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Life History, Ecology, and Status of Klamath River Steelhead

By Joshua A. Israel

INTRODUCTION

The Klamath River drains over 12,000 square miles of land from its headwaters in Southern Oregon's high desert mountains to its mouth located in Northern California's temperate redwood rainforests. This heterogeneous landscape, shaped by active geological and hydrological processes, has resulted in the necessity for aquatic organisms to develop behavioral and physiological mechanisms for coping with an increased level of disturbance. In particular, coastal steelhead (*Oncorhynchus mykiss irideus*) in this basin have evolved multiple life history and reproductive strategies for persisting in a system where critical habitat parameters are highly variable. Klamath River steelhead are recognized to constitute two distinct reproductive ecotypes that migrate from the ocean into tributaries during different time periods (Busby et al., 1996). However, different life stages of steelhead are found in the Klamath mainstem every month of the year, including a run of immature fish (commonly referred to as the "half-pounder") that overwinters in freshwater before migrating back into the ocean the following spring (USFWS, 1998).

Klamath River steelhead are an anadromous form of coastal rainbow trout (*O. mykiss irideus*). Their relationship to redband trout (*O. mykiss newberri*) has not been adequately evaluated to determine whether steelhead in the Klamath River are genetically derived from this upper Klamath basin fish. Steelhead exhibit the largest geographic range and most complex suite of traits of any salmonid species. Steelhead share many of the characteristics of rainbow trout that contribute to their ability to adapt to systems that are highly unpredictable and undergo frequent disturbance. Particularly important characteristics of Klamath River steelhead include anadromy (meaning migrating to the ocean and returning to spawn in freshwater) or nonadromous freshwater residency, iteroparity (meaning participating in multiple reproductive events), and natal homing.

Watershed disturbances caused by agriculture, timber harvest practices, past mining and water diversions have negatively affected the fishery resources within the basin (KRBFTF, 1991). During the past century, managing salmonid species for commercial and recreational

purposes have focused on artificially producing large numbers of fish in hatcheries. Natural environmental fluctuations (climatic cycles and marine conditions) have likely played less of a role in the decline of this species than these human-induced impacts. However, the Klamath River and its tributaries support the largest population of coastal steelhead remaining in California (McEwan and Jackson, 1996). Klamath River steelhead are part of the Klamath Mountains Province Evolutionary Significant Unit (ESU), which the National Marine Fisheries Service (NMFS) determined was not warranted for listing under the Endangered Species Act (NMFS, 2001). This paper reviews the ecology of steelhead and the diverse life histories they utilize on the Klamath River, as well as discusses their status and conservation actions necessary for their protection.

IDENTIFICATION

Steelhead and rainbow trout are variable in color and body shape (Moyle, 2002). Juvenile trout display 5-13 oval parr marks along the lateral line, white to orange tips on the dorsal and anal fins, and have few or no spots on the tail (Figure 1A). When compared to other salmonids, the interspaces on juvenile steelhead are wider than the parr marks. Their head is blunt with a short jaw that does not extend past the eye. Adult steelhead reach up to 45 inches, appear silver with an iridescent pink to red lateral line, and have a square-shaped tail fin with radiating spots unlike any other adult salmonid in the Klamath River. Numerous small, circular black spots also cover their back and adipose and dorsal fins (Figure 1B).

LIFE HISTORY

Nonanadromous Phenotype

O. mykiss irideus in the Klamath-Trinity River basins display one of the most diverse sets of life history patterns found in the *Oncorhynchus* genus. This species encompasses two distinct phenotypes. Typically, the resident form (called a rainbow or redband trout) spends their entire life in fresh water isolated above natural barriers (e.g., waterfalls, landslides, subsurface stream flows). This natural form of *O. mykiss irideus* is apparently uncommon in the Klamath River. However, nonanadromous trout have been observed in the summer below Iron Gate Dam and are potentially late releases of hatchery steelhead progeny that residualized (meaning remaining nonanadromous because smoltification stops) within this reach of the river (CDFG, 2001). The



A. Juvenile steelhead (Photo: Mark Capelli)



B. Adult steelhead (from http://www.krisweb.com/krisweb_kt/trtour/steelhd.htm).

Figure 1. A. This juvenile steelhead is distinguished by the spacing of its parr marks, blunt head, and orange/white tipped pelvic fins. B. This adult steelhead is distinguished by black spots radiating along its tail and heavy spotting on its body.

