthroat Trout and declined by 24% for Rainbow Trout and hybrids. Fish 100–200 mm in length made up the bulk of the abundance estimates for both Yellowstone Cutthroat Trout (64% on average) and Rainbow Trout and hybrids (64%), whereas large fish (≥300 mm) comprised a small proportion of Yellowstone Cutthroat Trout (8%) and an even smaller proportion (3%) of Rainbow Trout and hybrids.

Capture efficiency for each removal averaged 38% and ranged from a low of 23% for the first removal of 2014 (when stream flow was the highest for any removals) to a high of 52% for the 2012 removal (when flow was the lowest for any removals; Table 2). Capture efficiency generally increased as fish size increased.

The proportion of the total catch comprising Yellowstone Cutthroat Trout increased slowly over time, from 67% (across all size-classes combined) in 2010 to 86% by the second removal in 2015 (Figure 2). However, within each size-class, the proportion of the total catch that Yellowstone Cutthroat Trout comprised 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; this constituted only a 17% increase in Cutthroat Trout composition. 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 consisting 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),

TABLE 2. Number of marked fish (m) and capture efficiency (CE; i.e., the proportion of marked fish caught in the recapture run) for various size-groups of Yellowstone Cutthroat Trout during six different removal efforts from 2012 to 2015 in Palisades Creek, Idaho.

	2012		2013 (1)		2013 (2)		2014 (1)		2014 (2)		2015 (1)		Combined	
Size-group (mm)	m	CE	m	CE	m	CE	m	CE	m	CE	m	CE	m	CE
100–149	13	0.00	13	0.00	24	0.13	35	0.14	24	0.13	44	0.23	153	0.14
150–199	32	0.38	16	0.25	20	0.50	38	0.21	12	0.33	12	0.17	130	0.31
200–249	33	0.45	15	0.20	25	0.24	19	0.26	21	0.43	17	0.76	130	0.39
250–299	44	0.64	13	0.08	30	0.57	6	0.33	10	0.60	19	0.47	122	0.52
300–349	20	0.85	13	0.54	22	0.32	8	0.63	10	0.70	9	1.00	82	0.63
350–499	8	0.75	11	1.00	8	0.25	12	0.17	7	0.71	4	1.00	50	0.60
Total	150	0.52	81	0.32	129	0.35	118	0.23	84	0.40	105	0.45	667	0.47

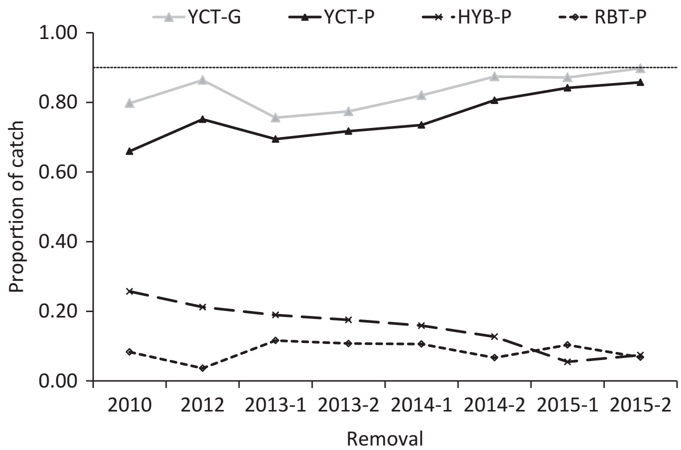

FIGURE 2. Proportion of the catch during eight backpack electrofishing removals of Yellowstone Cutthroat Trout (YCT), Rainbow Trout (RBT), and hybrids (HYB) in Palisades Creek, Idaho. Phenotypic (P) and genotypic (G) proportions of the catch are shown for Cutthroat Trout, whereas only phenotype is depicted for Rainbow Trout and hybrids. The dashed horizontal bar represents the goal of at least 90% of the trout are composed of Cutthroat Trout.

