STRAYING OF LATE-FALL-RUN CHINOOK SALMON FROM THE COLEMAN NATIONAL FISH HATCHERY INTO THE LOWER AMERICAN RIVER, CALIFORNIA

A Thesis

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Gena R. Lasko

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Department of Biological Sciences

Abstract

of

STRAYING OF LATE-FALL-RUN CHINOOK SALMON FROM THE COLEMAN NATIONAL FISH HATCHERY INTO THE LOWER AMERICAN RIVER, CALIFORNIA

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Pacific salmon (*Oncorhynchus* spp.) are generally anadromous fishes that spawn in fresh water. When young salmon have grown and matured to what is called the smolt stage (ocean ready), they move into the ocean to mature and grow into adulthood. When they have reached sexual maturity, they return to fresh water to spawn and then die. Salmon typically home to their natal streams when returning to fresh water to spawn. Straying, however, is a natural behavior for a small fraction of individuals in a population, and may even have an adaptive advantage under some circumstances. Straying can also occur as a result of various factors including natural habitat disruption, modification of the watershed, or human intervention in salmonid reproduction.

In the winter of 2006/2007, tens of thousands of late-fall-run Chinook salmon (*Oncorhynchus tshawytscha*) reared in the Coleman National Fish Hatchery, a US Fish and Wildlife Service facility on Battle Creek in the upper Sacramento River basin, were released at several downstream locations as part of a Sacramento-San Joaquin River Delta survival study. Two years later, in the winter of 2008/2009, at the end of the annual

Department of Fish and Game lower American River escapement survey for fall-run Chinook salmon, a new pulse of fish was found to be spawning in the American River. These fish turned out to be stray late-fall-run Chinook salmon from the Coleman National Fish Hatchery, spawning in the American River where the fall-run Chinook salmon were completing their spawning run. Late-fall-run Chinook salmon have not been known to spawn in the American River and understanding the reason for this unusual behavior was the basis for this project. Currently the only run of Chinook salmon in the lower American River is the fall-run. The Department does not want late-fall-run Chinook salmon to establish themselves in the river because of potential disruption of fall-run Chinook salmon nest success due to an overlap in run timing, potential interbreeding, and limited available spawning habitat.

This study was based on the hypothesis that salmon released in close proximity to the mouth of the American River are more likely to stray into the river during their return spawning migration than fish released farther from the river's mouth. Coded-wire tag inland return data from for the 2006 brood year of late-fall-run Chinook collected from 2007/2008 through 2010/2011 were used for this study. The tags were collected primarily from salmon found during river escapement surveys and those that returned to hatcheries in the Sacramento River watershed. The return data were analyzed using Chi-square statistical analyses to determine if there was a difference in the number of salmon straying into the American River with respect to the distance they were released from the mouth of that river, and a Spearman noncollated rank analysis was used to describe the

overall relationship between release distance from the American River and percent straying into the river.

Results indicated that straying did increase with proximity of release location to the mouth of the American River and with respect to downstream releases in general. No salmon released in the vicinity of the Coleman National Fish Hatchery were recovered in the lower American River. This study indicates that release location should be carefully evaluated if future downstream releases are conducted by Sacramento River watershed hatcheries.

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Date

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Members of the Family Salmonidae (order Salmoniformes) are a relatively ancient group of teleost fishes (McDowall 1993, Quinn 2005) and they begin to appear in the fossil record during the Eocene between 34-56 million years ago (Moyle 2002). Salmonids have soft fin rays and are generally distinguished by a fatty adipose fin and fusiform shaped body, forked tail, axillary scales located at the base of the pelvic fins and juvenile parr marks (Moyle 2002). This family of fishes is composed of highly successful predators, exhibiting genetic plasticity enabling them to survive the highly stochastic geological and climatic conditions of the northern hemisphere, including the great ice incursions and retractions of the Pleistocene. They are the dominant group of fishes in the cold freshwaters of the North Pacific and Eurasia (Moyle & Cech 2000) and are one of the most economically valuable groups of fishes both historically and currently in the United States and particularly in the Pacific Northwest. These fishes provide extensive commercial and recreational fisheries, and have various cultural, nutritional, and ecological values (Moyle & Cech 2000, Quinn 2005). They are also the center of exhaustive research and the focus of extensive habitat restoration in a great deal of their range. Where they have not dispersed naturally, humans have taken them, and they are now common in freshwater systems throughout the world (Moyle & Cech 2000, Pascual 2001).

There are seven species of anadromous salmon and trout in the genus *Oncorhynchus* native to the eastern Pacific Ocean that spawn in North American watersheds. They include: Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and pink salmon (*O. gorbuscha*), steelhead (*O. mykiss*) and cutthroat trout (*O. clarki*) (Quinn 1997, Moyle 2002). Salmonids of the North Pacific have highly variable life histories (Gross 1987, Thorpe 1994, Brunner et al. 2001, Crespi & Teo 2002) and have evolved with episodic glaciations over most of their range. Pleistocene glaciations have had a prominent role in the genetic variation patterns and organization of many animal species, including salmonids (Taylor et al. 1996). The last glacial advance (Wisconsinan) covered a large portion of North Asia and North America, and only two main refugia are believed to have remained for salmonids in the region during this time (Taylor et al. 1996, Quinn 2005). Most of the extant species have probably been around for millions of years (Stearly 1992) and it is believed that the majority of the current Pacific salmonid phylogeny, diversity, and distribution has occurred in the period since the last glacial retreat about 15,000 years ago (Taylor et al. 1996, Brunner et al. 2001, Quinn 2005).

Nearly all salmon and trout species spawn in fresh water and many have anadromous life histories (Quinn 1997, Moyle 2002, Quinn 2005). Anadromy is a form of diadromy. Diadromy is a migratory life history pattern in which the fish is born and undergoes early rearing in one habitat, as a juvenile migrates across the freshwater-sea boundary for adult rearing, and finally returns as a mature adult to the original habitat for spawning (Gross 1987, McDowall 1993). Anadromous fish hatch in fresh water and rear in the ocean and return to fresh water to spawn; catadromous fish hatch in the ocean, rear in freshwater and return to the ocean to spawn. Anadromy is thought to be an ancient and stable strategy in salmonids (McDowall 1993). It is adaptive for fish that experience catastrophic events and episodic disturbance, and is a method of dispersal to new environments for colonization, to avoid intraspecific competition, or to exploit new niche opportunities (Gross 1987). The most important factor for the adoption of an anadromous lifestyle, however, seems to be accessing the higher productivity in the ocean to maximize growth (Gross et al. 1988). There are also populations of landlocked salmonids of some species that are capable of producing anadromous offspring such as steelhead and kokanee (Taylor et al. 1996, Pascual et al. 2001). Anadromous salmon are also semelparous, meaning that they reproduce once and then die. This life history strategy contributes to the ecology of their local habitat in streams by bringing nutrients from the ocean up into freshwater streams (Quinn 2005).

Homing is closely tied to the anadromous life history strategy in salmon. Homing refers to the fact that salmon typically return to their natal stream to spawn. Homing serves to genetically isolate populations of the same species born in different waterways from each other and allows populations to adapt to local conditions in a stream (Quinn et al. 2000, Beacham et al. 2002, Keefer et al. 2008). Also, fish that home have usually evolved compatibility to the natal habitat such as adaptations for temperature tolerance or resistance to the parasites in the stream, and are generally far more successful at spawning than occasional strays which will be selected against (Quinn 2005).

Straying is when salmon either intentionally or unintentionally spawn in a stream other than the one in which they were born. It is not known why some salmon stray and the explanation is likely complex. The tendency to home or stray may be genetically inherited and the pattern and stability of salmon distribution may be a reflection of ecological constraints for the species (Quinn 2005). Straying may be a response to environmental conditions, or some sort of disturbance event preventing them from reaching or spawning in their natal spawning grounds. Salmon may also wander, explore new habitats for suitability, follow schools of salmon from other rivers or opportunistically spawn in another stream with favorable conditions (Jonsson et al. 2003, Keefer et al. 2008). They may also be distracted by odors or flows from a river they are passing or may simply get lost or confused by some combination of signals they encounter during upriver migration.

