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Straying of late-fall run Chinook salmon from the Coleman National Fish Hatchery into the lower American River, California

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Salmon typically home to their natal streams when returning to spawn in fresh water. Straying, however, is a natural behavior for a small fraction of individuals in a population, and may have an adaptive advantage under some circumstances. In the winter of 2006–2007, tens of thousands of late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) reared in the Coleman National Fish Hatchery (CNFH) were released at several downstream locations as part of a Sacramento-San Joaquin River Delta survival study. In the winter of 2008–2009, biologists observed a pulse of late-season spawners in the American River, which turned out to be stray late-fall run Chinook salmon from the CNFH, spawning where the American River fall-run Chinook salmon were completing their spawning. 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. We used coded-wire tag inland return data to test the hypothesis that salmon released close to the mouth of the American River are more likely to stray into the river during their return spawning migration than are fish released farther from the river's mouth. Results indicated that straying increased relative to 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 CNFH 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.

Key words: American River, anadromous, California, coded-wire tag, Coleman National Fish Hatchery, escapement, hatchery, homing, late-fall run Chinook salmon, *Oncorhynchus tshawytcha*, release location, straying

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Nearly all species of salmon and trout (family Salmonidae) spawn in fresh water, and many have at least facultative anadromous life histories (Quinn 1997, Quinn 2005, Railsback et al. 2014). Homing, the behavior of adult salmonids returning to spawn in their natal stream, is a major part of the anadromous life history (Quinn et al. 2000, Beacham et al. 2002, Keefer et al. 2008). Homing serves to genetically isolate populations of the same species spawning in different waterways, thus allowing for eventual adaptation to local conditions (Quinn et al. 2000, Beacham et al. 2002, Keefer et al. 2008). This could include evolved compatibility to natal habitat conditions via adaptations for temperature tolerance or resistance to pathogens in the stream, as locally adapted salmonids are generally far more successful at spawning than occasional strays (Quinn 2005). Overall estimates for natal area fidelity via homing in Pacific salmon (*Oncorhynchus* spp.) are 80%–100%, based primarily on hatchery data (Quinn 1997). Imprinting, or olfactory learning, of anadromous salmonids to their natal stream appears to occur before and during the parr-smolt transformation, as well as during emigration, although to a lesser extent during earlier life stages in some Pacific salmon of hatchery origin (Dittman et al. 1994, Dittman and Quinn 1996, Quinn 1997, Dittman et al.1996, Lema and Nevitt 2004, Yamamoto et al. 2010).

The term "straying," as used in this paper, refers to anadromous salmonids that either intentionally or unintentionally return to and spawn in a non-natal stream. Anadromous salmonids that spawn in a river or stream other than the one of their origin exhibit the "truest" sense of straying (Quinn et al. 1991), which Keefer et al. (2008) referred to as permanent straying. It is not known why some anadromous salmonids stray and the explanation is likely complex. The tendency to home or stray may be genetically inherited, and the pattern and stability of anadromous salmonid distributions may be a reflection of ecological constraints on the fish (Quinn 2005). Straying may occur in response to environmental conditions, or in response to disturbance events that prevent the fish from reaching or spawning in their natal stream (Quinn 2005, Waples et al. 2009). Anadromous salmonids may also wander, explore new habitats for suitability, follow schools of conspecifics from other rivers, or opportunistically spawn in another stream with favorable conditions (Jonsson et al. 2003, Keefer et al. 2008). Furthermore, anadromous salmonids may be distracted by odors or flows from a river they are migrating past, or simply get lost or confused by some combination of cues that they encounter during their upriver migration. Straying can be adaptive through rapid colonization of newly available habitat after events such as landslides, forest fires, or low flows and high temperatures resulting from drought or ice melt and glacial recession (Quinn 1997, Moyle 2002, Quinn 2005, Waples et al. 2009). Straying likely results in gene flow between different populations in the system (Quinn 2005). Strays might be the only successful spawners following a major climatic or catastrophic event, such as the eruption of Mount St. Helens which rendered natal streams inaccessible or unsuitable for spawning (Quinn 2005). In effect, straying can provide a kind of insurance in space from these types of events (Thorpe 1994).

There is great variability in salmon straying rates from year to year and between populations, by size and age (Quinn and Fresh 1984), and across species (Quinn 1997). Salmonids of hatchery origin appear to stray at a higher rate than salmonids that are of natural-origin, and straying also appears to increase with increased hatchery selection (Jonsson et al. 2003). It may be that this bias towards greater straying by salmonids of hatchery origin is due to fewer studies of straying behavior in wild populations (Quinn 1995). Straying may increase when salmonids of hatchery origin are released away from their natal hatchery, and may also increase with greater release distance from the hatchery (Newman 2008). Different rivers seem to vary in their attractiveness to Pacific salmon strays, possibly because of flow or temperature variations 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 upstream and downstream from an individual's natal stream. Johnson et al. (1990) found only a rough correlation between straying rate and release distance from the natal stream.

