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ARTICLE

Maximum Likelihood Estimation of the Proportion of Hatchery-Origin Fish on Spawning Grounds Using Coded Wire Tagging and Parentage-Based Tagging

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Abstract

For salmon populations in the Columbia River and Snake River basins, many of which are listed under the U.S. Endangered Species Act of 1973, reliable estimates of the proportion of hatchery-origin adults in spawning areas (*p*) are needed to assess population status and the genetic and demographic interactions of hatchery- and natural-origin fish. Some hatchery fish receive visible marks, coded wire tags (CWTs), parentage-based tags (PBTs), or all three. This allows one to identify whether fish recovered after release are of hatchery origin. Parentage-based tagging involves genotyping hatchery broodstock and uses parentage assignments as "tags" that identify the origin and brood year of their progeny. We derived a maximum likelihood estimator of *p* and applied it to the 2012 and 2013 carcass survey data for spring–summer Chinook Salmon *Oncorhynchus tshawytscha* in the South Fork Salmon River, Idaho. Maximum likelihood estimation was also applied to CWT data and, for investigating the importance of expected tag recoveries on precision, to simulated PBT data for fall Chinook Salmon spawning in the Hanford Reach of the Columbia River. Precision of *p* from maximum likelihood

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estimation increased with the expected number of tag recoveries in a carcass survey, whether CWTs or PBTs. In the South Fork Salmon River application, there were 340% more PBT recoveries than CWT recoveries, leading to greater precision in release-specific values of *p* from maximum likelihood estimation. The maximum likelihood estimation procedure provides fisheries managers a method to design a tagging and sampling program aimed at estimating *p*, a valuable measure of the potential for interaction of wild- and hatchery-origin fish on the spawning grounds. To design a program for estimating *p*, we recommend selecting a target level of precision and then choosing a tagging fraction and sampling rate that delivers that precision in the most cost-effective way.

Assessment of the status of salmon populations in the Columbia and Snake River basins, many of which are listed under the U.S. Endangered Species Act of 1973, requires reliable estimates of the proportion of hatchery-origin spawners on the spawning grounds, or p (McClure et al. 2003). Currently, demographic and ecological effects of hatchery-origin fish on spawning grounds are not well understood (Pearsons 2008), but estimates of their proportions are critical to fully evaluate potential risks of all 178 hatchery programs in the region (Mobrand et al. 2005; HSRG 2009). If p is unknown, a downward trend in natural-origin spawners could be masked by an upward trend in hatchery-origin inputs to the spawning grounds (Hinrichsen 2003; McClure et al. 2003). A reliable estimate of p provides a better understanding of the spatial and temporal distribution of hatchery-origin spawning as a means to identify demographic and ecological interactions (Pearsons 2008) and the potential for gene flow between natural- and hatchery-origin fish on spawning grounds (Ford 2002). It also can be used to identify trends in the numbers of natural-origin adult fish on spawning grounds (McClure et al. 2003).

An estimate of p is also needed to determine the extent of genetic, demographic, and ecological impacts resulting from interactions between hatchery- and natural-origin spawners. Studies of relative reproductive success have demonstrated that hatchery-origin fish spawning in the wild may reduce the genetic fitness of natural populations for several generations (Waples 1991; Araki et al. 2007; but see Hess et al. 2012), particularly when p approaches 10% (Ford 2002). Genetic effects are greater when broodstock are mostly composed of hatchery-origin fish and less when they are primarily of natural origin (Hess et al. 2012).

In the Columbia River basin, estimating p has been possible because some hatchery releases of juvenile fish have a visible mark (VM), a coded wire tag (CWT), or both, allowing discrimination between hatchery- and natural-origin individuals. Visible marking (e.g., clipping the adiposefin or tagging with visible elastomer implants) of hatchery releases is a widespread practice among hatchery operators in the Columbia River basin. Millions of hatchery fish are tagged with CWTs (Jefferts et al. 1963), which are coded magnetic wire tags implanted in the snouts of juvenile fish. These CWTs identify the hatchery of origin and release group of returning adult fish. To estimate p, field workers conduct carcass surveys that record the numbers of adults that have a VM only, a CWT only, or VM and CWT, and collect CWTs for future reading.

Currently, several published approaches for estimating p, including Bayesian (e.g., Geiger 1994; Barber et al. 2011) or frequentist (e.g., Hankin 1982; Hinrichsen et al. 2012) methods of estimation are based on tagging or marking (CWTs, otolith marks, or adipose fin clips) of juveniles prior to release. Dauer et al. (2009) proposed a modified mark–recapture method for iteroparous steelhead *Oncorhynchus mykiss* based on spawn checks (reabsorption of scales during previous freshwater migration due to high energy demands of egg or milt production, which Rideout et al. (2005) identified in upriver migrating adults). However, the method of Hinrichsen et al. (2012), which was originally applied to CWT and VM data, is the only published approach that produces release-specific estimators of p and their standard errors when there are multiple hatchery releases contributing fish to the spawning grounds. In the Columbia River basin, fish originating from different source hatcheries are known to stray into the same spawning area (McClure et al. 2008; Hinrichsen et al. 2012).

A recent alternative to the coded-wire-tagging approach for estimating p is a genetic-tagging approach of hatchery releases, called parentage-based tagging, which can be used to mark a high percentage of juvenile salmon released with a parentage-based tag (PBT). In this alternative approach, some juveniles are marked with a VM, a PBT, or both. Parentage-based tagging involves genotyping hatchery broodstock (parents) and adding these genotypes to a database (Anderson and Garza 2005, 2006; Steele et al. 2011, 2013). Genotyped progeny of these parents, collected as juveniles or adults, can be assigned back to their parents, thus identifying their hatchery of origin and age.

In this study, we estimated p using maximum likelihood estimation (MLE) that applies to both PBT and CWT data. We chose the MLE framework because it has a well-developed theory and desirable statistical properties including asymptotic normality, function invariance, and consistency (Mood et al. 1974). This MLE framework has several advantages over the generalized least-squares estimation (GLSE) used previously by Hinrichsen et al. (2012). In contrast to the GLSE approach of Hinrichsen et al. (2012), the MLE approach allows non-VM carcasses to be checked for tags, does not require a known sample rate, and explicitly accounts for tag and VM loss due to carcass decay, which, if ignored, can introduce bias (Mohr and Satterthwaite 2013).

Our goal was to develop a reliable estimator of p, apply it to field data, and demonstrate its use in the design of a program based on PBTs. We also sought to show how the precision of p from the MLE approach changes with tagging fraction (whether CWTs or PBTs are used). Releases of fish with CWTs typically have lower tagging fractions than those with PBTs. We developed an MLE of

p and applied it to PBT and CWT data from the spawning population of spring–summer Chinook Salmon *O. tshawytscha* in the South Fork Salmon River, Idaho. Additionally, we applied MLE to CWT data from the fall Chinook Salmon spawning population in Hanford Reach of the Columbia River, which has adult fish inputs from multiple source hatcheries. Using alternative study designs for the implementation of parentage-based tagging in this population, we showed how the precision of p using the MLE approach varies with carcass sampling rate and PBT fractions.

METHODS

Here we describe data, study protocol, the maximum likelihood estimation procedure, applications to real data, and study design investigations. The joint likelihood function was maximized using Fisher's Scoring Method (Jennrich and Sampson 1976). A web-based tool that implements the MLE approach, including R-code and program documentation, is available online at: www.onefishwofish.net/hatchPBTE. The notation is summarized in Table 1 and the main assumptions are provided in Table 2.

Study Protocol and Probability Model

Our method explicitly treats carcass recoveries that, due to carcass decay, have undetermined VM status at release, undetermined PBT status at release, or both. The PBT status at release could be either "tagged" if, at release, a fish can be assigned back to its parents, or "untagged" if it cannot, for whatever reason. For convenience, "undetermined VM" and "undetermined PBT" indicate that, due to carcass decay, it was impossible to determine whether a fish examined as a carcass was visibly marked or parentage-based tagged at release, respectively. For our analysis, counts of VM fish and non-VM fish on the spawning ground excluded the undetermined VM fish: the undetermined VM fish were placed in their own category. Likewise, undetermined PBT fish were placed in their own category separate from PBT and non-PBT fish.

We assumed a two-step sampling protocol. In step 1, a random sample of size N was drawn from the fish on the spawning grounds. This sample consisted of three groups: VM, non-VM, and undetermined VM fish. In step 2, random subsamples of size n_1, n_2, and n_3 were drawn from the VM, non-VM, and undetermined VM groups, respectively, and these were tested for PBTs. The total subsample size is $n = n_1 + n_2 + n_3$. At one extreme, researchers would genotype all fish in the total spawning ground sample ($n = N$) or, at the other extreme, researchers would genotype a small subsample of the total spawning ground sample ($n << N$).

