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ARTICLE

Genetic-Based Estimates of Adult Chinook Salmon Spawner Abundance from Carcass Surveys and Juvenile Out-Migrant Traps

Daniel J. Rawding, Cameron S. Sharpe,[1] and Scott M. Blankenship*[2]
Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501-1091, USA

Abstract

Due to the challenges associated with monitoring in riverine environments, unbiased and precise spawner abundance estimates are often lacking for populations of Pacific salmon *Oncorhynchus* spp. listed under the Federal Endangered Species Act. We investigated genetic approaches to estimate the 2009 spawner abundance for a population of Columbia River Chinook Salmon *Oncorhynchus tshawytscha* via genetic mark–recapture and rarefaction curves. The marks were the genotyped carcasses collected from the spawning area during the first sampling event. The second sampling event consisted of a collection of juveniles from a downstream migrant trap located below the spawning area. The parents that assigned to the juveniles through parentage analysis were considered the recaptures, which was a subset of the genotypes captured in the second sample. Using the Petersen estimator, the genetic mark–recapture spawner abundance estimates based on the binomial and hypergeometric models were 910 and 945 Chinook Salmon, respectively. These results were in agreement with independently derived spawner abundance estimates based on redd counts, area-under-the-curve methods, and carcass tagging based on the Jolly–Seber model. Using a rarefaction curve approach, which required only the juvenile offspring sample, our estimate of successful breeders was 781 fish. Our genetic-based approaches provide new alternatives to estimate adult Pacific salmon abundance in challenging environmental conditions or for populations with poor or unknown estimates of precision.

Many populations of Pacific salmon *Oncorhynchus* spp. from southern California to northern Washington are listed for protection under the U.S. Endangered Species Act 1973 (ESA). In the area of ESA Pacific salmon population recovery planning, the National Oceanic and Atmospheric Administration (NOAA) has provided guidance for status and trends monitoring based on Viable Salmonid Population (VSP) indictors (McElhany et al. 2000; Crawford and Rumsey 2011). The VSP indicators include adult spawner abundance, productivity, spatial distribution, and diversity. The legal statutes mandating protective action and the monitoring recommendations associated with these actions highlight the need for reliable population information to evaluate the merits of regulatory decisions and conservation efforts. Despite considerable effort being directed toward Pacific salmon monitoring activities, reported population abundance estimates often do not meet NOAA's guidelines for unbiased estimates with a coefficient of variation (CV) of less than 15% (Crawford and Rumsey 2011); thus, the development of alternative methods to estimate abundance in the fisheries field is warranted.

In Pacific salmon population assessment and management, the most common abundance metric used is spawner abundance or escapement (i.e., the number of fish returning to spawn after harvest) (Hilborn and Walters 1992; Good et al. 2007; Crawford and Rumsey 2011). In contrast, conservation biology refers to

*Corresponding author: scott.blankenship@fishsciences.net
[1]Present address: Oregon Department of Fish and Wildlife, Corvallis Research Laboratory, 28655 Highway 34, Corvallis, Oregon 97333, USA.
[2]Present address: Cramer Fish Sciences, GENIDAQS Division, 3300 Industrial Way, Suite 100, West Sacramento, California 95691, USA.
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the number of adults present in the population as the census size (i.e., N_c) (Luikart et al. 2010). For the methods described in this study, we defined N_c as the number of adult salmon present at the time of spawning, which is consistent with the above definitions of abundance. Another measure of abundance is the number of successful breeders (N_b), which is defined as the number of spawners that produced at least one offspring during one reproductive season (Schmeller and Merilä 2007). Since many salmon populations in the Pacific Northwest are listed for protection under the ESA, the number of successful breeders may be a better metric for assessing extinction probabilities due to the loss of genetic diversity and depensation (Waples 2002; Barrowman et al. 2003). For semelparous species such as Pacific salmon, N_c equates to the number of successful breeders (N_b) plus the number of spawners that produced no offspring.

Juvenile Pacific salmon out-migration and adult spawner abundance are commonly estimated, with this life-stage-specific information analyzed using spawner–recruit relationships to estimate freshwater productivity and capacity (Hilborn and Walters 1992; Barrowman et al. 2003) or the effectiveness of habitat restoration for salmon populations (Bradford et al. 2005). If adult and juvenile genetic sampling is incorporated into this established monitoring framework, then the use of genetic approaches to estimate N_c and N_b in a population can be pursued as alternatives to more traditional visual count methods. As each individual in a population is characterized by a unique genetic profile, often referred to as a molecular tag or genetic mark, DNA-based methods have been developed to determine the number of animals sampled and to estimate the population size using mark–recapture and rarefaction models (Lukacs and Burnham 2005a; Frantz and Roper 2006). The use of genetic markers to estimate population abundance is common in wildlife investigations (Marucco et al. 2011); however, adaptations of these approaches to aquatic systems appear well suited for estimating Pacific salmon population abundance. Genetic mark–recapture approaches designed to estimate abundance are based on mark–recapture theory and are varied (Lukacs and Burnham 2005a). They may be structured to directly recapture the same individual (Palsbøll et al. 1997; Taberlet et al. 1997) or recover a parent's genotype through its offspring via parentage analysis (Jones and Avise 1997; Pearse et al. 2001). Here, we employed a modification of the latter technique to estimate spawner abundance (N_c) via the Petersen estimator (Williams et al. 2002). We used multilocus genotypes from sampled adult carcasses to establish a set of "marks," with "recaptures" of parental marks accomplished through parentage analysis of genotyped juveniles trapped in the following year, which we termed transgenerational genetic mark recapture (tGMR).

The number of adults that produced offspring (N_b) can be estimated by analyzing the observed sibling relationships among genotyped juveniles using genetic rarefaction curves (Israel and May 2010). The rarefaction curve approach was originally designed to estimate species diversity in an area based on species accumulation curves (Colwell and Coddington 1994), but the method has been extended to estimate the number of individuals in a population (Kohn et al. 1999; Eggert et al. 2003). This approach involves fitting the cumulative number of examined genotypes to the number of unique genotypes within an identified population to estimate the asymptote of the curve, which is the population estimate of successful breeders. In genetic rarefaction curves, multiple equations may be used to estimate N_b; however, different equations often lead to different results (Frantz and Roper 2006). As with genetic mark–recapture studies, the genetic rarefaction approach is typically applied to adults, but the method has been used to estimate the number of Green Sturgeon *Acipenser medirostris* breeders in the Sacramento River based on juvenile collections (Israel and May 2010). We investigated the genetic rarefaction approach in parallel with tGMR, which we termed transgenerational genetic rarefaction curves (tGRC).

