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[Article]

Potential Consequences of Climate Change to Persistence of Cutthroat Trout Populations

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Abstract.—Warmer water, changes in stream flow, and the increasing frequency and intensity of other disturbances are among the factors associated with climate change that are likely to impact native trout populations in the western USA. We examined how three of these factors—increased summer temperatures, uncharacteristic winter flooding, and increased wildfires—are likely to affect broad-scale population persistence among three subspecies of cutthroat trout *Oncorhynchus clarkii*. Our results suggest that as much as 73% of the habitat currently occupied by Bonneville cutthroat trout *O. c. utah*, 65% of that occupied by westslope cutthroat trout *O. c. lewisi*, and 29% of that occupied by Colorado River cutthroat trout *O. c. pleuriticus* will be at high risk from one or more of the these three factors. Within the next 50 years, wildfire, floods, and other disturbances may have a greater impact on population persistence than increasing water temperature alone. Our results also suggest that the risk will vary substantially within subspecies. For each subspecies, our analyses identified large portions of their ranges where all populations either currently fail to meet basic persistence criteria, are at high risk from climate change, or both, indicating a high likelihood of losing the genetic and life history diversity in those areas. Stress from climate change is likely to compound existing problems associated with habitat degradation and introgression from introduced salmonids. Recognition of the increased risk from climate change may warrant altering the management paradigm of isolation and require increased control efforts for invasive nonnative species. Regardless of the management avenue chosen, more populations are likely to become isolated and vulnerable in the near future. Our results argue for immediate restoration actions within certain subbasins to increase the resistance and resilience of at-risk populations and habitats to additional disturbances caused by rapid climate change.

Native trout and salmon are sensitive to habitat degradation and generally require streams and lakes with cold, high-quality water that are free of nonnative salmonids. As a result of habitat declines (Dunham et al. 1997; Lee et al. 1997) and increased risk of competition, predation, and introgressive hybridization from introduced salmonids (Dunham et al. 2002a; Peterson et al. 2004), many species and subspecies have been listed as endangered or threatened pursuant to the U.S. Endangered Species Act and others are under review for potential future listing. Instream barriers (e.g., culverts and dams), invasions of nonnative fishes, habitat degradation, and management strategies of isolating native populations in headwater reaches above artificial barriers have all contributed to the creation of highly fragmented native cutthroat trout distributions, resulting in many small, isolated populations (Dunham et al. 2003; Neville et al. 2006a). Larger, interconnected populations in higher-order stream systems now are rare (Colyer et al. 2005), and most inland cutthroat trout subspecies currently occupy only 10–30% of their historic range, primarily in upper elevation headwater streams (Young 1995).

Small, inland cutthroat trout populations are already at risk of extinction from two primary causes. First, their small stream habitats are vulnerable to disturbances such as wildfire, flood, or prolonged drought (Dunham et al. 2003). Second, small, isolated popula-

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tions also are at increased risk of extinction because of demographic and genetic factors associated with their reduced population sizes and loss of interpopulation connectivity (Neville et al. 2006b). Fausch et al. (2006) recently summarized current threats to persistence of small, isolated salmonid populations, which included loss of genetic variability, loss of resilience, demographic stochasticity, environmental stochasticity, and natural and human-caused catastrophes.

In many cases, climate change will exacerbate declining habitat and population trends. Rahel et al. (1996) estimated losses of habitat in Wyoming's North Platte drainage of up to 76% for populations of brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis*, and rainbow trout *Oncorhynchus mykiss* as a result of warmer summer conditions. They also predicted increasing population fragmentation as fish retreated to remaining cooler waters in headwater stream reaches. In the Interior Columbia River basin, populations of bull trout *Salvelinus confluentus* may lose 18–92% of thermally suitable natal habitat as a result of warmer conditions associated with climate change (Rieman et al. 2007). Flebbe et al. (2006) found significant losses and increased population fragmentation in their examination of increased warming on brown trout, brook trout, and rainbow trout in the southern Appalachian Mountains. Depending on which climate model was used, trout habitat was predicted to decrease by 53–97% (Flebbe et al. 2006).

Increased stream temperatures are one of the primary, but not the only, potential outcomes of a rapidly changing climate. Reduced snowpack, earlier spring runoff, reduced summer flows, increased floods, and drought will pose additional stressors for freshwater fish populations (Clark et al. 2001; Poff 2002; Poff et al. 2002). Additionally, watersheds will be exposed to warmer air temperatures, increased evaporation rates, and earlier spring thaws, which will lead to longer wildfire seasons and fires of higher intensity (DellaSala et al. 2004; McKenzie et al. 2004; Westerling et al. 2006). Although native salmonids are well adapted to dealing with disturbances in their environment (Pearsons et al. 1992; Dunham et al. 2003; Dunham et al. 2007), disturbances such as wildfire or flooding can be lethal to at-risk populations if they are isolated from downstream cohorts and habitats that provide refuge from disturbance and sources of recolonization (Rieman and Clayton 1997; Gresswell 1999). As fire increases in extent, duration, and magnitude as predicted with climate change (McKenzie et al. 2004; Westerling et al. 2006), direct mortality and habitat impacts from fire may put many populations at risk, particularly those in isolated or already-degraded habitats (e.g., Brown et al. 2001; Dunham et al. 2003). Anthropogenic changes in watershed condition, such as loss of vegetative cover or increases in impervious surfaces, can compound disturbance risk (Wissmar et al. 2004). Additionally, native trout may be negatively affected by rapid changes in flood magnitude, timing that create a mismatch between the hydrological regime and spawn timing, or both. For instance, successful invasions of introduced rainbow trout likely have been limited in some regions by such a mismatch between spawning behavior and the hydrological regime of novel habitats (Fausch et al. 2001). It is likely that native populations facing hydrological changes in their native habitats will face similar challenges.

Changes associated with a rapidly warming climate already are apparent in the streams and watersheds in the Rocky Mountains of the western USA. In Colorado, earlier emergence of a mayfly *Baetis bicaudatus* has been observed since 2001 because of earlier peak stream runoff associated with warmer stream temperatures during dryer years (Harper and Peckarsky 2006). Since the mid-1980s, there has been a 60% increase in the frequency of large wildfires in the northern Rockies that is associated with increased spring and summer temperatures and earlier spring snowmelt (Westerling et al. 2006). Such observations increase the importance of analyzing increased risk to native trout populations in these areas.

The objective of our study was to examine the increased risk to local extirpations posed by multiple predicted climate change impacts to habitats and populations of native trout in the western USA and to identify the spatial characteristics of these risks and consequent conservation needs. We used a geographical information systems (GIS) approach to examine population persistence and climate change risk associated with increasing temperatures and altered flood and wildfire regimes for three native subspecies of cutthroat trout *O. clarkii* in the Intermountain West: Bonneville cutthroat trout *O. c. utah*, Colorado River cutthroat trout *O. c. pleuriticus*, and westslope cutthroat trout *O. c. lewisi*. Previous studies have examined likely impacts of increasing temperatures on fish distributions, but few, if any, have examined increased temperatures in conjunction with likely changes in flooding and wildfire events.