Anadromous salmonid hatcheries supplement natural populations to support fisheries and to enhance, conserve, and restore natural populations. Salmonids reared in hatcheries can quickly become adapted to their artificial environments (Araki et al. 2008). Unintended genetic changes have been documented in cultured populations as a result of historical hatchery practices, with loss of alleles through drift, artificial selection, non-random mating, and the relaxation of sexual selection (Meffe 1986, Waples 1999). An overarching effect is that fitness may be compromised (Hatchery Scientific Review Group 2009). Straying hatchery-origin salmonids can place natural populations at risk both through potential interbreeding and through ecological interactions with natural-origin spawners (Bakke 1997, Leider 1997). They also have the potential to disrupt the genetic composition of natural populations, and beneficial genes in locally adapted natural-origin salmonids may become diluted by mating with hatchery-origin individuals. The greatest risk is if the hatchery fish have been selected for domestication or are from a non-native stock (Keefer et al. 2008).

Release strategies for Chinook salmon produced in hatcheries in the Sacramento River system in California's Central Valley (Figure 1) include releases at downstream locations, as well as from the hatchery itself. The rationale behind downstream releases is that by being released closer to the ocean, Chinook salmon smolts avoid potential sources of mortality that they would otherwise encounter in the rivers in route to the ocean. Mortality may be either direct or indirect from sources that include impaired rearing and migratory habitat, predation by both native and introduced piscivorous species, and entrainment into water diversions). The goal of downstream releases is to increase survival of Chinook salmon produced in the hatcheries, and hence increase the number of fish available to fisheries and returning to the hatcheries for spawning. Coded-wire tag recoveries provide evidence that this goal is being attained; results of 2010 and 2012 Chinook salmon ocean harvest and spawner escapement surveys showed that downstream net-pen releases in the San Francisco Bay made significant contributions to ocean fisheries. In some instances, these contributions were greater compared to upstream releases (Kormos et al. 2012, Palmer-Zwahlen and Kormos 2013).