While genetic-based approaches to estimating abundance have proven successful, care must be taken in study design development, genetic analysis, use of software for matching genetic samples or obtaining parental assignments, and application to statistical models (Marucco et al. 2011). Lukacs and Burnham (2005a) indicated that the equal capture and correct identification of marked and unmarked assumptions should be carefully examined in genetic mark–recapture studies. For example, individual heterogeneity in capture probabilities will lead to a violation of the equal capture assumption and can be addressed through study designs and statistical models (Lukacs and Burnham 2005b; Miller at al. 2005; Marucco et al. 2011). In addition, marked and unmarked individuals can be correctly identified by ensuring the number of chosen loci has sufficient power to differentiate related individuals and laboratory procedures and genetic assignment software can minimize genotyping and assignment errors (Mills et al. 2000; Waits and Leberg 2000). Violation of genetic-based model assumptions will lead to biased abundance estimates (Lukacs and Burnham 2005a).

We tested genetic-based approaches to estimate abundance on a population of Chinook Salmon *Oncorhynchus tshawytscha* in a well-monitored lower–Columbia River tributary system (Coweeman River, Washington). We compared the accuracy and precision of the genetics-based approaches to independent estimates of abundance based on redd surveys (Gallagher and Gallagher 2005), area-under-the-curve (AUC) methods (English et al. 1992), and Jolly–Seber carcass tagging (Sykes and Botsford 1986). We report the results of this comparison and describe and discuss the challenges of implementing genetic approaches, such as genotyping error, the accuracy of parentage-based assignments, and the affect that variability of reproductive success has on heterogeneity of capture probabilities.

METHODS

Study Site and Species

The Coweeman River is a third-order tributary to the Cowlitz River located in Cowlitz County, Washington (46.107222 N,

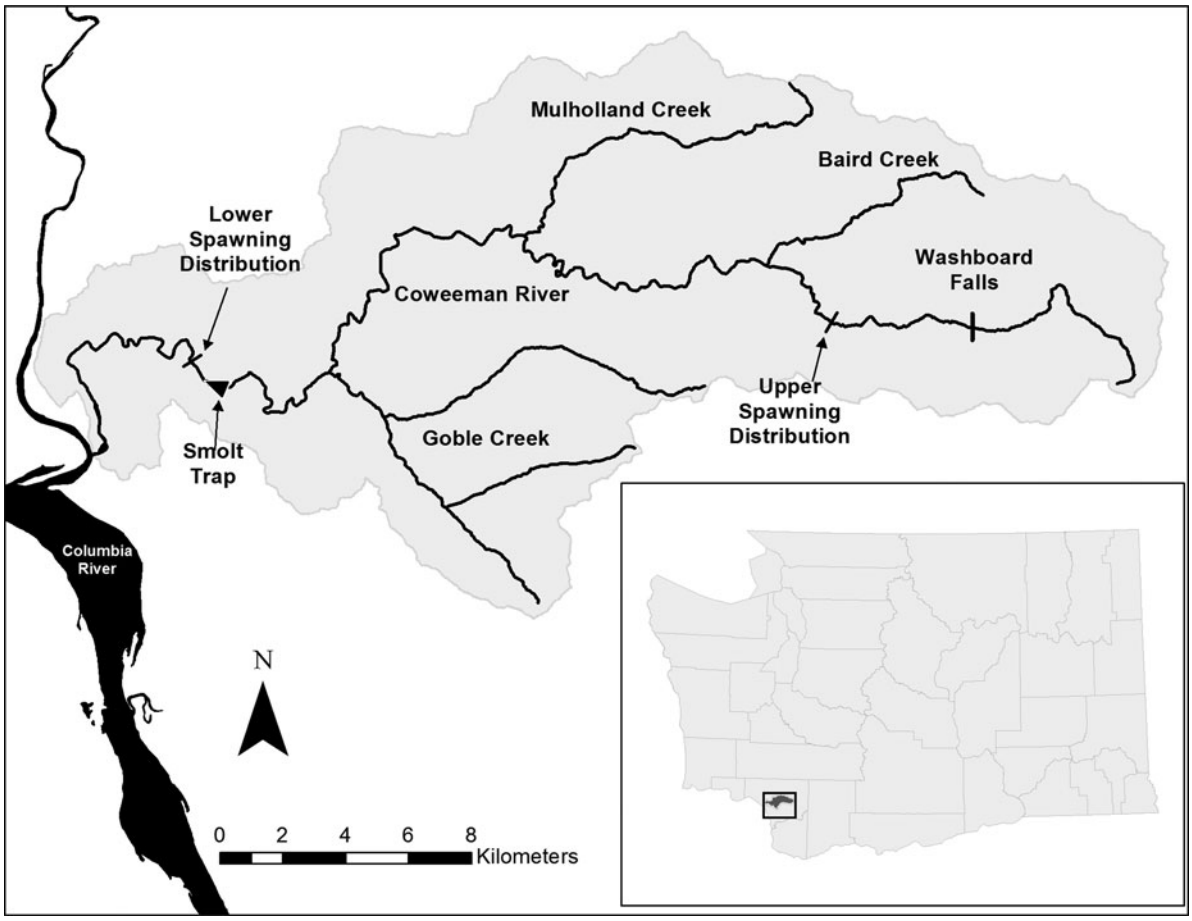

FIGURE 1. Map of the study area in Washington State showing the Coweeman River basin, 2009 spawning distribution, smolt trap location, and Washboard Falls, which is a barrier to Pacific salmon migration.

122.889444 W) with elevations ranging from near sea level at the river mouth to 846 m at Coweeman Lake near the headwaters (Figure 1). This basin drains approximately 329 km^2, and the watershed is managed for timber production with limited residential and commercial development near the mouth. Extensive Chinook Salmon surveys have documented that most spawning occurs within the area from river kilometer (rkm) 9 (measuring from the Coweeman River mouth) up to the Washboard Falls (rkm 50), a barrier to migratory Pacific Salmon (Sharpe et al. 2009). Spawning is intermittent in the lowest portions of Coweeman River tributaries including Baird, Mulholland, and Goble creeks.

Sexually mature Chinook Salmon enter the watershed from late August through the end of October. Most Coweeman River Chinook Salmon return as mature adults at 3 or 4 years of age, depending on sex and brood year strength. Spawning occurs shortly after entry from early September through early November. Eggs incubate in the gravel through early winter, and emergence begins around February 1, depending on spawning time and water temperature. The out-migration of juvenile Chinook Salmon in the watershed is bimodal (Healey 1991; Sharpe et al. 2009), consisting of a fry migration from February through May and a parr or subyearling smolt migration from June through August, with a very small percentage of the population continuing to emigrate into the fall in some years.