cause for residualization of steelhead progeny in the Klamath River is poorly understood. Possible hypotheses on this phenomena include accelerated growth rate of fish in hatcheries or excessively high water temperatures downstream delaying outmigrant behavior in these fish (Healey, 1991; Viola and Schuck, 1995). Steelhead have also residualized above recent manmade barriers in the basin like Lewiston, Iron Gate, and Dwinnell Dams, although the genetic integrity of these fish is questionable given the stocking of nonnative rainbow trout into the waterbodies. These potadromous fish remain migratory and utilize tributaries to these reservoirs.

The relationship of steelhead to nonanadromous Upper Klamath redband trout (*O. mykiss newberri*, Benhke 1992) remains unknown, although redband trout inhabit the upper Klamath basin in Oregon now isolated by dams along the mainstem. Prior to the construction of Copco Dam in 1917, steelhead migrated up to the falls at the outlet of Klamath Lake. Benhke (1992) suggested that *O. mykiss irideus* did not reside above this location and designated the migratory Upper Klamath trout as a separate subspecies, *O.m. newberrii*. Isolated trout in Jenny Creek, above a waterfall, and in the upper Williamson and upper Sprague Rivers have meristic (meaning physically measurable) characteristics and biochemical characters that suggest a common origin, but are quite distinctive from all other trout (Benhke, 1992). Moyle (2002) suggested that steelhead invaded the upper Klamath basin during the Pleistocene and

nonanadromous coastal rainbow trout are present above Klamath Lake. Snyder (1930) and Fortune et al. (1996 in Hardy and Addley, 2001) both suggested that steelhead utilized tributaries above Upper Klamath Lake. It is likely that redband trout moved downstream of the outlet falls. The questions of potential reproductive interactions between the two forms, and whether the redband trout become anadromous remain questions requiring further investigation.

Anadromous Phenotype

The second phenotype of coastal steelhead is the more common anadromous form. In the Klamath River basin, these fish display a variety of life history patterns constituting different freshwater and saltwater rearing strategies (ODFW, 1995). The differences between these different life history patterns are not well understood, and scientists group anadromous steelhead “races” depending on the timing of adult migration into the Klamath River. The classification of different adult migratory run-timings is not agreed upon (Table 1). Snyder (1933) found the timing of fall steelhead into the Shasta River to be earlier than other rivers.

Steelhead race	KRSIC (1993)	Hopelain (1998)	USFWS (1979)	Busby et al (1996)	Moyle (2002)
Spring/Summer	May- July	March-June	April-June		April- June
Fall	August- October	July-October	August-November		
Winter	November- February	November-March	November-February		November-April
Stream-maturing				April- October	
Ocean-maturing				September-March	

Table 1. Classification of different run-timings and reproductive ecotypes of steelhead found in the Klamath River basin.

NMFS does not classify Klamath River basin steelhead “races” based on run-timing of adults, but instead recognizes two distinct reproductive ecotypes of coastal steelhead in the Klamath based upon their reproductive biology and freshwater spawning strategy (Busby et al., Table 1). Burgner et al. (1992) identified the stream-maturing type as entering the river sexually immature and still requiring several months before ripening to spawning condition. In the Klamath River, Busby et al. (1996) called these summer steelhead and found they migrated upstream between April and October with a peak in spawning behavior during January. The second type, ocean-maturing, enter the Klamath River between September and March with a peak in spawning in March. These fish enter the river sexually mature and spawn shortly after reaching spawning grounds (Busby et al., 1996). The overlap in migration and spawning periods make differentiating these ecotypes difficult (Roelofs, 1983). A genetic study determined that

different runs of steelhead within a particular subbasin of the Klamath-Trinity system shared more genetic similarities than populations of similar run-timings in adjacent basins (Reisenbichler et al., 1992).

