

ARTICLE

Genetic Status and Conservation of Westslope Cutthroat Trout in Glacier National Park

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Abstract

Invasive hybridization is one of the greatest threats to the persistence of Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*. Large protected areas, where nonhybridized populations are interconnected and express historical life history and genetic diversity, provide some of the last ecological and evolutionary strongholds for conserving this species. Here, we describe the genetic status and distribution of Westslope

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Cutthroat Trout throughout Glacier National Park, Montana. Admixture between Westslope Cutthroat Trout and introduced Rainbow Trout *O. mykiss* and Yellowstone Cutthroat Trout *O. clarkii bouvieri* was estimated by genotyping 1,622 fish collected at 115 sites distributed throughout the Columbia, Missouri, and South Saskatchewan River drainages. Currently, Westslope Cutthroat Trout occupy an estimated 1,465 km of stream habitat and 45 lakes (9,218 ha) in Glacier National Park. There was no evidence of introgression in samples from 32 sites along 587 km of stream length (40% of the stream kilometers currently occupied) and 17 lakes (2,555 ha; 46% of the lake area currently occupied). However, nearly all (97%) of the streams and lakes that were occupied by nonhybridized populations occurred in the Columbia River basin. Based on genetic status (nonnative genetic admixture $\leq 10\%$), 36 Westslope Cutthroat Trout populations occupying 821 km of stream and 5,482 ha of lakes were identified as “conservation populations.” Most of the conservation populations ($N = 27$; 736 km of stream habitat) occurred in the Columbia River basin, whereas only a few geographically restricted populations were found in the South Saskatchewan River ($N = 7$; 55 km) and Missouri River ($N = 2$; 30 km) basins. Westslope Cutthroat Trout appear to be at imminent risk of genomic extinction in the South Saskatchewan and Missouri River basins, whereas populations in the Columbia River basin are widely distributed and conservation efforts are actively addressing threats from hybridization and other stressors. A diverse set of pro-active management approaches will be required to conserve, protect, and restore Westslope Cutthroat Trout populations in Glacier National Park throughout the 21st century.

The Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* is the most widely distributed subspecies of Cutthroat Trout *O. clarkii* in western North America, historically occupying portions of the Columbia, Fraser, Missouri, and South Saskatchewan River drainages in the United States and Canada (Allendorf and Leary 1988; Behnke 1992; Shepard et al. 2005; Trotter 2008). However, native populations have dramatically declined due to nonnative species introductions, habitat degradation, fragmentation, overexploitation, and climate change (Shepard et al. 2005; Trotter 2008; Muhlfeld et al. 2014). Human-induced hybridization, which occurs via the widespread stocking of nonnative salmonids and subsequent genetic introgression among species, has been especially detrimental to Westslope Cutthroat Trout (Allendorf and Leary 1988; Allendorf et al. 2005). Nonhybridized populations now persist in less than 10% of their historic range in the United States (Shepard et al. 2005) and less than 20% of their historic range in Canada (COSEWIC 2006). Most nonhybridized populations are restricted to small, fragmented headwater habitats in protected areas (e.g., national parks, wilderness areas, and roadless areas), where their status and long-term sustainability are uncertain. Consequently, protected areas have become increasingly important for the conservation and long-term persistence of Westslope Cutthroat Trout.

Glacier National Park, Montana, is considered a rangewide stronghold for Westslope Cutthroat Trout (Liknes and Graham 1988; Behnke 1992; Shepard et al. 2005), representing one of the last remaining reserves where predominantly lacustrine populations persist throughout the subspecies' former range (Liknes and Graham 1988; Marnell 1988). Westslope Cutthroat Trout are native to three major continental drainages (the Columbia, Missouri, and South Saskatchewan River basins) that originate within Glacier National Park: streams west of the Continental Divide drain into the Pacific Ocean

(via the Flathead River and the Clark Fork of the Columbia River), and streams east of the Continental Divide drain into Hudson Bay (via the South Saskatchewan River) and the Atlantic Ocean (via the Missouri and Mississippi rivers). Westslope Cutthroat Trout occupy a wide variety of aquatic habitats throughout the park—from small headwater streams to large rivers and glacial lakes—and express a diversity of life history strategies throughout these habitats (i.e., resident, fluvial, adfluvial, and lacustrine-adfluvial forms; Downs et al. 2011; D'Angelo and Muhlfeld 2013). This environmental and biotic diversity has likely provided the critical heterogeneity that is necessary for adaptation, resilience, and long-term persistence (Taylor et al. 2003).

Over the past century, native populations of Westslope Cutthroat Trout have been adversely impacted by widespread introductions of nonnative salmonids and subsequent introgressive hybridization with nonnative Rainbow Trout *O. mykiss* and Yellowstone Cutthroat Trout *O. clarkii bouvieri* (Marnell 1988; Hitt et al. 2003; Boyer et al. 2008). Using protein electrophoresis (i.e., allozymes), Marnell (1988) examined the genetic status of Westslope Cutthroat Trout in 33 lakes of Glacier National Park and found that introduced populations of Yellowstone Cutthroat Trout and Westslope Cutthroat Trout \times Yellowstone Cutthroat Trout hybrids were established in several lakes throughout the three major continental river drainages. Moreover, Marnell (1988) did not find any native populations east of the Continental Divide in the Missouri River or Saskatchewan River drainages within the park boundary. More recently, studies in the upper Columbia River basin have shown that hybridization between nonnative Rainbow Trout and native Westslope Cutthroat Trout is rapidly spreading upstream into native populations in the North Fork and Middle Fork Flathead River, including several populations in Glacier National Park (Hitt et al. 2003; Boyer et al. 2008; Muhlfeld et al. 2009c, 2014). Nevertheless, the current genetic status and threats to the

genetic integrity of Westslope Cutthroat Trout throughout Glacier National Park remain unknown.

Glacier National Park and surrounding waters contain some of the most ecologically and economically important Westslope Cutthroat Trout populations remaining in western North America (Shepard et al. 2005). Loss of these populations would damage the ecological integrity of Glacier National Park and the subspecies as a whole, since these populations likely contain unique genetic and behavioral adaptations representing important evolutionary potential that is critical for the subspecies' survival. Thus, protecting the genetic integrity of native Westslope Cutthroat Trout is a high priority for conservation and management programs in the park and rangewide. An understanding of the Westslope Cutthroat Trout's genetic status and distribution in Glacier National Park is needed to inform management decisions, provide recreational opportunities, and conserve the evolutionary heritage of this native trout for future generations.

Here, we provide the first comprehensive genetic status assessment of Westslope Cutthroat Trout throughout their historical range in Glacier National Park. Our objectives were to (1) define the current distribution and genetic status of Westslope Cutthroat Trout populations by using a spatially explicit analysis; (2) identify populations that managers can conserve for genetic integrity; and (3) evaluate hybridization threats to conservation populations throughout this iconic ecosystem.

STUDY AREA

Glacier National Park is the world's first International Peace Park, a Biosphere Reserve, and a World Heritage Site designated by the United Nations Educational, Scientific, and Cultural Organization. The park is centered in one of the most intact aquatic ecosystems in North America: the Crown of the Continent Ecosystem. The study area included the stream and lake habitats throughout the three major river drainages of Glacier National Park (Figure 1), including the upper Columbia River, upper Missouri River, and upper South Saskatchewan River drainages in the United States. The information was partitioned into and is reported based on fourth-level (8-digit) hydrologic unit codes (HUCs) from the National Hydrography Dataset (NHD; USGS 2016).