Field Data Collection

Carcass sampling.—The collection of adult biological data for this study was consistent with American Fisheries Society salmonid monitoring protocols (Johnson et al. 2007). To collect a representative carcass sample, the entire spawning distribution was surveyed weekly with equal effort from September 15 through November 11, 2009, which encompassed the entire spawning period. Biological and tagging data were collected from every carcass encountered (e.g., length, sex, origin, and scales). Additional data were collected using standard protocols for traditional salmonid abundance estimators. A small portion of tissue from all carcasses was excised from the operculum and placed in a labeled vial with 100% nondenatured ethanol for subsequent genetic analysis. To prevent duplicate sampling of Chinook Salmon, all carcasses were mutilated following tissue collection. Due to lower flows in the fall of 2009, the spawner distribution was limited to the main stem up to rkm 42 (Figure 1).

Juvenile sampling.—A rotary screw trap, with a 1.5-m-diameter cone, was used to capture juvenile Chinook Salmon out-migrants. The trap was installed January 31, 2010, and was operated essentially 24 h a day through August 23, 2010. There were isolated trap outages during the juvenile out-migration period. The trap was operated in three different configurations at the same site to maximize the efficiency of capturing juveniles. From February through June, the trap was located in the pool to maximize fishing time in high water. In June the trap was moved to the head of the pool to improve trap efficiency. The final configuration occurred from late June through the end of the season and consisted of adding panels above the trap to direct most of the river flow into the trap. Tissue samples were collected in daily batches with small pieces of fin tissue stored directly in ethanol.

An estimate of total juvenile out-migrant abundance was necessary for achieving proportional juvenile sampling. Standard rotary trap protocols were used to collect juvenile out-migrant data (Volkhardt et al. 2007), and total juvenile abundance was estimated based on a modification of Bonner and Schwarz (2011) and Schwarz and Bonner (2012) to account for three trap configurations using the diagonally stratified Petersen estimator with error. To achieve representative sampling, we controlled for potential bias caused by juvenile mortality. Specifically, the concern was that survival to the trap was not the same for a 40-mm fry trapped in February and a 90-mm parr trapped in August. To estimate the fry equivalents for the later-emigrating subyearling migrants, we adjusted our weekly out-migrant abundance estimate using the instantaneous mortality (z) based on Beverton–Holt's mortality model and the von Bertalanffy growth model (Hilborn and Walters 1992, page 424). The adjusted weekly estimate of juvenile out-migrants was used to proportionally subsample tissues for genotyping.

Genetic Data Collection

Genotyping.—We performed polymerase chain reaction (PCR) amplification on carcass and juvenile tissues using the 13 fluorescently end-labeled microsatellite marker loci standardized as part of the Genetic Analysis of Pacific Salmonids project (Seeb et al. 2007) and an additional locus *Ssa197* (O'Reilly et al. 1996). The PCR was performed following Seeb et al. (2007), with reaction volumes of 10 μL using 25 ng of template DNA. All PCR components were supplied from Promega (Madison, Wisconsin). All thermal cycling was conducted using either a PTC200 thermal cycler (MJ Research) or 9700 (Applied Biosystems). All PCR products were visualized by electrophoresis on an ABI 3730 automated capillary sequencer (Applied Biosystems). Fragment size analysis was completed using GeneMapper 3.7 software (Applied Biosystems). Fragment sizes were standardized to the Genetic Analysis of Pacific Salmonids database following Seeb et al. (2007). Carcass samples were extracted and genotyped in duplicate to minimize the potential for inaccurate recording of the parental genotypes (i.e., determination of marks). Carcass and juvenile samples were analyzed independently by two people to reduce the occurrence of process errors.

Genetic analysis.—Standard population genetic tests were performed to determine whether genotype data were of sufficient quality for parentage analysis. Both within- and among-collection genetic diversity were evaluated. Observed heterozygosity and unbiased gene diversity (i.e., expected heterozygosity) was measured following Hedrick (1983) and Nei (1987), respectively. For each locus and collection (i.e., carcasses or juveniles), Hardy–Weinberg equilibrium was assessed using an exact test following a modified version of the Guo and Thompson (1992) Markov-chain random walk algorithm. Gametic-phase linkage disequilibrium was calculated for pairs of loci following a likelihood ratio test, with statistical significance determined using a permutation procedure (Excoffier and Slatkin 1998). To determine whether allele frequency distributions from carcass and juvenile collections were statistically equivalent (i.e., samples drawn from the same underlying distribution), an exact test was used following a Markov-chain procedure described by Raymond and Rousset (1995). Tests for departures from Hardy–Weinberg and linkage equilibrium and allele frequency comparisons were implemented using ARLEQUIN 3.5 software (Excoffier et al. 2005).

Parentage analysis.—Categorical allocation methods are designed to identify the single most likely parent from a group of nonexcluded parents (Meagher and Thompson 1986; Kalinowski et al. 2007; Riester et al. 2009). These methods have been shown to be accurate and to perform better than exclusion (Wang 2004; Kalinowski et al. 2007; Harrison et al. 2013). The maximum likelihood method developed by Wang and Santure (2009), as implemented in COLONY 2.0, was used for simultaneous parentage and sibship analyses. The statistical framework was appropriate for the polygamous mating system of Chinook Salmon (Bentzen et al. 2001) and produced the necessary inputs for both genetic-based statistical methods used. The intrinsic coupling of sibship and parental reconstruction in COLONY allowed the assignment of all trapped juveniles to both sampled and unsampled adults (Emery et al. 2001). This information was required when estimating spawning abundance using the hypergeometric distribution or tGRC methods. Stochastic genetic errors (includes misscore, mutations, and data entry) were allowed at a rate of 0.001 alleles per locus (~1.5% of genotypes). This error rate was chosen given published observations (Talbot et al. 1995; Morin et al. 2010), and a low assumed genotyping error rate would cause the parentage analysis to be conservative by reducing the likelihood of false positives. Inferred maternity and paternity were accepted at a posterior probability of 1.0. All full-sib and half-sib designations were accepted, because the vast majority of the posterior probabilities were greater than 0.95 for sibling relationships. The maximum likelihood algorithm developed by Riester et al. (2009) in FRANz was used as a complementary parentage analysis method. Default FRANz

settings were used and a maximum population size of N = 1,000 was assumed. A maximum of one mismatch per parent–offspring pair and two mismatches per parent-pair–offspring trio were allowed for parentage assignment.