We defined variables in terms of parentage-based tagging, but the method generalizes to coded wire tagging as well, and we applied the MLE procedure to PBT and CWT data. We began with notation that is used to specify the probability model. We let p_i represent the fraction of fish on the spawning grounds that originated from release i. We let λ_i represent the VM fraction applied to release i, let $\phi_{i,1}$ represent the PBT fraction that was applied to VM fish in release i, and let $\phi_{i,2}$ represent the PBT fraction that was applied to non-VM fish in release i. We further assumed that the total number of fish on the spawning grounds sampled was N (fixed), that x_1 represented the number of sampled fish that had a VM, x_2 represented the number of sampled fish that did not have a VM (i.e., non-VM fish), and $x_3 = N - x_1 - x_2$ represented the number of sampled fish with an undetermined VM. The probability that a fish had determinable VM was θ.

The numbers of fish from release i determined to have a PBT were denoted y_i (VM fish), z_i (non-VM fish), and w_i (undetermined VM fish). The numbers of fish with undetermined PBT status for the VM, non-VM, and undetermined VM groups were denoted by u_1, u_2, and u_3, respectively. The probability that a fish with determinable VM status can be genotyped was γ_1, and the probability that a carcass with undeterminable VM status can be genotyped was γ_2. The assumptions in Table 2 allowed us to express the joint distribution of counts of fish on the spawning grounds as a product of multinomial probability distributions:

$$
\begin{aligned}
f(x_1,x_2,x_3,y_1,\ldots y_m,z_1,\ldots z_m,w_1,\ldots w_m) &= \binom{N}{x_1,x_2,x_3} \\
&\left(\theta\sum_{i=1}^{m}\lambda_i p_i\right)^{x_1}\left[\theta\left(1-\sum_{i=1}^{m}\lambda_i p_i\right)\right]^{x_2}(1-\theta)^{x_3} \\
&\times\binom{n_1}{y_1,\ldots,y_m,u_1,n_1-\sum_{i=1}^{m}y_i-u_1} \\
&\prod_{i=1}^{m}\left(\frac{\lambda_i\gamma_1\phi_{i,1}p_i}{\sum_{j=1}^{m}\lambda_j p_j}\right)^{y_i}(1-\gamma_1)^{u_1}\left(\gamma_1-\frac{\gamma_1\sum_{i=1}^{m}\lambda_i\phi_{i,1}p_i}{\sum_{j=1}^{m}\lambda_j p_j}\right)^{n_1-\sum_{i=1}^{m}y_i-u_1} \\
&\times\binom{n_2}{z_1,\ldots,z_m,u_2,n_2-\sum_{i=1}^{m}z_i-u_2} \\
&\prod_{i=1}^{m}\left[\frac{(1-\lambda_i)\gamma_1\phi_{i,2}p_i}{\left(1-\sum_{j=1}^{m}\lambda_j p_j\right)}\right]^{z_i}(1-\gamma_1)^{u_2}\left[\gamma_1-\frac{\sum_{i=1}^{m}(1-\lambda_i)\gamma_1\phi_{i,2}p_i}{\left(1-\sum_{j=1}^{m}\lambda_j p_j\right)}\right]^{n_2-\sum_{i=1}^{m}z_i-u_2} \\
&\times\binom{n_3}{w_1,\ldots,w_m,u_3,n_3-\sum_{i=1}^{m}w_i-u_3} \\
&\prod_{i=1}^{m}\left\{\left[\lambda_i\phi_{i,1}+(1-\lambda_i)\phi_{i,2}\right]\gamma_2 p_i\right\}^{w_i}(1-\gamma_2)^{u_3} \\
&\times\left[\gamma_2-\sum_{i=1}^{m}\left[\lambda_i\phi_{i,1}+(1-\lambda_i)\phi_{i,2}\right]\gamma_2 p_i\right]^{n_3-\sum_{i=1}^{m}w_i-u_3}
\end{aligned}
\tag{1}
$$

TABLE 1. Notation used for equations (1) and (2) in the text. NA = not applicable.

Symbol	Definition	Range of possible values
	Release variables	
m	Number of releases.	1, 2, …
$\phi_{i,j}$	(PBT fraction): fraction of the fish from release i that have a PBT for VM fish ($j = 1$) and non-VM fish ($j = 2$).	[0, 1]
λ_i	(VM fraction): fraction of fish from release i that have a VM.	[0, 1]
S_i	Number of families in release i (PBT data only).	0, 1, …
G_i	Number of tagged families in release i (PBT data only).	0, 1, …, S_i
	Spawning ground variables	
N	Number of adult fish on spawning grounds sampled, $N = x_1 + x_2 + x_3$.	0, 1, …
x_1	Number of VM fish on spawning grounds in sample of size N.	0, 1, …, N
x_2	Number of non-VM fish on spawning grounds in sample of size N.	0, 1, …, N
x_3	Number of undetermined VM fish on spawning grounds in sample of size N.	0, 1, …, N
θ	Probability that the VM status of a fish at release can be determined when it is recaptured as a carcass.	[0, 1]
γ_1	The probability that the tag status of a fish at release can be determined when it is recaptured as a carcass whose VM status at release can be determined.	[0, 1]
γ_2	The probability that the tag status of a fish at release can be determined when it is recaptured as a carcass whose VM status at release cannot be determined.	[0, 1]
p	True proportion of hatchery-origin fish on spawning grounds.	[0, 1]
p_i	True proportion of hatchery-origin fish on spawning grounds from release i.	[0, p]
n	Subsample of fish on spawning grounds tested for PBTs, $n = n_1 + n_2 + n_3$.	0, 1, …, N
n_1	Subsample of VM fish on spawning grounds tested for PBTs.	0, 1, …, x_1
n_2	Subsample of non-VM fish on spawning grounds tested for PBTs.	0, 1, …, x_2
n_3	Subsample of undetermined VM fish on spawning grounds tested for PBTs.	0, 1, …, x_3
y_i	Number of VM fish on spawning grounds in subsample determined to be from release i using PBTs.	0, 1, …, n_1
z_i	Number of non-VM fish on spawning grounds in subsample determined to be from release i using PBTs.	0, 1, …, n_2
w_i	Number of undetermined VM fish on spawning grounds in subsample determined to be from release i using PBTs.	0, 1, …, n_3
u_1	Number of VM fish on spawning grounds in subsample with undetermined PBT status.	0, 1, …, n_1
u_2	Number of non-VM fish on spawning grounds in subsample with undetermined PBT status.	0, 1, …, n_2
u_3	Number of undetermined VM fish on spawning grounds in subsample with undetermined PBT status.	0, 1, …, n_3
$F_{i,j}$	Family size on the spawning grounds from release i and family j (PBT data only).	0, 1, …
	Estimation	
*	Indicates a bootstrap data set, replication, or estimate.	NA
^	Indicates a maximum likelihood estimate. For example, $\hat{p}_i$ is the MLE of the proportion of hatchery-origin fish on the spawning grounds from release i.	NA

The right-hand side of equation (1) is the product of four probability distributions: the probability distribution for the VM status of carcasses recovered on the spawning grounds, and the conditional probability of distributions for the PBT status of VM carcasses, non-VM carcasses, and undetermined carcasses.

We used this joint probability distribution function to form a joint likelihood function of the unknown parameters: $\theta, \gamma_1, \gamma_2, p_1, p_2, ..., p_m$, which was then used to calculate the MLE of the proportion of hatchery-origin fish on the spawning grounds, $\hat{p} = \sum_{i=1}^{m} \hat{p}_i$, and its variance, where the circumflex symbol (^) is used to indicate the MLE of a parameter. The multinomial distribution assumed that sampling was with replacement. However, when sampling is without

TABLE 2. Assumptions for estimating the proportion of hatchery-origin Chinook Salmon on spawning grounds (p).

Assumption
1. For each release, the fraction of fish with VMs is known.
2. For each release, the fraction of fish with PBTs is known and is allowed to differ between fish with and without VMs.[a]
3. Every individual fish on spawning grounds has the same probability of being sampled, and the probability is not zero.
4. All fish on the spawning grounds from the same release have the same probability of having a VM.
5. All fish with VMs on the spawning grounds from the same release have the same probability of having a PBT.
6. All fish with no VM on the spawning grounds from the same release have the same probability of having a PBT.
7. Whether a carcass is sampled has no effect on the probability that any another carcass is sampled.
8. An individual from a particular hatchery release has the same probability of surviving to the spawning grounds as any other individual from that same release.

[a]This assumption is not necessary if fractions with VMs are identical for all releases.

replacement, the multinomial distribution often provides a good approximation of the true probability model, the multivariate hypergeometric. This approximation works best when sample size is small compared with population size (Jobson 1992). In equation (1), the realized spawning ground PBT and VM fractions for hatchery fish in the absence of carcass decay were unknown, and were estimated as the PBT and VM fractions at release, respectively. This is a common assumption in tagging studies (e.g., Hankin 1982; Hinrichsen et al. 2012; Satterthwaite et al. 2015).

