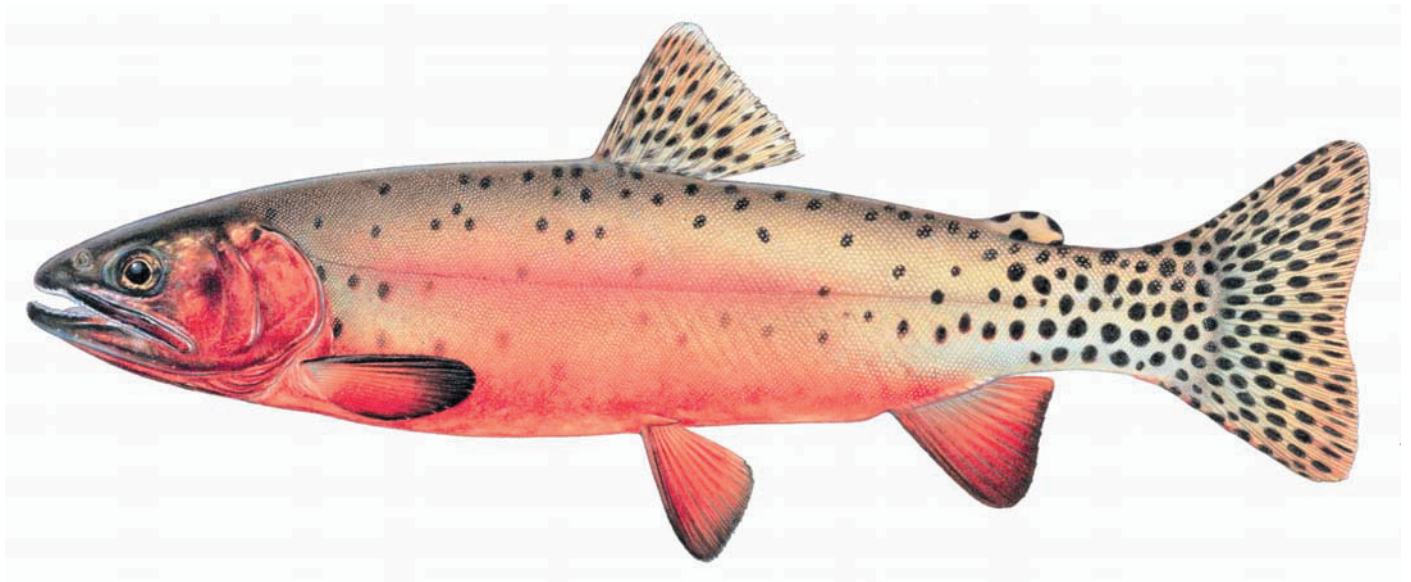


**Greenback Cutthroat Trout
(*Oncorhynchus clarkii stomias*):
A Technical Conservation Assessment**



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

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COVER ILLUSTRATION CREDIT

Illustration of the Greenback Cutthroat Trout (*Oncorhynchus clarkii stomias*) by © Joseph Tomelleri.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE GREENBACK CUTTHROAT TROUT

Status

Greenback cutthroat trout (*Oncorhynchus clarkii stomias*) was once presumably distributed throughout the colder waters of the South Platte and Arkansas River basins in Colorado and southeastern Wyoming. Primarily a fluvial species, greenback cutthroat trout may have occupied 10,614 to 13,231 km of streams above 1,800 m in these basins. Nevertheless, the distribution of greenback cutthroat trout has dramatically contracted since the mid-1800's, particularly from lower-elevation sites. Rebounding from a low of two populations occupying a few kilometers of small streams in 1970, populations regarded as greenback cutthroat trout now occupy up to 72 streams and lakes, 23 of which meet criteria for populations to count toward delisting under the Endangered Species Act. The bulk of these populations are found on federal lands, and many in the South Platte River basin are in Rocky Mountain National Park. Recent genetic evaluations, however, indicate that many populations considered historical remnants of greenback cutthroat trout may be Colorado River cutthroat trout. Individuals of both taxa were often mixed to develop recovery broodstocks, so the number of non-introgressed wild populations of greenback cutthroat trout is uncertain.

With the enactment of the Endangered Species Act in 1973, the greenback cutthroat trout was listed as endangered but subsequently downlisted to threatened in 1978. Presently, the U.S. Fish and Wildlife Service is conducting a review to determine whether this designation remains appropriate.

Primary Threats

Historically, habitat alteration from mining, agriculture, and water development contributed to the extirpation or reduction of large numbers of populations of greenback cutthroat trout, whereas introductions and invasions of nonnative trout probably represent the greatest cause of recent declines and the major impediment to restoration of this fish in much of its historical range. Many populations appear to remain vulnerable to this threat either because barriers to ongoing invasions are absent or because existing barriers may be temporary or have nonnative fish passed over them illegally. Ironically, the barriers themselves provide a limitation to dispersal, resulting in most populations of greenback cutthroat trout being restricted to short, headwater stream segments. Lack of connectivity to other populations renders them vulnerable in the short term to extirpation from natural disturbances such as fire, post-fire debris torrents, or floods and in the long term to loss of genetic variability and the potential for evolving in response to changing environmental conditions. This lack of connectivity also contributes to the greatest future threat to the persistence of this subspecies—climate change—because model projections suggest some suitable habitats may shift to higher elevations and precipitation patterns imply there may be large declines in late summer flows. Because these habitat changes are likely to be coupled with greater resource demands (particularly for water) by a rapidly growing human population in the Rocky Mountains, the future for stream populations of greenback cutthroat trout remains uncertain. The prospects for greenback cutthroat trout may be better in the many lakes used for conservation actions, with the understanding that such waters are unlikely to constitute historically occupied habitats. The potential effects of climate change on lake populations are uncertain, but isolation in such environments is likely to alter the genetic structure of some populations.

Primary Conservation Elements, Management Implications, and Other Considerations

Conservation of greenback cutthroat trout will require attention to both short-term and long-term threats. In the short term, preventing invasions by nonnative trout through the judicious use of barriers can protect some populations of greenback cutthroat trout, but perhaps the most successful long-term strategy will be to eliminate nonnative trout from downstream waters and expand the distribution of greenback cutthroat trout into larger basins exhibiting greater connectivity. Removal of nonnative trout and reintroduction of greenback cutthroat trout into formerly occupied habitats will also reduce the probability of losing all local populations simultaneously as well as offering the potential to conserve the remaining genetic variability represented in extant populations. Habitat improvement may have beneficial effects, particularly if combined with whole-basin changes in activities that degrade habitats,

although acknowledging the inherent temporal variability in habitat quality is essential. Given that habitat change is inevitable, managing to permit the continued evolution of this subspecies may be fundamental to its long-term persistence. Systematic conservation planning could prove to be an efficient and successful process for guiding future conservation efforts.

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INTRODUCTION

This assessment of the greenback cutthroat trout (*Oncorhynchus clarkii stomias*) is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2). The greenback cutthroat trout is listed as threatened under the Endangered Species Act and for the purposes of this assessment is regarded as a sensitive species in Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of a significant current or predicted downward trend in abundance or habitat quality that would reduce its distribution (FSM 2670.5 (19)). Because of concerns about its viability and abundance, a sensitive species requires special management, so knowledge of its biology and ecology is critical.

Goal

The purpose of this species conservation assessment is to provide forest managers, scientists, and the public with a thorough discussion of the current understanding of the biology, ecology, conservation status, and management of greenback cutthroat trout. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations. Rather, it provides the ecological background upon which management can be based and focuses on the consequences of changes in the environment from natural and anthropogenic sources that are relevant to the management of greenback cutthroat trout. Furthermore, it considers the implementation and success of management recommendations for the conservation of this species. Admittedly, any assessment of the biology, threats, and possible management of a species reflects the expertise and biases of the author. Herein I emphasize science and management directed toward the understanding, conservation, and restoration of indigenous populations and their phenotypic and genotypic diversity, and devote little attention to populations established or maintained primarily for recreation. Although there is much we do not know about ecosystem processes, I stress a conservative and precautionary approach that favors restoring those processes as opposed to more direct intervention that often has unintended consequences; in other words, adopting the physician's (and ecologist's; Leopold 1949) creed of do no harm. Other perspectives

would highlight different ecological aspects, threats to persistence, and management opportunities.

Scope

This assessment focuses on greenback cutthroat trout within the USFS Rocky Mountain Region. Although the vast majority of literature on cutthroat trout and nonanadromous salmonids in montane habitats originates from research elsewhere (see below), this document places that literature in the context of the geographical, ecological, and cultural characteristics of the central Rocky Mountains. Similarly, this assessment emphasizes the biology, ecology, and status of greenback cutthroat trout with respect to the current environment. Nevertheless, it includes consideration of historical conditions deemed essential to understanding the evolutionary history and trajectory of this species, as well as those factors influencing the potential for future conservation.

Resources consulted for this assessment included the peer-reviewed literature, non-refereed publications, agency reports, and data from resource management agencies. Not all documents on greenback cutthroat trout are referenced in the assessment, nor are all materials considered equally reliable. The assessment gives greater credence to peer-reviewed literature because these publications have received formal scientific scrutiny. Less stringently reviewed materials and unpublished data were occasionally used when they were the best available information, but greater caution must be applied in their interpretation. Agency reports and expert opinion that were specific to particular waters were sometimes included because these represent the bulk of information on this subspecies. Much of the present document adopts verbatim the text from an assessment on Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) (Young 2008) because of the ecological and evolutionary similarities between these taxa. This assessment also relies extensively on Young et al. (2002), which reviewed all available literature on conservation activities related to greenback cutthroat trout until 2000. Because there has been little published documentation of actions taken since that time, discussions in this assessment are largely confined to activities conducted during this period.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against

observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, logical thinking, and models must be relied on to guide the understanding of ecological relations (Hilborn and Mangel 1997). In this assessment, the strength of evidence for particular ideas is noted and alternative explanations are described where appropriate. Nonetheless, many of these explanations should be regarded as working hypotheses until supported or refuted by scientific or management experiments.

Application and Interpretation Limits

Although salmonids are one of the best-studied groups of fishes in the world, cutthroat trout have not received attention comparable to that received by other taxa. For example, a search of the Aquatic Sciences and Fisheries Abstracts database (accessed 19 December 2006) revealed that since 1970, 439 peer-reviewed articles have appeared that include “cutthroat trout,” “*Oncorhynchus clarkii* (or *clarki*),” or “*Salmo clarki*” in the abstract. Over this same interval, however, 1,020 articles have included the common or scientific name of brook trout *Salvelinus fontinalis*, 2,015 have named brown trout *Salmo trutta*, and 7,745 have named rainbow trout *O. mykiss*. Studies of these nonnative species also appear to exceed those of the inland subspecies of cutthroat trout, even when the papers on brook, brown, and rainbow trout are restricted to Colorado, Wyoming, and Utah (**Figure 1**). This search located only nine peer-reviewed papers published on greenback cutthroat trout since 1970. In addition, most populations of greenback cutthroat trout still extant in Region 2 are restricted to small headwater habitats, yet most research on cutthroat trout has focused on larger, migratory forms of other subspecies. Thus, few conclusions about the biology, ecology, and management of greenback cutthroat trout can be drawn directly from published research and rely largely on syntheses of studies of related taxa (often in dissimilar environments) and on an understanding of salmonid biology as a whole. Consequently, I have generally been conservative in my interpretations, but urge the reader to recognize these limitations with respect to our knowledge of greenback cutthroat trout in Region 2 and to use caution in applying this information.

Publication on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site (<http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml>). Making documents available via the Internet makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, Web publication facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer-reviewed prior to their release on the Web. This report was reviewed through a process administered by the American Fisheries Society, which chose two recognized experts (on this or related taxa) to provide critical input on the manuscript. Peer review was designed to improve the quality of communication and to increase the rigor and general management relevance of the assessment. A number of other individuals contributed their comments to earlier versions of this document; they are noted earlier in the acknowledgments.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

With the enactment of the Endangered Species Act in 1973, the greenback cutthroat trout was listed as endangered but subsequently downlisted to threatened in 1978 (Young et al. 2002). Presently, the U.S. Fish and Wildlife Service (USFWS) is conducting a review to determine whether this designation remains appropriate (U.S. Fish and Wildlife Service 2005). The American Fisheries Society also considers this fish to be threatened (Williams et al. 1989).

The Natural Heritage Program rank for cutthroat trout is G4 (global rank: uncommon but not rare; some cause for long-term concern due to declines or other factors), and for this subspecies it is T2 (intraspecific rank: at high risk of extinction due to very restricted range, very few populations [often 20 or fewer], steep declines, or other factors). Within states, ranks are S2 (Colorado: believed to be imperiled because of rarity due to very restricted range, very few populations [often 20 or fewer], steep declines, or other factors making it

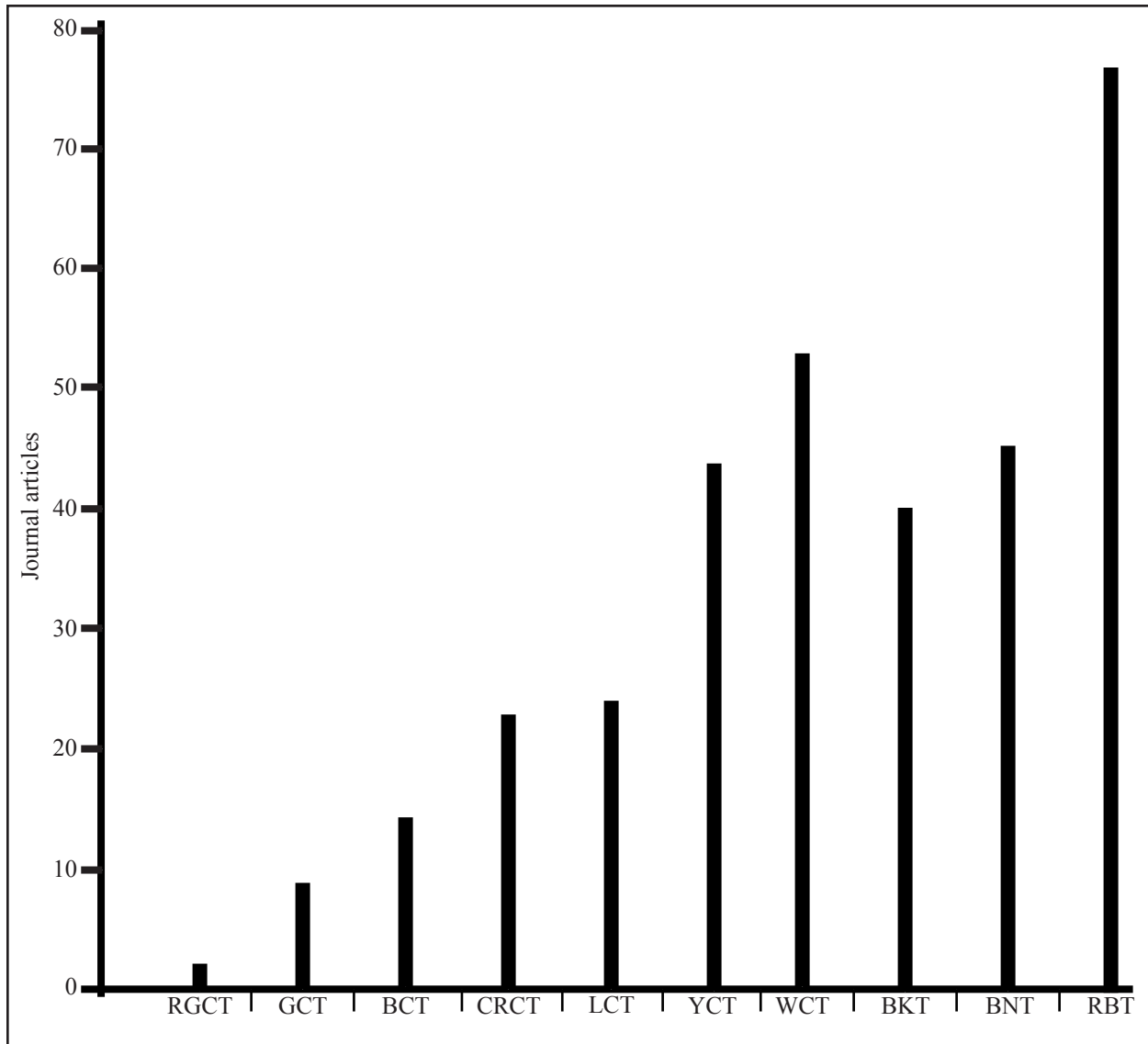


Figure 1. The number of peer-reviewed journal articles on subspecies of inland cutthroat trout and nonnative trout, based on a search of common and scientific names in the Aquatic Sciences and Fisheries Abstracts database on 19 December 2006. The search was restricted to papers published since 1970, and search terms had to appear in the article abstract. In addition, articles on nonnative trout had to include Colorado, Wyoming, or Utah in the abstract. RGCT, Rio Grande cutthroat trout; GCT, greenback cutthroat trout; BCT, Bonneville cutthroat trout; CRCT, Colorado River cutthroat trout; LCT, Lahontan cutthroat trout; YCT, Yellowstone cutthroat trout; WCT, westslope cutthroat trout; BKT, brook trout; BNT, brown trout; and RBT, rainbow trout.

very vulnerable to extirpation) and SX (Wyoming: extirpated) (NatureServe 2007).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The original recovery plan for greenback cutthroat trout was completed in 1977 (Greenback

Cutthroat Trout Recovery Team 1977), and revisions were adopted in 1983 (U.S. Fish and Wildlife Service 1983) and 1998 (U.S. Fish and Wildlife Service 1998). Within Region 2, this latest revision guides management of greenback cutthroat trout on the Pike-San Isabel and Arapaho-Roosevelt National Forests. The objective of the recovery plan is the delisting of this subspecies. To meet that objective, the plan requires that there be 20 stable populations of greenback cutthroat trout—at least

five of which must be in the Arkansas River basin—occupying at least 50 ha of lentic habitats and 50 km of streams within its historical range. Stable populations must be allopatric and are further characterized as those that have: 1) a biomass of at least 22 kg per ha of wild fish; 2) 500 or more adults, which are considered to be fish >120 mm; 3) evidence of successful recruitment in 2 of 5 years, and 4) a migration barrier preventing upstream-directed invasions of nonnative trout species (U.S. Fish and Wildlife Service 1998). That there be at least 2 ha of habitat in all stable populations appears to constitute a fifth criterion, but there is some ambiguity about this standard (Young and Harig 2001). Actions directed at achieving this objective include monitoring, protecting, improving, and where necessary isolating habitat; establishing, monitoring, and surveying for populations; controlling and halting introductions of nonnative fishes and diseases; creating broodstocks; restricting harvest; conducting an information and education campaign; promoting interagency cooperation and engaging outside groups; and developing a long-term management plan. In 2007, biologists familiar with this subspecies began developing a range-wide status assessment, largely following the protocol used for a similar assessment of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; Shepard et al. 2005) and Colorado River cutthroat trout (Hirsch et al. 2006). Results of this work should be forthcoming soon.

In addition, nongovernmental organizations and individuals have actively advocated for conservation of greenback cutthroat trout. The most notable example may be the development and release of the nationally recognized short documentary film “Incredible Journey of the Greenback Cutthroats” that was produced by Hugh Gardner for a Colorado television station. The recent re-release of this film was made possible by a grant from Patagonia, an outdoor clothing manufacturer, which as part of its World Trout Project has funded conservation activities by the Colorado chapter of Trout Unlimited on greenback cutthroat trout. Other actions have included the short-lived Western Native Trout Campaign formed by The Center for Biological Diversity, Biodiversity Conservation Alliance, Pacific Rivers Council, and Trout Unlimited to promote restoration of healthy populations of nonanadromous salmonids in the western United States, primarily via participation in public processes associated with federal land and species management plans. The Nature Conservancy, a national land trust whose mission is the preservation of biodiversity, has not targeted particular waters for the conservation of this subspecies. It is working on a large-scale initiative related to ecologically sustainable water management (Richter et al. 2003) and has crafted an ecoregional plan

that specifies larger basins in which conservation may be a priority (Neely et al. 2001). Trout Unlimited, a national organization with state and local chapters dedicated to conservation of wild trout, has collaborated with a number of state and federal agencies and grassroots organizations to enhance and restore populations and to improve habitats in specific watersheds through their Embrace-a-Stream program. They also maintain public awareness via press releases, educational materials, and organizational initiatives. For example, Trout Unlimited is devising a Conservation Success Index to gauge the effectiveness of conservation measures for native trout and to prioritize future efforts.

Biology and Ecology

Systematics and general species description

The greenback cutthroat trout is in the order Salmoniformes and family Salmonidae. The genus *Oncorhynchus* in North America comprises cutthroat trout (until recently, *O. clarkii*), rainbow trout, five species of Pacific salmon, Gila trout (*O. gilae gilae*), Apache trout (*O. g. apache*), Mexican golden trout (*O. chrysogaster*), Baja California rainbow trout (*O. m. nelsoni*), and several undescribed Mexican trout (Behnke 1992, Hendrickson et al. 2002). It is one of 14 subspecies of cutthroat trout in the western United States (Behnke 1992), some of which remain undescribed, may be of questionable validity, or represent a polyphyletic group with members warranting designation as individual subspecies (Martin et al. 1985).

The phylogenetic relationships among members of *Oncorhynchus* are poorly known and currently in dispute (Stearley and Smith 1993, Utter and Allendorf 1994, Oakley and Phillips 1999, Hendrickson et al. 2002). Behnke (1992) hypothesized that the major phylogenetic lines (i.e., coastal (*O. clarkii clarkii*), westslope, and Yellowstone cutthroat trout (*O. c. bouvieri*), were probably established over one million years ago, after which an interbasin transfer from the upper Snake River to the upper Green River permitted the spread of cutthroat trout in the Colorado River basin and the eventual evolution of Colorado River cutthroat trout. According to this perspective, glacial periods from 100,000 to 10,000 years ago resulted in stream captures from the Colorado River basin into the South Platte, Arkansas, and Rio Grande basins that led to the evolution of greenback cutthroat trout (*O. c. stomias*) and Rio Grande cutthroat trout (*O. c. virginalis*). In contrast, Smith et al. (2002; also see Minckley et al. 1986) proposed—based on mtDNA

sequence divergence rates and fossil records—that the progenitor of cutthroat trout initially occupied waters of the Great Basin perhaps 8 million years ago, which it may have accessed by following the ancient course of the Snake River through southern Oregon, and began to differentiate into subspecies nearly 5 million years ago. This is in accordance with Stearley's (1992) hypothesized pre-Pleistocene occupation of Lake Lahontan by cutthroat trout. Smith et al. (2002) also argued for substantial connections among waters in the Great Basin, Colorado River, and Rio Grande from 9 million to 5 million years ago. Based on restriction fragment length polymorphisms of mitochondrial and ribosomal DNA, Dennis Shiozawa and Paul Evans (Brigham Young University, personal communication and unpublished data) have hypothesized that a cutthroat trout exhibiting an archaic haplotype occupied habitats in all of these basins (as well as the South Platte and Arkansas River basins) and gave rise to Rio Grande, greenback, and Colorado River cutthroat trout, although the precise geographic and phylogenetic origins of each are uncertain. They also suggested that the structure of an additional haplotype in Colorado River cutthroat trout appears consistent with more recent evolutionary exposure to Yellowstone cutthroat trout, as Behnke (1992) proposed. Although sampling has been limited, individuals with the archaic haplotype are uncommon in the northern portions of the historical range (and could be restricted to isolated headwater habitats there), yet such fish may constitute the sole form present in the San Juan River basin. Only this presumptively older haplotype has been found in samples of greenback cutthroat trout and Rio Grande cutthroat trout, suggesting that their contact with Colorado River cutthroat trout had ceased prior to the latter's exposure to Yellowstone cutthroat trout. Metcalf et al. (2007) reported that the lineages leading to Colorado River cutthroat trout and greenback cutthroat trout diverged 0.7 to 2.0 million years ago, based on molecular clock estimates.

The greenback cutthroat trout is among the most colorful of the subspecies. Individuals display the light to deep red pigmentation of the gular folds that give the species its common name, as well as having large black spots concentrated posteriorly and dorsally. The back tends to be brownish or olivaceous, the sides somewhat paler and often with parr marks even in adult fish, and the belly may be pale to light yellow (particularly in females) or melon orange to bright red (particularly in males). The opercula also exhibit these bright colors. Mature males display particularly intense coloration from autumn through the spawning season. Behnke (1992) observed that this subspecies averaged 189 to 217 scales in the lateral series, and 44 to 53 scales

above the lateral line, which were much greater than counts in all other subspecies except Colorado River cutthroat trout.

Distinguishing greenback cutthroat trout from its two closest relatives can be difficult. Rio Grande cutthroat trout possess similar coloration, but usually have fewer scales in and above the lateral line and more irregularly shaped spots on the caudal peduncle. Although greenback cutthroat trout tend to have somewhat larger spots and more scales in and above the lateral line (Behnke and Benson 1980, Behnke 1992), there is substantial overlap in appearance with Colorado River cutthroat trout. Male greenback cutthroat trout in lakes are reputed to become a brighter shade of red during spawning, but male Colorado River cutthroat trout in similar habitats also adopt this appearance, which may be more of a reflection of the availability of carotenoid-containing prey (Putnam 1992) than of an inherent difference between subspecies. Even attempts to use genetic methods to discriminate between these subspecies have been unsuccessful (Leary et al. 1987, Kanda et al. 2002), but recent work with microsatellites (Metcalf et al. 2007) appeared to identify several diagnostic markers.

Other factors obscure a complete understanding of the taxonomic relations among these groups. The paucity of historical records leaves considerable uncertainty about the original distribution of greenback cutthroat trout. It is possible that the type specimen for greenback cutthroat trout originated from the Green River basin in Wyoming, that the presumably extinct yellowfin cutthroat trout (*Oncorhynchus clarkii macdonaldi*) was the only subspecies present east of the Continental Divide in this region and perhaps found only in the Arkansas River basin (Behnke 1992), and that greenback and Colorado River cutthroat trout represent forms of cutthroat trout that colonized portions of the Colorado River basin at different times. Moreover, although these two subspecies may once have been easily differentiated based on their distribution—whatever that may have been—inter- and intra-basin stocking has made this unreliable. Metcalf et al. (2007) believed that several populations in the South Platte and Arkansas River basins that had been treated as greenback cutthroat trout were instead Colorado River cutthroat trout that may have been established after 1896 when large numbers of Colorado River cutthroat trout were introduced on both sides of the Continental Divide (W. Wiltzius, Colorado Division of Wildlife, unpublished data). These authors also concluded that at least one presumptively pure population of Colorado River cutthroat trout in the upper Colorado River

basin may be greenback cutthroat trout, and further sampling has suggested that fish genetically resembling both subspecies are relatively widely distributed in the Colorado River basin (K. Rogers personal communication 2008). Because individuals from both kinds of populations were used in earlier taxonomic assessments, there may be less overlap in morphological and genetic characteristics between subspecies than previously assumed. Consequently, the taxonomic relations among greenback cutthroat trout, Rio Grande cutthroat trout, and the presumptively archaic and recent forms of Colorado River cutthroat trout merit continued investigation. Fully resolving this problem may not be possible, but additional field sampling, complemented by genetic evaluations of historical collections, may address some of the aforementioned issues.

Distribution and abundance

For the purposes of this assessment, I consider the historical range of greenback cutthroat trout to include the colder waters of the South Platte River basin in north-central Colorado and southeastern Wyoming and the Arkansas River basin in central Colorado from the Huerfano River basin north (but not including the Cucharas River basin [Behnke 1979]; **Figure 2**). As noted earlier, this distribution probably resulted from the arrival and spread of a cutthroat trout from the Great Basin via ancient major river connections or relatively contemporaneous headwater transfers (Minckley et al. 1986, Smith et al. 2002).

Regardless of the uncertainties associated with the historical range of greenback cutthroat trout, subsequent climatic and geological events within this region further delimited their range. The last glacial maximum in the Rocky Mountains was about 29,000 to 23,000 years ago with rapid recession of these glaciers 18,000 to 17,000 years ago throughout the central and southern Rockies (Menounos and Reasoner 1997, Licciardi et al. 2004, Pierce 2004, Benson et al. 2005). Thereafter, a modest glacial advance 13,000 to 11,000 years ago during the Younger Dryas period formed and filled additional glacial cirques in the mountains of Colorado and Wyoming (Menounos and Reasoner 1997, Licciardi et al. 2004, Pierce 2004). During cold periods, large valley glaciers 200 to 450 m thick were common in the higher mountain ranges in Colorado, and their lower termini often extended downslope to elevations of 2,200 to 2,700 m (Madole 1976, Madole et al. 1998). The snowline was also 600 to 1,000 m lower than at present, and portions of southern Wyoming, such as at or near the present locations of Laramie and Cheyenne, were subject to permafrost (Mears 1987, 2001; Whitlock

et al. 2002). Average summer temperatures may also have been 10 to 15 °C below those presently observed (Mears 1987, Pierce 2004). These glacial periods would have prevented fish from occupying nearly all high-elevation lakes and headwater streams, and displaced them downstream into larger, warmer waters. The ensuing warming and melting—in which mean annual temperatures may have risen 7 to 10 °C in less than 20 years (Whitlock et al. 2002)—marked the end of transbasin movements via stream capture, but it also permitted reoccupation of streams that were previously too cold for successful recruitment. Nevertheless, the glacial legacy of steep channels and hanging valleys limited later colonization of many of these sites, as did two additional processes. First, mountain landscapes have been undergoing isostatic rebound in response to the declining mass of ice (a process which can be surprisingly swift; Watts 2001, Clague and James 2002), with different faults rising at different rates (Hetzel and Hampel 2006) producing nickpoints in stream profiles. Second, streams have been differentially downcutting through resistant and nonresistant rock in response to reduced sediment availability since deglaciation. Together, these processes are likely to have produced many of the geological barriers to fish movement that are currently present as well as isolating some extant indigenous populations (for comparable examples with other salmonids, see Berg 1985, Castric et al. 2001).