Methods

Our assessment of extirpation risk to local populations of native cutthroat trout is based on the combined stressors of habitat fragmentation and climate change. We first analyze the current distribution of Bonneville cutthroat trout, Colorado River cutthroat trout, and westslope cutthroat trout to determine the likelihood of

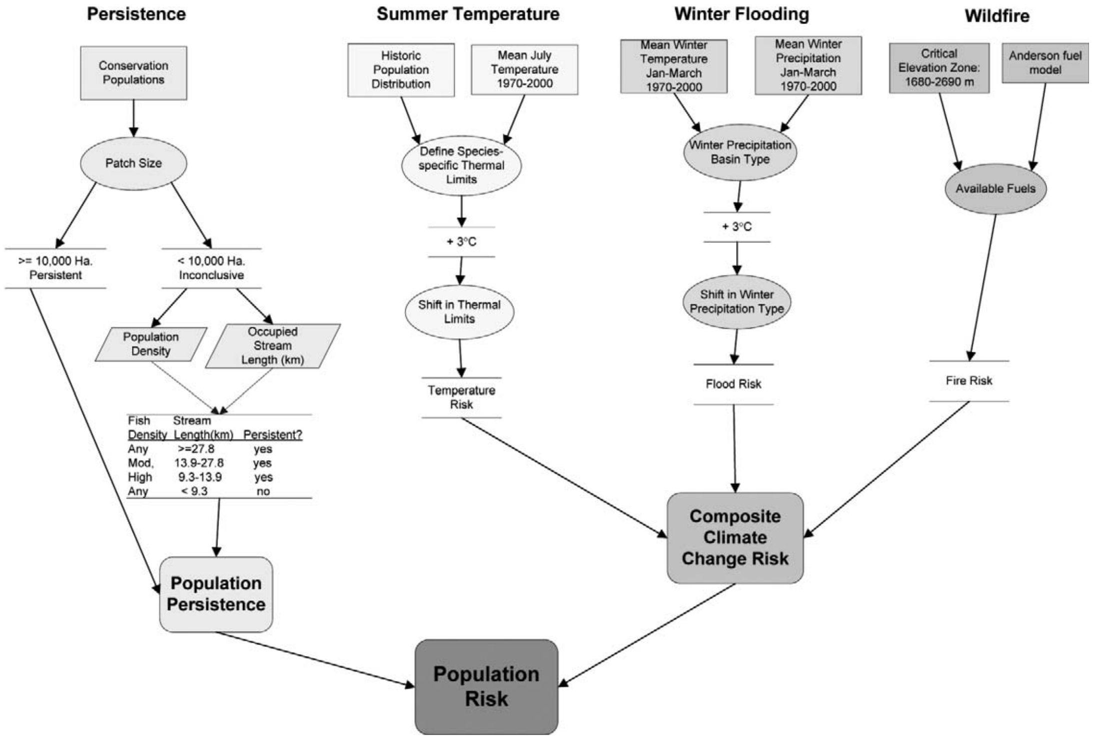

FIGURE 1.—Schematic showing how the current analysis of population persistence is influenced by climate change risk models to produce an overall description of population risk.

population persistence (under current conditions) based on relationships drawn from the literature between persistence and fish abundance, habitat connectivity and patch size for several trout species. We then analyze climate change-driven environmental effects and combine these results with the results of the persistence analysis to provide a spatially explicit characterization of local extinction risk in the context of climate change (Figure 1).

Population persistence.—Our analysis integrated available population data with persistence thresholds to develop a decision process for determining the likelihood of persistence for individual populations (expressed in terms of numbers of populations and amount of stream habitat they occupy), and whether the subspecies as a whole is likely to maintain its current geographic extent under existing conditions. Our approach relies on use of the conservation success index (CSI) geographic information, an analytical framework for evaluating the status of coldwater fishes at various geographic scales based on current distribution, population and habitat conditions, and security from future threats. Description of the CSI is beyond the scope of this paper, and we refer the reader to a detailed overview of data sources and methodology in Williams et al. (2007a). Briefly, for the species evaluated in this paper, population and distribution data used in the CSI were taken from recent rangewide assessments for Bonneville cutthroat trout (May and Albeke 2005), Colorado River cutthroat trout (Hirsch et al. 2006), and westslope cutthroat trout (Shepard et al. 2003). We utilized data for "conservation populations," which were defined as meeting genetic purity requirements according to their respective assessments. Population data were aggregated from stream reaches to subwatersheds (sixth level hydrologic unit code; see U.S. Geological Survey 2008) for the persistence analysis, and the subsequent results were aggregated to subbasins (fourth level hydrologic unit code) and larger river basins for rangewide interpretation. For Bonneville and Colorado River cutthroat trout, we also refer to geographic management units (GMUs), which are usually equivalent to larger river basins and are delineated by agency work-groups generally based on documented (or assumed, from geographic isolation) genetic distinctiveness (e.g., see Moritz 1994; Hirsch et al. 2006).

For small stream populations, we followed persistence criteria of Hilderbrand and Kershner (2000), who combined the amount of available stream habitat with population density to determine whether populations met the goal of 2,500 individuals (>75 mm), which corresponds to a frequently targeted effective population size of 500 (Franklin 1980). Based on their analysis, we assumed that the following combinations of stream habitat availability and population densities were necessary to meet persistence criteria: 9.3–13.9-km stream habitat with greater than 93 fish/km; 13.9–27.8-km habitat with greater than 31 fish/km; or greater than 27.8-km habitat with any fish density. Any stream with less than 9.3 km of habitat did not meet persistence criteria regardless of fish density. For larger rivers or interconnected stream systems, we relied on previous analyses of bull trout and Lahontan cutthroat trout *O. c. henshawi*, suggesting that populations in greater than 10,000 ha of habitat have a high likelihood of persistence, whereas populations in less than 5,000 ha face a substantially higher probability of extinction (Dunham and Rieman 1999; Dunham et al. 2002b; Rieman et al. 2007).

Persistence criteria were examined for each population, summed at the subbasin scale, and compared with a goal of having five populations that meet or exceed persistence criteria within each subbasin (Rieman et al. 2007). We also scored subbasins as fully meeting persistence criteria if one metapopulation occupied an entire subbasin or if two to three well-connected populations occupying 25,000-ha patch size or greater each occurred within a subbasin.

Climate change analysis.—The analyses of increased risk from warmer summer temperatures, winter flooding, and wildfire were conducted at the subwatershed scale in a GIS environment. For each subwatershed within a subspecies' historic range, we assigned a relative risk for each element individually as well as a composite characterization of low, moderate, or high risk from climate change. These risk scores were integrated with the results of the persistence analysis to identify subbasins and other geographic areas where large proportions of populations are predicted to be high risk of extirpation.

