2. Steelhead Biology and Ecology

"[W]e must constantly keep in mind that variation, i.e., deviation from the norm, is one of the most marked characteristics of animal life. And of the vertebrates, the trout are among the most variable of all. Further, of the trout the steelhead is one of the most variable forms. . . . As an example, in the coastal streams most fish migrate in their first year, third, fourth, or fifth years, or do not migrate at all."

Leo Shapovalov and Alan C. Taft,
Life Histories of Steelhead Trout and Silver Salmon, 1954

2.1 SPECIES TAXONOMY AND LIFE HISTORY

Oncorhynchus mykiss is one of six Pacific salmon in the genus *Oncorhynchus* that are native to the North American coast. *O. mykiss*, along with other species of Pacific salmon exhibit an anadromous life history, which means that juveniles of the species undergo a physiological change that allows them to migrate to and mature in salt water before returning to their natal rivers or streams (*i.e.,* where they were originally spawned) to reproduce (Benke 2002, 1992).

Two principal steelhead recovery objectives are to increase abundance of steelhead and to preserve the expression of their diverse life history strategies. A schematic illustration of the various life history strategies that occur in the SCCCS Recovery Planning Area is shown in Figure 2-1. The figure is best understood by tracing the various pathways a freshwater juvenile may follow. Those pathways may remain entirely within freshwater ecosystems or transition between freshwater, estuarine and marine ecosystems. The use of these different environments confers advantages or disadvantages to the survival and reproductive success of the individual depending on the conditions of those environments. Even though neighboring watersheds can differ, a viable population of steelhead may contain individuals expressing many, if not all, the diverse life history strategies exhibited by the species. See discussion below in Section 2.6, South-Central California Coast Steelhead Freshwater Life Cycle Habitat Use.

Steelhead are a highly migratory species. Adult steelhead (Figure 2-2) spawn in coastal watersheds; their progeny (Figure 2-3) rear in freshwater or estuarine habitats prior to migrating to the sea. Within this basic life history pattern, the species exhibits a greater variation in the time and location spent at each life history stage than other Pacific salmon within the genus *Oncorhynchus* (Hayes *et al*. 2012, 2011, Quinn 2005, Hendry *et al.* 2004, Hendry and Stearns 2004).

The life cycle of steelhead generally involves rearing in freshwater for one to three years before migrating to the ocean and spending from one to four years maturing in the

marine environment before returning to spawn in freshwater. The ocean phase provides a reproductive advantage because individuals that feed and mature in the ocean grow substantially larger than native freshwater residents, and larger females produce proportionately more eggs; however, the freshwater phase provides protected rearing environment, relatively free of competition and predators. This life history strategy is referred to as "fluvial-anadromous". Out-migration to the ocean (*i.e.,* emigration) usually occurs in the late winter and spring. In some watersheds, juveniles may rear in a lagoon or estuary for several weeks or months prior to entering the ocean. The timing of emigration is influenced by a variety of factors such as photoperiod, streamflow, temperature, and breaching of the sandbar at the river's mouth. These out-migrating juveniles, termed smolts (Figure 2.4), live and grow to maturity in the ocean for one to four years before returning to freshwater to reproduce (Jacobs *et al.* 2011, Beakes *et al*. 2010, Borg 2010, Haro *et al*. 2009, Leder *et al.* 2006, Quinn 2005, Davies 1991, Groot and Margolis 1995, 1991, Martin 1995, Northcote 1958, Shapovalov and Taft 1954).

The ocean phase of steelhead has not been studied extensively, and is an important area for research. Though marine migration studies of other species of *Oncorhynchus* have encountered only isolated specimens of *O. mykiss* and as a result it is believed that the species does not generally congregate in large schools like other Pacific salmon of the genus *Oncorhynchus* (Grimes *et al*. 2007, Aydin *et al.* 2005, Burgner *et al*. 1992, 1980, Groot and Margolis 1991, Myers *et al.* 2000, 1996, Hartt and Bell 1985). Consequently, the movement patterns of steelhead at sea are poorly understood. Some anadromous salmonids have been found in coastal waters relatively close to their natal rivers, while others may range widely in the North Pacific (Quinn 2005, Quinn and Myers 2005, Myers *et al.* 1996, Groot and Margolis 1991, Burgner *et al*. 1992, 1980, McNeil and Himsworth 1980).

Returning adults may migrate from several to hundreds of miles upstream to reach their spawning grounds. The specific timing of spawning can vary by a month or more among streams within a region, occurring in winter and early spring, depending on factors such as run-off and sandbar breaching (Jacobs *et al.* 2011, Fukushima and Lesh 1998, Shapovalov and Taft 1954). Once they reach their spawning grounds, females use their caudal fin to excavate a nest (redd) in streambed gravels where they deposit their eggs. After fertilization by the male, the female covers the redd (often during construction of additional upstream redds) with a layer of gravel, where the embryos and alevins incubate within the gravel. Hatching time varies from about three weeks to two months depending on water temperature. The young fish emerge from the gravel two to six weeks after hatching. Adult steelhead do not necessarily die after spawning and may return to the ocean, sometimes repeating their spawning migration one or more times. It is rare for steelhead to spawn more than twice before dying, and most that do so are females (Moyle *et al. 2008*, Moyle 2002, Beacham and Murray 1993, 1990). The frequency of repeat spawning among SCCCS DPS populations has not been investigated, and it is therefore unknown how it may differ from other populations, or the role repeat spawning plays in the population dynamics in South-Central California. Additional details regarding this species' life history can be found in Barnett and Spence (2011), Quinn (2005), Bjornn and Reiser (1991), Barnhart (1986, 1991), and Shapovalov and Taft (1954).

This species may also display a non-anadromous life history pattern (*i.e.*, a "freshwater-resident" strategy). It has been common practice to refer to non-anadromous individuals that complete their entire life history cycle (incubating, hatching, rearing, maturing, reproducing, and dying) in freshwater as rainbow trout, while referring to those emigrating to and maturing in the ocean as steelhead. However, this terminology does not capture the complexity of the life history cycles exhibited by native *O. mykiss*. Individuals can complete their life history cycle completely in freshwater, or they can migrate to the ocean after one to three years, and spend two to four years in the marine environment before returning to freshwater rivers and streams to spawn.

Additionally, "rainbow trout" which have completed their life history cycle entirely in freshwater sometimes produce progeny which become anadromous and emigrate to the ocean and return as adults to spawn in freshwater. Conversely, it has also been shown that steelhead may produce progeny which complete their entire life cycle in freshwater. This switching of life history strategies has been demonstrated by studying the microchemistry of *O. mykiss* otoliths (small inner ear bones), where time spent in marine and fresh waters can effectively be tracked by the presence or absence of certain ocean-derived elements in the bone tissue (Zimmerman 2005). Zimmerman and Reeves (2000) used this technique to uncover occasional life history switching in *O. mykiss* populations in Oregon. *O. mykiss* in the SCCCS Recovery Planning Area have not yet been examined in this way, but various lines of evidence (*e.g.*, native inland resident fish in systems such as the upper Old Creek and Arroyo Grande Creek exhibiting smolting characteristics, river systems producing smolts with no regular access for adult steelhead) indicate that switching between freshwater and anadromous life cycles is likely occurring (M. Capelli, personal communication). The cues that trigger this phenomenon are unknown, but may be linked to environmental variation (Hayes *et al.* 2012, Satterthwaite *et al.* 2012, 2010, 2009, Sogard *et al.* 2011). For example, juvenile residency can be strongly influenced by the hydrologic cycle in South-Central California, where extended droughts can cause juveniles to become land-locked and therefore unable to reach the ocean (Boughton *et al*. 2009, 2006).

Lastly, there is a third type of life history strategy displayed by *O. mykiss* that is referred to as "lagoon-anadromous." Bond (2006), working at a study site in northern Santa Cruz County, has shown that each summer a fraction of juvenile *O. mykiss* over-summered in the estuary of their natal creek. Like South-Central California estuaries, this estuary was cut off from the ocean during the summer a sandbar, creating a seasonal lagoon. Bond (2006) showed that many juveniles grow fast enough after their first year of lagoon rearing to migrate to the ocean, and most enter the ocean at a larger size than the same year class fish rearing in freshwater habitats of the stream system. Larger size generally enhances survival in the ocean, and the lagoon-reared fish represented a large majority of the returning adult spawning population (Hayes *et al.* 2008, Bond 2006). Steelhead populations in the SCCCS Recovery Planning area have not been investigated to determine whether or to what extent they may exhibit this life history strategy, though estuarine conditions in many watersheds are similar those which have been investigated and documented in watersheds north of the SCCCS DPS.