METHODS

Current distribution.—We described the current distribution of *Oncorhynchus* spp. in Glacier National Park by using site-, reach-, stream-, and lake-specific genetic data. Data were entered into a geographical information systems database by directly editing the 1:24,000-scale NHD in ArcGIS version 10.1 (ESRI 2012). Each stream, stream reach (segment), and lake was attributed with a standard set of population and habitat characterizations, including genetic status, fish stocking history, presence of nonnative fish species, elevation

(m), stream reach gradient (%), and lake surface area (ha; 3D Analyst Extension in ArcGIS version 10.1). Each water body (stream segment, stream, or lake) that was currently occupied by *Oncorhynchus* spp. was treated as a single, independent habitat segment to which genetic status (e.g., admixture proportion) was assigned. The following steps were taken to identify and exclude unoccupied waters: (1) ephemeral stream reaches or lakes were excluded unless survey data indicated the presence of *Oncorhynchus* spp.; (2) perennial stream reaches were excluded if they were disjunct from the NHD network after the removal of ephemeral reaches (all <1 km in length and unlikely to be fish bearing); (3) stream reaches with a gradient of 10% or higher and disjunct lakes with a surface area of 1 ha or less were excluded unless survey data indicated the presence of *Oncorhynchus* spp.; and (4) stream reaches and lakes were excluded if they were upstream of physical barriers to fish movement and/or extensive surveys suggested an absence of *Oncorhynchus* spp. in those systems (e.g., upper Kintla Creek; Meeuwig et al. 2008; D'Angelo and Muhlfeld 2013). Natural and anthropogenic barriers included waterfalls, high-gradient cascading stream sections, culverts, dams, and other features that prevented *Oncorhynchus* spp. movement and occupancy.

Available records of fish stocking and species surveys were reviewed, and the resulting information was included for each stream segment or lake in Glacier National Park (Montana Fish, Wildlife, and Parks 2015; C. C. Muhlfeld, unpublished data). The focus of the review was on nonnative fish species that had the potential to hybridize with native Westslope Cutthroat Trout, including Rainbow Trout and Yellowstone Cutthroat Trout.

Sample collection.—From 2008 to 2012, a total of 1,622 tissue samples from *Oncorhynchus* spp. were collected in 111 stream reaches and 37 lakes within Glacier National Park (Figure 1). Samples were aggregated into 115 sample sites after pooling tissue samples from proximate stream reaches (Figure 2; Supplementary Table S.1 available in the online version of this article). We also included fish population data collected in the Canadian portions of Sage, Spruce, and Kishenehn creeks (upper Columbia River basin) to determine the genetic status of Westslope Cutthroat Trout populations in those transboundary watersheds (R. Leary, University of Montana, unpublished data). Hook-and-line sampling, electrofishing, and gillnetting were used to capture fish in streams and lakes. Fish TL was recorded, and a small ($\leq 2 \times 2$ mm) portion of fin tissue was excised and stored in 1–2 mL of 99% ethanol. The DNA was extracted from a portion of each individual fin clip by using a DNeasy Blood and Tissue kit (Qiagen) via the manufacturer's standard protocol.

Genetic analysis.—We primarily used species-diagnostic single-nucleotide polymorphisms (SNPs) to estimate population and individual-level admixture in Westslope Cutthroat Trout populations. The 95-SNP genotyping assay included 59 loci with species-diagnostic alleles: 19 were

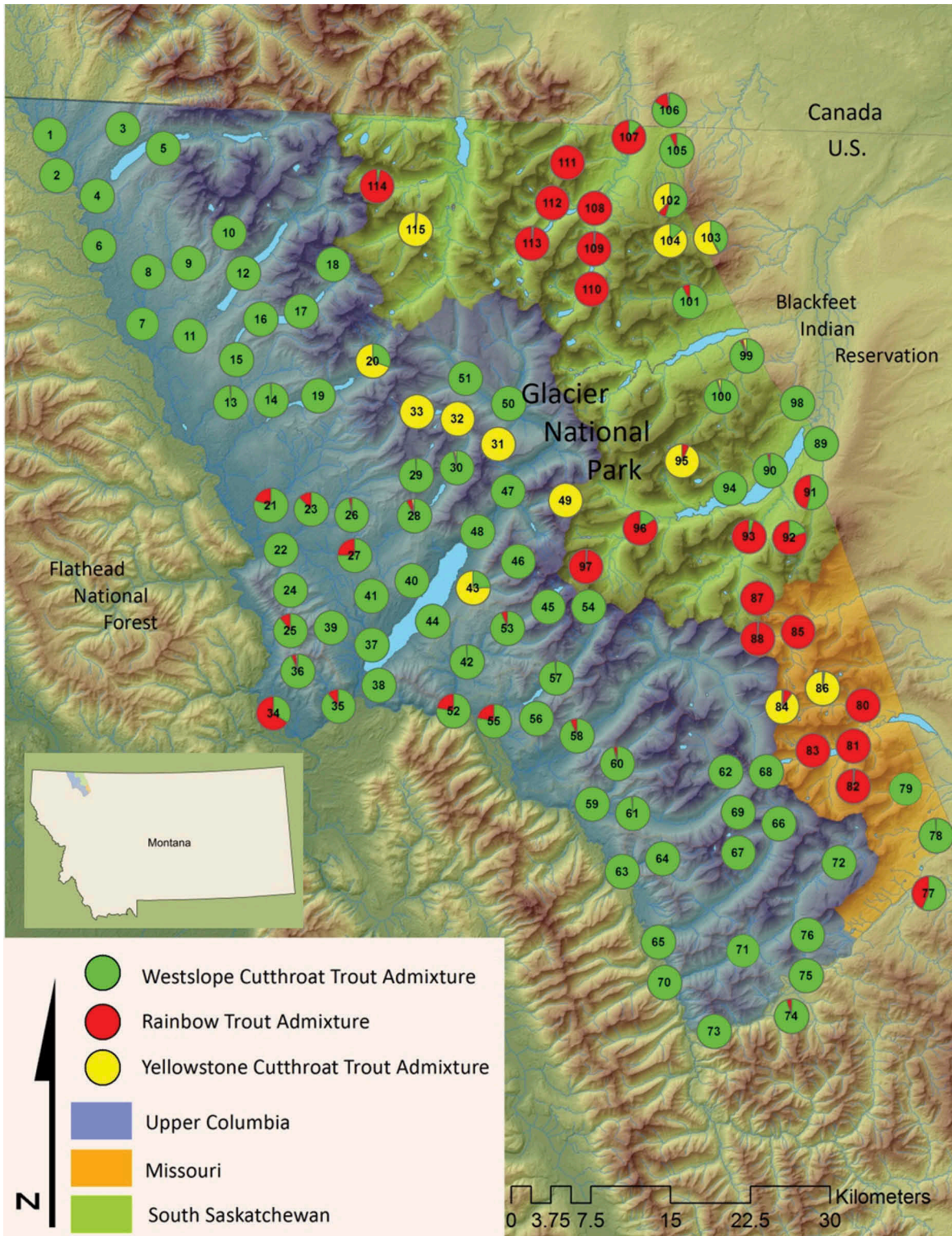


FIGURE 1. Sampling sites ($N = 115$) where genetic samples were collected from Westslope Cutthroat Trout and/or hybrid populations surveyed in Glacier National Park (2004–2012). These sites were used to assign genetic data to stream segments and lakes in the study area. Site numbers correspond to those in Supplementary Table S.1. Sites 7, 71, and 79 showed evidence of *Oncorhynchus mykiss* introgression admixture; calculations were inappropriate because of significant linkage disequilibrium.

diagnostic for Rainbow Trout, 20 were diagnostic for Westslope Cutthroat Trout, and 20 were diagnostic for Yellowstone Cutthroat Trout (Amish et al. 2012). A species-diagnostic SNP locus is fixed for alternative nucleotide bases in the parental species. At each diagnostic SNP locus, an individual trout can have zero, one, or two non-Westslope Cutthroat Trout alleles. Our SNP assays provided high power for precisely estimating population- and individual-level admixture (Amish et al. 2012; Hohenlohe et al. 2013) and fine spatial mapping of hybridization and introgression patterns throughout Glacier National Park (Sprowles et al. 2006; Blankenship et al. 2011; Hohenlohe et al. 2011, 2013; Amish et al. 2012). For example, with a sample size of 12 individuals (the average sample size per site in this data set), the power to detect either 1% or 10% Rainbow Trout admixture is 0.99 with 39 diagnostic loci.

