CENTRAL VALLEY STEELHEAD
Oncorhynchus mykiss irideus

Moderate Concern/Low Concern. Status Score = 3.0/4.6 out of 5.0. This taxon, which includes resident trout, is in little danger of extinction but current Central Valley stream conditions appear to favor resident life histories over anadromous life histories. Over time, life history diversity could be lost increasing extinction risk for the taxon as a whole. The first score only reflects the status of the steelhead life history, including both hatchery and wild fish, while the second score reflects the potential for maintaining large, highly adaptable rainbow trout populations that include steelhead as a life history option.

Description: Steelhead and rainbow trout vary greatly in color and body shape (Moyle 2002). Juvenile trout display 5-13 oval parr marks centrally located along the lateral line, with interspaces being wider than the parr marks. The color of the dorsal and anal fins ranges from white to orange, and there is little or no spotting on the slightly forked tail. The head is blunt with a short jaw that does not extend past the eye. Historically, adult CV steelhead rarely exceeded 60 cm FL. Newly arrived adults appear silvery, sometimes showing an iridescent pink to red lateral line, and have a square-shaped caudal fin with radiating spots, which is unlike other salmonid species within the Sacramento-San Joaquin Rivers. Many small, black spots also cover the back, adipose, and dorsal fins. As adults remain in freshwater they darken, taking on the greenish hue on the back and the iridescent pink and red sides characteristic of resident rainbow trout. The scales are small, with 110-160 pored scales along the lateral line. Basibranchial teeth are absent, with 16-22 gill rakers on each arch and 9-13 branchiostegal rays. Steelhead typically have 10-12 primary dorsal fin rays, with 8-12 primary anal rays, 9-10 primary pelvic rays, and 11-17 primary rays making up the pectoral fin.

Taxonomic Relationships: Central Valley (CV) steelhead are part of the coastal rainbow trout complex in the Central Valley and are broadly defined as anadromous rainbow trout from the region. However, the CV steelhead does not hold up well as a distinct taxonomic unit.

NMFS (1998) found that CV steelhead formed an Evolutionary Significant Unit (ESU) that was genetically distinct from the Central Coast ESU, which includes fish found in tributary streams to San Francisco Bay. The ESUs also included non-anadromous rainbow trout, so to "clarify" the situation the ESU designation was changed in 2005 to a Distinct Population Segment (DPS), which only listed threatened anadromous (sea-run) individuals (NMFS 2016). To further complicate the listing designation, only fish "originating below" dams and other barriers are counted. Resident trout are not included as part of this DPS and are therefore not listed under the ESA even where they interbreed with sea-run fish. All *O. mykiss* above Central Valley reservoirs are also excluded from the DPS, even steelhead-like forms (adfluvial rainbow trout) with spawning migrations into tributary streams and which use reservoirs like below-dam steelhead use the ocean. These migratory fish would presumably be part of the DPS if the dams did not exist. The changes happened despite the official DPS Policy, which states that a group of organisms form a distinct population segment if it is "markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, and behavioral factors." [61 *Federal Register* 4722 (Feb. 7, 1996)]. A basic problem is that CV steelhead are not "markedly separated" from resident rainbow trout. For more explanation of distinctions between an ESU and a DPS, see the Northern California winter steelhead account.

Curiously, the CV steelhead DPS officially includes steelhead from the Feather River and Coleman National fish hatcheries. “NMFS determined that these artificially propagated stocks are no more divergent relative to the local natural population(s) than what would be expected between closely related natural populations within the DPS” (NMFS 2016, p 4.). NMFS excluded fish reared in the Nimbus Fish Hatchery on the American River because these fish had been heavily hybridized with fish from the North Coast, primarily Eel and Mad rivers. These fish were brought to the hatcheries to increase adult size and improve angler satisfaction. The hatchery plans to eventually stop rearing the mixed strain fish and replace them with steelhead closer to the native strains, perhaps from above-dam populations (NMFS 2016). Mokelumne Hatchery recently switched from raising fish from the American River Hatchery to using Feather River Hatchery stocks prompting NMFS (2016) to recommend including these fish in the DPS as well.

In contrast to patterns typical of coastal steelhead, a recent genetic study found that Central Valley *O. mykiss* above and below dams within the same watershed were not each others’ closest relatives. Most below dam samples clustered closely with hatchery steelhead (Pearse and Garza 2015). The authors also found no relationship between genetic and geographic distance among below-dam populations suggesting that a long history of translocations of hatchery trout and steelhead and pervasive habitat alteration have effectively “scrambled” populations creating a single heavily hatchery-influenced below-dam population.

Central Valley steelhead is not a well-defined taxon. The mish-mash of which populations and life history forms to include or exclude from the DPS comes with some curious assumptions, namely that: (a) the resident and anadromous forms do not significantly interbreed, (b) that steelhead from various hatcheries do not stray and mix, (c) that steelhead-like fish above reservoirs have diverged significantly from steelhead below the rim dams so they no longer serve as part of the DPS, and (d) decades of widely planting resident rainbow trout of hatchery origin (multiple strains) have not influenced the genome of the DPS. Faults with each of these assumptions are addressed below.