Closely related to these life history strategies is steelhead use of a wide variety of habitats over their lifespan, including river mainstems, small montane tributaries, estuaries, and the ocean. Steelhead move between these habitats because each habitat supports only certain aspects of what the fish require to complete their life cycle. Populations frequently differ in the timing and habitats they use while pursuing the general pattern of the anadromous life cycle; these differences may reflect the evolutionary response of populations to environmental opportunities, subject to a variety of biological constraints that are also a product of evolution.

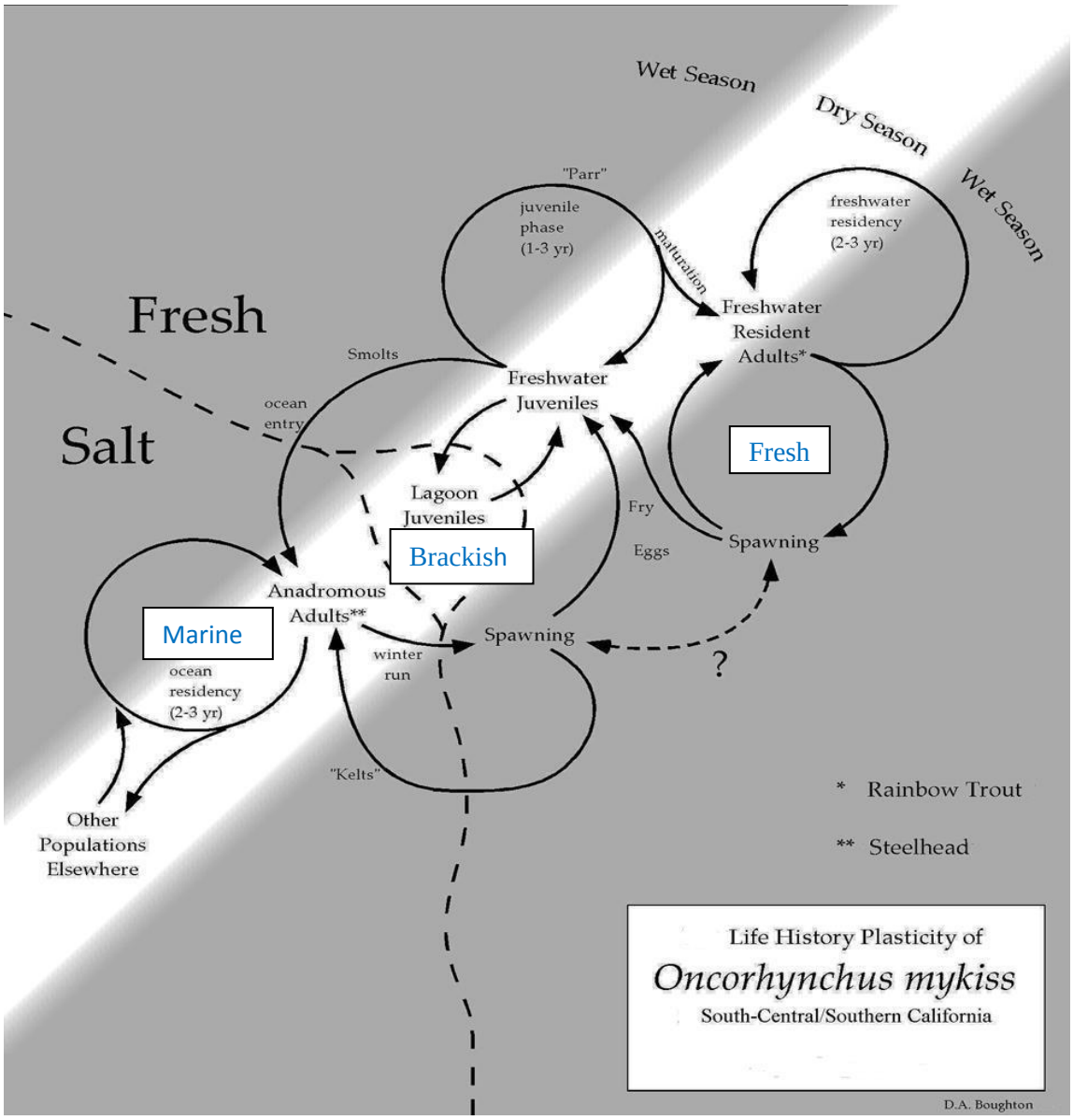

Figure 2-1. Summary of the various life history strategies exhibited by South-Central California Coast *O. mykiss* and the life stage specific terminology.

Within each of the three basic life history strategies (fluvial-anadromous, freshwater-resident, and lagoon-anadromous), there is additional variation, including examples of finer-scale habitat switching, such as multiple movements between lagoon and freshwater habitats in the course of a single

summer in response to fluctuating habitat conditions; and also so-called "adfluvial" populations that inhabit freshwater reservoirs but spawn in tributary creeks (Hayes *et al.* 2012, 2011, 2008, M. Capelli, personal communication).

Figure 2-2. Adult Steelhead (*O. mykiss)* (*c.* 75 cm), Uvas Creek, Pajaro River, Santa Clara County, 2012.

Figure 2-3. Juvenile *O. mykiss* (*c.* 10 cm), Trout Creek, Salinas River, Monterey County, 2008. (Courtesy Jenna Voss)

Figure 2-4. Steelhead smolts (*c.* 19 cm), Arroyo Seco, Salinas River, Monterey County, 2011 (Courtesy Monterey County Water Resources Agency)

2.2 SPECIES FRESHWATER DISTRIBUTION AND POPULATION STRUCTURE

Differences between the historical and current distributions of South-Central California Coast steelhead illustrate their present threatened status. Many anadromous populations have become reduced to critically low levels or extirpated, *e.g.,* in the Salinas River and in the southern extent of their range (Boughton *et al.* 2006, 2005, Boughton and Fish 2003, Augerot 2005). Individual anadromous populations within this SCCCS Recovery Planning Area have been severely reduced or in some cases extirpated (Table 2-1, Figure 2-5). Some smaller watersheds may have originally supported only sporadic steelhead runs, or intermittent native resident populations that experienced repeated local extinctions and recolonizations by anadromous immigrants in dry and wet cycles, respectively. This aspect of the freshwater distribution and population structure of *O. mykiss* has not been extensively studied, and as a result is not well understood (Boughton *et al*. 2006).

NMFS conducted an extensive *O. mykiss* population survey (targeted primarily at juveniles) in 2002 of most of the coastal watersheds within the South-Central California Coast Steelhead (SCCCS) Recovery Planning Area (Boughton and Fish 2003). Of the 39 watersheds in which steelhead were known to have occurred historically, virtually all were still occupied by either native resident *O. mykiss* or steelhead. One of these watersheds was considered unoccupied by steelhead because it was dry (Old Creek), and one was considered unoccupied because the survey found no current evidence of *O. mykiss* (Cayucos Creek). However, *O. mykiss* have subsequently been observed in both of these watersheds (M. Capelli, personal communication). (Table 2-1, Figure 2-5).

One of the objectives of this Recovery Plan is to maintain the current distribution of steelhead and restore distribution to a variety of previously occupied areas. Reduced flow and fish-passage barriers (and therefore opportunities to migrate) appear to have played a large role in watershed-wide reductions or extirpations of SCCCS steelhead; however, in many cases, ancestors of sea-run steelhead continue to persist as native resident populations above barriers in these same stream systems, and in some cases produce progeny that emigrate downstream, past the barriers to the ocean as smolts. In an investigation of the contraction of the southern range of California steelhead limit of *O. mykiss*, it was found that the majority (68%) of anadromous population extirpations were associated with anthropogenic barriers which restricted the use of upstream habitats for spawning and rearing by the anadromous form of *O. mykiss.* Between 58% and 65% of these stream systems maintain *O. mykiss* populations, either above or below the anthropogenic barriers (Boughton *et al.* 2005). Land use and water management practices, in combination with anthropogenic barriers to anadromy, have also contributed significantly to the reduction in steelhead distribution, particularly in mainstem habitats such as the Pajaro and Salinas Rivers in the Interior Coast Range BPG, and Pismo and Arroyo Grande Creeks in the Luis Obispo Terrace Biogeographic BPG.