Abundance Estimation

Genetic mark–recapture approach.—We used a "pooled" or "simple" Petersen estimator to estimate the spawner abundance (Seber 1982) as follows:

$$N_c = \frac{(n_1)(n_2)}{(m_2)},$$

where N_c is the estimated adult spawner abundance at the time of tagging. Specific to tGMR, the marks (n_1) are the number of successfully genotyped carcasses in the first sampling event, the recaptures (m_2) are the number of genotyped carcasses that were assigned as parents of genotyped juveniles from the second sampling event, and the captures (n_2) are the number of genotypes obtained from juveniles sampled in the second event. Two statistical models are typically used to estimate spawner abundance using the Petersen estimator. The first uses the binomial distribution, which is based on sampling with replacement (Seber 1982; Hilborn and Walters 1992). Under this tGMR model, all observed juvenile recaptures are used in the estimator even if they originated from the same parents. The binomial estimator of N_c (Nc_{BIN}) was calculated using $m_2 \sim$ Binomial (n_2,p) and $n_1 \sim$ Binomial (Nc_{BIN},p), where p is an estimate of the proportion of the population that is marked. Regarding n_2, as each juvenile has a male and female parent (i.e., two potential parental assignments), a single juvenile actually represents two captured genotypes in the binomial model. A juvenile that assigned to two genotyped carcasses would result in two recaptures, a juvenile that assigned to one genotyped carcass would represent one recapture, and a juvenile that did not assign back to any genotyped carcasses would represent zero recaptures. When estimating the male or female spawning abundance separately, each genotyped juvenile was considered a single capture and assigned a 0 or 1 based on its recapture status relative to the genotyped male or female carcasses.

If only the first observed recapture or capture is used from multiple capture events, this is termed sampling without replacement, and the hypergeometric distribution is appropriate for the estimation of N_c (Seber 1982; Rivot and Prévost 2002). In our application of the hypergeometric model, we only used the first encountered genotype and ignored subsequent assignments to that genotype. We calculated N_c (Nc_{HYP}) using $m_2 \sim$ Hypergeometric (n_1, n_2, Nc_{HYP}), where the marks (n_1) and unique recaptures (m_2) are as described above, but the captures (n_2) are the total number of unique parental genotypes inferred by COLONY from the juvenile genotype data. Seber's Goodness of Fit (GOF) test, which is a modification of the z-test, was used to test the null hypothesis that there was no difference in population estimates (Seber 1982; Parken et al. 2003).

Key tGMR assumptions.—We made two key assumptions for our tGMR models: (1) all marked and unmarked fish are correctly identified and assigned and (2) all fish have an equal capture probability in the first sampling event (Lukacs and Burnham 2005a).

First, we minimized the identification and assignment errors for marked and unmarked genotypes by using standard laboratory procedures (Paetkau 2003), independent analysis of genetic samples by two people, and simulations to assess the degree to which missed and incorrectly assigned "marks" may occur in our genotype dataset. For the simulation, two sets of genotypes for 100 dams and 100 sires were created using the software MYKISS (Steven Kalinowski, Montana State University, unpublished) from observed allele frequency distributions derived from the carcass genotype data. Each set of 100 parent pairs were then sampled without replacement to create 10,000 juvenile offspring. The error structure of Wang (2004) was used, with assumed error rates chosen to approximate those used for the parentage analysis described above (~1.5%). The two simulated datasets (100 dams, 100 sires, 10,000 offspring) only differed for the assumed proportion of unsampled parents (10% and 75%). Parentage was determined for simulated datasets using FRANz following the protocol stated above. Accuracy was measured as the percentage of parents correctly assigned (by sex), or correctly unassigned, given the actual parent was present or absent in the candidate pool. For sibship inference among simulated juvenile offspring, accuracy was measured by the percentage of full-sib and unrelated offspring correctly identified.

Second, since our study was transgenerational and heterogeneity exists for the number of offspring per spawner (Anderson et al. 2011), the most straightforward sampling design to meet the equal catchability assumption is a representative collection of marked fish in the first sample with respect to their reproductive success. Given individual reproductive success is highly variable for Chinook Salmon (Williamson et al. 2010) and it is impossible to predetermine individual reproductive successes, we sampled the entire spawning distribution using equal weekly effort throughout the spawning period to obtain a representative sample of carcasses.

The Petersen estimate is unbiased relative to the equal capture assumption when the probability of being tagged in the first sample and the probability of being captured in the second sample are independent or not correlated (Junge 1963). Since it was not possible to test for an equal capture probability of marks based on the sampling design, an alternate approach was pursued to assess the independence of the carcasses collected relative to their reproductive success. We used general linear models (GLMs) to explore the relationship between the offspring (response) and variables believed to influence individual reproductive success and carcass recovery (Zhou 2002; Murdoch et al. 2010; Williamson et al. 2010). Statistical models were used to partition the data into a defined structure and random variation. The null model would indicate there was no

relationship between response and predictors or the data were the result of random variation (Faraway 2006).

We used a logistic regression to assess the influence of covariates for the hypergeometric abundance estimator, where the response was binary (i.e., carcasses either produced zero or at least one offspring). Negative binomial regression was used for the binomial abundance estimator, as there was sampling with replacement and multiple offspring from the same adult were used in this estimator. The global GLM had five predictor variables: age, sex, origin (hatchery or wild), recovery location (rkm), and statistical recovery week. The fit of the negative binomial model to the data was assessed using Pearson's χ^2 test and Nagelkerke's pseudo-R^2, while the Hosmer–Lemeshow test was used to test the fit of the logistic regression model. To evaluate the difference between the models, we started with the global model and then used the backwards stepwise procedure and likelihood ratio tests (LRTs) to compare the reduced model (Hilbe 2009). The significance level for the LRTs was set at 0.05. If the reduced model was not rejected, the process was repeated until either the null or intercept-only model remained.

Genetic rarefaction curve approach.—We used models to fit the cumulative number of juvenile genotypes to the cumulative number of parent genotypes (Kohn et al. 1999). As there should be fewer new unique parental genotypes observed after each successive juvenile sampling event, an asymptote is reached that is a function of the unique parental genotypes. The asymptotic curve estimates the total number of successful spawners (N_b) represented by the juvenile collection. For this analysis we used two equations evaluated by Petit and Valiere (2006), which include the Beverton–Holt (BH) model as proposed by Kohn et al. (1999) and Eggert's model (Eggert et al. 2003), which is the same as a Continuous Smooth Hockey Stick model (Froese 2008).