In total, 1,131 tissue samples from *Oncorhynchus* spp. collected at 93 locations were genotyped at the 59 species-diagnostic SNPs. Samples were genotyped by using the default settings in Fluidigm SNP Genotyping Analysis software (version 3.1.2). We used a variety of quality control procedures, including positive and negative controls and data quality filters (e.g., screens for allelic dropout, criteria for missing data, etc.). Additionally, 5% of all samples were randomly re-extracted and re-run to confirm initial genotypes and to monitor for potential genotyping errors. In each population, we further screened the genotypic distributions to identify population-specific ancestral polymorphisms that complicate the calculation of ancestry and admixture, as described by Powell (2014; see below). Any problematic data were discarded.

We also included genotypic data from several recent studies, including data from 456 individuals (collected at 19 sites) that were genotyped at seven microsatellite loci diagnostic for Rainbow Trout (Boyer et al. 2008; Muhlfeld et al. 2009c; R. Leary, Montana Fish, Wildlife, and Parks, unpublished data); 18 individuals (collected at 2 sites) that were genotyped by using species-diagnostic, paired interspersed nucleic elements (Hitt et al. 2003); and 17 individuals (collected from one site) that were genotyped at eight allozyme loci diagnostic for Rainbow Trout and Yellowstone Cutthroat Trout (Marnell et al. 1987).

Statistical assessment of admixture.—For each sample, we calculated the maximum likelihood estimates of the proportion of alleles in the population that originated from Rainbow Trout, Westslope Cutthroat Trout, and Yellowstone Cutthroat Trout. In samples that included all three hybridizing species, we used the expectation-maximization (EM) algorithm to calculate the maximum likelihood estimate for each species' genetic contribution to each individual in the population using formulas presented by Kalinowski (2010). After estimating the three species' genetic contribution to each individual, we calculated each species' mean genetic contribution to the population as a

whole. A percentile bootstrap confidence interval (10,000 replicates) was calculated by bootstrapping across loci and then across individuals (Tang et al. 2005). For samples that contained all three hybridizing species, the EM algorithm was run in each bootstrap replicate. The 2.5th and 97.5th percentiles of the bootstrap distributions were taken as the bounds of the 95% confidence interval for the proportion of alleles in the population that were contributed by each parental species.

To test whether nonnative alleles were randomly distributed across loci in samples (except from sites 7, 71, and 79; see Figure 1), we used the mixing degree statistic (m_d ; Kalinowski and Powell 2015). The P -values for these tests were calculated as the number of 5,000 random permutations of alleles across loci that resulted in an m_d value greater than or equal to the observed value. The false discovery rate correction of Benjamini and Yekutieli (2001) was applied (adjusted $\alpha = 0.0102$ based on 74 simultaneous comparisons), and samples with P -values less than or equal to the adjusted α were considered to have been drawn from an unmixed sample (i.e., a nonhybrid swarm).

Genetic status.—Streams and lakes that were occupied by Westslope Cutthroat Trout were classified based on admixture proportions. Lakes were treated as independent habitat segments, and lake classifications were not extrapolated to connected streams unless stream-specific data were unavailable. Stream reaches were assigned admixture values based on the nearest, most recent stream sample site. If different genetic results were obtained for multiple sample sites on the same stream, we estimated the midpoint on the NHD network as the dividing point between classifications. Reaches downstream of the lowermost site to the mouth of the next larger stream, lake, or park boundary were classified by using data from the lowermost site. Connected reaches upstream of the uppermost site to the $\geq 10\%$ gradient point, fish passage barrier, or lake were classified according to the uppermost site. Tributaries were classified based on their own data or based on data from the nearest main-stem site.

Stream and lake habitats containing Westslope Cutthroat Trout with less than 1% nonnative admixture (i.e., the 95% confidence interval included 1%) were classified as “unaltered” (Tables 1, 2). Streams and lakes occupied by Westslope Cutthroat Trout with greater than 1% nonnative admixture were considered to be “introgressed.” For cases in which genetic data were unavailable (3 lakes and portions of 11 streams and main-stem rivers), we used stocking records and the occurrence of potentially hybridizing species to classify the likelihood of introgression (Shepard et al. 2005). Westslope Cutthroat Trout were classified as “suspected unaltered” in streams, rivers, and lakes for which field surveys or stocking records indicated the absence of potentially hybridizing species; they were classified as “potentially altered” if any information indicated that potentially hybridizing species were

TABLE 1. Genetic classes used for assessing the hybridization status of Westslope Cutthroat Trout and their relative occurrence in streams (km) of the major river basins in Glacier National Park (GNP) as of 2012 (% of occupied = percentage of basin-specific occupied stream length or GNP total occupied stream length).

Genetic class	Upper Columbia River basin		Missouri River basin		South Saskatchewan River basin		GNP total	
	Km	% of occupied	Km	% of occupied	Km	% of occupied	Km	% of occupied
Tested; unaltered	569	49	0	0	18	10	587	40
Tested; $\geq 1\%$ and $\leq 10\%$ introgressed	161	14	19	14	37	20	217	15
Tested; $> 10\%$ and $\leq 25\%$ introgressed	190	17	0	0	14	8	204	14
Tested; $> 25\%$ introgressed	11	1	75	56	102	56	188	13
Suspected unaltered	124	11	0	0	0	0	124	8
Potentially altered	95	8	29	22	10	7	134	9
Mixed stock	0	0	11	8	0	0	11	1
River basin or GNP total	1,150	100	134	100	181	100	1,465	100

present. The lengths of stream occupied by each genetic category were summarized, and the spatial distributions were displayed and quantified (Tables 1, 2).

Conservation populations.—Stream and lake habitats occupied by Westslope Cutthroat Trout with 10% or less nonnative genetic admixture were considered to represent “conservation populations” (Shepard et al. 2005; Muhlfeld et al. 2015). “Core conservation populations” included stream and lake habitats containing Westslope Cutthroat Trout with less than 1% nonnative genetic admixture (i.e., unaltered). Populations with 1–10% nonnative genetic admixture (i.e., that included both unaltered and introgressed individuals) were considered to have “mixed genetic makeup.” Conservation populations were first

defined as encompassing habitat patches at approximately the 12-digit HUC scale because this scale is consistent with the habitat and genetic structure that define local populations of Westslope Cutthroat Trout in Glacier National Park (Boyer et al. 2008; Muhlfeld et al. 2009b, 2012). Aggregation of stream segments and/or lakes within each patch depended on the isolation or connectivity and likely genetic exchange among spawning individuals. In the absence of barriers to fish migration, stream segments and/or lakes that supported Westslope Cutthroat Trout and that met the above criteria were aggregated as part of a “connected” conservation population. In several cases, connected populations were likely part of a larger metapopulation (Hanski and Gilpin 1991). When fish

TABLE 2. Genetic classes used for assessing the hybridization status of Westslope Cutthroat Trout and their relative occurrence in lakes (ha) of the major river basins in Glacier National Park (GNP) as of 2012 (% of occupied = percentage of basin-specific occupied lake area or GNP total occupied lake area).