Early life history for steelhead in the Klamath River basin is better understood. Before establishing feeding locations, newly hatched steelhead move to the shallow, protected margins of the stream (Royal, 1972 in McEwan and Jackson, 1996). Once aggressive behavior is exhibited, territories become established and are defended (Shapovalov and Taft, 1954) in or below riffles, where food production is greatest. Moffett and Smith (1950) found steelhead fry (meaning individuals not yet surviving through a winter) favored tributary streams with a peak in downstream movement during the early summer on the Trinity River. Possible physical influences leading to a decline in this behavior included decreasing river flows and increasing water temperatures. As higher flows and lower water temperatures returned to the mainstem during the late fall and winter, Moffett and Smith (1950) observed an increase in downstream movement. Steelhead parr (meaning individuals surviving at least one winter) showed the greatest freshwater movement towards the end of their first year and spent their second year inhabiting the mainstem. The large majority of steelhead (86%) in the Klamath River basin apparently spend two years in fresh water before undergoing smoltification (the physiological process of preparing to survive in ocean conditions) and migrating to sea (Hopelain, 1998). Kesner and Barnhardt (1972) determined that steelhead rearing in fresh water for longer periods made their seaward migration more quickly. Klamath River basin steelhead remain in the ocean for one to three years before returning to spawn and their ocean migration patterns are unknown. It is believed that steelhead use their excellent homing sense to return to the same area they lived in as fry to spawn (Moyle, 2002).

The presence of “half-pounder” steelhead in the Klamath River basin is a distinguishing life history trait of steelhead found in the Klamath Mountains Province ESU. Half-pounder steelhead are subadult individuals who have spent 2-4 months in the Klamath estuary or nearshore before returning to the river to overwinter. They overwinter in the lower and mid-Klamath regions before returning to the ocean the following spring. The presence of half-pound fish is uncommon above Seiad Valley (Kesner and Barnhardt, 1972). The occurrence of half-pounders was greater in spawning fish of mid-Klamath region tributaries (86-100%) when compared to the Trinity River (32-80%). There is a negative linear relationship between rates of

half-pounder migration and first-time spawning size. The lowest occurrence of half-pounders was from Lower Klamath River winter-run steelhead (17%), which also demonstrated the greatest first-year growth rate (Hopelain, 1998). The proportion of “half pounders” that become stream- or ocean-maturing ecotypes is not known.

Iteroparity (meaning the ability to spawn more than once) is an important character of steelhead that makes them different from most all other *Oncorhynchus* species. Hopelain (1998) reported that repeat spawning varied between different run-timings. The frequencies of steelhead having undergone multiple reproductive events varied in range from 17.6 to 47.9% for fall run, 40.0 to 63.6% for spring run, and 31.1% for winter run. Females make of the majority of repeat spawners (Busby et al., 1996), and lay between 200 and 12,000 eggs (Moyle, 2002). Nonandromous coastal rainbow trout typically contain fewer than 1,000 eggs, while steelhead contain about 2,000 eggs per kilogram of body weight (Moyle, 2002).

ECOLOGY

Steelhead require different habitats for each stage of life in the Klamath River. The abundance of steelhead in a particular location is influenced by the quantity and quality of suitable habitat, food availability, and interactions with other species. Caution should be used when interpreting microhabitat data and optimal conditions described in the laboratory, because they may not correspond to the most favorable conditions in natural environments (Spence et al., 1996). Klamath River steelhead exemplify the need for this scrutiny because of the high variation of life history strategies they utilize to ensure survival. Regardless, during the first couple years of freshwater residence, steelhead require cool, clear, fast-flowing water (Moyle, 2002). Considerable knowledge gaps exist in our understanding of how abiotic factors and species interactions affect an individual trout's instinct to express one life history strategy over another. Do distinct run-timings of Klamath River steelhead have different juvenile feeding habits, habitat requirements, or interspecies interactions that dispose them to a particular life history strategy? What type of intraspecies' interactions exist between juveniles or adults of different run-timings? Can critical abiotic factors lead an entire streams cohort of juvenile steelhead to undergo a certain life history strategy (e.g., early smoltification)?

