

Central Valley Steelhead

Dennis R. McEwan

Abstract

Before extensive habitat modification of the 19th and 20th centuries, steelhead (*Oncorhynchus mykiss*) were broadly distributed throughout the Sacramento and San Joaquin drainages. Historical run size is difficult to estimate given the paucity of data, but may have approached 1 to 2 million adults annually. By the early 1960s run size had declined to about 40,000 adults. Natural spawning populations currently exist in the Sacramento and San Joaquin river systems but at much lower levels. Coastal rainbow trout populations can be polymorphic in their life-history, and progeny of one life-history form can assume a life-history strategy different from that of their parents. A polymorphic population structure may be necessary for the long-term persistence in highly variable environments such as the Central Valley. Despite the substantial introduction of exotic stocks for hatchery production, native Central Valley steelhead may have maintained some degree of genetic integrity. Primary stressors affecting Central Valley steelhead are all related to water development and water management, and the single greatest stressor is the substantial loss of spawning and rearing habitat due to dam construction. Central Valley anadromous fish management and research is primarily focused on chinook salmon (*Oncorhynchus tshawytscha*) and has led to less emphasis on steelhead monitoring and restoration. Much of the information on historical abundance and stock characteristics that exists for Central Valley steelhead is derived from an intensive DFG research program in the 1950s. Since this time there has been relatively little research directed at steelhead in the Central Valley, and efforts to restore Central Valley steelhead have been greatly hampered by lack of information. The National Marine Fisheries Service cited the ongoing conservation efforts of the Central Valley Project Improvement Act (CVPIA) and CALFED as justification for listing Central Valley steelhead as a threatened species under the Endangered Species Act, rather than endangered as proposed. Restoration actions identified in these programs are largely directed at chinook salmon recovery with comparatively little emphasis on specific actions needed to recover steelhead, or have not yet been implemented. The structure of rainbow trout populations has important management implications that can only be addressed through an integrated management strategy that treats all life-history forms occupying a stream as a single population. However, management

agencies have generally failed to recognize this, as exemplified by the federal government's decision to exclude the non-anadromous forms in the ESA listing for steelhead, despite their recognition that they are important to the persistence of the anadromous forms. Steelhead need to be managed separately from chinook salmon stocks if recovery is to be successful, and recovery strategies must include measures to protect and restore the ecological linkages between the different life-history forms and measures to restore steelhead to some of their former habitat.

Introduction

Steelhead are the anadromous form of rainbow trout¹ (*Oncorhynchus mykiss*), a salmonid species indigenous to western North America and the Pacific coast of Asia. Recognized as a prized and sought-after game fish, steelhead are also highly regarded as a quality-of-life indicator among the non-angling public. The California Department of Fish and Game (DFG), the U.S. Fish and Wildlife Service (USFWS), and the National Marine Fisheries Service (NMFS) all assert some form of management authority over rainbow trout populations.

In this paper I discuss important aspects of steelhead ecology and population biology that have direct bearing on management effectiveness (and ineffectiveness), historical abundance and current status of Central Valley steelhead, factors that are responsible for their decline, and assessment of current monitoring and research efforts. I conclude with a description of current management and recovery efforts, a discussion of the dominant paradigm of Central Valley steelhead management and associated problems, and what I believe to be necessary if recovery is to be successful.

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1. The terms "rainbow trout" and "resident rainbow trout" are often used to identify non-anadromous forms of *O. mykiss*. This convention is confusing and technically inaccurate because "rainbow trout" is the common name of the biological species *O. mykiss*, and the term "resident," used in this sense, ignores other, non-anadromous life-history forms and migratory behaviors. In this document, the term "rainbow trout" refers to the biological species *O. mykiss* regardless of life history, and the different life-history forms are referred to as anadromous (or steelhead), potamodromous, or resident, depending on their migratory behavior (or lack thereof in the case of residents). The term "non-anadromous" is used to refer collectively to all life-history types other than anadromous.

Biology and Status

Ecology, Life-History, and Structure of Rainbow Trout Populations

In North America, steelhead are found in Pacific Ocean drainages from southern California to Alaska. In Asia, they are found in coastal streams of the Kamchatka Peninsula, with scattered populations on the mainland (Burgner and others 1992) (Figure 1). In California, spawning populations are known to occur in coastal streams from Malibu Creek in Los Angeles County² to the Smith River near the Oregon border, and in the Sacramento and San Joaquin river systems. The present distribution and abundance of steelhead in California have been greatly reduced from historical levels (McEwan and Jackson 1996; Mills and others 1997).

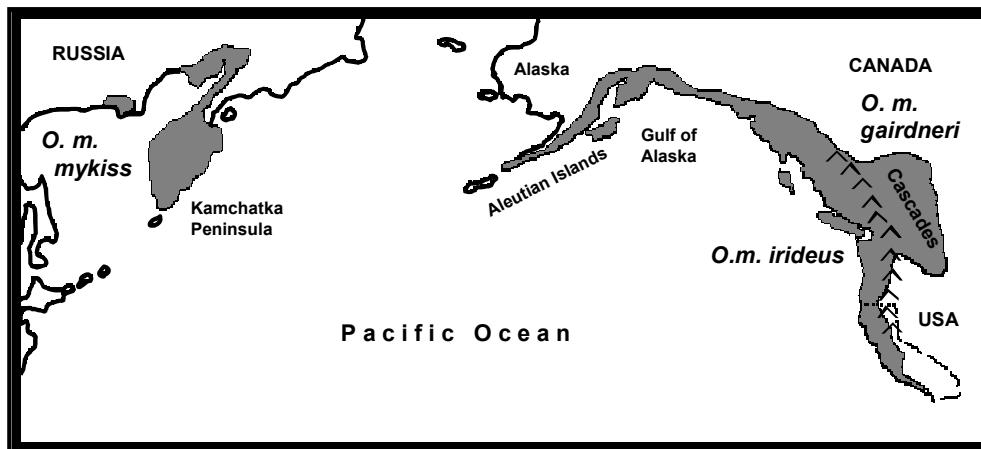


Figure 1 Endemic distribution of steelhead rainbow trout, *Oncorhynchus mykiss*. Modified from Burgner and others 1992.

2. The southernmost extent of steelhead distribution in North America is often reported as Malibu Creek because a known, persistent spawning population has been documented (McEwan and Jackson 1996; NMFS 1996a). However, streams south of Malibu Creek (for example, San Mateo Creek in San Diego County) appear to support at least occasional spawning and production (DFG 2000a) and most other streams are not adequately monitored to determine if steelhead are present. Thus, it is more correct to state that Malibu Creek is the known southern extent of persistent populations in North America.

Steelhead are similar to some Pacific salmon species in their ecological requirements. They are born in fresh water, emigrate to the ocean where most of their growth occurs, and return to fresh water to spawn. Unlike Pacific salmon, steelhead are iteroparous. Repeat spawning rates are generally low, however, and vary considerably among populations.

In California, peak spawning occurs from December through April in small streams and tributaries with cool, well-oxygenated water. The length of time it takes for eggs to hatch depends mostly on water temperature. Steelhead eggs hatch in about 30 days at 51°F (Leitritz and Lewis 1980). Fry usually emerge from the gravel four to six weeks after hatching, but factors such as redd depth, gravel size, siltation, and temperature can speed or retard this time (Shapovalov and Taft 1954).

The newly-emerged fry move to the shallow, protected areas associated with the stream margin (Royal 1972; Barnhart 1986) where they establish feeding stations (Fausch 1984) that they defend (Shapovalov and Taft 1954). Juveniles mainly inhabit riffles (Barnhart 1986) but they can use a variety of other habitat types (DFG Stream Evaluation Program, unpublished data). Relatively high concentrations occur in association with structural complexity, such as that provided by large woody debris (DFG Stream Evaluation Program, unpublished data). Juveniles also exhibit a significant movement to sites with overhead cover (Fausch 1993) and appear to select positions in streams in response to low light levels (Shirvell 1990). For juvenile steelhead, sites with light levels below a certain threshold, velocity refuges, and adjacent high velocity flows provide an optimal combination of safety from predators and aggressive conspecifics, as well as access to drifting invertebrate food resources.

The optimum water depth for steelhead spawning is approximately 14 inches and ranges from about 6 to 36 inches (Bovee 1978). Fry typically use water approximately 8 inches in depth and can use water 2 to 32 inches deep, while older juveniles typically use a water depth of about 15 inches but can use water 2 to 60 inches deep (Bovee 1978). In natural channels, water depth usually does not hinder adult migration because adult steelhead normally migrate during high flows. Depth can become a significant barrier or impediment in streams that have been altered for flood control purposes, especially those that do not have a low flow channel. It has been reported that seven inches is the minimum depth required for successful migration of adult steelhead (Thompson 1972, as cited in Barnhart 1986), although the distance fish must travel through shallow water areas is also a critical factor. Excessive water velocity and obstacles that impede swimming and jumping ability are more significant in hindering or blocking migration (Barnhart 1986).

Steelhead spawn in areas with water velocities ranging from 1 to 3.6 ft/s but most often in velocities of about 2 ft/s (Bovee 1978). The ability to spawn in higher velocities is a function of size: larger steelhead can establish redds and spawn in faster currents than smaller steelhead (Barnhart 1986). Steelhead have been reported to spawn in substrates from 0.2 to 4.0 inches in diameter (Reiser and Bjornn 1979). Based on the Bovee (1978) classification, steelhead use mostly gravel-sized material for spawning but will also use mixtures of sand-gravel and gravel-cobble. The gravel must be highly permeable to keep the incubating eggs well oxygenated.

Water temperature requirements for various life stages of steelhead have been studied (Bovee 1978; Reiser and Bjornn 1979; Bell 1986), although there are relatively little data specific to California (Myrick 1998). Egg mortality begins to occur at 56°F (Hooper 1973, as cited in Barnhart 1986), thermal stress has been reported at temperatures beginning at 66°F, and temperatures demonstrated to be lethal to adults have been reported at 70°F (Rich 2000). In California, low temperatures are not as much of a concern as high temperatures, particularly during adult migration, egg incubation, and juvenile rearing. The ability of steelhead to tolerate adverse temperatures varies depending on physiological conditions such as life stage, stock characteristics, and ecological conditions such as acclimation time, food availability, and access to cold water refugia within the stream (Nielsen and others 1994; Myrick 1998). Thus, determination of suitable temperature targets in regulated rivers is often a complex issue.

It should be noted that the preceding descriptions of habitat criteria are presented mainly as rough guidelines as determined by steelhead researchers on specific streams or under laboratory conditions. Often, temperature targets are established or proposed on regulated rivers based on laboratory studies that focus on temperature maxima that cause lethal and sublethal effects. Effects on growth rates, long-term survival, increased predation rate, and ecology usually are not addressed in these studies. Also, experimental work under controlled laboratory conditions does not take into account ecological conditions that may affect thermal tolerances, such as predation risk, inter- and intraspecific competition, and flow characteristics (Moyle and Baltz 1985, as cited in Myrick 1998). Because laboratory studies cannot approximate the complex conditions found in natural environments, water temperature requirements for steelhead in the wild are often subject to considerable debate, due primarily to misapplication and misinterpretation of thermal physiology studies and lack of standardization of methodologies (Rich 2000).

As noted above, steelhead in California exhibit life-history characteristics that are generally similar to Pacific salmon but there are some major differences: juvenile steelhead typically rear in freshwater for a longer period (usually from one to three years) and both adults and juveniles are more variable in the

amount of time they spend in fresh and salt water. Throughout their range, steelhead typically remain at sea for one to four growing seasons before returning to fresh water to spawn (Burgner and others 1992). Boydstun (1977) found that most Gualala River steelhead migrated to sea as two-year old fish and returned after spending two years in the ocean. In Scott and Waddell creeks, the majority of adults returning to the stream to spawn had spent two years in fresh water and one or two years in the ocean. However, steelhead from these streams occasionally exhibited other life-history patterns: scale analysis of adults indicated that they spent from one to four years in fresh water and from one to three years in the ocean (Shapovalov and Taft 1954).

Steelhead have traditionally been grouped into seasonal runs according to their peak migration period: in California there are well-defined winter, spring, and fall runs. This classification is useful in describing actual run timing but is misleading when it is used to further categorize steelhead. Seasonal classification does not reflect stock characteristics, spawning strategies, and run overlap between summer and winter steelhead. Run timing is a characteristic of a particular stock, but, by itself, does not constitute race or ecotype.

