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Examining the Causes and Consequences of Hybridization During Chinook Salmon Reintroductions: Using the San Joaquin River as a Restoration Case Study of Management Options

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ABSTRACT

Successful salmonid restoration efforts depend upon an understanding of the evolutionary processes that historically shaped population diversity, as well as the realities of currently available, altered river systems. Habitat alterations over the past century have dramatically changed the ecological forces that shaped salmonid speciation and evolution, bringing formerly separate and distinct populations into contact and in some cases leading to hybridization. Hybridization can threaten the genetic diversity within salmonid species and may affect the outcomes of restoration efforts. Here we use the San Joaquin River Restoration as a case study to discuss some of the genetic challenges of Chinook salmon restoration in a newly reopened habitat. We discuss a range of genetic management strategies—from passive reintroduction to tightly managed, active reintroduction—and the strengths and weaknesses of each approach.

INTRODUCTION

Hybridization between species or distinct populations presents a major challenge for conservation, particularly when one or both species are targeted for protection. Salmonid fishes exhibit many traits that, while largely responsible for their success at colonizing and diversifying throughout the western United States, also render them vulnerable to hybridization when ecological conditions are anthropogenically altered, for example by truncation or destruction of habitat from dam construction, as is the case in most of the river systems of the American West. Conservation of Pacific salmon has been a partial motivator to remove unnecessary dams and reopen river habitat, as in the recent Elwha River Restoration in Washington State (Pess et al. 2008; Brenkman et al. 2012). As habitats on other rivers undergo restoration, managers will need to consider the possible effects of hybridization. For this discussion, we define hybridization as the mating and production of offspring by individuals from genetically distinct groups, be they species or genetically divergent populations within a single species. Central Valley Chinook salmon are an excellent example of

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a group that faces genetic diversity loss and population structure collapse, in part from hybridization. In this paper we examine the role habitat modification plays in hybridization of salmonid fish. We then use the restoration of the San Joaquin River in Central California as a case study to discuss a range of management strategies and their potential genetic consequences for salmonid reintroduction.

Habitat Modification and Hybridization

Habitat reduction is one of the major factors that has contributed to the decline of anadromous Pacific salmonid diversity (Nehlsen et al. 1991; Yoshiyama et al. 2001). The construction of impassable dams and river barriers has eliminated access to more than 44% of historic anadromous salmonid spawning habitat on the west coast of the contiguous United States (McClure et al. 2008). With the truncation of spawning habitat, the ecological forces that drove and maintained salmonid diversification have been fundamentally changed.

Anthropogenic habitat modification has been recognized as a promoter of hybridization between species or divergently adapted populations of many animal species (Rhymer and Simberloff 1996; Scribner et al. 2001). Environmental heterogeneity is essential for maintaining distinct species and biologically diverse communities (Seehausen et al. 2008) and genetic diversity provides the capacity for future adaptation (Scribner et al. 2001). In cases of ecological speciation, in which no post-zygotic barriers exist, environmental heterogeneity is a force that drives incipient species formation. The breakdown of environmental heterogeneity can lead to "reverse speciation" or the loss of genetic and phenotypic diversity (Gilman and Behm 2011) and the collapse of species boundaries (Seehausen et al. 2008).

Fish taxa display a number of features that make hybridization a fairly common phenomenon (reviewed in Scribner et al. 2001), and resulting offspring are frequently viable (Thorgaard and Allendorf 1988). Salmonids are particularly vulnerable to interbreeding between distinct populations or species. Several cases of hybridization between members of the *Oncorhynchus* genus have been documented (Ferguson et al. 1985; Bartley and Gall 1990; Carmichael et al. 1993; Rosenfield 1998; Young et al. 2001), and in some cases have led to "hybrid swarms" in which the two groups completely merge into one new population or species (Forbes and Allendorf 1991; Allendorf et al. 2001).

Evolution of Salmonid Diversity

Chinook salmon possess a combination of characteristics that have led to their success at colonizing and thriving in the rivers of the western United States. The dynamic geological history of the West, forged by periods of tectonic uplift and volcanism, created a varied river landscape within which salmonids sub-specialized to inhabit distinct niches (Montgomery 2000). Anadromy allows salmon to use sheltered freshwater habitats to rear as vulnerable fry and also to exploit the abundant nutritional opportunities afforded by ocean living during periods of growth and maturation. The homing tendency to return to their specific natal stream is characteristic of anadromous salmonids and results in a degree of reproductive isolation and the development of genetic substructure within a single river system (McDowall 2001). This tendency to home is balanced by the propensity of some individuals to stray into non-natal streams to reproduce. Straying allows for the colonization of new habitat and increases the likelihood of persistence during periods of fluctuating habitat suitability or natural disasters (Quinn 1993). The delicate balance of straying and homing tendencies has enabled the development of a stunning diversity within the Chinook salmon species by promoting both phenotypically and genetically varied populations, while also providing for the colonization of novel habitats and the establishment of new populations (Waples et al. 2004).

In the case of Chinook salmon, the diverse environmental niches that enabled the specialization of different runs within California have been almost completely eliminated by anthropogenic change to river habitats, most notably by dams. Human alterations to California's Central Valley river systems are estimated to have reduced historical Chinook salmon freshwater habitat by as much as 95% (Myers et al. 1998). This situation has been exacerbated by translocations and hatchery practices, further disrupting run integrity and reproductive isolation. Chinook salmon are a prime example of a species which displays a striking amount of genetic and phenotypic diversity, but is also vulnerable to the loss of population structure and genetic diversity from the breakdown of pre-zygotic reproductive barriers. The propensity for inter-run hybridization is likely rooted in the relatively recent divergence between runs in California during the Pleistocene (Waples et al. 2008). In the current absence of varied spawning habitats, the forces that drove the evolution of Chinook run diversity and maintained population integrity are no longer present. With the removal of these ecological forces, there are few barriers to hybridization between runs, presenting a difficult set of conservation challenges for the species.