The approach used to fit each curve was a variation of the methods proposed by Petit and Valiere (2006). The juvenile multilocus genotypes were randomly resampled at 10% intervals of total sample size up to the total sample size, then at 150, 200, and 250%. For each subsampling interval, 10,000 bootstrap replicates were created, with the number of unique parents present in each replicate recorded. The model equations were applied to the bootstrap replicated datasets across all sampling intervals to estimate the asymptote mean, with the 2.5% and 97.5% percentiles used as the 95% confidence limits. Key assumptions for the tGRC method include a closed population, a representative juvenile sample, and a sample size that was sufficient to obtain a reliable estimate of the asymptote (i.e., the estimate of breeders). Analyses were conducted in the statistical software package R (Ihaka and Gentleman 1996).

RESULTS

Tissue samples were collected from a total of 266 carcasses; only 207 of these were successfully genotyped due to DNA degradation in the carcasses. Of the 207 carcasses, surveyors recorded the sex for 102 males and 99 females. These 201 individuals were used in genetic analysis, because COLONY requires parental sex be identified. We estimated a total juvenile out-migrant number of approximately 437,000 Chinook Salmon. Of the 2,000 juvenile out-migrants proportionally subsampled from our adjusted population estimate, 1,991 were successfully genotyped and used for analyses.

Genetic Analysis

Observed heterozygosity for microsatellite loci was high, ranging from 0.643 to 0.946 (mean, 0.872) for offspring and from 0.628 to 0.951 (mean, 0.867) for carcasses (Table 1). The mean number of alleles observed per locus was 25.9 and 23.2 for offspring and carcass collections, respectively. For adult carcass collection, 1 locus (*Ots213*) out of 14 deviated from Hardy–Weinberg equilibrium expectations, which was due to heterozygote deficit. Also, 1 locus (*Ogo4*) out of 14 showed associations among alleles between loci. For juvenile samples, 13 out of 14 loci deviated from expected Hardy–Weinberg genotype frequencies. All loci in the juvenile sample showed statistical evidence of gametic-phase linkage disequilibrium.

Parentage Analysis

Parental assignments were similar using FRANz and COLONY (data not shown), and subsequently there was no difference between abundance estimates using the different parental assignment software. Therefore, all abundance results reported were based on the algorithms implemented in COLONY. At least one offspring was assigned to 86 of the 99 female carcasses successfully genotyped, while 80 of the 102 male carcasses produced one or more offspring. We detected no difference in the sexes to produce at least one offspring ($\chi^2 = 1.94$, df $= 1$, $P = 0.16$). In addition to the 166 parents to which COLONY assigned at least one offspring, another 613 spawners were inferred by COLONY to have produced at least one sampled juvenile. The observed offspring per spawner ranged from 0 to 26 (mean $= 4.38$, variance $= 20.09$). The heterogeneity in the offspring per spawner was consistent with a negative binomial distribution (Figure 2; $\chi^2 = 7.44$, df $= 11$, $P = 0.76$).

Abundance Estimates

A total of 1,991 juvenile out-migrants were genotyped, corresponding to 3,982 "captured genotypes." We observed 880 "recaptures," carcass genotypes that were assigned as a parent to the out-migrating offspring. The median abundance estimate of N_c calculated using the binomial model (Nc_{BIN}) was 910 spawners (95% CI = 800–1,045) (Table 2). Using the hypergeometric model we estimated Nc_{HYP} as 948 spawners (95% CI = 900–1,010). There was no statistical difference between the tGMR spawner abundance estimates based on Seber's GOF test ($P = 0.59$). Using the binomial model, the abundance estimates were 433 females (95%

TABLE 1. Genetic data analysis summary. Abbreviations are as follows: HO is the observed heterozygosity, HE is the expected heterozygosity, HWE is the *P*-value for the Hardy–Weinberg equilibrium exact test, and LD is the proportion of significant chi-square values for the pairwise gametic-phase linkage disequilibrium permutation test. For example, statistical association between two loci (1 out of 13 locus-pair comparisons) is 0.08 or less.

	Offspring				Carcasses			
Locus	HO	HE	HWE	LD	HO	HE	HWE	LD
Ogo2	0.797	0.819	0.033	0.46	0.871	0.822	0.032	0.00
Ogo4	0.832	0.842	0.018	0.77	0.867	0.848	0.350	0.08
Oki100	0.925	0.941	0.000	0.69	0.912	0.935	0.428	0.00
Omm1080	0.938	0.952	0.000	0.62	0.951	0.949	0.272	0.00
Ots201b	0.900	0.898	0.000	0.08	0.918	0.898	0.141	0.00
Ots208b	0.972	0.965	0.000	0.92	0.917	0.965	0.159	0.00
Ots211	0.935	0.925	0.000	0.77	0.892	0.915	0.028	0.00
Ots212	0.938	0.926	0.000	0.85	0.940	0.918	0.941	0.00
Ots213	0.867	0.941	0.000	0.69	0.849	0.941	0.000	0.00
Ots3M	0.803	0.808	0.001	0.69	0.764	0.785	0.730	0.00
Ots9	0.643	0.635	0.874	0.31	0.628	0.636	0.873	0.00
OtsG474	0.820	0.808	0.011	0.15	0.828	0.814	0.815	0.00
Ssa408	0.895	0.899	0.000	0.77	0.900	0.897	0.329	0.00
Ssa197	0.946	0.946	0.000	0.85	0.915	0.944	0.124	0.00

CI = 357–525) and 483 males (95% CI = 397–585). Summing the separate estimates by sex yielded a total of 917 spawners (95% CI = 801–1,053). There was no statistical difference between the binomial adult and summed sex estimates ($P = 0.94$) and the hypergeometric adult and the summed sex estimates ($P = 0.69$). The CV of our population estimates ranged from 3% to 7%.

A total of 779 unique adults were estimated to have contributed to the offspring collection given the observed relatedness among juveniles. The estimates of N_b (successful breeders) using the tGRC approach fitted with the BH and Eggert's models were 966 (95% CI = 950–983) and 781 (95% CI = 775–788), respectively (Figure 3). There was no statistical evidence that N_b estimates calculated using BH were less than Nc_{HYP} and Nc_{BIN} ($P > 0.20$) in all cases. Yet, there was support that the N_b estimate calculated using Eggert's model was less than Nc_{HYP} and Nc_{BIN} ($P < 0.02$) in all cases.

