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Dear Mr. Pfister:

Thank you for the opportunity to review this "Range-wide status of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*): 2005" by Hirsch, Albeke, and Nesler. As requested in your letter, my general charge is to identify and characterize scientific uncertainties and to address four questions on the scientific validity of this document. Below please find my responses.

Overall, this document sets a new benchmark for the understanding of the historical and current status of Colorado River cutthroat trout that is a substantial improvement over previous assessments (e.g., Young et al. 1996). In most cases, I consider the methods employed by these authors to be reasonable and appropriate. There are a few instances where reconsideration of some perspectives, evaluation of data quality, or more detailed description of the methods might be appropriate.

1. Is the description and analysis of the population trends, population health, genetic status, and historical and current distribution of the species accurate?

Population trends
This report does not directly address trends i.e., long-term, consistent changes in populations of Colorado River cutthroat trout and data are not included that would permit such an evaluation (see population health, below).

Population health
Population health is defined as a complex of factors related to the risk of introgression, risk of disease, habitat size, population size, environmental influences on demography, and stream connectivity. These latter four variables are combined to create a general health assessment for conservation populations, and the meaning of each variable is well described in Box C. However, the four variables are then weighted differently and combined to produce a general health ranking. A justification for the weight assigned to each variable should be included.

I am skeptical about the evaluation of habitat size (synonymous with "Temporal Stability"). The downstream boundaries of many fish populations appear to be well known, usually because these are relatively accessible and are often near the sites chosen for fish abundance sampling. Also, these often define the beginning of allopatric populations of Colorado River cutthroat trout because a barrier precludes upstream migrations of nonnative fishes. However, I am uncertain how "populations" downstream from such barriers were treated. Barriers usually permit downstream passage of Colorado River cutthroat from upstream, and these fish may travel kilometers downstream from such barriers and form a modest to minor component of the fish community. Describing whether these fish were included or not included is recommended.

In contrast, the upstream boundaries of fish populations are rarely known. In these cases, expert opinion is likely to be highly subjective. For example, Young and Guenther-Gloss (2004) compared the actual lengths of stream habitat occupied by greenback cutthroat trout, based on whole-basin surveys, and the amount of habitat believed to be occupied based on expert opinion (and included in the recovery plan for this species). The mean difference between observed and estimated habitat size was 54% (range, 4-225%). Most of these differences were attributable to inaccurate assessments of upstream boundaries (M.K. Young, unpublished data). In the absence of whole-basin surveys to specifically identify upstream-downstream boundaries (also see Ganio et al. 2005; Cole et al. 2006), or those present within otherwise contiguous populations (Wofford et al. 2005), I suspect many of the estimates of habitat size are largely conjecture.

With regard to population size, the manuscript states (page 7) that the abundance of cutthroat trout larger than 150 mm approximates the effective population size, a term often used to describe the likely patterns of genetic drift and diversity through time of an idealized population. However, the abundance of adult fish is likely to be much less than the effective population size (e.g., about 50%; Rieman and Allendorf 2001).

More important may be how fish abundance is estimated. My understanding is that most quantitative population monitoring of Colorado River cutthroat trout in Colorado and Wyoming is based on periodic sampling e.g., every 4-5 years, of one to a few index reaches in each stream. 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. Although extrapolating counts or estimated abundance from single (or a few) reference, representative, or index reaches to entire streams is widespread in the western U.S., 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 accurately estimate fish abundance because it addresses spatial heterogeneity in abundance and defines the boundaries of occupied habitat (Hankin and Reeves 1988, Dolloff et al. 1993). Thus the estimates of abundance used in the manuscript cannot be regarded as reliable. Although the use of abundance classes reduces the magnitude of any bias, it does not remove it.

Finally, connectivity influences a number of factors used in the assessment of individual conservation populations, which is probably appropriate, but in some instances the ranking of connectivity depends on recognition of the presence of migratory life histories. In my experience, this is very poorly known, even among experts, so I found it difficult to give credence to these rankings.