Summer temperature.—For coldwater species, temperature is a critical habitat element. The correlation between air temperature and historical fish distributional limits, and the lack of regional temperature data for streams and lakes makes air temperature the most practical indicator of thermal changes in aquatic environments across large geographic areas (Rahel et al. 1996; Rahel 2002). We apply the methods of Rahel et al. (1996) who used changes in mean July air temperature, often the hottest month of the year in the Rocky Mountains, to analyze habitat loss due to global warming for a coldwater guild of brown trout, rainbow trout, brook trout, and cutthroat trout in the Rocky Mountains. We used the national data set of average monthly temperatures from the period 1970 to 2000 (PRISM 2007; spatial resolution = 800 m), and averaged the minimum and maximum July temperatures to establish a baseline from which to predict change.

Before analyzing the effects of increasing temperature, we characterized the thermal limits for each subspecies based on the relationship between each subspecies' historical distribution and air temperature, assuming that this reflects subspecies-specific preferences for and adaptations to local environmental conditions. For instance, less than 1% of the total historical distribution for westslope cutthroat trout and Colorado River cutthroat trout was found in streams with an average July air temperature greater than 22°C. In contrast, nearly 20% (1,400 km) of the Bonneville cutthroat trout historic distribution was associated with a mean July air temperature greater than 22°C. Based on this analysis, an upper thermal limit of 22°C was applied to westslope and Colorado River cutthroat trout, and 24°C was used for Bonneville cutthroat trout. Temperatures at or above these limits were considered "unsuitable." Recognizing that local conditions such as shading and flow can mitigate temperature, we also identified a "marginal" temperature range that is higher than the optimal range but is not necessarily precluded as habitat because it does represent a portion of the historic distribution and may be used at least seasonally. This marginal habitat range for westslope and Colorado River cutthroat trout was defined as 19.1–22.0°C, which included 12% and 11%, respectively, of their historically occupied ranges. For Bonneville cutthroat this "marginal" range was defined as 22.1–24.0°C, which included 14% of its historically occupied range. Any temperatures less than the lower end of these ranges were considered thermally suitable. By using historic rather than current distributions to define thermal limits, we hoped to minimize anthropogenic effects on species distribution and emphasize fish responses to natural habitat suitability.

Our analysis of global warming impacts on thermal suitability applied a 3°C temperature increase to the 1970–2000 mean July air temperatures. This increase has been projected as the most likely scenario for the western United States within this century (Climate Impacts Group 2004). We calculated an area-weighted average temperature under the global warming scenario for each subwatershed within each species' range. We scored each subwatershed for three levels of risk to local populations from increased summer air temperatures: 1 (suitable and below thermal limit, low risk), 2 (marginal and within thermal transition range, moderate risk), or 3 (unsuitable and above thermal limit, high risk).

Uncharacteristic winter floods.—Our intent in this analysis was to identify those subwatersheds at increased risk of uncharacteristic winter flooding as a direct result of warmer winter temperatures due to climate change. We have drawn on the findings of Hamlet and Lettenmaier (2007) who analyzed uncharacteristic winter flood events for the western USA as a result of global warming. They used midwinter temperature to define three types of basins: rain dominant, snow dominant, and transient between rain and snow. Winter flooding in rain-dominant basins is a function of the individual storm event as well as the size and runoff characteristics of the catchment. Flood events in these basins will not change due to rising temperatures without a corresponding increase in precipitation. Snow-dominant basins do not typically flood in midwinter but rather flooding occurs later as spring runoff. Low- to mid-elevation, snow-dominant basins currently near the freezing line, however, may experience a change in runoff timing and characteristics with warmer winter temperatures. Transient basins, where both rain and snowstorms occur in the winter months, are currently the primary location of significant flooding events for much of the western USA (O'Conner and Costa 2003; Hamlet and Lettenmaier 2007). The magnitude of the flood event depends on the intensity and duration of the rainstorm and the antecedent snowpack.

Because our focus was on changes in winter flooding regimes, we began by identifying basins that are dominated by winter precipitation and eliminated those areas that receive the majority of their annual precipitation in other seasons such that winter flooding is less likely to occur under existing precipitation patterns. To do this, we used PRISM average annual and monthly precipitation data for 1970–2000. We calculated the area-weighted mean annual and winter precipitation for each subwatershed. Subwatersheds where the three months of winter (January–March) precipitation comprised less than 25% of the annual precipitation were classified as having a non-winter-dominant precipitation regime and therefore were considered to be at low risk for uncharacteristic winter flooding. We recognize that some basins in wet regions may receive a significant amount of winter precipitation but not meet our 25% criteria.

After identifying the winter precipitation-dominant subwatersheds, we then characterized them based on the area-weighted mean winter temperature (January–March). Hamlet and Lettenmaier (2007) used −6°C and +5°C as the average temperature limits for their transient basins. However, their analysis covered a much larger geographic region (basins across the western USA) with a spatial resolution of one-eighth degree latitude–longitude (approximately 12 × 10 km) than our study, which was limited geographically to the historic ranges of our three subspecies and had a spatial resolution of 800 m. Therefore, we used a more narrowly defined range for transient basins of −1°C and +1°C. We assumed that subwatersheds with a mean winter temperature less than −1°C were snow dominant, while those with a mean winter temperature greater than +1°C were rain dominant. A 3°C temperature increase was added to the current winter mean temperature, and the subwatersheds were reclassified. The greatest risk was assigned to subwatersheds that change from snow dominant to transient or rain dominant. Given our narrow temperature range for transient basins, our analysis may err on the side of understating the risk of increased winter flooding.

Subwatersheds that change from transient to rain dominant were assigned a moderate risk score because they would be likely to experience more flood events in the near term, as they continue to receive some snow along with an increasing frequency of warm midwinter storm events, until they ultimately become rain dominant. Once this occurs, the winter flood risk may actually decline because there will no longer be an antecedent snow pack to contribute to high runoff. The cold, high-elevation subwatersheds that are likely to remain snow dominant as well as the valley bottoms that are currently rain dominant were classified as low risk. We recognize that these downstream reaches are likely to experience greater winter flows due to upstream events, but the complexity of dams and reservoir management makes it difficult to analyze downstream flood effects accurately.

Increased wildfire.—Our analysis for this element, unlike the previous two, does not incorporate a fixed temperature increase because wildfire does not have a temperature threshold like thermal limits for fish or the difference between rain and snow events. Rather, we assume that wildfire is a function of climate, fuels, and ignition and that changing climatic conditions for the western United States will continue to increase the likelihood of uncharacteristic wildfires (assuming the presence of fuels and an ignition source).

In order to define the spatial characteristics of increased wildfire risk we applied the findings of Westerling et al. (2006) who found that fire frequency and duration and, therefore, the total area burned, in the forested regions of the Rocky Mountains were closely associated with timing of snowmelt. Areas where snowmelt occurred earlier had more fires and a longer fire season because the fuels had more time to dry. They found that the topographic zone of 1,680–2,690 m

TABLE 1.—Persistence and climate change risk in geographic management units (GMUs) occupied by Bonneville cutthroat trout. Risk is quantified in terms of kilometers of stream habitat occupied and numbers of conservation populations.