Resident vs. anadromous. There is a conundrum in the relationships among steelhead and resident rainbow trout (Kendall et al. 2015). In general, the two forms are complementary because anadromous trout can give rise to resident trout and vice versa on a regular basis and the flexible life history has a strong genetic basis (Pearse et al. 2014). Recent research shows that anadromy is a polygenic (multi-gene) trait in rainbow trout with moderate heritability. This means that a large population of resident rainbow trout, such as the one in the lower Sacramento River, can continue to have individuals that express anadromy even if there is selection against behavior in many years (M. Miller, UC Davis, pers. comm. 2017). But the anadromy trait can also be maintained at low levels through the effects of environmental variation. If survival is low in the ocean or during down-stream migration for an extended period, then resident trout will have an adaptive advantage. If conditions in the ocean promote high survival and growth, then progeny of high-fecundity steelhead females will do well in fresh water. Resident trout can also thrive above natural barriers (e.g., landslides) and steelhead can recolonize streams from which resident fish have been eliminated from natural causes (e.g. volcanic eruptions). According to NMFS (2006) “It is unclear how long an *O. mykiss* population can persist if [it is] dependent entirely upon the productivity of resident fish in a dynamic freshwater environment, even if the resident forms are abundant (*Federal Register* 71(3), p 844.).”

Pearse et al. (2014) indicate that residency has a genetic basis reflecting strong selection pressure against anadromy in populations with little contact with sea-run fish. Conversely, in southern California many, if not most, returning "steelhead" likely originate as migratory smolts produced from resident headwater trout populations many of which persist *above* man-made and natural barriers to anadromy. The polygenic nature of the anadromy indicates that the trait can persist for a long time in a large resident population. This has been demonstrated in an Argentina river flowing to the Atlantic, where steelhead have developed from resident fish, apparently of California origin, with resident and migratory fish forming one interbreeding population (Pascual et al. 2001). In some cases, such as in the Calaveras River, the anadromous forms may be mainly female, while males remain as resident fish (McEwan 2001).

All Central Valley Hatchery steelhead are adipose fin clipped and it appears that a majority of steelhead, or at least of steelhead caught by anglers, are of hatchery origin. Steelhead resulting from natural spawning make up only a small percentage of fish returning to hatcheries or nearby streams in the Central Valley (NMFS 2016). Resident populations in tailwaters (e.g. in Sacramento River between Keswick dam and Red Bluff) generally contain few fish that had a steelhead mother (Zimmerman and Reeves 2000, Zimmerman et al. 2009). Presumably the large size, rapid growth rates and correlated greater fecundity of these resident fish, combines with low survival rates of fish that out-migrate through valley rivers and the Delta to go to the ocean, strongly selects for the resident life history in these habitats. It should be noted that some large resident trout enter hatcheries and are inadvertently used as part of the steelhead breeding program (NMFS 2016).

Straying of hatchery fish. Hatchery fish of all salmonids are notorious for straying to non-natal rivers at fairly high rates, especially if smolts are released at a location other than the hatchery. Thus, in the Central Valley where hatchery fish have often been released at downstream locations straying should be expected. Accordingly, straying of hatchery fish is presumably one reason why CV steelhead show little genetic structure among populations (Pearce and Garza 2015). In an earlier report to CDFW, Garza and Pearse (n.d.) found that genes from Eel River fish were found in both resident and anadromous fish throughout the Sacramento Basin, indicating widespread straying of fish raised at Nimbus Hatchery on the American River from Eel River stock.

Rainbow trout above dams. A number of large reservoirs that block former steelhead streams (e.g., Berryessa Reservoir) have steelhead-like fish that migrate from the reservoir into tributaries to spawn. This expression of the anadromy gene complex increases in frequency in direct proportion to reservoir size (Leitwein et al. 2016), hence the propensity of rainbow trout in the Great Lakes to take on an adfluvial life history. These adfluvial populations are now isolated from below-dam forms and presumably are on their own evolutionary pathways, although individuals may be washed downstream of dams and interbreed with fish in the CV rivers below. While genetic work on rainbow trout above reservoirs has not focused on migratory forms, wild rainbow trout of unspecified origin are genetically distinct from lineages below the dams (Pearse and Garza 2015), providing a reason not to include them in the DPS. These fish would have been part of the DPS before dams were constructed and today may better represent the pre-dam steelhead genome than the lineages presently below the dams. No evidence was found that out-of-basin rainbow trout stocked to support fisheries have contributed to the genomes of the above-reservoir rainbow trout populations. We do not know if the migratory form in reservoirs are of hatchery origin or developed from natural populations present when the dams were built. Research is needed on the genomes and life histories of migratory fish in and above reservoirs, including their relationships with resident forms.

Genetic impacts of hatchery fish on wild populations. In general, wide-scale planting of catchable-size hatchery rainbow trout above dams has not resulted in long-term introgression of hatchery genes into wild resident rainbow trout populations in California (Pearse and Garza 2015). Presumably hatchery populations become adapted to hatchery conditions and their domesticated genomes do not do well in the wild. Even where they survive long enough to breed with wild fish it is assumed that their off spring which inherit domesticated genes have limited reproductive success in the wild thus limiting the flow of hatchery genes into wild trout populations. Below dam CV populations, in contrast, appear to have heavily introgressed with hatchery stocks (Pearse and Garza 2015).

These diverse lines of evidence indicate that the Central Valley steelhead is not a well-defined taxon, or even a DPS. We see two basic ways the taxon can be treated for management: (a) continuing with the status quo or (b) recognizing that all rainbow trout in the Central Valley belong to one broad, genetically diverse taxon, perhaps an ESU.

Status quo. This means to continue to recognize virtually any sea-run rainbow trout in the Central Valley as CV steelhead, except those from the American River. Rainbow trout populations above dams (including adfluvial forms) would continue to be excluded from the DPS. This strategy keeps steelhead of hatchery origin as the mainstay of the run, with only occasional individuals originating from tail-water rainbow trout populations or above dam populations. If the status quo is to be pursued, improved monitoring techniques and genetic methods will need to be widely used to limit interbreeding with America River steelhead or large resident rainbows that sometimes enter hatcheries masquerading as steelhead.