These resident populations could include fish that are considered naturally persistent residents, descendants of steelhead that have been blocked from downstream emigration by barriers (including irregular or inadequate flows to the ocean) and have been forced to adopt a resident life cycle strategy (*i.e.*, "residualized" populations), or in some cases perhaps progeny of stocked *O. mykiss* found above barriers to steelhead migration (Boughton *et al.* 2005).

Table 2-1. South-Central California Coast watersheds historically occupied by populations of steelhead (listed from north to south). Several watersheds with historical populations now have barriers that block migration to portions of the watershed (modified after Boughton *et al.* 2006).[1]

WATERSHED	EXTANT?
Pajaro River	Yes
Salinas River	Yes
Carmel River	Yes
San Jose Creek	Yes
Malpaso Creek[2]	Yes
Garrapata Creek	Yes
Rocky Creek	Yes
Bixby Creek	Yes
Little Sur River	Yes
Big Sur River	Yes
Partington Creek	Yes
Big Creek	Yes
Vicente Creek[2]	Yes
Mill Creek	Yes
Prewitt Creek	Yes
Plaskett Creek	Yes
Willow Creek - Monterey	Yes
Alder Creek	Yes
Villa Creek Monterey	Yes
Salmon Creek	Yes
San Carpoforo Creek	Yes
Arroyo de la Cruz	Yes
Little Pico Creek	Yes
Pico Creek	Yes
San Simeon Creek	Yes
Santa Rosa Creek	Yes
Villa Creek – SLO	Yes
Cayucos Creek	Negative obs.[3]
Old Creek	Dry[4]
Toro Creek	Yes
Morro Creek	Yes
Chorro Creek	Yes
Los Osos Creek[2]	Yes
Islay Creek	Yes
Coon Creek	Yes
Diablo Canyon	Yes
San Luis Obispo Creek	Yes
Pismo Creek	Yes
Arroyo Grande Creek	Yes

[1] A watershed includes all of the tributaries and main-stem which share a common outlet to the ocean.
[2] Data from: Becker, *et al. 2008,* Boughton *et al. (2005),* Sleeper *(2002),* Titus *et al. (2010), M. Capelli, NOAA-NMFS, personal communication (2007-2012),* M. Larson, *CDFW*, personal communication (2007-2011).
[3] "Negative obs." means juveniles were not observed during a spot-check of best-occurring summer habitat in 2002; however, such spot observations should not be interpreted as definitive determinants of absence of *O. mykiss*. Old Creek has an adfluvial population above of *O. mykiss* above Whale Rock Reservoir, and adult steelhead have been reported in Old Creek below Whale Rock reservoir as recently as 1998 (National Marine Fisheries Service 1998).
[4] "Dry" indicates the stream had no discharge in anadromous reaches during the summer of 2002; because of the high variability of the hydrologic regime, such spot-checks do not necessarily reflect the potential suitability of such reaches for migration, spawning, or rearing of *O. mykiss*.; however, such an assumption may not be warranted since rearing juvenile steelhead can make use of ephemeral reaches (Boughton *et al. 2009).* See Boughton *et al. (2005)*.

Several reports describe the historical steelhead populations of the SCCCS Recovery Planning Area (Boughton *et al*. 2005, Boughton and Goslin 2006, Boughton *et al*. 2006). Using this information, the TRT proposed a structure for steelhead of the SCCCS Recovery Planning Area composed of four BPGs (Table 2-2). The division of steelhead populations into BPGs followed two basic rules: First, populations were sorted into a coastal super-group and an inland super-group, based on whether or not the most potential freshwater habitats lay on an ocean-facing watershed subject to marine-based climate inversion and orographic (*i.e.,* lifting) precipitation from offshore weather systems. Second, within the coastal and inland super-groups, populations were sorted into groups defined by contiguous areas with broadly similar physical geography and hydrology. The combinations of these physical characteristics represent differing natural selective regimes for the steelhead populations occurring in the individual watersheds. These differing physical characteristics have led to life history and genetic adaptations that enable the populations to persist in the widely varying and distinctive habitat regimes represented by the four BPGs. The purpose of delineating the BPGs is to guide recovery efforts across the SCCCS Recovery Planning Area to ensure the preservation and recovery of the range of natural diversity of the SCCCS Recovery Planning Area. From north to south, these BPGs are known as: Interior Coast Range, Carmel River, Big Sur Coast, and San Luis Obispo Terrace (Figure 2-5).

Table 2-2. Ecological characteristics of BPGs in the South-Central California Coast Steelhead Recovery Planning Area (originally Table 4 in Boughton *et al*. 2007b).

South-Central California Coast Steelhead ESU/DPS					
	Ecological Characteristics				
Population Group	**Migration Corridor**	**Migration reliability**[1]	**Summer Climate Refugia**[1]	**Intermittent Streams**	**Winter Precipitation**
Interior Coast Range[2]	Long alluvial valleys	Moderate/Low	Montane	Many	Mostly <75 cm (highlands)[3]
Carmel River	Medium Valley	Moderate	Marine+ Montane	Some	30 – 90 cm3
Big Sur Coast	Short, steep	High	Marine	Few	75 – 135 cm
San Luis Obispo Terrace	Coastal Terrace	Moderate	Marine +Montane	Some	60 – 90 cm (highlands)

[1] Inferred reliability under an un-managed flow regime, that is conditions prior to European settlement.
[2] The migration corridor of the mainstem crosses alluvial valleys, which renders the migration of adults, and especially smolts, problematic, particularly in dry years - while much of its best freshwater habitat currently occurs in the redwood forest at the southern end of the Santa Cruz Mountains – ecologically quite different from the chaparral watersheds of the other east-slope populations.
[3] Except in the Santa Cruz Mountains of the Pajaro system, which are wetter.

In characterizing the historical, pre-European settlement population structure of the SCCCS Recovery Planning Area, the TRT: 1) identified the original anadromous *O. mykiss* populations and attempted to determine which ones were still extant; 2) delineated the potential unimpaired geographic extent of each population on a watershed scale; 3) estimated the relative potential viability of each population in its (hypothetical) unimpaired state; and 4) assessed the potential demographic independence of each population in its (hypothetical) unimpaired state (Boughton and Goslin 2006, Boughton *et al.* 2006, Helmbrecht and Boughton 2005). This analysis entailed a consideration of available historical and current data on distribution and abundance of *O. mykiss*, new genetic data, landscape data, climate data, and stream discharge data. However, data limitations, particularly a lack of long-term adult steelhead run-size data, prevented the TRT from providing definitive characterizations of pre-European or current anadromous *O. mykiss* populations, including the geographic extent of individual populations, their intrinsic viability, or demographic independence. For a discussion of the constraints imposed by limited relevant data see Boughton and Goslin (2006) and Boughton *et al*. (2006). See Appendix B, Watershed Intrinsic Potential Rankings, Appendix C, Composition of SCCCS Recovery Planning Area BPGs.

The separate watersheds comprising each BPG are generally considered as individual *O. mykiss* populations (*i.e.,* one watershed = one population of steelhead). Single BPGs encompass multiple watersheds and multiple *O. mykiss* populations. However, many watersheds in the Big Sur Coast and San Luis Obispo Terrace BPGs are relatively small, and may be capable of supporting only small steelhead runs. The basis for the persistence of steelhead populations in these small watersheds is uncertain. The TRT proposed that at least three scenarios (not necessarily mutually exclusive) are plausible for explaining the persistence of these smaller populations (Boughton *et al.* 2007b):

1. Some of the populations in the coastal BPGs, though small, may be exceptionally stable and their continued presence may depend in part on steelhead dispersal between neighboring watersheds (an independent population supporting one or more dependent populations, thus forming a metapopulation). See Appendix A for a definition of an independent population.
2. Adult dispersal between neighboring watersheds within a coastal BPG may occur frequently enough to knit together the steelhead in individual watersheds into a small number of "trans-watershed" populations (an independent population comprised of the fish from two or more neighboring streams, thus forming a metapopulation).
3. The populations in the smaller coastal watersheds (*e.g.,* in the Big Sur Coast and San Luis Obispo Terrace BPGs) may depend on occasional or frequent adult dispersal pulses from populations in the larger inland watersheds (*e.g.,* Interior Coast Range or Carmel River BPGs).

