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Genetic Considerations for Sourcing Steelhead Reintroductions: Investigating Possibilities for the San Joaquin River

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ABSTRACT

Steelhead trout (*Oncorhynchus mykiss*) historically occurred in all major watersheds along the west coast of the United States. They can be a vital part of a healthy riverine ecosystem, are highly valued for fishing, and have been greatly affected by human activities. Given these traits, and that the San Joaquin River in the Central Valley of California is under consideration for steelhead reintroduction, emphasis has recently been placed on conservation efforts to reintroduce steelhead into streams in which they were once native. There are many issues to consider when deciding how, where, and in what manner to reintroduce steelhead, including genetic considerations. One primary factor is determining the source population for reintroduction. In this paper, we consider the many important genetic aspects to consider when determining the source for steelhead reintroduction, and outline the genetic data needs when determining sources for reintroduction. We discuss the lessons learned from previous reintroductions in relation to a reintroduction scenario in the San Joaquin River, and recommend potential source populations.

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KEY WORDS

Steelhead, reintroduction, genetic management, hatchery, rainbow trout, restoration, San Joaquin River, anadromy, *Oncorhynchus mykiss*

INTRODUCTION

Steelhead trout (*Oncorhynchus mykiss*) historically occurred in all major watersheds along the west coast of the United States. They can be a vital part of a healthy riverine ecosystem, are highly valued for fishing, and have been greatly affected by human activities (McEwan 2001). Given these traits, conservation efforts to reintroduce steelhead into streams to which they were once native have recently been emphasized (Busby et al. 1996). There are many issues to consider when deciding how, where, and in what manner to reintroduce steelhead, including genetic considerations. Conserving genetic diversity and the evolutionary processes that generate, preserve, and maintain diversity (sensu Moritz 2002) is particularly relevant to steelhead reintroduction efforts. Genetic diversity has been correlated with species' resilience to disturbance (Reusch et al. 2005; Worm et al. 2006) and fitness (Reed and Frankham 2003); loss of diversity and inbreeding depression can

limit adaptive response, reduce tolerance to environmental stress, and cause life history and morphological changes (Bijlsma and Loeschcke 2012; Naish et al. 2013). Genetic diversity in salmonid populations provides many valuable functions, including maximizing potential for populations to adapt to environmental change, increasing population viability, and reducing the likelihood of extinction (reviewed in Fraser 2008). Through careful genetic planning, some of the roadblocks associated with reintroduction efforts (i.e., inbreeding or outbreeding depression, genetic bottlenecks) can be successfully navigated or avoided and the probability of success can be greatly improved (Huff et al. 2011; Witzenberger and Hochkirch 2011). One primary factor in genetic planning is determining the source population for reintroduction.

Oncorhynchus mykiss has a very diverse life history, with two ecotypes: an anadromous form ('steelhead') and a freshwater resident form ('rainbow' or 'redband' trout). While there often is not complete separation between the two ecotypes (see the "Above-Barrier Versus Below-Barrier Sources" section for a full discussion), our focus here is on reintroduction efforts of the imperiled steelhead (*O. mykiss irideus*) life history. Steelhead from Washington, Oregon, and California spend, on average, 2 years in freshwater before smolting and migrating out to sea (Busby et al. 1996). Hatchery-raised juveniles usually smolt after 1 year because of hatchery conditions that increase growth. After outmigration, steelhead generally spend 1 to 3 years (predominantly 2 years) in salt water before returning to their natal stream to spawn. The timing of the spawning migration varies by location and run, with the different runs named for the timing of freshwater entry (winter, spring, summer, and fall run steelhead). Unlike most Pacific salmonids, steelhead are iteroparous with the ability to spawn multiple times; however the frequency of multiple spawning varies among populations (Busby et al. 1996). Most of the steelhead Distinct Population Segments (DPSs, formerly classified as Evolutionary Significant Units [ESUs]) on the west coast of the United States are listed as threatened and/or endangered under the U.S. Endangered Species Act (Fed.

Reg. 50 CFR Parts 223 and 224, Jan. 5, 2006), while resident stocks of *O. mykiss* are thriving and have been introduced in almost all the water bodies in California (Moyle 2002).

In this paper, we explore the many genetic considerations associated with choosing a source population for steelhead reintroduction efforts. Our broad goal is to present for the first time in one paper all the relevant genetic information for considering a steelhead reintroduction source. We first conduct a broad literature review relevant to steelhead reintroductions in general and then use the San Joaquin River reintroduction scenario as a case study. In our analysis and recommendations, we assume that reintroduction efforts are for conservation, and reintroductions are only being considered in ecosystems where steelhead were once native members of the community. We first review the relevant literature concerning sources for steelhead reintroductions, considering naturally produced populations—both within-basin and out-of-basin sources and above-barrier versus below-barrier populations—along with hatchery produced sources. We also discuss the numbers needed to start a reintroduction effort and issues associated with using one or multiple source populations. We outline the general genetic data needed to evaluate potential source populations for steelhead reintroduction efforts and then, as a case study, discuss the steelhead reintroduction scenario in the San Joaquin River, which is currently undergoing a large-scale restoration project via the San Joaquin River Restoration Program.

Many additional factors have to be considered when a population is reintroduced, such as risk of disease transfer, effects on source populations, habitat suitability of release sites, and release strategies. We do not evaluate these factors in this paper, but they should be thoroughly considered before a reintroduction effort is initiated. Additionally, there are scenarios where it may be preferable to allow natural re-colonization to occur through removing dams, adding fish passage, and/or restoring/re-watering habitat, rather than through active reintroduction.

The purpose of this paper, however, is to investigate the genetic considerations for determining source populations when an active reintroduction has been decided upon.

WILD POPULATIONS

When wild populations are being considered to source a steelhead reintroduction, programs can evaluate within-basin and out-of-basin sources, as well as populations that occur above and below barriers to migration. Each of these potential sources has different genetic considerations that must be evaluated.

Within-Basin Versus Out-of-Basin Sources

"Local" or within-basin sources are frequently recommended when potential sources for reintroduction are considered (IUCN 1998; HSRG 2004; Fraser 2008). Strong legal (Allendorf et al. 2001) and biological justifications exist for staying within a DPS when a reintroduction source is selected, and the use of within-basin local sources, where available, can be a more conservative approach to reintroduction sourcing. Using within-basin sources likely involves fewer genetic and ecological risks (discussed in Young 1999; Garcia de Leaniz et al. 2007), including increased fitness from local adaptation and decreased risks from increased straying. Salmonids typically exhibit strong local adaptation to their spawning environment (Taylor 1991; Adkison 1995; Quinn 2005) and genetic support for local adaptation in *O. mykiss* specifically suggests that it should be considered as a factor in reintroduction efforts for this species (e.g. Narum et al. 2010; Pearse et al. 2011; Miller et al. 2012) because their use as sources may lead to a higher probability of reintroduction success. Local or within-basin salmonid sources originate from the same DPS and likely share greater genetic similarity with the historic population or the extant populations near a reintroduction area. However, landscape heterogeneity can result in divergent selection among differing habitats and local adaptation

can be difficult to identify definitively (Fraser et al. 2011).