	Totals		Percent meeting persistence criteria		Percent meeting persistence criteria at high climate risk	
GMU	Stream habitat (km)	Population	Steam habitat	Population	Stream habitat	Population
Bear River	1,752	32	96	69	59	68
Northern Bonneville	1,319	65	70	22	76	86
Southern Bonneville	144	21	18	10	100	100
West Desert	94	31	10	1	0	0
Total	3,309	149	79	25	71	76

had the most pronounced earlier snowmelt and also more and larger wildfires.

Because large portions of the ranges of our three subspecies fall within the geographic region evaluated by Westerling et al. (2006), we used their topographic zone of increased wildfire to identify subwatersheds at greatest risk of wildfire. We calculated the area-weighted average elevation for each subwatershed, and those that were within 1,680–2,690 m were identified as potential high fire risk pending further evaluation (see below), while those that fell above or below this zone were classified as low risk for wildfire. To further classify risk within the focal elevational zone, we relied on the Anderson fire behavior fuel model (Anderson 1982) as updated by the U.S. Forest Service and Department of the Interior's LANDFIRE program (e.g., www.landfire.gov). This spatial data set identifies 13 different fuel types based on satellite imagery collected between 1999 and 2003 with a spatial resolution of 30 m. Using the description of fire behavior associated with each of the fuel types, we assigned the grassland- and mesic shrubland-classes a low risk and the others a high risk. Converted lands and nonfuel categories (such as urban areas, agricultural lands, and barren ground) were classified as a zero risk. We then calculated an area-weighted average score for each subwatershed to determine a fire risk classification for subwatersheds within 1,681–2,690-m elevation. Those that were less than 50% high risk fuels were classified as low risk, subwatersheds that were 50–75% high risk fuels were classified as moderate risk, and subwatersheds greater than 75% high risk were ranked as high risk.

Composite climate change risk.—After completing our analyses of the three elements, we scored each subwatershed as low, moderate, or high composite risk based on the highest score from each of the three elements. For example, if a watershed was scored as low risk for both temperature and winter flooding but was at high risk for fire, its composite risk was high. These results were then combined with the results of our population persistence analysis to evaluate the risk of extirpation.

Results

Population Persistence

The range of Bonneville cutthroat trout is divided into four GMUs: Bear River, Northern Bonneville, Southern Bonneville, and West Desert (May and Albeke 2005). The amount of stream habitat available to conservation populations ranges from 94 km in the West Desert GMU to 1,752 km in the Bear River GMU. More than 90% of habitat currently occupied by conservation populations occurs in the wetter regions of the Bear River and Northern Bonneville GMUs, where stream populations comprise a combination of interconnected metapopulations and more isolated populations restricted to headwater streams. Sixty-nine percent of populations currently meet persistence criteria in the Bear River GMU, whereas 22% meet persistence criteria in the Northern Bonneville (Table 1). The Southern Bonneville and West Desert GMUs are more xeric and cutthroat trout populations occur primarily in small, isolated stream fragments (Figure 2). Only 10% of populations in the Southern Bonneville GMU currently meet persistence criteria. One population in the West Desert meets persistence criteria. Adequate habitat often exists downstream of existing populations, but these stream sections typically are inhabited by introduced salmonids that pose a significant conservation threat to native trout (Fausch et al. 2006).

The Colorado River cutthroat trout occurs in eight major river basins–GMUs within the upper Colorado River drainage. Four GMUs each contain at least 400 km of stream habitat occupied by conservation populations, but the other four contain smaller amounts of habitat, and three of these (Dolores, Lower Colorado, San Juan) each contain less than 100 km of occupied stream habitat. Those GMUs with larger amounts of occupied habitat typically also contain higher percentages of populations and habitat meeting

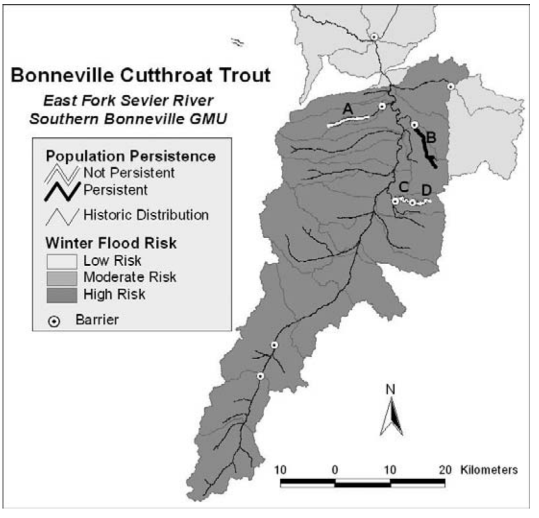

FIGURE 2.—Existing population status of Bonneville cutthroat trout in the East Fork Sevier River of the Southern Bonneville GMU. Three of four existing populations (A, C, D) fail to meet persistence criteria because their small populations occupy 3.6, 4.3, and 7.8 km of stream habitat, respectively. The one population (B) meeting persistence criteria in the East Fork Sevier occupies 10.5 km of stream. All populations are located in areas rated as high risk from winter flooding.

persistence criteria (Table 2). For example, a total of 1,046 km of stream habitat is occupied in the Upper Green GMU, and 33% of those populations and 69% of habitat currently meet persistence criteria. Conversely, there is only 80 km of stream habitat occupied in the Lower Colorado GMU and only 14% of those populations meet persistence criteria. An exception is the Lower Green GMU, where fewer, but larger, populations meet persistence criteria. Populations within three GMUs have both low numbers of populations and amounts of habitat meeting persistence criteria: Gunnison, San Juan, and Dolores. Like the Bonneville cutthroat trout, those GMUs containing smaller amounts of habitat for the Colorado River cutthroat trout also have most existing populations isolated in smaller headwater streams.

The westslope cutthroat trout has a much larger amount of habitat currently occupied when compared with either the Bonneville cutthroat trout or Colorado River cutthroat trout. Five of 13 major river basins–GMUs have more than 1,000 km of stream habitat, and two of these have more than 10,000 km: Clark Fork (11,854 km) and Salmon (11,701 km). Most GMUs, especially those with larger amounts of available habitat, have large majorities of populations and habitat that meet persistence criteria (Table 3). Many of these populations occur across larger stream systems and in watersheds with high connectivity and few instream barriers. An exception is in the Madison GMU, where despite more than 1,000 km of occupied stream habitat, only 12% of populations and 27% of habitat meet persistence criteria. Those GMUs with less-occupied habitat and fewer populations meeting persistence criteria include the Marias (19% of populations meeting persistence criteria), Middle Missouri (11%), Upper Missouri (5%), and Musselshell (0%). Although the St. Mary and Upper Columbia have a higher percentage of populations meeting persistence criteria, they are of greater concern than some other GMUs because of relatively smaller amounts of habitat currently occupied. Nonetheless, the westslope cutthroat trout contains many more interconnected populations exhibiting fluvial life histories than do the Bonneville or Colorado River cutthroat trout.

Climate Change Risks

Although Bonneville cutthroat trout include several large, interconnected populations, our analysis suggests they are at a relatively high risk from climate change

TABLE 2.—Persistence and climate change risk in GMUs occupied by Colorado River cutthroat trout. Risk is quantified in terms of kilometers of stream habitat occupied and numbers of conservation populations.