One broad taxon. The reality of the Central Valley is that below dams resident rainbow trout and steelhead, regardless of origin, form one interbreeding population (Pearse and Garza 2015). Central Valley hatchery programs strongly select for the anadromous life history while habitat conditions in the highly altered contemporary rivers strongly select for the resident life history in the year-round, cool tail water habitats directly below dams. Until recently, two hatcheries (Nimbus, Mokelumne) also selected for larger fish, favoring the introduced north coast phenotype over the Central Valley phenotype. Thus the anadromous steelhead life history is maintained in the Central Valley largely through artificial selection. In addition, rainbow trout living in tailwaters below dams also experience a very different selection regime than their pre-dam predecessors once did, one that seems to favor a resident life history.

Careful investigation of adfluvial populations above major dams – which likely better represent ancestral CV steelhead lineages than populations presently below dams – could result in finding individuals of native ancestry that could contribute migratory life history diversity to valley floor populations. This overall approach of acknowledging the biological interdependence of different life history traits could better support steelhead fisheries without concerns about 'contamination' of CV steelhead genomes with genetic material from other populations.

Life History: CV steelhead, like all steelhead populations, exhibit flexible and diverse life history strategies, which allow for persistence in spite of variable conditions in rivers and the ocean (McEwan 2001). General aspects of steelhead life history are portrayed in Moyle (2002) and the North Coast winter steelhead account, while interactions of steelhead with resident trout are reviewed in Kendall et al. (2015). While we accept recognition of all rainbow trout below dams as a unified population in the Central Valley, in this account we focus on fish with the anadromous steelhead life history and their interactions with resident trout living in tailwater habits below Central Valley dams. Broader accounts can be found in Moyle (2002) and in the coastal rainbow trout account. This account necessarily over-simplifies the adaptive life history variations in rainbow trout.

At present steelhead found in the Central Valley undertake spawning migrations during winter. There is indication that before the era of large rim dams that summer-run (late-maturing) steelhead, such as those that still exist in the Klamath River, once existed in the system (McEwan 2001). In the American River, summer steelhead apparently migrated upstream in May-July, and were fairly abundant (Gerstung 1971). Because summer steelhead over-summer in deep pools found in mid- to high elevation streams, they were extirpated by the large dams that blocked migration into upstream areas, despite an effort to propagate them (Gerstung 1971). For winter steelhead, peak immigration seems to have occurred historically from late September to late October, with some creeks such as Mill Creek showing a small run in mid-February (Hallock 1989). Juvenile CV steelhead generally migrate out of the system from late December through the beginning of May, with a peak in mid-March. There is a much smaller peak in the fall (Hallock 1961).

Juvenile CV steelhead are opportunistic, voracious predators on anything available in their rearing streams, from aquatic and terrestrial insects, to small fish, frogs and mice (Merz and Vanicek 1996, Merz 2002). However, benthic aquatic insect larvae are the mainstay of their diet, especially those of caddisflies (*Trichoptera*), midges (*Chironomidae*), and mayflies (*Ephemeroptera*). Below reservoirs, zooplankton may be important as well. Diets shift with season and size of juveniles. At times, salmon eggs, juvenile salmon, sculpins, and suckers may be important prey for yearling steelhead (Merz 2002) and these high calorie, seasonal forage items are especially important for growth. Curiously, Merz (2002) did not observe a change in average prey size with fish size, and even adult steelhead were observed feeding on small insects. In the Mokelumne River, Merz (2002) found that most juveniles tended to have relatively limited movement within their rearing area.

CV steelhead historically spent 1 (29%), or 2 (70%) years within their natal streams, with a small percentage (1%) spending three years before becoming smolts and migrating out of the Sacramento-San Joaquin system (Hallock 1961). It is not known to what extent, if at all, this anadromous life history diversity is still present today. As discussed in other accounts, the relationship between anadromous and resident forms of the same species is complex, but populations that have both basic life history strategies, as is true in the CV, are likely to have an evolutionary advantage. Resident fish persist when ocean conditions cause poor survival of anadromous forms, while anadromous forms can recolonize streams in which resident populations have been wiped out by drought, fire or other natural disasters. Anadromous steelhead produce many more than do resident fish and thus improve gene flow among rivers, increasing genetic diversity of the meta-population. Eggs are large which confers an advantage on sea-run females, which attain greater size and therefore produce more and larger eggs than their resident counterparts. Small resident males, on the other hand can still produce sufficient sperm to fertilize many eggs from large females. For this reason anadromy seems to confer a greater benefit on females (Ohms et al. 2014).

Habitat Requirements: The habitat requirements of CV steelhead *sensu lato* are similar to those of Central Coast steelhead and coastal rainbow trout. Water quality is a critical factor during freshwater residence, with cool, clear, well-oxygenated water needed for maximum survival (Moyle 2002). Optimal spawning temperatures are 4˚-11˚C, with embryos starting to die at 13˚C (McEwan and Jackson 1986). Fry, after emerging from gravel, usually migrate into shallow (< 36 cm) areas such as stream edges or low gradient riffles, often in open areas with large substrates (Everest and Chapman 1972, Everest et al. 1986, Fontaine 1988). With increasing size, fry move into higher-velocity, deeper, mid-channel areas in the late summer and fall (Fontaine 1988). Fry prefer water depths of 25-50 cm, and optimal growth occurs at temperatures of 15-19°C (Richter and Kolmes 2005). Juvenile steelhead (ages 1+ and 2+) prefer deeper water in summer than fry, and show a preference for pool habitat, especially deep pools near the thalweg with ample cover, as well as higher-velocity rapid and cascade habitats (Bisson et al. 1982, 1988; Dambacher 1991). In general, juveniles and resident adults prefer complex habitat with large physical structures such as boulders, submerged clay and undercut banks, and large woody debris that provide feeding opportunities, segregation of territories, refuge from high velocities, and cover from fish and bird predators. These features are characteristic today of small tributaries and they are uncommon in rivers below major dams. However, much of the complex cover in the Sacramento and San Joaquin rivers and their tributaries was removed in the 19^{th} century as part of 'desnagging' efforts to improve channels for navigation. CV steelhead now spawn in mainstem rivers, as do resident fish. Merz (2002) observed good growth and feeding of presumed steelhead in the Mokelumne River below Camanche Dam. The Sacramento River above Red Bluff supports resident rainbow trout, with some becoming steelhead.