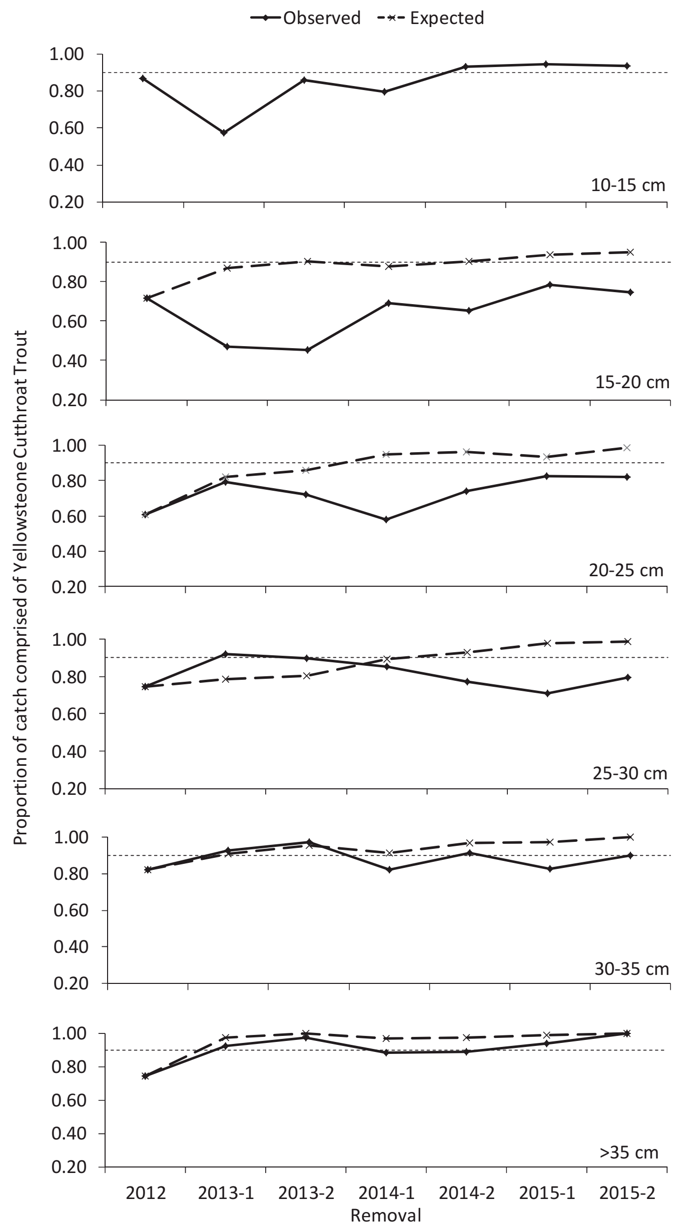

FIGURE 3. Observed proportion of captured fish by 50-mm size-groups that were Yellowstone Cutthroat Trout during eight backpack electrofishing removals from 2010 to 2015 in Palisades Creek, Idaho. Also plotted are expected proportions (starting in 2013) based on the initial composition of the fish population and subsequent capture efficiencies achieved each year; for the smallest size-group expectations could not be calculated (see text for details). Dashed horizontal bars represent the goal of at least 90% of the trout are composed of Cutthroat Trout.

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 with 67% of the fish being phenotypic Cutthroat Trout. By the final removal effort of 2015, an estimated 90% of the alleles were Cutthroat Trout compared with 86% of the fish that were phenotypic Cutthroat Trout. The gap between the number of alleles and the number of fish that were Cutthroat Trout 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). However, among the subsample of fish that were genotyped, the proportion of parentals, F_1 generation fish, and backcrosses did not differ from 2012 to 2015 (Kolmogorov–Smirnov goodness-of-fit test: D = 0.27, P = 0.66; Figure 4).

Purification of the stream worked better in the upper reaches of the stream relative to the lower reaches (Figure 5). 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

Palisades Creek is a relatively wide, steep, swift, and deep mountain stream that is difficult to sample effectively with backpack electrofishers, as evidenced by the 23–52% capture efficiencies we achieved across all removals. However, even in much smaller streams that are less complex and with significantly less stream flow, achieving capture efficiency above 50% with backpack electrofishers can be difficult (Peterson

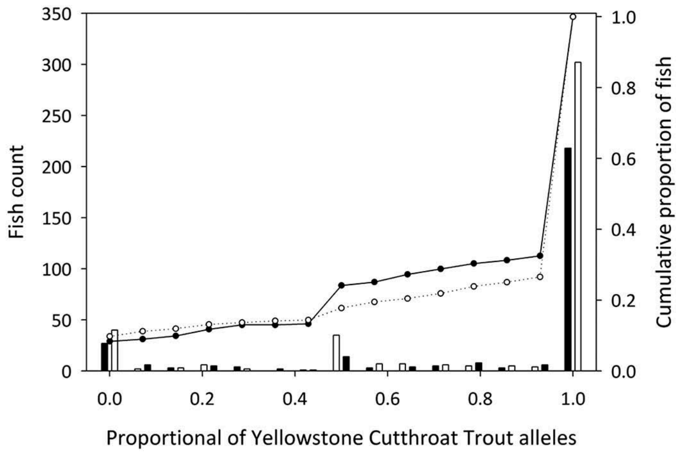

FIGURE 4. Count and cumulative proportion of genotyped fish with varying levels of Yellowstone Cutthroat Trout alleles in 2012 (solid circles and bars) and 2015 (open circles and bars) in Palisades Creek, Idaho.

