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Conserving Peripheral Trout Populations: the Values and Risks of Life on the Edge

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ABSTRACT: Peripheral populations—generally defined as those at the geographic edge of the range—often have increased conservation value due to their potential to maximize within-species biodiversity, retain important evolutionary legacies, and provide the fodder for future adaptation. However, there has been little exploration of their conservation value in aquatic systems. Inland cutthroat trout (*Oncorhynchus clarkii*) subspecies provide a unique opportunity to evaluate the distribution of peripheral populations and patterns of persistence across a wide range of environmental conditions. Our assessment analyzed range-wide losses of peripheral and core populations since the 1800s, and evaluated the likelihood of persistence for remaining populations of five cutthroat trout subspecies: Bonneville, Colorado River, Yellowstone, Rio Grande, and westslope. For all five, we found that core and peripheral populations have declined substantially, but the amounts of habitat occupied by peripheral populations generally have declined at a greater magnitude. The more isolated peripheral populations typically exhibited the greatest declines. Remaining peripheral populations often failed to meet minimum persistence criteria. Our characterization of peripheral populations and their losses emphasizes the need for closer evaluation of conservation priorities and management actions for cutthroat trout and other fishes if the values of peripheral populations are to be maintained.

Conservación de poblaciones periféricas de trucha: valor y riesgo de vivir en los límites

RESUMEN: las poblaciones periféricas –definidas como aquellas que habitan en el borde de la distribución geográfica- han incrementado su valor de conservación debido al potencial que tienen con respecto a la maximización de la biodiversidad intraespecífica, a que retienen importantes legados evolutivos y a que comprenden materia prima para el proceso adaptativo. No obstante, poco se ha explorado en cuanto a su valor de conservación en ecosistemas acuáticos. La subespecie de la trucha de agua dulce (*Oncorhynchus clarkii*) representa una oportunidad única para evaluar la distribución de las poblaciones periféricas y patrones de persistencia a través de un amplio rango de condiciones ambientales. En la presente evaluación se analiza la pérdida extensiva de poblaciones periféricas y centrales desde 1880 así como también la verosimilitud de persistencia de poblaciones remanentes de cinco subespecies de la trucha degollada: Bonneville, Río Colorado, Yellowstone, Río Grande y westslope. En todos los casos se encontró que las poblaciones centrales y periféricas han declinado sustancialmente pero la cantidad de hábitat ocupado por poblaciones periféricas se ha reducido aún más. Aquellas poblaciones periféricas con mayor grado de aislamiento, típicamente presentan las mayores pérdidas. Con frecuencia, las poblaciones periféricas remanentes no cumplen con los criterios mínimos de persistencia. Si el objetivo principal es mantener el valor de las poblaciones periféricas, su caracterización y pérdida debieran enfatizar la necesidad de contar con evaluaciones precisas de las prioridades de conservación y acciones de manejo dirigidas a la trucha degollada y a otros peces.

Introduction

The conservation of population diversity is imperative to the conservation of species (McElhany et al. 2000; Luck et al. 2003; Gustafson et al. 2007), which has created a need to prioritize populations deserving management attention. Whereas there are many aspects of populations to consider, the conservation of peripheral populations has received increasing attention in the conservation biology literature. Peripheral populations can be defined generally as those at the geographic edge of a species' range, though their attributes can be quite different depending on whether they are continuous with, or disjunct from, the rest of the range (Bunnell et al. 2004). From a conservation perspective, peripheral populations are often assumed to have certain characteristics that may increase their value for maximizing within-species biodiversity and species persistence.

Peripheral populations are generally more isolated than populations closer to the core of a species range, and are often assumed to occupy marginal habitat and have lower abundances (but see Sagarin and Gaines 2002; Sagarin et al. 2006). As a result, peripheral populations should experience increased genetic drift and selective pressures, which may be expected to cause a suite of unique and potentially adaptive genetic characteristics unlikely to be found in larger, more stable populations (Lesica and Allendorf 1995; Nielsen et al. 2001). Many peripheral populations also have had a unique history during recent glacial periods, either being derived from refugia (Nielsen 1999; Hampe and Petit 2005), or acting as the leading edge of colonization following glacial retreats (Taylor et al. 2003). Consequently, it is often argued that peripheral populations merit higher conservation priority because collectively they maximize within-species diversity, retain an important evolutionary legacy, and provide the fodder for future adaptation and speciation (Lesica and Allendorf 1995; Nielsen 1999; Nielsen et al. 2001).

Peripheral populations may also become increasingly important for species persistence in light of on-going human impacts (e.g., land development and the introduction of nonnative species) as well as in the context of climate change. As air temperatures increase with global climate change, peripheral populations farther from the Equator are likely to provide the leading edge for range shifts, and protection of these populations and their habitats may provide essential stepping stones as species attempt to track their changing environment (Gibson et al. 2009). Populations at the trailing edge of range shifts may also be important because they may harbor unique genetic diversity or adaptations that could be beneficial in a changing climate, such as higher temperature tolerances (Flebbe et al. 2006; Beatty et al. 2008). Thus, there may be a variety of reasons for prioritizing at least some peripheral populations along the entire edge of a range, and a general strategy of preserving populations across the environmental gradients experienced by a species may be our best bet for maximizing future adaptive potential (Smith et al. 2001; Moritz 2002).

Evaluating conservation needs with respect to peripheral populations in fishes is difficult because to date aquatic systems have been highly underrepresented in research on peripheral populations (see Hampe and Petit 2005). The inland cutthroat trout (*Oncorhynchus clarkii*) subspecies of the western United States provide a unique opportunity to evaluate the distribution of core and peripheral populations, reveal patterns of persistence across the ranges of multiple subspecies, and provide rare insight into distributional patterns of aquatic fauna. First, they occupy a wide range of environmental conditions across varying latitudes and are separated by natural geographic dispersal barriers (Behnke 1992). Second, they are also confronted with various human impacts and in general are a highly imperiled fauna (Young 1995; Behnke 2002). Our objective was to compare the distribution and persistence of peripheral populations within and among five subspecies of cutthroat trout: Bonneville cutthroat trout (*O. c. utah*), Colorado River cutthroat trout (*O. c. pleuriticus*), Yellowstone cutthroat trout (*O. c. bouvieri;* including the Snake River fine spotted form), Rio Grande cutthroat trout (*O. c. virginalis*), and westslope cutthroat trout (*O. c. lewisi*) (Figure 1). Contrasts in the distribution and persistence of peripheral and core populations among subspecies of cutthroat trout could provide insight valuable for prioritizing conservation needs across these fishes' ranges at a time of rapid environmental change.

Methods

Our assessment analyzed range-wide losses of peripheral populations relative to core populations since the 1800s and evaluated the likelihood of persistence for remaining populations. We first classified historical populations of Bonneville, Colorado River, Yellowstone, Rio Grande, and westslope cutthroat trout as core, continuous peripheral, or disjunct peripheral using a standardized rule set based on hydrologic connectivity and topographic isolation within and among populations. In our approach, core areas have a higher degree of interpopulation connectivity and drain into a common river system, whereas peripheral populations are more disconnected from central river systems. We then analyzed data from the latest available status surveys for each subspecies and compared current distributions to historical distributions to document extirpation of each type of population. Finally, we analyzed the likelihood of persistence for remaining peripheral populations based on fish abundance, amount of occupied stream habitat, and habitat patch size.

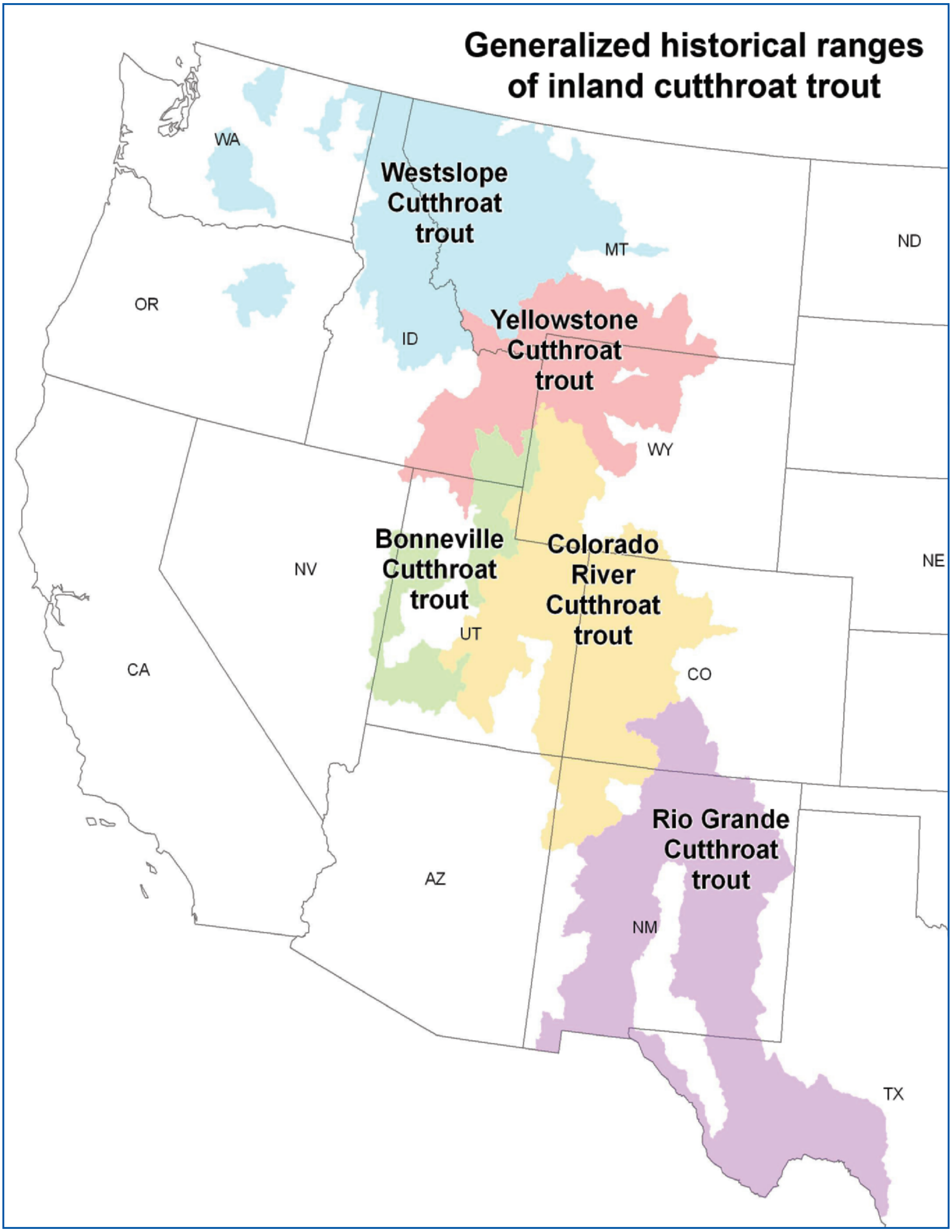
Defining peripheral populations based on historical distribution

There are many definitions of peripheral populations but most make a distinction between those that are geographically marginal (distant from the core of the species' range) and those that are ecologically marginal (occupy a different environment; Lesica and Allendorf 1995; Bunnell et al. 2004). Although geographically marginal populations are often ecologically marginal as well, we rely on a spatial definition because of the difficulty in defining ecological marginality across entire species ranges.

