

The Population Genetic Structure of Central Valley Steelhead Rainbow Trout

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Introduction

In 1999 the Department of Fish and Game (DFG) obtained funding from the CALFED Bay-Delta Program, the Ecosystem Restoration Program, and the US Fish and Wildlife Service's (USFWS) Anadromous Fish Restoration Program (AFRP) to conduct a comprehensive baseline genetic analysis of coastal rainbow trout (*Oncorhynchus mykiss irideus*) in the Central Valley. This species exhibits great variation in life history, with anadromous (steelhead) and resident forms being the extremes of a continuum of life-history types. Central Valley steelhead have experienced declining abundance and their range has been greatly reduced due to the loss of historical habitat above dams. The federal Biological Review Team that conducted the status review for west coast steelhead concluded that resident rainbow trout should be included in the steelhead distinct population segments or Evolutionarily Significant Units (ESU) where they have the opportunity to interbreed (Busby and others 1996). However, National Oceanic and Atmospheric Administration (NOAA) Fisheries listed only the anadromous life-history form under the Endangered Species Act (ESA)¹. In 1998, the Central Valley California Steelhead ESU was listed as threatened. Unfortunately, the genetic profiles and relationships of the different populations and life-history types occurring in the Central Valley were not investigated and described prior to major impacts to the species, such as extensive habitat modification, habitat loss through construction of dams, and the introduction of nonnative coastal rainbow trout (both anadromous and resi-

1. NOAA Fisheries published a new proposed rule on June 14, 2004, that includes resident rainbow trout where the two forms co-occur.

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dent). NOAA Fisheries reviewed existing genetic analyses and conducted some additional analyses to delineate ESUs for purposes of the ESA (Busby and others 1996). However, their analyses did not provide sufficient detail necessary to distinguish populations within ESUs (McEwan 2001). DFG initiated this study to elucidate the genetic profiles of native Central Valley steelhead rainbow trout¹ and to describe population genetic structure in relation to anadromous and resident life-history types and anadromous hatchery populations.

The information from the Central Valley steelhead rainbow

trout study will enable development of management actions that will accelerate the species' recovery. Analysis of the remaining amount and pattern of genetic variation within and among Central Valley steelhead populations will be used to estimate population structure and genetic diversity. Knowing the amount and pattern of genetic diversity will allow us to prioritize research and management to retain remaining genetic and biological diversity; to avoid mixing different groups of fish, which would lead to reduced genetic diversity; identify populations with relatively low diversity; identify populations of interbreeding individuals; and identify metapopulation structure. This study will help us identify the most appropriate steelhead stock to use as donors to reintroduce steelhead to stream systems where they have been extirpated. If native non-anadromous rainbow trout—which have been recently isolated from the ocean due to construction of impassable dams—prove to be genetically similar to anadromous forms in the same stream, these nonanadromous populations may have the potential to provide brood stock for reintroduction projects. Identification of these isolated populations, if they exist, could greatly enhance our ability to reintroduce native steelhead to Central Valley streams where they have become extirpated without risking reductions in genetic diversity. Another benefit will be the clarification of the genetic relationship of natural stocks with hatchery stocks. This will allow managers to (1) assess whether hatchery practices are having unintended genetic effects on the natural populations, such as introgression and loss of genetic variation, and (2) assess whether hatchery populations are significantly different from the natural populations from which they were founded.

Objectives

- Describe and compare genetic profiles and relationships between steelhead rainbow trout populations inhabiting specific stream systems within the Central Valley.
- Describe genetic profiles of Central Valley hatchery steelhead populations and compare to naturally spawning, presumed native populations of steelhead and isolated resident rainbow trout.
- Analyze genotypes of self-sustaining, presumed native Central Valley rainbow trout populations that are now isolated above artificial barriers to determine their phylogenetic relationship to anadromous and non-anadromous rainbow trout populations and strains.
- Evaluate the genetic structure of naturally spawning Central Valley steelhead populations.

Methods

Sampling locations for tissue collections are shown in Figure 1 and described in Table 1. DFG collected, or coordinated

the collection of, tissue samples from steelhead rainbow trout at 21 locations throughout the Central Valley. Several other agencies and consultants assisted with collections at various locations. USFWS made collections from upper and lower Clear Creek and Coleman National Fish Hatchery (CNFH) for a related study. Data from these locations are included in the analyses and results for a total of 24 sampling locations. Tissue samples were collected from rainbow trout captured in anadromous reaches and above artificial barriers, and taken from anadromous fish hatcheries from 1999 to 2003. Collections made above artificial barriers were below historical natural barriers and within the historical range of steelhead, as described in McEwan (2001) and Yoshiyama and others (1996). Fish were collected at each sampling location throughout a continuous stream reach (i.e., there are no barriers between actual collection sites within each sampling location) to minimize collection of closely related individuals that would bias the population genetic results.