Genetic class	Upper Columbia River basin		Missouri River basin		South Saskatchewan River basin		GNP total	
	Ha	% of occupied	Ha	% of occupied	Ha	% of occupied	Ha	% of occupied
Tested; unaltered	2,555	45	0	0	0	0	2,555	28
Tested; $\geq 1\%$ and $\leq 10\%$ introgressed	146	3	0	0	0	0	146	2
Tested; $> 10\%$ and $\leq 25\%$ introgressed	0	0	0	0	0	0	0	0
Tested; $> 25\%$ introgressed	188	3	214	42	439	14	841	9
Suspected unaltered	2,781	49	0	0	0	0	2,781	30
Potentially altered	0	0	291	58	2,604	86	2,895	31
Mixed stock	0	0	0	0	0	0	0	0
River basin or GNP total	5,670	100	505	100	3,043	100	9,218	100

migration between stream segments was impeded by barriers, we subdivided these stream segments into discrete, “isolated” populations. One exception was an isolated conservation population in a reach containing multiple barriers (e.g., upper McDonald Creek), in which case the lowermost barrier was used to delineate the downstream end of the conservation population. The information about each designated conservation population was summarized according to the amount of occupied stream habitat (length, km) and lake habitat (surface area, ha).

Hybridization risk.—We developed a genetic risk assessment to evaluate hybridization threats to individual conservation populations of Westslope Cutthroat Trout (Table 3). Hybridization risk was assessed in terms of co-occurrence between Westslope Cutthroat Trout and Rainbow Trout or Yellowstone Cutthroat Trout. Multiple studies have shown that nonnative genetic admixture declines with upstream distance from sites containing high amounts of nonnative admixture (e.g., Rubidge and Taylor 2005; Boyer et al. 2008; Bennett et al. 2010; Yau and Taylor 2013). Hybridization risk was measured based on (1) the distance between the location of interest and the closest stream or lake habitat where Rainbow Trout or Yellowstone Cutthroat Trout introgression was detected at admixture levels greater than 10% within Glacier National Park or surrounding waters (Boyer et al. 2008; Muhlfeld et al. 2014) and (2) the existence of barriers that would preclude contact with the conservation population (Table 3; Table S.1).

RESULTS

Currently Occupied Waters

We estimated that *Oncorhynchus* spp. currently occupied 1,465 km of stream habitat and 9,218 ha of lake habitat (45 lakes) in Glacier National Park (Tables 1, 2). The upper Columbia River drainage (e.g., Middle Fork and North Fork Flathead River) contained the greatest amount of occupied stream habitat (1,150 km; 79% of occupied), far exceeding the amounts occupied in the South Saskatchewan River (181 km; 12%) and Missouri River (134 km; 9%) drainages (Table 1). The length of stream occupied above dispersal barriers was similar among the major river drainages, but such habitats were more common in the Missouri River (51 km; 38% of total occupied stream habitat) and South Saskatchewan River (64 km; 35%) drainages than in the upper Columbia River basin (76 km; 7%). Occupied lake habitat was distributed among the upper Columbia River (5,670 ha [17 lakes]; 62% of total occupied lake area), South Saskatchewan River (3,043 ha [11 lakes]; 33%), and Missouri River (505 ha [6 lakes]; 5%) drainages. The total and relative amounts of lake habitat occupied above dispersal barriers differed among the Missouri River (6 lakes, 505 ha; 100% of occupied lake area in the basin), upper Columbia River (13 lakes, 734 ha; 13%), and South Saskatchewan River (11 lakes, 439 ha; 14%) drainages (Table 2).

Westslope Cutthroat Trout and other *Oncorhynchus* spp. were not detected in 254 km of potentially fish-bearing stream habitat (<10% gradient) within Glacier National Park. This

TABLE 3. Genetic risk and associated attributes that were assigned to Westslope Cutthroat Trout (WCT) populations that were designated as “conservation populations” within Glacier National Park.

Degree of genetic risk	Risk attribute	Conservation significance
Low	Hybridizing species cannot interact with the existing WCT population because a complete passage barrier is in place or because hybridizing fish are not present in the same drainage or any adjacent drainage.	Hybridization and introgression with nonnative salmonids are among the leading factors in declines of native WCT.
Medium-low	Hybridizing species are in the same stream and/or drainage farther than 10 km from a WCT population but not in the same stream segment as WCT or within 10 km of WCT where a barrier currently exists (though that barrier may be at risk of failure).	
Medium-high	Hybridizing species are in the same stream and/or drainage within 10 km of a WCT population and no barrier exists. However, hybridizing species are not yet found in same stream segment as the WCT population.	
High	Hybridizing fish are sympatric with the WCT population and/or the segment is directly connected to a hybrid source.	

estimate includes three isolated stream networks where waterfall barriers prevent upstream dispersal of *Oncorhynchus* spp.: 43 km in the Nyack Creek watershed (upper Columbia River drainage), 23 km in the Kintla Creek watershed (upper Columbia River drainage), and 27 km in the Waterton River headwaters (South Saskatchewan River drainage). *Oncorhynchus* spp. were apparently absent from 28 km of potentially fish-bearing stream habitat upstream of Lake Sherburne in the South Saskatchewan River drainage; it is unknown whether *Oncorhynchus* spp. were present in these habitats prior to the construction of Sherburne Dam. Additionally, Westslope Cutthroat Trout and other *Oncorhynchus* spp. were not detected in 1,603 ha of lake habitat within Glacier National Park. Occupancy status was unknown for approximately 50 km of potentially fish-bearing stream habitat and 586 ha of lake habitat due to the logistical challenges of sampling remote backcountry locations.

Stocking records indicated that *Oncorhynchus* spp., including Westslope Cutthroat Trout, Rainbow Trout, and Yellowstone Cutthroat Trout, were introduced into approximately 48 lakes (8,101 ha) and 32 streams (stream kilometers unknown) within or directly connected to Glacier National Park (C. Downs, National Park Service, unpublished data). Due to these introductions, hybridized populations occur in 23 lakes (987 ha) within Glacier National Park: 9 lakes (439 ha) in the South Saskatchewan River drainage; 9 lakes (334 ha) in the Columbia River drainage; and 5 lakes (214 ha) in the Missouri River drainage.

Genetic Status

In total, 1,622 individual *Oncorhynchus* spp. were genotyped from 115 sites in Glacier National Park, including 78 stream sites (59 unique streams) and 37 lakes (Figure 1; Table 4; Table S.1). Populations from 49 sites ($N = 32$ stream sites, 41% of sampled sites; $N = 17$ lakes, 46% of sampled lakes) were genetically unaltered (>99% Westslope Cutthroat Trout), whereas populations from 66 sites ($N = 46$ stream sites, 59%; $N = 20$ lakes, 54%) had at least 1% nonnative genetic admixture (Figure 1; Table S.1). Of the 66 sites with least 1% nonnative admixture, 43 sites ($N = 26$ stream sites, 33%; $N = 17$ lakes, 46%) were found to have over 10% admixture. Admixture could not be calculated for three genetic samples (Figure 1; Table S.1), but analysis of allele frequencies for those sites suggested low levels of introgression. The genetic contribution of hybridizing species varied among introgressed sites and included Westslope Cutthroat Trout populations that were introgressed with Rainbow Trout ($N = 31$ sites), Yellowstone Cutthroat Trout ($N = 9$ sites), or both ($N = 19$ sites); hybridized populations of Rainbow Trout and Yellowstone Cutthroat Trout ($N = 2$ sites); and populations of nonintrogressed Rainbow Trout ($N = 3$ sites) and Yellowstone Cutthroat Trout ($N = 2$ sites; Figure 1; Table S.1).

Genetic data were used to assign genetic status to 1,196 km of stream (82% of the stream habitat [km] occupied by

Oncorhynchus spp.) in Glacier National Park (including the Canadian portions of the Spruce, Sage, Kishenehn, and Starvation Creek watersheds, upper Columbia River basin) and 3,542 ha of lake habitat (38% of the lake area occupied by *Oncorhynchus* spp.; Figure 2; Tables 1, 2). Genetic results showed no evidence of introgression in samples from 587 km of stream length (40% of occupied stream habitat) and 2,555 ha of lake habitat (28% of occupied lake area). Westslope Cutthroat Trout were suspected to be unaltered in an additional 124 km of stream length (8% of occupied) and 2,781 ha of lake habitat (30% of occupied). Nonhybridized fish were present in a mixed-stock population in only 11 km of stream length (1% of occupied). Therefore, at most, 711 km of stream length (48% of occupied) and 5,336 ha of lake habitat (58% of occupied) in Glacier National Park supported genetically unaltered Westslope Cutthroat Trout. Most of the stream habitat (569 km, 97%) and all of the lake area (5,336 ha) that contained genetically unaltered Westslope Cutthroat Trout occurred in the upper Columbia River drainage. Moreover, genetic results indicated the presence of low levels of introgression (1–10%) in samples from 217 km of stream length (15% of occupied) and 146 ha of lake habitat (2% of occupied).

