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SOME RESEARCH QUESTIONS ON RECOVERY OF STEELHEAD ON THE SOUTH-CENTRAL AND SOUTHERN CALIFORNIA COAST

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U.S. DEPARTMENT OF COMMERCE
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Introduction

Steelhead (*Oncorhynchus mykiss*) occur in stream systems of the southern and south-central California coast (Swift *et al*., 1993; Boughton *et al*., 2005) but have been placed on the US Endangered Species List due to population declines (Busby *et al*., 1996; Good *et al*., 2005). Recovery of steelhead requires the improvement of abundance, productivity, diversity and spatial structure in a series of populations distributed broadly throughout the various biogeographic regions of the coast (Boughton *et al*., 2007; McElhany *et al*., 2000). Because the intent of the Endangered Species Act is "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved" (16 U.S.C. §§1531§2(b)), the basis for a species' recovery lies in its natural habitats, the processes that maintain those habitats, and the way the species uses those habitats.

The processes maintaining the freshwater and marine habitats of steelhead are broadly intertwined with climate, watershed condition, and human activities. Modifying these processes to support species recovery is a social process inevitably involving scientists, stakeholders, and much uncertainty, and is beyond the scope of this report (see Boughton, 2010a for a general scientific framework).

The focus here is on research questions that address the second aspect of recovery: the way in which the species uses its habitats, such that it achieves long-term viability. Many of these questions can probably be addressed in a traditional scientific manner, less tied to a social process involving stakeholders.

Rebuilding a steelhead population involves three parallel tracks: 1) taking steps to improve VSP parameters (abundance, productivity, life-history diversity, and spatial structure of populations); 2) taking steps to learn the level of improvement necessary to achieve low risk ("viability criteria"), and 3) monitoring the progress of steelhead populations toward meeting those criteria. The efforts involved in these three parallel tracks often overlap and reinforce each other.

Two previous reports by the Technical Recovery Team for south-central/southern California coast (Boughton *et al.* 2006, 2007) identified a variety of research topics that fall along these three parallel tracks. Here I have gathered this information into one report, expanded on some of the topics, and organized them under headings reflecting the three parallel tracks:

1. Identify ecological factors that promote anadromy

2. Clarify population structure (and refine viability criteria accordingly)

3. Monitor progress toward recovery

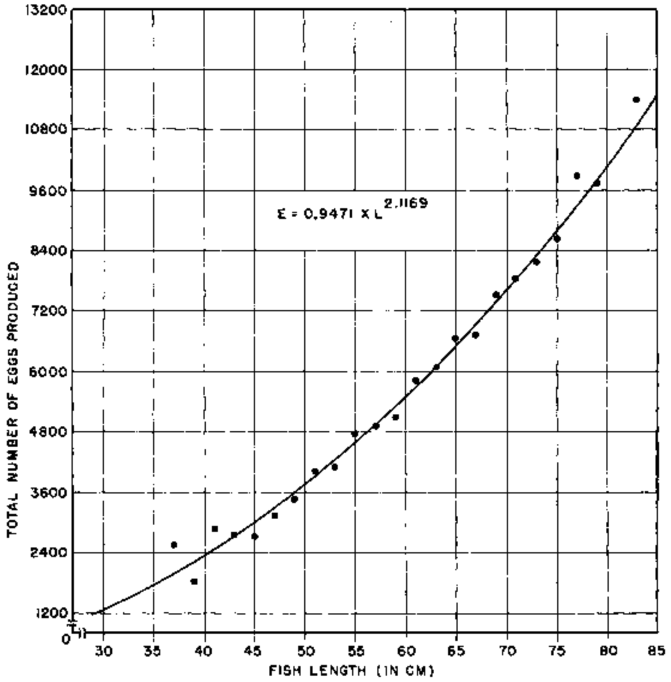

Figure 1. Fecundity as a function of body size for female steelhead sampled from Scott Creek in Santa Cruz County. Reproduced from Shapovalov and Taft (1954).

Identify Ecological Factors that Promote Andromy

Rainbow trout is a form of the species *O. mykiss* that does not migrate to the ocean, but instead stays resident in freshwater for its entire life cycle. It is widespread in the region's creeks and is not currently considered at risk of extinction. In contrast, the sea-going (anadromous) form is much rarer and is considered highly at risk. So, the focus of recovery is to recover and secure the anadromous form, and that involves restoring ecological conditions that specifically promote its abundance.

Obviously, it is necessary to have migration corridors for steelhead to reach a spawning area, but this does not necessarily imply that they will out-compete the freshwater residents that spawn in the same area. At present it is not clear what ecological conditions specifically promote the sea-going form, though there are some important clues. These clues present a prime opportunity for research that would lead to more effective recovery actions.

The most settled question is the definite fecundity advantage of sea-going females. As shown in Figure 1, the egg production of an adult female scales exponentially to its body length, and adult *O. mykiss* are generally able to attain much larger sizes in the ocean than in freshwater. Thus, a typical female rainbow trout might attain a length of 35cm, enabling her to produce 1800 eggs annually, whereas a medium sized steelhead female at 60cm could produce over 3½ times that number. This factor alone gives the sea-going form a distinct advantage, and all else being equal (and assuming the two forms breed true), over time the sea-going form should come to dominate any stream system with migration connectivity to the ocean. The resident forms would become confined to streams that lack migration connectivity. This pattern occurs, for example, in the Deschutes River in Oregon (Zimmerman and Reeves, 2000).