Overdispersion

We anticipated that when PBT fractions were less than one, observed variance would be higher than the theoretical variance derived from equation (1) because of overdispersion of family size of the hatchery releases, as measured by PBT counts on the spawning grounds. Heterogeneity in family size may result from differences in reproductive output of breeding pairs or differences in survival probability of their offspring from tagging to their return to the spawning grounds (Satterthwaite et al. 2015). When family sizes are distributed as a Poisson, they are equally dispersed and reproduction is equivalent to that of a "Wright–Fisher" population (Hartl and Clark 2007). In this case, a correction for overdispersion was not needed for the variances produced by equation (1). For each brood year, we tested for overdispersion in the family sizes of fish on spawning grounds by testing whether the overdispersion parameter (variance/mean) estimate was significantly greater than one using the Fisher's index of dispersion (Potthoff and Whittinghill 1966; Böhning 1994),

$$\frac{\sum_{j=1}^{G_i}\left(F_{i,j}-\bar{F}_i\right)^2}{\bar{F}_i}, \qquad (2)$$

where G_i is the number of tagged families in brood year i, $F_{i,j}$ is the observed family size in the spawning ground sample of the of the jth family from brood year i, and $\bar{F}_i$ is the sample mean of family sizes from brood year i. Under the null hypothesis of equi-dispersion, Fisher's index of dispersion has a chi-square distribution with $G_i - 1$ degrees of freedom (Hoel 1943). When family sizes follow a Poisson distribution, then Fisher's index of dispersion divided by the degrees of freedom is close to one (i.e., the sample mean and variance are approximately equal). This test was performed on each brood year of data that contributed fish with PBTs to the spawning grounds.

To incorporate the potential effects of overdispersion of family sizes into our analyses, we developed a bootstrap approach that used observed family sizes on the spawning grounds (Efron and Tibshirani 1993). We generated 10,000 bootstrap data sets, applied the MLE procedure to each of these, and then calculated the bootstrap estimates of standard errors. The boostrap estimate of SE was the sample SD of the 10,000 bootstrap replicates of the MLE. These bootstrap estimates of SE, which include effects of overdispersion, were then compared with the SEs that assumed equal dispersion (standard MLE approach). Details of the bootstrap procedure are provided in the Appendix.

South Fork Salmon River Application

We estimated the proportion of hatchery-origin spring–summer Chinook Salmon on the spawning grounds of the South Fork Salmon River in 2012 and 2013 using MLE from PBT and CWT data (Table 3). Since 2008, all hatchery broodstock from the Snake River basin collected in Idaho, including broodstock from McCall Fish Hatchery, Idaho, the primary local hatchery contributing fish on the spawning grounds (Young and Blenden 2011), have been genotyped annually as part of a regional parentage-based tagging program to genetically tag hatchery releases (Steele et al. 2011). The parameters needed for the estimation procedure were derived from visible marking and genetic tagging data at McCall Hatchery, the only hatchery that contributed tagged fish to the spawning ground sample, and carcass surveys in South Fork Salmon River spawning areas downstream from the weir (Figure 1).

Broodstock in 2008 (n = 1,920), 2009 (n = 946), and 2010 (n = 781) at the McCall Hatchery were genotyped using a panel of 96 single nucleotide polymorphisms (SNPs) markers (described in Ackerman et al. 2012; Steele et al. 2011). This process resulted in genetic tagging of nearly all the released juvenile Chinook Salmon from these cohorts. In 2010, 149 adults were part of an integrated broodstock program, and 632

TABLE 3. Visible marking and parentage-based tagging at McCall Hatchery, which provided adult Chinook Salmon inputs to South Fork Salmon River spawning area in 2012 and 2013. For the spawning survey in 2012, the following inputs were used: $n = N = 218$, $n_1 = x_1 = 64$, $n_2 = x_2 = 154$, $n_3 = x_3 = 0$, ($u_1 = 5$, $u_2 = 24$, and $u_3 = 0$; PBT data), and ($u_1 = u_2 = u_3 = 0$; CWT data). For the spawning survey in 2013, $n = N = 153$, $n_1 = x_1 = 52$, $n_2 = x_2 = 89$, $n_3 = x_3 = 12$, ($u_1 = 12$, $u_2 = 28$, and $u_3 = 0$; PBT data), and ($u_1 = u_2 = u_3 = 0$; CWT data). Variables are defined in Table 1; SBS = segregated broodstock program, IBS = integrated broodstock program.

		PBT data				CWT data			
Brood year	VM fraction, λ	PBT fraction, ϕ	Number of tags in VM subsample, y	Number of tags in non-VM subsample, z	Number of tags in undetermined VM subsample, w	CWT fraction, ϕ	Number of tags in VM subsample, y	Number of tags in non-VM subsample, z	Number of tags in underdetermined VM subsample, w
					2012 Survey				
2007	0.98	0.00	0	0	0	0.24	3	0	0
2008	0.98	0.98	42	2	0	0.20	9	1	0
2009	0.98	0.96	1	0	0	0.19	0	0	0
					2013 Survey				
2008	0.98	0.98	6	1	1	0.20	1	0	0
2009	0.98	0.96	28	0	3	0.19	4	0	0
2010 (SBS)	0.98	0.99	2	0	0	0.16	0	0	0
2010 (IBS)	0.00	1.00	0	2	0	1.00	0	2	0

adults were part of a conventional or segregated broodstock program (see Mobrand et al. 2005) to distinguish between integrated and segregated programs. Since PBT was initiated in brood year 2008 (BY2008), age-5 salmon returns in 2012 were not tagged with PBT.

We developed p estimates from all regional hatcheries for salmon returns to the South Fork Salmon River spawning grounds, not just those from a single facility. However, the McCall Hatchery was the only one that contributed to recoveries of tagged fish from the spawning grounds on the South Fork Salmon River. If other hatcheries besides McCall Hatchery had contributed tagged fish to the spawning grounds, then VM and genetic tag data would be needed for those hatcheries as well. Otherwise, it would be impossible to estimate the nonzero contributions of those additional hatcheries to the spawning population. Surveys conducted prior to 2012 revealed that less than 2.0% of the carcasses recovered in the South Fork Salmon River did not originate from the McCall Hatchery (Young and Blenden 2011).

Juvenile Chinook Salmon released from the McCall Hatchery were ostensibly all visibly marked by removing the adipose fin, with the exception of BY2010 fish that were part of the integrated broodstock program; 100% were coded-wire-tagged and none were visibly marked. However, approximately 2% inadvertently received no adipose fin clip (B. Leth, Idaho Fish and Game, personal communication), and we adjusted the VM fractions downward accordingly to account for these "misclips."

Cross information (i.e., mating records) for broodstock was used to enumerate the total number of unique crosses made at McCall Hatchery each year from 2008 to 2010. The PBT rate of offspring was then calculated as the number of crosses in which both parents were successfully genotyped divided by the total number of unique mating crosses. Estimates of PBT fractions for releases from McCall Hatchery are presented in Table 3. For each release, the same PBT fraction was applied to both VM and non-VM fish. In the 2012 survey, 218 samples were drawn, and all of these were tested for a PBT; 29 failed to provide the genotype due to carcass decay. The broodstock in BY2007 were not genotyped, yielding a PBT fraction of zero, but it was still possible to infer p for BY2007. The p for BY2007 was estimated as the total p (estimated from VM data), minus the sum of the ps for BY2008 and BY2009 (estimated from PBT data). In the 2013 survey data $N = 153$, and 40 failed to provide genotype due to carcass decay. Data used for estimation of p in 2012 and 2013 are given in Table 3.

Carcass samples were collected from weekly, ground-based, spawning ground surveys in the South Fork Salmon River from mid-August through mid-September 2012 and 2013. Surveys were performed in conjunction with extensive area, multiple-pass, redd counts and supplemented with additional carcass recovery surveys at other times to maximize the number of carcasses collected. Tissue samples were collected from individuals for PBT analysis. All carcasses were visually inspected for an adipose fin clip and scanned using a CWT detector. Snouts were removed from all carcasses containing a CWT. The caudal fin was removed from all sampled carcasses to prevent duplicative sampling on subsequent surveys. Unlike the PBT data, we assumed that it could always be determined whether a CWT was present or absent.