	Totals		Percent meeting persistence criteria		Percent meeting persistence criteria at high climate risk	
GMU	Stream habitat (km)	Population	Stream habitat	Population	Stream habitat	Population
Upper Green	1,046	76	69	33	24	32
Lower Green	493	26	71	4	33	12
Yampa	545	53	66	25	57	54
Upper Colorado	484	75	25	9	76	71
Gunnison	149	25	13	4	0	0
Dolores	23	4	0	0		
Lower Colorado	80	14	31	14	52	50
San Juan	67	12	21	8	0	0
Total	2,887	285	56	20	37	39

TABLE 3.—Persistence and climate change risk in GMUs occupied by westslope cutthroat trout. Risk is quantified in terms of kilometers of stream habitat occupied and numbers of conservation populations; na = not applicable.

GMU	Totals: Stream habitat (km)	Totals: Population	Percent meeting persistence criteria: Steam habitat	Percent meeting persistence criteria: Population	Percent meeting persistence criteria at high climate risk: Stream habitat	Percent meeting persistence criteria at high climate risk: Population
Clark Fork	11,854	231	90	47	71	81
Clearwater	8,726	4	100	100	81	100
Coeur d'Alene	4,050	6	100	67	74	75
John Day	406	16	76	25	64	75
Kootenai	394	35	71	46	75	88
Madison	1,046	147	27	12	24	22
Marias	217	16	63	19	26	33
Middle Missouri	141	9	60	11	85	100
Musselshell	12	2	0	0	na	na
St. Mary	243	8	91	62	6	20
Salmon	11,701	15	99	53	65	38
Upper Columbia	307	17	80	47	90	75
Upper Missouri	328	57	15	5	100	100
Total	39,425	563	93	33	88	71

impacts (Table 4). A small portion of this increased risk is from higher summer temperatures (Figure 3). Most of the greater risk is associated with increased winter flooding. Within the historic range, 48% of current habitat and 46% of historic habitat face high risks from winter flooding. This includes many subwatersheds in the Bear River and Northern Bonneville GMUs, which contain nearly all of existing strongholds for this cutthroat trout subspecies (Figure 4). Numerous subwatersheds in the Southern Bonneville GMU also are at high risk from increased flooding, but most of this habitat is currently unoccupied by native cutthroat trout. Increased wildfire risk affects fewer subwatersheds than flood risk, but again is greatest in the Bear River and Northern Bonneville GMUs, where existing stronghold populations could be jeopardized (Figure 5). Combining areas at high risk from increased summer temperatures, winter flooding, and wildfire results in 73% of current habitat being ranked at high risk from one or more of these factors. This was a higher percentage of habitat predicted to be at high risk than for either Colorado River cutthroat or westslope cutthroat trout.

Overlaying climate risk with existing population persistence projections suggests that nearly all Bonneville cutthroat trout populations in the Southern Bonneville and West Desert GMUs are at high risk of extinction (Table 1). In fact, all but one of the populations in the West Desert are at high risk under current climate conditions. Only 18% of existing populations in the Southern Bonneville meet persistence criteria, and all of those are at high risk from climate change impacts. In these areas, climate change risk compounds the existing threats to small, isolated populations. The Northern Bonneville and Bear River GMUs have existing strongholds and interconnected populations that are naturally more resistant to climate change impacts. Nonetheless, large portions of the populations in these two GMUs that meet persistence criteria are at high risk from climate change.

Less of the current habitat of the Colorado River cutthroat trout was ranked at high risk from climate change impacts compared with the other two subspe-

TABLE 4.—Increased risk from climate change for historic and current habitat of three subspecies of inland cutthroat trout. The numbers are the percentages of currently occupied or historic habitat.

Subspecies	Habitat	Increased temperature risk: High	Increased temperature risk: Medium	Increased temperature risk: Low	Increased flood risk: High	Increased flood risk: Medium	Increased flood risk: Low	Increased wildfire risk: High	Increased wildfire risk: Med	Increased wildfire risk: Low	Composite risk: High	Composite risk: Medium	Composite risk: Low
Bonneville	Current	8	16	76	48	7	45	39	39	22	73	16	11
	Historic	28	18	54	46	20	34	20	45	35	78	14	8
Colorado River	Current	5	23	72	12	0	88	17	22	61	29	17	54
	Historic	21	30	49	18	4	78	15	34	51	44	21	35
Westslope	Current	3	35	62	31	7	62	37	19	44	65	28	7
	Historic	8	42	50	26	5	69	27	18	55	57	35	8

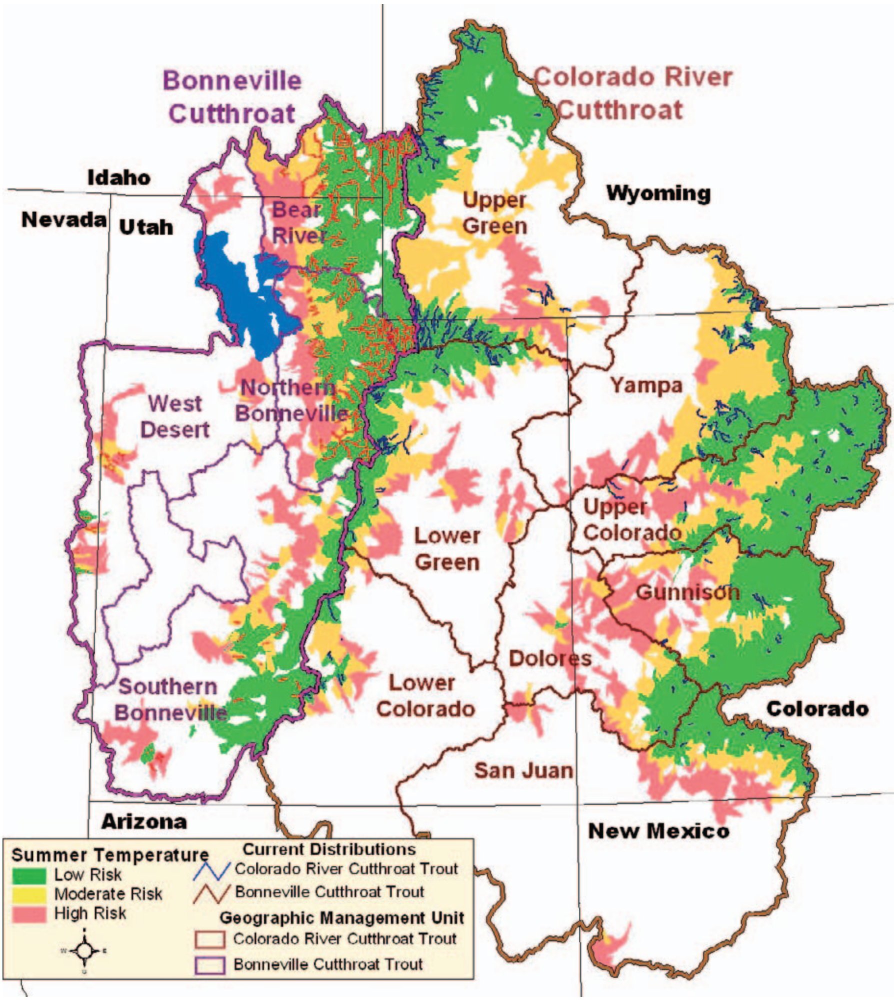

FIGURE 3.—Risk of increased summer temperature within the historic ranges of Bonneville cutthroat trout and Colorado River cutthroat trout, by subwatershed.