Additionally, individuals from locally adapted populations stray less than those from transplanted populations (pink salmon: Bams 1976; Chinook salmon: McIsaac and Quinn 1988 and Pascual et al. 1995; coho salmon: Labelle 1992) and the use of non-local sources reared in a hatchery setting can also increase straying rates (e.g., Schroeder et al. 2001). While naturally low stray rates support metapopulation dynamics that can be important for long-term population viability, unnaturally high stray rates can have negative consequences for surrounding populations, including increased introgression (but see Waples 1999 for other important factors). Increased straying may also decrease the likelihood of reintroduction success if fish fail to successfully colonize and migrate back to the reintroduction area.

Several caveats exist for the 'local is best' assertions for reintroductions (reviewed in Weeks et al. 2011). Climate change may yield very different adaptive environments in both the short- and long-term (Sgro et al. 2011), making it difficult to determine which populations will fare best in a reintroduction; however, the ability of salmonids to evolve rapidly in response to climate change has been demonstrated (e.g. pink salmon: Kovach et al. 2012). Additionally, managers' use of presumed locally adapted stocks at the expense of establishing populations with more genetic variation and evolutionary potential may result in the selection of inbred or genetically suboptimal sources (Weeks et al. 2011). Concern over maladaptation of non-local stocks may not warrant primary consideration in a restoration effort; rather, starting genetic diversity, drift, and inbreeding depression could trump local adaptation in importance (reviewed in Stockwell and Leberg 2002).

Despite any possible benefits of using non-local sources, however, the potential negative effects of introducing non-local stocks on extant surrounding populations should always be seriously considered (see the inbreeding/outbreeding discussion in the "Single Versus Multiple Sources" section). The genetic

population structure of any nearby or within-DPS populations should be examined to understand the level of connectivity and similarity among existing populations; this should be used as a guide, to attempt to preserve existing distinctions while fostering genetic diversity (Ryman 1991; McClure et al. 2008). If the effect of a non-local stock introduction on surrounding populations is highly uncertain, it will be better to err on the side of protecting the extant populations. Additionally, it may be best to err on the side of conserving unique genetic assemblages and avoid intentional hybridization between populations, unless there is evidence of inbreeding depression (Edmands 2007).

Applying a 'genetic similarity' criterion for selecting a steelhead donor source population may not be a straightforward process and can be problematic if there are no genetically similar extant populations. In some situations, nearby local or within-basin sources may not be the closest genetically to the historical population in a reintroduction area. There are multiple examples where the proximal *O. mykiss* population does not represent the most genetically similar stock, because of natural colonization processes, anthropogenic alteration of habitat, or introgression from divergent non-native or hatchery lineages (e.g., Garza and Pearse 2008; Pearse et al. 2011). While analysis of historical samples can reveal the historical genetic composition of extirpated populations (e.g., Guinand et al. 2003; Palstra and Ruzzante 2010; Pearse et al. 2011; Iwamoto et al. 2012; see review in Nielsen and Hansen 2008), such samples are not always available or of sufficient numbers or quality for genetic analysis. Furthermore, neutral genetic markers, which are often used to measure similarity, may or may not be a good predictor of organismal survival (see Reed and Frankham 2001) or reintroduction success (Lawrence and Kaye 2011). Therefore, consideration of non-neutral or adaptive genetic variation is also warranted.

Above-Barrier Versus Below-Barrier Sources

One possible source for reintroductions of steelhead is 'residualized' rainbow trout—populations of *O. mykiss* that historically had access to the ocean via downstream migration but have been cut off from the ocean by man-made dams and barriers. Almost all major rivers in California have been dammed. Approximately 80% of habitat thought to have been historically available to anadromous *O. mykiss* in the Central Valley is now behind impassable dams (Lindley et al. 2006). This has both decreased available habitat and left residualized populations trapped above dams with no access to the ocean. It has been proposed that these populations may be good sources for below-dam reintroductions (McEwan 2001; Deiner et al. 2006; Lindley et al. 2006; Hayes et al. 2012), though some have cautioned against their use because the above-barrier populations have been subject to strong selection against anadromy and/or smoltification over many generations (Lindley et al. 2006; Garza and Pearse 2008).

When the feasibility of above-dam populations as reintroduction sources is evaluated, the first question one must address is whether residualized populations can regain anadromy. At the population level, anadromy is not a binary trait with two distinct conditions (anadromous, resident). Rather, it often exists as a continuum, with ancestry and environmental conditions affecting the expression of the trait (Quinn and Myers 2004; Narum et al. 2011; Hayes et al. 2012). This polymorphic life history may be what allows populations to persist in areas with highly variable climate and hydrology (Lindley et al. 2006).

Several studies have found evidence for a genetic basis to anadromy, though there is also evidence for high plasticity in this trait (Nichols et al. 2008; Narum et al. 2011; Martínez et al. 2011; Hecht et al. 2012a, 2012b). The potential for smoltification likely varies by population and studies of residualized populations have shown that the potential for smoltification can remain after many decades of impoundment (e.g. Thrower and Joyce 2004; Hayes

et al. 2012; Holecek et al. 2012). In the Deschutes River (Oregon), Zimmerman and Reeves (2000) analyzed otolith microchemistry signatures and found that female steelhead produce only steelhead offspring and female rainbow trout produce only rainbow trout offspring. However, in the nearby Babine River (Oregon), there are steelhead of maternal resident rainbow trout origin and rainbow trout of steelhead maternal origin (Zimmerman and Reeves 2000). Spawning habitat for the two life history forms is more segregated in the Deschutes River than in the Babine River, which may contribute to this pattern. The ability of resident and residualized *O. mykiss* to produce smolts has also been documented for several additional populations (Ruzycki et al. 2001; Thrower and Joyce 2004; Riva-Rossi et al. 2007; Hayes et al. 2012). In Southeast Alaska, Thrower and Joyce (2004) found that residualized *O. mykiss* that had been trapped behind a dam for 70 years were able to produce smolts, though their offspring had marine survival rates four to five times lower than smolts from anadromous parents. An introduced population of *O. mykiss* in the Santa Cruz River in Argentina was most likely introduced from resident rainbow trout from the McCloud River in California (Riva-Rossi et al. 2004), however both the resident and anadromous form now exist in the Santa Cruz River. They are long-lived, highly iteroparous, and the resident and anadromous forms do not appear genetically distinct (Pascual et al. 2001). Each life history type is able to produce both resident and anadromous offspring (Riva-Rossi et al. 2007). Thrower et al. (2004) found high heritability (i.e. narrow-sense heritability = 0.726 ± 0.134) of smolting in fish from Sashin Lake and Sashin Creek (Alaska), and conclude that the genetic potential for smolting can remain dormant within the genome or can be maintained through an interaction between early maturation and smolting. They state that this potential for smolting can be maintained for decades, even in the face of selection against the anadromous phenotype, suggesting that there may be potential for using residualized rainbow trout to conserve threatened anadromous populations. Environmental conditions can also play a major role

in *O. mykiss* life history determination, because some environmental conditions may favor one form over another (Satterthwaite et al. 2009, 2010; Hausch and Melnychuk 2012; Berejikian et al. 2012).