Of the 115 populations sampled, 34 (~29%) contained hybrid swarms ($m_d: P > 0.0102$). Hybrid swarms were detected in all three major river basins (upper Columbia River: $N = 20$; South Saskatchewan River: $N = 9$; Missouri River: $N = 5$). Interestingly, only 21 (32%) of the 66 sites with at least 1% nonnative admixture contained hybrid swarms. Twenty-seven (79%) of the 34 hybrid swarms were detected in streams or lakes with records of *Oncorhynchus* spp. stocking.

Conservation Populations

We identified 36 Westslope Cutthroat Trout conservation populations, which occupied 821 km of stream habitat (56% of occupied stream length) and 5,482 ha of lake habitat (60% of occupied lake area; Figure 3; Table 5); of these, 19 were core conservation populations (497 km of stream habitat; 2,298 ha of lake habitat; Table 6). Twenty-seven conservation populations occurred in the upper Columbia River drainage (736 km of stream habitat; 5,481 ha of lake habitat), seven were found in the South Saskatchewan River drainage (55 km of stream habitat), and only two occurred in the Missouri River drainage (30 km of stream habitat; Table 6). Most (89%) of the stream habitat and all of the lake habitat occupied by conservation populations occurred in the upper Columbia River drainage; 7% and 4% of the stream habitat occupied by conservation populations were situated in the South Saskatchewan and Missouri River drainages, respectively. Individual conservation populations occupied 0.4–81 km of lotic habitat (median = 20 km) and 2–2,794 ha of lake habitat (median = 89 ha).

TABLE 4. Temporal comparison of the genetic classification by Marnell et al. (1988) and the current status review for lake-dwelling Westslope Cutthroat Trout (WCT) and hybrid populations in Glacier National Park (RBT = Rainbow Trout; YCT = Yellowstone Cutthroat Trout).

Lake	Genetic ID, 1988 (Marnell et al. 1988)	Genetic ID, 2010–2012 (proportion admixture; present study)	Area (ha)	Elevation (m)	Population origin
Upper Columbia River basin					
Kintla	WCT	WCT (0.996), YCT (0.004)	694	1,222	Indigenous
Akokala	WCT	WCT (1.000)	10	1,241	Indigenous
Bowman	WCT	WCT (0.995), RBT (0.005)	698	1,228	Indigenous
Cerulean	WCT	WCT (0.994), RBT (0.006)	20	1,420	Indigenous
Quartz	WCT	WCT (1.000)	352	1,346	Indigenous
Middle Quartz	WCT	WCT (0.997), RBT (0.003)	19	1,340	Indigenous
Lower Quartz	WCT	WCT (0.998), RBT (0.002)	68	1,277	Indigenous
Grace	YCT × WCT	YCT (0.693), WCT (0.307)	33	1,207	Introduced
Logging	WCT	WCT (0.995), RBT (0.005)	451	1,161	Indigenous
Evangeline	YCT	YCT (0.998), WCT (0.002)	29	1,599	Introduced
Camas	YCT	YCT (1.000)	7	1,547	Introduced
Arrow	WCT × YCT	WCT (0.962), RBT (0.011), YCT (0.027)	24	1,241	Indigenous
Trout	WCT	WCT (0.989), RBT (0.011)	87	1,190	Indigenous
Rogers	WCT	WCT (0.921), RBT (0.050), YCT (0.092)	34	1,156	Indigenous
Upper Howe	WCT	WCT (0.997), RBT (0.003)	8	1,252	Indigenous
Lower Howe	WCT	WCT (0.997), RBT (0.002), YCT (0.001)	3	1,253	Indigenous
Hidden	YCT	Assumed YCT, no access by other species	110	1,943	Introduced
Avalanche	WCT	WCT (1.000)	23	1,190	Indigenous
Snyder	WCT	WCT (1.000)	2	1,597	Indigenous
Fish	WCT × YCT	YCT (0.752), WCT (0.244)	3	1,264	Introduced
McDonald	WCT	WCT (based on tributaries)	2,781	961	Indigenous
Lincoln	WCT	WCT (1.000)	14	1,402	Indigenous
Harrison	WCT	WCT (0.996), RBT (0.004)	163	1,126	Indigenous
Upper Isabel	WCT	WCT (1.000)	5	1,826	Indigenous
Isabel	WCT	WCT (1.000)	18	1,742	Indigenous
Ole	WCT	WCT (0.999), YCT (0.001)	2	1,697	Indigenous
Missouri River basin					
Oldman	YCT	YCT (0.902), RBT (0.086), WCT (0.012)	18	2,026	Introduced
Katoya	YCT	YCT (0.983), WCT (0.017)	4	1,941	Introduced
Medicine Grizzly	N/A	RBT (0.990), WCT (0.010)	16	1,696	Introduced
Morning Star	YCT	Fishless	4	1,757	Introduced
South Saskatchewan River basin					
Otokomi	YCT × RBT	YCT (0.934), RBT (0.066)	9	1,976	Introduced
Gunsight	N/A	RBT (0.987), WCT (0.013)	46	1,629	Introduced
Upper Slide	YCT × RBT	YCT (0.875), WCT (0.125)	16	1,838	Introduced
Lower Slide	YCT × RBT	YCT (0.578), WCT (0.410), RBT (0.012)	3	1,825	Introduced
Red Eagle	RBT × YCT	RBT (0.801), WCT (0.194), YCT (0.004)	56	1,439	Indigenous
Elizabeth	N/A	RBT (0.991), WCT (0.009)	79	1,491	Introduced
Glenns	N/A	RBT (0.982), WCT (0.018)	106	1,482	Introduced
Cosley	N/A	RBT (1.000)	90	1,476	Introduced

Most ($N = 30$; 83%) of the 36 conservation populations were classified as weakly to strongly connected populations (Table 5), and they occupied much more stream length (732 km; 89% of conservation population-occupied stream habitat) and lake habitat area (4,933 ha; 85% of conservation

population-occupied lake habitat) than isolated populations (stream length = 89 km, 11%; lake area = 549 ha, 10%; Table 6). Twenty of the connected populations occupied stream habitat only (465 km), whereas 10 of the connected populations occupied both stream (267 km) and lake (4,933