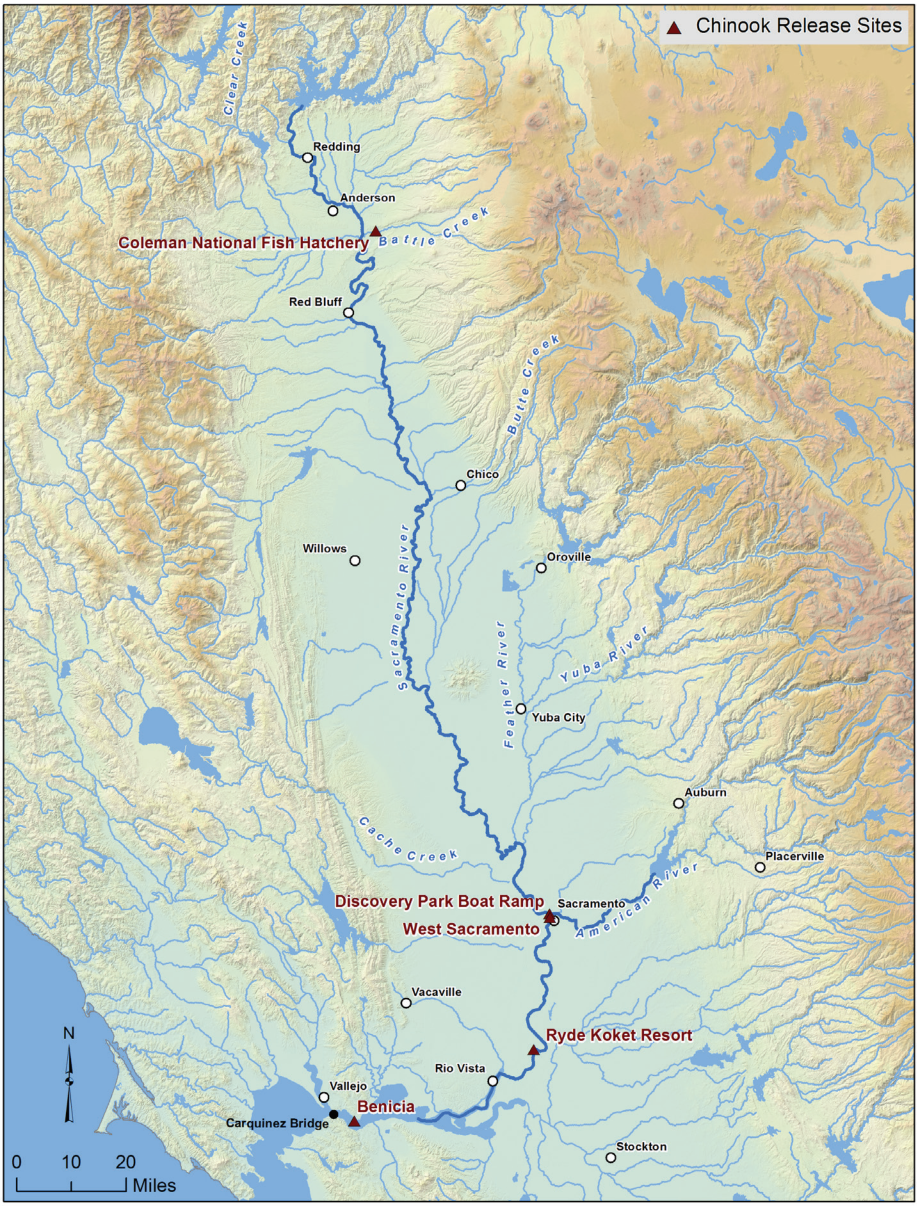

FIGURE 1.—Map of the Sacramento River watershed including Coleman National Fish Hatchery and release sites at Discovery Park, West Sacramento, Ryde Koket Resort, and Benicia during winter, 2006-2007. Map created by Daniel Rankin, California Department of Fish and Wildlife.

Release location of hatchery-origin Chinook salmon may affect their straying rates (Quinn 1997), perhaps because the fish released away from the hatchery do not acquire the sequence of cues that fish released at the hatchery acquire as they migrate downstream. Both the distance between release site and the hatchery facility, and location of the release site within the watershed, can affect homing (Quinn 1997). Downstream releases may result in improved survival, but at the cost of impaired homing (McCabe et al. 1983). However, Pacific salmonids released long distances of 100 km or more (Ebel 1980) from their rearing site still may return to the hatchery (Ebel et al. 1973, Slatick et al. 1975).

In January 2009, a late pulse of fresh-run adult Chinook salmon appeared in the lower American River, a major tributary to the lower Sacramento River (Figure 1). These fish were observed at what would have normally been the end of the 2008–2009 fall-run Chinook salmon spawner escapement survey on the lower American River. To determine the origin of these fish, the spawner escapement survey was extended through February 2009. Most of the late arriving Chinook salmon were adipose fin-clipped and coded-wire tagged, which indicated that they were of hatchery origin. Through recovery of the coded-wire tags, these fish were determined to be strays of 2006 brood-year releases of late-fall run Chinook salmon that had been produced at Coleman National Fish Hatchery (CNFH) in the upper Sacramento River system (Figure 1). These late-fall run Chinook salmon came from downstream, experimental release groups and were part of a juvenile Chinook salmon survivorship study conducted in the Sacramento-San Joaquin River Delta during the winter of 2006–2007 (P. Brandes, U.S. Fish and Wildlife Service, personal communication, 2011).

Fall-run Chinook salmon (Table 1) are currently the only naturally extant run of Chinook salmon on the lower American River (Williams 2001). They are produced at the Nimbus Fish Hatchery (at river km 36) and also occur as a natural population that spawns in the river. Late-fall run Chinook salmon (Table 1) arriving in January could negatively impact fall-run Chinook salmon production on the American River by competing for spawning space, or by excavating or superimposing their redds on those of fall-run Chinook salmon that had already spawned in the river. The presence of a significant number of late-fall run Chinook salmon in the American River posed itself as a management concern to the California Department of Fish and Wildlife (CDFW), thus warranting further study and analysis.

Table 1.—Timing and characteristics of Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) 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

The purpose of this study was to determine the relationship between straying by adult late-fall run Chinook salmon into the American River, and downstream release locations of juvenile CNFH late-fall run Chinook salmon from the 2006 brood year. This information will inform fishery managers about the relative risk of straying into Sacramento River tributaries, such as the American River, when making decisions about downstream release locations for hatchery-produced Chinook salmon. Because of the variability in straying between river systems and populations, this research is most pertinent to the lower American River, but may have application to other river systems with hatcheries and naturally spawning populations.