Genetic status

In this manuscript, genetic status pertains to the risk or degree of hybridization with nonnative rainbow trout or nonindigenous cutthroat trout. These are valid and crucial concerns, but there is much more to the genetic status of Colorado River cutthroat trout that warrants evaluation. Dennis Shiozawa at Brigham Young University has done extensive testing of Colorado River cutthroat trout from throughout its historical range during the past two decades, and his data suggest that two forms of this taxon may exist: one that exhibits relatively recent exposure (during glacial times) to Yellowstone cutthroat trout, and a much older form that does not. The relative distribution of these two forms is unknown, but my interpretation of these reports is that although the archaic form may only be found in isolated headwaters in the more northerly portions of its range, it may constitute the only form found in more southerly areas e.g., the San Juan River basin. This distinction has relevance for the management of populations and broodstocks, and thus the status of Colorado River cutthroat trout, throughout its historical range.

A related issue is the absence of information on the distribution of Colorado River cutthroat trout derived from Trappers Lake, Colorado. Fertilized eggs of Colorado River cutthroat trout were collected from Trappers Lake from 1914 to 1941 and from 1954 at least until 1965 (Snyder and Tanner 1960; Drummond 1966), and fish were released throughout Colorado (see Young et al. 1996 for many examples of Colorado River cutthroat trout populations outside the Trappers Lake basin with historical records of such stocking). Fish from this source were also exposed to Yellowstone cutthroat trout after 1943, and as late as 1959 fish recognized as this subspecies were observed spawning (Snyder and Tanner 1960). Consequently, the distribution of fish of Trappers Lake origin is probably relevant to the genetic status of a number of populations, both in terms of potential hybridization and the mixing of fish from this basin with indigenous stocks elsewhere within the historical range.

Historical and current distribution

As defined in this manuscript, the historical range of Colorado River cutthroat trout is believed to represent the distribution of this subspecies in 1800. The physical definition of the historical range is defined as those waters above 6,000’ (or 5,500’ on northern exposures) that were likely to be accessible (i.e., have no geological barriers to fish movement). Elevational limits are a reasonable way to describe historically occupied habitat, but the manuscript does not provide support for why these limits were chosen. There is substantial evidence that close relatives of Colorado River cutthroat trout were found in waters at much lower elevations e.g., greenback cutthroat trout near the present city of Greeley, Colorado, and Bonneville cutthroat trout in Lake Utah (Wiltzius 1985; Behnke 1992), so it would seem plausible that at least some populations of Colorado River cutthroat trout (and likely some very large ones) would be found at lower elevations. Moreover, there is no evidence that a formal review of historical documents was conducted. Two recent examples from the literature (Hamilton et al. 2005; Kaczynski and

Alvarado 2006) demonstrated that reviews of historical documents provided much more accurate depictions of the historical range of salmonids than did current expert opinion.

The second issue is the definition of historically accessible waters. Again, this is dependent on expert opinion, but a rule set for determining whether a water would have been historically accessible is not given. In many areas throughout the Northern Hemisphere, indigenous populations of salmonids are commonly found upstream from barriers that formed as a consequence of isostatic rebound following recision of glacial ice (Berg 1985; Castric et al. 2001). I am aware of several streams within the historical range of Colorado River cutthroat trout that possess geological barriers to fish migration but also contain presumably indigenous populations of this subspecies (which this manuscript also considers indigenous). Without a set of guidelines, designation of some streams with a geological barrier as historical habitat and others as outside historical habitat strikes me as arbitrary (although I agree that there will be streams in both categories). Providing objectives rules for making this distinction is needed.

2. Does the report provide accurate and adequate review and analysis of the factors affecting the species (habitat loss and modification, overutilization, disease, predation, regulatory mechanisms, and genetic fitness)?

