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COMMENTS

Comment: First Documented Case of Anadromy in a Population of Introduced Rainbow Trout in Patagonia, Argentina

Pascual et al. (2001) contributes important information on the basis for anadromous and resident life history forms of rainbow trout *Oncorhynchus mykiss* introduced into a new environment. I agree with the authors that this is phenomenon well-deserving of ''further research.'' My comment concerns two points that I believe can contribute to any further research. The first point concerns the possible range of diversity of rainbow trout that were introduced into the Rio Santa Cruz; this relates to the origins of *O. mykiss* that were propagated and distributed during the early 1900s. The McCloud River was not the sole or even the first source of rainbow trout used in early propagation. The second point concerns the conclusion that there is not reproductive isolation between anadromous and resident life history forms of *O. mykiss* in the Rio Santa Cruz and the implications of that conclusion. I suggest an alternative nongenetic method for testing this hypothesis.

The assumption that the origin of virtually all hatchery rainbow trout can be traced to the McCloud River has persisted in the literature for more than 100 years. Pascual et al. state: ''All early shipments of rainbow trout and Pacific salmon, including those directed to the Santa Cruz Hatchery, came directly from California [citations]. At that time, most of the eggs exported by the United States were obtained from the Baird Hatchery on the McCloud River in California (Scott et al. 1978).'' Scott et al. (1978) concerns the documentation of the origin of the rainbow trout of New Zealand; they wrote: ''With few exceptions, American fisheries literature has perpetuated the belief that Baird Station on the McCloud River in California was the source of nearly all exports of rainbow trout eggs to other countries including New Zealand.'' They cite Dollar and Katz (1964), who state: ''From these McCloud River trout have been developed most of the hatchery trout stocks used today in the U.S., Europe, New Zealand, and other countries.''

Scott et al. (1978) discovered that New Zealand rainbow trout are derived from an 1883 shipment of eggs from a private hatchery that was propagating steelhead from Sonoma Creek, California. In regard to the Rio Santa Cruz trout, it is interesting to note that the descendents of the Sonoma Creek steelhead became resident rainbow trout in New Zealand. New Zealand does have anadromous introduced populations of chinook salmon *Oncorhynchus tshawytscha* and sea-run brown trout *Salmo trutta* but no steelhead. Scott et al. (1978) mention that on the island of Tasmania, the stocking of rainbow trout in rivers with access to the sea was terminated because the stocked fish were lost to seaward migration.

A brief summary of the early propagation of rainbow trout is given in my monograph on trout of the western United States (Behnke 1992); further details and citations are given in Behnke (1990). My sources are the comments of Livingston Stone in the annual reports of the U.S. Fish Commissioner (from the first report of 1872–1973 to the 1888 report) and information on propagation and distribution found in the biennial reports of the State Board of California Fish Commissioners (from the first report of 1870–1871 to the 1888–1890 report).

Propagation of rainbow trout from the McCloud River drainage began in 1877 when J. B. Campbell and Myron Green (assistant to Livingston Stone) began propagating rainbow trout on Campbell Creek, a tributary to the McCloud River, on Campbell's property. These eggs were supplied to the California Acclimatization Society for hatching and distribution. It is not known if the eggs were taken from resident rainbow trout, steelhead, or both.

The U.S. Fish Commission's involvement with rainbow trout propagation at the Baird Station began in 1880 at Crooks Creek (later Greens Creek) on the McCloud. This operation lasted until 1888. During this time, about 2.6 million eggs where shipped to state and federal hatcheries for distribution and for the establishment of broodstocks. Thus, shipments of rainbow trout eggs to Argentina that began in 1905 did not come directly from the Baird Station.

Livingston Stone was unsure about the trout propagated at the Baird Station. Resident stream trout, referred to by Stone as ''red-banded trout,'' from tributary streams and large, silvery ''salmon-trout'' (steelhead) that appeared in the McCloud

River in late December were both kept in holding ponds. Stone speculated on the question: did the red-banded and salmon-trout represent two different species? Although unsure of the taxonomic status of the steelhead and resident trout, Stone stated that the two forms were ''indiscriminately mixed'' during egg taking and fertilization.