Studies on the genetic relationships between resident and anadromous forms in the same watershed support the finding that the line between life history types is not clear (Docker and Heath 2003; Narum et al. 2004; Olsen et al. 2006; McPhee et al. 2007). Narum et al. (2004) looked at anadromous and resident forms in the Touchet and Walla Walla rivers, WA. Interestingly, steelhead and rainbow trout within the Walla Walla River are distinct from each other, while the two forms found within the Touchet River are not. Olsen et al. (2006) found no genetic difference between sympatric steelhead and resident *O. mykiss* in Copper River (Alaska), and suggest that geographic proximity— rather than life history type —should be what determines which populations are used in restoration when the two forms are sympatric and genetically similar, but that conservation efforts should work to maintain the two life history forms. Similarly, McPhee et al. (2007) suggest that pristine populations of steelhead will exhibit partial anadromy and they conclude that managing the resident and anadromous forms separately without showing there is reproductive isolation is erroneous.

The second factor to consider when the feasibility of using above-dam *O. mykiss* as reintroduction sources is investigated is the genetic makeup of the above-dam population and relationship to surrounding populations. Available studies show that the relationship between these populations can vary depending on the watershed of interest and its history (e.g. genetic distinction between above- and below-barrier populations: Deiner et al. 2006; Garza and Pearse 2008; Narum et al. 2008; Pearse et al. 2011; genetic similarity between populations: Clemento et al. 2009; Winans et al. 2010). Natural barriers may represent ancient events that led to differentiation between populations within a watershed through vicariance, where man-made barriers are more contemporary and similarities between populations separated by artifi-

cial barriers may remain (Kostow 2003; Deiner et al. 2006). In the Russian River (California) watershed, *O. mykiss* found above man-made dams are not differentiated from their below-barrier counterparts, but all of the populations found above natural barriers are highly divergent from the below-barrier populations (Deiner et al. 2006). In the Central Valley, genetic diversity is higher in below-barrier populations compared to many above-barrier populations, though this may result from the introgression with hatchery strains in below-barrier populations (Garza and Pearse 2008; Pearse et al. 2011). In south-central California, *O. mykiss* above and below dams within the same basin are often the most closely related and there are no differences in measures of genetic diversity (Clemento et al. 2009). In contrast, *O. mykiss* populations in the Pacific Northwest above natural barriers have lower genetic diversity and are distinct from anadromous populations (Narum et al. 2008). In these systems, there is less differentiation among steelhead populations across rivers compared to differentiation between populations above and below-barriers in the same river.

Hatchery stocking history can have a large influence on relationships between above and below barrier populations. In the Central Valley, CA, most of the above-barrier populations cluster together with the San Francisco Bay populations, but the below-barrier Central Valley populations cluster with northern California populations (Garza and Pearse 2008; Pearse et al. 2011). This is most likely results from Central Valley hatcheries using northern California hatchery stocks as broodstock, which then spread throughout the below-barrier populations by straying. Despite this, studies suggest that the wild *O. mykiss* trapped upstream by dam construction have not been replaced by out-planted hatchery rainbow trout (Garza and Pearse 2008; Pearse et al. 2011).

Wild Populations Summary

In summary, steelhead sources used in reintroductions should, where available, originate from within the target basin, provided that these actually represent a genetically and ecologically similar stock relative to the historical population or nearby extant populations. Where within-basin stocks are not available or suitable, from extirpation, low abundance and/or diversity levels, or genetic contamination, the use of out-of-basin stocks, or a mix of within-basin and out-of-basin stocks, may be considered with the caveats that the out-of-basin stocks or hybrid offspring from mixed stocks may not be best adapted to the current or future reintroduction area (e.g. Huff et al. 2011) and their use should not endanger any nearby extant populations. Additionally, if mixed stocks are used, it will be very important to monitor the success of the different stocks and their crosses to detect any outbreeding depression (see "Single Versus Multiple Sources" section and the discussion in Baerwald et al. 2011, Sec. 4.2.3).

The body of evidence from the available studies suggests that there may be potential for using residualized populations that possess the targeted genetic history in reintroduction efforts, though there is great uncertainty about whether these populations, once given the chance, will regain anadromy. The conditions found in the reintroduction area will also likely play a role in determining rates of anadromy (see Satterthwaite et al. 2009, 2010). In the status review of west coast steelhead DPS's, the NMFS Biological Review Team (BRT) (Good et al. 2005) concluded that the likelihood a resident fish will give rise to anadromous fish with enough frequency to produce a self-sustaining anadromous population is low enough to warrant just focusing on the anadromous form in the risk assessment for the status review of each DPS; however, the presence of numerous, native resident *O. mykiss* is considered a mitigating risk factor for some populations. The studies reviewed herein also suggest that populations that were once anadromous but have been residualized because of man-made barriers might be good candidates for reintroduction

downstream in the same watershed. Great caution should be taken, however, and the necessary genetic data collected in advance, to evaluate the relationships of these residualized populations to surrounding populations to ensure they are not predominantly influenced by hatchery out-planting and to ensure they are not inbred. Given the extensive history of *O. mykiss* propagation and introduction, it may be difficult to determine which stocks are 'wild' and which are influenced by past hatchery stocking (Good et al. 2005; Deiner et al. 2006).

HATCHERY STOCKS

The history of artificial propagation and introduction of salmonid species in North America is long and complex (Lichatowich 1999). Each year along the Pacific coast, over four billion hatchery-reared salmonids are released and make their way into the Pacific Ocean (Naish et al. 2008). Historically, artificial propagation was used to improve fishing opportunities. Focus then shifted to mitigation for dams, hydroelectric projects, and other anthropogenic factors that decreased fish populations and harmed fisheries (Good et al. 2005). In recent years, propagation efforts have emphasized conservation more because salmonid populations are being reintroduced to areas from which they have been extirpated and populations are being supplemented to prevent extinction (Flagg et al. 1999; Bowlby and Gibson 2011). Given the often already depleted nature of wild steelhead populations, it may be tempting to source a steelhead reintroduction using the available abundant hatchery populations.

Historically, there have been widespread releases of hatchery *O. mykiss* throughout the Pacific Northwest and California, often in areas above dams that were no longer accessible to anadromous steelhead (Good et al. 2005). The four steelhead hatchery production programs in the Central Valley are operated to mitigate damages that Central Valley dams cause the native steelhead population. The assumption has been that hatcheries can increase survival during what can

be the most limiting life history stage: the egg-to-smolt stage (Naish et al. 2008).