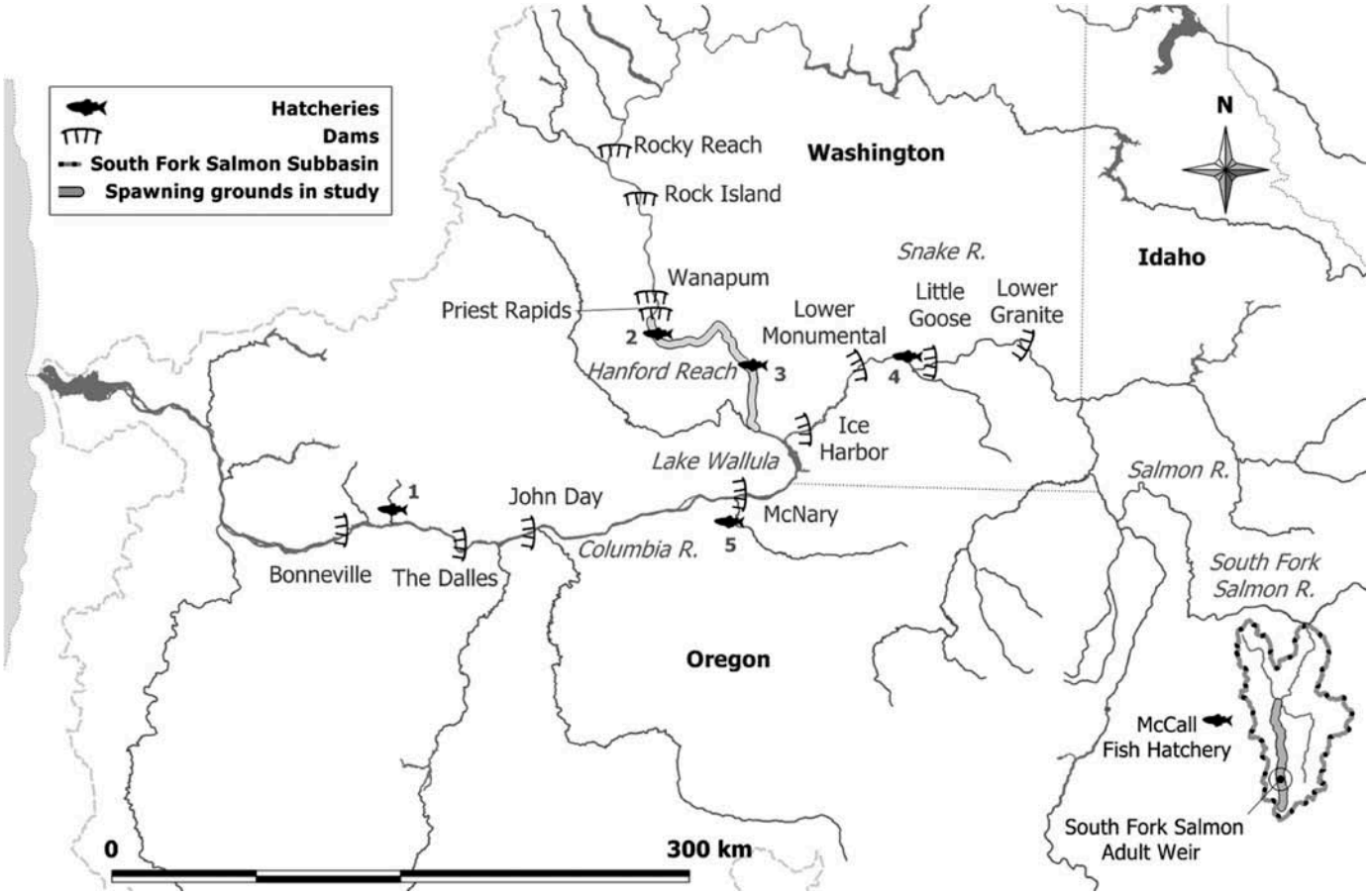

FIGURE 1. Spawning areas of the study are located in the South Fork Salmon River, Idaho, and the Hanford Reach, Washington. South Fork Salmon River spawning areas surveyed are downstream of the adult weir, where only the McCall Hatchery contributed tagged Chinook Salmon in the 2012 and 2013 surveys. The Hanford Reach, a 82-km stretch of the Columbia River extending from the upper end of McNary Dam reservoir to Priest Rapids Dam (river kilometer 639), where 2010 carcass surveys recovered CWTs. The numbered hatcheries shown contributed coded-wire-tagged fall Chinook Salmon to the Hanford Reach spawning grounds; the numbers correspond to those in Tables 4 and 6.

Samples from carcasses were genotyped following protocols in Ackerman et al. (2012) and parentage assignments were conducted using the software SNPPIT (Anderson 2010), version August 12, 2012 (https://github.com/eriqande/snppit/commits/master). An assignment criterion of a log-likelihood ratio (LOD) greater than 14 was used because parentage assignments of known-origin offspring showed this criterion to optimize the trade-off between false positive and false negative assignments (M. W. Ackerman, unpublished data). The South Fork Salmon River Chinook Salmon population p estimates are based on spawning survey data from 2012 and 2013.

To compare estimates based on parentage-based tagging with those derived from coded wire tagging for the South Fork Salmon River Chinook Salmon population, we also developed the appropriate set of inputs for the estimation procedure by ignoring PBT data and using coded-wire-tagging fractions and recoveries instead (Table 3). The goal was to determine whether PBT and CWT data yielded similar estimates and whether precision was reduced by using CWT recoveries, which are typically much lower than PBT recoveries. When CWT data were used instead of PBT data, the total sample sizes and numbers of fish tested for a tag were unchanged from the values used for PBT data (Table 3). Furthermore, the visible marking fractions were the same as those used in the PBT application. The CWT fractions used in the 2012 and 2013 surveys were calculated from data in the Fish Passage Center hatchery release database (http://www.fpc.org/; October 2013) and are provided in Table 3. The CWT recoveries from the surveys also are given in Table 3.

When PBT data were used, we tested for overdispersion of observed family sizes on the spawning grounds by applying Fisher's index of dispersion (Potthoff and Whittinghill 1966). We applied the bootstrap procedure provided in the Appendix to gauge the influence of variation in family size on the precision of the MLEs.

Hanford Reach Application

To further demonstrate the use of the MLE method and show how it may be used to develop a program for estimating the proportion of hatchery-origin fish on spawning grounds, we applied it to the 2010 fall Chinook Salmon carcass survey data in the Hanford Reach. The Hanford Reach is a 82-km stretch of the Columbia River in Washington extending from the upper end of Lake Wallula (created by McNary Dam) to Priest Rapids Dam (river kilometer 639) (Figure 1). These data were collected using CWTs instead of PBTs. We applied our MLE method to the Hanford Reach because its spawning grounds receive fish from multiple hatcheries (which complicates estimation), specific hatchery contribution estimates were available, and the carcass survey methods were known (Hinrichsen et al. 2012). Here, our approach was to evaluate several study design variables such as PBT fractions, VM fractions, carcass sample sizes, and numbers of carcasses tested for PBTs, to gauge their effects on the precision of the MLE. We evaluated alternative tagging, marking, and sampling programs by calculating the precision that they would deliver for p from the MLE approach.

In 2010, hatcheries contributing fish with CWTs on spawning grounds in the Hanford Reach portion of the river included Little White Salmon BY2005, Lyons Ferry (Snake River) BY2006, Priest Rapids BY2005 and BY2007, Ringold Springs BY2006 and BY2007, and Umatilla BY2007 (Table 4). For convenience, we treated each hatchery-brood year pair as a separate release in equations describing the estimators and their variances. Thus, there were a total of seven releases ($m = 7$). Of the $N = 9,791$ carcasses sampled in 2010, $x_1 = 331$ had an adipose fin clip, $n = 331$ were tested for a CWT, and $n_1 = 331$ of those tested for a CWT were marked with an adipose fin clip; note $n_2 = 0$. Since only VM fish were tested for a CWT, the CWT fractions for the non-VM fish do not enter the estimation: the CWT fractions given in Table 4 are for the VM releases. Some wild-born juvenile salmon in Hanford Reach were also visibly marked and coded-wire-tagged and then were recovered as adults in the 2010 carcass survey. Wild-origin presmolts have been marked with adipose fin clip and CWT since 1985 (Fryer 2014). Wild-born carcass recoveries (19 total) from these releases were not counted as hatchery-origin fish on spawning grounds; instead, in our estimation, they were treated as a part of the unmarked sample. All the necessary inputs for the MLE procedure, including VM fractions and CWT fractions (used in place of PBT fractions) as well as numbers of CWTs recovered from each hatchery are given in Table 4. Field technicians did not test any unmarked carcasses for a CWT. Data on undetermined VM and CWT counts were unavailable and assumed to be zero in this application. Standard errors for p and p_i from the MLE approach were calculated as the square root of variances derived from maximum likelihood theory (Mood et al. 1974).

Study Design Explorations

Design exploration 1.—To show how a parentage-based tagging program may be designed for the Hanford Reach, we used MLEs of the proportions of hatchery-origin fish on spawning grounds from the releases described in the previous section. First, we assumed that the PBT fraction applied to all releases was $\phi_i = 0.98$, $i = 1, 2, \ldots, 7$ (the mean of the observed PBT fractions in the 2013 South Fork Salmon River spawning population study). We also assumed that the PBT fraction was the same for both VM and non-VM fish, 26% of the sampled carcasses could not be genotyped (consistent with the 2013 South Fork Salmon River study), and that all carcasses had determined VM status (i.e., $x_3 = 0$). As an initial sensitivity analysis, we varied the subsample numbers (total numbers of sampled carcasses tested for

TABLE 4. Visible marking and coded wire tagging at hatcheries that provided adult Chinook Salmon inputs to Hanford Reach spawning area. The numbers in the first column correspond to those in Figure 1. The following inputs were used: $N = 9,791$, $x_1 = 331$, $x_2 = 9,460$, $n = 331$, $n_1 = 331$, and $n_2 = 0$. Variables are defined in Table 1. Since only carcasses with VMs were tested for a CWT, (i.e., $z_i = 0$ for $i = 1, 2, \ldots 7$), the CWT fractions of non-VM releases do not enter the estimation and are therefore ignored. The CWT fractions given are only for the fish with VMs.