Processes over shorter timescales have also altered the distribution of greenback cutthroat trout. Climate cycles at intervals of decades to centuries, exemplified by the El Niño/Southern Oscillation and the Pacific Decadal Oscillation and driven in part by irregularities in the earth's orbit around the sun (Mantua et al. 1997, Whitlock et al. 2002, Hessburg et al. 2005), have probably led to repeated extinctions, but headwater refugia during droughts and main-stem river or low-elevation lake refugia during wetter periods facilitated recolonization of accessible waters. Similarly, fire-related debris flows or storm-related mass failures may have eliminated or isolated some populations of greenback cutthroat trout, and barrier failure and fish migration may have restored this subspecies to some waters. Consequently, the historical range noted earlier represents a snapshot in time of the complex interplay between climate, geology, and disturbance, and the evolutionary history, demographic resilience, and dispersal ability of greenback cutthroat trout.

The majority of suitable habitats within modern times have included headwater tributaries, larger streams, and portions of main-stem rivers. Glacial advances and retreats probably rendered all but a

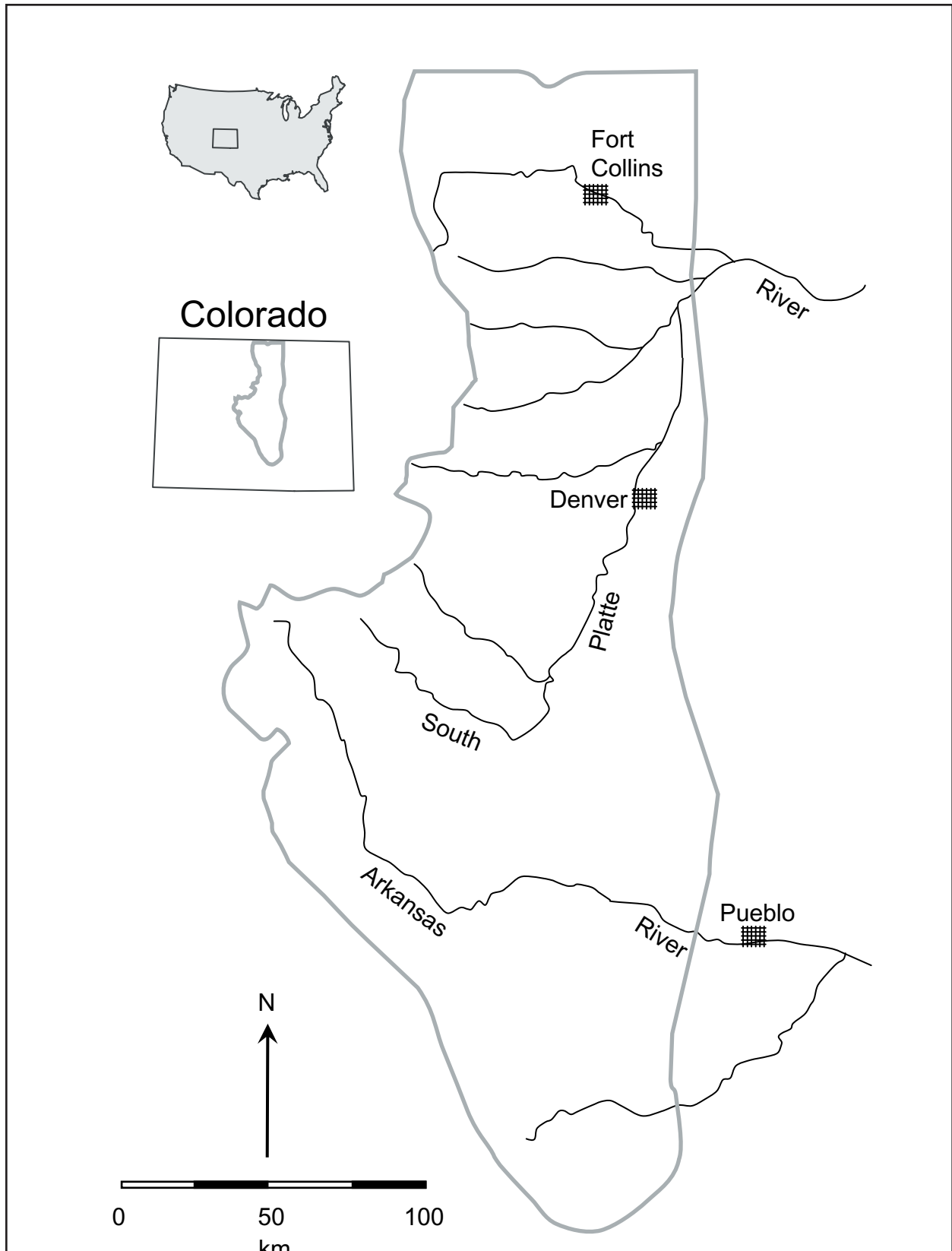


Figure 2. The putative historical range of greenback cutthroat trout in Colorado east of the Continental Divide circa 1850.

few lakes, e.g., Twin Lakes in the Arkansas River headwaters, inhospitable or inaccessible to greenback cutthroat trout (cf. Bahls 1992, Bowman et al. 2002). Their current presence in most lakes is a result of fish stocking over the last four decades (Young et al. 2002). In addition, nearly all presumably indigenous populations are found only in high-elevation basins protected by natural barriers to fish movement, which may indicate that these populations were translocated to these sites (Young and Harig 2001).

The loss and anthropogenic transfer of populations began long before the range of this species was described, so our knowledge of historically occupied locations is at best approximate. Based on the assumption that the downstream limit of greenback cutthroat trout extended to the foothills (e.g., it was common in the South Platte River near Denver and present as far downstream as the mouth of the Cache la Poudre River in the vicinity of Greeley; Wiltzius 1985), Young and Harig (2001) estimated that greenback cutthroat trout may have occupied up to 6,276 km of streams in the Arkansas River basin and 6,955 km of streams in the South Platte River basin at elevations above 1,800 m. A more recent tally—10,416 km overall—attempted to account for streams with physical barriers or cold summer water temperatures (B. Rosenlund personal communication 2007). Nevertheless, it is evident that the distribution of greenback cutthroat trout has dramatically contracted since the mid-1800s, particularly from lower-elevation sites. In addition, portions of main-stem rivers that are currently regarded as uninhabitable by trout because of high turbidity or warm summer temperatures may have been used seasonally or for overwintering (cf. Clapp et al. 1990), particularly in those basins in which modern land uses have contributed to habitat degradation. Finally, it is also likely that there were latitudinal clines in the downstream distribution of greenback cutthroat trout related to water temperature (Dunham et al. 1999).

Population trend

Concurrent with the decline in distribution was the loss in the number and size of populations. The declines followed the arrival of large numbers of Euro American settlers and resulted from extensive mining pollution (Ubbelohde et al. 1976), stream dewatering for agriculture (Jordan 1891), and harvest for commercial sale (Wiltzius 1985). Perhaps as important was the widespread introduction of nonnative trout species that had begun as early as 1872 (Wiltzius 1985). Although greenback cutthroat trout were purportedly

still present in many tributaries to the Arkansas River in 1919 (Carhart 1950), one authority regarded them as extinct throughout their historical range within the next two decades (Green 1937). By 1970, however, a few kilometers of two small streams were thought to contain genetically pure representatives of this taxon, and recovery efforts began in earnest with its listing under the Endangered Species Act.

Young et al. (2002) provided a comprehensive review of the characteristics of the 68 waters included as part of recovery efforts from 1957 to 1999. Habitats consisted of 170 km of 39 streams and 148 ha of 29 lakes, the bulk of which were at relatively high elevations (mean elevation of the downstream bound of fluvial populations, 2,783 m; mean lake elevation, 3,158 m). The vast majority of populations are found on USFS lands, but many in the South Platte River basin are in Rocky Mountain National Park. Not all attempts at recovery were successful because some habitats were unsuitable, chemical treatments sometimes failed to remove all nonnative trout, artificial barriers occasionally collapsed or were passed by nonnative species, or anglers transported nonnative fish above barriers (Harig et al. 2000). See Young et al. (2002) for further details on these populations, such as their year of origin or discovery; sampling dates and fish density or catch-per-unit-effort; the results of genetic analyses; the dates of chemical treatments; the presence of fish migration barriers; and the source, spawning history, and distribution of broodstocks used to found or supplement populations. Note that these details are subject to change pending the release of the status assessment (B. Rosenlund personal communication 2007).

Until recently, greenback cutthroat trout were believed to occupy 58 to 72 streams and lakes, 23 of which met criteria for populations to count toward delisting (Colorado Division of Wildlife and U.S. Fish and Wildlife Service, unpublished data). Unfortunately, many historical populations may be Colorado River cutthroat trout (Metcalf et al. 2007), and these fish were often mixed with greenback cutthroat trout to develop the broodstocks used to establish populations under the recovery program (Young et al. 2002). In addition, the absence of this subspecies from rivers and most larger streams with apparently suitable habitat implies that the average size of populations has decreased from historical norms. For example, Young et al. (2005) observed that a doubling in occupied stream length equated to a doubling of the square root of abundance of greenback cutthroat trout and Colorado River cutthroat trout.

Activity patterns and movements

The last two decades have seen a paradigmatic shift in our beliefs about movement of salmonids in streams. Previously, most stream fishes, among them cutthroat trout, were believed to complete their entire life cycle in short stream reaches or in just a single pool (Funk 1957, Miller 1957, Gerking 1959). This conclusion, however, was partly a result of the methodology used to study movement. Typically, these studies relied on sampling and marking fish annually within the same relatively short reaches. When resampled, the majority of marked fish that were recovered were found in the same location in which they had been marked, which led investigators to conclude that most stream fish did not move long distances. However, a very small proportion of the marked fish were generally recaptured, and sample reaches usually represented a tiny fraction of all available habitat (Gowan et al. 1994, Albanese et al. 2003). With the advent of radiotelemetry (Clapp et al. 1990), simple two-way traps (Gowan and Fausch 1996), individually recognizable tags (e.g., passive integrated transponder tags; Braennaes et al. 1994), sophisticated genetic techniques (Neville et al. 2006b), and elemental analyses of bony structures (Rieman et al. 1994), researchers have begun to portray a more comprehensive picture of the role of movement in the life histories of stream fishes. Several of these studies have examined cutthroat trout, but few have been specific to greenback cutthroat trout. The inferences below are drawn from studies of the movements of several salmonid species, and they are believed to represent those historically or currently undertaken by greenback cutthroat trout.

Territoriality

As do many salmonids, cutthroat trout often become territorial and defend a foraging space from competitively subordinate (usually smaller) fish (Nakano et al. 1998, Gowan and Fausch 2002). Within territorially structured populations, dominant individuals occupy the most bioenergetically favorable positions, such as the head of a pool, with subordinate fish likely to be downstream and to either side in less optimal sites (Lewynsky 1986, Hughes 1992). Such structuring might be regarded as antithetical to notions of mobility, but territory size is plastic and compresses when food is abundant (Chapman 1966). Furthermore, dominant individuals may occupy particular sites only until bioenergetic demands exceed available resources; they then move in search of new sites offering greater returns (Gowan and Fausch 2002, Gowan 2007). Conversely, when resources are less predictable in time and space (e.g., the punctuated streamside inputs

of terrestrial macroinvertebrates), different positions are bioenergetically equivalent (e.g., locations within beaver ponds), or food can be rapidly depleted (e.g., forage fish), territoriality may break down completely with fish forming less spatially stable dominance hierarchies or adopting individual “floater” strategies. Territorial dominance, subordination, and floating may exist simultaneously among different individuals in a single system (Nielsen 1992). Territoriality may also dissolve when fish occupy positions for reasons other than foraging, as in the winter aggregations of cutthroat trout in pools (Jakober et al. 1998).

Diel movements

Studies of movement patterns of cutthroat trout at short temporal scales of hours to a day are rare, and the results may be more of a reflection of the seasons and habitats evaluated than of the actual diversity in movement over this interval. Young et al. (1997a) examined the hourly positions of Colorado River cutthroat trout for six, 24-h cycles from mid-July to late August in the North Fork Little Snake River in Wyoming. They found that median distances traveled during the diel cycle varied from 27 to 90 m and declined over the summer, whereas home ranges were smaller (median <27 m) and did not show a statistically significant decline with time. The study also revealed that Colorado River cutthroat trout were most active during the day, less so during crepuscular periods, and largely inactive at night, although changes in position were unrelated to time of day. Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) had comparable summer diel home ranges, with peaks in movement at dawn and dusk (Hilderbrand and Kershner 2000). Schmetterling and Adams (2004) found that subadult westslope cutthroat trout tended to move at night in summer; this has also been reported for other juvenile salmonids during outmigrations (Jonsson and Antonsson 2005). Other trout species, studied in larger systems, have displayed more extensive movements and alternate activity patterns that may, in part, reflect different foraging strategies (e.g., piscivory) (Young et al. 1997b, Young 1999).

Diel movements have also been examined in winter, typically in association with changes in position in the water column rather than location within a stream. During winter, individuals small enough to conceal within the stream substrate will do so during the day, and re-emerge at night (Vore 1993, Bonneau and Scarnecchia 1998). Larger fish sometimes congregate in pools during the day, and move to shallower, moving waters at night (Harvey et al. 1999, Jakober et al.

2000). This diel shift is thought to be in response to an increased vulnerability to diurnal predators caused by a reduction in swimming burst speed at very cold temperatures (Jakober et al. 2000). This behavior is common to many species of salmonids, and it has been observed in summer when water temperatures decline below 10 °C (Hillman et al. 1992, Thurow et al. 2006).

Seasonal movements

Spawning migrations often constitute the most dramatic movements made by salmonids, but movements associated with seasonal changes may also be substantial. Schmetterling and Adams (2004) observed that 14 to 48 percent of westslope cutthroat trout in different segments of a 2nd-order stream moved during a 3-week interval in mid-summer, and the median distance traveled by mobile fish was 91 m. Young (1996) observed that Colorado River cutthroat trout occupied summer home ranges of 11 to 652 m (median, 45 m) in a 3rd-order Wyoming stream and that weekly movement declined as summer progressed (also see Young et al. 1997a, Hilderbrand and Kershner 2000). Fluvial Bonneville cutthroat trout in tributaries of a large basin also occupied summer home ranges under 300 m (Schrunk and Rahel 2004, 2006). Increases in abundance of Colorado River cutthroat trout in two streams as flows declined from July to August also implied that these fish moved during summer (Herger et al. 1996).

Declining temperatures in autumn appear to trigger substantial movements in many populations of cutthroat trout. Fluvial westslope cutthroat trout in tributaries to the Middle Fork Salmon River in September and October moved downstream an average of 91 km by the following February (Zurstadt and Stephan 2004), whereas movements of fish with a resident life history or occupying smaller basins have been shorter (Brown and Mackay 1995b, Jakober et al. 1998, Lindstrom 2003). For example, Brown (1999) observed that about half of the westslope cutthroat trout radio-tagged in August had moved on average 1.0 km as temperatures declined to 3 to 4 °C in late October, and that all fish had moved by late November when temperatures approached 0 °C. Thereafter, many of these fish aggregated in deep pools and ceased further movement; however, some fish again moved a comparable distance apparently after being displaced by anchor ice (also see Lindstrom 2003). In contrast, Colorado River cutthroat trout in the headwaters of the North Fork Little Snake River in Wyoming did not alter their positions during the summer-autumn transition (Young 1998).

Although mid-winter movements in small streams with ice or snow cover tend to be limited (Chisholm et al. 1987, Brown 1999, Hilderbrand and Kershner 2000), movements in larger systems can be substantial. Colyer et al. (2005) reported that fluvial Bonneville cutthroat trout occupied average home ranges of 300 and 1,900 m in two years in a river main stem during winter where warmer water temperatures (2 to 4 °C) may have permitted continued foraging and growth.

Life-history-related movements

Most spawning movements in cutthroat trout are initiated as flows increase in spring or early summer, with the peak often coinciding with annual peak flow (Benson 1960, Bernard and Israelsen 1982, Schmetterling 2001, Zurstadt and Stephan 2004). Adults usually remain for a fairly brief period in the spawning streams (e.g., 2-19 d, Brown and Mackay 1995a; 9-11 d, Magee et al. 1996; 22-52 d, Schmetterling 2001; 17 d, De Rito 2004) before departing back to summer growth sites. The magnitude of pre- and post-spawning migrations greatly varies and probably is dictated by stream connectivity. Young (1996) reported that post-spawning migrations (and by inference, pre-spawning migrations) for small (<250 mm total length) Colorado River cutthroat trout in an isolated 3rd-order stream were up to 1.8 km. Brown and Mackay (1995a) observed that spawning westslope cutthroat trout (median fork length 330 mm) above a fish barrier moved a median of 3.5 km to spawning sites and 2.4 km on return migrations. In contrast, cutthroat trout with unimpeded access to larger waters moved extensively. Westslope cutthroat trout migrated 2 to 72 km up the Blackfoot River on spawning runs (Schmetterling 2001) and Yellowstone cutthroat trout in the Yellowstone River moved 1 to 53 km to tributaries to spawn (Clancy 1988). Large (236-503 mm) Bonneville cutthroat trout with access to the main-stem Bear River or its major tributaries, the Smiths Fork and Thomas Fork, moved 0.5 to 86.0 km (Schrunk and Rahel 2004, Colyer et al. 2005).

Following emergence from spawning substrates, cutthroat trout fry shift to nearby shallow, low-velocity habitats (Moore and Gregory 1988, Bozek and Rahel 1991b). Thereafter, however, the few studies on movements of cutthroat trout fry indicate that they can be quite mobile, particularly the offspring of fluvial or adfluvial forms (Northcote 1992). Benson (1960) noted that in a Yellowstone Lake tributary, fry emerged about 30 days after eggs were deposited and their outmigration to the lake peaked in late July and ended by late October. Nearly 90 percent of all outmigrants were recently emerged fry, and the remainder were age

1 or 2 (also see Gresswell et al. 1994, 1997). Snyder and Tanner (1960) and Drummond (1966) observed comparable patterns for Colorado River cutthroat trout fry in tributaries to Trappers Lake in Colorado; they also noted that these migrations were nocturnal. Recently emerged Bonneville cutthroat trout left their natal stream from August to November to overwinter in a river main stem (Bernard and Israelsen 1982). Not all studies, however, have indicated that fry migrate shortly after emergence. For example, Young and Guenther-Gloss (2004) demonstrated spatial differences in abundance of adult and age-1 greenback cutthroat trout in South Platte River tributaries, which implied that movements of many juveniles were delayed until at least one year after emergence, although the timing of these movements was unknown. Westslope cutthroat trout juveniles reared for up to three years in streams before migrating to main-stem rivers (Schmetterling 2001), a pattern similar to that observed for Colorado River cutthroat trout in tributaries to the North Fork Little Snake River (M.K. Young, unpublished data). Late summer sampling in that basin failed to detect substantial downstream movements of juveniles (Jespersen 1981, M.K. Young, unpublished data), and it is assumed that outmigrations are concomitant with high spring flows.

In summary, it is evident that cutthroat trout life histories are characterized by movements of many life stages in many seasons. The ubiquity of movement probably applied historically to greenback cutthroat trout, and may characterize the behavior of some extant populations. Moreover, it is important to note that lack of movement within a particular season or life history stage is not conclusive evidence of a sedentary life history strategy. Monitoring at annual intervals has demonstrated that fish do not necessarily show high fidelity to positions they have previously occupied. Bjornn and Mallet (1964) marked westslope cutthroat trout along a 120-km reach of the Middle Fork Salmon River from June to October, and resampled this reach annually for three years. Over 65 percent of fish were recaptured over 3 km from where originally found, and over 40 percent were more than 16 km away (also see Zurstadt and Stephan 2004). After a year, nearly 40 percent of marked Bonneville cutthroat trout in a much smaller stream were recaptured 331 to 3,292 m from where initially caught (Hilderbrand and Kershner 2000). Similarly, a 5-year study of Colorado River cutthroat trout in the North Fork Little Snake River basin revealed that at least 40 percent of marked fish occupied new locations in different summers, with between-year changes in location of up to 7.5 km (M.K. Young, unpublished data).

Finally, directionality in movements cannot be assumed. Although cutthroat trout in some large river systems consistently moved downstream after spawning (Bjornn and Mallet 1964, Schrank and Rahel 2004, Zurstadt and Stephan 2004), elsewhere individuals in both small and large basins moved up- or downstream after spawning (Clancy 1988, Brown and Mackay 1995a, Young 1996, Hilderbrand and Kershner 2000, Schmetterling 2001) and during fall and winter (Brown and Mackay 1995b, Brown 1999, Lindstrom 2003).

Habitat

Greenback cutthroat trout have occupied relatively steep, coldwater streams and rivers and accessible high-mountain lakes in the South Platte and Arkansas river basins for millennia. Their habitat use resembles that of other salmonid fishes in mountain environments, and probably reflects a shared evolutionary history. Some aspects of habitat use (e.g., spawning habitat and juvenile habitat) have been addressed elsewhere in this document; the following discussion highlights a few additional elements of this well-studied subject.

Temperature

Cutthroat trout, like all salmonids, are ectothermic; water temperature drives many physiological processes and thus dictates the suitability of habitats. Although it is well known that trout mortality can be severe at very high water temperatures, the designation of biologically meaningful temperature maxima has varied depending on the method used. For example, using constant temperatures, Bear (2005) found that 50 percent of westslope cutthroat trout had died after 60 days at 19.6 °C. Johnstone and Rahel (2003) used laboratory experiments to identify 24.2 °C as the 7-day upper incipient lethal temperature for Bonneville cutthroat trout when temperatures were held constant, and noted that environments cycling between 16 and 26 °C were not fatal but induced sublethal effects. These effects include a decline or halt in feeding and growth and appearance of heat stress proteins at temperatures above 22 to 24 °C (Dickerson and Vinyard 1999, Meeuwig et al. 2004). Nonetheless, field observations indicate that cutthroat trout occupy waters that temporarily exceed these thresholds. Schrank et al. (2003) reported that Bonneville cutthroat trout apparently experienced maximum daily temperatures of 27 °C in a western Wyoming stream, and these fish neither died nor moved. They regarded the relatively short period that temperatures remained this warm, as well as the large diel fluctuations in temperature, as mitigating possible lethal effects (also see Dunham et al. 2003a).

Many populations of cutthroat trout are exposed to very cold water temperatures (near 0 °C) during winter. This does not represent a substantial physiological challenge for most age-1 and older fish, but that is not the case for fry that emerged during the previous growing season (Cunjak and Power 1987). It is the average summer temperature, however, that dictates the risk of winter mortality through its effects on the duration of incubation and period of post-emergence growth. If cutthroat trout fry have not grown sufficiently in the interval between emergence and the onset of cold winter temperatures (<4.0 °C), mortality rates are generally high (Coleman and Fausch 2007a) and may be related to recruitment failures observed in several streams (Harig and Fausch 2002, Peterson 2002, Coleman and Fausch 2007b). A similar pattern has been observed for brown trout at high latitudes in Scandinavia (Borgström and Museth 2005). For Colorado streams, the probability of successful establishment of populations of greenback cutthroat trout or Rio Grande cutthroat trout was predicted in part by mean July water temperature, with successes associated with streams above 7.1 °C (Harig and Fausch 2002). Additional field and laboratory studies confirm that this summer temperature threshold is between 7.0 and 8.5 °C, or a threshold of about 900 degree-days during the growing season (Coleman and Fausch 2007a,b).

Optimal temperatures for growth fall between these two extremes. Bear (2005) determined that growth rates of westslope cutthroat trout peaked at a constant temperature of 13.6 °C (see Meeuwig et al. 2004 for similar results with Lahontan cutthroat trout). Similarly, the scope for activity, a measure of the oxygen physiologically available to an individual fish, peaked near 15 °C (Dwyer and Kramer 1975). These laboratory studies of individual growth and survival, however, require field validation, and can be informed by an appreciation of the population-scale effects of water temperature. For example, westslope cutthroat trout tended to occupy tributaries to the Madison River in Montana that had average summer temperatures below 12 °C and maximum average summer temperatures below 16 °C (Sloat et al. 2002). Similarly, Isaak and Hubert (2004) found that abundance of trout, including cutthroat trout, in the Salt River basin of western Wyoming and eastern Idaho peaked at mean summer water temperatures of 12 °C and declined at warmer or cooler temperatures. While this dome-shaped pattern probably applies in general to greenback cutthroat trout, optimal temperatures may vary with other habitat conditions.

Channel units and structure

The importance of pools to salmonids has long been recognized, and cutthroat trout are not exceptional in this regard; they disproportionately used pools relative to riffles during summer observations (Young 1996, Young et al. 1997a). As daytime foraging sites, the heads of pools usually provide the greatest energetic returns at the least cost in small to medium-sized streams (Hughes 1992, Gowan and Fausch 2002) because macroinvertebrate production in upstream riffles is often high and has not been cropped by other fish, and the reduced velocity in pools requires less energy for fish to maintain position. It should be noted, however, that adult cutthroat trout do not solely occupy pools. Adult Colorado River cutthroat trout were found to move through up to five habitat units over a single 24-hour period in summer, and activity patterns suggested that they were feeding in all habitats (Young et al. 1997a). Furthermore, when introduced into long reaches of a fairly large stream from which all dominant competitors had been removed, individual Colorado River cutthroat trout disproportionately, but not exclusively, chose to inhabit pools (Young et al. 1998). Many occupied sites within riffles provided pool-like habitats (M.K. Young, personal observation), suggesting that the scale at which cutthroat trout select habitats could decouple the perceived relation between pools and fish abundance (see Spatial patterns and temporal dynamics, below).

In mid-winter, deep pools or those with surface ice are oft-used habitats, as are beaver ponds or portions of streams receiving warmer groundwater (Chisholm et al. 1987, Brown and Mackay 1995b, Jakober et al. 1998, Lindstrom 2003). These habitats minimize bioenergetic expenditures, provide security from predators during the day, and may be the most stable habitats under varying ice conditions, such as when frazil and anchor ice form during the supercooling of surface water exposed to the sky (Brown 1999). The severity of winter conditions and the need for these habitats can vary with respect to the longitudinal position of fish in a stream. For example, in the Snowy Range in southeastern Wyoming, deep snow above 2900 m prevented ice formation over streams whereas surface ice completely covered them below 2500 m. At intermediate elevations, streams exhibited a mix of snow cover, surface ice, and open water, with the latter periodically influenced by anchor ice; such locations may represent the most extreme winter conditions for salmonids (Chisholm et al. 1987). Similar instability may develop in areas downstream from groundwater sources (Lindstrom 2003).

Channel properties also influence the abundance and production of cutthroat trout. Platts (1979) noted that cutthroat trout appeared to reach their highest densities in 2nd - to 4th -order streams, which afford the habitats most suitable for spawning and juvenile rearing. These sites also may be more productive because of the relatively high allochthonous inputs, such as terrestrial macroinvertebrates and litter, from riparian zones (Vannote et al. 1980, Baxter et al. 2005). Several studies have indicated that there is a minimum threshold in stream size below which cutthroat trout presence is unlikely (Kruse et al. 1997, Dunham et al. 2002b, Harig and Fausch 2002).

In general, cutthroat trout appear to occupy higher-gradient sites than other trout species in many Rocky Mountain streams (Fausch 1989, Bozek and Hubert 1992), and it has been suggested that these represent the most suitable reaches for cutthroat trout (Griffith 1988). More likely, however, is that nonnative trout are largely excluding cutthroat trout from lower-elevation, lower-gradient stream segments, and that the steep, high-elevation habitats are the least suitable for nonnative species or are more likely to contain fish migration barriers, permitting cutthroat trout to persist there (Fausch 1989). A sampling scheme that corrected for the covariation between gradient and elevation revealed that gradient had little effect on trout biomass in Wyoming and Idaho streams (Isaak and Hubert 2000).

Cover and complexity

Cover is thought to represent one of the most fundamental habitat needs of salmonids in streams (despite that the presence of cover reduces the feeding efficiency of cutthroat trout; Wilzbach and Hall 1985, Wilzbach et al. 1986). Its primary role seems to be as a sanctuary from predators (Helfman 1981) although it may also offer shelter from high flows (Harvey 1998, Harvey et al. 1999). Yet because many habitat elements can serve as cover—large wood, overhanging or submerged vegetation, roots of bankside trees and shrubs, beaver dams, rubble and boulders, deep or turbulent water, or undercut banks—it may rarely be limiting in unaltered streams. Perhaps for this reason, Young (1996) found no difference in the proximity to cover of sites used by and available to Colorado River cutthroat trout. More critical may be the hydraulic and physical complexity of channels that generates an array of microsites. Channel complexity has been related to the density of cutthroat trout (Kershner et al. 1997). Although a number of geomorphic elements can influence complexity (e.g., boulders, Warren

and Kraft 2003; streamside vegetation, Kershner et al. 1997), large wood (also known as coarse woody debris) plays a dominant role in many montane streams where greenback cutthroat trout persist. Deposition of large wood affects sediment scour and deposition, energy dissipation, and channel form (Montgomery et al. 2003), and creates pools, stores spawning gravels, affords overhead cover, and provides refuge during high flows (Dolloff and Warren 2003). For Colorado River cutthroat trout in a Wyoming stream, pools formed by large wood were disproportionately occupied relative to other pool types (Young 1996). Removals or additions of large wood have caused declines or increases in local salmonid abundance (Dolloff 1986, Bisson et al. 2003).