Habitat Utilization

Although steelhead have a greater physiological tolerance than other salmonids, certain requirements must be met for a watershed to support these highly-adaptable fish, including cool water throughout their life history (Table 2). Many physiological cues during their lifecycle depend on temperatures remaining within these critical ranges. Length of time for eggs to hatch from the redd is a function of water temperature and dissolved oxygen. Hatchery steelhead take 30 days to hatch at 10.5°F (Leitritz and Lewis, 1980 in McEwan and Jackson, 1996), and emergence from the gravel occurs after two to six weeks (Moyle, 2002; McEwan and Jackson, 1996). Egg mortality begins at 13.3°C (McEwan and Jackson, 1996). Redd construction typically occurs in gravel substrates of 0.5 to 10.0 cm in diameter (Reiser and Bjornn, 1979 in Spence et al., 1996). Water velocities over the redd is between 20 and 155 cm/sec, and depths are often 10 to 150 cm (Moyle, 2002). Low levels of sedimentation (>5% sand and silt) can reduce redd survival and emergence due to decreased permeability of the substrate and dissolved oxygen concentrations available for the incubating eggs (McEwan and Jackson, 1996). Once out of the gravels, steelhead fry can survive at a greater range of temperatures, but have difficulty obtaining oxygen from the water at temperatures above 21.1°C (McEwan and Jackson, 1996). When physiologically stressed, steelhead have a more difficult time acquiring food, defending territories, avoiding predators, and are more likely to succumb to infectious diseases and parasites (Spence et al., 1996).

Life History Stage	McEwan and Jackson (1996)	Moyle (2002)
Spawning	3.8 to 11	NR
Incubation and emergence	8.8 to 11	10 to 15
Fry and juvenile rearing	7.2 to 11	15 to 18
Smoltification	7.2 to 15	NR
Adult migration	7.7 to 11	NR
Summer steelhead holding	10 to 15	10 to 15

Table 2. Utilized (McEwan and Jackson, 1996) and optimal (Moyle, 2002) water temperatures (°C) for various steelhead life history stages. NR= Not Reported.

Steelhead have a body form useful for holding in fast water; it is more cylindrical than other salmonids with short median fins and large paired lobes. These differences in body shape were found to contribute to steelhead being better swimmers than cutthroat trout. Hawkins and Quinn (1996) found that the critical swimming velocity for juvenile steelhead was 7.69 body

lengths/sec compared to juvenile cutthroat trout that moved between 5.58 and 6.69 body lengths/sec. Adult steelhead swimming ability is hindered at water velocities above 3 to 3.9m/sec (Reiser and Bjornn, 1979 in Spence et al., 1996). Preferred holding velocities are much slower, and range from 0.19m/sec for juveniles and 0.28m/sec for adults (Moyle and Baltz, 1985). Physical structure like boulder, large woody debris, and undercut banks create hydraulic heterogeneity that increase the habitat available for steelhead in the form of cover from predators, visual separation of juvenile territories, and refuge during high flows (Everest et al., 1985). Reiser and Peacock (1985 in Spence et al., 1996) reported the maximum leaping ability of steelhead to be 3.4m and they require water approximately 18cm deep for passage (Bjornn and Reiser, 1991 in Spence et al., 1996).

Summer steelhead do not utilize the majority of Klamath River tributaries like the more common fall and winter steelhead. In particular, summer steelhead utilize Red Cap, Bluff, Elk, Dillon, Clear, Wooley, and Canyon Creeks and the Salmon, North and South Fork Trinity and New Rivers. These rivers drain portions of the Klamath and Trinity Mountains providing deep pools (> 3) for refugia through the summer for subadults to mature sexually. Nielsen and Lisle (1994) found coldwater pockets in these thermally-stratified pools to be 3.5°C cooler than midday ambient stream temperatures of 36-29°C. In the New River, summer steelhead were found to occupy covered areas under bedrock ledges and boulders. Densities of these fish were highest where water velocities averaged 9.3cm/sec (Nakamoto, 1994).

Growth rate and feeding habits.

The growth rate of steelhead is quite rapid after emergence from the redd and by the end of the first year individuals can reach between 10 and 12 cm (Moyle, 2002). Increased water temperature, which is one factor influencing production of aquatic invertebrates (Allan, 1995), accelerates growth rates until early fall (Moffett and Smith, 1950). By the end of the second year, steelhead are often 16 to 17 cm in length and sustain a short growth spurt during their third spring to prepare them for smoltification (Moyle, 2002). Smolts from Klamath River subbasins known to contain fall-runs of steelhead entered the ocean at 21-23 cm (Hopelain, 1998).