While increased survivorship can be beneficial when initiating a reintroduction, studies have shown that the potential benefits of hatchery production also have serious negative consequences. Recent work has shown that hatchery propagation can cause decreased survival rates (Caroffino et al. 2008), rapid and cumulative negative genetic effects and fitness declines in the first generation (Araki et al. 2008; Christie et al. 2012), and modifications to life history traits (WDFW 2008; HSRG 2009). Berntson et al. (2011) compared wild and hatchery populations of steelhead in Little Sheep Creek (Oregon). Hatchery broodstock was originally made of wild spawners followed by incorporation of a combination of wild and hatchery origin individuals into the broodstock. They found the relative reproductive success of hatchery origin fish was 30% to 60% of wild spawners, despite having wild-origin fish in the broodstock. The most likely cause for the observed decrease in fitness is domestication selection—positive selection on traits for hatchery growth that come at the expense of traits suitable for performance in the wild (Araki et al. 2008; Christie et al. 2012). It is outside the purview of this manuscript to detail all the known negative aspects of hatchery propagation, but we recommend the reader see Naish et al. (2008) and Araki and Schmid (2010) for excellent reviews of the pitfalls of hatchery propagation.

The history of broodstock collection is one primary aspect of potential hatchery sources that must be evaluated to determine their suitability as a source. In a review of fitness effects of hatchery production, Araki et al. (2008) found that the relative fitness of hatchery produced individuals (compared to wild individuals) is below 1, and much lower than 1 when broodstock is of non-local origin. The poorest fitness performance of hatchery fish relative to wild fish occurs in non-local hatchery strains that have been in captivity for more than five generations or have experienced artificial selection (reviewed in Fraser

2008). Additionally, the use of non-local stocks can increase straying rates (Schroeder et al. 2001).

Given the negative aspects of domestication selection and the use of non-native stocks in hatchery propagation, the Scientific Review Team (SRT 1998), in a review of all federally funded hatchery programs in the Columbia River Basin, concluded that stock transfers and introductions of non-native stocks from hatcheries should be discontinued and hatcheries should be used only temporarily to increase abundance and not for long-term production. The California Hatchery Scientific Review Group (California HSRG 2012) also recommends that the use of non-local broodstocks be discontinued in California hatcheries and that hatchery operation should be modified, or the hatchery population size should be minimized, to reduce the negative effects of hatchery propagation on wild popualtions.

The health of wild populations decreases when hatchery fish are present in a system (Araki et al. 2008). Therefore, the potential negative effect of using hatcheries for reintroductions in basins where wild fish are present should be given serious consideration. Even if there are no wild populations in the reintroduction area, wild populations in nearby watersheds can be negatively affected by hatchery out-plants through straying. In a review of California's steelhead populations, Moyle et al. (2008) report that hatchery production of steelhead has negative affects on wild steelhead in the Central Valley through prey competition, predation, competition for limited spawning habitat, and hybridization of Central Valley steelhead with steelhead introduced from outside the basin.

It may be quite difficult for reintroduction efforts to find an appropriate hatchery source that has not incorporated non-native stocks. Of ten California steelhead hatchery programs reviewed by Good et al. (2005), three to four use local broodstock with moderate genetic divergence ("no more than observed between similar populations within DPS") from the natural, native population into which they are released. Three use non-local broodstock and have

substantial ("comparable to divergence observed within entire DPS") to extreme genetic divergence from the natural populations they supplement.

There are a few examples where hatchery production appears to have avoided some of the pitfalls of artificial propagation (e.g., Hayes et al. 2004; Berejikian et al. 2008; Van Doornik et al. 2010; Heggenes et al. 2011; Kostow 2012). Key components to these successes are practices that reduce domestication selection, minimize the number of years of artificial propagation, preserve natural genetic diversity, and reinforce natural life history characteristics present in the wild populations. A good example is the Hamma Hamma River Steelhead Supplementation Project in Washington (Berejikian et al. 2008; van Doornik et al. 2010). This steelhead reintroduction effort used no artificial spawning, collected eggs from a large proportion of the naturally spawned redds in the system, allowed natural age-at-smoltification, used relatively low numbers of captively-reared released fish, and released both smolts and adults that were reared in captivity, all in an effort to decrease the negative effects of hatchery rearing while supplementing the population (Berejikian et al. 2008). They found an increase in naturally spawning fish when they reared wild caught eggs to the adult stage in the hatchery and then allowed the captively reared adults to spawn in the wild. They also found that releasing hatchery-reared adults to spawn in the wild resulted in a higher number of total redds produced in the wild (compared to the number of redds produced with just wild fish present) without decreasing the number of redds produced by naturally spawned fish. However, they did find that the hatchery-released adults showed an earlier spawning time than the wild adults. A study completed after the supplementation program found slight increases in genetic diversity and the effective number of breeders, which they attribute to collecting eggs from a large proportion of the wild population to rear in captivity (van Doornik et al. 2010).

Hatchery Stocks Summary

Given the complex genetic histories of steelhead hatchery populations, it is imperative to thoroughly evaluate the broodstock history of any hatchery stock considered for reintroduction efforts and to exercise great caution when deciding to use a hatchery population to source a reintroduction. The decreased fitness often experienced by hatchery fish compared to wild fish (Berntson et al. 2011; Gow et al. 2011), could greatly hinder reintroduction efforts—leading to a longer need for managed reintroduction and greater expenditure of resources—and jeopardize surrounding extant populations. Steelhead population structuring can exist at a finer scale than the level of basin or DPS (e.g. Wellband et al. 2012). Therefore, it is imperative that the genetic relationship of potential hatchery source stocks to the populations in the surrounding reintroduction area be fully examined in order to avoid contaminating nearby extant populations with non-local and/or lower-fitness genotypes (Flagg et al. 1999).

Hatchery programs that have a better chance of avoiding negative effects of artificial propagation and with higher likelihood of reintroduction success are those that have continuous and substantial input from local, wild populations into the broodstock (Frankham 2008), use artificial propagation or rearing over very short time-frames (Williams and Hoffman 2009; Bowlby and Gibson 2011) and use broodstock from the closest available watershed or, at a minimum, within the DPS (*sensu* Laikre et al. 2010). If a hatchery population that meets these criteria is identified as a good source for a reintroduction and using a wild population is unfeasible, taking adults from the hatchery and allowing them to spawn naturally in the reintroduction area—rather than out-planting juveniles, which are likely to stray to other areas to spawn due to minimal imprinting in the restoration-area water—can be an additional way to minimize negative impacts (e.g. Berejikian et al. 2008).