Peripheral populations also differ based on their spatial relationships with core populations. Lesica and Allendorf (1995) used a continuum of spatial distance from the core to assess the relative conservation value of populations that are more or less disjunct. Channell and Lomolino (2000a and b) used an index of centrality to compare populations based on their inclusion in equal area bands within the historical range designating peripheral and central regions. Bunnell et al. (2004) recognized two discrete types of peripheral populations: continuous and disjunct. They defined disjunct populations as being isolated from the core such that genetic interactions are precluded, whereas continuous populations occupy the outer edge of a species' range. Because the aquatic systems on which we focus have different attributes from the more commonly-referenced terrestrial systems, we used the classifications described by Bunnell et al. (2004) but have modified their methods for distinguishing between disjunct and continuous peripheral populations. We used the historical distribution of each subspecies to define disjunct peripheral populations as those that were not hydrologically connected within the same river basin and therefore with no practical opportunity for gene flow, whereas continuous peripheral populations were connected hydrologically within the same river basin but were at the far downstream extent from the core populations.

We first identified core populations based on a geographic information systems (GIS) analysis of the connectivity of his-

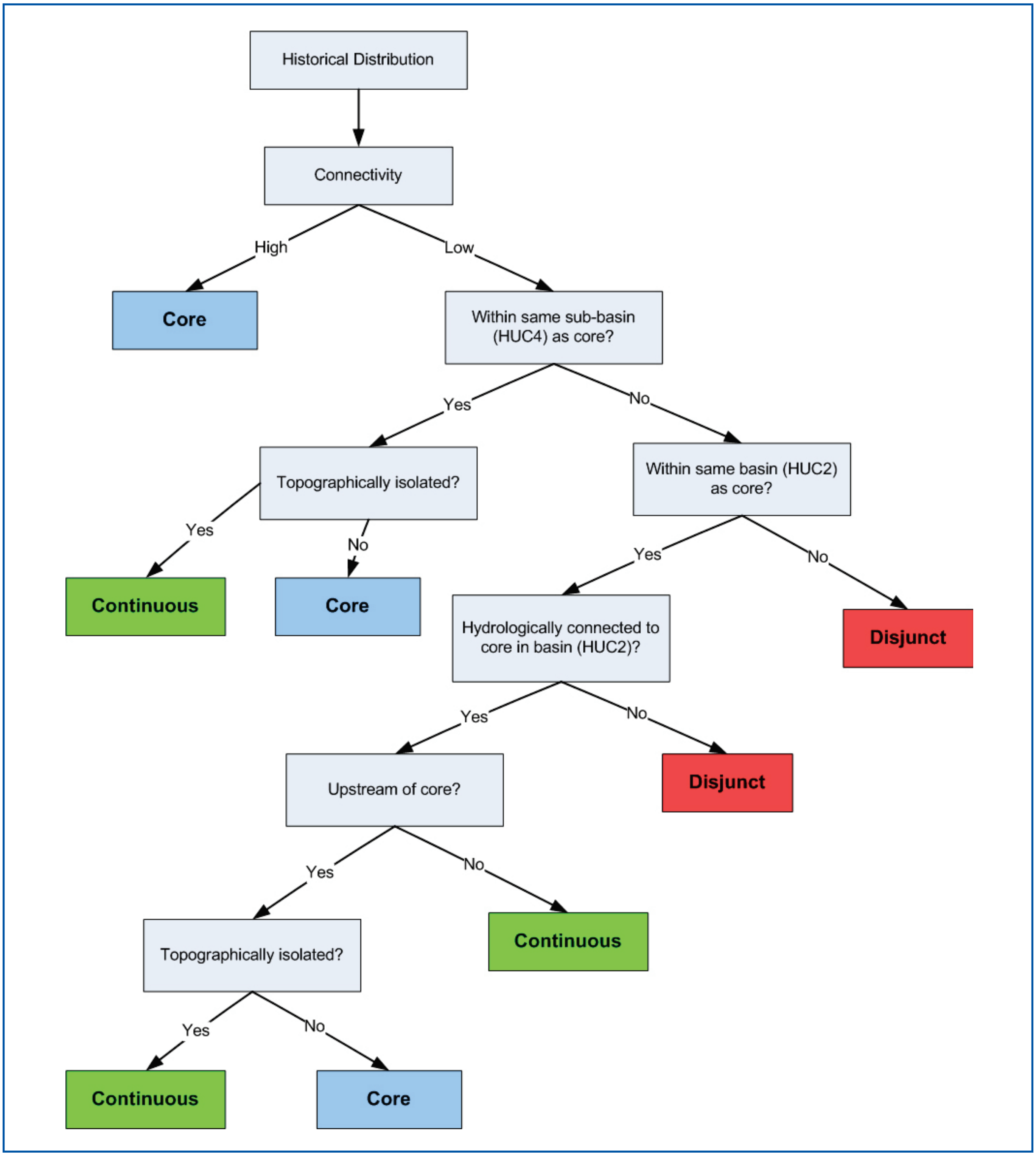
Figure 1. Historical ranges of cutthroat trout subspecies analyzed in this paper.



torical populations. Hydrologic networks that were spatially discrete from other systems but internally interconnected were identified from the historical distribution, then broken into four classes based on total length of the connected network using a "natural breaks" classification (Jenks 1967). This method identifies groupings of stream networks that minimize variance within groups and maximize variance among groups. All networks in the three groups with highest connectivity were classified as core, whereas the remaining group with the lowest connectivity was further analyzed.

The low connectivity populations were then evaluated to determine if they should be considered part of the core populations. Figure 2 provides a graphical depiction of our population classification. Low connectivity populations within a

Figure 2. Decision tree for determining how historical populations of cutthroat trout were classified as core, continuous peripheral, or disjunct peripheral.



sub-basin (4th Hydrologic Unit Code) that contained core populations were classified as core if they were topographically connected (i.e., occurred along the same mountain range) to core populations. Low connectivity populations within a river basin (2nd Hydrologic Unit Code) containing core populations were classified as core if they were hydrologically connected to the main stem river upstream of a designated core population and drained from the same topographic feature (e.g., mountain range) as a core population. If they drained from an isolated mountain range or connected to the main stem river at the downstream extent of the core they were classified as continuous peripheral. The remaining populations were classified as disjunct peripheral, being low connectivity populations with no hydrologic connectivity to the core.

Spatial data on historical distributions, current population extents, and population sizes were taken from the recent range-wide assessments for Bonneville cutthroat trout (May and Albeke 2005 as updated by the Bonneville Cutthroat Trout Working Group in 2009, pers. comm.), Colorado River cutthroat trout (Hirsch et al. 2006), Yellowstone cutthroat trout (May et al. 2007), westslope cutthroat trout (Shepard et al. 2003), and Rio Grande cutthroat trout (Alves et al. 2007) with supplements in the Texas portion of the range from Garrett and Matlock (1991), and are described in Trout Unlimited's Conservation Success Index (Williams et al. 2007).

Current distribution and persistence of core and peripheral populations

Using the above framework, we evaluated the current distribution of populations in each category compared to their historical distribution to determine the relative magnitude of losses in each category. We also examined the likelihood of persistence for peripheral populations that were classified as "conservation populations" in the range-wide assessments. Generally, conservation populations were identified in these range-wide assessments as having sufficient genetic purity and habitat to provide conservation value (e.g., Alves et al. 2007). Assessments also contained information on population density and extent of occupied habitat of conservation populations, which facilitates further analysis of their likely persistence.

After identifying those peripheral populations receiving conservation population status, we then determined their likelihood of persistence. Our persistence analysis followed Hilderbrand and Kershner (2000) for small cutthroat trout streams, and Dunham, and Rieman's (1999) work on bull trout (*Salvelinus confluentus*) for larger rivers or interconnected stream systems. We integrated the findings of these two studies such that populations occupying both a patch size greater than 5,000 ha and a stream extent of at least 13.9 km were considered persistent. Populations occupying less than 5,000 ha or less than 13.9 km of habitat required certain combinations of stream habitat availability and population density to meet persistence criteria. We generally followed Hilderbrand and Kershner's (2000) target of a census size of 2,500 individuals (> 75 mm TL), which is assumed to equate to an effective population size of 500 spawning adults, but because the assessment data used in this study report abundances only for individuals 150 mm or longer TL, we targeted an approximate census size of 1,250. Densities reported in the assessments were given in ranges, which we categorized such that "low" = < 31 fish/km, "moderate" = 31–93 fish/km, "high" > 93 fish/km. Using these categories, populations with "moderate" densities occupying 13.9–27.8 km habitat (see Hilderbrand and Kershner 2000), or "high" densities occupying 9.3–13.9 km stream habitat were considered persistent. Populations occupying greater than 27.8 km of habitat at any density were considered persistent, whereas those with less than 9.3 km of stream habitat did not meet persistence criteria regardless of fish density (Hilderbrand and Kershner 2000).