On the south-central/southern California coast, three ecological factors could potentially counteract the size advantage of anadromous females, so that the resident form is sometimes favored in anadromous waters. First, the migration corridor could be unreliable. Second, mortality may sometimes be much higher in the ocean than in freshwater, counter-acting the potential size advantage of sea-going fish. Third, juveniles of the freshwater form may survive better or compete better in freshwater than juveniles of the sea-going form, which could also counteract the natural size advantage of the sea-going form. Of these three possibilities, the first two are supported by various lines of evidence, and the third has some suggestive evidence. The need is to move beyond existing evidence to a quantitative understanding of ecological mechanism, so that specific recovery strategies can be linked to desired outcomes.

Reliability of Migration Corridors

Question: What is the relationship between reliability of migration corridors and anadromous fraction?

Migration corridors in this arid region are clearly unreliable, but it is not clear precisely how reliable they must be for the anadromous form to persist over the long term, nor how to best characterize reliability. Answers would probably be useful for stream systems with managed flows but are likely to be system-specific.

Recommendation: The relationship between flow patterns in managed rivers, the reliability of migration opportunities, and the long term persistence of steelhead runs is likely to be system-specific but could be characterized through the establishment of a long-term monitoring effort that tracks abundance and timing of steelhead runs, and the timing of smolt runs, in specific systems of interest. This would provide a framework by which management actions, in the form of managed flow regimes, could be related to outcomes, in the form of migrant abundance and timing. However, answers would probably emerge only over the long term, and numerous confounding factors would also need to be taken into account by the monitoring framework.

Steelhead-Promoting Nursery Habitats

Another factor that might counter-act the fecundity advantage of steelhead over rainbow trout is low marine survival, which if low enough could cancel or even outweigh the fecundity advantage. For example, continuing with the previous thought experiment in which a steelhead female produces about 3½ times more eggs than a rainbow trout female, if mortality during the first year in the ocean is 3½ times greater than the mortality of trout staying in freshwater, the fecundity advantage of the steelhead would, on average, be erased. Mortality that is higher yet—say, 10 times higher than in freshwater—would favor the freshwater form outright. In reality, the fact that the freshwater-resident and the ocean-going forms both occur in the region suggests that conditions sometimes favor one phenotype and at other times favor the other.

In general, ocean survival varies quite a bit among salmonids, ranging from 25% to well below 1% (Logerwell *et al.*, 2003; Peterson and Schwing, 2003) (also Ward 2000). At first blush, it would seem that improving the marine survival rate of steelhead would be beyond the scope of most strategies, since steelhead are rarely fished and other sources of ocean mortality are largely uncontrollable. However, mortality rates of many marine fishes are strongly size-dependent. Consistent with this general pattern, young steelhead migrating to the sea tend to survive much better if they have a larger size at ocean entry (Ward *et al.*, 1989; Bond, 2006). Thus their growth opportunities in freshwater may influence their subsequent marine survival.

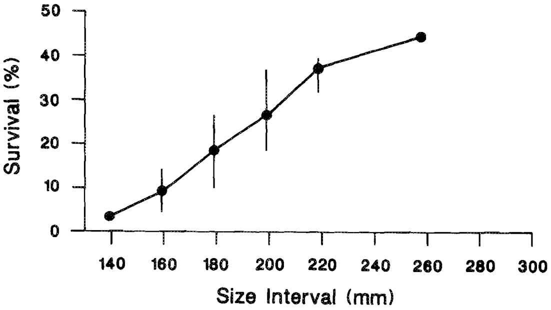

Figure 2. Marine survival of steelhead as a function of body size at ocean entry. Data from the Keogh River steelhead population described by Ward *et al.* (1989). Shown is average survival to spawning of smolts emigrating in years 1977 - 1982.

The most complete data on this phenomenon are from the Keough River steelhead population in British Columbia (Ward, 2000; Ward *et al.*, 1989), reproduced here in Figure 2. According to Figure 2, an outgoing smolt that has a forklength of 14cm has about a 3% chance of surviving to spawn, but a 16.5cm smolt's chances are at least 3½ times better (c. 10%), and a 22cm smolt's chances are an order of magnitude better (37%). Thus, mortality effects of size at ocean entry can be of the same order as the aforementioned fecundity advantages of migrating to the ocean in the first place.

A similar relationship between survival and size at ocean entry was observed by Bond (2006) in Scott Creek in Santa Cruz County, which is much closer geographically to our study area. However, the average marine survival was observed to be lower, on the order of 3% rather than the 10% to 20% observed in the Keogh River population. Thus the line in Figure 2 would presumably have a similar slope, but be displaced significantly downward. In any case, size at ocean entry appears to be at least as important as final spawning size in modulating the relative abundances of the freshwater and ocean-going forms of *O. mykiss*.[1]

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[1] Its importance can vary over time, however. Ward 2000 observed that after 1989, marine survival drastically declined in the Keogh River population, and the relationship disappeared between marine survival and size at ocean entry. This was attributed to a change in ocean conditions and indicates that the survival advantage of being a large smolt varies over time.

Overall, this suggests that the recovery prospects for steelhead runs would be drastically improved by identifying, restoring, and protecting those freshwater habitats that tend to produce large smolts. These areas would qualify as steelhead "nursery habitats," defined as juvenile habitats that produce adult recruits out of proportion to their spatial extent relative to other habitats (Beck *et al.*, 2001).