There are two steelhead ecotypes: stream-maturing steelhead, which enter fresh water with immature gonads and consequently must spend several months in the stream before they are ready to spawn; and ocean-maturing steelhead, which mature in the ocean and spawn relatively soon after entry into fresh water. This corresponds to the accepted classification that groups steelhead into two seasonal "races": summer and winter steelhead (Withler 1966; Royal 1972; Roelofs 1983; Barnhart 1986; Burgner and others 1992). Stream-maturing steelhead (summer steelhead) typically enter fresh water in spring, early summer, and fall. They ascend to headwater tributaries, hold over in deep pools until mature, and spawn in winter. Ocean-maturing steelhead (winter steelhead) typically begin their spawning migration in fall, winter, and spring and spawn relatively soon after freshwater entry. Ocean-maturing steelhead generally spawn January through March, but spawning can extend into spring and possibly early summer months. Before the intensive water development of this century and the resultant loss of a considerable amount of holding habitat, summer steelhead were probably more common in California than they are today. At present, summer steelhead are found only in north coast drainages, mostly in tributaries of the Eel, Klamath, and Trinity river systems. Winter steelhead are also present in north coast drainages, and are also found in the Central Valley and central and south coast drainages.

The above classification scheme is based on behavioral and physiological differences and may not reflect genetic or taxonomic relationships (Allendorf 1975; Allendorf and Utter 1979; Behnke 1992). Genetic similarity appears to be mostly a reflection of geographical relationships. For example, summer steel-

head occupying a particular river system are more genetically similar to winter steelhead of that system than they are to summer steelhead in other systems. Allendorf (1975) found that summer steelhead from several coastal streams in Washington were genetically indistinguishable from coastal winter steelhead of the same streams, but showed no genetic affinities with inland (upper Columbia River) summer steelhead.

Rainbow trout have also been classified on the basis of life history. Steelhead and non-anadromous rainbow trout were classified as two different subspecies and even different species by early researchers (Jordan and Gilbert 1882; see Allendorf 1975, Behnke 1992). However, little or no morphological or genetic differentiation has been found between anadromous and non-anadromous forms inhabiting the same stream system (Behnke 1972; Allendorf 1975; Allendorf and Utter 1979; Busby and others 1993; Nielsen 1994). Anadromous and non-anadromous rainbow trout apparently did not arise from two distinct evolutionary lines (Behnke 1992), rather, the different forms reflect the phenotypic plasticity of the species.

Behnke (1972), Allendorf (1975), Allendorf and Utter (1979), and Wilson and others (1985) conclude that rainbow trout cannot be separated taxonomically by immigration timing and status of gonadal maturity (summer vs. winter steelhead) or their tendency for anadromy (steelhead vs. non-anadromous forms). Rather, rainbow trout are taxonomically structured on a geographic basis (coastal vs. inland forms). Similarly, Behnke (1992) identifies three subspecies of rainbow trout that have anadromous life-history forms: coastal rainbow trout (*O. m. irideus*), Columbia River redband trout (*O. m. gairdneri*), and *mikizha* or Kamchatka rainbow trout (*O. m. mykiss*). All steelhead life-history forms of *O. m. gairdneri* are summer steelhead (Behnke 1992; Burgner and others 1992) and occupy upper Columbia River tributaries east of the Cascades. *Oncorhynchus m. mykiss* is found in streams along the west coast of the Kamchatka peninsula of Russia. *Oncorhynchus m. irideus* is distributed along coastal rivers and streams from California to Alaska and consists of both summer and winter steelhead (Figure 1). All steelhead in California are *O. m. irideus* (Behnke 1992).

The present taxonomic classification recognizes the extreme polymorphism that occurs among rainbow trout populations (Behnke 1992). Rather than the different life-history forms comprising distinct taxa or populations, studies and observations indicate that coastal rainbow trout can form a single, panmictic population in streams systems where there is access to the ocean. These populations are comprised of individuals with different life-history traits and a continuum of migratory behaviors, the two extremes being anadromy (strongly migratory) and residency (non-migratory). Within these extremes are potamodromous, and possibly estuarine and coastal (weakly anadromous) forms that are typical of coastal cutthroat trout (*O. clarki*) populations

(Northcote 1997). This type of population structure has been observed in Kamchatka rainbow trout populations in several rivers in western Kamchatka, where steelhead, coastal, and riverine (potamodromous and resident) life-history polymorphisms have been identified, and appear to form a single interbreeding population within each river system (Savvaitova and others 1973, 1997). Mature male parr have been observed spawning with female steelhead in California streams (Shapovalov and Taft 1954; DFG Stream Evaluation Program, unpublished data). Lack of genetic differences provides additional evidence that anadromous and non-anadromous life-history types can form a single interbreeding population within the anadromous reaches of a stream system.

In trout populations that have anadromous life-history forms, it is not uncommon for males to assume a non-anadromous life history and mature in fresh water as parr (see Thorpe 1987; Titus and others forthcoming), or for progeny of one life-history form to assume a life-history strategy that differs from their parents. On the Santa Clara River in Ventura County, for example, an annual average of 172 steelhead smolts has been captured in a downstream migrant trap at the Vern Freeman Diversion Facility from 1994 through 1997, although apparently very few adult steelhead have returned to the river. In fact, less than five adult steelhead have been observed using the diversion dam fish ladder (Entrix, Inc. 1994, 1995, 1996, 1997). A recent study that examined the microchemistry of juvenile rainbow trout otoliths has provided additional evidence for this. By comparing the ratio of strontium (Sr) to calcium (Ca) in the primordia and freshwater growth regions of the otolith, the life-history form of the maternal parent can be determined. The study found conclusive evidence that, in some populations, non-anadromous females produce steelhead progeny and steelhead females produce non-anadromous progeny (Zimmerman 2000).

A polymorphic life-history structure and resultant flexibility in reproductive strategies allows for persistence in the face of unstable and variable climatic, hydrographic, and limnological conditions that frequently exist at the margins of a species' range. For rainbow trout, this includes stream systems in the Central Valley and those south of San Francisco Bay, and Kamchatka on the other end of the range. Stream systems in California are subject to extreme variations (both within and among years) in rainfall which can result in high volume, flash flood runoff, or droughts lasting several years. Natural stream flow in these streams can vary greatly, both seasonally and annually. It is not uncommon, even under unimpaired conditions, for the lower reaches of many streams to become interrupted during the dry season (and longer), restricting the population to the perennial headwaters, and these conditions may persist for years. Thus, a polymorphic population structure allows persistence in an environment that is frequently suboptimal and not conducive to consistent, annual recruitment of migrants to the ocean, and may be necessary for the

long-term persistence of a population in these types of environments. Having several different life-history strategies among a single population effects “bet-hedging” against extinction, and has been proposed as a reason for the occurrence of similar polymorphic population structure in coastal populations of cutthroat trout (Northcote 1997) and brown trout (*Salmo trutta*) (Jonsson 1985, as cited in Northcote 1997; Titus and Mosegaard 1992) occupying highly variable environments.

Life-History of Central Valley Steelhead

Presently, the Central Valley drainages are known to contain only winter steelhead. However, there are indications from fish counts made before the era of large dam construction that summer steelhead were present in the Sacramento River system as well (Needham and others 1941; USFWS and DFG 1953). The presence of suitable over-summering habitat, a stable hydrology strongly influenced by spring snowmelt runoff, and the widespread occurrence of spring-run chinook salmon (*Oncorhynchus tshawytscha*), which have a similar life history to summer steelhead, are further indications that summer steelhead occurred throughout the Central Valley system. Because of the need of adults to over-summer in deep pools in mid- to high-elevation tributaries, summer steelhead were probably eliminated with commencement of the large-scale dam construction period in the 1930s.

The peak period of adult immigration before the occurrence of large-scale changes to the hydrology of the system appears to have been in fall, with a smaller component immigrating in winter (Bailey 1954; Van Woert 1958; Hallock and others 1961; Hallock 1989) (Figure 2A). Hallock and others (1961) found that the peak migration into the upper Sacramento River above the mouth of the Feather River from 1953 to 1959 was in late September. Adult counts at Clough Dam on Mill Creek for a 10-year period beginning in 1953 indicated that the peak of adult migration into that stream occurred in late October, with a smaller peak about mid-February (Hallock 1989). Examination of adult steelhead counts at Red Bluff Diversion Dam indicates that run timing on the upper Sacramento River does not appear to have changed appreciably: adult counts from 1969 to 1982 also show this same pattern (Hallock 1989), as do counts from 1983 to 1986 (USFWS unpublished data) (Figure 2B).

Hallock and others (1961) found that juvenile steelhead migrated downstream during most months of the year, but the peak period of emigration occurred in spring, with a much smaller peak in fall. The emigration period for naturally-spawned steelhead juveniles migrating past Knights Landing on the lower Sacramento River in 1998 ranged from late December through early May, and peaked in mid-March (DFG unpublished data). Most naturally-produced Central Valley steelhead rear in freshwater for two years before emigrating to

the ocean. Scale analysis indicated that 70% had spent two years in freshwater before emigrating to the ocean, 29% had spent one year, and 1% had spent three years (Hallock and others 1961). A current generalized life-stage periodicity for Central Valley steelhead is shown in Figure 3.

Recent microchemical analysis of Sr:Ca ratios in otoliths extracted from three rainbow trout from the Calaveras River provides evidence that some Central Valley rainbow trout populations are polymorphic. All three fish were adults with spent gonads indicating they had recently spawned. One was a 25-inch female steelhead that was the progeny of a steelhead female; one was a non-anadromous male (but whose scale circuli showed accelerated growth that may be indicative of having undertaken an estuarine migration) that was the progeny of a steelhead female; and one was a non-anadromous male that was the progeny of a non-anadromous female (Titus 2000). Thus, in a sample of just three fish from the population, we see two, possibly three different life-history expressions, at least one of which was different from that of its mother.

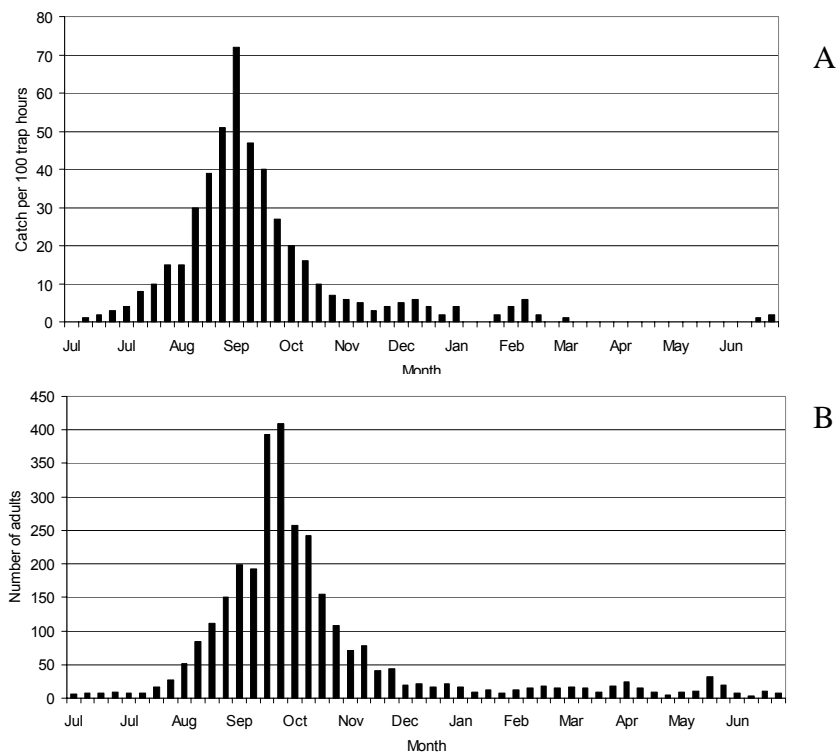


Figure 2 Time pattern of Sacramento River adult steelhead migration. Figure 2A shows migration timing from July through June of 1953 through 1959, determined by trapping upstream migrants in the Sacramento River just upstream of the confluence with the Feather River (from Hallock and others 1961). Figure 2B shows the weekly average number of adult steelhead counted at Red Bluff Diversion Dam from July through June of 1983 through 1986.

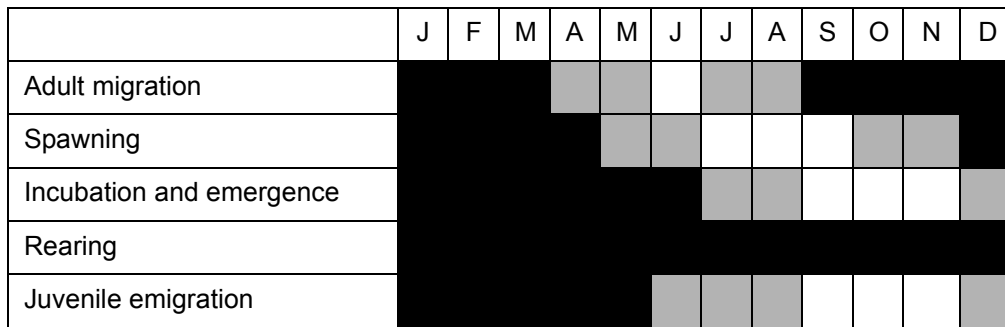


Figure 3 Central Valley steelhead life stage periodicity. Shaded areas represent months when the life stage is present; black shading indicates months of peak occurrence.