Results

General distributions and declines

For all subspecies, the majority of historical populations (83–91%) were categorized as core, with the remaining populations falling in the two peripheral categories except for Bonneville cutthroat trout, for which no populations met our criteria for continuous peripheral (Table 1). We found that core and peripheral populations of all five cutthroat trout subspecies have declined substantially since historical times, but the amounts of stream habitat occupied by peripheral populations generally have declined at a greater magnitude. The more isolated disjunct peripheral populations typically exhibited the greatest declines and have been completely extirpated in Rio Grande cutthroat trout. The status of westslope cutthroat trout populations was better when compared to other subspecies, but even here declines of disjunct peripheral populations were nearly twice that of core populations.

Bonneville cutthroat trout occur in four geographic areas mostly in Utah: the Bear River, Northern Bonneville, Southern Bonneville, and West Desert. For Bonneville cutthroat trout, disjunct peripheral populations historicalally occurred in the Southern Bonneville outside of the Sevier River drainage as well as all occupied habitats in the West Desert (Figure 3). No populations were classified as continuous peripheral for this subspecies. All historical populations in the Bear River and Northern Bonneville areas as well as those in the Sevier River drainage (Southern Bonneville) were classified as core populations. Comparisons to recent surveys (May and Albeke 2007) show declines of 62% for habitat occupied by core populations and 91% for habitat occupied by disjunct peripheral populations (Table 1). Only 124 km of habitat is still occupied by remaining disjunct peripheral populations (Figure 4). Recent translocations of Bonneville cutthroat trout to streams in the West Desert area for conservation purposes have provided an additional 71 km of habitat for disjunct peripheral populations, bringing the total to 195 km. Populations throughout the Southern Bonneville have been severely fragmented and isolated, particularly in the Sevier River drainage, which historically was a relatively intact core system.

Colorado River cutthroat trout exhibited substantial and almost equal declines among all population classes

(Table 1). Historically, core populations were prevalent in headwater areas of the Upper Green, Yampa, Lower Green, Upper Colorado, Gunnison, Dolores, and San Juan basins. Comparisons between historical distribution and a recent status review (Hirsch et al. 2006) found substantial declines in all basins (ca. 90%). Remaining stronghold areas are primarily in the Upper Green, Lower Green, and Yampa basins with very few populations remaining in the San Juan and Dolores basins. Historically, peripheral populations in most basins were scattered in lower elevation regions or areas draining from isolated mountain ranges, including all populations in the Lower Colorado (Figure 5). Continuous peripheral populations have declined by 87% and disjunct peripheral populations by 90%, with 440 km of stream habitat remaining for disjunct and continuous peripheral populations combined (Figure 6). The only remaining disjunct peripheral populations are found in the Dolores and Lower Colorado basins.

Historically, core populations of Yellowstone cutthroat trout were widely distributed in four of the five geographic areas inhabited by this subspecies: Bighorn, Yellowstone, Upper Snake, and Lower Snake (Figure 7). Peripheral populations historically occurred primarily along the northern and eastern flanks of the Bighorn Mountains in Wyoming and Montana, including the Tongue River drainage, and in the western and southern-most portions of the Lower Snake basin, primarily in Idaho. Compared to historical distributions, core populations have declined less for Yellowstone cutthroat trout than other subspecies examined except for westslope cutthroat trout, but still approximately half the populations have been extirpated (Table 1). Disjunct peripheral populations have declined by 84% while continuous peripheral populations declined by 86%. Remaining historical peripheral populations are located in Idaho's Camas Creek drainage, Wyoming's lower Bighorn drainage, and the Snake River near the Idaho/Utah border (Figure 8). Existing populations of Yellowstone cutthroat trout have been augmented somewhat by translocations that have resulted in 909 km of additional stream habitat, occupied by core and peripheral populations, including disjunct populations in the headwaters of the Tongue River.

All population groups of Rio Grande cutthroat trout have declined substantially, including the extirpation of all disjunct peripheral populations (Table 1). Historically, disjunct peripheral populations were located in isolated portions of the Upper and Lower Pecos River basins in southeastern New Mexico and western Texas as well as the Caballo geographic area of the Rio Grande (Figure 9). Remaining peripheral populations were classified as continuous peripheral and consisted of 89 km of occupied habitat in the Lower Rio Grande geographic area in New Mexico (Figure 10). Rio Grande cutthroat trout have been introduced into 75 km of stream habitat, which were all classified as core.

Disjunct peripheral populations of westslope cutthroat trout historically occurred in the Upper Columbia (Washington), John Day (Oregon), and Musselshell (Montana) drainages (Figure 11). Continuous peripheral populations currently occur in the Idaho/Washington border area of the Coeur d'Alene basin and have shown no declines since historical times (Figure 12). Historical populations in all remaining river drainages were classified as core. Recent assessment data (Shephard et al. 2003) shows substantial disjunct peripheral population losses in all three areas as well as habitat fragmentation and isolation of remaining core populations in the following drainages: Clark Fork, Marias, Middle Missouri, Upper Missouri, and Madison. Remaining populations are now increasingly vulnerable because of the amount of habitat lost and the location of these areas outside of the remaining core. Overall, stream habitat occupied by core populations decreased by approximately 37%, the lowest decline of any subspecies examined, while disjunct peripheral populations declined by 73% (Table 1).

Table 1. Classification of historical cutthroat trout populations and the fate of these populations since historical (ca. 1850) times. Extent of historical, current, and extirpated populations is given in km of occupied stream habitat. Introduced populations are classified based on the location of the donor population.

Classification	Historical (km)	Current (km)	Extirpated (km)	Extirpated (%)	Introduced (km)
Bonneville Cutthroat Trout					
Core	9,497	3,645	5,852	62%	15
Continuous peripheral	0	0	0	–	0
Disjunct peripheral	1,376	124	1,252	91%	71
Colorado River Cutthroat Trout					
Core	30,784	4,426	26,358	86%	0
Continuous peripheral	2,490	329	2,161	87%	0
Disjunct peripheral	1,107	111	996	90%	0
Yellowstone Cutthroat Trout					
Core	22,539	11,202	11,337	50%	791
Continuous peripheral	3,365	473	2,892	86%	31
Disjunct peripheral	1,341	216	1,124	84%	87
Rio Grande Cutthroat Trout					
Core	9,901	1,138	8,762	89%	75
Continuous peripheral	527	89	438	83%	0
Disjunct peripheral	417	0	417	100%	0
Westslope Cutthroat Trout					
Core	83,341	52,221	31,120	37%	0
Continuous peripheral	382	382	0	0%	0
Disjunct peripheral	7,242	1,981	5,260	73%	0

Persistence of remaining peripheral populations

The percentages of conservation populations meeting persistence criteria varied widely among subspecies, and between continuous and disjunct peripheral populations (Table 2). Only 6 disjunct populations of Yellowstone cutthroat trout remain, but four of these (67%)

Figure 3. Historical distribution of core and peripheral populations of Bonneville cutthroat trout.

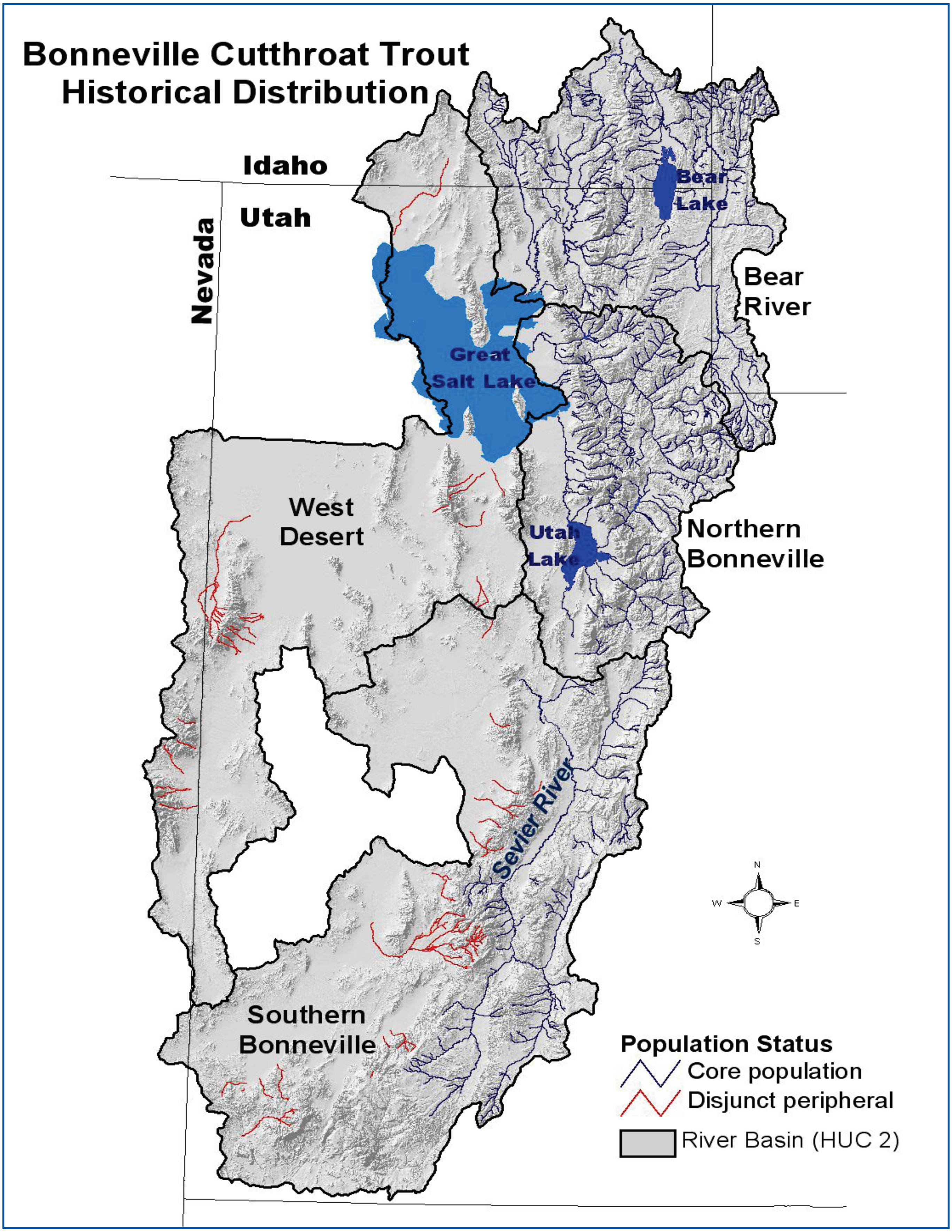


Figure 4. Current distribution of core and peripheral populations of Bonneville cutthroat trout. Note that some populations (shown by dotted lines) have been introduced into previously unoccupied stream segments but still within their historical range.

