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Quantifying the Effectiveness of Conservation Measures to Control the Spread of Anthropogenic Hybridization in Stream Salmonids: a Climate Adaptation Case Study

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MANAGEMENT BRIEF

Quantifying the Effectiveness of Conservation Measures to Control the Spread of Anthropogenic Hybridization in Stream Salmonids: a Climate Adaptation Case Study

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Abstract

Quantifying the effectiveness of management actions to mitigate the effects of changing climatic conditions (i.e., climate adaptation) can be difficult, yet critical for conservation. We used population genetic data from 1984 to 2011 to assess the degree to which ambient climatic conditions and targeted suppression of sources of nonnative Rainbow Trout \textit{Oncorhynchus mykiss} have influenced the spread of introgressive hybridization in native populations of Westslope Cutthroat Trout \textit{O. clarkii lewisi}. We found rapid expansion in the spatial distribution and proportion of nonnative genetic admixture in hybridized populations from 1984 to 2004, but minimal change since 2004. The spread of hybridization was negatively correlated with the number of streamflow events in May that exceeded the 75th percentile of historic flows ($r = -0.98$) and positively correlated with August stream temperatures ($r = 0.89$).

Concomitantly, suppression data showed a 60% decline in catch per unit effort for fish with a high proportion of Rainbow Trout admixture, rendering some uncertainty as to the relative strength of factors controlling the spread of hybridization. Our results illustrate the importance of initiating management actions to mitigate the potential effects of climate change, even where data describing the effectiveness of such actions are initially limited but the risks are severe.

Species with limited capacities for range shifts are anticipated to be especially vulnerable under global climate change (Walther et al. 2002; Thomas et al. 2004; Calkins et al. 2012). In lieu of rapid evolutionary adaptation or phenotypic plasticity (Bradshaw and Holzapfel 2006; Donelson et al. 2012; Vedder

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et al. 2013), management actions to reduce limiting factors in response to changing climatic conditions (i.e., climate adaptation; West et al. 2009) represent the most plausible means to enhance persistence of dispersal-limited species or populations (IPCC 2007; Petorelli 2012). The effectiveness of management and conservation actions within a climate adaptation framework, however, is often poorly understood (Lawler et al. 2010; Morecroft et al. 2012).

In many cases, data collected to specifically assess the relative influence of climate change on biological patterns and processes among other stressors are limited, forcing managers to assemble existing data and adjust conservation strategies under an adaptive framework (Lawler et al. 2010; Nichols et al. 2011; Cross et al. 2013). Here, we present a climate adaptation case study where we evaluate the benefits of early actions to control the spread of hybridization between native Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* and nonnative Rainbow Trout *O. mykiss*, the most widely introduced salmonid worldwide (Halverson 2011). Rainbow Trout are successful in a wide range of environmental conditions, and their introduction has led to the establishment of wild populations with a widespread geographic distribution (Currie et al. 1998). Cutthroat Trout and Rainbow Trout have considerable overlap in life history and behavior and readily interbreed, making anthropogenic hybridization a primary factor in the decline of the many of the subspecies of inland Cutthroat Trout in North America (e.g., Busack and Gall 1981; Campbell et al. 2002; Peacock and Kirchoff 2004; Pritchard et al. 2007; Metcalf et al. 2008; Rasmussen et al. 2010). Introgressive hybridization can disrupt locally adapted gene complexes that confer ecological adaptations in native populations and can lead to genomic extinction of the native taxon (Rhymer and Simberloff 1996; Allendorf et al. 2001; Roberts et al. 2010).

Several studies have illustrated a strong linkage between ambient climate conditions and the prevalence of hybridization between Westslope Cutthroat Trout and Rainbow Trout within stream networks (Fausch et al. 2001; Muhlfeld et al. 2009b; Bennett et al. 2010; Rasmussen et al. 2010; Yau and Taylor 2013). However, a paucity of empirical data exists describing how climate change may influence the spread and severity of hybridization over time. Understanding the mechanisms that influence hybridization (e.g., Marchetti et al. 2004) is imperative for developing effective conservation and management programs in freshwater systems. In many cases, hybridization is likely to increase if source populations with high proportions of nonnative genetic admixture are not reduced or eliminated. Suppression treatments have been implemented in several systems in the western United States to conserve key populations of native Cutthroat Trout. For example, piscicides (e.g., USFS 2006), isolation strategies (e.g., High et al. 2008), and fish removals (e.g., Noringer and Rahel 2003) have been used to mitigate the spread of hybridization and to protect nonhybridized populations. To our knowledge, however, no studies have assessed the effectiveness of such control measures in connected metapopulations over time. Here, we capitalize on existing genetic samples collected over the past 30 years to (1) evaluate the spread in severity and spatial distribution of hybridization between native Westslope Cutthroat Trout and nonnative Rainbow Trout, (2) identify whether climate attributes are associated with the changes in distribution, and (3) adaptively assess the effectiveness of controlling source populations to stem the spread of hybridization.