Hatchery	Brood year	VM fraction, λ	CWT fraction, ϕ_2	Number of tags in VM subsample, y	Number of tags in non-VM subsample, z
1. Little White Salmon National Fish Hatchery	2005	1.00	0.25	1	0
2. Priest Rapids Hatchery	2005	0.27	0.11	3	0
	2007	0.04	1.00	7	0
3. Ringold Springs Hatchery	2006	0.07	1.00	2	0
	2007	0.79	0.09	7	0
4. Lyons Ferry Hatchery[a]	2006	0.51	0.99	1	0
5. Umatilla Hatchery	2007	1.00	1.00	2	0

[a] Some Lyons Ferry Hatchery juveniles were visually marked with a visual implant elastomer tag. In this application, however, only fish that were marked with an adipose fin clip were considered visually marked.

PBTs) over alternative values, n = 500, 1,000, and 9,791, where the large subsample size of 9,791 was equal to the total sample size in the 2010 Hanford Reach carcass survey. For this study design, we assumed that $N = 9,791$, and x_1, x_2, x_3, n_1, n_2, n_3, y, z, and w were equal to their expected values. We reported the SE values for the MLEs of the proportions of hatchery-origin fish on spawning grounds for each of the alternative designs. To elucidate why certain designs yielded greater precision in p and p_i from MLE we calculated the expected number of tag recoveries (by release) for each alternative design. We assumed Wright–Fisher reproduction (Satterthwaite et al. 2015).

Design exploration 2.—Here, we varied the hatchery tagging rate and the carcass subsample rate (r) as a fraction of the total sample size of $N = 9,791$, where $r = n/N$. We then constructed a contour plot showing lines of equal coefficient of variation of p from MLE using hatchery tagging rate as values on the y-axis and carcass subsample rate as values on the x-axis of the plot. For this study we varied the tag fractions (PBTs or CWTs) over ϕ = 0.10, 0.15, …, 1.00 (at all hatcheries), and the subsample rate over r = 0.10, 0.15, …, 1.00 at the Hanford Reach spawning area, yielding 361 unique alternative designs. As in design exploration 1, we assumed that x_1, x_2, x_3, n_1, n_2, n_3, y, z, and w were equal to their expected values, the PBT fraction was the same for both VM and non-VM fish, 26% of the sampled carcasses could not be genotyped, and that all carcasses had determined VM status (i.e., $x_3 = 0$). We used a plot to show the relationship between the expected tag recoveries and CV in this study design using all of the 361 alternative pairs of values of tagged fractions and subsample rates. We assumed Wright–Fisher reproduction (Satterthwaite et al. 2015).

RESULTS

South Fork Salmon River Application

The numbers of tag recoveries identified in the 2012 and 2013 surveys in the South Fork Salmon River varied among years (BY2007–2010) and tag type (Table 3). In BY2007, which preceded the PBT program, there were three CWT recoveries. In other brood years, the PBT recoveries matched or exceeded those of CWTs. Notable were tags from BY2008 in the 2012 survey (44 PBTs, 10 CWTs) and BY2009 in 2013 (31 PBTs, 4 CWTs). Overall the respective recoveries were 88 PBTs and 20 CWTs (17 CWTs from brood years when both tag types were deployed).

The PBT-based MLE of p in 2012 was 32.4% (SE = 3.4%), where most of the hatchery-origin Chinook Salmon on spawning grounds were 4-year-old (23.8% BY2008) and 5-year-old fish (8.1% BY2007), as well as a few 3-year-old jacks (0.6% BY2009; Table 5). The CWT-based MLE of p in 2012 was similar, 30.3% (SE = 3.1%), where fish from BY2008 contributed 24.4% of the total fish on the spawning grounds, BY2007 contributed 5.9%, and BY2009 contributed none (Table 5).

The PBT-based MLE of p in 2013 was 41.8% (SE = 4.6%), where the majority of the hatchery-origin salmon on spawning grounds were 4-year-old (30.7% BY2009) and 5-year-old fish (7.5% BY2008), along with a few 3-year-old jacks (3.6% BY2010; Table 5). The CWT-based MLE of p was similar, 38.4% (SE = 4.1%), where salmon from BY2009 contributed 29.9% of the total fish on the spawning grounds, BY2008 contributed 7.2%, and BY2010 contributed 1.3% (Table 5).

When relatively large differences in CV were produced by the PBT and CWT data, the CVs based on PBT data were smaller. For example, see BY2007 and BY2008 contributions

TABLE 5. Maximum likelihood estimates of proportions of hatchery-origin adult Chinook Salmon in South Fork Salmon River spawning areas in 2012 and 2013 using PBT and CWT data; SBS = segregated broodstock program, IBS = integrated broodstock program, NA = not applicable. The asterisk (*) indicates a bootstrap estimate.

	PBT data					CWT data		
Brood year	p	SE	CV	SE*	CV*	p	SE	CV
				2012 Survey				
2007	0.081	0.021	0.264	0.022	0.266	0.059	0.031	0.531
2008	0.238	0.032	0.134	0.032	0.135	0.244	0.040	0.164
2009	0.006	0.006	1.036	0.005	0.954	0.000	0.000	NA
Total	0.324	0.034	0.105	0.034	0.104	0.303	0.031	0.104
				2013 Survey				
2008	0.075	0.026	0.342	0.025	0.340	0.072	0.044	0.617
2009	0.307	0.044	0.143	0.044	0.143	0.299	0.055	0.183
2010 (SBS)	0.018	0.013	0.715	0.013	0.741	0.000	0.000	NA
2010 (IBS)	0.018	0.012	0.689	0.013	0.737	0.013	0.009	0.705
Total	0.418	0.046	0.111	0.047	0.113	0.384	0.041	0.107

to the spawning grounds in 2012 and BY2008 and BY2009 contributions to the spawning grounds in 2013 in Table 5. The rest of the CVs associated with nonzero contributions were similar between PBT and CWT data, not differing by more than 6%.

Tests for overdispersion in observed family sizes detected a statistically significant overdispersion in a single case: the dispersion parameter (sample variance/sample mean) of tagged family sizes was 1.17 for families originating from BY2008 and recovered as carcasses in the 2012 survey, which was significantly greater than 1.0 ($P < 0.001$). The bootstrap estimates of SE, which included the effects of variation in family size, differed little from the standard SEs, which assumed Wright–Fisher reproduction. Using 10,000 bootstrap replications, the bootstrap SEs were within 0.001 of the standard SEs for the 2012 and 2013 survey data (Table 5).

Hanford Reach Application

The MLE of p for the Hanford Reach was 7.66% (SE = 0.91%) using CWT data (Table 6). The largest estimated contribution of hatchery-origin Chinook Salmon on spawning grounds came from Priest Rapids Hatchery (4.0%) and Ringold Springs Hatchery (3.6%). The smallest contribution came from the Lyons Ferry and Umatilla hatcheries, each contributing about 0.02% of the total fish on spawning grounds. Little White Salmon Hatchery contributed 0.05%. The MLEs were similar to the generalized least-squares estimates derived in Hinrichsen et al. (2012).

Study Design Explorations

Design exploration 1.—By varying subsample size, n, in the Hanford Reach spawning area, we found that SEs for the MLEs of the proportions of hatchery-origin fish on spawning grounds declined sharply with subsample size (Figure 2). The largest decreases in SEs occurred when increases were made at lower values of n. Specifically, diminishing returns were evident in the relationship between SEs and subsample size. Using PBT data, with a subsample size of $n = 100$, SEs of $\hat{p}$ and $\hat{p}_i$ were larger than those estimated when the original CWT ($n = 331$) data were employed. As the subsample size increased to $n = 500$ and greater, the SE of $\hat{p}$ was less than what the original CWT data showed. The PBT data did not yield substantially smaller SEs in the case of the contributions from the Little White Salmon (BY2005), Lyons Ferry (BY2006), and Umatilla (BY2007) hatcheries. This occurred because CWT recoveries were relatively high for fish originating from these hatcheries, and we found that CVs of $\hat{p}_i$ decreased with expected number of tag recoveries (Figure 3).