Three primary hypotheses about late-fall run Chinook salmon straying were tested in this study: (1) late-fall run Chinook salmon produced at CNFH and released downstream are more likely to stray than those released at or in close proximity to CNFH; (2) downstream releases of late-fall run Chinook salmon increase the net straying rate into the American River; and (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.—Coded-wire tag release and return data from CNFH's 2006 brood-year of late-fall run Chinook salmon 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. Release data by coded-wire tag number included brood year, release location and date, and the number of fish tagged in each release group. Coded-wire tag return data for this cohort were recovered in the American River and other inland spawning locations and hatcheries in the Sacramento River Basin (see Results for locations). This included recoveries by the United States Fish and Wildlife Service (USFWS) and CDFW. This allowed for the comparison of the number of fish found to have strayed into the lower American River or elsewhere in the watershed to the number of fish that homed to CNFH. The 2006 brood-year return data included corresponding return data over several years from winters 2007–2008 through 2010–2011 (capturing 2-5 year-old fish). 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 available for use at www.rmpc.org.

Escapement surveys.—Field surveys were conducted as an extension of the lower American River escapement surveys conducted by CDFW in survey years 2008–2009 through 2009-2010 (two season span). Surveys also occurred in 2010–2011 but were limited because of high river flows and turbidity. When river conditions allowed, the Chinook salmon carcass surveys were conducted weekly in the spawning reaches of the lower American River, primarily from a short distance below Nimbus Dam down to the crossing of the Sunrise Bridge in Sacramento, CA (approximately 4 km). All carcasses encountered during these surveys were collected and evaluated for the presence of a coded-wire tag; carcasses were selected by the absence of the adipose fin. If the adipose fin was absent, therefore indicating the possible presence of a coded-wire tag, the head was removed by machete, labeled, and retained for tag recovery. Recovery of the coded-wire tag data (reading and recording tag information) collected in the lower American River was conducted by CDFW. For more information regarding CDFW's lower American River escapement surveys, see Vincik and Mamola (2010).

Data analysis.—Three hypotheses were tested using a Chi-square test for independence to compare: (1) 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); (2) 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; and (3) the observed counts of fish that were recovered in the American River (strayed) to the counts of fish recovered at the CNFH (not strayed) based on the release location (distance) from the American River. The Chi-square tests assessed whether the tendency to stray was associated with release location. Note that *df*=1 when observations from all downstream release locations were grouped together in comparisons with observations associated with releases made upstream at CNFH.

The Spearman Rank correlation coefficient was used to determine the strength of the relationship between distance of release site to the mouth of the American River, to the percentage of individuals from each release site that were observed straying into the lower American River.

The relationship between survival and release site for 2006 brood-year late-fall run Chinook salmon was assessed using Chi-square tests for independence to determine if there was a difference in survival between fish released from CNFH compared to fish released at downstream sites. In this analysis, adult return rates were used as an index of survival.

We also assessed other coded-wire tag recoveries of 2006 brood-year late-fall run Chinook salmon that were not related to straying, including smolt recoveries made in the Sacramento-San Joaquin Delta (Delta). This investigation was conducted to determine if smolt entrainment at the Central Valley Project (CVP) or the State Water Project (SWP) pumping facilities may have impacted adult recovery statistics. In addition, Chi-square tests for independence were used to determine if release location contributed to either ocean or freshwater fisheries returns, and if spawning returns differed with the inclusion of fisheries returns. In all statistical tests used in this study, α=0.05.

Results

Overall results.—USFWS released 1,070,896 coded-wire tagged juvenile late-fall run Chinook salmon from the 2006 brood-year raised at CNFH. Of these, 854,496 were released in close proximity to the hatchery and 216,400 were released at downstream locations that included: Discovery Park; Sacramento River at West Sacramento; Sacramento River at Ryde Koket Resort; Georgiana Slough, and Benicia (Table 2, Figure 1). The nearest downstream location to the American River was Discovery Park, over 300 river km south of Battle Creek. Direct counts of recorded recoveries (returns) of 2–5 year-old adults, excluding the ocean and freshwater fisheries, from the 2006 brood-year were made from 2007–2008 through 2010–2011. A total of 6,487 adults returned to spawn in the Sacramento River watershed, and 6,103 (94%) of those Chinook salmon homed back to CNFH, while 384 (6%) strayed to other locations within the watershed. Of the strays, 279 (73%) were recovered in the lower American River, captured either at Nimbus Hatchery or in the river during the Chinook salmon carcass surveys. The percentage of returning late-fall run Chinook salmon that were released proximate to CNFH and homed was 99.3%, while the percentage released downstream that homed back to CNFH was 34.0%. Of the Chinook salmon released at the hatchery, 0.70% survived to be captured in the watershed, while 0.24% of the fish released downstream survived (Table 2).