SAN JOAQUIN RIVER: RESTORATION CASE STUDY

Central Valley Chinook Salmon

Chinook salmon is the predominant salmonid species in California, estimated to have once numbered in the millions (Yoshiyama et al. 1998). Four distinct runs are recognized—fall, late fall, winter, and spring—and are named for the season in which salmon re-enter fresh water during migration to their spawning grounds. Each run's peak spawning occurs during a different time of year, with some degree of temporal overlap between the fall and spring runs (Moyle 2002). Winter-run and spring-run Chinook salmon historically favored spawning habitat in the upper reaches of rivers, while the fall and late-fall runs spawned in lower elevation reaches (Fisher 1994). Three Chinook salmon Evolutionarily Significant Units (ESUs) have been recognized within the Central Valley—spring run, winter run, and fall/late fall run (Waples 1995), each of which is listed as endangered, threatened, or a species of concern by the state or federal government (Fed Regist. 50 C.F.R. Parts 223 and 224 [2006a, 2006b]). Variation in spawn timing and river location has been an important factor in maintaining the separate Chinook salmon ESUs in the Central Valley (O'Malley et al. 2007).

Historically both fall-run and spring-run Chinook salmon were widely distributed throughout the Sacramento–San Joaquin river system (Figures 1, 2). However, fishing pressure, habitat degradation from hydraulic mining, and extensive water diversions for agricultural uses have decreased Chinook numbers drastically (Yoshiyama et al. 1998). In addition to contributing to lowering abundances, the construction of impassable river impoundments on many of the primary salmon rivers in the Central Valley has caused the breakdown of the spatial segregation between the spring and fall runs, in particular, leaving them susceptible to introgression. Major dams, such as Friant and Oroville dams, prevent spring-run Chinook salmon from entering historical spawning grounds in the upper reaches of rivers, relegating remaining spring-run salmon to the lower river reaches typically used by fall-run salmon for spawning. Because of the temporal overlap between the spring- and fall-run spawning periods, these two runs are particularly vulnerable to introgression, which may compromise the genetic integrity of the two runs and the degree of genetic diversity between populations.

Several studies have identified genetic distinctions between the spring and fall runs in the Central Valley (Nielsen et al. 1994; Kim et al. 1999; Banks et al. 2000; Garza et al. 2008). There remains considerable spatial genetic diversity within the spring run, with the individual tributaries retaining unique genetic signatures (Garza et al. 2008). Feather River spring-run salmon have experienced significant introgression with fall-run salmon and genetically group most closely with the Feather River fall-run salmon rather than other extant populations of spring-run salmon (Garza et al. 2008). The fall run has consistently