The percentage of correctly inferred parental assignments was greater than 99.5% for both simulated data sets that consisted of either 10% or 75% unsampled parents (Table 3). Yet, correct assignment rates were slightly lower for simulated data constructed with 75% of contributing parents being unsampled, with correct assignment of dams, sires, and parent pairs (i.e., dam–sire–offspring trios) being 99.74, 99.88, and 99.63%, respectively (Table 3). For the 75% unsampled parents' dataset, the observed 99.63% correct-parent pair assignment rate suggested a 0.15% and 0.23% false positive and false negative rate, respectively. Regarding proper enumeration of full-sibs, 666 false negative determinations of full-sib relationships were observed out of 152,769 total full-sib comparisons, equating to a $P(\text{FS}|\text{FS}) = 99.56\%$ and a $P(\text{Unrelated}|\text{Unrelated})$ approaching 1. There did not appear to be a bias in assignment error, with false positive and false negative rates being of the same magnitude. Simulation results suggested that parentage assignments were accurate and would not contribute to a bias in the determination of parentage.

A total of 181 of the 201 genotyped carcasses had associated sex, origin, age, location, and timing data. In this subset,

TABLE 2. Spawner abundance estimates (N_c) for different genetic mark–recapture models applied to the Coweeman River Chinook Salmon population for the 2009 spawning season.

Model	Sex	n_1	n_2	m_2	Nc	95% CI	CV
Binomial	Adult	201	3,982	880	910	800–1,045	0.07
Hypergeometric	Adult	201	779	166	948	900–1,010	0.03
Binomial	Females	99	1,991	457	433	357–525	0.10
Binomial	Males	102	1,991	423	483	397–585	0.10
Binomial	Males	99	1,991	423	917	801–1,053	0.07
	Females	102	1,991	457			

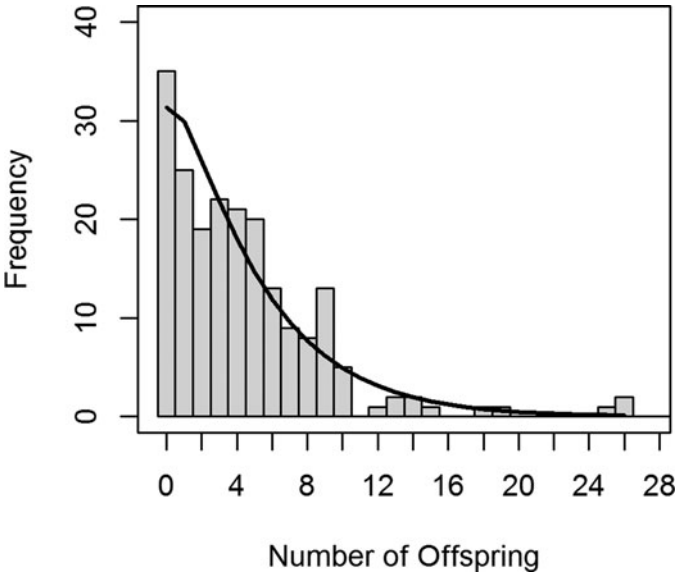

FIGURE 2. The observed distribution for the number of inferred offspring per spawner from carcass samples for the Chinook Salmon population in the Coweeman River for the 2009 spawning season, and the expected fit (black line) based on the negative binomial distribution.

TABLE 3. Summary of parental assignment from simulated parent–offspring sets. Assumed rate of unsampled parents was **(A)** 10% and **(B)** 75%. False positives were instances of offspring being assigned to a parent that was not present in the candidate pool and false negatives were instances of offspring not being assigned to a parent that was present in the candidate pool.

Parentage category	Count	False positive	False negative	% of Total
	A = 10%			
Dams error	9	7	2	0.09%
Dams correct	9,991			99.91%
Sires error	6	3	3	0.06%
Sires correct	9,994			99.94%
Pairs error	15	10	5	0.15%
Pairs correct	9,985			99.85%
	B = 75%			
Dams error	26	7	19	0.26%
Dams correct	9,974			99.74%
Sires error	12	8	4	0.12%
Sires correct	9,988			99.88%
Pairs error	37	15	23	0.37%
Pairs correct	9,963			99.63%

we had data for one 2-year-old male (jack) and one 5-year-old fish. Given the paucity of information in these age categories, they were not included in the analysis. There was no strong evidence that any of the considered variables substantially affected the production of at least one offspring (logistic model) or the number of offspring (negative binomial model). For the global negative binomial model the factors tested explained very little of the variability in individual relative reproductive success (Nagelkerke's pseudo-$R^2 = 0.07$). Based on Pearson's χ^2 test, the global negative binomial model did not fit the data (deviance $= -923.46$, df $= 173$, $P = 0.04$), but we could not reject the null hypothesis that the null model did not fit the data (deviance $= -932.70$, df $= 178$, $P = 0.07$). For the global logistic regression, the Hosmer–Lemeshow GOF test was consistent with the data ($\chi^2 = 5.46$, df $= 8$, $P = 0.71$). As with the negative binomial model, the LRTs favored the null logistic regression model.

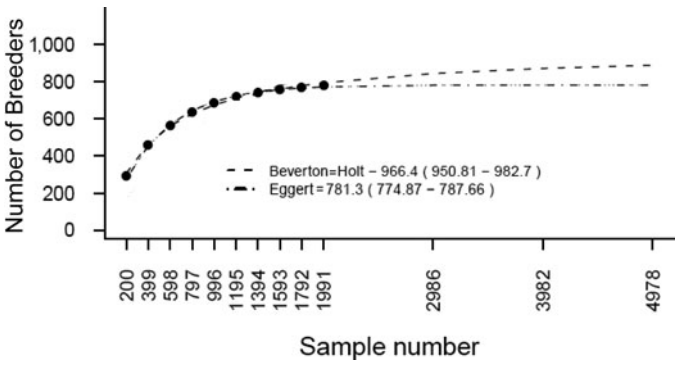

FIGURE 3. The mean accumulation curves from 10,000 bootstrap iterations based on Beverton–Holt's (BH) and Eggert's models used to estimate successful breeders (N_b). Black circles are the individual data points estimated from parental reconstruction. Sampling intervals up to the total actual sample size ($N = 1{,}991$) are in 10% increments. Beyond the total actual sample size, the number of breeders was forecasted at 150, 200, and 250% of the total actual sample size. Estimates of N_b (with 95% CI in parentheses) are given next to the model name.

We compared the traditional escapement estimators using redd counts, AUC, and carcass tagging based on the Jolly–Seber model for adults, females, and males in this well-monitored watershed to the tGMR estimates (Figure 4). For the adults, there was no statistical difference between the genetic and any of the traditional estimates ($P > 0.06$). For females, there was no statistical difference between any of the estimates ($P > 0.84$) and the comparison for males also yielded a nonsignificant result ($P > 0.17$).