Hypothesis 1: *Hatchery produced late-fall run Chinook salmon released at downstream locations are more likely to stray than those released at or in close proximity to the CNFH.* — The overall stray rate of late-fall run Chinook salmon released at downstream locations was 66.0%, while that for late-fall run Chinook salmon released near CNFH was 0.06% (Table 3), and this difference was highly significant (X^2_1=3624, P<0.001). Therefore, for brood-year 2006, the stray rate was significantly higher for downstream releases than it was for releases made at or in close proximity to CNFH.

Table 2.—Summary of coded-wire tag data releases and adult returns for late-fall run Chinook salmon (*Oncorhynchus tshawytscha*), 2006 brood-year, Coleman National Fish Hatchery, California.

Total juveniles released	1,070,896
Total juveniles released at hatchery	854,496
Total juveniles released downstream	216,400
Total adults returned	6,487 (0.61%)
Total adults returned that were released at hatchery	5,970
Total adults returned that were released at downstream locations	517
Total homed to natal hatchery	6,103
Total strayed	384 (6%)
Total homed released at natal hatchery	5,927
Total strayed released at natal hatchery	43 (0.07%)
Total homed released at downstream locations	176
Total downstream releases that strayed	341 (66%)
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

Table 3.—Late-fall run Chinook salmon (*Oncorhynchus tshawytscha*), brood-year 2006, that strayed or homed as a function of release location, California.

Release Location	Total Returns	Homed	Strayed	Percent Strayed	Standard Error (95% CI)
Hatchery	5,970	5,927	43	0.07%	0.1%
Downstream	517	176	341	66.0%	2.1%

Hypothesis 2: *Downstream releases of 2006 brood-year late-fall run Chinook salmon increased straying into the American River*.—Among releases of 2006 brood-year late-fall run Chinook salmon, 54% of those released at downstream locations strayed into the American River, while 0% of those released in close proximity to CNFH did so (Table 4), and this difference was highly significant (X^2_1=3786, P<0.001).

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.—Releases of late-fall run Chinook salmon at West Sacramento had the highest stray rate (88%), followed by Discovery Park (64%), Ryde Koket (42%), Benecia

Table 4.—Number of late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) that strayed into the American River that were released at the Coleman National Fish Hatchery or downstream locations in the Sacramento River and Sacramento-San Joaquin Delta, California.

Release Location	Total Returns	Homed	Strayed into American River (*n*)	Strayed into American River (%)	Standard Error (95% CI)
Hatchery	5,970	5,927	0	0.0	0.0%
Downstream	517	176	279	54.0	2.2%

Table 5.—Brood-year 2006 late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) from the Coleman National Fish Hatchery that strayed into the American River or returned elsewhere in the watershed, as a function of release site. Approximate distance from mouth of the American River: Discovery Park, 0 km; West Sacramento, 2 km; Ryde Koket, 48 km; Benecia, 113 km; Coleman National Fish Hatchery (NHF), 322 km.

Location	Total Returns	Returned Elsewhere	Number Strayed[a]	Percent Strayed[a]
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

[a] Strays that entered the American River

(12%), and lastly CNFH, which had no observed strays into the American River (Table 5). These observed differences in frequencies of straying relative to proximity of release point to the American River were highly significant (X^2_4=4246, P<0.001). Generally, the fidelity of returning adult late-fall run Chinook salmon to their release locations was high, relative to their returns elsewhere in the Sacramento River system, including CNFH (Figure 2).

Correlation analysis.—The Spearman Rank Correlation coefficient indicated a strong negative relationship between stray rate and distance of release location from the American River (r_s = -0.90, P=0.037). Generally, stray rates decreased with increasing release location distance from the lower American River (Figure 3).

Survival by release location.—There was a significant difference in adult return rates between releases of 2006 brood-year late-fall run Chinook salmon made at CNFH and those made at downstream release locations (X^2_4=616.8, P<0.001). Return rates were highest in association with releases made at CNFH (0.70%) followed by those made at Benicia (0.39%). The other three downstream release locations had similar return rates to one another (0.21%–0.23%; Table 6 and Figure 4).