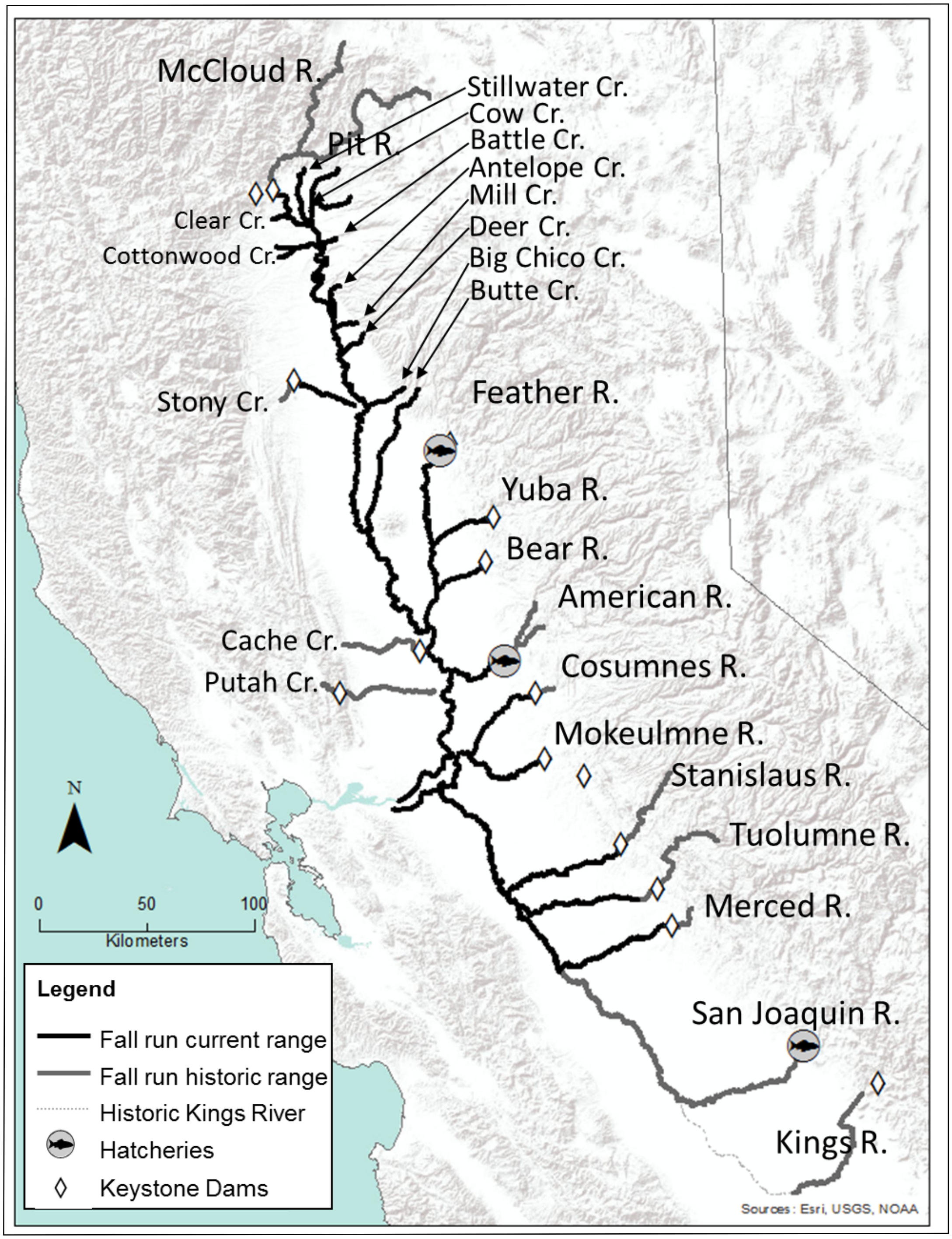

Figure 1 Current and historical Central Valley fall-run Chinook salmon distribution. The current distribution, shown in solid black, is overlaid on the historic distribution, shown in dark grey. Historical connection between the Kings and upper San Joaquin rivers is shown by the dotted light grey line. Keystone dams, defined as the first major barrier to anadromy, are indicated by open diamonds or by circle with fish icons to denote associated hatcheries, as in the case of Friant Dam on the San Joaquin and Oroville Dam on the Feather River. (Source: data derived from Schick et al. 2005)

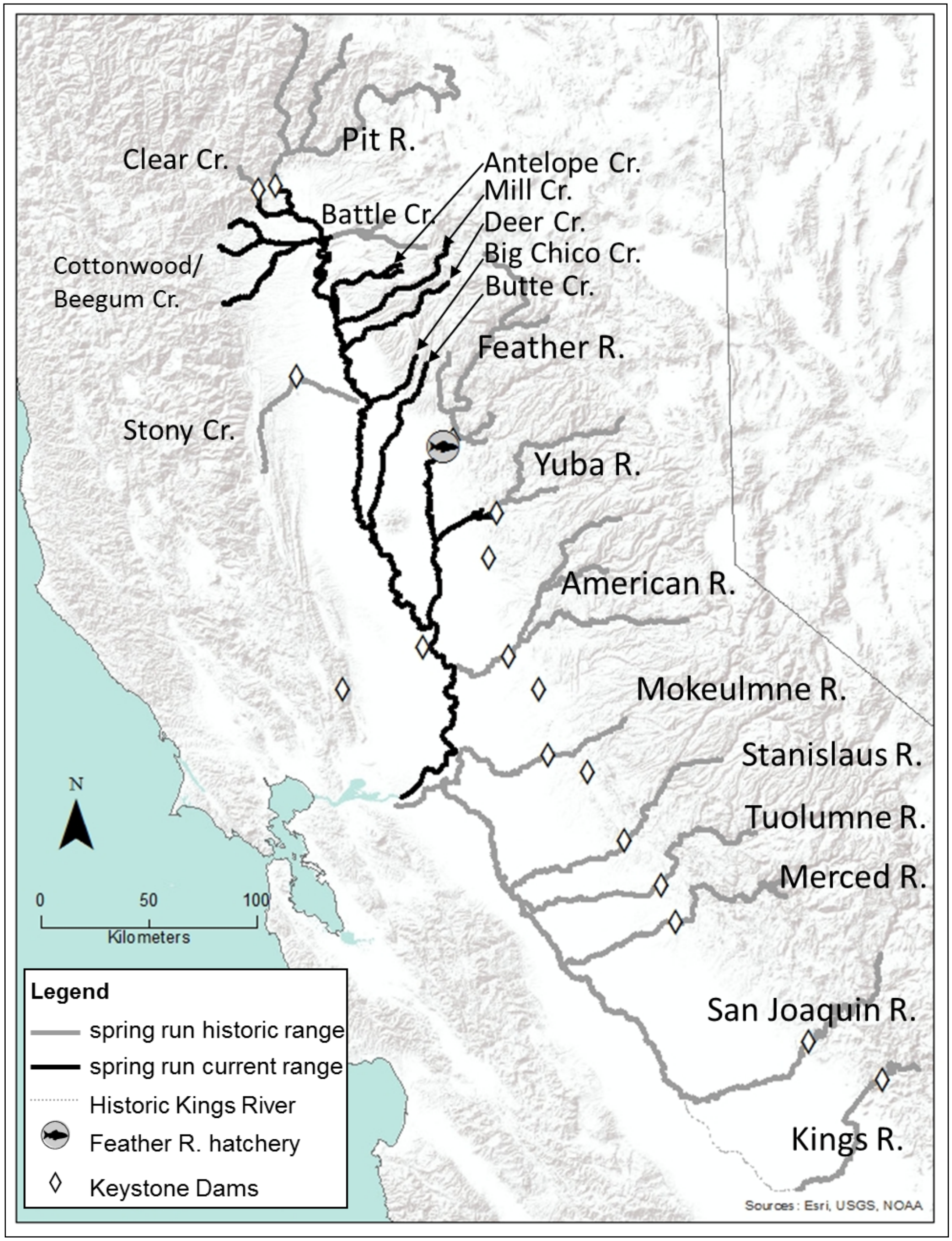

Figure 2 Current and historical Central Valley spring-run Chinook salmon distribution. The current distribution in solid black is overlaid on the historic distribution in light grey. Keystone dams, defined as the first major barrier to anadromy, are shown by open diamonds. Feather River Hatchery is likely to be used as the source population for spring-run Chinook salmon reintroductions to the San Joaquin River. (Source: data derived from Schick et al. 2005)

been found to have little spatial population structure and demonstrates a high rate of gene flow between Central Valley tributaries (Williamson and May 2005; Garza et al. 2008).