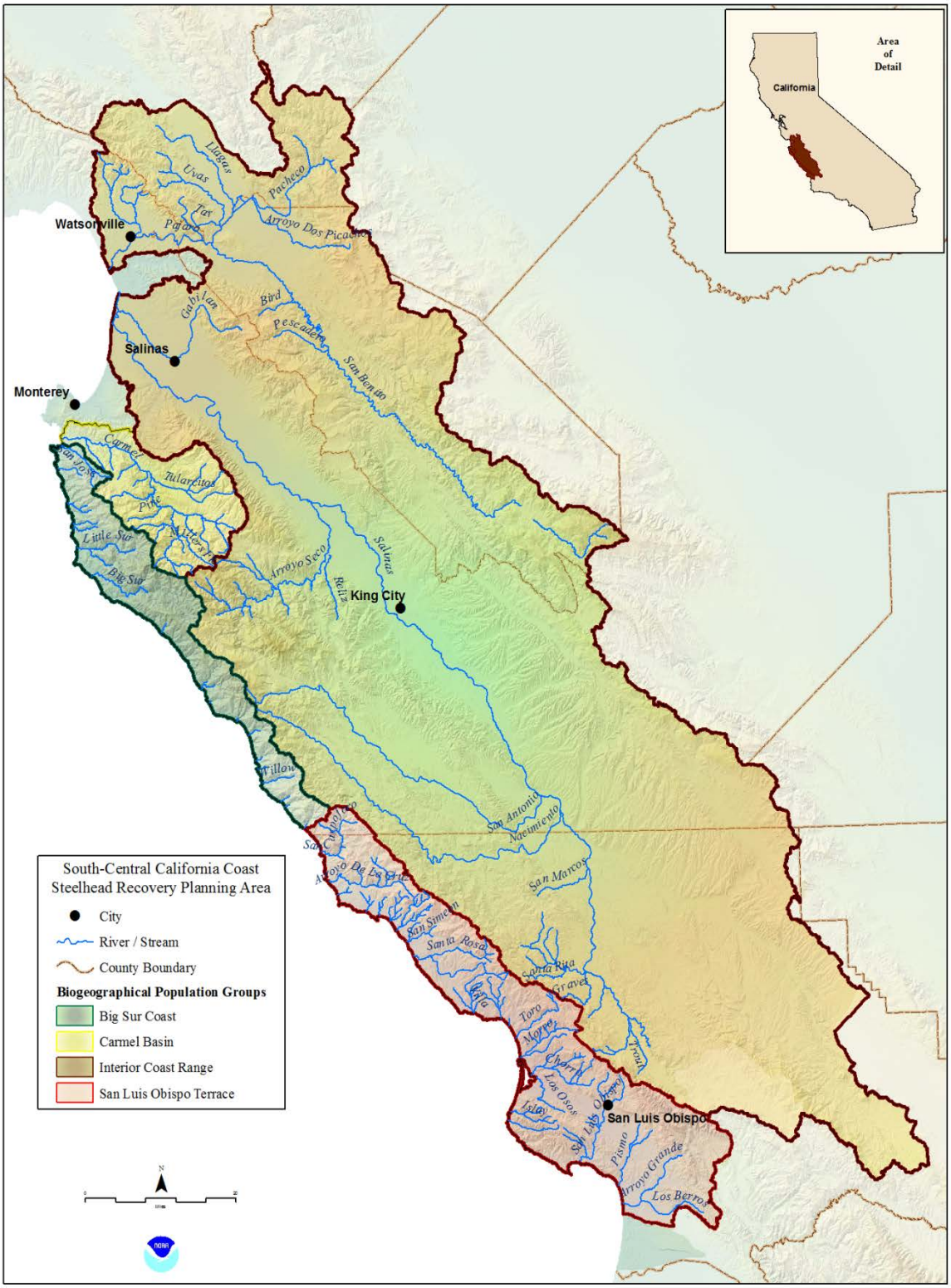

Figure 2-5. Biogeographic Population Groups (BPGs) in the South-Central California Coast Steelhead Recovery Planning Area (after Boughton *et al.* 2007b).

2.3 SPECIES ABUNDANCE

One of the recovery objectives in this recovery plan is to increase the abundance of steelhead, including the expression of all life history forms and strategies. The limited documentation on current abundance suggests the overall population in the SCCCS DPS is extremely small. Estimating the magnitude of the departure of the population from historical conditions is further hampered because the run size for most watersheds continues to be poorly characterized and major impacts leading to subsequent declines occurred prior to most modern fish investigations in the SCCCS DPS. The sporadic presence of steelhead in many watersheds in the SCCCS DPS further confounds assessment efforts.

The status of steelhead populations along the West Coast was assessed in 1996 by the NMFS Biological Review Team (BRT) (Busby *et al*. 1996). In 2002 NMFS conducted an extensive survey of the geographic distribution of *O. mykiss* within south-central and southern California (Boughton and Fish 2003). Of the 39 watersheds that historically supported anadromous runs, virtually all continue to be occupied by native *O. mykiss*, though most of the populations are at historically low levels.

As a follow-up West Coast Status review Good *et al*. (2005) reported three new significant pieces of information for the SCCCS DPS: 1) an updated time-series data set regarding adult spawner counts at San Clemente Dam on the Carmel River; 2) NMFS' 2002, assessment of the geographic distribution of *O. mykiss* within its historical range (see above); and 3) changes in harvest regulations for *O. mykiss*[1].

The status of the steelhead within California was subsequently reviewed by Helmbrecht and Boughton (2005), and again in 2011 (Williams *et al*. 2011). The following summarizes the findings from these status reviews:

The steelhead populations in this region have declined dramatically from estimated annual runs totaling 27,000 adults near the turn of the century to approximately 4,740 adults in 1965 to several thousand total adults, with a large degree of inter-annual variability (Busby *et al*. 1996, Good *et al*. 2005, Williams *et al.* 2011). However, this run-size estimate is based on information from only five major watersheds with steelhead (Pajaro, Salinas, Carmel, Little Sur, and Big Sur Rivers) located in the northern portion of the SCCCS Recovery Planning Area. Run-size estimates from coastal and inland watersheds south of the Big Sur have not been estimated or recorded. Watersheds in the Big Sur Coast BPG have had relatively less disturbance than other BPGs and have most likely experienced less dramatic declines, while those within the San Luis Obispo Terrace BPG with a larger population and more extensive watershed developed, are likely to have experienced more dramatic declines (Boughton and Fish 2003, Boughton *et al.* 2005). Additionally, available run-size estimates represent only average annual estimates, and do not describe the wide annual variation in run-size that would be expected in a region with a highly variable climate and habitat conditions.

The BRT further noted that information was available to compute a trend for adult escapement for only one population within the DPS – the Carmel River above San Clemente Dam. These Carmel River data indicate a significant decline of 22 percent per year from 1963 to 1993, with an average five-year adult count of only 16 adult spawners recorded at San Clemente Dam for these years (Busby *et al*. 1996, Good *et al*. 2005; see also, Monterey County Peninsula Water Management District 1991-2013, and Chapter 10, Carmel River Basin Biogeographic Population Group).

While -the BRT believed that general trends in the SCCCS DPS could be inferred from this

[1] Subsequent to these investigations additional historical records of *O. mykiss* have been identified (see Becker & Reining 2008).

early-1960 to early-1990 data, they also noted the relationship between anadromous and non-anadromous *O. mykiss*, including possibly residualized populations upstream of impassible dams, while unclear, was likely to be important in the management of this species years (Busby *et al*. 1996, Good *et al*. 2005).

Data collected from the Carmel River since the 2005, BRT status review indicates the abundance of anadromous *O. mykiss* spawners in the Carmel River has increased since the 1987-1992 drought, but that the average run-size has decreased since the early 1960s. Continuous data have been collected for the period from 1988 through 2012 (however these counts are incomplete because fish spawning below San Clemente Dam are not included). Counts from the start of the 1988-2002 period included three consecutive years when no adult steelhead were detected (1988, 1989, and 1990). A pen rearing program was established for juvenile *O. mykiss* using facilities at the Monterey Bay Salmon and Trout Project and the Granite Canyon Marine Lab; fry from the artificially spawned adults were released above San Clemente Dam in the early 1990's. Steelhead counts increased from a single adult reported in 1991, to 775 adults reported in 1997 (see additional discussion in Chapter 10, Section 10.3). The BRT noted that the rapid increase in the number of returning adult anadromous *O. mykiss* spawners to the Carmel River could be attributed to a combination of factors, including improved freshwater conditions, improved resilience of populations, high dispersal rates, or ability of native resident *O. mykiss* to produce smolts. The BRT also noted that while some component of the increase is probably due to improved ocean conditions during this period, it should not be assumed that comparable increases have occurred in other watersheds for the SCCCS DPS.