With good management practices, the risks associated with artificial propagation can be reduced, but never eliminated, so any fish taken from a hatchery stock inherently comes with additional risks compared to individuals from wild populations (McClure et al. 2008). Hatchery-origin fish can be used to prevent extinction in the very short term for some stocks, but after a few generations of propagation, the negative genetic effects can outweigh any benefits from increased abundance (Bowlby and Gibson 2011). An assessment of risk–benefit trade-offs should be conducted before any hatchery releases (Waples and Drake 2004; Laikre et al. 2010).

OTHER REINTRODUCTION SOURCING CONSIDERATIONS

Single Versus Multiple Sources

Another factor to consider in a reintroduction is whether one or multiple sources should be used to found the new population. Using a single source may increase the risk of inbreeding depression in small, introduced populations (Vergeer et al. 2004) and there are, indeed, examples where using multiple source populations has increased the chances of successful establishment in reintroductions (Godefroid et al. 2011; Maschinski et al. 2013). However, concern over disruption of co-adapted gene complexes and outbreeding depression has largely precluded the use of multiple sources in reintroduction efforts (Frankham et al. 2011).

Inbreeding can be exacerbated in reintroduction efforts because of a small number of founding individuals, unbalanced sex ratios, and genetically homogenous source populations (Favé et al. 2008). Inbreeding can cause changes in fitness related traits, such as decreased adult size and weight, altered spawn timing, and decreased survival to the adult stage (Keller and Waller 2002; Thrower and Hard 2009; Naish et al. 2013). Inbreeding can particularly be an issue in small, isolated populations, where gene flow from neighboring populations may be important for persistence (Sato and Harada 2008). Using multiple source populations, along with measures such as equalizing the sex-ratio of introduced individuals and starting the population with several rounds of supplementation, can ameliorate any suspected inbreeding

(Tallmon et al. 2004; Favé et al. 2008; Naish et al. 2013).

Gene flow among multiple sources may, indeed, help maintain genetic diversity in reintroduced and recolonizing populations (Fraser et al. 2006), however, outbreeding has been shown to negatively affect fitness in reintroduced vertebrate populations (Leberg 1993; Marshall and Spalton 2000; Edmands 2007; Huff et al. 2011). Intraspecific outbreeding in salmonids has been implicated in decreasing disease resistance (Currens et al. 1997), negatively altering behavior (Tymchuk et al. 2007), and reducing spawner return rates (Gilk et al. 2004). Alternatively, hybridization of different groups has also been shown to be beneficial ('hybrid vigor'), in some cases increasing fitness or creating new genotypic combinations that have adaptive advantage (Rieseberg et al. 2003). The negative consequences of outbreeding, however, are often not realized until two or more generations later (Edmands 2007). The outcome of hybridization between groups and any resultant changes in fitness can be hard to forecast and depends on the interactions between environment and genetic composition (Arnold and Hodges 1995; Keller and Waller 2002). It is important to remember that though outbreeding depression can have serious negative fitness consequences, outbreeding itself does not inherently lead to outbreeding depression (Edmands 2007). In fact, a meta-analysis of outbreeding experiments in fish shows it is not currently possible to forecast with any certainty situations where outbreeding depression will result (McClelland and Naish 2007).

Our limited ability to predict what the relative importance of inbreeding and outbreeding depression will be to reintroduction success complicates the decision for using one or multiple sources in a reintroduction (McClelland and Naish 2007; Fraser 2008; McClure et al. 2008). It is important that the population genetic structure and current and historical relationships among potential sources and the populations surrounding the donor area be considered (Frankham et al. 2011). One guideline that has been suggested is to consider mixing populations when the inbreeding

coefficient (F) of individual populations gets above 0.25 (Margan et al. 1998).

Reintroduction Numbers

An important additional consideration is the number of individuals to use in reintroductions. The recommended number of individuals for a reintroduction depends on several factors, including: source population size, stability, and genetic diversity; whether one or multiple sources will be used; life-stage(s) to be used; method(s) of reintroduction and their associated mortality rates; and whether a hatchery will be used for supportive rearing or production. Ultimately, the target population size—the estimation of which should account for present and projected future habitat carrying capacity (Cheyne 2006; Osborne and Seddon 2012)—will also drive the number of individuals used in reintroduction efforts.

The benefits of a relatively large population size are well established and highly relevant for population reintroductions. The duration of a reintroduced population's persistence increases with its initial size (Griffith et al. 1989; Fischer and Lindenmayer 2000, Robert et al. 2007; Godefroid et al. 2011) and population size and fitness have been found to be correlated (Reed and Frankham 2003; Reed 2005). The introduction of insufficient or inbred individuals can lead to loss of genetic diversity from inbreeding depression or genetic drift (Frankham et al. 2002; Pierson et al. 2007; Naish et al. 2013) and negative fitness effects (i.e., decreased weight, length, and earlier return timing) have been observed in inbred hatchery steelhead populations (Naish et al. 2013). Smaller populations with lower diversity may also be less adaptable to changing or novel environments (Reed and Frankham 2003). Furthermore, increasing population size early in a reintroduction is critical to reaching a point where demographic stochasticity (and the extinction vortex) does not dominate species persistence (Menges 1991, 2008).

Attempts to recommend minimum viable population sizes for species conservation have at times been met

with some reservation and skepticism (Robert et al. 2007; Traill et al. 2007, 2010). Likewise, a wide range of recommendations exists for the number of individuals or breeding pairs to use in a reintroduction or captive broodstock to conserve genetic diversity (50 to 5,000; see Frankel and Soule 1981; Allendorf and Ryman 1987; Pavlik 1996; Whitlock 2000, McGlaughlin et al. 2002; Miller and Kapuscinski 2003; Reed 2005; Moyer et al. 2009). If a hatchery is used to source a reintroduction, starting with a larger hatchery broodstock population will likely capture more source population genetic diversity (Allendorf and Ryman 1987; Frankham et al. 2002). Another approach to determine the number of individuals to use is to evaluate the sample size needed to maintain a given level of genetic diversity over a particular timeframe. For example, an evaluation of spring-run Chinook salmon using microsatellite genetic data found that an effective number of breeders (Nb) of 300 fish per year for 4 years would yield an effective population size (Ne) of 1,200 fish, which was expected to capture the majority of the genetic diversity in a given source population (Bork and Adelizi 2010). Fraser (2008) reviewed recommendations for hatchery populations and found that recommendations ranged from retaining 90% of genetic diversity (e.g. allelic richness, heterozygosity) over a 100-year period (Frankham et al. 2002) to allowing a maximum decrease in mean heterozygosity of 1% per generation (but see Franklin 1980; Frankel and Soule 1981; Naish et al. 2008). If source populations are unable to support a given level of extraction for the purposes of a reintroduction, fewer individuals may be used and the reintroduction effort may compensate by drawing from the source(s) for a longer duration to ensure genetic representation (Moyer et al. 2009). Additionally, if multiple sources are used, they should be incorporated in as close to equal proportions as possible to maximize the benefit of using multiple sources.