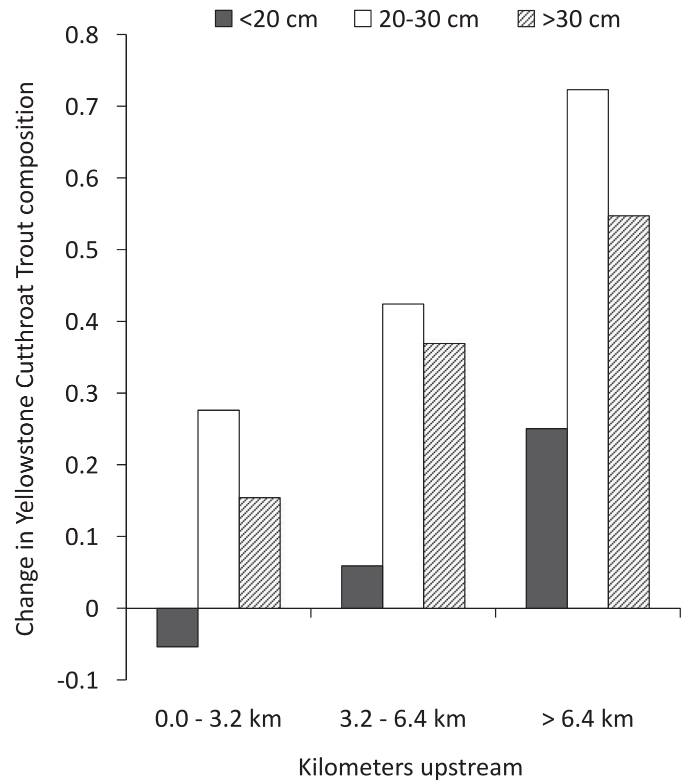

FIGURE 5. Longitudinal differences in the change (from the first to the last removal effort) in the proportion of the trout population comprised of Yellowstone Cutthroat Trout in Palisades Creek, Idaho.

et al. 2004; Meyer and High 2011). Capture efficiency was highest for larger fish, which is typical of backpack electrofishing (Mahon et al. 1979; Meyer and High 2011). Higher removal efficiency of spawning-sized fish should have minimized recruitment of Rainbow Trout and hybrids in our study over time (except in 2011 when high flows damaged the weir and interrupted operation), but the abundance of the smallest Rainbow Trout and hybrids diminished at a slower rate than expected. Nevertheless, the capture efficiencies we achieved should have been adequate to reduce the number of non-Cutthroat Trout fish in the stream to 6%, instead of the 14% level that we observed.

The difference between observed and expected levels of reduction in Rainbow Trout and hybrid abundance in Palisades Creek for the smallest fish suggests one or more of the following factors diminished the success of the removals. First and foremost, this was at least partly an artifact of our inability to capture small fish, with capture efficiency for the smallest size-class in our study (100–150 mm) averaging only 0.11 and for fry being inherently even lower (though we did not empirically evaluate this). Moreover, as mentioned previously, extremely high flows throughout 2011 prevented weir operation and precluded electrofishing removals that year, so age-0 and age-1 Rainbow Trout and hybrids at the start of the study were not appreciably vulnerable to removal by electrofishing for the first several years of the study (until they reached a size large enough to effectively capture them). Unusually high flows in 2011 theoretically should have diminished spawning success of Rainbow Trout and hybrids (Fausch et al. 2001), but the catch of Rainbow Trout and hybrids in later years indicated that 2011 was in fact a productive year for *O. mykiss* recruitment. These observations support the conclusion that the lack of removals and weir failure in 2011, and our general inability (throughout the study) to capture fry and juvenile Rainbow Trout and hybrids with backpack electrofishers, were two of the primary reasons why expectations lagged behind observed reductions in *O. mykiss* alleles.