Recent trends, based on the reported annual count (May 2009) of adult steelhead show a significant decrease: 95 fish at San Clemente Dam, and 21 fish at Los Padres Dam. These counts compare to average counts of 429 and 129 fish at San Clemente Dam and Los Padres Dam, respectively, since the end of the last drought in 1991 (Williams *et al.* 2011). The most recent (2012-2013) counts for the Carmel River indicate 452 adults at the San Clemente Dam, and 204 adults at the Los Padres Dam, and reflect the effects of the most recent drought years 2007-2009 (Monterey Peninsula Water Management District 2012). Since the listing of South-Central California steelhead, there have been some increased efforts to periodically document observations of adults as well as more systematic monitoring on a few watersheds with recently constructed fish passage facilities or active restoration efforts. For example, there are fish trapping and monitoring efforts on the Pajaro, lower Salinas River and the Carmel Rivers.

Finally, the BRT reported that the California Department of Fish and Wildlife (CDFW) has prohibited sport harvest in the ocean (incidental ocean harvest is rare), and imposes significant angling restrictions within the anadromous waters of the SCCCS DPS (*e.g.*, restrictions on timing, location, and gear used for angling). However, CDFW continues to allow summer trout fishing in significant parts of the Salinas River system (*i.e.*, upper Arroyo Seco, Nacimiento River above barriers, upper Salinas River, Salmon Creek, and the San Benito River in the Pajaro River system, with zero bag limits); additionally, there is currently take allowed of hatchery fish in some systems, including the Pajaro River.[2] While some of these areas are above impassable fish passage barriers, and currently do not provide accessible spawning and rearing habitat for anadromous *O. mykiss*, these upper watershed do have the potential to produce smolts from native resident *O. mykiss* that have the potential to contribute to the anadromous population if they can successively emigrate out of the watershed to the ocean.

[2] Angling regulations are subject to periodic modification. The CDFW's annual Sport Fishing Regulations should be consulted for current restrictions on angling for *O. mykiss* (both resident and anadromous).

However, the San Benito River flows on the east side of the Gabilan Range, and is considerably drier, with limited shading, and limited potential to provide over-summering habitat for rearing juvenile steelhead. Additionally, a few other creeks have summer catch-and-release regulations designed to minimize impacts to native *O. mykiss* from angling activities. While there is indirect evidence that such fishing pressure has resulted in minimal or no mortality to native *O. mykiss*, the reduction in risk to listed *O. mykiss* cannot be estimated quantitatively from the existing data because the natural abundance of *O. mykiss* is not quantitatively known.

In summary, while a majority of watersheds historically supporting *O. mykiss* are still occupied (often with individuals currently able to express only a resident life history strategy), steelhead run sizes are sharply reduced. The three watersheds most likely exhibiting the largest annual anadromous runs (*i.e.*, Pajaro, Salinas, Carmel) have experienced declines in adult run size of 90 percent or more (Busby *et al*. 1996, Good *et al*. 2005, Williams *et al.* 2011). Present population trends within individual watersheds that continue to support steelhead runs are generally unknown, and may vary widely between water-years. Available run-size estimates for all watersheds represent only average annual estimates that likely include wide inter-annual variations expected in a region with a highly variable climate. However, these averages are extremely small, and raise the question of how such small runs of anadromous fish persist (potentially either by dispersal from some source population, and/or by consistent production of smolts by local populations of freshwater, non-anadromous *O. mykiss)*. The consensus of the most recent BRT assessment was that the status of the SCCCS DPS has not changed appreciably in either direction since publication of the initial status review (Busby *et al.* 1996), and that SCCCS DPS is still in danger of extinction and the threatened status has not changed (Williams *et al*. 2011).

2.4 SPECIES GENETIC STRUCTURE AND DIVERSITY

A recovery objective for steelhead is to restore and conserve genetic diversity and interchange of genetic material between and within populations. Since the late 1990s, a number of genetic studies have been conducted to elucidate the structure of *O. mykiss* populations within the SCCCS Recovery Planning Area (Martìnez, *et al.* 2011, Clemento *et al.* 2009, Pearse and Garza 2008, Girman and Garza 2006, Nielsen 1999, 1994, Nielsen *et al.* 2001, 1997, 1994c). These studies have provided insights into the historical distribution of the species, as well as the potential influence of past (and current) stocking practices within the watersheds historically occupied by native *O. mykiss*. Berg and Gall (1988) surveyed steelhead populations throughout California. They discovered considerable variability among California populations, but did not discern a clear geographic pattern to the variation. Busby *et al.* (1996) also reported a high level of genetic variability in California coastal populations, including four from the SCCCS Recovery Planning Area. Busby *et al.* (1996) also reported an allozyme allele fixed in some populations but entirely absent in others, which is unprecedented in anadromous salmonids, except when comparing populations at the extreme ends of their ranges.

Sundermeyer (1999) examined five microsatellite loci from fourteen populations of *O. mykiss* collected from 11 tributaries (including several of the larger tributaries from both the upper and lower reaches) in the Pajaro River. Most of these populations were found to be closely related to two populations from the San Lorenzo River which is immediately north but outside of the SCCCS Recovery Planning Area, and the source of hatchery-reared *O. mykiss* planted in the Pajaro River system. Native non-anadromous *O. mykiss* above barriers to upstream migration were less closely related to the San Lorenzo populations than those *O. mykiss* located below barriers. The *O. mykiss*

from four locations above barriers to upstream migration (Llagas, upper Uvas, Bodfish, and Dos Picachos Creeks) were the mostly distantly related from the San Lorenzo River fish, and from each other, a genetic reflection of their relative physical isolation.

Recent genetic investigations have shed light on the relationship between steelhead and the *O. mykiss* above barriers within the SCCCS Recovery Planning Area. Girman and Garza (2006) and Clemento *et al.* (2009) reported above-barrier *O. mykiss* were more closely associated with below-barrier populations than to populations from other watersheds; also, that they were more closely related to the steelhead below the barrier than to any other geographically proximate populations. In addition, their results supported the idea that planted hatchery fish from other watersheds have had no detectable influence on the genetics of above-barrier populations. These results indicate that the above-barrier populations are not the descendants of hatchery fish. They are most likely the descendants of contiguous *O. mykiss* populations – where most of these areas have historical accounts of steelhead populations prior to construction of the barriers (Becker *et al.* 2008, Swift *et al.* 1993, Benke 2002, 1992, Hubbs 1946, Jordan and Gilbert 1881).

While the fish that remain above barriers do not have an opportunity to interbreed with adult steelhead, they can, and in some cases do, produce progeny that emigrate downstream past the barriers to the ocean as smolts and return as adults, and thus have the potential to contribute to the persistence and therefore the viability of the anadromous population.

2.5 HABITAT CHARACTERISTICS OF THE SOUTH-CENTRAL CALIFORNIA COAST STEELHEAD RECOVERY PLANNING AREA

The major steelhead watersheds in the SCCCS Recovery Planning Area include the Pajaro, Salinas, Carmel, Little and Big Sur Rivers (Good *et al*. 2005, Busby *et al*. 1996,). South of the Big Sur Coast, several major drainages and a number of smaller streams also support runs of anadromous *O. mykiss* (of unknown size and frequency); these include the San Carpoforo, Arroyo de la Cruz, Pico and Little Pico, San Simeon, Santa Rosa, San Luis Obispo, Pismo, and Arroyo Grande Creeks (Titus *et al*. 2010, Becker *et al.* 2008, Swift *et al.* 1993).

Significant portions of the upper watersheds within the SCCCS Recovery Planning Area are contained within the Northern District of the Los Padres National Forest. This forest is managed primarily for water production and recreation, with limited grazing and oil, gas, and mineral production (United States Forest Service, 2005a, 2005b, 2004, Berg *et al*. 2004, Stephenson and Calcarone 1999). Additionally, a significant amount of land within the SCCCS Recovery Planning Area is protected within military installations, and in the southern portions, within large scale conservation easements. Urban development is centered in coastal areas and inland valleys, with the most expansive and densest urban development located within the Pajaro, Carmel, and Salinas River valleys, and in southern San Luis Obispo County (Kier Associates and National Marine Fisheries Service 2008a, 2008b, Hunt & Associates 2008a, Hornbeck 1983, Lantis *et al*. 1981, Lockmann 1981).