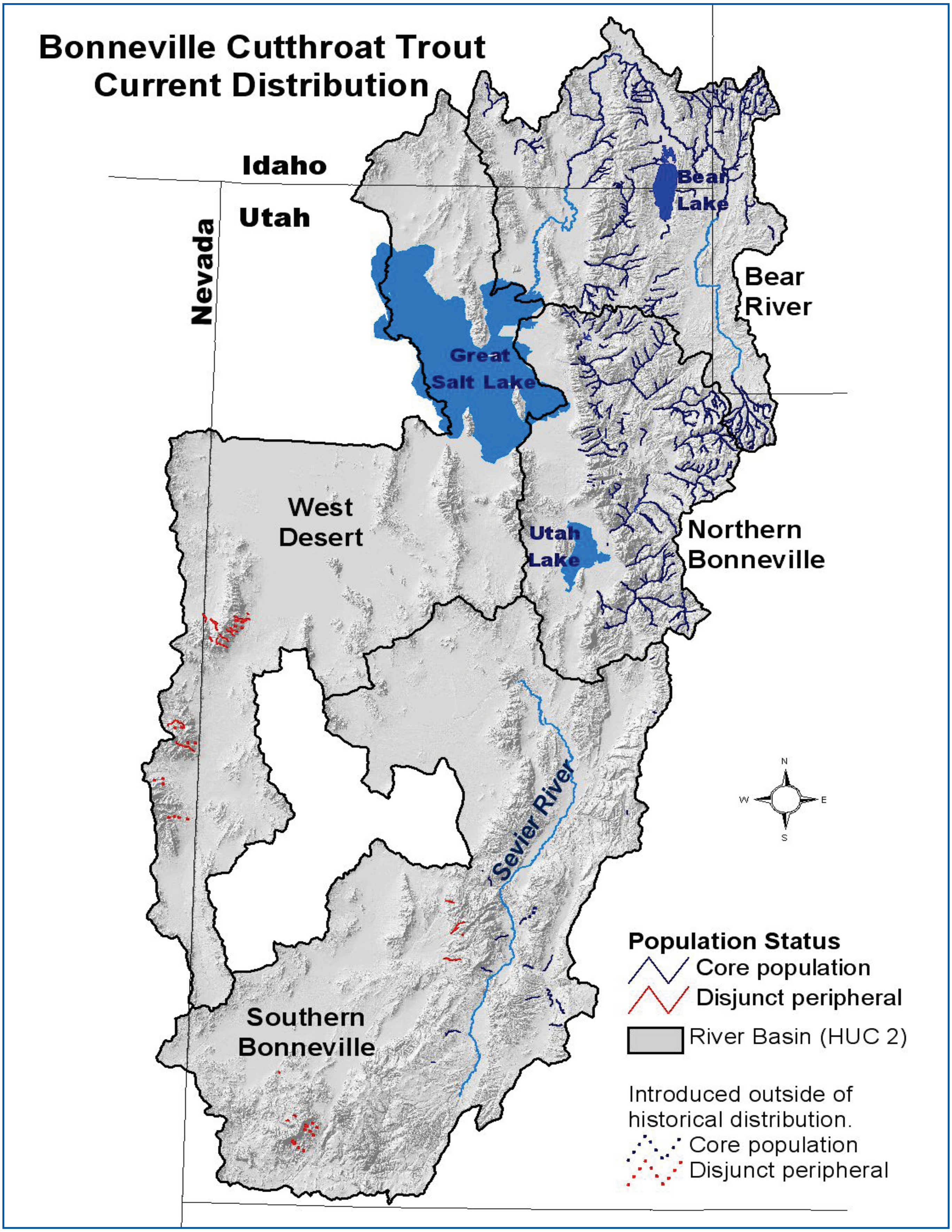


Figure 5. Historical distribution of core and peripheral populations of Colorado River cutthroat trout.

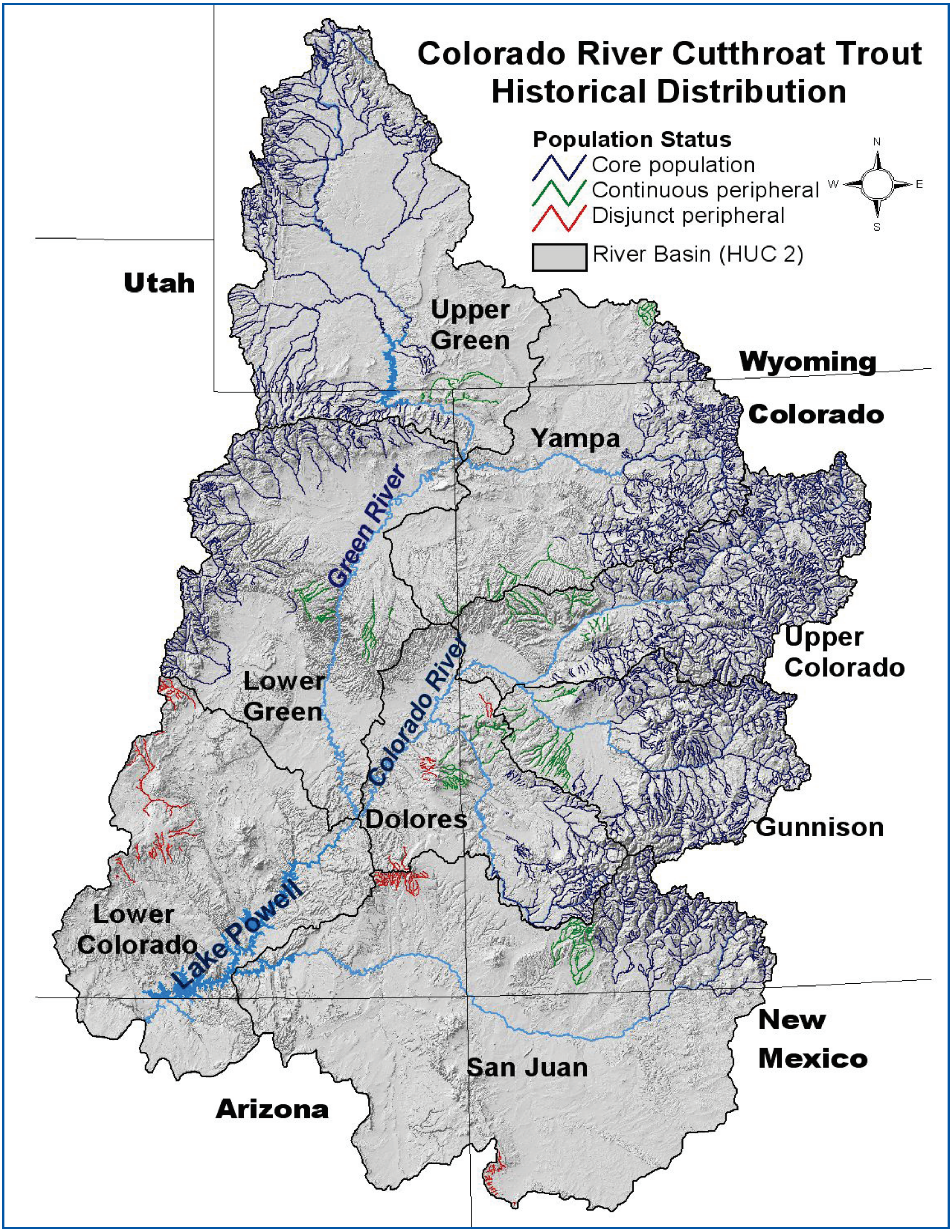
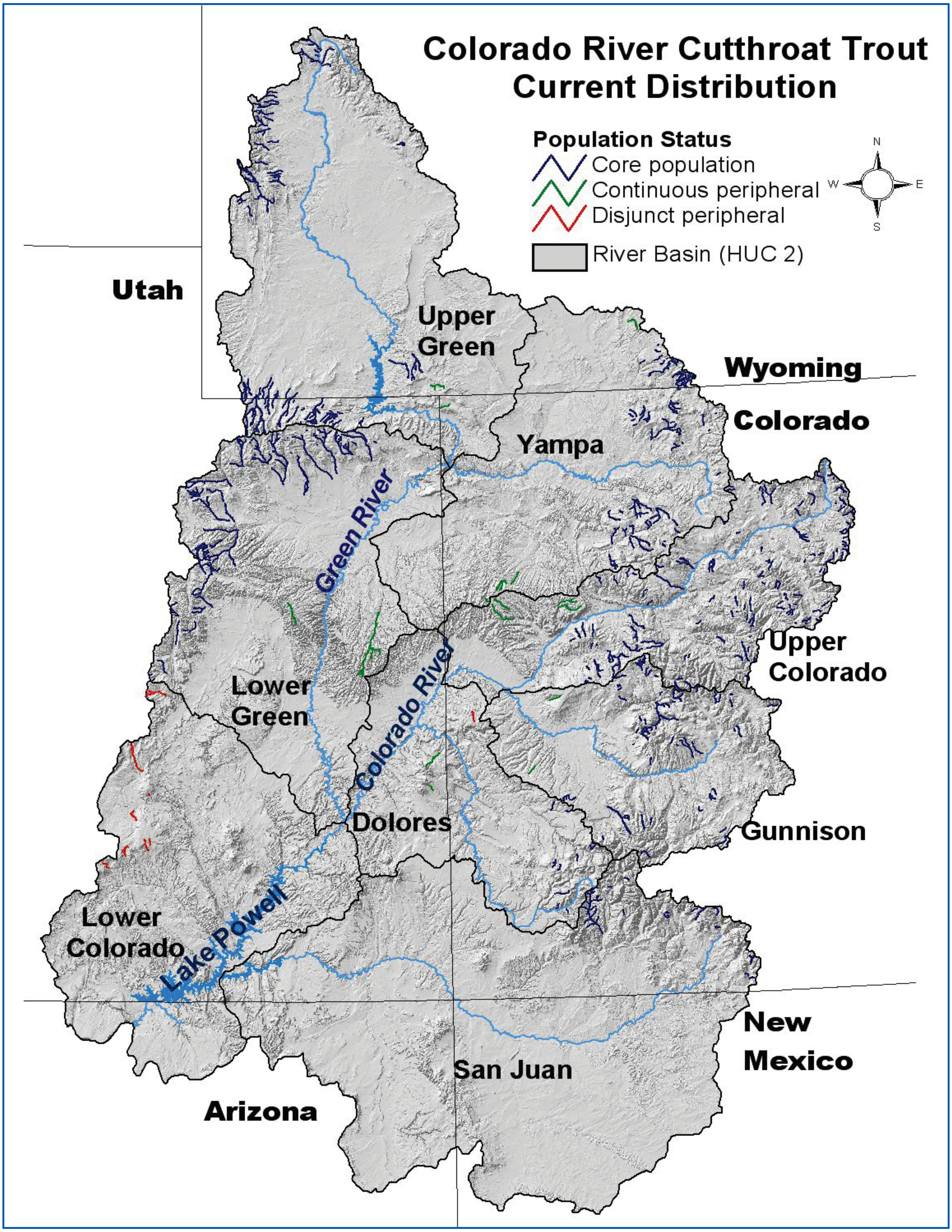