**METHODS**

**Study site.**—Our study area included tributaries to the North Fork, Middle Fork, and main-stem Flathead rivers in the upper Flathead River drainage in northwestern Montana and southeastern British Columbia (Figure 1). The basin encompasses approximately 10,086 km² and is largely under public ownership (98%). The study area is topographically diverse with elevations ranging from 953 to 3,040 m, and vegetation is dominated by native conifer Coniferae and poplar *Populus* spp. Climate within the study area is characterized by relatively cold, wet winter and spring months and relatively warm, dry summers. Streamflows are typical of the northern Rocky Mountains with highest spring flows during May and June, which taper throughout the summer and early winter. The stream network includes approximately 6,857 km of connected streams; while natural barriers do exist, the majority of these occur in the upper portions of tributary streams.

Despite agency stocking of over 20 million Rainbow Trout into the lower Flathead River, from the late 1800s and ending in 1969 (Hitt et al. 2003), the upper Flathead River system is considered a rangewide stronghold for nonhybridized Westslope Cutthroat Trout (Shepard et al. 2005). This interconnected drainage contains migratory (fluvial and adfluvial) and resident populations of Westslope Cutthroat Trout, a species of special concern in Montana and a blue-listed species at risk in British Columbia. Westslope Cutthroat Trout exhibit complex life histories, and adults migrate from Flathead Lake and Flathead River in Montana to spawn in streams within the North Fork and Middle Fork drainages (Muhlfeld et al. 2009a). Spawning typically occurs during the descending limb of the hydrograph (late May to mid-June).

**Genetic sampling.**—Genetic sampling occurred during the summer months (late July through early September) of 1984, 1998, 2004, 2008, and 2011, and included samples from 60 sites within the study area (Figure 1). The number of repeat samples at any given site varied from one to four based on logistical constraints. Fish were captured via electrofishing methods in stream reaches ranging from 250 m to 1 km to minimize sampling of related individuals. Additionally, we took the following measures to minimize the possibility of introducing a bias to our admixture estimates by sampling full siblings: (1) samples were collected over extensive stream reaches to account for any localized philopatry; (2) no more than 10% of any sample was composed of fry, and any fry that were sampled were collected...
FIGURE 1. A map of the study area including genetics sampling locations (black circles) and source of nonnative Rainbow Trout (grey triangle) in the Flathead River basin in northwest Montana and southern British Columbia; the upper inset demonstrates the location of the Flathead River basin in North America, and the lower inset is a magnified view of the box indicating the locations of (A) Abbot Creek, (B) Ivy Creek, (C) Rabe Creek, (D) Sekokini Creek, and (E) Third Creek, where removal efforts were used to reduce the source population of fish with high proportions of Rainbow Trout admixture.
from distant locations along the sampling reach (it can take several months for emerging fry to disperse from the redd); and (3) genetic samples from each time period contain a minimum of three, and may contain as many as five year-classes (based on length). Total lengths were recorded, and a portion of the fish tissue was excised and stored in a 95% solution of ethanol.

The vast majority (90%) of sampled trout were less than 200-mm TL (age 1, age 2, and age 3). The total number of individuals varied across years, including 214 fish from nine sites in 1984, 346 fish from 20 sites in 1998, 847 fish from 32 sites in 2004, 382 fish from 18 sites in 2008, and 506 fish from 20 sites in 2011. Sample sizes included all fish (pure Cutthroat Trout and hybrids). Based on the lengths of the sampled fish and the time of year they were collected, all sampled individuals were either resident life history forms or the juvenile progeny of resident or migratory life history forms. Therefore, our samples almost undoubtedly represent individuals produced from natural reproduction in the stream from which they were collected.

We used species-specific diagnostic loci to genotype individuals and estimate the proportion of admixture in populations. The proportion of admixture was calculated as the average frequency of diagnostic Rainbow Trout alleles among individuals in a sample. Hybridization was declared present in a tributary if Rainbow Trout alleles were detected in the sample at one or more loci. A tributary was considered to be nonhybridized (i.e., pure Westslope Cutthroat Trout) if no Rainbow Trout alleles were detected in the sample.