Smolt recoveries.—We summarized coded-wire tag recovery data for CNFH 2006 brood-year late-fall run Chinook salmon smolts that were recovered at various locations in the Delta, including at the SWP and CVP pumping facilities (Table 7). There were so few smolt recoveries made relative to their corresponding release numbers (0.06% of total

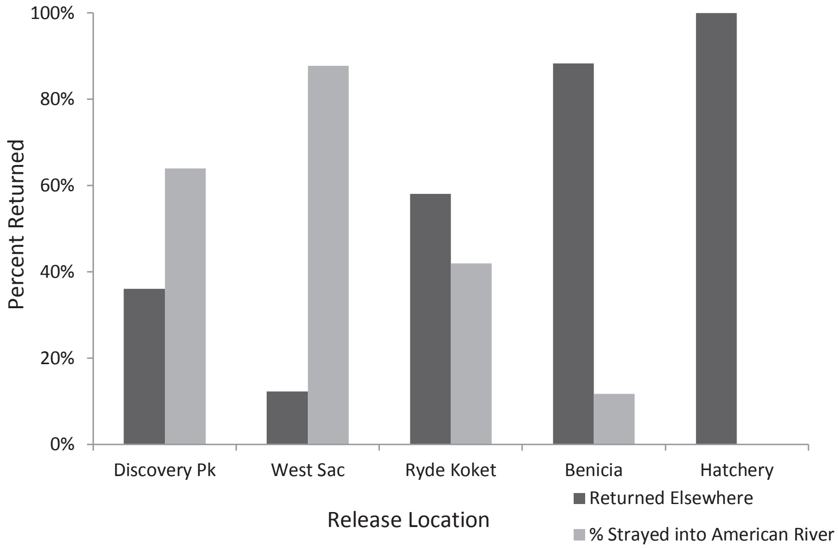

Figure 2. —Percent of adult 2006 brood-year late-fall-run Chinook salmon (*Oncorhynchus tshawytscha*) from the Coleman National Fish Hatchery that strayed into the American River compared to percent adult returns released at Discovery Park, West Sacramento, Ryde Koket Resort, Benicia, and hatchery collected between 2008 and 2011.

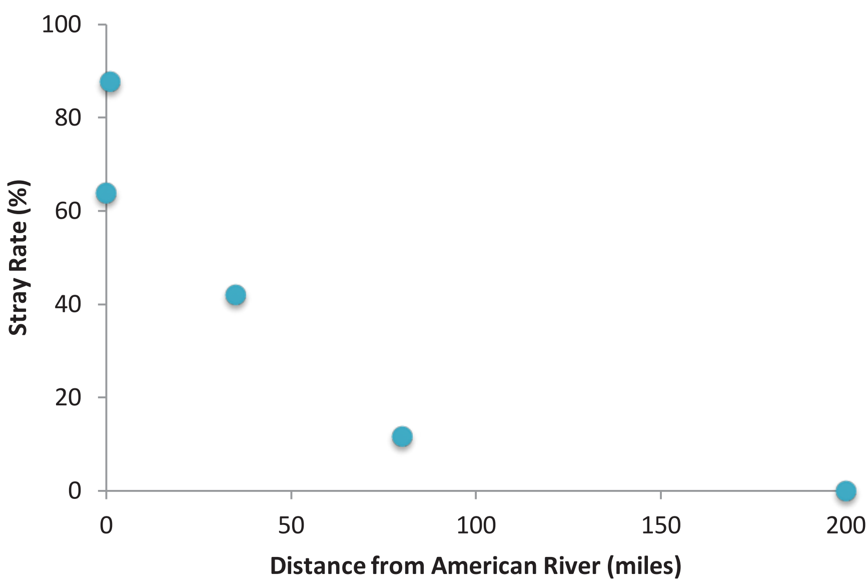

Figure 3. —Stray rate of adult 2006 brood-year late-fall-run Chinook salmon (*Oncorhynchus tshawytscha*) from the Coleman National Fish Hatchery into the American River versus distance of release site from the American River collected between 2008 and 2011. There is a significant negative relationship; stray rates decrease as distance of release site from the American River increases.

Table 6.—Brood-year 2006 total count of inland late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) adult 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

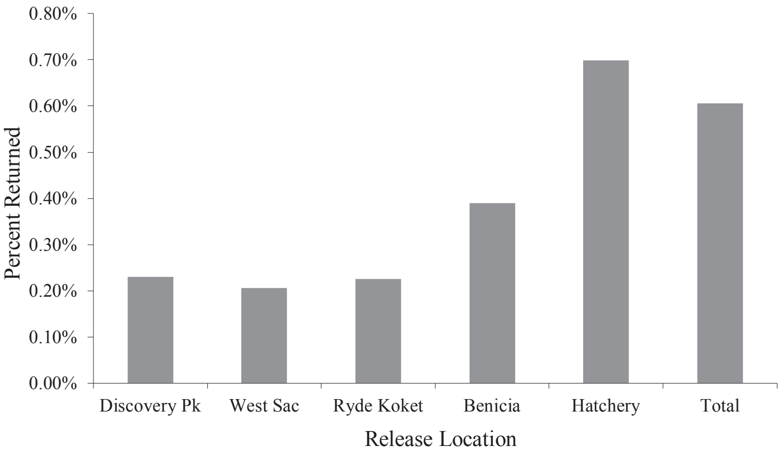

Figure 4. —Percent survival of 2006 brood-year late-fall run adult Chinook salmon (*Oncorhynchus tshawytscha*) in total and that returned by release location collected between 2008 and 2011.