Table 1 Steelhead production in Central Valley anadromous fish hatcheries

<i>Facility (river system)</i>	<i>Purpose of mitigation</i>	<i>Production goal (yearlings)</i>	<i>Average annual production, 1984-1985 through 1993-1994</i>	
			<i>Fingerlings^a</i>	<i>Yearlings</i>
Coleman National Fish Hatchery (Sacramento R.)	Shasta Dam (USBR Central Valley Project)	700,000 to 800,000	245,378	526,602
Feather River Hatchery	Oroville Dam (DWR State Water Project)	400,000 to 450,000	489,366	406,421
Nimbus Hatchery (American R.)	Folsom Dam (USBR Central Valley Project)	430,000	407,381	369,870
Mokelumne R. Hatchery ^b	Camanche Dam (East Bay Municipal Utility District)	100,000	35,734	179,125
All Hatcheries			1,177,859	1,482,018

^a Includes fry, advanced fingerlings, and sub-yearlings.
^b Because the steelhead run in the Mokelumne River is so small, eggs are procured from Nimbus Hatchery.

Hallock and others (1961) reported that the composition of naturally-produced steelhead in the population estimates for the 1953-1954 through 1958-1959 seasons ranged from 82% to 97% and averaged 88%. This is probably not reflective of present stock composition in the Central Valley, due to the loss of spawning and rearing habitat and increase in hatchery production. During the period of the Hallock and others study, only Coleman and Nimbus hatcheries were in operation. Today, four Central Valley anadromous fish hatcheries (Mokelumne River, Feather River, Coleman, and Nimbus hatcheries) collectively produce approximately 1.5 million steelhead yearlings annually (Table 1, Figure 4)³.

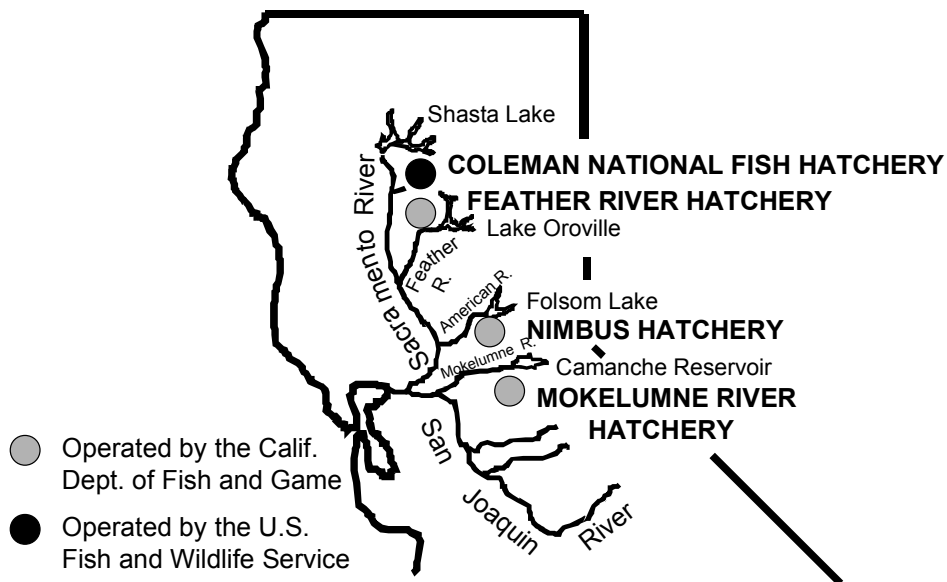


Figure 4 Central Valley anadromous fish hatcheries that raise steelhead

There has been substantial introduction of exotic steelhead stocks in the Central Valley (McEwan and Nelson 1991; NMFS 1996a). The degree of introgression or replacement of native stocks has not been determined, however, there is evidence that native Central Valley steelhead may have maintained some degree of genetic integrity. NMFS conducted a genetic analysis using allozymes from rainbow trout collected from Coleman, Nimbus, and Feather River hatcheries, Deer and Mill creeks, and the Stanislaus and American rivers. They found that the Stanislaus River, Coleman and Feather River hatcheries, and Deer and Mill creek populations formed a genetic group distinct from all

3. There are five anadromous fish hatcheries in the Central Valley; however, Merced River Hatchery does not have a steelhead program.

coastal samples of steelhead (Busby and others 1996; NMFS 1997a). In contrast, the American River samples (wild fish and those from Nimbus Hatchery) were genetically most similar to a sample from the Eel River (NMFS 1997a), which accurately reflects the founding history of Nimbus Hatchery (McEwan and Nelson 1991).

Distribution and Abundance

There is little documentation of historical steelhead distribution in the Central Valley. This is probably because it is difficult to assess or monitor steelhead (as will be discussed further). However, available information indicates that steelhead were well-distributed throughout the Sacramento and San Joaquin river systems. Steelhead were found from the upper Sacramento and Pit river systems south to the Kings River (and possibly Kern river systems in wet years) and in both east- and west- side tributaries of the Sacramento River (Clark 1929a; Wales 1939; Needham and others 1941; Murphy 1946, 1951; Beland and Braun 1952; Fry 1952; Vestal 1965; Painter and others 1977; DFG 1952, 1955, 1967, 1978a, 1978b, 1979; McEwan and Jackson 1996; Yoshiyama and others 1996; DFG unpublished data) (Figure 5).

The broad historical distribution of chinook salmon in the Central Valley (Yoshiyama and others 1996, 1998, this volume) corroborates the conclusion that steelhead were widely distributed. A comparison of the distributions of the two species in recent fish sampling in the lower Klamath River tributaries demonstrates that steelhead are present in all tributaries that contain chinook salmon, and, in nearly all cases, steelhead were found in tributaries and reaches further upstream (Voight and Gale 1998).

Further evidence supporting the assumption that steelhead distribution can be inferred from chinook salmon distribution is provided by an extensive review done by CH2M Hill (1985). In this review of salmonid distribution in the anadromous portions of the entire Klamath-Trinity river system, only one tributary containing chinook salmon but lacking steelhead was documented: all other tributaries that supported chinook salmon had steelhead as well and, in nearly all cases, steelhead were distributed at higher elevations in the stream than were chinook salmon. Thus, Yoshiyama and others' (1996) conclusion that steelhead were more broadly distributed than chinook salmon appears to be justified:

[Steelhead were] undoubtedly more extensively distributed [than chinook salmon in the Central Valley]. Due to their superior jumping ability, the timing of their upstream migration, which coincided with the winter rainy season, and their less restrictive preferences for spawning gravels, steelhead could have used at least hundreds of miles of smaller tributaries not accessible to the earlier-spawning salmon.

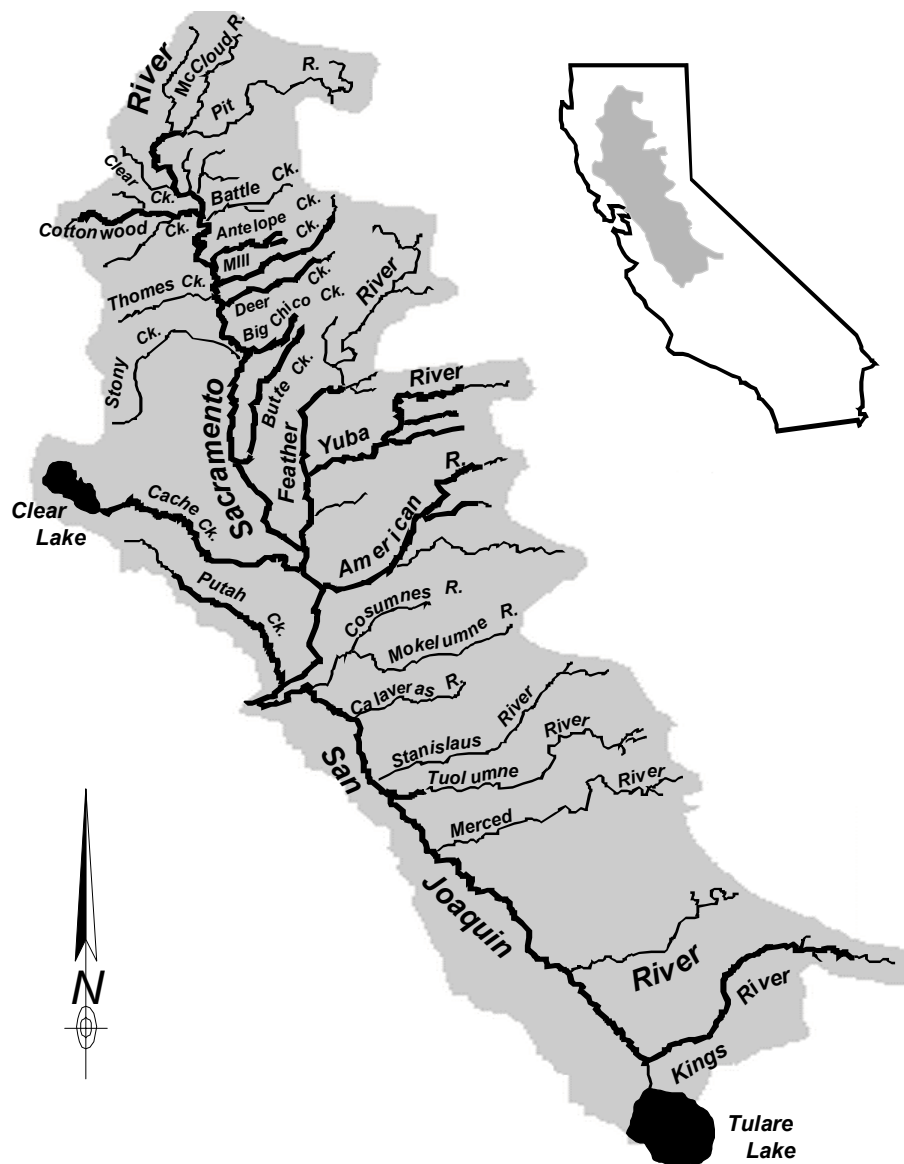


Figure 5 Historical distribution of steelhead in Central Valley drainages. Thick lines represent streams and stream reaches that have documented historical evidence of steelhead (see text for references). Thin lines represent likely distribution of steelhead based on documented occurrence of chinook 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.

The present distribution of steelhead in the Central Valley has been greatly reduced (Figure 6), mostly due to construction of impassable dams that block access to essential spawning and rearing habitat. Although a comparison of Figures 5 and 6 indicates a considerable reduction in distribution, it does not effectively convey the impact of the loss of habitat, because many of the stream reaches included as present distribution are at low elevations and were used by steelhead mostly as migration corridors. Clark (1929b) estimated that 80% of the spawning grounds in the Central Valley have been blocked due to power and irrigation dams. The California Advisory Committee on Salmon and Steelhead Trout (CACST 1988) estimated that there has been a 95% reduction in spawning habitat for Central Valley anadromous fish. Similarly, Yoshiyama and others (1996) estimated that 82% of chinook salmon spawning and rearing habitat in the Central Valley has been lost, and they state that the percentage of lost habitat for steelhead is undoubtedly higher because steelhead extended further into the drainage.

Naturally-spawning stocks of rainbow trout that support anadromy are known to occur in the upper Sacramento River and tributaries, Mill, Deer, and Butte creeks, and the Feather, Yuba, American, Mokelumne, Calaveras, and Stanislaus rivers. The presence of naturally spawning populations appears to correlate well with the presence of fish monitoring programs, however, and recent implementation of monitoring programs has found steelhead smolts in streams previously thought not to contain a population, such as Auburn Ravine, Dry Creek (DFG unpublished data) and the Stanislaus River (Demko and Cramer 1997, 1998; Demko and others 1999). It is possible that naturally spawning populations exist in many other streams but are undetected due to lack of monitoring or research programs.

Until very recently, steelhead were considered by some to be extinct in the San Joaquin River system (see Reynolds and others 1990; Cramer and others 1995). However, this conclusion was based on little information and no field studies. The presence of steelhead in the San Joaquin River is controversial, however, substantial evidence shows there is an extant, self-sustaining steelhead run in the San Joaquin River system:

- Numerous yearling-sized steelhead exhibiting smolt characteristics have been captured during an annual chinook salmon Kodiak trawl survey on the lower San Joaquin River from 1987 to the present (DFG unpublished data; USFWS unpublished data).
- A small number of steelhead smolts has been captured in rotary screw traps in two locations in the Stanislaus River every year for the past six years (Demko and Cramer 1997, 1998; S.P. Cramer & Associates unpublished data) (Figure 7). These fish do not appear to be progeny of straying adult Mokelumne River Hatchery steelhead: recent genetic analysis of

rainbow trout (discussed previously) captured in the reach below Goodwin Dam show that this population has closest genetic affinities to upper Sacramento River steelhead (NMFS 1997a). In contrast, Nimbus Hatchery steelhead, the source of eggs for the Mokelumne River Hatchery steelhead program, appear to be genetically similar to coastal steelhead, which were used to found the Nimbus Hatchery steelhead program when the hatchery first began production. Mokelumne River Hatchery is the only steelhead hatchery in the San Joaquin River system, and juvenile steelhead are not stocked anywhere in the San Joaquin basin except the Mokelumne River.