Inputs of large wood are controlled by a variety of processes. Mass mortality of riparian stands from fire, insect damage, or wind are important sources (Veblen et al. 1994, Bragg 2000), as well as individual treefall from bank undercutting or self-thinning or pulsed contributions from landslides or debris torrents (Cannon 1999, May and Gresswell 2003, Reeves et al. 2003b). Large wood abundance is characterized by high spatial and temporal variability among and within streams in the Rocky Mountains (Richmond and Fausch 1995, Hauer et al. 1999, Young et al. 2006). It is hypothesized to loosely track forest succession and snag availability, with large wood loads peaking shortly after disturbance and during the old-growth phase (Minshall and Brock 1991, Bragg et al. 2000, Gregory et al. 2003).

Spatial patterns and temporal dynamics

The preceding paragraphs noted an array of habitat features that may be needed to sustain cutthroat trout populations. Although a number of models have been developed that relate habitat to trout abundance in small streams (e.g., Hickman and Raleigh 1982, Clarkson and Wilson 1995), these models often perform poorly, particularly when applied outside the systems for which they were developed (Fausch et al. 1988). Although this flaw is to some degree inherent to habitat models, their imprecision also arises from neglecting the spatial context of habitats, whether within the sampled reaches, between adjacent reaches, or among tributaries within a basin (Fausch et al. 2002). Dunning et al. (1992) introduced four concepts useful in evaluating how the abundance and distribution of habitats affects population size and persistence: habitat complementation, habitat supplementation, source-sink structure, and neighborhood effects. Habitat complementation refers to the spatial distribution of essential habitats that are not substitutable (e.g., spawning gravels, foraging sites, and overwintering refuges). Habitat supplementation

deals with substitutable habitats, such as a feeding site for obtaining drift and a feeding site for exploiting terrestrial infauna. Source-sink structure refers to the demographic support provided by those areas that produce a surplus of individuals to areas in which populations may not be sustainable. Neighborhood effects involve how adjacent habitats affect local abundance and how permeable habitat boundaries are to movement of individuals. Schlosser (1991, 1995) recognized the interaction between fish movement and each of these elements. For example, a basin with high habitat complementarity could support fish populations with low movement rates and no evident population sources or sinks, whereas a basin with suitable spawning gravels in only one segment or stream and little complexity has low habitat complementarity that forces fish to migrate to reproduce and has a strong source-sink structure. Schlosser and Angermeier (1995; also see Schlosser 1998, Schlosser and Kallemyn 2000) further explore these and related concepts with respect to fish populations.

How small- to large-scale patterns in habitat distribution and abundance affect populations of cutthroat trout, or most other salmonids, has not been fully explored. Nevertheless, Fausch et al. (2002) described some promising avenues for investigation, and a few studies suggest the importance of habitat complementarity and supplementarity, source-sink structure, and neighborhood effects to cutthroat trout. For example, Dunham et al. (1997, 2002b) concluded that the probability of presence of Lahontan cutthroat trout was related to the size of habitat patches and whether other waters to which they were connected also contained populations. Torgersen et al. (2004) found periodicity in the distribution of cutthroat trout at three spatial scales that were related to characteristics of the streams and basins, and Ganio et al. (2005) noted how this varied among streams. Large Bonneville cutthroat trout migrated from spawning sites in small tributaries and the presumably warmer and more productive feeding grounds where they overwintered (Colyer et al. 2005). Young and Guenther-Gloss (2004) found that longitudinal patterns in abundance of adult greenback cutthroat trout differed from those of juveniles in headwater streams, and that neither displayed consistent downstream-upstream trends. Putative nursery areas for Colorado River cutthroat trout (Bozek and Rahel 1991b) were not related to the abundance or distribution of suitable rearing habitat; instead, they were associated with reaches containing spawning gravels. Finally, Young et al. (2005) observed that the square root of abundance of Colorado River cutthroat trout and greenback cutthroat trout increased in proportion to

stream length and that this variable accounted for about 80 percent of the variation in abundance. They also showed that measures of individual habitat components were not strongly related to abundance, and concluded that larger streams may support disproportionately large populations because they provide a greater diversity of habitats (or higher complementarity) than do smaller streams. There is also a rapidly growing literature on predicting fish species occurrence or abundance based on landscape-scale habitat patterns (e.g., Angermeier et al. 2002, Olden and Jackson 2002, Feist et al. 2003, Peterson and Dunham 2003) that is likely to prove useful in understanding the relation between habitat abundance and distribution and cutthroat trout population size.

The importance of riparian zone structure to fish populations is also beginning to be acknowledged. Schlosser (1991) pointed out the importance of nutrient exchange between riparian zones and stream channels, highlighting the terrestrial contributions of leaf matter to secondary productivity in streams. More recently, the two-way trophic linkages between streams and their riparian zones have been recognized (Baxter et al. 2005), and the effects of riparian vegetation composition and disturbance on fish community composition are being explored. Little has been done with inland cutthroat trout in this regard, but there can be strong effects of riparian zone vegetation and structure on aquatic macroinvertebrate production, terrestrial macroinvertebrate infauna, and fish abundance (Molles 1982, Snyder et al. 2002, Allan et al. 2003, Kawaguchi et al. 2003, Perry et al. 2003). The apparent response of cutthroat trout to small-scale changes in primary productivity and light associated with forest openings (Wilzbach 1985, Wilzbach et al. 2005) and the variation in diet correlated with different riparian vegetation types (Romero et al. 2005) imply that riparian zone structure may account for some of the spatial variation in cutthroat trout abundance.

An additional perspective that is key to understanding the size and distribution of cutthroat trout populations is that habitats are dynamic and respond to processes recurring at daily, seasonal, annual, and multi-decadal intervals. In particular, disturbances that dramatically alter channels or riparian zones—debris torrents, landslides, extreme floods, and severe fires—will change the discharge-sediment transport regime, re-set forest succession and large wood dynamics, and redistribute suitable and unsuitable habitat in a basin, sometimes for decades or centuries (Reeves et al. 1995, Benda et al. 1998). These rare events, and the locations of refugia from them, can dictate the size, structure, distribution, and persistence

of fish populations (Schlosser and Angermeier 1995, Labbe and Fausch 2000).

Diet

Cutthroat trout are sight-feeding predators that consume zooplankton, aquatic and terrestrial macroinvertebrates, and occasionally fish or other small vertebrates. Because maximum prey size in salmonids is constrained by gape width, fry may consume very small prey that are not bioenergetically worthwhile to larger fish (Bozek et al. 1994). Nevertheless, the small average size of most invertebrates results in substantial overlap in the sizes of items consumed by juvenile and older age classes. The high taxonomic overlap between prey and drifting macroinvertebrates indicates that cutthroat trout are opportunistic foragers (Young et al. 1997a, McGrath 2004). Nevertheless, they also exhibit a certain degree of prey selectivity, particularly for terrestrial macroinvertebrates during summer (Young et al. 1997a, Hilderbrand and Kershner 2004), which can constitute a third to a half of the annual energy intake of salmonids in small streams (Allan et al. 2003, Baxter et al. 2005, Romero et al. 2005). There is little incidence of piscivory among populations of fish with resident life histories in small streams (Bozek et al. 1994, Dunham et al. 2000, Hilderbrand and Kershner 2004, McGrath 2004). Keeley and Grant (2001) attributed this to the general absence of forage fish and suggested that the growth of trout would decline or cease once they reached 15 to 20 cm, which is reasonably concordant with observations of cutthroat trout found in such environments (Downs et al. 1997, Hilderbrand and Kershner 2004, Young and Guenther-Gloss 2004). Piscivory may be more typical of cutthroat trout in or originating from larger streams, rivers, and lakes. For example, predation by large Bonneville cutthroat trout in Strawberry Reservoir, Utah, reduced overwinter survival of stocked cutthroat trout fingerlings to 1 percent (Baldwin et al. 2000). Similarly, predation on fry by adult greenback trout may have limited recruitment in Zimmerman Lake, Colorado (D.A. Winkelmann, Colorado State University, unpublished data). Also, Snyder and Tanner (1960) reported that adult Colorado River cutthroat trout still present in spawning streams contained an average of 61 fry during the late summer outmigration of juvenile fish to Trappers Lake (cf. Benson 1960).

Behnke (1992) argued that adult habitat was most often limiting in fluvial trout populations, yet the substantial influence of food availability on trout growth, density, and behavior has long been recognized (Chapman 1966). In small exclosures within streams, the addition of food markedly increased growth of

age-1 cutthroat trout relative to fish not receiving supplemental food, whereas additions of cover had no effect (Boss and Richardson 2002; also see Wilzbach 1985). Direct or indirect additions of food had similar effects on other small-stream salmonids (e.g., Warren et al. 1964, Mason 1976), and with the plethora of recent papers on links between stream productivity and allochthonous inputs, such as salmon carcasses (Wipfli et al. 2004) or particular forms of riparian vegetation (Baxter et al. 2005), there is substantial evidence that food availability is dynamic at decadal and successional scales and has a large role in structuring cutthroat trout populations (Dunham and Vinyard 1997, Railsback and Harvey 2002, Young and Guenther-Gloss 2004).

Spawning

With few exceptions (Carl and Stelfox 1989), cutthroat trout spawn in lotic environments. Although they generally choose small, perennial streams (Clancy 1988, Magee et al. 1996), they sometimes use springbrooks in the river floodplain (Joyce and Hubert 2004), alluvial side channels of main-stem rivers (Henderson et al. 2000, De Rito 2004), or even intermittent channels that remain flowing until fry have emerged (Gresswell et al. 1997). Spawning may begin as early as April and conclude as late as July in response to elevational gradients in flow and temperature (Benson 1960, Snyder and Tanner 1960, Quinlan 1980, Brown and Mackay 1995a, Schmetterling 2001, Zurstadt and Stephan 2004). This species tends to spawn during or after snowmelt-driven peaks in discharge (Quinlan 1980, Jespersen 1981, Thurow and King 1994, Schmetterling 2000, 2001, De Rito 2004), which probably evolved as a mechanism to avoid egg and fry incubation during channel-scouring flows. With regard to temperature, Thurow and King (1994) and Magee et al. (1996) observed that spawning began after mean daily temperatures exceeded 7 to 10 °C, but Quinlan (1980) found that spawning in high-elevation tributaries in southern Wyoming began when maximum daily temperatures reached these levels.

The length of incubation and time to fry emergence also varies with temperature. Snyder and Tanner (1960) reported that Colorado River cutthroat trout eggs hatched after 30 days at 10 °C, with each 0.6 °C decline corresponding to a 2-day increase in this period. Similarly, Yellowstone cutthroat trout eggs hatched 25 to 49 days after deposition when the sum of mean daily temperatures reached 278 to 365 °C (Gresswell et al. 1994). Time to emergence after spawning was 570 to 600 degree-days for Colorado River cutthroat trout (Coleman and Fausch 2007a). Because greenback

cutthroat trout in many high-elevation streams do not appear to conclude spawning until early July, fry emergence is often in late August through early October (Young 1995, Coleman and Fausch 2007b).

Cutthroat trout are assumed to home to natal streams for reproduction, as do most anadromous salmonids (Quinn 2005a), but there is little information on this. Gresswell et al. (1994) reported that less than 5 percent of migrating Yellowstone cutthroat trout that ascended Yellowstone Lake tributaries to spawn had strayed. Schmetterling (2001) noted that westslope cutthroat trout that spawned in consecutive years used the same tributary in each year, but not the same location. Why salmonids stray or home has received less attention, but the preponderance of evidence implies that the selective advantage of local adaptation disproportionately favors homing, whereas temporal variation in habitat quality, such as from floods or drought, seems to be related to straying (Hendry et al. 2004).

The characteristics of sites chosen for spawning, known as redds, have been the focus of many studies. Females deposit eggs from 10 to 25 cm deep in spawning gravels (Snyder and Tanner 1960, Young et al. 1989), and burial depths are related to female size (Crisp and Carling 1989). Substrates chosen for egg deposition contain particles ranging from much less than 1 mm up to 100 mm, with a median diameter frequently between 10 and 30 mm (Thurrow and King 1994, Schmetterling 2000). Kondolf and Wolman (1993) concluded that females could use substrates with median particle sizes of about 10 percent of fish length, but sizes actually used were constrained by what was available. Substrate composition, particularly the proportion of fine particles, has been shown to be related to the survival from egg deposition to fry emergence (Chapman 1988). Young et al. (1991) confirmed this in laboratory studies of Colorado River cutthroat trout, but demonstrated that measures of the central tendency of substrate composition accounted for a greater proportion of the variation in survival to emergence than did measures of fine sediment alone. Other common characteristics of redds include water velocities of 0.4 to 0.6 m per s and depths of 10 to 20 cm (Thurrow and King 1994, Schmetterling 2000).

Locations with suitable velocity, depth, and substrate for spawning can be found in channels of many different configurations and created by a variety of channel features and lithologies (Bozek and Rahel 1991b, Kondolf and Wolman 1993, Magee et al. 1996). Kondolf et al. (1991) observed that in reaches

with gradients averaging 7 to 17 percent, salmonid spawning areas were in sites near obstructions such as boulders or log jams that reduced local gradients to 0.4 to 3.6 percent. Many greenback cutthroat trout redds in small streams are associated with the shallow tails of pools where channel shape favors downwelling and deposition of appropriate-sized substrate (M.K. Young, personal observation). Although Magee et al. (1996) could not relate reach-scale variables to spawning gravel availability, Buffington et al. (2004) noted that channel roughness was related to the availability of spawning gravels, with steeper channels requiring bar formation or obstructions such as large wood to promote gravel storage. Low-gradient alluvial valleys also promote groundwater-surface water exchange that salmonids may favor for spawning (Baxter and Hauer 2000).

Demography

Life history characteristics

A life history is defined as the repertoire of actions an animal performs to complete its life cycle and enhance its fitness (Stearns 1992); it can include any phenotypic or behavioral variation that contributes to demographic and evolutionary success. Some of these characteristics have been previously discussed (see Activity patterns and movements, above) and can influence the viability of populations. The following discussion focuses on those aspects most directly related to population demography. Salmonids in general (Willson 1997) and cutthroat trout in particular (Gresswell et al. 1994, Waples et al. 2001) exhibit some of the most striking life history variation among fishes. Unfortunately, studies of this variation do not exist for many populations of cutthroat trout, and are essentially absent from the literature on subspecies from the central and southern Rocky Mountains. Consequently, most inferences are based on data from other taxa and should be regarded as tentative.

Within a particular population, sexual maturity of cutthroat trout is more closely related to length than to age. Several studies have indicated that males will mature at shorter lengths and younger ages than females (McIntyre and Rieman 1995, Meyer et al. 2003). Downs et al. (1997) determined that for westslope cutthroat trout in headwater streams, 50 percent of males had reached maturity at 135 mm fork length (range, 110-160 mm) and 50 percent of females were mature at 157 mm fork length (range, 150-180 mm). Males began maturing at age 2, and all were mature by age 4; whereas females began maturing at age 3, but not all were mature until age 6. Similarly, Quinlan (1980) reported that on

average Colorado River cutthroat trout from a cold southern Wyoming stream reached maturity at 146 mm total length. The age at which cutthroat trout will reach maturity is largely determined by the productivity and temperature of a stream. For example, the mean length of age-1 fish (56 mm) in a high-elevation stream was much less than that of the mean lengths of age-1 fish (77 and 128 mm) in two mid-elevation streams in Colorado (Peterson et al. 2004a). Finally, the maximum age of cutthroat trout varies. The oldest fish observed by Downs et al. (1997) was age 8, but at least one fluvial individual in a largely unexploited population reached age 11, and 7 percent of marked fish were at least age 7 (Fraley and Shepard 2005).

The fecundity of female salmonids is related to their length, which usually accounts for about half of the variation in egg number (e.g., Downs et al. 1997). Because the majority of greenback cutthroat trout populations are found in small, high-elevation streams with short growing seasons, fish larger than 250 mm are often rare (Jespersen 1981, Scarnecchia and Bergersen 1986, Young et al. 2005) and egg numbers are relatively low. In a small sample of Colorado River cutthroat trout, Quinlan (1980) reported that fecundity ranged from 95 to 281 eggs for females from 149 to 210 mm in a high-elevation Wyoming watershed. In comparable environments, westslope cutthroat trout females between 150 and 175 mm fork length produced 166 to 264 eggs, those from 175 to 199 mm produced 198 to 553 eggs, and those from 200 to about 250 mm produced 224 to 664 eggs (Downs et al. 1997). Cutthroat trout with fluvial or adfluvial life histories typically attain greater sizes and produce more eggs (Gresswell 1995, McIntyre and Rieman 1995, Meyer et al. 2003). For example, female Colorado River cutthroat trout from Trappers Lake, Colorado, averaged 290 mm and contained a mean of 667 eggs (Snyder and Tanner 1960). These length-fecundity relations should be regarded as representative rather than predictive because they are often species- and site-specific (Gresswell et al. 1994, Downs et al. 1997).

Spawning is bioenergetically demanding, and energy consumption and weight loss by spawning trout is often high. Males expend much of this energy during competition with other males for access to females, females invest it in egg production, and mobile forms of both sexes engage in energetically costly spawning migrations (Jonsson et al. 1991). Consequently, post-spawning mortality of cutthroat trout can be high (13 to 89 percent; Gresswell et al. 1994, 1997, Vinyard and Winzeler 2000, Schmetterling 2001). Furthermore, because food availability and the growing season are

often limited in headwater populations, female cutthroat trout there may only be able to accumulate enough energy to spawn in alternate years. Willson (1997) suggested that this was a typical pattern for female salmonids, but there is substantial variability among different populations of cutthroat trout. Schmetterling (2001) noted that less than half of a group of radio-tagged fluvial westslope cutthroat trout spawned in consecutive years (also see Shepard et al. 1984, De Rito 2004). Similarly, Snyder and Tanner (1960) estimated that about 16 percent of Colorado River cutthroat trout in Trappers Lake spawned in consecutive years, but they could not account for fish that strayed to other streams or died in the interim. In contrast, the frequency of spawning varied by tributary and year for Yellowstone cutthroat trout from Yellowstone Lake (Gresswell et al. 1994).

Sex ratios of mature fish have been variously estimated as favoring females or males, but this probably reflects the life history being sampled and the sampling approach. Surveys of fish during migratory runs e.g., at weirs near stream mouths, often suggest that females outnumber males (Snyder and Tanner 1960, Gresswell et al. 1994), whereas surveys of fish on spawning grounds imply the reverse (Downs et al. 1997). This pattern might obtain because the tradeoffs between increased fecundity, bioenergetic costs, and predation risk are more favorable for migratory females. Males can mature at small sizes and adopt alternative mating tactics that might be as successful as those of large males that defend females (Jonsson et al. 2001). That males can mature at smaller sizes even in resident populations implies that the adult sex ratio in general may be male-biased.

Population structure: survival rates and temporal patterns

Spatial variation among size classes or density related to habitat within a stream was discussed earlier (see Spatial patterns and temporal dynamics, above). In addition, the among-stream variation in survival rates and age structures is high and appears to be environmentally mediated. For example, annual survival rates of adult Colorado River cutthroat trout in high-elevation streams (0.53-0.57) were substantially greater than those of adults in mid-elevation Colorado streams (0.35-0.37) (Peterson et al. 2004a). These populations also differed with respect to the presence of younger age classes, which were absent in the high-elevation systems. Greenback cutthroat trout populations exhibited similar variation in size structure and probably survival because the coldest

streams tended to have populations with relatively few individuals in the youngest age classes and the largest proportion of adult fish exceeding 200 mm, whereas warmer streams often contained populations with higher densities, a large proportion of the population consisting of younger individuals, and relatively few large adults (Young and Guenther-Gloss 2004). These results imply that in colder, higher-elevation systems, populations may be sustained by occasional reproductive bonanzas and the stockpiling of slow-growing but long-lived adults (cf. Kennedy et al. 2003), whereas in warmer, lower-elevation streams, year class failure may be relatively rare, density dependence among cohorts may be strong, and adult survival may be reduced (cf. Lobón-Cerviá 2005).

A number of studies have demonstrated that fluctuations in the size of salmonid populations can sometimes be extraordinary (Platts and Nelson 1988, House 1995), but sampling a limited number of reaches of individual streams at different times during different years probably exaggerated this pattern (Decker and Erman 1992). Nonetheless, assessments partitioning the spatiotemporal variance in salmonid population size have found the temporal component to be substantial (Wiley et al. 1997, Dunham et al. 2002b, M.K. Young, unpublished data) and sometimes to be more important than spatial factors (Isaak and Thurow 2006). The spatial extent of synchrony in such fluctuations has not been comprehensively evaluated, but Young (unpublished data) found a strong positive correlation in the changes in abundance of Colorado River cutthroat trout among 14 stream segments in the North Fork Little Snake River basin over four years. Other evaluations of salmonids have detected synchrony among populations up to 30 to 50 km apart (Rieman and McIntyre 1996, Myers et al. 1997, Lobón-Cerviá 2004), but the geographic extent of events affecting fish survival will dictate this scale. For example, a severe fire would depress at most a few adjacent populations, whereas effects of climate-driven changes could extend across river basins or the entire historical range. Finally, the degree of synchrony may be related to the status of populations. Isaak et al. (2003) found that synchrony among individual Chinook salmon (*Oncorhynchus tshawytscha*) populations increased as these populations underwent a regional decline, heightening the risk of simultaneous extirpation of many populations.

Population models

Population viability models are often developed to identify those life history parameters (or vital rates) that have the greatest influence on population growth

and persistence, and to simulate how variation in those parameters changes model predictions of the deterministic population growth rate or the distribution of times to extinction. There is a lively discussion in the literature on the value of such models. Their detractors contend that population viability models are rarely validated, require hopelessly large amounts of data to correctly parameterize, and produce results that are too biased, imprecise, or simplistic to generate useful predictions (Ludwig 1999, Coulson et al. 2001, Ellner et al. 2002, Lindenmeyer et al. 2003). Those defending their use often concede these points to some degree (Brook et al. 2002), but note that developing a population viability model compels the user to specifically describe the life history of the species of concern, to acknowledge assumptions about that life history, and to recognize critical gaps in knowledge (Morris and Doak 2004). This process also represents a reasonably objective method for making predictions about management effects and population persistence, and some model predictions have proven accurate (Brook et al. 2000). Consequently, there is either grudging or enthusiastic support that population viability models have heuristic value because they demonstrate trends in population persistence or the response of demographic parameters to management alternatives or stochastic variation, and they have been widely adopted in the conservation field (Beissinger and McCullough 2002, Morris and Doak 2004).

Development of population viability models for conservation of cutthroat trout is limited. Hilderbrand (2003) created a projection matrix model for generic headwater stream populations of cutthroat trout (see Stapp and Hayward 2002 for a model representing an adfluvial population). Estimates of vital rates were derived from studies of Colorado River cutthroat trout (Peterson et al. 2004a), westslope cutthroat trout (Shepard et al. 1997), and the opinions of experts familiar with Colorado River and Bonneville cutthroat trout (**Table 1**). Fecundities, egg survival to fry emergence, and fry survival to the following summer were condensed into a single parameter that differed by female size. Estimates thereafter were length-based rather than age-based to reflect the influence of length on maturity, and it was assumed that half of the surviving individuals would transition to a later stage and half would remain within a particular stage. The population growth rate (λ) for this model was 1.06.

Hilderbrand (2003) explored variation in model outcomes by subjecting vital rates to deterministic and stochastic variation and constraining population growth with a density-dependence function and one of several

Table 1. Table 1. Parameter values for the components of the matrix population model for cutthroat trout developed by Hilderbrand (2003), and ranges of values (if more than one) for those parameters from Downs et al. (1997), Vinyard and Winzeler (2000), Stapp and Hayward (2002), and Peterson et al. (2004a). Following Hilderbrand (2003), subadults are <150 mm, small adults are 150-200 mm, and large adults are >200 mm.

Parameter	Value	Range
Fecundity (150-200 mm female)	139	166-553
Fecundity (200+ mm female)	231	224-664
Survival to emergence of fry	0.40	0.06
Fry overwinter survival	0.27	0.37
Age-0 to subadult survival	0.22	0.02-0.37
Subadult to subadult survival	0.16	0.23-0.42
Subadult to small adult survival	0.16	0.23-0.42
Small adult to small adult survival	0.23	0.35-0.57
Small adult to large adult survival	0.23	0.35-0.57
Large adult to large adult survival	0.23	0.11-0.57

levels of carrying capacity, as well as by mimicking the influence of different levels of immigration and population synchrony, in simulations of the probability of population persistence for 100 years. Unsurprisingly, deterministic reductions in vital rates that reduced the population growth rate below 1.0 resulted in extinction over that interval, and larger population sizes (as measured by carrying capacity) were necessary to ameliorate the tendency of greater stochastic variation to reduce the probability of persistence. Increasing rates of immigration disproportionately improved the probability of persistence of the smallest populations, as would be expected for marginal populations dependent on larger ones for their reproductive largesse. However, synchrony in population size reduced the positive effect of immigration, because when populations were large, the need for and space available to immigrants was reduced, and when populations declined, the number of available immigrants declined.

A few additional caveats about the generality of these results are warranted. Because of the diversity of life history strategies exhibited by cutthroat trout (Rieman and Dunham 2000) and the uncertainty about and inherent variability in parameter values, population viability models are most useful for indicating relative effects of changes in vital rates, rather than demonstrating specific outcomes (Beissinger and Westphal 1998). The relative importance of vital rates also relies on the underlying model assumptions about regulating processes and population structure. For example, Hilderbrand (2003) reported that changes in survival from the subadult to small adult stage and the young-of-the-year to subadult stage had the greatest influence on population growth rate in the matrix model

for cutthroat trout. In contrast, a comparable model for white-spotted charr (*Salvelinus leucomaenis*) in Japan that assumed similar fecundities, lengths, and ages but slightly different growth rates and a different form of density dependence identified adult survival rate as having the greatest effect on population growth rate (Morita and Yokota 2002). Furthermore, elasticities—the values for judging the relative influence of vital rates—are only accurate for small changes in those parameters (e.g., perhaps much less than 20 percent; Mills et al. 1999). Greater variation, particularly in the relative importance of different vital rates in different habitats, can markedly alter the elasticity rankings of vital rates among models (Mills and Lindbergh 2002, Morris and Doak 2004, Norris 2004). As was noted earlier, habitat-specific variation in vital rates for headwater populations of cutthroat trout is common. In addition, an assumption in the aforementioned cutthroat trout model (and others; Fefferman and Reed 2006) is that age structures will remain fairly constant in any given stream, but this may not be realistic. For example, Hesthagen et al. (2004) observed substantial annual variation in the mean age of maturity in female Arctic charr (*S. alpinus*) and brown trout over a 13-year interval. Also, the repeated evolution of migratory strains suggests that fecundity may play a large role in the success of populations, at least in evolutionary time (Willson 1997), despite its relative unimportance in the previously noted demographic models. Consequently, the use of demographic models to gauge population growth and persistence can be informative, but the results must be treated with caution in the absence of long-term data (at least 4 years; Morris and Doak 2004) specific to the life history characteristics and habitat being modeled.

Genetic structure

The genetic structure of cutthroat trout populations reflects their evolutionary history and may dictate their evolutionary future. The relatively high levels of genetic variation within the family Salmonidae are thought to have arisen from an autopolyploidization event (Allendorf and Thorgaard 1984). The extraordinary phenotypic diversity of salmonids, particularly in their life histories (Willson 1997), may in part be linked to this genetic variation as well as the diversity of environments they occupy (Waples et al. 2001). In cutthroat trout, there is often substantial genetic differentiation among local populations. Population genetic structure often displays a geographic cline in many salmonids—in that network distance sometimes explains relatedness of populations and much of the diversity is partitioned among major river basins—yet a more common pattern among cutthroat trout is to exhibit high interpopulation genomic diversity unrelated to geographic distance (Allendorf and Leary 1988, Waples et al. 2001, Taylor et al. 2003, Young et al. 2004, Cegelski et al. 2006, Neville et al. 2006a; for comparable structure in brook trout in their native range, see Castric et al. 2001). Preliminary studies of Colorado River cutthroat trout in streams draining the Uinta Range in Utah indicated that separate clades existed in streams draining the southern and northern slopes, and that differences among populations within clades accounted for much of the overall genetic variation (D. Shiozawa and P. Evans, Brigham Young University, unpublished data). Elsewhere, cutthroat trout populations linked by migratory individuals (e.g., Yellowstone cutthroat trout in the main-stem Yellowstone River and connected tributaries) often show less divergence (Allendorf and Leary 1988, Neville et al. 2006a), but even in the presence of straying, adjacent streams less than 2 km apart have developed distinct populations (Wenbug and Bentzen 2001). A further complication is that fish with different life histories (e.g., migrants and residents) may be derived from the same set of parents or constitute the same deme (Jonsson and Jonsson 1993, Yamamoto et al. 1999, Kinnison and Hendry 2004), yet also be under selection favoring one form or the other (Klemetsen et al. 2003, Adams and Huntingford 2004).

Physical isolation, at the scale of individual streams, imposes a different set of conditions on genetic structure. Isolated populations of salmonids have shown reduced genetic diversity relative to downstream populations, a pattern that has been attributed to the pronounced effect of genetic drift on small populations of salmonids (Carlsson and Nilsson 2001, Castric et al. 2001), including cutthroat trout (Taylor et al.