Straying can be adaptive by allowing for the rapid colonization of newly available habitat after events such as landslides, forest fires, or low flows and high temperatures due to drought or ice melt and glacial recession (Quinn 1997, Moyle 2002, Quinn 2005, Waples et al. 2009). Straying can provide a kind of insurance in space (Thorpe 1994). Straying also provides gene flow between different populations in the system (Quinn 2005) and strays might be the only successful spawners after some sort of a climatic or catastrophic event such as the eruption of Mount St. Helens (Quinn 2005) that renders their natal stream inaccessible or unsuitable for spawning. Salmon that spawn in rivers other than their natal rivers or streams exhibit the “truest” sense of straying (Quinn et al. 1991), which Keefer et al. (2008) referred to as permanent straying.

The overall estimate for salmon homing, based primarily on hatchery data, is thought to be between 80%-100% (Quinn 1997). Imprinting, or olfactory learning, of salmon to their natal stream appears to happen during smolt emigration as well as during earlier life stages, though likely to a lesser extent (Dittman et al. 1994, Quinn 1995, Dittman et al.1996, Yamamoto et al. 2010). There is apparently a great amount of variability in salmon straying rates from year to year and between populations, and by size and age (Quinn & Fresh 1994), and across species (Quinn 1997). Hatchery fish appear to stray more and straying also appears to increase with increased hatchery selection (Jonsson et al. 2003). Straying may increase when hatchery fish are released away from their natal hatchery and may also increase the greater the distance they are released from the hatchery (Newman 2008). Different rivers seem to vary in their attractiveness to strays because of flow or temperature variation from year to year (Quinn et al. 1991, Carmichael 1997, Crateau 1997, Phillips et al. 2000), and strays might choose a river resembling their natal stream (Quinn et al. 1991). There also appears to be considerable variation in the amount of straying based on location, and straying can occur both above and below a salmon's natal stream, though Johnson et al. (1990) found only a rough correlation to geographical distance.

Chinook salmon are an extremely valuable native species in California, and they were once one of the most abundant fishes in the Sacramento River watershed (Moyle 2002, Lichatowich 2012). There are four recognized Chinook salmon runs in the Central Valley (fall, late-fall, spring, and winter runs) which represent distinct life history strategies and are named based on the season when the adults generally move into freshwater to spawn (Table 1; Fry 1961, Fisher 1994). Central Valley Chinook have undergone severe declines since the arrival of European settlers into modern times due to factors such as the loss of access to spawning habitat with the building of dams and other

Table 1. Basic timing and characteristics of Central Valley Chinook salmon runs. From Fisher (1994).

Central Valley Chinook salmon run	Migration period	Spawning period	Fork length at ocean entry
Late-fall run	October-April	Early January-early April	160 mm
Winter run	December-July	Late April-early August	120 mm
Spring run	March-July	Late August-early October	80 mm
Fall run	June-December	Late September-December	80 mm

man-made barriers, habitat destruction, decline in water quality, introductions of non-native species, and the alteration of natural geomorphic and hydrologic processes and flows.

There are three recognized Evolutionarily Significant Units (ESUs) of Chinook salmon in the Sacramento River watershed (Evolutionarily Significant Units are treated as species under the Endangered Species Act, Federal Register 1991). Three of the four runs of salmon described above are considered separate Evolutionarily Significant Units by the National Marine Fisheries Service. Currently fall and late-fall runs are lumped into one Evolutionarily Significant Unit, though they are genetically distinct (Moyle 2002) and at high risk for extinction (Katz et al. 2012). Evolutionarily Significant Units were applied to salmon by Waples in 1991 as a strategy to conserve salmon populations (Waples 1991, Quinn 2005). Evolutionarily Significant Units are populations of interbreeding groups of animals that are substantially distinct in that they are isolated by life history, ecological and genetic differences, though not necessarily completely isolated reproductively (Botsford & Brittnachere 1998, Waples 2009). In the Sacramento River watershed, Sacramento River winter-run Chinook salmon are listed as endangered, Central Valley spring-run Chinook are threatened and Central Valley fall and late-fall run Chinook are currently species of concern under the Federal Endangered Species Act.

The beginnings of artificial salmon culture in North America began in 1872 by Livingston Stone for the American Fish Culturists Association. He established the first hatchery on the McCloud River in California (Black 2001, Sharp 2001). Early hatcheries were built to supply or enhance fish populations for human consumption and recreation, and later to compensate for depleted stocks (Stickney 1994, Black 2001). The premise behind the use of hatcheries continues to be that they can enhance fish populations that are depleted primarily by human consumption and human activities resulting in habitat loss, modification, and degradation (Moyle 2002). Additionally, for several decades, hatcheries have been used for conservation purposes where populations are facing possible extinction (Stickney 1994, Waples 1999, Einum & Fleming 2001). Hatcheries are sometimes used as genetic banks to maintain diversity in severely depleted populations (Hatchery Scientific Review Group 2009). In some cases, it has become acceptable to sacrifice habitat and natural populations where hatcheries can be used to compensate for these losses in lieu of addressing human impacts such as pollution, blockage to fish passage, and overfishing (Waples 1999). This view, however, has been changing, particularly in the last couple of decades (McMichael et al. 1997). Waples (1999) called this a paradigm shift, one that has resulted in growing efforts to reduce the impacts of hatchery programs on wild fishes. Scientists and fisheries managers have begun to look more carefully at the interactions of hatchery produced fishes with wild residents in the environment. Today, there is growing concern that production and supplementation hatcheries may be threatening the survival of the salmon populations they are intended to supplement and protect (Moyle 2002). It is expected that in California, a review of existing hatchery practices is on the immediate horizon (http://www.fws.gov/cno/press/release.cfm?rid=83), and this process has already been underway in the Columbia River Basin (Hatchery Scientific Review Group 2009). Precedent, continued uncertainty and fear hinder major changes to hatchery operations.

Even where there is will for change, powerful economic interests continue to push for hatchery supplementation to supply fish for both recreational and commercial use (Stickney 1994).

Fishes reared in hatcheries quickly become adapted to their artificial environment. Genetic changes are unavoidable in cultured populations because of the loss of alleles through drift, artificial selection, non-random mating, and the relaxation of sexual selection (Meffe 1986, Waples 1999). Fitness may be compromised (Hatchery Scientific Review Group 2009) because sources of natural mortality during spawning and early life history stages in the hatchery may be removed (Waples 1999). Hatchery fish usually experience high densities, little if any habitat complexity or variation, and learn no predator response behaviors such as avoiding overhead shadows or seeking cover, and are not adapted to feeding on natural food sources (McMichael et al. 1999, Waples 1999, Einum & Fleming 2001). The results are fish that are generally adapted to the hatchery, and that tend to have lower survival rates than wild fish even if wild fish are smaller (Waples 1999, Einum & Fleming 2001). These and other possible effects on fish raised in hatcheries create populations of domesticated fish that will be released into the environment (Waples 1999) and will potentially interact and interbreed with wild fish affecting their success and genetic fitness. Reduced fitness due to genetic effects of captive breeding programs has been seen within a relatively short time (Araki et al. 2007, Araki et al. 2012). Also, there is evidence of a carry-over effect of reduced fitness to wild-born offspring of captive bred parents and their descendants in subsequent generations (Araki et al. 2012).

Straying salmon from hatcheries have the potential to disrupt the genetic composition of wild populations, and beneficial genes in locally adapted wild salmon may become diluted by hatchery fish, particularly if they have been selected for domestication, or are from a non-native stock (Keefer et al. 2008). Hatchery strays place native fish at risk both through potential interbreeding and through ecological interactions with wild spawners (Bakke 1997, Leider 1997).

In an attempt to increase survival of Sacramento River Chinook salmon, and hence the number of fish available in fisheries and returning to hatcheries, some fisheries managers release juvenile salmon downstream rather than releasing them into the rivers where the fish were cultured in hatcheries. The rationale for downstream releases is that, by releasing fish closer to the ocean, the fish can potentially avoid the substantial mortality factors that they would encounter in the rivers enroute to the ocean, e.g., predation by larger fish or possible entrainment in water diversions. Indeed, recent results of 2010 ocean harvest and escapement surveys showed that downstream net-pen releases in the San Francisco Bay proportionately had the greatest contribution to ocean fisheries compared to upstream releases (Kormos et al. 2012).