To produce rapidly growing juvenile fish, a habitat must produce abundant food. Although young steelhead feed mostly on invertebrates, food productivity ultimately traces down the food chain to the primary productivity of plants, which of course require sunlight and nutrients. Unfortunately, sunlight can also heat up streams rather rapidly, and in our region the streams cool enough for steelhead are mostly well-shaded, which precludes high levels of primary productivity. One would expect that where steelhead nursery habitats exist, they embody some mechanism that allows cool water temperatures and high primary productivity to co-exist during the summer growing season. This appears to be the case of the Scott Creek population, in which the seasonal lagoon at the creek's confluence with the ocean serves as steelhead nursery habitat (Bond, 2006).

Or, steelhead nursery habitats might develop where cool-water habitats receive large terrestrial inputs of food items. Terrestrial insects often fall in the water (Douglas *et al.*, 1994; Harvey *et al.*, 2002) and can provide a significant component of the diet of young steelhead (Rundio and Lindley, 2008). The study by Rundio and Lindley (2008) in the Big Sur area found terrestrial insects were a sporadic occurrence in the diet of *O. mykiss*, but each item had large mass and thus was highly profitable to the fish. Habitats with more frequent inputs of terrestrial insects might offer large growth opportunities.

Finally, some habitats might produce rapid growth if there is a mechanism to keep juvenile densities low, so that individuals have expanded feeding opportunities. For example, it might be the case that intermittent streams provide expanded feeding opportunities during their wet season, because their dry season prevents the establishment of a large permanent population of resident rainbow trout.

Recommendation: The identification and restoration of steelhead nursery habitats is a prime research opportunity with large potential payoffs for steelhead recovery. Nursery habitats would likely be estuarine or freshwater habitats that support rapid growth of young fish during the first or possibly second year of life, since large body size of migrants at ocean entry substantially improves their subsequent survival in the ocean. The simplest type of study to identify such habitats would be to use mark-recapture techniques to track growth and survival of juveniles as a function of habitat use. A more complete study would also track the consequences for marine survival.

Comparative Evaluation of Seasonal Lagoons

One type of steelhead nursery habitat is obviously the freshwater lagoons that form in the estuaries of many stream systems during the dry season. In some of these seasonal lagoons, juvenile steelhead can grow very quickly and enter the ocean at larger sizes, where they survive relatively well and thus contribute disproportionately to returning runs of spawners (Bond, 2006). Smith (1990), however, has observed that some lagoons can be quite vulnerable to rapid degradation in quality, and others may never be suitable, due to local environmental factors that can produce anoxic conditions or poor feeding opportunities. So there is a need to determine which lagoons have the potential to play a positive role in anadromy-targeted recovery efforts.

Question: What specific ecological factors contribute to lagoon quality (survival, growth) for steelhead rearing? What ecological factors contribute to lagoon reliability?

The existing information on the role of lagoons mostly comes from Santa Cruz County, focusing on a few systems. As described above, this work suggests that lagoons can comprise steelhead nursery habitat but can also be vulnerable to various natural and anthropogenic disturbances (Smith, 1990).

Seasonal lagoons are a specific kind of estuary, and in general estuaries are highly dynamic interfaces between two other much larger ecosystems: freshwater stream networks on the terrestrial side and the ocean ecosystem on the marine side. This accounts for estuaries' dynamism, complexity, and sensitivity to external influences but also for much of their productivity (Hofmann, 2000; Jay *et al.*, 2000).

On the south-central/southern California coast, there appears to be a general unity in function across many of the small estuaries, due to the general similarity of climate, terrestrial watershed conditions, and the raised coast (e.g Rich and Keller, 2009). However, there is also much variation and one would expect that small differences in, say, watershed condition or coastal wind and current patterns would sometimes translate into large differences in the suitability of lagoons as steelhead nursery habitat (J. J. Smith, pers. comm.).

Recommendation: Comparative studies on the environmental controls for productivity and reliability of lagoon habitat (including how to restore it if necessary) would aid in identifying those estuaries capable of serving as reliable steelhead nursery habitat. Such studies should focus on factors enabling rapid growth of juvenile steelhead and factors conferring resiliency against catastrophic failure of habitat quality (anoxia, premature breaching, *etc.*).

Potential Nursery Role of Mainstem Habitats

There may be other freshwater habitats that support high survival and robust growth of juveniles and so constitute nursery habitat specifically for the anadromous form of the species.

Low-gradient mainstem habitats, such as the trunks of the Santa Ynez, Ventura, Santa Clara, and Pajaro Rivers, may also have once supported rapid growth of juveniles, particularly if reaches received enough sunlight to support primary productivity, but artesian flows or other groundwater inputs kept water cool in the summer (C. Swift, personal communication). Most mainstem habitats have now been highly altered by agricultural clearing and groundwater pumping, so determining their upside potential for steelhead recovery would require some effort.

Question: Can mainstem habitat be restored to support high juvenile survival and possibly growth? What are the key ecological constraints?

Recommendation: The potential nursery role of mainstem habitat is much more speculative than the nursery role of lagoons. Initial assessment of the potential nursery role could take the form of 1) empirical study of mainstem habitat use by juvenile steelhead, at broad and fine scales; and 2) water-temperature modeling that accounts for effects of climate, insolation, and groundwater interaction on mainstem water temperatures, especially during summer. The empirical work would be most useful if it applied mark-recapture techniques to assess growth and survival as a function of habitat use and, in managed rivers, as a function of the flow regime.

Potential Positive Roles of Intermittent Creeks

Juvenile *O. mykiss* are common in intermittent creeks (Boughton 2008), but it is unclear whether these simply function as sink habitat (a net drain on productivity) or play a more positive role in population viability. The sheer amount of intermittent stream habitat available to, and used by, the species begs the question of its role or significance.