The technology used to obtain genetic data has evolved tremendously in the last three decades, and this is evident in the range of techniques and marker types used to genotype samples from trout populations considered in this study. Allozyme electrophoresis (six diagnostic allozymes) was used to obtain genotypes from samples collected in 1984; genotype data from 1998 was obtained using paired interspersed nuclear element PCR (PINE PCR; six diagnostic PINES) techniques; samples collected in 2004 and 2008 were genotyped using 7 and 11 microsatellites, respectively; and 2011 samples were genotyped using 13 diagnostic indel–microsatellites. Specific details on diagnostic loci and allele frequencies have been documented previously (Huston 1988; Hitt et al. 2003; Boyer et al. 2008; Leary 2011).

Although the class (i.e., allozyme, PINE, microsatellite, insertion or deletion) of genetic marker differed and the number of diagnostic loci varied somewhat across sampling periods, estimates of population admixture are nonetheless comparable across sites through time. For example, with the population sample sizes and number of diagnostic loci considered here, the probability of detecting as little as 1% genetic admixture from Rainbow Trout in a hybrid swarm was greater than 0.95 for all sample sites and years (Boecklen and Howard 1997). Furthermore, high concordance between SNP- (single nucleotide polymorphism) and microsatellite-based estimates of population admixture has been observed for salmonids (Spruell et al. 2001; Hohenlohe et al. 2013), indicating that this population genetic parameter can reliably be compared across marker classes.

**Nonnative removal data.**—Radiotelemetry (Muhlfeld et al. 2009a) and genetic data (Hitt et al. 2003; Boyer et al. 2008) were used to identify sources of Rainbow Trout hybridization and patterns of invasion in the Flathead River system. Based on these data, fish managers implemented a hybrid trout suppression program using a combination of trapping and electrofishing to capture and remove mature hybrids with high proportions of Rainbow Trout admixture from the known source population and spawning tributaries.

Beginning in 2000, a migrant weir was installed at the mouth of Abbot Creek, a tributary downstream of an historical, but currently defunct, private Rainbow Trout hatchery that operated from 1969 through 1997, which is considered the major source of Rainbow Trout in the study area (Hitt et al. 2003). The trap was operated continuously from March through May during the spawning period; trapping efficiency was relatively high, although there were brief periods during peak runoff events when some fish were able to swim around the trap leads. In 2005, suppression efforts were expanded to four additional tributary source populations based on results from continued monitoring and research (Boyer et al. 2008; Muhlfeld et al. 2009a). At all five tributaries, electrofishing was conducted 2 to 3 times/week during the peak spawning period to capture mature fish staging at tributary mouths prior to completing their spawning migration. Morphological traits such as the uniform distribution of spots anterior and posterior of the dorsal fin, white fin tips, and faint or absent throat slash coloration were used to identify hybrid trout for removal. While hybrid trout exhibit a wide range of phenotypes intermediate to those of the parental types (Leary et al. 1996), individuals with a high proportion of Rainbow Trout admixture tend to exhibit visual characteristics typical of that taxon and thus are reliably identified in the field (Meyer et al. 2006; Muhlfeld et al. 2009a).

**Factors associated with the changes in severity and distribution of hybridization.**—We used ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, California) to measure the flow-routed distances to each of the sample locations for estimates of distance to source (i.e., Abbott Creek). Our use of a relatively small data set (total sample size = 83) across five time periods and of mixed temporal extent at any given site prohibited the use of a multiple-model approach (e.g., Burnham and Anderson 2002) and models accounting for spatial and temporal autocorrelation (e.g., Lichstein et al. 2002). Therefore, we fitted a two-parameter negative exponential decay function to the data for each sample year to quantify the relationship between distance to the source (i.e., Abbott Creek) and the proportion of admixture at individual sites. We then calculated the area under the curve (AUC) by taking the integral of the area under the fitted curves for a relative measure of the extent of admixture for each sampling period.

Given the large amount of public land within our study area and relatively small changes in landscape associated
with development, we focused our analyses on climate-related attributes likely to influence the prevalence of Rainbow Trout proximate to the source population. We integrated the AUC measures with ambient climate data to assess relationships between the extent of admixture and climate-related variables. Specifically, we included measures of spring flows and summer stream temperatures, which are known to influence Rainbow Trout invasions. Rainbow Trout within the study area typically spawn on the ascending limb of the hydrograph (Muhlfeld et al. 2009a), and the timing and magnitude of spring flows can influence when Rainbow Trout spawn as well as recruitment success (Fausch et al. 2001). Elevated stream temperatures during the summer months are likely to facilitate upstream invasion of Rainbow Trout and increase the likelihood of hybridization events (Bear et al. 2007; Muhlfeld et al. 2009b).