- A DFG creel census on the Stanislaus River has documented the catch of rainbow trout greater than 20 inches (DFG unpublished data). Examination of scale samples from these larger trout by DFG biologists shows an accelerated growth period typical of estuary or ocean residence (DFG 1997). DFG (1985) also observed large numbers of juvenile rainbow trout in several age classes, including young-of-the-year.
- In 1996, DFG (unpublished data) observed large numbers of rainbow trout in the Tuolumne River during a snorkel survey. In 1997, naturally spawned young-of-the-year rainbow trout were captured in the Tuolumne River by beach seining. Rotary screw trap catches in the past few years also contain young rainbow trout.
- In January 2001, a 28-inch rainbow trout was captured by a DFG fisheries biologist while angling in the lower Tuolumne River. The fish was a male with a hooked kype and prominent red coloration along the lateral line and operculae, indicating that it was ready to spawn. An 11-inch steelhead smolt was captured by the same biologist a few days later near the same location (DFG 2001).
- A 24-inch rainbow trout was captured by electrofishing at the confluence of the Merced and San Joaquin rivers in 1996-1997.
- In February 2000, an angler caught a 31-inch rainbow trout in the Calaveras River downstream of New Hogan Dam. Several weeks later, one adult female and two adult male rainbow trout were collected from the river after a fish kill occurred. Microchemical analysis of the otoliths found that the female was a spawned-out steelhead and one of the males was the progeny of a steelhead mother, but itself was non-anadromous (Titus 2000). In April 2000 a 9-inch juvenile steelhead exhibiting obvious smolt characteristics was captured (DFG 2000b).

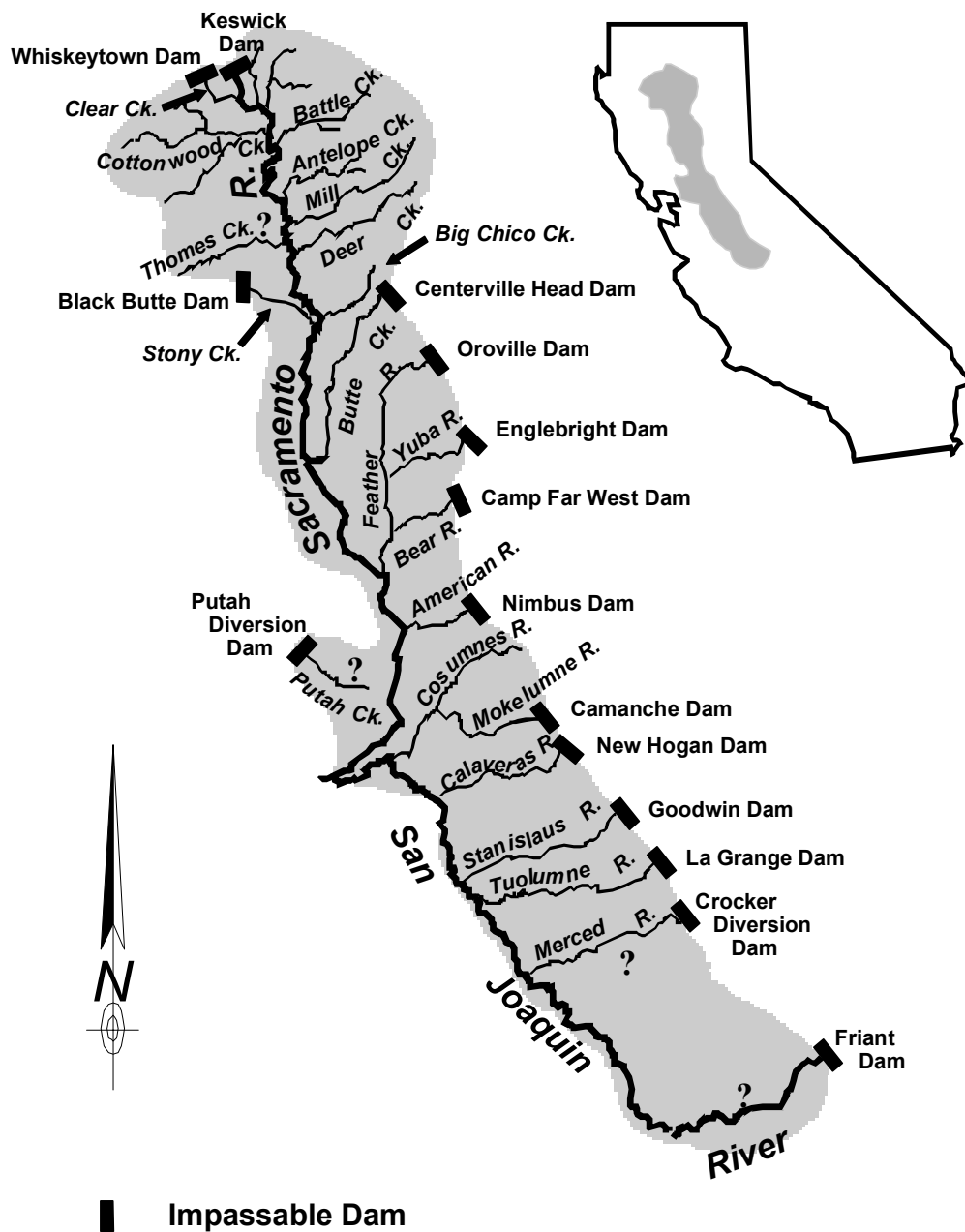


Figure 6 Present distribution of steelhead in Central Valley drainages. Shading represents an estimation of present range within which steelhead likely occur in numerous tributaries not shown on map. Question marks denote streams and stream reaches where steelhead currently have access but their presence is unknown.

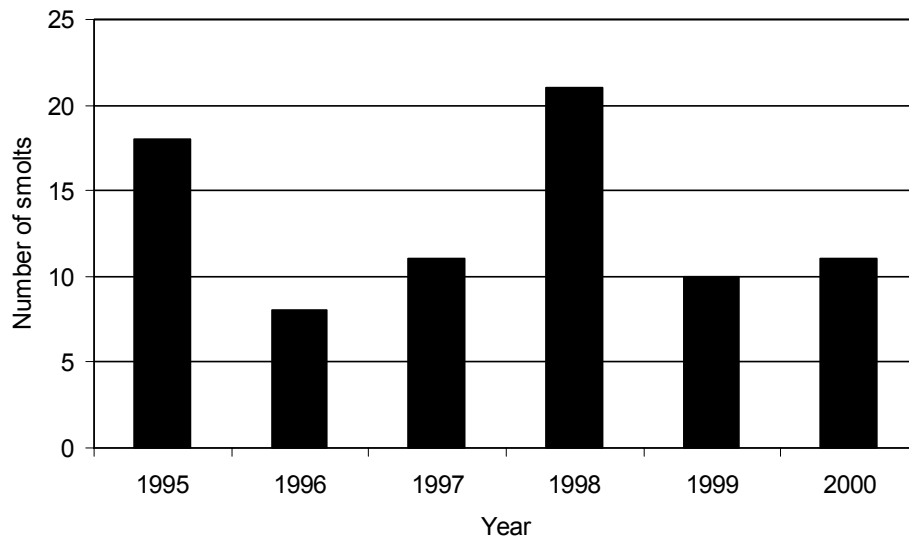


Figure 7 Number of smolt steelhead captured in rotary screw traps in the Stanislaus River. Data have not been adjusted for sampling effort, and effort has not been consistent between years. Data for 1999 is preliminary and data for 2000 is preliminary and partial.

The California Fish and Wildlife Plan (DFG 1965) estimated there were 40,000 adult steelhead in the Central Valley drainages in the early 1960s. In the 1950s, Hallock and others (1961) estimated the average annual steelhead run size was 20,540 adults in the Sacramento River system above the mouth of the Feather River. Estimating steelhead abundance before extensive water development and habitat modification is difficult given the paucity of historical information. However, historical steelhead abundance can be grossly estimated by examining chinook salmon and steelhead production in relatively unimpaired river systems.

From 1938 to 1975, counts were made of adult chinook salmon and steelhead at the Benbow Dam fishway on the South Fork Eel River. A decline in numbers of both chinook salmon and steelhead using the fishway began in the early 1960s, indicating that major effects to the Eel River probably occurred after 1960. Examination of the relative abundance of chinook salmon and steelhead during the years 1938 through 1960 shows, that of the 19 years of counts, there were two years when adult steelhead abundance was slightly less than chinook salmon, seven years when it was slightly more, and 14 years when steelhead abundance was more than twice that of chinook salmon. For the entire Eel River system, the California Fish and Wildlife Plan (DFG 1965) estimates the steelhead run size to be 160% of the chinook salmon run size.

Table S-3 of the California Fish and Wildlife Plan (DFG 1965) shows that for most northern California river systems, the steelhead run size in the early 1960s was at least that of the chinook salmon run size and in several streams steelhead were more than twice as abundant⁴. Even if a 50% ocean harvest rate for chinook salmon is considered, steelhead run size was only slightly less than chinook salmon in most streams and was the same or higher in some.

Thus, historical chinook salmon abundance may be viewed as an approximation of steelhead historical abundance. Assuming this is true, historical steelhead numbers in the Central Valley would have approached 1 to 2 million adults annually, which is the historical abundance of chinook salmon in the Central Valley estimated by Yoshiyama and others (1998). However, it should be noted that historical steelhead abundance in the Columbia River may have been significantly less than that of chinook salmon, based on historical commercial landings of chinook salmon and steelhead (R. Behnke, personal communication, see "Notes"). Also, given their larger size at ocean entry, juvenile steelhead would require greater resources than the smaller-sized salmon, therefore, fresh water habitat may not have been able to support as many juvenile steelhead as chinook salmon. The greater resource limitations for steelhead could have been attenuated by the fact that steelhead utilize the more numerous smaller tributaries for spawning and rearing than do chinook salmon, and greater ocean survival due to the larger size of steelhead smolts at ocean entry. Nevertheless, it is difficult to estimate historical abundance in the absence of any real data, so the above estimate of 1 to 2 million adult steelhead should be viewed as a best guess.

An accurate estimate of current steelhead abundance in the Central Valley is also not available. However, in the early 1990s, the total annual run size (hatchery and wild) for the entire system, based on Red Bluff Diversion Dam (RBDD) counts, hatchery counts, and past natural spawning escapement estimates for some tributaries, was estimated to be no greater than 10,000 adult fish (McEwan and Jackson 1996). A more reliable indicator of the magnitude of the decline of Central Valley hatchery and wild stocks is the trend in the RBDD counts. Steelhead counts at the RBDD have declined from an average annual count of 11,187 adults for the ten-year period beginning in 1967, to 2,202 adults annually in the 1990s (McEwan and Jackson 1996). Natural spawning escapement estimates above RBDD for the period 1967 to 1993 averaged 3,465 and ranged from 0 (1989 and 1991) to 13,248 (1968) (Figure 8). Natural escapement has shown a more substantial decline than hatchery (Coleman National Fish Hatchery) escapement.

4. The only exceptions were the Scott, Shasta, and Trinity rivers. Chinook salmon run size was estimated to be higher than steelhead in these rivers and might be explained by severely degraded conditions and blocked access in the Scott and Shasta river tributaries and chinook salmon hatchery production in the Trinity River.

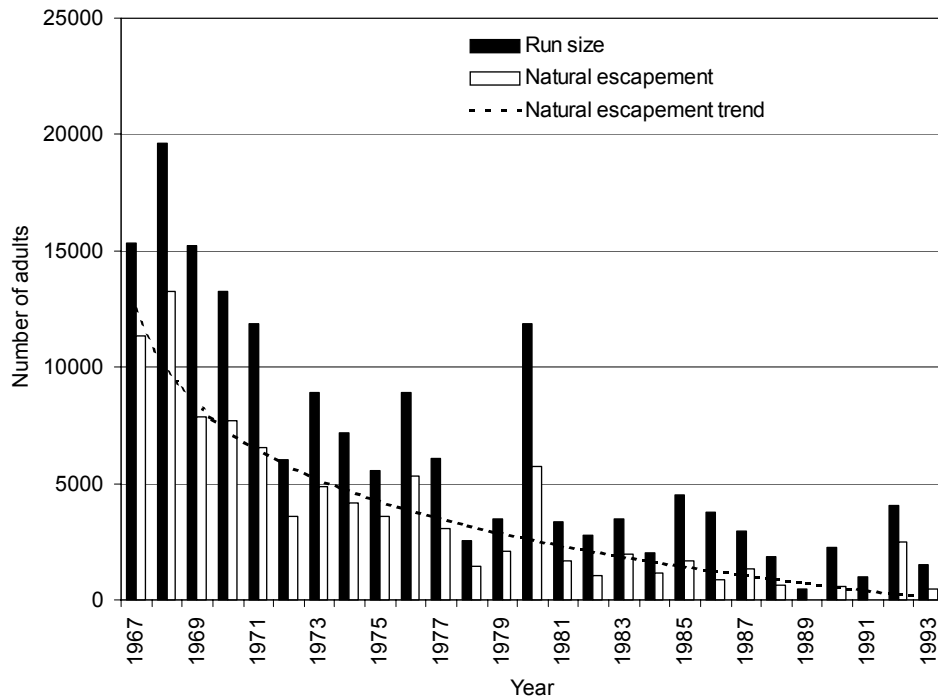


Figure 8 Steelhead population trends in the upper Sacramento River from 1967 to 1993. Run size is the adjusted steelhead counts at Red Bluff Diversion Dam and includes hatchery and natural spawners. Natural escapement was calculated by applying an estimated harvest rate of 16% (DFG unpublished data) to run size, then subtracting Coleman National Fish Hatchery escapement.