Question: Do intermittent creeks serve as steelhead nursery habitat, positively influence the anadromous fraction of *O. mykiss* populations, or otherwise enhance viability of the anadromous form of the species?

Obviously the species uses intermittent creeks extensively and intensively. Boughton (2008) observed that during the early summer in a moderately wet year, densities of young-of-the-year *O. mykiss* were nearly identical in the perennial and intermittent creeks of the Arroyo Seco watershed in Monterey County. Many sections of the intermittent creeks dried up and killed juveniles later in the summer. Such mortality has been observed in the region for many years (Shapovalov, 1944), although it is also common to find scattered residual pools or reaches packed with fish in late summer.

The important issue is identifying the potential positive, rather than negative, roles of intermittent creeks in sustaining the viability of steelhead populations.

The most obvious positive potential role is that intermittent creeks can provide migration corridors to perennial creeks during the wet season. Perennial reaches often occur in low-order streams upstream of intermittent sections, so the corridor role increases the amount of accessible perennial habitat, and thus the size of the steelhead population that can be supported. In dry years, the corridor function would fail in some areas. The research need here was stated earlier, about the relationship between migration reliability and persistence of steelhead runs.

Boughton (2008) found that most spawning habitat in the Arroyo Seco system tended to occur in intermittent streams and argued that hydrologic and geomorphic processes would tend to produce such a pattern in general. This suggests a second positive function of intermittent streams—vastly expanding the amount of spawning habitat beyond what is available in perennial streams—but it also suggests a need for an additional corridor function. In this case, the corridor function is for young-of-the-year to emigrate to perennial streams or residual pools before the summer dry season traps and kills them.

It is possible that intermittent streams enable a high-risk, high-reward strategy on the part of young steelhead. Many individuals may be killed during the summer drying season, but those surviving in the residual pools may benefit from enhanced growth. One mechanism for enhanced growth may be cannibalism of trapped compatriots. Another mechanism for rapid growth may be rapid recolonization of the dried stream channels as flows become re-established with cooler, wet weather in the fall.[2] Such fish would

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[2] Fall rains can re-establish flows, but I have also observed flows to be re-established by cooler fall weather, which presumably lowers the transpiration demands of riparian vegetation, leaving more groundwater to maintain base flows in the stream channels.

find few competitors and perhaps even an enhanced opportunity to feed on eggs and fry of the following winter's spawners (Ebersole *et al.*, 2006). In this manner, intermittent creeks could serve as steelhead nursery habitat

In wet years, the seasonal drying may be vastly reduced, increasing summer survival and allowing large pulses of juveniles to be recruited to the subpopulation of adult steelhead in the ocean. Under some scenarios, such as a highly plastic life-history strategy (see next section), it is possible that such pulses would be the primary mode of production for anadromous individuals and sustain the anadromous form of the species over the long term.

Recommendation: Intermittent creeks comprise a large proportion of freshwater *O. mykiss* habitat in the region. Despite an obvious negative role in the species ecology, they may have important positive roles as well. These potentially positive roles have the status of hypotheses with general implications for recovery strategies and viability targets and should be tested.

Other Lentic Habitats

Rapid growth of juvenile steelhead has been observed in artificial water impoundments, such as Sprig Lake in Mount Madonna Park in Santa Clara County (J.J. Smith, personal communication). This raises the possibility that artificial impoundments may have a positive and disproportionately effective role to play in enhancing the anadromous fraction of *O. mykiss* populations in the study area. However, artifical water impoundments can also have negative impacts, such as providing habitat for warm-water species that prey on *O. mykiss*, and so this hypothesis would have to be carefully evaluated.

Natural lentic habitats have been lost throughout the region. For example, there was once a series of ponds and small lakes between Salinas and Castroville (Gordon, 1996), which have since been drained; and there was originally a series of coastal ponds in Pismo Beach, connecting the mouths of Pismo Creek and Arroyo Grande. Both these lentic habitat systems (and others) are in the summer fog zone and may have stayed cool enough and productive enough in summer to support rapid growth of juvenile *O. mykiss*, comparable to estuaries.

Question: Are there situations where freshwater lentic habitats did or could serve as nursery habitat for anadromous *O. mykiss*, and if so, what are their ecological parameters?

Recommendation: This general question could be addressed in a number of ways: review of historical information, hydrologic and water-temperature modeling that identifies geographic settings in which lentic habitats would stay cool enough for *O. mykiss* during the summer or wet enough during the fall, and experimental studies of survival and growth in existing ponds or water impoundments. Obviously, lentic habitats have to be connected to stream systems via migratory corridors to serve as useful habitat for steelhead.

Spawner Density as an Indicator of Viability

The viability criteria described in Boughton *et al.* (2007) include not just overall abundance but also sufficient population density, under the assumption that high spawner density is an indicator of a healthy and robust population occupying productive habitat. However, there are not sufficient existing data to set a specific density threshold that indicates a viable population. Empirical research is needed before proposing such a threshold.

Question: What spawner density (at what spatial and temporal scale) is sufficient to indicate a viable population of steelhead?

Recommendation: This is an empirical question, and answering it requires one or more healthy and robust anadromous populations to be carefully characterized. The answer is more useful in the long term, as an indicator of progress toward recovery, than it is in the short term for achieving recovery, but the most useful data would be a time series of observations of spawner density over many years. Thus, the sooner the relevant observations begin being collected, the better. A natural locus for collecting the relevant data are the life-cycle monitoring stations proposed in the monitoring plan. Redd surveys (see section on monitoring), if suitably georeferenced, would automatically provide the relevant information.