2003, Neville et al. 2006a, Pritchard et al. 2007b). The existence of multiple barriers within a particular basin has led to fine-scale population structuring (Pritchard et al. 2007b), often with the incremental loss of genetic diversity observed among population segments found farther upstream (Wofford et al. 2005). However, these small populations, if they persist, may simultaneously be subject to strong natural selection and become locally adapted, a process that can be relatively rapid (Ford 2004, Hendry et al. 2004; also see Genetic concerns, below).

Metapopulations

Geographically distinct populations that are demographically linked by migrants are considered to constitute metapopulations. The specific metapopulation structure depends on the size and demographic contribution of each subpopulation; the frequency, direction, and extent of migration among subpopulations; and the rates of subpopulation extinction. The key, however, is that individuals can move among locations, thereby promoting persistence in the face of localized environmental catastrophes and reducing the long-term loss of genetic variation. This connectivity appears to buffer some populations from extirpation (Dunham et al. 1997), but it need not be continual for metapopulations to form. Rather, connectivity can be ephemeral and appear at the scale of decades or centuries (Rieman and Dunham 2000, Schlosser and Kallemeyn 2000), such as might be expected during the pre- and post-glacial history of greenback cutthroat trout. Although salmonids are believed to form metapopulations where circumstances permit and this concept has been a rich source of theoretical predictions (Rieman and Dunham 2000), detailed descriptions of metapopulation structure in salmonids remain rare (but for studies on aspects of metapopulations, see Dunham et al. 1997, Dunham and Rieman 1999, Koizumi and Maekawa 2004, Johansen et al. 2005, Neville et al. 2006a).

Community ecology

Sympatric vertebrates

Because they are currently largely restricted to high-elevation headwater streams and previously fishless lakes, greenback cutthroat trout are often the only native fish species present. Historically, greenback cutthroat trout were found in warmer, larger streams and rivers and a few accessible lakes, where they were at least seasonally sympatric with a much larger array of species that may have included longnose

dace (*Rhinichthys cataractae*), creek chub (*Semotilus atromaculatus*), flathead chub (*Platygobio gracilis*), white sucker (*Catostomus commersonii*), longnose sucker (*C. catostomus*), Johnny darter (*Etheostoma nigrum*), and perhaps brook stickleback (*Culaea inconstans*) (Woodling 1985). Greenback cutthroat trout were also sympatric with yellowfin cutthroat trout (*Oncorhynchus clarkii macdonaldi*) in the Twin Lakes at the headwaters of the Arkansas River basin (Behnke 1992). The historical dynamics of these communities are a matter of speculation because of the current prevalence of nonnative species and anthropogenic disruption of large stream habitats.

The influence of competition with or predation by native fish species on greenback cutthroat trout has not been studied. Incidental predation by terrestrial vertebrates, such as dipper (*Cinclus mexicanus*), belted kingfishers (*Ceryle alcyon*), great blue heron (*Ardea herodias*), osprey (*Pandion haliaetus*), mink (*Mustela vison*), and otter (*Lutra canadensis*), was probably historically common. Researchers using radiotelemetry regularly find some transmitters on stream banks (e.g., Schmetterling 2001, Lindstrom 2003, De Rito 2004, M.K. Young, personal observation) and treat these as instances of predation, although they sometimes cannot be distinguished from the scavenging of already dead fish or angler harvest. In some areas, spawning runs may have attracted large numbers of predators, comparable to the concentrations of grizzly bears (*Ursus arctos horribilis*) and other predators that until recently exploited large spawning runs of Yellowstone cutthroat trout from Yellowstone Lake (Haroldson et al. 2005). Such spawning runs probably formed a significant energy subsidy to upland and riparian environments, but the absence of these runs for about the last century has probably represented a major trophic shift for some stream ecosystems in the central Rocky Mountains.

Parasites and diseases

There is little information on the parasites and diseases of greenback cutthroat trout. The trematode *Gyrodactylus* has been found in at least one wild population of Colorado River cutthroat trout (Jespersen 1981), and the water mold *Saprolegnia* has been detected in many others, particularly in mature individuals after the spawning season (Binns 1977, M.K. Young, personal observation). Many pathogens, such as *Aeromonas salmonicida* (the causative agent of furunculosis), *Renibacterium salmoninarum* (cause of bacterial kidney disease), *Tetracapsula bryosalmonae* (cause of proliferative kidney disease), *Flavobacterium psychrophilum* (cause of bacterial coldwater disease),

and infectious hematopoietic necrosis virus are widespread in salmonids, of sometimes unknown geographic origin, and can result in high mortality rates among hatchery populations, particularly those under stress. Their prevalence in or influence on wild populations of greenback cutthroat trout has not been thoroughly evaluated, but preliminary examinations found no indication of these diseases (U.S. Fish and Wildlife Service 1998).

Envirogram

I developed an envirogram to describe the factors that directly and indirectly influence the abundance and viability of greenback cutthroat trout (Andrewartha and Birch 1984; **Figure 3**). The envirogram is divided into five panels: reproduction, growth and survival, biotic hazards, abiotic hazards, and demographic and evolutionary hazards. Because our understanding of the biology of this subspecies is incomplete, these diagrams should be regarded as hypotheses about the ecological relations between different life stages, their habitats, and their communities. However, the greatest value of this framework may be to serve as a heuristic tool for managers and to challenge researchers to test these hypotheses or propose alternatives (Graves 2001).

CONSERVATION

Potential Threats

The highly restricted current range of greenback cutthroat trout in high-elevation streams and lakes represents a historical anomaly in their distribution. Rather than focus on these few systems, this discussion takes a broader perspective by considering threats to many of the waters previously occupied by greenback cutthroat trout and still suitable for them.

Nonnative fishes

Brook trout

Brook trout have probably been responsible for the greatest loss of headwater populations and represent the greatest immediate threat to the persistence of remaining populations of greenback cutthroat trout. As of 2000, brook trout had invaded about 19 of 65 stream sites recently harboring greenback cutthroat trout (Young et al. 2002), and replacement of populations of greenback cutthroat trout by brook trout is ongoing (U.S. Fish and Wildlife Service 1998, McGrath 2004). This nonnative species is ubiquitous throughout the historical range of greenback cutthroat trout in Colorado

1. Reproduction

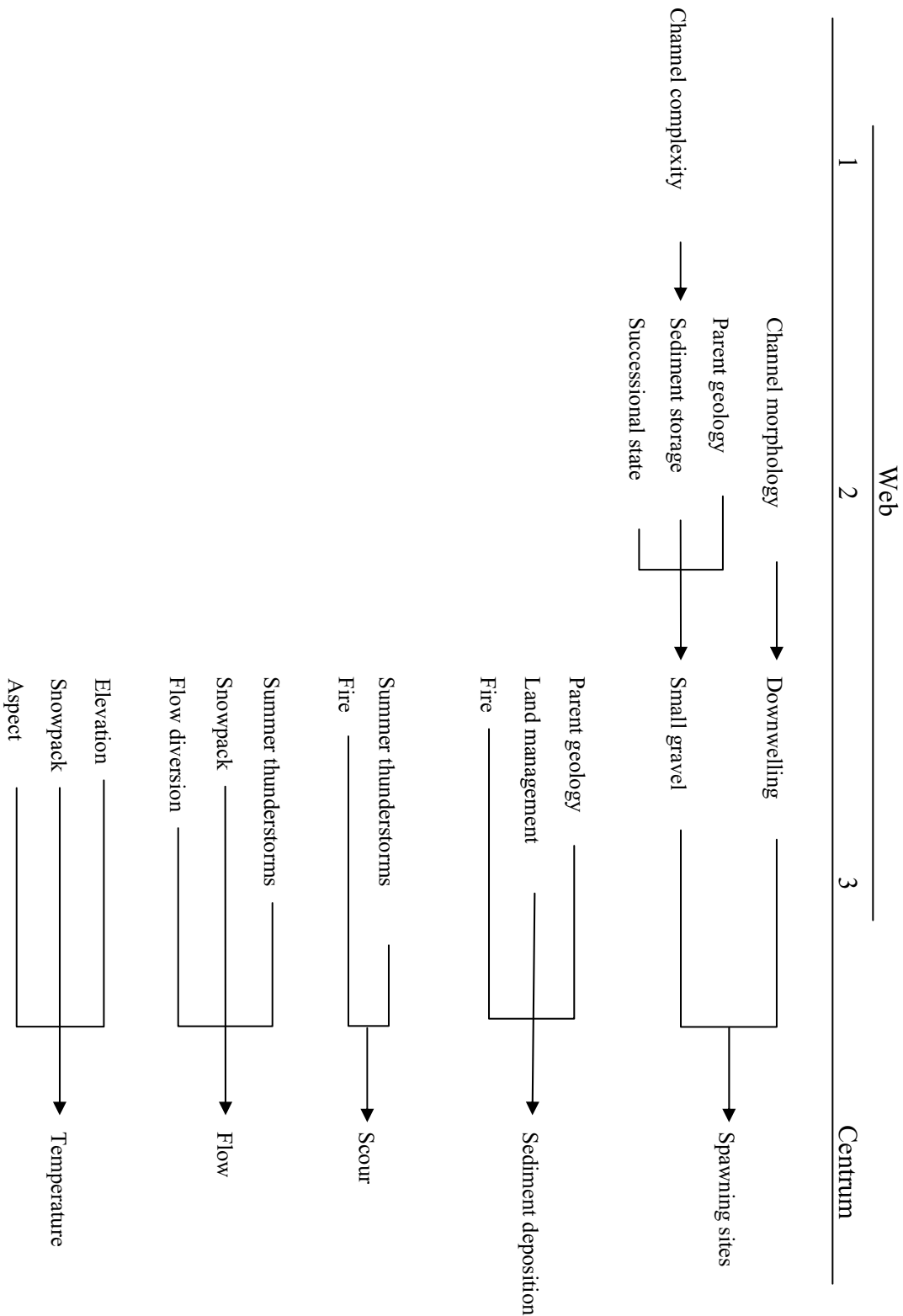
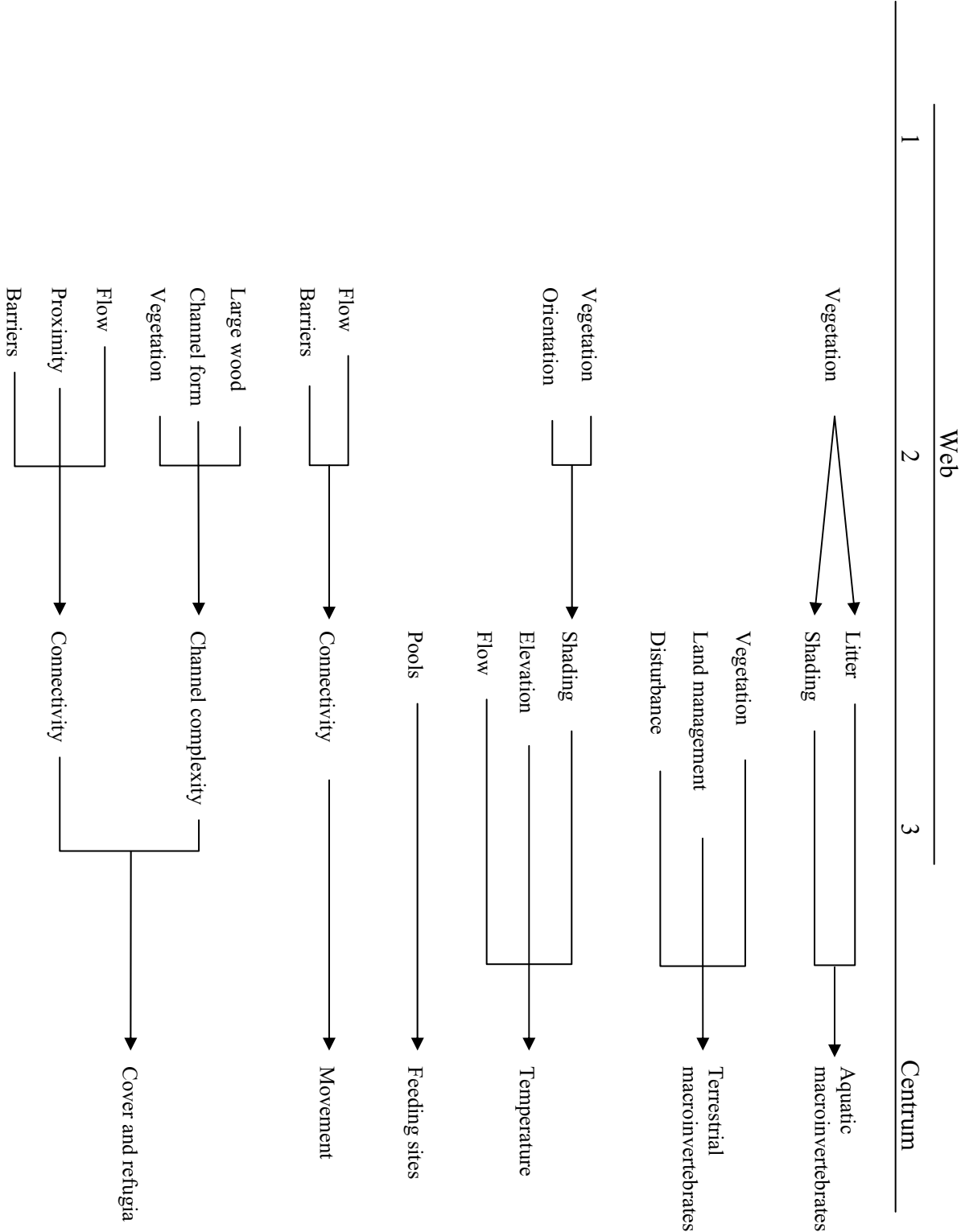
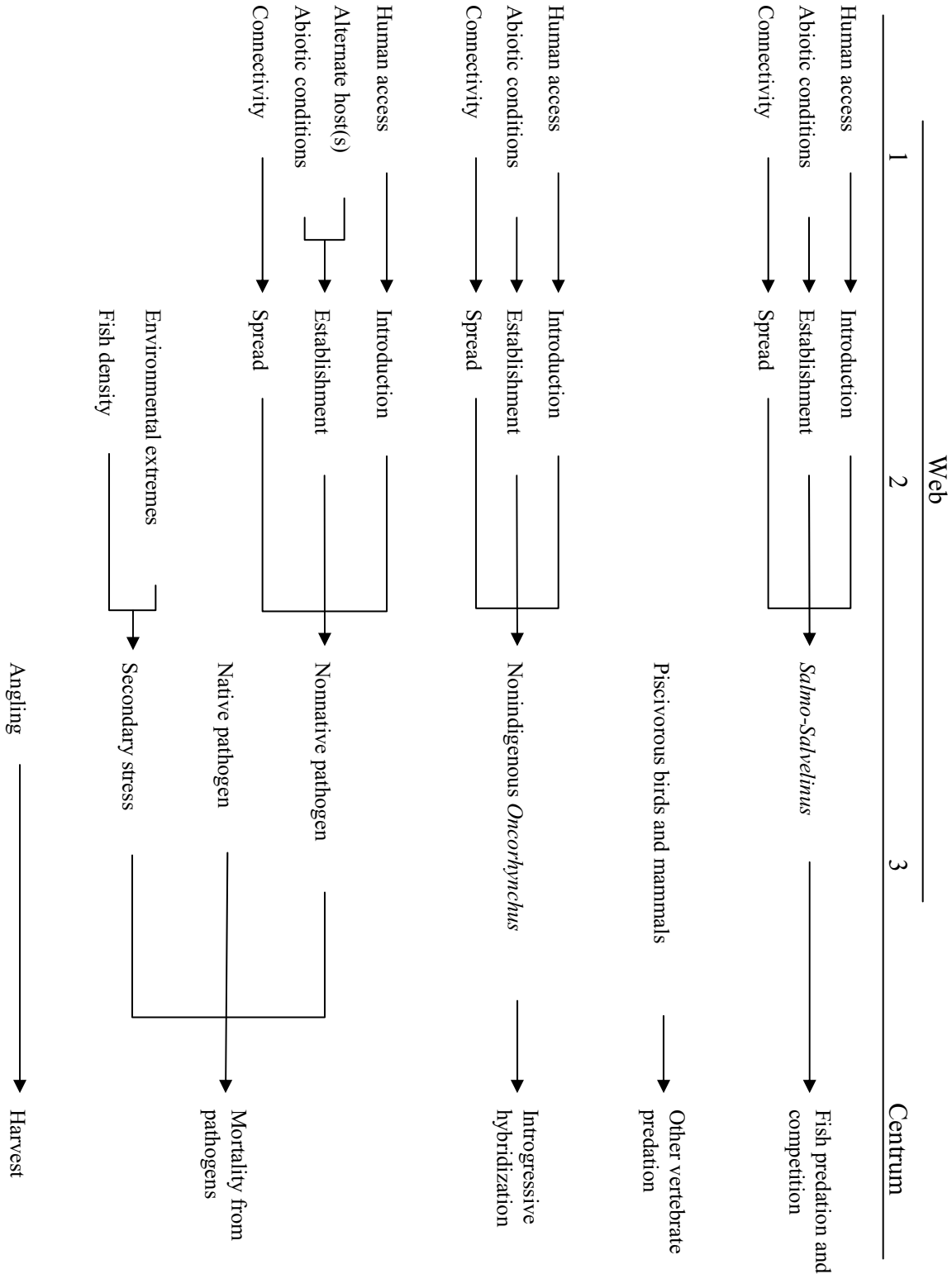


Figure 3. Envirogram of factors important to the different life stages of greenback cutthroat trout. Panels address reproduction (1), growth and survival (2), biotic hazards (3), abiotic hazards (4), and demographic and evolutionary hazards (5).

2. Growth and survival



3. Biotic hazards



4. Abiotic hazards

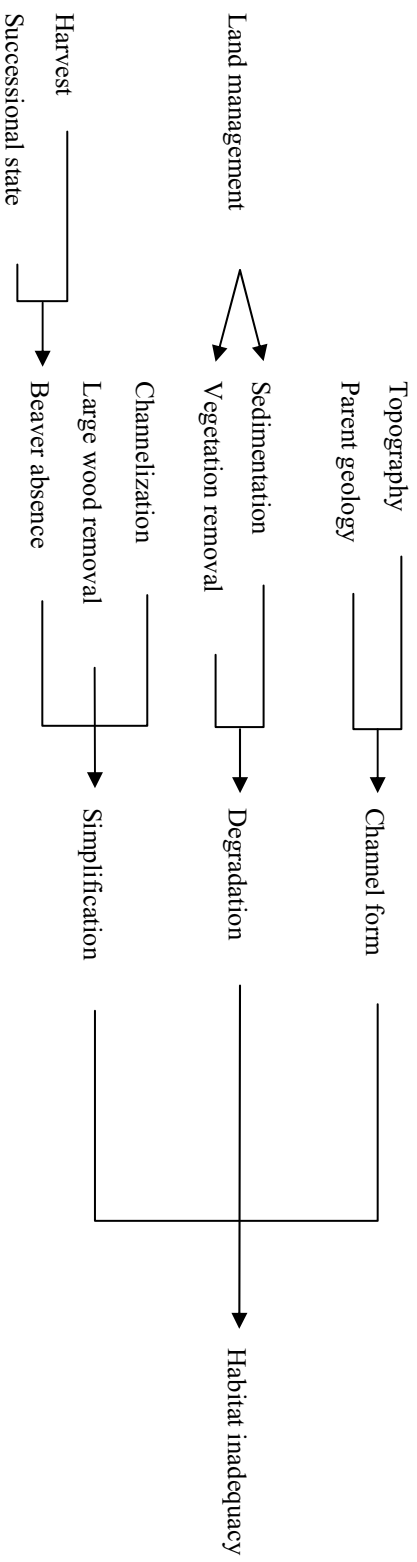
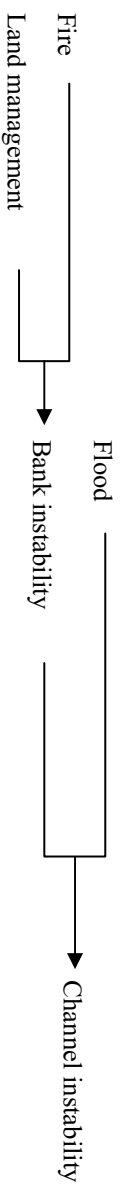
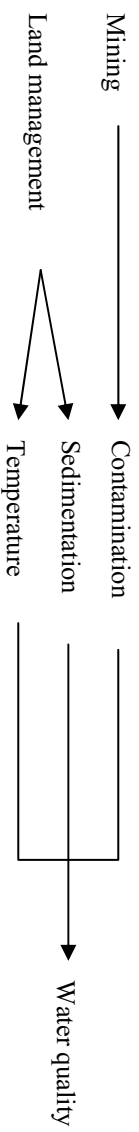
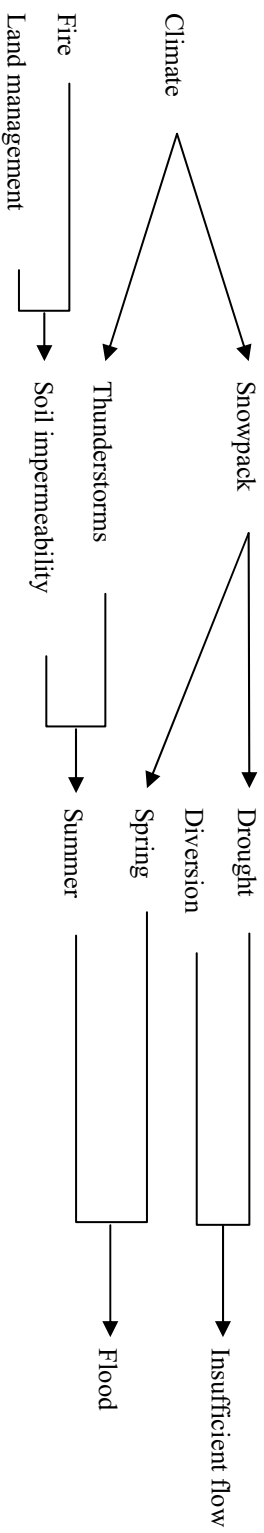
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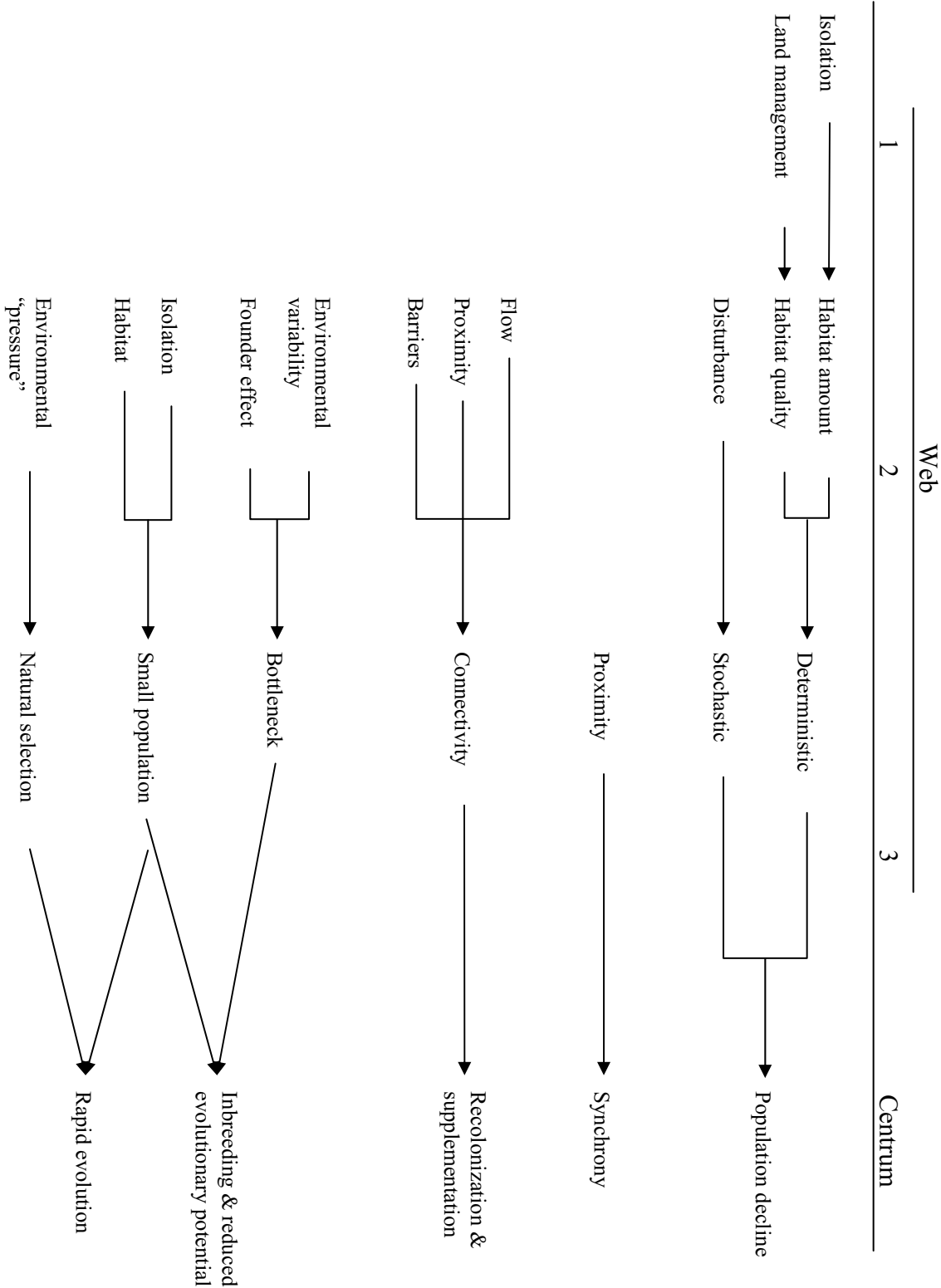
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5. Demographic and evolutionary hazards



and Wyoming, typically inhabiting the small streams that constitute the bulk of waters currently occupied by greenback cutthroat trout. In favorable habitats, brook trout mature at younger ages and exhibit greater size-specific fecundity than do cutthroat trout (Adams 1999, Kennedy et al. 2003); however, their overall biomass may be comparable to that of the displaced cutthroat trout population (Shepard et al. 2002) or somewhat greater (McGrath and Lewis 2007).

Often, the mortality rates of young cutthroat trout exposed to brook trout are high enough to result in recruitment failure (Dunham et al. 2002a, Shepard et al. 2002, McGrath 2004, M.K. Young, unpublished data). Peterson et al. (2004a) demonstrated that age-0 Colorado River cutthroat trout survival was near zero in the presence of brook trout, and that the suppression of brook trout led to large increases in survival of age-0 and age-1 fish. Yet the mechanism by which brook trout replace cutthroat trout remains an enigma. There is substantial diet overlap between brook trout and cutthroat trout (Dunham et al. 2000, Hilderbrand and Kershner 2004, McGrath and Lewis in press), so a number of studies have focused on competition. However, these have been conducted under artificial settings, and their relevance to wild populations is uncertain. For example, in laboratory or enclosure trials, juvenile and adult brook trout occasionally dominated same-age or -size Colorado River cutthroat trout by achieving greater short-term growth rates or survival, but often only at exceptionally high water temperatures or fish densities (De Staso and Rahel 1994, Novinger 2000, Hilderbrand and Kershner 2004). Moreover, these necessarily narrowly focused experiments have not addressed the spatial and temporal variation in foraging exhibited by each species in circumstances other than the diurnal, mid-summer conditions emulated in the laboratory or monitored in the field. Predation by brook trout would represent a more direct explanation for the declines in age-0 and age-1 cutthroat trout, but field observations offer little support for it (Dunham et al. 2002a, McGrath 2004, B. Shepard personal communication 2007, M.K. Young, unpublished data). Nevertheless, even small brook trout have exhibited piscivory (Levin et al. 2002, Mohler et al. 2002), and there may be a particular temporal window (e.g., immediately after cutthroat trout fry emergence) when predation is substantial. As noted earlier, this period was characterized by intense cannibalism by cutthroat trout on their own fry (Benson 1960, Snyder and Tanner 1960), and the combined effects of both species may be responsible for declines in fry survival.

There is little evidence for substantial biotic resistance by greenback cutthroat trout to invasions by brook trout, based on the commonly observed pattern of greenback cutthroat trout persisting in the extreme headwaters of a basin, with brook trout dominating all remaining suitable waters downstream (cf. Fausch 1989, Benjamin et al. 2007, M.K. Young, personal observation). Although physical barriers to upstream migration often separate these species, there are some examples of coexistence of greenback cutthroat trout and brook trout in the absence of barriers (e.g., George Creek; Young and Guenther-Gloss 2004). It is uncertain whether these represent a transient sympatric phase (i.e., a snapshot of an ongoing invasion; Peterson et al. 2004a), a “stagnant” invasion dependent on future habitat or population disruption before proceeding further (Griffith 1988, Adams et al. 2001, Shepard 2004), or the partitioning of suitable habitats by each species. It should be noted that during a protracted invasion—over several decades—these alternatives may be indistinguishable (Spens et al. 2007). Another possibility is that life history diversity may confer an advantage to cutthroat trout found elsewhere. Yellowstone cutthroat trout in the Yellowstone River basin, westslope cutthroat trout in many rivers west of the Continental Divide in Montana and Idaho, Bonneville cutthroat trout in the Logan River, and Colorado River cutthroat trout in larger streams draining the southern slopes of the Uinta Range have persisted in sympatry with brook trout for decades. A shared characteristic among these basins is the existence of migratory forms of cutthroat trout that are larger and more fecund than resident forms. As noted earlier, offspring of some of these migratory fish migrate from spawning streams shortly after emergence. Because evidence indicates that juvenile cutthroat trout suffer high mortality rates in the presence of brook trout, fry migrating from waters occupied by brook trout may be achieving greater survival, thus facilitating cutthroat trout persistence. If so, the widespread fragmentation of stream networks with anthropogenic barriers (e.g., water diversions, culverts, or desiccated stream reaches; see Habitat fragmentation, below) that is probably responsible for the current absence of most migratory forms of greenback cutthroat trout, may also be compromising the ability of many populations of this subspecies to persist in the face of invasions by brook trout.