The San Joaquin River is the southern-most extent of Chinook salmon's native range in North America and once supported productive fall and spring Chinook salmon runs (Myers et al. 1998; Yoshiyama et al. 1998). Massive agricultural water exports greatly altered the natural river hydrology and had a particularly devastating effect on the San Joaquin River fish community. With the construction of Friant Dam in 1942 (Figure 3), 100% of the water in the upper San Joaquin was designated for agricultural use (Yoshiyama et al. 1998), and stretches of the river ran dry, extirpating both the spring and fall runs from the upper San Joaquin River. A modest number of fall-run salmon has persisted in the lower San Joaquin River and its tributaries; however, despite hatchery support on the Merced and Mokelumne rivers, spawning adult populations have continued to decline. Returns have increased modestly in recent years, but remain far below their historical levels (Yoshiyama et al. 2001; Azat 2012).

The San Joaquin River Restoration Program

The San Joaquin River Restoration Program (SJRRP) is a comprehensive multi-agency effort to restore water flows and healthy fish populations to California's upper San Joaquin River. In 2006, the Natural Resources Defense Council obtained a settlement agreement[1] in their lawsuit against the U.S. Bureau of Reclamation that resulted in a mandate to restore both spring-run and fall-run Chinook salmon to the upper San Joaquin River, between Friant Dam and the confluence with the Merced River, by December 2012 (NRDC et al. v. Kirk Rodgers et al. 2006). This region, referred to as the "Restoration Area," is shown in Figure 3. In fall 2009, water releases were initiated to restore continuous water flows from Friant Dam to the Sacramento–San Joaquin Delta. Chinook salmon are expected to return to the upper San Joaquin River in the coming years, either through direct reintroductions or natural recolonization by strays from populations in the Central Valley. The San Joaquin River Salmon Conservation and Research Facility—hereafter referred to as the Conservation Facility—is being used to propagate fish for release and will aid in the reintroduction of spring-run and fall-run Chinook salmon to the San Joaquin River.

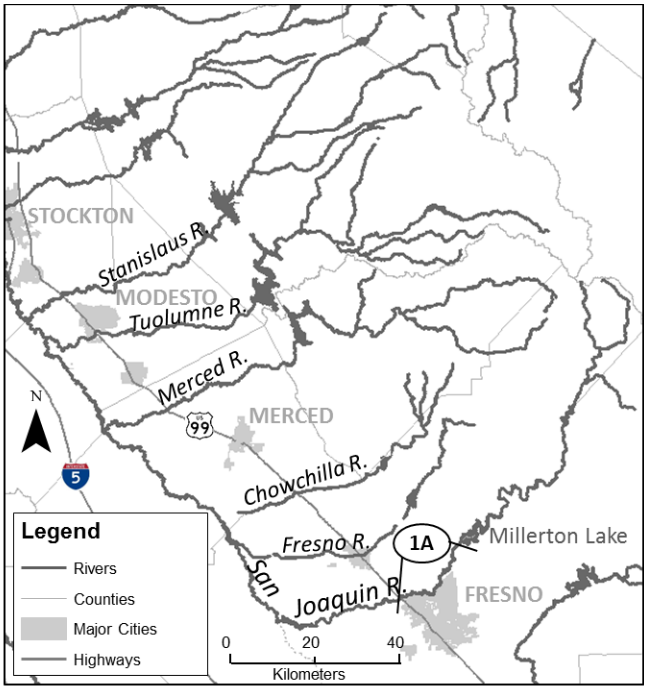

Figure 3 The San Joaquin River Restoration Area is located between Millerton Lake and the confluence of the Merced River and the San Joaquin River. Reach 1A is denoted by hash marks and is the likely site of future in-river spawning grounds.

A stated goal of the SJRRP is to restore fall-run and spring-run Chinook salmon populations that (1) are specifically adapted to conditions in the upper San Joaquin River, (2) are genetically diverse, (3) are demographically diverse, and (4) and show no significant signs of hybridization with each other or with non-target hatchery stocks. As the spring-run ESU is federally listed under the Endangered Species Act

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[1] Full text of legal settlement agreement available from: *http://www.revivethesanjoaquin.org/sites/default/files/Settlement%20Agreeent%20Final.pdf*

(ESA), here we make the assumption that the spring run will continue to be prioritized over federally unlisted fall-run Chinook salmon during the restoration (FMWG 2010).

Hybridization and the San Joaquin River Restoration Program

One of the most obvious challenges to meeting the goals of the restoration is that the San Joaquin River is likely to effectively hold only one ecological niche for Chinook salmon. In contrast to the historical San Joaquin River, in which the spring run spawned upriver of present-day Friant Dam, both spring- and fall-run salmon will be confined to the geographic area formerly used by fall-run salmon for spawning. Spawning habitat availability in the Restoration Area is likely to be initially scarce, with the majority of salmon expected to spawn in Reach 1A (river mile 267–243) (Meyers 2012; TAC 2009). Competition for limited spawning sites and superimposition of redds may increase the incidence of hybridization between the reintroduced spring and fall runs. Maintaining two phenotypically and genetically distinct runs in that environment is likely not possible without intensive and sustained management.

Although some level of historical hybridization between runs may have naturally occurred, in the absence of genetic analysis of samples pre-dating the construction of Friant Dam, it is impossible to estimate historic levels of introgression in this system. However, in the absence of evidence for historical introgression, limiting hybridization between the spring and fall runs in the San Joaquin is the conservative approach, particularly given the potential negative consequences of rampant admixture between runs. Outbreeding of locally adapted stocks can result in reductions in fitness (outbreeding depression) and loss of local adaptation, as well as reduction or loss of original run phenotypes (Edmands 2007); however, it is difficult to predict which outcrosses will have negative fitness consequences (McClelland and Naish 2006). Low levels of gene flow between populations have proven beneficial in selected situations where populations suffer from inbreeding depression and local adaptation is not strong, by providing an infusion of genetic diversity (Verhoeven et al. 2011). From a policy standpoint, hybridization between runs may have negative implications for protection of the ESA-listed spring-run ESU, which further supports avoiding hybridization between the spring and fall runs. Currently, there is no universal policy for how to treat hybrids under the ESA and a large degree of genetic introgression with a non-listed ESU may be grounds for reconsideration of ESA protection (Allendorf et al. 2001, 2004).