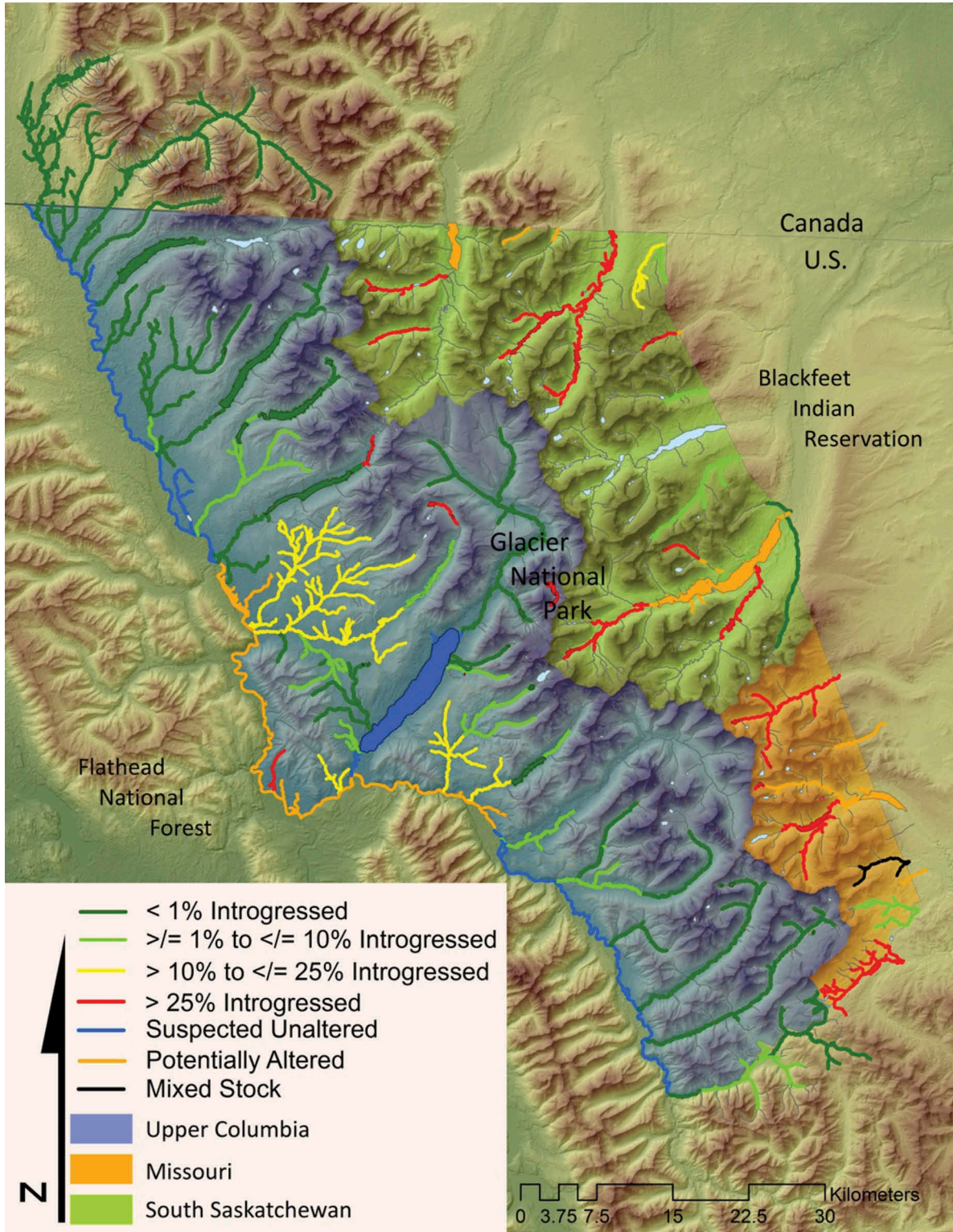


FIGURE 2. Genetic status of Westslope Cutthroat Trout populations in streams and lakes of the upper Columbia, Missouri, and South Saskatchewan River basins, Glacier National Park, as of 2012.

TABLE 5. Population type, distance to the nearest hybrid source (>10% introgressed), hybridization risk (see Table 3), total occupied drainage area, total occupied stream length, and total occupied lake area for Westslope Cutthroat Trout conservation populations in Glacier National Park.

Conservation population	Population type	Nearest hybrid source (km)	Hybridization risk	Drainage area (km ²)	Stream length (km)	Lake area (ha)
Upper Columbia River basin						
Spruce Creek	Connected	29.6	Medium-low	44.0	31.7	0
Kishenehn Creek	Connected	27.3	Medium-low	208.0	72.2	0
Sage Creek	Connected	33.6	Medium-low	98.3	81.3	0
Starvation Creek	Connected	24.7	Medium-low	42.9	20.8	0
Kintla Lake	Connected	21.2	Medium-low	47.7	6.7	694
Ford Creek	Connected	13.0	Medium-low	33.5	20.6	0
Akokala Creek	Connected	0.0	High	103.4	61.3	10
Bowman Lake	Connected	6.7	Medium-high	144.1	26.4	704
Lower Quartz Lake	Connected	4.2	Medium-high	72.2	35.3	68
Quartz Lake	Isolated	N/A	Low	64.7	5.2	391
Logging Lake	Connected	0.0	High	80.4	22.1	451
Rogers Lake	Connected	0.0	High	7.8	0.4	34
Trout Lake	Isolated	0.0	High	30.9	4.5	111
Camas Tributary	Connected	0.0	High	5.2	3.5	0
McGee Creek	Connected	0.0	High	25.2	21.1	0
Lake McDonald	Connected	0.0	High	184.5	55.5	2,794
Upper McDonald Creek	Isolated	N/A	Low	244.7	53.0	0
Avalanche Lake	Isolated	N/A	Low	37.4	4.1	23
Lincoln Creek	Connected	0.0	High	51.1	21.3	14
Harrison Lake	Connected	0.0	High	33.9	4.4	163
Nyack Creek	Connected	5.8	Medium-high	50.8	13.5	0
Coal Creek	Connected	14.6	Medium-low	134.8	41.0	0
Muir Creek	Connected	26.7	Medium-low	35.2	8.2	0
Park Creek	Connected	35.9	Medium-low	83.0	25.9	0
Lake Isabel	Isolated	N/A	Low	7.6	3.1	24
Ole Creek	Connected	40.3	Medium-low	112.5	33.7	2
Bear Creek	Connected	49.2	Medium-low	146.6	60.0	0
Missouri River basin						
Railroad Creek	Isolated	N/A	Low	30.4	18.8	0
Midvale Creek	Connected	0.0	High	25.9	11.1	0
South Saskatchewan River basin						
Divide Creek	Connected	7.1	Medium-high	36.0	15.0	0
Wild Creek	Connected	7.7	Medium-high	11.6	2.7	0
Two Dog Creek	Connected	1.6	Medium-high	6.7	0.6	0
Rose Creek	Connected	0.0	High	0.6	0.9	0
Boulder Creek	Connected	25.8	Medium-low	70.4	23.1	0
Lower Kennedy Creek	Connected	12.2	Medium-low	41.1	6.8	0
Julie Creek	Connected	0.0	High	3.8	5.1	0

TABLE 6. Numbers of Westslope Cutthroat Trout conservation populations and the number of stream kilometers occupied (km) in the upper Columbia, Missouri, and South Saskatchewan River basins within Glacier National Park (GNP), presented for each population type (isolated or connected) and each rationale for designation.

Rationale for designation	Isolated		Connected		Total		
	Number	Km	Number	Km	Number	Km	%
Upper Columbia River basin							
Core conservation population	4	65	13	414	17	479	58
Mixed genetic makeup	1	5	9	252	10	257	31
Missouri River basin							
Mixed genetic makeup	1	19	1	11	2	30	4
South Saskatchewan River basin							
Core conservation population	0	0	2	18	2	18	2
Mixed genetic makeup	0	0	5	37	5	37	5
GNP total							
Core conservation population	4	65	15	432	19	497	61
Mixed genetic makeup	2	24	15	300	17	324	39

ha) habitat. Isolated conservation populations consisted of both single isolates ($N = 3$; stream length = 26 km; lake area = 47 ha) and isolated metapopulations ($N = 3$; stream length = 63 km; lake area = 502 ha). With the exception of the Quartz Lake population (isolated by an artificial barrier), isolated populations were located upstream of natural waterfall barriers. Four of the six isolated conservation populations occupied both stream (17 km) and lake (549 ha) habitat, while the other two isolated populations occupied stream habitat only (72 km; Table 5; Table S.1).

Hybridization Risk

Nineteen conservation populations (526 km of stream habitat; 1,468 ha of lake habitat) were classified as having a medium-low to medium-high risk of hybridization (mean distance to hybrid source = 21 km; Figure 3; Tables 3, 5). Twelve conservation populations (211 km; 3,577 ha) were at a high risk of hybridization, and five populations (84 km; 438 ha) were at a low risk of hybridization. All of the low-risk populations were isolated upstream of fish passage barriers.