cies (Table 4). Because Colorado River cutthroat have already been extirpated from much of the lower and mid-elevation habitats, most existing high-elevation populations are unlikely to be impacted by increased summer temperatures (Figure 3). Only 5% of current habitat is predicted to be at high risk from increasing summer temperatures compared with 21% of historic habitat. Increased flood risk is also relatively low for many Colorado River cutthroat populations, including stronghold areas in the Upper Green, Lower Green, and Yampa GMUs (Figure 4). Increased wildfires pose a slightly greater risk to Colorado River cutthroat, as 17% of current habitat was predicted to be at high risk. These high risk areas are scattered but include some stronghold populations in the Upper Green GMU (Figure 5). Combining areas at high risk from increased summer temperatures, winter floods, and wildfire results in 29% of current habitat being ranked as high risk from one or more of these factors, which was the lowest amount of habitat at high risk among the three subspecies examined. In addition, 54% of current habitat was predicted at low risk for all three risk factors. These low risk areas are concentrated along the eastern portions of the subspecies' range in the Yampa, Upper Colorado, and Gunnison GMUs, but also cover much of the High Uintas (Utah), which contain population strongholds in the Upper Green and Lower Green GMUs.

Because of existing habitat fragmentation and small population sizes, many Colorado River cutthroat populations already are at risk in the Gunnison, Dolores, Lower Colorado and San Juan GMUs (Table 2). Of

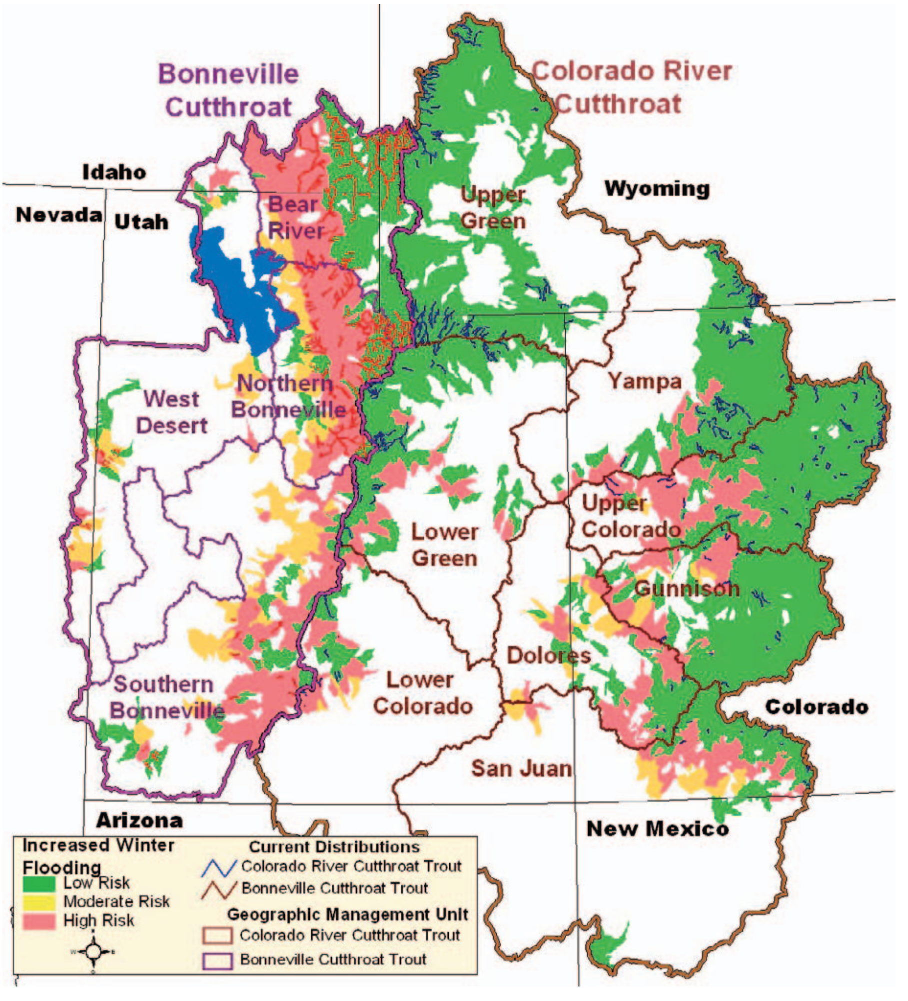

FIGURE 4.—Risk of increased winter floods within the historic ranges of Bonneville cutthroat trout and Colorado River cutthroat trout, by subwatershed.

those four GMUs, climate change poses the greatest increased risk in the Lower Colorado, where 52% of those populations currently meeting persistence criteria fall under high climate change risk. Climate change also compounds risk in the Lower Colorado, Upper Colorado, and Yampa GMUs, where more than half of populations meeting persistence criteria are at high risk from climate change. Increased risk from climate change impacts is lowest in the Upper Green and Lower Green GMUs. Overall, climate change risk is likely to be less of a factor for Colorado River cutthroat trout than for other subspecies.

Current westslope cutthroat trout habitat generally is at lower risk for increased summer temperature but at varied risk for increased flood and wildfire risks. Only 3% of current habitat is predicted to be at high risk from increased summer temperatures, whereas 31% is at high risk from increased flooding and 37% from increased wildfire (Table 4). High-risk areas for winter flooding are centered in the Coeur d'Alene, Kootenai, Clearwater, and Clark Fork GMUs as well as major river corridors in the Salmon GMU. High wildfire risk is concentrated more in the southern and eastern portions of the range, including substantial habitat areas within the Upper Missouri, Madison, and Salmon GMUs and the Flathead drainage. If risk from winter flooding, wildfire, and temperature are combined, 65% of the current range of westslope cutthroat trout is rated at high risk from climate change, and those high-risk habitats are distributed across all GMUs (Figure 6).