Distribution: CV steelhead were historically part of a single meta-population with resident rainbows. The meta-population consisted of distinct populations in the Sacramento and San Joaquin Rivers and in most of their tributaries (Figure 1). Lindley et al. (2006) modeled the likely historical distribution of steelhead in the Central Valley based on habitat characteristics, and concluded there were possibly 81 discrete populations from the San Joaquin Valley north to the Pit River drainage, although a number of the 'populations' they identified are in areas not accessible to anadromous fish, indicating the close link between anadromous and resident fish.

The distribution of steelhead life history in the Central Valley today is greatly reduced from the historical distribution. This is the result of impassable dams and water diversions that block access to historical spawning and rearing areas (Figure 2). Estimates on the loss of habitat for Central Valley salmonids ranges from 80-95% (Clark 1929, CACSST 1988, Yoshiyama et al. 2001, Lindley et al. 2006). Populations of resident rainbow trout that have anadromous components within them are found in the Upper Sacramento River and tributaries, Mill, Deer, and Butte Creeks, and the Feather, Yuba, American, Mokelumne, Tuolumne, and Calaveras Rivers (McEwan 2001). A wider implementation of monitoring programs would probably turn up other populations, as has happened on Dry Creek, Auburn Ravine and the Stanislaus River (McEwan 2001). The Cosumnes River, which historically had steelhead, provides rearing habitat to non-natal steelhead from adjacent basins in wet years (NMFS 2014). However, most fish living below dams in tailwaters are resident rainbows; where cold water exists above dams, resident and adfluvial rainbows occupy such habitat.

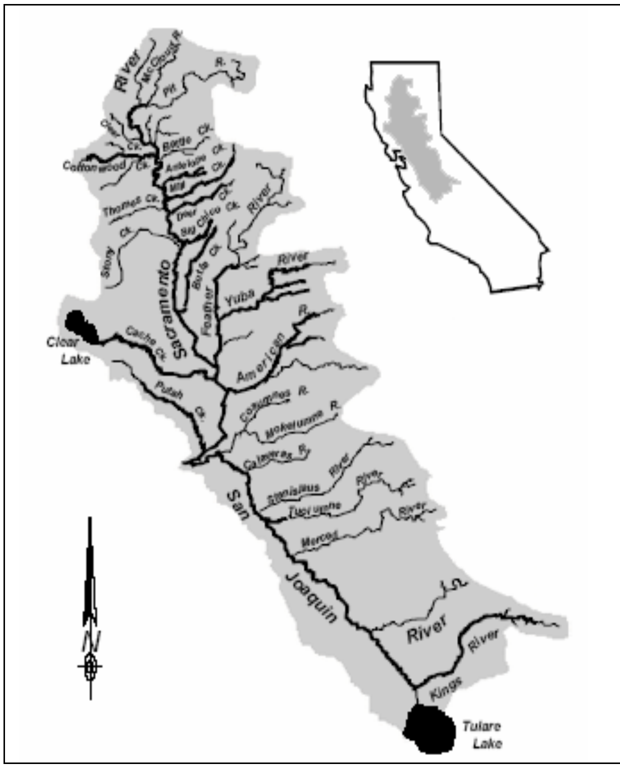

Figure 1. Historical distribution of steelhead in Central Valley drainages. Thick lines represent stream reaches that have documented historical evidence of steelhead. Thin lines represent likely distribution of steelhead based on documented occurrence of Chinook salmon or lack of natural barriers above documented steelhead occurrences. Shading represents an estimation of historical range within which steelhead likely occurred in numerous small tributaries not shown on map. From McEwan 2001.

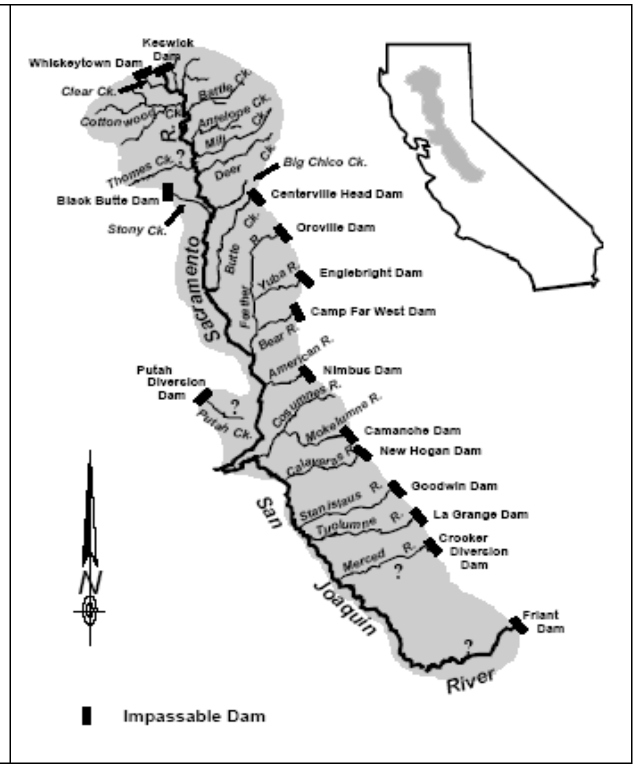

Figure 2. Present distribution of steelhead in Central Valley drainages. Shading represents an estimate of present range within which steelhead likely occur including tributaries not shown on map. Question marks denote streams and stream reaches where steelhead currently may have access but their presence is unknown. From McEwan 2001.