Other roles of habitat in facilitating or hindering brook trout invasions may be important. At a large scale, regional climate patterns could influence brook trout success. Fausch et al. (2001) demonstrated that the

annual timing of peak flow with respect to the period of egg incubation, fry hatching, and fry emergence affected the reproductive success of rainbow trout and dictated whether invasions by this species would be successful at a global scale. An apparent difference in the invasion success of brook trout east and west of the Continental Divide in Montana may be linked to differences in winter climate (Fausch et al. 2006). At smaller scales, the distribution of habitats serving as demographic sources and sinks could be controlling brook trout establishment and spread (Adams 1999, Castric et al. 2001, Petty et al. 2005, Benjamin et al. 2007). For example, despite widespread stocking, brook trout are rare in much of the upper Snake River basin in Wyoming except in a few watersheds with headwater lakes (M. Novak, Bridger-Teton National Forest, unpublished data). Although advances by brook trout have been attributed to habitat disruption (Griffith 1988), invasions of brook trout are also common in relatively pristine habitats that have not undergone recent disturbance, such as the headwaters of the Colorado River in Rocky Mountain National Park (Fausch 1989, Behnke 1992). Greenback cutthroat trout in waters with very cold summer temperatures may suffer frequent recruitment failure (Peterson et al. 2004a, Young and Guenther-Gloss 2004), but these conditions also reduce growth rates of brook trout and increase their age at maturity (Adams 1999, Kennedy et al. 2003). It may be that greenback cutthroat trout adults in such conditions have greater annual survival than adult brook trout and experience punctuated recruitment in the occasional years when low snowpack or unusually warm summer temperatures facilitate post-emergence growth of fry and their subsequent overwinter survival. Under these circumstances, cutthroat trout may resist invasions by brook trout because such waters can represent a demographic sink for brook trout (Adams 1999), although the presence of a demographic source in warmer waters downstream could promote the repeated upstream movements of brook trout that would interact with cutthroat trout in the headwaters (Peterson and Fausch 2003). Alternatively, the conditions supporting recruitment in brook trout and greenback cutthroat trout may be unlikely to occur simultaneously, favoring one species or the other in different years and promoting their coexistence (cf. Seegrist and Gard 1972).

Brown trout

Although brown trout are implicated in the loss of many populations of Rio Grande cutthroat trout (Calamusso and Rinne 2004, Paroz 2005), instances where they may have replaced greenback cutthroat trout are less apparent because there is so little overlap between species. Nevertheless, brown trout have been

shown to be competitively superior to cutthroat trout in laboratory trials (Wang and White 1994) and field enclosures (McHugh and Budy 2005), and there is evidence that brown trout displace wild cutthroat trout. For example, de la Hoz Franco and Budy (2005) believed that the presence of brown trout truncated the downstream distribution of Bonneville cutthroat trout in the Logan River, and McHugh and Budy (2006) observed an array of subtle but significant changes in the growth and behavior of cutthroat trout in the presence of brown trout. Yet the relative distribution of these two species in this system has apparently been stable for decades (cf. Bernard and Israelsen 1982), and Bonneville cutthroat trout in the Smiths Fork and Thomas Fork Bear River in Wyoming and Yellowstone cutthroat trout in the Yellowstone River basin have persisted in long-term sympatry with brown trout. An important element that may be facilitating coexistence is that brown trout tend to be found in larger streams at lower elevations and do not occupy many tributaries used by cutthroat trout for spawning, which might restrict any deleterious interactions between brown trout and juvenile cutthroat trout. This downstream-upstream partitioning of stream habitats by brown trout and other salmonids (Weigel and Sorensen 2001) and their absence from small, high-elevation streams in the central Rocky Mountains (Bozek and Hubert 1992, Rahel and Nibbelink 1999) is thought to be related to their poor recruitment at low water temperatures (Jensen and Johnsen 1999, Lobón-Cerviá and Mortensen 2005, McHugh and Budy 2005). Because brown trout eggs and fry are also vulnerable to high flows during the latter part of incubation through the early stages of emergence (Jensen and Johnson 1999, Lobón-Cerviá 2004, Lobón-Cerviá and Mortensen 2005), the timing of peak discharge in these environments may also present an obstacle to more-upstream invasions.

Rainbow trout and nonindigenous cutthroat trout

Rainbow trout and nonindigenous subspecies of cutthroat trout, particularly Yellowstone cutthroat trout (Young et al. 1996), have been widely introduced into waters originally containing greenback cutthroat trout. Unlike brook trout or brown trout, these congeneric taxa do not replace greenback cutthroat trout but instead hybridize with them (Allendorf and Leary 1988, Forbes and Allendorf 1991, J. Metcalf, University of Colorado, unpublished data). Although introductions of nonnative stocks do not always result in hybridization (Weigel et al. 2003), the probability of hybridization tends to rise with the number of introductions (Bischoff 1995, Colautti 2005). These hybrids are fertile and capable

of backcrossing with genetically pure fish of either source and with other hybrids, leading to introgression of nonnative genes into the cutthroat trout population. If mating between cutthroat trout and rainbow trout or nonnative cutthroat trout is nonselective (which it may not be; see Baumsteiger et al. 2005 and Ostberg and Rodriguez 2006 for examples of assortative mating) and continues for a number of generations and if hybrids do not show reduced fitness, genes of nonnative stocks will pervade virtually all remaining individuals to produce a hybrid swarm within a particular area (Allendorf et al. 2001). There are many examples of the development of hybrid swarms between greenback cutthroat trout and rainbow trout (J. Metcalf and A. Martin, University of Colorado, unpublished data). Although laboratory studies have suggested that hybrids may suffer greater juvenile mortality (Leary et al. 1995, Allendorf et al. 2004), results from field studies have been equivocal (Allendorf et al. 2004, Rubidge and Taylor 2004, Baumsteiger et al. 2005, Rubidge and Taylor 2005).

Spatial patterns in the distribution of nonnative genes are complex. Weigel et al. (2003) reported that proximity to a source of stocked fish was only weakly related to hybridization between cutthroat trout and rainbow trout. Instead, larger streams at lower elevations were more likely to contain hybridized populations regardless of stocking location. They argued that isolating mechanisms, such as different spawning and emergence times or habitat preferences between adults of each species, were preventing hybridization from developing in headwater populations of cutthroat trout (also see Henderson et al. 2000, Ostberg and Rodriguez 2006). In contrast, Hitt et al. (2003) and Rubidge and Taylor (2005) detected the upstream progression of hybrids between rainbow trout and cutthroat trout over time, and concluded that hybrid swarms would eventually occupy most of these waters except those with migration barriers. The spread of nonnative genes appeared to rely on straying by hybrid cutthroat trout rather than pure nonnative trout (Hitt et al. 2003, Rubidge and Taylor 2004), but self-sustaining feral populations of rainbow trout in river main stems or a reservoir were also implicated (Weigel et al. 2003, Rubidge and Taylor 2005). To add further complexity, De Rito (2004) argued that introgression in resident populations of Yellowstone cutthroat trout progressed much faster than it did among fluvial populations because the latter exhibited greater temporal segregation from rainbow trout during spawning. Because artificial barriers protecting many populations of greenback cutthroat trout are prone to failure (Harig et al. 2000), the risk of hybridization with nonindigenous *Oncorhynchus* remains a long-term threat.

Once introgressive hybridization of greenback cutthroat trout populations has begun, options for restoring a genetically pure stock are few. Although removals of obvious hybrids have been conducted with the aim of reducing the rate of transmission of nonnative genes to future generations of salmonid populations (Busack and Gall 1981, Dowling and Childs 1992), these efforts have failed (in the absence of a thorough and sustained campaign; Campbell et al. 2002) for two reasons. First, whereas it is often possible to recognize first-generation hybrids between rainbow trout and cutthroat trout visually, backcrosses and later-generation individuals can be indistinguishable from genetically pure adults without the aid of genetic testing (Leary et al. 1996). Second, if introgressive hybridization has progressed through several generations, nearly all individuals will carry at least some introduced genes, and reducing this influence to undetectable levels is probably futile (Allendorf et al. 2001).

Conservation of these hybridized stocks is a dilemma for managers. Such populations are less desirable because they are not genetically pure, and thus are poor choices for establishing new populations or supplementing existing ones (Allendorf et al. 2001). However, because introgressed populations may contain the sole remnants of portions of the genome or display unique life history attributes, their elimination or further genetic erosion would result in the permanent loss of this evolutionary legacy (Peacock and Kirchoff 2004). Favoring one perspective over the other has introduced some inconsistencies in the management of cutthroat trout subspecies (Allendorf et al. 2004, Campton and Kaeding 2005), including their status for listing under the Endangered Species Act (Allendorf et al. 2005). Currently, those populations of greenback cutthroat trout exhibiting less than 1 percent introgression are prioritized for conservation and considered suitable to found broodstocks or new populations, whereas those with 1 to 10 percent introgression are deemed worthy of conservation if they display novel genetic or life history characteristics (Utah Division of Wildlife Resources 2000). However, because the level of introgression detected will vary depending on the genetic technique used (Pritchard et al. 2007a), these thresholds might better serve as guidelines rather than rigid categories.

Further complicating this issue is the likely transfer of closely related taxa, such as Colorado River cutthroat trout or Rio Grande cutthroat trout, into or upstream from waters historically containing greenback cutthroat trout and vice versa. Before 1896, greenback cutthroat trout were cultured and sometimes released on the west side of the Continental Divide; thereafter, stocking of

Colorado River cutthroat trout was more common and included many waters on the east side of this divide (W. Wiltzius, Colorado Division of Wildlife, unpublished data). Using genetic procedures to determine which subspecies are represented in many extant populations is an important issue for the conservation of both.

Other nonnative species

The number of additional nonnative species that have been introduced into the United States is large. Despite a growing sensitivity to the consequences of these introductions, they will likely continue because of the increasing globalization of commerce and the speed and ubiquity of human-assisted dispersal (Cox 2004). Invasions of some aquatic species, such as New Zealand mudsnails (*Potamopyrgus antipodarum*), could dramatically alter aquatic ecosystems, but whether these will directly affect greenback cutthroat trout is unknown.

Because of the global rise in aquaculture, among the largest threats may be nonnative pathogens in cultured fish. This is believed to be the pathway followed by the myxosporean parasite *Myxobolus cerebralis*, the causative agent of whirling disease (Bergersen and Anderson 1997). This European species was detected in the United States in the 1950's and may have originated from an international shipment of frozen rainbow trout (Gilbert and Granath 2003). The subsequent distribution of infected fish resulted in its establishment in wild salmonid populations throughout the Rocky Mountain states by the 1990's. This parasite reduces survival of juvenile trout, and is believed to be responsible for dramatic declines in several wild trout populations (Nehring and Walker 1996, Vincent 1996). *Myxobolus cerebralis* requires the annelid *Tubifex tubifex* as an intermediate host, and the susceptibility of salmonid populations varies with habitat suitability (generally areas with large amounts of fine sediment; Gilbert and Granath 2003), genotype of the annelid (Beauchamp et al. 2002), water temperature, the abundance of infective spores, and the age of fish exposed (Thompson et al. 1999). The extent of infection also appears to vary temporally (Downing et al. 2002), so while the magnitude of population-level effects of an infection are unknown, overall survival is expected to decline.

Cutthroat trout are susceptible to infection and mortality from whirling disease (Thompson et al. 1999), but no wild populations of greenback cutthroat trout are known to have been exposed (U.S. Fish and Wildlife Service 1998, McGrath 2004, D.A. Winkelman,

Colorado State University, unpublished data). Although agency-sponsored stocking of infected fish in waters containing greenback cutthroat trout or the migration of infected fish from nearby waters are the most likely pathways, other methods of spread of the parasite or its intermediate host are possible. Yellowstone cutthroat trout in tributaries to Yellowstone Lake have become positive for whirling disease despite the absence of fish stocking (of salmonids other than lake trout [*Salvelinus namaycush*]), which has led to speculation that white pelicans (*Pelecanus erythrorhynchos*) may be acting as a disease vector (T. Koel, National Park Service, unpublished data). Illegal introductions of infected salmonids by anglers may also contribute to its spread, and anglers may inadvertently transport the parasite via sediment on fishing or boating equipment. Because greenback cutthroat trout generally occupy cold, high-gradient streams that are unlikely to support large populations of *Tubifex tubifex*, these trout populations may have low vulnerability to infection by *Myxobolus cerebralis*. However, populations occupying streams with low-gradient segments where fine sediment is abundant, such as in reaches with beaver ponds, those draining fine-grained parent material, or areas degraded by land management, may be at risk.

Genetic concerns

Inbreeding depression and loss of genetic variation

Genetic variation is the fodder for evolution of populations and species. Maintenance of genetic variation relies on a balance between natural selection, mutation, and genetic drift. Mutation rates appear to be relatively low, but natural selection and drift can operate more rapidly. Population size plays a critical role in retention of genetic variation because heterozygosity is predicted to decline exponentially with time as a function of the effective population size, with smaller populations suffering more rapid declines than larger ones (Frankham 2005). This loss of heterozygosity is also directly proportional to the inbreeding coefficient (Allendorf and Ryman 2002). A further issue is that genetically effective population sizes can be much smaller than census population sizes. The effective population size has been demonstrated to be 10 to 20 percent of the census population size of adults for many taxa (Waples 2002, Frankham 2005). For inland salmonids, this range has been 10 to 50 percent (Palm et al. 2003, Jensen et al. 2005), with the most optimistic estimates based on the assumption that fish of several age classes reproduce in any given year (Rieman and Allendorf 2001).

Inbreeding depression is the reduction in fitness of offspring produced by breeding among relatives, and it is inevitable in small, isolated populations (Allendorf and Ryman 2002). The effects of inbreeding are thought to result from the fixation and expression of deleterious recessive alleles (Allendorf and Ryman 2002). Although it has been posited that populations that survive bottlenecks (periods of extremely low abundance) will purge these alleles, theoretical and field studies have demonstrated that purging will have at most a modest effect on inbreeding depression (Allendorf and Ryman 2002, Frankham 2005). Moreover, that a population persists after a severe bottleneck is evidence neither of successful purging nor of the absence of inbreeding depression in that population.

The consequences of inbreeding depression and the loss of genetic variation in wild populations are a point of contention. Arguments have been made that by the time populations decline to the degree that inbreeding effects would be manifest, demographic or environmental factors alone would likely drive these populations to extinction (Lande 1988), or that inbreeding depression occurs but may have no effect on population viability (Caro and Laurenson 1994). Nonetheless, comprehensive assessments have confirmed that inbreeding decreases the fitness of a large array of taxa (Lacy 1997, Keller and Waller 2002, O'Grady et al. 2006), and that this effect may be more pronounced in wild populations than in captive ones (Crnokrak and Roff 1999). Although population viability models indicate that inbreeding can substantially increase extinction risk, the paucity of field studies that have reached a similar conclusion (Allendorf and Ryman 2002, Frankham 2005) creates some uncertainty about the magnitude of the effect. In addition, polyploid taxa such as salmonids may be less susceptible to inbreeding depression (O'Grady et al. 2006). Nevertheless, because the consequences of inbreeding depression (or the simple lack of genetic variation) may be most pronounced during intermittent intervals of stress (e.g., bouts of drought, disease, or unstable or degraded habitats) when mortality may be increasing for several reasons, they may be considerable yet difficult to detect (Allendorf and Ryman 2002).

There is compelling evidence from studies of the recent isolation of salmonid populations (Neville et al. 2006a) and of populations isolated above waterfalls (Castric et al. 2001, Pettersson et al. 2001, Pritchard et al. 2007b) of declines in genetic diversity. Although some studies have failed to demonstrate a positive correlation between population size and genetic variability in salmonids (Heath et al. 2002, Laikre et al.

2002, Østergaard et al. 2003), in some of these cases, straying individuals may be maintaining high levels of genetic diversity despite low effective population sizes (Consuegra et al. 2005), or numbers may have rebounded after undergoing a severe bottleneck (Pritchard et al. 2007b). In addition, there is likely to be genetic structuring within populations caused by the presence of physical barriers to upstream migration, with the upstream-most segments having the least genetic variation (Wofford et al. 2005). These apparent "within-population" barriers may be relatively common (M.K. Young, personal observation).

Unintentional selection

The artificial culture of salmonids is widely practiced in the western United States, and its development has tracked advances in the transportation and exploitation of fish stocks (Wiltzius 1985). Other than severe inbreeding, early managers of hatcheries often ignored genetic concerns associated with cultured stocks, focusing more on growth rates, survival to harvest, and ease of culture. Concerns about the genetic health of hatchery stocks have arisen because their use to found or supplement wild populations, particularly of increasingly rare salmonid taxa (Flagg et al. 2004, Mobrand et al. 2005), may substantially erode the fitness of wild stocks (Goodman 2005). Brannon et al. (2004) pointed out that there is nothing inherently wrong with hatcheries or cultured fish, but both have often failed to live up to their potential with respect to the conservation of indigenous stocks. In that regard, a symposium (Nickum et al. 2004), journal issue (Journal of Fish Biology 65[Supplement A]), and spate of recent papers (e.g., Levin et al. 2001, Brannon et al. 2004, Mobrand et al. 2005) have addressed the many advantages, shortcomings, and strategies related to using hatchery stocks to achieve conservation goals. Although there is agreement that hatchery stocks can play a role in the genetic management of wild populations (Brannon et al. 2004, Wares et al. 2004), concerns about artificial production of salmonids remain, in part because some degree of unintentional selection of those populations, even with infusions of genes from wild fish, is inescapable (Ford 2002, Quinn 2005b, Wedekind et al. 2007; with respect to greenback cutthroat trout, A. Martin, J. Mitton, and J. Metcalf, University of Colorado, unpublished data).

A ubiquitous goal of conservation plans for cutthroat trout (e.g., U.S. Fish and Wildlife Service 1998, CRCT Conservation Team 2006b) has been the development of hatchery broodstocks to promote both conservation and sport fishing. Mobrand et al. (2005)

noted that these goals are distinctive enough to warrant separate hatchery strategies, and fundamental to the use of hatcheries for conservation is a genetic management plan to identify how genetic variation will be maintained and artificial selection avoided in hatcheries as well as how genetic effects of introductions of hatchery fish to supplement or found wild populations will be monitored (for a partial example, see Wares et al. 2004). With respect to maintaining genetic variation and avoiding artificial selection, Campton (2004) asserted that hatcheries should strive to achieve an even sex ratio, maximize the effective population of breeders, ensure an equal opportunity to spawn, and in particular avoid the practice of mixing the milt of multiple males (also see Wedekind et al. 2007). Such practices are included in the management plans for two Colorado River cutthroat trout broodstocks in Wyoming (Wyoming Game and Fish Department 2007).

Although rarely considered, another example of unintended selection involves the rapid evolution of isolated populations of formerly mobile salmonids (Stockwell et al. 2003). Changes in the migratory opportunities of salmonid populations can lead to selection for different life history forms and divergence in the genetic structure, and these changes can develop in surprisingly few generations (Hendry 2004). Koskinen et al. (2002) concluded that selection was largely responsible for the divergence among isolated populations of grayling (*Thymallus thymallus*) introduced 80 to 120 years earlier, despite the potential for severe founder effects and genetic drift. Ironically, whereas a number of migratory runs of salmonids have been established far outside their historical ranges (Withler 1982), there has been little success at reestablishing native salmonid populations with mobile life histories, especially in complex environments (Withler 1982, Healey and Prince 1995, Ford 2004). In some cases, isolated salmonid populations still produce occasional migrants, but downstream conditions have been altered to the extent that migrants are no longer adapted to these environments and most fail to return (Waples et al. 2001, Nelson et al. 2002). Isolation in fairly uniform habitats also poses the additional risk that populations may specialize, speciate, and lose the plasticity necessary to persist in changing environments (Gislason et al. 1999). Finally, research on sympatric forms exhibiting resident and anadromous life histories suggests that headwater isolation of cutthroat trout may produce strong yet conflicting selection. Morinville and Rasmussen (2003) concluded that low-productivity habitats led to slow growth and fish that were likely to adopt mobile life histories. In contrast, nutrient-rich environs that enabled faster growth and early maturation

were associated with greater probabilities that fish would adopt residency (Willson 1997, Klemetsen et al. 2003). Thus, it appears plausible that the abrupt isolation of populations in cold, unproductive headwaters might simultaneously select for migratory life histories in juveniles because of growth limitations, and select against migration when adults are unable to return over barriers to spawn in natal habitats. Strong selection for adapted life histories under such circumstances would be unsurprising, as would substantial alteration from the historical genotypes and phenotypes present in a drainage. Despite all of these concerns, there are examples of large numbers of migrants attempting to return to their natal waters despite over a century of isolation (see Habitat improvement, below), suggesting that this life history strategy may be strongly conserved in some populations.

Harvest and recreation

Although exploitation historically played a role in the decline and extirpation of many populations of greenback cutthroat trout (Wiltzius 1985), there is no evidence that angler harvest is contributing to the continued depression of populations. Restrictive angling regulations—limited or no harvest and gear restrictions—apply to virtually all populations of this taxon (U.S. Fish and Wildlife Service 1998, Colorado Division of Wildlife, unpublished data), and the remote locations of and limited access to most waters with this subspecies, as well as the small asymptotic length of most adult fish in streams, undoubtedly reduces fishing mortality. It is more difficult to determine whether angling in and of itself might contribute to a decline in populations of this subspecies. Paul et al. (2003) developed a model that suggested that incidental mortality of cutthroat trout in a no-harvest fishery might be sufficient to favor brook trout, for which harvest was permissible, when both species were present. However, this result relied on model assumptions rather than on empirical observations, and it appears questionable given that Yellowstone cutthroat trout in the Yellowstone River below Yellowstone Lake were captured an average of nine times each summer without obvious declines in that population (Schill et al. 1986). Evaluation of some of the more popular fisheries for greenback cutthroat trout could shed light on this issue.

Other forms of human recreation generally are regarded as relatively benign with respect to cutthroat trout. Concentrated human use in riparian zones has led to habitat degradation, but these effects are localized and unlikely to threaten entire populations. More critical may be the intentional or inadvertent role of

humans as vectors for non-native species. Although agency-sponsored stocking of sport fishes was the primary means of arrival of many nonnative salmonids, illegal introductions by anglers have been responsible for much of the recent spread of these fishes (Rahel 2004). Hepworth et al. (2002) noted that over the last 25 years, anglers have moved nonnative fish into most southern Utah reservoirs larger than 100 ha, including several used for cutthroat trout recovery. These introductions may also be fostering the dissemination of pathogens (Whirling Disease Initiative, Montana Water Center, unpublished data). Recent studies are using forensic techniques to identify the water or hatchery of origin of nonnative species (e.g., Munro et al. 2005), but this may do little to alter the process of introduction. Also at issue is the dissemination of nonnative species or diseases on angling gear or vehicles. Controlling the spread of nonnative species by either means may require manipulation of the transportation system (e.g., eliminating stream fords or closing roads to render intentional redistribution of nonnative fish more difficult).

Abiotic events and processes

Habitat fragmentation

As suggested by Smith et al. (2002) for fishes of the Great Basin, the distribution of greenback cutthroat trout has probably been characterized by expansion into low-elevation rivers and perhaps greater connectivity during periods of glacial development and greater precipitation, interspersed with retreats into smaller, accessible, high-elevation habitats that promoted greater isolation among populations during warmer, more arid times. Further habitat fragmentation undoubtedly arose following glacial retreat as stream downcutting and isostatic rebound contributed to the formation of waterfalls and cascades that terminated upstream migrations of greenback cutthroat trout and isolated small populations in many streams throughout its range. However, the relatively recent exclusion of this subspecies from cool, mid-elevation rivers by nonnative trout, habitat alteration, and exploitation, and the inadvertent or intentional anthropogenic isolation of small-stream populations have resulted in population insularity perhaps without precedent in the modern evolutionary history of this taxon.

Anthropogenic habitat fragmentation has resulted from several sources: impassable culverts, stream desiccation or vertical barriers associated with water diversions, thermal or chemical barriers (or long reaches of unsuitable habitat) from habitat degradation, and

downstream biotic barriers consisting of a gauntlet of nonnative species. These different types of barriers are widespread (Pepin et al. 2002), and in many instances the locations of the more prominent ones are known (U.S. Fish and Wildlife Service 2004).

The genetic consequences of population isolation, particularly of small populations, were described earlier. Demographic risks include susceptibility to environmental catastrophes that can extirpate entire populations, such as the debris torrents triggered by thunderstorms in recently burned watersheds that eliminated populations of Gila trout (Brown et al. 2001). Variability in habitat suitability from annual fluctuations in precipitation and discharge may be high in the headwater habitats currently occupied by most populations of greenback cutthroat trout, and the demographic variation that results can lead to population loss even when population growth rates are greater than 1 (Morris and Doak 2004). Alternatively, newly isolated habitats may lack resources critical to the survival of all life stages of cutthroat trout populations, which would likely result in a deterministic decline, sometimes to extinction, of such populations. In all cases, isolation prevents the natural demographic rescue of declining populations or refounding of extirpated ones.

Several studies have provided direct or indirect evidence of the consequences of habitat size for persistence of isolated salmonid populations. Harig and Fausch (2002) noted that successful introductions of Rio Grande or greenback cutthroat trout were more likely in watersheds greater than 14.7 ha. Similarly, watershed area or stream network size was positively correlated with the probability that bull trout (*Salvelinus confluentus*) (Dunham and Rieman 1999), Lahontan cutthroat trout (Dunham et al. 2002b), or Dolly Varden (*S. malma*) (Koizumi and Maekawa 2004) would be present in a stream segment. Probably the best evidence of isolation effects, however, comes from studies of white-spotted charr in Japan. Morita and Yamamoto (2002) found that the time since isolation increased the risk of population extirpation and the size of the watershed above a barrier decreased this risk. These authors also forecast the loss of 12 additional populations; although these habitats were still occupied, they regarded the sites as too small to support populations indefinitely based on their model. The extended time to extinction of populations doomed to fail because deterministic growth rates were less than 1 (or infrequent stochastic events were inevitable) has been predicted elsewhere (Morita and Yokota 2002, Hilderbrand 2003). Such populations have been described as “the living dead” (Hanski et al. 1996)

and contradict the notion that because cutthroat trout populations occasionally are found in very short stream segments, such habitats represent adequate habitat for cutthroat trout. Soulé (1987) termed this logic “the fallacy of the accident” because it ignores the likelihood that far greater numbers of populations in such habitats have already gone extinct.

Anthropogenic habitat degradation

Recounting the vast number and extent of activities that have reduced the quality of habitat for greenback cutthroat trout is beyond the scope of this manuscript. The consequences of various forms of land management for salmonid habitat quality have been the subject of a thorough review (Meehan 1991), and an excellent overview of changes in Colorado rivers and streams wrought by human activity is given by Wohl (2001; and of rivers throughout the country, Wohl 2004). The effects of the major activities will be briefly reviewed here, but the reader is encouraged to consult the extensive literature for more details (see Winters et al. 2004 for a summary).

Historical changes in habitat quality from human activity were associated with the arrival of Euro-Americans in the early to mid-1800’s. Trapping led to declines in the abundance and distribution of beaver (*Castor canadensis*)—and more importantly, their dams—from low-gradient stream reaches. The loss of beaver dams and ponds reduced water storage that would have otherwise sustained late summer low flows, removed winter habitat and refugia, and increased stream flashiness as channel roughness decreased (Collen and Gibson 2001). This probably reduced overall abundance of greenback cutthroat trout in larger systems, and led to extirpations in smaller ones where such habitats were critical. Although beaver have recovered somewhat, they are believed to have reached only 10 to 25 percent of their historical abundance (Naiman et al. 1986).

Various forms of mining led to the wholesale loss of populations in waters of all sizes. Stream-based mining, such as sluicing, hydraulic mining, or dredging, completely altered stream channels (and sometimes valleys) and created sediment loads without historical precedent. Toxicants introduced from underground sources as well as the intentional or accidental disposal of solvents used to extract metals from raw ore rendered streams uninhabitable for many forms of life. Colorado has over 7,000 abandoned mines, and mine drainage influences over 2,600 km of streams (Rueth et al. 2002). Recovery from channel alteration

may require centuries, and heavy metal leaching from hardrock mines may be difficult to mitigate for the foreseeable future. Currently, mining undergoes much more stringent environmental regulation, but this has not removed the possibility of catastrophic events, as was demonstrated in the late 1980’s by the sodium cyanide spill and biotic sterilization of a long reach of the Alamosa River following the heap leach pond failure at the Summitville Mine. That the 1872 Mining Law continues to hold sway suggests that future effects of mineral development on fish populations are possible. Recreational hydraulic mining for small deposits of precious metals probably has localized effects from increased suspended sediment concentrations (Thomas 1985).