1. The term “steelhead rainbow trout” is used to refer collectively to all life-history types.

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Figure 1 Sampling locations for Central Valley steelhead rainbow trout.

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Adult steelhead were collected whenever possible. However, our collections focused mostly on juvenile fish because they are much easier to sample. Fish were captured by electrofishing, hook and line, rotary screw traps, and beach seining.

We took caudal fin tissue samples (approximately 2 square millimeters) from 50 to 100 individuals per sampling location. Fish were returned to the stream alive after sampling. Tissue samples were air dried, processed at DFG’s Salmonid Genetic Tissue Archive, and shipped to the geneticist. Both DFG and USFWS subcontracted with Dr. Jennifer Nielsen from the US Geological Survey’s Alaska Science Center, Conservation Genetics Laboratory, to perform the genetic analyses¹. A total of 1,570 steelhead rainbow trout tissue samples were analyzed.

DNA was extracted from the tissue samples, amplified, and analyzed using standard methods. Thirteen microsatellite loci from the published literature were used. Tissue samples were analyzed for microsatellite allelic diversity within and among populations. Genetic data were analyzed using a variety of software from different statistical packages. Two loci were found to be out of Hardy-Weinberg equilibrium in over 80% of the sample populations and were dropped from further analysis. Genetic distance values reflecting the proportion of shared alleles between individuals and groups of individuals were determined and used to graphically depict genetic relationships and population structure. An unrooted

Neighbor-Joining tree (NJ) was generated. Genetic relationships depicted in the consensus NJ tree were tested using random bootstrap replications (n = 2,000) to assess the reproducibility of branching patterns (Nielsen and others 2003). Bootstrap values are expressed as percentages.

Table 1 Central Valley steelhead rainbow trout sampling locations.

Sample Location Above/Below Barrier Comments

1. Sacramento River mainstem below

Keswick Dam

Below barrier Collection focused on "river trout" to determine if they differ genetically from steelhead and are reproductively segregated

2. Battle Creek Weir at hatchery

3. Cottonwood Creek Below barrier Self-sustaining stocks in headwaters within steelhead historical range

4. Mill Creek Below barrier Mill and Deer creeks represent one of the last remaining intact and accessible small stream systems in the Sacramento River system, and have healthy, self-sustaining populations; hence, they

are good candidates to examine population structure of relatively unimpacted populations

5. Deer Creek, downstream of lower falls. Self-sustaining stocks in headwaters within steelhead historical range

6. Stony Creek Above barrier Self-sustaining stocks above Lake Berryessa

7. Putah Creek Above barrier Self-sustaining stocks above Lake Berryessa

8. Feather River Below barrier Low-flow channel

9. Feather River Hatchery

10. Lower Yuba River Below barrier Below Englebright Dam

11. Upper Yuba River Above barrier Above New Bullards Bar Dam

12. Lower American River Below barrier Below Nimbus Dam

13. Middle Fork American River Above barrier Below Rubicon River confluence

14. Nimbus Fish Hatchery

15. Antelope Creek Below barrier Below confluence of north and south forks

16. Calaveras River Below barrier Below New Hogan Dam

17. Lower Stanislaus River Below barrier Below Goodwin Dam

18. Upper Stanislaus River Above barrier Below Beardsley Dam

19. Lower Tuolumne River Below barrier Below La Grange Dam

20. Upper Tuolumne River Above barrier Between New Don Pedro Reservoir and Yosemite National Park Boundary

21. Kings River Above barrier Self-sustaining stocks in headwaters within steelhead historical range

1. The final technical report submitted to DFG and USFWS was written by Nielsen and others (2003); it includes the results from both studies. The original report is available from the author.

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Results and Conclusions

This study found that there is significant steelhead genetic population structure throughout the Central Valley (Nielsen and others 2003). Pairwise population comparisons showed significant differentiation in all but 2% of the population-pair comparisons. Analysis of molecular variance showed that microsatellite diversity was highest within populations

(88.67%) and lowest among populations (11.33%). After dividing the populations into the two primary drainages, the same analysis showed that microsatellite diversity was highest for individuals within populations (92.39%) and was lowest between the Sacramento and San Joaquin drainages (0.13%). The lack of genetic divergence between the Sacramento and San Joaquin river drainages most likely reflects a common ancestry. However, there is a relatively high level of genetic population structuring within the individual rivers of each drainage area. This genetic diversity and population structuring should be carefully considered before carrying out any future conservation and restoration actions to preserve existing patterns of genetic diversity.