Trends in Abundance: Data on the historical abundance of CV steelhead is lacking because of a combination of factors, including: (a) adult migration takes place during winter high flows, when streams were turbid, (b) steelhead do not aggregate in large numbers like the more conspicuous Chinook salmon, (c) early observers did not discriminate between steelhead, resident trout, and small salmon – they tended to be lumped as "salmon-trout" - and (d) much of 'steelhead' spawning apparently took place in smaller streams, after which many adults headed back to the ocean. Given the sheer size of available habitat and abundance of food resources for juvenile steelhead (*e.g.* small salmon, larval suckers and minnows, abundant insects generated by dead salmon nutrients), an estimate of annual adult numbers in 50,000-100,000 range would be reasonable.

The apparent precipitous decline of steelhead that lead to listing was obtained by looking at returns to the upper Sacramento River, which are based mainly on counts from fish ladders and hatchery returns, from an average of 6,574 fish in 1967-1991 to an average of 1,282 from

1992 to 2006 (Figure 3). Data from Coleman National Fish Hatchery on Battle Creek, (Sacramento River Rkm 534), shows a small but relatively stable return of 100-300 natural-origin adults per year (Figure 3). NMFS (2016) estimated total annual runs of steelhead to be around 4,600, including fish returning to hatcheries, with an additional 1,700 fish returning to the Nimbus Fish Hatchery and American River. However, all estimates are highly uncertain and should treated as best guesses.

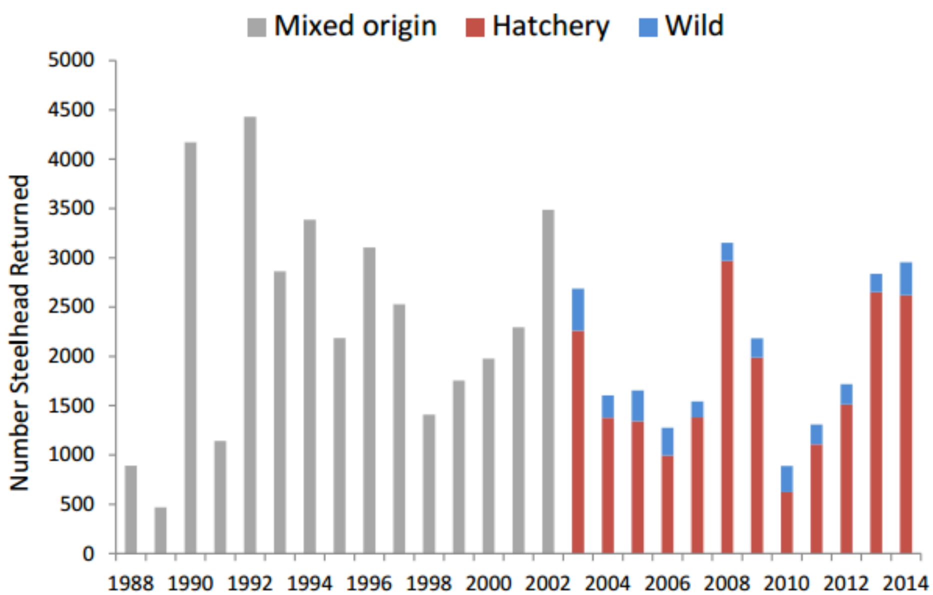

Figure 3. Adult steelhead returns to Coleman National Fish Hatchery, 1988-2014. From NMFS 2016, Fig. 1, pg. 12. *Prior to 2003, origins of returning fish were not classified.

Factors Affecting Status: Many stressors have contributed to the decline of steelhead life history in the Central Valley, including: major (rim) dams, diversions, barriers (small dams and other structures), levees and bank protection, dredging and sediment disposal, mining, contaminants, alien species, fisheries, and hatcheries (Upper Sacramento FRHAC 1989; Reynolds et al. 1989, 1993; CALFED 2000; CMARP Steering Committee 1999; McEwan 2001). Most of the factors affect steelhead in a manner similar to Chinook salmon, so are treated in the Central Valley fall Chinook salmon account.

Dams. Probably the single largest cause of loss of rainbow trout exhibiting steelhead life history has been the loss of historical holding, spawning and rearing habitat now above impassable dams. It is likely that somewhere between 80 and 95% of steelhead spawning and rearing habitat is no longer accessible to anadromous individuals. This habitat was mainly smaller tributary streams at higher elevations, but steelhead also likely ascended many mainstem rivers to higher elevations (McEwan 2001). Where cold releases from dams are present throughout the summer, resident populations of trout are present, which support tailwater fisheries. Migratory steelhead life histories have largely been replaced in the Central Valley by resident trout who spend their entire lifecycle in the tailwater releases from dams. Upstream reservoirs created by these same dams often support populations of migratory adfluvial trout.