Factors Affecting the Decline of Central Valley Steelhead

Stressors affecting abundance, persistence, and recovery have been identified for anadromous fishes in the Sacramento and San Joaquin River systems and these apply reasonably well to Central Valley steelhead. Stressors affecting Central Valley anadromous fishes include water diversions and water management; entrainment; dams and other structures; bank protection; dredging and sediment disposal; gravel mining; invasive aquatic organisms; fishery management practices; and contaminants (Upper Sacramento River FRHAC 1989; Reynolds and others 1990, 1993; CALFED 2000; CMARP Steering Committee 1999). Stressors affecting steelhead on the west coast generally include the stressors listed above plus logging, agriculture, urbanization, disease, predation, and natural factors (NMFS 1996b; NMFS 1997b). McEwan and Jackson

(1996) state that the primary stressors specific to Central Valley steelhead are all related to water development and water management.

Most of the stressors commonly thought to affect Central Valley steelhead were first identified as factors that constrain chinook salmon populations and have been applied to steelhead secondarily because they are an anadromous fish with a somewhat similar life history. It is often assumed that steelhead have been affected by the identified stressors to the same degree as chinook salmon; hence, it is a common perception that alleviation of the stressor to the level that it no longer affects a chinook salmon population will result in steelhead population increases. However, some stressors cause greater effects to steelhead than they do to many chinook salmon populations. For example, high water temperatures affect juvenile steelhead to a greater degree than juvenile fall-run chinook salmon because most salmon have emigrated to the ocean by early summer before high water temperatures occur, whereas steelhead must rear through summer and fall when water temperatures are more likely to become critical.

The single greatest stressor on Central Valley steelhead is the catastrophic loss of spawning and rearing habitat due to construction of impassable dams (IEP Steelhead PWT 1999). Because juvenile steelhead must rear in fresh water for one year or longer, water temperatures must remain suitable year-round. For the most part, this occurred naturally only in the mid- to high-elevation reaches and tributaries, resulting in adult steelhead migrating higher into the drainage to spawn. Because 82% to 95% of their historical spawning and rearing habitat has been lost (Yoshiyama and others 1996; CACSST 1988), mostly due to dam construction, juvenile steelhead rearing is mostly confined to lower elevation reaches where high water temperatures during late-summer and fall are a major stressor (IEP Steelhead PWT 1999; CMARP Steering Committee 1999).

The creation of large impoundments with well-stratified waters has allowed better management of water temperatures in river reaches below large dams. However, hypolimnetic releases to create suitable water temperatures have been made mostly to benefit winter-run chinook salmon populations, and, until very recently, relatively little effort has been made to use this water to maintain suitable temperatures for rearing steelhead during the critical late summer and early fall periods. Although steelhead benefit from water temperature control actions in reaches where they are sympatric with the chinook salmon life stage that is the target of the action (such as rearing winter-run chinook salmon in the upper Sacramento River) focusing actions exclusively on chinook salmon can cause, and has caused, severe temperature effects for steelhead in tributaries where they are sympatric only with fall-run chinook salmon.

Some dams in the Central Valley were constructed with inadequate release structures that make it difficult to optimize releases from the hypolimnion. Other reservoirs may not have adequate minimum pool storage requirements. Consequently, many reservoirs currently are not able to provide releases necessary to maintain suitable temperatures for steelhead rearing through the critical summer and fall periods, especially during dry and critically-dry years. Water demands and power generation also affect the ability to provide suitable temperatures for steelhead.

In the early 1960s, all major Central Valley dams (except Oroville) and most minor dams were already in place, consequently the amount of spawning and rearing habitat available to steelhead probably has not changed appreciably from the late 1950s to the present. The greatest decline of natural steelhead in the system probably took place before the 1960s as a consequence of the reduction in habitat quantity as dam construction was incrementally isolating adults from the tributary spawning and rearing habitats. The decline since the 1960s can probably be mostly attributed to reduction in habitat quality, as increasing water demands – as reflected in the amount of water exported from the system by the State Water Project (SWP) and Central Valley Project (CVP) pumping facilities in the Sacramento-San Joaquin Delta-estuary (Figure 9) – and land use practices diminished the production capability of the existing accessible habitat. Before 1967 when the SWP began operation, the amount of water exported annually from the south Delta-estuary by the CVP pumping facility averaged 1,109,146 acre-feet per year. Since 1967 with both projects operating, the average has nearly quadrupled (4,133,516 acre-feet per year).

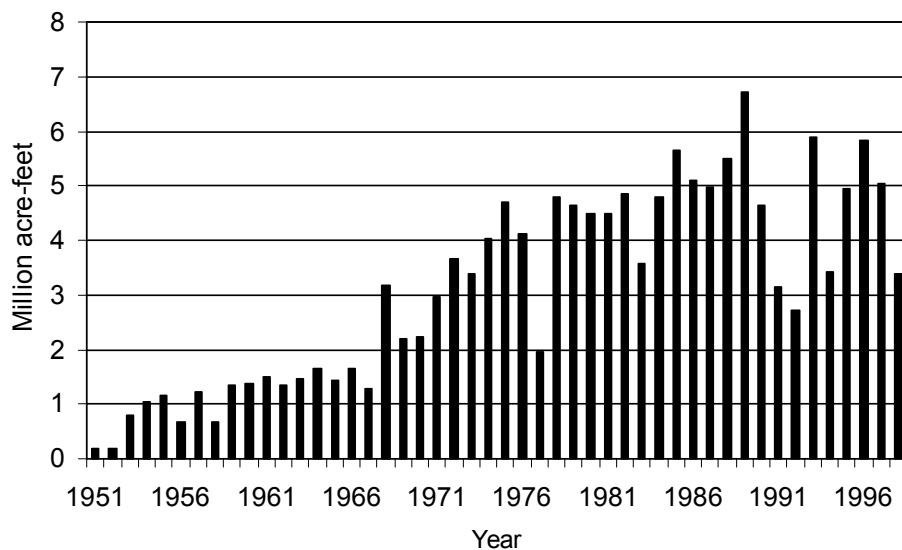


Figure 9 Combined State Water Project and Central Valley Project water exports from the Sacramento-San Joaquin Delta and Estuary, 1951 to 1998

A demographic shift towards the non-anadromous life-history forms brought about by anthropogenic effects could cause a decline in the relative abundance of the individual steelhead life-history forms, although this may not be a stressor on the population as a whole. Among polymorphic salmonid populations, the life-history fate of juveniles appears to be partially controlled by density-dependent factors: the growth rate during early life-history of a particular fish appears to be the factor that determines whether it will later smolt and migrate to the ocean, or become sexually mature in the stream as a parr (Thorpe 1987). Low juvenile densities or abundant resources leads to rapid growth rates, which triggers relatively rapid development which, in turn, leads to a higher frequency of parr maturation in the population, especially among males (Thorpe 1987; Titus and Mosegaard 1992). Conversely, it has been shown that high juvenile densities cause greater resource competition and juveniles that cannot establish and defend suitable stream positions are forced to migrate (Elliott 1994). The greater productivity and more abundant food resources in tailwater reaches may allow an increased growth potential among juvenile rainbow trout, which may skew the population towards the non-anadromous life-history forms. This may be a contributing factor in the growth of the non-anadromous "river trout" population in the upper Sacramento River below Keswick Dam.

Another potential population stressor is the disruption of interrelationships among Central Valley rainbow trout subpopulations. Due to highly variable natural conditions in the Central Valley, inter-population dynamics may be essential to the persistence of rainbow trout populations in the smaller stream systems. Historically, larger source populations occupying more stable habitats (for example, upper Sacramento, Feather, Yuba, and American rivers) provided a source for recolonization and gene flow to the smaller, less-persistent sink populations occupying more hydrologically unstable stream systems. Conversely, the long-term persistence of the source populations may be affected by the diversity and viability of the smaller subpopulations. The precipitous decline of Central Valley steelhead has been alarming not only from the standpoint of reduction in absolute numbers, but also in the elimination of the populations that occupied the many tributaries. A reduction in the large-river source populations may also explain the precipitous decline of steelhead in smaller streams, in spite of the large amount of quality habitat that still exists in these systems. Thus, restoration that focuses only on increasing absolute numbers and ignores the need to increase population diversity may be inadequate.

Monitoring and Research

Past Monitoring and Research Efforts

What is known about Central Valley steelhead is mostly due to a six-year monitoring and research program begun in 1953 by the DFG (Hallock and others 1961). The study, *An Evaluation of Stocking Hatchery-reared Steelhead Rainbow Trout (Salmo gairdnerii gairdnerii) in the Sacramento River System*, focused on hatchery steelhead but also provided valuable information on natural steelhead stocks, including status, abundance, and life history. Much of the baseline information that exists for Central Valley natural steelhead is derived from this study. Unfortunately, this program was canceled due to “lack of interest in steelhead...by administrators” (Hallock 1989). The cancellation of this program, and steelhead research programs in other areas of California, coincided with the implementation of monitoring programs to gather information to promulgate ocean harvest regulations for salmon. In more recent years, efforts to restore Central Valley steelhead has been hampered by a paucity of baseline information.

Other important steelhead investigations in the Sacramento River system include studies on the time pattern of migration of steelhead into the upper Sacramento River (Bailey 1954; Van Woert 1958); a survey of anadromous fish losses in irrigation diversions from the Sacramento and San Joaquin rivers (Hallock and Van Woert 1959); an evaluation of the steelhead fishery (Smith 1950); and an investigation into the status and potential effects of Shasta Dam on upper Sacramento River steelhead (Hanson and others 1940). In addition, several significant studies were undertaken in Sacramento River tributaries, including an assessment of the Yuba River steelhead run size and harvest rates (DFG 1984); an evaluation of the effects of the Oroville Project on the Feather River (Painter and others 1977); and an evaluation of steelhead angling on the American River (Staley 1976). Apparently, no studies or reports on San Joaquin River steelhead have been done.

Recent Monitoring and Research Efforts

In response to the recent listing of Central Valley steelhead under the ESA, steelhead monitoring and research efforts have increased. However, the Hallock and others (1961) study remains the only comprehensive investigation on Central Valley steelhead. Other recent studies and monitoring programs of a broad-based nature that have been completed include an evaluation of juvenile salmonid emigration in the upper Sacramento River (Snider and Titus 1996) and the aforementioned genetic analysis (NMFS 1997a). Significant ongoing investigations include abundance and distribution patterns in juvenile salmonids near the Red Bluff Diversion Dam; a Sacramento-San Joaquin

basin-wide angler survey; upper Sacramento River juvenile salmonid monitoring; and lower Sacramento River juvenile salmonid emigration studies. In addition to these, there are currently anadromous fisheries investigations ongoing on several major tributaries such as the Feather, American, and Mokelumne rivers, and minor tributaries such as Auburn Ravine and Dry Creek. The California Department of Water Resources (DWR) and U.S. Bureau of Reclamation (USBR) recently completed a biological assessment of Central Valley water management operations on steelhead and spring-run chinook salmon. This document provides a good synthesis of available information on steelhead and potential impacts (DWR and USBR 1999).

The Interagency Ecological Program Steelhead Project Work Team (IEP Steelhead PWT) identified 82 Central Valley anadromous fish monitoring and research projects operating in 1998 and classified these projects into four categories based on the objectives of the project and the degree to which they obtained information on steelhead: "salmon exclusive," "salmon focused," "anadromous salmonid focused," and "steelhead focused" (IEP Steelhead PWT 1999). Of the four categories, only the latter three provided any meaningful information on steelhead.

"Salmon exclusive" monitoring and research projects had objectives aimed at obtaining information on chinook salmon, used methods and periods of operation to accomplish these objectives, and provided no meaningful information on steelhead. Of the 82 projects reviewed, 42 (51%) were of this type. "Salmon focused" projects were similar to "salmon exclusive" projects in design and scope, but some useful steelhead information was collected incidentally: 12 (15%) were of this type. "Anadromous salmonid focused" projects had objectives that were designed to collect both salmon and steelhead information and used methods and periods of operation to accomplish this: 20 (24%) were of this type. "Steelhead focused" projects had objectives designed to collect steelhead information and used methods and periods of operation designed to collect steelhead information exclusively: eight (10%) were of this type. This analysis demonstrates that despite the recent emphasis on obtaining information on steelhead, the focus of Central Valley anadromous fish monitoring and research efforts is still overwhelmingly on chinook salmon.