There are significant differences in the allelic frequencies between steelhead rainbow trout samples collected above impassable dams and those collected below dams on several large rivers: American, Stanislaus, Tuolumne, and Yuba rivers. This suggests some degree of genetic separation. A more thorough analysis may allow inference on the direction and duration of such isolation between populations above and below barriers in the Central Valley (Nielsen and others 2003).

Hatchery populations (CNFH, Nimbus Hatchery, and Feather River Hatchery) are genetically similar to steelhead rainbow trout populations in close proximity, suggesting gene flow among these populations or the common ancestry and local origins of the hatchery stock (Nielsen and others 2003). CNFH stock was derived from steelhead collected from the upper Sacramento River from 1947 through 1984. Feather River Hatchery stock is from local origins, but Nimbus Hatchery stock is of mixed origin and includes fish originally collected from the Eel River. The hatchery-wild gene flow is found only at the local scale regardless of hatchery origin. Nielsen and others (2003) note that because hatchery stocks do not have unique diagnostic microsatellite alleles we cannot estimate rates of gene flow or introgression. Other molecular markers and fine scale sampling are needed to obtain this type of information.

Genetic relationships and population structure depicted in the unrooted NJ tree (Figure 2) show some population associations that are intuitive and are supported by relatively high bootstrap values. The clustering of the three hatchery populations with nearby natural populations is well supported by the bootstrap values (the branching pattern shown was observed in > 50% of the 2,000 bootstrap replicates). Samples from CNFH and the upper Sacramento River cluster together, as do samples from Feather River Hatchery and the lower Feather River, and Nimbus Hatchery and the lower American River. Samples from Deer, Mill, and Antelope creeks, which are close to each other geographically, also

cluster together.

Other associations were more difficult to interpret, such as the grouping of the upper portions of the Tuolumne, Stanislaus, American, and Yuba rivers. A more thorough investigation is needed to determine if there is shared ancestry of these populations not influenced by hatchery fish or if these associations are due to the influence of introduced rainbow trout stocked above dams (Nielsen and others 2003). Until further studies are conducted we cannot make any conclusions about the presence of presumed native populations above these barriers or their potential use as donor stock. Other associations—such as the Kings River and Stony Creek and the grouping of the Calaveras River, Putah Creek, lower American River, and Nimbus Hatchery—will also need further examination.

Lastly, the genetic analyses showed that most Central Valley steelhead rainbow trout stocks have undergone a recent reduction in population size.

Recommendations for Future Studies

Although this study provided much-needed information on the genetic and population structure of Central Valley steelhead, there are still several questions that can only be answered by conducting additional studies. Recommended research includes:

- A complete genetic analysis of all Central Valley hatchery rainbow trout stocks to get better information on the distribution of hatchery and wild stocks, and impacts of hatchery fish on wild fish genetic diversity.

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Figure 2 Unrooted Neighbor-Joining tree based on Cavalli-Sforza and Edwards chord distance for the Central Valley system derived from allelic variation at 11 microsatellite loci. Branches with bootstrap values (2,000 replicate trees) are provided.

- Additional genetic analysis of steelhead rainbow trout populations above and below barriers to determine if native stocks of steelhead remain isolated above artificial barriers. These studies should be done on a finer scale for specific watersheds such as the American, Merced, San Joaquin, Stanislaus, Tuolumne, and Yuba rivers.
- Genetic analysis to describe and compare the genetic profiles and relationships of naturally spawning Central Valley steelhead populations with naturally spawning populations along the California coast.

This work is currently being conducted by the NOAA Fisheries' Southwest Fisheries Science Center in Santa Cruz.

Detailed examination of hatchery stocking records may provide some insight into several of the unexplained relationships

shown in the NJ tree.

Next Phase

DFG has obtained funding from AFRP to evaluate the distribution and relationship of different life-history forms of rainbow trout within the Central Valley. This will build on the genetic population structure study and provide complementary information on population structure using a different technique. The question we are asking is: do the different life-history forms (e.g., steelhead, resident, potamodromous, estuarine) of Central Valley rainbow trout maintain distinct, reproductively isolated populations or do they comprise a single, polymorphic population within stream systems? The life history of individual fish will be determined by comparing strontium to calcium ratios across a transect of the otolith (i.e., ear bones). This will allow us to determine both the life history of the individual fish, as well as the mother. If the life histories of the fish and its mother are different, this indicates that fish are capable of producing offspring that differ in their life-history expression; hence the life-history forms are not reproductively isolated. Recent microchemical analysis of strontium to

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calcium ratios from three rainbow trout from the Calaveras River provides evidence that some Central Valley rainbow trout populations are polymorphic (McEwan 2001).

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