Agriculture. In reality, agriculture is the single largest cause of steelhead decline because most dams in the CV were constructed in good part to provide water for irrigation. Agriculture also dried up some streams (e.g., San Joaquin River), created diversions that sucked up fish and water, dumped pollutants and warm-return water into streams, and generally degraded water quantity and quality in low elevation streams. On the other hand, summer flows below dams, either to satisfy downstream diverters or to protect fisheries, have created additional habitat for salmonids, especially rainbow trout. The Sacramento River, for example, has higher flows in summer than it did historically, and now maintains a wild trout fishery from Keswick Dam to Red Bluff. Although steelhead use these tailwaters, the resident life history is favored. In addition, concern for the affects of large diversions on salmon and steelhead has led to extensive screening of most large diversions to reduce mortality (Moyle and Israel 2005). NMFS (2016) emphasizes the many projects that are in place to mitigate for the impacts of agriculture.

Fire. Wildfires are having an increasing impact on streams supporting native rainbow trout populations above dams. NMFS (2016, p.35) states: "...Drier-than-normal conditions can increase the intensity and severity of wildfires. According to CalFire (www.calfire.ca.gov), in 2014, fire crews responded to 4,266 fires which burned over 191,000 acres (which was similar to the year-to-date average of 4,508 wildfires on 109,888 acres burned), and in 2015, there have been 6,284 fires and over 307,595 acres burned." How this landscape level change will affect rainbow trout and steelhead is not known, but it may contribute to increasing water temperatures and reduced cold water pools in reservoirs (see Climate Change).

Hatcheries. There are four hatcheries that raise steelhead in the Central Valley producing on average 1.5 million yearlings per year: Coleman National Fish Hatchery on the Sacramento River, Feather River Hatchery, Mokelumne River Hatchery, and Nimbus Hatchery on the American River (McEwan 2001). Steelhead reared in the first three hatcheries are considered to be part of the DPS (NMFS 2016). Williamson et al. (2011) regard hatcheries as a major threat to sustainable wild steelhead populations. The fish produced by hatcheries can negatively affect wild steelhead and rainbow trout in a number of ways including, displacing wild juveniles through competition and predation, competition between hatchery and wild adults for limited spawning habitat, hybridization with fish from outside the basin, and spread of disease. The first two effects are well documented for salmonids and may be responsible for the estimate that only 10-30% of returning steelhead in the upper Sacramento River are of natural origin (Reynolds et al. 1990). However, it is likely that, in the long run, hatcheries are causing a gradual decline in survival of both hatchery fish and naturally-spawned fish of hatchery origin. Reproductive fitness in steelhead can decrease rapidly when fish are raised in hatcheries. Araki et al. (2007) estimate that fitness of steelhead decreases almost 40% per generation of hatchery culture. When wild fish are brought into hatcheries there is a reproductive loss of 15% in the first generation and a further loss of 37% with each successive generation. This research indicates a major problem with using hatcheries to maintain or restore wild populations: steelhead of hatchery origin are quite different from steelhead of wild origin when it comes to long-term persistence in California streams and rivers. Currently, there seems to be strong natural selection favoring resident rainbow trout life history in tailwaters, presumably in part due to the poor ability of steelhead of either hatchery or wild origin to survive and contribute to populations.

The use of steelhead from outside the Central Valley as hatchery broodstock is well documented, although the effects of outside stocks on wild fish are not known. Outside stocks have been used in all four hatcheries, but Busby et al. (1996) and Pearse and Garza (2015) found that Coleman Hatchery and Feather River Hatchery fish are genetically most similar to naturally spawning Central Valley steelhead while Nimbus hatchery fish are most similar to Eel River steelhead. The Mokelumne River Hatchery fish at that time was rearing fish from the Nimbus Hatchery but has subsequently switched to rearing fish derived from returnees to the hatchery.

Whether or not these fish have actually harmed CV steelhead is not known; it can be argued that the increase in genetic diversity that results from hybridization, which is widespread in the CV steelhead/rainbow trout population, is potentially a positive attribute, allowing more flexibility for adapting to climate and other change. However, outbreeding depression between natural- and hatchery-origin fish could lead to an overall loss of genetic diversity in the population.

Estuarine alteration. Predation on steelhead smolts migrating through the highly altered lower Sacramento River and Delta may be heavy because of lack of cover, low outflows, and other factors. Confusing hydrology during periods of low-outflow in winter/spring may also direct smolts to areas with unfavorable conditions, such as agricultural ditches and fields. High rates of mortality of out-migrating smolts may select against the steelhead life history strategy.

Fisheries. Harvest of naturally spawned steelhead is prohibited within the Central Valley. Take is limited to one hatchery fish per day and every hatchery fish is marked. Because hatchery fish are raised for harvest and are not particularly suitable to augment wild stocks, their catch is not detrimental to the steelhead population as a whole. It is not clear what affect the incidental catch and release of wild steelhead has on the CV steelhead population as a whole, but some mortality is most likely occurring. However, steelhead are buffered somewhat by the presence of large populations of resident rainbows, which can reach 60+ cm FL, which make up most of the rainbow trout caught. See NMFS (2016) for discussion of angling effects on CV steelhead.

Alien species. Predation on steelhead and other salmonids by striped bass (*Morone saxatilis*), largemouth (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*), and other alien predators is just one cause of mortality of juvenile steelhead, as is predation by native predators from fish to birds to sea lions. Such predation may be a major proximate cause of death, but the ultimate causes are severe habitat alteration (Grossman 2016).