Feeding habits of steelhead varied through the different periods of their life, although mean growth rates in juveniles were similar between run-timings and tributaries (Hopelain, 1998). In general, trout seem to specialize on an aquatic organism or terrestrial bug of choice, although they also seem to be somewhat opportunistic (Moyle, 2002). In April, Trinity River

steelhead were found with ants in their stomachs (Boles, 1990). As they grow, their diets change to include larger prey, with fish being more important to nonanadromous trout than parr preparing for smoltification. Kesner and Barnhardt (1972) observed Trichoptera larvae to be the primary food found in half-pounder steelhead stomachs. They also determined that half-pounders more frequently contained food in their stomachs compared to steelhead on a spawning migration. In the ocean, a large part of steelhead's diet seems to be other fish, squid, and crustaceans (Barnhardt, 1986).

Community associations and species interactions

Steelhead trout are found in two distinct assemblages depending on their phenotype (Moyle, 2002). *O. mykiss irideus* are found above and below barriers to anadromy. Above barriers in cold, fast-moving tributaries in the Lower Klamath River coastal rainbow trout are found alone or with coastal cutthroat trout (Moyle, 2002). Large coastal cutthroat trout are piscivorous, and I have observed them preying on young-of-the-year steelhead trout in Freshwater Creek (Humboldt County). The anadromous form of rainbow trout are found in an assemblage that includes other salmon, Klamath smallscale suckers, speckled dace, and marbled sculpin species in the Klamath River. This species association is a product of the physical landscape as well as interspecies interactions between fish. Potentially, environmental fluctuations keep the populations of each species from reaching a size where competition and territoriality is important (Moyle, 2002). Alternatively, in the reaches of streams where this diverse assemblage is observed, a high degree of habitat heterogeneity allows segregation of species into microhabitats and may eliminate interspecies interactions.

In the presence of other juvenile salmonids (coho and chinook), steelhead have been observed to distribute themselves in microhabitats different from the other species (Everest and Chapman, 1972). Steelhead are successful competitors and can display aggressive behavior to defend territories (Jenkins, 1969 in Moyle, 2002). Juvenile rainbow trout have a positive interaction with suckers in the Sacramento River, and possibly form the same relationship in the Klamath River. In the Sacramento, juveniles were observed to follow large suckers around and feed on invertebrates disturbed by the suckers feeding (Baltz and Moyle, 1984). Studies of intraspecies interactions have reported steelhead segregating themselves spatially within the same stream into microhabitats (Moyle, 2002; Keeley and McPhail, 1998). However little is known about the relationship between different cohorts, including half-pounders, in the Klamath

River. In one study on a coastal California stream (Harvey and Nakamoto, 1997), the intraspecific interactions among different cohorts were dependent on the habitat occupied by the fish. In deep water, Harvey and Nakamoto (1997) observed larger steelhead in the presence of small steelhead to grow faster than when these fish were observed together in shallow waters. Food availability has a larger impact on territory size than body size, and juvenile steelhead were observed to intrude into adjacent steelhead territories to capture food (Keeley and McPhail, 1998). Moffett and Smith (1950) observed schools of steelhead parr in the thalweg along the bottom during extended winter dry periods on the Trinity River. This may be favored habitat because this deeper, faster water contains more invertebrate drift (Britain and Eikeland, 1988) and offers greater protection from predators.

STATUS

The management of steelhead in the Klamath River exemplifies the difficulty of grouping steelhead stocks into “races” based on run-timings. Evaluating the status and management of these distinct populations is complicated by the fact that NMFS aggregates all populations from each of the rivers into the Klamath Mountains Province ESU. Although this designation is based upon the uniqueness of life-history traits and distinguishing genetic characteristics of steelhead north of Redwood Creek, CA and south of the Elk River, OR, it may not conserve steelhead life history diversity on a subbasin watershed scale.

No long-term data is available to evaluate Klamath River steelhead population trends. The *California Fish and Wildlife Plan* (1965) estimated a basinwide annual run size of 283,000 adult steelhead (spawning escapement + harvest). Busby et al. (1994) reported winter steelhead runs in the basin to be 222,000 during the 1960s. Based on creel and gill net harvest data (Hopelain, 2001), the winter-run steelhead population was estimated at 10,000 to 30,000 adults annually in the early 1980s. Population estimates of summer steelhead have also declined precipitously during the 1990s (Table 3). The apparent decrease in population size of steelhead in the Klamath River has multiple causes. Main factors impacting steelhead in the Klamath Basin include hatcheries, harvest, hydroelectric operations, and human impacts.