Clarify Population Structure

Population structure concerns the ecological and biological factors that cause fish to naturally group into functional units known as independent populations. Independent populations are defined as "a collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations" (McElhany *et al.*, 2000).

In other words, if groups of fish regularly exchange individuals, they are members of the same population, whereas if exchange is rare or does not significantly affect population dynamics, they are members of separate populations. This definition of "separateness between, exchange within" means that the proper context of most management strategies is the independent population: a strategy that directly affects only a portion of a population will soon have significant indirect effects on the rest of the population but few immediate effects on other populations.[3]

The independent population is also the fundamental functional unit of species persistence, and hence viability. So, many of the viability criteria described by Boughton *et al.* (2007) are defined in terms of population traits such as anadromous fraction and mean spawner abundance over time. The groupings of fish to which these criteria should be applied are a function of what is known about the patterns of exchange of fish among breeding units. Open questions about patterns of exchange lead to uncertainty about how to apply the criteria.

A simple quantitative model led Boughton *et al.* (2007) to conclude that an annual adult abundance of 4,150 fish was sufficient for an independent population to be considered viable. But it was unclear, due to questions of exchange patterns, whether the criteria should be applied:

…to anadromous fish in a particular basin,

…to the sum of anadromous fish across several basins,

…to the sum of anadromous and freshwater-resident fish in a particular basin, or

…to the sum of anadromous and freshwater-resident fish across several basins.

The answer of course has large implications for the scope and scale of recovery efforts. The answer depends on the level of exchange of fish across separate coastal basins, and on the level of exchange between the anadromous and resident forms of the species within a particular basin—termed "dispersal" and "life-history crossovers" respectively. A life-history crossover is a freshwater parent that has anadromous fish among its progeny, and/or vice versa. Questions about dispersal and life-history crossovers, and the implications for viability criteria, are key issues addressed in this section.

Partial Migration and Life-History Crossovers

Partial migration is the phenomenon in which a population consists of both migratory and resident individuals (Jonsson and Jonsson, 1993), implying the regular or at least occasional occurrence of life-history crossovers. A diversity of crossover patterns have been observed in the small number of studies conducted on *O. mykiss* to date. Zimmerman and Reeves (2000) observed no crossovers in resident and anadromous *O. mykiss* of the Deschutes River in Oregon, implying two demographically distinct (independent) populations. For one natural and eight hatchery populations in California, Donohoe *et al.* (2008) found that anadromous females sometimes produced resident progeny, but resident females did not produce anadromous progeny, suggesting a one-way flow of crossovers away from the anadromous form. The Babine River *O. mykiss* in British Columbia apparently exhibit modest levels of crossover (c. 9%) in both directions (Zimmerman and Reeves, 2000), suggesting a single population that is partially subdivided, whereas J.R. Ruzycki (personal communication in Donohoe *et al.* 2008, p. 1072) reports a high level of bidirectional crossover in various tributaries of the Grande Ronde River in Oregon (0% to 33% of anadromous adults were progeny of resident females, and 44% of resident adults were progeny of anadromous females), indicating a fully integrated population in which the two life-history forms functionally co-exist.

This continuum has profound implications for viability criteria. Are the populations in our area fully integrated? Or, does each form more or less breed true, implying demographically independent populations that share stream systems but play no role in supporting one another and perhaps even compete? Boughton *et al.* (2007) made recommendations that embodied bet-hedging for these two possibilities (actually two endpoints of a continuum): On the one hand, one should specify criteria that would secure the ocean-going fish if they turn out to comprise a demographically independent population. On the

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[3] Over the longer term, a permanent change in population dynamics would be expected to trickle out to other independent populations, due to occasional exchanges of individuals. Occasional exchanges are expected to drive important processes such as gene exchange and recolonization of stream systems following a drought.

other hand, one should specify criteria that secure the ocean-going fish if they turn out to depend on the resident form with which they coexist. However, one can imagine that resolution of the uncertainty would eliminate some of the need for hedging and thus lead to a more efficient and effective recovery plan. Resolution would involve two fundamental questions:

Question 1: What is the mechanism for, and frequency of, life-history crossovers in the south-central and southern California regions?

Question 2: How does crossover affect the persistence of the anadromous form?

Answering the first question will take some time. Currently, S. Sogard (NOAA Fisheries) and M. Mangel (UC Santa Cruz) are leading a research effort to better understand life-history crossovers in California steelhead; Mangel and Satterthwaite (2008) give an overview of the framework being used. The hypothesis being examined is that the anadromy / residency "decision" made by individual O. *mykiss* is cued by the environment, using a mechanism similar to what has been observed in Atlantic salmon (*Salmo salar*), a better-studied species that also exhibits variation in the timing of the smolting decision during life history.

Specifically, the hypothesis is that the smolting/residency "decision" is made by individual fish during a sensitive period some months before the actual process of smolting is observed, and that the cues for the "decision" are the fish's size and growth rate during the sensitive period. This makes sense because size and growth in the freshwater habitat integrate information about the quality of that habitat, as well as about the expected survival and fecundity in the marine environment versus the freshwater environment. I have put quotes on "decision" because no cognitive process is implied; what is hypothesized is a physiological (and perhaps hormonal) mechanism that processes information from the environment to produce an adaptive life-history decision.