Timber harvest began in earnest coincident with the demand for mine timbers and fuel, but it reached an initial peak upon the arrival of the railroad in the late 1800’s, with its requirement for railroad ties (Wroten 1956). Because no road system existed, streams channels were used to transport up to tens of millions of railroad ties annually to railheads farther downstream. These tie drives were conducted during high spring flows after the winter-long harvest of timber. Streams were often ponded behind temporary dams, which were blown out to release a rush of water and wood. To prevent jams from developing, streams were often cleared of large wood and boulders with dynamite before the drives began. This has left a legacy of simplified stream channels and early successional riparian zones that probably support cutthroat trout populations at reduced densities relative to historical levels, and will continue to do so until riparian stands become large enough to contribute large wood to channels (Young et al. 1994).

Overall, logging on federal lands in the Rocky Mountains has decreased as recreational use of those areas has increased (Rueth et al. 2002). Riparian timber harvest has largely ended, thus the likelihood of large wood contributions from riparian zones to stream channels is increasing (Fausch and Young 2004). In part, more recent timber management has had a lesser effect on stream channels simply because of a larger road network, but that network has been a chronic contributor of sediment (Eaglin and Hubert 1993, Trombulak and Frissell 2000) and the cause of fish barriers in the form of impassable culverts (see Habitat fragmentation, above) and simplified habitats from channelization of streams adjacent to roads.

Livestock grazing was also historically far more intensive than at present, but in certain areas it still degrades habitat of streams with greenback cutthroat

trout. Although grazing effects are often confounded with other factors and sometimes difficult to isolate (Rinne 1999), the preponderance of evidence suggests that concentrations of livestock in riparian zones often lead to bank damage, higher sediment delivery, and the removal of woody and herbaceous vegetation (Belsky et al. 1999, Agouridis et al. 2005), all of which can contribute to trout population reductions. However, different grazing systems are likely to have different effects on stream channels. For example, relative to high-intensity, short-duration grazing by cattle, season-long grazing was associated with declines in terrestrial macroinvertebrate infall and aquatic macroinvertebrate drift and reduced trout density and biomass in Wyoming streams (Saunders and Fausch 2007). In addition, use of channels by cattle that coincides with the incubation of trout eggs and alevins may lead to redd trampling and reduced embryo survival (J. Brammer, Beaverhead-Deer Lodge National Forest, unpublished data).

The magnitude of water development within the range of greenback cutthroat trout is staggering. Colorado has over 67,000 points of water diversion on or within 10 km of national forests and grasslands, and statewide, diversions have legally binding water rights that are 150 times the mean historical runoff for the entire state (Pepin et al. 2002). Although the primary problem associated with water development has been habitat fragmentation, the altered timing and magnitude of flows has also contributed to a lessened capacity to support cutthroat trout populations. Diversions often reduce discharge during the late summer irrigation season, which is also the time of greatest growth in cutthroat trout, hence water removal is essentially equivalent to a reduction in the amount of habitat and thus the size a population can attain. Diversion structures can also entrain large numbers of downstream-migrating fishes that fail to escape from irrigation channels when flow is discontinued (Zydlewski and Johnson 2002, De Rito 2004). For example, greenback cutthroat trout were found trapped below a diversion structure in an irrigation ditch draining Como Creek, one of the few waters with a historical population of this subspecies (M.K. Young, personal observation). In addition, snow-making operations associated with ski areas may alter the hydrograph by shrinking autumnal flows and promoting larger and later snowmelt runoff that could depress recruitment in cutthroat trout populations. Localized cloud seeding for enhancing winter snowpack could have a similar effect on peak flows, but both practices might beneficially enhance late summer base flows.

Finally, urbanization is likely to be detrimental to greenback cutthroat trout populations. The Rocky Mountain states are experiencing some of the fastest growth in the country; the annual growth rate was 3 percent compared to 1 percent in the rest of the United States in the 1990's (Theobald and Hobbs 2002). In Summit County, Colorado, the population tripled between 1975 and 2000, and Douglas County, Colorado was one of the fastest growing counties in the nation in the 1990's (Travis et al. 2002). By 2030, an additional 1.5 million people are projected to live in Colorado (U.S. Census Bureau, unpublished data; available at <http://www.census.gov/population/www/projections/projectionsagesex.html>). The primary risk of increasing population growth is the lack of a concomitant decline in per-capita resource use. This is likely to reduce management flexibility to restore cutthroat trout populations because of other demands for resources, particularly the consumptive use of water and schemes to route it to locations of greatest demand. Intensified use of public lands for a variety of purposes, greater occupation of private land adjacent to or surrounded by federal lands, and litigation associated with both appear likely to constrain opportunities to retain or restore natural disturbances that may be essential to habitat formation. This suggests that action to promote greenback cutthroat trout conservation may be easier now than it will be in coming decades. Finally, an indirect consequence of this growing population is air pollution. Although the most widespread effects of fossil fuel consumption by a growing population are probably being manifest in a changing climate (see below), burning of hydrocarbons in conjunction with agricultural fertilization has increased the deposition of atmospheric nitrogen in nearby mountains, which could result in localized acidification of waters draining basins that lack sufficient buffering (e.g., along the Colorado Front Range; Bowman et al. 2002).

It is difficult to address the cumulative effects of these activities for any particular population of greenback cutthroat trout. However, it is telling that the vast majority of relict populations of Colorado River cutthroat trout in Colorado and Wyoming are found on public rather than private lands, and that they disproportionately occur in USFS wilderness areas and in national parks that are largely free from the aforementioned forms of land management (Hirsch et al. 2006). A similar pattern has been observed for many salmonids in the Rocky Mountains and Pacific Northwest (Kershner et al. 1997, Lee et al. 1997, Thurow et al. 1997, Shepard et al. 2005).

Natural disturbance

Because cutthroat trout evolved with the natural disturbance regimes of the Rocky Mountains, it is assumed that these disturbances did not represent a widespread threat to their persistence. The currently restricted distribution of greenback cutthroat trout has altered the risks that natural disturbance can pose, but such disturbance may also present opportunities for enhancing or restoring populations of cutthroat trout.

Fire: The immediate and long-term effects of wildfire on aquatic ecosystems and fish populations are receiving greater attention in the literature (Young et al. 2003). Occasionally, thermal or water chemistry changes associated with severe wildfire have led to direct mortality of trout populations (Rinne 1996, Howell 2006); however, many populations have endured such fires with few or no ill effects or showed only temporary declines (Rieman and Clayton 1997, Gresswell 1999, Burton 2005, Sestrich 2005). More problematic may be post-fire floods, blackwater events, and debris torrents triggered by summer thunderstorms that have reduced or eliminated salmonid populations (Bozek and Young 1994, Brown et al. 2001). Cannon (1999) observed that the probability of some form of post-fire debris flow was about one in three in portions of the Rocky Mountains, and was largely dependent on storm events in which rainfall intensity exceeded soil infiltration capacity. Given such storms, the proportion of a tributary basin burned by high-severity fire was the best predictor of the location of a debris torrent (Hyde 2003). Nevertheless, the majority of events are in small (<2.6 km²), steep (>20%) basins (Parrett et al. 2003), and these would usually not threaten entire populations (Rieman and Clayton 1997, but see Brown et al. 2001). The probability of such events often declines rapidly in subsequent years (Cannon 1999).

Secondary effects of fire may depress or boost populations. Channel stability often declines following fire because of the loss of riparian vegetation, increases in stream flow produced by reductions in evapotranspiration, and increases in sediment, but regrowth and resprouting of vegetation eventually attenuate off-channel contributions of sediment and water. Infall of fire-killed snags will spike in the first few decades following fire (Lyon 1984, Bragg 2000), which may lead to extremely complex channels with an array of complementary habitats. Growth rates of salmonids in burned streams often increase dramatically (J. Dunham, U.S. Geological Survey, unpublished data). Although this may in part be attributable to temporary changes in water chemistry, it

is more likely that decreased shading increases primary productivity that leads to greater macroinvertebrate abundance and food availability (Wilzbach et al. 2005). Because water temperatures are directly related to the amount of solar radiation reaching the water surface (Johnson 2004), post-fire temperatures are expected to increase. This may harm or bolster population growth rates depending on the pre-fire temperature regime (Dunham et al. 1999, Harig and Fausch 2002, Schrank et al. 2003). Streams previously too cold for consistent reproduction may support larger, more stable populations, whereas those that are already relatively warm may become seasonally uninhabitable. Both conditions will gradually revert to their original state as canopy cover and stream shading increase.

Fish community changes have also been hypothesized following fire. For example, nonnative species might invade post-fire habitats because the increased light, water temperature, sediment transport and deposition, and channel instability typical of such sites may favor nonnative salmonids (Dunham et al. 2003b). What little evidence exists, however, does not support this position. Sestrich (2005) found that brook trout invaded one system following fire but were depressed in several others, whereas westslope cutthroat trout tended to recover rapidly and sometimes exceeded pre-fire abundances in most streams. In another basin, all native and nonnative salmonids reestablished themselves in streams after undergoing fire-related fish kills (Howell 2006).

Fire occurrence in the central Rocky Mountains appears to be somewhat predictable. Schoennagel et al. (2005) found that large fires in subalpine forests of Rocky Mountain National Park were disproportionately associated with the coincidence of certain phases of multi-year climate cycles—the negative phase of the Pacific Decadal Oscillation and La Niña events—that promoted extreme drought in the year of the fire. In these and other high-elevation Rocky Mountain forests, antecedent conditions (e.g., weather in previous years) had little effect on fire incidence.

Other forest disturbance: Two other forest disturbances that may influence cutthroat trout populations are prevalent in the central Rocky Mountains: large-scale blowdown and stand mortality from insects. With regard to blowdowns, their highly localized nature is unlikely to affect large numbers of streams (Lindemann and Baker 2001). Those that do undergo blowdown may be heavily shaded for decades, which may reduce primary productivity and stream temperature, but will also represent a

source of large wood that will contribute to habitat complexity and possibly a series of temporary barriers to fish movement.

Insect-related mortality of conifers is a growing issue throughout the Rocky Mountains (Harris 2004). However, many of its effects are expected to be comparable to those of fire—decreased shading and pulsed deposits of large wood in stream channels (Bragg 2000)—and may represent a net benefit for cutthroat trout populations, particularly in those systems from which large wood has been lost as a result of human activities. It is presumed that the increased abundance of large wood will increase local fire intensity and fish mortality, but the interaction between fallen trees, fire characteristics, and management is highly controversial and has not been scientifically resolved (Rieman et al. 2003, Beschta et al. 2004, Karr et al. 2004).

Floods and drought: High flows following snowmelt are believed to reduce abundance of juvenile nonnative salmonids in Rocky Mountain streams (Nehring and Anderson 1993, Latterell et al. 1998), but because cutthroat trout generally spawn after flows peak in spring, the likelihood of redd scouring is low. However, the monsoonal thunderstorms in late summer typical of southern Wyoming and Colorado (Fausch and Young 2004) coincide with the period of egg incubation and fry emergence of cutthroat trout, and eggs, alevins, and fry may be susceptible to storm flows. Occasionally, such storms are severe enough to cause localized debris flows with more pronounced effects on trout populations and habitats (Roghair et al. 2002, Sato 2006). A minor debris torrent in the headwaters of the North Fork Little Snake River associated with a late August thunderstorm in 1999 effectively eliminated Colorado River cutthroat trout from a 600-m stream reach, and densities remained low in subsequent years (M.K. Young, unpublished data). The dendrochronological age of an alluvial plug above an abandoned channel in a nearby tributary provided evidence of a somewhat larger event 40 years earlier in this basin (M.K. Young, unpublished data).

In contrast, drought is a common, broad-scale phenomenon recurring at the interval of decades to centuries in the Rocky Mountains (Kittel et al. 2002), and drought-related declines in discharge reduce trout abundance and growth rates because of high temperatures and less available habitat (Elliott et al. 1997, Hakala and Hartman 2004, Harvey et al. 2006). Persistent drought has extirpated several populations of Colorado River cutthroat trout (Brauch and Hebein 2003), but the low flows and extended growing seasons probably promoted successful recruitment in the

coldest perennial streams (Isaak and Hubert 2004). Until recently, it appeared that droughts had relatively temporary effects on greenback cutthroat trout, but historical climate patterns may no longer apply.

Climate change

Climate change is an accepted fact among climate scientists. There is unequivocal evidence that the atmosphere is warming—0.74 °C in the last 100 years, with the last 50 years likely the warmest in the past 1300 years—and there is little doubt that anthropogenic activities are partly responsible (Intergovernmental Panel on Climate Change 2007). Because of the link between climate change, atmospheric carbon dioxide concentrations, and fossil fuel consumption, there is every reason to believe that warming will continue. For example, the U.S. Department of Energy (2006) forecasts that global consumption of coal will nearly double by 2030 (in large measure to fuel the demand for electricity, which is expected to more than double). Combustion of coal is the leading contributor to the anthropogenic production of greenhouse gases, and global carbon dioxide emissions are also expected to double in the next 25 years.

The environmental effects of climate change are being felt worldwide and in the Rocky Mountains. Snowpacks in the western United States are now melting 1 to 4 weeks earlier than they did 50 years ago, flows are peaking earlier, and late-summer baseflows are declining (Mote et al. 2005, Stewart et al. 2005). The biota are responding as well; the spring arrival of migrating birds and emergence of hibernating mammals in the Colorado Rockies have advanced several weeks over the past few decades (Inouye et al. 2000), the range of macroinvertebrate species in northern Europe has begun to retract uphill and farther north (Franco et al. 2006), and similar changes in phenology or distribution are being exhibited by disparate taxa throughout the world (Parmesan and Yohe 2003, Root et al. 2003). The effects of climate change on specific populations of greenback cutthroat trout are difficult to predict because of site-to-site variation in the contribution of groundwater and surface flow to discharge, the uncertain applicability of predictions from global circulation models to particular regions, and the challenges of forecasting climate in montane environments (Christensen et al. 2007). Nevertheless, the regional trends and forecasts have profound implications for the viability of this subspecies. The consensus from climate model predictions is that high-latitude and high-elevation sites will receive greater winter precipitation but more of this precipitation will fall as rain and the snowline will

rise (Kittel et al. 2002, Christensen et al. 2007). These predictions are consistent with the observed changes in hydrology over the last 50 years (Mote et al. 2005, Stewart et al. 2005). Recent simulations are suggesting that summer temperatures in the western United States are expected to rise 2 to 5 °C in the next 34 to 63 years (Running 2006) whereas summer precipitation will decline (Christensen et al. 2007). In particular, models and recent evidence indicate that most of Colorado and Utah will develop climatology in the coming decades in which the levels of aridity encountered during the Dust Bowl of the 1930's or the mid-century drought will become the new standard (Seager et al. 2007). If these forecasts are correct, populations of all trout, including greenback cutthroat trout, may be confined to smaller, more upstream habitats affording perennial flow (Keleher and Rahel 1996, Flebbe et al. 2006), potentially including some that are currently uninhabitable because of cold water temperatures (Isaak and Hubert 2004, Cooney et al. 2005). Regional droughts coupled with changes in snowmelt timing could also lead to the synchronous drying of small streams throughout large portions of the South Platte and Arkansas river basins. Given that migration barriers probably restrict the upstream extent of many populations of greenback cutthroat trout (cf. Kruse et al. 1997), the overall effect would likely be a net reduction in the abundance and distribution of greenback cutthroat trout and an increase in their susceptibility to small-population phenomena such as inbreeding and vulnerability to disturbance. Recent work on disturbance has linked an increase in fire frequency, size, and duration at mid-elevation sites to the earlier snowmelt typical of the last few decades (Westerling et al. 2006); thus in a warming climate, isolated populations of greenback cutthroat trout are likely to be at greater risk from fires and post-fire floods (cf. Brown et al. 2001). This risk may also be high at lower elevations where fire suppression has had the greatest effects on forest stand structure (e.g., ponderosa pine [*Pinus ponderosa*] forests) or where extensive stands of conifers have died from insect attacks (Keane et al. 2002). The probability of intense storms also appears to be increasing (Intergovernmental Panel on Climate Change 2007), which could heighten the threat of damaging floods. Another risk is that brown trout and rainbow trout either require higher temperatures or are more tolerant of them than are cutthroat trout (Bear 2005, Lobón-Cerviá and Mortensen 2005), which could favor replacement or more rapid introgression of cutthroat trout populations where these species co-occur. It should be pointed out that greenback cutthroat trout, and all of the flora and fauna of the Rocky Mountains, have endured climatic conditions more

extreme than those at present or likely to exist in the near future (Whitlock et al. 2002). The present cause for concern is that migratory routes to new habitats or persistent refugia have been altered by human water development, barriers to movement, and invasions of nonnative species. Overcoming this problem by relying on human transfers of stocks has a different set of implications for the persistence of this subspecies that are described elsewhere in this document.

Intentional manipulation of climate, such as cloud seeding to increase winter snowpack, is underway in this region (e.g., the Sierra Madre and Snowy Range of Wyoming; Wyoming Water Development Commission, unpublished data). In the absence of overall climate change, such practices might decrease mid-summer water temperatures while increasing base flow in streams with greenback cutthroat trout, and could have positive or negative effects on populations. Predictions regarding current and future outcomes, however, are uncertain because the full magnitude of climate change remains somewhat speculative.

Conservation Status in Region 2

Primarily as a consequence of a variety of anthropogenic events, the distribution, abundance, and diversity of greenback cutthroat trout is greatly reduced relative to historical levels, including on lands administered by Region 2. Based on Young et al. (2002), the majority of populations are restricted to relatively small (<4.5 km) and unproductive headwater (above 2,700 m) streams and small (<5.1 ha), high-elevation (above 3,100 m) lakes. Virtually all migratory life history forms have been lost and cannot be reestablished in the existing fragmented habitats. Larger, more productive low-elevation streams and rivers that supported migratory fish are now occupied by nonnative fish species and surrounded by human development. The many barriers that protect greenback cutthroat trout populations from nonnative fish invasions simultaneously isolate them and prevent neighboring populations from providing demographic support or individuals for refounding extirpated populations (Fausch et al. 2006). Extant populations remain at risk from ongoing invasions, barrier failure or unauthorized human introductions that permit nonnative trout to invade, and catastrophic environmental events (e.g. wildfire) that could eliminate individual populations or groups of isolated populations in a basin. It is likely that many populations, particularly the smallest and least productive, are losing genetic variation and a few others are introgressed with genes from nonnative

congeners. Climate change and a rapidly growing human population in the Rocky Mountains are likely to exacerbate many of these problems.

Overall, the majority of populations regarded as greenback cutthroat trout in the recovery plan are in the South Platte River basin, and many of these are in Rocky Mountain National Park (Young and Harig 2001). It seems unlikely that local environmental phenomena, such as fire or post-fire debris torrents, would endanger considerable numbers of populations, however few populations are replicated and the risk of losing portions of the genome is high. Moreover, the concentration of populations in Rocky Mountain National Park does represent a risk in the event of large-scale environmental events, perhaps driven by climate change, that could simultaneously threaten many populations, and result in reduced population sizes that are vulnerable to other effects (such as genetic bottlenecks or disturbances to which populations would normally be resilient) or lead to outright extirpation. Land management, such as mining, grazing, road building, and timber harvest, and water management, such as water withdrawals or additions and diversion structures, degrade and fragment some habitats and probably depress some populations, but effects vary among streams. Land management is unlikely to be the sole cause of wholesale population losses, but in concert with other anthropogenic activities or natural disturbances could tip some populations toward extinction. Most lake populations have been unaffected by land management because of their remote locations, and are probably more secure than populations in streams (except in the event of climate alterations that might lead to widespread winterkill or cooling of spawning areas). These sites, however, probably were not occupied historically.

Substantial investments in management and research have been directed at the conservation of greenback cutthroat trout since 1957 (U.S. Fish and Wildlife Service 1998, Young et al. 2002, and references therein). The security of this taxon was thought to be vastly improved by this work until the recent finding that many populations may consist instead of Colorado River cutthroat trout or inadvertent hybrids between greenback cutthroat trout and Colorado River cutthroat trout (Young et al. 2002; Metcalf et al. 2007). Moreover, the remaining populations show reduced levels of genetic variation relative to other cutthroat trout populations (Metcalf et al. 2007). If these findings are correct, the status of greenback cutthroat trout is uncertain. Until comprehensive genetic testing of recovery populations is completed, perhaps guided by the reconstructed

pedigree of each introduced population (Young et al. 2002), the number and distribution of populations of greenback cutthroat trout remains uncertain. Conserving the nonintrogressed remnants of this taxon represents a critical challenge.

Potential Management in Region 2

Implications and potential conservation elements

Complete restoration of greenback cutthroat trout to its historical range is presently unattainable, largely because invasions of nonnative fish in large systems seem irreversible and habitat loss associated with water diversion is unlikely to be mitigated. Nonetheless, the conservation status of this taxon can be improved in a number of ways. A number of guidelines (see McElhany et al. 2000 and Fausch et al. 2006 for a comprehensive discussion) merit consideration with respect to ensuring the long-term persistence of populations of greenback cutthroat trout throughout their historical range and in Region 2:

- ❖ Replicating indigenous populations in other waters in a particular basin can reduce the risk of loss of unique portions of the genome. This is a commonly recommended tactic for many species of rare salmonids (Apache Trout/Little Colorado River Spinedace Recovery Team 2000, U.S. Fish and Wildlife Service 2003). Increasing the number of populations also reduces the overall risk of extinction of the subspecies.
- ❖ Increasing the size of individual populations beyond particular thresholds (hundreds to thousands of adults; McIntyre and Rieman 1995, Allendorf et al. 1997) can improve the probability of persistence of populations and their retention of genetic variation.
- ❖ Improving habitats could increase productivity and resilience with respect to demographic insults, but it should be recognized that habitats are dynamic and that restoring habitat-forming processes may prove more successful and enduring than altering habitat directly (Beechie and Bolton 1999, Roni et al. 2002).
- ❖ Those populations with access to stream networks could show increased persistence because of greater habitat complementarity,

availability of refugia, and connectivity to other population segments that might escape deleterious effects of disturbance or management. Populations occupying complex and predictable environments may also be more stable (Schosser 1995, Schlosser and Angermeier 1995). In addition, restoring populations of greenback cutthroat trout to basins in different stages of forest succession or different basin configurations reduces the likelihood that a single disturbance, such as a stand-replacing fire or localized downburst, will simultaneously depress all populations (Rieman and Clayton 1997, Miller et al. 2003, Rieman et al. 2003). If such basins are part of the same connected network, habitat complementarity would greatly increase.

- ❖ Restoration of larger, more fecund fish with a migratory life history to waters would increase population resilience to habitat alteration from human or natural causes (Rieman and Clayton 1997, Rieman and Dunham 2000), and might facilitate their persistence despite the presence of nonnative salmonids.
- ❖ Given that the future is uncertain but that change is inevitable, of critical importance may be favoring management of wild populations that have the opportunity to evolve (Ruckelshaus et al. 2002). Stated another way, Stockwell et al. (2003) argued that particular populations be viewed not as static repositories of traits but as dynamic reserves of evolutionary potential. Or to quote Cox (2004): “The best protection we can give species unique to our land, freshwater, and ocean areas is the potential to adapt by evolution and dispersal to conditions of a rapidly changing environment.” This favors maintaining populations in a wide array of habitats that enable expression of a variety of phenotypes (Healey and Prince 1995) and discourages population maintenance via anthropogenic supplementation (unless conditions become particularly dire; see Minckley 1999). Northcote (1997) contended that management by isolation and periodic supplementation simplified large-scale diversity, and some authors (e.g., Willson 1997) consider such isolated populations as evolutionary dead ends (for an alternate view, see Scudder 1989).

- ❖ Introductions of this subspecies into formerly fishless waters may harm other organisms (Dunham et al. 2004) and the consequences deserve attention. Other management activities for cutthroat trout, such as the application of toxicants, can also be deleterious for non-target organisms.
- ❖ Because financial and human resources are limited and managers are confronted by an array of decisions about what to do and where to do it, a strategic, efficient approach to conservation is important (Margules and Pressey 2000). A suite of streams for restoration of greenback cutthroat trout has been identified (U.S. Fish and Wildlife Service 1998), but rules for prioritizing restoration actions among these have not. Also, landscape-scale considerations might identify a different set of candidate waters (Dave Winters, U.S. Forest Service, personal communication).

It should be noted that other perspectives on the value of greenback cutthroat trout would list a much different set of conservation elements. Quist and Hubert (2004) argued that there appears to be little ecological difference between cutthroat trout and introduced trout species and that the social and economic values of nonnative species usually exceed or at worst are equal to native cutthroat trout. Consequently, they questioned the merit of substantially investing in their conservation beyond maintaining a few token populations given what they perceived to be the inevitable loss of nearly all populations of cutthroat trout. This ignores the legal mandate for conservation of some subspecies of cutthroat trout established by the Endangered Species Act, as well as making evident that it is much less expensive to conserve existing populations than to establish new ones. In addition, there is growing evidence to counter their perspective; for example, it appears that the various salmonid species differentially alter trophic pathways in aquatic and terrestrial ecosystems (Baxter et al. 2005). One thing, however, is certain: the wholesale loss or introgression of indigenous populations of greenback cutthroat trout would reroute the course of millions of years of evolutionary history, and at this point the outcome is not likely to be appreciated or understood (for a similar perspective with respect to brown trout, see Araguas et al. 2004). Consequently, preserving the potential for all foreseeable conservation alternatives seems prudent.

That said, it should be acknowledged that the success of greenback cutthroat trout conservation may have less to do with tactics and strategies than with cultural values and the flexibility and openness of biologists, agencies, and the public to new solutions. Lichatowich et al. (1999) pointed out that as early as the 1880s, as a society we understood what caused declines in salmon populations in the Pacific Northwest, yet many of these populations were subsequently decimated or extirpated. They argued that this resulted from an inherent societal belief in a harvestable excess, faith in the efficacy of technological solutions for ecological problems, and an unwillingness to recognize signs of failure because of an ideological certainty in the correctness of a particular solution. For these reasons, they doubted that many biologically focused management proposals would improve prospects for Pacific salmon. Along the same lines, Lackey et al. (2006) related that fisheries professionals often expressed public optimism about salmon recovery efforts but were privately pessimistic, and concluded that these professionals recognized that efforts at salmon conservation were destined to be futile without policy and institutional change. One such change might be to practice adaptive management (Walters 1986), a style of resource management that emphasizes learning by doing, but despite much fanfare, it has not been widely adopted or consistently applied with success (Ludwig and Walters 2002, Sabine et al. 2004, Stankey et al. 2005). Allan and Curtis (2005) believed resistance to adaptive management, with its emphasis on reflection, learning, and embracing complexity, arose from existing management styles that favor activity, control, comfort, and certitude about outcomes (also see McAlpine et al. 2007). Minns et al. (1996) reached a similar conclusion with regard to fish habitat restoration, in that to some agencies it was more important to be seen doing something than it was to try to understand the correct thing to do. Nevertheless, the partial successes in some case studies of adaptive management—improved integration between management concerns and research priorities and greater appreciation of the critical role of monitoring—illustrate its potential value for addressing complex ecosystem management problems (Bormann et al. 2007). Regardless of the approach, experimenting with institutional change warrants consideration equal to that given to the application of particular strategies or adoption of protocols in the conservation of greenback cutthroat trout in Region 2.

Tools and practices

Population and habitat monitoring

A review of the literature indicates that there is a burgeoning interest in statistically sound, politically necessary, and ecologically meaningful monitoring programs (e.g., Fitzpatrick et al. 1998, Urquhart et al. 1998, Kaufmann et al. 1999, Stevens and Olson 1999, Williams et al. 2002). Also abundant are critiques arguing that most monitoring designs are neither robust nor relevant, rendering them almost useless (e.g., Bisbal 2001, Yoccoz et al. 2001, Legg and Nagy 2006). Because adequate inventorying and monitoring is fundamental to identifying the location, extent, and size of fish populations, the kind and amount of habitat, and the variation and trends in both, the importance of their thoughtful development cannot be exaggerated.

Bisbal (2001) offered a seven-step outline for developing a sound monitoring program for fish and wildlife in the Columbia River basin (see Thompson et al. 1998 for a more generic though comprehensive review of monitoring). These steps include: (1) adopting an ecological management framework that integrates an agency vision for a species and its ecosystem in the context of society and natural events; (2) identifying what could be monitored (e.g., any characteristic of a greenback cutthroat trout population or its habitat) and at what scale (e.g., range-wide, region-wide, or forest-wide) to achieve this vision; (3) establishing what will be monitored (i.e., what subset of possible indicators will provide the essential information on the status of the species and ecosystem of concern, what design best captures that information, and what thresholds will trigger a management response) and performing a pilot study to validate the selections; (4) creating a data archive that captures what is already being done and what should be added; (5) procuring that additional information; (6) managing the data by ensuring that quality control and assurance are practiced, and data are accessible, formatted for ready analysis, and regularly updated; and (7) conducting three forms of evaluation: a) scientific evaluation to ensure that the monitoring system is valid and the data are credible, b) policy evaluation to determine whether the data are sufficiently informative to make management decisions (which may lead to changes in objectives as well as the monitoring strategy), and c) public evaluation, including review of the data and inclusion in decision making, to promote accountability of managers and politicians.

A full discussion of all aspects of a sound monitoring program for greenback cutthroat trout is beyond the scope of this manuscript. Nevertheless, the recovery plan for greenback cutthroat trout (U.S. Fish and Wildlife Service 1998) specifies that several types of monitoring will be conducted and these points are discussed in greater detail below.