	1978	1982	1986	1990	1994	1996	Max (yr)
Bluff Cr	NS	37	73	14	4	4	73 (1986)
Camp Cr	NS	NS	0	3	0	0	7 (1989)
Red Cap Cr	NS	45	NS	7	0	1	45 (1982)
Dillon Cr	NS	295	NS	74	NS	43	300-500 (1983)
Clear Cr	1810	610	428	91	58	24	1810 (1978)
Indian Cr	421	5	NS	12	61	8	154 (1989)
Elk Cr	408	249	NS	31	26	13	249 (1982)
Salmon		120	NS	15	NS	27	128 (1988)
N. Fk. Salmon	NS	41	6	12	20	9	69 (1980)
S. Fk. Salmon	NS	223	13	21	47	35	166 (1980)

Table 3. Preliminary estimates of summer steelhead population, 1979-1996. NS= Not Surveyed (summarized from McEwan and Jackson, 1996).

Hatcheries

Two hatcheries are currently operated by the California Department of Fish and Game (CDFG) as mitigation for lost habitat beyond Iron Gate and Lewiston Dams. While hatchery production has primarily relied upon native broodstock, numerous transfers of fish from outside the basin are documented. Prior to 1973, transfers came from the Sacramento, Willamette, Mad and Eel Rivers (Busby et al., 1996). Since the length of freshwater occupancy of juvenile Klamath River steelhead is long, wild fish are at a potentially increased risk from hatcheries. About 1,000,000 smolts per year are produced by the two hatcheries (Busby et al., 1994 in Moyle 2002). In 2003, 191,000 steelhead yearlings were released from Iron Gate hatchery using a volitional release that started on March 28. About half the fish moved downstream on their own, while the other half were released by CDFG on May 9 (Kim Rushton, Per. Comm.). Historic returns of steelhead to both hatcheries are shown in Figure 2, and population size fluctuations in the two basins do not seem correlated.

No studies have been carried out to evaluate the impact of hatcheries releases on wild steelhead and other salmonids in the Klamath River, but studies elsewhere have shown that releases of large numbers of fish result in negative competitive interactions between wild steelhead and hatchery fish for food, habitat, and mates (Nickelson et al., 1986). Also, carrying capacity of rivers is often exceeded during the outmigration of hatchery smolts decreasing food

availability (Steward and Bjornn, 1990 in Spence et al 1996). Hatchery steelhead have been documented to displace a large percentage of wild steelhead (79%, McMichael et al., 1999). Other risks from hatcheries include disease transmission (Steward and Bjornn, 1990 in Spence et al., 1996), alterations of migration behavior in wild fish (Hillman and Mullen, 1989 in Spence et al., 1996), and genetic changes in the wild population (Waples, 1991). The behavioral and genetic interactions of residualized hatchery steelhead wild steelhead on the Klamath River has not been evaluated but is recognized as an issue requiring attention (CDFG, 2001).