DISCUSSION

Genetic Mark–Recapture Data

We used transgenerational genetic tagging to estimate spawner abundance for a Chinook Salmon population by relating adult parents collected as carcasses from spawning ground surveys with juveniles recovered at an out-migrant trap. We found no statistical difference between genetics-based Petersen abundance estimates calculated using either hypergeometric or binomial models and no difference between the genetic-based estimates and the traditional estimates. The traditional visual-based estimates presented here excluded small males, so it is not surprising that the tGMR estimates were closer for females and tended to be slightly higher than those for males and adults (Figure 4). The precision (CV) of our genetic-based estimates

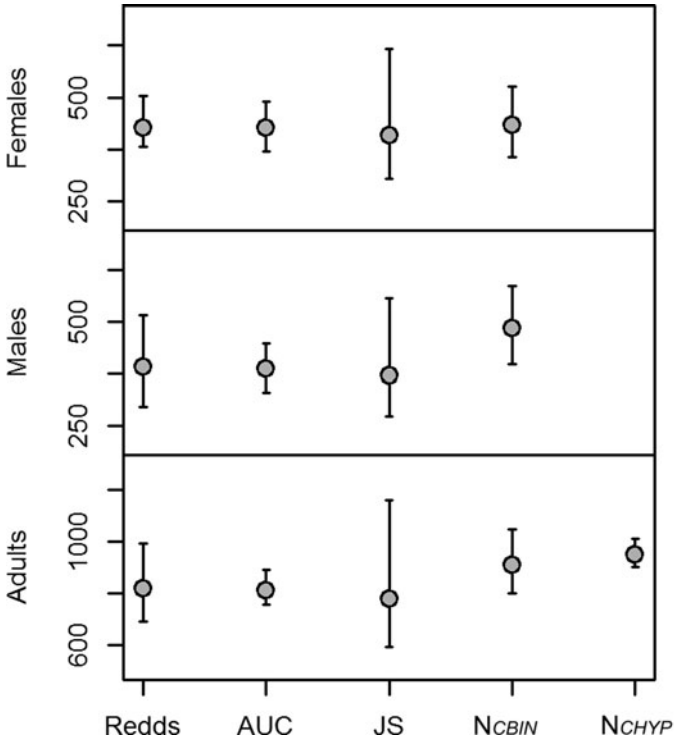

FIGURE 4. A comparison of spawner census estimates for genetics-based and non-genetics-based estimators. Non-genetics-based estimates from Redds, AUC, and JS correspond to redd count expansion, area-under-the-curve, and Jolly–Seber carcass tagging estimates, respectively. Genetics-based estimates from Nc_{BIN} and Nc_{HYP} correspond to the binomial and hypergeometric estimators, respectively. Grey circles show median values and black bars correspond to 95% CIs.

was less than the NOAA guideline of 15%. We obtained precise population estimates because the dataset comprised a total 814 adult genotypes (observed directly from adults or inferred from juveniles), which is over 82% of the genetic-based population estimates of N_c.

Schwarz and Taylor (1998) indicated the Petersen estimator provides an unbiased estimate if the following assumptions are met: (1) there is no mark loss, (2) there are no marking effects, (3) the population is closed, (4) all marked and unmarked fish are correctly identified and enumerated, and (5) all fish in the population have an equal probability of capture. Our genetic-based approaches meet the no-tag-loss and no-marking-effects assumptions, because genotypes were permanent markers and genetic marks were obtained from carcasses or nonlethally from juveniles.

The closure assumption requires that within the study period there are no additions to the population through births or immigration and no deletions through death or emigration. In this study, the closure assumption is not testable and is likely violated by adults failing to produce offspring; however, the Petersen estimator is unbiased with respect to the population at time of tagging if mortality was random (Seber 1982; Williams et al. 2002). Therefore, our estimate of N_c is unbiased relative to the closed population assumption if our carcass collection was unbiased regarding the production of at least one offspring and the mortality (i.e., lack of spawning success) was equal for sampled and unsampled carcasses. We have no a priori reason to believe our carcass sampling was not representative relative to the production of at least one offspring. Regarding juveniles, it is unlikely that immigration occurred since our trap was located at rkm 10, which would be a substantial upstream migration for juvenile Chinook Salmon from other populations.

Laboratory procedures and simulation results suggest the tGMR estimator would not be biased with regard to correct identification and reporting of tagged or marked fish (assumption 4), which is also supported by parentage algorithms power analysis (Wang 2004; Kalinowski et al. 2007). Heterozygote deficits such as those observed for locus *Ots213* could contribute to unrecovered marks, but the simulation results indicate the effect of potential parental assignment errors on abundance estimates would be minimal. The genetic disequilibrium observed in the juvenile sample was not unexpected (Allendorf and Phelps 1981) and would not affect the accuracy of parentage algorithms. Improperly identified alleles were compensated for by using the group method, where genotypes for all siblings are jointly considered in the likelihood calculations (Wang and Santure 2009). Given the genetic diversity, number of loci, and percentage of adults sampled in our study, correct assignment rates in COLONY should approach 100% based on the results reported by Harrison et al. (2013).

We implemented a representative carcass sampling design to obtain a sample of parents to meet the fifth assumption of equal capture probabilities, which is considered the Petersen estimator's "Achilles heel" (Arnason et al. 1996). For tGMR, differences in individual parental reproductive success create unequal capture probabilities for parents in the second sampling event. Therefore, reliance on mixing or random sampling in the second event to meet the equal capture probability assumption, as conducted in standard mark–recapture studies (Schwarz and Taylor 1998), could lead to biased abundance estimates. When repeatedly sampling the same individual, the heterogeneity in capture probabilities can be addressed using the models of Otis et al. (1978) or mixture models (Pledger 2005), but application of these models for the tGMR approach is not currently possible.

There are many possibilities for the Petersen estimator to be consistent relative to the equal capture assumption and this occurs when the probability of being tagged in the first sample and captured in the second sample are independent or not correlated (Junge 1963; Schwarz and Taylor 1998). Since we could not directly test the equal capture assumption in the tagging event, we provided two sources of evidence suggesting the correlation between the two sampling events was likely small in our study. First, the tGMR estimate agreed with three other traditional estimates, and second, the results of the GLM analysis indicated there was no strong evidence that variables believed to affect carcass sampling in the first sample explained

reproductive success (and therefore likely capture probability) in the second sample.

We presented two tGMR estimators to address heterogeneity in the number of offspring per spawner if carcass sampling was not representative. When carcass recoveries are sex biased (Zhou 2002; Parken et al. 2003; Murdoch et al. 2010), our approach of estimating abundance for females and males separately should provide consistent estimates. The few published carcass selectivity studies for Chinook Salmon indicate carcass recoveries appear biased toward larger and possibly more productive fish, which would cause an underestimate in abundance using tGMR with proportional sampling in the second event (Zhou 2002; Murdoch et al. 2010). The bias in estimates of N_c due to size selectivity in carcass recoveries is likely to be small because of the weak relationship between reproductive success and body size for Pacific salmon (Dickerson et al. 2005, Williamson et al. 2010; Richard et al. 2013). However, when there are concerns with heterogeneity, the hypergeometric tGMR estimator will likely be less sensitive to violations of the equal capture assumption, because the heterogeneity in individual capture probabilities is reduced by restricting the number of offspring per spawner from many to one.