Factor	Rating a	Rating b	Explanation
Major dams	High	Low	Much former SH habitat is above dams; but RRT use much of former SH habitat; RRT in tailwaters.
Agriculture	Medium	Low	Habitats have been degraded through diversions, warm return water, and associated pollutant inputs.
Grazing	Low	Low	Livestock are pervasive on public and private lands bordering trout streams.
Rural/ residential development	Low	Low	Cumulative effects of numerous roads and rural development can negatively affect habitats.
Urbanization	Medium	Low	SH must pass through river sections leveed to protect cities, water diversions reduce flows overall but increase flows in summer. RBT fisheries are valued in tailwaters.
Instream mining	Low	Low	Gravel mining has impacts in limited areas.
Mining	Low	Low	Legacy effects of hard-rock mining are potentially severe in localized areas.
Transportation	Medium	Low	Roads present along many streams.
Logging	Low	Low	Both legacy effects and on-going impacts degrade aquatic habitats; most logging upstream of dams.
Fire	Low	Low	Fires have regional affects on water quality above dams.
Estuary alteration	High	N/A	The Delta /SF Estuary is a partial barrier to migration of SH, with poor water quality etc.
Recreation	Low	Low	Boating and other recreation may alter behavior.
Harvest	Low	Low	Recreational fisheries take mainly hatchery SH and RRT.
Hatcheries	Medium	Low	SH largely maintained by hatcheries; wild trout have legacy hatchery affects (genetics).
Alien species	Medium	Low	Hatchery SH juveniles eaten by striped bass and other predators (including natives).

Table 1. Major anthropogenic factors limiting, or potentially limiting, (a) viability of the steelhead (SH) life history in the Central Valley and (b) viability of the entire rainbow trout meta-populations, including both steelhead and resident (RRT) populations. Factors were rated on a five-level ordinal scale where a factor rated "critical" could push a species to extinction in 3 generations or 10 years, whichever is less; a factor rated "high" could push the species to extinction in 10 generations or 50 years whichever is less; a factor rated "medium" is unlikely to drive a species to extinction by itself but contributes to increased extinction risk; a factor rated "low" may reduce populations but extinction is unlikely as a result. A factor rated "n/a" has no known negative impact. Certainty of these judgments is moderate. See methods for explanation.

Effects of Climate Change. Moyle et al. (2013) did not rate the effects of climate change on CV steelhead because of uncertainty of what fish should be included in the rating. Climate change models generally agree that the climate is/will be more variable than in the past 100 years, with long droughts more frequent, lower stream flows with higher temperatures in summer in most years, and larger floods in some years. This variability will increase the difficulty of managing large dams to maintain sufficiently large pools of cool water that can enable cold-water flows for salmonids through the hot, dry summers, including the cold water needed to maintain hatchery operations for steelhead. During droughts, habitat for rainbow trout in general will shrink although resident rainbow populations are capable of rapid (2-3 years) recovery if favorable conditions return. Presumably steelhead will have additional difficulties in maintaining their life history under extended periods of low flows, even in hatcheries. Our general prediction for climate change effects is that resident rainbow trout will persist in most places, but with more variable and often smaller population sizes. The persistence of CV steelhead life history, however, is problematic without major hatchery inputs.

Drought and climate change are related, and more frequent and intense droughts are likely to become more common in California. Drought has had a negative impact on Central Valley steelhead populations recently (NMFS 2016). From 2012-2016, historic drought likely reduced limited habitat quality and range for CV steelhead. In the lower American River, drought reduced coldwater pool upstream of Folsom Dam, impacting water releases and thus reduced survival of wild steelhead parr (NMFS 2016). While steelhead populations in the Central Valley have historically overcome periodic droughts, current low abundance and productivity may cause some populations to become extirpated during long dry spells (NMFS 2016). Prospects for re-establishing these populations in highly altered landscapes and habitats throughout the Central Valley are troubling.

Status Score = 3.0/4.6 out of 5.0. Moderate Concern/Low Concern. The first score only reflects the status of the steelhead life history, including both hatchery and wild fish. The second score reflects the potential for maintaining large, highly adaptable rainbow trout/steelhead populations below dams, assuming the steelhead life history would develop or disappear in response to changing environmental conditions. We view the second score as representing a Central Valley rainbow trout meta-population that includes steelhead life history as one option. Other options include adfluvial life history in large rivers, and various resident life history options. Using the NMFS definition of CV steelhead, Moyle et al. (2008) and Katz et al. (2012) rated the status of CV steelhead as 2.5 and 2.4, respectively, using similar rating systems.

The DPS was first listed as a threatened species under the ESA by NMFS in 1998 and was reevaluated and confirmed in 2005, 2010 and 2015. It is managed by CDFW as a sport fish with limited take of hatchery fish. NMFS (2016, p 3) affirmed the status of CV steelhead as a threatened species, based on the following summary:

> "Many watersheds in the Central Valley are experiencing decreased abundance of CV steelhead. Dam removal and habitat restoration efforts in Clear Creek appear to be benefiting CV steelhead as recent increases in non-clipped (wild) abundance have been observed. Despite the positive trend in Clear Creek, all other concerns raised in the previous status review remain, including low adult abundances, loss and degradation of a large percentage of the historical spawning and rearing habitat, and domination of smolt production by hatchery fish. Many other planned restoration and reintroduction efforts have yet to be implemented or completed, or are focused on Chinook salmon, and have yet to yield demonstrable improvements in habitat, let alone documented increases in naturally produced steelhead. There are indications that natural production of steelhead continues to decline and is now at very low levels. Their continued low numbers in most hatcheries, domination by hatchery fish, and relatively sparse monitoring makes the

> continued existence of naturally reproduced steelhead a concern. We therefore conclude that CV steelhead remain listed as threatened, as the DPS is likely to become endangered within the foreseeable future throughout all or a significant portion of its range."