Release site of hatchery-origin salmon may affect salmon straying rates (Quinn 1997), perhaps because the fish released away from the hatchery do not acquire the landmarks and cues that fish released at the hatchery would acquire. Both the distance between release site and the rearing facility and location within the watershed of the release site can affect homing (Quinn 1997). Downstream releases may show improved survival but impaired homing (McCabe et al. 1983), though salmon released long distances from their rearing site may still return (Ebel et al. 1973, Slatick et al. 1975).

Coleman National Fish Hatchery is located on Battle Creek in Anderson, California, about 4.8 km (3 miles) east of the Sacramento River. The mouth of Battle Creek is located approximately at river kilometer 438 (mile 272) of the Sacramento River upstream from the Carquinez Bridge. The Coleman National Fish Hatchery was established in 1942. It was constructed to mitigate for the salmon spawning habitat that was lost with the construction of the Shasta Dam (Leitritz 1970). Some hatcheries, including the Coleman National Fish Hatchery, have at times practiced downstream releases of juvenile salmon for the purpose of research and for maximizing post-release survival. The Coleman National Fish Hatchery, operated by the US Fish and Wildlife Service, produces late-fall-run Chinook salmon and has conducted and provided fish for downstream releases. All Coleman National Fish Hatchery produced late-fall-run Chinook salmon are marked with both an adipose fin clip (removal) and a coded-wire tag.

When what would have normally been the end of the 2008/09 fall-run Chinook salmon escapement survey (the portion of an anadromous fish population that escapes the commercial and recreational fisheries to reach the fresh water spawning ground) on the lower American River, an unusually large number of freshly spawning salmon were observed in the river in January 2009. In order to determine the origin of these fish, the survey was extended through February of 2009. The late arrivals were primarily found to be adipose fin clipped and had coded-wire tags. Through recovery and reading of the coded-wire tag, implanted in the snout of a juvenile and retained in the snout of the adult salmon carcass, these fish were determined to be stray late-fall-run Chinook salmon from the 2006 brood year. The origin of the fish collected that winter was the Coleman National Fish Hatchery, and they were fish from downstream juvenile release groups that were part of a Sacramento-San Joaquin River Delta survivorship study conducted in the winter of 2006/2007 (Brandes 2011).

Fall-run Chinook salmon are currently the only active run in the lower American River. Fall-run Chinook salmon are produced at the Nimbus Fish Hatchery and occur as an established wild, native run of fall-run Chinook salmon that spawn in the river. The Nimbus Fish Hatchery is located below Nimbus Dam on the American River at river kilometer 37 (mile 23) above the confluence with the Sacramento River. The Nimbus Fish Hatchery was established in 1955 and was built to mitigate for the loss of spawning habitat lost by the construction of the Folsom-Nimbus project (Leitritz 1970). Late-fall-run Chinook salmon arriving in January could presumably create competition with the fall-run Chinook salmon by competing for space, or digging up or superimposing their redds over the nests of the fall-run Chinook salmon that were still or had just finished spawning. This could potentially threaten wild fall-run Chinook salmon survival in the river, and Department of Fish and Game biologists do not want a new run of salmon to become established at this time, particularly with the limited remaining spawning habitat in the river.

The purpose of this study is to determine if straying of adult late-fall-run Chinook salmon from Coleman National Fish Hatchery into the American River is related to the downstream releases of juvenile salmon from the 2006 brood year. If so, it can help hatchery managers and researchers make decisions about the placement of reasonable downstream release locations with respect to Sacramento River tributaries such as the American River and reduce the risk of straying. Because of the great amount of variability in straying between rivers, systems and populations, this research is novel and pertinent to the lower American River.

Hypotheses

I tested three primary hypotheses about late-fall-run Chinook salmon straying, namely:

1. Late-fall-run Chinook salmon produced at and released downstream are more likely to stray than those released at or in close proximity to the Coleman National Fish Hatchery.
2. Downstream releases of late-fall-run Chinook salmon increase straying into the American River.
3. Salmon released in close proximity to the mouth of the American River are more likely to stray into the American River than those released farther from the river's mouth.

MATERIALS AND METHODS

Data Collection

This study includes compiled data collected throughout the Sacramento River watershed. The main focus area and field portion of the study took place on the lower American River, tributary to the Sacramento River, from a short distance below Nimbus Dam down to the crossing of the Sunrise Bridge in Sacramento, CA. Late-fall-run Chinook salmon reared in the Coleman National Fish Hatchery were released at several downstream locations during the months of December 2006 and January 2007. Over 850,000 late-fall-run smolts were released near the Coleman National Fish Hatchery and more than 200,000 smolts were released from the downstream locations in the Sacramento River watershed (Figure 1) including Discovery Park, West Sacramento, Ryde Koket Resort and Benicia.

Coded-wire tag release and return data for late-fall-run hatchery raised Chinook salmon from brood year 2006, originating from the Coleman National Fish Hatchery, were analyzed in this study. One hundred percent of the 2006 brood year late-fall-run Chinook salmon were coded-wire tagged and adipose fin clipped. The release data by coded-wire tag number includes brood year, release location and date, and the number of fish tagged in each release group. Therefore, any fish with a readable coded-wire tag can be identified by the above information. I used the coded-wire tag return data for the same cohort of late-fall-run Chinook salmon collected in the American River and all other inland returns of these fish to spawning locations recorded in the Sacramento River