Figure 6. Current distribution of core and peripheral populations of Colorado River cutthroat trout.

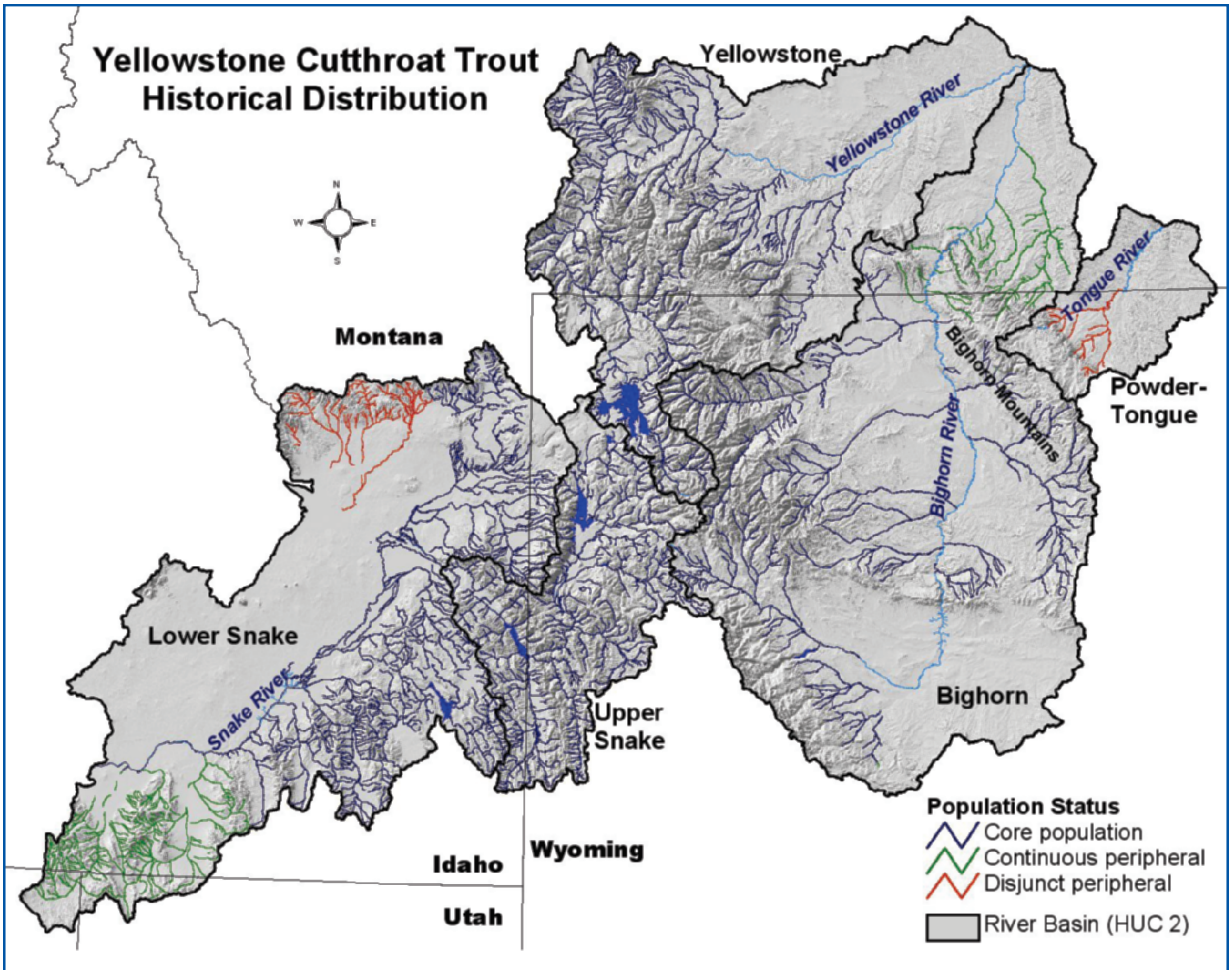


were considered persistent. The majority of continuous peripheral populations have also been extirpated already for this subspecies (Table 1), and though 32 remain, only 6 (19%) were considered persistent. Both continuous and disjunct peripheral populations classified as persistent for Yellowstone cutthroat trout occupy, on average, more than 50 km of streams, considerably more than persistent peripheral populations of other subspecies (Table 2). For westslope cutthroat trout, all remaining peripheral conservation populations are disjunct, and 21/43 (49%) of these met persistence criteria. Fifty percent of remaining continuous peripheral populations of Colorado River cutthroat trout were considered to be persistent, but less than 2/14 (14%) of disjunct populations were. All disjunct peripheral populations of Rio Grande cutthroat trout have been extirpated. Of 8 remaining continuous peripheral Rio Grande cutthroat trout populations, only 2 (25%) were considered persistent. Historically, Bonneville cutthroat trout had no continuous peripheral populations. Of remaining disjunct peripheral populations, only 5/39 (13%) were characterized as persistent, and these populations occupy an average of less than 13 km of stream habitat. The disjunct peripheral populations that were not considered persistent averaged only 4 km of occupied habitat.

Discussion

The conservation value of an individual population is generally gauged in the context of a species' abundance, and its genetic, ecological, and life history diversity range-wide (e.g., Gustafson et al. 2007). Without full knowledge of these characteristics across all populations, however, alternative means are needed for evaluating conservation priorities. Identifying peripheral populations may be a useful approach for assigning conservation values because of their assumed contribution to within-species biodiversity, arising from often unique evolutionary histories and the potential for distinct future evolutionary trajectories (Lesica and Allendorf 1995; Taylor et al. 2003). Assessing conservation needs relative

Figure 7. Historical distribution of core and peripheral populations of Yellowstone cutthroat trout.



to range distributions in fishes is especially difficult because peripheral populations of fishes have received relatively little attention in the scientific literature. In a recent review, Hampe and Petit (2005) found that only 4% of studies on peripheral populations were focused on aquatic systems, and we know of no studies that have attempted explicitly to define peripheral populations (sensu Schwartz et al. 2003; Channell and Lomolino 2000a, b) in trout. Identification of peripheral populations using geography, as done herein, can serve as a useful first step to characterizing potential historical within-subspecies diversity and understanding what may have already been lost, to guide future conservation needs (e.g., Gustafson et al. 2007).

In general, inland cutthroat trout are characterized by high among-population genetic diversity (Loudenslager and Gall 1980; Allendorf and Leary 1988; Neville et al. 2006; Peacock and Kirchoff 2007). This differentiation may be magnified in peripheral populations with distinct population dynamics (e.g., population fluctuations and/or bottlenecks) and colonization histories (Hedrick 1999; Nielsen 1999; Taylor et al. 2003), emphasizing their potential for disproportionate contributions to within-species biodiversity. In our study, the majority of peripheral populations have already been lost, and many of those remaining have a low likelihood of persistence because of small population sizes and limited habitat extents, due primarily to habitat degradation and fragmentation (Horan et al. 2000). Particularly in light of rapid environmental change, remaining peripheral populations may merit special focus to conserve potentially unique genetic characteristics and/or adaptations such as higher temperature tolerance (Nielsen 1999; Taylor et al. 2003; Flebbe et al. 2006; Rieman et al. 2007; Beatty et al. 2008) and for consideration for introduction efforts in the event that current habitats are eliminated.

The spatial patterns associated with peripheral populations and their losses differ even among subspecies of cutthroat trout and will need to be evaluated on a subspecies-by-subspecies basis. The cutthroat trout subspecies we evaluated had vary-

Figure 8. Current distribution of core and peripheral populations of Yellowstone cutthroat trout. Note that some populations (shown by dotted lines) have been introduced into previously unoccupied stream segments but still within their historical range.