Strictly speaking, the report does not review and analyze the factors affecting this subspecies (with one exception on page 15). Instead, it tabulates characteristics of those factors for each population, based on which it offers a ranking of health or risk for each population. I believe the report does a good job in this regard. It is very conservative in its interpretation of land management effects and habitat restoration effects, and I think rightly so in both cases. Mortality from fishing is briefly and adequately addressed. The treatment of nonnative species is adequate. Probably most surprising is the emphasis placed on disease risks given the paucity of data indicating that disease represents a substantial threat to the persistence of most populations of cutthroat trout. Although clinical trials indicate that whirling disease is fatal to juvenile Colorado River cutthroat trout, the majority of the habitats it currently occupies—cold, often steep, headwater streams—may be unlikely to support the causative agent of the disease or its intermediate hosts. And although the report considers many other diseases to also represent a threat, in a recent review of the literature I was unable to find evidence that diseases were a concern for most wild populations. Moreover, discussions I had with fish pathologists suggested that the vast majority of wild populations are never tested for disease, so substantive conclusions about the risk or presence of disease seem misplaced. If this supposition is incorrect, data supporting these conclusions should be included.

The analysis on page 15 is problematic because it appears to be post-hoc, and does not address an apparent problem with heterogeneity in the data.

The report does not address any aspects of genetic fitness (i.e., allelic diversity, average heterozygosity, or genetic population structuring).

3. Are there any significant oversights, omissions, or inconsistencies in the report?

The report is quite thorough but I believe it could be improved in three respects. On page 4, the report states that all data are associated with a relative degree of reliability. I believe that an analysis of the reliability of the results for each factor (e.g., knowledge of barrier locations or effectiveness, habitat lengths, or presence of nonnative species or diseases) is warranted. Currently, all items are treated as though the conclusions rest on data of equal quality, which seems unlikely. A related point is that a fuller description of how some factors were identified e.g., complete vs. partial barriers or the various levels of habitat quality, is desirable.

Second, it seemed surprising that in the initial analysis of stream segments, for many variables there were no data (e.g., genetic purity or occupied stream width), but for risk assessments of conservation populations, the "unknown" category was rarely apparent.

The third point involves the identification of possible waters for restoration. The logical conclusion of this exercise is that waters that are currently barren are those most favored for introduction of new populations or expansions of existing ones. However, would not such waters be among those least likely to support fish (because they currently fail to do so)? Moreover, even if successful, would not such populations also be among those most at risk of loss because of small size, lack of migratory fish, and lack of connectivity? It strikes me as ironic that the objective of restoration would be to create populations at immediate risk of extinction. Finally, this also seems odd because of recommendations by the American Fisheries Society, the professional society representing fisheries biologists throughout North America, to avoid using waters for introductions that do not constitute historical habitat (Williams et al. 1988), which fishless waters presumably do not.

4. Are the conclusions logical and supported by the evidence provided?

Beyond presenting summaries of the tabulations, the report does not venture far in its conclusions. A notable exception is the concluding paragraph of the executive summary, for which I could find no related text or support in the remainder of the report.

Two additional minor points:
1. On page 6, the report describes populations as sources and sinks. The ecological literature has adopted much different definitions of these terms with respect to fish populations for over a decade (e.g., Schosser 1995). Sources are considered to be to be populations in which recruitment exceeds mortality over the long term i.e., the net population growth rate is greater than 1. Sinks are habitats in which population growth rates are less than 1. One-way movement of fish from one habitat to another is not necessarily evidence of a population source or sink. Better terminology for the patterns described in the report might be "donor" and "recipient," particularly as they refer to individuals (or genes).

2. On page 9, the report mentions removing all ditches from the database. However, the Belvidere Ditch in the Little Snake River basin in Wyoming is listed as a water supporting a conservation population.

On the whole, the report is a very good summary of the status of Colorado River cutthroat trout and I commend the authors for their efforts.

Sincerely,

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