Both the Feather and Trinity rivers provide examples of dammed systems in which spring-run and fall-run Chinook salmon exhibit introgression as a result of habitat compression from dam construction (Fisher 1994; Kinziger et al. 2008). Lewiston Dam was constructed on the Trinity River in 1964, cutting off the spring run from its historic upstream spawning grounds, likely contributing to observations of introgression between spring-run and fall-run individuals (Kinziger et al. 2008). On the Feather River, spring-run fish began spawning below Oroville Dam after its construction in 1968 (Lindley et al. 2004). Because of compaction of habitat below the dam and hatchery practices that failed to distinguish between (or intentionally crossed) the spring and fall runs, the Feather River spring run has significant historical and ongoing hybridization with fall run (Fisher 1994) individuals. Genetic analysis of putatively neutral loci suggests that the Feather River fish which exhibit a spring-run phenotype have been heavily introgressed with fall-run genes (Garza et al. 2008), to the point that they group genetically with fall-run fish, yet still hold a remnant of the spring-run genetic signature. The Feather River is of particular interest because the Feather River Hatchery has been selected as the likely source of spring-run broodstock for San Joaquin River restoration (Bork and Adelizi 2010; Baerwald et al. 2013).

Feather River migration phenotypes reflect the observed genetic hybridization between the spring and fall runs. Tagging studies performed at the

Feather River Hatchery have found that some offspring from Feather River spring-run matings return as fall-run fish, and vice versa (California Department of Fish and Game 1998). From 2004 to 2007, hatchery offspring from spring-run parents and fall-run parents were tagged with coded wire and their return times were recorded to test run–time fidelity (Cavallo et al. 2009). Over this period, an average of 17.6% (range 6% to 32%) of the selected fish returning in the spring period had fall-run parents. During the same period, the selected fish returning in the fall period had spring-run parents an average of 50.9% (range 28% to 62%) of the time (Cavallo et al. 2009). Thus, the extensive hybridization in the Feather River appears to correlate with significant crossover between the spring-run and fall-run phenotypes. Because genetic data from before construction of Oroville Dam is unavailable, the natural level of hybridization and crossover between these populations is unknown. A spring-run phenotype (i.e., arriving early and spawning in fall) currently persists among Feather River Chinook salmon in spite of hybridization, although this may in part be a result of the Feather River Hatchery's breeding program, which is designed to select for two distinct phenotypes.

Certain conditions in the Restoration Area will likely be similar to those in the Feather River. Overlap in migration timing and lack of spatial separation between mature spring-run and fall-run Chinook salmon will likely create conditions that encourage introgression. In the absence of measures to prevent interbreeding, this introgression will almost certainly lead to the loss of distinct fall-run and spring-run phenotypes and/or genotypes. Introgression may lead to a hybrid swarm in which either or both run phenotypes are lost and the population consists predominantly of hybrids. Alternatively, run timing phenotypes may be preserved, but the genetic distinction between runs may be lost. In this case, genetically spring-run fish may spawn in the fall and genetically fall-run fish may spawn in the spring, similar to the situation in the Feather River. Measures to protect the spring-run phenotype and associated genotypes will likely require both use of an effective fish weir to physically separate the runs as well as adoption of practices that identify and exclude fall-run fish from spring-run matings in the conservation facility.

Given the goals of the restoration and the ecological realities of the restored San Joaquin River, managers face a number of choices as they reintroduce and maintain Chinook salmon populations in the Restoration Area. These challenges are not unique to the San Joaquin River and include deciding on method of reintroduction (passive versus active), the degree of hatchery support, and the degree of sustained intervention required to meet population targets. With the current trend of dam removals in the Pacific Northwest and restoration projects aimed at aiding struggling salmonid populations (Brenkman et al. 2012; Crane 2011), managers elsewhere will likely be faced with similar questions of how best to repopulate newly reopened river habitat. Strategies range from passive reintroductions to direct and intensively managed reintroduction. Here we discuss three types of reintroduction options for the San Joaquin that fit into the continuum of minimal to intensively managed strategies.

Strategy #1: Passive Reintroduction

In a passive reintroduction, habitat is reopened and fish are allowed to recolonize the area naturally. In the San Joaquin River, this would likely lead to recolonization by fall-run individuals because of their increased prevalence in the San Joaquin River system, the fact that the reopened habitat corresponds to historical fall-run habitat, and the high observed straying rates of Central Valley fall-run Chinook salmon. One of the factors that affects escapement by strays is water quality: straying fish tend to enter rivers with higher water quality (Quinn 1993). The water flow out of the San Joaquin River into the Delta can be composed of more than 20% agricultural runoff during dry periods (Nichols et al. 1986). The high contaminant input—in the form of salts, selenium, and boron—to the San Joaquin River is one of the most important factors that affects ecosystem health in the Bay–Delta system (Quinn et al. 2004). As the water quality of the San Joaquin improves with increasing flows during the restoration period, larger numbers of strays may be expected in the San Joaquin River. The potential for large numbers of fall-run strays to enter the Restoration Area necessitates a plan for how these fish will be managed. It is likely that a fall-run Chinook salmon population would re-establish itself in the Restoration Area, but unlikely that a spring-run population would naturally recolonize, given the absence of historic spring-run habitat or any nearby current spring-run populations.