It should be noted that though the research effort of Sogard and Mangel is important progress on the anadromy/residency ambiguity in steelhead recovery planning, it has important limitations at this time.

First, it has the status of a hypothesis and at this writing no one has actually experimentally induced life-history crossovers in O. *mykiss* by manipulating size or growth rates or any other environmental factor.

Second, even if the Atlantic salmon model is useful for understanding life-history plasticity in O. *mykiss*, there are almost certain to be important differences and indeed surprises in the O. *mykiss* story. It would be surprising if there were no surprises.

Finally, the existence of a plastic life-history strategy does not preclude the possibility of important genetic constraints. For example, one might expect that even if the model is broadly correct, the specific timing of sensitive periods, and the thresholds for the size and growth cues, would probably vary quite markedly among populations of steelhead due to genetic differences. In short, the responses to environmental cues would likely have a heritable component, and this component would likely exhibit local adaptation to specific conditions. A response that is adaptive in one basin may be selected against in another basin, depending on environmental factors such as those discussed in the previous section.

Recommendation: It is essential for the research effort on the mechanisms of life-history plasticity in O. *mykiss* to stay on track over the long term, for it is difficult to envision a successful recovery effort without a better understanding of the functional relationship between resident and anadromous fish. The current effort of Sogard, Mangel and coworkers should yield useful information over time, but it focuses on two systems outside our region: Soquel Creek in Santa Cruz County (a coastal redwood forest system) and the American River near Sacramento (a large Central Valley River system). One should expect local adaptation of steelhead populations in the southern and south-central region.

Because of local adaption, it might be useful and practical to address some related questions about the frequency of life-history crossovers and their implications for recovery planning in the southern and south-central coastal region. In particular, one should:

Identify environmental factors that specifically promote anadromy (this was discussed in the previous section). It seems clear that the abundance of anadromous fish needs to be increased, and identifying relevant environmental factors would usefully inform this goal. The principal uncertainty is how much the abundance of anadromous fish needs to be increased, a separate question that depends on the frequency of life-history crossovers and the mechanisms underlying them. This question can be addressed over the longer term as more is learned about the mechanism and used to refine the viability criteria described by Boughton *et al.* (2007).

Estimate the frequency of life-history crossovers in populations of interest, to determine whether it even occurs with any regularity. The most practical method for doing so is by analyzing otolith microchemistry of juvenile O. *mykiss* (see Donohoe *et al.*, 2008 for an example), but unfortunately this requires lethal sampling of juveniles. Fortunately, modest lethal sampling of juveniles (as opposed to adults) is likely to pose only a negligible increase extinction risk, due to the low reproductive value of juveniles (most sampled juveniles would die in nature anyway before reaching reproductive age).

Tackle Question 2 above, "How does crossover affect the persistence of the anadromous form?" This could be done using existing frameworks in population modeling, such as individually-based models or integral projection models, but would require assumptions about typical mortality and growth rates in freshwater and marine environments, as well as about frequency of life-history crossovers. However, it would probably produce important insights.

Rates of Dispersal

Just as life-history crossovers may knit resident and anadromous *O. mykiss* into integrated populations, frequent movement of anadromous fish through the ocean to neighboring river basins may knit neighboring *O. mykiss* into integrated "trans-basin" populations. If interbasin dispersal is common, the most effective recovery strategies might be those that emphasize integration of recovery efforts across a set of linked basins. If interbasin dispersal is rare, the most effective strategies would be those that identify basins having stable conditions that protect small, inherently vulnerable populations.

The places where the implications of the single-basin versus trans-basin scenarios are most distinct are those areas along the coast where numerous small coastal basins occur in close proximity. These areas are the Big Sur Coast, the coast of San Luis Obispo County, the south coast of Santa Barbara County, and the small basins draining the Santa Monica Mountains just north of Los Angeles. Unfortunately, it is not clear if it is practical to try to estimate dispersal rates in these regions.

Question: How common is dispersal, and how does it relate to population structure, especially in small coastal basins?

Recommendation: Dispersal is difficult to document, because it may be too rare to detect yet still have an important impact; and because of the difficulty of tracking the origin and fates of migrating fish. A combination of genetic tags and RFID tags may make the question tractable, particularly in small basins where it is possible to sample a significant fraction (perhaps all) of a given cohort of adults. This is fortunate because small basins are where the question is most relevant to management issues. Longer-term efforts that integrate demographic monitoring (abundances of various life stages) and genetic sampling may also prove informative over time. The difficulty of addressing this question suggests that it might be deferred, unless key recovery actions depend for their success on it being answered.

Revision of Population Viability Targets

In the framework described by Boughton *et al.* (2007), the key criterion for establishing population viability was that a population be demonstrated to sustain a long-term mean run size of 4150 anadromous spawners per basin per year. However, the authors noted that the criteria were chosen to be precautionary due to scientific uncertainty about key issues, and that better information might allow the criteria to be revised without increasing the risk of extinction. There were three types of information that seemed most likely to lead to useful revisions of the viability criteria:

1. The threshold run size might be able to be revised downward from 4150 spawners per year if it was learned that year-to-year variation in run size was modest enough to be consistent with a lower threshold. The necessary information—annual estimates of run size over several decades—would come from the types of monitoring programs described in the section "*Monitoring steelhead recovery*."

2. Data on the frequency of life-history crossovers might justify that the 4150 threshold could include some fraction of adult resident fish, rather than the 100% anadromous fraction currently recommended (*i.e.* because the resident and anadromous forms are shown to comprise functionally integrated populations). Useful information would come from addressing the questions in the section "*Partial migration and life-history crossovers*."