Table 7.—Chinook salmon (*Oncorhynchus tshawytscha*) recoveries of brood-year 2006 smolts at the Central Valley Project (CVP), State Water Project (SWP), or other locations combined (Chipps Island, Sherwood Harbor, and others); NFH = National Fish Hatchery.

	Release location					
Recovery 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	21	137	46	2	236	1442
Total	41	163	51	2	362	619

releases) that it is unlikely that loss of these tags would have a significant impact on adult return statistics in this study.

Fisheries returns.—Late-fall run Chinook salmon released at CNFH contributed proportionately more to the freshwater fishery in the Sacramento River than individuals from all downstream release groups combined (X^2_1=9.1, P=0.0025). Conversely, releases made at CNFH did not contribute proportionately more to the ocean fisheries (X^2_1=0.038, P=0.85). Releases made at CNFH and at downstream release locations contributed equally to the ocean fishery (Table 8).

Table 8.—Summary of 2006 brood-year ocean and freshwater late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) adult catches. Percent catch is based on returns divided by total released downstream or at the Coleman National Fish Hatchery.

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

Finally, we found that there was no significant difference in percentage of adult returns for 2006 brood-year late-fall run Chinook salmon when comparing returns used for this straying study (adults intercepted in river escapement surveys and hatcheries only) to adult returns that included fishery returns by release location or as total returns (for all cases, X^2_1≤1.8, P≥0.17).

Discussion

Homing and straying are natural behaviors in anadromous salmonids (Quinn 1984, Kaitala 1990, Quinn 2005). Salmonids 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 generally higher rates than those of natural origin (Jonsson et al. 2003). The results of this study suggest that when late-fall run Chinook salmon reared at CNFH are released at downstream locations, straying of these fish increases in the Sacramento River system, including into the lower American River. Additionally, the results suggest that the closer juvenile releases are to the mouth of the American River, the more likely they are to stray into the river as adults. It is worth noting in this regard that although releases made at Discovery Park had a lower stray rate than those made at West Sacramento, the proximity of the two locations is very close (within about 1.6 river km). Thus, the distance between these two locations may not have been a significant factor in the difference between their corresponding stray rates (Table 5).

Fish released near the mouths of other Sacramento River tributaries might also be more likely to stray into those rivers as well; however, there were no data to test this assumption. Because this study did not include downstream release locations between CNFH and the American River, it is unknown if stray rates would be similarly high in such instances. There is possibly a release distance upstream at which stray rates into the American River would also be high before dropping off and approaching stray rates associated with releases made at CNFH, unless this distance puts the fish in proximity of other potentially attractive tributaries.

Notably, none of the 2006 brood-year late-fall run Chinook salmon strays detected in the American River originated from releases made in proximity to CNFH. It is possible that some may have strayed there, but were undetected. However, given that adult returns from releases made at CNFH numbered more than 11 times the number of adult returns from releases made at downstream locations, the data strongly support the hypothesis that downstream releases increase straying of late-fall run Chinook salmon into the American River.

Downstream releases of hatchery-origin Chinook salmon will likely continue, to some extent or another, in the Sacramento River system, particularly if downstream net-pen releases yield high returns for ocean fisheries (Kormos et al. 2012), and in light of degraded water quality and habitat conditions, including drought effects, water diversions, and predation by introduced species, in the Sacramento-San Joaquin River and Delta system. As these practices continue in future, we recommend that releases not occur near the mouth of the American River. Results from this study suggest that releases should be made some distance, to be determined by further study, above the American River and away from other tributaries, or farther downstream in the system, as is feasible. We also recommend that all individuals in downstream release groups be marked and tagged, and that adult returns be scrutinized based on release location. This approach would be consistent with current CDFW protocols for releases of hatchery-produced fall-run Chinook salmon used for enhancement purposes or field experiments; 100% of fall-run Chinook salmon are uniquely tagged from Feather River and Mokelumne River Hatchery enhancement programs (K. Shaffer, California Department of Fish and Wildlife, personal communication). If only a portion of the downstream releases of late-fall run Chinook salmon observed in this study had been marked and coded-wire tagged, stray rates would likely have been greatly underestimated, or these strays may have gone undetected entirely.