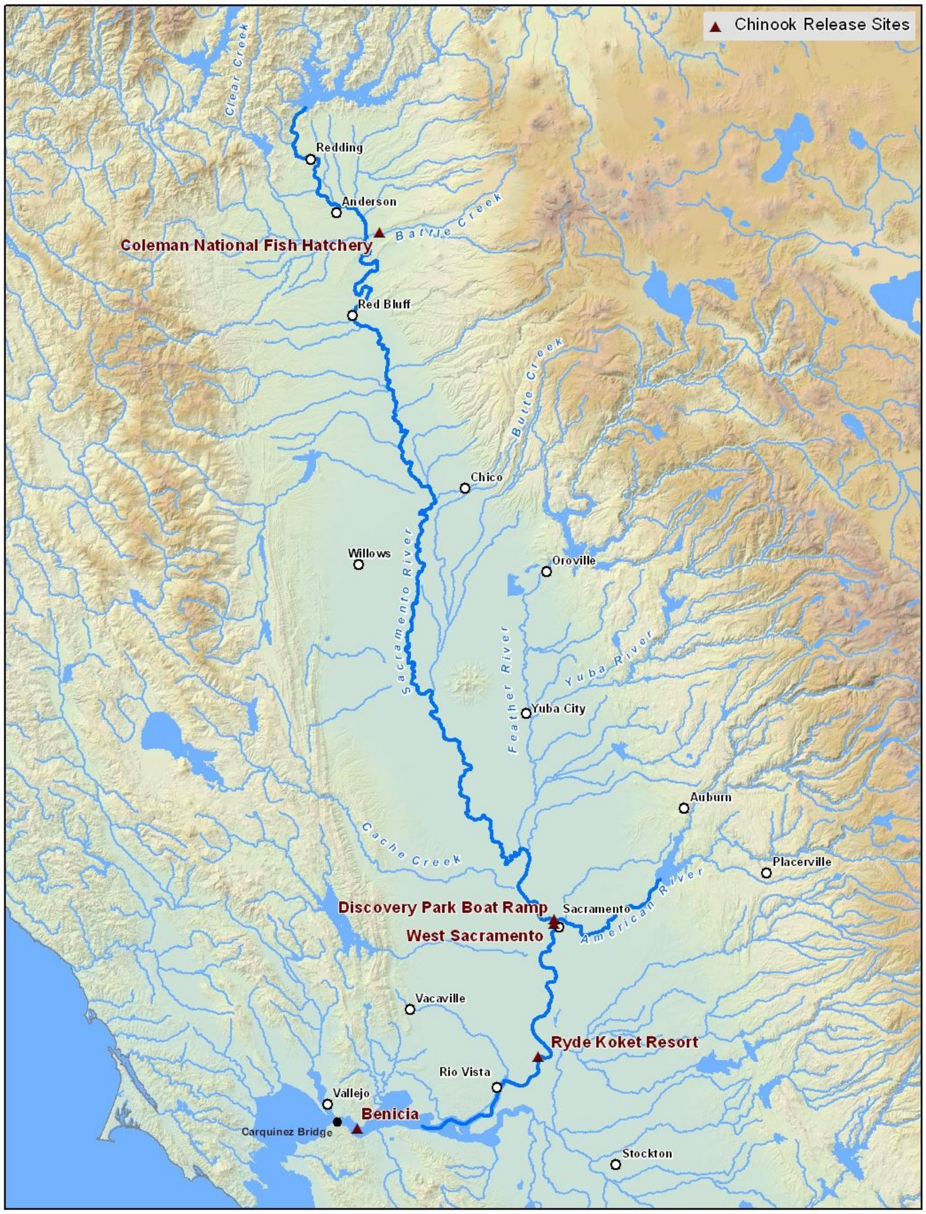

Figure 1. Map of Sacramento River Watershed including Coleman National Fish Hatchery and release sites at Discovery Park, West Sacramento, Ryde Koket Resort and Benicia. Map provided by Daniel Rankin.

watershed, including counts done by the US Fish and Wildlife Service and the Department of Fish and Game, for the analyses in this study. Data included counts of late-fall-run Chinook salmon that returned to spawning grounds or hatcheries in the watershed as adults, allowing the comparison of the number of fish found to have strayed into the lower American River to the number of fish that homed to the Coleman National Fish Hatchery. Late-fall-run Chinook salmon spawn during the winter-early spring and may return at different ages (2-5 years old). Therefore, the 2006 brood year return data includes corresponding return data over several years from winters 2007/8 through 2010/11. All coded-wire tag data used in this study were obtained from the Regional Mark Processing Center (RMPC) where coded-wire tag release and recovery data are uploaded. These data are made available for use at www.rmpc.org. Examples of release and return data for late-fall-run Chinook salmon from the Coleman National Fish Hatchery can be found in the Appendix.

Escapement Surveys

The field surveys for this project were conducted as an extension of the lower American River escapement surveys conducted by the Department of Fish and Game in the survey years of 2008/09 through 2009/2010 (two season span). Surveys were limited in 2010/2011 because of river conditions and high flows. When conditions allowed, American River carcass surveys were conducted weekly in the spawning reaches of the lower American River. All carcasses encountered during these surveys were collected and evaluated for the presence of a coded-wire tag, generally indicated by the presence of a clipped adipose fin, and if the head was present with enough tissue that the tag was still likely to be present. If there was the possibility of finding a coded-wire tag, the head was removed by machete, labeled and retained for recovery of coded-wire tag data. Recovery of the coded-wire tag data (reading and recording tag information) collected in the lower American River was conducted by the Department of Fish and Game. For more information regarding Department of Fish and Game lower American River escapement surveys, please see Vincik and Mamola (2010).

Data Analysis

Hypothesis 1 was tested using a Chi-square test for independence to compare the total number of recovered fish from the 2006 brood year found to have strayed or not strayed by release location (hatchery or downstream release).

Hypothesis 2 was tested using a Chi-square test for independence to compare the percent of returning fish that strayed into the American River from the 2006 cohort that were released at the hatchery to the percent that strayed into the American River from the downstream release groups.

Hypothesis 3 was tested using a Chi-square test for independence to compare the observed counts of fish that were recovered in the American River (strayed) to the counts of fish recovered at the Coleman National Fish Hatchery (not strayed) based on the release location (distance) from the American River.

A Spearman Rank correlation was used to determine the strength of the relationship between the distance of the release locations from the mouth of the American

River and the percent observed straying by individuals from the release groups (by release location) into the lower American River.

Survival by release location was tested using a Chi-square test for independence to determine if there was a difference in survival between fish released from the Coleman National Fish Hatchery compared to fish released from downstream locations.

Finally, I looked at recoveries not related to straying. These inquiries included investigating smolt recoveries from the same 2006 cohort in the Sacramento-San Joaquin Delta to see if smolt entrainment in the Central Valley Project or the State Water Project pumps might impact adult recovery statistics. I also used Chi-square tests for independence to determine if release location contributed to either ocean or freshwater fisheries returns, and if spawning returns differed with the inclusion of fisheries returns.

RESULTS

Overall Results

U.S. Fish and Wildlife Service released 1,070,896 coded-wire tagged juvenile late-fall-run Chinook salmon from the 2006 brood year that had been raised at the Coleman National Fish Hatchery. Direct counts of recorded recoveries (returns) of 2-5 year-old adults, excluding the ocean freshwater fisheries, from the 2006 brood year were made from 2007/2008 through 2010/2011 and were compiled and analyzed. A total of 6,487 adults returned to spawn in the Sacramento River watershed, and 6,103 of those fish homed back to the Coleman National Fish Hatchery while 384 fish strayed to other locations within the watershed. Of the strays, 279 ended up in the lower American River, captured either in the Nimbus Hatchery or in the river itself. The percent of fish returned that were released from the Coleman National Fish Hatchery and homed was 99.3%, and the percent released downstream that homed was 34.0%. Only 0.70% of Coleman National Fish Hatchery releases survived to be captured in the watershed while 0.24% of the fish released downstream survived. Table 2 gives a summary of coded wire tag release and return data.

Testing of Hypotheses

Hypothesis 1. Late-fall-run Chinook salmon produced at and released downstream are more likely to stray than those released at or in close proximity to the Coleman National Fish Hatchery.

Table 2. Summary of Coded Wire Tag Data Releases and Adult Returns for Late-Fall-Run Chinook salmon 2006 Brood Year from Coleman National Fish Hatchery.

Total juveniles released	1,070,896
Total juveniles released at hatchery	854,496
Total juveniles released downstream	216,400
Total adults returned	6487 (0.61%)
Total adults returned that were released at hatchery	5970
Total adults returned that were released at downstream locations	517
Total homed to natal hatchery	6103
Total strayed	384 (≈ 6%)
Total homed released at natal hatchery	5927
Total strayed released at natal hatchery	43 (0.07%)
Total homed released at downstream locations	176
Total strayed released at downstream locations	341 (66%)
Total downstream releases that strayed	341 (89%)
Released downstream & strayed into American River	279 (73%)
Released downstream & strayed elsewhere	62
Percent homed of all returns that were released at hatchery	99.3%
Percent homed of all returns that were released downstream	34.0%
Percent returned/survived released at hatchery	0.70%
Percent returned/survived released downstream	0.24%

A contingency table with a Chi-square test for independence was used to analyze the relationship between two discrete variables (stray rates and release location). This test resulted in $\chi 2$ of = 977 and $p < 0.001$ (df = 1). The data used in this analysis are presented in Table 3. Results indicate that with the resulting p value being so small that I can conclude that stray rate and release location are not independent, therefore, for brood year 2006, the stray rate is statistically higher for downstream releases than the rate for those released at or in close proximity to the Coleman National Fish Hatchery.

Hypothesis 2. Downstream releases of late-fall-run Chinook salmon increases straying into the American River.

A contingency table with a Chi-square test for independence was used to analyze the relationship between two discrete variables (stray rates and release location). This test resulted in $\chi 2$ of = 3367 and $p < 0.001$ (df = 1). However, because no salmon from Coleman National Fish Hatchery releases strayed into the American River (Table 4), a Chi-square test for this analysis is unreliable, because the Chi-square test requires each cell to have a value of at least 5. Though no hatchery fish were detected in the lower American River, it is possible that some may have strayed there, but were undetected. Given that no fish were detected having strayed into the American River from the returning hatchery released fish, and that Coleman National Fish Hatchery released returns numbered more than 11 times that of downstream releases returns, the data strongly support the hypothesis that downstream releases increase straying of fish into the American River.

Table 3. Brood year 2006 strayed vs. homed by hatchery or downstream release group.