3. Data on dispersal might justify that the 4150 threshold include spawners from neighboring basins (*i.e.* because dispersal rate is sufficiently high that the fish in neighboring basins comprise a single, trans-basin population). Useful information would come from addressing the questions in the section "*Rates of dispersal*."

Data for item 1 would arise over time as a byproduct of a comprehensive monitoring program, which is necessary to assess risk in any case. The priority item is probably item 2, since the integration of the resident and anadromous forms is not well understood at all but has profound implications for a very diverse set of management issues beyond just revision of recovery criteria.

Monitoring Steelhead Recovery

Monitoring involves two rather different, but related activities:

Status Monitoring: Monitoring the condition of the population as a whole, to judge its status (progress toward recovery or further decline toward extinction)

Effectiveness Monitoring: Monitoring the response of the population to specific recovery actions, to learn what works and what doesn't.

Status monitoring is designed to gather data for assessing the viability criteria described in Boughton *et al.* (2007). The most important such activity is monitoring the annual run size of populations, and how this might be done is my focus here. Status monitoring attempts to characterize the entire population.

Effectiveness monitoring is designed to assess the impact, positive or negative, possibly quantitative, of some specific recovery action. An action's effect should change status, and thus in principle should be detectable in data from status monitoring. In practice, the signal-to-noise ratio is generally too small to discern such effects, and any detectable signal that does exist is ambiguous if it cannot be compared to one or more controls (monitored populations lacking recovery actions). Effectiveness monitoring will generally be more powerful if it focuses on the specific life stage impacted by recovery actions in particular habitats, and if it compares it to the same life stage in similar unaffected habitats that serve as controls.

There are various ways that effectiveness and status monitoring can be integrated with one another, but this is beyond to scope of this report. Below I focus on status monitoring, and in particular the monitoring of run size for anadromous adults. Run-size monitoring involves many technical challenges in the south-central/southern California domain and remains an ongoing challenge. Below, I briefly review what appear to be three promising techniques. All these techniques necessarily involve two components:

1. Observed counts for some life-history stage of *O. mykiss* that contains information about run size.

2. Some method for estimating the number of unobserved fish.

For the first component, the observed count may actually be the run, but if it is some other life-stage, there is a need to collect data to estimate a conversion factor. For example, if redds are counted, it is necessary to estimate redds per female and sex ratio to get an estimate of the full run size (Gallagher and Gallagher, 2005).

The second component is necessary because observations confound the true number of fish with the detection rate of the observer: A large population with poor observing conditions looks the same as a small population with excellent observing conditions. Thus, one must also estimate the number of unobserved fish, which corresponds to estimating the detection rate of the observer.

There are numerous ways to do this (Williams *et al.*, 2001, is an excellent technical review), but they all involve making repeated observations (often just two times) of the same group of fish. It is tempting to view this redundancy as wasted effort, but it is absolutely necessary for estimating unobserved fish. Doing so, and getting an estimate of the full population, is often far more informative than obtaining partial counts in which abundance and detection rate are confounded, because detection rates can be so variable (Rosenberger and Dunham, 2005).

Redd Counts

Gallagher and Gallagher (2005) have shown that salmon and steelhead runs can be estimated using redd counts. The abstract of their paper:

"We developed and evaluated a stratified index redd area method to estimate Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* escapement in several coastal streams in northern California based on the assumption that redd size is related to the number of redds a female builds. Sources of error in redd counts were identified, including the use of logistic regression to classify redd species (necessary due to temporal overlap in the spawning of these species in coastal northern California). Redd area escapement estimates were compared with estimates from more conventional methods and releases above a counting structure. Observer efficiency in redd detection ranged from 0.64 (SE = 0. 10) to 0.75 (SE = 0. 14) and was significantly associated with stream- flow and water visibility (analysis of variance [ANOVA]: F = 41.8; $P < 0.001$). Logistic regression reduced uncertainty in redd identification. Redd area and date observed were significant in predicting coho salmon and steelhead redd species (Wald's z = 11.9 and 18.09, respectively; $P < 0.001$). Pot substrate and redd area were significant in classifying Chinook and coho salmon redds (Wald's z = 5.88 and 4.03; P = 0.015 and 0.04, respectively). Stratified index redd area escapement estimates and estimates based on capture- recapture experiments, area-under-the-curve estimates, and known releases above the counting structure (coho salmon only) were not significantly different (ANOVA: F < 13.6; P > 0.06). Escapement estimates assuming one redd per female were only significantly different from other methods for steelhead (ANOVA: F = 13.11; P = 0.006). Redd counts were significantly correlated with escapement estimates (r > 0.82; P < 0.04). Reduction of counting errors and uncertainty in redd identification, biweekly surveys throughout the spawning period, and the use of redd areas in a stratified index sampling design produced precise, reliable, and cost-effective escapement estimates for Chinook salmon, coho salmon, and steelhead." (Gallagher and Gallagher, 2005)

This method has much promise but has not been tried in the southern California setting, where stream turbidity and channel geomorphology may make redds difficult to detect in wintertime conditions (though redds do persist and are often detectable through the spring). The method has high personnel requirements, because it requires the survey reaches to be visited biweekly throughout the spawning season. On the other hand, it is simple, requires only modest training of field personnel, and has modest costs other than the hiring of personnel.