Constraints to Steelhead Monitoring and Research

Constraints to steelhead monitoring and research have led to significant knowledge gaps. These constraints fall mainly into two categories: institutional and biological. Institutionally, the lack of adequate funds for anadromous fish monitoring often necessitates that monitoring programs adopt a narrow focus. Because chinook salmon are commercially exploited, highly visible, and politically sensitive, they have received the majority of monitoring funds and effort. This narrow focus was reinforced by the belief among

resource agencies that steelhead suffer from the same level of impacts as do chinook salmon, and assessment of impacts would be similar for steelhead.

Life-history traits common to all Central Valley steelhead can hamper steelhead monitoring and research. Adults tend to migrate during high flow periods, making them difficult to observe. In addition, maintaining counting weirs and other monitoring equipment and structures during these high flow periods can be challenging. Carcass surveys, a reliable method to estimate chinook salmon spawning escapement, is not applicable to steelhead because many survive spawning and most others do not die on spawning grounds. Although steelhead redds can be discerned from salmon redds, they are hard to observe because steelhead spawn at higher flows than do chinook salmon. Trap efficiencies appear to be lower for juvenile steelhead because emigrating juveniles can probably escape trapping more readily because of their larger size, relative to chinook salmon (R. Titus, personal communication, see "Notes").

Knowledge Gaps

Significant knowledge gaps hinder our ability to design restoration actions and monitor their effectiveness. The most important knowledge gaps and monitoring elements needed to address them include the following.

Current Distribution and Abundance of Naturally Spawning Populations

Comprehensive Monitoring. Recent monitoring projects have shown that naturally spawning steelhead exist in the upper Sacramento River and tributaries, Mill, Deer, and Butte creeks, and the Feather, Yuba, American, and Stanislaus rivers. Naturally spawning populations may exist in many other streams as well, but are undetected due to lack of monitoring or research programs. More comprehensive monitoring is needed to determine system-wide distribution.

Run Size Estimation. From 1967 to 1993, run size estimates were generated for steelhead using counts at the fishway on the Red Bluff Diversion Dam (RBDD). From these counts, estimates of natural spawning escapement for the upper Sacramento River above RBDD were made. Because of effects to winter-run chinook salmon, the operation of RBDD was changed so that the dam gates were raised earlier in the season, and this eliminated the ability to generate run-size estimates. Another method of generating run-size estimates for the upper Sacramento River system, or perhaps an index, needs to be developed.

Determination of Origin. Beginning with broodyear (BY) 1997, all steelhead produced in Central Valley hatcheries were marked with an adipose fin clip. This program will continue as a permanent hatchery practice at these hatcheries. Marked juvenile fish were captured in smolt emigration studies in 1998 and

marked adult steelhead began returning in winter 1999 (DFG unpublished data). Capture of non-clipped juvenile steelhead will help elucidate the location of naturally spawning populations.

Life Stage Determination. The IEP Steelhead PWT has developed a Steelhead Life Stage Assessment Protocol and is proposing that it be used by all Central Valley monitoring projects (IEP Steelhead PWT 1998). The protocol classifies rainbow trout by developmental life stage and includes diagnostics for determining the degree of smolting using a set of characteristics that is well-established (for example, Folmar and Dickhoff 1980; Wedemeyer and others 1980). Implementation of a standardized protocol to assign individual fish to one of several life-stage categories (yolk-sac fry, fry, parr, silvery parr, or smolt) will yield valuable information regarding behavior, development, and disposition of juvenile steelhead and distribution of steelhead throughout the Central Valley.

Spawning and Rearing Habitat Characteristics and Use

Assessment of Habitat Structure and Availability Below Dams. Because the majority of steelhead historical habitat is inaccessible to immigrating adult steelhead, research on habitat characteristics and suitability in tailwater reaches below dams needs to be done. A suite of studies on this subject should be initiated, which includes temperature modeling (both river and reservoir); instream flow evaluations to determine suitable migration, spawning, and rearing flows; habitat preference studies to determine how juvenile steelhead use microhabitat; and assessment of habitat conditions and factors limiting steelhead production.

Determination of Temperature Requirements in Specific Streams. To gain a better understanding of thermal requirements and the relationship between water temperature and juvenile steelhead survival, growth, and productivity, thermal bioenergetic investigations need to be conducted on a site-specific basis. Methods using data collected *in situ* have been developed and would provide more accurate site-specific thermal preference information based on field (rather than laboratory) studies (A.A. Rich & Associates 2000).

Population and Habitat Assessment in Low Elevation Tributaries. Steelhead and non-anadromous rainbow trout will use seasonal habitats of intermittent streams for spawning and rearing (Shapovalov 1944; Everest 1971, 1973; Erman and Leidy 1975; Erman and Hawthorne 1976; Maslin and McKinney 1994). Also, steelhead have been found in some small, low elevation Sacramento River tributaries (for example, Dry and Auburn Ravine creeks) that do not contain suitable habitat year-round, or are limiting in one or more suitable habitat characteristics (DFG unpublished data). Habitat characteristics and use, the extent of use of these streams by steelhead, and life-history characteristics

(spawning and emigration timing, size and age at emigration, and so on) need to be determined.

Genetic and Population Structure

Assessment of Maturation Status. Determining maturation status of rainbow trout captured by the various monitoring projects is incorporated into the Steelhead Life Stage Assessment Protocol. Parr maturation, especially in males, is common in steelhead and other polymorphic salmonid populations (reviewed by Titus and others, forthcoming.). When collected systematically throughout the system in conjunction with life stage and condition, these data will provide much needed information about developmental variation in steelhead and population structure.

Central Valley Steelhead Comprehensive Genetic Evaluation. The genetic analysis done by NMFS as part of the west coast steelhead Endangered Species Act status review provided useful information for delineation of Evolutionarily Significant Units (ESUs), but did not have the detail necessary to provide meaningful information within ESUs. More comprehensive information and analysis on the relationship of Central Valley steelhead to each other and to other populations of coastal rainbow trout is needed, as is information on the phylogenetic relationships between putative native rainbow trout, naturally spawning steelhead, and presumably non-native hatchery steelhead. This information will be useful in estimating the structure and genetic diversity within and among Central Valley rainbow trout populations.

Assessment of Reintroduction of Steelhead from Non-anadromous Forms. Provided that native Central Valley rainbow trout populations isolated above artificial barriers can be identified through the comprehensive genetic analysis described above, the next step would be to determine if the steelhead life-history form can be recreated and reintroduced into stream systems where they are presently extirpated.

Miscellaneous Research

Access Restoration Evaluation. Restoring access for steelhead above impassable dams needs to be considered on some streams to address the large-scale habitat loss that has occurred in the Central Valley. Restoration of access to the upper reaches of the Yuba and American rivers has been proposed. Also, the *CALFED Ecosystem Restoration Program Plan* (CALFED 2000) identifies the Yuba River and Battle and Clear creeks as locations in which passage above existing barriers is most feasible. An evaluation should be done in two phases. The first phase would assess spawning and rearing habitat availability above the dams. If suitable habitat can be identified or restored, then a feasibility study

of the best means to provide access (dam removal, passage facility installation, trap-and-truck operation, etc.) should be initiated.

Hatchery Evaluations. Intra- and inter- specific effects of hatchery fish on naturally spawning steelhead need to be investigated. This should include an evaluation of the degree of straying of hatchery steelhead both within and between basins. If there is a significant amount of in-river spawning of hatchery adults, then the potential exists for introgression of hatchery stocks with putative native populations. This is especially of concern for hatcheries that were founded with non-native broodstock, such as Nimbus Hatchery. The degree of straying of hatchery steelhead into other basins needs to be investigated as well. This can be accomplished by applying an external mark to a constant fraction of hatchery production or through thermal mass-marking and subsequent analysis of otolith microstructure. The use of native strains as broodstock needs to be evaluated.

Evaluation of Delta Water Operations on Steelhead Emigration and Rearing. SWP and CVP water diversions from the Sacramento-San Joaquin Delta-estuary have caused significant adverse effects to many riverine, estuarine, and anadromous species (Herbold and Moyle 1989). Attempts to mitigate these adverse effects have spawned much research and monitoring, particularly for chinook salmon, striped bass (*Morone saxatilis*), and delta smelt (*Hypomesus transpacificus*). However, no studies on the effect of the Delta water operations on steelhead in the Delta have been done. The effect of water operations on emigrating juvenile steelhead needs to be assessed. Specifically, timing of smolt emigration through the Delta, magnitude of diversion and entrainment of smolts toward the SWP and CVP pumping facilities, and the effect of the loss of estuary rearing habitat should be evaluated.

Recovery and Management

Endangered Species Act and Recovery Programs

In 1994, the Oregon Natural Resources Defense Council and 15 other organizations petitioned NMFS to list all steelhead stocks in Washington, Idaho, Oregon, and California under the ESA, citing declines in numerous west coast stocks resulting from water development, logging, drought, and other activities. NMFS found that the petition contained credible information and initiated a status review. In 1996, NMFS published a proposed rule designating 15 steelhead ESUs in the four states, ten of which they proposed to list, including all six ESUs in California. They proposed to list the Central Valley ESU, which includes all anadromous reaches of the Sacramento River system and the San

Joaquin system downstream of the confluence of the Merced River (including the Merced River), as endangered.

In August 1997, NMFS published a Final Rule announcing the listing of the Southern California ESU as endangered, and the South-Central California Coast and the Central California Coast ESUs as threatened. They deferred the decisions on the other California ESUs. In May 1998, NMFS listed the Central Valley ESU citing ongoing conservation efforts as justification for listing as threatened, rather than endangered, as originally proposed. Specifically cited were the Central Valley Project Improvement Act (CVPIA), an act passed by Congress in 1992 to remedy habitat and other problems associated with the operations of the Central Valley Project, and the CALFED Bay-Delta Program, a joint State and federal program to develop a long-term solution to address Central Valley ecosystem restoration, water supply reliability, and other issues.

The Anadromous Fish Restoration Plan (AFRP) was developed in 1995 to achieve the mandated CVPIA goal of doubling the natural production of anadromous fish by 2002 (USFWS 1997). The AFRP lists actions, such as specified increased flows below CVP reservoirs, intended to recover six species of anadromous fish, including steelhead. Some measures of the AFRP have been implemented, such as increased flows for fish.

Like many other management and restoration plans for Central Valley anadromous fisheries, actions identified in the AFRP are largely driven by chinook salmon restoration, and less emphasis is placed on specific actions needed to recover steelhead. For example, minimum flows in the San Joaquin River system were set according to the needs of fall-run chinook salmon, and because juvenile fall-run chinook have largely emigrated by early summer, no provisions of flows to maintain cold water temperatures through the summer were established. AFRP-specified flows for Clear Creek and the upper Sacramento River below Keswick were also designed specifically for chinook salmon. The AFRP needs to consider rearing flows and temperatures necessary to support over-summering juvenile steelhead.

The institutional predilection for chinook salmon in monitoring and assessment efforts discussed previously is also prevalent in recovery and management strategies, and this has been the dominant paradigm in steelhead management and restoration efforts initiated in the past ten years (see Upper Sacramento River FRHAC 1989; Reynolds and others 1990, 1993; USFWS 1997)⁵. Although most restoration measures designed to recover chinook salmon stocks do benefit steelhead or are benign in that regard, focusing restoration solely on chinook salmon leads to inadequate measures to restore steelhead because of their different life histories and resource requirements, particularly that of rearing juveniles.

The other large-scale ecosystem restoration action, the CALFED Bay-Delta Program, goes much farther than the CVPIA in recognizing the need to identify and implement actions to restore steelhead, separate from those to restore chinook salmon, especially in the San Joaquin River system:

It is important to note that all of the agreed upon or proposed flows (AFRP, Tuolumne River Settlement Agreement, FERC, VAMP, Davis-Grunsky, and DFG recommended flows) in the Stanislaus, Tuolumne, and Merced rivers were designed to facilitate chinook salmon recovery, and little or no consideration was given to steelhead recovery in the design of these flow strategies. Flow and temperatures requirements of steelhead will need to be evaluated and integrated into the proposed flow regimes (CALFED 2000).

CALFED has identified specific measures for steelhead recovery in the Ecosystem Restoration Program Plan, yet this program is in its infancy, and many of the identified actions are still in their initial stages. It may be several years in the future before many of these actions are implemented.