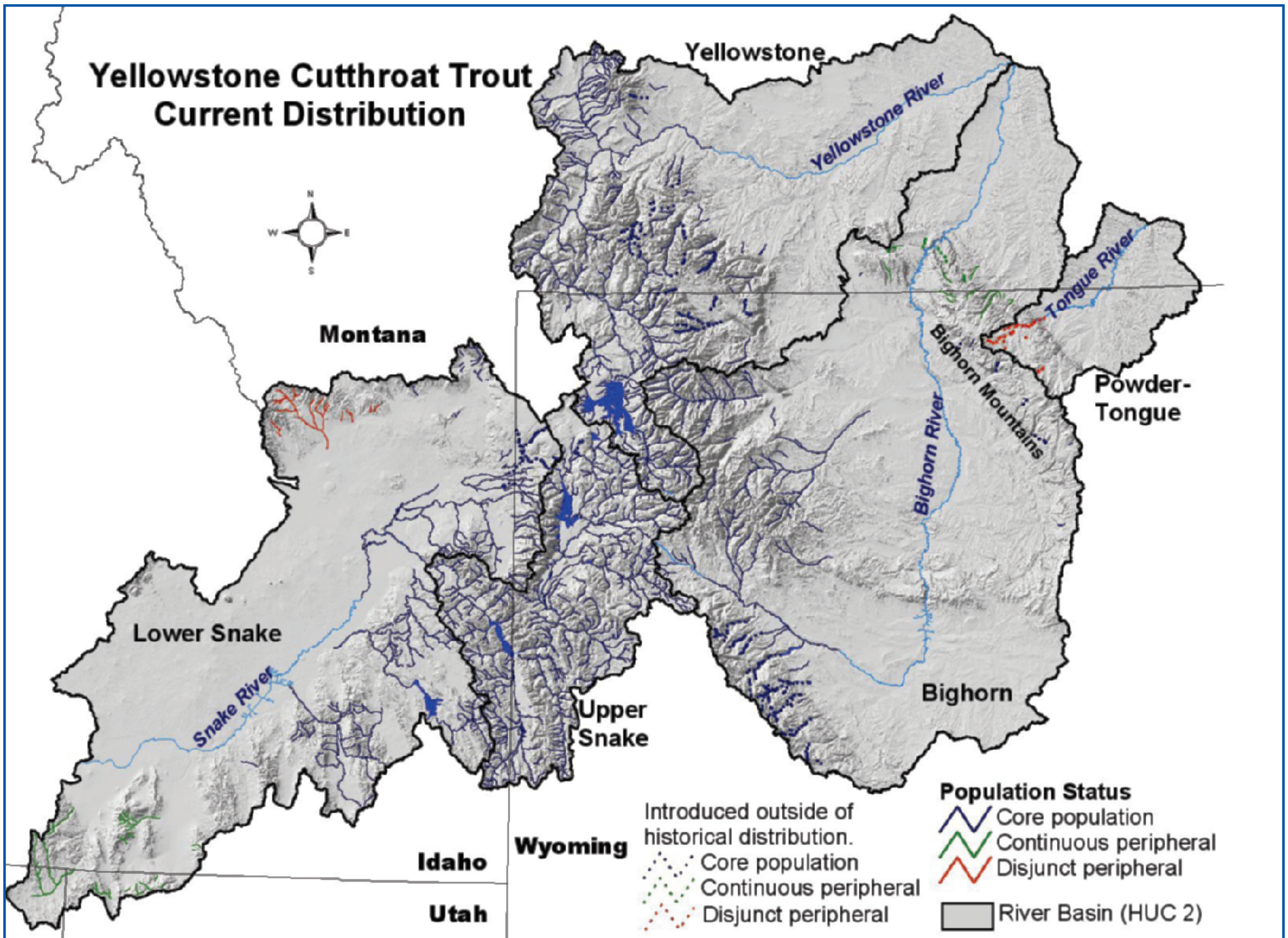


Figure 9. Historical distribution of core and peripheral populations of Rio Grande cutthroat trout.

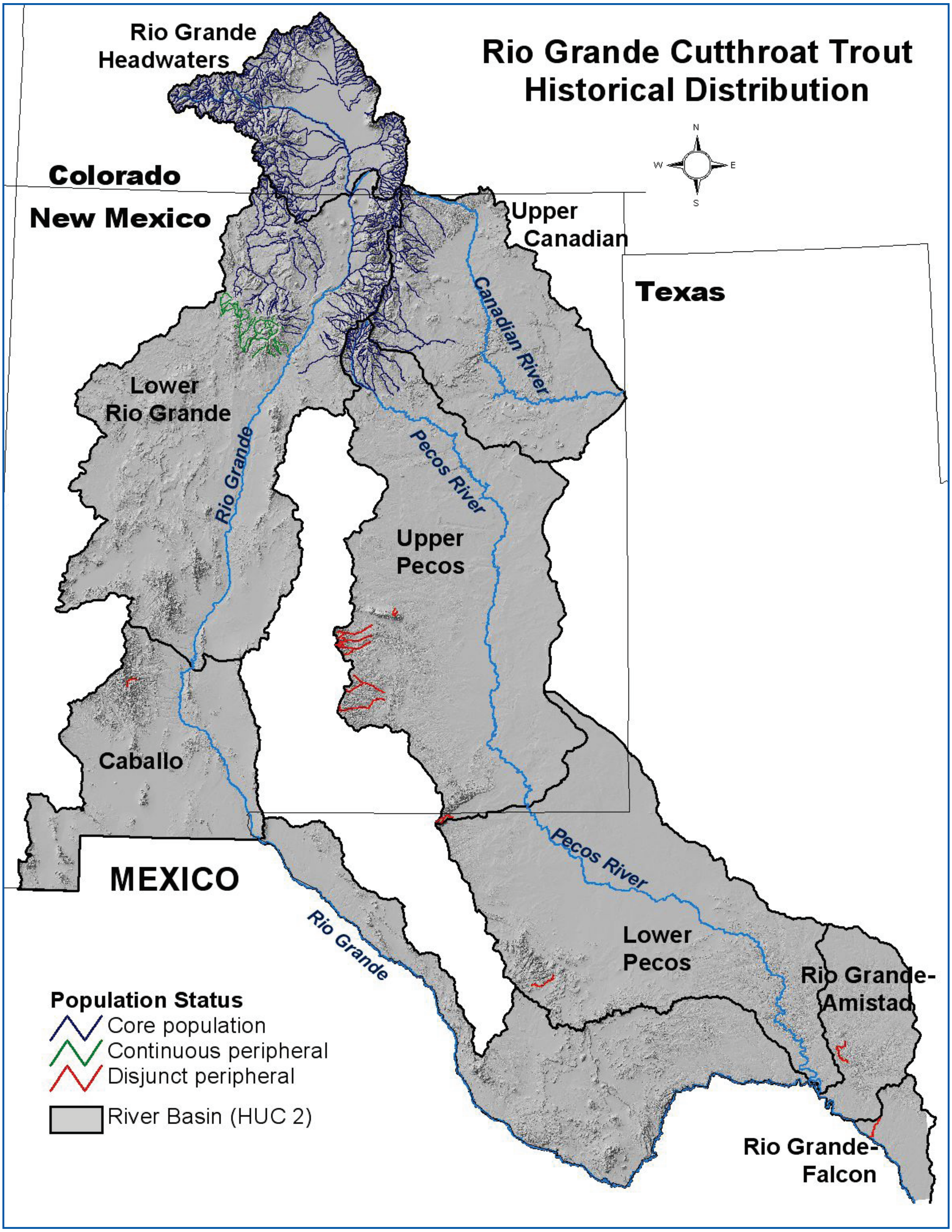
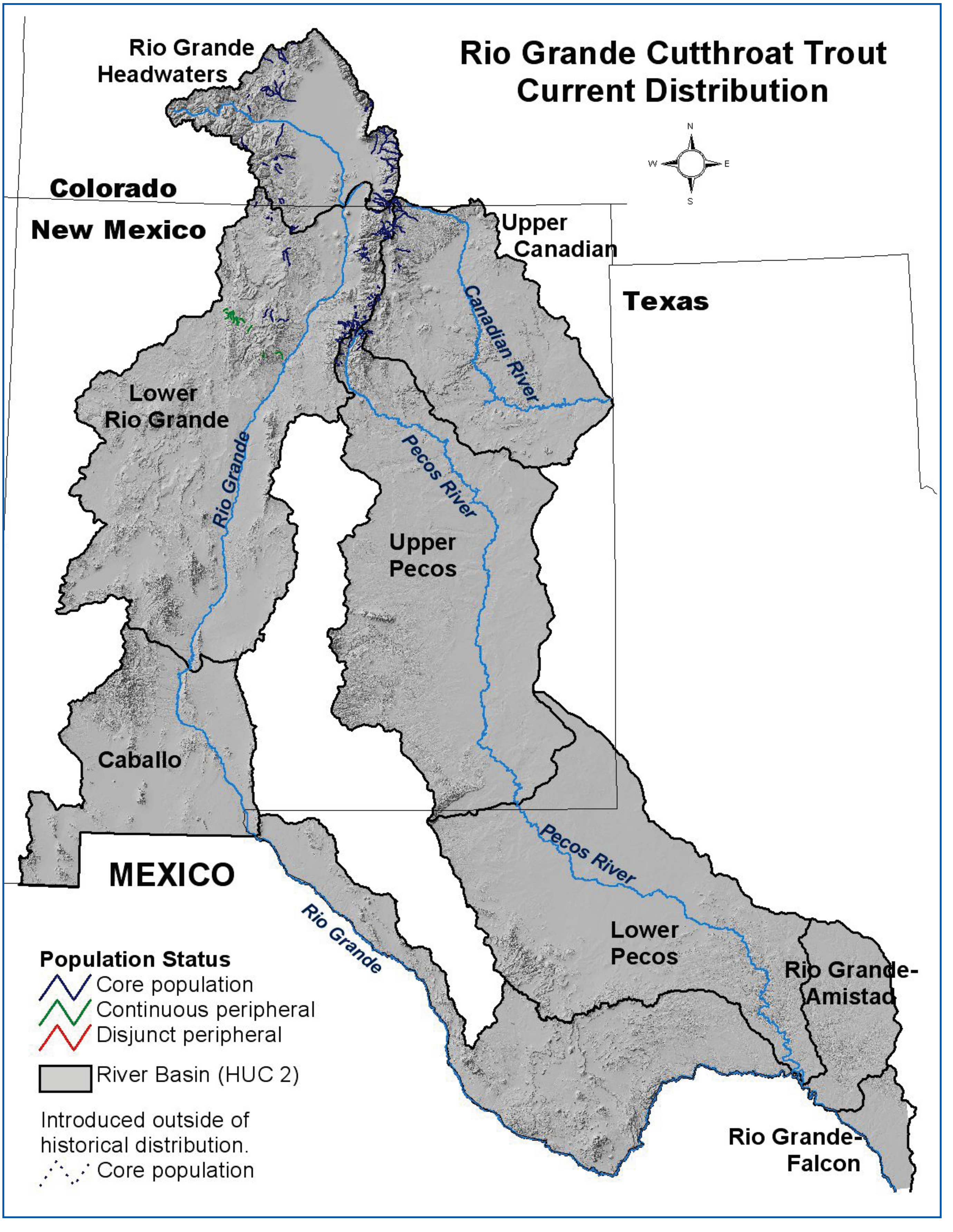