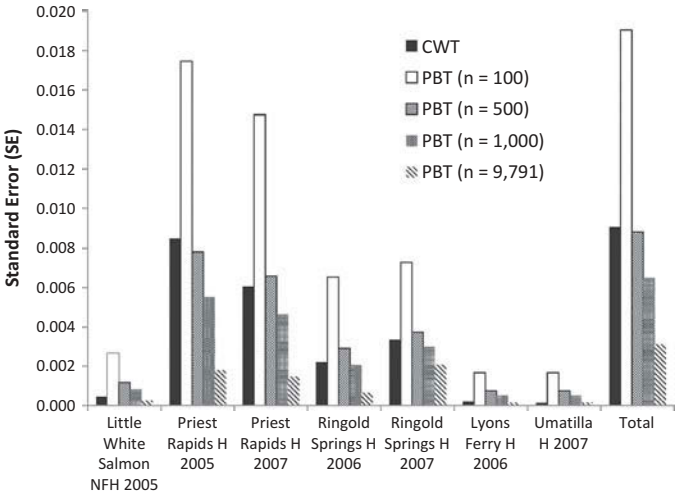

FIGURE 2. Standard errors for the proportions of hatchery-origin Chinook Salmon on spawning grounds from the MLE approach using study designs with alternative carcass subsample sizes, n. For reference, the SEs using the original Hanford Reach CWT data are included, where $n = 9{,}791$. In the remaining studies, it is assumed hypothetical PBT data were used.

Design exploration 2.—The second design exploration showed the range of the tagged fraction (CWT or PBT) and subsample sizes that yielded the same fixed CV of $\hat{p}$. The values of CV ranged from 0.04 to 0.25. The minimum CV was attained when r and ϕ both were at their maximum value

TABLE 6. Estimates of hatchery inputs of adult Chinook Salmon to Hanford Reach spawning grounds in 2010. Standard errors of estimates are given in parentheses. MLE = maximum likelihood estimate, GLSE = generalized least-squares estimates. GLSE are from Hinrichsen et al. (2012).

		MLE			GLSE		
Hatchery	Brood year	p	SE	CV	p	SE	CV
1. Little White Salmon National Fish Hatchery	2005	0.0005	0.0005	0.8882	0.0005	0.0005	0.8756
2. Priest Rapids Hatchery	2005	0.0241	0.0085	0.3520	0.0241	0.0085	0.3514
	2007	0.0161	0.0061	0.3778	0.0161	0.0061	0.3768
3. Ringold Springs Hatchery	2006	0.0031	0.0022	0.7070	0.0031	0.0022	0.7044
	2007	0.0324	0.0034	0.1040	0.0324	0.0033	0.1023
4. Lyons Ferry Hatchery[a]	2006	0.0002	0.0002	0.9997	0.0002	0.0002	0.9710
5. Umatilla Hatchery	2007	0.0002	0.0001	0.7070	0.0002	0.0001	0.6661
Total (all years and hatcheries)		0.0766	0.0091	0.1185	0.0766	0.0090	0.1179

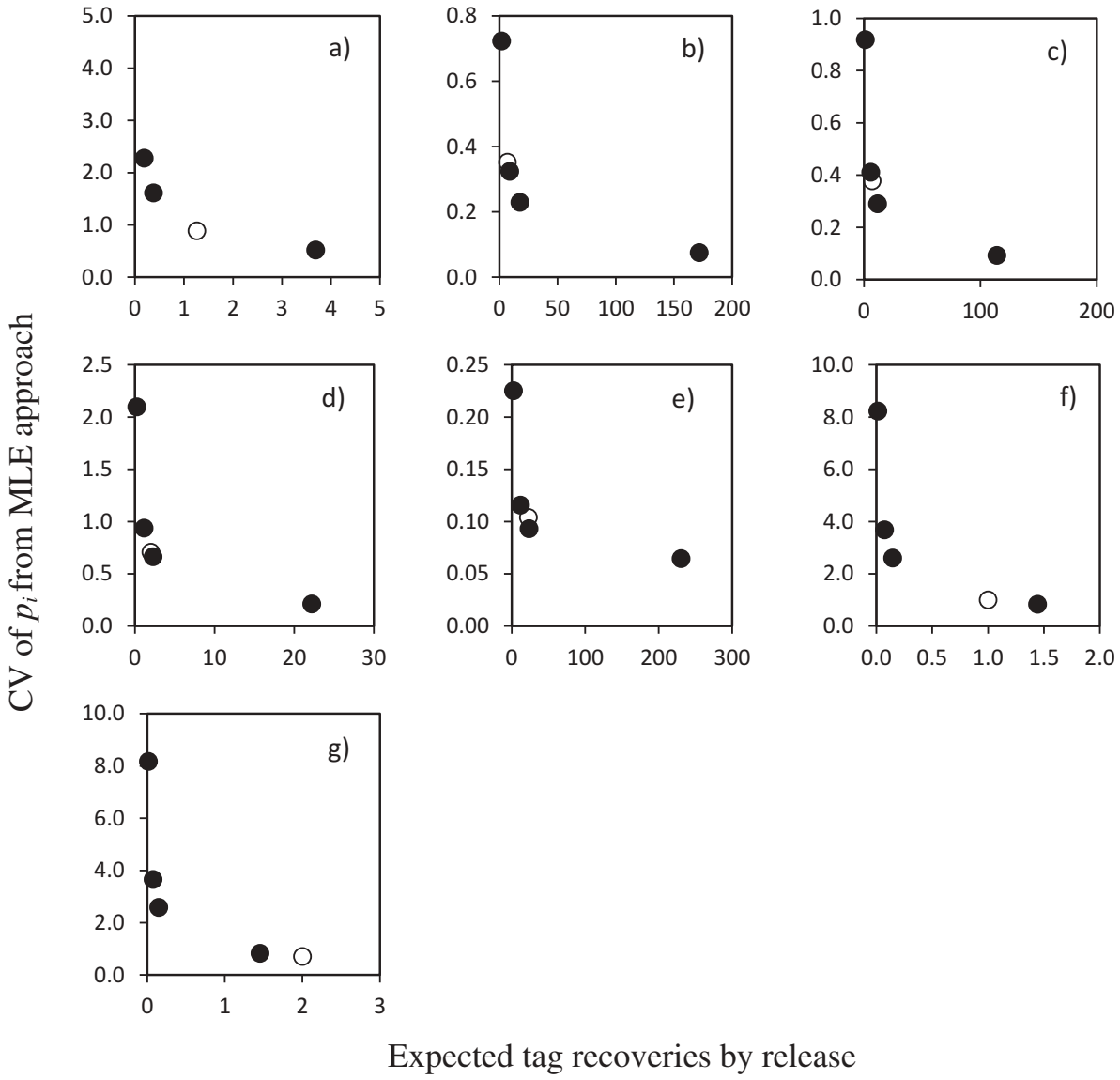

FIGURE 3. Coefficient of variation of p_i from the MLE approach plotted against the expected tag recoveries in the study design exploration 1 for Chinook Salmon released at (**a**) Little White Salmon (BY2005), (**b**) Lyons Ferry (Snake River) (BY2006), (**c**) Priest Rapids (BY2005), (**d**) Priest Rapids (BY2007), (**e**) Ringold Springs (BY2006), (**f**) Ringold Springs (BY2007), and (**g**) Umatilla (BY2007) hatcheries. Filled circles are CVs from hypothetical PBT data and open circles denote CVs from the original CWT data.

of 1.0, and the maximum CV was attained when r and ϕ both were at their minimum value of 0.1. The CV contours displayed a symmetry whereby for any pair of values of the tagged fraction, ϕ, and subsample rate, r, their values could be exchanged and the CV of $\hat{p}$ would be unchanged (Figure 4). For example, when $\phi = 0.85$ and $r = 0.20$, then CV = 0.07; $\phi = 0.20$ and $r = 0.85$ also gave CV = 0.07. This showed that the tagged fraction and subsample rate had the same influence on the precision of p from the MLE approach. Furthermore, when the tagging fraction was larger, then achieving a target CV required a lower subsample rate. For example, when the tagging fraction was $\phi = 0.20$, then achieving a CV of 0.08 required a subsample rate of $r = 0.60$; when the tagging fraction was $\phi = 0.80$, then achieving a CV of 0.08 required a subsample rate of $r = 0.15$ (Figure 4).

The CVs calculated in design exploration 2 were a monotonically decreasing function of the expected number of tag recoveries. Designs that delivered high precision for p from the MLE approach were those that delivered a large expected number of tag recoveries (Figure 5). Due to diminishing returns evident in the relationship between CV and the expected number of tag recoveries, there was little decrease in CV as expected tag recoveries increased beyond 100.