"New" Concepts for Steelhead Management

The diverse structure of rainbow trout populations described in the preceding sections is not a new concept: the extreme variability in life history and the close relationship between non-anadromous and anadromous forms was recognized early-on (Jordan 1894, 1895; Snyder 1928; Taft 1934; Shapovalov and Taft 1954) and is illustrated by the following quote from Jordan (1895):

It is said by anglers that the brook trout exist in the mountains and the salmon trout come up from the sea and "promiscuously mix with it." This

5. Another example of the chinook salmon emphasis in Central Valley anadromous fish programs was evident at the Salmonid Symposium—of the 18 papers presented at the symposium, 14 dealt with chinook salmon exclusively, three with anadromous fish in general, and only this one addressed steelhead.

*seems another way of saying that the brook trout (irideus) and the salmon trout (gairdneri) are but forms or states of the same fish.*⁶

Although classified originally as different species and later as different subspecies, the taxonomic relationship of the anadromous and non-anadromous rainbow trout forms posed considerable difficulties to early taxonomists (Jordan 1894; Kendall 1921; Taft 1934). Taft (1934) and Shapovalov and Taft (1954) aptly described the variability in rainbow trout population structure. In recent years, these concepts appear to have been largely ignored in the application of rainbow trout management, and non-anadromous and steelhead rainbow trout are usually treated as separate stocks in management schemes.

This management dichotomy is brought about not only by an incomplete understanding or appreciation of the complexity of rainbow trout population structure, but is also largely due to institutional limitations. In many cases, such as within the DFG, coordination of management and policy development for non-anadromous and steelhead rainbow trout are under the auspices of different organizational divisions, and in the case of federal ESA jurisdiction, two different cabinet-level departments (Interior and Commerce departments, respectively).

The latter example has led to a curious and biologically questionable decision by the federal government in the promulgation of the ESA for steelhead. NMFS stated in the Final Rule listing some ESUs of steelhead (NMFS 1997b) that “available evidence suggests that resident rainbow trout should be included in listed ESU’s...where resident *O. mykiss* have the opportunity to interbreed with anadromous fish below natural or man-made barriers...”; and “NMFS believes that resident fish can help to buffer extinction risks to an anadromous population.” Further, “NMFS believes that available data suggest that resident rainbow trout are in many cases part of steelhead ESUs.” Despite these findings, NMFS deferred to USFWS, who asserted their ESA jurisdiction for resident (non-anadromous) fish. USFWS stated that there was no evidence to suggest that non-anadromous rainbow trout needed ESA protection and concluded that only the anadromous forms of each ESU could be listed under the ESA by NMFS (NMFS 1997b). Because of this, non-anadromous rainbow trout were specifically excluded from the listing. Thus, we have a unique and potentially problematic situation (from a recovery standpoint) where some individuals of a listed species may be protected under the ESA, while their progeny are not. This is also problematic from an enforcement and protection standpoint because the life-history fate of a juvenile rain-

6. Use of the specific epithets *irideus* and *gairdneri* indicates that Jordan was referring to non-anadromous and steelhead rainbow trout, not *Salvelinus fontinalis* or other Pacific salmon species.

bow trout is indeterminable unless the fish has smolted, thus ESA protection may be denied for the component of the population that most needs it.

The likelihood that anadromous and non-anadromous rainbow trout can form a single interbreeding population in a particular stream has important management implications, which can only be addressed through an integrated management strategy that treats all rainbow trout occupying a stream or continuous stream reaches as a single population, regardless of life history differences within the population. Management of steelhead must include measures to protect and restore non-anadromous rainbow trout, and especially the ecological linkages between the different forms. The large-scale disruption of this linkage that has occurred in the Central Valley through the placement of impassable dams on many streams may go a long way in explaining the significant decline of Central Valley steelhead stocks.

The necessity of a strategy that integrates the management of non-anadromous and steelhead rainbow trout was recognized by Snyder (1928) long ago, who made this insightful, yet mostly unheeded statement:

We have steelheads and stream trout, and conservation of the one depends absolutely upon conservation of the other. We burn the candle at both ends when we overfish both the steelheads and stream trout. We are awakening to the fact that we can not both destroy the steelheads and maintain the rainbows.

We may have begun to awaken in the 1920s, but apparently we hit the snooze button and went back to sleep. If we are to effectively manage and recover Central Valley steelhead, we must bring our management and restoration strategies more in line with rainbow trout population structure and dynamics and we must recognize that steelhead need to be managed separately from chinook salmon stocks. Because most of their historical habitat is now inaccessible, the most effective recovery strategies will be those that focus on restoring access to former habitats, where natural conditions are conducive to spawning and rearing and the resiliency that is inherent in a diverse population structure can be fully expressed. This may have ancillary benefits to water users as well, given that in many regulated stream systems today, steelhead can only be maintained by providing suitable flows and cool water temperatures, and this can and does exact a significant water cost. Allowing steelhead to spawn and rear in their former habitats will likely alleviate the need to provide these conditions in the downstream reaches below dams.

References

- AA Rich & Associates. 2000. The relationship between water temperature and juvenile steelhead growth and productivity in the Corte Madera Creek watershed, Marin County, California. Project proposal submitted for CALFED funding dated 5/15/2000.
- Allendorf FW. 1975. Genetic variability in a species possessing extensive gene duplication: genetic interpretation of duplicate loci and examination of genetic variation in populations of rainbow trout [Ph.D. thesis]. University of Washington. 97 p.
- Allendorf FW, Utter FM. 1979. Population genetics. In: Hoar W, Randall D, Brett J, editors. Fish Physiology. Volume VIII. New York: Academic Press. p 407–55.
- Bailey ED. 1954. Time pattern of 1953–54 migration of salmon and steelhead into the upper Sacramento River. DFG unpublished report. 4 p.
- Barnhart RA. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)—steelhead. USFWS Biol Rep 82(11.60). US Army Corps of Engineers, TR EL–82–4. 21 p.
- Behnke RJ. 1972. The systematics of salmonid fishes of recently glaciated lakes. J Fish Res Board Can 29(6):639–71.
- Behnke RJ. 1992. Native trout of western North America. American Fisheries Society Monograph nr. 6. 275 p.
- Beland TJ, Braun EL. 1952. A report on Mendocino National Forest stream improvement. Project 7X–301.
- Bell MC. 1986. Fisheries handbook of engineering requirements and biological criteria. Fish Passage Development and Evaluation Program. Portland (OR): U.S. Army Corps of Engineers, North Pacific Division. 290 p.
- Bovee KD. 1978. Probability-of-use criteria for the family Salmonidae. Instream flow information paper 4. US Fish and Wildlife Service, FWS/OBS–78/07. 79 p.
- Boydston LB. 1977. California's steelhead program. In: Hassler T, VanKirk R, editors. Proceedings of the genetic implications of steelhead management symposium, 1977. Calif. Coop. Fish. Res. Unit special report 77–1. p. 26–30.
- Burgner RL, Light JT, Margolis L, Okazaki T, Tautz A, Ito S. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the north Pacific Ocean. International North Pacific Fisheries Commission. Bull. nr. 51.

- Busby PJ, Johnson OW, Wainwright TC, Waknitz FW, Waples RS. 1993. Status review for Oregon's Illinois River winter steelhead. US Department of Commerce, NOAA technical memo. NMFS-NWFSC-10. 85 p.
- Busby PJ, Wainwright TC, Bryant GJ, Lierheimer LJ, Waples RS, Waknitz FW, Lagomarsino IV. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. US Department of Commerce, NOAA technical memo. NMFS-NWFSC-27.
- [CACST] California Advisory Committee on Salmon and Steelhead Trout. 1988. Restoring the balance. 1988 annual report. 84 p.
- [CALFED] CALFED Bay-Delta Program. 2000. Ecosystem Restoration Program Plan, volume 1. Ecological attributes of the San Francisco Bay-Delta watershed. Programmatic EIS/EIR technical application.
- [DFG] California Department of Fish and Game. 1952. Interoffice correspondence from A.C. Taft to files regarding steelhead run in Putah Creek, Yolo County dated 5 February 1952.
- [DFG] California Department of Fish and Game. 1955. Letter from L. Shapovalov to R.E. Dederick dated 2 March 1955.
- [DFG] California Department of Fish and Game. 1965. California Fish and Wildlife Plan.
- [DFG] California Department of Fish and Game, Water Projects Branch. 1967. Sacramento Valley east side investigations: Appendix C – Fish and wildlife. California Department of Water Resources. Bulletin nr. 137. p 177–295.
- [DFG] California Department of Fish and Game. 1978a. Observations on downstream migration of salmonid smolts in Cottonwood Creek. California Department of Fish and Game unpublished report.
- [DFG] California Department of Fish and Game. 1978b. Inventory of fishes of Cottonwood Creek, California. California Department of Fish and Game unpublished report.
- [DFG] California Department of Fish and Game. 1979. A summary of fish and wildlife studies and recommendations for the US Army Corps of Engineers' proposed Cottonwood Creek Project. California Department of Fish and Game unpublished report.
- [DFG] California Department of Fish and Game. 1984. Yuba River steelhead run during winter of 1976–77. Memorandum from Ron Rogers to Yuba River files dated 2 March 1984.

- [DFG] California Department of Fish and Game. 1985. Memorandum from B. Loudermilk to files regarding Stanislaus River snorkel and faceplate survey for chinook salmon dated 23 August 1985.
- [DFG] California Department of Fish and Game. 1997. Letter from J. Schafer to G. Griffen (NMFS) regarding DFG comments on Proposed Rule to list steelhead under the Endangered Species Act, dated 6 January 1997.
- [DFG] California Department of Fish and Game. 2000a. Steelhead rainbow trout in San Mateo Creek, San Diego County, California. Report submitted to the National Marine Fisheries Service. 22 p.
- [DFG] California Department of Fish and Game. 2000b. Memorandum from R. Baxter to D. McEwan regarding Calaveras River smolt steelhead sampling dated 21 April 2000.
- [DFG] California Department of Fish and Game. 2001. Memorandum from K. Kundargi to files regarding observation of steelhead in the Tuolumne River dated 21 January 2001.
- [DWR and USBR] California Department of Water Resources, US Bureau of Reclamation. 1999. Effects of the Central Valley Project and State Water Project operations from October 1998 through March 2000 on steelhead and spring-run chinook salmon. Biological Assessment. 211 p.
- CH2M Hill. 1985. Klamath River basin fisheries resource plan. Prepared for the US Department of Interior.
- Clark GH. 1929a. Sacramento-San Joaquin salmon fishery in California. California Division of Fish and Game. Fish Bulletin 137.
- Clark GH. 1929b. Sacramento River salmon fishery. California Fish and Game 15(1):1-10.
- CMARP Steering Committee. 1999. Recommendations for the implementation and continued refinement of a comprehensive monitoring, assessment, and research program. 142 p.
- Cramer SP, Alley DW, Baldrige JE, Barnard K, Demko DB, Dettman DH, Farrell B, Hagar JM, Keegan TP, Laird A, Mitchell WT, Nuzum RC, Orton R, Smith JJ, Taylor TL, Unger PA, Van Dyke ES. 1995. The status of steelhead populations in California in regards to the Endangered Species Act. Special report submitted to the National Marine Fisheries Service on behalf of the Association of California Water Agencies. 190 p.
- Demko DB, Cramer SP. 1997. Outmigrant trapping of juvenile salmonids in the lower Stanislaus River, Caswell State Park Site 1996. Final report submitted to the US Fish and Wildlife Service under subcontract to CH2M Hill. 144 p.

- Demko DB, Cramer SP. 1998. Outmigrant trapping of juvenile salmonids in the lower Stanislaus River, Caswell State Park Site 1997. Final report submitted to the US Fish and Wildlife Service under subcontract to CH2M Hill. 101 p.
- Demko DB, Gemperle G, Cramer SP, Philips A. 1999. Outmigrant trapping of juvenile salmonids in the lower Stanislaus River, Caswell State Park Site 1996. Final report submitted to the US Fish and Wildlife Service under subcontract to CH2M Hill. 131 p.
- Elliott JM. 1994. Quantitative ecology and the brown trout. Oxford University Press. 304 p.
- Entrix, Inc. 1994. Results of fish passage monitoring at the Vern Freeman Diversion Facility, Santa Clara River, 1994. Prepared for the United Water Conservation District.
- Entrix, Inc. 1995. Results of fish passage monitoring at the Vern Freeman Diversion Facility, Santa Clara River, 1994. Prepared for the United Water Conservation District.
- Entrix, Inc. 1996. Results of fish passage monitoring at the Vern Freeman Diversion Facility, Santa Clara River, 1994. Prepared for the United Water Conservation District.
- Entrix, Inc. 1997. Results of fish passage monitoring at the Vern Freeman Diversion Facility, Santa Clara River, 1994. Prepared for the United Water Conservation District.
- Erman DC, Hawthorne VM. 1976. The quantitative importance of an intermittent stream in the spawning of rainbow trout. *Trans Am Fish Soc* 105:675-81.
- Erman DC, Leidy GR. 1975. Downstream movement of rainbow trout fry in a tributary of Sagehen Creek, under permanent and intermittent flow. *Trans Am Fish Soc* 3:467-73.
- Everest FH. 1971. An ecological and fish cultural study of summer steelhead in the Rogue River, Oregon. Annual progress report. Oregon State Game Commission Anadromous Fish Project, AFS-31.
- Everest FH. 1973. Ecology and management of summer steelhead in the Rogue River. Fishery research report nr. 7. Oregon State Game Commission.
- Fausch KD. 1984. Profitable stream positions for salmonids: relating specific growth rates to net energy gain. *Can J Zool* 62:441-51.
- Fausch KD. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. *Can J Fish Aquatic Sci* 50:1198-1207.