DISCUSSION

Large protected areas, where nonhybridized populations are interconnected and express historical life history and genetic diversity, provide some of the last ecological and evolutionary strongholds for conserving native species. Here, we demonstrate how genetic and hybridization assessments across widely distributed populations can help to identify populations and drainages containing native trout of crucial conservation concern. Moreover, we provide a much-

needed template for conserving native Westslope Cutthroat Trout in one of the few strongholds remaining within their range. Our assessment indicates that extensive translocations of and invasions by nonnative salmonids have led to introgressive hybridization with Westslope Cutthroat Trout populations in many watersheds within Glacier National Park and pose an imminent threat to many extant populations of high conservation value. Introgressive hybridization between introduced Rainbow Trout and native Westslope Cutthroat Trout tends to spread quickly (Hitt et al. 2003; Weigel et al. 2003; Rubidge and Taylor 2004; Bennett et al. 2010; Yau and Taylor 2013; Muhlfeld et al. 2014; Lowe et al. 2015) and can reduce fitness (Muhlfeld et al. 2009a; Kovach et al. 2015), genomic integrity (Allendorf and Leary 1988), and, ultimately, native species diversity (Allendorf et al. 2001). Furthermore, hybridization is exacerbated by habitat modification (Allendorf et al. 2001) and climate change (Muhlfeld et al. 2014), so this problem will probably become more serious with increasing land use and global climate change. Glacier National Park is an area of critical refugia from the ongoing threats of habitat loss, invasive species, and climate change; therefore, a diverse set of management approaches will be needed to conserve the remaining native Westslope Cutthroat Trout populations within the park and in the surrounding waters.

Genetic Status and Distribution West of the Continental Divide

Our results indicate that in Glacier National Park, numerous nonhybridized Westslope Cutthroat Trout populations persist west of the Continental Divide in tributaries to the North Fork and Middle Fork Flathead River. These populations

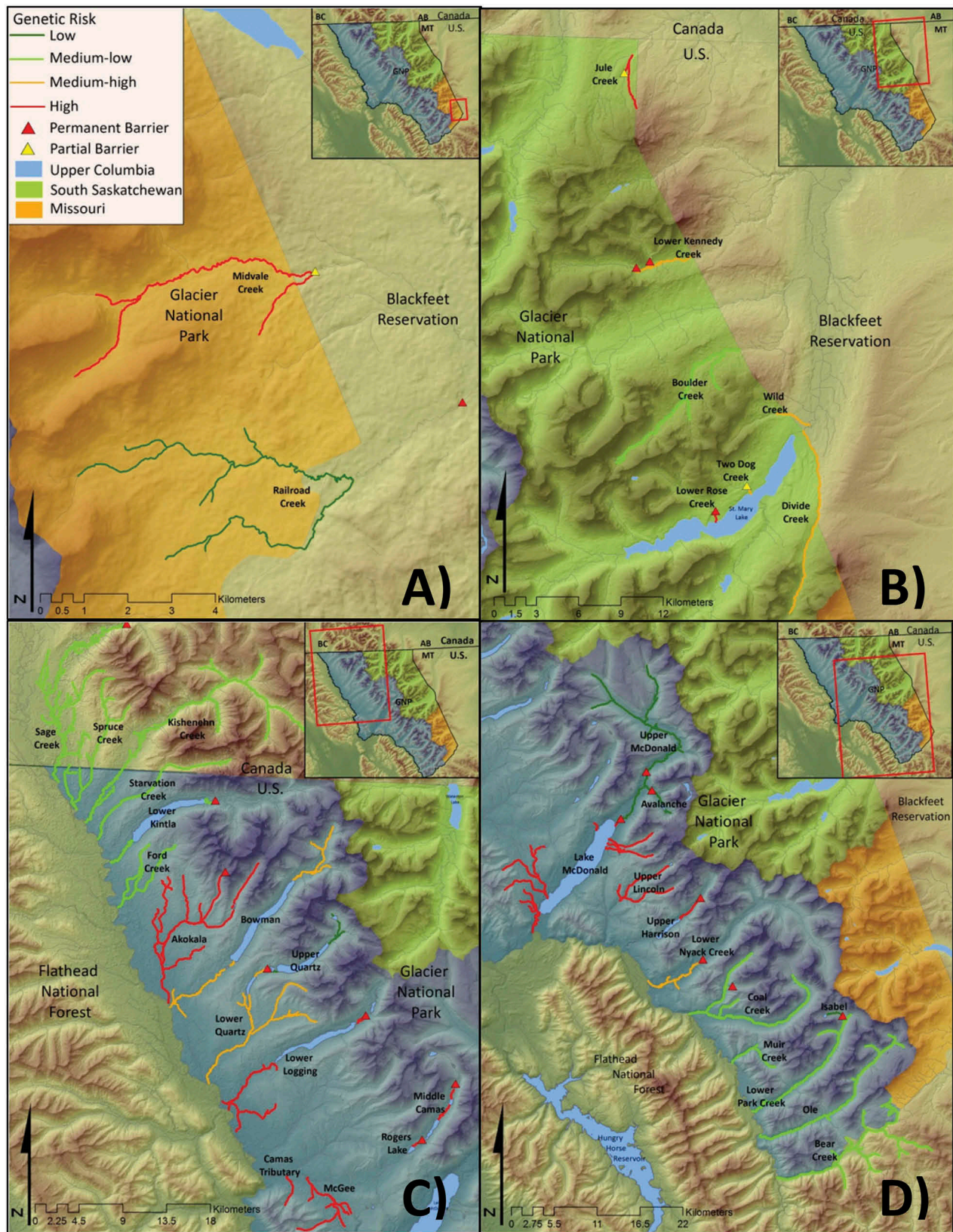


FIGURE 3. Westslope Cutthroat Trout conservation populations in Glacier National Park: (A) Missouri River basin; (B) South Saskatchewan River basin; and (C) Middle Fork Flathead River, upper Columbia River basin; and (D) North Fork Flathead River, upper Columbia River basin. The line color indicates the degree of genetic risk (see Table 3).

represent the vast majority of nonhybridized Westslope Cutthroat Trout remaining in the park. Moreover, these areas support some of the final remaining enclaves of nonhybridized lacustrine populations throughout the Westslope Cutthroat Trout's range (Liknes and Graham 1988; Marnell 1988; Shepard et al. 2005). However, continued invasions by Rainbow Trout and Westslope Cutthroat Trout \times Rainbow Trout hybrids from sources within and outside of Glacier National Park threaten the connected conservation populations within the park (e.g., Akokala Creek, Bowman Lake, lower Quartz Lake, Logging Lake, Camas Tributary, lower McDonald Creek, Lincoln Creek, and Harrison Creek). Hybridized Westslope Cutthroat Trout \times Rainbow Trout populations within the park now include those occurring in Camas, Anaconda, and Dutch creeks; a few unnamed tributaries in the lower North Fork Flathead River; and in the lower portions of Lincoln, Harrison, and Nyack creeks (Middle Fork Flathead River system).

Headwater populations of nonnative Yellowstone Cutthroat Trout threaten downstream Westslope Cutthroat Trout populations in a few drainages of the North Fork Flathead River (e.g., Logging Lake and Camas Tributary) and Middle Fork Flathead River (e.g., McDonald Creek). However, the spread of hybridization with Yellowstone Cutthroat Trout does not appear to be as frequent and severe as hybridization with Rainbow Trout in the park and elsewhere (Behnke 1992; Shepard et al. 2005; Trotter 2008). More research is needed to assess the impacts and spatiotemporal patterns of genetic introgression between native Westslope Cutthroat Trout and introduced Yellowstone Cutthroat Trout.