Population inventory: Although an understanding of the distribution of many lesser-known fishes in this region would benefit from predictions based on statistical models of habitat (Angermeier et al. 2002, Olden and Jackson 2002), the inventory of populations of greenback cutthroat trout is probably approaching completion because this taxon has been the subject of focused efforts for decades. Nonetheless, previously undiscovered populations continue to be found, often in waters once thought too small, steep, or isolated to contain greenback cutthroat trout. Consequently, these and any remaining unreported populations are likely to be small but may be valuable because they are likely to constitute novel components of the genomic diversity of this taxon.

The recovery plan for greenback cutthroat calls for a systematic search of waters that may contain relict populations (U.S. Fish and Wildlife Service 1998), but it does not specify a particular strategy. The location of populations has usually relied on developing a list of streams with suitable environmental characteristics (i.e., likely trout streams) that were not believed to have been invaded by nonnative salmonids or to have been stocked, followed by field surveys relying on observations from stream banks or spot samples with electrofishing (Hepworth et al. 2001, Colorado Division of Wildlife, unpublished data). These surveys are typically informal and provide semi-quantitative information on the size, structure, and longitudinal distribution of individual populations. More structured sampling that facilitated predictions about presence and habitat relations has been conducted for other salmonids in the Rocky Mountains (Paul and Post 2001, Rich et al. 2003), and still more rigorous inventories have been proposed (Peterson et al. 2002).

There have also been many inventories of the genetic status of greenback cutthroat trout populations (Young et al. 2002). These surveys were generally conducted to evaluate the level of introgression of greenback cutthroat trout populations with nonindigenous *Oncorhynchus*. Because of the costs of analyses or risks to the population from lethal sampling for allozyme studies, such sampling has

been less comprehensive than population detection or monitoring. Sampling is becoming more commonplace because the techniques currently available to evaluate mitochondrial, ribosomal, and nuclear DNA are increasing the probability of detection of introgression (primarily due to the increase in diagnostic markers and ability to use non-lethal tissue samples; Neville et al. 2006b) while reducing the expense of analyses and effects on sampled populations. One caution is that populations can never be conclusively demonstrated as being free from introgression. Instead, it can be stated that with a given level of confidence the percentage of nonindigenous genes is below some value (e.g., there is a 95 percent probability that the proportion of rainbow trout genes present is ≤ 1 percent), with the caveat that these values will vary based on which method is used and what part of the genome is examined (Pritchard et al. 2007a). A second issue is that sometimes little attention is given to the spatial distribution of fish sampled for genetic analyses. Fish collected from a single site may be unrepresentative of the entire population (Bischoff 1995, Weigel et al. 2003).

Population monitoring: As alluded to above, how population monitoring is conducted should reflect why monitoring is needed. For example, objectives that involved understanding population size, structure, distribution, trend, response to management, variability, synchrony, or probability of extinction (Thompson et al. 1998, Staples et al. 2005) could dictate different forms of population monitoring. A goal of the recovery plan for greenback cutthroat trout is the establishment of 20 populations containing at least 500 fish over 120 mm, supporting a biomass of at least 22 kg per ha, and exhibiting successful periodic natural recruitment (U.S. Fish and Wildlife Service 1998), which implies that estimates of population size and biomass, and indirectly of habitat size, will be important targets of a monitoring scheme.

Presently, most quantitative population monitoring of greenback cutthroat trout is based on periodic sampling (e.g., every 3 to 5 years) of one to a few index reaches in each stream (Young et al. 2002), but some basinwide sampling of occupied habitats has been done (U.S. Fish and Wildlife Service and Colorado Division of Wildlife, unpublished data). Index reaches tend to be about 100 m long, and block nets are sometimes installed at each end of the index reach during sampling. Crews typically make two or three electrofishing passes and use estimators based on the removal method to calculate abundance of juvenile and adult fish, but not of age-0 individuals (Colorado

Division of Wildlife, unpublished data). Most current inventories do not appear to address the within-stream distribution of cutthroat trout.

Measuring in-stream distribution: Knowing the upstream-downstream boundaries of a population are crucial if abundance estimates are extrapolated from sampled reaches, and in some areas, whether particular stream reaches harbor fish affects management of adjacent riparian and upland forests (Cole et al. 2006). Biologists have devised a number of methods to estimate the longitudinal distribution of inland trout populations within streams. Harig and Fausch (2002) identified the extent of greenback cutthroat trout in study streams by walking upstream from a known fish barrier while observing fish from the stream bank or probing cover to disturb concealed individuals, an effective procedure because cutthroat trout tend to be active and visible during the day (Young 1996). They ceased observations upon encountering an obvious fish barrier or stream channels so narrow (≤ 1 m wetted width) that the numbers of cutthroat trout present, if any, would not be appreciable (Harig and Fausch 2002). Occupied stream length was then measured with a geographic information system. Young and Guenther-Gloss (2004) and Young et al. (2005) used a similar visual method to define the downstream-upstream limits of populations of greenback cutthroat trout or Colorado River cutthroat trout, but they measured channel length in the field with a drag tape. They also continued visual observations for 500 m past the last fish detected or until wetted stream width was ≤ 0.5 m. This was followed by electrofishing at systematic intervals (usually ≤ 250 m) to verify conclusions about trout distribution. Similar approaches for assessing inland trout distributions have been used elsewhere (Propst and Stefferud 1997, Jones et al. 1998, Sloat et al. 2002, Bateman et al. 2005, Cole et al. 2006). It should be recognized that trout populations may contract or expand their upstream or downstream limits depending on environmental conditions (Larson et al. 1995, Jones et al. 1998), but these shifts tend to be relatively minor for fish with resident life histories (Cole et al. 2006, Fransen et al. 2006, but see Clapp et al. 1990 and Colyer et al. 2005 for an example of how the timing of sampling would influence estimates of downstream limits). In addition, barriers and other unsuitable environments can restrict populations to a fraction of the available perennial stream habitat (Angermeier et al. 2002, Wofford et al. 2005), so map-based estimates (Fransen et al. 2006) in lieu of field surveys are likely to be unreliable.

Measuring in-stream abundance: Three techniques are frequently used to count trout: stream

bank observations, snorkeling, and electrofishing. In general, stream bank counts are the least robust because large numbers of fish are not detected, and detection depends on fish behavior and viewing conditions (Heggenes et al. 1990, Bozek and Rahel 1991a, Young and Guenther-Gloss 2004, Young et al. 2005). As noted above, however, visual counts have been helpful in describing fish distributions (Harig and Fausch 2002) and are less labor intensive than other methods. Nighttime spotlighting has also been effective (Hickey and Closs 2006), but visibility depends on fish behavior and habitat complexity. Snorkel surveys have been widely used for estimating fish abundance (e.g., Mullner et al. 1998, Wildman and Neumann 2003), and protocols for effective sampling have been described (Dolloff et al. 1996). Counts obtained during day or night snorkeling sometimes differ substantially, with counts at night often being much higher in streams with cold temperatures (Roni and Fayram 2000, Thurow et al. 2006). Although snorkel counts of many species tend to be less than those obtained by electrofishing (Rodgers et al. 1992, Thurow and Schill 1996, Thurow et al. 2006), these are often correlated, and snorkeling may be favored because it requires less effort (Hankin and Reeves 1988, Roni and Fayram 2000).

Electrofishing is the most widely used method for obtaining counts of greenback cutthroat trout to obtain abundance estimates. The basics and nuances of proper technique have been thoroughly addressed (Bohlin et al. 1989, Cowx 1990, Cowx and Lamarque 1990), but approaches for optimizing effectiveness are still being developed (Miranda and Dolan 2003, 2004; Beaumont et al. 2005, 2006). Despite that electrofishing usually generates greater counts than other methods, not all fish are caught because the vulnerability to capture varies with fish length (Zalewski 1985, Dolan and Miranda 2003, Peterson et al. 2005), habitat complexity (Peterson and Cederholm 1984, Habera et al. 1992), habitat size (Riley et al. 1993, Rosenberger and Dunham 2005), water depth (Gardiner 1984), conductivity (Zalewski and Cowx 1990), fish species (Peterson et al. 2004b), fish density (Kruse et al. 1998), and whether an area has recently been electrofished (Cross and Stott 1975, Riley and Fausch 1992). This variation in capture efficiency has important ramifications for obtaining unbiased estimates of trout abundance, depending on the estimator that is used, but high capture efficiencies are necessary for precise estimates regardless of model choice (White et al. 1982). This must be balanced with the risk of injury to some fraction of the fish population (Reynolds 1996, Barton and Dwyer 1997, Snyder 2003), particularly of rare or federally listed species (Nielsen 1998).

The two most commonly used estimators are removal (or depletion) estimates and mark-recapture (also known as Petersen or Lincoln-Petersen) estimates (Seber 1982, Gatz and Loar 1988, Williams et al. 2002). Removal estimates are based on the notion that a constant effort will result in a constant rate of removal (i.e., the number of fish removed on each sampling pass is a fixed proportion of those present). The accuracy of removal estimates relies on meeting several assumptions: (1) for all practical purposes, the population is closed (i.e., there are no births, deaths, emigrants, or immigrants) during sampling; (2) all fish have an equal probability of capture; and (3) probability of capture remains constant during all sampling intervals. Mark-recapture estimates consisting of a single marking run and recapture run, as practiced by most stream biologists wishing to obtain an abundance estimate, also depend on (1) and (2) above, and that all marked individuals are recognized.

To meet the first assumption, biologists have sometimes installed block nets at the upstream and downstream ends of sampling reaches to prevent fish from escaping during sampling. However, many biologists forego using block nets because they do not believe that many fish attempt to swim a great distance to avoid capture, that numbers of escaping fish are low relative to total numbers of fish present, and that installation of block nets may cause fish to flee from or into the sampling area and bias capture totals (Bohlin et al. 1989, Amiro 1990a, Heggenes et al. 1990). Peterson et al. (2005) demonstrated that substantial numbers of bull trout and rainbow trout moved during electrofishing and advocated that block nets be used, but noted that movement (or the lack thereof) of rainbow trout was explained more by the presence of rubble on the stream bottom than the presence of a block net. In contrast, Young and Schmetterling (2004) found that very few fish left 200-m sampling sections between mark and recapture runs, and that ignoring fish movement would have resulted in positive biases in abundance estimates of 3 to 8 percent. Regardless, the installation of block nets represents a substantial investment in time and labor that might cause crews to forego additional sampling. This tradeoff, and defining *a priori* an acceptable level of this sampling bias, may be important to a monitoring plan.

The second assumption of equal catchability among all individuals has long been known to be false because electrofishing is a size-selective technique. Consequently, biologists usually develop separate population estimates based on the catchability of fish of different lengths (Büttiker 1992) or forego estimates of fish below a given size (for example, age-0 fish). More

problematic is the implicit assumption that the catchable population equals the total population. Bohlin and Sundström (1977) suggested that some proportion of the population could avoid capture based on physiology or behavior, and that these fish were not visually distinguishable from other members of the population. It is difficult to correct for this bias in population estimates, which can also be generated by unequal catchability among marked and unmarked fish (such as from a nonrandom distribution of each or inherent differences in vulnerability to electrofishing; Peterson and Cederholm 1984). Heterogeneity in capture among individuals can be incorporated into more sophisticated models (Williams et al. 2002), but these are rarely used for routine population estimation.

The assumption of equal detectability during all sampling intervals is the most difficult to meet. Recently electrofished trout undergo physiological and behavioral changes for about 24 h that may render them less vulnerable to recapture by electrofishing (Mesa and Schreck 1989). To overcome this problem, biologists may wait several hours to several days between marking and recapture runs (Vincent 1983, Rodgers et al. 1992, Peterson et al. 2004b, Rosenberger and Dunham 2005, Temple and Pearsons 2006). However, those performing multi-pass removal estimates often repeat sampling passes at much shorter intervals (≤ 1 h), which appears to reduce catchability of fish on successive passes (Riley and Fausch 1992, Peterson et al. 2005). The resulting negative bias in removal estimates is sometimes severe (>50 percent) and has long been recognized (Cross and Stott 1975, Heggberget and Hesthagen 1979, Mahon 1980, Bohlin 1982, Amiro 1990b, Libosvářský 1990). Consequently, mark-recapture methods tend to estimate abundance more accurately than removal methods do (Peterson and Cederholm 1984, Rosenberger and Dunham 2005), but these estimates also suffer from bias when model assumptions are not met (Robson and Regier 1964, White et al. 1982, Peterson and Cederholm 1984). Whichever model is chosen, greater capture efficiency and greater effort typically results in more precise and less biased estimates (Robson and Regier 1964, Randall 1990, Rosenberger and Dunham 2005).

A more fundamental issue with monitoring populations of greenback cutthroat trout may be dealing with spatial variation in abundance. Although extrapolating counts or estimated abundance from single (or a few) reference, representative, or index reaches to entire streams is typical, the method lacks inferential power because of the untenable assumption of uniform fish densities throughout a stream (Thompson et al. 1998, Yoccoz et al. 2001, Williams et al. 2002, Williams

et al. 2004). Many studies have demonstrated high spatial variation in abundance in salmonid populations (Jones et al. 1998, Mitro and Zale 2000, Young and Guenther-Gloss 2004), even among adjacent reaches (Amiro 1990b). Consequently, sampling from the entire occupied portion of a stream channel is essential to estimate fish abundance accurately because it addresses spatial heterogeneity in abundance and defines the boundaries of occupied habitat (Hankin and Reeves 1988, Dolloff et al. 1993).

Limited budgets and time have caused biologists to seek methods that produce sufficiently precise abundance estimates yet capture the spatial heterogeneity in populations. Foremost among these in recent years is the basinwide inventory (Hankin and Reeves 1988, Dolloff et al. 1993), which relies on double sampling and a spatially comprehensive, systematically drawn sample of habitat units. All selected units are censused with a less precise technique, such as snorkeling or single-pass electrofishing, and counts from these units are calibrated by comparing them to counts obtained with a more precise method, such as multi-pass electrofishing, from a subsample of these units. The number, kind, and size of sampling locations are predicated on acceptable levels of precision in abundance estimates (Hankin and Reeves 1988, Thompson et al. 1998, Young and Guenther-Gloss 2004). In general, the use of calibrated single-pass electrofishing catches as an index of whole-stream population abundance is gaining popularity (Strange et al. 1989, Lobón-Cerviá and Utrilla 1993, Jones and Stockwell 1995, Jones et al. 1998, Kruse et al. 1998, Wyatt 2002, Young and Guenther-Gloss 2004, Young et al. 2005). Nevertheless, this approach still suffers from the negative bias associated with abundance estimators, particularly that are attributable to environmental variability in catchability (Thompson 2003, Peterson et al. 2004b, Rosenberger and Dunham 2005, Sweka et al. 2006). However, spatial variation in abundance may vastly outweigh imprecision or bias associated with estimates at particular sites (Mitro and Zale 2000, Bateman et al. 2005). Because obtaining highly precise and accurate abundance estimates from large portions of individual streams is time consuming and expensive, quantifying and balancing these different sources of error will be essential to crafting a defensible yet practical approach to gaining reliable information on population size.

The point of many monitoring schemes is to detect temporal variation in terms of population trends, overall fluctuation, or synchrony. A vital issue for managers is the period of monitoring that may be necessary to

detect a change in population size, which is contingent on the precision of population estimates, the temporal fluctuation in abundance, the magnitude and direction of change to be detected, and the level of confidence one hopes to have in the prediction (Peterman 1990, Thompson et al. 1998). For example, in a recent assessment on detecting trends in bird populations in North America, Bart et al. (2004) recommended a monitoring scheme that yielded 80 percent power to detect a 50 percent decline within 20 years based on annual monitoring, noting that detecting smaller declines at shorter intervals was impractical. Few attempts have been undertaken to assign specific values to each of these variables for salmonids, and the results from those have not been encouraging. For example, it may require decades to detect even very large changes in population size (Korman and Higgins 1997, Maxell 1999, Ham and Pearsons 2000, Maxwell and Jennings 2005), mainly because of the high temporal variability in abundance (also see Platts and Nelson 1988 on salmonids and Peterman and Bradford 1987 on marine fishes). In general, the power to detect a change will decrease as the size of the change decreases, the imprecision or variability in abundance estimates increases, and the interval of observation and number of censuses decreases. In addition, annual sampling of permanent monitoring stations may be more efficient at detecting changes than random annual allocations of sites (Quist et al. 2006). However, the underlying assumptions of such monitoring schemes are that salmonid populations decline proportionally throughout occupied habitats or that adjacent waters will have populations that fluctuate synchronously, which may or may not be true (Rieman and McIntyre 1996, Pess et al. 2002, Isaak and Thurow 2006; for a nonsalmonid example, see Shackell et al. 2005). Either way, this has important ramifications for the distribution of monitoring sites or streams to detect trends (Strayer 1999, Jonzén et al. 2005). A final consideration is weighing the levels of risk and cost that are acceptable (i.e., is it more important to respond to apparent trends [such as a decline in a population of concern] and accept the cost of responding when it may not be necessary, or is it worthwhile to be more certain about even very small changes that demand large investments in monitoring? [Legg and Nagy 2006]). Several authors were concerned about detecting population declines rather than increases because the former may warrant management intervention (e.g., Maxwell and Jennings 2005). In addition, because of these difficulties and the uncertainties associated with abundance estimates, Staples et al. (2005) favored monitoring based on estimating risks to populations. However, this strategy relies on the existence of a

comprehensive, long-term data set to quantitatively gauge risk, a luxury that is probably lacking for most populations of greenback cutthroat trout.

Many of these population monitoring issues may also apply to other characteristics of greenback cutthroat trout populations, such as size structure and demographic parameters (Kritzer et al. 2001, Vokoun et al. 2001) or year class strength (Cowx and Frear 2004), but these have not been explored. Though not addressed in the recovery plan (U.S. Fish and Wildlife Service 1998), a critical addition may be the monitoring of genetic characteristics of greenback cutthroat trout, such as population genetic structure (Nielsen and Sage 2001, 2002), the geographic distribution of genetic variation among and within populations (Wenbug and Benson 2001, Wofford et al. 2005), or historical and current gene flow (Neville et al. 2006a). Schwartz et al. (2007) suggest some guidelines for genetic monitoring.

Habitat inventory and monitoring: The recovery plan for greenback cutthroat trout makes only passing mention of habitat monitoring (U.S. Fish and Wildlife Service 1998), so the following discussion is predicated on the notion that a monitoring scheme will be necessary for the long-term management plan. Much like it is for fish populations, developing a successful inventory and monitoring strategy for habitat is challenging. For example, an ideal variable for detecting trends in and describing quality of physical habitats would be one that has a strong influence on fish population size or viability, may be altered by management activities or disturbance, has little inherent within-stream spatial or temporal heterogeneity, and can be measured without error and at little cost. Such a variable—other than perhaps the presence or absence of water—does not exist, which has contributed to the development of an extensive literature on habitat inventory and monitoring (e.g., Dolloff et al. 1993, Overton et al. 1997, Fitzpatrick et al. 1998, Urquhart et al. 1998, Bain and Stevenson 1999, Kaufmann et al. 1999, Stevens and Olson 1999, Peck et al. 2001, Reeves et al. 2003a, Henderson et al. 2004, Hixon et al. 2004, Larsen et al. 2004). Much of this literature has targeted salmonid habitats and is summarized elsewhere (Roni 2005, Stalnack et al. 2005). Consequently, this discussion will only touch on some of the major points.

Vast arrays of habitat variables that are presumably biotically relevant have been included in monitoring schemes for salmonids. Quite problematic, however, is the lack of a quantitative understanding of the relation between trout abundance (and population viability) and these habitat characteristics (including

their range and dynamics), which leads to ambiguity in the apparent response of populations to habitat changes other than the most obvious ones (cf. Bryant et al. 2005, Rosenfeld and Hatfield 2006). For example, because low water temperature appears to play a strong role in controlling the year class success of high-elevation populations (Harig and Fausch 2002, Coleman and Fausch 2007a,b), it may be a key variable for monitoring and may be sensitive to management and natural disturbance. In contrast, the abundance of pools, despite their importance to Colorado River cutthroat trout and greenback cutthroat trout (Young 1996, Harig and Fausch 2002), were poorly correlated with abundance compared to the length of occupied channel (Young et al. 2005).

Many variables are routinely monitored to assess the effects of management activities or natural disturbance. However, detecting changes attributable to these factors is contingent on two properties: 1) that the magnitude of change of a habitat component exceeds its inherent variability and the error associated with its measurement, and 2) that the habitat component responds in a predictable way. Assessments that have sought variables satisfying these requirements have found the list to be surprisingly short (Kaufmann et al. 1999, Archer et al. 2004). In some cases, variables were associated with high amounts of observer error (e.g., the percentage of fine sediment, or the size, number, or depth of pools; Poole et al. 1997, Roper et al. 2002, Williams et al. 2004), high within- and among-stream variability (e.g., large wood counts; Archer et al. 2004, Young et al. 2006), or both (e.g., several measures of riparian vegetation; Coles-Ritchie et al. 2004, Henderson et al. 2004). Even within a limited set of variables, some respond in surprising ways. Kershner et al. (2004) surveyed reaches of over 250 streams throughout the interior Columbia River basin, and found significant differences between managed and reference sites for eight of 12 variables. Predictably, residual pool depths and measures of bank stability and undercut were greater in reference streams, but contrary to expectation, the median particle size was also lower. In addition, there was no difference in the percentage of pools between managed and reference sites, despite that this difference had been observed elsewhere in the basin (McIntosh et al. 2000). They attributed this discrepancy in part to the absence of large wood in most of their monitoring reaches (because riparian zones adjacent to monitored reaches were infrequently forested; Kershner et al. 2004), which emphasizes how site selection and geomorphic position can shape the outcome of a monitoring plan (Montgomery and MacDonald 2002).

Monitoring schemes must be scaled to satisfy the objectives of monitoring (Williams et al. 2004). The whole-basin monitoring protocols for addressing objectives of the Northwest Forest Plan and PACFISH/INFISH effectiveness monitoring are designed to detect changes at scales of entire river basins or geographic regions (Reeves et al. 2003a), but they might be successful at detecting changes across smaller landscapes such as individual national forests as long as sampling intensity was high (e.g., 35 to 90 sampling sites) (Henderson et al. 2004; see Larsen et al. 2004 for a similar suggestion). If the objectives are to detect meaningful stream- or site-specific trends, more intensive sampling within and among streams, often at permanent sample sites, of variables likely to respond to particular management activities will be necessary (Archer et al. 2004, Kershner et al. 2004), and in many cases these standards will be difficult to achieve. Regardless of the protocol followed, there is consensus that extensive training is essential to produce reliable results (Roper and Scarnecchia 1995, Henderson et al. 2004).

Population and habitat management approaches

Habitat improvement: The physical manipulation of streams to improve fish habitat, stream channel and riparian stability, and water quality are common practices throughout the United States, with annual expenditures exceeding \$1 billion (Bernhardt et al. 2005). Those wishing to install structures or rework stream channels can find extensive guidance in the literature (e.g., Hunter 1991, Jenkinson et al. 2006). Although remediation of point sources of habitat or population degradation (e.g., screening irrigation ditches, restoring fish passage where culverts prevent access to suitable habitat, rebuilding meanders in artificially straightened channels, shading revegetated banks, or halting sediment contributions from road surfaces) can have readily discernable immediate and long-term benefits, the addition of in-stream structures, even when apparently successful (Binns et al. 2004), is more problematic (Independent Scientific Advisory Board 2003).

Several of the kinds of structures used today were first designed in the 1930's (Thompson 2006). Many of these have relatively short working lives because flows often damage them or make them ineffective (Frissell and Nawa 1992, Thompson 2006). Even when structures persist and appear to be functioning, they may lead to unintended consequences. For example, Cowx and van Zyll de Jong (2004) reported that in a log-driven

Canadian stream, habitat structures were added with the goal of increasing the abundance of brook trout. Brook trout did not become more abundant in response to these installations, but a competitor, juvenile Atlantic salmon (*Salmo salar*), did. Gowan and Fausch (1996) concluded that increases in trout abundance associated with log-drop structures in Colorado streams were probably attributable to redistribution, not increases in population size. Moreover, Thompson (2006) argued that the greater angler catch rates often associated with structures reflected both a redistribution of fish and an increase in angler effort, which actually led to net declines in overall fish abundance; in essence, structures became ecological traps for trout attracted to them.

Typically, fish-related habitat improvement assumes that we know which factors limit fish populations in a given location and that artificially manipulating habitat composition will relax the limitations and increase fish abundance. A critical problem is that it is difficult to verify these assumptions because of the rarity of post-project monitoring (Bash and Ryan 2002, Bond and Lake 2003, Reeve et al. 2006). In two cases where extensive monitoring was conducted, the authors concluded that the factors limiting fish abundance were not addressed because either they were misidentified or they were upstream or downstream of the habitat improvement area (Reeves et al. 1997, Ward 2000). In addition, the absence of untreated control streams weakened any inferences that could have been drawn (Independent Scientific Advisory Board 2003).

As alluded to above, many questions related to spatial scale and stream management remain to be answered (Jensen et al. 2001). Fausch et al. (2002) contended that many researchers and managers have neglected to appreciate the scale of habitats at which trout perceive their environment and questioned whether we can manage habitats at that scale. The grain (i.e., the smallest habitat unit of relevance) and extent (i.e., the size or spatial distribution of these habitats) to which trout respond are probably inherent properties (Fausch et al. 2002). Moreover, combining these with variation in environmental quality can contribute to the spatial heterogeneity in abundance (Schooley 2006), and these patterns in salmonids have only recently come under scrutiny (e.g., Torgersen et al. 2004, Ganio et al. 2005).

Because of our incomplete understanding of the relations between habitat characteristics and cutthroat trout abundance, it may be simpler and more biologically defensible to increase the amount of habitat available to fish by increasing the length of stream that

a population can occupy (e.g., by moving existing anthropogenic barriers farther downstream) rather than altering instream habitat, and to favor the restoration of natural processes—or the cessation of damaging activities—throughout an entire watershed that will enable habitat appropriate for a particular system to develop (Beechie and Bolton 1999, Reeve et al. 2006). Although a biologist familiar with stream restoration and our desire to effect change once quipped “for most Americans, instant gratification isn’t fast enough” (also see Minns et al. 1996 for a similar position, and Reeve et al. 2006 on how the way that funding has been awarded reinforces this shortcoming), a longer-term, larger-scale perspective on habitat restoration may ultimately be more successful. Again, a review of individual tactics or best management practices is beyond the scope of this paper, but examples range from the large-scale buyout of federal grazing leases or changes in grazing systems that diminish livestock effects to the site-specific reduction in water losses in irrigation canals by installing pipe (and the negotiated return of the water savings to salmonid spawning and rearing streams).

Increasing habitat size or stream network connectivity can have an additional benefit, the restoration of migratory populations of cutthroat trout. Swanberg (1997), Schmetterling (2003), and Schmetterling and McFee (2006) transported mature bull trout, westslope cutthroat trout, and largescale suckers (*Catostomus macrocheilus*) over a dam on the main-stem Clark Fork River in Montana that had been impassable to upstream migrants for over 90 years, and they found that these individuals moved long distances (up to 100 km) to reproduce in what were presumably their natal waters. This suggests that despite isolation that selected against such migrants for tens of generations, this life history form was still extant in these populations (although elsewhere extirpation of mobile forms has resulted; Nelson et al. 2002).

Nonnative species: prevention of invasions:

Although habitat degradation can depress or extirpate a fish population, it has the advantage of occasionally being reversible. In most cases, invasions by nonnative fishes are not reversible, and preventing invasions is far easier than attempting to manage them. Unfortunately, the simplest form of prevention (i.e., not introducing nonnative fish in the first place) has been rendered moot by over a century of agency-sponsored and publicly supported sport-fish stocking, and the subsequent spread and establishment of these fishes. Although stocking of nonnative fish within the historical range of greenback cutthroat trout continues, this practice has

ceased in waters that contain remnant or reintroduced populations (U.S. Fish and Wildlife Service 1998). More problematic recently has been the redistribution of nonnative fishes by members of the public (Rahel 2004). In several instances, the appearance of nonnative trout above apparently functioning fish migration barriers has been attributed to such illegal introductions (U. S. Fish and Wildlife Service 1998, M.K. Young, unpublished data). This practice threatens conservation work that often required hundreds of hours of labor and tens of thousands of dollars, yet prosecution of offenders is virtually impossible because of the ease of committing these transgressions and the limited law enforcement presence on public lands. Where feasible, one strategy could be to limit motorized access near some waters, particularly near barriers, by closing or rerouting roads; it appears less likely that nonnative fish would be transported alive over long distances by hand. A more draconian measure would be to establish refuges closed to fishing, with the belief that this would reduce public desire for fishing in those waters (and perhaps the probability of transfer of pathogens on fishing equipment), but this could produce a public backlash that might result in targeting those waters for nonnative introductions and reduce support for conservation activities.

Legal introductions of nonnative fish by private entities, such as for recreational fishing ventures, also represent a risk to conservation efforts. This is a likely pathway for the introduction of new pathogens (see Parasites and diseases, above), particularly if cultured fish can be released into waters that permit them to mix with wild populations. In one case, a natural waterfall that had been effective in repelling nonnative trout (and native mountain whitefish) from moving upstream among a population of Colorado River cutthroat trout was scaled when a private landowner downstream stocked and grew outsized rainbow trout that were able to leap over the falls (Medicine Bow-Routt National Forest, unpublished data).

The primary tactic for halting an invasion, or preventing reinvasion of habitats from which nonnative fish have been removed, is the installation of a barrier. Fausch et al. (2006, and references therein) exhaustively consider the consequences of intentional isolation as a management strategy, as well as describe the effects of nonnative salmonid invasions on native salmonids and the issues that should be addressed when considering the tradeoff between invasion and intentional isolation. The remainder of this discussion will highlight some aspects of prophylactically managing nonnative species.