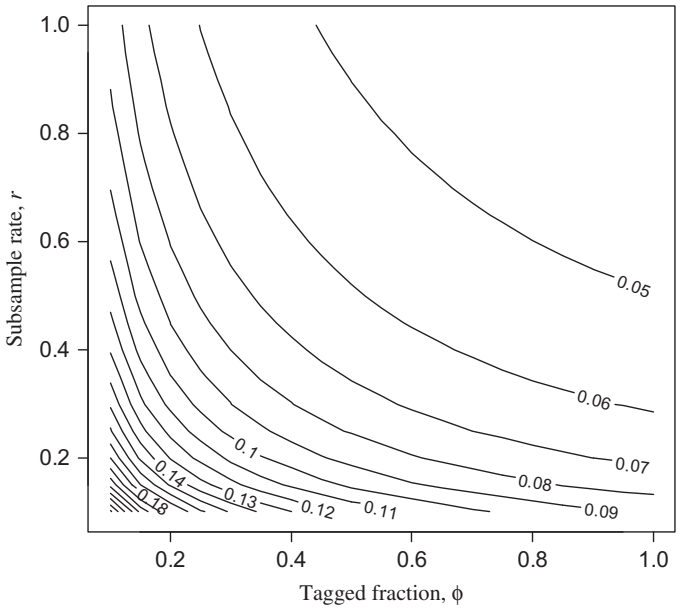

FIGURE 4. Contour plot of the CV of p from the MLE approach with varying tagging fraction and subsample rate $r = n/N$. Each contour represents all possible pairs of values of tagging fraction and subsample rates that yield a fixed value of the CV of p estimated by MLE.

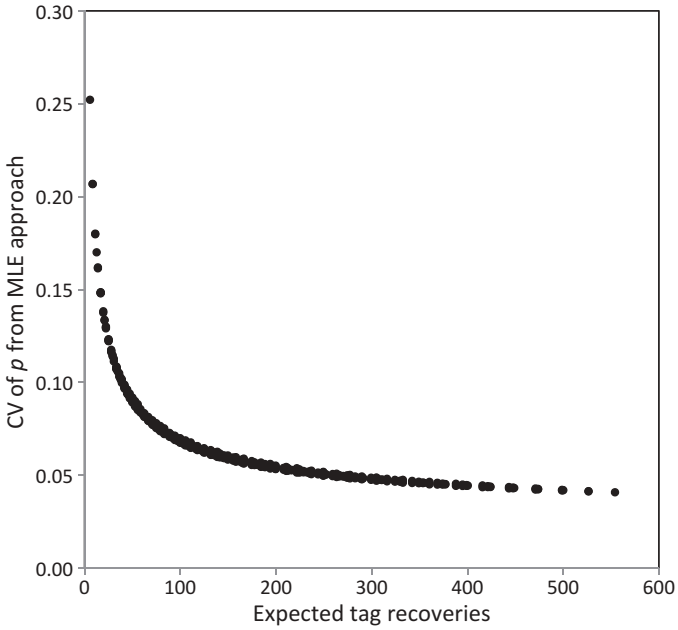

FIGURE 5. Coefficient of variation of p from the MLE approach plotted against the expected tag recoveries derived from the 361 pairs of alternative subsample rates and tagged fractions used in the Hanford Reach study design.

DISCUSSION

Our study demonstrated an MLE method to estimate the proportions of hatchery-origin fish on spawning grounds using VM and tagging data (PBT or CWT). The method produced not only MLEs but SEs as well. When we applied this estimation procedure to South Fork Salmon River Chinook Salmon data, estimates based on CWTs versus PBTs were similar. Precision of the proportions of hatchery-origin fish on spawning grounds estimated from the MLE approach increased with the expected tag recoveries in spawning ground surveys. When CWT or PBT recoveries were low, precision suffered. In the South Fork Salmon River application, PBT-based estimates of age-specific p tended to be more precise than CWT-based estimates because PBT recoveries were greater than CWT recoveries.

Our findings can aid fisheries managers in designing a tagging program aimed at estimating p, which is a valuable measure of the potential for interaction of wild- and hatchery-origin fish on spawning grounds (HSRG 2009). Because precision is gained by increasing expected tag recoveries, greater precision is obtained by increasing sampling rate of carcasses on the spawning ground, tagging more releases, or both. Either CWTs or PBTs (or both) could be used to achieve reliable estimates of p, and each has its potential advantages. When CWTs are used, a simple portable hand-held wand test allows one to detect whether a carcass carries a tag. No such test exists for fish with a PBT. However, if nearly all hatchery releases are visibly marked and parentage-base tagged, the potential advantage of wand detection of a CWT disappears, because a mark would indicate that a fish is almost certainly parentage-base tagged; thus, a VM can serve as the equivalent of a "positive wand test" for fish with a PBT. (Note, however, that carcass decay can obscure VM status and thus may limit the ability to use it as an indicator for presence of PBTs.) Regardless, tag detection is only the first step in determining the hatchery of origin for a tagged fish. Reading a CWT requires extracting the tag and examining it in a laboratory, while a PBT is "read" by genotyping a tissue sample in a genetics laboratory.

Caution is advised when directly comparing CWT and PBT tagging fractions if Wright–Fisher reproduction does not apply (e.g., Moyer et al. 2007) and tagging fractions are less than 100%. When CWT and PBT tagging fractions are identical and less than one, using PBT data can reduce precision (Satterthwaite et al. 2015). This occurs when family size counts are overdispersed, which increases the variation in the realized tagging fractions. Thus, whenever parentage-based tagging is employed, observed family sizes on the spawning grounds should be examined for overdispersion, and the bootstrapping technique described in the Appendix applied. When overdispersion in family size is sufficiently small (i.e., the dispersion parameter is close to one), SE does not increase appreciably beyond that predicted from a maximum likelihood approach that ignores family size. Such was the case for the 2012 and 2013 South Fork Salmon River Chinook Salmon survey data. Note, however, when PBT fractions are 100%, there will be no loss in precision due to variation in family size (Satterthwaite et al. 2015).

The current practice of estimating proportions of hatchery-origin fish on the spawning grounds in the South Fork Salmon River uses VM (adipose fin clip) data alone, and the accuracy of these VM-only estimates is adequate for most current management applications. The point estimates calculated by visible marking for 2012 (30.0%) and 2013 (37.6%; authors' unpublished results) were similar to those for parentage-based tagging. Incorporating methods developed here and including PBT data would eliminate a major drawback to relying on visual marks only: the lack of precision (or unknown precision) in estimators of p. In addition, using our MLE method to estimate the contributions of fish from multiple brood years and source hatcheries would greatly assist management decisions that consider the composition of hatchery fish on the spawning grounds.

Applying our MLE procedure to field data has potential pitfalls that must be considered. For one, carcass decay produces PBT loss when a decomposing carcass can no longer be genotyped effectively. In the South Fork Salmon River spawning surveys, there was an estimated 13% PBT loss due to carcass decay in the 2012 survey and 26% PBT loss in the 2013 survey. These PBT losses were explicitly accounted for in the likelihood function. One possible solution to the problem of PBT loss is to conduct PBT sampling on live fish trapped at a weir instead of on carcasses. This would potentially reduce tag loss to nearly zero. However, this would not be possible at the majority of spawning locations, including the portion of the South Fork Salmon River used in this study. Furthermore, when sampling at a weir, one would not know whether the fish spawned, which can be determined for some of the carcasses. When carcass sampling is unavoidable, it may be possible to decrease PBT loss by collecting tissue samples more frequently or from alternative tissues or locations on the carcass that degrade at a slower rate.

Another potential difficulty is VM loss, which affects both the CWT-based and PBT-based estimates of p. Due to carcass decay, it was impossible to determine whether 8% of the carcasses in the 2012 survey were visibly marked. Visible mark loss was explicitly accounted for in the likelihood function by the parameter θ, the probability that a carcass's VM status at release can be determined.

Furthermore, mark-selective fisheries can potentially reduce the fractions of hatchery fish having VMs on the spawning grounds (PSC 2005) by removing marked hatchery-origin fish, but not unmarked fish. This can bias estimation of p because we assume that expected the VM fractions on the spawning grounds equal those at release. One solution is to adjust the VM fractions according to the harvest rate. However, when harvest rate is unknown, another solution must be found. When the fractions of releases with VMs are nearly 100% or zero (as in the case of the South Fork Salmon River application), then no such adjustments are necessary, because, in these cases a mark-selective fishery would leave the marked to unmarked ratio of hatchery-origin fish on the spawning grounds unchanged. Thus, when a mark-selective fishery changes the ratio of fish with VMs to those without VMs, one solution is to break each release into two releases: one with no VMs and one with 100% VMs, thereby allowing separate estimates of their contributions to the overall proportion of hatchery-origin spawners. For example, if a release of 10,000 fish marked at 80% is split into two releases, 2,000 fish will have a marking fraction of 0, and 8,000 fish will have a marking fraction of 1.0. This technique relies on tagging non-VM releases and testing some sampled non-VM fish for a tag. Such an approach would be compatible with double-index tagging release strategies meant to aid in the estimation of mark-selective fishery impacts (PSC 2005).

Although estimates of p from MLE and GLSE approaches are nearly equal for the Hanford Reach application, advantages remain for using the MLE. The GLSE (as formulated in Hinrichsen et al. 2012) was less general than the MLE because it did not allow for testing non-VM carcasses for a tag, did not allow testing a subsample of carcasses with VMs for a tag, and did not explicitly handle tag loss due to carcass decay. Furthermore, the GLSE was based on a known sampling rate (which may be unknown), while the MLE was based on a fixed sample size (which should always be known). One could modify the GLSE to be comparable with the MLE approach. However, the MLE has properties that are optimal and well known (Mood et al. 1974), while properties of the GLSE are less well known. Furthermore, the MLE formulation can be used to calculate model selection criteria, such as the Akaike information criterion (Burnham and Anderson 2002), or explore Bayesian approaches, which begin with a specification of the likelihood function (Gelman et al. 2003).