Location	Total Returns	Homed	Strayed	Percent Strayed	Standard Error (95% confidence interval)
Hatchery Releases	5970	5927	43	0.07%	0.1%
Downstream Releases	517	176	341	66.0%	2.1%

Table 4. The number number of fish that strayed into the American River that were released at the Coleman National Fish Hatchery or downstream.

Location	Total Returns	Homed	Number Strayed (into American River)	Percent Strayed (into American River)	Standard Error (95% confidence interval)
Hatchery Releases	5970	5927	0	0.0	0.0%
Downstream Releases	517	176	279	54.0	2.2%

Hypothesis 3. Salmon released in close proximity to the mouth of the American River are more likely to stray into the American River than those released farther from the river's mouth.

A Chi-square test for independence resulted in $\chi 2 = 3931$ and $p < 0.001$ (df = 4). Again, the Chi-square test is unreliable because no Coleman National Fish Hatchery strays were detected in the lower American River (Table 5). Releases of young salmon at West Sacramento had the highest stray rate followed by Discovery Park, Ryde Koket, Benecia and then the Coleman National Fish Hatchery, which had no observed strays into the American River. Though Discovery Park had a lower stray rate than West Sacramento, the proximity of the two sites is very close (within about 1 river mile), so the distance between these two sites might not be the significant factor in the difference between the two stray rates. Figure 2 illustrates the percent of fish that strayed into the American River versus returned elsewhere.

Additional Results

Spearman Rank Correlation

The Spearman Rank Correlation indicated a strong negative relationship between stray rate and release site distance from the American River ($r = -0.90$ and $p = 0.037$, df = 3; data have not been transformed). Generally, stray rated decreased with increasing release site distance from the lower American River as depicted in Figure 3.

Table 5. Brood year 2006 late-fall-run Chinook salmon from the Coleman National Fish Hatchery that strayed into the American River vs. returned elsewhere in the watershed, by release site. Approximate distance from mouth of the American River: Discovery Park 0 miles; West Sacramento 1 mile; Ryde Koket 30 miles; Benecia 70 miles; Coleman National Fish Hatchery 200 miles. NFH = National Fish Hatchery.

Location	Total Returns	Returned Elsewhere	Number Strayed (into American River)	Percent Strayed (into American River)
Discovery Park	122	44	78	63.9
West Sacramento	139	17	122	87.8
Ryde Koket	162	94	68	42.0
Benecia	94	83	11	11.7
Coleman NFH	5970	5970	0	0
Total	6487	6208	279	4.3

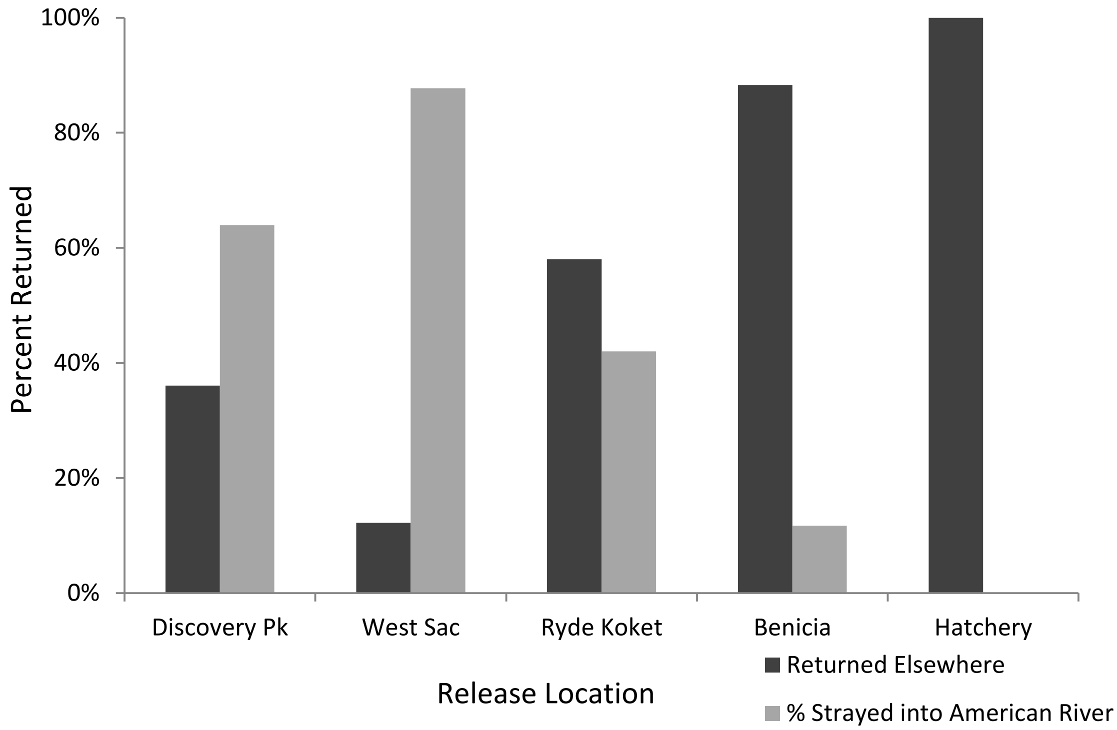

Figure 2. The percent of adult late-fall-run Chinook salmon from the Coleman National Fish Hatchery that strayed into the American River compared to percent adults returned elsewhere in the Sacramento River Watershed. No salmon released from the Coleman National Fish Hatchery were found in the lower American River returns.

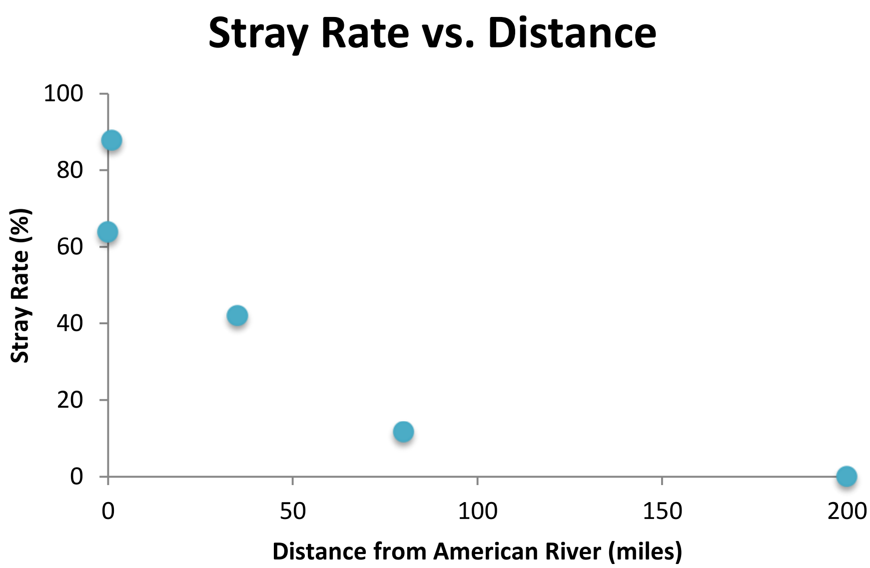

Figure 3. Stray rate into the American River versus distance of release site from the American River. There is a significant negative relationship; i.e., stray rates decrease as distance of release site from the American River increases.

Survival by Release Location

The relationship between return rates (a proxy for survival) and release locations for the 2006 brood year late-fall-run Chinook salmon was also tested. A Chi-square test for independence for the return rates with respect to release sites resulted in $p < 0.001$ and $\chi 2 = 616.8$ (df = 4). The null hypothesis here, that there is no difference in return rates for fish released from the Coleman National Fish Hatchery and for fish released in downstream locations can be rejected and the test supports the conclusion that there is a difference in return rates between hatchery release and downstream release locations. The Coleman National Fish Hatchery had the greatest return rates followed by Benicia. The other three downstream release sites had similar return rates (Table 6 and Figure 4).