GENETIC NEEDS FOR REINTRODUCTIONS

In summary, the process of determining which population of steelhead is most prudent and appropriate for a reintroduction effort requires genetic data from many populations – not only in the targeted restoration area, but also in the populations within the DPS. This includes information about wild and hatchery populations, resident and anadromous populations, and their genetic relationships with each other. Below is a list of genetic data needs that management agencies should focus on while undertaking complex reintroduction sourcing decisions:

- Evaluate genetic diversity indices for–and genetic relationships among–all populations within the DPS, including those residualized populations found above artificial barriers.

- If hatchery stocks are being considered, determine the genetic diversity of all available hatchery stocks within the DPS and review the history of broodstock use. Evaluate hybridization levels of hatchery populations with sources outside the DPS and practices that may have increased domestication selection.

- Determine the history of hatchery stocking in within-DPS steelhead populations and whether stocking appears to have genetically altered these populations.

- Determine census and effective population sizes of potential source populations to evaluate if individuals can be taken from the population with little to no negative effect on the source population.

- Develop a clear genetic monitoring program to track the progress of the reintroduction, determine changes in genetic diversity, evaluate reintroduction strategies, and avoid negative effects on other salmonid populations. This should include tracking:

  - Effective population size

  - Expected heterozygosity

  - Allelic richness (if using microsatellites)

  - Hardy–Weinberg equilibrium

- Linkage disequilibrium

- Allele frequency change (if using microsatellites)

- Genetic differentiation among populations

- Inbreeding estimates

- Correlation between genetic and spatial distance

(All of these genetic indices can be calculated with the same dataset, therefore do not require different sampling efforts for each index. See the appendix in Baerwald et al. 2011 for an overview of these genetic parameters).

Armed with the relevant genetic information, managers can improve the likelihood of a successful reintroduction and work toward improving the health and viability of the overall DPS through the restoration of steelhead populations.

SAN JOAQUIN RIVER STEELHEAD REINTRODUCTION

Background

Approximately 60 miles of the San Joaquin River, downstream of Friant Dam, have been dry for over 60 years because of impoundment and water diversions for agriculture. This has led to the extinction of once abundant Chinook salmon and steelhead populations in the upper San Joaquin River. The San Joaquin River Restoration Program (Program) is charged with re-watering and restoring the river downstream of Friant Dam (for an overview see *http://www.restoresjr.net*). As part of a legal settlement (Natural Resources Defense Council et al. v. Kirk Rodgers et al.), one of the Program's goals is "to restore and maintain fish populations in 'good condition' in the main stem of the San Joaquin River below Friant Dam to the confluence of the Merced River, including naturally reproducing and self-sustaining populations of salmon and other fish." To achieve this goal, the Program will reintroduce spring-run Chinook salmon to the upper San Joaquin

River and may eventually look to reintroduce steelhead once habitat conditions could support such a population. In this section, we use this as a case study for evaluating potential source populations for steelhead reintroduction in this area—based on the genetic considerations reviewed in previous sections—and provide recommendations.

Within-Basin Naturally Reproducing Populations

The San Joaquin River is within the Central Valley steelhead DPS, which is listed as threatened under the federal Endangered Species Act and covers the Sacramento and San Joaquin River basins (see Figure 1; Good et al. 2005). Given the listed status of the Central Valley DPS, great care must be taken when deciding on which populations to source the reintroduction to ensure minimal harm to both the source population and any extant neighboring populations. Most extant populations of steelhead in the Central Valley DPS are now limited to non-historical or remnant spawning and rearing habitat below artificial barriers. These populations have been heavily influenced by hatchery production meant to mitigate for habitat loss and to support sport fisheries (Lindley et al. 2006). Naturally spawning steelhead populations in the Central Valley DPS are known to occur in the upper Sacramento River and tributaries: Mill Creek, Deer Creek, Butte Creek, Feather River, Yuba River, and American River (McEwan 2001). It is possible that wild populations are found in other tributaries in the Central Valley but have gone undetected because of a lack of sufficient monitoring (IEP 1998; McEwan 2001; Eilers 2008).

The presence of extant, wild, and naturally reproducing steelhead populations in the San Joaquin River basin is controversial, though there is some evidence to suggest there may be populations in the Stanislaus, Calaveras, and Tuolumne rivers (see Figure 1; McEwan 2001; Zimmerman et al. 2009). There are both hatchery-origin and natural-origin *O. mykiss* in the Mokelumne River. In a study of movement patterns of natural and hatchery origin *O. mykiss* in the Mokelumne River, Real et al. (2012) found
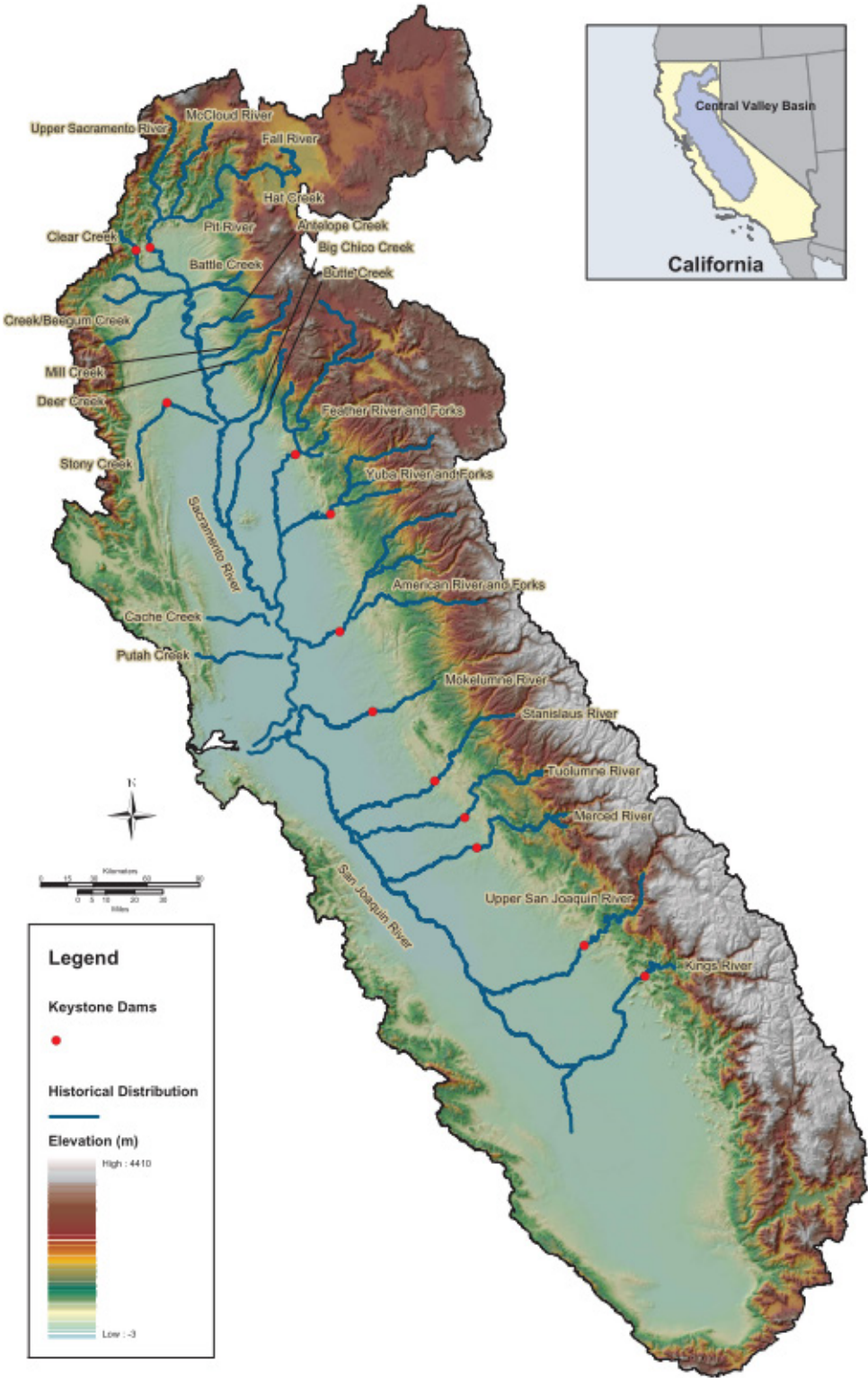
Figure 1 Historic distribution of Central Valley steelhead, from Schick et al. (2005). It is likely that steelhead historically moved farther into the smaller tributaries than shown. See Schick et al. (2005) for details.