A passive approach would have mixed outcomes for the restoration effort. The goal to establish a spring-run Chinook salmon population would likely not be met. In addition, the speed of a fall-run re-colonization is unknown. A population may reestablish itself within a few years, as they are expected to in the case of the removals of Elwha Dam and Glines Canyon Dam on Washington's Elwha River (Peninsula Daily News 2012). However, it could also take several years for a viable population to re-emerge in the San Joaquin River, perhaps not meeting the time-frame mandated by the legal settlement. On the other hand, this strategy might yield the best outcome in terms of not only reintroduction of Chinook salmon to the San Joaquin River, but also conservation of the evolutionary processes of the species. Allowing a new population to evolve within the ecological conditions of the current San Joaquin River would likely lead to a more locally adapted population than would be produced by hatchery supplementation (Taylor 1991). Passive reintroduction would likely meet restoration goals of having a locally adapted Chinook population, however it would likely not lead to the establishment of a spring-run population in the Restoration Area. The emphasis on restoring spring-run Chinook salmon makes this a less desirable option for the restoration program and will not be implemented in this case; however this option may be useful for other reintroduction programs.

Strategy #2: Assisted Reintroduction

An assisted reintroduction strategy in the San Joaquin River would involve the use of a conservation hatchery to propagate and actively release spring-run fish into the river. In this scenario, passive re-colonization by fall-run salmon would likely also occur for the reasons listed above. If both spring-run and fall-run salmon were present in the Restoration Area, hybridization between spring-run and fall-run individuals would likely be a major issue. It is possible that run-timing segregation could arise naturally through differences in habitat preference or behavioral differences between the runs; however, this is unlikely because of the truncated region of suitable salmon habitat in the Restoration Area. Without the existence of geographically and ecologically separate niches for the fall and spring runs, there likely will not be a selective force strong enough to maintain the different runs.

In the absence of any managed separation, a likely result is a heavily admixed population of both spring-run and fall-run origin. The risks associated with this strategy are substantial, the first being the risk of fall-run fish impeding establishment of a spring run in the Restoration Area. Second, there is a much greater risk of introgression between runs, which may be impossible to reverse once present in the system. Lastly, strays from a hybridized San Joaquin River run might negatively affect the genetic integrity of Chinook salmon in other Central Valley tributaries.

The use of a hatchery may also negatively affect the fitness of the introduced population, and continued supplementation may hinder the process of local adaptation. A growing body of evidence suggests that hatchery-reared fish display lower fitness than their naturally reproducing counterparts (Araki et al. 2008). A recent study of steelhead (*Oncorhynchus mykiss*) found that even one generation of hatchery rearing led to a significant loss of reproductive success in the wild (Christie et al. 2012). Hatchery rearing tends to lead to lower rates of survival, growth, and reproductive success, as well as reductions in genetic diversity and effective population size (Araki and Schmid 2010). However, this is a controversial topic in ecology, and there is also evidence that not all hatchery supplementation has negative effects on wild fish (Waples 1999). Limited use of a conservation hatchery could benefit a newly established population. See the *San Joaquin River Hatchery Genetic Management Plan* for guidelines aimed at reducing the potential negative effects of hatchery influence while offering a means to supplement the San Joaquin River (Bork and Adelizi 2010).

Intraspecific competitive interactions between hatchery and natural-origin fish are known to occur (reviewed in Tatara and Berejkian 2012), and may be relevant in the Restoration Area if hatchery fish of either spring-run or fall-run origin are allowed to enter the upper San Joaquin River during the time that spring-run or fall-run Chinook salmon of natural origin are spawning. For example, Chinook salmon experiments in Alaska have demonstrated higher levels of agonistic behavior by both hatchery-origin stocks and hatchery–wild hybrids when compared to wild-origin stock (Wessel et al. 2006). Williamson et al. (2010) showed that hatchery-origin fish produce half the number of progeny per parent compared to natural-origin, spring-run Chinook salmon when spawning in the wild; their observed correlations between fitness and several variables (size and age, upstream spawning location, and early run timing) suggest that if hatchery-origin fish are allowed to out-compete fish of natural origin during spawning, the mean population fitness will decline.

This is a complicated situation given the high level of hatchery influence on extant salmon populations in the Central Valley, but it is an important topic and warrants consideration. The potential harm of continued hatchery influence on restoration populations should be carefully weighed against the potential benefit. If a spring-run population is to be established, some hatchery supplementation will be necessary. While some hatchery influence is unavoidable, reducing the period of active hatchery supplementation by the conservation facility, and implementing measures to improve hatchery practices in all Central Valley facilities, may reduce the potential negative effects of hatchery-origin fish on the San Joaquin Chinook population (see CHSRG 2012 for recommendations). Once a naturally reproducing population has been established, hatchery supplementation should cease or be kept to a minimum to allow the in-river population to locally adapt.

The assisted reintroduction strategy would meet some of the goals of the restoration, but would fall short of others. Hatchery-assisted establishment of a spring-run population could allow for the introduction of genetically diverse individuals, improving the chances of establishing a genetically diverse local population. The use of active reintroduction is almost certainly necessary to met the goal of having spring-run individuals in the Restoration Area because it is unlikely that a spring-run population will be re-established through straying. However, the goal of having two non-introgressed runs is less likely to be accomplished in this scenario. The presence of what is effectively a single ecological niche will almost certainly lead to some level of hybridization between spring-run and fall-run salmon, potentially leading to a hybrid swarm.

Strategy #3: Intensive Reintroduction

Perhaps the single most important challenge to maintaining two separate fall and spring runs in the San Joaquin River is the loss of spawning grounds upstream of Friant Dam, historically used by spring-run Chinook salmon. Without natural spatial and temporal separation of the spring and fall runs, it will likely be impossible to maintain two distinct runs without sustained management and imposition of spatial segregation during spawning. In an intensive reintroduction scenario, managers would depend on the use of one or more seasonal weirs to segregate the spring and fall runs during spawning periods, leading to artificial selection for two populations.