Other 2006 Brood Year Coded-Wire Tag Recoveries

Smolt Recoveries

Coded-wire tag smolt recovery data are summarized in Table 7 for Coleman National Fish Hatchery 2006 brood year late-fall-run Chinook that were recovered from water project pumps and from seining and trawl surveys conducted at various locations in the Delta. There were so few recoveries compared to the release numbers (0.06% of total releases) that it is unlikely that they would have a significant impact on adult recovery statistics in this study.

Table 6. Brood year 2006 total count of inland returns (excluding fish caught in the fresh water fishery). NFH = National Fish Hatchery

Location	Number Released	Number Returned	Percent Returned
Discovery Park	52,948	122	0.23
West Sacramento	67,500	139	0.21
Ryde Koket	71,853	162	0.23
Benicia	24,099	94	0.39
Coleman NFH	854,496	5,970	0.70
Total	1,070,896	6,487	0.61

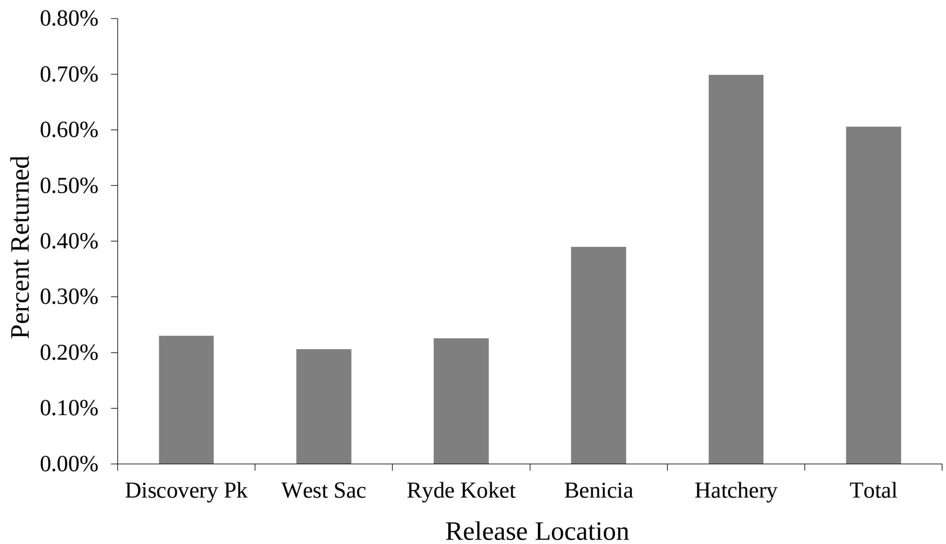

Figure 4. Percent survival of 2006 brood year late-fall-run Chinook salmon adults that returned by release location.

Table 7. Summary of brood year 2006 smolt recoveries. CVP = Central Valley Project; SWP = State Water Project; other capture locations include Chipps Island, Sherwood Harbor and others. NFH = National Fish Hatchery.

	Release location					
	Ryde Koket	Discovery Park	West Sacramento	Benecia	Coleman NFH	Total
CVP	6	10	3	0	63	82
SWP	14	16	2	0	63	95
Other locations	21	137	46	2	236	442
Total	41	163	51	2	362	619

Fisheries Returns

Fish released from Coleman National Fish Hatchery contributed proportionately more to the freshwater fishery than individuals from the downstream release groups. A Chi-square test for independence resulted in $\chi2 = 9.1$ and $p = 0.0025$ ($df = 1$). Conversely, hatchery releases did not contribute more proportionately to the ocean fishery. Both hatchery and downstream releases groups contributed almost equally to the fishery with a Chi-square test for independence resulting in $\chi2 = 0.038$ and $p = 0.85$ ($df = 1$). See Table 8.

The statistics also showed that there was no significant difference in the percent returns when comparing spawning returns used for this straying study (adult fish captured in river escapement surveys and hatcheries only) compared to adult spawning returns combined with fishery returns by release location or total returns. Chi-square tests for independence for returns of hatchery releases resulted in $\chi2 = 1.6$ and $p = 0.21$ ($df = 1$); returns of downstream releases $\chi2 = 0.24$ and $p = 0.62$ ($df = 1$); and for total returns $\chi2 = 1.8$ and $p = 0.17$ ($df = 1$).

Table 8. Summary of 2006 brood year ocean and freshwater catches. Percent Catch is based on returns divided by total released (downstream or Coleman National Fish Hatchery).

Location	Ocean Fishery	Freshwater Fishery	Percent Catch	
			Ocean	Freshwater
Released Downstream	4	13	0.0018%	0.0060%
Released at Hatchery	15	124	0.0018%	0.0145%
Total	137	19		

DISCUSSION

Straying and homing in anadromous salmon are natural behaviors (Quinn 1984, Kaitala 1990, Quinn 2005). Salmon from different watersheds stray at different rates and different rivers have varying levels of attractiveness to returning fish (Quinn et al. 1991). Also, hatchery fish tend to stray at higher rates than natural origin salmon (Jonsson et al. 2003). Based on this study, it appears that when late-fall-run Chinook salmon reared in the Coleman National Fish Hatchery are released downstream, straying, in general, increases in the Sacramento River watershed. Also, downstream releases increase straying into the lower American River. Additionally, the study shows that the closer releases are to the mouth of the American River, the more likely returning adult salmon are to stray into this river. Fish released near the mouths of other Sacramento River tributaries might also be more likely to stray into those rivers as well, though there were no data to test this assumption. Since this study did not include downstream release locations between Coleman National Fish Hatchery and the American River, it is unknown if stray rates would be similarly high in such instances, though there is possibly a release distance upstream where stray rates into the lower American River would also be high before dropping off and approaching hatchery release stray rates, unless this distance puts the fish in proximity of other potentially attractive tributaries.

It is likely that downstream releases will continue to some extent for hatchery-raised salmon in the Sacramento River watershed, particularly if downstream net-pen releases yield high returns for ocean fisheries (Kormos et al. 2012). If these practices do continue in the future for fishery enhancement, it is recommended that they not be released near the mouth of the American River. Results from this study should encourage managers to release the fish some distance to be determined above the American River and away from other tributary mouths or release them farther down the system as is feasible. It is recommended that all individuals in downstream release groups be marked and tagged, and close attention should be paid to returns based on release site. If only a portion of the downstream releases of late-fall-run Chinook observed in this study had been marked, there could have been a great underestimate as to the stray rate.

Results of this study do not support the use of downstream releases for increased escapement. It does not appear that escapement increased for late-fall-run Chinook salmon from any of the downstream release groups. Decreases of this potential benefit to salmon released downstream as compared to hatchery releases could have been due to several factors such as environmental conditions, handling and release methods, trucking practices, holding practices, holding pens, release locations, water quality issues, entrainment, and predation. Smolt recovery data were very low in the Sacramento-San Joaquin Delta. Recoveries in the State and Federal water project facilities were also low with respect to this study, however, it is unknown what percent of coded-wire tags from these small fish are not recoverable at these facilities.

There are indications that the reduction of intraspecific competition between wild and hatchery juveniles could reduce the impact of hatchery stock on wild fish (Nickelson 2003, Reese et al. 2009). With this in mind, there may be some value to using downstream releases to spatially and temporally minimize interactions between hatchery and wild juveniles.

Challenges Encountered

The biggest challenge with this study was that there was only one brood year from which return escapement data in the American River were collected over multiple years for downstream release groups. Downstream releases of late-fall-run Chinook salmon were conducted in other years, but carcass surveys on the lower American River were not extended to recover late-fall-run strays in all years. Also, in the winter of 2010/2011, high flows washed out nearly the entire carcass survey season for both fall and late-fall runs. If that year’s data had been available, it is foreseeable that the stray rate into the American River might have been higher than was recorded.

Another challenge is that the 2006 brood year might be an outlier, as evidenced by the fact that this brood year's returns to the river attracted attention that apparently other brood years, from which downstream releases were conducted, did not instigate extended surveys. It might also be due to conditions in the river when the smolts were released causing them to imprint unusually to the river or during adult immigration such as strong attraction flows during the spawning run when the fish were passing the American River.

Methods used during the extended period of the escapement surveys in the lower American River for late-fall-run Chinook recoveries were another challenge encountered in this study. Standard protocols of mark-and-recapture for abundance estimation were not used. Heads were collected but carcasses were not marked for recapture later.