In some streams, natural barriers in the form of waterfalls, cascades, bedrock chutes, or even subterranean reaches may already exist (whether waters upstream of such features constitute historical habitat is considered below). In the absence of a natural barrier, installation of an artificial one is an alternative, albeit an expensive one. Costs to install barriers to protect Apache trout in small (3 to 12 m) streams in Arizona ranged from \$150,000 to \$3,000,000 (Avenetti et al. 2006). Specifications for a wide array of barriers being used to impede upstream migrations of nonnative fish are available elsewhere (Hepworth et al. 2002, <http://wildfish.montana.edu/projects/barrier/browse.asp>) and will not be discussed further. However, the presence of an artificial barrier is no assurance that an invasion of nonnative fish will be averted. Harig et al. (2000) found that nearly all structures built to stop invasions of nonnative fishes into streams occupied by greenback cutthroat trout had eventually been breached by nonnative fish.

Artificial barriers fail for a number of reasons. In some cases, they are porous or too short, or developed a jump pool that enabled nonnative fish to scale them (also see Thompson and Rahel 1998). Barriers may also fail because they are ill-designed for the hydraulic characteristics of a site. Outright collapse or partial destruction of barriers, usually during high flows, is common (M.K. Young, personal observation). Such barriers are often undersized for the locations where they are installed, or better sites for construction (i.e., channels confined between hillslopes of exposed bedrock) were not available or were overlooked. In one case, a barrier consistently failed not because it was damaged, but because bedload transport aggraded the channel and obliterated the nick point (M.K. Young, personal observation). Nevertheless, installation of barriers is ongoing, and it is hoped that more recently constructed barriers will be more successful.

An alternative to new barrier construction may be the use of an existing barrier installed for another purpose. Although some (e.g., culverts) are prone to being washed out during relatively modest floods, others (e.g., diversion structures designed to capture water for agricultural and municipal use) are constructed to higher engineering standards than those designed by biologists. Some diversions already function as barriers, and others might be retrofitted to do so. If reauthorization for these must be granted periodically by a federal agency, additional construction could be recommended as part of that process.

Regardless, even the best-designed and -placed barrier will require regular maintenance for the life of the structure (estimated annual repair costs of the aforementioned structures in Arizona was \$3,000 to \$15,000; Avenetti et al. 2006), and it will be likely to fail during extreme events such as debris torrents. All things considered, an artificial barrier should be regarded as a stopgap measure; ultimately, the only permanent method for securing populations of greenback cutthroat trout will be removal of nearby nonnative trout populations and reestablishment of connectivity to larger stream networks (Hepworth et al. 2002).

Nonnative species: removal and control:

Because nonnative trout species appear to preclude the reoccupation of many waters by greenback cutthroat trout, removal of these species has been a priority. The number of techniques available, however, is limited, and new approaches have not developed beyond the experimental stage (e.g., pheromone-based removals of brook trout; Young et al. 2003). Probably the most popular approach is chemical treatment with rotenone or antimycin, which have a long history of use in the western United States. Ironically, one of the most extensive treatments was intended to eradicate native and nonnative fish species, probably including fluvial Colorado River cutthroat trout, from the Green River in Wyoming and Colorado prior to the filling of Flaming Gorge Reservoir (Minckley and Deacon 1994). Since that time, toxicants have been repeatedly administered to remove nonnative trout from waters prior to the introduction or reestablishment of trout species native to these basins (Rinne et al. 1981, Gresswell 1991, Hepworth et al. 2002), including greenback cutthroat trout (U.S. Fish and Wildlife Service 1998, Young et al. 2002). Details of how to conduct treatments are described elsewhere (Finlayson et al. 2000, Hepworth et al. 2002); only a few key points will be addressed here. First, although some projects have involved relatively large stream networks (e.g., 93 km in LaBarge Creek and 78 km in the North Fork Little Snake River; Wyoming Game and Fish Department 2007), most waters targeted for nonnative fish removal are single streams with low summer discharge ($<0.4 \text{ m}^3$ per s; Hepworth et al. 2002, Brauch and Hebein 2003). Second, these authors noted that in complex streams with numerous side channels, springs, or beaver ponds, single treatments were generally ineffective at removing all nonnative fish. Consequently, toxicants are often applied annually for 2 to 4 years to assure complete removal (Hepworth et al. 2002, Shepard and Nelson 2004, B. Wengert personal communication 2006). In

some instances, biologists may notch or remove beaver dams or log jams shortly before chemical application to simplify habitats and to increase the efficacy of an individual treatment. Subsequent beaver activity or trapping of debris during high flows often rebuilds these habitats (M.K. Young, personal observation). Although they are relatively successful, chemical applications are increasingly difficult to conduct because of the growing public controversy associated with their use. This may involve concerns about chemicals applied to drinking water supplies (Finlayson et al. 2000) or the loss of valued nonnative trout fisheries (Hepworth et al. 2002). Furthermore, federal policy has been inconsistent with regard to where such treatments will be appropriate, and extended delays in these projects from litigation or administrative review have been commonplace (Finlayson et al. 2005). Often, the costs associated with bureaucratic issues have rendered projects in smaller waters uneconomical (Hepworth et al. 2002).

In part because of these problems, managers have increasingly relied on intensive electrofishing to eliminate nonnative trout from streams in which cutthroat trout will be introduced (Brauch and Hebein 2003, Shepard and Nelson 2004). Initially, attempts to remove nonnative trout often employed a single removal conducted in one or a few years, but this was ineffective because even multiple electrofishing passes over a short period of time do not capture all fish present and small numbers of reproducing adults can quickly repopulate a stream (Thompson and Rahel 1996, Shepard et al. 2002, Meyer et al. 2006a). Successful eradication was associated with more intensive removal efforts (6 to 10, 2-pass removals over 1-3 years; Kulp and Moore 2000, Shepard and Nelson 2004). Shepard and Nelson (2004) recommended focusing the first year on reproductive adults, conducting removals twice before spawning and once afterwards (when remaining adults had schooled and juvenile fish had grown enough to be susceptible to this technique), and concentrating the second year on juvenile fish and the few remaining adults. As with chemical treatments, this approach is generally only effective in small streams (<4 m wide) with simple channels and little overhanging riparian vegetation (Shepard and Nelson 2004).

In circumstances where removal of nonnative trout may be unlikely, partial control of their populations has been promoted as a method to enhance survival of cutthroat trout (Thompson and Rahel 1996, Peterson et al. 2004a). Nevertheless, this must be viewed as a temporary measure that will fail unless permanent removal is the ultimate goal, in part because enthusiasm for such projects tends to wane rapidly (Meyer et

al. 2006a). For example, annual trap netting and electrofishing removals of brook trout helped promote survival of a population of greenback cutthroat trout in Hidden Valley Creek in Rocky Mountain National Park. With the cessation of these efforts, brook trout rapidly multiplied and greenback cutthroat trout disappeared (B. Rosenlund, U.S. Fish and Wildlife Service, unpublished data). Selective angling targeting brook trout in this stream was also attempted, but harvest was insufficient to cause a decline (U.S. Fish and Wildlife Service 1998; also see Paul et al. 2003). There is also a concern that in mixed species fisheries, anglers will be unable to distinguish between cutthroat trout and the species designated for harvest (Stelfox et al. 2001).

Treatments of mountain lakes have historically relied on toxicants, either applied in late summer and mixed throughout the water column by mechanical means (B. Rosenlund, U.S. Fish and Wildlife Service, unpublished data) or, perhaps most often in lakes without outlets, applied in autumn before or during turnover and allowed to persist overwinter. In some circumstances, intensive gill netting has exterminated nonnative trout populations (Knapp and Matthews 1998). Finally, a more unusual approach was the apparently effective introduction of sterile tiger muskies (*Esox lucius x masquinongy*) to high-elevation Idaho lakes (K. Meyer personal communication 2005; also see Grisak and Marotz 2002), but this has not been thoroughly evaluated. These actions may be effective in isolated lakes, but those with inflows or outflows would additionally require the approaches described above for streams.

Population establishment, maintenance, and salvage: Translocating (or stocking) fish to establish populations is one of the most common tactics employed by biologists. Stockwell and Leberg (2002) noted that about 80 percent of recovery plans for fish listed under the Endangered Species Act called for translocation. These authors addressed a number of issues related to using this method, as did Williams et al. (1988); some of these are described in more detail below.

Many populations of cutthroat trout have been established from introductions of hatchery stocks (U.S. Fish and Wildlife Service 1998, 2004) and direct transfers of wild fish (Hepworth et al. 2002), but the former has been more common with greenback cutthroat trout (Young et al. 2002). Hepworth et al. (2002) noted that direct transfers of 100 to 200 wild fish were adequate to start new cutthroat trout populations in small streams, but when the objective was to establish a fishery for native trout in larger water bodies (e.g.,

reservoirs), the much larger numbers of fish afforded by hatchery production were desirable. Typically, most plants of cutthroat trout have consisted of age-0 or age-1 fish (Young et al. 2002). Based on a stage-structured matrix model used to predict population persistence, Hilderbrand (2002) suggested that one-time stocking of a relatively large number of adults (10 percent of potential carrying capacity) was the most successful strategy, but even small introductions spread out over a decade or two increased persistence. Hilderbrand (2002) argued that if individual populations become increasingly isolated in the future and at greater risk of extinction from chance events or inadequate habitat, periodic artificial supplementation (i.e., roughly equivalent to the current practice of mountain-lake stocking where reproduction is unreliable) of greenback cutthroat trout may become the norm. However, under these scenarios, it is difficult to envision that artificial selection would be avoided; thus, supplementation might be viewed as a last resort for maintenance of a particular population. Alternatively, introducing new individuals to particular populations to avoid inbreeding (i.e., genetic rescue) may hold promise, but it requires substantial knowledge about the genetic status of source and donor populations to avoid eroding the genetic integrity of an existing population (Tallmon et al. 2004).

New introductions in a particular river basin have usually been of hatchery stocks derived from a mixture of populations indigenous to that basin (Young et al. 2002). However, the tendency for cutthroat trout to show high between-population differentiation (see Genetic structure, above) implies that developing a broodstock representative of a particular basin is a nontrivial exercise because each indigenous population may carry a unique portion of the genome in that basin (cf. Youngson et al. 2003). Moreover, in those cases where indigenous populations no longer exist, the dilemma becomes whether to introduce fish from an adjacent river basin or use stocks of mixed origin. Aspects of this problem have been explored elsewhere (Krueger et al. 1981; more recently McKay et al. 2005 for plants).

Finally, managers are increasingly adopting the practice of emergency salvage i.e., removing fish from a stream and holding them elsewhere when the loss of a population is perceived as imminent, such as from post-fire flooding or drought (U.S. Fish and Wildlife Service 2004). One of the few published accounts of this approach involves Gila trout that were salvaged by electrofishing from a New Mexico stream after a stand-replacing fire but before monsoon rains arrived (Propst et al. 1992). An intense thunderstorm shortly thereafter

apparently eliminated all fish from the basin, which was repopulated several years later with descendants of the salvaged fish after the stream channel had begun to stabilize (Brown et al. 2001). Despite this successful example, managers might consider two issues before adopting this tactic: 1) whether salvage is necessary and 2) where and how long fish are to be held. As noted earlier, severe fire is not inevitably followed by debris torrents that might extirpate fish populations, and even those streams experiencing debris torrents rarely suffer complete extirpation of fish populations because native trout readily recolonized from less affected areas up- or downstream (Rieman and Clayton 1997, Sestrich 2005). Alternatively, in the event of extreme drought, cutthroat trout populations may decline dramatically but still persist if refugia such as springs or beaver ponds are present. More problematic might be that drought tends to be a regional rather than local phenomenon, and many populations might be simultaneously threatened. Thus, prioritizing salvage efforts and identifying where to put salvaged stocks might best be done long before the need arises. In addition, because of the potential genetic and disease consequences of holding and possibly propagating wild populations outside their native habitat (or even their outright loss from unforeseen accidents such as power failures at hatcheries; also see Unintentional selection, above), detailed planning before conducting salvage appears sensible. Brooks (2006) provides an example of a salvage plan for Gila trout.

Systematic conservation planning:

Conservation is expensive and incremental, and we cannot conserve everything (Meir et al. 2004), a point stressed by Quist and Hubert (2004) with respect to cutthroat trout management in the western United States. Societal desires (e.g., the popularity and economic benefits of fisheries for charismatic nonnative species) and management realities (e.g., removal of nonnative species from large watersheds is not feasible) constrain the number and kind of watersheds available for the protection or restoration of populations of cutthroat trout, a situation typical of that encountered in establishing reserves for terrestrial species (Soulé and Sanjayan 1998, Margules and Pressey 2000). Most reserves for cutthroat trout have probably been created opportunistically as funding, access, and agency cooperation permitted, or they exist by default (e.g., above water diversion structures or natural waterfalls). Such approaches to establishing reserves are unlikely to include the waters most suitable for the long-term conservation of cutthroat trout, in part because the waters least prized for other purposes were most likely to be selected (Pressey 1994).

In contrast, systematic reserve planning strives to preserve all existing (or historical) biodiversity and to maintain its persistence (or restore it; Margules and Pressey 2000). It explicitly attempts to maximize the chances of representing all biodiversity elements, is transparent and defensible, permits a more efficient allocation of resources (and more efficient conservation of biodiversity), and enables the evaluation of unexpected conservation opportunities (Leslie et al. 2003). The prioritization of conservation actions based on systematic conservation planning can help realize conservation goals given limited resources, as well as identify areas where data are needed to make good decisions (Margules and Pressey 2000). Conservation planning for greenback cutthroat trout has considered some of the aforementioned points (see U.S. Fish and Wildlife Service 1998), but full implementation of this strategy for freshwater fishes has not been attempted (but see Higgins et al. 2005 for a generic model based on habitat and Allendorf et al. 1997 for work on Pacific Northwest salmon).

The elements of a systematic conservation plan have been tailored for individual groups of species, environments, or regions (e.g., Leslie et al. 2003, Roberts et al. 2003), but most follow an outline similar to that developed by Margules and Pressey (2000). These elements can be summarized in five steps. First, measure and map the units of conservation, which could include populations of a particular size, different life histories, the array of genetic diversity or habitat diversity, some degree of connectivity, or other aspects of individual populations (see below). Second, identify conservation goals, which could include maintaining or establishing specific numbers and locations of populations based on those conservation units. Third, review existing reserves to assess representativeness. In other words, address whether the number and distribution of existing reserves represent all of the important conservation elements. Fourth, classify potential reserves based on a set of criteria that improves the chances of meeting the goals. These criteria vary greatly among plans but typically include some version of the following two variables. One is irreplaceability, which is the likelihood that a site will be required in a conservation plan to achieve specific targets or its unavailability will disproportionately reduce the options for meeting those targets (Ferrier et al. 2000); restated, it is the proportion of biodiversity within the planning region that would be lost if the site was lost (Meir et al. 2004). Another criterion is cost, which can be measured in a variety of ways. Cost is often viewed as a representation problem, where one attempts to maximize representing all conservation targets in the fewest sites (Cabeza and

Moilanen 2001). It also might include the expense of acquiring sites for conservation (e.g., on private lands), rendering existing sites more suitable (e.g., by removing nonnative fish), or the political cost of performing an action (e.g., where anglers are likely to be dissatisfied at the loss of a nonnative trout fishery). Finally, selection of reserves—and the prioritization for action—is based on a ranking of these criteria with respect to the original conservation goals. Two of the variables that are usually included at this stage are complementarity and vulnerability. Complementarity is based on the notion that if the site (or population) representing the highest conservation value (whether it be population size, diversity, number of connected populations or size of connected habitat, or some measure of irreplaceability or representativeness) is chosen for a reserve, the next site (or population) chosen will contain the maximum amount of biodiversity (or greatest value) not already represented in the first site (Margules and Pressey 2000). Therefore, it reflects information on reserves already chosen and on those not yet selected. The second variable often included in reserve prioritization is vulnerability, which is simply the risk of loss (often of an existing population or the opportunity to conserve it) within a particular period of time. Although prioritization of reserves can be based on simple rankings of value and vulnerability over a limited geographic area (Allendorf et al. 1997), comprehensive assessments of biodiversity (or alternatively, the various forms of diversity represented by a single species such as greenback cutthroat trout) may require an approach that is more efficient though computationally intensive (Cabeza and Moilanen 2001, Leslie et al. 2003).

In a systematic conservation plan, the first question to answer might be “what is the unit of conservation?” Within the United States, units of conservation recognized under the Endangered Species Act are evolutionarily significant units or distinct populations segments (Young and Harig 2001). These effectively equivalent terms require that to merit designation, one or more populations must be essentially reproductively isolated and constitute an important component of the evolutionary legacy of the species; this approach prioritizes groups based on existing patterns of variation. Yet Ruckelshaus et al. (2002) cautioned that what needs to be conserved are not only the genetic or ecological novelties that have arisen, but also the capacity for continued evolution (also see Healey and Prince 1995, Waples et al. 2001). Along these lines, Northcote (1992) argued that because environments will undoubtedly continue to change, maintaining the diversity in life history strategies is the best insurance for uncertain times. Ruckelshaus et al. (2002) also suggested that

conservation be based to some extent on the recency of evolved traits and the number of times they have arisen. For example, the repeated derivation of resident life histories from migrant ones (Berg 1985, Stearley 1992) implies that this would be a readily “recovered” trait whereas the most complex life histories are probably unique and perhaps unrecoverable if lost. In the absence of data on evolutionary phylogeny of these traits, an alternative is to use the diversity in habitats and associated life histories as the basis for selection of forms to conserve (Northcote 1992, Healey and Prince 1995). Allendorf et al. (1997) suggests other criteria for defining conservation value.

Prioritizing where to work can also be based on other factors. Hepworth et al. (2002) noted there was little opposition to cutthroat trout restoration in small, isolated tributaries, but much less support for work in streams supporting existing fisheries; they suggested prioritizing restoration based on threats and what was attainable. The recovery plan for greenback cutthroat trout identified six criteria—based on barriers, feasibility of nonnative fish removal, and adequate habitat—for candidate waters for introductions (U.S. Fish and Wildlife Service 1998). Most of the 20 candidate waters closely resemble habitats currently occupied. Although pragmatic from a political and management perspective, such waters would be likely to support relatively small populations susceptible to extirpation and in need of frequent management intervention. A ranking scheme that also favored restoration in streams potentially supporting more robust populations that were resilient to stochastic variation, because they provided greater amounts of habitat or connectivity to additional waters, might suggest some additional priorities for restoration (cf. Feist et al. 2003). Balancing these two perspectives could be a useful element of a prioritization scheme.

On a related note, distinctions are sometimes made between using waters for restoration that were once inhabited by a particular species versus those that were historically barren (Young and Harig 2001). A policy statement from the American Fisheries Society regarded stocking outside historically occupied waters as unacceptable unless formerly occupied habitats were unavailable or unrestorable (Williams et al. 1988). Nevertheless, historically fishless waters have frequently been adopted by agencies charged with recovering rare or threatened taxa, including greenback and Colorado River cutthroat trout (U.S. Fish and Wildlife Service 1998, CRCT Task Force 2001). For example, inaccessible high-elevation lakes have been widely used for introductions because

they serve as more stable environs unlikely to lose stocked populations except from winterkill or lack of reproduction. Likewise, many headwater stream segments above waterfalls are fishless, and they may be deemed the most suitable sites for introductions for that reason (Hirsch et al. 2006; see above). At least three issues, all noted earlier, deserve consideration with respect to these uses of historically fishless waters. First, introductions in these areas may harm other indigenous species (Dunham et al. 2004). Second, absence of fish from such reaches may indicate that they are unsuitable trout habitat. Harig and Fausch (2002) and Young et al. (2005) suggested that mean summer water temperature and occupiable stream length could be used as screens to select suitable habitats. Finally, establishing populations in such habitats exposes them to strong natural selection, which probably has little effect in the short term but has long-term implications for maintaining the genetic variability that was exhibited historically. Nonetheless, use of such waters may be unavoidable if climate change and human uses render habitats within the historical range unsuitable.

Information Needs

Many gaps in our understanding of the evolution and ecology of greenback cutthroat trout have been identified throughout this paper, but a few warrant further development because they may address crucial short-term issues. One of the most critical needs among biologists working on conservation of native cutthroat trout of all subspecies is a clearinghouse of information on efforts, techniques, and strategies. Syntheses such as this one are a useful start, but more precious—partly because of their rarity—are summaries by practitioners of what worked and what did not (e.g., Hepworth 2002). The websites on barrier construction (<http://wildfish.montana.edu/projects/barrier/browse.asp>) and stream restoration (see Jenkinson et al. 2006) also serve as examples. More controversial but perhaps no less important is greater availability of population size and trend data for many rare and threatened species (in this regard the status assessment [Hirsch et al. 2006] is an excellent example). Availability of this information would invite public participation and independent evaluation of population and species management, which might be uncomfortable for agencies used to controlling access to such data, but it could also lead to more successful management and less controversy over management decisions because of greater public involvement (Safford 1995, James 1999). Dedicated databases are also associated with more cost-efficient and successful conservation (Lundquist et al. 2002).

Whereas it is likely that most extant populations of greenback cutthroat trout have been located, comprehensive inventories of the spatial characteristics of most of these populations—their upstream and downstream extent, the presence of natural or anthropogenic barriers that bound them or structure otherwise connected populations by restricting upstream migration (Wofford et al. 2005, Cole et al. 2006, Fransen et al. 2006)—probably remain incomplete. This was the case for many populations of greenback cutthroat trout, despite the management attention directed at the comparatively few populations of this federally listed taxon (Young and Guenther-Gloss 2004). Such surveys would permit refined estimates of population size and barrier permanence. Moreover, the identification of existing or potential barriers would have implications for the management of greenback cutthroat trout populations in a changing climate.

Fundamental to modeling or managing greenback cutthroat trout populations is the ability to define them (cf. Dunham et al. 2001). Though seemingly intuitive, identifying geographic boundaries of cutthroat trout populations is complicated by the presence of individuals that migrate or stray, by the intermittent suitability of some habitats, and by the continuity of connectivity to or isolation from other waters. Techniques for assessing the genetic distance among individuals or defining genetic neighborhoods (Neville et al. 2006b), stable isotope analyses that permit identification of natal streams of migratory fish (Rieman et al. 1994), and traditional demographic and movement studies will be necessary to understand whether a body of water contains one or more viable populations, represents a demographic sink for surplus fish produced elsewhere, or provides complementary habitat for a population ranging over a much longer stream network. In waters permitting substantial connectivity, autocorrelation in phenotypic or genotypic character sets has been used to define geographic population structure (Diniz-Filho and Telles 2002). In addition, populations have been geographically defined based on their homing to particular spawning locations (Dunham et al. 2001), whether they are within a single stream or distributed among different streams in a network. Alternatively, the entire home range of a group of fishes (Danancher et al. 2004) could serve the same purpose. Although it has been expedient to associate individual greenback cutthroat trout populations with a named body of water (e.g., Young et al. 2002), this has little *a priori* justification unless known barriers confine individuals to a lake or a headwater stream segment. Individuals found below such barriers may represent migrants that are lost from the upstream population, constitute a

separate population with a similar or entirely different migration strategy, or both. In addition, as noted earlier, multiple barriers within particular streams may produce semi-independent populations linked by one-way migrations (i.e., under most circumstances, individuals can only move downstream) that may exhibit very different dynamics than single populations occupying a connected patch of similar size. Studies of fish movement and genetic population structure, coupled with the aforementioned stream inventories, will be necessary to address this issue.

Although genetic approaches have proven to be reliable at detecting hybridization, they remain costly, and managers continue to explore the use of visual techniques for preliminary evaluations (e.g., as a screen for determining whether populations warrant genetic testing). Some of these methods have been at least partly successful. De Rito (2004) was fairly accurate in detecting pure Yellowstone cutthroat trout, whereas recognition of pure rainbow trout and of hybrid individuals was unreliable (also see Campbell et al. 2002, Meyer et al. 2006b). Similar results were obtained with classifications of coastal cutthroat trout, steelhead, and their hybrids (Baumsteiger et al. 2005). More promising was a relatively robust classification tree model for discriminating westslope cutthroat trout from their hybrids with rainbow trout based on the prominence of the throat slashes, basibranchial teeth presence, spot shape, and relative head length (Weigel et al. 2002). Constructing comparable models for greenback cutthroat trout would require extensive sampling coupled with genetic assessment of individuals, but collection of individuals for genetic testing may already be planned, and structured visual assessments might be added in the field with little additional effort (e.g., 2 minutes per fish; Weigel et al. 2002).

As noted earlier, extensive sampling has been done to evaluate the genetic purity of many populations of greenback cutthroat trout (Young et al. 2002). Beyond the question of purity, however, is the phylogeography and genetic population structure of these populations and their relationship to yellowfin cutthroat trout. Relating measures of genetic diversity within populations to fitness may also help elucidate whether inbreeding depression represents a substantial threat.

Because nonnative trout, particularly brook trout, likely represent the greatest current threat to the persistence of many populations of greenback cutthroat trout, evaluations of many aspects of these invasions

may be crucial. For example, knowledge about the typical rate of advance and demographic establishment of invading fish would give managers some notion of the amount of time they may have to respond before a population of cutthroat trout may be beyond saving. Furthermore, despite their widespread success, brook

trout invasions do not appear to be inevitable in all waters, and the environmental characteristics that inhibit those invasions could suggest management approaches for reducing or eliminating brook trout elsewhere, or identify relative levels of risk of particular waters to invasion by brook trout.

DEFINITIONS

Adfluvial – a life history form that uses lakes for rearing and growth but migrates to streams to spawn.

Allopatric – not overlapping in distribution with another species.

Anadromous – a life history form that uses the ocean for rearing and growth but migrates to streams to spawn.

Anchor ice – submerged ice that is attached to the stream bottom; often referred to as frazil ice when dislodged or floating in the water column.

Anthropogenic – of human origin.

Burst speed – the maximum speed of swimming.

Carotenoid – a reddish pigment.

Caudal peduncle – the tapering portion of a fish's body between the posterior edge of the anal fin base and the base of the caudal fin.

Debris torrent – a flood consisting of water, sediment, rock, and wood that can result when short-duration, high-intensity rainfall exceeds soil infiltration capacity and leads to channeling of surface runoff; such floods usually originate in small, steep basins and often consist of much more than 50 percent sediment, rock, and wood, in contrast to hyperconcentrated flows (sometimes known as blackwater events) that consist of less than 50 percent of these particles.

Deme – a local population that is largely isolated from other populations of the same species.

Deterministic – referring to events that have no random or probabilistic aspects but proceed in a fixed predictable fashion.

Diel – over a 24-h period.

Diurnal – during the day.

Effective population size – the number of adults in an idealized population (e.g., with an equal sex ratio and equal contributions among individuals) that would have the same temporal variation in gene frequencies as a population in question.

Extinction – loss of a taxon from all of its range; often also used to refer to the loss of a population (thus synonymous with extirpation), which is probably appropriate for cutthroat trout because of their local population structuring.

Extirpation – loss of a taxon from part of its range.

Fluvial – a life history form that migrates from rivers or larger streams to small streams to spawn; it also means of rivers or streams (as opposed to lacustrine).

Genetic drift – a random change in the frequencies of alleles that is often inversely proportional to population size and connectivity; drift frequently leads to loss of alleles and reductions in genetic variability.

Genome – the total genetic material of an individual or species.

Glacial maximum – furthest southward and downward extent of glaciers.

Haplotype – one of the alternative forms of the genotype of a gene complex.

Heterozygosity – having two or more alleles at a particular locus; may apply to an individual or a population.

Homing – returning to reproduce in the same location where born (in contrast to straying).

Hybrid swarm – a complete admixture of genetic material from separate taxa within a single population.

Hybridization – production of offspring from mating of separate taxa.

Indigenous population – a population native to a water body; this does not include populations in the Colorado River basin that were stocked into historically unoccupied waters, regardless of their hydrologic connection.

Introgression – movement of genetic material from one taxon to another; introgressive hybridization results from production of fertile hybrid offspring that mate with other hybridized or pure individuals.

Isostatic rebound – in this case, land-level rise following the loss of glacial ice; the earth's crust is buoyant, floating on the hot mantle; removal of water, ice, or sediment from the earth's surface enables those portions to rise, often differentially along fault lines.

Lateral line – a fish organ that runs horizontally under the skin along the sides of a fish.

Macroinvertebrates – with respect to fish, usually invertebrates (e.g., insects, spiders, annelids) that are large enough to constitute part of the diet.

Migration – directed, often long-distance movements by fish as an element of their life history.

Parr marks – oval, vertically oriented markings on the sides of many salmonids, particularly juveniles.

Piscivory – consuming fish as part of the diet.

Refugia – typically, habitat sanctuaries from extreme environmental events.

Resident – a life history form that confines its migrations to small- to medium-sized streams; the distinction between this and a fluvial life history is somewhat arbitrary and may depend more on the presence of a known barrier restricting the former; sometimes collectively referring to all freshwater life histories in contrast to anadromy.

Salmonid – a member of the family Salmonidae, including trout, charr, salmon, grayling, and whitefish.

Springbook – a channel in alluvium fed by groundwater that is often adjacent to a larger river.

Stochastic – random.

Stream capture – the redirection of flows from one basin to an adjacent basin, typically by ice or erosion; often responsible for interbasin transfer of fish populations during post- and pre-glacial times.

Sympatric – co-occurring with a particular species.

Vital rates – demographic characteristics, such as fecundity and age-specific survival, that determine population growth rate.

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