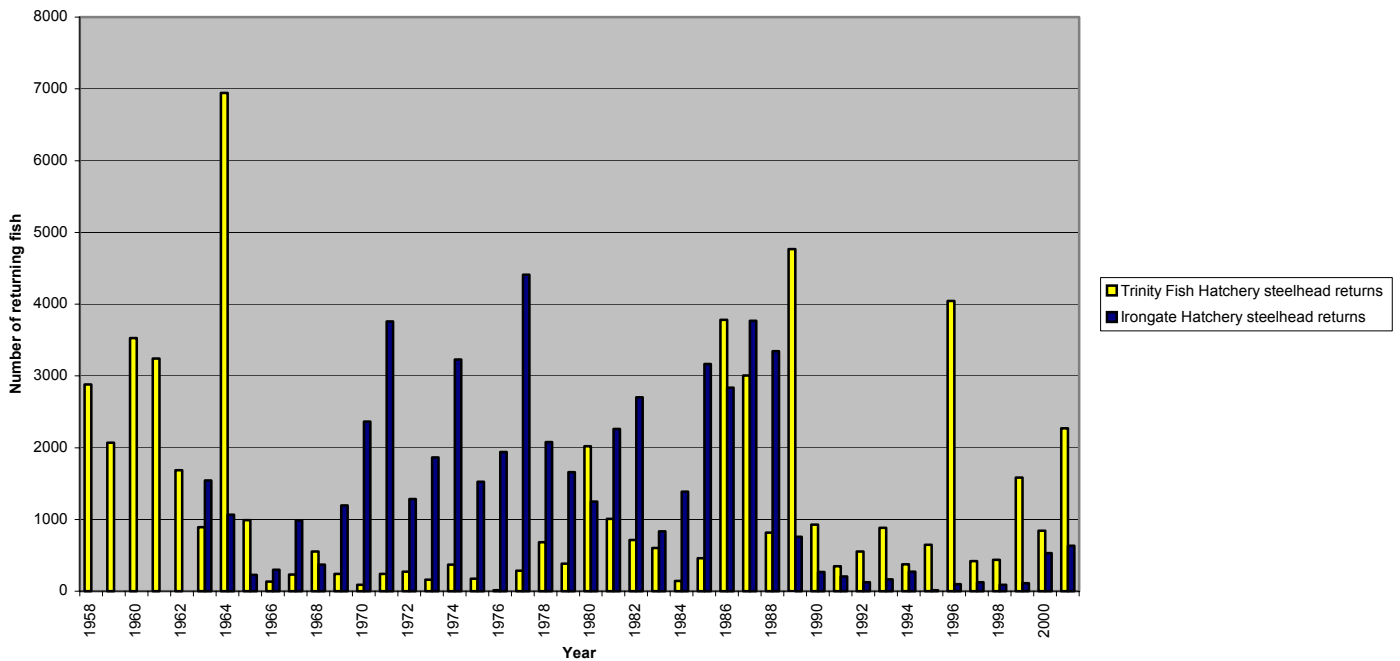


Figure 2. **Historical steelhead returns at two hatcheries in the Klamath River basin.**

Harvest

A sportfishery for Klamath River steelhead and other salmonids provides economic benefits to the local Klamath River economy. The net annual economic benefit of steelhead in the Klamath River is over 12 million dollars per year (Meyer Resources, Inc. (1988) in McEwan and Jackson, 1996). Currently, sportfishery regulation prohibits take of wild winter steelhead and does not allow fishing of summer steelhead. Poaching may pose a problem for these fish because of their concentration over a long period in particular locations (Eric Gerstung, pers. Comm. in McEwan and Jackson, 1996).

Hydroelectric Operation

Iron Gate Dam (and all the other dams in the basin) breaks the upstream-downstream connectivity of the Klamath River. A primary impact to steelhead is the elimination of free passage beyond these barriers upstream to historic spawning grounds and downstream to the ocean. Another direct impact Iron Gate Dam has on Klamath River steelhead is the alteration of natural flow regimes. A river's flow regime controls the physical and hydrological processes of a river, and therefore is responsible for habitat and food availability, temperature regimes, and the concentration of dissolved gases (Spence et al., 1996). The loss of habitat from decreased flows intensifies inter- and intraspecies competition for suitable rearing and feeding of juvenile steelhead (Spence et al., 1996). The discontinuity of the river above and below each dam resets the nutrient cycling in the Klamath River, and may impact food availability for steelhead, although this has not been investigated.

Iron Gate Dam is responsible for changes in flow and these impact the temperature regime on the mainstem Klamath River. Steelhead continuously exposed to temperatures above 24°C are unable to survive (Moyle, 2002). While water from Iron Gate Dam is not released at this temperature, the quantity of water released impacts the variability of downstream water temperatures. Larger volumes have greater thermal inertia, thus tripling mainstem flows would dampen daily fluctuations into water temperatures above critical values for steelhead (Deas, 2000 in Class Reader, 2003). However, these greater flows might potentially increase downstream minimum temperatures and would eliminate the thermal benefits from mainstem tributaries. [refer to (Anderson, 2003 and Litton, 2003) in this volume for more detail].

Human Impacts

Klamath River steelhead spend a considerable part of their life in the tributaries where cool, high-quality water is typically common. Recent reports have documented the degradation of this habitat and potential impacts to juvenile salmonid production (Ricker, 1997; Jong, 1997; Borok and Jong, 1997). Particular impacts caused by increased sedimentation of spawning grounds include reduction of egg survival and sac fry emergence rates. Potential impacts from upslope erosion created by logging and road construction may negatively impact steelhead spawning ([refer to Bezemek, 2003) in the volume for more detail]; Burns, 1972). In many smaller Klamath River tributaries, where impacts from these activities are greatest, steelhead rely

on unimpacted habitat for supporting the production and survival of juveniles. In some subbasins, road construction and placement of culverts has created barriers to migration.