The SCCCS Recovery Planning Area is comprised of geologically young mountainous topography with a number of inland valleys and coastal terraces. The geomorphology (*i.e.,* the shape and composition of the land surface) is strongly influenced by tectonic activity and various other signs of stress (*e.g.*, highly folded and faulted rocks of varying types), including metamorphic formations (*i.e.,* rocks that have changed under pressure and heat over time). The Coast Ranges (consisting of the Diablo, Temblor, and Santa Lucia Mountains) are made up of sedimentary formations (*i.e.*, sediment deposited out of the air, ice, and/or water flows), granitic formations (*i.e.,* formed from cooled

magma), and the widespread Franciscan formation (comprised of sandstones derived from erosion of volcanic highlands into deep marine basins). The legacy of tectonic activity and other physical stresses has created the steep slopes and unconsolidated rock formations that characterize this region. These geological factors combined with an active, annual fire-cycle and intense winter storms have created spatially complex and frequently unstable river and stream habitats to which anadromous fishes and other aquatic species have adapted through evolutionary processes (Boughton *et al*. 2006, Sugihara *et al.* 2006, Norris and Webb 1990, Faber *et al*. 1989, Endler 1986, 1977, Felton 1965, Mayer *et al.* 1988).

The SCCCS Recovery Planning Area is characterized by ten broad native terrestrial plant communities within the Californian floristic province: Estuarine Wetlands, Beach and Dunes, Riparian Forests, Coastal Prairie, Coastal Sage Scrub, Oak Woodlands, Chaparral, Valley Grasslands, Vernal Pools, and South Central California Conifer Forests (Barbour *et al*. 2007, Holland 1996, Ferren *et al*. 1995, Sawyer and Keeler-Wolf 1995, Baldwin *et al.* 2012). Upland areas of the northern portion of the SCCCS Recovery Planning Area are dominated by a mix of Chaparral, Valley Grasslands, Oak Woodlands, and South-Central California Conifer Forests. Upland areas of the southern portion of the SCCCS Recovery Planning Area are dominated by South-Central Coastal Scrub, Valley Grassland, Oak Woodland, and South-Central California Conifer Forests. Both of these upland areas are subject to catastrophic wildfires (Sugihara *et al.* 2006, Davis and Borchert 2006). Riparian forests consist of deciduous species. Large segments of the valley grasslands and riparian forests have been converted for agricultural, residential, and a variety of other commercial land-uses (Berg *et al*. 2004, California Department of Fish and Wildlife 2003, Stephenson and Calcarone 1999, Holland 1996, Kreissman 1991, Mayer and Laundenslayer 1988, Warner and Hendrix 1984, Capelli and Stanley 1984). However, the interior uplands within the U.S. National Forest are largely undeveloped, as are large portions of state parks, military bases, and reserves on non-federal lands.

The climate in the California floristic province is Mediterranean, with long dry summers and short, sometimes intense cyclonic winter storms. Rainfall is restricted almost exclusively to the late fall, winter months and early spring months (November through May). The California floristic province is subject to an El Niño/La Niña weather cycle which can significantly affect winter precipitation, causing highly variable rainfall between years. Additionally, there is wide disparity between winter rainfall from north to south, as well as between coastal plains and inland mountainous areas. Mean annual precipitation ranges along the coast (north to south) from 32 to 24 centimeters (cm) per year, with larger variations (24-90 cm/year) from the coast to inland areas (west to east) due to the orographic effects of the various mountain ranges. Fog along the coastal areas is typical in late spring and summer, extending inland along coastal reaches with valleys extending into the interior. This fog has been shown to moderate conditions for rearing *O. mykiss* in these lower, coastal reaches. Seasonally high, down slope winds during the early fall and winter are warm and dry and can exacerbate brush or forest fires, especially under drought conditions (Mastrandrea *et al*. 2009, Miller and Schlegel 2006a, 2006b, Haston and Michaelsen 1997, Philander 1990, Leipper 1994, Stine 1994, Ryan and Burch 1992, Hornbeck 1983, Karl 1979, Felton 1965).

River flows vary greatly between seasons, and can be highly "flashy" (rapidly increased flows with high volume but short duration) during the winter season, changing by several orders of magnitude over a few hours in response to winter storms. Snow accumulation is generally very small and of extremely short duration, and does not contribute significantly to peak run-off. Baseflows in some river reaches can be influenced significantly by groundwater stored

and transported through faults and fractured rock formations. Many rivers and streams naturally exhibit interrupted baseflow patterns (alternating channel reaches with and without perennial surface flow) controlled by geological formations, and a strongly seasonal precipitation pattern characteristic of a Mediterranean climate. Water temperatures are generally highest during summer months, but can be locally controlled by springs, seeps, and rising groundwater, creating micro-aquatic conditions suitable for salmonids (Sloat and Osterback 2013, Atkinson *et al.* 2011, Boughton, *et al*. 2007a, Faber *et al.* 1989, Mount 1995, Jacobs *et al.* 1993, Reid and Wood 1976).

Within the SCCCS Recovery Planning Area steelhead habitat occurs in chaparral ecosystems which differ in significant ways from steelhead habitats found in snow-fed and/or conifer-covered ecosystems in the Sierra Nevada or the North Coast of California. From the perspective of steelhead ecology, it is useful to divide these chaparral ecosystems which dominate the SCCCS Recovery Planning Area into two categories: coastal watersheds draining directly westward into the ocean, and inland watersheds set back from the coast, often separated from it by extensive mountain ranges. The inland watersheds are relatively few, large, and have a continental climate whereas the coastal watersheds tend to be small, numerous and have a heavily marine-influenced climate. These differences (and others that result from them, such as the reliability of suitable summer temperatures) likely impose different sorts of selective regimes/limiting factors on steelhead populations such as those in the Pajaro and Salinas Rivers. Coastal watersheds are often characterized by a "mountain-terrace" system, where a broad coastal terrace is backed by a steeper mountain range. These types of areas occur along the southern coast of San Luis Obispo County. The mountains harvest orographic rain from incoming storm systems, creating flashy streamflows that carve out well-shaded step-pool systems in the uplands, and braided gravel-bed streams and pool-riffle systems in the terraces. They also produce seasonal lagoons at the interface of the stream with the ocean. Each of these parts of the stream system produces suitable habitat for a particular life stage of steelhead. Due to the movement of water, sediment and fish, stream systems function as integrated wholes with steelhead acting as effective strategists using the entire suite of resources provided them by the coastal and inland watersheds of the SCCCS Recovery Planning Area.

2.6 SOUTH-CENTRAL CALIFORNIA COAST STEELHEAD FRESHWATER LIFE CYCLE HABITAT USE

Steelhead spend much of their life in the ocean, but must enter freshwater to reproduce. Dominant patterns in the region are one or two years in freshwater and one to two years in the ocean before returning to spawn in freshwater. Understanding the interaction between steelhead and their freshwater habitats is critical for effective steelhead recovery and management. Many of the naturally limiting factors (which are part of the natural selective regime) described in this section that affect the growth and survival of juvenile steelhead in their freshwater phase are exacerbated by anthropogenic modification of freshwater habitats and/or watershed processes that create and sustain these habitats. The freshwater habitats used by steelhead within the SCCCS Recovery Planning Area occur in two types of watersheds featuring distinctly different environmental regimes. One type is the series of rivers that flow through hot inland valleys and cut through coastal ranges to the sea, where the lowland coastal plain portion of these watersheds present natural ecological constraints to fish passage. In the Pajaro River system, the lower mainstem and the lowland reaches of Llagas, Uvas, and Salsipuedes/Corralitos Creeks, are subject to significant streambed percolation into the aquifers, and reaches have a tendency to dry up in the spring, or even between storms in dry

winters, with extended periods between storms. The Salinas River and the lower reaches of one of its major tributaries, the Arroyo Seco, also percolates large volumes of surface flow and goes seasonally dry, thus inhibiting fish passage of both adults and smolts. These watersheds have warm seasonal climates and are in coastal rain shadows. The other freshwater habitats are the small, steep coastal watersheds with higher rainfall, lower air temperatures, and a greater proportion of perennial streams (Boughton *et al*. 2006, Boughton *et al.* 2007b).