Results of this study do not support the use of downstream releases to increase escapement of late-fall run Chinook salmon. Escapement did not increase for late-fall run Chinook salmon from any of the downstream release groups. The absence of increased survival among Chinook salmon released downstream as compared to those released at CNFH could have been due to several factors such as environmental conditions, handling and release methods, trucking practices, holding pens or practices, release locations, water quality conditions, entrainment, and predation. Associated smolt recoveries were very low in the Delta. Recoveries at the State and Federal water project facilities were also low for this particular cohort. However, it is not known what percentage of coded-wire tags from fishes as small as late-fall run Chinook salmon smolts are not recoverable at these facilities.

There are indications that the reduction of intraspecific competition between juveniles of hatchery and natural origin could reduce the impact of hatchery stock on natural-origin Pacific salmon (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 natural-origin juvenile Chinook salmon. Also, coded-wire tag results for fall-run Chinook salmon suggest that net-pen releases into the San Francisco Bay estuary can enhance ocean fisheries (Kormos et al. 2012, Palmer-Zwahlen and Kormos 2013).

Challenges encountered.—The greatest challenge with this study was that the extended escapement surveys on the lower American River covered only a single cohort, brood-year 2006, which had multiple downstream release groups as smolts. 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 those strays in all corresponding return years. Also, during the winter of 2010–2011, high flows washed out nearly the entire carcass survey season for both fall and late-fall runs on the American River. If the carcass survey had been successfully conducted during that additional recovery season for the 2006 brood year, it is foreseeable that the overall stray rate of 2006 brood-year late-fall run Chinook salmon into the American River might have been higher than was estimated in this study.

Another challenge, and indication for further study, is that the 2006 brood-year may have been an outlier, as evidenced by the fact that the brood year's returns to the American River attracted attention that apparently other brood year returns, from which downstream releases were conducted, did not. The 2007 brood-year of late-fall run Chinook salmon at CNFH also had downstream releases, and some strayed into the lower American River, but did not instigate extended carcass surveys by CDFW. High stray rates may have also been due to conditions in the river. Timing of releases and river conditions could have caused smolts to imprint unusually strongly to the American River, or strong attraction flows could have affected adult immigration when upstream migrating Chinook salmon adults were passing the American River.

Methods used during the extended period of the escapement surveys on the lower American River were another challenge encountered in this study. Standardized protocols of mark-and-recapture for abundance estimation were used. Heads were collected for coded-wire tag recovery, but carcasses were not marked for recapture later. Consequently, 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 estimate the total number of 2006 brood-year late-fall run Chinook salmon that strayed into the lower American River. Instead, we were relegated to using only the actual, raw return numbers, which underrepresent 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. Strays may excavate or superimpose their redds on redds of fall-run Chinook salmon that have completed spawning. There may also be competition between the juveniles of each run in the river (Reese et al. 2009), although late-fall run juveniles would be smaller and theoretically less competitive than the older and larger fall-run juveniles. Spatial separation between the runs could possibly exist if the entire historical spawning habitat for Chinook salmon on the American River was still available. However, it is not known if there was an historic late-fall run of Chinook salmon on the American River (Williams 2001).

Some potential problems of straying might be mitigated by factors related to the life history of the two runs. Isolation between the runs occurring during the juvenile life stages could reduce potential impacts of late-fall run Chinook salmon on fall-run Chinook salmon. Fall-run Chinook salmon in the Central Valley are considered ocean-type, which rear in the river for a short time (days to a few months) before emigrating to the Pacific Ocean, and late-fall run Chinook salmon are considered river or stream-type, and rear in the freshwater environment for a longer period of time (up to one 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 the thermal preference of juvenile Chinook salmon. Therefore, juvenile late-fall run Chinook salmon survival might be very low (R. Titus, California Department of Fish and Wildlife, 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. Smaller late-fall run Chinook salmon might even deflect predation from juvenile fall-run Chinook salmon (Reese et al. 2009).

Additional recommendations.—Analysis of late-fall run Chinook salmon spawning returns from past downstream releases of different brood years should be conducted. All future downstream release groups should be monitored for adult returns to Central Valley anadromous salmonid hatcheries. In-river surveys for late-fall run Chinook salmon should be conducted on the lower American River to determine if the 2006 brood year was an outlier, and to gain a better idea of straying patterns in the river and across the Sacramento River Basin.

Late spawning season surveys should be conducted on 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 aging and micro-chemical analysis that may yield watershed origin and migratory history of the fish. These data would provide information on stock composition of Chinook salmon spawning in the American River, including if there are offspring or spawning adults of late-fall run Chinook salmon from CNFH.

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

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