- Folmar LC, Dickhoff WW. 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. *Aquaculture* 21:1-37.
- Fry DH, Jr. 1952. Fisheries problems of the Feather River with especial reference to the proposed Oroville Dam. California Department of Fish and Game memorandum report.
- Hallock RJ. 1989. Upper Sacramento River steelhead, (*Oncorhynchus mykiss*), 1952-1988. Report to the Fish and Wildlife Service. 85 p.
- Hallock RJ, Van Woert WF. 1959. A survey of anadromous fish losses in irrigation diversions from the Sacramento and San Joaquin rivers. *California Fish and Game* 45(4):227-96.
- Hallock RJ, Van Woert WF, Shapovalov L. 1961. An evaluation of stocking hatchery-reared steelhead rainbow trout (*Salmo gairdnerii gairdnerii*) in the Sacramento River system. California Department of Fish and Game. Fish Bulletin 114. 74 p.
- Hanson HA, Smith OR, Needham PR. 1940. An investigation of fish-salvage problems in relation to Shasta Dam. 166 p.
- Herbold B, Moyle PB. 1989. The ecology of the Sacramento-San Joaquin Delta: a community profile. US Fish Wildl Serv Biol Rep 85(7.22). 106 p.
- Hooper DR. 1973. Evaluation of the effects of flows on trout stream ecology. Emeryville (CA): Pacific Gas and Electric. 97 p.
- [IEP Steelhead PWT] Interagency Ecological Program Steelhead Project Work Team. 1998. Steelhead life-stage assessment protocol. 4 p.
- [IEP Steelhead PWT] Interagency Ecological Program Steelhead Project Work Team. 1999. Monitoring, assessment, and research on Central Valley steelhead: status of knowledge, review of existing programs, and assessment of needs. In: Comprehensive monitoring, assessment, and research program plan technical appendix VII-A-11.
- Jonsson B. 1985. Life-history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Trans Am Fish Soc* 114:182-94.
- Jordan DS. 1894. Salmon and trout of the Pacific coast. 13th biennial report of the State Board of Fish Commissioners of the State of California for the years 1893-1894.
- Jordan DS. 1895. Notes on the fresh-water species of San Luis Obispo County.
- Jordan DS, Gilbert CH. 1882. Synopsis of the fishes of North America. *Bull US Nat Muse*. volume III, nr. 16.

- Kendall WC. 1921. What are rainbow trout and steelhead trout? *Trans Am Fish Soc* 50:187-199.
- Leitritz E, Lewis RC. 1980. Trout and salmon culture (hatchery methods). *California Fishery Bulletin* nr. 164. University of California.
- Maslin PE, McKinney WR. 1994. Tributary rearing of Sacramento River salmon and steelhead. Interim report dated 30 October 1994. 45 p.
- Mayott CJ. 1997. Operation of the Hills Ferry Salmon Barrier, 1996. California Department of Fish and Game, Region 4 report dated 29 June 1999.
- McEwan D, Jackson TA. 1996. Steelhead restoration and management plan for California. California Department of Fish and Game.
- McEwan D, Nelson J. 1991. Steelhead restoration plan for the American River. California Department of Fish and Game. 40 p.
- Mills TJ, McEwan DR, Jennings MR. 1997. California salmon and steelhead: beyond the crossroads. In: Stouder D, Bisson P, Naiman R, editors. *Pacific salmon and their ecosystems: status and future options*. New York (NY): Chapman & Hall. p 91-111.
- Moyle PB, Baltz DM. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow requirements. *Trans Am Fish Soc* 114:695-704.
- Murphy GI. 1946. A survey of Stony Creek, Grindstone Creek, and Thomes Creek drainages in Glenn, Colusa, and Tehama counties. California Department of Fish and Game, Inland Fisheries Branch administrative report 46-15. 16 p.
- Murphy GI. 1951. The fishery of Clear Lake, Lake County, California. *California Fish and Game* 37(4):439-84.
- Myrick CA. 1998. Temperature, genetic, and ration effects on juvenile rainbow trout (*Oncorhynchus mykiss*) bioenergetics [PhD dissertation]. University of California, Davis.
- [NMFS] National Marine Fisheries Service. 1996a. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. NOAA technical memo. NMFS-NWFSC-27. 260 p.
- [NMFS] National Marine Fisheries Service. 1996b. Factors for decline: a supplement to the Notice of Determination for west coast steelhead under the Endangered Species Act. 83 p.
- [NMFS] National Marine Fisheries Service. 1997a. Status review update for deferred and candidate ESUs of west coast steelhead. Prepared by NMFS West Coast Steelhead Biological Review Team.

- [NMFS] National Marine Fisheries Service. 1997b. Endangered and threatened species: listing of several Evolutionary Significant Units (ESUs) of West Coast steelhead. Federal Register 62(159):43940-1.
- Needham PR, Smith OR, Hanson HA. 1941. Salmon salvage problems in relation to Shasta Dam, California, and notes on the biology of the Sacramento River salmon. Transactions of the American Fisheries Society. 17th annual meeting.
- Nielsen JL. 1994. Molecular genetics and stock identification in Pacific salmon (*Oncorhynchus* spp.) [Ph.D. thesis]. University of California, Berkeley. 167 p.
- Nielsen JL, Lisle TE, Ozaki V. 1994. Thermally stratified pools and their use by steelhead in northern California streams. Trans Am Fish Soc 123:613-26.
- Northcote TG. 1997. Why sea run? An exploration into the migratory/residency spectrum of coastal cutthroat trout. In: Hall JD, Bisson PA, Gresswell RE, editors. Sea-run cutthroat trout: biology, management, and future conservation. Corvallis (OR): Oregon Chapter, American Fisheries Society. p 20-26.
- Painter RE, Wixom LH, Taylor SN. 1977. An evaluation of fish populations and fisheries in the post-Oroville project Feather River. Report submitted to the California Department of Water Resources in accordance with Federal Power Commission License nr. 2100.
- Reiser DW, Bjornn TC. 1979. Habitat requirements of anadromous salmonids. General technical report PNW-96. Portland (OR): USDA, Forest Service, Pacific Northwest Forest and Range Experiment Station. 54 p.
- Reynolds FL, Mills TJ, Benthin R, Low A. 1993. Restoring Central Valley streams: a plan for action.
- Reynolds FL, Reavis RL, Schuler J. 1990. Central Valley salmon and steelhead restoration and enhancement plan. California Department of Fish and Game. 115 p.
- Roelofs TD. 1983. Current status of California summer steelhead (*Salmo gairdneri*) stocks and habitat, and recommendations for their management. Report to the US Forest Service, Region 5. 77 p.
- Rich AA. 2000. Water temperature requirements for chinook salmon and steelhead trout. Testimony submitted to the State Water Resources Control Board, Yuba River hearings, 1 May 2000 (Exhibit S-DFG- 39). 12 p.
- Royal LA. 1972. An examination of the anadromous trout program of the Washington State Game Department. Washington Department of Game. 176 p.
- Savvaitova KA, Kuzishchin KV, Maksimov SV, Pavlov SD. 1997. Population structure of mikizha, *Salmo mykiss*, in the Utkholok River (western Kamchatka). Translated from Voprosy Ikhtiologii in volume 37 nr. 2. J Ichthyology 37(3):216-225.

- Savvaitova KA, Maksimov VA, Mina MV, Novikov GG, Kokhmenko LV, Matsuk VE. 1973. The noble trouts of Kamchatka: systematics, ecology, and possibilities of using them as the object of trout-culture and acclimatization. Russia: The Voronezh University Publishers.
- Shapovalov L. 1944. Preliminary report on the fisheries of the Santa Ynez River system, Santa Barbara County, California. Calif. Dept. of Fish and Game, Inland Fisheries Branch administrative report 44-14. 22 p.
- Shapovalov L, Taft AC. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Department of Fish and Game. Fish Bulletin 98. 373 p.
- Shirvell CS. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Can J Fish Aquat Sci 47:852-61.
- Smith SH. 1950. Upper Sacramento River sport fishery. US Fish and Wildlife Service Special Scientific Report: Fisheries. Nr. 34. 44 p.
- Snider B, Titus R. 1996. Evaluation of juvenile anadromous salmonid emigration monitoring in the Sacramento River near Knights Landing, November 1995-July 1996. California Department of Fish and Game report.
- Snyder JO. 1928. California trout. California Fish and Game 14(2):121-2.
- Staley JR. 1976. American River steelhead, *Salmo gairdnerii gairdnerii*, management, 1956-1974. California Department of Fish and Game Anadromous Fisheries Branch administrative report nr. 76-2. 41 p.
- Taft AC. 1934. California steelhead experiments. Transactions of the American Fisheries Society. 64th annual meeting.
- Thompson K. 1972. Determining stream flows for fish life. In: Proceedings, Instream Flow Requirement Workshop. Vancouver (WA): Pacific NW River Basin Comm. p 31-50.
- Thorpe JE. 1987. Smolting vs. residency: developmental conflict in salmonids. In: Dadswell MJ, Klauda RJ, Moffitt CM, Saunders RL, Rulifson RA, Cooper JE, editors. Common strategies of anadromous and catadromous fishes. Proceedings of the American Fisheries Society Symposium 1. Boston, MA. p 244-252.
- Titus RG. 2000. Adult steelhead collected in the Calaveras River below New Hogan Dam in March 2000. California Department of Fish and Game Stream Evaluation Program report. 9 p.
- Titus RG, Erman DC, Snider WM. History and status of steelhead in California coastal drainages south of San Francisco Bay. Forthcoming.

- Titus RG, Mosegaard H. 1992. Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. *J Fish Biol* 41:239-55.
- [Upper Sacramento River FRHAC] Upper Sacramento River Fisheries and Riparian Habitat Advisory Council. 1989. Upper Sacramento River Fisheries and Riparian Habitat Management Plan. Report prepared for The Resources Agency, State of California. 158 p.
- [USFWS] US Fish and Wildlife Service. 1997. Revised draft restoration plan for the anadromous fish restoration program.
- [USFWS and DFG] US Fish and Wildlife Service, California Department of Fish and Game. 1953. A plan for the protection and maintenance of salmon and steelhead in the American River, California, together with recommendations for action. Unpublished report dated 20 July 1953. 47 p.
- Van Woert W. 1958. Time pattern of migration of salmon and steelhead into the upper Sacramento River during the 1957-58 season. California Department of Fish and Game, Inland Fisheries Branch administrative report nr. 58-7.
- Vestal EH. 1965. Observations on the fish and wildlife resources of the upper Kings River, middle and south forks, Fresno County, with recommendations for management. California Department of Fish and Game unpublished report.
- Voight HN, Gale DB. 1998. Distribution of fish species in tributaries of the lower Klamath River: an interim report, FY 1996. Technical Report No. 3. Yurok Tribal Fisheries Program, Habitat Assessment and Biological Monitoring Division. 71 p.
- Wales JH. 1939. General report of investigations of the McCloud River drainage in 1938. *California Fish and Game* 25(4):272-309.
- Wedemeyer GA, Saunders RL, Clarke WC. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Mar Fish Rev* 42:1-14.
- Wilson GM, Thomas WK, Beckenbach AT. 1985. Intra- and inter-specific mitochondrial DNA sequence divergence in *Salmo*: rainbow, steelhead, and cutthroat trouts. *Can J Zool* 63:2088-94.
- Withler IL. 1966. Variability in life-history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. *J Fish Res Board Can* 23(3):365-93.
- Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 1996. Historical and present distribution of chinook salmon in the Central Valley drainage of California. In: Sierra Nevada ecosystem project: final report to Congress. Volume III: assessments, commissioned reports, and background information. Davis (CA): University of California, Centers for Water and Wildlife Resources. p 309-61.

- Yoshiyama RM, Fisher FF, Moyle PB. 1998. Historical abundance and decline of chinook salmon in the Central Valley region of California. *N Am J Fish Manage* 18:487-521.
- Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. In: Brown RL, editor. *Fish Bulletin 179: Contributions to the biology of Central Valley salmonids*. Volume 1. Sacramento (CA): California Department of Fish and Game.
- Zimmerman CE. 2000. Ecological relation of sympatric steelhead and resident rainbow trout in the Deschutes River, Oregon [PhD thesis]. Corvallis (OR): Oregon State University. 116 p.

Notes

- Titus R. (California Department of Fish and Game). Telephone conversation with author in November 1999.
- Behnke R. (Colorado State University). Written correspondence with author in February 2001.