Monitoring runs using the DIDSON Acoustic Camera

Dual-frequency identification sonar (DIDSON) is an off-the-shelf device that uses high frequency sound waves to produce near video-quality images of underwater objects. It can potentially be used to identify and count all migrating steelhead at some survey point in a stream system, for the entire spawning season. Its advantages are similar to those of using a weir to make counts, but it has two additional advantages that are key. First, there is no need for a full weir or other device that impedes flow, and so fouling, destruction by high-flow events, *etc.*, are not a major constraint. Second, it can see through turbid waters (unlike a regular video camera). These two traits appear well suited to the flashy, turbid conditions typical of southern California streams.

DIDSON has been successfully used to estimate adult salmon escapement in high-abundance rivers in Alaska, Idaho, and British Columbia. Operational and technical guidance on successfully using the DIDSON in our region is described in detail by Pipal *et al.* (2010).

The principal disadvantages of the DIDSON are 1) the cost of the device, and 2) deployment constraints for getting good images. These constraints have to do with maintaining a good "insonified region" of the channel being monitored for migrants. Some channel shapes are better than others, and there also need to be strategies for maintaining a completely insonified cross-section during the advance and retreat of high flow events. In addition, there is a need to learn how to interpret poor images when they occur. However, the method has the promise to solve some of the intractable problems of monitoring steelhead in southern California: counting modest numbers of migrants in turbid waters during and after flashy high-flow events.

Tagging Juveniles and Monitoring Migrants

Steelhead runs can potentially be estimated by tagging juveniles with RFID tags[4] during their freshwater phase and subsequently monitoring migrants using in-stream tag readers.

The tagging phase uses standard block-netting and electro-fishing techniques during the summer low-flow season. Depletion-sampling can be used to estimate juvenile abundances. However, Rosenberger and Dunham (2005) found that capture-recapture methods gave more robust estimates than depletion-sampling, and Temple and Pearsons (2006) showed that the customary 24-hour waiting period in capture-recapture sessions can be shortened to one or two hours, which simplifies logistics so that capture-recapture sampling can have a time-efficiency similar to that of depletion-sampling.

The monitoring phase is accomplished using in-stream tag readers, such as those described by Zydlewski *et al.* (2001, 2006); Bond *et al.* (2007); Ibbotson *et al.* (2004). These must be deployed for the duration of the migration season (both outgoing and incoming) every year.

The design has promise for monitoring runs of steelhead for which many other methods are problematic. Precision of run size estimates is primarily controlled by the number of tagged spawners that ultimately return and get detected. The number required is modest: around 30 to 90 tagged spawners are necessary to obtain 50% confidence intervals that stay below one-third of the estimated run size (Boughton, 2010b). However, with marine survival typically falling between 0.3% and 3%, the required tagging effort would usually be between 3,400 and 45,000 juvenile fish tagged per generation per population to achieve this modest number of tagged spawners. This large tagging effort could perhaps be spread across a set of populations, if one were willing to assume uniform marine survival across the populations.

The estimation method is robust to imperfect detection of tagged fish by the in-stream tag readers, as long as there are at least two readers that inde-

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[4] Radio frequency identification tags, also known at PIT tags (passive integrated transponder tags).

pendently scan for tags. Reach-sampling allows the entire run to be estimated using fish from a sample of reaches. In the simulations, the number of reaches needed for acceptable precision could be as low as 30-40 under scenarios of high marine survival, a sampling fraction of around 2% in large watersheds, such as the Arroyo Seco watershed used in the simulations. Under low marine survival, the necessary sampling fraction was around 10% in the simulations.

A nice side-benefit of this method is that one would obtain very good estimates of ocean survival. This is useful because it allows the overall trajectory of steelhead runs to be decomposed into marine and freshwater components. This, in turn, will deliver greater statistical power for analyzing patterns in the freshwater component. In short, one would have greater statistical power for effectiveness monitoring at the scale of the entire stream basin, by removing the confounding noise of ocean survival (which can be quite variable and thus mask improvement on the freshwater side).

Sampling Young-of-the-Year Otoliths

This method is similar to tagging juveniles and monitoring migrants, in that it uses reach-sampling, block-nets, and summer electrofishing to make estimates of total juvenile abundance in a stream system. However, instead of subsequently tracking the survival of tagged juveniles to estimate run size, one would collect some fraction of the juveniles, and examine their otoliths and genetic relatedness. From this, one could estimate the number of anadromous mothers (and as a byproduct, non-anadromous mothers) for each annual cohort of young-of-the-year fish. This would provide an estimate of the female component of the steelhead run.

This method would dispense with the need to implant RFID tags in fish and the need to maintain in-stream tag readers during difficult winter conditions. All fieldwork would consist of eletrofishing for juveniles at randomly-sampled stream reaches early each summer. However, the method would require the time and expense of otolith analysis, and it would require intentional take of juveniles for purposes of extracting otoliths (extraction is lethal).

This method is at the moment undeveloped but has promise as a relatively simple and efficient way to estimate run sizes using established and familiar field methods. A big drawback is the need to kill juveniles to get their otoliths.

However, a small amount of take of juvenile fish would be expected to have negligible effects on viability, because young-of-the-year fish have relatively low reproductive value. This is a technical way of saying that most of them are going to die before they reach reproductive age anyway - perhaps only 0.1% or less will reproduce - so that sampling them will have negligible effects on viability, especially if the sampling is done before density-regulation occurs late in the summer low-flow season. The key unknowns at this point are how many fish would have to be sampled to get a reasonable estimate of the number of anadromous mothers and whether the sampling does in fact pose a negligible increase in risk.

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