the natural origin fish are predominantly resident *O. mykiss* (78%) but a minority demonstrate anadromous behavior (22%). Hatchery-origin fish, however, show a much greater incidence of anadromy (59%). In a study of San Joaquin River basin *O. mykiss* downstream of artificial barriers, Zimmerman et al. (2009) found evidence from otoliths showing that female rainbow trout do produce steelhead smolts. The California Department of Fish and Wildlife has documented non-adipose fin-clipped juvenile emigrants leaving the lower San Joaquin River beginning in 1987, though it is unknown from which tributary they are emigrating from (CDFW 1997, Letter from Jacqueline Schafer to Garth Griffen (NMFS) regarding CDFG comments on Proposed Rule to list steelhead under the ESA, dated 6 January 1997, as cited in IEP 1998). Unfortunately, very little is known about these steelhead, including genetic diversity or abundance, so it is difficult to evaluate their potential as reintroduction sources. However, in an analysis of Central Valley *O. mykiss*, Garza and Pearse (2008) found evidence for introgression of the Kamloops trout hatchery strain (*O. mykiss gairdneri*) into Calaveras River steelhead. The Calaveras River was also stocked with Nimbus Fish Hatchery (Gold River, California) stocks in 1992 and 1995 (Nielsen et al. 2005). We recommend that further information be collected, including abundance, genetic diversity, and relationship to the rest of the Central Valley DPS, to evaluate these San Joaquin River basin populations.

Above-Barrier Populations

There is limited information available on the history of *O. mykiss* populations found above artificial barriers in the San Joaquin River basin or their relationship to the below-barrier populations. In an analysis of Central Valley steelhead, Garza and Pearse (2008) found monophyly among all sampled Central Valley *O. mykiss* populations, regardless of whether they came from above or below dams. They found that below-barrier Central Valley populations cluster with northern California coastal steelhead populations, likely attributable to the documented historical use

of Eel River broodstock at Nimbus Fish Hatchery to reestablish the American River steelhead run after dam construction. The Nimbus Fish Hatchery was then the source of eggs for the Mokelumne River Hatchery (McEwan 2001). These Eel River genes subsequently spread throughout the below-barrier populations, likely via hatchery-origin strays. Studies have shown that above-barrier Central Valley populations cluster with one another. However these studies did not include above-barrier samples from the San Joaquin, Merced, Mokelumne, or Calaveras Rivers (Nielsen et al. 2005; Garza and Pearse 2008). Garza and Pearse (2008) suggest hatchery rainbow trout stocking has not eliminated the residualized native steelhead in the above-barrier populations studied. Rather, these selected above-barrier populations may represent the relatively non-introgressed ancestral genetics of steelhead in the Central Valley. However, they did find that over 10% of the fish sampled from above the Stanislaus River barrier assigned to hatchery stocks. Garza and Pearse (2008) also found close relationships among Sacramento River basin *O. mykiss* and reduced gene flow between Sacramento River and San Joaquin River basin populations. They found that measures of genetic diversity were higher in below-barrier populations compared to above-barrier populations, though this may be from the introgression with hatchery strains. They explain that it is unknown if current patterns are from historical relationships or if contemporary hatchery stocking and increased rates of straying have altered historical relationships.

Further genetic evaluation of the populations above artificial barriers in the Central Valley should be conducted to determine the relationships among above-barrier and below-barrier populations, if any represent native populations versus hatchery outplants, and to assess genetic diversity, integrity, and their feasibility as sources for reintroductions below dams (McEwan 2001). The above-barrier populations in the San Joaquin Basin may be important reintroduction sources and targets for conservation if they are not highly introgressed with hatchery out-plants, as they are potentially the only extant representatives

of a unique segment of the DPS (Lindley et al. 2006). If genetic analyses determine above-dam populations on the San Joaquin represent native *O. mykiss* lineages, then it could be worthwhile to pursue them as a reintroduction source, however the above barrier populations are excluded from the legal definition of the DPS, which could cause legal complications for their use in reintroduction efforts. Agencies should also be cautious when considering these populations as the usefulness of fish from above-barrier populations for recovering steelhead may be diminished due to the presumed selection against anadromy they have experienced since impoundment (Lindley et al. 2006; Garza and Pearse 2008). It could be very informative to test juvenile *O. mykiss* above the barriers for the level of skin reflectance and Na+, K+, -ATPase activity as indicators of smoltification (e.g., Holecek et al. 2012), conduct seawater challenges to see if smoltification can be induced (Ugedal et al. 1998), and/or look for genetic signatures of anadromy/smoltification (e.g. Nichols et al. 2008; Hecht et al. 2012a).