The Hills Ferry Barrier (HFB) is a sliding pipe weir, intended to prevent adult salmon from ascending into the upper San Joaquin River. It is located on the main stem San Joaquin River, roughly 150 meters upstream from the confluence with the Merced River, and is installed on private land based on annual temporary access agreements (Gates 2007). Since 1992, the California Department of Fish and Wildlife (CDFW, formerly CDFG) and the California Department of Water Resources (CDWR) have been operating the barrier annually from mid-September to early December (Gates 2007, 2011).

Monitoring of the HFB showed that salmon that encounter the barrier when it is in place may go (1) up the Merced River; (2) back downstream into the mainstem San Joaquin River, where some may ascend other lower San Joaquin River tributaries (e.g., Tuolumne River); or (3) escape through the barrier up to the Restoration Area (Portz et al. 2011). Evaluation of HFB operation under increased San Joaquin River restoration flows starting in 2010 shows that the barrier is ineffective and requires redesign or possibly relocation to a more suitable location to prevent salmon from moving into the upper San Joaquin River (Portz et al. 2011). It is questionable whether logistically feasible weir locations exist or whether construction would impose unnecessary habitat destruction to spawning gravels. For the sake of discussion, here we make the assumption that such weirs could be built and operated in the Restoration Area. The feasibility of placement, construction, and operation of one or more effective, seasonal weirs on the San Joaquin River is outside the scope of this discussion, and should be addressed elsewhere.

One possible use of weirs could involve the operation of a single seasonal weir to allow spring-run salmon to move into the Restoration Area but then later to exclude fall-run salmon access. Because of the overlap in the natural spawning times of the fall and spring runs, the use of a single weir could likely exclude the majority of fall-run salmon but would necessitate the use of a somewhat arbitrary cut-off date to mark the end of the spring-run migration and the start of the fall-run migration, after which the weir would be closed and fish would be excluded from entering the upper San Joaquin River. In this scenario, depending on the choice of weir closure date, some spring-run salmon would either be excluded or some fall-run salmon would be erroneously admitted to the Restoration Area. Installing a weir at a date when the majority of spring-run fish have passed could be achieved using guidance from other systems (Kinziger et al. 2008) and other Central Valley spring-run populations (Williams 2006; Cavallo et al. 2009). This scenario would reduce, but not completely eliminate, the hybridization concern. It would also prevent the natural establishment of a fall-run population, because of the absence of spawning habitat below the Merced River confluence.

To meet the goal of having two genetically and phenotypically distinct runs, managers may need to use multiple weirs to tightly control individual access to spawning areas. This is no simple task because we cannot definitively assign individuals to either the spring run or fall run without the use of genetic identification at the weir. Even for individual genotypes that have current marker panels, we are unable to consistently and accurately assign individuals when high levels of introgression have already occurred (Garza et al. 2008). In the San Joaquin River, spring-run fish used in the conservation hatchery will likely be of Feather River Hatchery origin (Bork and Adelizi 2010; Baerwald et al. 2013). Because of the historical hybridization between the fall and spring runs in the Feather River system, genetic stock identification will continue to be a challenge.

The SJRRP Technical Advisory Committee recommends using later-returning fall-run salmon and/or late fall-run salmon to establish fall and spring runs with increased temporal distinction in the Restoration Area (TAC 2009). Selection for late-fall fish would minimize overlap with spring-run fish. This approach would ideally lead to the establishment of temporally separated runs. One advantage of this option is that it may allow the establishment of both spring-run and fall-run Chinook salmon in the Restoration Area; however, because this strategy is based on run timing and not genetic assessment, the spring and fall runs that develop may not preserve the historical genetic distinction between runs, as is the case in the Feather River.

Another option that would require intensive management employs a permanent weir with fish passage, allowing inspection of each fish and permitted passage of only marked Chinook salmon. This option requires that juveniles be marked comprehensively upon outmigration from the Restoration Area so they could be selected for access as returning adults. It would require all outmigrating juveniles to be tagged before they exited the Restoration Area, since some spring-run fish are expected to be spawned naturally in the river and would lack a mark from the conservation facility. This scenario could be applied to allow only spring-run individuals into the Restoration Area, or allow only spring-run fish access up to a certain cutoff date, after which all fish could pass. A conservative approach would be to start with only spring-run access and then use adaptive management to determine an appropriate cut-off date to use. The benefits of this strategy would be increased control over the individuals spawning in the Restoration Area at certain times and the ability to exclude spring-run and fall-run strays. One disadvantage of this option is that it would prevent the establishment of a fall-run Chinook salmon population in the Restoration Area, at least initially. If fall-run salmon are allowed access to the Restoration Area after a cutoff date, there is still the potential for hybridization between the fall run and late-spawning spring run populations.

An intensive, artificial selection scenario would only meet some of the stated goals of the restoration. It could lead to the establishment of phenotypically and genotypically distinct runs and limit introgression. The populations may become locally adapted, but only to the artificial conditions imposed by managers. This intensive level of management would need to continue indefinitely. If intensive management were to cease, the selection pressures would change and there would likely be extensive interbreeding between the two runs that would then occupy the same ecological niche.

Meeting Restoration Goals

None of the reintroduction strategies listed above would lead to a total fulfillment of all of the stated SJRRP goals. There are trade-offs for each scenario and in this case, managers will need to decide which goals to prioritize. This is an example of a legally mandated set of reintroduction goals that is not fully compatible with the biological realities of the target species, nor the ecological realities of the restored habitat. There does not appear to be a strategy that would completely meet the legal settlement's expectations. Taken within the context of salmonid evolution, it is somewhat unreasonable to expect the truncated habitat of the upper San Joaquin to support two distinct salmon runs, which evolved to fill two very different ecological niches that are no longer present, without some level of artificial selection imposed by the use of weirs.