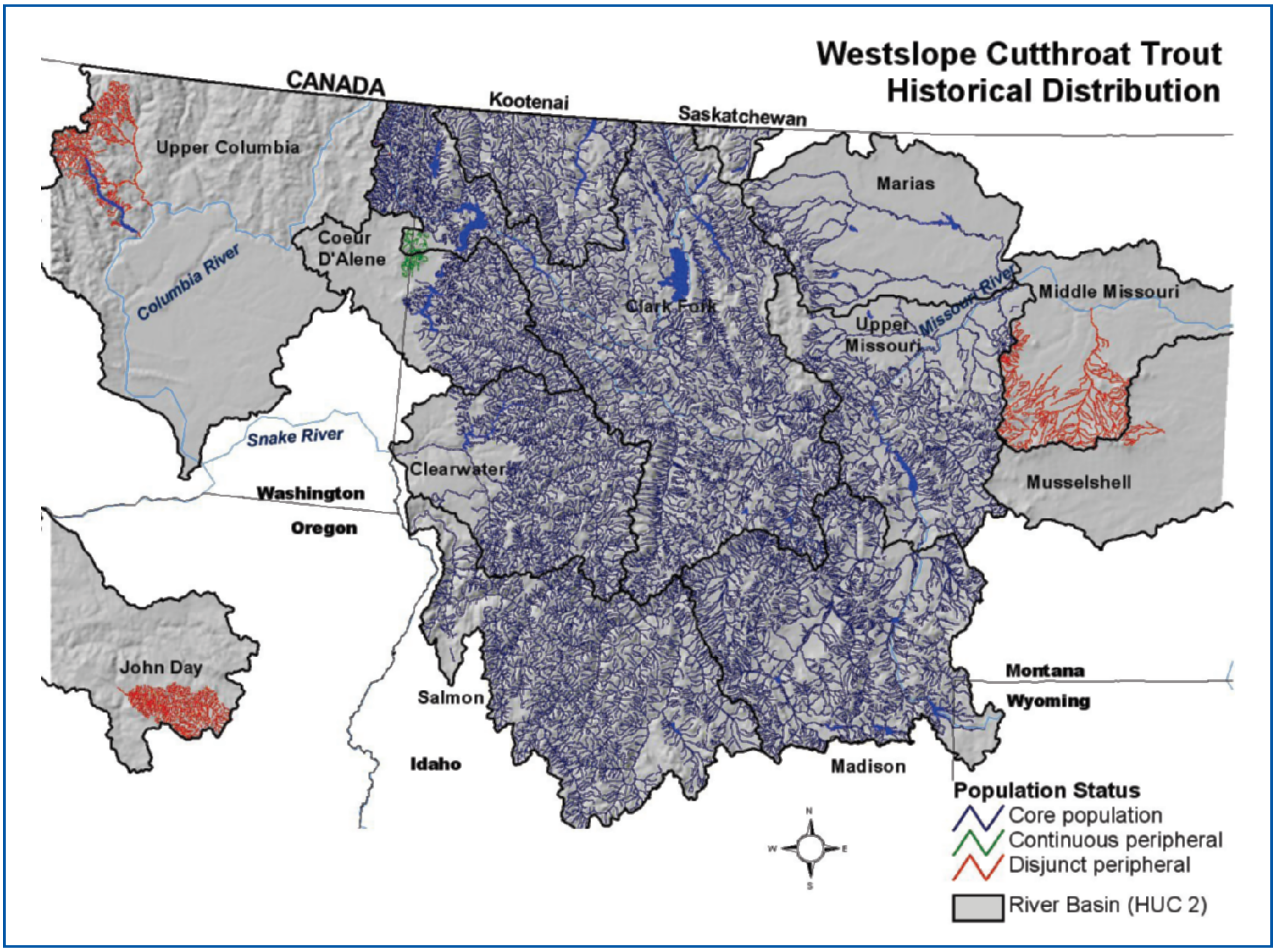
Figure 10. Current distribution of core and peripheral populations of Rio Grande cutthroat trout. Note that some populations (shown by dotted lines) have been introduced into previously unoccupied stream segments but still within their historical range.



ing patterns in terms of the proportion, geographic distribution, and magnitude of extirpation of peripheral populations related to latitude and hydrologic boundaries, but peripheral populations of all subspecies had high magnitudes of decline relative to core populations. Bonneville, Colorado, and Rio Grande cutthroat trout historical distributions extended south to warmer latitudes where suitable habitats are primarily associated with isolated mountain ranges that were occupied by disjunct peripheral populations. Most of these have now been extirpated or have low likelihood of persistence. In contrast, the westslope and Yellowstone cutthroat trout have the northern-most ranges and tended to have peripheral populations on the eastern and western extent of their distribution, because their distributions centered on core areas of the Rocky Mountains and are naturally constrained to the south by drainage basin boundaries. Likewise, patterns of loss were also not consistent geographically; westslope and Yellowstone cutthroat trout ranges have contracted to the center of their distribution, Bonneville and Rio Grande cutthroat trout distributions are contracting to the north, and the Colorado River cutthroat trout distribution is contracting to the north and the higher elevations of the Colorado River Basin. These contrasting spatial patterns among subspecies (sensu Sagarin and Gaines 2002) suggest that simple rules for classifying peripheral populations and identifying patterns of population loss based solely on range margins do not apply here, and that core-peripheral population designations and associated inferences about conservation value need to be considered on a case-by-case basis. However, despite spatial differences among subspecies, the magnitude of loss of peripheral populations across all subspecies is noteworthy.

Our results regarding losses of peripheral populations are clearly dependent on our approach to defining peripheral versus core populations. The aquatic systems on which we focus have different attributes from the more commonly-referenced terrestrial systems in that physical connectivity and opportunities for dispersal among populations are constrained by river systems, which originate in high-elevation mountain ranges and can drain towards or away from the center of the range. This makes defining the "core" and "periphery" complex, and not necessarily related to the geographic center or edge of the range. We based our definition on hydrologic and topographic connectivity in the hopes of maximizing the likelihood that the regions we defined as core versus periph-

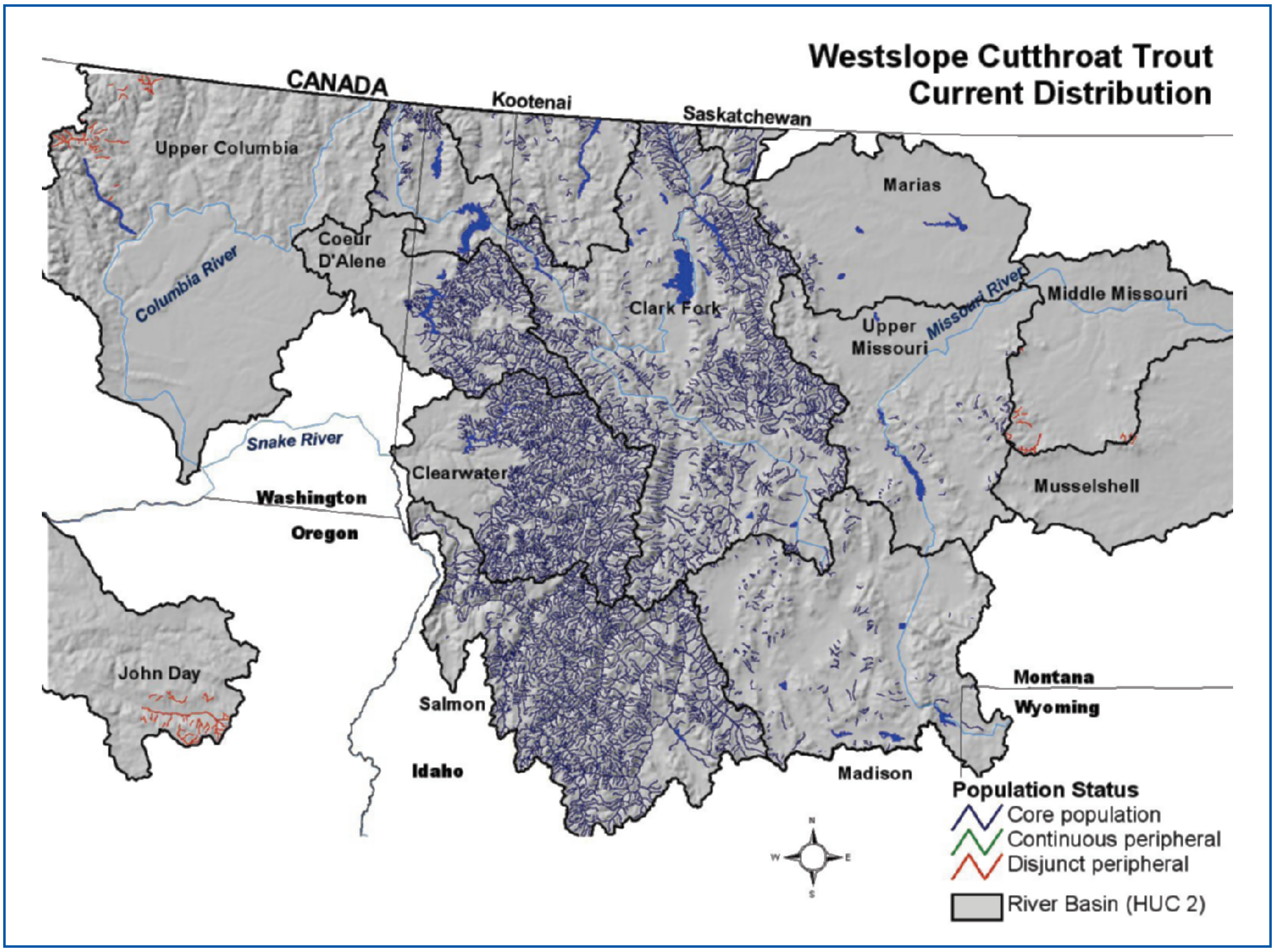
Figure 11. Historical distribution of core and peripheral populations of westslope cutthroat trout.