This hereditary basis for migratory behavior in the trout propagated at the Baird Station was noted by Pascual et al. when they mentioned that the early importations to the Santa Cruz Hatchery ''presumably contained a mixture of anadromous and resident rainbow trout, as steelhead existed at sites where the Baird Station collected fish.'' But, there's more to the early history of rainbow trout propagation and possible sources of intraspecific diversity.

Oncorhynchus mykiss of the McCloud River drainage was not the first source of rainbow trout used in artificial propagation. In 1870, the California Acclimatization Society began propagation of rainbow trout taken from around the San Francisco Bay region. Stone described their operation in the U.S. Fish Commission report of 1872–1873. Holding ponds were constructed at San Pedro Point, San Mateo County. Trout in the ponds came from San Pedro Brook and San Andreas Reservoir (large, silvery trout). Until 1877 when J. B. Campbell sent McCloud trout from Campbell Creek, various unnamed sources were used in the first propagation of rainbow trout. Because steelhead ran up all suitable tributaries of San Francisco Bay, including San Leandro Creek (the type locality of the name *irideus*) and the site of the San Leandro ''hatching house'' of the Acclimatization Society, it is likely that, similar to the broodstock at the Baird Station, the first artificial propagation of rainbow trout contained steelhead ancestry.

In 1875, Seth Green obtained rainbow trout eggs from the California Acclimatization Society and established a broodstock at his Caldonia, New York, hatchery. Descendents from this broodstock were widely disseminated to other hatcheries. Mac Crimmon (1971) gives this date as 1874 and mistakenly believed that the eggs first shipped to Seth Green came from the McCloud River. In 1876, rainbow trout eggs from the Acclimatization Society were shipped to a private hatchery at Northville, Michigan. In 1880, the Northville hatchery was leased by the U.S. Fish Commission and became an important component of the federal program for the propagation and distribution of trout. In 1878, the Caldonia, New York, and Northville, Michigan, hatcheries received McCloud River trout eggs from Campbell Creek shipped by the Acclimatization Society. Exchanges among federal, state, and private hatcheries were common during the early years of fish culture (Mac Crimmon 1971), and by 1890, after about 2.6 million eggs from the Baird Hatchery were infused into state and federal hatcheries from 1880 through 1888, various hatchery broodstocks of rainbow trout should have contained diversity from different parental sources that included both steelhead and resident rainbow trout ancestry.

Mac Crimmon and Gots (1972) mentioned that ''eastern hatcheries'' encountered problems with rainbow trout broodstocks in the 1890s and that such broodstocks were replaced by or supplemented with rainbow trout propagated by the California Fish Commission from the Klamath River. It is not known if the Klamath trout were steelhead, resident rainbow trout, or both.

The first mention of steelhead propagation found in U.S. Fish Commission reports is in 1896. Steelhead propagation continued for many years into the 1900s. The major egg sources came from northern California (Redwood Creek and Klamath River) and Oregon (mainly the Rogue and Willamette rivers). The half-pounder life history characteristic of Rogue and Klamath steelhead is particularly pertinent to the life history of the Rio Santa Cruz steelhead.

Following Jordan and Evermann's (1896) classification of rainbow trout as *Salmo irideus* and steelhead as *Salmo gairdneri,* the U.S. Fish Commission (which became the U.S. Bureau of Fisheries in 1904) kept separate records for the propagation and distribution of steelhead (*S. gairdneri*) and rainbow trout (*S. irideus*). Pascual et al. cite Tulian (1908)[1] to establish the earliest stocking records of rainbow trout in the Rio Santa Cruz. Rainbow trout were first introduced in 1906 from a shipment of 25,000 eggs of ''*Salmo irideus.*'' Most probably these trout came from one of the U.S. Bureau of Fisheries broodstocks that had been captively bred since the 1880–1888 egg-taking operation on the McCloud River. It is also possible, even probable, that these broodstocks contained an influence from the trout propagated by the California Acclimatization Society and shipped to the Northville, Michigan, hatchery in 1876 and 1878

[1] This paper was presented at the Fourth International Fishery Congress, Washington, D.C., September 22–26, 1908. It was published in the Bulletin of the United States Bureau of Fisheries, volume 28 for 1908, but this volume was not published until 1910.

and to the Caldonia, New York, hatchery in 1875 and 1878. Another possible source of diversity in early broodstocks could have been the previously mentioned replacement and supplementation of many established broodstocks in the 1890s with Klamath River rainbow trout (possibly steelhead).