Because of existing habitat fragmentation and small population sizes, most westslope cutthroat trout

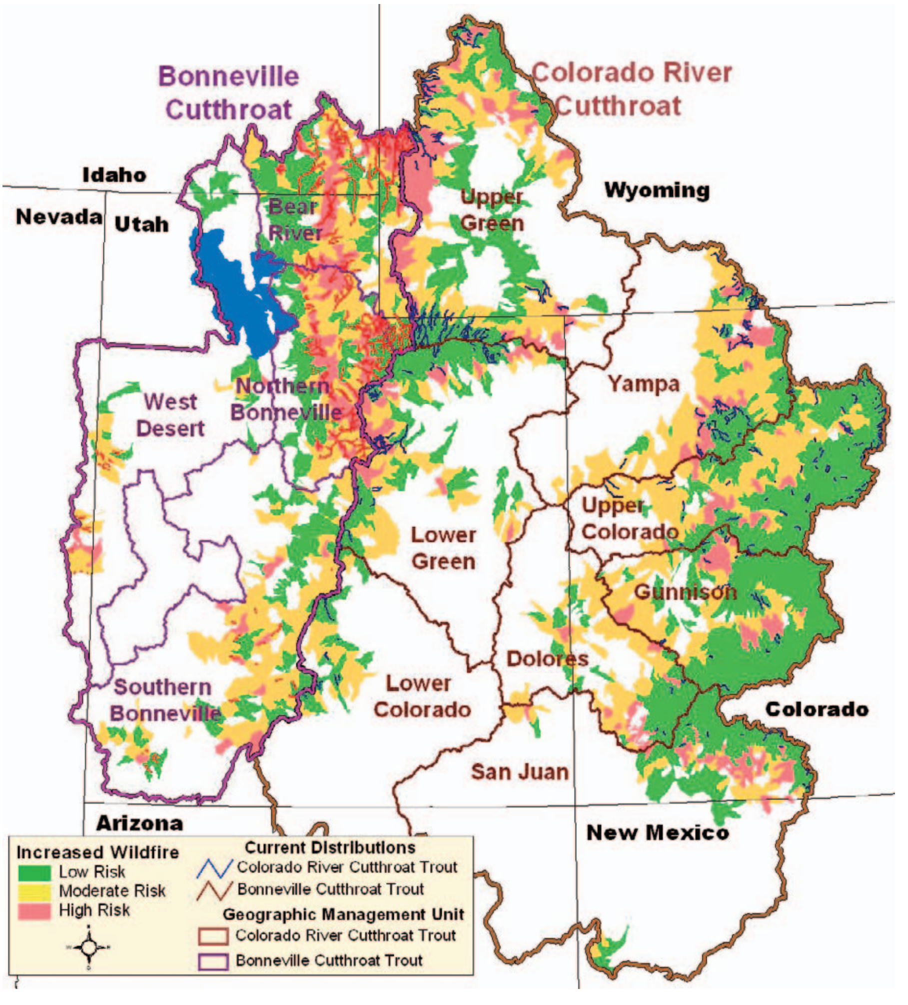

FIGURE 5.—Risk of increased wildfire within the historic ranges of Bonneville cutthroat trout and Colorado River cutthroat trout, by subwatershed.

populations in the Madison, Musselshell, and Upper Missouri GMUs (Table 3) do not currently meet our minimum persistence criteria and therefore are already considered at risk. We predict that climate change will exacerbate this risk, particularly in the Upper Missouri, where 100% of existing populations meeting persistence criteria under current conditions are at high risk from winter floods and wildfires. Although more habitat is available in other GMUs, impacts from climate change still may be severe. Even in the Clearwater GMU, where 100% of existing populations meet persistence criteria, 81% of those are at high risk from climate change. The composite climate change risk is high for more than 50% of populations meeting persistence criteria in Clark Fork, Clearwater, Coeur d'Alene, John Day, Kootenai, Middle Missouri, and Salmon GMUs. The Upper Columbia GMU in Washington also has a large proportion of habitat at high risk. In most basins, increased wildfire risk and increased flooding are major factors.

Discussion

Our work is intended to provide a broad-scale perspective on the relative magnitude and nature of climate change impacts across species ranges, which we believe emphasizes the urgency of conservation needs for many regions currently supporting or with potential to support inland cutthroat trout. Many of the populations we have considered are already at risk, existing as small, isolated populations in fragmented and degraded habitat. Our analyses suggest that these risks will be further compounded by climate change,

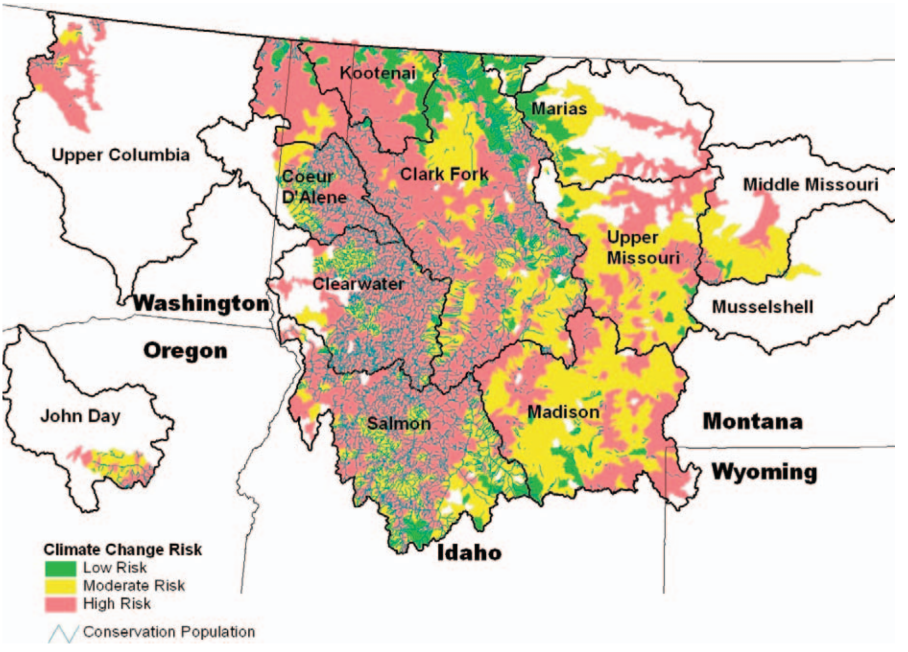

FIGURE 6.—Composite climate change risk for subwatersheds within the historic range of westslope cutthroat trout.

and some populations that are currently considered to be in relatively good condition are likely to suffer negative consequences from climate change. According to our projections, the impacts of climate change on cutthroat trout will not be evenly spread among subspecies or subwatersheds, owing to factors such as existing population status and current land use patterns, topography of watersheds, elevation, and latitude. These geographic patterns of risk may have significant evolutionary and ecological implications, and we address these first before discussing important caveats and assumptions of our analyses and outlining conservation strategies we hope can ensure the future of these subspecies.

As is the case with many salmonid species (see Gustafson et al. 2007), historic extirpations within inland trout have not represented just numerical losses of populations, but the loss of major components of life history, ecological and genetic diversity (Rieman and McIntyre 1993). Because of geographic patterns in land use practices, barriers and irrigation diversions, and the introduction and invasion of nonnative trout, fluvial migratory fish that use lower-elevation, large main-stem habitats have already been extirpated in many areas. Remaining populations are generally relegated to smaller, isolated headwater habitats. Not surprisingly, our analysis suggests that some of the remaining populations in lower-elevation habitats will be at risk from increased temperatures, increased winter flooding, or both. The loss of such a major component of life history diversity may have important implications for remaining populations (Rieman and McIntyre 1993). Migratory fish are highly fecund, contribute to important genetic exchange, and are thought to provide a buffering effect through spatial segregation within populations and metapopulation dynamics among populations (Dunham et al. 2003; Neville et al. 2006a). Further degradation of low-elevation, main-stem habitats and losses of migratory life histories may therefore have significant impacts on the persistence and evolutionary trajectories of some populations, and maintaining and restoring these habitats should be a conservation priority.