eral historically supported trout populations with different dispersal patterns and levels of population connectivity. Intuitively, populations occupying isolated stream networks that infiltrate completely into historical lake beds (e.g., West Desert Bonneville cutthroat populations; Figure 13) are easily classified as disjunct peripheral populations. Classifying continuous peripheral populations can be more tenuous, but these populations may still have different ecological and genetic characteristics than truly core populations (Bunnell et al. 2004). Factors such as elevation (Angers et al. 1999), habitat heterogeneity (Fausch et al. 2002), and natural barriers (Costello et al. 2003; Taylor et al. 2003; Wofford et al. 2005; Neville et al. 2006) can also isolate and differentiate trout populations even within what we consider to be core habitats.

Similarly, our criteria for persistence were necessarily coarse due to the nature of available data, and in some cases may not capture the true probability of persistence in terms of the complicated demographic, genetic, and environmental factors that promote or reduce persistence (e.g., Hilderbrand and Kershner 2000). Therefore, in many cases our estimates of persistence may be optimistic. It is important to note as well that prioritizing peripheral populations for conservation is not without controversy, and often in the related literature the attributes of peripheral populations are broadly assumed but empirically untested. For instance, some have argued that the reduced abundance, and therefore greater extirpation risk, of these populations means they should not be considered as viable components of biodiversity because scarce resources may be wasted on trying to conserve them (see discussion in Bunnell et al. 2004 and Hampe and Petit 2005). Yet peripheral populations do not always show reduced abundances (see Sagarin and Gaines 2002; Sagarin et al. 2006) and many peripheral populations have persisted through major climatic shifts, founder events, and extreme selective pressures, and in this sense have already withstood the test of time and demonstrated remarkable long-term viability (Nielsen 1999; Bunnell et al. 2004; Hampe and Petit 2005; Antunes et al. 2006). The somewhat opposing theoretical expectations regarding the genetic characteristics of these populations also make it difficult to assign conservation value consistently. From one perspective, the assumed attributes of populations in peripheral, marginal habitats (small, fragmented, unstable, swamped by gene flow from the core) are thought to constrain their abil-

Figure 12. Current distribution of core and peripheral populations of westslope cutthroat trout.



ity to adapt to local environments – possibly a primary reason why range limits exist where there are no barriers to dispersal (Kirkpatrick and Barton 1997; Kawecki 2008). At the same time, others argue that the frequent population bottlenecks and founder events experienced by small fragmented populations at the edge of species' ranges can set the stage for the fixation of beneficial alleles and genetic reorganization events that would be unlikely in larger, more stable populations experiencing weaker selection pressures (Lesica and Allendorf 1995; Nielsen et al. 2001).

As with many things in ecology, it is likely that the evolutionary and conservation value of peripheral populations is partially context-dependent (sensu Stockwell et al. 2003), and population-specific information such as abundance, ecological uniqueness, genetic characteristics, and levels of migration should be evaluated before making conservation and management decisions for these populations. However, both theory and empirical data would suggest these populations should be characterized by high levels of among-population differentiation and potentially unique genetic variants, and therefore collectively represent a disproportionate amount of within-subspecies diversity. The oft-cited tenet of conservation "save all the pieces" (Leopold 1949) would argue for careful consideration of their conservation value, particularly in light of an uncertain future where maintaining diversity and adaptive potential will be critical for long-term viability. We hope that our geographical characterization of peripheral populations and their losses will emphasize the need for closer evaluation of conservation priorities for peripheral populations in inland cutthroat trout and other fishes.

Management implications

Our study indicates that additional management actions may need to be directed towards peripheral native trout populations. Of course, the results of broad-scale assessments, including ours, should be augmented with finer-scale stream and population data to inform management decisions, but our results may be useful in identifying those populations that are in greatest need of management attention. For example, peripheral populations that fall far below persistence thresholds and/or are in high-risk areas for climate change-driven disturbance (Rieman et al. 2007; Williams et al. 2009) should receive initial attention. Declines of remaining peripheral populations are not likely to be consistent across all river basins or geographic areas. Yet to maximize within-species biodiversity, it is important to conserve at least some minimum number of populations across all river basins. Rieman et al. (2007) recommended that five populations meeting persistence thresholds be maintained in each subbasin (4th Code Hydrologic Unit) for long-term conservation of bull trout. Because of natural limitations on available habitat in some of the more arid regions occupied by peripheral populations, this goal may not be realistic or even possible in areas such as the West Desert for Bonneville cutthroat trout, or the San Juan Basin for Colorado River cutthroat trout. In these instances, it is advisable to maintain as many populations as possible given restrictions on available habitat. Even if habitat cannot be expanded, restoring the quality and extent of riparian zones and thermal refugia may help buffer stream systems from disturbance and on-going impacts of climate change (Seavy et al. 2009). In general, larger populations and those in higher quality and more heterogeneous stream systems are more likely to survive prolonged drought, flooding, or wildfire in their watersheds (Dunham et al. 2002, 2003; Neville et al. 2009).

More frequent monitoring will aid in the conservation of peripheral populations (Dauwalter et al. 2009). Because of their small geographic extent, many peripheral populations are vulnerable to disturbance, including relatively small increases in stressors. Frequent monitoring can help with the early detection of detrimental physical or biological changes. Although usually somewhat isolated and removed from hydrologic connections that would facilitate non-native species invasion, if introduction does occur in peripheral habitats, a non-native species could quickly spread through the system, and there is growing concern that such invasions may be facilitated by climate change (Fausch 2008). Initial

Table 2. Number of peripheral populations and their cumulative stream habitat that meet or fail to meet persistence criteria. The populations reported here include only those considered to be "conservation populations" within historically occupied habitat as defined by state fish and wildlife agencies. This includes introduced populations that are considered to be "conservation populations."

Cutthroat subspecies	Peripheral cassification	Persistent populations		Non-persistent populations	
		Number of populations	Stream habitat (km)	Number of populations	Stream habitat (km)
Bonneville	Disjunct	5	62	34	132
	Continuous	0	0	0	0
Colorado River	Disjunct	2	35	12	45
	Continuous	5	78	5	41
Yellowstone	Disjunct	4	209	2	7
	Continuous	6	305	26	147
Rio Grande	Disjunct	0	0	0	0
	Continuous	2	34	6	33
Westslope	Disjunct	21	748	22	114
	Continuous	0	0	0	0

Figure 13. Peripheral populations of Bonneville cutthroat trout persist in small streams draining Utah's Deep Creek Mountains along the western edge of the subspecies' range. (Photos: Warren Colyer and Amy Harig)

genetic assessments are needed for many peripheral populations to understand their genetic distinctiveness, "health," and conservation needs (Dunham et al. 1999). If collected over time, genetic data can be an efficient and effective way to monitor changes in factors such as effective population size, inbreeding, or hybridization (Schwartz et al. 2006).

Translocations of native trout from peripheral populations into new or former habitat could provide conservation benefits, but are often unsuccessful (Harig and Fausch 2002) and are not without risk. Translocating fish into novel habitat spreads the risk of extinction for that species, and may put other species at risk (Ricciardi and Simberloff 2009) and establish a new evolutionary trajectory for the translocated population when compared to the original donor populations (Stockwell and Leberg 2002; Stockwell et al. 2003). Differential selection and founder effects are common when establishing new populations from a small number of individuals (Wilcox and Martin 2006; Yamamoto et al. 2006). These risks can be minimized if translocations are repeated over time (if not detrimental to the source population) and if fish are moved between similar habitats within their historical range. In general, translocations should only occur between habitats in the same river basin or geographic area. In some instances, a lack of sufficient available habitat within the same river basin or geographic area may make translocations problematic: Harig and Fausch (2002) found that a minimum watershed area of 14.7 km^2 is likely needed for a successful translocation, and Hilderbrand and Kershner's (2000) minimum stream habitat threshold of 9.3 km for long-term persistence is another useful guideline for gauging necessary amounts of habitat for cutthroat trout. Meeting population size criteria for long-term population persistence may be difficult and managers should not underestimate risks associated with small population sizes (Traill et al. 2009).

Conservation of peripheral populations will help preserve remaining genetic, life history, and evolutionary diversity within native trout. Retaining within-species biodiversity to allow for adaptation to fringe areas, small habitats, and harsh conditions should provide a substantial evolutionary advantage during periods of rapid environmental change, which are likely to characterize the future of coldwater fishes.

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