Future directions of our research may prove fruitful for multiple fisheries applications. One direction is to develop estimators that use all the mark and tag data at once, including any type of VM (e.g, fin clips, dorsal and ventral fin erosion, visual implant elastomer marks), otolith marks, and tags including CWTs, PBTs, and PIT tags (IEAB 2013). The estimator could also be applied to hatchery versus wild composition of fisheries catch or to run contributions of releases from multiple hatcheries or brood years at dams such as Bonneville and Lower Granite dams on the Columbia and Snake rivers, respectively, which can contribute around 30 hatchery–brood year groups using nonlethal sampliing (e.g., J. E. Hess and colleagues, Columbia River Intertribal Fish Commission, unpublished results). Estimates of hatchery–brood year run contributions at Bonneville and Lower Granite dams could aid run reconstruction (Starr and Hilborn 1988) efforts in the Columbia and Snake River basins (e.g., Copeland et al. 2014) and validate run composition estimates (e.g., Schrader et al. 2013).

From this study, we conclude that a program that uses low tagging of releases and high spawning ground sampling can be replaced by one that uses high tagging of releases and low spawning ground sampling without changing the

precision of p from the MLE approach. Ideally, both tagging and spawning ground sampling would be high, but practically, cost is a restriction (Satterthwaite et al. 2015). Although parentage-based tagging has been fully implemented in the Snake River basin and is currently expanding to encompass the Columbia River basin, scenarios under which a cost-effective, coast-wide, parentage-based tagging program that could be implemented are explored by Satterthwaite et al. (2015). From the standpoint of estimating p reliably, we recommend developing a program that delivers the desired level of statistical precision at the lowest cost, whatever tagging technology or combination thereof is employed. However, there are many purposes for the use of tagging and marking data besides estimation of p (e.g., stock-specific harvest rate estimation), and these must also be considered in the design of a cost-effective, coast-wide, tagging and marking program.

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Appendix: Description of Bootstrap Procedure to Incorporate Heterogeneity

The following is a detailed description of the bootstrap procedure that we developed to incorporate the effect of heterogeneity in family size on the precision of the maximum likelihood estimates (MLEs). For each release i, we let S_i be the number of families and G_i be the number of these families that are tagged. The numbers of fish from these individual families that arrive on the spawning grounds are unknown since the spawning ground survey represents a sample of the population and carcass decay can cause tag loss. We assume that each fish on the spawning ground has an equal probability of being sampled, and therefore the distribution of proportions of fish from each family arriving on the spawning grounds from release i can be estimated as

$$q_{i,j} = \frac{F_{i,j}}{\sum_{i=1}^{G_i} F_{i,j}} \tag{A.1}$$

where $F_{i,j}$ is the observed family size of the jth family that is tagged. After fitting the MLE procedure to the actual data, the bootstrap data sets are constructed as follows:

1. Draw a random sample of release-specific hatchery contributions and wild contributions to a sample of size N using a multinomial distribution:

$$\left(H_1^*, H_2^*, \ldots H_m^*, W^*\right) \sim \text{Mult}(N, \hat{p}_1, \hat{p}_2, \ldots, \hat{p}_m, 1-\hat{p}), \tag{A.2}$$

where H_i^* is the simulated number of sampled hatchery fish on the spawning grounds from release i, W^* is the simulated number of sampled wild fish on the spawning grounds, $\hat{p}_i$ is the MLE of the proportion of hatchery-origin fish from release i, and $\hat{p}$ is the MLE of the overall proportion of hatchery-origin fish on the spawning grounds.

2. For each release i, draw at random from the distribution of observed proportions of fish arriving to the spawning grounds by sampling at random and with replacement from $q_{i,1}, q_{i,2}, \ldots q_{i,G_i}$ to obtain a simulated set of S_i family size proportions, $q_{i,1}^*, q_{i,2}^*, \ldots q_{i,S_i}^*$ The simulated sampled family sizes in the spawning ground sample are then given by

$$F_{i,j}^* = \left\lfloor H_i^* q_{i,j}^* \right\rfloor \quad j = 1, 2, \ldots S_i \tag{A.3}$$

Use the sum of the first G_i of the simulated family sizes as the simulated number of tagged fish in release i, or T_i^*. The sum of the remaining $S_i - G_i$ family sizes is the simulated number of untagged hatchery contribution of release I, or U_i^*.

3. Partition the simulated number of tagged and untagged carcasses into marked, unmarked, undetermined mark, and undetermined tag groups according to the relevant

multinomial distribution. For example, the tagged carcasses from release i, are partitioned according to the following multinomial distribution:

$$\left(a^*_{i,1}, a^*_{i,2}, \ldots, a^*_{i,6}\right) \sim \text{Mult}\Big[T^*_i, \hat{\gamma}_1\hat{\theta}\lambda_i, \hat{\gamma}_1\hat{\theta}(1-\lambda_i), \hat{\gamma}_2\left(1-\hat{\theta}\right), (1-\hat{\gamma}_1)\hat{\theta}\lambda_i, (1-\hat{\gamma}_1)\hat{\theta}(1-\lambda_i), (1-\hat{\gamma}_2)\left(1-\hat{\theta}\right)\Big], \quad \text{(A.4)}$$

where $a^*_{i,1}$, $a^*_{i,2}$ and $a^*_{i,3}$ represent the originally tagged fish on the spawning grounds with a determined tag that are marked, unmarked, or of undetermined mark status, respectively, while $a^*_{i,4}$, $a^*_{i,5}$ and $a^*_{i,6}$ represent the originally tagged fish with an undetermined tag that are marked, unmarked, or of undetermined mark status, respectively. Similarly, the untagged hatchery fish on the spawning grounds can be partitioned into $\left(b^*_{i,1}, b^*_{i,2}, \ldots, b^*_{i,6}\right)$, using the same cell probabilities and similar definitions as in equation (A.4), but noting that the number of trials is U^*_i. The simulated wild fish on the spawning grounds can be partitioned according to

$$\left(c^*_1, c^*_2, \ldots, c^*_6\right) \sim \text{Mult}\Big[W^*, 0, \hat{\gamma}_1\hat{\theta}, \hat{\gamma}_2\left(1-\hat{\theta}\right), 0, (1-\hat{\gamma}_1)\hat{\theta}, (1-\hat{\gamma}_2)\left(1-\hat{\theta}\right)\Big], \quad \text{(A.5)}$$

where c^*_1, c^*_2 and c^*_3 represent the wild fish on the spawning grounds with determined tag status that are marked, unmarked, or of undetermined mark status, respectively, while, c^*_4, c^*_5 and c^*_6 represent the wild fish on the spawning grounds with undetermined tag status that are marked, unmarked, or of undetermined mark status, respectively.

4. Construct the bootstrap data set used in the MLE procedure by summing the appropriate cell counts in step 3:

$$x^*_1 = \left(\sum_{i=1}^{m} a^*_{i,1} + a^*_{i,4} + b^*_{i,1} + b^*_{i,4}\right) + c^*_1 + c^*_4 \quad \text{(A.6)}$$

$$x^*_2 = \left(\sum_{i=1}^{m} a^*_{i,2} + a^*_{i,5} + b^*_{i,2} + b^*_{i,5}\right) + c^*_2 + c^*_5 \quad \text{(A.7)}$$

$$x^*_3 = \left(\sum_{i=1}^{m} a^*_{i,3} + a^*_{i,6} + b^*_{i,3} + b^*_{i,6}\right) + c^*_3 + c^*_6 \quad \text{(A.8)}$$

$$y^*_i = a^*_{i,1} \quad \text{(A.9)}$$

$$z^*_i = a^*_{i,2} \quad \text{(A.10)}$$

$$w^*_i = a^*_{i,3} \quad \text{(A.11)}$$

$$u^*_1 = \left(\sum_{i=1}^{m} a^*_{i,4} + b^*_{i,4}\right) + c^*_4 \quad \text{(A.12)}$$

$$u^*_2 = \left(\sum_{i=1}^{m} a^*_{i,5} + b^*_{i,5}\right) + c^*_5 \quad \text{(A.13)}$$

$$u^*_3 = \left(\sum_{i=1}^{m} a^*_{i,6} + b^*_{i,6}\right) + c^*_6 \quad \text{(A.14)}$$

5. Apply the MLE procedure to bootstrap data set to obtain bootstrap replications of the parameter estimates.

Repeat steps 1 through 5 to obtain B bootstrap replications of the parameter estimates. A bootstrap estimate of the SE of an estimator is obtained by applying the sample standard deviation formula to all B bootstrap replications of the estimate.