For each sample year, we quantified the stream temperature and streamflow conditions of the 3 years prior to the genetics sampling using empirical data collected in the study area (Figure 2). We considered the 3 years prior to the genetic sampling the most appropriate as these periods were contemporaneous with the likely reproduction events, resulting in the ages of fish sampled (i.e., age 1 to age 3). We summarized streamflow (U.S. Geological Survey [USGS] site number 12355500) and stream temperature data (USGS site number 12363000) from continuous, proximate (<10-km) gauges within the study area (USGS 1981–2011) as follows: (1) the number of days within
each month that streamflow was less than or greater than the 25th and 75th percentiles of daily flow conditions (1910–2012), respectively, during the Rainbow Trout spawning period (April to June; Muhlfeld et al. 2009a); and (2) average stream temperatures during the summer months (June–September). We used Pearson’s product-moment correlation analyses (R Core Development Team 2013) to evaluate the associations between the annual measures of AUC (i.e., the extent of hybridization) and climate conditions.

**RESULTS**

Our results indicated a rapid expansion in the spatial distribution of hybridization and proportion of nonnative Rainbow Trout admixture in hybridized populations from 1984 to 2004 (Figure 3, A–F), but minimal change in the extent of admixture since 2004 (Figure 3A). Overall, we observed the strongest correlations between AUC (extent of admixture) and the number of streamflow events in May exceeding the 75th percentile of historic flows \(r = -0.98\) and August stream temperatures \(r = 0.89\); Tables 1, 2).

From 1984 to 2004, we found little indication of changes in the proportion of admixture at the source (i.e., intercept) but observed substantial declines in the decay parameter, suggesting pronounced regional expansion in the proportion of Rainbow Trout admixture during this period (Table 3; Figure 3A–F). The proportion of admixture among sites, quantified through

**FIGURE 3.** Maps illustrating the source population (black circle), the natural fish barriers (black crosses), and the predicted spatial extent of (A–C; blue) 1% and (D–F; green) 10% admixture from the exponential decay models in (A, D) 1984, (B, E) 1998, and (C, F) 2004 within the Flathead River basin.
TABLE 1. Average, monthly stream temperature data (°C) from the Middle Fork Flathead River, Montana, for the 3 years prior to each genetic sampling event and the correlation (r) with AUC, a measure of the extent of hybridization in the upper Flathead River basin.

<table>
<thead>
<tr>
<th></th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981–1983</td>
<td>8.8</td>
<td>11.2</td>
<td>13.7</td>
<td>9.1</td>
</tr>
<tr>
<td>1995–1997</td>
<td>9.1</td>
<td>13.6</td>
<td>15.0</td>
<td>12.9</td>
</tr>
<tr>
<td>2001–2003</td>
<td>9.6</td>
<td>14.9</td>
<td>15.6</td>
<td>13.4</td>
</tr>
<tr>
<td>2005–2007</td>
<td>10.2</td>
<td>15.9</td>
<td>15.4</td>
<td>12.8</td>
</tr>
<tr>
<td>Correlation (r) with AUC</td>
<td>0.6</td>
<td>0.82</td>
<td>0.89</td>
<td>0.86</td>
</tr>
<tr>
<td>P-value</td>
<td>0.25</td>
<td>0.11</td>
<td>0.04</td>
<td>0.06</td>
</tr>
</tbody>
</table>

The lack of change in the spatial extent and degree of hybridization post-2004 was highly correlated with decreasing stream temperatures and an increase in the number of days with high (>75%) streamflow events (Figure 4A). The apparent slowdown of hybridization also coincided with marked declines in catch rates of nonnative Rainbow Trout and hybrid trout (Figure 5). From 2000 to 2012, 1,633 adult Rainbow Trout and hybrids were removed from Abbot Creek and nearby tributaries. Adult trapping data at Abbot Creek indicated little change in measures of AUC from 2000 to 2005 (mean CPUE = 1.42; SD = 0.70), but CPUE from 2006 to 2011 (mean CPUE = 0.56; SD = 0.39) decreased by 60% compared with earlier efforts (Figure 5A). Catch-per-unit-effort estimates in 2003 were likely biased low due to high streamflows and possible trap avoidance during the spawning migration; omission of those data revealed considerably higher measures of Rainbow Trout and hybrid trout abundance (mean CPUE = 1.67; SD = 0.38). Results from electrofishing efforts (number of fish/ electrofishing-day) were generally congruent with the trapping results, as average CPUE of Rainbow Trout and hybrid trout declined by 62% (range = 43–78%) between the early (prior to 2006) and later (2006–2012) periods of the study (Figure 5B). Interestingly, however, we observed a slight increase in