Genetic Rarefaction Curves

In our study, Eggert's model yielded estimates of breeders that were 82% to 86% of the tGMR census estimate, while the BH estimate was greater than the point estimate of the tGMR census estimate. It is biologically impossible for the number of successful breeders to exceed the number of spawners, suggesting the BH model overestimates the number of breeders. It should be noted that the asymptotic estimate of successful breeders in the BH model is based on an infinite number of juveniles, which is biologically unrealistic for any population. This extrapolation may explain the consistent overestimates in the BH model when using rarefaction curves (Eggert et al. 2003; Frantz and Roper 2006; Petit and Valiere 2006). Yet, the BH model may be one option to estimate the N_b if the asymptote is not well defined. Since our asymptote was well defined, we did not evaluate this condition. Our empirical results were consistent with the published simulations, finding that the Eggert's model produced reliable estimates of abundance providing the sample size was sufficiently large (Eggert et al. 2003; Frantz and Roper 2006; Petit and Valiere 2006). Petit and Valiere (2006) indicated that CI coverage was too narrow for genetic rarefaction curves compared with genetic mark–recapture methods, with Lukacs and Burnham (2005a) indicating these differences may be due to the more complete use of all available data by genetic mark–recapture models.

Despite the issues raised with tGRC interval coverage, rarefaction curves may be the best option for estimating escapement in some river systems with high, turbid water and small population sizes, as visual methods are impossible and carcass recoveries are rare. While tGRC would likely yield a consistent estimator for trend analysis using only juvenile samples, additional research is needed to clarify the relationship between N_b (to fry stage) and N_c (adult abundance) to maximize the utility of tGRC for Pacific salmon managers. We recommend the N_b approach be used on populations where abundance is suspected as being underreported due to challenging environmental conditions for sampling or poor sampling designs, as N_b would provide a conservative abundance estimate from a sample of juvenile out-migrants. Another area where estimates of N_b may be preferred is for small at-risk populations because the number of successful breeders may better identify genetic bottlenecks or populations near depensation thresholds compared with census estimates.

Extension of tGMR Method

We report the efficacy of the genetic approaches for the Coweeman River population of Chinook Salmon, but these methods could be extended to other populations and species. Despite the promise of genetic methods, further consideration of sampling designs and bias will be necessary if the method is to be applied to a wider range of river systems, population sizes, and types of genetic markers. Crawford and Rumsey (2011) indicated there was a need for unbiased estimates of hatchery fish presence, age structure, sex ratio, and coded wire tags for Pacific salmon populations. Representative spawning ground sampling designs (Courbois et al. 2008) to obtain these metrics would be consistent with tGMR carcass sampling requirements. Another area in which the tGMR approach could be readily implemented is in reproductive success studies that measure the success of hatchery spawners to the juvenile stage relative to natural-origin spawners, since relative reproductive success and tGMR study designs are similar (Williamson et al. 2010; Richard et al. 2013).

The genetic methods we describe can be used with other anadromous salmonids that immigrate to the ocean shortly after emergence, such as Chum Salmon *Oncorhynchus keta* and Pink Salmon *O. gorbuscha*. Yet, additional considerations are needed to extend this application to anadromous salmonids with yearling life histories, such as spring Chinook Salmon, Coho Salmon *O. kisutch*, and Atlantic Salmon *Salmo salar*. Further, Atlantic Salmon and steelhead *O. mykiss* produce unique challenges because smolts may be the offspring of anadromous fish or resident fish or both (Zimmerman and Reeves 2000; Richard et al. 2013). Using our methods, the N_c and N_b for steelhead would include the combined resident and anadromous spawning population, which may not meet manager needs, as the anadromous life history form is listed for protection under the ESA, while individuals exhibiting a resident life history are not listed. Yet, conservation biologists may find the N_b estimator more informative for assessing extinction probabilities than traditional spawner abundance estimates that are based only on the anadromous phenotype.

One approach to estimate steelhead abundance may be to use angling or partial weirs to capture adults or kelts (Mayer et al. 2006; Nelson et al. 2005). Since juveniles rear for 1 to 4 years before emigrating to the ocean as smolts (Leider et al. 1986),

this residency suggests that there is an opportunity to collect juveniles through other methods, such as seining, electrofishing, or baited minnow traps (Bryant 2000; Hahn et al. 2007; Temple and Pearsons 2007) before emigration. All fry should emerge by midsummer and could be collected using representative sampling designs over the spawning distribution (Richard et al. 2013). Otolith microchemistry could then be used to identify if the fry were from anadromous mothers (Zimmerman and Reeves 2000), and an abundance estimate for steelhead females could be obtained using the binomial tGMR and expanded to males based on an observed or expected anadromous sex ratio.

The tGMR approach could also be extended to estimate adult abundance using only returning adults. Rather than the second sampling event consisting of juvenile captures, the second event would be a capture of returning adults. By aging the scales from returning adults, the adults could be assigned to the appropriate brood year based on scale ages, and tGMR could then be used to estimate spawner abundance for relevant brood years. Another variant of the genetic mark–recapture design is to estimate smolt abundance via "back-calculation" (Volkhardt et al. 2007). In this approach the smolts are the marks and the returning adults are the recaptures and captures.

Conclusions

This is the first application we are aware of applying genetics-based abundance estimators to a Pacific Salmon population. Given the existing monitoring effort in the Pacific Northwest to estimate juvenile out-migrant abundance and the representative sampling required for adult age, sex, origin, and coded wire tag data, there are many opportunities to incorporate and refine the approach we have developed. This approach provides an opportunity to estimate adult abundance for populations in which the precision of the estimate is unknown, does not meet management needs, or pertains to populations where access and high, turbid water prohibit more traditional techniques. These methods are likely to be most effective for small Pacific Salmon populations, and they have limited biological impacts on ESA-listed salmon spawners because the collection of tissue for genotyping can be obtained from carcasses and nonlethally from juveniles. Although there is more work required in the area of study design and statistical analysis, integrating carcass and juvenile sampling has the benefits of unifying census estimation with improved VSP monitoring to better understand the population dynamics of anadromous Pacific Salmon and their interactions with hatchery salmonids.

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