GENETIC MONITORING

Regardless of the direction managers take in the case of the San Joaquin River, genetic monitoring can provide valuable information about the outcomes of different management options and about the overall health of a newly established population. Genetic monitoring is a critically important, but often neglected, aspect of large-scale reintroductions (Laikre et al. 2010) and it is imperative that conservation and restoration efforts conduct sufficient monitoring to evaluate the success of reintroduction methods. To gauge the success of Chinook salmon restoration and better predict long-term sustainability in the San Joaquin River, the following objectives are recommended for monitoring:

1. Identify recolonizer origins.
2. Evaluate genetic diversity indices of the fall-run and spring-run populations in the Restoration Area.
3. Detect hybridization between the fall and spring runs, if possible.

4. Quantify survival and recruitment of Chinook salmon releases from the conservation facility.
5. Detect signatures of selection and local adaptation.
6. Create a shared Central Valley Chinook salmon database.

We recommend the implementation of a comprehensive genetic monitoring program in the San Joaquin River that would entail the sampling of all hatchery fish released into the river, the parents of these fish, and all individuals returning to the San Joaquin River (see Box 1 for specific monitoring suggestions). This would require a large commitment to sample collection, but would yield valuable information about the outcomes of the reintroduction effort. A comprehensive single nucleotide polymorphism (SNP) genotyping program would allow for the assessment of genetic health of San Joaquin River Chinook salmon populations. This data would allow for yearly assessment of genetic diversity indices and the identification of trends in changing levels of genetic diversity or inbreeding in the population (Baerwald et al. 2013). A comprehensive monitoring program would also enable the use of parentage-based tagging (Anderson and Garza 2006). If conducted from the initiation of reintroduction efforts, this type of sampling regime would enable a pedigree reconstruction of the newly forming San Joaquin River population(s). This information would allow managers to evaluate the success of hatchery releases, determine the proportion of returning fish that were naturally spawned in the Restoration Area, and identify straying rates into the upper San Joaquin River from other tributaries. Unfortunately, the current 96-SNP panel widely used in the Central Valley cannot reliably distinguish fall-run individuals from Feather River spring-run Chinook salmon, likely because of the extent of historical admixture in that river. This will be problematic if Feather River spring-run Chinook salmon are used as the broodstock source for spring-run supplementation. The advancement of sequencing technology has made the development of SNP markers much easier, and may enable more precise genetic stock identification (M. Meek, UC Davis, unpublished data).

Box 1: Recommended Genetic Monitoring

1. If feasible, use genetic stock identification or parental-based tagging to identify and track the origin of re-colonizers.
2. Conduct otolith microchemistry analysis on a subset of spawned carcasses to assess trends in spawner origin in the Restoration Area (Kawamura et al. 2010)
3. Identify and monitor introgression between spring- and fall-run individuals using genetic markers, as possible.
4. Conduct initial yearly assessment of genetic diversity indices (Ne, Nc, Ho, He, LD, FIS, FST, etc.) in both natural fall-run re-colonizers and actively released fish, until returns reach targets set by the SJRRP.
5. Continue assessment of genetic diversity indices every 3 to 4 years during the later stages of the reintroduction.
6. Coded-wire tag (CWT) all juveniles released into the Restoration Area.
7. Assess survival, recruitment, and straying rates of released fish annually via CWT data.
8. Otolith mark eyed eggs if used for reintroduction in-river so return rates of these fish can be assessed upon carcass survey.
9. Identify and assess genes that are important for local adaptation, as methods improve.

As techniques in the field of population genetics and genomics continue to advance, so too should the methods used to monitor populations. As genetic analyses of Central Valley Chinook salmon continue, we may one day be able to achieve more precise genetic stock identification and reliable assessment of the Feather River spring run versus the fall run. Future analysis of the Chinook genome may also enable the identification of genes under selection in the Restoration Area and enhance our understanding of local adaptation. A combination of established and emerging approaches should be considered to maximize the ability to evaluate the genetic integrity of the restored population and gain valuable insight into the strategies that promote or inhibit long-term reintroduction success.

We strongly advocate for the formation of a central common database to house genetic data on Central Valley Chinook salmon, and possibly other California salmonids. Such a database would facilitate information exchange among researchers, government agencies, and organizations, and would eliminate unnecessary duplication of research efforts. The Genetic Analysis of Pacific Salmonids (GAPS) consortium (Seeb et al. 2007) provides a model for the development of a similar data consortium for California. Ideally this database consortium would include academic institutions and state and local government agencies involved in salmonid research. Sufficient funding would be needed to create and maintain such a database and could potentially be funded through user membership.

CONCLUSION: LESSONS OF THE SAN JOAQUIN FOR FUTURE RESTORATIONS

Reintroductions often occur in a complex landscape where they must incorporate knowledge of historical processes and contemporary ecological pressures to build a population that will be successful into the future. The reintroduction of Chinook salmon to the San Joaquin River is an example of a case in which the desire to maintain separate runs must be balanced with the threat of likely introgression. The complexity of the San Joaquin River Restoration cannot be overstated, given the admixed genetic background of fish likely to be reintroduced, the level of straying in the Central Valley, the planned active introduction of spring-run Chinook salmon, and the potential future passive recolonization by fall-run individuals. The restoration has three types of options for reintroduction strategy: passive, assisted, or intensive. Our view is that it is unlikely that any one of these options will achieve all of the program goals. Given our knowledge of Chinook salmon history and biology, the program must weigh the trade-offs of different approaches to define reintroduction priorities and select a strategy that is likely to succeed in the current political and legal climate. The Restoration Area is a blank slate for the establishment of new salmonid populations and offers the ability to evaluate the success of reintroduction and management strategies, given adequate monitoring. We hope this case will provide an example to inform future salmonid restoration efforts facing similar genetic concerns.

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