TABLE 2. The total number of days streamflow conditions near the source population were below or exceeded the 25th and 75th percentiles of historic flows, respectively, during the 3 months during nonnative Rainbow Trout spawning and rearing for the 3 years prior to each sample year and the correlation (r) with AUC, a measure of the extent of hybridization in the upper Flathead River basin.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Apr 25th</th>
<th>Apr 75th</th>
<th>May 25th</th>
<th>May 75th</th>
<th>Jun 25th</th>
<th>Jun 75th</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981–1983</td>
<td>24</td>
<td>12</td>
<td>17</td>
<td>24</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td>1995–1997</td>
<td>8</td>
<td>31</td>
<td>18</td>
<td>16</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td>2001–2003</td>
<td>27</td>
<td>21</td>
<td>50</td>
<td>8</td>
<td>36</td>
<td>27</td>
</tr>
<tr>
<td>2005–2007</td>
<td>0</td>
<td>45</td>
<td>29</td>
<td>15</td>
<td>22</td>
<td>3</td>
</tr>
<tr>
<td>2008–2010</td>
<td>53</td>
<td>3</td>
<td>46</td>
<td>13</td>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td>Correlation (r) with AUC</td>
<td>0.23</td>
<td>0.09</td>
<td>0.9</td>
<td>-0.98</td>
<td>0.76</td>
<td>-0.21</td>
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<td>P-value</td>
<td>0.71</td>
<td>0.89</td>
<td>0.04</td>
<td>0.005</td>
<td>0.14</td>
<td>0.74</td>
</tr>
</tbody>
</table>

TABLE 3. Sample year, intercept, decay parameter (b), SE, and parameter significance from two-parameter exponential decay models describing the proportion of nonnative Rainbow Trout admixture with Westslope Cutthroat Trout by distance from Rainbow Trout source population in the Flathead River, Montana.

<table>
<thead>
<tr>
<th>Year</th>
<th>Intercept</th>
<th>SE</th>
<th>P-value</th>
<th>b</th>
<th>SE</th>
<th>P-value</th>
</tr>
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<td>1984</td>
<td>92</td>
<td>0.79</td>
<td>&lt;0.0001</td>
<td>0.43</td>
<td>11.5</td>
<td>0.97</td>
</tr>
<tr>
<td>1998</td>
<td>97.1</td>
<td>5.1</td>
<td>&lt;0.0001</td>
<td>0.11</td>
<td>0.01</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2004</td>
<td>84</td>
<td>5.8</td>
<td>&lt;0.0001</td>
<td>0.04</td>
<td>0.005</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2008</td>
<td>95</td>
<td>4.5</td>
<td>&lt;0.0001</td>
<td>0.06</td>
<td>0.008</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2011</td>
<td>84.7</td>
<td>7.3</td>
<td>&lt;0.0001</td>
<td>0.05</td>
<td>0.008</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

FIGURE 4. (A) Estimates of AUC from exponential decay functions describing the proportion of Rainbow Trout admixture by sample year in the Flathead River basin, and (B) the number of days streamflow exceeded the 75th percentile of record (black) and average August stream temperatures (white) in the 3 years prior to each sample year.
CPUE from trapping data between 2010 (0.19) and 2012 (0.55), while CPUE from electrofishing continued to decline during this period (Figure 5A, B).

DISCUSSION

Over the past several decades, the northern Rocky Mountains have experienced considerable warming, which has contributed to increasing stream temperatures, modified hydrologic regimes, and increases in disturbance events (e.g., wildfire, debris flows) in mountain streams (Pederson et al. 2010; Isaak et al. 2012). Climate adaptation remains as a key piece of what natural resource managers can do to increase the resistance and resilience of species and ecosystems to changing climatic conditions (Lawler et al. 2010; Pettorelli 2012). Here, we illustrated the conservation benefits of using existing data within an adaptive framework to quantify the effects of proactive management actions to ameliorate the effects of an invasive species under a changing climate.