The Bear River in Utah, Wyoming, and Idaho illustrates how climate change threatens even some of our most robust native trout populations. Unlike many western native trout populations, Bear River populations have maintained a fluvial life history strategy, overwintering in lower-elevation, main-stem habitats and spawning in headwater tributaries (Schrank and Rahel 2004; Colyer et al. 2005). Arguably, it is this migratory strategy that has allowed Bonneville cutthroat to persist in seasonally marginal habitats and to resist introgression and competition with nonnative competitors (e.g., Fausch et al. 2006). Nearly 100% of the main-stem migration corridors in the Bear River watershed fall within the moderate-risk category. Loss of those habitats would reduce occupied stream habitat from 1,150 to 553 km, degrade migration corridors, and further isolate tributary resident populations in upstream reaches of the watershed. Under this scenario, the distribution of Bear River populations would be relegated to high-elevation tributary streams as is the case with most other cutthroat trout subspecies.

Perhaps one of the greatest direct risks from climate change, however, is the predicted loss of isolated populations on the periphery of cutthroat trout distributions. In some cases, our analysis shows that the persistence of entire GMUs is apparently tenuous because of such threats. For instance, the West Desert GMU for Bonneville cutthroat trout currently supports one population that meets the criteria we used as metrics for ensuring a high probability of persistence, and though portions of the Southern Bonneville GMU do, this remainder is predicted to be jeopardized by climate change. Rather than considering these populations to be conservation write-offs, we feel these populations may have disproportionate conservation value given their peripheral nature as well as their location in the southernmost part of the subspecies range. Because of their isolation, existence in what is often marginal habitat, and vulnerability to genetic drift, peripheral populations are often genetically divergent and collectively contain a large proportion of a species' genetic, life history and ecological diversity (Lesica and Allendorf 1995; Hampe and Petit 2005). Emerging fossil and phylogeographic evidence also suggests populations at the "trailing edge" (southern latitude) of species' ranges contribute greatly to speciation and evolutionary divergence (Hampe and Petit 2005).

Southern-edge populations such as those in the West Desert and Bonneville GMUs may also have unique adaptations for persisting in marginal habitats that may become particularly important as climate change proceeds. For instance, with eastern brook trout there is some indication that populations at the southern edge of the species range have a higher temperature tolerance and possess unique adaptations that may prove important in dealing with climate change (Flebbe et al. 2006). Such populations, especially those outside of areas at highest risk of climate change, appear to warrant increased conservation attention in order to maintain the evolutionary potential and diversity they provide for the species as a whole (Waples 1995).

We emphasize caution in interpreting our results because broad-scale studies tend to mask important local variations (such as the presence of nonnative species) that are critical to consider when making management prioritizations. Our projections are also certainly affected by many assumptions and unpredictable or uninvestigated factors. For instance, our use of historical distributions to define trout temperature tolerances is a logical but imprecise substitution for empirical data and might make our assessments diverge from on-the-ground reality. Additionally, our assumptions about the minimum patch sizes that would likely support cutthroat trout are based on recent empirical work estimating patch size requirements of bull trout (see Rieman et al. 2007) and Lahontan cutthroat trout (Dunham et al. 2002b), and results from these two taxa may not be directly transferable to the cutthroat trout we considered. Futhermore, barriers to dispersal were not included in patch size estimates, and, in reality, the entirety of most "patches" is not actually accessible to fish, making our estimates of current patch size generous. Nonnative species may also pose additional risks to populations related to climate change that were not incorporated into our analyses. In many cases, nonnative species such as rainbow trout and brook trout may actually benefit from climate change, adding an unpredictable but important component of risk for native species in the future (Rieman et al. 2006, 2007).

We also do not consider the capacity for adaption or migration in response to a changing climate, but on these fronts we are not terribly optimistic. Salmonids as a whole have demonstrated a remarkable ability to adapt in the face of historical environmental changes, and there are several cases where Pacific salmon are demonstrating rapid evolution in the face of dramatic climate and habitat alterations (Gustafson et al. 2007). Yet inland trout perhaps face more severe limitations compared with their coastal relatives. Many taxa may have the ability to migrate to new geographic areas supporting their required environmental niches, but because the trout we consider live in largely landlocked linear aquatic habitats that follow elevation gradients, their migration patterns are particularly constrained. Fish will increasingly move into cooler water in response to rising temperatures, but where migratory corridors are inaccessible they will only be able to move so far, and this process of truncating habitat will lead to greater fragmentation overall. Furthermore, the many factors that have caused these fish already to be of conservation concern (e.g., habitat degradation, fragmentation, and nonnative species) have also likely eroded genetic diversity in many populations, further restricting their ability to respond adaptively to environmental influences (Waples 1994; Williams and Williams 2004).

We believe there are many actions that can be taken to improve the resistance and resiliency of inland trout in light of climate change to help ensure their future survival (Williams et al. 2007b). A primary strategy should focus on expanding small, isolated populations to achieve an effective population size of at least 500 (e.g., Hilderbrand and Kershner 2000) by increasing available habitat and improving existing habitat quality. Trout will have a much better chance of persisting in the face of increasing environmental threats if they have access to heterogeneous habitat and refugia, both seasonally and during disturbance (Dunham et al. 2003). Secondly, ecological and life history diversity could potentially be restored by providing instream flows and reconnecting stream systems to allow access to migratory habitats by removing instream barriers. Finally, existing habitat stressors (such as livestock grazing, road development, and water withdrawals) should be curtailed. In habitats where conditions are predicted to be suitable in the future, these restoration activities may provide opportunities for reintroductions, allowing for expansion of populations across more of the historic distribution of these species and providing a stronger foundation for the maintenance and evolution of future diversity. Many of these actions may necessitate control or elimination of nonnative species, which is one of the principal threats facing native trout in the western United States (Fausch et al. 2006). Such ecologically based strategies offer proven effectiveness in the face of increasing environmental uncertainty (Williams and Williams 2004).

We conclude that impacts from climate change are likely to increase the extinction risk for the three cutthroat trout subspecies evaluated, particularly where they exist as small, isolated populations. Managers already face a conundrum in their treatment of these small populations (Fausch et al. 2006). On the one hand, there is a need to expand habitats and populations because these isolated populations are at increased risk of extinction from stochastic events. But on the other, it is often desirable to ensure their isolation through the construction of instream barriers because downstream populations of introduced salmonids pose a risk from introgressive hybridization, competition, predation, or the spread of diseases if they have access to the native populations. Because climate change poses additional threats to isolated populations, information about relative risks may further inform the tradeoff between invasion and isolation (Peterson et al. 2008). Regardless of the management avenue chosen, more populations are likely to become isolated and vulnerable as a result of rapidly changing climate in the near future. Loss of these populations will degrade the genetic and ecological legacies of their species.

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