The Westslope Cutthroat Trout population inhabiting upper McDonald Creek represents the largest and most secure conservation populations within Glacier National Park. Barrier waterfalls isolate the population, which occupies approximately 55 km of high-quality stream habitat. Protection of and improvements in stream and riparian habitats and road crossings along the Going-to-the-Sun Road will be vital for maintaining the high-quality habitats that support this important conservation population.

Genetic Status and Distribution East of the Continental Divide

In Glacier National Park east of the Continental Divide, Westslope Cutthroat Trout populations in the Missouri and South Saskatchewan River drainages appear to be at imminent risk of genomic extinction, as only a few populations remain in spatially limited stream habitats and those populations are generally at risk of invasive hybridization. We detected only nine Westslope Cutthroat Trout populations with hybridization levels $\leq 10\%$ in streams east of the Continental Divide. In the upper Missouri River drainage (Marnell 1988), we found two remaining conservation populations within the park boundary: Midvale and Railroad creeks. The Midvale Creek population

is at a high risk of genetic introgression because there is no permanent barrier to prevent Westslope Cutthroat Trout \times Rainbow Trout hybrids from leaving the lower portion of the stream network. Railroad Creek supports a nonhybridized Westslope Cutthroat Trout population and is isolated by a geologic barrier falls outside the park boundary on the Blackfoot Reservation. However, nonnative Brook Trout *Salvelinus fontinalis* occurring upstream of the barrier falls pose an immediate threat to the persistence of the conservation population in Railroad Creek. The seven conservation populations that were identified in the South Saskatchewan River drainage (Jule, Kennedy, Boulder, Wild, Two Dog, Rose, and Divide creeks) occupy short stream sections that are connected to hybrid and nonnative source populations. These seven populations are generally confined to headwater areas and are likely subject to the demographic, genetic, and environmental risks that are inherent to small populations.

Populations in the South Saskatchewan and Missouri River drainages in Montana represent some of the furthest inland distributions of Westslope Cutthroat Trout throughout the subspecies' historic range in the United States (Shepard et al. 2005; Haak et al. 2010). These peripheral populations (i.e., occurring at the geographic edge of the subspecies' historic range) are at a higher risk than populations in the core of the range (e.g., the Flathead River system) because they occupy small headwater areas and experience limited interpopulation genetic exchange; thus, they are more likely to suffer effects from inbreeding depression (Lesica and Allendorf 1995; Taylor et al. 2003). In a rangewide status assessment of Westslope Cutthroat Trout in the United States, Shepard et al. (2005) reported that native populations largely occur in core areas of the historical range, whereas they are sparsely distributed near the range margins, particularly in the Missouri River drainage within Montana. However, peripheral populations are frequently subject to different selective pressures than core area populations and may contain genetic diversity that is important for adaptation to changing environmental conditions (Haak et al. 2010). Therefore, conservation strategies that increase the occupied stream length while reducing threats from nonnative species (e.g., via barrier installation or the suppression/eradication of nonnative fish) are needed in the Missouri and South Saskatchewan River drainages to protect the few remaining populations of Westslope Cutthroat Trout.

Conservation Management

Although protecting the remaining genetic integrity and diversity of Westslope Cutthroat Trout in Glacier National Park will be challenging, numerous management opportunities exist. Conservation management strategies that protect nonhybridized populations and that eliminate or reduce nonnative species and hybridized populations will be necessary to maintain the subspecies' genetic integrity and ecological diversity within the park.

Isolation by artificial barriers is often used as a conservation strategy for protecting native inland trout from nonnative species in headwater streams (Fausch et al. 2009), but this approach can increase the risk of extinction due to small population size and inbreeding depression (Peterson et al. 2008). By contrast, maintaining large areas of connected habitat is also an important conservation strategy, with the goal of (1) allowing Westslope Cutthroat Trout to express all life history traits and (2) reducing the stochastic environmental and demographic risks that are inherently associated with small population sizes. However, for some connected populations, this strategy increases the risks of introgression, competition with and predation by nonnative fish, and disease. Balancing these trade-offs will require difficult and context-specific decisions for protecting the genetic and ecological diversity of Westslope Cutthroat Trout in Glacier National Park. For example, a recent case study assessing various artificial barrier placement scenarios in terms of their potential impacts on Westslope Cutthroat Trout populations in the Akokala Creek watershed, Glacier National Park, helped fisheries managers to identify an optimal strategy that minimized negative impacts on population demography and genetic diversity (Muhlfeld et al. 2012).

Suppression or eradication of hybridizing trout species within Glacier National Park and surrounding areas is likely needed to conserve and protect extant conservation populations of Westslope Cutthroat Trout. Projects that involve physical or chemical removal of nonnative species have proven effective for eliminating or reducing invasive species' impacts on many native trout species, including Westslope Cutthroat Trout. For example, chemical eradication of hybrid and Rainbow Trout source populations in several lakes within the Bob Marshall Wilderness and Jewel Basin was used to effectively eliminate hybrid sources threatening nonhybridized downstream populations in the South Fork Flathead River (Boyer 2012). Suppression of hybrid and Rainbow Trout source populations in the lower Flathead River upstream of Flathead Lake reduced the abundance and spread of hybridization with Rainbow Trout (Al-Chokhachy et al. 2014). These types of pro-active suppression programs will be increasingly important as the climate continues to warm, evoking changes in streamflow and temperature regimes (Muhlfeld et al. 2014).

Replication of genetically pure populations across the landscape will also be an important management strategy for conserving Westslope Cutthroat Trout in Glacier National Park. This type of approach will be particularly useful for restoring Westslope Cutthroat Trout to areas within their historical range in the Missouri and South Saskatchewan River drainages, where only a few populations persist in small, fragmented streams with little opportunity for gene flow. Conservation introduction (moving species to areas outside of their previous range, where conditions are predicted to be more suitable) is another translocation strategy that fisheries managers can use to establish new conservation populations in areas of refugia (Galloway et al. 2016).

In most locations where we detected 1% or greater levels of nonnative admixture, genotypic distributions deviated from random mating, suggesting that many populations have not yet become hybrid swarms. This result is not surprising, as various ecological and evolutionary phenomena occurring in this region contribute to nonrandom mating—especially the continuous dispersal of highly admixed individuals into populations with low admixture (Boyer et al. 2008; Kovach et al. 2015), assortative mating due to differences in reproductive timing between species (Muhlfeld et al. 2009c), and natural selection acting against nonnative introgression (Muhlfeld et al. 2009a; Kovach et al. 2015). Even for randomly mating populations that are not experiencing migration, selection, or assortative mating, hybrid swarm formation takes multiple generations because of physical genetic linkage (Allendorf et al. 2013), and many hybridization events are likely recent (Muhlfeld et al. 2014). Importantly, the observation that many hybridized populations within Glacier National Park are not yet hybrid swarms suggests that parental genotypes (i.e., largely nonhybridized Westslope Cutthroat Trout individuals) are still present and that active suppression of highly nonnative individuals may be particularly beneficial in these areas (Al-Chokhachy et al. 2014). Nonetheless, several hybrid swarms with a high proportion of nonnative admixture have been identified in streams outside of the park's boundary (Hitt et al. 2003; Boyer et al. 2008; R. Leary, Montana Department of Fish, Wildlife, and Parks, unpublished data), thereby threatening nonhybridized populations within the park.

Conclusions

We have provided baseline genetic status and distribution information that can be used for prioritizing management efforts to protect and restore the genetic integrity of Westslope Cutthroat Trout populations in Glacier National Park. We recommend maintaining and periodically updating these data to monitor changes in genetic status and distribution over time. Conservation strategies that prioritize genetic integrity, large population sizes, and a broad mosaic of connected, cold, complex habitats free of nonnative salmonids are needed to maintain and restore the Westslope Cutthroat Trout's genetic and ecological diversity and persistence in Glacier National Park throughout the 21st century.

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