The importance of the upper Flathead River system as a regional and rangewide stronghold for nonhybridized Westslope Cutthroat Trout under current and future climate conditions (Wenger et al. 2011) predicated the need to initiate conservation actions to slow or stop the spread of hybridization. We found that the spread of hybridization was strongly correlated with warming stream temperatures during the summer months and the number of high-flow events during May from 1984 to 2011. High spring flow events are known to limit young-of-year survival and recruitment of introduced Rainbow Trout (Fausch et al. 2001; Warren et al. 2009), and stream temperature is strongly associated with the distribution patterns of Cutthroat Trout and nonnative Rainbow Trout hybrids within stream networks (Muhlfeld et al. 2009b; Bennett et al. 2010; Rasmussen et al. 2010). Warming stream temperatures may also favor Rainbow Trout growth due to its broad thermal tolerances (Bear et al. 2007) and result in increased overwinter survival in the early life stages of development (Quinn and Peterson 1996). While the relative influence of summer stream temperatures or reductions in the number of high streamflow events is unclear from our results, these data suggest that favorable climate conditions likely provided “windows” of opportunity for Rainbow Trout expansion in the system (Fausch et al. 2001).

Since 2005, trends of warming climate and reduced flows have slowed and remained relatively constant, a pattern similar to our predictions of the extent of admixture as measured by AUC (Figure 4). Anticipated changes in climate suggest this recent pattern is likely to be short lived, as regional air temperatures are expected to continue to increase by 2.3°C by 2090 (Jones et al. 2013). Future warming will continue to increase the amount of habitat within the optimal thermal niche for nonnative Rainbow Trout (Arim et al. 2006; Rahel and Olden 2008), and our results suggest pronounced expansions for the future unless control measures are continued. Warming temperatures imply earlier snowmelt events (Luce and Holden 2009), and predictions averaged across climate models (Elsner and Hamlet 2010) suggest streamflows in our study area are likely to increase during May. Our results suggest such shifts in the hydrologic regime may be less favorable for Rainbow Trout and hybrid recruitment due to substantial increases in May discharge. However, salmonids can exhibit phenotypic plasticity in the timing of reproduction in relation to annual and climate-driven differences in hydrology and temperature (Warren et al. 2012); thus, there is considerably uncertainty as to how shifting hydrographs will affect future recruitment.

It remains somewhat unclear whether the observed stasis of the hybrid zone since 2004 is due to climate variation or management actions, including nonnative Rainbow Trout removal efforts, as we found CPUE steadily declining since the inception of the program in 2000. Propagule pressure, the number and dispersal frequency of individual nonnatives (Lockwood et al. 2005), plays an important role in the establishment and spread of exotic species, including the occurrence of hybridization between nonnative Rainbow Trout and Cutthroat Trout in
North America (Bennett et al. 2010; Kozfkay et al. 2011; Yau and Taylor 2013). Larger source populations are also likely to facilitate nonnative adaptation to local conditions (Westley et al. 2012). While characteristics such as increased elevation and decreasing stream size may act in slowing down invasion (Weigel et al. 2003; Yau and Taylor 2013), uncontrolled invasive populations often exhibit pronounced phases of expansion until suitable habitat is saturated (Arim et al. 2006); a pattern recently observed for unchecked nonnative Rainbow Trout populations in Idaho (High et al. 2011). The order of magnitude decline in relative abundance indicates the removal efforts are associated with the observed slowdown of hybridization in the upper Flathead River system. We acknowledge, however, that recent increases in CPUE in trapping data from removal efforts suggests continued monitoring is warranted.

While it is not possible to precisely determine the relative role that changing climatic conditions and recent control efforts have played in regulating the spread of Rainbow Trout hybridization, our results suggest that continuing or even increasing nonnative Rainbow Trout control efforts remains the most conservation-oriented approach. If the spread of hybridization is largely driven by factors associated with climate change (e.g., Moyle and Light 1996), the observed rate at which native Westslope Cutthroat Trout populations become introgressed with Rainbow Trout are likely to increase given the congruence of predictions across climate models (Nakicenovic et al. 2000; Rahel and Olden 2008). In the context of climate warming, suppressing source populations of nonnative Rainbow Trout and hybrids may provide a buffer for managers to develop additional tools to prevent further spread of hybridization (Pyke et al. 2008). Our results also highlight the need for additional monitoring to better understand the mechanisms by which such control efforts and climatic change influence the spread of hybridization (sensu Beever et al. 2013), and furthermore consideration as to how to increase effectiveness by specifically targeting years where high recruitment is likely.

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