Because of this, it was not possible to apply any of the expansion models that are generally used to estimate escapement from mark-and-recapture carcass survey data (Bergman et al. 2012) to get an escapement estimate for late-fall-run Chinook salmon into the lower American River. This resulted in only being able to use actual return numbers and therefore resulted in under-representing the number of strays in the lower American River.

Implications of Increased Straying into the Lower American River

There are potential problems with late-fall-run Chinook salmon spawning in the American River. They may be digging up or superimposing their redds on the redds of the fall run that had just finished spawning. There might also be competition between the juveniles of each run in the river (Reese et al. 2009), though the late-fall run would be smaller and theoretically less competitive than the older and larger fall-run juveniles. Spatial separation between the runs would probably exist if all of the historical spawning habitat was still available, though it is not known for sure if there was an historic late-fall run of Chinook salmon in the American River in the past (Williams 2001).

Potential problems might be mitigated by factors related to the life history of the two runs. A source of isolation between the runs occurring during the juvenile life stages might reduce potential impacts of late-fall-run Chinook salmon on the fall-run salmon. Fall-run Chinook salmon in the Central Valley are considered ocean type which rear in the river for a short time before emigrating to the ocean and late-fall-run salmon are considered river or stream type, and rear in the freshwater environment for a longer period of time, up to a year, before emigration (Fisher 1994, Burke 2004). Late-fall-run Chinook salmon may not persist because summer water temperatures in the lower American River typically exceed thermal preferenda for juvenile Chinook salmon, and therefore juvenile late-fall-run Chinook survival might be very low (R. Titus, California Department of Fish and Game, California State University, Sacramento, personal communication,). If juveniles of both runs are present together, they may or may not be competing for resources but may be occupying slightly different niches in the habitat, and the smaller late-fall Chinook might even deflect predation from the fall-run Chinook juveniles (Reese et al. 2009).

Additional Recommendations

Analysis of hatchery returns of past downstream releases of different brood years should be conducted. All future downstream release groups should be monitored for returns to hatcheries, and in-river surveys for late-fall-run Chinook salmon should be conducted in the lower American River to determine if 2006 was an outlier year and to get a better estimate of straying patterns in the river and in the watershed.

Surveys should be conducted in the American River for spawned unmarked late-fall-run Chinook salmon. Data collected should include tissue samples for genetic analysis to help determine stock origin, scales for aging, and otoliths for microchemical analysis that may yield watershed origin and migratory history of the fish. This would provide managers and researchers the means to determine the composition of individuals of late-fall-run Chinook salmon spawning in the American River, and if these are offspring of the late-fall-run salmon from the Coleman National Fish Hatchery or if they were spawned in the lower American River or elsewhere.

Even if 2006 was an unusual year, this study highlights straying trends and informs fisheries management to be cautious when using downstream release programs for late-fall or other runs of hatchery Chinook salmon in the Sacramento River watershed, particularly keeping in mind potential effects upon the fall-run Chinook salmon that spawn in the American River.

Appendix: Examples of Release and Return Data

Example of coded-wire tag release data. NFH = National Fish Hatchery

CWT number	brood year	first release date	number released	comment	release site	fish origin
53381	2006	20061129	78346	First spring Chinook salmon surrogate release group for broodyear 2006	COLEMAN NFH	COLEMAN NFH
53379	2006	20070116	17668	Delta Study release group #2	SAC R AT DISCOVERY PARK	COLEMAN NFH
53371	2006	20061206	11965	Delta Study release group #1	SAC R AT RYDE KOKET	COLEMAN NFH
52991	2006	20070119	12289	Delta Study release group #2	BENICIA	COLEMAN NFH
53377	2006	20061204	16538	Delta Study release group #1	SAC R AT WEST SACRAMENTO	COLEMAN NFH
53383	2006	20070103	95986	Production	COLEMAN NFH	COLEMAN NFH

Example of raw return data collected in the 2008/09 American River Escapement Survey. NFH = National Fish Hatchery; CAR = carcass survey

headtag	**run name**	**recovery date**	**recovery type**	**coded-wire tag code**	**Brood year**	**hatchery**	**releasite**
67699	Late Fall	02-Feb-09	CAR	052991	2006	Coleman NFH	Benicia
67697	Late Fall	02-Feb-09	CAR	052992	2006	Coleman NFH	Discovery Park
67677	Late Fall	02-Feb-09	CAR	052988	2006	Coleman NFH	Ryde-koket
67737	Late Fall	02-Feb-09	CAR	053375	2006	Coleman NFH	West Sacramento
67674	Late Fall	02-Feb-09	CAR	052992	2006	Coleman NFH	Discovery Park
67676	Late Fall	02-Feb-09	CAR	052993	2006	Coleman NFH	Discovery Park
67698	Late Fall	02-Feb-09	CAR	053375	2006	Coleman NFH	West Sacramento
67671	Late Fall	02-Feb-09	CAR	053380	2006	Coleman NFH	Discovery Park
73454	Late Fall	09-Feb-09	CAR	052992	2006	Coleman NFH	Discovery Park
73458	Late Fall	09-Feb-09	CAR	053378	2006	Coleman NFH	West Sacramento
73481	Late Fall	09-Feb-09	CAR	052993	2006	Coleman NFH	Discovery Park
67681	Late Fall	09-Feb-09	CAR	052993	2006	Coleman NFH	Discovery Park

LITERATURE CITED

Araki, H., B. Cooper, and M.S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100-103.

Araki, H., B. Cooper, and M.S. Blouin. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. Biology Letters 5:621-624.

Bakke, B. 1997. Straying of hatchery fish and fitness of natural populations. In: Genetic effects of straying of non-native hatchery fish into natural populations: proceedings of the workshop. W. Stewart Grant (editor) U.S. Department of Commerce, NOAA Tech Memo. NMFS-NWFSC-30, 130pp.

Beacham, T.D., K.J. Supernault, M. Wetklo, B. Deagle, K. Labaree, J.R. Irvine, J.R. Candy, K.M. Millar, R.J. Nelson, & R.E. Withler. 2002. The geographic basis for population structure in Fraser River Chinook salmon (*Oncorhynchus tshawytscha*). Fishery Bulletin 101:229-242.

Bergman, J.M., R.M. Nielson, and A. Low. 2012. Central Valley Chinook salmon in-river escapement monitoring plan. Fisheries Branch Administrative Report Number: 2012-1 for the California Department of Fish and Game, Natural Resources Agency.

Black, M. Shasta salmon salvage efforts: Coleman National Fish Hatchery on Battle Creek, 1985-1992. In: Contibutions to the biology of Central Valley salmonids. Randall L. Brown (editor). California Department of Fish and Game. Fish Bulletin. 1:177-263.

Botsford, L.W., and J.G. Brittnacher. 1998. Viability of Sacramento River winter- run Chinook salmon. Conservation Biology 12: 65-79.

Brandes, P. 2011. Unpublished draft report on the 2006-2007 Mark and recapture experiments for Delta Action 8.

Brunner P.C., M.R. Douglas, A. Osinov, C.C. Wilson & L. Bernatchez. 2001. Holarctic phylogeography of Arctic charr (*Salvelinus alpinus* L.) inferred from mitochondrial DNA sequences. Evolution 55:573-586.

Burke, J.L. 2004. Life histories of juvenile Chinook salmon in the Columbia River Estuary, 1916 to the present. Master of Science Thesis. Oregon State University.

Carmichael, R.W. 1997. Straying of Umatilla River hatchery origin fall-run Chinook salmon into the Snake River: proceedings of the workshop. W. Stewart Grant (editor) U.S. Department Commerce, NOAA Tech Memo. NMFS-NWFSC-30, 130pp.

Crateau, E. 1997. Straying of hatchery origin spring/summer-run Chinook salmon in the Grande Ronde Basin: proceedings of the workshop. W. Stewart Grant (editor) U.S. Department Commerce, NOAA Tech Memo. NMFS-NWFSC-30, 130pp.

Crespi, B. & R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56:1008-1020.