Another factor that may have diminished the success of *O. mykiss* allele reduction (relative to expectations) is the possibility that the weir on Palisades Creek did not completely block upstream-migrating Rainbow Trout and hybrids during operation, or was not 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 in the lowermost portion 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 (High, unpublished data), (2) the proportion of the catch at the weir consisting of Rainbow Trout and hybrids is already very low in most years (about 6% on average: 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 presence of the few artificial ponds that reside on private property adjacent to the lower 3 km of the treatment reach. In Idaho, the Idaho Department of Fish and Game oversees fish stocking regulations and enforcement for private ponds, and in the South Fork of the Snake River drainage any Rainbow Trout stocked by landowners on their property must be 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); fish from this source 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.

Another possible explanation is that we assumed the capture efficiency for Rainbow Trout and hybrids was equivalent to Yellowstone Cutthroat Trout so that we could remove every Rainbow Trout and hybrid we captured during the study, rather than marking and releasing them during the marking runs. However, if capture efficiency was actually lower for Rainbow Trout and hybrids then we may have overestimated our ability to remove Rainbow Trout and hybrids from the stream. Capture efficiency can vary between salmonid taxa with widely disparate, instream behavioral patterns (Peterson et al. 2004), but Yellowstone Cutthroat Trout, Rainbow Trout, and their hybrids are behaviorally very similar (Behnke 2002; Seiler and Keeley 2007a, 2007b, 2009; Gresswell 2011). Moreover, at the nearest electrofishing reach annually monitored on the South Fork of the Snake River, capture efficiency from 2010 to 2015 for Yellowstone Cutthroat Trout and Rainbow Trout plus hybrids averaged 0.10 and 0.08, respectively (High, unpublished data), suggesting that differing capture efficiency between taxa is unlikely to explain our findings.

One final possibility explaining why observed *O. mykiss* suppression for small fish lagged expectations is that Rainbow Trout and hybrids of this size may have an interspecific competitive or selective advantage over Yellowstone Cutthroat Trout. For Cutthroat Trout, a competitive disadvantage with nonnative Brook Trout 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; Gresswell 2011). Nevertheless, in a series of laboratory experiments on juvenile fish, Seiler and Keeley (2007a, 2007b, 2009) found that juvenile Yellowstone Cutthroat Trout had less success in occupying feeding stations, captured a lower proportion of food, had a lower sustained swimming velocity, and had lower growth rates than did juvenile Rainbow Trout and hybrids when in sympatry. Rainbow Trout and hybrids tend to spawn earlier than Yellowstone Cutthroat Trout (Henderson et al. 2000; DeRito et al. 2010), 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 of the 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 the results of a number of studies suggest that hybrids have reduced fitness compared with parental Westslope Cutthroat Trout *O. clarkii lewisi* (Muhlfeld et al. 2009; Kovach et al. 2015, 2016), this may not hold true for Yellowstone Cutthroat Trout. If Rainbow Trout or hybrids had even a slight competitive or survival advantage over Yellowstone Cutthroat Trout in Palisades Creek, we would have overestimated Cutthroat Trout proportions when projecting the proportions of each taxa within a given size-class forward in time.

In reality, several of these explanations probably contributed to the finding that Rainbow Trout and hybrid removals did not fully meet our Cutthroat Trout purification expectations. Despite this, we found that after eight removals over 5 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 achieved.

We observed a stronger response to the removal of Rainbow Trout and hybrids in upstream reaches of the study area. 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 from the barrier, any influx of Cutthroat Trout at the upper end of our study area would have artificially increased the rate of Rainbow Trout reduction relative to that in lower reaches of the stream. Downstream migration of individuals from isolated upstream Coastal Cutthroat Trout *O. clarkii clarkii* populations has been investigated (Gresswell and Hendricks 2007), but the magnitude of this type of movement for inland subspecies of Cutthroat Trout is poorly understood.

Conclusions

While previous studies have demonstrated that removing Rainbow Trout and hybrids from portions of hybridized Cutthroat Trout populations led to reduced levels of introgression in the population (Host 2003; 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. mykiss* 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 (Kovach et al. 2016).

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 the installation of a downstream barrier or weir. A weir can function as a barrier throughout the entire year but has the added advantage of allowing biologists to pass pure Cutthroat Trout over the weir to augment the existing resident population. Populations targeted for such projects 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. While differentiation of these taxa is relatively straightforward in Yellowstone Cutthroat Trout populations (Meyer et al. 2017), delineating taxa can be more difficult for other subspecies of Cutthroat Trout (Weigel et al. 2002; Baumsteiger et al. 2005). 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 (Young et al. 2016; Muhlfeld et al., in press). 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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