The *O. mykiss* life cycle can be conceptualized as a biological network in which environmental opportunities can be represented as a set of parallel and serial linkages:

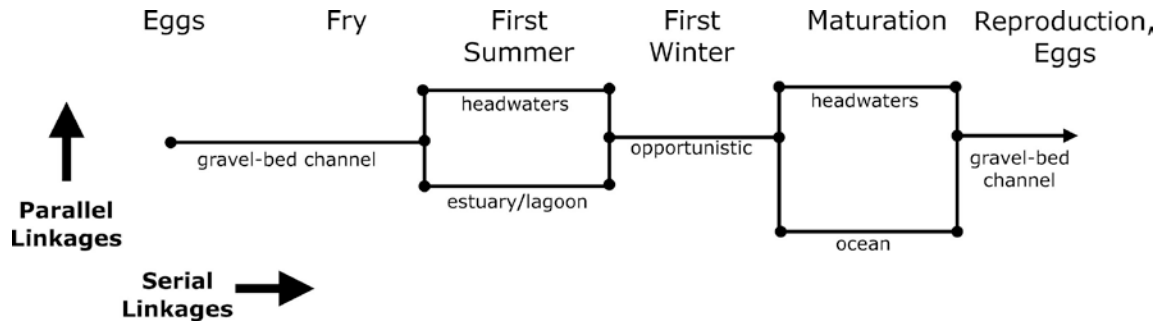

Figure 2-6. South-Central California Coast *O. mykiss* Life Cycle Habitat Linkages (Schwing *et al.* 2010, after Boughton).

The sequence of habitats required for the fish to complete the egg-to-egg life cycle involves a series of linkages, the loss of any of which prevents the completion of the life cycle. While serial linkages are a source of vulnerability, some of the linkages can be realized through alternative pathways: for example, over-summering in different sorts of thermal refugia, such as tributary headwaters or seasonal lagoons/estuaries next to the ocean; or maturation in freshwater versus the ocean. These alternative pathways in the network increase the resilience of the population to extirpation, because if one pathway fails in a particular year, some members of the population can still complete their life cycle by pursuing an alternative pathway.

The following provides a more detailed discussion of the freshwater life cycle phases of steelhead and the environmental factors that control the successful transition between freshwater life cycle phases prior to entering the ocean life cycle phase (Schwing, *et al.* 2010, after Boughton, *et al*. 2006).

Spawning Migration. Steelhead passage limitations arising from periodic drought (or longer term climate change) is one of the principal limiting factors affecting adult steelhead (Boughton *et al.* 2006). Steelhead are iteroparous (*i.e.,* can reproduce more than once), and, to realize the evolutionary benefits of repeat spawning, must have an opportunity to both enter and exit the stream system. The migration of steelhead into freshwater spawning and rearing streams is strongly associated with higher winter and spring flows which provide a continuous hydrological connection between the ocean and upstream spawning and rearing habitats. Some steelhead adults in this domain may remain in freshwater after spawning, and can become trapped in deep residual pools in

the summer (M. Capelli, personal communication). This sort of trapping is probably a function of the precise timing, duration, and magnitude of storms in a given winter. Periodic droughts further constrain migration opportunities during dry periods, and may have a bigger effect on repeat-spawning, which requires both an in- and out-migration opportunity in a given year, followed by an in-migration opportunity a year or two later. Finally, spawning efforts may be abrogated by one or more successive high flow events following spawning that erodes the spawning redds and exposes or flushes recently laid eggs out of the redd, exposing them to predation, or terminating the incubation process prematurely.

Initial Spring Feeding. The development and hatching of *O. mykiss* eggs is controlled by temperature and dissolved oxygen, which is itself influenced by flow rates, ambient air temperature, riparian cover, and groundwater input. Following the hatching and emergence from spawning gravels juvenile *O. mykiss* (fry) either stay near the redds from which they were hatched and establish territories, or disperse to favorable feeding areas (Boughton *et al.* 2009, Quinn 2005). Rainfall and conditions conducive to adult upstream migration and spawning are also conducive to initial rearing conditions for the first spring growth of juvenile steelhead. As flows drop later in the spring and summer, rearing fish may move out of initial rearing reaches, or may continue to reside in deeper pools, where they may be trapped between temporary dry reaches of stream channel until the following winter rains reconnect perennial reaches.

An increase in rearing temperatures, either as a result of inter-annual, seasonal variability or longer-term climatic changes will likely produce warmer conditions during early rearing. If temperatures stay below about 17° Celsius, a warming or an increase in week-scale variability of temperature can increase the growth rate of salmonids if food is abundant. However, warmer temperatures also increase metabolic demand and can reduce growth if food is limiting (Sloat and Osterback 2013, Boughton *et al*. 2007b, Smith and Li 1983, Brett 1971). Consequently, the effect of warmer conditions on growth is crucially dependent on per-capita food availability, which in turn depends on a host of other factors, such as primary productivity of the stream network, biomass of terrestrial insects caught in stream drift, and stream geomorphology as it affects the territorial dynamics of juvenile *O. mykiss*.

First Rearing Summer (unimpaired conditions). The hot, rain-free summers in the SCCC DPS require that juvenile *O. mykiss* occupy stream reaches which remain wetted and where temperatures do not exceed their thermal tolerance. Regionally, there are two alternative mechanisms that create thermal refugia: the temperature lapse rate (*i.e.,* the decrease in temperature with an increase in altitude), which maintains cool, montane uplands, and the ocean heat sink, which maintains cool conditions proximate to the coast. In many small coastal watersheds these two mechanisms merge geographically, whereas in inland watersheds the operation of these mechanisms may be separated by a long stretch of dry or warm channel that creates a summer-long barrier to movement. Numerous tributaries draining various mountain ranges provide a high level of redundancy of rearing refugia in the montane thermal refugia.

Probably as important as air temperature in maintaining cool water temperatures during the summer is reduced solar incidence which is often the single biggest source of heat flux into a stream (Hannah *et al.* 2008, Evans *et al*. 1998). Wind effects can also be significant, particularly in estuaries (Bogan *et al*. 2004, 2003). In coastal areas, fog and onshore winds provide shade and cooling wind, respectively. In the montane refugia, the closed tree canopy appears necessary to maintain suitably cool water conditions (Leipper 1994, D. Boughton, unpublished data). Therefore, the resilience of

montane thermal refugia to current inter-annual seasonal or longer-term climatic changes is probably highly dependent on the presence of a properly functioning riparian canopy.

Mountain refuges appear more vulnerable than coastal refuges to thermal increases in water temperature during the summer (Snyder *et al*. 2002), where the latter are buffered by a maritime climate. An alteration of fire regime, flood regime, and/or sediment may eliminate a properly functioning closed riparian canopy by burning trees, increasing the depth to the water table, or destroying trees via debris flows or floods (Bendix and Cowell 2010b, May and Gresswell 2004, Bendix and Hupp 2000). The water table can be lowered not just by increased sediment deposition, but also by decreased summer base flows, driven by lowered rainfall or greater evaporative demand of plants (Tague *et al*. 2009).

Lowered summer water tables may not just indirectly affect rearing juveniles via alteration of riparian trees; it may also affect the fish directly by reducing the summertime surface flow, and eliminating it entirely in portions of the watershed that fall within a rainshadow or in reaches with deep alluvium or already impaired flows. The gravel-bedded reaches used for spawning tend to have deep alluvium, and therefore can be especially vulnerable to loss of surface flow or incomplete riparian shading (Boughton *et al*. 2009). Timing is important for young-of-the-year development in gravel-bedded channels followed by retreat into "hydro-thermal" refugia once growth and size permits; large amounts of juvenile movement and stranding are commonly observed in the SCCCS DPS (see for example, Shapovalov 1944).

Groundwater inputs and heat-exchange with the channel-bed can buffer daily and annual temperature fluctuations in a stream (Hannah *et al*. 2004, Tague *et al*. 2009, 2008). In a stable climate the ground stores heat seasonally (absorbing heat in summer and supplying heat in winter), but should have an annual net flux close to zero, that is negligible heat increase or loss (Bogan *et al*. 2004). Decreased base flows during the summer may actually help the ground (channel-bed) buffer stream temperatures more effectively, by increasing the surface area of the bed-water interface, relative to the volume of water in the stream and the air-water surface area. The magnitude of such a buffering is not known, but would probably shrink the amount of fish habitat and feeding opportunities for rearing juvenile fish.