In 1908, Tulian took 300,000 steelhead (*S. gairdneri*) eggs and 50,000 rainbow trout (*S. irideus*) eggs to Argentina. The rainbow trout came from Germany. The first rainbow trout shipped to Germany came from the Northville, Michigan, hatchery in 1882. The first shipment of McCloud trout from the Baird Station to Northville was 1880. The 1882 shipment of eggs to Germany most probably was from a broodstock established from the 1876 or 1878 shipments from the California Acclimatization Society. Mac Crimmon (1971) cites ''steelhead'' eggs being sent to German hatcheries in 1896, 1898, and 1902. By 1908, when rainbow trout from Germany were shipped to Argentina, German broodstocks were probably derived from mixed parental sources with diverse life histories including migratory behavior. Thus, the shipments of *O. mykiss* to Argentina and introduced into the Rio Santa Cruz in 1906–1908 were not monotypic. Diversity of ancestral life history forms could have provided the hereditary basis resulting in a migratory steelhead-like population and a resident rainbow trout population, comparable to what has occurred in the Great Lakes (Mac Crimmon and Gots 1972). Pascual et al. (2001) concluded that resident and anadromous *O. mykiss* of the Rio Santa Cruz are not genetically differentiated and, thus, not reproductively isolated. But this question is not yet resolved. Where steelhead and resident rainbow trout populations coexist in sympatry, some hybridization will probably occur. Steelhead populations typically contain a small proportion of residual males that mature sexually before smolting, and they might then mate with resident females. Resident males can act as ''sneakers'' and fertilize some eggs during steelhead spawning. A slight amount of genetic interchange between resident and anadromous populations will make it difficult, perhaps impossible, to establish unambiguous genetic differentiation between the two. The basic question in need of resolution is: does like give rise to like? Do steelhead produce steelhead and do resident rainbows produce resident rainbows, at least in the overwhelming majority of cases? Pascual et al. (2001) rejected this hypothesis (or accepted the null hypothesis) on the basis of statistical analysis of genetic data. This hypothesis should be retested using a nongenetic method. Zimmerman and Reeves (2000) used the strontium–calcium ratio in otolith nuclei to determine if individuals in sympatric populations of steelhead and resident rainbow trout had steelhead or rainbow trout mothers. In the Deshutes River, Oregon, of 20 steelhead, all had steelhead mothers, and all of 38 resident rainbow trout had rainbow trout mothers. In the Babine River of British Columbia, 1 of 24 steelhead had a rainbow trout mother and 2 of 9 resident rainbow trout had steelhead mothers (one or both could have been residual steelhead).

For listing under the Endangered Species Act (ESA), the National Marine Fisheries Service grouped steelhead populations into Evolutionarily Significant Units (ESUs). ''Substantial reproductive isolation'' is a prerequisite for ESUs (Busby et al. 1996). In this regard, Pascual et al. make a broad extrapolation from their conclusion that Rio Santa Cruz anadromous and resident rainbow trout are ''not reproductively isolated'' to claim that over the entire natural range of the species from California to Alaska ''wild steelhead and resident rainbow trout co-occur and do not seem to be reproductively isolated.'' This statement is unwarranted because it ignores studies such as Zimmerman and Reeves (2000); it can also be potentially harmful by providing a ''scientific'' basis for anti-ESA rhetoric.

Before hasty conclusions are reached on the hereditary basis for anadromy and residency in salmonid fishes, I suggest a critical reading of W. E. Ricker's 1972 classic work on hereditary and environmental factors affecting life histories (and reproductive isolation) in salmonid populations. I particularly call attention to Ricker's final comment: ''My strong opinion is that we should avoid any appeal to conservatism in such questions. Time and again it has been discovered that nature is more complex than anyone dreamed possible.''

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