Agricultural and ranching land use practices can negatively impact adjacent waterbodies containing steelhead and other anadromous fish. The trampling and removal of riparian vegetation by grazing livestock destabilizes and denudes streambanks increasing sediment and temperature in the streams (Platts et al, 1991 in Spence et al., 1996). On the Klamath River, these activities have led to a reduction in canopy over the stream channel and siltation of pools necessary for juvenile rearing (Moyle, 2002). Agriculture practices can directly impact steelhead because of the massive alterations of the riparian and aquatic systems resulting from effort to increase the quantity of land converted for food production (Spence et al., 1996). This includes stream channelization, large woody debris removal, and armoring of banks (Spence et al., 1996). All of these activities homogenize the aquatic habitat to temperature and water conditions that are not favored by steelhead or other native biota, but do enhance the invasion of nonindigenous fish (Harvey et al., 2002). Humans have introduced 13 alien species in the Klamath River, although none have been observed to negatively impact steelhead. However, in other Northern California rivers, invasive species have played a role in the decline of steelhead through predation and competition (Brown and Moyle, 1991).

CONCLUSION

Fall-winter steelhead populations in the Klamath River are the healthiest in California, although they have declined for historic levels and appear to still be declining. Summer steelhead populations remain the most imperiled *O. mykiss* runs in the Klamath River and are holding onto a small number of key populations. Steps necessary to restore steelhead to historic numbers and protect all life-history types will potentially require management and societal changes within the basin. Considerable development has gone into the formation of conservation strategies for steelhead throughout California (McEwan and Jackson, 1996; CDFG, 2001). Key elements of the *Steelhead Restoration and Management Plan for California* (McEwan and Jackson, 1996) for the Klamath River included greater flow releases through Iron Gate and Lewiston Dams and emphasized increasing naturally produced stocks. The plan recognized the importance of protecting functioning subbasins where natural processes take precedence to human impacts causing severely degraded habitat conditions. Greater effort by managers to take

measures focusing on restoring favorable instream conditions that benefit multiple species and desired ecosystem function instead of single species, would help steelhead in the Klamath River. Creation of a basinwide restoration program involving stakeholders, managers, and policymakers from the upper and lower basins would be a good first step towards beginning to identify physical and hydrological processes and conditions that are necessary for conserving the aquatic communities of the Klamath basin.

Watersheds identified by McEwan and Jackson(1996) requiring stream restoration to benefit steelhead included the South Fork of the Trinity, Scott, and Shasta Rivers. Many subbasins of the Klamath River are predominantly within public ownership and have been designated key watersheds as part of the Northwest Forest Plan. Further steps will be necessary on private lands to restore functioning aquatic habitats and steelhead populations, particularly on tributaries with minimal federally protected reaches. Fisheries and watershed restoration opportunities will bring necessary monies into rural parts of the Klamath River basin where the economy can no longer depend on timber and mining dollars. Better hatchery management focused on conserving the *O. mykiss* gene pool, limiting interactions between wild and hatchery fish, and decreasing residualization of hatchery trout will benefit conservation of Klamath River steelhead. However, without increased flows and suitable water quality (ie: cool and sediment-free), the effectiveness of restoration will be marginalized (Wu et al., 2000). Great potential exists for steelhead to become a trophy fishery on the Klamath and this would bring additional local economic benefits to communities along the lower river and large subbasins. The importance of steelhead and a healthy Klamath River on the economies of Klamath basin communities has yet to be realized.

Managers would benefit from a better understanding of the physical and biological cues that lead to the diverse migration patterns of steelhead in the Klamath River. Uncertainty of the genetic relationships of half-pounder steelhead and redband trout to the different run-timings of steelhead will continue to disguise impacts of sports fisheries on certain “races” of steelhead on the Klamath River. Spawning escapement rates for wild steelhead are essential data for acknowledging the viability and persistence of individual subbasin populations. Many questions still exist in our understanding of steelhead on the Klamath River, and for an accurate assessment of these populations, monitoring and research of these fish must increase within the basin. Additional information regarding the genetics, ecology, and behavior of the remarkable Klamath

River steelhead will contribute to society's recognition of this river as a distinct and important aquatic system.

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