The coastal thermal refugia are closely tied to the heat dynamics of the ocean and maritime air and to the future pattern of seasonal upwelling and winds along the coast. Many tributaries and the lower sections of mainstems fall within the climatic influence of the marine inversion layer that develops in summertime. Except for the mainstems of large coastal rivers such as the Salinas and Pajaro, many of these coastal streams also benefit thermally from the temperature lapse rate in the coastal mountains, as well as receiving orographic precipitation in the wintertime - the converse of the streams in the rain shadow of inland areas. The coastal area is probably significantly more resilient to the consequences of climate change (*e.g.*, ambient air and water temperatures) than inland areas because of the moderating effects of the marine environment, and highly productive per unit of habitat. However, it is a very narrow band and so its effect to overall productivity of the SCCCS DPS is limited.

Each watershed occupied by SCCC steelhead terminates at the coast with some type of estuary-lagoon system. In South-Central California, seasonal lagoons currently tend to form each summer when decreased streamflows allow marine processes to build a sand berm at the mouth of each watershed. Juvenile steelhead over-summer in these lagoons, where they often grow so rapidly that they can undergo smoltification at age one and enter the ocean large enough to experience enhanced survival to adulthood (Hayes *et al*. 2008, Bond 2006). Both effects should increase the resilience of the

steelhead life history component of *O. mykiss*. In contrast, juveniles over-summering in some montane thermal refugia often display very little or no growth during the summer (Sogard *et al*. 2012, 2009, Hayes *et al.* 2008, Boughton *et al*. 2007a, Bond 2006) .

Fall and Winter Rearing (unimpaired conditions). Steelhead rearing ecology during the fall and winter is less documented, but is likely less constrained than earlier life phases (incubation, hatching, and emergence) or later over-summering phases. Baseflows rebound in some creeks as the weather cools in September and October, and sections of channel that were dry during the summer months begin flowing again, even before the first rains of the fall. This is due to reduced evaporative demand by riparian plants. Initial rainstorms of fall have relatively little effect on stream flows, as most precipitation percolates into the ground, and larger interior watersheds may require considerably more rain to re-initiate surface flows. The cooling of the weather and the rebounding of baseflows releases over-summering fish that were trapped in small residual pools and thermal refugia, so that a relatively small number of fish potentially gain access to a large extent of stream habitat (Boughton *et al*. 2009).

In some areas in the SCCCS DPS, this time of the year is marked by peak emergence of aquatic arthropods and inputs into streams of terrestrial arthropods, suggesting the opening of increased feeding opportunities to the fish that survived the summer. Arthropod productivity appears sensitive to local geologic and vegetative factors (Rundio 2009), but where it occurs it may allow juvenile steelhead to transform relatively warm temperatures into opportunities for rapid growth (Rundio and Lindley 2008). If these opportunities occur in sparsely populated intermittent creeks, the conditions are conducive to potential rapid growth into large smolts.

The timing of these peaks of productivity and growth opportunities is likely to be modified by current inter-annual as well as longer climatic changes. Because warmer autumns would increase metabolic costs as well as well as scope for growth (Boughton *et al*. 2007a), the impact on *O. mykiss* growth and survival could be either negative or positive, depending on a sensitive balance of factors. Compared to fall feeding, winter-feeding and growth is presumably more constrained by cooler temperatures, less arthropod production, and disturbances associated with high-flow events.

Smolting and Outmigration. Intensive studies of steelhead populations in the redwood systems of Santa Cruz County, California, indicate most *O. mykiss* become smolts and migrate to the ocean at age two or three, but a small proportion smolt at age one (Hayes *et al*. 2011, Sogard *et al*. 2009, Hayes *et al*. 2008, Shapovalov and Taft 1954; see also Atkinson 2010). Since larger size at ocean entry greatly increases ocean survival (Hayes *et al*. 2008, Bond 2006, Ward *et al*. 1989), smolting at age one is probably only a viable strategy for fish that have achieved rapid growth during their first year (Satterthwaite *et al*. 2009). Bond (2006) has shown that fish over-summering in lagoons can achieve such growth. It is possible that rapid growth can be achieved in other habitats as well (see for example, Casagrande 2012, 2010, Moore 1980), but most studies have shown growth to be slower in upland tributaries.

Quantitative data on growth and life history are not yet available for the chaparral and coastal terrace systems of the SCCCS Recovery Planning Area. It is likely that age at smolting of individual fish is based on local adaptations, including a "decision" as to whether to smolt versus maturing in freshwater. Local adaptation is likely dominated by a tradeoff between ocean mortality and greater fecundity that fish achieve by growing to a larger size in the ocean (Satterthwaite *et al*. 2009). Since ocean survival appears so strongly sensitive to size at ocean

entry, the balance of anadromous versus native freshwater-resident fish may be sensitive to juvenile growth rates. As noted above, warmer temperatures offer the possibility of either reducing or accelerating juvenile growth, depending on food availability, which itself may respond inter-annual and longer climatic effects on precipitation, riparian vegetation, and life cycle patterns sensitive to temperature, and nonlinear food-web dynamics.

An increase in the frequency, intensity, or duration of multi-year droughts limits migration opportunities for smolts. Loss of surface flow appears to occur more commonly in the deep alluvium of downstream reaches rather than in headwater tributaries (Boughton *et al*. 2009, Bêche *et al.* 2009). Additionally, sandbar barriers at the mouths of estuaries sometimes fail to breach in dry years, so drought would probably have greater impacts on migrating smolts (and migrating adults) than on the *O. mykiss* maturing in headwater tributaries (for estuary moth opening patterns, see Jacobs *et al*. 2011). The loss of opportunity would force a higher proportion of fish to adopt a freshwater-maturation strategy rather than the anadromous strategy. Since freshwater native resident *O. mykiss* are significantly less fecund than steelhead, the resulting population would be less resilient to extirpation, and gene flow among populations by straying steelhead would also be reduced. All these potential outcomes would tend to reduce the capacity of *O. mykiss* populations to recover from and adapt to changing conditions.

Subsequent Years in Freshwater; Maturation in Freshwater. The majority of juvenile *O. mykiss* that do not smolt their first year must again cycle through stages of spring-feeding, over-summering, and fall and winter feeding, although at a larger body size. Most of these fish probably smolt at age two or three or adopt the freshwater-resident strategy, maturing and eventually spawning in a suitable section of the stream network; the proportions adopting these pathways (*i.e.,* either multiple pre-smolts rearing years or freshwater maturation and reproduction) are unknown and probably sensitive to both growth and survival at all stages of life history (Satterthwaite *et al*. 2009).

The over-summering stage probably poses the greatest constraint to survival. Compared to young-of-the-year, older fish appear to require deeper water for over-summering (Spina 2007, Spina *et al.* 2005, Spina 2003, Spina and Johnson 1999), and may be more restricted to the parts of the watershed that provide well-shaded perennial pools of sufficient depth. Because of the geology and topography, these appear to be concentrated in headwater streams well-fed by orographic precipitation, where baseflows are stable, and geomorphic processes produce an abundance of pools (Boughton *et al*. 2009, Harrison and Keller 2006). The pool-forming mechanisms in these uplands are highly variable, involving self-formation of step-pools, scour around boulders that roll off hillsides, and rock outcrop which create force-pools.

The upland habitats used by older juvenile fish are a subset of the upland habitats used by the fish initially in their first summer. Consequently, vulnerabilities to repeated inter-annual seasonal changes (and longer-term climate changes) are similar to those described previously (*e.g.*, loss of baseflow, loss of riparian cover). Additional factors influencing productivity of upland habitats relied upon by rearing fish for multiple years are: (1) a lower level of redundancy, due to the more restricted distribution of high-quality pool habitat; (2) the vulnerability of pools to being transiently filled by fine sediments following wildfires; and (3) the long-term robustness of step-pools and bedrock force-pools, which should tend to re-scour after being filled, and are presumably resilient to a broader range of conditions compared to the reaches further downstream (Chin *et al*. 2009, Montgomery and Buffington 1997).

In summary, while freshwater habitats provide important spawning and rearing opportunities to steelhead, the inherent instability of these habitats can limit productivity depending on the pre-smolting growth patterns of individual fish, the pattern of rainfall, run-off, and input of sediments from natural hill-slope and channel erosion processes (accelerated, by periodic wildfires).