Hatcheries

There are four steelhead hatcheries in the Sacramento and San Joaquin river basins: Coleman National Fish Hatchery, Feather River Fish Hatchery, Nimbus Fish Hatchery, and Mokelumne River Hatchery. The National Marine Fisheries Service determined two programs on Sacramento River tributaries (Coleman National Fish Hatchery and Feather River Fish Hatchery) are important for restoration efforts of local populations based on genetic similarity. These hatcheries both started with their respective local stocks, continue to incorporate moderate to few wild-origin fish in their broodstock, have no more than moderate divergence from the native wild populations, and are, therefore, considered a part of the Central Valley DPS (Good et al. 2005). Steelhead at Nimbus Fish Hatchery and Mokelumne River Hatchery are not considered part of the Central Valley DPS (Drake et al. 2003) and the California HSRG recommends that the steelhead broodstock

at the Nimbus Fish Hatchery be replaced entirely with local broodstock more appropriate for the American River (California HSRG 2012). At some point, all four programs have incorporated non-local eggs or releases into their programs (NMFS 1998; Drake et al. 2003). Over the years from the late 1950s to the 1980s, the Coleman National Fish Hatchery incorporated releases from the Feather River Fish Hatchery, Nimbus Fish Hatchery, Mad River Hatchery *O. mykiss*, and some releases of Kamloops trout (*O. mykiss gairdneri*). While the U.S. Fish and Wildlife Service does not recommend that the Coleman stock be used to supplement wild populations of steelhead in Deer and Mill creeks, it states that this stock may be useful to assist recovery of Central Valley steelhead in other areas (NMFS 1998). The Feather River Fish Hatchery has used mostly local stocks for their broodstock, yet several times throughout their operation they, too, have incorporated releases from the Nimbus Fish Hatchery (NMFS 1998) and out-of-basin Skamania and Iron-Gate fish hatcheries (California HSRG 2012). Hatchery-origin adults in the Feather River exhibit higher rates of anadromy than wild-origin *O. mykiss* in the system (Kurth 2012). Additionally, the Coleman National Fish Hatchery—and possibly the other hatcheries—engaged in selective breeding for larger-sized individuals up until the 1990s (Drake et al. 2003). This selective breeding likely increased domestication selection in these hatchery stocks. Unlike the Feather River Fish Hatchery and Coleman National Fish Hatchery, hatchery stocks at the Nimbus Fish Hatchery on the American River and the Mokelumne River Fish Hatchery exhibit significant genetic divergence from local steelhead populations. This is almost certainly results from past use of non-local broodstock. It is also likely that the Nimbus Fish Hatchery has incorporated hatchery rainbow trout strains commonly raised at other Central Valley hatcheries into their steelhead stocks (Garza and Pearse 2008).

San Joaquin River Recommendations: A Decision-Making Example

As outlined above, there is much uncertainty about the genetic status of steelhead in the San Joaquin River basin, and further data are needed to fully evaluate potential reintroduction sources. Any decision about the ideal source population for a steelhead reintroduction should incorporate the following traits:

- High genetic diversity (high heterozygosity and effective population size, low levels of inbreeding)

- No to low levels of introgression from hatchery or outside DPS stocks

- Locally adapted: preferably from within the drainage or, at a minimum, from within the DPS

- Evidence for anadromy or an account of the anadromous life history

- Census population size that can withstand removing individuals for reintroduction without jeopardizing the persistence and viability of the source population

Decisions about steelhead reintroduction efforts conducted in the San Joaquin River should follow an adaptive management framework, as outlined by the Fisheries Management Working Group (FMWG 2010). Additionally, active reintroduction may negatively affect any steelhead that naturally recolonize the area and/or reintroduced or recolonizing Chinook salmon. Potential negative effects include competition (Tatara and Berejikian 2012)–though the likely effects of intra-specific competition are much greater than inter-specific competition (McMichael et al. 1997)–or predation (Naman and Sharpe 2012). A full analysis of these interactions is outside the purview of this manuscript, though they should be given full consideration in any reintroduction effort.

Genetic relationships of *O. mykiss* should be a consideration, for example comparing *O. mykiss* above Friant Dam and above the barriers on the Merced, Mokelumne, and Calaveras rivers to the populations analyzed in Garza and Pearse (2008). The within-

population genetic diversity of the above-barrier fish should also be evaluated and the level of inbreeding should be determined. If the population above Friant Dam, for example, has maintained high diversity levels compared to the rest of the natural populations in the DPS and does not appear to be introgressed with hatchery-origin fish, it should be given strong consideration because it might allow the population to regain the anadromous life history. However, as mentioned before, these populations may have undergone many generations of selection against anadromy. An investigation into the potential for smoltification traits in this population would be very informative and should be conducted before active reintroduction.

Alternatively, to source the San Joaquin River reintroduction, the most viable naturally reproducing population found downstream of barriers, could be considered. Examples in the San Joaquin Basin may be the Tuolumne or Stanislaus River steelhead. However, before choosing these sources, the census and effective size of these populations should be determined to be high enough to ensure their persistence after individuals are removed for the reintroduction project. These populations have experienced some level of introgression with hatchery stocks through straying or stocking, though individuals from the upper portion of these rivers may be better sources because they appear to be less introgressed with hatchery fish (Garza and Pearse 2008).

If the *O. mykiss*, found in locations such as above the Friant Dam, appear to be genetically similar to wild, native *O. mykiss*, with little hatchery influence but with low diversity levels from bottlenecks, another experimental option may be to take individuals from above the barrier and introduce them along with individuals from locations such as the Tuolumne or Stanislaus rivers. Taking a mixed-stock approach may alleviate inbreeding depression, restore historical genotypes, regain the anadromous life history, and provide sufficient genetic diversity for natural selection to act upon the population and allow it to withstand stochasticity. However, outbreeding depression can be a risk when mixing stocks (discussed

earlier, see also discussion in Baerwald et al. 2011, Sec. 4.2.3, and Huff et al. 2011). If this or any multi-stock option is chosen, it should be conducted in an experimental framework with a clear monitoring plan to evaluate the fitness of each stock and any crosses that result in the restoration area, because little is known about which reintroduction source, or combination thereof, will be most successful.

The last resort should typically be sources such as the Feather River Fish Hatchery steelhead. However, consideration must be given to the risks associated with using hatchery stocks for reintroduction and recovery (discussed earlier) and whether the fitness risks to nearby populations (e.g. Tuolumne and Stanislaus rivers) from straying and introgression outweigh the benefits of reintroduction. We do not recommend using stocks from hatcheries such as Coleman, Mokelumne, or Nimbus Hatcheries for reintroduction; they have incorporated of stocks from outside the DPS and have a recent history of selective breeding. California coastal steelhead are also an example of what should *not* be considered as sources, because these populations are outside the Central Valley DPS.

Whatever option is taken, reintroduction should be done within an adaptive management framework, and great caution should be taken to avoid any negative effects on surrounding steelhead populations or on introduced or naturally colonizing spring-run Chinook salmon. Genetic monitoring will be imperative to evaluate the success of the reintroduction (Schwartz et al. 2007; Laikre et al. 2010). We suggest that all released fish be marked so they can be identified if they stray into other areas, that genetic samples be taken from all reintroduced individuals to allow for Parental Based Tagging analyses (Anderson and Garza 2006), and diligent monitoring be maintained to track the abundance, effective population size, genetic diversity, fitness, and straying rates of the reintroduced population. By doing this, reintroduction strategies can be evaluated based on the data gained, and modified, as appropriate.

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