Dittman, A. H., T. P. Quinn, W. W. Dickhoff, and D. A. Larsen. 1994. Interactions between novel water, thyroxine and olfactory imprinting in underyearling coho salmon (*Oncorhynchus kisutch*, Walbaum). Aquaculture and Fisheries Management 25:157-169.

Dittman, A. H., T. P. Quinn, and G. A. Nevitt. 1996. Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 53:434-442.

Ebel, W. J., D. L. Park, and R. C. Johnsen. 1973. Effects of transportation on survival and homing of Snake River Chinook salmon and steelhead trout. Fishery Bulletin. U.S. 71:549-563.

Einum, S., and I.A. Fleming. 2001. Implications of stocking: ecological interactions between wild and released salmonids. Nordic Journal of Freshwater Resources 75:56-70.

Federal Register. 1991. Policy on applying the definition of species under the Endangered Species Act to Pacific salmon. 56:58612-58618.

Fisher, F. W. 1994. Past and present status of Central Valley Chinook salmon. Conservation Biology 8:870-873.

Fry, D.H. 1961. King Salmon spawning stocks of the California Central Valley, 1949-1959. California Fish and Game 47:55-71.

Gross. M.R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14-25.

Gross, M.R., R.M. Coleman, & R.M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239:1291-1293.

Hatchery Scientific Review Group. 2009. Columbia River hatchery reform system-wide report. 271pp. plus appendices. http://www.hatcheryreform.us/hrp/reports/system/welcome_show.action

Johnson, S. L., M. F. Solazzi, and T. E. Nickelson. 1990. Effects on survival and homing of trucking hatchery yearling coho salmon to release sites. North American Journal of Fisheries Management 10:427-433.

Jonsson, B., N. Jonsson and L.P. Hansen. 2003. Atlantic salmon straying from the River Imsa. Journal of Fish Biology 62:641-657.

Kaitala, V. 1990. Evolutionary stable migration in salmon: a simulation study of homing and straying. Annales of Zoologici Fennici 27:131-138.

Katz, J., P.B. Moyle, R.M. Quinones, J. Israel, and S. Purdy. 2012. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environmental Biology of Fishes. Published online first, 2012.

Keefer M. L., C. C. Caudill, C. A. Peery and C. T. Boggs. 2008. Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system. Journal of Fish Biology 72:27–44.

Kormos, B., M. Palmer-Zwahlen, & A. Low. 2012. Recovery of coded-wire tags from Chinook salmon in California’s Central Valley escapement and ocean harvest in 2010. Fisheries Branch Administrative Report 2012-02.

Leider, S. 1997. Straying and gene flow between hatchery and natural populations. In: Genetic effects of straying of non-native hatchery fish into natural populations: proceedings of the workshop. W. Stewart Grant (editor) U.S. Department Commerce, NOAA Tech Memo. NMFS-NWFSC-30, 130pp.

Leitritz, E. 1970. A history of California’s fish hatcheries 1870-1960. California Department of Fish and Game. Fish Bulletin 150.

Lichatowich, J. 2012. Plenary Address. Salmonid Restoration Federation. 30th Annual Salmonid Restoration Conference, Davis CA.

McDowall, R.M. 1993. A recent marine ancestry for diadromous fishes? Sometimes yes, but mostly no! Environmental Biology of Fishes 37:329-335.

McCabe, G.T., C.W. Long, and S.L. Leek. 1983. Survival and homing of juvenile coho salmon, *Oncorhynchus kisutch*, transported by barge. Fishery Bulletin 81:412-415.

McMichael, G.A., T.N. Pearsons, and S.A. Leider. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. North American Journal of Fisheries Management 19:948-956.

McMichael, G.A., C.S. Sharpe, and T.N. Pearsons. 1997. Effects of residual hatchery-reared steelhead on growth of wild rainbow trout and spring Chinook salmon. Transactions of the American Fisheries Society. 126:230-239.

Meffe, G.K. 1986. Conservation genetics and the management of endangered fishes. Fisheries 11:14-23.

Moyle, P.B. 2002. Inland fishes of California. University of California Press, Berkeley, CA. 502 pp.

Moyle, P.B. & J.J. Cech, Jr. 2000. Fishes: an introduction to ichthyology. Prentice-Hall, Inc., Upper Saddle River NJ. 612pp.

Newman, K.B. 2003. An evaluation of four Sacramento-San Joaquin River Delta juvenile salmon studies. US Fish and Wildlife Service, Stockton, CA. 181pp. Avaliable: www.science.calwater.ca.gov/.

Pascual, M., P. Bentzen, C.R. Riva Rossi, G. Mackey, M.T. Kinnison, R. Walker. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. Transactions of the American Fisheries Society 130:53-67.

Phillips, J.L., J. Ory, and A. Talbot. 2000. Anadromous salmonid recovery in the Umatilla River Basin, Oregon: a case study. Journal of the American Water Resources Association 36:1287-1308.

Quinn, T. P. 1984. Homing and straying in Pacific salmon. In: J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (editors), Mechanisms of migration in fishes. Plenum Press, NY. p. 357-362.

Quinn, T. P. 1997. Homing, straying, and colonization. In: Genetic effects of straying of non-native hatchery fish into natural populations: proceedings of the workshop. W. Stewart Grant (editor) U.S. Department of Commerce, NOAA Tech Memo. NMFS-NWFSC-30, 130pp.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, WA. 378 pp.

Quinn, T. P., and K. Fresh. 1984. Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. Canadian Journal of Fisheries and Aquatic Sciences 41:1078-1082.

Quinn, T. P., R. S. Nemeth, and D. O. McIsaac. 1991. Homing and straying patterns of fall Chinook salmon in the lower Columbia River. Transactions of the American Fisheries Society 120:150-156.

Quinn, T.P., M.J. Unwin, & M.T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. Evolution 54:1372-1384.

Reese, C., N. Hillgruber, M. Sturdevant, A. Wertheimer, W. Smoker, and Rick Focht. 2009. Spatial and temporal distribution and the potential for estuarine interactions between wild and hatchery chum salmon (*Onchorhynchus keta*) in Taku Inlet, Alaska. Fishery Bulletin 10:433-450.

Sharp, G.D. 2001. A brief overview of the history of fish culture and its relation to fisheries science. Proceedings of the Tenth Biennial Conference of the International Institute of Fisheries Economics and Trade, July, 2000. Available on CD-Rom from IIFET Secretariat, OSU, Corvallis Oregon. http://sharpgary.org/BriefOverviewHistory.pdf

Slatick, E., D. L. Park, and W. J. Ebel. 1975. Further studies regarding effects of transportation on survival and homing of Snake River Chinook salmon and steelhead trout. Fishery Bulletin 73:925-931.

Stearly, R.F. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus*. In R.L. Mayden, ed. Systematics, historical ecology, and North American freshwater fishes. Stanford, CA. Stanford University Press. Pages 622-658.

Stickney, R.R. 1994. Use of hatchery fish enhancement programs. Fisheries 19:6-13.

Taylor, E.B., C. J. Foote, and C.C. Wood. 1996. Molecular genetic evidence for parallel life-history evolution within a pacific salmon (sockeye salmon and kokanee *Oncorhynchus nerka*). Evolution 50:401-416.

Thorpe, J.E. 1994. Strategies for survival: salmonids in marginal habitats. Transactions of the American Fisheries Society 123:606-612.

Vincik, R., and M. Mamola. Lower American River fall-run Chinook salmon escapement survey October 2009-January 2010. California Department of Fish and Game, Draft Report.

Waples, R.S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53:11-22.

Waples, R.S. 1999. Dispelling some myths about hatcheries. Fisheries 24:12-21.

Waples, R.S., T. Beechie, and G.R. Pess. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific Salmon populations. Ecology and Society 14:3.

Williams, J.G. 2001. Chinook salmon in the lower American River, California's largest urban stream. In: Contibutions to the biology of Central Valley salmonids. Randall L. Brown (editor). California Department of Fish and Game. Fish Bulletin. 2:1-38.

Yamamoto, Y., H.Hino, and H. Ueda. 2010. Olfactory imprinting of amino acids in lacustrine sockeye salmon. PLoS One 5:e8633.