The NMFS status of threatened is based on a rather narrow view of steelhead that depends on their numbers being independent of the rest of the rainbow trout complex of which they are part, a requirement for a DPS. This status is not based on biology but on a somewhat arbitrary distinction between anadromous and resident rainbow trout, reflecting only the populations of fish below the rim dams around the Central Valley. The decision notes that both natural and hatchery steelhead are in decline, suggesting that the life history strategy itself is not sustainable. It also implies that low numbers could be an effect of limited monitoring as well. In contrast, the tailwater 'resident' trout populations appear to be thriving, as are populations above dams. The status of adfluvial trout populations above dams is not known, but their life history is similar to that of steelhead except a reservoir with abundant forage fishes takes the place of the ocean. Pearse et al. (2014) indicate that resident status can evolve very rapidly from ancestral steelhead.

NMFS (2016) indicates that while hatchery steelhead are part of the DPS, their main concern is naturally produced steelhead, although continuing to raise hatchery fish appears to directly conflict with that goal. Below dams in the Central Valley, resident trout and steelhead, including hatchery steelhead, form one genetic population, without much structure and featuring significant genetic input from introduced North Coast hatchery steelhead. Clearly, the selection pressures in the current CV environment favor fish adapted for resident life history, which has a genetic basis and can evolve rapidly (Pearse et al. 2004). Fish with the low rated steelhead life history will be abundant only if conditions that favor steelhead improve, but the life history seems likely to continue to be expressed at low rates regardless.

Metric	Score a	Score b	Justification
Area occupied	4	5	Steelhead are present in small numbers in at least 5 rivers, plus 3 hatcheries.
Estimated adult abundance	3	5	Steelhead include hatchery fish; based on NMFS estimate.
Intervention dependence	2	4	Steelhead life history increasingly dependent on hatcheries; valley floor rainbow trout depend on tailwaters below dams.
Tolerance	4	5	Rainbow trout are one of most tolerant salmonids but conditions in lower rivers/Delta may exceed tolerances of migrating steelhead.
Genetic risk	4	4	Appears to be one genetically diverse population with little genetic structure.
Climate change	2	4	Populations below dams that maintain cool water pools most threatened, especially steelhead life history. Upstream populations less so.
Anthropogenic threats	2	5	Score of 2 if only steelhead considered, 5 if entire meta-population considered.
Average	3.0	4.6	a = 21/7; b = 32/7.
Certainty (1-4)	3	4	Well studied but steelhead/rainbow trout interactions need more study.

Table 2. Metrics for determining the present status of steelhead/rainbow trout populations in the CV. Score a is for the steelhead life history whether of wild or hatchery origin; score b is for all naturally produced rainbow trout below dams, whether migratory or non-migratory. For individual metrics, 1 is a major negative factor contributing to status, 5 is a factor with no or positive effects on status, and 2-4 are intermediate values. Certainty of these judgments is moderate to high. See methods for explanation.

Management Recommendations:

Habitat. Current habitat conditions and dam operations in Central Valley rivers select against the anadromous steelhead life history, while hatchery operations select for anadromy. We must trust in the natural adaptability of rainbow trout and focus management on sustaining diverse, fishable, wild trout populations in tailwaters downstream of dams. When restoration actions improve conditions so that the migratory life history is once again favored, steelhead abundance will rebound. Habitat conservation efforts should be focused on the few streams that have track records of producing wild steelhead, such as Deer and Battle creeks. However**,** management of rivers to benefit naturally spawning Chinook salmon, especially late fall, winter, and spring runs should also benefit rainbow trout by providing both habitat protection and cold-water flows. For example, coldwater releases below Shasta Dam for winter-run Chinook provide habitat for a thriving, highly prized resident trout population.

NMFS (2016) provides a detailed, but not exhaustive, list of the many large-scale projects underway or proposed that should benefit steelhead, even if aimed mainly at Chinook salmon. These included restoring Clear Creek and Battle Creek, tributaries to the Sacramento River. In Clear Creek, barriers have been removed and passage to upstream areas improved, increasing steelhead numbers (NMFS 2016). For Battle Creek, dams have been identified for removal, with those remaining having passage improved. The Clear Creek and Battle Creek projects should be regarded as first steps towards a broader program of stream restoration, with more actions focusing on steelhead. In addition, significant actions associated with the operation of the State Water Project in the Central Valley under a 2009 NMFS Biological Opinion are likely to positively benefit CV steelhead survival.

Hatcheries. Interbreeding between hatchery and natural-origin steelhead likely reduces the reproductive capacity and inhibits the recovery of natural steelhead populations in the Central Valley. Hatchery steelhead should be excluded from the DPS and hatchery management should focus on reducing interactions between hatchery fish and naturally spawning steelhead while producing fish to support the fishery. Studies are also needed on why so few juvenile hatchery steelhead survive after being released. Delisting hatchery stocks would also allow loosening permitting restrictions on sampling of steelhead and rainbow trout for scientific research to better support recovery of naturally spawning populations.

A major effort should be made to understand the genetics and life histories of rainbow trout populations in and above reservoirs to determine the value of resident and adfluvial fish for future restoration efforts and well as simply to document their presence. We recommend against using "CV steelhead," however defined, in attempts to restore anadromous fish above dams (such as trap and haul programs), as proposed by NMFS (2016). Such programs do not work well where they have been tried (Lusardi and Moyle 2017) and steelhead face the particular problem of already-established rainbow trout populations above dams that include large adfluvial fish. In addition, genetic evidence suggests that current above-dam populations may better represent historical CV steelhead lineages than do anadromous individuals returning to the Central Valley today.

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